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Research Article

Integrative taxonomy of *Micrurus ibiboboca* (Merrem, 1820) (Serpentes, Elapidae) reveals three new species of coral snake

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The elapid coral snake genus *Micrurus* is a group of Neotropical venomous snakes divided into two clades composed of species with monadal and triadal colour patterns. Historically, several studies have considered the triadal *Micrurus ibiboboca* a species complex. Here, we evaluate the cryptic diversity of the *M. ibiboboca* species complex based on a molecular phylogenetic analysis performed on a dataset that comprised 25 described species of *Micrurus* and five sequenced genes (one nuclear and four mitochondrial). Furthermore, we contrasted our molecular results with a comprehensive morphological study using external and hemipenial characters. Our phylogenetic results recovered three well-supported clades for triadal colour patterns: (1) *M. ortoni*, *M. surinamensis*, *M. potyguara*, *M. filiformis*, *M. lemniscatus*, *M. carvalhoi*, *M. diutius*, and *M. helleri*; (2) *M. dissoleucus* and *M. mipartitus*; and (3) *M. frontalis*, *M. brasiliensis*, *M. obscurus*, *M. altirostris*, *M. baliocoryphus*, *M. pyrrhocryptus*, and the *M. ibiboboca* species complex. Based on our results, we redescribe *M. ibiboboca* and describe three new species of coral snake from Northeastern and Southeastern Brazil, previously confused with *M. ibiboboca.*

http://zoobank.org/urn:lsid:zoobank.org:pub:44DE4ADA-1DE3-46E1-A288-CBC5E37105E5

Key words: Atlantic Rain Forest, Caatinga, cryptic diversity, hemipenial morphology, molecular phylogeny, neotropical snakes, systematics

Introduction

Micrurus Wagler, 1824 is a genus of Neotropical elapids widely distributed in South America (Roze, 1996; Silva, Buononato, et al., 2016, 2021). Currently, this group has more than 80 recognized species distributed from the southeastern United States to southern South America (Rio Negro Province, Argentina). Campbell and Lamar (2004), following Roze and Bernal-Carlo (1987), recognized four groups within *Micrurus* based mainly on their colour patterns: (1) The Central American triadal group, (2) the South American triadal group, (3) the South American bicolored group, and (4) the South American monadal group.

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Traditionally, many taxonomic studies of *Micrurus* were based mainly on morphological evidence (Bernarde et al., 2018; Di-Bernardo et al., 2007; Feitosa et al., 2007a, 2007b, 2015; Nascimento et al., 2019; Passos & Fernandes, 2005; Pires et al., 2014, 2021; Silva & Sites, 1999). However, although morphological characters play a pivotal role in diagnosing the diversity in coral snakes, several previous studies have emphasized the necessity of more thorough analyses to delimit species within this group (Feitosa et al., 2007a, 2007b, 2015; Nascimento et al., 2019; Pires et al., 2014, 2021). On the other hand, studies based on molecular evidence have unveiled the cryptic diversity in particular groups of *Micrurus*, for example, within the *M. lemniscatus* (Linnaeus, 1758) and *M. frontalis* (Duméril, Bibron & Duméril, 1854) species complexes; these studies have

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highlighted the vast overlap of morphological characters among named species, showing that a more integrative approach is necessary to achieve an accurate taxonomic delimitation (Hurtado-Gómez et al., 2021; Jowers et al., 2019; Pires et al., 2021).

Among the 35 species of *Micrurus* distributed in Brazil, 22 belong to the triadal group (Silva, Feitosa, et al., 2021). This group is characterized by having a short and bilobed hemipenis that can be capitate or non-capitate, and by the presence of a triad sequence of three black rings, separated by two white rings and interspersed by two red rings (Campbell & Lamar, 2004; Roze, 1996; Silva, Buononato et al., 2016, 2021).

The classification of the triadal group has been marked by taxonomic confusion, leading to an underestimation of its diversity (Bernarde et al., 2018; Nascimento et al., 2019; Pires et al., 2021; Silva & Sites, 1999, 2001). As an example, Silva and Sites (1999) identified seven morphologically distinct groups within *Micrurus frontalis*, which was later supported by a molecular phylogenetic study (Silva & Sites, 2001). Furthermore, Silva, Pires et al. (2016) have shown a cryptic diversity in the *Micrurus lemniscatus* species group, revealing three distinct populations delimited by morphological characters, which was further corroborated by Pires et al. (2021).

Within the triadal group, the *Micrurus ibiboboca* (Merrem, 1820) species complex represents a taxonomic challenge. Species classified in this complex have already been confused with other sympatric coral snakes in Northeastern Brazil, including *Micrurus brasiliensis* Roze, 1967, *Micrurus carvalhoi* Roze, 1967, and *Micrurus potyguara* Pires et al., 2014. These species exhibit morphological similarities in terms of their colour patterns (e.g., the presence of a black band in the posterior middle third of the head) and in the shape of cephalic scales (e.g., posterior reduction of the frontal and supraocular scales), rendering accurate identification difficult and leading to an increased occurrence of taxonomic errors (Pires et al., 2014; Roze, 1967; Silva, Feitosa et al., 2021; Silva, Pires et al., 2016).

Micrurus ibiboboca has an entangled taxonomic history and has undergone several reclassifications over the years. This species was originally described as *Elaps ibiboboca* by Merrem (1820), and its locality was described "Habitat in Brasilia". However, Amaral (1926) reclassified *E. ibiboboca* into the genus *Micrurus*. In a subsequent publication, Amaral (1927) proposed that *M. ibiboboca* should be considerated synonymous with *M. lemniscatus*, while Hoge (1953) recognized it as a subspecies of *M. lemniscatus* (*M. l. ibiboboca*). Furthermore, Roze (1966) analysed specimens from the Wied-Neuwied collection and observed that *Elaps ibiboboca* (Merrem, 1820) and *Elaps marcgravii* (Wied-Neuwied, 1820a) had been described based on the same specimen. Following the priority law established by ICZN (1999), the specimen described by Merrem (1820) –AMNH 3911, was recognized by Roze (1966) as the holotype of *M. lemniscatus ibiboboca*. The specific taxon hails from the region of Vila de Belmonte in Bahia state (Wied-Neuwied, 1820b, 1820c), currently known as Rio Jequitinhonha (Vanzolini & Myers, 2015). Further, Campbell and Lamar (1989), through their comprehensive compilation of data on snakes inhabiting Latin America, finally recognized *M. ibiboboca* as a full species.

In this perspective, *Micrurus ibiboboca* emerged as a group with concealing cryptic diversity. Several studies have emphasized relevant facts about morphological variation among different populations of *M. ibiboboca* (Argôlo, 2004; Rodrigues, 2003; Silva, 2007; Silva, Feitosa et al., 2021; Silva, Pires et al., 2016; Silva & Sites, 2001; Vanzolini et al., 1980). Nevertheless, no study has yet been focused on the taxonomy of the *M. ibiboboca* species complex based on an integrative approach.

Here, we comprehensively evaluate the molecular and morphological diversity of the *Micrurus ibiboboca* species complex, aiming to ascertain the presence of cryptic species within this group. Our results provide evidence of the existence of three new species of coral snake from Northeastern and Southeastern Brazil that can be distinguished genetically and morphologically from *M. ibiboboca*, and which are described herein.

Material and methods

Taxon and gene sampling

Our molecular data matrix comprises 128 terminals sequenced for five genes: four mitochondrial (16S – 16S Large Subunit Ribosomal RNA gene; 12S – Small Subunit Ribosomal RNA gene; *cyt-b* – Cytochrome b gene; and *nd4* – NADH Dehydrogenase 4 gene) and one nuclear gene (*c-mos* – Oocyte maturation factor Mos). We sequenced 46 new DNA fragments (23 for 16S and *nd4*) for two species of *Micrurus*: *M. ibiboboca* and *M. potyguara* (see Table 1, Supplemental Table S1) (GenBank accession nos.: PP392932-PP392954 and PP405216-PP405238). We also included sequences available in GenBank (https://www.ncbi.nlm.nih.gov) for 23 species of *Micrurus*, plus one *Sinomicrurus macclellandi* (Reinhardt, 1844), and one *Micruroides euryxanthus* (Kennicott, 1860) (Supplemental Table S1). Additionally, we included 62 sequences belonging to the Booidea and Caenophidia radiations, obtained from Zaher et al. (2019) and Hurtado-Gómez et al. (2021).

Table 1. List of primers used in this study.

Gene	Primer	Sequences	References
16S	L2510mod (16Sar)	5′ CCGACTGTTTAMCAAAAACA 3′	Palumbi *et al*. (1991)
	H3056mod (16Sbr)	5′ CTCCGGTCTGAACTCAGATCACGTRGG 3′	Palumbi *et al*. (1991)
nd4	ND4ab	5′ CACCTATGACTACCAAAAGCTCATGTAGAAGC 3′	Arevalo *et al*. (1994)
	H-Leu	5′ ATTACTTTTACTTGGATTTGCACCA 3′	Stuart and Parham (2004)

We rooted our phylogenetic tree using Booidea (*Eryx colubrinus* and *Boa constrictor*).

DNA sequencing

DNA was extracted from scales, liver, or muscle tissue using the PureLink extraction kit (Invitrogen, Massachusetts, USA), following the manufacturer's protocol. Sequences were amplified by Polymerase Chain Reaction (PCR) using the Promega PCR Master Mix kit following the amplification protocols described in Grazziotin et al. (2012) for both the 16S and *nd4* genes. Amplified fragments were purified with shrimp alkaline phosphatase and exonuclease I (GE Healthcare, Piscataway, NJ). Both strands were sequenced on an ABI 3100 Genetic Analyzer automated sequencer (Life Technologies, Courtaboeuf, France) at Museu Paraense Emílio Goeldi. Both strands were quality-checked and, when necessary, edited manually. The consensus of both strands was generated using Geneious Prime 2022.1.1.

Molecular analyses

Sequences were aligned using MAFFT 1.3.6 (Katoh & Standley, 2013) through a plugin implemented in Geneious Prime. The 16S and 12S sequences were aligned under the E-INS-I algorithm, while *nd4*, *cyt-b*, and nuclear genes were aligned under the G-INS-i algorithm. We used default parameters for gap opening and extension. The protein-coding gene alignments were visually checked using Geneious Prime to verify that all sequences follow the correct reading frame. All genes were concatenated using Geneious Prime.

We used PartitionFinder 2 (Lanfear et al., 2012) to identify the combined best-fitting of partitioning schemes and models of molecular evolution. Our input matrix was divided in 11 partitions (coding genes were partitioned by codon positions and each rRNA was analysed as a separate partition) and was analysed using the greedy option. We performed a run allowing the program to select (using the Akaike Information Criterion with correction: AIC) for molecular evolution models implemented on RAxML (models GTR and GTR + G). We performed a maximum likelihood (ML) analysis using RAxML 8.2.3 (Stamatakis, 2014). The ML tree was estimated using the RAxML algorithm that conducts a rapid bootstrap analysis and searches for best scoring ML tree in the same run (option-*f a*). We ran 1000 bootstrap replicates, and the best scoring ML tree was estimated 200 times using as a starting tree each 5th bootstrap tree.

Additionally, to evaluate the relationships among populations of the *Micrurus ibiboboca* complex, haplotype networks were built based on our concatenated mitochondrial genes (16S and *nd4*) under an infinite site model (i.e., uncorrected, or Hamming distance) using R package *pegas* (Paradis, 2010). Additionally, we also calculated uncorrected genetic distance (*p-distance*) using PAUP 4.0 (Swofford, 2003) for *nd4*.

Specimens and characters examined for morphological analysis

We examined a total of 677 specimens of the *M. ibiboboca* complex and three specimens of *M. potyguara* (see Supplemental Appendix 1). To correctly identify all examined specimens and compare with other sympatric species of *Micrurus*, we used the available information in the literature, including previous taxonomic revisions and information available in the original descriptions (Feitosa et al., 2007a; Pires et al., 2014; Silva, Feitosa et al., 2021; Silva, Pires et al., 2016; Silva & Sites, 1999).

We used our molecular phylogenetic tree as a framework to evaluate both external and internal morphology in search of diagnostic character. We measured snout–vent length (SVL), tail length (TL), and head length (HL) to the nearest 1 mm by carefully stretching the specimen along a graduated ruler, and for other measurements we used a digital caliper to the nearest 0.1 mm. For definition of external morphological characters (pholidosis and morphometrics) we followed Feitosa et al. (2007b).

To verify colour characters, we counted the number of body and tail triads and measured the length of the rings of the reference triad following Pires et al. (2014). We analysed the colour pattern through photographs and specimens deposited in herpetological collections, considering males and females. The description of colour pattern followed Silva, Buononato et al. (2016). The

definition of scale markings followed Silva, Buononato et al. (2016), who described as one-third or two-thirds of the posterior region of the scale marked with black. We evaluated the colour of the snout, considering the rostral, nasal, and internasal scales (see Supplemental Fig. S2). We measured the following rings that compose the triads: length of the anterior red ring (ARR); length of the anterior black ring (ABR); length of the anterior white ring (AWR); length of the median black ring (MBR); length of the posterior white ring (PWR); length of the posterior black ring (PBR); and length of the posterior red ring (PRR).

We analysed hemipenial morphology across the *M. ibiboboca* complex distribution and compared it with the triadal species, using data available in the literature and material available in institutions. The preparation of hemipenis from specimens fixed in 10% formaldehyde followed Manzani and Abe (1988), Pesantes (1994), and Zaher and Prudente (2003). Hemipenial terminology follows Slowinski (1995), Roze (1996), and Zaher (1999). For the comparison and description of the hemipenes, we analysed the following characters: hemipenis shape; length of lobes; lobes ornamentation; arrangement of spines; body ornamentation; arrangement of the spermatic sulcus; arrangement of the capitular sulcus.

All examined specimens are deposited in the following institutions (acronyms in parentheses): Brazil: Laboratório de Anfíbios e Répteis, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, under the care of Adrian Antônio Garda (AAGARDA); Laboratório de Herpetologia do Instituto de Biociências, Universidade de São Paulo, São Paulo, under the care of Miguel Trefaut Rodrigues (MTR); Centro de Assistência Toxicológica, Campus João Pessoa, Paraíba (CEATOX); Coleção Herpetológica da Universidade Nacional de Brasília, Distrito Federal (CHUNB); Coleção Zoológica Gregório Bondar, Ilhéus, Bahia (CZGB); Instituto Butantan, São Paulo, São Paulo (IB); Instituto Vital Brazil, Rio de Janeiro, Rio de Janeiro (IVB); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Rio de Janeiro (MNRJ); Museu Paraense Emílio Goeldi, Belém, Pará (MPEG); Museu de Zoologia da Universidade Estadual de Feira de Santana, Bahia (MZUEFS); Museu de Zoologia da Universidade de Santa Cruz, Ilhéus, Bahia (MZUESC); Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo (MZUSP); Federal da Paraíba, João Pessoal, Paraíba (UFPB); Universidade Federal do Piauí, Teresina, Piauí (UFPI). United States of America: American Museum of Natural History, New York (AMNH). France: National Museum of Natural History, Paris (MNHNP). United Kingdom: British Museum of Natural History, London (BMNH).

