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A new species of *Sibon* (Serpentes, Dipsadini) from French Guiana and amended diagnosis of *Sibon nebulatus*

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Abstract

Specimens of snakes from Mexico to northeastern Brazil have been assigned to the taxon *Sibon nebulatus*. Recent molecular data confirmed the previous suspicions that these specimens in fact belong to distinct species. After examination of the holotype and recently collected specimens, we provide an amended diagnosis and restrict the range of *S. nebulatus* to northern South America, implying that Central American populations belong to one or several undescribed species. We also describe *Sibon nigralbus* **sp. nov.**, a new species from the Guiana region. Further investigation is needed to clarify the status of populations in Pará state, Brazil, and in the Magdalena valley in Colombia, where additional species possibly occur.

Key words: Amazonia, DNA, Neotropics, Herpetology, Phylogeny, Taxonomy

Introduction

The Neotropics harbor more species of vertebrates than any other region (Jenkins *et al.*, 2013). However, basic information on the number and distribution of species remains largely incomplete, even for terrestrial vertebrates such as squamates (Guedes *et al.* 2018). This hampers our understanding of the processes responsible for species diversification and impairs informed biodiversity conservation. Considering the current threats faced by tropical biodiversity (Gomes *et al.* 2019; Albert *et al.* 2023), it is urgent to fill this information gap.

Almost all DNA-based studies focusing on groups of neotropical squamates have revealed lineages that correspond to undescribed species. For example, many species of snakes previously thought to be widespread have been found to actually represent species complexes (e.g. Passos *et al.* 2017; Torres-Carvajal & Hinojosa 2020). This is notably the case within *Sibon*, a genus of snail-eating snakes comprising 22 recognized nominal species distributed throughout Central America and northern South America (Arteaga *et al.* 2018). *Sibon nebulatus*, described by Linnaeus (1758) as *Coluber nebulatus*, with a type locality designated as "America" by Anderson (1899), is a name that has been used to designate snail-eating snakes occurring from Mexico to northeastern Brazil, including all the countries in between (Colombia, Ecuador, Venezuela, Guyana, Suriname and French Guiana). However, recent studies combining morphology and molecular data (Sheehy 2012; Arteaga *et al.* 2018; Arteaga & Batista 2023) suggested that many different species are hidden under that name. Some of these works even described a few of these lineages as new taxa from Central America and the trans-Andean regions of South American (Arteaga & Batista 2023). The phylogenetic analyses of this last contribution support a South American clade (considered as the *Sibon nebulatus* species complex hereafter) including *S. bevridgelyi*, *S. dunni*, *S. hartwegi*, *S. leucomelas*, *S. vieirai*, and *S. nebulatus*. In this work, *S. nebulatus* is considered to occur in northern South America and is more closely related to the five other nominal species than to a Central American clade formed by three lineages identified as *S.* aff. *nebulatus*, thus rendering *S. nebulatus* paraphyletic. The restriction of the type locality and the correct

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assignment of modern material to *S. nebulatus* is thus crucial to be able to describe the remaining unnamed species in this group.

There are three specimens in the collection Museum Regis Adolphi Friderici that could have been used by Linnaeus (1758). Andersson (1899) stated that only the type specimen NHRM60 (http://linnaeus.nrm.se/zool/herp/images/H00060.jpg) corresponds to *Sibon* (the two others are *Siphlophis cervinus*), thus designating it as holotype. However, there are considerable disagreements about the geographical origin of this specimen. Smith & Taylor (1950) report the type locality to be in Mexico without any explanation. On the contrary, Arteaga & Batista (2023) considered that the northern South American lineages (formed by two samples from Colombia and Trinidad) correspond to *Sibon nebulatus*, also without explaining their decision. Peters (1960) considered that *Sibon n. nebulatus* (other subspecies have subsequently been elevated to the species rank) is widespread from Mexico to Guyana but recognized that there is "considerable variation between populations of this subspecies, as would be expected from the wide geographical area covered in its range". Peters also stated that "Specimens from Middle America usually possess regular, clearly defined, dark-brown or black dorsal blotches, which are fairly sharply contrasted with the rich chocolate-brown of the interblotches and are continuous from the vertebral row to the ventrals, and often extend well onto two or more ventrals and fuse across the midventer. On the other hand, individuals from northern South America often have small, poorly defined dorsal blotches, occupying only the vertebral and paravertebral rows. The blotches seldom extend onto the belly, and are never fused with the opposite blotch across the ventrum. The blotches are a light brown, with the interspaces very light brown or grayish. These differences are not perfectly constant, however, and cannot be used alone to distinguish members of the two populations. Variations in each part of the color description given above for the Middle American material can be observed, so that no one point can be selected as a basis for taxonomic separation". Given that Peters was not aware that what he considered *S. nebulatus* comprised several species in both South America and Central America, we assume that at least part of the variation he observed could be fixed across species and that the area of the type locality of *S. nebulatus* sensu stricto could be narrowed down.

We have collected specimens of *Sibon nebulatus sensu lato* from French Guiana and Ceará, Brazil (Appendix 1) that differ from each other on morphology and DNA sequence data. Some of them are genetically and morphologically most closely related to specimens from Trinidad, Colombia, and northeastern Brazil, thus widely occurring along the coast of northern South America. They are also morphologically similar to the holotype of *Sibon nebulatus* (NHRM60; see Results) and distinct from Central American specimens, thus agreeing with Arteaga & Batista (2023) that the species is probably restricted to northern South America. The other one is distinct from any other nominal species of *Sibon*, and so far, only known from French Guiana. Therefore, we here provide an amended diagnosis of *Sibon nebulatus* and describe the other one as a new species.

Material and Methods

Field work and deposition of specimens. We collected six specimens (one of *Sibon nebulatus* and five of *S. nigralbus* sp. nov.) and four tissue samples of *Sibon* from French Guiana and 21 specimens and one tissue sample from Pará and Ceará (Brazil) (all of *Sibon nebulatus*). Specimens were euthanized with 2% benzocaine, fixed in 10% formalin, and stored in 70% ethanol. They are deposited in the Museum National d'Histoire Naturelle (Paris, France) (MNHN) and at Coleção Herpetológica do Núcleo Regional de Ofiologia da Universidade Federal do Ceará (CHUFC). We also examined: two specimens of *S. nebulatus* from the Brazilian state of Pernambuco (Herpetological and Paleontological Collection of Universidade Federal Rural de Pernambuco, CHP-UFRPE); 11 specimens of *S.* aff. *nebulatus* from Central America (from Senckenberg Natural History Museum, SMNS); four specimens of *S. nebulatus* from northern South America (one from SMNS and three from MNHN); pictures of the holotype of *S. nebulatus* at the Swedish Museum of Natural History, including measurements and scale counts directly taken from the holotype by the curator; pictures of the holotypes of *L. affinis* and of *S. hartwegi*. A complete list of museum specimens examined is presented in Appendix 1.

We also examined available occurrence records of *Sibon nebulatus* from the literature and from the iNaturalist citizen science platform in South American east of the Llanos (since other related species occur in the Llanos and the Andean foothills that cannot be properly identified using pictures only) in order to evaluate the possible extent of the range of the species. We also considered additional records of the new species in French Guiana from iNaturalist and Faune-Guyane platforms (Appendix 2).

Morphology. Our terminology for Dipsadini cephalic shields follows proposals by Peters (1960) and Harvey and Embert (2008). Diagnoses and descriptions generally follow Fernandes *et al.* (2010) and ventral and subcaudal counts follow Dowling (1951). We also included counts of dorsal and ventral markings. Morphological measurements were taken with measuring tapes to the nearest 1 mm for SVL and TL, or with digital calipers to the nearest 0.1 mm for cephalic measurements. Abbreviations are as follows: Snout-Vent Length (SVL); Tail Length (TL); Total Length (TOL; = SVL + TL); Head length (HL); Head Width (HW); Eye Diameter (ED); Eye-Nostril Distance (END); Inter-Nasal Distance (IND); Inter-Orbital Distance (IOD). Sex was determined by establishing the presence/absence of hemipenes through a subcaudal incision at the base of the tail unless hemipenes were already everted. Preparation and description of hemipenes follows Zaher (1999).

Principal Component Analyses were undertaken using Head length (HL); Head Width (HW); Eye Diameter (ED); Eye-Nostril Distance (END); Inter-Nasal Distance (IND); Inter-Orbital Distance (IOD), number of ventral scales and number of ventral markings. We excluded Tail Length (TL); Total Length (TOL), and number of caudal scales because some specimens missed the tip of the tail and also excluded dorsal markings because they were difficult to count reliably in some specimens. We did not include cephalic scales because the variation was very low. We undertook an additional analysis using the residuals of the linear regression between all the variables and the SVL to remove the effect of the body size.

