THE DEFENSIVE REPERTOIRE OF NEW WORLD CORAL SNAKES: EVOLUTION AND NATURAL HISTORY

Authors and Affiliations

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ABSTRACT

The defensive repertoire of New World coral snakes is diverse, but its evolutionary history remains poorly understood. We compiled 280 records of 11 defensive behaviors across 85 species of *Micrurus* and one species of *Micruroides* from the literature and contributions by researchers, naturalists, and wildlife photographers. Fifty-seven records represented behaviors not previously documented for the respective species. Using mitochondrial ND4 sequences, we inferred a Bayesian phylogeny, reconstructed ancestral states, and evaluated phylogenetic signal of the defensive behaviors. Tail-raising and coiling, dorsoventral body flattening, erratic movements, and head-hiding were reconstructed in the common ancestor of *Micruroides* and *Micrurus*, indicating a broadly conserved ancestral defensive repertoire. Erratic movements and head-hiding showed significant individual phylogenetic signal, and the combined profile of the four widespread behaviors was also phylogenetically structured. Hemipenis eversion was reconstructed as a synapomorphy of the sampled *Micrurus frontalis-M. spixii* clade, with an independent origin in *M. boicora*. Ventral exposure, cloacal popping sounds, and other less frequent behaviors also showed independent origins. These findings reveal a defensive repertoire combining deep evolutionary conservation with repeated origins of more restricted behaviors, while highlighting major gaps in behavioral sampling.

INTRODUCTION

Finding food and avoiding predators are among the most recurrent ecological challenges faced by reptiles (Greene, 1988). Thus, predation is a major ecological challenge faced during foraging activities and has driven the evolution of multiple morphological, chemical and behavioral defenses in this group (Greene 1988; Kikuchi et al. 2023). Because predation unfolds through successive stages, from detection and identification to attack, subjugation, and consumption (Endler 1986), different defensive traits may act at different points of a predator–prey encounter (Toledo et al., 2011). Therefore, many of the aforementioned behaviors can be used together, and predation-avoidance is usually a holistic behavioral process (Kikuchi et al. 2023). Although each behavior constitutes a single defensive trait, those repeatedly deployed together may become integrated into multi-behavior defensive strategies (Kikuchi et al. 2023). Therefore, different behaviors driven by distinct selective pressures imposed by different predators might have contributed to the emergence and evolution of a holistic defense repertoire (Kikuchi et al. 2023). Among reptiles, snakes possess a great variety of antipredator behaviors (Greene 1988), and some groups, such as coral snakes, often employ multiple defensive behaviors in unison (Greene 1988; Roze 1996).

In the Americas, the snake family Elapidae is represented by two genera: the monotypic *Micruroides* (Schmidt 1928) and *Micrurus* (Wagler 1824), which currently comprises 85 species of coral snakes (Campbell and Lamar 2004; Reyes-Velasco et al 2020; Uetz et al 2023; Nascimento et al 2024). Although members of this family are regarded as the most dangerous snakes in the world, most are small and generally pose little threat to humans (Campbell and Lamar, 2004). Coral snakes are typically associated with aposematic red coloration, and many of them exhibit diverse patterns of banding including red and other colors (Amaral 1925; Bosque et al. 2016). Although the defensive mechanism of aposematism has been a commonly studied topic in terms of ecology and evolution of coral snakes (Kikuchi et al 2021; Bosque et al 2022), little attention has been given to the evolution of defensive behaviors.

Coral snakes exhibit a broad repertoire of morphological and behavioral patterns that are interdependent (Roze 1982). Among the defensive behaviors documented for most New World coral snakes are: flattening the body while performing erratic (unpredictable) movements, hiding the head beneath the body coils, raising a coiled tail, and repeated biting (Greene 1973; Jackson 1979; Greene 1988; Roze 1996; Test et al 1996; Greene 1997; Martins and Oliveira 1998; Campbell and Lamar 2004; Silva Júnior 2016). These defensive displays

aim to confuse or intimidate potential predators (Jackson 1979; Roze 1996; Test et al 1996; Campbell and Lamar 2004; Silva Júnior 2016). Although these behaviors can be observed in isolation, coral snake defense is a holistic process in which the aforementioned behaviors, combined with aposematic coloration, are employed as a survival strategy (Roze 1982; Test et al 1996). In any case, it is important to highlight that the most commonly observed response (when disturbed by humans or other animals) is escaping, whether into the leaf litter, crevices, or burrows (Martins and Oliveira 1998; Campbell and Lamar 2004; Marques and Sazima 2021).

The above-mentioned defensive behaviors are innate and stereotyped (Carpenter and Ferguson 1977; Senter 2022) and, as such, their evolution can be studied in a phylogenetic context, where each behavior is considered an independent phenotypic character (Greene 1994; Senter et al 2014; Joy et al 2016; Senter 2022). One basic hypothesis is that these behaviors will have originated in a common ancestor and, hence, exhibit strong phylogenetic signal, i.e., the tendency of phylogenetically related taxa to present similar characters (Berger 1988; Blomberg et al 2003; Blomberg and Garland 2002). The evolution of different snake behaviors has been investigated, such as constrictive feeding (Greene 1994), defensive displays of intimidation with an open mouth (Greene 1994), courtship behaviors and male combat (Senter et al 2014; Senter 2022). However, the information on such behaviors is often based on scattered, anecdotal, and species-specific records in the literature (see Getelina et al 2018; Gonzalez and de Oliveira 2020; Cruz et al 2021; Flórez et al 2022; Smith et al 2023). Hence, there is an important knowledge gap on coral snake behavior in the wild, likely due to the rarity and elusive (fossorial and semifossorial) habits of these species (see Roze 1996). Most studies on coral snakes often mention defensive behaviors in general terms, without detailing which species exhibit them, and behavior descriptions tend to be brief or limited to photographs (as seen in Roze, 1996; Silva Júnior, 2016; Silva Júnior et al. 2021a).

In this study, we aimed to (1) synthesize records of defensive behaviours in New World coral snakes from the literature and contributed observations; (2) investigate the evolutionary history and phylogenetic structure of their defensive repertoire; and (3) evaluate the putative functions and contexts of these behaviours using available natural-history evidence. We hypothesized that widespread behaviours constitute an ancestral, broadly conserved repertoire inherited from the common ancestor of *Micruroides* and *Micrurus*, whereas less frequent behaviours evolved independently one or multiple times in particular lineages. Accordingly, we expected the combined profile of widespread behaviours to show phylogenetic structure, with the remaining behaviours displaying more restricted and homoplastic distributions. We

compiled 11 defensive behaviours across 85 *Micrurus* and one *Micruroides* species and provided the first comparative reconstruction of their defensive repertoire.

MATERIALS AND METHODS

Defensive Behavior Compilation

We compiled 11 defensive behaviors related to the genus *Micruroides* and *Micrurus*: tail-raising and coiling (TC), dorsoventral body flattening (BF), erratic movements (TR), cloacal discharge (CD), hemipenis eversion (EH), climbing behavior (CB), thanatosis (TH), head-hiding (HH), tail-striking (TS), cloacal sound production ("cloacal popping sounds") (CP), and ventral display (VE). Evidence of defensive behaviors was obtained using two complementary approaches: (1) a thorough literature review, searching for previously described defensive behaviors for specific species; (2) direct contact with researchers and wildlife photographers to obtain personal field-notes, observations and records of defensive behaviors. For the literature review, we included records based on either formal descriptions or photographic documentation of coral snakes' defensive behavior, even if the study's primary focus was not behavioral (e.g., Marques et al 2006). We used Google Scholar for the literature review, using terms such as: coral snakes, defense, defensive behavior, behavior, snakes and natural history.

Contact with researchers and photographers was made via email, with many addresses retrieved from scientific articles and books, as well as by searching for photographic records showing behavioral evidence on social media platforms (Instagram, iNaturalist and Flickr). All records (photos and videos) were used with the permission of their respective authors (see Acknowledgements). Adhering to the principles of open science, all behavior records are fully available: obtained photographic records are presented in plates, and the videos are in the supplementary material.

The compiled behavior records (photos and videos), along with those available in the literature, were analyzed for evidence of defensive behavior. We considered images such as those presented in Campbell and Lamar (2004), specifically: Plate 77 (*Micrurus diastema sapperi*), Plate 113 (*Micrurus hippocrepis*) and Plate 219 (*Micrurus ancoralis jani*) as evidence

that these species are capable of exhibiting tail-raising and coiling behavior (see Campbell and Lamar 2004). We also regarded the flattening of the posterior body region and arboreal behaviors as evidence that these species can display dorsoventral flattening (Figure 1) and use trees for defense, as described by Getelina et al. (2018). Because we had access to the specific geographic location of all records provided by their authors, we assigned behaviors to different species or lineages based not only in the external morphological characteristics of each record, but also on the location of each record and the known distribution of the corresponding taxa.

We built a heatmap (Figure 2) to facilitate the visualization of each behavior depicted by all species in our dataset using R v4.3.2 (R Core Team 2023). The packages used to build the heatmap were: *dplyr* (Wickham et al. 2023), *tidyr* (Wickham et al. 2024), *openxlsx* (Schauberger and Walker 2023), *ggplot2* (Wickham 2016), *knitr* (Xie 2015), *viridis* (Garnier et al. 2024) and *forcats* (Wickham 2023). We also used Adobe Photoshop to discriminate which behaviors are new additions to the literature within the heatmap.

Figure 1. (a) *Micrurus ancoralis*, from Ibarra Canton, Ecuador, displaying tail-raising and coiling along with flattening of the posterior body region. Photo: Bill Hagan; (b) *Micrurus obscurus,* near Vila Makuma, Ecuador. Exhibiting a defensive display. Note the hidden head and the raised, curled and flattened tail in evidence. Photo: Dwain Holmes.; (c) *Micrurus nigrocinctus* from Guanacaste, Costa Rica, in a defensive display. Detail of the flattened body, hidden head and raised, curled tail. Photo: Michael Franzen.; (d) *Micrurus nigrocinctus*, from la Cangreja, Costa Rica showing ground level view of the tail raising and coiling, along with dorsoventral body flattening. Photo: César Barrio Amorós.

