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Phylogeography of West Indies Coral snakes (*Micrurus*): Island colonisation and banding patterns

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Abstract

In this study, we analyse New World coral snakes in a phylogenetic framework based upon an increased molecular data set, including novel sequences for the only two sympatric species known from an island (Trinidad, West Indies). Their presence in Trinidad and absence in Tobago offers a unique system to study the phylogeography of the region. We assess the tempo and mode of colonisation of *Micrurus* on the island, in addition to discussing the phylogenetic relationships for the genus *Micrurus* concerning two phenotypic traits, body and tail banding patterns. These relationships are analysed for the first time on statistical coalescent phylogeographic discrete ancestral reconstruction. We find a robust phylogenetic component in these characteristics, where strongly supported clades are recovered: prior to the onset of the Early Miocene, a triadal and tricolour tail clade composed of species from South America, and a second clade dating to the Middle-Late- Miocene with monadal and bicolour tails widely distributed from North to South America. The divergence between clades dates to the Oligocene and suggests an ancient pre-isthmus divergence supporting the arrival of the triadal clade into South America, before the connection between Central and South America was established. We find the two coral snakes present in the West Indies, *M. diutius* and *M. circinalis*, belong to the triadal and monadal clades, respectively. Guyana and Trinidad *Micrurus diutius* share the same haplotypes suggesting a Late Pleistocene–Holocene vicariance when sea level rises separated Trinidad from the mainland. A second lineage of *diutius*-like snakes is present in Guyana and is confirmed as *M. lemniscatus* which is assigned as a voucher and restricts the type locality for *M. lemniscatus.*

KEYWORDS
colour, dispersal, monadal, phylogenetics, triadal, Trinidad

1 | INTRODUCTION

Coral snakes and their aposematic colouration have attracted the attention of evolutionary biologists for centuries. Recently, they have been proposed as drivers of snake evolution, increasing phenotypic snake diversity in the regions they inhabit (Rabosky et al., 2016; Wallace, 1867). The Neotropical coral snake genus *Micrurus* currently contains 78 species, with eight species described since 2000 (Uetz, Freed, & Hošek, 2017). Current evidence suggests that *Micrurus* includes two lineages that can be distinguished by their patterns (Gutberlet & Harvey, 2004; Marques, Pizzatto, & Santos, 2013; Slowinski, 1995).

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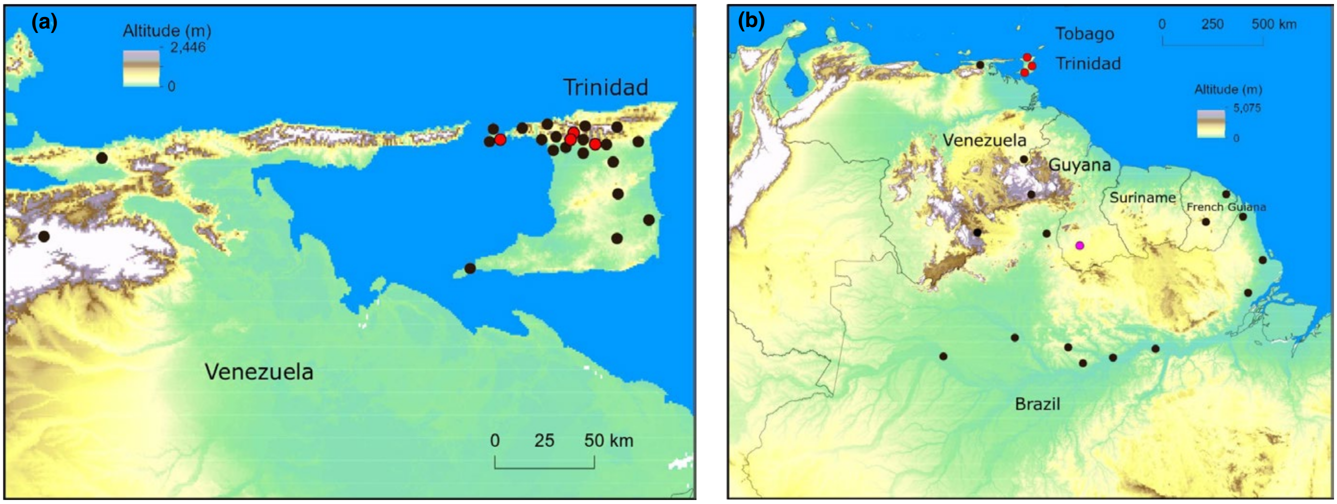

FIGURE 1 (a) Left map represents records for *Micrurus circinalis* from Trinidad and northern Venezuela, and right map (b) indicates records of *M. lemniscatus* localities based on museum samples. The red dots indicate sequenced *M. circinalis* and *M. diutius*. The purple dot on the right map indicates the sequenced undescribed *M. lemniscatus* locality from Guyana (voucher CAS257629). This Figure was generated in ArcGis.

Following previous authors, one lineage possesses the monadal pattern (one black ring, or annulus, between two white or yellow annuli separated by red annuli, the monadal lineage; Supporting Information, Figure 1a). The lineage also shares a suite of morphological and life history traits. The monadal patterned coral snakes share long-tails and an elongate, deeply divided hemipenes (Slowinski, 1995). Monadal coral snakes are mainly distributed in North and Central America, and some have expanded southward into cis-Andean and trans-Andean South America. Marques et al. (2013) linked a suite of life history traits to this clade that includes females that are larger than males, the absence of male–male combat and seasonal vitellogenesis that occurs in spring synchronous with mating. Oviposition occurs from late spring to summer, and hatchlings emerge from late summer to autumn. Spermatogenesis peaks during autumn, and males store sperm in the ductus deferens over winter, until the mating season.