Quantitative comparisons

To evaluate the existence of cryptic species using morphological evidence, we defined four OTUs (Operational Taxonomic Units) for the *Micrurus ibiboboca* species complex based on the lineages recovered in our molecular phylogenetic analysis and the colour pattern as follows: (OTU 1) *Micrurus* sp. 1, (OTU 2) *Micrurus* sp. 2, (OTU 3) *Micrurus ibiboboca*, and (OTU 4) *Micrurus* sp. 3. For localities of each OTUs see Supplemental Appendix 1.

We implemented statistical analysis to compare the patterns of variation of morphological characters and to characterize and describe the recognized OTUs. We calculate the range of variations (minimum and maximum), mean ($\bar{X}$), and standard deviation (SD) for each taxon using the basic R v. 4.3.2 (R Core Team, 2023) packages. We checked and removed outliers from our data using the *dplyr* (Wickham, François et al., 2023) R package.

The normality of the variables was evaluated one by one using the Kolmogorov–Smirnov test through the basic R package. To assess the existence of sexual dimorphism, the variables were submitted to Wilcoxon–Mann–Whitney and chi-square tests for continuous and discrete variables, respectively. Sexual dimorphism analysis was performed using the basic package available in R.

To investigate character variation among OTUs, we implemented multivariate analyses using R, as follows: (1) robust principal component analysis (RPCA) based on our original dataset; (2) robust principal component analysis (RPCA); and (3) robust linear discriminant analysis (RLDA) based on a simulated equalized dataset.

Because the sample size of some OTUs was small, we equalized our dataset, following the pipeline reported by Graboski et al. (2023). We simulated an equalized dataset from our original data using the *boot* (Canty & Ripley, 2022) and *dplyr* (Wickham, François et al., 2023) R packages. We simulated 100 samples per OTUs.

The RPCA and RLDA analyses were performed using the robustbase (Maechler et al., 2021), scales (Wickham, Pedersen et al., 2023), and MASS (Venables & Ripley, 2002) R packages. The results of multivariate analysis were plotted using ggplot2 (Wickham, 2016) R package. All R scripts used in these analyses and our original and simulated dataset are available on Zenodo (https://zenodo.org/doi/10.5281/zenodo.10418791).

Maps of species distribution

We built a geographic dataset with 492 specimens registered in 130 localities for the *Micruurus ibiboboca*

species complex. We included in the geographic dataset registers taken directly from the localities of specimens examined in collections (see Supplemental Material). We only used specimens whose identification and origin were confirmed. We standardized the coordinates in decimal degrees using the WGS 84 datum. The coordinates were confirmed using the Google Earth Pro software version 7.3 (Google LLC). We used QGIS version 3.18.2 (QGIS Team Developer, 2021) to plot distribution points. Additionally, we used the global ecoregions shape 200 WWF (Olson & Dinerstein, 2002) to verify the ecoregions of described taxa and to associate them with the distribution limits of each species.

Results

Phylogenetic analysis

Our concatenated alignment totalized 2905 base pairs (509 bp for 12S, 517 bp for 16S, 650 bp for *cyt-b*, 660 bp for *nd4*, and 569 bp for *c-mos*). PartitionFinder identified a best-fit scheme composed of nine partitions with the GTR + G model.

The resulting ML topology for the higher-level affinities was similar to those presented by previous studies (Hurtado-Gómez et al., 2021; Jowers et al., 2019; Lee et al., 2016; Renjifo et al., 2012; Zaher et al., 2016, 2021). The New World coral snake (*Micruroides* and *Micrurus*) is monophyletic with moderate bootstrap support (79%), as a sister group to the Asian *Sinomicrurus* (see Supplemental Fig. S1). The clade comprising the New World coral snake and *Sinomicrurus* was recovered as strongly supported, with 95% bootstrap (Supplemental Fig. S1). The genus *Micrurus* was recovered as a maximally supported clade (Supplemental Fig. S1). Within *Micrurus*, two divergent and well-supported clades were recovered (Supplemental Fig. S1): Clade 1, composed of monadal species (100% bootstrap support); and Clade 2 composed by the triadal species, including the bicolor species, *Leptomicrurus narduccii* (Jan, 1863) (= *Micrurus narducci*) and *Micrurus mipartitus* (Duméril, Bibron, & Duméril, 1854) (80% bootstrap support).

Leptomicrurus narduccii (= *Micrurus narduccii*) was recovered as sister to the remaining triadal species (including *M. mipartitus*), with moderate bootstrap support (72%) (Fig. 1; Supplemental Fig. S1). The triadal species (Clade 2) were composed of three distinct clades, as follows (bootstrap values are given in parentheses): Clade A (99%) containing *Micrurus hemprichii* (Jan, 1858), *Micrurus surinamensis* (Cuvier, 1816), and *M. lemniscatus* complexes; Clade B (100%) composed of *Micrurus dissoleucus* (Cope, 1860) and *M. mipartitus*; and Clade C (99%) composed of the *M. frontalis* and *M. ibiboboca* complexes. Clade A was moderately strongly (72%) recovered as sister group of Clades B + C (Fig. 1; Supplemental Fig. S1). Clade C comprised four main subclades (Fig. 1; Supplemental Fig. S1), as follows (bootstrap values in parentheses): Subclade 1 (100%), composed of specimens of *Micrurus* sp. 1 from the municipalities of Cristalândia and Palmeiras, Bahia state; Subclade 2 (91%) composed of *M. frontalis* and *M. brasiliensis*; (3) Subclade 3 (37%) composed of *M. obscurus* (Jan, 1872), *M. altirostris* (Cope, 1860), *M. baliocoryphus* (Cope, 1860), and *M. pyrrhocryptus* (Cope, 1862); and (4) Subclade 4, composed of three lineages of the *M. ibiboboca* species complex (100%): *M.* sp. 2, from the municipality of Quissamã, Rio de Janeiro state (99%); *M. ibiboboca*, from the municipality of Uruçuca and Trancoso, Bahia state (100%); and *M.* sp. 3, from Northeastern Brazil (92%) (Fig. 1; Supplemental Fig. S1).

Haplotype network and genetic distance

We evaluated the genetic structure among four populations of the *M. ibiboboca* complex. The haplotype network of the concatenated mitochondrial genes (16S and *nd4*) indicates a strong genetic differentiation among these lineages, totalling 14 unique haplotypes (Fig. 2), as follows: *Micrurus ibiboboca* with a single haplotype (I), including specimens from the municipalities of Trancoso and Uruçuca, Bahia state; *Micrurus* sp. 1 with two exclusive haplotypes (VIII and VI), including specimens from the municipalities of Cristalândia and Palmeiras, Bahia state; *Micrurus* sp. 2 with a single haplotype (II), including specimens from the municipality of Quissamã, Rio de Janeiro state; and *Micrurus* sp. 3 with 10 unique haplotypes (III, IV, V, VIII, IX, X, XI, XII, XIII, and XIV), presenting a genetic differentiation between them of one to four mutations (out of a total alignment of 957 base pairs), from Northeastern Brazil.

Micrurus ibiboboca is genetically distinct from *Micrurus* sp. 1, *Micrurus* sp. 2, and *Micrurus* sp. 3, presenting 16, 26, and 35 mutations (out of a total alignment of 957 base pairs), respectively. *Micrurus* sp. 2 differs genetically from populations 3 and 4 presenting 10 and 19 mutations (out of a total alignment of 957 base pairs), respectively, while *M. ibiboboca* differs from *Micrurus* sp. 3 in nine mutations (out of a total alignment of 957 base pairs). For *nd4*, the genetic distance (*p*-distance) between *M. ibiboboca* and *M.* sp. 1 is 4.1%, between *M. ibiboboca* and *M.* sp. 2 is 1.9%, and between *M. ibiboboca* and *M.* sp. 3. is 2.8%.

Quantitative variation

In the robust principal components analysis (RPCA) using 16 variables (discrete, continuous, and ratios), based on

Figure 1. Maximum likelihood tree summarizing the relationships of the triadal *Micrurus* species (Clade 2–C2). Branch colours and terminal taxa highlight the species of the *Micrurus ibiboboca* complex: *Micrurus* sp. 1 = *Micrurus janisrozei* sp. nov. (green); *Micrurus* sp. 2 = *Micrurus anibal* sp. nov. (orange); *Micrurus ibiboboca* (red); and *Micrurus* sp. 3 = *Micrurus bonita* sp. nov. (blue). The numbers above or below the branches represent bootstrap support values ≥70%.

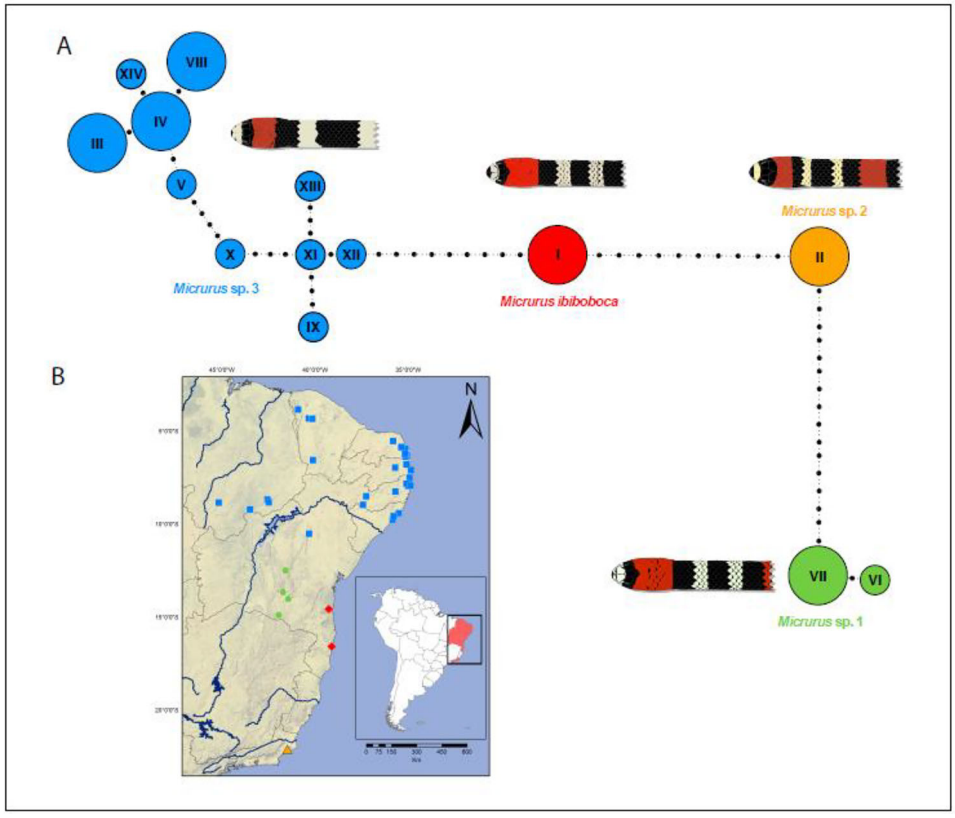


Figure 2. Haplotype network of concatenated mitochondrial genes (16S and nd4) and distribution map for the sequenced species. Populations are represented by colours. **A**. Circles represent different haplotypes with size proportional to their relative frequency. Population 1 – *Micrurus janisrozei* sp. nov. (green circles); Population 2 – *Micrurus anibal* sp. nov. (orange circles); Population 3 – *Micrurus ibiboboca* (red circles); and Population 4 – *Micrurus bonita* sp. nov. (blue circles). **B**. Distribution map of individuals sequenced to construct the haplotype network: *Micrurus janisrozei* (green circles); *Micrurus anibal* (orange triangles); *Micrurus ibiboboca* (red diamonds); and *Micrurus bonita* (blue squares).

the original dataset (see Supplemental Appendix 2), the first two components explained 75% (26% and 49%, respectively) of the total variance for females (Supplemental Fig. S5A). For males, the first two components explained 73% (23% and 47%, respectively) of the total variance (Supplemental Fig. S5B). For females and males, the results obtained by RPCA, based on the original dataset, showed a large overlap of variables among OTUs (Supplemental Fig. S5A, B).

In the RPCA using 16 variables (discrete, continuous, and ratios), based on the simulated dataset, the first two components explained 88% (56% and 32%, respectively) of the total variance for females (Fig. 3A). While for males, the first two components explained 94% (63% and 31%, respectively) of the total variance (Fig. 3B). For females and males, the results obtained by simulated RPCA showed four distinct groups, as follows: (1) *Micrurus* sp. 1, comprising specimens distributed in the elevated regions of Chapada Diamantina, in the upper portion of the southern Caatinga, following to the middle region of the Caatinga; (2) *Micrurus* sp. 2, comprising specimens distributed in mountainous region of the state of Rio de Janeiro, and in forest regions of the Upper Paraná to Restingas region; (3) *Micrurus* sp. 3, comprising specimens distributed in north of the Caatinga, in enclaves of high and dry forests, and in the coastal forests of Pernambuco and Bahia states; and (4) *Micrurus ibiboboca* (Fig. 3A, B).

In the robust linear discriminant analysis (RLDA) using six variables (continuous and ratios) based on the simulated dataset, the first two linear discriminants explained 98% (82% and 16%, respectively) of the total variance for females (Fig. 3C). For males, the first two linear discriminants explained 94% (59% and 35%, respectively) of the total variance (Fig. 3D). The simulated RLDA analysis for females and males showed the same four distinct groups found in the simulated RPCA analysis.