Molecular analyses. We gathered all the Cytb and ND4 sequences available in GenBank for the *Sibon nebulatus* clade in Arteaga & Batista (2023) (Appendix 3). We employed BLASTN to verify that no other sequence deposited on GenBank after the aforementioned works clustered with the species used in this study. We collated these public data with our nine newly generated sequences. These sequences were aligned on the MAFFT7 online server under default parameters except the E-INS-i strategy, which is designed for sequences with multiple conserved domains and long gaps (Katoh *et al.* 2019). We trimmed the alignment to keep only the region where most sequences overlap, resulting in a final alignment of 1739 base pairs (bp). We investigated the phylogenetic relationships among a total of 77 terminals under a Maximum Likelihood (ML) approach, applying a GTRCAT model with RAxML v.8.2.4 (Stamatakis 2014). All RAxML analyses were performed on the CIPRES Science Gateway online server (Miller *et al.* 2010). Nonparametric bootstrapping values (Felsenstein 1985) were estimated using 1,000 pseudoreplicates.

Results

Molecular phylogeny. The *Sibon nebulatus* clade previously recovered by Arteaga & Batista (2023) is also strongly supported here (Fig. 1). The new species from French Guiana is recovered (although poorly supported) as the sister species to a sample labeled *S.* aff. *hartwegi* 2 in Arteaga & Batista (2023), but herein considered as *S.* sp. "Magdalena" since it is morphologically distinct to *S. hartwegi*. These two lineages altogether form a clade sister to all the other South American samples of the *Sibon nebulatus* species complex but this position is poorly supported.

The other species occurring in French Guiana is genetically almost identical to the two previously documented populations from Trinidad and Colombia (Magdalena valley), and related, although more distantly (ND4: 2.5%; Cytb: 2.6% p-dist), to the population from Ceará in northeastern Brazil. All these populations are considered as *S. nebulatus* sensu stricto hereafter, and are closely related to *S. hartwegi* (sensu Arteaga & Batista 2023) from Colombia (ND4: 4.2%; Cytb: 3.7% p-dist, Appendix 4). Another lineage labeled *S.* aff. *hartwegi* (following Arteaga & Batista 2023) forms a poorly supported clade with *S. nebulatus* + *S. hartwegi*.

Morphometrics. The PCA based on raw morphometric measurements of the *Sibon nebulatus* complex accumulated 77 % of the total variation in the first two components (Fig. 2A). The first principal component (PC1) explains 58.4 % of the variation, all variable coefficients are highly positively correlated to body size which does not clearly segregate the different groups. The second principal component (PC2) explains 19.1% of the variation and segregates *S. nigralbus* sp. nov. from the rest. The holotype is notably nested within the widespread northern South American species considered to correspond to *S. nebulatus* sensu stricto hereafter. Using residuals (Fig. 2B), a very similar pattern is observed. However, it is noteworthy that the holotype is located equally near *S. nebulatus* sensu stricto and *Sibon* aff. *nebulatus*, suggesting that the species identity cannot be ascertained solely based on body proportions.

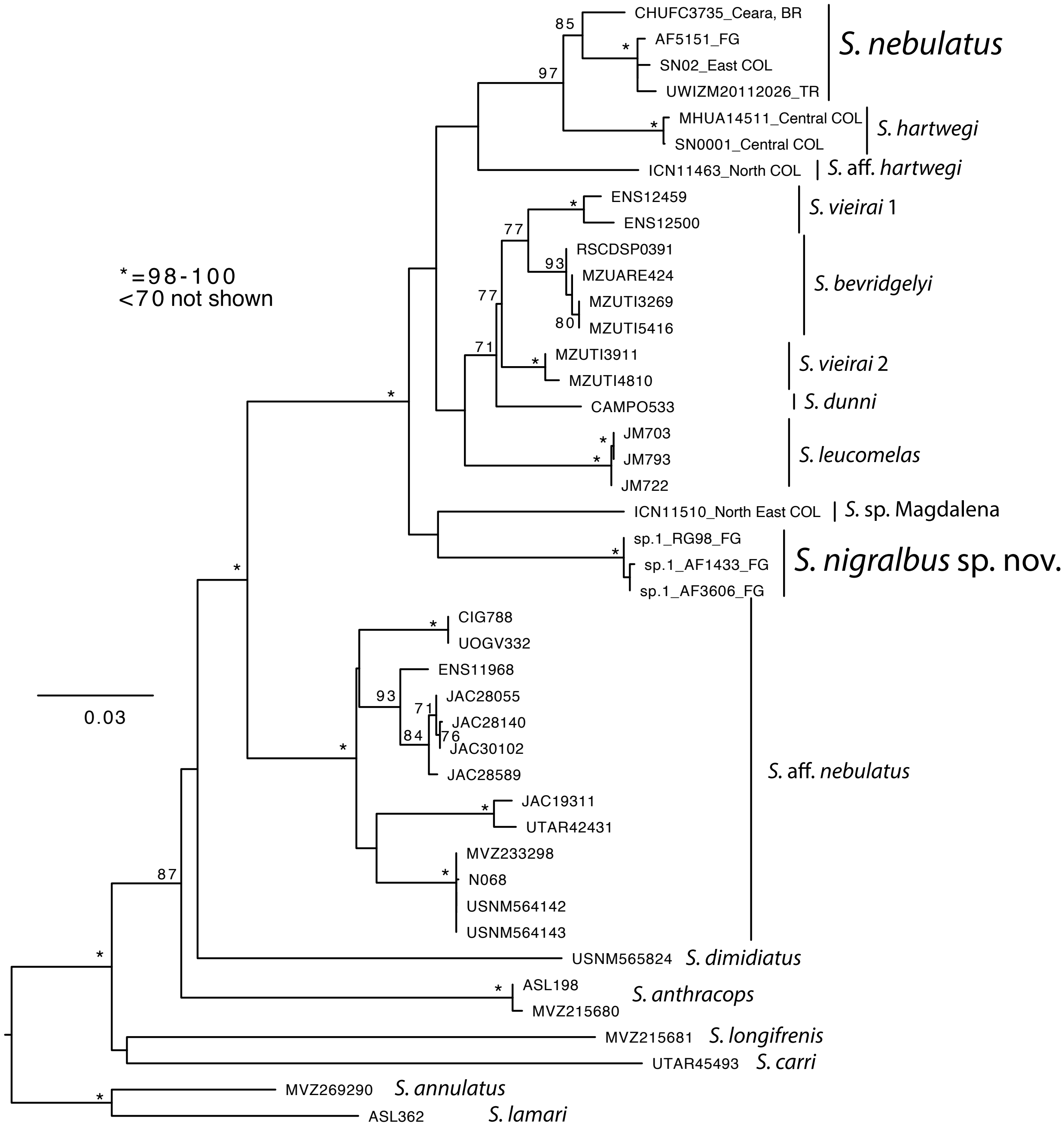

FIGURE 1. Maximum-Likelihood phylogram based on the concatenated Cytb and ND4 gene fragments. Bootstrap supports are indicated on the top left of the nodes and "*" depict values above 97%. The existence of two lineages of *S. vierai* in the tree is merely due to the absence of overlap of the loci across samples.

Nevertheless, the boxplot of selected variable and ratio with SVL (Fig. 2C, Table 1) indicate that the number of black ventral patches, the Eye Diameter and the Inter-Nasal Distance can be used to diagnose the species. Additional characters of coloration (higher number of ventral patches, postcephalic dark patch and light orange colored dorsal spots), and the shape of some of the cephalic scales (elongated temporals, elongated dorsal between parietals) also differentiate the northern South American and the Central American species, with the holotype clearly corresponding to the South American lineage (see comparisons below).

TABLE 1. Meristic and morphometric summary.