The second lineage, the triadal lineage, has a pattern of three black annuli separated by white or yellow annuli, and each triad is separated from the next by a red annulus (Supporting Information, Figure 1b). The triadal, short-tailed clade share not only the pattern but a slightly bi-lobed short hemipenes, and a South American distribution. Marques et al. (2013) also linked a suite of life history traits to the triadal clade. Males are larger than or equal in size to females; males have ritualised combat behaviour, mating in autumn is synchronous with both spermatogenesis and vitellogenesis, and requires females to store sperm until ovulation in the spring. The triadal clade contains species that are cis-Andean and trans-Andean. The remaining species have not been included in molecular studies, and some have ambiguous colour patterns. The two clades are ecologically similar and frequently occur in sympatry, as they do on the island of Trinidad (West Indies). Coral snakes usually have similarly coloured heads and tails to confuse predators. When attacked, coral snakes place their head under coils of their bodies and raise and curl their tail, imitating their head (Green, 1973; Jackson, 1979). Coral snake tails can be bicoloured or tricoloured.

The phylogeography of New World coral snakes does not allow for a straightforward interpretation based on local geographical or environmental events. Gutberlet and Harvey (2004) argue that *Micruroides,* (the sister to all other Western Hemisphere coral snakes) found in the western United States and northern Mexico, points to an ancient diversification of coral snakes following a southern migration from northern America. They propose that the more ancestral groups are North and Central American, while the South American clades are likely to have colonised via the Panamanian isthmus. However, as noted by the authors, the position of *M. fulvius* and *M. tener* are highly divergent to the ancestral clade (i.e. *Micruroides*), a more likely northern diversification from South America. The proto-Antilles volcanic arc connected North and South America (Crother & Guyer, 1996) on several occasions throughout the Cretaceous-early Tertiary, until it moved eastward with the drifting Caribbean Plate (Zamudio & Greene, 1997). The reestablishment of the Panamanian isthmus dates to the Late Miocene–Pliocene (3–5 Mya, Bacon et al., 2016; Marshall, Butler, Drake, Curtis, & Tedford, 1979; Raven & Axelrod, 1974), though recent data suggest 2.8 Mya (O'Dea et al., 2016), and the presence of basal clades and species diversity suggest a pre-isthmian connection (Gutberlet & Harvey, 2004). This scenario seems to fit well with recent work on ancestral character state reconstruction of red black-banded pattern based on mitochondrial and nuclear data in snakes, dating to an Eocene arrival of coral snakes to the New World (Rabosky et al., 2016).

Pre-isthmus colonisation of South America through semi-emergent island chains suggests that New World Coral snakes are efficient island colonisers, but the lack of coral snakes in the Greater Antilles does not favour such an idea (Gutberlet & Harvey, 2004). Nevertheless, the island of Trinidad (Figure 1a) is the only island in the world where two *Micrurus* are found in sympatry, the large, *M. l. diutius* (triadal clade) and the smaller, *M. circinalis* (monadal clade). The geographic position of Trinidad within the Lesser Antilles and its proximity to northern South America (Figure 1b) offers a rare opportunity to understand the possible timing and colonisation mode of Trinidad and may prove to be an important piece in the puzzle to understanding speciation patterns of triadal and monadal *Micrurus*. Descriptions of *M. circinalis* patterns have suggested some variation that spans the two clades (Campbell & Lamar, 2004; Schmidt, 1957). *Micrurus circinalis* inhabits Venezuela's coastal range, Trinidad and two islands in the Bocas Group: Gaspar Grande and Monos Islands. The South American species *M. lemniscatus* (Linnaeus 1758) is generally recognised (Campbell & Lamar, 2004) as a widespread, polytypic species with five subspecies. *Micrurus l. helleri* (Schmidt & Schmidt, 1925) is found in the Amazon region of northern Brazil, Southern Venezuela, Colombia, Ecuador, Peru and Bolivia; *M. l. diutius* (Burger, 1955) inhabits Trinidad and extends from the eastern versant of the Andes to East Venezuela, Guyana, French Guiana, Suriname and Amapa, Brazil and southward to the Amazon; *M. l. carvalhoi* (Roze, 1967) occurs in Brazil, Argentina and Paraguay and *M. l. frontifasciatus* (Werner, 1927) inhabits Bolivia and Brazil (see Supporting Information Table S1 and legend for explanation of subspecies delimitations).

Recent evidence suggests that the evolutionary development of putative Batesian mimetic antipredator strategies, through the development of tricoloured ring patterns, is dependent primarily on size and diet composition (Pyron & Burbrink, 2009). Thus, the evolution of body size affects phenotypic colour pattern traits. Larger snakes with a large gape and diet preferences show more drab, cryptic or disruptive break-up colour patterns, while smaller snakes exhibit higher aposematism through tricoloured ringed patterns. Here we examine the body and tail colour for each species and relate the colouration to the clades they belong to determine whether the two clades are indeed consistent with their colour pattern. That is, are there any monadal patterned snakes in the triadal clade, or the reverse. We hypothesise that different monadal and triadal banding patterns are likely phylogenetic and related to body size, which may be selected through predators, venom composition and environmental adaptation.

We sequenced mitochondrial genes and a nuclear marker from six *Micrurus circinalis* individuals (five from the island of Trinidad and one from the nearby satellite island of Gaspar Grande), and four *M. lemniscatus* (three from Trinidad Island and another from Guyana), and we compare them to all extant sequences available in Genbank for those loci. Our purposes are to (a) assess the phylogenetic relationships of all available *Micrurus* species and, determine their position within the monadal vs. triadal clades and tricoloured vs. bicoloured tails; (b) examine phylogeographic patterns within the genus including the distribution of the species within the monadal and triadal clades; (c) examine the timing and mode of colonisation of Trinidad *Micrurus*; and (d) assess the taxonomy of the *M. l. diutius* from Trinidad and South America and other *M. lemniscatus* ssp. from South America data.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling and laboratory analyses

DNA extraction, purification and amplification protocols follow Jowers, Lehtinen, Downie, Georgiadis, and Murphy (2015). DNA was extracted from samples of *Micrurus circinalis* and *M. lemniscatus* spp. adults (Table 1). Specimens of both species were collected from fieldwork expeditions from 2011 to 2016 and from the University West Indies Zoological Museum (UWIZM) collections, and tissues from two museum specimens were supplied from Guyana and Trinidad by the California Academy of Science (CAS) (Table 1). Primers are listed in Supporting Information Table S2. Templates were sequenced on both strands, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v.4.9. Sequences were aligned in Seaview v.4.2.11 (Gouy, Guindon, & Gascuel, 2010) under ClustalW2 (Larkin et al., 2007) default settings. Nucleotide translation into proteins had no stop codons. Genbank sequences for this study are in Supporting Information Table S3.