Colour patterns

We found significant differences in the colour pattern of populations of *Micrurus ibiboboca* related to snout colour, number, and length of triadal rings and colour pattern of the first white rings of the triads (black

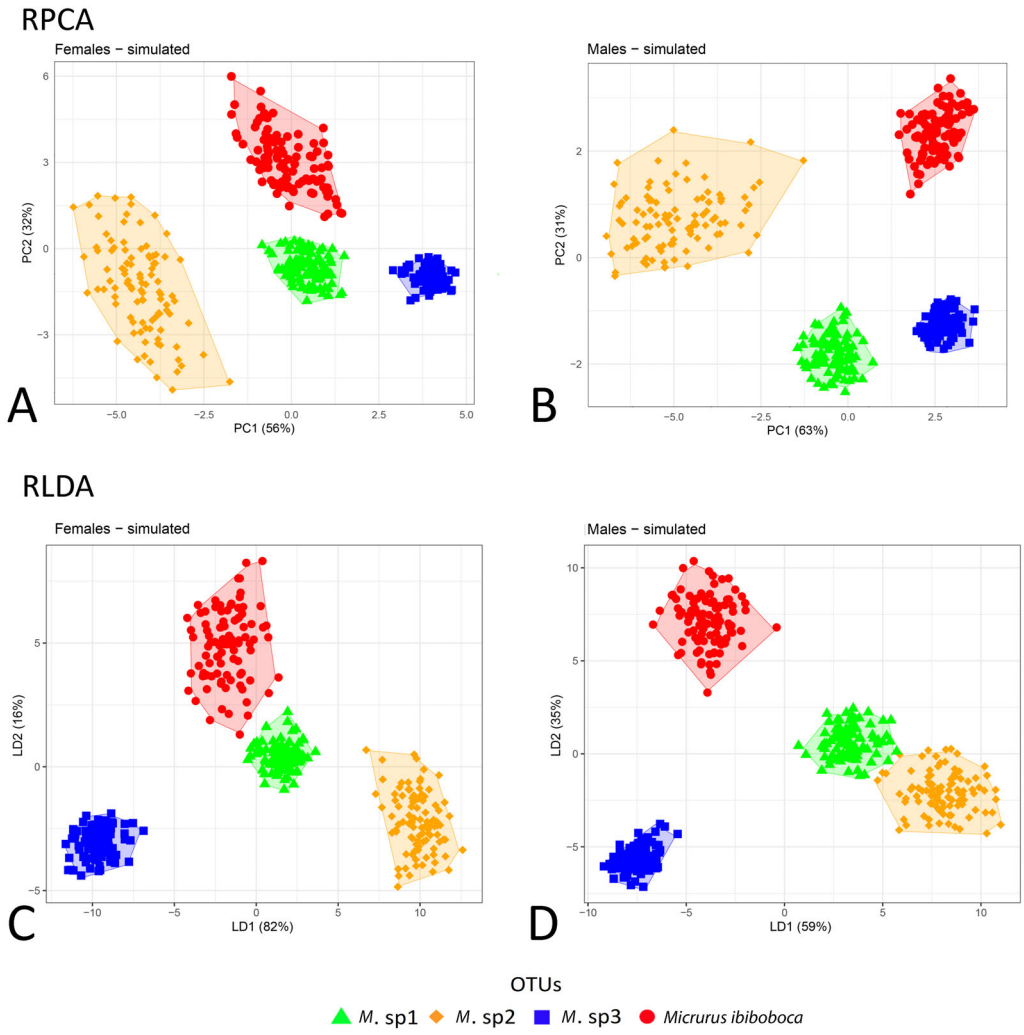


Figure 3. Results of robust principal component analysis (RPCA) and linear robust discriminant analysis (RLDA) using the simulated dataset based on 16 and six characters respectively for four OTUs. **A**. RPCA of female; **B**. RPCA of male; **C**. RLDA of females; **D**. RLDA of males. Species are colour coded according to OTUs (species colour OTUs on below of the graph). Legend: green triangles = *M.* sp1; orange lozenges = *M.* sp2; red lozenges = *Micrurus ibiboboca*; blue squares = *M.* sp3.

markings). *Micrurus ibiboboca* presents a completely black snout, without any white spot, followed by a defined transverse white band; border of prefrontal scales with few black spots; anterior scales in the ventral region of the head marked with black, followed by a white band that crosses the anterior genials; body triads with long black and white rings of the same length; and white rings of the first body triad with black-spotted scales (Fig. 4A, B).

Micrurus sp. 1 is characterized by having a predominantly white snout with few black spots; extremities of parietal scales marked with black; ventral region of the head with mental and first pair of supralabials black, white band crossing the first pair of genial scales, followed by a narrow black line in the anterior portion of the second pair of genials; body triads with long black and white rings of similar lengths; and white rings of the first body triad with black-tipped scales (Fig. 4C, D).

Micrurus sp. 2 has a black snout, without white spots; well-defined white prefrontal stripe, without black spots; wider interorbital transverse cephalic band, always ending in the middle third of the parietals; ventral region of the head with a narrow white band crossing the anterior genial scales; triads with short black and white rings of similar lengths; and white rings of the first body triad with black-spotted scales (Fig. 4E, F).

Micrurus sp. 3 has a predominantly white snout, with few black spots on the rostral and internasal scales, shorter interorbital transverse cephalic band; ventral region of the head with a half-moon-shaped white postmental band; scales of the white rings of the first triad of the body are immaculate, triads with white rings

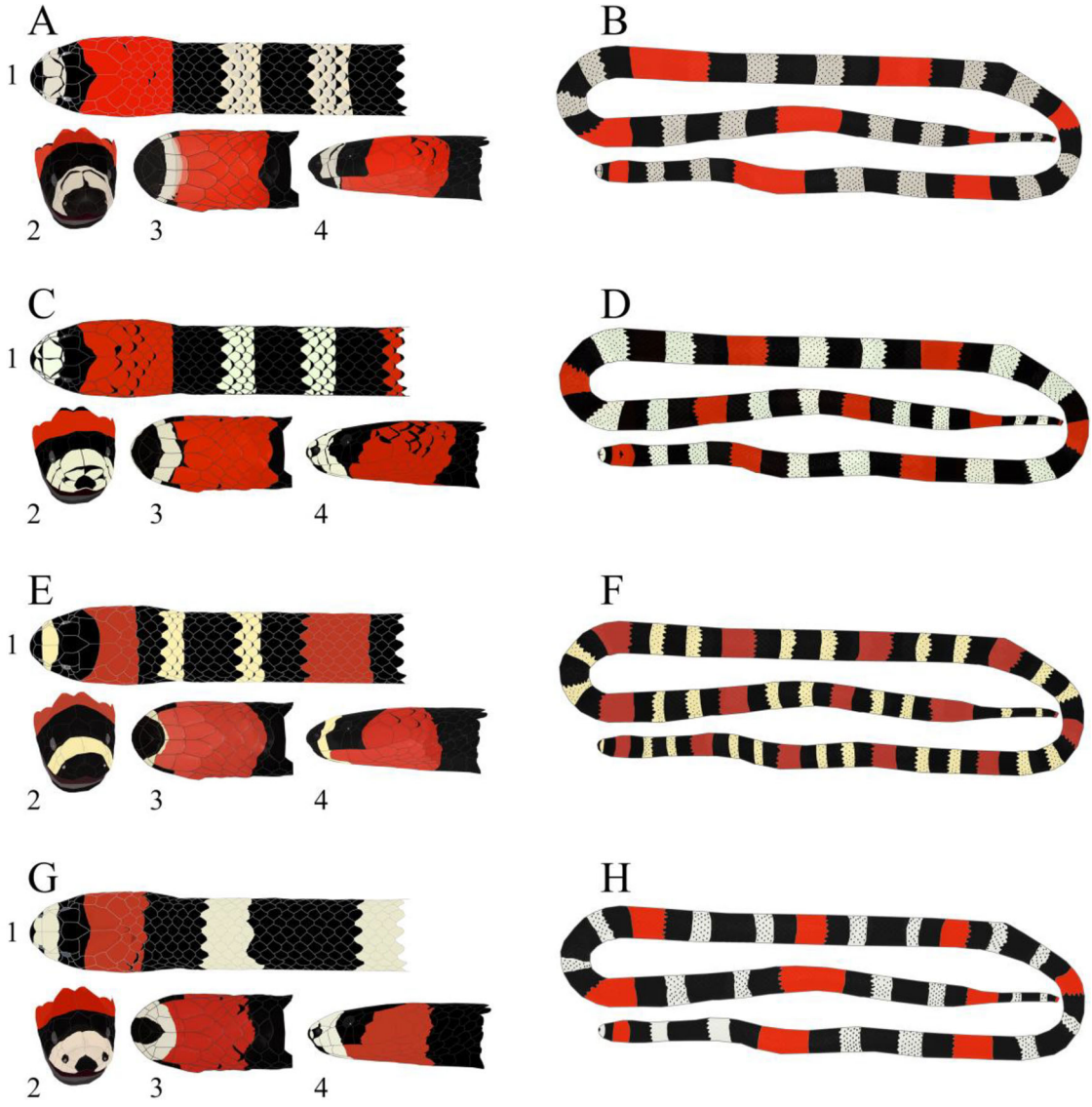


Figure 4. Comparison of the colour patterns observed in the different taxa delimited from our analyses. General cephalic and body patterns of: **A**, **B**. *Micrurus ibiboboca*; **C**, **D**. *Micrurus janisrozei* sp. nov.; **E**, **F**. *Micrurus anibal* sp. nov.; **G**, **H**. *Micrurus bonita* sp. nov. Legend: 1. Dorsal cephalic pattern; 2. Snout pattern; 3. Ventral cephalic pattern; 4. Lateral cephalic pattern.

shorter than the black rings; and central black rings of the triads longer than the outer rings (Fig. 4G, H).

Hemipenial morphology

Micrurus ibiboboca and *Micrurus* sp. 2 have hemipenes like those of *M. carvalhoi* and *M. potyguara* (Fig. 5H, I), with long bodies and lobes (Fig. 5A–C). In contrast, *Micrurus* sp. 1 and *Micrurus* sp. 3 have hemipenes with short bodies and lobes (Fig. 5B–D), more like those of *M. decoratus* and *M. frontalis* (Fig. 5E–G).

The hemipenes differed also in the arrangement of the capitular sulcus and the shape of the extremity of the lobes. In *M. ibiboboca* the capitular sulcus is in the proximal third, while in *Micrurus* sp. 2 it is in the basal third (Fig. 5A–C). There are also notable differences in the extremities of the lobes, with *Micrurus* sp. 1 having rhomboid ends, and *Micrurus* sp. 3 slender ends (Fig. 5B–D).

Species accounts

Based on the results of our phylogenetic tree, in combination with multivariate morphological analyses, we recognize three new species of South American *Micrurus* and redefine *M. ibiboboca*. Following the redescription of *M. ibiboboca*, we proceed below with the formal description of *M.* sp1, *M.* sp2, and *M.* sp3, respectively. Comparisons are provided for new species,

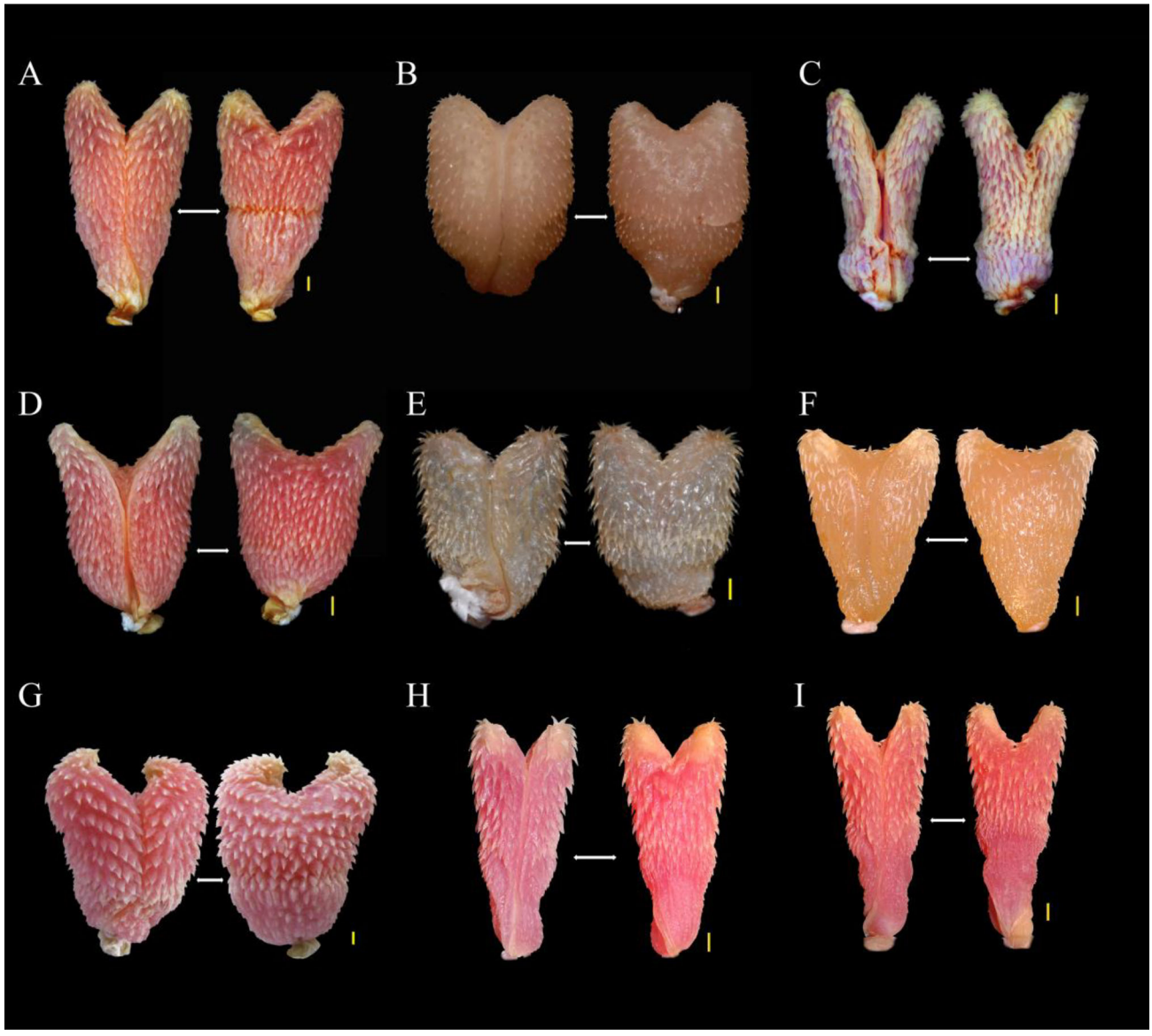


Figure 5. Comparisons of hemipenial morphology: **A**. *Micrurus ibiboboca* (CZGB 901) from Camacã municipality, Bahia, Brazil; **B**. *M. janisrozei* sp. nov. (IBSP 42254) from the municipality of Brumado, Bahia, Brazil; **C**. *M. anibal* sp. nov. (MNRJ 18191) from the municipality of Iguaba Grande, Rio de Janeiro, Brazil; **D**. *M. bonita* sp. nov. (CZGB 484) from the municipality of Petrolândia, Pernambuco, Brazil; **E**. *M. decoratus* (IBSP 54841) from the municipality of Ribeirão Pires, São Paulo, Brazil; **F**. *M. brasiliensis* (adapted from Pires et al., 2014); **G**. *M. frontalis* (adapted from Silva, Buononato et al., 2016); **H**. *M. carvalhoi* (adapted from Pires et al., 2014); **I**. *M. potyguara* (adapted from Pires et al., 2014). Legend: white arrows = level of constriction of the capitular sulcus; yellow lines = 1 mm scale.

sympatric and morphologically related species, these being: *M. brasiliensis*, *M. carvalhoi*, *M. corallinus*, *M. frontalis*, *M. paraensis*, and *M. potyguara.*

Micrurus ibiboboca (Merrem, 1820)
(Figs 4A, B, 6A–E)

Elaps ibiboboca Merrem, 1820: 142; *Elaps marcgravii* (Wied-Neuwied, 1820, p. 109); *Micrurus lemniscatus* Amaral (1926, p. 29). *Micrurus ibiboboca* (Amaral, 1927, p. 29); *Micrurus lemniscatus ibiboboca* (Hoge, 1953, p. 195); *Micrurus ibiboboca* (Campbell & Lamar, 1989, p. 120; Roze, 1967, p. 30; Silva, Feitosa et al., 2021, p. 198; Silva, Pires et al., 2016, p. 120).