Species	Tot. length	SVL	tail	HL	HW	ED	END	IND	IOD	Preoc.	Postoc.	Supral.	Supral.eye	Infral.	Temp.	Chinshields	Dor.1	Dor.2	Dor.3	V.scales	Subc.	D.patches	V.patches
S. aff. *nebulatus* (n=11)	577	438	151	14.3	11.5	3.5	2.8	4	6.2	1	2	7	4–5	8.91	1+2(1)	3.18	15.3	15.1	15	181.4	86.7	34.18	38.09
S. nebulatus holotype	640	470	170	11.4	10.3	2.6	2.3	5.1	6.5	2	2	7	4–5	9	1+2	3	15	15	15	184	83		66
S. nebulatus (n=25)	575	426	149	13.7	10.8	3.2	2.7	3.8	5.9	1	2	7.08	4(5)–5(6)	8.4	1+2	2.96	15.1	15.04	15	183	83.6	45.04	48.24
S. nigralbus sp. nov. (n=5)	587	413	174	10.8	9.38	3.3	2.3	3.1	4.9	1.8	2	7.33	4(5.6)–5(6.7)	8.4	1(2)+2(3)	3.2	14.6	15	15	196.8	104	56	58.6

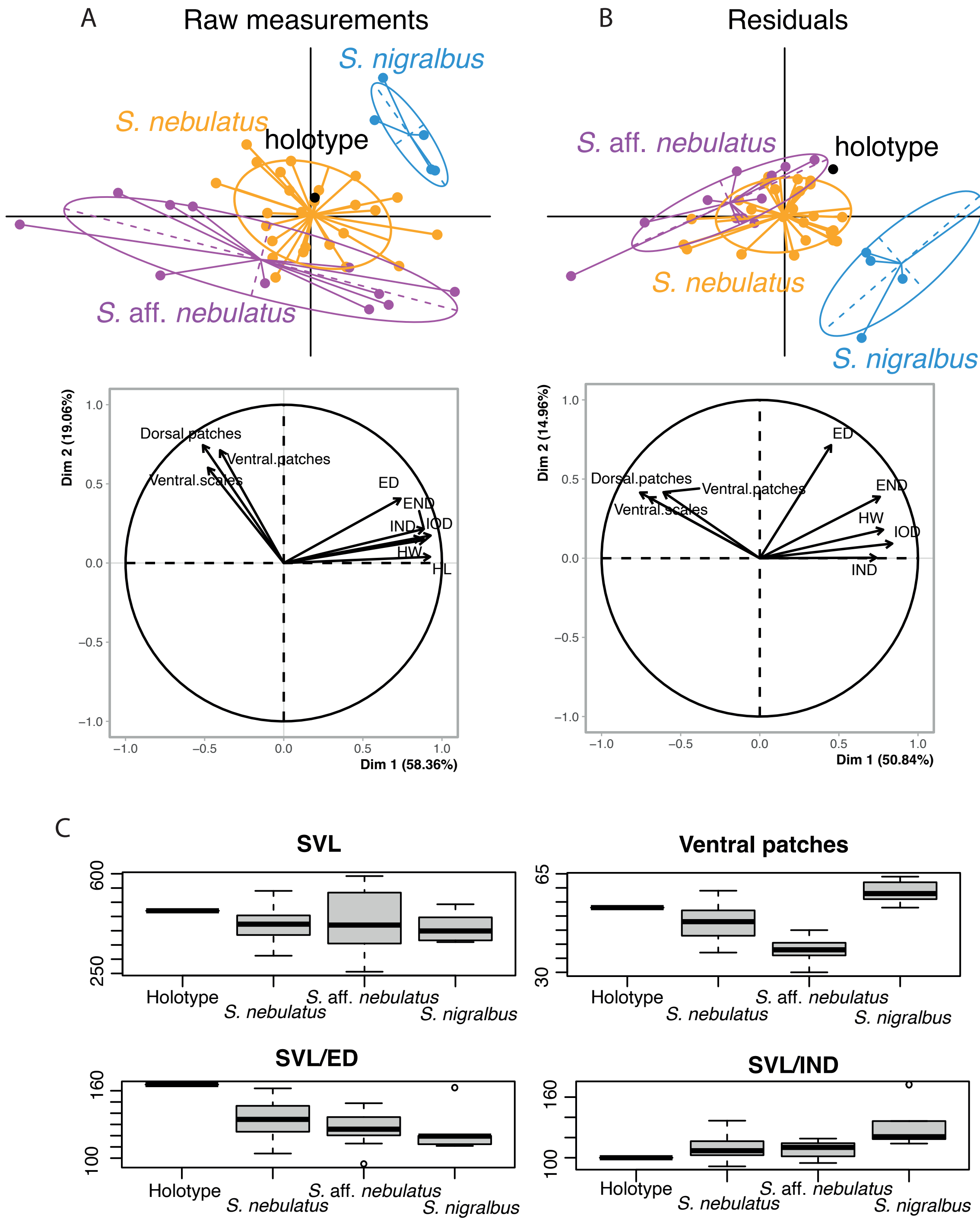

FIGURE 2. Principal component analyses of the (A) raw morphometric data and (B) of the residuals of the linear regression of the measurements on SVL showing the absence of overlap between the new species and the other ones as well as the position of the holotype of *S. nebulatus*. (C) Boxplot of the SVL, of the number of ventral patches, and of the ratio between SVL and ED and SVL and IND showing the lack of overlap between some species pairs.

Taxonomic accounts

After morphological examination of the holotype and specimens collected throughout the putative range of *Sibon nebulatus* (Central America and northern South America: Colombia, Tobago, French Guiana, Brazil) (Fig. 3), we conclude that the nominal species should be restricted to northern South America. These specimens, considered hereafter *S. nebulatus*, can be differentiated morphologically (meristics, morphometrics, and coloration) (Figs 2,4,5) from other co-occurring species as well as from Central American species previously assigned to that taxon (see below). The large geographic range of this species, which inhabits open habitats along the coast of Northern South America, strengthens the idea that it corresponds to the type specimen collected in the 18th century, although the type locality remains vague.

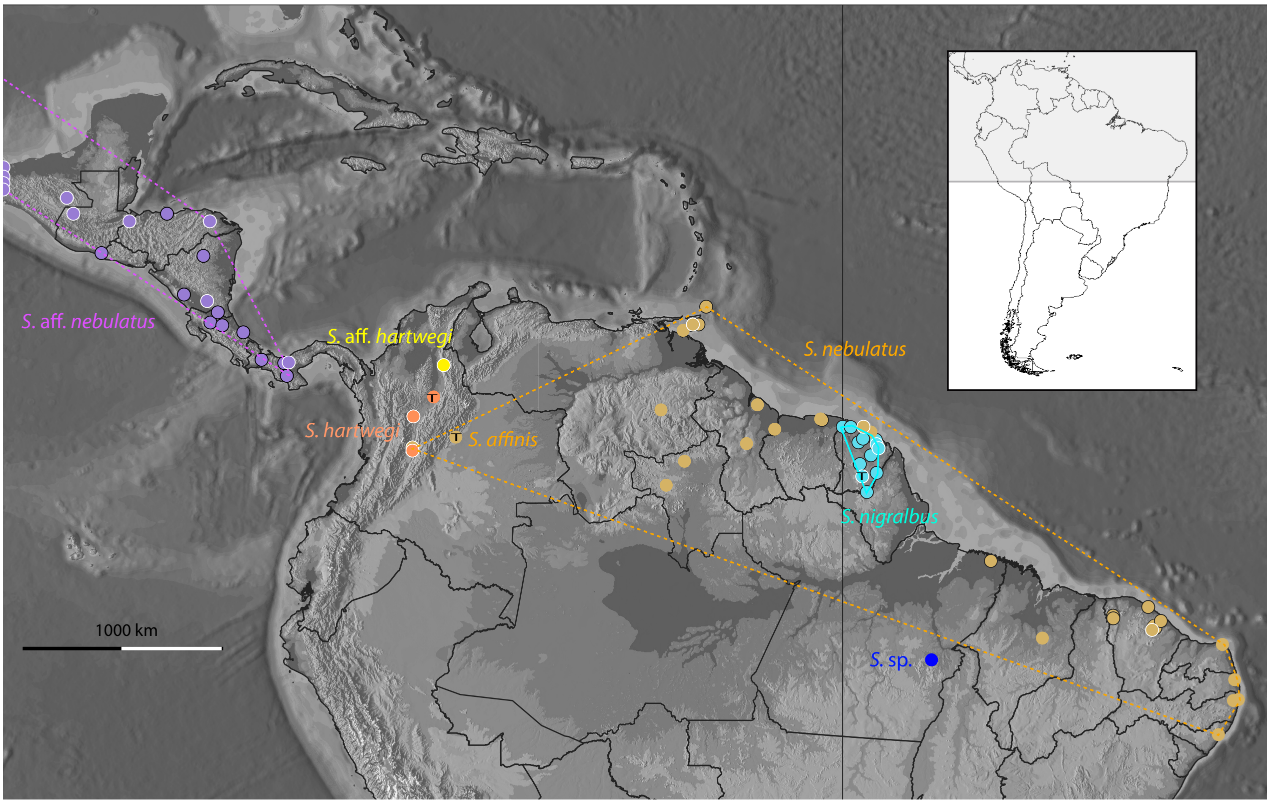

FIGURE 3. Occurrence records of *Sibon* spp. from northern South America and central America that have been associated with the name *S. nebulatus*. White-bordered circles indicate records supported by molecular data; black-bordered circles indicate specimens that have been examined morphologically; points without contour indicate records from iNaturalist, Faune Guyane or other credible sources. "T" symbols indicate type localities. The northernmost records in Mexico are out of the focal area.