2.2 | Phylogenetic analyses

We used PartitionFinder v.2 (Lanfear, Frandsen, Wright, Senfeld, Frandsen, Wright, Senfeld, & Calcott, 2017) to choose the optimal partitioning strategy under a greedy search scheme (Lanfear, Calcott, Ho, & Guindon, 2012). The most appropriate substitution models for the Bayesian Inference (BI) and RAxML analyses were determined by the Bayesian information criterion (BIC). Phylogenetic inference was based on 666 base pairs of the NADH subunit 4. Adjacent tRNA genes (Histidine, Serine, and partial Leucine, 184 bp) were excluded from analyses because over half of the alignment missed this fraction. Also, molecular clock calibrations were based

TABLE 1 Species sequenced for this study, vouchers, and localities

Species	Voucher	Locality	GPS coodinates
Micrurus circinalis	UWIZM.2011.19.7	Trinidad, Pt. Baleine, Gaspar Grande Island	10°39'58.39"N – 61°39'18.79"W
Micrurus circinalis	UWIZM.2016.12.2	Trinidad, Arima Valley	10°41'5.02"N – 61°16'57.27"W
Micrurus circinalis	UWIZM.2012.9.4	Trinidad, Driveway, Spinghill Estate	10°41'0.29.73"N – 61°17'15.99"W
Micrurus circinalis	UWIZM.2012.27.60	Trinidad, Arima Valley	10°43'5.17"N – 61°17'54.27"W
Micrurus circinalis	UWIZM.2016.22.1	Trinidad, Caura Valley	10°41'49.64"N – 61°20'56.22"W
Micrurus circinalis	UWIZM.2012.38.4	Trinidad, Arima Valley	10°42'0.36'76"N – 61°17'45.49"W
Micrurus diutius	UWIZM.2012.4	Trinidad, Gran Sual Trace, Mamal Main Road	10°27"01.10"N – 61°16'46.19"
Micrurus diutius	UWIZM.2016.24	Trinidad, Fishing Pond	10°32'52.23"N – 61°02'16.39"W
Micrurus diutius	CAS231787	Trinidad, coast rd, between Blanchisseuse and Las Cuevas10	10°48'00.63"N – 61°19'46.62"W
Micrurus lemniscatus	CAS257629	Guyana, Upper Takutu-Upper Essequibo Region	25°5'26.37"N – 58°44'14.55"W

only on ND4 by codon partition, and this small fraction could deviate from estimates. The best partition scheme for the ND4 alignment (used for phylogenetic inference) supported a codon partition for all analyses (BEAST, BI, RAxML); codon 1 (HKY+I+G), codon 2 (HKY+G) and codon 3 (TIM+G).

Test runs were carried out with all published *Micrurus* ND4 sequences from Genbank, included in a large preliminary phylogeny. However, this database represents substantial sampling biases (e.g. *M. fulvius*, *M. tener*) and we therefore only covered some of these that represented independent lineages, or from geographically distant localities (Supporting Information Table S4). Previous phylogenetic studies have found the genus *Leptomicrurus* to be nested within *Micrurus* (Castoe, Smith, Brown, & Parkinson, 2007; Gutberlet & Harvey, 2004; Slowinski, 1995). We, therefore, reference *Micrurus* inclusive of the *Leptomicrurus* spp. in all analyses, except if noted. We assigned the most primitive known coral snake, *Micruroides*, as the outgroup (Gutberlet & Harvey, 2004). Bayesian inference trees were built in MrBayes v. 3.2 (Ronquist & Huelsenbeck, 2003) under codon partition models, with default priors and Markov chain settings and with random starting trees. Each run consisted of four chains of 20,000,000 generations, sampled every 10,000 generations. Convergence was reached after few generations with 10% of the trees resulting from the analyses discarded as burn-in. We used a maximum likelihood (ML) approach implemented in the software RAxML v7.0.4 (Silvestro & Michalak, 2012), using the default settings and codon partition (Figure 2, Supporting Information Figure S2). Preliminary analyses with and without codon partition analyses in all tree-building methods employed did not alter the topologies significantly. All analyses were performed through the CIPRES platform (Miller, Pfeiffer, & Schwartz, 2010).

We performed statistical coalescent and phylogeographic analyses using BEAST v1.8.2 (Drummond, Suchard, Xie, & Rambaut, 2012). First, we specified nucleotide substitution and molecular clock models for the ND4 gene fragment and strict clock under a Yule speciation model. To time-calibrate the tree, we fixed the mutation rate in the ND4 genes fragment to 1.4×10^{-8} substitutions/site/year following Castoe et al. (2007), which has recently been employed to calibrate *Micrurus* phylogenies based on mitochondrial data (Streicher et al., 2016). We co-estimated the trait history using a discrete phylogeographic (ancestral state reconstruction) model also implemented in BEAST (Lemey, Rambaut, Drummond, & Suchard, 2009) with two traits: (a) body banding pattern; triadal, monadal and bicolour (Figure 3), and (b) tail banding pattern; tricolour, bicolour, both tricolour and bicolour (Figure 4). Because not all selected models could be implemented in BEAST v.1.8.2, we employed a similar model (HYK+I+G) with codon partition (1,2,3). Test runs under different models (and with or without I+G) did not alter the tree topologies significantly. As priors for the rates, we selected the approximate reference (CTMC) prior (Ferreira & Suchard, 2008). Given that our geographic sampling of populations is uneven and our state-space is low, we chose a symmetric continuous time rate matrix. The discrete Bayesian analyses were run for 10 million generations and sampled every 1,000 generations. The resulting trees were summarised using TreeAnnotator v1.8.2 (Rambaut & Drummond, 2010), where a maximum clade credibility (MCC) tree with mean values was generated under heights=ca (Heled