Phylogenetic Inference, Ancestral Reconstruction and Phylogenetic signal

Despite recent advances (Nascimento et al., 2019; Nascimento et al., 2024), coral snake taxonomy remains unstable and some GenBank sequences have conflicting species assignments, so we adopted a conservative sequence-selection procedure. We selected one ND4 sequence for each of 48 *Micrurus* species and one *Micruroides* species, except for *M. nigrocinctus*, which was represented by two recognized lineages (Jowers et al. 2019, 2023). Sequence assignments followed the phylogenetic and taxonomic evidence of Jowers et al. (2019, 2023), Reyes-Velasco et al. (2020), and Nascimento et al. (2024). These studies provide broad taxonomic coverage and, in some cases, evidence of migration and gene flow useful for assigning sequences to currently recognized species. This single-locus approach allowed us to maximize taxon coverage while minimizing uncertainty in assigning GenBank sequences to nominal species, while also avoiding the high proportion of missing character data present in some multilocus datasets with incompletely sampled taxa.

All ND4 sequences used for the molecular phylogeny were retrieved from genbank and entries are detailed in the supplementary material. We used MEGA11 software (Tamura et al 2021) to visualize the sequences and align them using the MUSCLE algorithm using the default parameters (Edgar 2004). The multiple sequence alignment was visually inspected and poorly-aligned flanks were manually trimmed, resulting in a final alignment of 500 bp.

We used ModelFinder (Kalyaanamoorthy et al 2018) implemented in IQTREE v1.6.12 (Minh et al 2020) to estimate the best nucleotide substitution model, constraining it to the models available in BEAST (Suchard et al 2018). We partitioned the data into the three codon positions (Chernomor et al 2016), and the evolutionary models estimated for each codon position were: GTR + F + I for the first position, and TN + F + G4 for the second and third positions.

We used BEAST v1.10.4 (Suchard et al 2018) and BEAGLE v4.0.1 (Suchard and Rambaut 2009; Ayres et al 2012, 2019) to run a Bayesian inference (BI) phylogenetic analysis and ancestral state reconstructions for the defensive behaviors. The input in nexus format containing the DNA sequences and coded behaviors for each species was loaded into the

BEAUti v1.10.4 program (Suchard et al 2018) in order to define model parameters and priors. We used an uncorrelated relaxed clock (Drummond et al 2006), a Yule speciation model (Yule 1925), a tree density model by Gernhard (2008), and a discrete gamma distributed rate heterogeneity model (Yang 1994). In addition, we used an asymmetric distribution model (Edwards et al 2011) for the coded behaviors.

We modified the transition and transversion priors to the rates obtained in ModelFinder (Kalyaanamoorthy et al 2018), and the ND4 mutation rate calculated by Castoe et al. (2007) and Jowers (2019) ($1.4 \times 10{-}8$ substitutions/site/year). For each behavior, we calculated its observed frequency by dividing the number of terminal taxa showing evidence of that behavior by the total number of terminal taxa included in the alignment (n = 50). This calculation was performed separately for each behavior, and the resulting value was used as the prior frequency in the ancestral-state reconstruction analyses. These adjustments were important to reduce the computational effort of *Monte Carlo Markov Chain* (MCMC) searches. We used Adobe Photoshop to color the phylogenetic tree, add information about the coral snakes and figures corresponding to the behaviors for the ancestral reconstruction.

Finally, for phylogenetic signal estimates, we used the Fritz and Purvis (2010) D statistic for all the behaviors. We used the *ape* (Paradis and Schliep 2019), *caper* (Orme et al 2023) and *readxl* (Wickham and Bryan 2025) packages implemented in RStudio (R Core Team 2023). We calculated the estimated value of D, the probability of E(D) resulting from: no (random) phylogenetic structure and a Brownian motion evolution model. We also calculated the M statistic for the most common behaviors as a trait group (Yao and Yuan 2025). For the M statistic, we adapted the script of Yao and Yuan (2025), using the same packages: tidyverse, *readxl* (Wickham and Bryan 2025), *foreach* (Microsoft and Weston 2022), *ape* (Paradis and Schliep 2019), *phylobase* (Hackathon et al 2024), *cluster* (Maechler et al 2025) and *phylosignalDB* (Yao and Yuan 2025). All the scripts can be found in the supplementary material.

RESULTS

Behavior

We compiled a total of 280 defensive behavior records, 57 of which were provided by researchers or photographers and were not previously described in the literature (see Figure 2), suggesting that these may represent new behavior descriptions. All behaviors are represented

in Figure 2, with the source of each behavior specified in the supplementary material. Among 85 species in the genus *Micrurus*, only ten remain without information on defensive behavior: *Micrurus elegan*s, *M. frontifasciatus*, *M. margaritiferus*, *M. michoacanensis, M. oligoanellatus*, *M. pacaraimae*, *M. petersi*, *M. serranus*, *M. spurrelli* and *M. stuarti*.

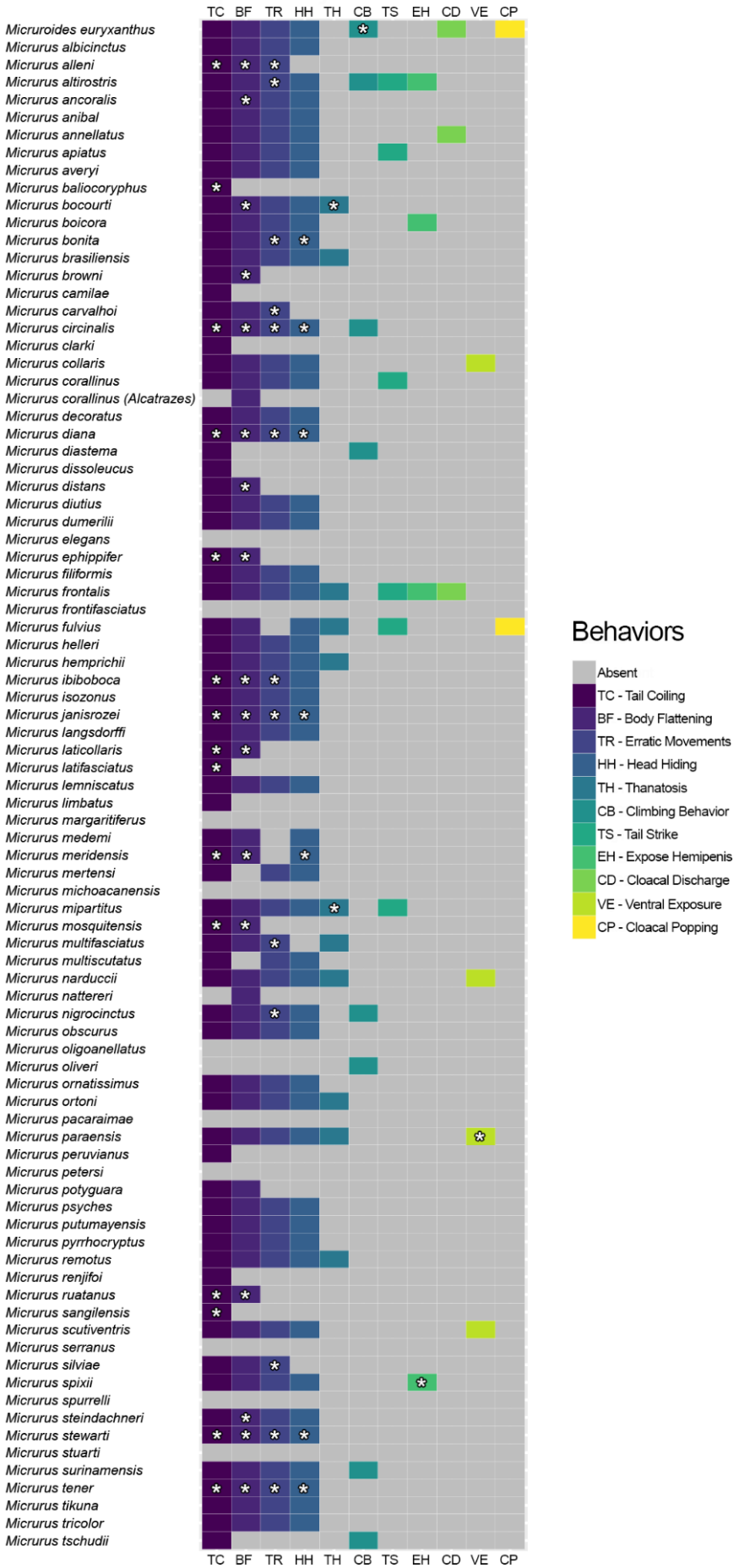
Species by behaviour
TC BF TR HH TH CB TS EH CD VE CP
Micruroides euryxanthus
Micrurus albicinctus
Micrurus alleni
Micrurus altirostris
Micrurus ancoralis
Micrurus anibal
Micrurus annellatus
Micrurus apiatus
Micrurus averyi
Micrurus baliocoryphus
Micrurus bocourti
Micrurus boicora
Micrurus bonita
Micrurus brasiliensis
Micrurus browni
Micrurus camilae
Micrurus carvalhoi
Micrurus circinalis
Micrurus clarki
Micrurus collaris
Micrurus corallinus
Micrurus corallinus (Alcatrazes)
Micrurus decoratus
Micrurus diana
Micrurus diastema
Micrurus dissoleucus
Micrurus distans
Micrurus diutius
Micrurus dumerilii
Micrurus elegans
Micrurus ephippifer
Micrurus filiformis
Micrurus frontalis
Micrurus frontifasciatus
Micrurus fulvius
Micrurus helleri
Micrurus hemprichii
Micrurus ibiboboca
Micrurus isozonus
Micrurus janisrozei
Micrurus langsdorffi
Micrurus laticollaris
Micrurus latifasciatus
Micrurus lemniscatus
Micrurus limbatus
Micrurus margaritiferus
Micrurus medemi
Micrurus meridensis
Micrurus mertensi
Micrurus michoacanensis
Micrurus mipartitus
Micrurus mosquitensis
Micrurus multifasciatus
Micrurus multiscutatus
Micrurus narduccii
Micrurus nattereri
Micrurus nigrocinctus
Micrurus obscurus
Micrurus oligoanellatus
Micrurus oliveri
Micrurus ornatissimus
Micrurus ortoni
Micrurus pacaraimae
Micrurus paraensis
Micrurus peruvianus
Micrurus petersi
Micrurus potyguara
Micrurus psyches
Micrurus putumayensis
Micrurus pyrrhocryptus
Micrurus remotus
Micrurus renjifoi
Micrurus ruatanus
Micrurus sangilensis
Micrurus scutiventris
Micrurus serranus
Micrurus silviae
Micrurus spixii
Micrurus spurrelli
Micrurus steindachneri
Micrurus stewarti
Micrurus stuarti
Micrurus surinamensis
Micrurus tener
Micrurus tikuna
Micrurus tricolor
Micrurus tschudii
TC BF TR HH TH CB TS EH CD VE CP
Behaviors
Absent
TC - Tail Coiling
BF - Body Flattening
TR - Erratic Movements
HH - Head Hiding
TH - Thanatosis
CB - Climbing Behavior
TS - Tail Strike
EH - Expose Hemipenis
CD - Cloacal Discharge
VE - Ventral Exposure
CP - Cloacal Popping