Holotype. Adult male, AMNH R-3937, collected by Wied-Neuwied on an expedition in Brazil between 1782–1867. Described by Merrem (1820) with the

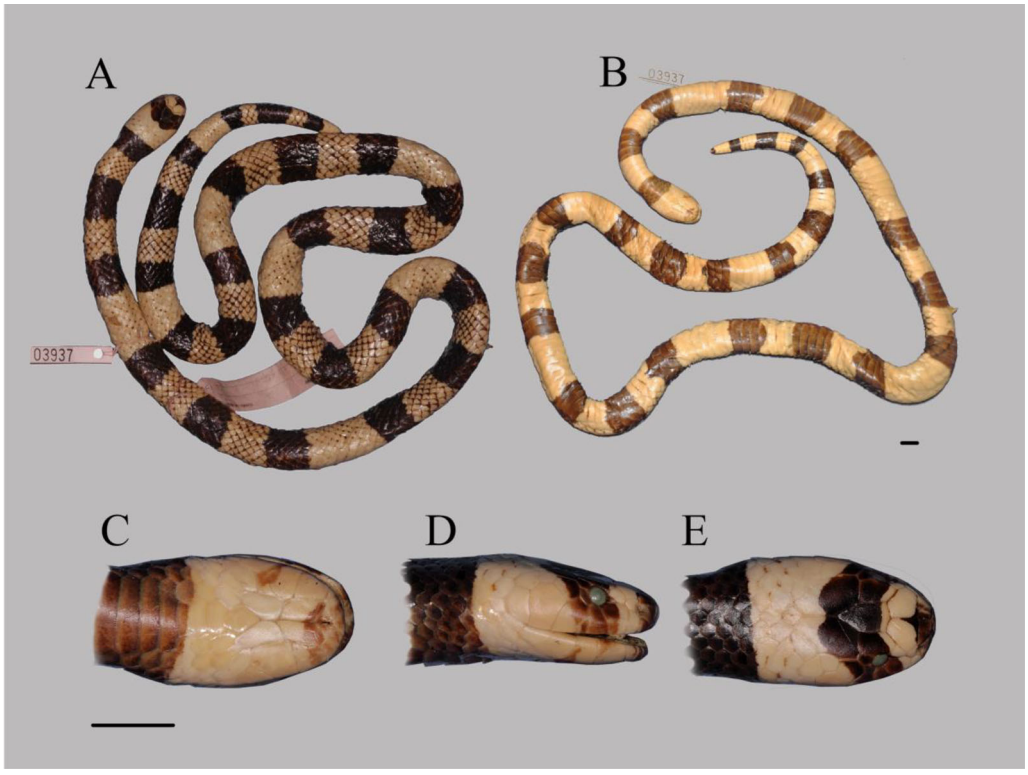


Figure 6. *Micrurus ibiboboca* holotype (AMNH R-3937, SVL 780 mm). **A**. dorsal view of the specimen; **B**. ventral view of the specimen; **C**. ventral view of the head; **D**. lateral view of the head; **E**. dorsal view of the head. Type locality: Municipality of Belmonte, state of Bahia, Brazil. Black line = 5 mm scale.

location "Habitat in Brasilia" and in the same year also described by Wied-Neuwied (1820a) with the location "boca do Rio Belmonte", currently known as Rio Jequitinhonha (15°51′38.0″S, 38°53′21.9″W) (Vanzolini & Myers, 2015; Silva, Feitosa et al., 2021) (Fig. 6).

Revised diagnosis. *Micrurus ibiboboca* can be distinguished from all congeners by the combination of the following characters: black snout; middle and posterior borders of prefrontals marked with black; mental, first and second pair of infralabials spotted or completely black; body triads 7–11; ventrals 198–237 in males and 201–238 in females; subcaudals 17–35 in males and 16–32 in females; hemipenis long, bilobed, capitate and ornamented with calcified spines; presence of capitular sulcus in the proximal third; basal pocket not very evident and ornamented by few spines.

Comparisons. *Micrurus ibiboboca* differs from *M. janisrozei* sp. nov. by having a black snout and a long hemipenis with a poorly developed basal pocket (vs. white snout with black-tipped scale and a short hemipenis with a well-developed basal pocket); differs from *M. anibal* sp. nov. by having a black cephalic band ending before the middle third of the parietals and hemipenis with capitular sulcus dividing the organ in the proximal third (vs. black cephalic band extending to the middle third of the parietals and hemipenis with capitular sulcus dividing the organ in the distal third, just above the base); differs from *M. bonita* sp. nov. by having a black snout, first two white rings of the first triad with maculate scales and a long hemipenis with a conspicuous capitular sulcus (vs. predominantly white snout, scales of the white rings of the first triad immaculate, short hemipenis with a discrete capitular sulcus); differs from *M. brasiliensis* by having a black snout, a long black cephalic band reaching up to the sixth pair of supralabials, and an elongate hemipenis with long lobes (vs. white snout with black-tipped scale, laterally shorter black cephalic band reaching only part of the third and fourth supralabials, and elongate hemipenis with short lobes); differs from *M. corallinus* and *M. paraensis* by having a triadal colour pattern and absence of a black cephalic cap (vs. monadal colour pattern and a cephalic cap covering from the snout to the parietals); differs from *M. frontalis* in that it has a black snout with the posterior edges of the prefrontal scales marked with black, only the anterior third of the

parietals is black, and hemipenis with capitulum and body similar in size (vs. black snout with white scale edges, parietals marked with black up to the posterior third and hemipenis with a capitulum longer than the body); differs from *M. carvalhoi* having a black snout with a white prefrontal transverse band curved, central black rings of triads tending to be longer than the outer rings, and white rings of triads black spotted on the posterior third of the scales (vs. black snout with a white narrow prefrontal transverse band, central black rings of triads tending to be shorter than the extremities, and white rings of triads heavily marked with black); and differs from *M. potyguara* in having most of the head red and a half-moon-shaped prefrontal transverse band (vs. most of the head black and a regular, well-delimited prefrontal transverse band) (Figs 4, 5, and 7; Tables 2 and 3).

Redescription of holotype. AMNH R-3937, male, adult, 210 ventrals, 24 subcaudals, SVL 780 mm, TL 54.3 mm, HE 26.2 mm (Fig. 6). Described based on preserved colour pattern. Black snout (rostral, first pair of supralabials, internasals, and anterior edge of prefrontals); second pair of supralabials, nasals and most of the prefrontals pale yellow; prefrontals with anterior borders, up to the first one-third, and posterior borders marked with black; anterior border of the frontal, preocular, supraocular and third pair of supralabials pale yellow (Fig. 6A–E). Black cephalic band covering most of the frontal, supraoculars, third pair of supralabials,

Figure 7. *Micrurus* species with triadal pattern compared in this study. **A**. *Micrurus ibiboboca* (predating an *Amphisbaena alba*), Campo Formoso, Bahia, Brazil; **B**. *M. janisrozei* sp. nov., municipality of Seabra, Bahia, Brazil; **C**. *M. anibal* sp. nov., municipality of Jaconé, Rio de Janeiro, Brazil; **D**. *M. bonita* sp. nov., municipality of Catimbau, Pernambuco, Brazil; **E**. *M. brasiliensis*, municipality of Mambaí, Goiás, Brazil; **F**. *M. decoratus*, municipality of Petrópolis, Rio de Janeiro, Brazil; **G**. *M. frontalis*, municipality of Viçosa, Minas Gerais, Brazil; **H**. *M. carvalhoi*, municipality of Santa Cruz do Rio Pardo, São Paulo, Brazil; **I**. *M. potyguara*, municipality of João Pessoa, Paraíba, Brazil. Photos: Roberto L. Froes (A); Reinaldo Brito (B); Nelson J. da Silva Jr. (C and E); Marco A. Freitas (D); Breno Hamdan (F); Afonso Santiago (G); Antônio Bordignon (H), Cláudio Sampaio (I).

posterior border of the preoculars, post-oculars, fourth pair of supralabials, anterior half of parietals, anterior temporals and fifth pair of supralabials; the remaining cephalic scales are pale yellow (Fig. 6D–E). Ventrally, the mental and first pair of infralabials are marked with black; anterior border of the anterior genials and second infralabials and posterior region of the third left infralabial also marked with black; there is an irregular black marking between the fifth and sixth right infralabials; the other scales of the ventral region are pale yellow (Fig. 6C). Eight complete body triads (8 pale yellow rings, 16 white rings, and 24 black rings); pale yellow rings (ARR and PRR) longer than the others; ring scales pale yellow slightly marked with black at the posterior border; first black body ring (ABR) shorter than the others, starting in the middle of the third dorsal row (four scales in length); first and second white rings (AWR and PRR, 4–5 scales long) of the triads with black-tipped scales posteriorly; middle black ring of the first triad (MBR, six scales long) longer than the outer black rings; the other black rings (ABR, MBR, and PBR, 4–5 scales long) of the body are of similar lengths (Fig. 6A, B). Tail with a complete triad (one pale yellow ring, two white rings, three black rings), outer black rings (ABR and PBR, three scales in length) are shorter than the middle ring (MBR, five scales in length); white rings (AWR and PWR) three scales in length and a pale yellow ring (ARR) three scales in length; tip of tail with a black scale on the dorsal region and another on the ventral region (Fig. 6A, B).

Quantitative variation. ($n = 175$, see Supplemental Appendix 1). Ventrals 198–237 in males (mean = 217.2; SD = 9.3; $n = 126$), 201–238 in females (mean = 217.4; SD = 8.6; $n = 49$); subcaudals ($t = -2.43$, $p < 0.01$) 17–35 in males (mean = 23.3; SD = 3.1; $n = 126$), 16–32 in females (mean = 22.4; SD = 3.1; $n = 49$); snout–vent length ($t = -3.22$, $p < 0.01$) 190–1480 in males (mean = 676.6; SD = 288.2; $n = 126$), 205–1449 in females (mean = 502.1; SD = 264.5; $n = 49$); tail length ($t = -4.34$, $p < 0.01$) 12.3–92.8 in males (mean = 42.4; SD = 17.4; $n = 126$), 12.1–68 in females (mean = 31.5; SD = 14.8; $n = 49$); head length ($t = 3.08$, $p < 0.01$) 9.9–34.5 in males (mean = 19.1; SD = 5.6; $n = 126$), 10.1–34 in females (mean = 16; SD = 5.5; $n = 49$); body triads 7–11 in males (mean = 8.7; SD = 0.9; $n = 126$), 7–11 in females (mean = 8.7; SD = 1; $n = 49$).

Colour pattern in life. Snout black, reaching the anterior border of the prefrontals; prefrontal white transverse band curved starting in the middle of the first pair of supralabials reaching to the anterior border of the frontals; middle and posterior borders of prefrontals marked with black; black cephalic band starting in the middle third of the third pair of supralabials, extending to the anterior third of the parietals; red cephalic region from the anterior third of the parietals to the fourth dorsal scale row; mental, first and second pair of infralabials spotted or completely black; anterior region of the third pair of supralabials and anterior one-third of genials white with scales marked with black at the borders; postmental red region starts in the anterior third of the third pair of infralabials and posterior third of the anterior genials to first 1–2 ventrals (Figs 4A, 8A). First triad begins after the red dorsal and ventral rows in the cephalic region; AWR and PWR with posterior third of dorsal scales marked with black; MBR of the first triad longer than ABR and PBR; ARR and PRR rings of the triads with black-tipped scales (Fig. 4B). In preserved specimens ($n = 170$), red corresponds to light yellow and white to beige (Fig. 6). White spots may occur on the borders of the black nasal and internasal scales (Fig. 8A).

Hemipenial morphology. ($n = 3$, CZGB 901; MNRJ 8277; MZUSP 8908). Long, bilobed, capitate hemipenis, uniformly ornamented with calcified spines on both sides (Fig. 5A); sulcus spermaticus centripetal, deep, bifurcated at the base of the lobes, running centripetally along the lobes to the apices; sulcus spermaticus delimited by longer spines in relation to those of the body and capitulum; short lobes (21% of the total length), ornamented with spines longer than the spines in the body, which reduce in size towards the apex, arranged radially from the distal end to the proximal third before the capitulum; interlobular region with few spines, smaller in relation to the capitulum, arranged in short rows; capitular sulcus evident in the proximal third, delimiting the organ in the body in the first third and capitulum in the distal two-thirds; capitular sulcus narrower and deeper on the sulcate side, and wider and shallower on the asulcate side; capitulum (29% of the total length) ornamented by long spines in relation to those of the body, arranged in diagonal rows, gradually decreasing in size and number towards the apical region of the lobes; larger spines on the sulcate side; body (50% of the total length) covered by smaller spines and in greater number on the sulcate side, arranged in vertical rows, reducing in size and quantity towards the base; distal region close to the base ornamented by few spines; basal pocket poorly developed and ornamented by few spines (Fig. 5A).

Distribution. *Micrurus ibiboboca* occurs in coastal forests in eastern Bahia and in inland forests in the state of

Table 2. Quantitative variation among the triad species of *Micrurus* described in this study. Legend: VE = ventrals; SC = subcaudals; and TriB = number of body triads.

		***Micrurus ibiboboca* (*n* = 176)**			***Micrurus janisrozei* sp. nov. (*n* = 124)**			***Micrurus anibal* sp. nov. (*n* = 28)**			***Micrurus bonita* sp. nov. (*n* = 353)**		
		Range	**mean**	**SD**	**Range**	**mean**	**SD**	**Range**	***mean***	**SD**	**Range**	**mean**	**SD**
VE	♂	198–237	217.2	9,3	209–244	223.6	5.8	210–208	218.5	5.3	203–247	227.1	6.4
	♀	201–238	217.4	8,6	212–240	226.2	5.2	208–252	221.1	6.3	214–257	230.9	7.7
SC	♂	17–35	23.3	3,1	20–27	23.1	2.5	20–25	22.8	1.5	18–33	24.9	2.5
	♀	16–32	22.4	3,1	17–26	22.1	2.0	18–29	20.9	2.5	15–34	23.5	2.7
TriB	♂	7–11	8.7	0,9	8–12	10.2	1.2	9–14	11.9	1.4	6–12	8.6	1.0
	♀	7–11	8.7	1,1	8–12	10.2	1.2	8–16	12.3	1.8	7–12	8.6	0.9

Bahia, following the coast to inland forest areas in the state of Pernambuco. It is present in areas of mangroves and sandbanks (restingas), as well as in the Caatinga region (Fig. 9).

Micrurus janisrozei sp. nov.

(Figs 4C, D, 10A–E)

Micrurus carvalhoi (Jowers et al., 2019, p. 5, fig. 2). *Micrurus ibiboboca* (Hurtado-Gómez et al., 2021, p. 234, fig. 3; Pires et al., 2014, p. 574, fig. 4d; Silva, Feitosa et al., 2021, p. 198, fig. 112; Silva, Pires et al., 2016, p. 120). *Micrurus lemniscatus* (Renjifo et al., 2012, p. 139, fig. 7; Silva & Sites, 2001, p. 4, table 1).

Holotype. Adult male: MUFAL 11876, specimen locality: Caetité municipality (14°02′52.1″S, 42°28′46.6″W), Bahia state, Brazil (Fig. 10).