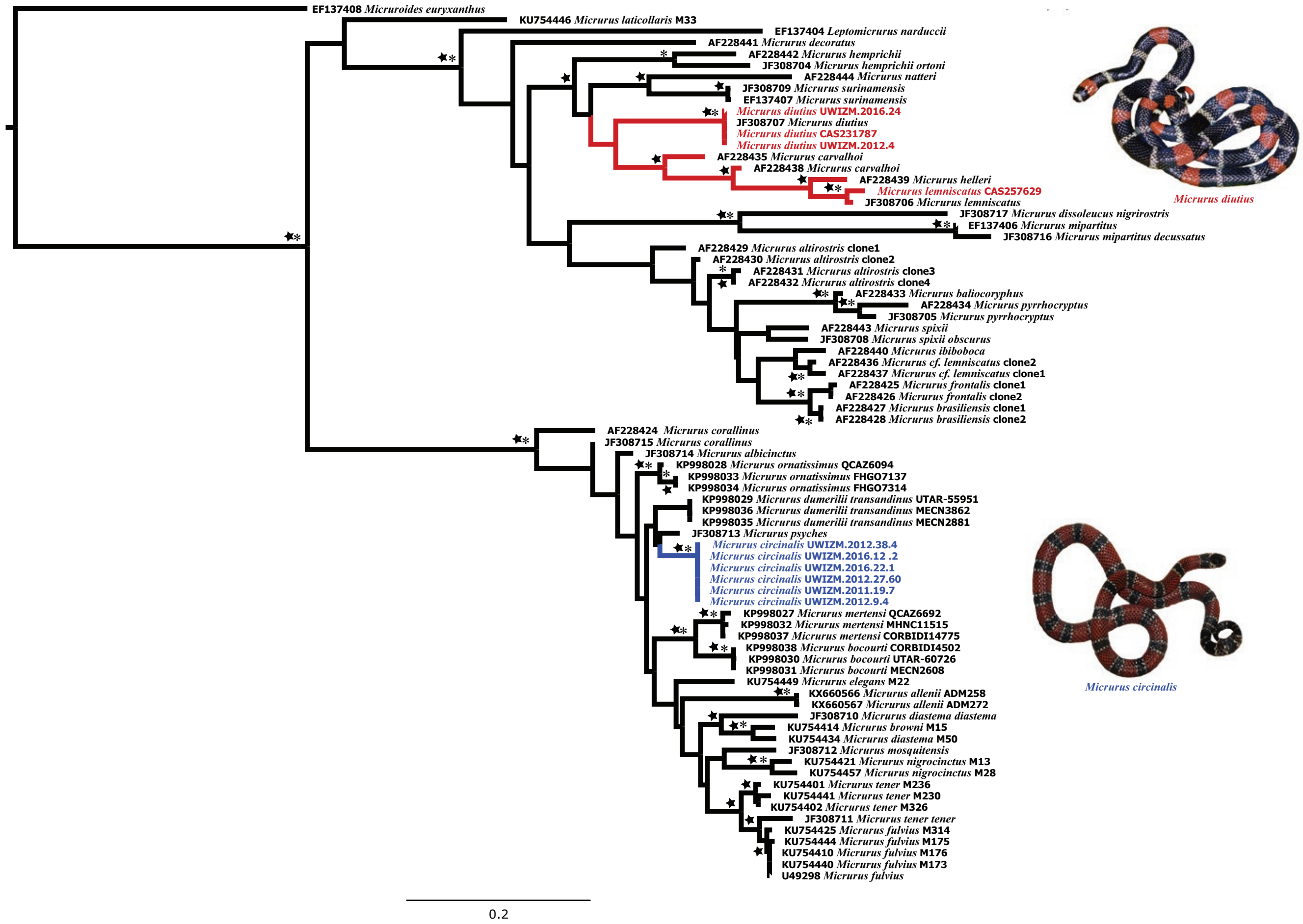

FIGURE 2 Best maximum likelihood tree recovered from the RAxML analyses for the ND4 fragment. BI posterior probabilities (>0.95) and ML bootstraps (>95%) are indicated on nodes as * and as black stars, respectively. In red are the *Micrurus lemniscatus* and in blue *M. circinalis* sequenced for this study. Note: *Micrurus natteri* is part of the former polytypic *M. surinamensis*.

& Bouckaert, 2013). Independent runs were evaluated for convergence and mixing by observing and comparing traces of each statistic and parameter in Tracer v1.6 (Rambaut & Drummond, 2007). We considered effective sampling size (ESS) values >200 to be good indicators of parameter mixing. In an attempt to assess the monophyly of the monadal and triadal banding patterns with nuclear markers, we run a minimum spanning network (Bandelt, Forster, & Röhl, 1999) in PopART (http://popart.otago.ac.nz) of all available c-mos sequences in Genbank (Supporting Information Figure S2).

2.3 | Genetic distances within *Micrurus circinalis* and *M. lemniscatus*

Four further loci were amplified (12S rDNA; 420 bp, 16S rDNA; 487 bp, cyt- *b*; 303 bp, c-mos; 505 bp) but could not be used in the phylogenetic analyses as too few Genbank *Micrurus* sequences are available for those markers. We report on genetic distances within *Micrurus circinalis* and *M. lemniscatus*. Uncorrected genetic *p*-distances (partial deletion 95%, Table 2) and standard error (%) were calculated using Mega 7 (Kumar, Stecher, & Tamura, 2016).

2.4 | Morphology and hypothetical species assignment to clades

Using the morphological data from Roze (1996), Campbell and Lamar (2004), and the relationships recovered in our tree (Figure 3), we inferred what clade species were likely to belong to if they were not already included in out molecular data set. The colour of the body and tail was determined for the description of species in the literature and the examination of photographs. Patterns were coded as monadal (m), triadal (t), and bicoloured (b). Distributions were summarised from written descriptions in the literature previously noted. In species described post-2004 the original species, descriptions were consulted. Subcaudal counts were used as a proxy for actual tail lengths since data on tail lengths in all coral snake species is not available from the literature. The