Figure 2. Distribution of all sampled defensive behaviors for coral snakes. *Micrurus corallinus* (Alcatrazes) refers to the population from Alcatraz Island. White asterisks represent the new behavior records described in the present study for the particular species..

Phylogeny

We recovered, with a high degree of support (posterior > 0.95), *Micruroides euryxanthus* (Kennicott 1860) as the sister group of all *Micrurus* species. We also recovered a second clade with high support, containing the two known monophyletic groups of coral snakes, the triads (snakes that have three black rings between the red ones) and the monads (one black ring between other rings). Our results recovered a topology very similar to those obtained in other recent phylogenies (Jowers et al 2019, 2023; Nascimento et al., 2024); hence, we are confident that our phylogenetic hypothesis provides the necessary evidence for robust evolutionary inferences.

Overall, while our tree agrees with the general structure of recent phylogenies, some differences in monads and triads are evident in relation to the *M. nigrocinctus* lineages/group, the *M. ibiboboca* species complex, *M. mipartitus* and *M. decoratus* (see Jowers et al 2019, 2023; Nascimento et al 2024). The following taxa represent the different *Micrurus nigrocinctus* lineages shown in Jowers et al (2023): *M. nigrocinctus* MG974666 (lineage 3 - L3), *M. nigrocinctus* OP481993 (lineage 1 from Panama - L1), and *M. ruatanus* (lineage 2 - L2).

The major clades broadly corresponded to differences in banding pattern, tail length, and aquatic habits (Figure 3). Most triadal species were short-tailed, although *M. narduccii* and *M. mipartitus* differed from the typical triadal pattern (Roze 1967; Campbell and Lamar 2004). A separate group comprised short-tailed aquatic and semi-aquatic species (Sazima and Abe 1991; Martins and Oliveira 1998; Campbell and Lamar 2004; Barbo et al 2011; Starace 2013; Natera et al 2015). Among the long-tailed monadal *Micrurus* clade, only *M. elegans* differed from the others, exhibiting a triadal pattern (Lomonte et al 2021).

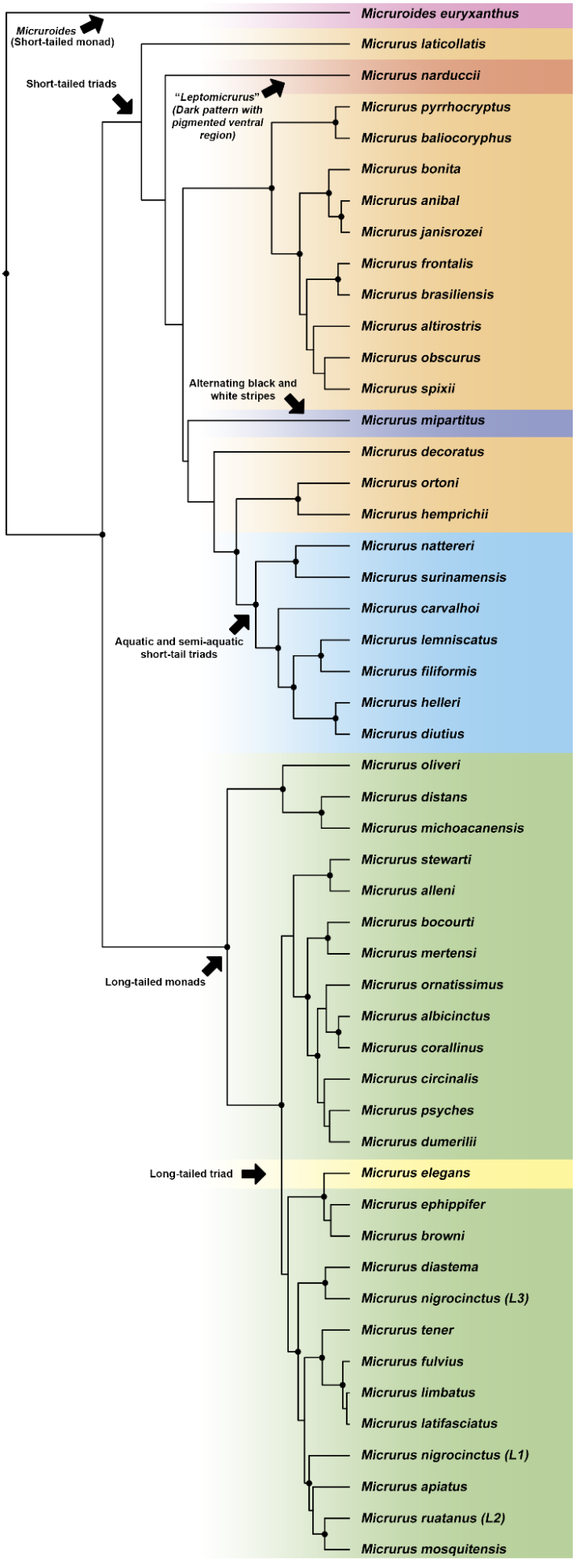
Micruroides euryxanthus
Micrurus laticollatis
Micrurus narduccii
Micrurus pyrrhocryptus
Micrurus baliocoryphus
Micrurus bonita
Micrurus anibal
Micrurus janisrozei
Micrurus frontalis
Micrurus brasiliensis
Micrurus altirostris
Micrurus obscurus
Micrurus spixii
Micrurus mipartitus
Micrurus decoratus
Micrurus ortoni
Micrurus hemprichii
Micrurus nattereri
Micrurus surinamensis
Micrurus carvalhoi
Micrurus lemniscatus
Micrurus filiformis
Micrurus helleri
Micrurus diutius
Micrurus oliveri
Micrurus distans
Micrurus michoacanensis
Micrurus stewarti
Micrurus alleni
Micrurus bocourti
Micrurus mertensi
Micrurus ornatissimus
Micrurus albicinctus
Micrurus corallinus
Micrurus circinalis
Micrurus psyches
Micrurus dumerilii
Micrurus elegans
Micrurus ephippifer
Micrurus browni
Micrurus diastema
Micrurus nigrocinctus (L3)
Micrurus tener
Micrurus fulvius
Micrurus limbatus
Micrurus latifasciatus
Micrurus nigrocinctus (L1)
Micrurus apiatus
Micrurus ruatanus (L2)
Micrurus mosquitensis
Micruroides
(Short-tailed monad)
Short-tailed triads
"Leptomicrurus"
(Dark pattern with
pigmented ventral
region)
Alternating black and
white stripes
Aquatic and semi-aquatic
short-tail triads
Long-tailed monads
Long-tailed triad
4.0E-4

Figure 3. Phylogenetic relationships of New World coral snakes recovered by Bayesian inference in BEAST. Black circles indicate posterior probabilities ≥ 0.95. Black arrows and background colors identify groups defined by banding pattern, relative tail length, and aquatic or semi-aquatic habits. Purple represents *Micruroides euryxanthus*, the short-tailed, monadally patterned representative of the sister genus of *Micrurus*. Orange represents predominantly short-tailed, triadally patterned *Micrurus*. Within this clade, red indicates *M. narduccii*, representing the former genus *Leptomicrurus* and characterized by a predominantly dark dorsum and brightly pigmented ventral markings; dark blue indicates *M. mipartitus*, which has alternating narrow pale and black rings rather than a typical triadal pattern; and light blue represents short-tailed aquatic and semi-aquatic species. Green represents predominantly long-tailed, monadally patterned *Micrurus*, whereas yellow indicates *M. elegans*, the triadally patterned exception within this group.

Defensive Behaviors and Ancestral Reconstruction

In the ancestral state reconstruction we recovered four widely distributed defensive behaviors, present since the common ancestor of *Micrurus* and *Micruroides*, namely: TC, BF, TR and HH. EH was reconstructed in the *M. frontalis*-*M. spixii* clade and showed significant phylogenetic signal under the D statistic (Table 1). Considering the available evidence, the other behaviors seem to have arisen independently in groups and/or species. To appropriately depict the evolution of these defensive behaviors they were divided into four trees (Figures 4, 5 and 6). Results for the phylogenetic signal, D statistic, are shown in Table .