Sibon nebulatus hartwegi has been elevated from subspecies to full species status by Arteaga & Batista (2023) based on mtDNA topology, the morphological similarity between one of the genotyped specimens (MHUA14511) with the holotype (notably the large dark bands in the anterior part of the body) (Fig. 5) and the fact that, like the holotype, the samples came from the lowlands of the Río Magdalena valley. However, there are four distinct lineages in this *S. nebulatus-hartwegi* group in the Río Magdalena valley, and the one assigned to *S. hartwegi* is the closest to *S. nebulatus*. Therefore, the status of *S. hartwegi* is still unclear and deserves further investigation that is out of the scope of this paper.

***Sibon nebulatus* amended diagnosis.** The following diagnosis is based on the holotype and 25 specimens examined from Colombia, Tobago, Pará and Ceará states (Brazil), and French Guiana (Appendix 1); (1) 15–16/15/15 smooth dorsals with enlarged vertebral row (2× as wide as adjacent rows); (2) loreal and prefrontal in contact with orbit; (3) 7–9 supralabials, 4th and 5th contacting orbit; (4) 7–9 infralabials,1st–6th in contact with chinshields, first pair of infralabials in contact behind symphysial; (5) 178–189 ventrals in males, 167–192 in females; (6) 76–100 divided subcaudals in males, 73–83 in females; (7) dorsal background color gray with 35–53 black bands (1–2 dorsal scales long distant by 2–4 dorsal scales from one another) bordered by light orange speckles in life, white in preservative (Fig. 2), ventral surfaces cream white 42–66 black bands interrupted medially and with smaller black speckles, dorsal aspect of head black with cream and orangish speckles and blotches, a large circular ocelli or a collar delimited by orangish scaled is often present (Figs 4,5), throat with cream white background with a few small black blotches and spots, iris light gray variegated with black reticulations; (8) 312–540 mm SVL in males, 384–530 mm in females; (9) 126–203 mm TL in males, 120–160 mm in females.

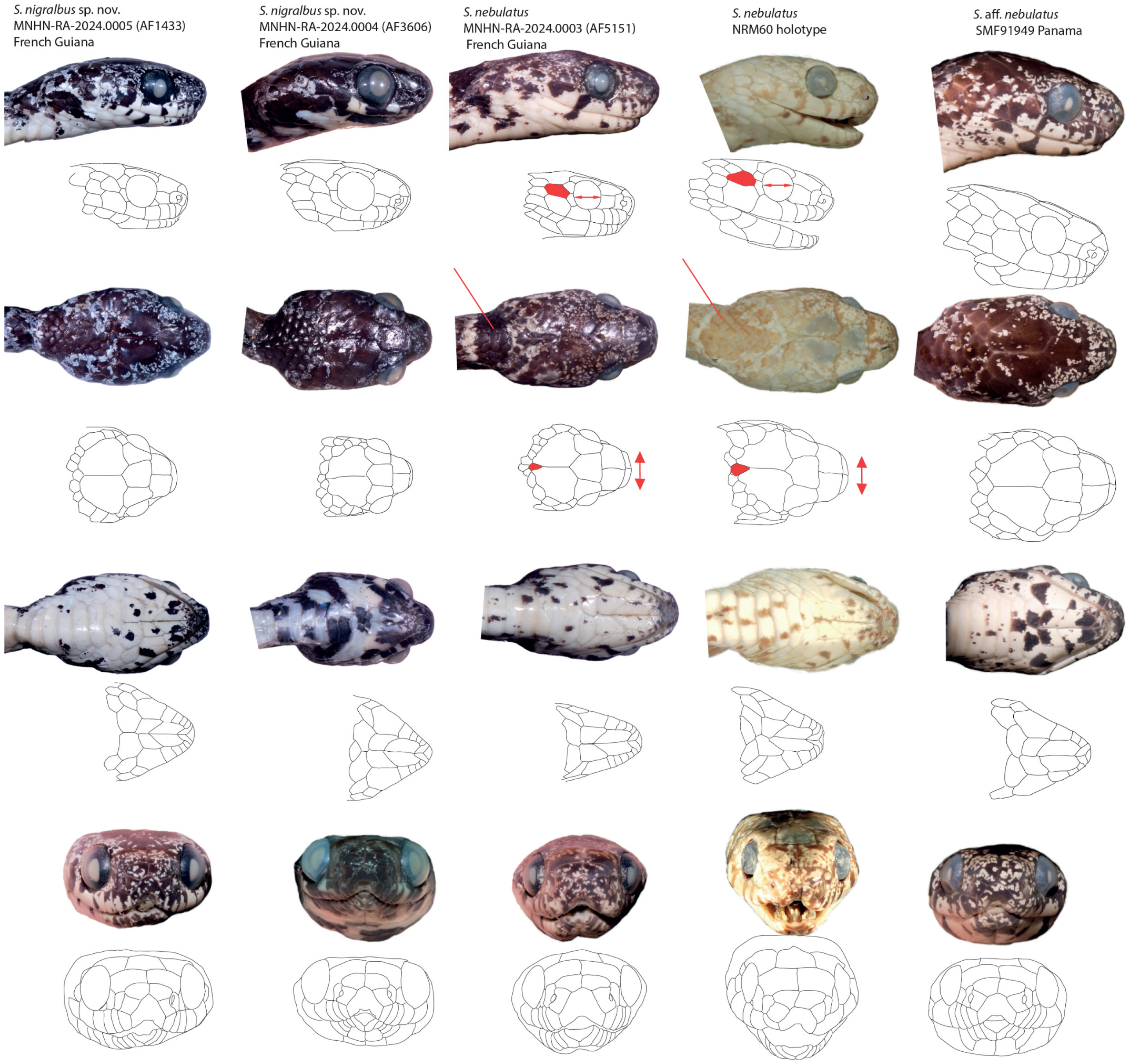

FIGURE 4. Pictures of preserved specimens of the *Sibon nebulatus* species complex and schematic drawings of the head in lateral, dorsal, ventral and frontal views. From left to right: two specimens of *S. nigralbus* sp. nov., a specimen of *S. nebulatus* from French Guiana, the holotype of *S. nebulatus*, and a specimen of *S.* aff. *nebulatus* from Central America. Some scales in the drawings are filled in red to highlight important differences in shape and a thin red line indicates the postcephalic dark patch.

Sibon nebulatus can be differentiated from the Central American species previously referred to as *S.* aff. *nebulatus* by Arteaga & Batista (2023) by generally having a greater number of dorsal and ventral dark patches (x=48.9 range=40–66 vs. x=38.1 range=30–45 in *S.* aff. *nebulatus*), these ventral patches are also thinner than in *S.* aff. *nebulatus*, and a large nuchal black mark, that is rarely seen in Central American specimens whereas some specimens in northern South America have patches almost identical to the one of the holotype (Fig. 5). *Sibon nebulatus* is less bulky but this does not appear in the PCA once size is corrected. Finally, *S. nebulatus* differs from species previously referred to as *S.* aff. *nebulatus* by having an elongated temporal (vs enlarged posteriorly) and parietals with posterior elongations resulting in an oak tree leaf pattern, and notably a dorsal scale nested between the two parietals dorsally (vs. posteriorly rounded parietals with no dorsal scale nested between them in *S.* aff. *nebulatus*).

FIGURE 5. Pictures of preserved (including types) and in life specimens of *S. nebulatus*, *S.* aff. *nebulatus* and *S. hartwegi*.

From the other South American species, *S. nebulatus* differs from *S. ayerbeorum* by having a higher number of supra and infralabials (7 and 7–9, respectively vs 6 and 6), a higher number of ventrals (167–192 vs 136–155) and a dorsal coloration with black bands (vs irregular middorsal and ventrolateral dark-bordered ocelli). From *S. dunni* by having a higher number of supralabials (7 vs 6), a higher number of ventrals (167–192 vs 136–145) and a gray dorsal coloration with black bands (vs light brownish-cream with a vertebral series of small, irregular, ovate, chocolate-brown spots). From *S. marleyae* by presenting a lower number of subcaudals (73–100 vs 109–143) and a gray dorsal coloration with black bands (vs olive to yellow with maroon bands). From *S. hartwegi* by having a lower number of supralabials (7 vs 8). *Sibon nebulatus* differs from both *S. leucomelas* and *S. vieirai* by having a conspicuous dark nuchal band as well as a drab and ochraceous background dorsal coloration (vs blackish or dark gray). *Sibon nebulatus* differs from *S. bevridgelyi* by having whitish dorsal markings on a primarily ochraceous background color (vs golden yellow dorsal markings and rusty brown to deep maroon background).