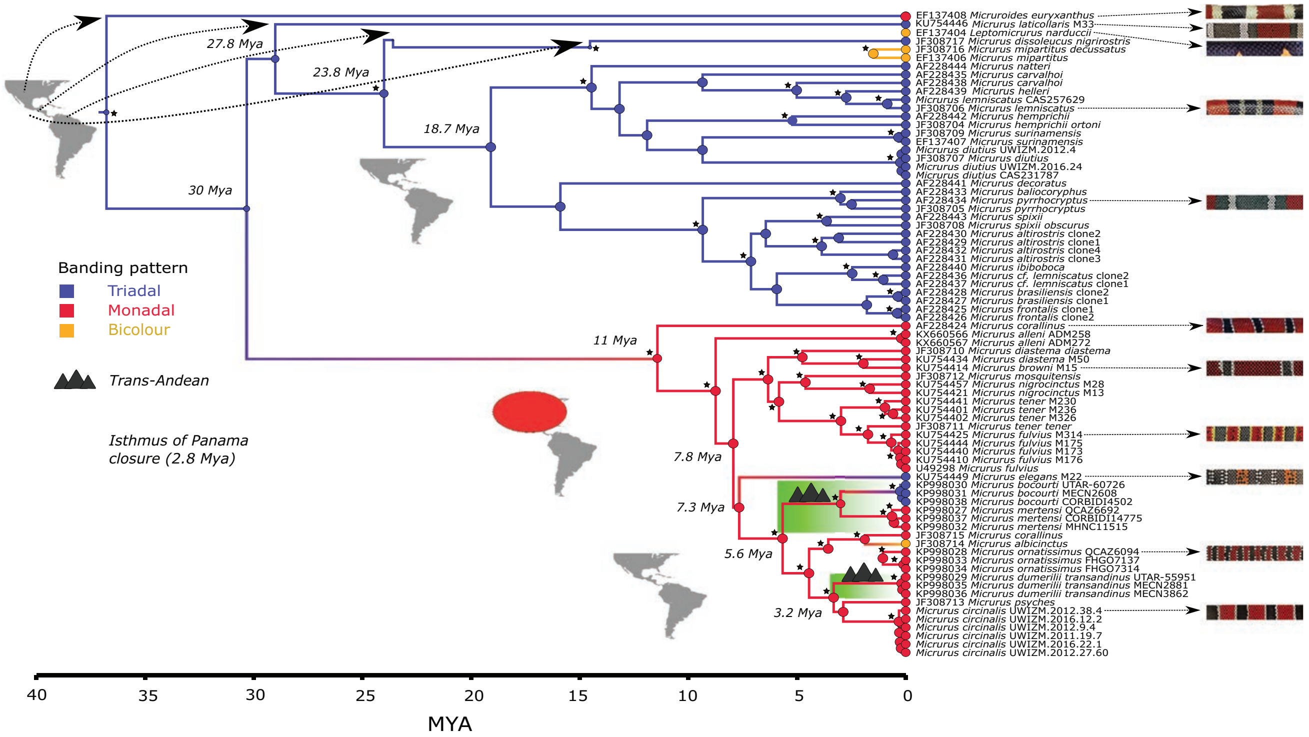

FIGURE 3 MCC discrete coalescent tree of body colour patterns (triadal, monadal and bicolour) in *Micrurus*. Node circles are colour coded by traits and sizes correspond to the probability of the trait origin. Stars by nodes are posterior probabilities (>0.95) from the Bayesian analysis. Values in yellow spheres by nodes indicate mean heights (HPD) in millions of years. Orange and green clades denote Central and North American and the trans-Andean *Micrurus*, respectively. The right of the tree shows some of the triadal and monadal patterns.

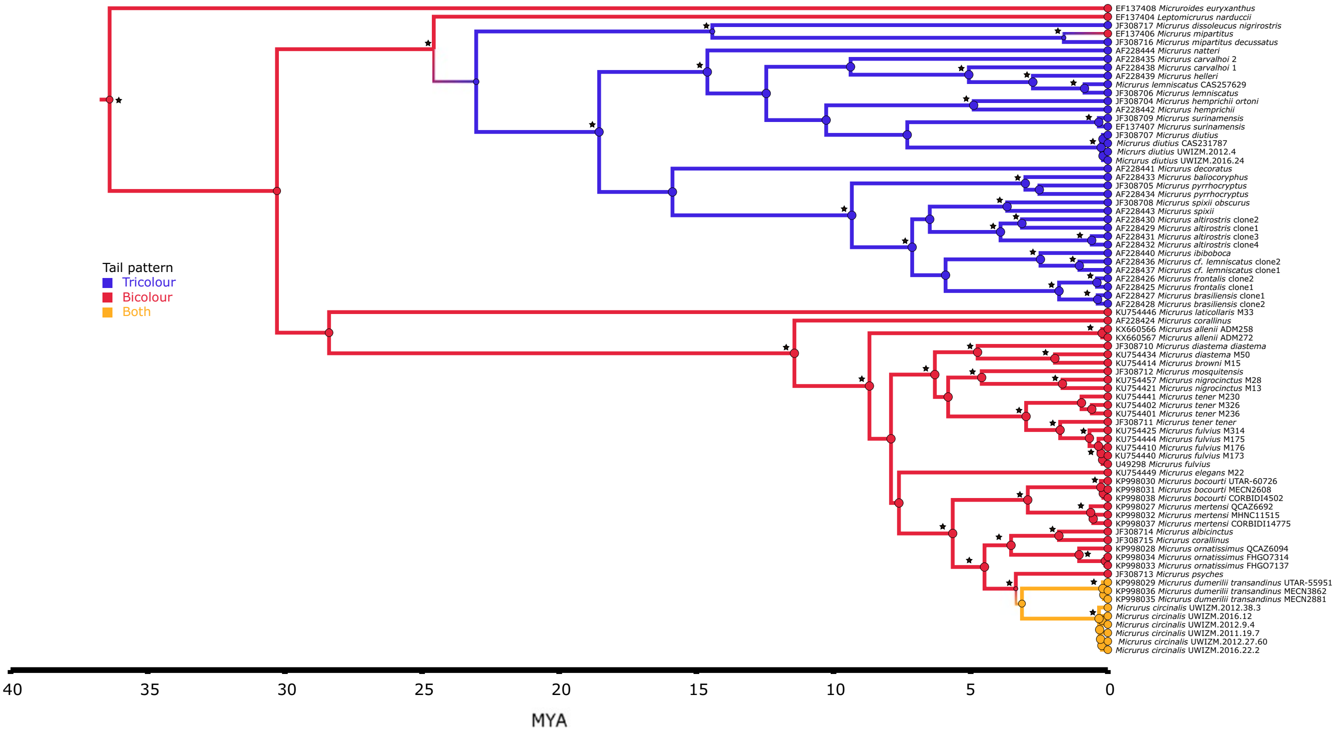

FIGURE 4 MCC discrete coalescent tree of tail banding patterns in *Micrurus*. Node circles are colour coded by localities and sizes correspond to the probability of the trait origin. Stars by nodes are posterior probabilities (>0.95) from the Bayesian analysis.