We recovered TC as a practically universal behavior for New World coral snakes, being inherited by all living groups since the common ancestor with *Micruroides euryxanthus*, and absent or not sampled in only four species in our phylogeny (Figure 5a). In accordance, there was no support for phylogenetic signal in TC. The CD was recovered in two species of coral snakes, *Micruroides euryxanthus* and *Micrurus frontalis* (Figure 5a). This behavior had a significant phylogenetic signal according to the D statistic (Table 1). In addition, we recovered a significant phylogenetic signal for EH (Table 1) in the group formed by *M. frontalis*, *M. brasiliensis*, *M. altirostris*, *M. spixii* and *M. obscurus* (Figure 5a). Within this group, only *M. brasiliensis* and *M. obscurus* did not display or were not recorded reversing their hemipenis.

We also recovered BF as an almost universal defense behavior for coral snakes (Figure 5b), with no phylogenetic signal support (Table 1). This behavior is shared and it was likely inherited by all living groups since the common ancestor between *Micruroides* and *Micrurus* , being absent or not sampled in eight species in our phylogeny (Figure 5b). CB was recovered in several parts of the phylogenetic tree; hence, this behavior seems to have independently arisen seven times, once in *Micruroides euryxanthus*, in two triad species, and three monad species (Figure 5b). There is no support for phylogenetic signal in CB (Table 1). CP probably

arose independently in *Micruroides euryxanthus* and *Micrurus fulvius* (Figure 5b). There is statistical support for a phylogenetic signal in CP (Table 1).

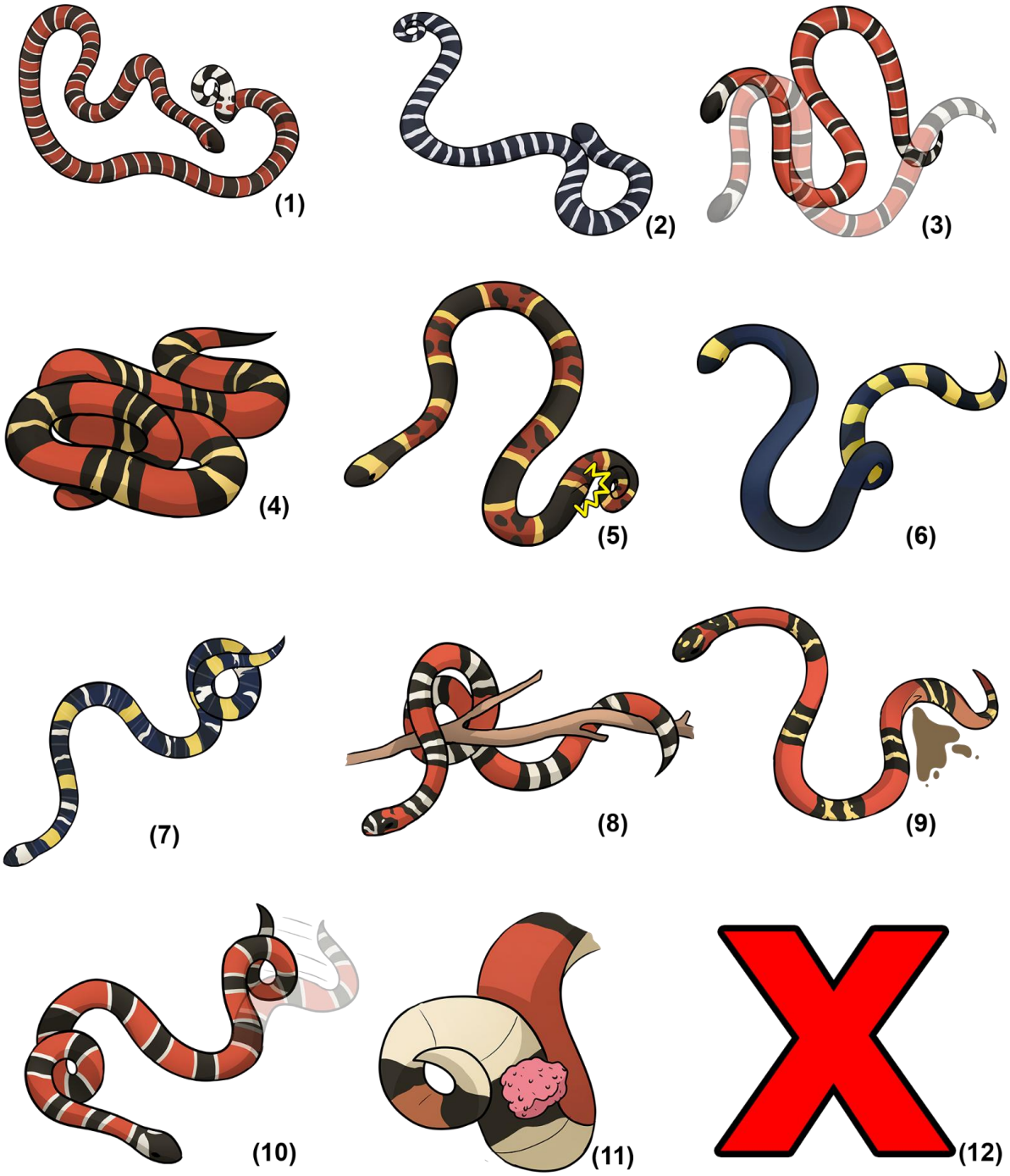

Figure 4. Legend of the illustrations as depicted in Figures 5 and 6 for the ancestral defensive reconstructions of New World coral snakes. Behaviors: TC - raising and coiling the tail (1); BF - dorsoventral flattening of the body (2); TR - erratic movements (3); HH - hiding the head (4); CP - producing cloacal popping

sounds (5); VE - exposing the venter (6); TH - thanatosis (7); CB - climbing (8); CD - cloacal discharge (9); TS - striking with the tail (10); EH - exposing the hemipenis (11); Behaviors accompanied by a red X indicate absence of the behavior in the group/species (12). Illustrations by Ilusea Studio: *Micrurus ornatissimus* (1); *M. annellatus* (2); *M. corallinus* (3); *M. surinamensis* (4); *M. fulvius* (5); *M. narduccii* (6); *M. ortoni* (7); *M. altirostris* (8); *M. frontalis* (9); *M. corallinus* (10); *M. spixii* (11).

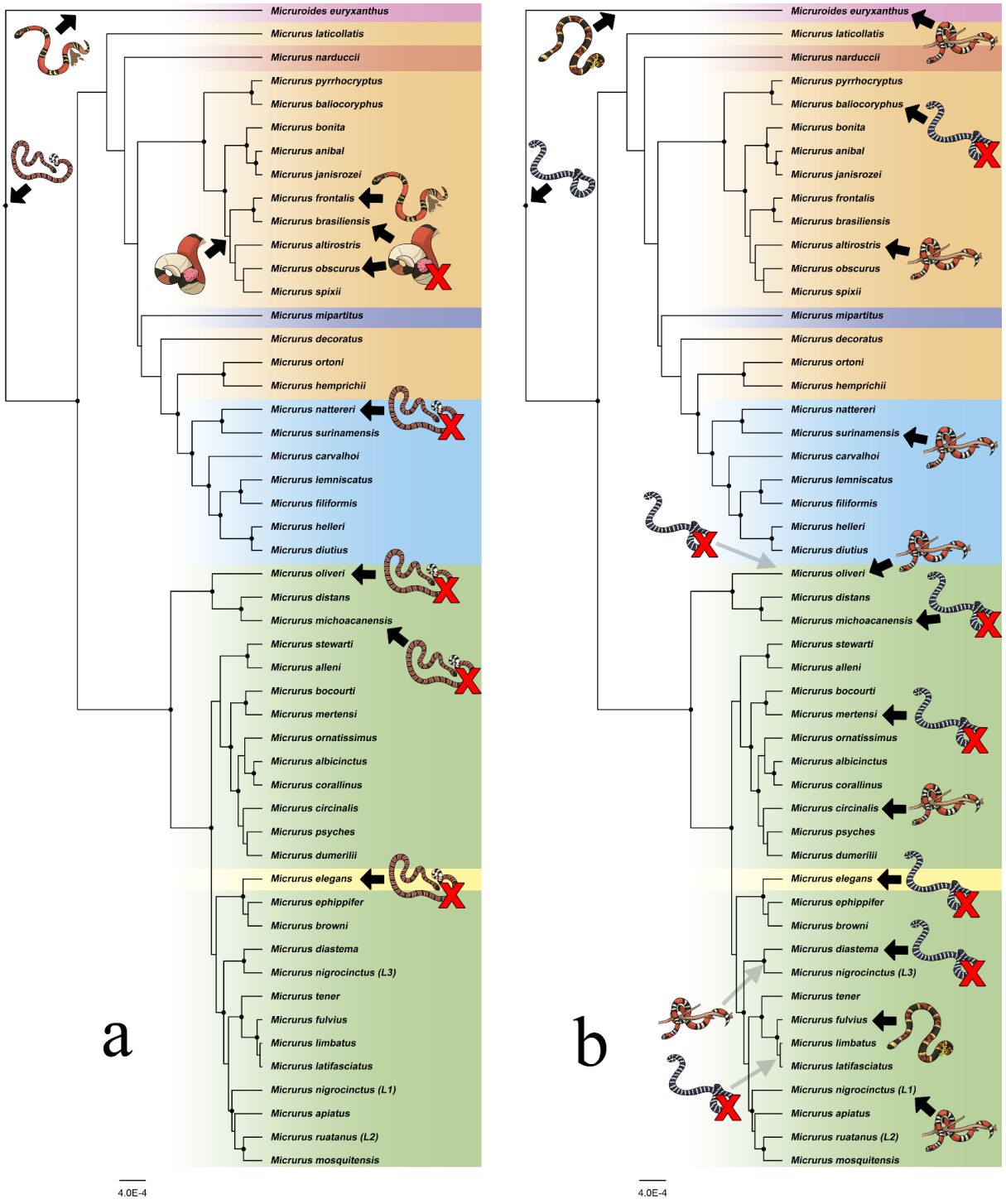

Figure 5. Ancestral reconstruction of defensive behaviors of New World coral snakes. Tree "a" represents three behaviors: (1) TC: raising and curling the tail, (2) EH: exposing the hemipenis and (3) CD: cloacal discharge. Tree "b" also represents three behaviors: (1) BF: dorsoventral flattening, (2) CB: climbing behavior and (3) CP: cloacal popping sounds. Black circles represent a posterior value above 0.95. Tree color refers to the groups established by the black arrows in Figure 3.