Paratypes. All from Brazil ($n = 5$). Adult female, MZUESC 5654, Jequié municipality (13°51'03.8"S, 40°04'52.2"W), Bahia state. Adult male, MZUESC 5683, Jequié municipality (13°51'03.8"S, 40°04'52.2"W), Bahia state. Adult male, MZUESC 5727, Jequié municipality (13°51'03.8"S, 40°04'52.2"W), Bahia state. Adult male, MZUESC 6423, Piatã municipality (13°09'08.1"S, 41°46'05.8"W), Bahia State. Adult male, MZUESC 20837, Rio de Contas municipality (13°40'10.7"S, 41°42'51.7"W), Bahia State (Supplemental Fig. S3).

Diagnosis. *Micrurus janisrozei* sp. nov. can be distinguished from all congeners by the unique combination of the following characters: snout predominantly white, with black bordered scales; black-tipped parietals; body triads 8–12 (average 10); ventrals 209–238 in males and 212–244 in females; subcaudals 17–27 in males and 16–26 in females; hemipenis short, slightly bilobed, capitate and ornamented with calcified spines; presence of capitular sulcus; basal pocket developed and ornamented by a few small spines.

Comparisons. *Micrurus janisrozei* sp. nov. differs from *M. ibiboboca* in having a predominantly white snout with black bordered scales and a short hemipenis with a developed basal pocket (vs. black snout, long hemipenis with poorly developed basal pocket); differs from *M. anibal* sp. nov. in having a predominantly white snout with black-bordered scales, black cephalic band ending in the anterior third of the parietals and short hemipenis with capitular sulcus dividing the organ in the proximal third (vs. black snout with narrow prefrontal transverse white band, black cephalic band ending in the middle third of the parietals and long

Table 3. Quantitative variation among *Micrurus* species of congener triads to those described in this study. Legend: VE = ventrals; SC = subcaudals; and TriB = number of body triads.

		Micrurus brasiliensis (*n* = 55)			*Micrurus frontalis* (*n* = 695)			*Micrurus carvalhoi* (*n* = 129)			*Micrurus potyguara* (*n* = 9)		
		Range	**mean**	**SD**	**Range**	**mean**	**SD**	**Range**	**mean**	**SD**	**Range**	**mean**	**SD**
VE	♂	210–243	226.5	7.8	190–254	225.3	8.3	224–263	237.6	8.3	231–237	234.7	3.2
	♀	219–237	226.9	5.9	197–252	224.6	11.5	222–267	253.4	9.3	253–263	257.3	5.1
SC	♂	17–28	22.5	2.7	14–28	21.9	2.0	25–39	31.7	3.0	34–38	36.0	2.0
	♀	14–36	23.3	5.7	14–28	21.0	2.8	26–38	30.1	2.9	29–35	33.0	3.5
TriB	♂	10–16	11.6	1.7	9–18	13.6	1.3	10–15	12.7	1.3	9–11	10.0	1.0
	♀	9–13	10.8	1.1	10–17	13.1	1.4	9–16	12.5	1.6	11–12	11.7	0.6

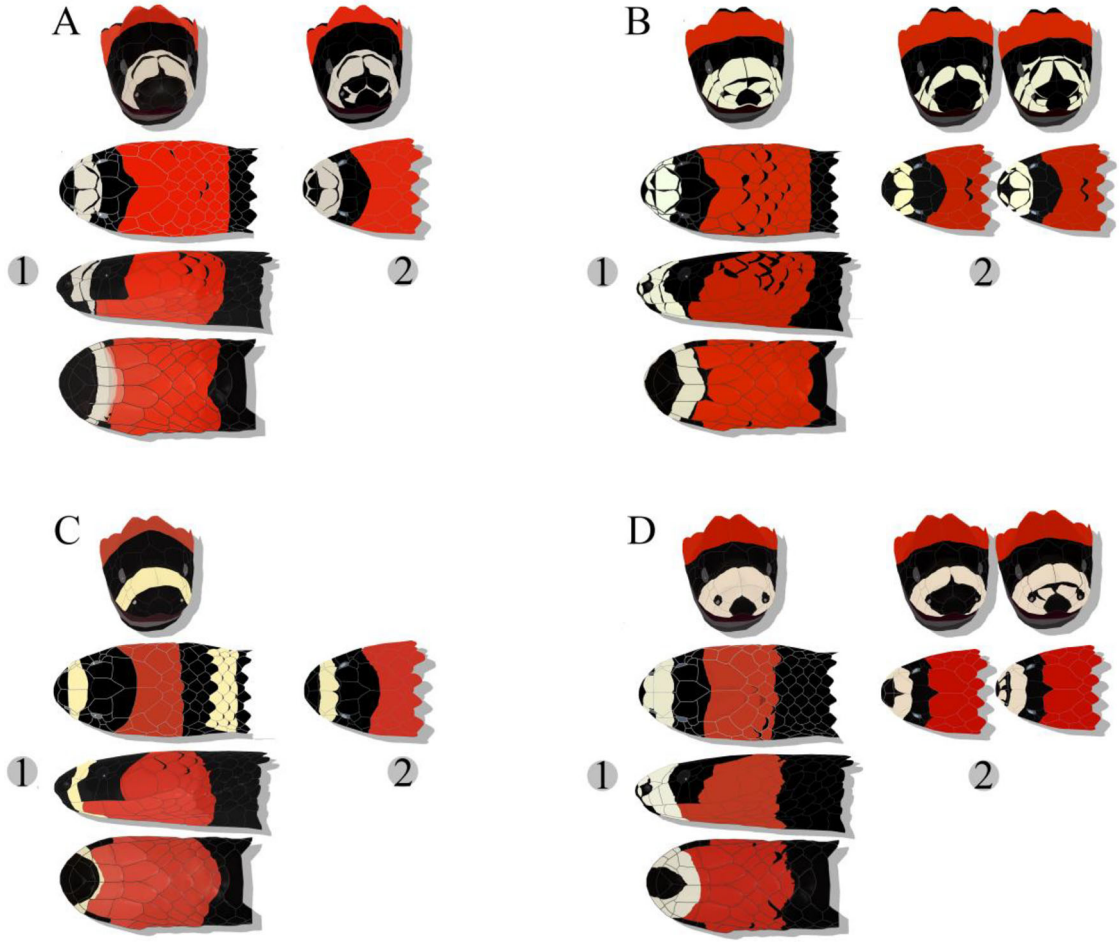
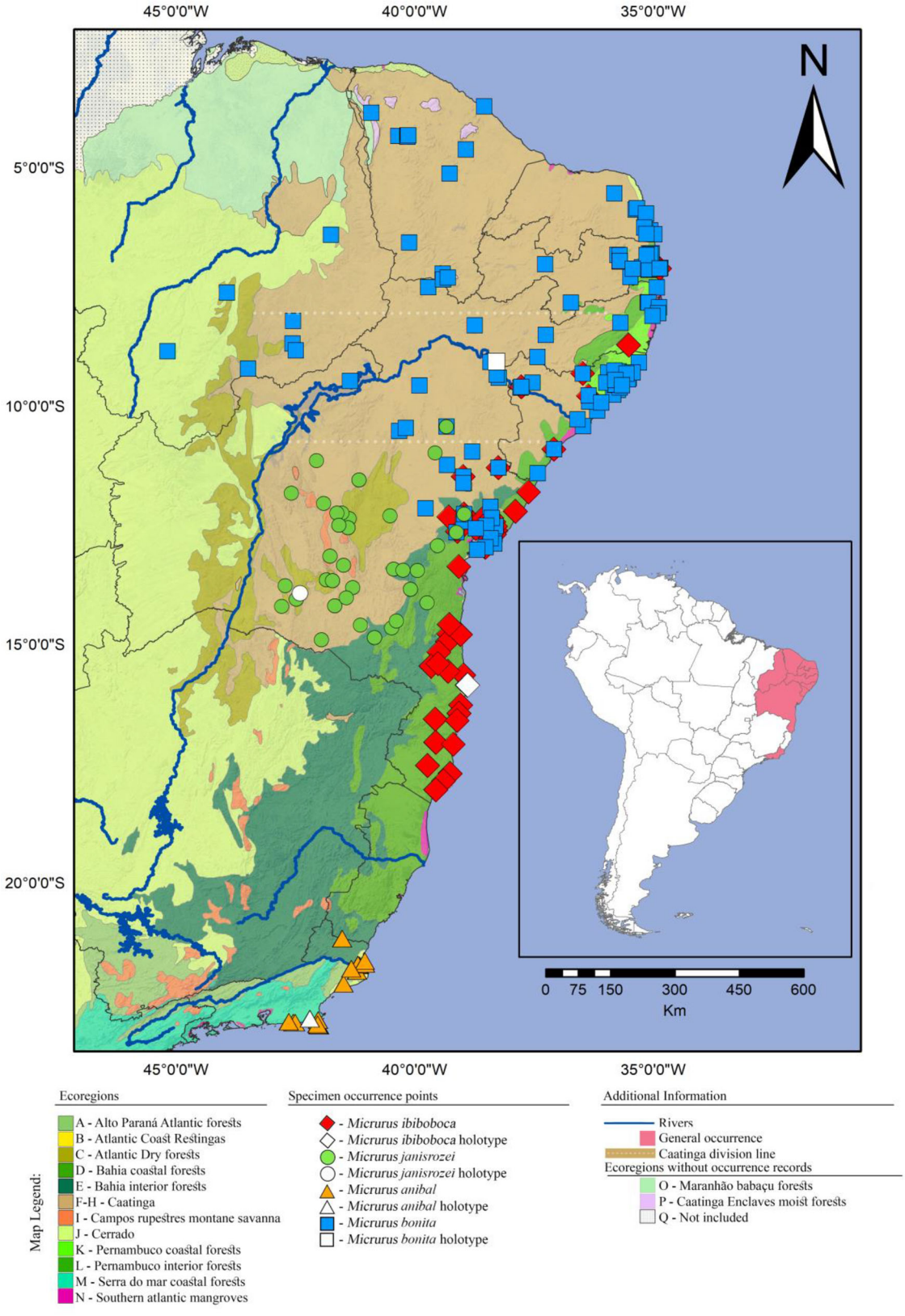


Figure 8. Comparison of the cephalic colour pattern (1) and pattern variations (2) in **A**. *Micrurus ibiboboca*; **B**. *M. janisrozei* sp. nov.; **C**. *M. anibal* sp. nov.; and **D**. *M. bonita* sp. nov.

hemipenis with capitular sulcus dividing the organ in the distal third, just above the base); differs from *M. bonita* sp. nov. in having a predominantly white snout with black-bordered scales, white rings of the first triad are maculate and hemipenis with short and blunt lobes (vs. predominantly white snout with tip of the snout or occasionally spotted with black, immaculate white ring of the first triad and hemipenis with short, narrow lobes); differs from *M. brasiliensis* by having a longer black cephalic band reaching three pairs of supralabials on the lateral region of the head, black triad rings equal to or longer than the white ones, short hemipenis with a deep capitular sulcus (vs. shorter black cephalic band reaching two pairs of supralabials on the lateral region of the head, longer black rings, elongated hemipenis with a discrete capitular sulcus); differs from *M.*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0 75 150 300 450 600
Km
Map Legend:
Ecoregions
A - Alto Paraná Atlantic forests
B - Atlantic Coast Restingas
C - Atlantic Dry forests
D - Bahia coastal forests
E - Bahia interior forests
F-H - Caatinga
I - Campos rupestres montane savanna
J - Cerrado
K - Pernambuco coastal forests
L - Pernambuco interior forests
M - Serra do mar coastal forests
N - Southern atlantic mangroves
Specimen occurrence points
- Micrurus ibiboboca
- Micrurus ibiboboca holotype
- Micrurus janisrozei
- Micrurus janisrozei holotype
- Micrurus anibal
- Micrurus anibal holotype
- Micrurus bonita
- Micrurus bonita holotype
Additional Information
Rivers
General occurrence
Caatinga division line
Ecoregions without occurrence records
O - Maranhão babaçu forests
P - Caatinga Enclaves moist forests
Q - Not included

corallinus and *M. paraensis* in having a triadal colour pattern and lacking a black cephalic cap (vs. monadal colour pattern and presence of a cephalic cap from the snout to the parietals); differs from *M. frontalis* in that it has a predominantly white snout, predominantly red parietals and black triad rings that are equal to or longer than the white rings (vs. predominantly black snout, most or all of the parietals black and shorter black triad rings); differs from *M. carvalhoi* in that it has a predominantly white snout, white triad rings spotted on the posterior third of the scales and short hemipenis with short, blunt lobes (vs. black snout, white triad rings with black tipped scales, and elongated hemipenis with short and narrow lobes); differs from *M. potyguara* in having a predominantly white snout, predominantly red parietals and short hemipenis with short and blunt lobes (vs. black snout and predominantly black parietals and elongated hemipenis with short and narrow lobes) (Figs 4, 5, 7; Tables 2 and 3).

Description of the holotype. MUFAL 11876, male, adult, 230 ventrals, 22 subcaudals, SVL 753 mm, TL 44 mm, HE 18.4 mm (Fig. 10A–E). Described based on preserved colour pattern. Rostral black; first, second, and third pair of supralabials, internasals, prefrontals and preoculars pale yellow with black borders; black cephalic band covering posterior half of third pair of supralabials, frontal, supraoculars, posterior border of preoculars, postoculars, fourth pair of supralabials, anterior region of parietals, fifth pair of supralabials and anterior border of the anterior temporals; the other cephalic scales pale yellow; posterior tip of the parietals with a elliptic black spot including the first dorsal scale (Fig. 10D, E). Ventrally, the mental, first and second pair of infralabials completely black; borders of the anterior genials and anterior region of the third pair of infralabials black; a thin black line in the gular region formed on the posterior borders of the third pair of infralabials and posterior border of the anterior genials; posterior border of the fourth supralabial marked with black; the other ventral cephalic scales of the gular region are pale yellow (Fig. 10B, C). Ten complete triads (10 pale yellow rings, 20 white rings and 30 black rings); pale yellow rings (ARR and PRR) longer than the others; pale yellow ring scales black-tipped; first black body ring (ABR) starting in the middle of the fourth dorsal row (four scales in length); anterior and posterior white rings (AWR and PWR, 3–4 scales long) of triads with black markings. Tail with a complete triad (one pale yellow ring, two white rings, three black rings), the outer black rings (ABR and PBR, three scales in length) are shorter than the middle black ring (MBR, five scales in length); white rings (AWR and PWR) three scales in length and pale yellow rings (ARR and PRR) three scales in length; tail end with a black scale on the dorsal and another on the ventral region (Fig. 10A, B).