TABLE 2 ND4 *p*-uncorrected distances of all recently attributed species of *Micrurus lemniscatus* subspecies and closely related species within the monophyletic clade (see Renfijo et al., 2012). *M. natteri* is part of the former polytypic *M. surinamensis*

Species	CAS257629	all Trinidad	JF308706	AF228435	AF228438	AF228439	AF228444	JF308709	EF137407	AF228437	AF228436
M. lemniscatus (CAS257629 Guyana)	–										
M. diutius (all Trinidad+JF308707 Guyana)	0.0667	–									
M. lemniscatus (JF308706 Brazil)	0.0121	0.0667	–								
M. carvalhoi (AF228435 Brazil)	0.0970	0.0803	0.0939	–							
M. carvalhoi (AF228438 Brazil)	0.0576	0.0742	0.0515	0.0500	–						
M. helleri (AF228439 Brazil)	0.0379	0.0818	0.0348	0.0939	0.0470	–					
M. natteri (AF228444 Colombia)	0.1167	0.1076	0.1167	0.1015	0.1061	0.1091	–				
M. surinamensis (JF308709 Peru)	0.0924	0.0727	0.0924	0.0970	0.0955	0.0985	0.0803	–			
M. surinamensis (EF137407 Brazil)	0.0924	0.0697	0.0924	0.0939	0.0955	0.0985	0.0803	0.0030	–		
M. cf. lemniscatus (AF228437 Brazil)	0.1439	0.1379	0.1439	0.1045	0.1212	0.1273	0.1076	0.1333	0.1333	–	
M. cf. lemniscatus (AF228436 Brazil)	0.1485	0.1424	0.1485	0.1061	0.1242	0.1273	0.1106	0.1348	0.1348	0.0121	–

subcaudal count used was the maximum number reported for males of each species (Supporting Information Table S5 and S6).

3 | RESULTS

3.1 | Phylogenetic analyses

Two well-supported clades were identified, a triadal clade with tricolour tail and a monadal clade with a bicolour tail. Runs showed high effective sample size (ESS) convergence (>200), indicating adequate sampling of the posterior distribution. All trees (BI, ML and MCC) recovered similar clade relationships, with a clade constituted primarily by triadal body colour pattern and tricolour tail, and another by monadal body colour pattern and bicolour tail. These two clades are highly supported in all analyses except with the exception of *M. laticollaris*, recovered in the monadal with bicolour tail clade (Figure 4).

MCC discrete trees show deep trait characters of the triadal pattern (28 Mya, 24–32 Mya, 95% highest posterior density (HPD), and ~24 Mya (95% HPD; 20–28), excluding *M. laticollaris*, see below), much older and ancestral than the monadal clade (11 Mya, 9–13 Mya, 95% HPD). The timing between *Micruroides* and *Micrurus* (+*Leptomicrurus*) dates to a mean 36.5 Mya (95% HPD: 29–44 Mya), and the split between both triadal and monadal dates to 30 Mya (25–35 Mya, 95% HPD). The triadal clade (Figure 3) is composed by South American *Micrurus* while the monadal clade has members on all three western hemisphere land masses. *Micrurus corallinus* (AF228424) is the sister to the remaining members (*alleni+diastema+browni+mosquitensis+nigrocinctus+tener+fulvius*) suggesting that the extant members of the clade are mostly Central and North American with an ancestor in South America around 8 Mya (95% HPD: 6.6–9.1 Mya). The second portion of this clade has the Guatemalan *Micrurus elegans* as the sister to (*bocourti+mertensi+corallinus* (JF308715)+*albicinctus+ornatissimus+dumerilii+psyches+circinalis)* and suggests that evolution was tinkering with triadal patterns in this clade and that it diverged circa 7 Mya (95% HPD: 6–8.7 Mya). It also suggests the subclade had a North American origin that dispersed to South America. The South American monadal clade was recovered as a trans- and cis-Andean *Micrurus* with divergences at ~5 Mya (95% HPD: 4.4–7 Mya), and 3.2 Mya (95% HPD: 2.3–4.4 Mya). Our data suggest the non-monophyly of *M. corallinus* (Figure 3).

Results from the tail trait MCC tree (Figure 4) shows an ancestral bicoloured state and the appearance of a tricolour tail pattern within the triadal clade 22 Mya (19–26 Mya, 95% HPD). Excluding *Micrurus laticollaris*, the monadal clade bicolour tail dates to about 11 Mya (9–13.9, 95% HPD). The phylogenetic position of *Micrurus laticollaris* remains unresolved. We assessed the position of *M. laticollaris* without the assignment of trait and running longer chains, but remained weakly supported in all analyses (MCC M&T; 0.49 Bayesian posterior probability (BPP), MCC Tail; 0.46 BPP, MCC with no trait; 0.45 BPP (not shown), RAxML; 35 Bootstrap support (BS), BI; 0.63 BPP). The results from the minimum spanning network revealed little genetic variability and failed to recover the observed monophyly of both monadal and triadal clades (Supporting Information Figure S2).

All sequenced *Micrurus lemniscatus* recovered a Guyana (CAS257629) and Trinidad haplotype (CAS231787, UWIZM2012.4, UWIZM2016.24). There was a 100% match between the Trinidad haplotype and the Genbank sequence JF308707 from Guyana, which is mislabeled *M. l. lemniscatus*. *Micrurus diutius* is paraphyletic. However, *M. diutius* individuals from Trinidad and Guyana (CAS231787, JF308707) are monophyletic. *M. lemniscatus* (CAS257629 labelled *M. l. diutius*) from Guyana groups with another *M. lemniscatus* "*diutius*" from Brazil. *Micrurus circinalis* is monophyletic and well supported and sister clade to *M. psyches* in the ML tree and in the MCC colour pattern tree and these form a sister clade to *M. dumerili transandinus,* but are weakly supported in the ML and BI tree (Figure 2). *M. psyche* is sister to *M. circinalis* + *M. dumerilii transandinus* in the MCC tail tree (Figure 4). The MCC trees recovered a strongly supported monophyletic clade composed of *M. circinalis*, *M. psyches* and *M. dumerilii transandinus* (Figures 3 and 4). The position of this clade changes between analyses, positioned more central within the triadal and tricolour tail clade, in the BI and ML trees.