In general, TR appears to be a universal behavior in coral snakes (Figure 6a), inherited from their common ancestor between *Micrurus* and *Micruroides*, and with significantly supported phylogenetic signal (Table 1). This behavior is absent in a large group of monads (see the Discussion on this topic). VE was reconstructed as arising independently in *Micrurus narducci* and is characteristic to the group known as "*Leptomicrurus*" (Silva Júnior et al 2021a) of which our only representative in the phylogeny is *Micrurus narduccii* (see Figure 6a). However, VE is also present in another species, *Micrurus paraensis*, indicating that the behavior also arose in this monadal species. VE also has support for phylogenetic signal (Table 1). TS was recovered in only six coral snakes, it is present in three triadal and three monadal species and apparently arose independently in all species (Figure 6a). TS showed no significant phylogenetic signal and did not differ from a random distribution across the phylogeny (Table 1). However, its distribution differed significantly from the Brownian threshold expectation (Table 1).

HH is widely distributed and has support for phylogenetic signal (Table 1). It is present in almost all triads, except for four species, and present in most monads (Figure 6b). Finally, TH seems to have appeared independently six times, in the *Micrurus frontalis* + *M. brasiliensis* group, *M. hemprichii* + *M. ortoni*, *M. bocourti*, *M. fulvius*, *M. mipartitus* and *M. narducii*, also having statistical support for phylogenetic signal (Table 1, Figure 6b). Analyzing TC, BF, HH and TR as a trait group also presented statistical support for phylogenetic signal ($M = 0.766$, $P < 0.001$). Therefore, both hypotheses were supported: TC, BF, TR, and HH formed an ancestral, broadly conserved repertoire with significant multivariate phylogenetic structure, whereas less frequent behaviours showed more restricted and predominantly homoplastic distributions.

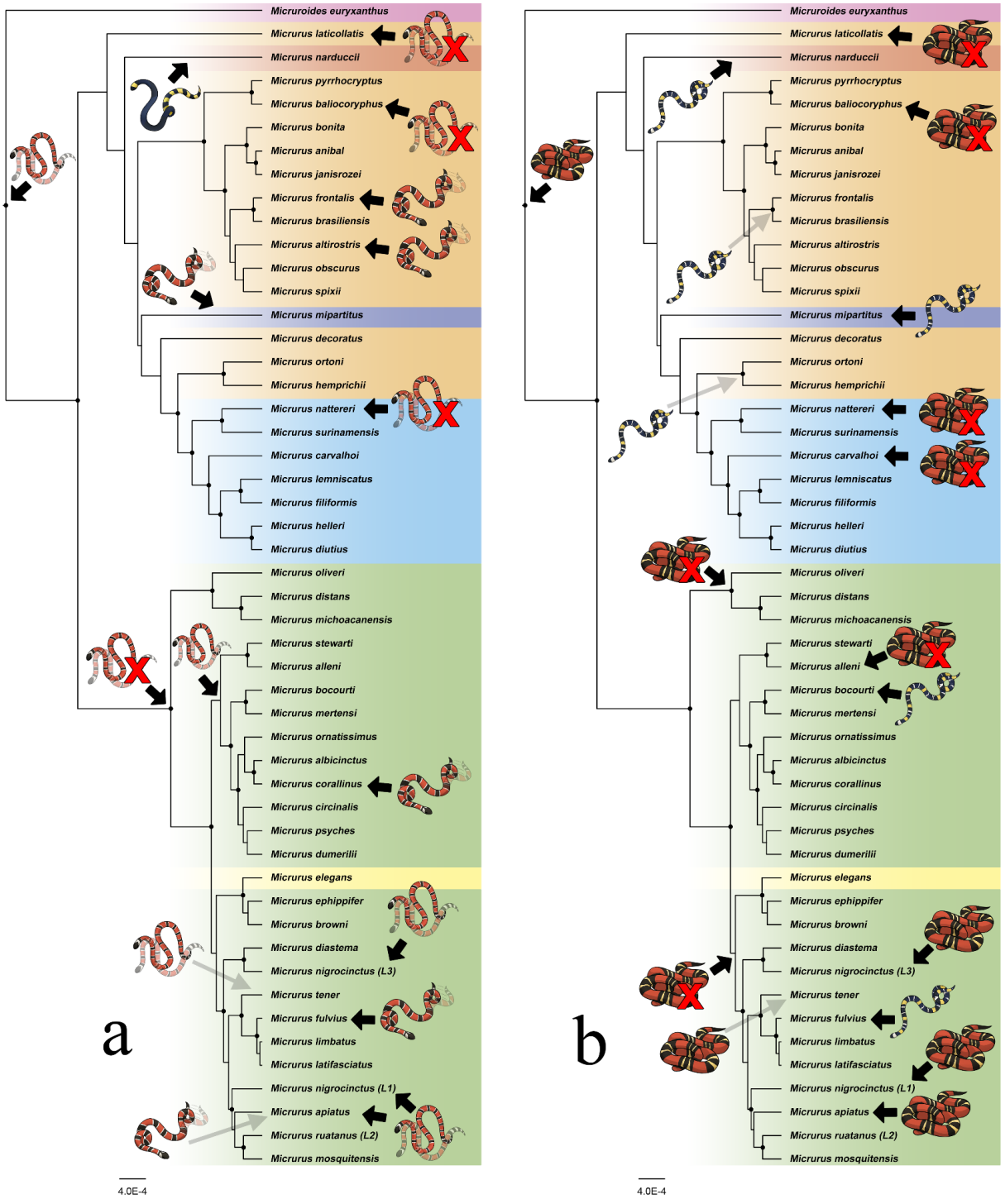

Figure 6. Bayesian analysis and ancestral reconstruction done in BEAST of the phylogenetic relationship and behavior evolution of New World coral snakes. Tree "a" represents three behaviors: (1) TR: erratic movements, (2) VE: ventral exposure and (3) TS: striking with the tail. Tree "b" represents two behaviors: (1) HH: hiding the head and (2) TH: thanatosis. Black circles represent a posterior value above 0.95. Tree color refers to the groups established by the black arrows in Figure 3.

Table 1. Results of phylogenetic structure estimation for each behavior, for the 50 taxa on the phylogeny. Columns represent behaviors, number of taxa where the behavior is present, number of taxa where the behavior is absent or not recorded, estimated D value, probability of E(D) resulting from no phylogenetic structure (random) and probability of E(D) resulting from Brownian phylogenetic structure. We used the following abbreviations for each behavior: tail-raising and coiling (TC), dorsoventral body flattening (BF), erratic movements (TR), cloacal discharge (CD), hemipenis eversion (EH), climbing behavior (CB), thanatosis (TH), head-hiding (HH), tail-striking (TS), cloacal popping sounds (CP), and ventral display (VE).

Behavior	Present (n = 1)	Absent (n = 0)	D	P(random)	P(Brownian)
TC	46	4	0.501	0.131	0.257
BF	42	8	0.554	0.075	0.121
TR	35	15	-0.034	<0.001	0.526
CD	2	48	-0.520	0.035	0.700
EH	3	47	-0.150	0.042	0.583
CB	8	42	0.592	0.092	0.110
TH	8	42	0.257	0.015	0.304
HH	34	16	0.318	0.002	0.226
TS	6	44	1.056	0.508	0.019
CP	2	48	-0.575	0.037	0.717
VE	1	49	-1.859	0.039	0.762

DISCUSSION

Our results show that defensive behavior is neither uniformly labile nor strictly constrained by ancestry. Instead, antipredator repertoires can evolve through the coexistence of deep phylogenetic conservatism in an ancestral core of important defensive behaviors, and repeated origins of more restricted responses. In New World coral snakes, TC, BF, TR, and HH were reconstructed as ancestral and jointly showed phylogenetic structure, whereas most less frequent behaviors showed lineage-specific or repeated origins. This pattern indicates that complex behavioral repertoires can diversify through evolutionary change in particular components while an ancestral group remains conserved. It also demonstrates that multivariate

analyses can reveal evolutionary structure obscured when widespread behaviours are examined separately.

Phylogenetic hypothesis

The general structure of our tree, which includes the genus *Micruroides* as a sister group to the *Micrurus* clades (triads and monads) is well supported and agrees with the results of other recent analyses (Jowers et al 2019, 2023; Nascimento et al 2024). Notably, many of the poorly supported groups/taxa (e.g. *M. laticollaris* and *M. narduccii*) have also been recovered in other phylogenies with low support (Jowers et al 2019, 2023; Nascimento et al 2024). Jowers et al. (2019) used a *single-locus* analysis and is subject to the same limitations as our work, although the alignment used for the ND4 mitochondrial gene is a larger fragment than the one used in this work. Even so, Jowers et al. (2023) used two mitochondrial genes, ND4 and CytB (cytochrome b), recovering *M. laticollaris* again at the same position, also with a low support value. Nascimento et al (2024) used four mitochondrial and one nuclear gene, and their results seem to have the same limitations we observed. These problematic nodes might only be strongly resolved using genomic-scale data..