Quantitative variation. Quantitative variation ($n = 123$, see Supplemental Appendix 1). Ventrals 209–238 in males (mean = 223.6; SD = 5.8; $n = 74$), 212–244 in females (mean = 226.2; SD = 5.2; $n = 49$); subcaudals (t = –2.87, $p = <0$), 18–27 in males (mean = 23.1; SD = 2.5; $n = 74$), 17–26 in females (mean = 22.1; SD = 2; $n = 49$); snout–vent length (t = –3.64, $p < 0.01$) 210–1095 in males (mean = 608.8; SD = 220.6; $n = 74$), 200–962 in females (mean = 498.5; SD = 199.5; $n = 49$); tail length (t = –3.99, $p < 0.01$) 14.3–68 in males (mean =38.7; SD =12.9; $n = 74$), 11.2–48 in females (mean =29.6; SD =10.6; $n = 49$); head length 1.9–28.3 in males (mean = 16.4; SD = 4.6; $n = 74$), 9.7–25.3 in females (mean = 15; SD = 3.6; $n = 49$); triads in the body 8–12 in males (mean = 10.2; SD = 1.2; $n = 74$), 8–12 in females (mean = 10.2; SD = 1.2; $n = 49$).

Colour pattern in life. Rostral spotted or completely black; snout mostly white with border of the scales of the second and third pair of supralabials marked with black; posterior nasals, preocular and prefrontal marked with black; black cephalic band starting in the middle one-third of the third pair of supralabials and extending to the anterior one-third of the parietals; red cephalic region from the posterior two-thirds of the parietals to the fourth dorsal scale; posterior edges of parietals marked with black (Fig. 4C). Mental and first pair of infralabials spotted or completely black; anterior region of the third pair of supralabials and anterior genials marked with black; a white postmental transverse band runs from the second pair of infralabials, and most of the anterior genials; a black thin line is formed on the posterior border of the third pair of infralabials and posterior border of the anterior genials; from the black line to the first ventrals, the colouration is red (Fig. 4C). First triad starts after 5–7 rows of red dorsal scales;

Figure 9. Distribution maps of the taxa delimited in this study with the records of occurrences, within the ecoregions delimited by WWF and within the political divisions of Brazilian states. Legend: Ecoregions (A–N); Localities of occurrence of specimens: red diamond = *M. ibiboboca*; white diamond = *M. ibiboboca* type locality; green circle = *M. janisrozei* sp. nov.; white circle = *M. janisrozei* sp. nov. type locality; orange triangle = *M. anibal* sp. nov.; white triangle = *M. anibal* sp. nov. type locality; blue square = *M. bonita* sp. nov.; white square = *M. bonita* sp. nov. type locality.

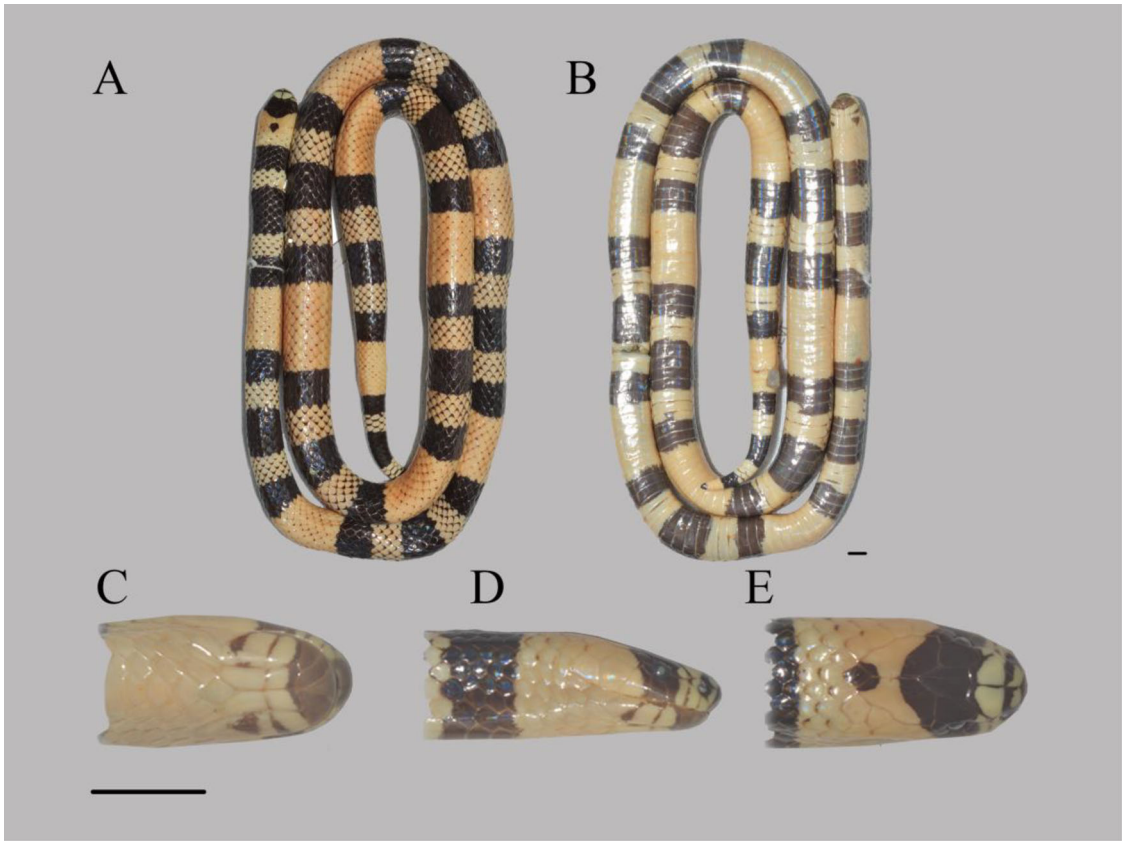

Figure 10. *Micrurus janisrozei* sp. nov. holotype (MUFAL 11876, SVL 753 mm): **A**. dorsal view; **B**. ventral view; **C**. ventral view of the head; **D**. lateral view of the head; **E**. dorsal view of the head. Type locality: Municipality of Caetité, state of Bahia, Brazil. Black line = 5 mm scale.

AWR and PWR with border of the posterior third of the scales marked with black MBR of the first triad longer than ABR and PBR; ARR and PRR of the triads are slightly marked with black (Fig. 4D). In preserved specimens, the red becomes pale yellow, and the white becomes beige (Fig. 10). Fusions of the spots on the edge of the snout scales may occur (Fig. 8B).

Hemipenial morphology. Hemipenial morphology ($n = 3$, IBSP 42254; MZUESC 20868, 20869). Hemipenis short, slightly bilobed, capitate and uniformly ornamented with calcified spines; centripetal spermatic sulcus, deep, bifurcated at the base of the lobes, following centripetally along the lobes to the apex (Fig. 5B); spermatic sulcus delimited by few spines, shorter in relation to the capitulum; short lobes (16% of the total length), ornamented with spines not much smaller than those on the capitulum, arranged in diagonal rows from the apex to the border with the capitular sulcus; interlobular region presents few smaller spines in relation to the body; deep capitular sulcus in the proximal third, delimiting the body in the first third and capitulum in the distal two-thirds; deep capitular sulcus on the sulcate face and wider on the asulcate face; capitulum (48% of the total length) ornamented by spines larger than those on the body, arranged in diagonal rows, gradually decreasing in size and number towards the apical region of the lobes; larger spines on the sulcate side; body (36% of the total length) covered by smaller spines and in greater number on the sulcate side, arranged in diagonal rows, reducing in size and quantity towards the base; distal region of the body close to the base ornamented by few spines, presence of a developed basal pocket and ornamented by few tiny spines (Fig. 5B).

Etymology. The specific name is a homage to Janis A. Roze, a distinguished herpetologist and expert on coral snakes, renowned for authoring numerous publications and books dedicated to this subject.

Distribution. Occurs in elevated regions of Chapada Diamantina, in the upper portion of the southern Caatinga, following to the middle region of the Caatinga. It is present in inland forests of Bahia, dry

Atlantic forests, and in rocky fields (Campos Rupestres) in the state of Bahia (Fig. 9).

Micrurus anibal sp. nov.

(Figs 4E, F, 11A–E)

Micrurus helleri (Jowers et al., 2019, p. 5, fig. 2). *Micrurus ibiboboca* (Hurtado-Gómez et al., 2021, p. 234, fig. 3; Pires et al., 2014, p. 580; Silva, Feitosa et al., 2021, p. 198; Silva, Pires et al., 2016, p. 120). *Micrurus lemniscatus* (Silva & Sites, 2001, p. 4, table 1; Renjifo et al., 2012, p. 139, fig. 7).

Holotype. Adult male, MNRJ 18191. Specimen locality: Iguaba Grande municipality (22°51'00.7"S, 42°11'35.3"W), state of Rio de Janeiro, Brazil (Fig. 11).

Paratypes. All from Brazil ($n = 4$).

Adult female, MNRJ 4900, Saquarema municipality (22°55'51.6"S, 42°29'47.2"W), Rio de Janeiro state. Adult male, MNRJ 8232, Jaconé municipality (22°55'00.0"S, 42°38'00.0"W), Rio de Janeiro State. Adult male, MNRJ 19013, Ubas, Iguaba Grande municipality (22°51'00.7"S, 42°11'35.3"W), Rio de Janeiro state. Adult female, MNRJ 19014, Ubas, Iguaba Grande municipality (22°51'00.7"S, 42°11'35.3"W), Rio de Janeiro state (Supplemental Fig. S3).

Diagnosis. *Micrurus anibal* sp. nov. can be distinguished from all congeners by the unique combination of the following characters: black snout to the anterior border of the prefrontal scales; well-defined prefrontal white transverse band, from the middle of the second pair of supralabials to the posterior border of the prefrontals; black cephalic band extending from the posterior border of the prefrontals to the middle third of the parietals; triads in body 8–16 (average 12), ventrals 210–228 in males, 208–252 in females; subcaudals 20–25 in males, 18–29 in females; hemipenis long, bilobed, capitate and ornamented with calcified spines;

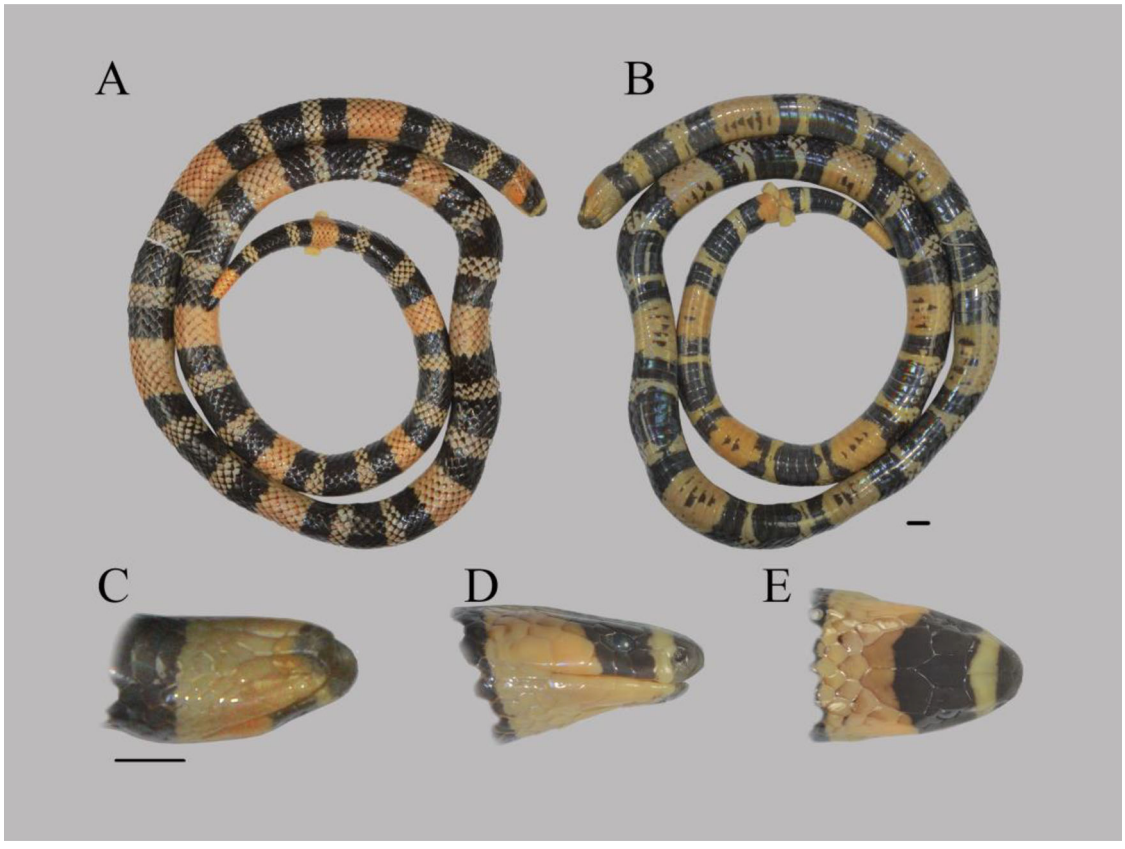

Figure 11. *Micrurus anibal* sp. nov. holotype (MNRJ 18191, SVL 620 mm): **A**. dorsal view; **B**. ventral view; **C**. ventral view of the head; **D**. lateral view of the head; **E**. dorsal view of the head. Type locality: Municipality of Iguaba Grande, state of Rio de Janeiro, Brazil. Black line = 5 mm scale.

hemipenis with capitular sulcus; capitulum longer than body; basal pocket developed and ornamented by few spines.

Comparisons. *Micrurus anibal* sp. nov. differs from *M. ibiboboca* in that it has a black cephalic band extending to the middle third of the parietals, hemipenis with capitular sulcus dividing the organ in the proximal region just above the base and capitulum larger than the body (vs. black cephalic band ending before the middle third of the parietals, capitular sulcus dividing the organ in the middle third and capitulum similar in size to the body); differs from *M. janisrozei* sp. nov. in having a black snout with a narrow white prefrontal band, a black cephalic band ending in the middle third of the parietals and an elongated hemipenis with a capitular sulcus dividing the organ in the proximal region just above the base (vs. predominant white snout with scales marked with black, black cephalic band ending in the anterior third of the parietals, and short hemipenis with capitular sulcus dividing the organ in the middle third); differs from *M. bonita* sp. nov. by having a black snout, all white triad rings with maculate scales and elongated hemipenis with capitular sulcus dividing the organ in the proximal region just above the base (vs. predominantly white snout, first white triad rings immaculate and short hemipenis with capitular sulcus dividing the organ in the middle third); differs from *M. altirostris* by having a black snout and a long black cephalic band reaching up to two-thirds of the parietal (vs. snout with black spots and a narrow black cephalic band reaching only the height of the frontal); differs from *M. brasiliensis* by having a black snout, white prefrontal transverse band, black cephalic band reaching more than three pairs of supralabials and hemipenis with long lobes (vs. predominantly white snout, absence of white prefrontal band, black cephalic band reaching less than three pairs of supralabials and hemipenis with long lobes); differs from *M. corallinus* and *M. paraensis* by having a triadal colour pattern and lacking a black cephalic cap (vs. monadal colour pattern and presence of a cephalic cap covering from the snout to the parietals); differs from *M. decoratus* in having maculate white rings of the triads and elongated hemipenis with long lobes (vs. white rings of the immaculate triads and short hemipenis with short lobes); differs from *M. frontalis* by having a completely black snout and two-thirds of the parietals black (vs. black snout with white borders and black parietals); differs from *M. carvalhoi* by having white triad rings marked in the posterior third, hemipenis with capitular sulcus in the proximal region and capitulum longer than the body (vs. white triad rings heavily marked with black, capitular sulcus in the middle third and capitulum length similar to the body); differs from *M. potyguara* in that it has two-thirds of the parietals black, hemipenis with capitular sulcus in the proximal region and capitulum longer than the body (vs. totally black parietals, capitular sulcus in the middle third and capitulum length similar to the body) (Figs 4, 5, 7; Tables 2 and 3).