Hemipenis. Based on the partially everted left hemipenis of the specimens CHUFC1278 and CHUFC15745. The organ is slightly bilobed, capitate; on the sulcate side the *capitulum* occupies 2/3 of the hemipenis length, the *capitulum* is covered by spinulate calyces and small spines; the *sulcus spermaticus* is centrolineal and bifurcates just after the *capitulum* base; spines on edges of *sulcus* smaller than those on lateral and median region of sulcate side; *truncus* with enlarged asymmetrical spines at the sulcate and asulcate sides.

Distribution and ecology. *Sibon nebulatus* is widespread throughout northern South America, from Colombia to state of Alagoas in Brazil. In Colombia, it is apparently distributed on each side of the eastern Cordillera. However, the record in the Magdalena valley needs verification since there is a single mtDNA sequence attesting this trans-andean distribution. Even if the origin of this sample is confirmed, introgression with *S. hartwegi* remains possible and the presence of the species across the Andes remains to be confirmed by nuDNA and morphology. The species seems to occupy open and transitional habitats between forest and savannas which explains the seemingly fragmented range of the species that is probably widespread in the Llanos and in the Rupununi savanna (Roraima) and possibly in the savannas throughout Pantepui. It also stretches along the coast of the Guiana region from Trinidad to French Guiana where it reaches a northeastern range limit. *Sibon nebulatus* also occurs in the Brazilian northeast. It is unclear if it occurs between the Guiana region and northeast Brazil along the lower course of the Amazon River (another species seems to occur in Pará, see below) and in the coastal savannas of Amapá.

Sibon nigralbus **sp. nov.**

Sibon nebulatus **Dewynter** ***et al.*** **(2021)**

Proposed standard English name: black and white snail-eating snake

Type material. Holotype: MNHN-RA-2024.0004 (AF3606) (Figs 4, 6), adult male collected by Antoine Fouquet, Elodie Courtois, Benoit Villette and Mael Dewynter, on 07 January 2016 at Mont Itoupé, French Guiana (3.02647 -53.07983; 800 m a.s.l.).

Paratypes: MNHN-RA-2024.0005 (AF1433), adult male collected by Elodie Courtois on 16 December 2013 at RN2 PK80, French Guiana (4.38526 -52.30456; 90 m a.s.l.). MNHN-RA-2024.0006 (RG86), adult female collected by Michel Blanc on 18 January 2013 at RN2 PK40, French Guiana (4.57989 -52.39734; 90 m a.s.l.). MNHN-RA-2024.0007 (RG98), adult male collected by Michel Blanc on 15 October 2016 at RN2 PK36, French Guiana (4.60042 -52.40194; 90 m a.s.l.). MNHN-RA-2024.0008 (RG9) adult male collected by Michel Blanc on 18 June 2001 at CD5 PK2, French Guiana (4.79283 -52.43410; 60 m a.s.l.).

Diagnosis. *Sibon nigralbus* sp. nov. is placed in the genus *Sibon* based on phylogenetic evidence (Fig. 1) and on having the penultimate supralabial conspicuously higher than all other supralabials. The species is diagnosed based on the following combination of characters: (1) 14–15/15/15 smooth dorsals with enlarged vertebral row (2× as wide as adjacent rows); (2) loreal and prefrontal in contact with orbit; (3) 7–8 supralabials, 4th and 5th, or 5–6, or 6–7 contacting orbit; (4) 8–9 infralabials, 1st–6th in contact with chinshields, first pair of infralabials in contact behind symphysial; (5) 194–200 ventrals in males, 199 in the single female; (6) 99–114 divided subcaudals in males, 101 in the single female; (7) dorsal background color gray with 47–67 black bands (1–3 dorsal black scales per band separated by 2–3 gray dorsal scales) boarded by light gray speckles (Fig. 5), ventral surfaces cream white 53–64 black bands interrupted medially and with smaller black speckles, dorsal aspect of head black with white speckles dorsally and white blotches laterally, throat with cream white background with black blotches and spots, iris light gray variegated with black reticulations; (8) 360–447 mm SVL in males, 493 mm in the single female; (9) 152–175 mm TL in males, 202 mm in the single female.

Comparisons. *Sibon nigralbus* sp. nov. is compared to other species of *Sibon* forming the *S. nebulatus* clade. *Sibon nigralbus* sp. nov. co-occurs in French Guiana with *S. nebulatus* (in parenthesis), from which it differs primarily on the basis of its light gray band with white flecks between black bands (vs dark gray with ochre/orange flecks and stripes), by having more ventral scales (194–200 vs 181–185 in males); more subcaudals (99–114 vs 73–100), a smaller head (2.1–2.9% vs 3.0–3.8% of SVL) and larger eyes (28–32 % vs 21–25% of HL).

TABLE 2. Variation in selected meristic characters across all nominal *Sibon* spp.

Species	DO	VE (M)	VE (F)	SC (M)	SC (F)	SL	IL
SOUTH AMERICAN SPECIES							
S. ayerbeorum	15/15/15	155	136–140	93	78–79	6	6
S. bevridgelyi	15/15/15	175–193	193	80–94	98	7–8	7–11
S. dunni	15/15/15	142–145	136–139	60–62	48–56	6	8–9
S. hartwegi	15/15/15	171–195	172–191	85–103	75–82	8	9
S. leucomelas	15/15/15	190–198	187–194	84–101	84–100	7	-
S. marleyae	15/15/15	186–204	176–193	130–143	109–128	7–8	8–9
S. nebulatus	15/15/15	178–189	167–192	76–100	73–83	7	7–9
S. nigralbus sp. nov.	14–15/15/15	194–200	199	99–114	101	7–8	8–9
CENTRAL AMERICAN SPECIES							
S. annulatus	15/15/15	170–192	161–186	108–135	113–126	7–8	7–9
S. anthracops	13/13/13	175–188	166–180	79–91	73–81	6–8	7–9
S. argus	15/15/15	181–201	186–192	112–121	95–108	6–9	6–9
S. canopy	15/15/15	180–189	170–185	113–130	107–124	6–8	6–8
S. carri	13/13/13	157–168	165–173	46–51	42–49	6–7	6–7
S. dimidiatus	15/15/15	184–200	171–196	113–126	100–122	7–9	7–12
S. irmelindicaprioae	15/15/15	187–196	174	110–128	117	7–9	8–10
S. lamari	15/15/15	162–163	168–171	77–108	112–119	7–8	8–10
S. linearis	15/15/15	-	155	-	70	9	-
S. longifrenis	15/15/15	147	147	101	101	7	7
S. manzanaresi	15/15/15	171–176	174	106–112	111	8	9–10
S. merendonensis	15/17/17	-	184	-	83	-	-
S. miskitus	15/15/15	170–180	168–171	106–112	95–100	-	-
S. aff. *nebulatus*	15–16/15-16/15	175–191	171–178	83–103	74–79	7	9
S. noalamina	15/15/15	170–177	-	80–96	-	5	6–7
S. perissostichon	15/17/15	-	186	-	108	6	7
S. vieirai	15/15/15	86–101	84–100	95–105	78–92	7–8	9–10

Sibon nigralbus sp. nov. can be further differentiated from the other nominal *Sibon* from South America by a combination of meristic characters (Table 2) and color pattern. From *S. vieirai* it differs by a higher number of ventrals (194–200 vs 84–105), presence of dorsal black bands (vs blackish blotches or incomplete bands) and a throat with black blotches and spots (vs black markings that form a checkerboard pattern). From *S. leucomelas*, the new species is differentiated by having higher number of subcaudals (99–114 vs 84–101) and a throat with black blotches and spots (vs throat entirely black). From *S. ayerbeorum*, the new species can be distinguished by its higher number of supra and infralabials (7–8 and 8–9 vs 6 and 6 respectively), higher number of ventrals (194–200 vs 136–155) and subcaudals (99–114 vs 78–93), and a dorsal coloration with black bands (vs irregular middorsal and

FIGURE 6. Holotype and one of the paratypes of *Sibon nigralbus* sp. nov. in preservative and picture of specimens in life.

ventrolateral dark-bordered ocelli). It can be differentiated from *S. bevridgelyi* by its higher number of ventrals (194–200 vs 175–193), higher number of subcaudals (99–114 vs 80–98), and a gray dorsal coloration with black bands (vs pale yellow with or without black bands and a black stippled disruptive pattern of irregular rusty to reddish brown blotches). From *S. dunni*, the new species differs by its higher number of supralabials (7–8 vs 6), higher number of ventrals (194–200 vs 136–145), and its gray dorsal coloration with black bands (vs light brownish-cream with a vertebral series of small, irregular, ovate, chocolate-brown spots). From *S. marleyae*, it differs by having a lower number of subcaudals (99–114 vs 109–143) and a gray dorsal coloration with black bands (vs olive to yellow with maroon bands). From *S. hartwegi*, it differs by its higher number of ventrals (194–200 vs 171–195) and subcaudals (99–114 vs 75–103).