In any case, Nascimento et al. (2024) recovered the species belonging to the *M. ibiboboca* complex as paraphyletic, whereas we recovered a monophyletic group. These differences can be attributed to the characteristics of the various molecular markers used in the different studies, nuclear and mitochondrial in the case of Nascimento et al. (2024) and the ND4 mitochondrial gene in our work. Disagreements between mitochondrial and genomic phylogenetic signals may be associated with factors of mitochondrial introgression between species and differences in the patterns of evolution between the mitochondrial and nuclear genomes, whether neutral or selective (Toews and Brelsford 2012). However, it is worth noting that large amounts of incomplete taxa can cause inaccuracies in phylogenetic analyses in certain scenarios (Wiens, 2003, 2006; Wiens and Moen, 2008; Wiens and Morrill, 2011; Streicher et al., 2016), in particular considering the ratio of incomplete taxa to the low number of characters (over 50% incomplete taxa in the aligment) in Nascimento et al. (2024). Although our work is limited to a single mitochondrial gene, and we acknowledge that our results reflect the history of coral snakes strictly as the history of ND4, we highlight that our results do not suffer from possible inaccuracies generated by incomplete taxa (Wiens, 2003, 2006; Wiens and Moen, 2008; Wiens and Morrill, 2011; Streicher et al., 2016), and that single mitochondrial locus phylogenies have also shown strong support when tested against genome scale data (Islam et al. 2024).

Ontogenetic variation

One obtained record (Supplementary Records: Alejandro Arteaga), shows *Micrurus steindachneri* from Tungurahua province, Ecuador, advancing toward the observer in a manner similar to *M. diastema*, but with much faster and more erratic movements. It is possible that some behaviors and/or defensive postures are imperfectly executed by juvenile coral snakes, although there has been little discussion on this aspect in these snakes. The aforementioned videos depict a similar posture used to advance toward an observer, which appears to be "better executed" by the adult *Micrurus steindachneri* compared to the juvenile *M. diastema*, which seems "inexperienced" or "uncoordinated" when performing the same posture to advance. Additionally, some records, such as Plate 219 (*Micrurus ancoralis jani*) in Campbell and Lamar (2004) and Supplementary Records (Dwain Holmes: *Micrurus ornatissimus*) in the present work, show juvenile individuals raising the tip of the tail but not coiling it, as observed in several other records of adult individuals.

Many birds show innate avoidance of the conspicuously banded coral snake pattern; there are records of birds distancing themselves and even giving warning calls in response to coral snake models (Smith 1975, 1976, 1977). Roze (1996) mentioned how these birds are capable of at least overcoming smaller coral snakes, perhaps this is further evidence of how the inexperience in executing defensive behavior by juvenile coral snakes can increase predation. However, future observational studies are needed to better elucidate behavioral differences based on the age of coral snakes.

Sampling biases

Although only ten species lack any recorded defensive behavior, there remains a significant sampling gap for most species, primarily because we may have assumed that a specific behavior is absent due to lack of documentation. One reason for this is the way data is collected in field situations. For example, Gonzalez and de Oliveira (2020) and Flórez et al. (2022) describe behaviors for *Micrurus hemprichii ortonii*, *Micrurus narduccii*, *Micrurus dumerilii dumerilii* and *Micrurus camilae* during encounters with these species. However, more intensive sampling has revealed less common behaviors: for example, Roze (1996) demonstrated that *M. fulvius* can produce cloacal popping sounds after experiencing intense stress and also described *M. brasiliensis* displaying thanatosis after being restrained multiple times.

This implies that to fully understand the complete defensive behavior repertoire, not only in coral snakes but snakes in general, the animal must be placed in a stressful situation simulating predation (e.g., touching, restraint, movements, shaking). Angarita-Sierra (2015) presented several defensive behaviors for *Ninia atrata* (Colubridae), showing that the more "predatory" stimuli the snake received, the more defensive behaviors it displayed, highlighting the usefulness of intensive sampling for describing a species range of defensive behaviors. Another example of this is the observation reported by Jackson (1979), where a specimen of *Micrurus corallinus* exhibited both defensive behaviors: tail-raising and coiling, as well as tail-striking only after being captured and shaken by a *Galictis* sp. (Mammalia, Carnivora) during predation. In any case, we should stress that intensive sampling must not be conducted without clear scientific aims and must be included in research projects with clear observational and handling protocols in line with animal welfare legislation and research permits.

Given the rarity of coral snakes in the wild and the fact that escape is the most common defensive response among these snakes, recording certain behaviors can be challenging, particularly erratic movements and tail-striking, which can only be documented through direct observation or video footage, not through photographs alone (Roze 1996; Martins and Oliveira 1998; Campbell and Lamar 2004; Marques and Sazima 2021).

Predator detection

It remains unclear how coral snakes detect and monitor the presence of potential predators. These snakes generally have small eyes, characteristic of animals with fossorial, crepuscular and nocturnal habits (Marques and Sazima 2021; Silva Júnior et al 2021b). They lack heat-sensoring organs, such as those found in some snakes of the family Boidae and the subfamily Crotalinae within the family Viperidae (Noble e Schmids 1937). Additionally, during their defensive displays, coral snakes do not appear to exhibit constant tongue-flicking, as seen in other species (e.g. *Crotalus durissus*), which serves to gather chemical information (Greene 1997). Snakes respond defensively to vibrations, whether in the air or on the ground, and these stimuli play a crucial role in predator avoidance (Wever 1978; Burger 1998; Young et al 2000). Vibrations are detected either through an inner ear apparatus, the mandible-quadrate-columella system, or via a somatic system of sensory cells distributed throughout the body, and possibly even through the lungs (Hartline 1971a,b; Wever, 1978).

The primary defensive posture of coral snakes involves keeping their head at ground level, along with much of the body (see Supplementary Records). This posture, in which the

body regions most sensitive to vibration remain in contact with ground, suggest that vibration may be the most important stimulus for detecting and defending against predators. Nonetheless, this hypothesis requires further testing.

Evolution of the defensive repertoire

In the present study, the most frequent defensive behaviors observed among New World coral snakes against humans, other than fleeing, are raising and curling the tail (TC), flattening the body dorsoventrally (BF), performing erratic movements (TR) and hiding the head (HH). Although some of these behaviors appear to be lost in large groups and reappear in smaller species or groups as if they had arisen independently, we interpret this information with some skepticism. Most of the evidence comes from literature or photos, and some of the contributors do not recall or have not observed additional defensive behaviors that may be underreported. This, combined with the rarity of the genus in nature (Roze 1996) and the fact that the most common defense of these snakes is flight (Martins and Oliveira 1998; Campbell and Lamar 2004; Marques and Sazima 2021), makes recording some behaviors problematic, especially erratic movements and striking with the tail, which can only be witnessed or filmed and cannot be observed only through photographs.

The ancestral-state reconstructions indicate that TC, BF, TR, and HH represent ancestral behaviors for *Micrurus*, inherited from the common ancestor shared with *Micruroides*. Because these behaviors occur in both genera, they can also be interpreted as symplesiomorphies within the sampled New World coral snake clade. Their reconstruction at this node does not necessarily indicate that they originated in the common ancestor of *Micruroides* and *Micrurus*, because they may have been inherited from an elapid ancestor. All these behaviors have not rejected the Brownian motion model, suggesting the possibility of gradual evolution (Felsenstein 1985). However, the most present behaviors, TC and BF, have no significant support for phylogenetic signal. Both TC and BF are more present in the New World coral snakes than TR and HH, both of which had support for phylogenetic signals, and both also rejected random distribution. This might be a consequence of the analysis, once these behaviors appear in almost all species in the tree, the presence of these behaviors in many terminal taxa who are distant could mask these traits as random distributed and, this deep ancestry with extreme trait prevalence can appear to lack structure under the D statistic (Fritz and Purvis 2010). When the four most prevalent behaviors were analyzed jointly (TC+BF+HH+TR), they exhibited a significant multivariate phylogenetic signal ($M = 0.766$, $P < 0.001$), indicating that closely related species tend to resemble one another in their overall behavioral profiles.

Multivariate analyses may reveal phylogenetic structure that is not apparent when traits are examined separately (Yao and Yuan 2025). It would not be surprising that these traits evolved together, since they are frequently used together, in a holistic defense of coral snake, as evidenced by the data we compiled in this work. In addition, the detection and interpretation of phylogenetic signal is dependent on the phylogenetic scale of the analysis, including the phylogenetic extent and grain represented by the sampled tree (Graham et al 2018). The widespread retention of these ancestral states across *Micrurus* suggests that the core defensive repertoire has remained broadly conserved throughout the diversification of the genus.

Body flattening (BF) is a behavior that maximizes the dorsal surface visible to predators, making the snake appear larger and potentially intimidating the predator (Greene 1988; Angarita-Sierra 2015). Greene (1988) described how many reptiles exhibit "crouching" behavior, where the animal flattens as much of its body as possible against the substrate. Since vibrations play an important role in snake's defense against predators, and the effectiveness of the vibration reception can vary based on substrate or soil, dorsoventral flattening "crouching" might serve to enhance the snake's ability to detect vibrations through the ground, this could occur via its somatic system and/or through the lungs, as most of its body remains in contact with the substrate, allowing the snake to better sense the presence of nearby predators (Hartline 1971a,b; Burger 1998; Young et al 2000).