3.2 | Genetic distances within *M. circinalis* and *M. lemniscatus* and closely related species

The *p*-uncorrected distances from *Micrurus lemniscatus* between the Guyana and Trinidad haplotypes were 2.5% (12S rDNA), 3.1% (16S rDNA), 7.2% (cyt- *b*), 6.67% (ND4) and 0.48% (c-mos) (Table 2). The 12S rDNA, 16S rDNA and c-mos *Micrurus circinalis* sequences recovered a unique haplotype while the cyt-*b* and ND4 fragments recovered four and two haplotypes, respectively. *M. circinalis* intra-species variability was low (mean 0.65%). ND4 genetic divergence between its closest sister species, *M. psyches,* and *M. dumerili* was low, 3.2% and 3.8%, respectively.

3.3 | Classification of body pattern clades and phylogeny

Micruroides euryxanthus is a North American polytypic species easily distinguished from *Micrurus* spp (including the four species previously placed in *Leptomicrurus*) by its black head, including the parietal scales, the presence of a single pair of enlarged chin shields, a short tail and small size. The pattern is described as monadal by most authors (Campbell & Lamar, 2004; Roze, 1996) but may be best considered a proto-monadal pattern due to it being highly variable between the recognised subspecies.

Micruoides is the sister to an odd group of lineages that included *M. mipartitus*, *Micrurus laticollaris, Micrurus* (*Leptomicrurus*) *narducci* and *M. dissoleucus*. These are small to large coral snakes with modified patterns that do not correspond particularly well to either triadal or monadal patterns. Most of the snakes in this sister group are bicoloured and tend to have slender bodies. The triadal-like patterns in these species (*M. laticollaris* and *M. dissoleucus*) may also be best considered proto-triadal. This group has a mean of 35.0 subcaudals (standard deviation, *SD* = 4.5) (Supporting Information Table S5). The inferred species based on morphological similarities (*n* = 10) have 32 subcaudals (Standard Deviation, *SD* = 7.25) (Supporting Information Table S6). The group contains species that previous authors have considered monadal (*M. dissoleucus*) and triadal clade (*M. laticollaris, M. mipartitus*) members. Tail length is more similar to the monadal than to the triadal clade, and *M. dissoleucus nigrorostris* has a tricoloured tail (Supporting Information Table S6).

Triadal clade. We also moved the Central American *M. multifasciata*, *M. multiscinctus* and *M. spurrelli* to the *Micruroides* sister group given their similarities to *M. mipartitus,* reported in Campbell and Lamar (2004); Supporting Information Table S5 and S6. The relationships of these snakes will be resolved when they are represented in the molecular database. This clade of *Micrurus* have short tails, with a mean of 31.7 subcaudals (*SD* = 6.75), and including the attributed species to the clade (*n* = 20), they have a mean of 30.95 subcaudals (*SD* = 6.72). All species are tricoloured with tricoloured tails (Supporting Information Table S6). These coral snakes have a South American distribution.

Monadal clade. These are coral snakes with a long tail, and their combined distributions range from Mexico, through Central and South America. They express bicoloured, triadal and monadal patterns; although most tend to be monadal. They tend to have long, bicoloured tails (based on the species in our trees, they average 50.4 subcaudals, *SD* = 3.9) and with species attributed to this clade (*n* = 49; 49.75 subcaudals, *SD* = 6.53). Most of the hypothesised species within this clade have bicoloured tails (40 out of 49) (Supporting Information Table S6).

4 | DISCUSSION

4.1 | Phylogenetic relationships of body and tail banding patterns

Our work confirms previous findings of two predominant clades of coral snakes, a triadal and a monadal clade

(Arbuckle, 2014; Gutberlet & Harvey, 2004; Lee, Sanders, King, & Palci, 2016; Renjifo et al., 2012) with modifications. The inclusion of 10 new species with molecular data totals at least 37 species, but the trees suggest the number of species present is likely 42 based upon the lineages recovered in the analyses. Previously, the complete molecular phylogeny included 27 species (Renfijo et al., 2012).

This study modifies the previous phylogenetic arrangement of colour patterns in coral snakes. Monadal species are not represented in the triadal clade. However, at least two triadal-like species (*Micrurus bocourti* and *M. elegans*) occur within the monadal clade and suggests a divergence of monadal and bicolour patterns within the clade. *Micrurus bocourti* is sometimes called the False Triad Coral Snake because it has only two black bands in the first triad and the lateral black bands barely extend beyond the white rings. *Micrurus elegans* also has an unusual triadal-like arrangement with long black bands and very narrow double white rings that may look more like spots than complete transverse bands (Roze, 1996). The polyphyletic position of *M. corallinus* (Figures 3 and 4) suggests the need for taxonomic revision and raises the question of the possibility of cryptic species.

The MCC discrete tail pattern tree recovered two clades, with a few exceptions, a bicoloured clade and a tricoloured clade. The monadal clade is composed of species with a bicoloured tail pattern, and the triadal clade is composed of species with a tricolour tail pattern. The association between body banding patterns and tail colour banding patterns (triadal pattern-tricolour tail and monadal pattern-bicolour tail) points to genetic linkage mechanisms maintaining such variation.

The position of the species formerly considered to be *Leptomicrurus* provides support for an ancestral bicoloured tail pattern, but the exclusion of such from the analyses would result in a sister clade relationship of both tail patterns. Campbell and Lamar (2004) recognise four groups of New World coral snakes by the colour patterns, body scales, hemipenis, size and geography. We find some coherence with their assigned grouping and our phylogenetic trees. The notable exceptions are the species that compose the older lineages, with a sister relationship to *Micruroides*. The Bayesian MCC coalescent trees indicate an old, rather than a recent evolution of both banding patterns. The monadal (body) and bicolour (tail) clades are composed of species from South, Central and North America. On the other hand, the triadal and tricolour tail clade consists solely of South American species.