Etymology. The specific epithet is the combination of the Latin words *nigrum* (meaning "black") and *albus* (meaning "white"). It refers to the color pattern of the species which consists of a succession of white, gray, and black bands.

Description of holotype. Adult male, SVL 366 mm, tail length 170 mm (46.4% SVL); head length 10.4 mm (2.8% SVL) from tip of snout to angle of jaw; head width 8.6 mm (82.8% head length) taken at broadest point; nostril-orbit distance 2.0 mm; head distinct from neck; snout short, blunt in dorsal outline and rounded in profile; rostral 2.2 mm wide, broader than high; internasals 3.0 mm wide, broader than long; prefrontals 4.4 mm wide, broader than long, entering orbit; supraocular 3.4 mm long, longer than broad; frontal 3.3 mm long, with a pentagonal shape, in contact with prefrontals, supraoculars, and parietals; parietals 5.4 mm long, longer than broad; nasal divided, in contact with two supralabials, loreal, prefrontal, internasal, and rostral; loreal 1.3 mm long, longer than high, entering the orbit; eye diameter 3.3 mm; pupil semi-elliptical; no preocular; two postoculars; temporals 1+2; seven supralabials, 4th and 5th contacting orbit; symphysial precluded from contacting chinshields by first pair of infralabials; eight infralabials,1st–6th contacting chinshields; two pairs of chinshields longer than wide; dorsal scales in 15/15/15 rows, smooth, without apical pits; 197 ventrals; 114 divided subcaudals; cloacal plate entire.

Hemipenis. Based on the partially everted left hemipenis of the paratype MNHN-RA-2024.0005 (AF1433). The organ is slightly bilobed, capitate; on the sulcate side the *capitulum* occupies 1/2 of the hemipenis size, the *capitulum* is covered by spinulate calyces and small spines; the *sulcus spermaticus* is centrolineal and bifurcates just after the *capitulum* base; spines on edges of *sulcus* smaller than those on lateral and median region of sulcate side; *truncus* with enlarged asymmetrical spines at the sulcate and asulcate sides.

Distribution and ecology. *Sibon nigralbus* sp. nov. is only known from French Guiana, (where it was so far mistaken with *S. nebulatus* whereas specimens of *S. nebulatus* sensu stricto were considered to belong to a new species) but it is widespread throughout the territory at the exception of the upper Maroni basin and along the coastal strip of savannas where *S. nebulatus* occurs (Dewynter *et al.* 2021). It is indeed a species found in close association with secondary and old growth forests. Therefore, it is very likely that this species also occurs in the forests of the neighboring Amapá state (Brazil) and Suriname. A picture of a specimen from Marabá, Pará state (Brazil), south of the Amazon river, is morphologically similar to *S. nigralbus* (*S.* sp. in Fig. 3). Several specimens have been observed feeding on snails in French Guiana. One specimen was observed at 05h30 am perched at about 6 m above the ground on a vine of the genus *Bauhinia* and disappeared in a cavity in the trunk.

Discussion

Amphibian or reptile species, including snakes, having a continuous distribution throughout Central America and northern South America are extremely rare (Nogueira *et al.* 2020). The presence of the Andes and the relatively recent connection between the two landmasses (Bacon *et al.* 2015) are obvious explanations for the sharp difference in biotic composition between Central and South America. In fact, almost all recent studies focusing on species of snakes supposed to have trans-Andean ranges (distributed across Central and South America) have resulted in taxonomic revisions with species being restricted to each sides (e.g., *Leptodeira annulata* in Costa *et al.* 2022; *Phrynonax poecilonotus* in Lopes & Passos 2023; *Oxybelis aeneus* and *O. fulgidus* in Jadin *et al.* 2020).

The existence of distinct species within *Sibon nebulatus* had been hypothesized for a long time (Peters 1960) and almost all described subspecies within *Sibon nebulatus* have been elevated to full species status already, notably by Arteaga and Batista (2023), but additional taxonomic changes are still required to fully represent the extant diversity. Parker (1960) already noticed differences in coloration between Central America and northern

South American populations of *S. nebulatus nebulatus* but there was two major obstacles: characterizing the extant diversity within both Central and South America (using molecular data herein), and identifying the morphological similarity between the holotype, whose type locality is unknown, and a comprehensive sampling of this diversity. Many taxa described by Linnaeus have vague type localities which hamper taxonomic revision because recent material and complementary lines of evidence, notably molecular data, cannot be associated with the type material (e.g., de Mello *et al.* 2024). These old names have been used for decades or even centuries to identify populations that in fact belong to distinct species, often across vast regions like the entire Amazonia (Moraes *et al.* 2022). The large distribution of many species is therefore often erroneous and hampers our understanding of the basic structure of biodiversity (Vacher *et al.* 2020). These unrecognized species are sometimes conspicuously distinct (Fouquet *et al.* 2016) or truly "cryptic" (Vacher *et al.* 2017), and in this second situation the challenge lies in identifying correctly the nominal species and thus obtaining enough information from type specimens. We partly filled this gap in this work, improving our understanding of the extant diversity and clarifying the taxonomic identity of previously documented lineages of *Sibon*.

The Central American lineage identified as *Sibon* aff. *nebulatus* remains widely distributed from Mexico to Panama and harbors a pronounced genetic structure suggesting that it probably includes more than one species. Similarly, records from Pará state and the existence of several mtDNA lineages in the Magdalena valley in Colombia suggest that additional species in northern South America exist. Even what we here consider as *S. nebulatus* sensu stricto can in fact correspond to several species since the northeastern Brazil populations are genetically distinct from the rest (see below). We hope that this study will foster further research to clarify the status of these populations that have been identified as *Sibon nebulatus* so far.

The distribution pattern of *Sibon nebulatus* is peculiar, since it occurs in the Llanos, the Rupununi savanna, and the coastal strip of the Guiana region and then in northeastern Brazil. Such a pattern is rare in squamates and amphibians and strengthens the idea that the distinction between the easternmost populations and the western ones deserve further study. Nevertheless, such a pattern is largely explained by the association of the species with open habitats that occur in isolated patches in northern South America. Moreover, this pattern is found in other species with similar ecology, including *Chironius carinatus*, *Pseudoboa neuwiedii*, *Thamnodynastes pallidus*, *Crotalus durissus* (Nogueira *et al.* 2020) and frogs such as *Dendropsophus minusculus* (Zina *et al.* 2014), *Scinax nebulosus* (Freitas *et al.* 2020), *Physalaemus ephippifer* (Nascimento *et al.* 2019). However, in some of these species, there cryptic diversity is also expected because clear genetic structures exist between the Guiana region and northeastern Brazil (Vacher *et al.* 2020).

On the contrary, the distribution pattern of *Sibon nigralbus* is found in a multitude of species of squamates (Ribeiro-Júnior & Amaral 2017; Nogueira *et al.* 2020) and amphibians (Vacher *et al.* 2020) that are endemic to the easternmost part of the Guiana region, a pattern explained by the barriers formed by the lower course of the Amazon River and climatic gradients. Nevertheless, the species could extend to Pará, which is rare in amphibians but not so much in lizards such as *Alopoglossus angulatus, Copeoglossum nigropunctatum, Tretioscincus agilis, Iphisa elegans, Neusticurus rudis,* and *Gymnophthalmus underwoodi* (Miralles & Carranza 2010; Ribeiro-Júnior & Amaral 2017) that are distributed throughout eastern Amazonia and have a trans-Amazon river distribution.