Erratic movements (TR), like the previously discussed behavior, is nearly universal within coral snakes. This behavior appears to have been lost in a large group of monads and reemerged in a few groups and species (Figure 6a). However, this is probably a consequence of the sampling and the groups present there. For example, one of the groups present there is the *Micrurus distans* species complex (*M. distans*, *M. michoacanensis* and *M. oliveri*) that was proposed by Reyes-Velasco et al. (2020). These species occur in nearby regions, and distribution data are still limited, which makes the identification of records difficult. In addition, the few defensive records described for *M. distans* were fractionated among these species, since the other species in its complex used to be subspecies of *M. distans* (see Reyes-Velasco et al 2020). Combined with the fact that most records are photographs, sampling this behavior is difficult, and it is possible that it is widespread as other nearly universal behaviors (e.g., TC). This behavior consists of a series of abrupt movements with brief or no pauses between them. Although these movements may seem random, the snake positions itself optimally for striking during these actions (Roze 1996). TR serves as a strategy to generate confusion for predators or observers, combined with the snake's coloration, these rapid movements can make it difficult

to spot on certain substrates, even when visible, it becomes challenging to distinguish between the snake's head and tail (see Supplementary Records: Germano Woehl Junior and Pedro Henrique) (Gehlbach 1970; Roze 1982). Considering the holistic nature of coral snake defense, this strategy, along with tail-raising and coiling not only frightens and intimidates potential predators but also positions the snake optimally for an attack (Roze 1996). It further confuses predators, making it harder for them to locate the snake's head, as many predators tend to target the head when attacking snakes (Jackson 1979; Egler et al 1996; Almeida-Santos et al 2000; Gómez-Martínez et al 2008; Matute et al 2024). Moreover, if the tail is attacked due to this confusion, the snake gains an opportunity to use chemical defenses more effectively (see discussion on cloacal discharge) (Jackson 1979; Egler et al 1996; Roze 1996; Oliveira and Santori, 1999; Almeida-Santos et al 2000; Gómez-Martínez et al 2008; Matute et al 2024).

Head hiding (HH) is also one of the near-universal behaviors. Similarly to erratic movements, it also presents phylogenetic signal, and the disappearance of this behavior in a large group of monads, and the independent emergence in some species is likely a consequence of sampling. Since many snake predators tend to target or neutralize the head, hiding the head serves as a natural defense to protect a vital region of the body (Jackson 1979; Egler et al 1996; Roze 1996; Oliveira and Santori 1999; Almeida-Santos et al 2000; Gómez-Martínez et al 2008). The laughing falcon (*Herpetotheres canchinnans*) prey on coral snakes, and it is one of the most common coral snake predators (Roze 1996; Skutch 1960). Many birds, including the laughing falcon, loggerhead shrikes (*Lanius ludovicianus*) and red-tailed hawks (*Buteo jamaicensis*), employ a decapitation or neutralizing the head strategy and heavy pecking, also directed towards the head (Brugger 1989; Howell 1957; Roze 1996; Skutch 1960; Stoddard 1978). In fact, birds, which appear to be the most frequent predators of coral snakes, tend to neutralize and remove the head of the coral snake with records of chickens that died to envenomation due to an internal bite of a swallowed coral snake (Howell 1957; Roze 1996; Stoddard 1978). Red-tailed hawks have also been reported to die due to coral snake envenomation (Brugger 1989). This behavior is commonly observed during the defensive displays of coral snakes, and in Supplementary Records: Pedro Henrique and Leandro Alves, *Micrurus surinamensis* and *Micrurus bonita* can be seen positioning their heads beneath the body. This not only protects the snake's head but also likely enhances the confusion caused by tail-raising and coiling, as the head becomes harder to spot, diverting the observer's attention toward the raised tail (see discussion on tail-raising and tail-striking).

Cloacal discharge (CD) has only been recorded in two coral snake species, *Micruroides euryxanthus* and *Micrurus frontalis*. The D statistic shows high phylogenetic signal, rejects random distribution but not Brownian model. However, this behavior is present in distant coral snake species. Therefore this behavior might suffer from the same trait prevalence that affects the D statistic, in this case being extremely absent in the tree (Fritz and Purvis 2010). The distribution of this behavior resembles more a homoplasy, since the species that exhibit it are relatively distant. Although it seems unlikely that other snakes in this group are incapable or simply do not employ cloacal discharge as a defensive behavior, it is curious that some well-sampled (e.g., *Micrurus corallinus*) lack such records. Here, with some skepticism, we reconstruct cloacal discharge as a homoplasy, arising independently in two species of the phylogenetic tree. Although we do not present a sequence of *M. annellatus* in our work, since it belongs to the group of monads (Campbell and Lamar 2004; Silva Júnior et al 2021a) and presents the behavior of CD, this behavior would probably have to be explained by the third independent emergence of this behavior in the monads, which would configure three species of true corals that exhibit this behavior (three convergent apomorphies). Paired post-cloacal scent glands are ubiquitous among snakes and appear to be a derived feature of the group, and the secretions from those glands can be far more offensive in odor than the snake's fecal matter (Underwood 1957; Greene 1994). These secretions, when used offensively during predator encounters, enhance the defensive effectiveness of cloacal discharge, and the presence of these glands in snakes may also be adaptively associated with a generalized foraging style (Greene 1994).

CD seems to be a response to being grasped, as observed by Egler et al. (1996) *Atractus torquatus* (Serpentes, Colubridae) used cloacal discharge after being grasped by *Bothrops atrox* (Serpentes, Viperidae), causing *B. atrox* to release the snake and rub its mouth on the ground, seemingly in aversion to the cloacal contents of *A. torquatus*. We have also observed cloacal discharge in several snake species from other families, such as Boidae (*Boa constrictor* and *Eunectes murinus*), Colubridae (*Atractus reticulatus*, *Chironius bicarinatus*, *C. exoletus*, *C. flavolineatus*, *C. laevicollis*, *Leptophis marginatus*, *Palusophis bifossatus*), Dipsadidae (*Boiruna sertaneja*, *Dipsas mikanii*, *D. neuwied*, *Leptodeira annulata*, *L. pulchriceps*, *L. tarairiu*, *Oxyrhopus guibei*, *O. petolarius*, *O. trigeminus*, *Philodryas olfersii*, *Phimophis guerrini*, *Pseudoboa nigra*, *Phalotris matogrossensis, Xenodon matogrossensis*, *X. merremii*, *X. neuwiedii*) and Viperidae (*Bothrops jararaca*, *Bothrops jararacussu*, *Crotalus durissus*) (personal observations by Felipe Paiva and Ricardo A. Kawashita-Ribeiro). All these species

exhibited CD only after being grasped or restrained, by the head, mid-body, or tail by hand. Given that many predators to which snakes are exposed in the wild use their mouths to capture or subdue prey (see Jackson 1979; Egler et al 1996; Matute et al 2024), cloacal discharge may function as a defense against such capture or restraint.

Everting the hemipenis (EH) was reconstructed as a synapomorphy of the sampled group formed by the *Micrurus frontalis* and *M. spixii* species complex. EH has been previously documented in the literature for *M. frontalis* and *M. altirostris*, in the present study, we describe this behavior for *M. spixii* as well. The D statistical test indicated high phylogenetic signal and rejected the random distribution but not the Brownian model, indicating a significant phylogenetic signal for this behavior. The shared presence of this behavior in the group is evidence that reinforces their evolutive relation. It is possible that other members of these species complexes may also exhibit this behavior (e.g. *M. brasiliensis*, *M. obscurus* e *M. diana, M. silviae*) and further studies and more intensive sampling will be necessary to clarify the occurrence of hemipenis exposure in the remaining species. Naturally, this complementary behavioral data might shed light on the presence, absence and strength of a phylogenetic signal. This behavior is observed in the group formed by the *Micrurus frontalis* and *M. spixii* species complexes and this group shares a close evolutionary relationship, as indicated by recent phylogenetic analyses, although there is variation in different works (Jowers et al 2019, 2023; Nascimento et al 2024). The presence of this behavior in these species complexes may provide additional evidence supporting their phylogenetic proximity. Moreover, EH is observed in at least one other coral snake species, *M. boicora*. This species belongs to the *Micrurus hemprichii* species complex (Bernarde et al 2018), along with *M. hemprichii* and *M. ortoni*. In the present study, we analyzed nine records of defensive behavior of *M. hemprichii* and *M. ortoni* from the literature, seven provided by contributors, and additional records through social media searches. No hemipenis exposure was observed or reported to us for *M. hemprichii* and *M. ortoni.* Therefore, given the present evidence, EH is observed in only one species outside of the complexes mentioned above and this behavior arose at least twice independently in the genus *Micrurus*, once for the *Micrurus frontalis* + *M. spixii* complex group (synapomorphy) and a second time in *M. boicora* (apomorphy). This behavior was suggested to be an epiphenomenon of fright, or that a defensive organ, such as a stinger was brought into play, basically a form of deimatic behavior (Allen 1940; Greene 1988; Wuster and Cox, 1992; Serafim and Ribeiro Duarte 2008). Azevedo (1960) compared his observations of hemipenis display in *Micrurus* with local folklore that these snakes “bite with their tails”. Wuster and Cox (1992) also

suggested that this behavior varies with size and/or age, due to their juvenile individuals of *Oligodon cyclurus* (Serpentes: Colubridae) displaying their hemipenis much more readily than the adults, who were more reluctant to extrude their larger and more conspicuous hemipenis. Mizsei and Uveges (2012) also mentioned that another possible explanation for the variation with age of this behavior, is the fact that younger specimens are more vulnerable, therefore easy to frighten. They also mentioned that because their hemipenis is less developed, thus easier to extrude (Mizsei and Uveges 2012). Despite the different views on the behavior, in all these observations, the hemipenis display managed to redirect the observer's attention to the tail (Allen 1940; Azevedo, 1960; Wuster and Cox 1992; Serafim and Ribeiro Duarte 2008; Mizsei and Uveges 2012). Most of the hemipenis displays happen very fast, and sometimes repeatedly, with the longest display reported in *Micrurus* lasting two minutes (Allen 1940; Azevedo, 1960; Wuster and Cox 1992; Serafim and Ribeiro Duarte 2008; Mizsei and Uveges 2012). Wuster and Cox (1992) also mentioned how the hemipenis color contrast could act as an aposematic signal, they also brought up how the hemipenis is fragile, and essential for reproduction, being one of the snake's least expendable body parts. Perhaps, the function of hemipenis eversion is to draw even more attention to the tail and, since it is a fragile and essential region, this act of successive eversion and retraction could be a way of drawing even more attention to the tail, which was successful in drawing the authors' attention, but also not exposing it for too long and protecting the hemipenis. The difference in the usage of this behavior and age also could be explained by our hypothesis that young individuals of snakes tend to be executed imperfectly by juvenile snakes, however this requires further testing. Furthermore, despite being labeled as inconspicuous in juveniles (Wuster and Cox 1992), this behavior might be more noticeable to the snake predators, since their vision is usually closer to ground level and to most of them, coral snakes appear to be significantly larger than compared to humans.