Description of the holotype. MNRJ 18191, male, adult, 217 ventral, 22 subcaudal, SVL 620 mm, TL 38 mm, HE 16 mm (Fig. 11A–E). Described based on preserved colour pattern. Rostral, first pair of supralabials, internasals and anterior region of prefrontals black; prefrontal transverse band covering second pair of supralabials, anterior region of preoculars, supraoculars, nasal, third pair of supralabials and middle third of prefrontals; black cephalic band covering posterior border of prefrontals, two-thirds of preoculars, frontal, supraoculars, postoculars, fourth pair of supralabials, anterior two-thirds of parietals, anterior region of anterior temporals and fifth pair of supralabials; all other cephalic scales after the black band are pale yellow (Fig. 11D–E). Ventrally, mental, first pair of infralabials, anterior region of the anterior genials and anterior region of the second infralabials black; other ventral cephalic scales and gular region pale yellow (Fig. 11A–E). Thirteen complete triads (13 pale yellow rings, 26 white rings, 39 black rings); pale yellow rings (ARR and PRR, 4–6 scales long) slightly longer than the others, with black-spotted scales at the posterior end; first black body ring (ABR) shorter than the others, starting in the middle of the second dorsal row (three scales in length); white rings (AWR and PWR, 2–3 scales long) short and with scales heavily black-tipped; middle black ring of triads (MBR, 4–5 scales long) slightly longer than the others (ABR and PBR, three scales long); tail has a complete triad (one pale yellow ring, two white rings, three black rings), outer black rings (ABR and PBR, three scales long) shorter than the middle ring (MBR, six scales long); short white rings (AWR and PWR, 2–3 scales long); long pale yellow ring (PRR, six scales long); tail tip with three black scales (Fig. 11A). Ventrally the white rings and pale-yellow rings have irregular black spots along the entire body (Fig. 11B).

Quantitative variation. Quantitative variation ($n = 27$, see Supplemental Appendix 1). Ventrals 210–228 in males (mean = 218.5; SD = 5.3; $n = 12$), 208–252 in females (mean = 22.1; SD = 6.3; $n = 15$); subcaudals 20–25 in males (mean = 22.8; SD = 1.5; $n = 12$), 18–29 in females (mean = 20.9; SD = 2.5; $n = 15$); snout–vent length 233–1060 in males (mean = 574.8; SD = 260.5; $n = 12$), 200–961 in females (mean = 428.6; SD = 231.4; $n = 15$); tail length 13.8–61.2 in males (mean

= 34.6; SD = 15.4; $n = 12$), 12.5–61 in females (mean = 29.8; SD = 15.8; $n = 15$); head length 11.6–24.3 in males (mean = 16.4; SD = 3.9; $n = 12$), 9.7–22.3 in females (mean = 14.8; SD = 4.1; $n = 15$); body triads 9–14 in males (mean =11.9; SD =1.4; $n = 12$), 8–16 in females (mean =12.3; SD =1.8; $n = 15$).

Colour pattern in life. Snout marked with black up to the height of the anterior border of the prefrontals; prefrontal white transverse band starting in the middle of the second pair of supralabials reaching the posterior edge of the prefrontals; black cephalic band starts in the middle third of the third pair of supralabials to the middle third of the parietals; red cephalic region from the middle third of the parietals up to the second row of dorsal scales (Fig. 4E1–E4). Ventrally, mental and first pair of infralabials spotted or entirely black; anterior region of the second pair of supralabials and anterior genials marked with black; narrow ventral white band starts on the anterior third of the second pair of infralabials, following the anterior third of the anterior genials; after the white stripe the other scales are red (Fig. 4E). First triad with AWR and PWR with black tipped scales; longer MBR than ABR and PBR; ARR and PRR slightly marked with black; (Fig. 4F). In preserved specimens, the red in life becomes pale yellow and the white becomes beige (Fig. 11). The black cephalic band may cover the posterior quarter of the prefrontals (Fig. 8C).

Hemipenial morphology. Hemipenial morphology ($n = 1$, MNRJ 18191). Hemipenis long, bilobed, capitate, uniformly ornamented with calcified spines; centripetal spermatic sulcus, deep, bifurcated at the base of the lobes, following centripetally along the lobes to the apex (Fig. 5C); sulcus spermaticus delimited by spines similar in size to the capitulum; long lobes (32% of the total length), ornamented with spines not much smaller than those of the capitulum, arranged in diagonal rows from the apex to the constriction of the capitular sulcus; interlobular region with few spines smaller in relation to the capitulum located in the intralobular base; capitular sulcus in the proximal third, delimiting the body in the first third and capitula in the distal two-thirds (Fig. 5C, white arrows); discreet capitular sulcus on the grooved side and wide on the non–grooved side; capitulum (51% of the total length) ornamented by spines larger than those on the body, arranged in diagonal rows, decreasing in size and number in the apical region of the lobes; larger spines on the furrowed face; body (17% of the total length) covered by smaller spines and in greater number on the furrowed face, arranged in vertical rows, reducing in size and quantity towards the base; proximal region of the hemipenis ornamented by few spines, presence of basal pocket developed and ornamented by few spines (Fig. 5C).

Etymology. The specific epithet is a noun in apposition referring to a memory of Anibal Rafael Melgarejo Gimenez, a Uruguayan based in Brazil, herpetologist and toxicologist who contributed to the studies of Brazilian snakes, including coral snakes.

Distribution. *Micrurus anibal* sp. nov. occurs in the mountainous region of the state of Rio de Janeiro, with records to the south in forest regions of the Upper Paraná and to the east in restinga regions (Fig. 9).

Micrurus bonita sp. nov.

(Figs 4G, H, 12A–E)

Micrurus ibiboboca (Vanzolini et al., 1980,p. 61, fig. 48–49; Slowinski, 1995, p. 326; Silva & Sites, 2001, p. 4, table 1; Argôlo, 2004, p. 89; Renjifo et al., 2012, p. 139, fig. 7; Pires et al., 2014, p. 577; Silva, Pires et al., 2016, p. 120, fig. 61; Jowers et al., 2019, p. 5, fig. 2; Silva, Feitosa et al., 2021, p. 198).

Holotype. Adult male, CZGB 484. Specimen locality: Petrolândia municipality (9°04'08.5"S, 38°16'57.6"W), Pernambuco state, Brazil (Fig. 12).

Paratypes. All from Brazil ($n = 5$).

Adult male, MUFAL 4104, Atalaia municipality (9°31'04.4"S, 35°58'51.4"W), Alagoas state. Adult female, MUFAL 6490, Coruripe municipality (10°06'09.0"S, 36°10'17.9"W), Alagoas state. Adult female, MUFAL 10425, Jarapatinga municipality (9°05'25.4"S, 35°17'45.3"W), Alagoas state. Adult female, MUFAL 13929, Barra de Santo Antônio municipality (9°25'15.0"S, 35°30'45.7"W), Alagoas state. Adult male, MUFAL 14344, Maceió municipality (9°36'52.7"S, 35°45'45.0"W), Alagoas state (Supplemental Fig. S3).

Diagnosis. *Micrurus bonita* sp. nov. can be distinguished from all congeners by the unique combination of the following characters: predominantly white snout; scales of the first white rings of the first 1–2 triads immaculate; middle black rings of the triads longer than the outer rings; body triads 6–12 (average 8); ventrals 203–247 in males, 214–257 in females; subcaudals 18–33 in males, 15–34 in females; hemipenis short, slightly bilobed, capitate and ornamented with calcified spines; capitulum longer than the body; poorly developed basal pocket ornamented by a few small spines.

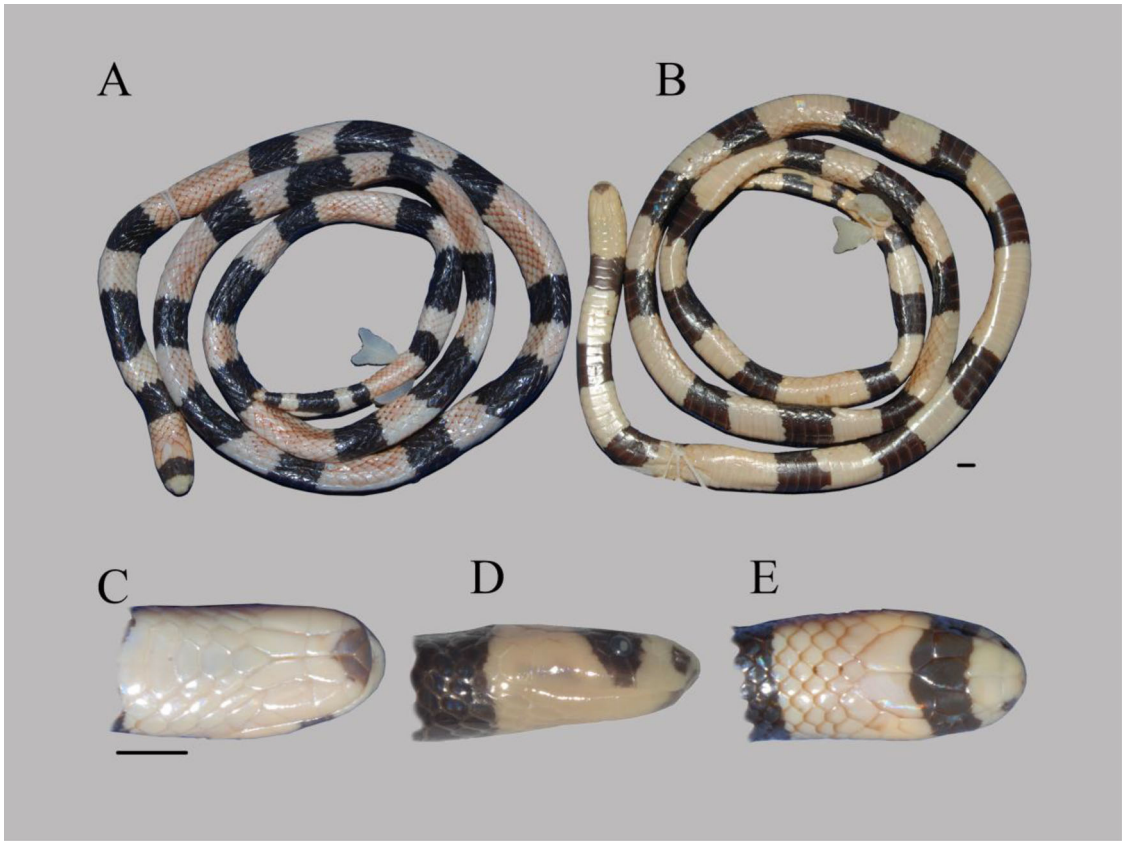

Figure 12. *Micrurus bonita* sp. nov. holotype (CZGB 484, SVL 795 mm): **A**. dorsal view; **B**. ventral view; **C**. ventral view of the head; **D**. lateral view of the head; **E**. dorsal view of the head. Type locality: Municipality of Petrolândia, state of Pernambuco, Brazil. Black line = 5 mm scale.

Comparisons. *Micrurus bonita* sp. nov. differs from *M. ibiboboca* in that it has a predominantly white snout, scales of the first white rings of the first triads immaculate and a short hemipenis with a capitulum longer than the body (vs. black snout; first white rings of triads marked with black and long hemipenis with capitulum similar in size to the body); differs from *M. janisrozei* sp. nov. in having a predominantly white snout, scales of the white rings of the first triads immaculate, hemipenis with short lobes and thin apices (vs. predominantly white snout with borders of the scales spotted with black, scales of the white rings of the first triad black-tipped, hemipenis with short lobes and blunt apices); differs from *M. anibal* sp. nov. in having a predominantly white snout, first white rings of triads immaculate and short hemipenis (vs. black snout, first white rings of triads with scales marked with black and long hemipenis); differs from *M. brasiliensis* by having a predominantly white snout, immaculate white ring scales of the first triad and short hemipenis with narrow apex lobes (vs. white snout with black-spotted edges of the scales, stained first white triad rings; elongated hemipenis with rhomboid apex lobes); differs from *M. corallinus* and *M. paraensis* in having a triadal colour pattern and lacking a black cephalic cap (vs. monadal colour pattern in and presence of a cephalic cap covering from the snout to the parietals); differs from *M. filiformis*, *M. lemniscatus*, *M. carvalhoi*, and *M. potyguara* by having a predominantly white snout, irregular or absent prefrontal transverse band (vs. black snout; regular and well-defined white prefrontal band); differs from *M. frontalis* in having a predominantly white snout and a black cephalic band covering only one-third of the parietals (vs. predominantly black snout and parietals completely black) (Figs 4, 5, 7; Tables 2 and 3).

Description of the holotype. CZGB 484, male, adult, 221 ventrals, 22 subcaudals, SVL 795 mm, TL 42 mm, HE 13 mm (Fig. 12). Described based on preserved colour pattern. Rostral, first and second pair of supralabials, internasals, nasals and prefrontals white; surroundings of the nasal cavities marked with black; black cephalic band starting at the posterior edge of the prefrontals covering the posterior half of the preoculars, third pair of supralabials, supraoculars, postoculars, fourth pair of supralabials, anterior temporals and fifth

pair of supralabials, anterior one-third of parietals, and entire frontal; after the black cephalic band all other cephalic scales are pale yellow (Fig. 12D–E). Ventrally, mental and first pair of infralabials completely black; anterior border of the anterior genials and anterior region of the second pair of infralabials slightly marked with black; other ventral cephalic scales and gular region pale yellow (Fig. 12C). Eight complete triads (eight pale yellow rings, 16 white rings, and 24 black rings); pale yellow rings (ARR and PRR, 6–11 scales long) longer than the others; white rings of the first triad immaculate; other white rings scales weakly marked with black; first and third black rings (ABR and PBR, 4–5 scales long) of the triads shorter than the middle black rings (MBR, 6–8 scales long) (Fig. 12A–B). Tail with a complete triad (one pale yellow ring, two white rings, three black rings), black outer rings (ABR and PBR, three scales long) shorter than the middle ring (MBR, five scales long); white rings (AWR and PWR) three scales in length and pale-yellow ring (PRR) two scales in length; tail tip with one black scale (Fig. 12A, B).