Interestingly, a South American clade notably formed by *Sibon nebulatus*, *S. nigralbus* sp. nov., *S. vieirai*, and *S. leucomelas* diverged from the Central America clade formed by *S.* aff. *nebulatus*, and are both nested within the other species of *Sibon* occurring in Central America. Therefore, we can assume that *Sibon* dispersed once from Central America, possibly with the progressive closure of the isthmus and was probably part of the pulse of dispersals of the late Miocene 8–6 Ma ago, which mirrors the pattern shared by many other lineages of amphibians, reptiles, fish, and birds (Bacon *et al.* 2015).

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APPENDIX 1. list of examined specimens.

Species	Voucher	Sex	Country	Province	Locality	Lat	Long	Altitude	Collection Date	Collector
S. aff. *nebulatus*	SMF77134	M	Costa Rica	Alajuela	Volcan Arenal	10.48000	-84.70000	709	03_11_1955	K. Janousek
S. aff. *nebulatus*	SMF79561	F	Nicaragua	Granada	Vulkan Mombacho,	11.83563	-85.98094	1100	7_18_1999	N. Valerio
S. aff. *nebulatus*	SMF79837	M	Nicaragua	Río San Juan	Bartola	10.97283	-84.33917	30	6_16_2000	G. Köhler
S. aff. *nebulatus*	SMF79879	M	Honduras	Atlantida	La Ceiba	15.7515	-86.80263	100	8_20_2000	J. Ferrari
S. aff. *nebulatus*	SMF81283	M	El Salvador	Ahuachapan	Parque Nacional El Imposible	13.84667	-89.98000	720	04_11_1998	G. Köhler, E. Köhler
S. aff. *nebulatus*	SMF83122	F	Nicaragua	Atlantico Norte	Parque Nacional Saslaya	13.70850	-85.03825	830	7_27_2004	G. Köhler
S. aff. *nebulatus*	SMF89598	M	Panama	Veraguas	PNSF: Cerro Mariposa	8.51223	-81.12142	933	06_06_2008	L. Stadler, N. Hamad
S. aff. *nebulatus*	SMF90209	M	Panama	Chiriqui	RFLF: Lost & Found Ecohostel	8.67462	-82.21958	1250	06_10_2009	S. Lotzkat, A. Hertz
S. aff. *nebulatus*	SMF91949	M	Panama	Veraguas	Finca La Providencia	7.89542	-80.99138	16	10_02_2011	G. Köhler
S. aff. *nebulatus*	SMF98956	M	Costa Rica	Limon	Moin	10.00357	-83.10438	22	4_27_2013	J. Vargas
S. aff. *nebulatus*	SMF100964	F	Costa Rica	Heredia	San Ramón de la Virgen	10.34315	-84.12447	414	07_06_2016	S. Lotzkat
S. nebulatus	NHRM60	Holotype	?							?
S. nebulatus	SMF67976	M	Tobago			11.24698	-60.66304			F. J. Landen
S. nebulatus	MNHN1997.2125	F	French Guiana		?					C. Marty
S. nebulatus	MNHN1997.2005	F	French Guiana		Synamary	5.35887	-52.94456	10		F. Starace, C. Marty
S. nebulatus	MNHN-RA-2024.0003	M	French Guiana		Crique canceler	5.42960	-53.03750	10		A. Baglan
S. nebulatus	CHUFC15747	M	Brazil	Ceará	Tianguá	-3.72742	-40.93850	740	26_01_2019	R. Avila
S. nebulatus	CHUFC15748	M	Brazil	Ceará	Ubajara	-3.85806	-40.92750	847	28_01_2019	R. Avila
S. nebulatus	CHUFC14581	F	Brazil	Ceará	Ubajara	-3.85806	-40.92750	840	?	R. Avila
S. nebulatus	CHUFC15745	M	Brazil	Ceará	Tianguá	-3.72742	-40.93850	867	26_01_2019	R. Avila
S. nebulatus	CHUFC15744	F	Brazil	Ceará	Tianguá	-3.72742	-40.93850	865	26_01_2019	R. Avila

......continued on the next page

APPENDIX 1. (Continued)

Species	Voucher	Sex	Country	Province	Locality	Lat	Long	Altitude	Collection Date	Collector
S. nebulatus	CHUFC14582	M	Brazil	Ceará	Ubajara	-3.85806	-40.92750	840	?	R. Avila
S. nebulatus	CHUFC2774	F	Brazil	Ceará	Ubajara	-3.85806	-40.92750	840	04_06_1999	NUROF-UFC
S. nebulatus	CHUFC2440	M	Brazil	Ceará	Pacoti	-4.22500	-38.92278	800	03_04_1990	NUROF-UFC
S. nebulatus	CHUFC2775	F	Brazil	Ceará	Mulungu	-4.30556	-38.99639	801	01_01_1991	NUROF-UFC
S. nebulatus	CHUFC2770	F	Brazil	Ceará	Pacoti	-4.22500	-38.92278	800	23_11_1997	NUROF-UFC
S. nebulatus	CHUFC2171	M	Brazil	Ceará	Pacoti	-4.22500	-38.92278	800	09_08_1997	NUROF-UFC
S. nebulatus	CHUFC2679	M	Brazil	Ceará	Pacoti	-4.22500	-38.92278	800	02_03_2006.	NUROF-UFC
S. nebulatus	CHUFC3819	F	Brazil	Ceará	Baturité	-4.32806	-38.88472	412	01_01_2000	NUROF-UFC
S. nebulatus	URCA5699	M	Brazil	Ceará	Trairí	-3.30789	-39.23357	9	?	R. Avila
S. nebulatus	CHUFC1278	M	Brazil	Pará	Bragança	-1.07593	-46.86192	4	28_03_1974	NUROF-UFC
S. nebulatus	CHUFC1350	F	Brazil	Ceará	Fortaleza	-3.79099	-38.43817	16	03_01_1988	NUROF-UFC
S. nebulatus	CHUFC2140	M	Brazil	Ceará	Ibiapina	-3.92528	-40.89528	878	07_03_1998	NUROF-UFC
S. nebulatus	CHUFC2139	M	Brazil	Ceará	Ibiapina	-3.92528	-40.89528	878	07_03_1998	NUROF-UFC
S. nebulatus	CHUFC4534	F	Brazil	Ceará	Mulungu	-4.30556	-38.99639	801	18_03_2022	NUROF-UFC
S. nebulatus	CHUFC4343	M	Brazil	Ceará	Pacatuba	-3.98389	-38.62000	600	01_08_2010	NUROF-UFC
S. nebulatus	CHUFC4533	M	Brazil	Ceará	Aratuba	-4.41778	-39.04500	830	18_03_2022	NUROF-UFC
S. nigralbus	MNHN-RA-2024.0005	M	French Guiana		RN2 PK80	4.38526	-52.30456	90	16_12_2013	A. Fouquet, E. Courtois, B. Villette, M. Dewynter
S. nigralbus	MNHN-RA-2024.0004	M	French Guiana		Itoupe	3.02302	-53.09547	800	07_01_2016	E. Courtois
S. nigralbus	MNHN-RA-2024.0006	F	French Guiana		RN2/PK 40	4.57989	-52.39734	90	18_01_2013	M. Blanc
S. nigralbus	MNHN-RA-2024.0008	M	French Guiana		CD5/PK 2	4.79283	-52.43410	60	18_06_2001	M. Blanc
S. nigralbus	MNHN-RA-2024.0007	M	French Guiana		RN2/PK 36	4.57989	-52.39734	90	15_10_2016	M. Blanc

APPENDIX 2. Additional occurrence records.