Cloacal Popping (CP) sounds have been recorded in only two New World coral snake species; here we reconstruct this behavior as a homoplasy, arising independently in *Micruroides euryxanthus* and *Micrurus fulvius* (convergent apomorphies). This behavior might suffer from the same problem as CD, since the results of both these behaviors are extremely similar in the D statistic test. Naturally CP also occurs in only two distant coral snake species, and despite the support for phylogenetic signal ($D = -0.575$, $P[random] = 0.037$), this behavior also seems to suffer from the trait prevalence, being too absent (Fritz and Purvis 2010). Therefore, this behavior also seems to have arisen independently twice. This defense method appears to be more common in *Micruroides euryxanthus*, as Roze (1996) only attributed this behavior to

Micrurus fulvius, following extensive handling, a stressful situation for the snake. The use of sound-based defense is seen in many snakes, such as the hissing of *Boa constrictor* or the rattling of rattlesnakes (Bogert 1960; Martins and Oliveira 1998). The mechanism behind cloacal popping is not very well understood, one hypothesis suggests that the snake may have adaptations allowing for the extension of the tubular cloacal structure and the intake of air, or it may involve air being expelled from the intestinal tract (Bogert 1960; Young 1997; Young et al 1999). The snake then compresses the cloacal region or intestinal tract, forcing air out through the cloacal lips, generating vibrations that produce the sound (Bogert 1960; Young 1997). Similar defense mechanisms are observed in other snakes, and cloacal popping sounds may be produced either during or independently of cloacal discharge (Bogert 1960; Young 1997; Young et al 1999).

Climbing behavior (CB) was recorded in eight terminal taxa and was reconstructed as having seven independent origins. It showed no significant phylogenetic signal (D = 0.592, P[random] = 0.092). CB as a defense appears to have arisen independently in seven species and in the *Micrurus nigrocinctus* (lineage 3) + *M. diastema group*. It is likely that with future sampling this behavior will prove to be more present in the genus, since it is susceptible to the same sampling problems already mentioned. As noted earlier, coral snake escape behavior is commonly directed toward ground shelters or leaf litter (Martins e Oliveira, 1998; Campbell and Lamar 2004; Marques e Sazima, 2021). It remains unclear whether CB occurs randomly, due to the snake's confusion, or if it is genuinely used to avoid a specific type of threat or predator.

Ventral exposure (VE) was recovered only for *Micrurus narduccii* (autapomorphy). The D statistic test showed high phylogenetic clumping, rejecting the random model but not the Brownian one; this is expected since there is only one species that exhibits this behavior in the tree, which can also be affected by the trait prevalence (Fritz and Purvis 2010). This might be a synapomorphy, characteristic of the group formed by *M. narduccii*, *M. scutiventris* and *M. collaris*, formerly allocated to the genus "*Leptomicrurus*". However, this behavior is also present in another species of coral snake for which no sequence is available, *M. paraensis*, therefore arising two times independently. Species from the former genus "*Leptomicrurus*" lack the dorsal ring pattern found in most coral snakes but have strongly pigmented ventral markings, these coral snakes reveal the posterior third or a large portion of their body, exposing their brightly colored, aposematic ventral surface (Greene 1997; Martins and Oliveira 1998; Silva Júnior et al 2021a; William Lamar personal communication). This behavior is also present

in *M. paraensis*, a species with the monadal ringed pattern typical of many coral snakes, however, it also has a strong tendency to melanism (Cunha and Nascimento 1973; Hoge et al 1977), which may explain its use of the aposematic ventral display, revealing bright red parts of the venter.

Tail coiling TC is an almost universal behavior in the sampling carried out in this study. Furthermore, the defensive TS with the tail arose independently six times. The distribution of TS was consistent with phylogenetic randomness and differed significantly from the Brownian threshold expectation (Table 1). It is likely that this trait has independently arisen multiple times. This behavior is challenging to document, similarly to TR, it can only be recorded through video or direct observation, given that photographs, the primary means of documenting these snakes, are not informative for this behavior. It is unsurprising that TS is present in some of the most frequently sampled species, such as *Micrurus corallinus*, *M. frontalis*, *M. altirostris*, *M. fulvius* and *M. apiatus*. Jackson (1979) reported that *M. corallinus* displayed its raised and coiled tail, as well as tail strikes, only after being grasped and shaken by a *Galictis* sp.. Since many behavioral records are based on photographs or observations following minimal contact with the snakes, it is likely that there is insufficient stimulus to elicit such behaviors in these contexts. As shown in Jackson (1979), TS serves as a form of intimidation toward predators, as *Galictis* sp. retreated with each tail strike, jumping backward away from the coral snake, giving it the chance to escape.

Coral snake defense is a holistic process (Roze 1982; Test et al 1996), with TS working in tandem with TC (see Jackson 1979). Greene (1973) discussed how some snakes may mimic the defensive display of venomous snakes of the genus *Naja* (Elapidae), and Serafim and Ribeiro Duarte (2008) noted the similarity between the defensive tail-coiling and raising display in *Micrurus* and the hood of a *Naja*. Indeed, to a human observer viewing the snake from above, the distinction between the tail and the head may be apparent (Figure 1a), while concealment of the head may still create some ambiguity (Figure 1b). However, for an observer at ground level, tail-coiling and raising can indeed resemble a snake displaying an intimidating vertical posture with a “hood”, especially when combined with BF (see Figure 1c and d).

This combination of behaviors, along with tail strikes, simulates a snake strike, as evidenced by Jackson (1979), who described how the attention of *Galictis* sp. constantly shifted between the real head and the raised, coiled tail. The tail strikes, mimicking false strikes of a defensive snake, caused Galictis sp. to retreat, jumping backward and providing *Micrurus corallinus* an opportunity to escape (Jackson 1979). This intimidation or confusion can be

further intensified through head-hiding, so that, with the head concealed, the tail becomes the central focal point of attention. Further studies are needed to reveal how coral snakes respond to different types of predators (birds, mammals, other snakes), how predators interact with various defensive behavior combinations used by coral snakes, and how the use of multiple behaviors enhances the antipredator impact of each behavior individually.

TH has apparently arisen independently six times in coral snakes, and it is present in the *Micrurus frontalis* + *M. brasiliensis* group, *M. hemprichii* and *M. ortoni* group, *M. mipartitus*, *M. bocourti*, *M. fulvius* and *M. narduccii*. The D statistic test showed a tendency to clumping and rejected the random model but not the Brownian one. However, the distribution of this behavior is scattered across the phylogenetic tree, indicating that it arose independently. This behavior is also present in a species for which no ND4 sequence is available, *Micrurus remotus*. Gonzalez and de Oliveira (2020) reported the behavior in *Micrurus ortoni* after handling, Roze (1996) reported TH in *M. brasiliensis* only after the snake was restrained repeatedly. This behavior is also subject to the problem of sampling, since the most sampled defensive behaviors are those most used by snakes, and TH may require more stimuli to be used in most cases. Thanatosis, also referred to as "death feigning" or "tonic immobility", in the literature is a posture of immobility assumed by animals, caused by interactions or contact with a possible predator and is considered a defensive tactic where the individual appears to be dead (Miyatake et al 2004; Humphreys and Ruxton 2018; Skelhorn 2018). There is little information on the efficacy and heredity of TH and most studies focus on invertebrate groups (see Miyatake, et al., 2004; Humphreys and Ruxton, 2018; Skelhorn, 2018). It is possible that TH is a visual defense that aims to reduce a certain stimulus received by the predator (Gonçalves and Biro 2018; Leavell and Bernal 2019). TH can reduce not only visual stimuli, but also sound stimuli due to immobility. As an example: some snake-predatory mammals, including *Micrurus*, although they use chemical stimuli, through smell and auditory stimuli to locate snakes, clearly have the perception of visual stimuli, since they can dodge blows delivered by snakes and can effectively locate and avoid the snake's head (Jackson 1979; Oliveira and Santori 1999; Almeida-Santos et al 2000; Gómez-Martínez et al 2008; Gonçalves and Biro 2018; Leavell and Bernal 2019).

Conclusion

In view of what was presented above, the "missing data" of defensive behaviors and sequences is still a major limitation for ancestral reconstruction and phylogenetic signal estimation, therefore some of the results obtained here will probably change with the addition of more information on defensive behaviors and availability of molecular data. The present

work demonstrates how natural history is a valuable source of information and contributes to studies on biology, ecology and evolution, and how this information can serve as a basis for elucidating unresolved macroevolutionary questions (Greene 1988; Martins and Oliveira 1998).

In addition, this work reaffirms the importance of researchers' and citizen science contributions to understanding the natural history of coral snakes. Given the rarity of the genus *Micrurus* in the wild (Roze 1996), citizen records comprise a valuable source of data for information such as distribution, defensive behaviors, period of activity, predation, use of shelters or habitat, among others. Overall, our results indicate that the defensive repertoire of *Micrurus* combines ancestral behaviors inherited from the common ancestor shared with *Micruroides* with more restricted behaviors that originated repeatedly in particular lineages.

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