Quantitative variation. Quantitative variation ($n = 352$, see Supplemental Appendix 1). Ventrals 203–247 in males (mean = 227; SD = 6.4; $n = 207$), 214–257 in females (mean = 230.9; SD = 7.7; $n = 145$); subcaudals showing sexual dimorphism ($t = -4.59$, $p < 0.01$) 18–33 in males (mean = 24.9; SD = 2.5; $n = 207$), 15–34 in females (mean = 23.5; SD = 2.7; $n = 145$); snout–vent length showing sexual dimorphism ($t = -3.91$, $p < 0.01$) 176–1375 in males (mean = 638; SD = 223.4; $n = 207$), 222–1005 in females (mean = 546.9; SD = 168.4; $n = 145$); tail length showing sexual dimorphism ($t = -5.48$, $p < 0.01$) 13–77.6 in males (mean = 39.3; SD = 12.9; $n = 207$), 12–74 in females (mean = 32.2; SD = 10 .3; $n = 145$); head length showing sexual dimorphism ($t = -4.96$, $p < 0.01$) 9.7–31 in males (mean = 17.1; SD = 3.8; $n = 207$), 7.5–24.5 in females (mean = 14.9; SD = 31; $n = 145$); body triads in males 6–12 (mean = 8.6; SD = 1; $n = 207$), in females 7–12 (mean = 8.6; SD = 0.9; $n = 145$).

Colour pattern in life. Predominantly white snout; rostral may be speckled with black; black cephalic band starts at the edge of the third pair of supralabials and up to the anterior third of the parietals; red cephalic region begins after the anterior third of the parietals (Fig. 4G1–G4). Ventrally, mental and two-thirds of the first pair of infralabials spotted with black; postmental transverse white band covers the middle third of the first pair of infralabials, the entire second pair of infralabials and two-thirds of the third pair of infralabials and anterior genials; after the white transverse band all other cephalic scales are red (Fig. 4G3). AWR and PWR scales from the first triad immaculate; MBR of all triads longer than ABR and PBR; ARR and PRR of triads with slightly marked scales (Fig. 4H). In preserved specimens, the red in life becomes pale yellow and the white in life becomes beige (Fig. 12). Black spots may occur on the snout or on the edge of the snout scales (Fig. 8D).

Hemipenial morphology. Hemipenial morphology ($n = 5$, MZUSP 10463, 6932, 7193; CZGB 484; MNRJ 13116;), Short, slightly bilobed, capitate hemipenis, uniformly ornamented with calcified spines (Fig. 5D); spermatic sulcus centripetal, deep, bifurcated at the base of the lobes, running centripetally along the lobes to the apex; sulcus spermatic delimited by shorter spines in relation to the capitulum; short lobes (28% of the total length), ornamented with spines slightly smaller in relation to the capitulum, arranged radially up to the capitulum; interlobular region presents few spines, smaller in relation to the capitulum; discrete capitular sulcus on both sides delimiting the body in the proximal third and capitulum in the distal two-thirds; capitulum (54% of the total length) ornamented by spines larger than those on the body, arranged in diagonal rows, gradually decreasing in size and number towards the apical region of the lobes; larger spines on the sulcate side; body (18% of the total length) covered by smaller spines than on the capitulum; spines in greater number on the sulcate side, arranged in vertical rows, reducing in size and quantity towards the base; proximal region ornamented by few spines; poorly developed basal pocket ornamented by a few tiny spines (Fig. 5D).

Etymology. The specific epithet is a noun in apposition referring to Maria Gomes de Oliveira, known as Maria "Bonita", the pioneering woman who joined a cohort of "Cangaceiros". The "Cangaço" was a social movement in northeast Brazil during the nineteenth and twentieth centuries and was characterized by armed nomads grouped in gangs. The "Cangaceiros" expressed discontent with the precarious conditions prevalent among the northeastern population, where power was concentrated in the hands of landowners. The "Cangaço" evolved into an emblematic symbol of Brazilian culture, inspiring a myriad of artistic and cultural expressions throughout the northeastern region of Brazil.

Distribution. Occurs from the central region to the north of the Caatinga, in enclaves of high and dry forests. It is present in areas of coastal forests and inland forests of Pernambuco and Bahia, with records in areas

of mangroves and restinga. West of the coast, it can be found in dry Atlantic Forest regions and in Cerrado regions connected to the Caatinga (Fig. 9).

Discussion

Diversity and distribution of the Micrurus ibiboboca *complex*

The description of three new species within the *M. ibiboboca* complex highlights the importance of ongoing analysis of the incompletely understood diversity of South American *Micrurus*. Our molecular and morphological analysis revealed three new species of *Micrurus*, distributed throughout the northeastern and southeastern parts of the Brazilian Atlantic Rain Forest (ARF) and Caatinga biomes.

The ARF is the second-largest tropical forest in Brazil. It comprises distinct vegetation or forest formations distributed in tropical and subtropical regions, with several studies defining areas with high species diversification (Marques et al., 2011; Myers et al., 2000; Siqueira et al., 2001). In contrast, the Caatinga is a large semi-arid ecological region located entirely within the northeastern quadrat of Brazil (Silva & Lacher, 2020). For a long time, it was thought that the Caatinga was homogeneous, with relatively few species. However, recent studies have discovered areas of endemism and biogeographic elements capable of delimiting populations throughout the ecological region (Cardoso & de Queiroz, 2010; Guedes et al., 2014; Silva et al., 2018; Velloso et al., 2002).

These ecological regions have been shown to be highly biodiverse areas, with the incidence of endemic and threatened species for several groups of organisms, such as in the Serra do Mar, and Bahia Coastal and Interior Forests areas in the ARF, and elevated areas of Caatinga, as Dry Atlantic Forest, Humid Forest enclaves (Brejos de Altitude), and the Chapada Diamantina complex (Graboski et al., 2015, 2022; Grazziotin et al., 2006; Rocha et al., 2007; Thomé et al., 2021). An example of endemic snakes with a similar distribution pattern to the new species of *M. ibiboboca* complex includes *Amerotyphlop*s (Graboski et al., 2015, 2023), with new species recently described from the Bahia Coastal and Interior Forests (*A. caetanoi* and *A. montanun*) and in Brejos de Altitude (*A. arenensis*). All the new *Micrurus* species described in the present study are endemic to these areas: *M. janisrozei* sp. nov. and *M. bonita* sp. nov. present a sympatric distribution with *M. ibiboboca*, in the Bahia Interior Forest. In contrast, *M. anibal* sp. nov. is restricted to Southeastern Brazil, distributed in the Coastal Forests in Serra do Mar. Although *M. bonita* sp. nov. can be found in the Bahia Coastal and Pernambuco Forests, this species is often associated with the Caatinga, in the Humid Forest enclaves, with some records in Cerrado. Additionally, *M. janisrozei* sp. nov. is associated with Caatinga and elevated areas of Dry Atlantic Forest in the south of this biome, in the Chapada Diamantina complex.

Taxonomy of the Micrurus ibiboboca *complex*

Regardless of the recent advances in our knowledge of South American coral snake diversity, many species of the genus *Micrurus* remain poorly known, with several divergent lineages included in species complexes (Hurtado-Gómez et al., 2021; Jowers et al., 2019; Pires et al., 2021; Silva & Sites, 1999). Traditionally, taxonomic and systematic studies have relied heavily on morphological characters alone, demanding the expertise of taxonomic specialists to accurately identify taxa, especially when dealing with cryptic species and phenotypic plasticity of traits (Feitosa et al., 2015; Nascimento et al., 2019; Pires et al., 2021; Silva & Sites, 1999).

Our results suggest the *Micrurus ibiboboca* complex contains three new species previously confused with *M. ibiboboca*. However, our phylogenetic results showed that only two of the new species described here, *M. anibal* sp. nov. and *M. bonita* sp. nov., are closely related to the *M. ibiboboca* complex. In contrast, *M. janisrozei* sp. nov. was recovered as phylogenetically distant from the *M. ibiboboca* species complex, recovered as sister group of the poorly supported clade composed of the *M. frontalis* and *M. ibiboboca* complexes.

Several studies based on morphological and distributional data of the *M. ibiboboca* species complex considered the new species described here and *M. ibiboboca* as a single taxon (Campbell & Lamar, 2004; Roze, 1996; Silva, Feitosa et al., 2021; Silva, Pires et al., 2016). For example, Pires et al. (2014) describe the hemipenis morphology of a specimen, with voucher number IBSP 42254, from the municipality of Brumado, Bahia state, as *M. ibiboboca*. However, our morphological results indicate that this is a specimen of *M. janisrozei* sp. nov.

Studies including molecular datasets are essential for thoroughly assessing and inferring the cryptic diversity of *Micrurus,* and are a powerful taxonomic tool to identify and discover new species (Funk et al., 2012; Passos et al., 2022; Sites & Marshall, 2004; Streicher & Meik, 2018). However, the correct identification of samples used in molecular studies has become a growing concern. The lack of knowledge of morphological characters in taxonomic studies can be problematic in identifying collection specimens. Consequently, using tissue samples without proper taxonomic confirmations

can lead to confusing assessments that do not improve our taxonomic knowledge in the study of several groups, especially for many species complexes involving the genus *Micrurus* (Arteaga et al., 2017; Mulcahy et al., 2022; Passos et al., 2022; Tautz et al., 2003).

An example of this problem occurred in the study of Silva and Sites (2001). Using molecular data, these authors identified specimens with voucher numbers IVB 1757 (from Arraial do Cabo municipality, Rio de Janeiro state) and CEPB 2312 (from Quebrangulo municipality, Alagoas state) as *M. lemniscatus*, and CEPB 024 (from Xingó municipality, Alagoas state) as *M. ibiboboca*. However, Pires et al. (2014) indicated that IVB 1757 and CEPB 2312 are morphologically closer to *M. ibiboboca*. Additionally, Renjifo et al. (2012) used these sequences in their phylogenetic analysis, suggesting a taxonomic change of *Micrurus lemniscatus* (an Amazonian taxon) to *M. lemniscatus carvalhoi* (a non-Amazonian taxon). Subsequently, some phylogenetic studies identified these two samples as *M.* cf. *lemniscatus* and *M. ibiboboca* (Jowers et al., 2019; Lee et al., 2016; Zaher et al., 2016, 2021). Recently, Hurtado-Gómez et al. (2021) followed the identifications proposed by Renjifo et al. (2012), while Jowers et al. (2019) used sequences AF228439 (IVB 1757) and AF228437 (CEPB 2312) identified as *M.* cf. *ibiboboca*, following the taxonomy proposed by Pires et al. (2014).

Silva and Sites (2001) clarified that the samples of *Micrurus lemniscatus* analysed at that time did not form a clade and that there are significant differences between the samples from the Amazon, Cerrado, and the coastal region of Brazil. Considering the possibility of a paraphyletic relationship of some specimens of *M. lemniscatus*, Silva and Sites (2001) indicated that a taxonomic revision is needed for *M. lemniscatus* and *M. ibiboboca* complexes. Our molecular results suggest that the specimen CEPB 2312 (former *M. lemniscatus*, AF228438) is *M. janisrozei* sp. nov. and that the specimen CEPB 024 (former *M. ibiboboca*, AF228440) is *M. bonita* sp. nov., while the specimen IVB 1757 (former *M. lemniscatus*, AF228439) is *M. anibal* sp. nov.

Comparative morphology of the Micrurus ibiboboca *complex*

During the last decades, most of the taxonomic and systematics studies of *Micrurus* have predominantly relied on morphology as the primary source of evidence for describing new species and defining groups (Bernarde et al., 2018; Di-Bernardo et al., 2007; Feitosa et al., 2015; Pires et al., 2014). Nevertheless, the exclusive use of phenotypic characters alone has presented taxonomic challenges due to the extreme variation in colour patterns and highly conservative morphological variation in the genus (Feitosa et al., 2007a, 2007b, 2015; Nascimento et al., 2019; Pires et al., 2014, 2021; Silva & Sites, 1999). An example of this was reported for the *M. frontalis*, *M. spixii*, and *M. lemniscatus* complexes, which have a conservable overlapping in the ranges of scales counting and in the number of triads of the body (Nascimento et al., 2019; Pires et al., 2014, 2021; Silva, Buononato et al., 2016, 2021; Silva & Sites, 1999).

The results of our morphological analysis support these previous studies, indicating a high level of morphological similarities. Notably, the distribution of morphological variables in multivariate space indicates a strong overlapping among species of the *M. ibiboboca* complex. However, our RPCA and RLDA results based on simulated data corroborated the existence of four distinct morphological groups. The use of central tendency measures, such as mean, mode, and median, has provided a better understanding of the *M. ibiboboca* species complex.

Additionally, the colour pattern of the head and the first triad of the body provides evidence for diagnosing the new species. *Micrurus ibiboboca* and *M. janisrozei* sp. nov. were easily confused by having black and white rings in the first triads, with similar lengths. However, *M. janisrozei* sp. nov. has, on average, a greater number of rings along the body, in addition to having a predominantly white snout. Otherwise, *M. bonita* sp. nov. has cephalic and body colours that are easily recognizable by the characteristic white snout and immaculate first two white rings of the first triad.

Furthermore, the hemipenial morphology is taxonomically informative in defining groups and delimiting species of *Micrurus* (Nascimento et al., 2019; Passos & Fernandes, 2005; Pires et al., 2014; Roze, 1996; Silva & Sites, 1999). Pires et al. (2014) described the lobes of the hemipenis of *M. ibiboboca*, *M. spixii*, and *M. frontalis* complexes as short and weakly bilobed. However, our analysis indicates that the hemipenis that Pires et al. (2014) referred to *M. ibiboboca* (IBSP 42254, from Brumado municipality, Bahia state), is instead *M. janisrozei* sp. nov. Additionally, the hemipenial morphology of *M. ibiboboca* (CZGB 901, from Camacã municipality, Bahia state) resembles that of the *M. lemniscatus* complex, exhibiting long and strongly forked lobes.

Our results suggest two distinct groups based on the general morphology of the hemipenis: (1) *M. ibiboboca* and *M. anibal* sp. nov. presenting the elongated form, as well as *M. brasiliensis*, *M. potyguara*, and *M. carvalhoi*; and (2) *M. janisrozei* sp. nov. and *M. bonita* sp. nov. presenting a short hemipenis, as well as *M. frontalis* and *M. decoratus*. The species with an elongated hemipenis, in general, have similar body and capitulum sizes,

except for *M. anibal* sp. nov. that presents a proximal capitular constriction.

Additionally, we observed similarities in the ornamentation of the capitulum and in the length of the lobes, where all species compared in our analysis have long spines arranged in vertical rows with long lobes, except for *M. brasiliensis*, which has intermediate sized lobes in comparison to the other species. Furthermore, the depth of the capitular sulcus is remarkably similar among species with short hemipenis. These species have smaller hemipenis bodies than the capitulum. Also, *M. janisrozei* sp. nov. and *M. bonita* sp. nov. have shorter spines than *M. frontalis* and *M. decoratus*.

Considering the comparison of the new taxa among congeners species, we observed significant variations concerning the position, depth, and boundaries of the capitular sulcus. The capitular sulcus, conspicuously visible on the asulcate side, clearly indicates the capitate condition of the hemipenis in all specimens analysed in our study, corroborating Pires et al. (2014). Furthermore, Slowinski (1995) also reported the partially capitate (almost capitate) condition in *M. brasiliensis* and *M. ibiboboca*. However, the hemipenis used by Slowinski (1995) for *M. ibiboboca* is instead a specimen of *M. bonita* sp. nov. (IBSP 51155, from Recife municipally, Pernambuco state).

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No potential conflict of interest was reported by the author(s).

Supplemental material

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Data availability statement

Data underlying this article will be shared upon reasonable request to the corresponding author.

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