Species	Source	Country	state	Locality	lat	lon
Sibon nebulatus	iNaturalist 191313826	Brazil	RR	Tepequem	3.75509	-61.71727
Sibon nebulatus	iNaturalist 146055486	Suriname		Orealla	5.30774	-57.33909
Sibon nebulatus	iNaturalist 1999388	Guyana		Iwokrama	4.61201	-58.70544
Sibon nebulatus	iNaturalist 45124684	Venezuela		Canaima NP	6.24302	-62.85409
Sibon nebulatus	iNaturalist 192413637	Trinidad		Coromandel Settlement	10.10118	-61.77844
Sibon nebulatus	iNaturalist 131657033	Guyana		Soesdyke-Linden highway	6.49182	-58.17777
Sibon nebulatus	iNaturalist 216924274	Suriname		Tamanredjo	5.75720	-55.04996
Sibon nebulatus	iNaturalist 194472561	Suriname		Meerzorg	5.80432	-55.11246
Sibon nebulatus	iNaturalist 140260030	Brazil	MA	Santo Antônio dos Lopes	-4.81554	-44.36246
Sibon nigralbus	iNaturalist 202231486	French Guiana		Saul	3.61851	-53.21184
Sibon nigralbus	iNaturalist 110738207	French Guiana		Nouragues	4.04063	-52.67641
Sibon nebulatus	iNaturalist 149476287	Brazil	RN	São Miguel de Touros	-5.12438	-35.63582
Sibon nebulatus	iNaturalist 218904517	Brazil	PE	Ilha de Itamaracá	-7.79365	-34.86406
Sibon sp. PA	iNaturalist 146306767	Brazil	PA	Marabá	-5.86861	-49.73789
Sibon nebulatus	iNaturalist 11264701	Trinidad		Bus Bush Wildlife Sanctuary	10.38306	-61.03571
Sibon nebulatus	França *et al.* 2018	Brazil	PE	CIMNC	-7.84077	-35.10124
Sibon nebulatus	França *et al.* 2012	Brazil	PR	Rio Tinto	-6.83121	-35.04242
Sibon nebulatus	Freire 1998	Brazil	AL	Rio Largo	-9.49170	-35.8305
Sibon nebulatus	Faune-Guyane	French Guiana		Kourou, golf	5.17083	-52.67669
Sibon nigralbus	Faune-Guyane	French Guiana		Piste Bushiman	5.42611	-54.04333
Sibon nigralbus	Faune-Guyane	French Guiana		Angouleme	5.41109	-53.65514
Sibon nigralbus	Faune-Guyane	French Guiana		Lipo lipo	2.25969	-52.87256
Sibon nigralbus	Faune-Guyane	French Guiana		Polydor	3.19269	-52.39807
Sibon nigralbus	Faune-Guyane	French Guiana		Trinité	4.67081	-53.28381
Sibon nigralbus	Faune-Guyane	French Guiana		St Eugene	4.85042	-53.06083

APPENDIX 3. GenBank accession numbers for loci and terminals of taxa and outgroups sampled in this study. Novel sequence data produced in this study are marked in bold and with an asterisk (*).

Species	Voucher	Cytb	ND4	Country	Locality	Latitude	Longitude
S. aff. *hartwegi*	ICN11463	NA	JX398532	Colombia	Río de Oro	8.27256	-73.40639
S. aff. *nebulatus*	CIG788	MZ287377	MZ287387	Mexico	Chiapas	-	-
S. aff. *nebulatus*	ENS11968	NA	JX398529	Mexico	Guerrero	17.35477	-99.45820
S. aff. *nebulatus*	JAC19311	NA	JX398534	Guatemala	Huehuetenango	15.87000	-91.22583
S. aff. *nebulatus*	JAC28055	JX398678	JX398535	Mexico	Colima	19.40784	-104.05303
S. aff. *nebulatus*	JAC28140	NA	JX398536	Mexico	Colima	19.22840	-104.20312
S. aff. *nebulatus*	JAC28589	NA	JX398537	Mexico	Colima	19.01834	-103.77038
S. aff. *nebulatus*	JAC30102	NA	JX398538	Mexico	Colima	19.37525	-103.94473
S. leucomelas	JM703	JX398679	JX398539	Panama	PN General Omar Torrijos	8.66670	-80.61670
S. leucomelas	JM722	JX398680	JX398540	Panama	PN General Omar Torrijos	8.66670	-80.61670
S. leucomelas	JM793	JX398681	JX398541	Panama	PN General Omar Torrijos	8.66670	-80.61670
S. aff. *nebulatus*	MVZ233298	EU728583	EU728583	Costa Rica	-	-	-
S. aff. *nebulatus*	N068	JX398682	JX398542	Nicaragua	-	11.32194	-84.73931
S. aff. *nebulatus*	UOGV332	NA	JX398546	Mexico	Chiapas	16.34425	-91.611528
S. aff. *nebulatus*	USNM564142	NA	JX398547	Honduras	Gracias a Dios	15.34181	-84.60604
S. aff. *nebulatus*	USNM564143	NA	JX398548	Honduras	Gracias a Dios	15.34181	-84.60604
S. aff. *nebulatus*	UTAR42431	JX398690	JX398549	Guatemala	Izabal	15.36000	-88.72300
S. annulatus	MVZ269290	MH375034	MH375053	Nicaragua	-	-	-
S. anthracops	ASL198	JX398657	JX398506	Costa Rica	Santa Rosa	10.84441	-85.56373
S. anthracops	MVZ215680	MH375035	MH375054	Costa Rica	-	-	-
S. bevridgelyi	MZUARE424	MH374990	NA	Ecuador	2 km N Palmales Nuevo	-3.65158	-80.09625
S. bevridgelyi	MZUTI3269	MH374962	NA	Ecuador	Reserva Buenaventura	-3.65343	-79.76722
S. bevridgelyi	MZUTI5416	MH374963	NA	Ecuador	Reserva Buenaventura	-3.65343	-79.76722
S. bevridgelyi	RSCDSP0391	JX398683	JX398543	Ecuador	cf. Guayas		
S. carri	UTAR45493	JX398665	JX398514	Guatemala	Zacapa	15.24011	-89.17680
S. dimidiatus	USNM565824	JX398668	JX398517	Honduras	Olancho	14.92883	-85.80492
S. dunni	CAMPO533	MH374991	NA	Ecuador	Pimampiro	0.39074	-77.94103
S. hartwegi	ICN11510	NA	JX398533	Colombia	Santander	6.54960	-73.12641
S. hartwegi	MHUA14511	GQ334556	GQ334662	Colombia	Antioquia	5.95257	-74.85040
S. hartwegi	SN0001	JX398684	JX398544	Colombia	Tolima	4.21852	-74.68138
S. lamari	ASL362	JX398670	JX398519	Costa Rica	Guayacan de Siquirres	10.06446	-83.54332
S. vierai 2	MZUTI3911	MH374964	NA	Ecuador	Reserva Itapoa	0.51307	-79.13401
S. vierai 2	MZUTI4810	MH374965	NA	Ecuador	Jardín de los Sueños	-0.83142	-79.21337
S. longifrenis	MVZ215681	MH375036	MH375055	Costa Rica	-	-	-
S. nebulatus	AF5151	**PV443854***	**PV443862***	French Guiana	Crique Canceler	5.42960	-53.03750
S. nebulatus	CHUFC3735	**PV443857***	**PV443861***	Brazil	Pacoti, Ceará	-4.22832	-38.92437
S. nebulatus	SN02	NA	JX398545	Colombia	Tolima	4.21852	-74.68138
S. nebulatus	UWIZM20112026	JX398687	JX398551	Tobago	Lopinot Valley	10.68464	-61.32633
S. nigralbus sp. nov.	RG98	NA	**PV443858***	French Guiana	RN2 PK36	4.57989	-52.39734
S. nigralbus sp. nov.	AF1433	**PV443855***	**PV443859***	French Guiana	RN2 PK80	4.38526	-52.30456
S. nigralbus sp. nov.	AF3606	**PV443856***	**PV443860***	French Guiana	Itoupé	3.02302	-53.09547
S. vierai 1	ENS12459	NA	JX398530	Ecuador	Esmeraldas	1.18333	-78.75349
S. vierai 1	ENS12500	NA	JX398531	Ecuador	Esmeraldas	1.18333	-78.75349

APPENDIX 4. p-distance matrix (lower left ND4; upper right Cytb).

	nigralbus	*nebulatus*	aff. *nebulatus*	*vierai*	aff. *hartwegi* 1	sp. Magdalena	*leucomelas*	*hartwegi*	*bevridgelyi*	*dunni*
S. nigralbus		0.0862	0.1088	0.0615	?	?	0.0720	0.0827	0.0607	0.0636
S. nebulatus	0.0764		0.1029	0.0629	?	?	0.0755	0.0368	0.0556	0.0661
S. aff. *nebulatus*	0.0820	0.0971		0.0903	?	?	0.0938	0.1019	0.0885	0.0929
S. vierai	0.0792	0.0774	0.1029		?	?	0.0410	0.0598	0.0193	0.0325
S. aff. *hartwegi* 1	0.0788	0.0621	0.1029	0.0767		?	?	?	?	?
S. sp. Magdalena	0.0665	0.0727	0.0885	0.0753	0.0780		?	?	?	?
S. leucomelas	0.0823	0.0702	0.0940	0.0717	0.0579	0.0760		0.0749	0.0350	0.0402
S. hartwegi	0.0803	0.0417	0.1045	0.0880	0.0689	0.0825	0.0848		0.0520	0.0621
S. bevridgelyi	0.0788	0.0738	0.0990	0.0316	0.0734	0.0750	0.0669	0.0853		0.0296
S. dunni	?	?	?	?	?	?	?	?	?	