From a phylogenetic context, the parameter values determining the drivers in *Micrurus* snake patterning are not straightforward. Still, some insights may be derived from both clades body and tail length ratios, and its evolutionary advantages in relation to habitat. Interestingly, aquatic, fossoriality, followed by arboreality are the three most significant phylogenetically habitat traits determining colour patterns in snakes (Allen, Baddeley, Scott, Scott-Samuel, Baddeley, Scott, Scott-Samuel, & Cuthill, 2013). Our findings of a larger triadal clade with short tails suggest a burrowing and or aquatic/semi-aquatic (e.g. the monophyletic *M. natteri, M. spixii, M. lemniscatus, M. diutius, M. carvalhoi, M. surinamensis, M. helleri*) ancestry, while the smaller monadal clade with longer tails suggests a more probable terrestrial ancestor that was active on the surface and may have climbed into low vegetation. Also, following the idea that higher aposematism is related to smaller bodies snakes (Pyron & Burbrink, 2009), it would suggest that triadal snakes are more aposematic than monadal *Micrurus*. However, this argument and the exact reasons for the origins of both patterns in *Micrurus* merit further investigation.

Trait colour congruence to mitochondrial genes in vertebrates is rare and has mostly been reported in allopatric coral reef fish (Drew, Allen, & Erdmann, 2010). However, the mechanisms and loci involved in banded colour pattern inheritance in Squamata remain largely unknown (Allen et al., 2013). MtDNA phylogenetic congruence to colour banding in New World coral snakes is likely the result of strong selection pressure from predators, resulting in aposematic patterns (Lomonte et al., 2016; Rabosky et al., 2016, but see Allen et al., 2013), that are probably reflected throughout the genome. Unfortunately, few other nuclear loci and the small sample size within *Micrurus* available in Genbank, limited testing such congruence with few species (Supplementary information Figure S2). It is apparent that further sequencing of other nuclear markers will be required to assess monadal vs. triadal patterns from nuclear-derived markers. However, the recovery of different monadal and triadal clades derived from other than mitochondrial based studies (Renfijo et al., 2012) suggests that this is likely the species tree. For example, it is noteworthy that *Micrurus* venoms (phospholipases A_2 [PLA_2] and "three-finger toxins" [3FTx]) show a historical, geographical dispersal pattern with their distribution, highly congruent to our phylogeny. Species with a PLA_2-rich venom are distributed throughout Central and North America, reaching northern South America (mostly the monadal clade), while those with 3FTx-rich venom are found in Central and South America (mostly the triadal species), with both venom factors present in Central America. A third venom component, the pain-inducing toxin (MITx) is found only in monadal snakes (Lomonte et al., 2016). Furthermore, phylogenetic analyses inferred from the combination of morphometric and allozyme data have also recovered the two clades, monadal and triadal (Slowinski, 1995).

4.2 | Phylogenetic relationships and timing of clades

Assessing the complex geology in the area is key to understand the phylogeography of *Micrurus* and dispersal vs.

vicariance. Our findings mostly agree with an ancestral pre-isthmus formation and suggest older and complex phylogeographic events. The split between *Micruroides* and *Micrurus* dates to the Eocene, 36 Mya, while the triad-monadal clades diverged in the Oligocene, 30 Mya. The ancestor of the tridal clade dates to the onset of the Early Miocene 24 Mya, while the monadal clade dates to the much more recent beginning of the Middle Miocene, about 11 Mya.

The divergence between triadal and monadal clades agrees with the early arrival of the ancestor of *Micrurus* to South America in the Early Tertiary when the ancient Isthmian link (the Proto-Antilles Arc) connected both continents (Savage, 1982, 2002). Our calibrations further support the idea of an ancestral stock of South American triadal *Micrurus* (Lomonte et al., 2016). The Panama Arc existed as a semi-emergent island chain circa 30 Mya, and collision of the arc at around 24 Mya continued until the present (Farris et al., 2011), with land mammal dispersals beginning at around 20 Mya (O'Dea et al., 2016). Deep straits resulted in massive inter-oceanic seawater exchange until these passages were extinguished at around 9 Mya, allowing more continuous crossing over (Newkirk & Martin, 2009; Osborne et al., 2014). This scenario fits well with the timing between monadal Central American and South American *Micrurus* to ~8 Mya, suggesting a likely northern migration from South America.

Similarly, the Guatemalan *Micrurus elegans* most recent common ancestor, with remaining monadal South American *Micrurus,* points to a secondary southern migration circa 7 Mya. The uplift of the northern Andes in the Late Miocene ~3–5 Mya is believed to have shaped the evolution of *Micrurus* through vicariance (Gutberlet & Harvey, 2004; Lomonte et al., 2016). Dates between trans- and cis-Andean monadal *Micrurus* support a Late Miocene divergence and could, therefore, be indicative of vicariant speciation. Formation of the isthmus sensu stricto dates to approximately 2.8 Mya (O'Dea et al., 2016), coinciding with the Great American Biotic Interchange (Stehli & Webb, 1985) over dry land. The divergence between Colombian and Panamanian *M. mipartitus* (1.4 Mya, 95% HPD: 0.7–2.3 Mya) supports a radiation event after the opening of the isthmus, as has been previously suggested for other *Micrurus* (Coates & Obando, 1996; Gutberlet & Harvey, 2004).

The older branches and divergence within this triadal clade agree with geography and earlier diversification. The weak positioning of the bicoloured tailed *M. laticollaris* (BPP; 0.46) alters the dating of such clade considerably to 24 Mya, even ancestral to the tricolour tail pattern in the Early Miocene, 21 Mya. Exclusion of this taxon results in a more credible origin of the bicolour tail pattern, in congruence with monadal body patterns to the beginning of the Late Miocene, ~11 Mya. The triadal clade contains about 20 species, 16 are cis-Andean and four that are Andean or trans-Andean. Note that we are excluding *M. laticollaris* from this clade based on its position in the tree. Overall, our timings inferred from the molecular clock estimates are similar to those of Rabosky et al.'s (2016) study reconstructed with three different tree-building methods (RLC-Bayesian random local clock, Parsimony and ML), but slightly older though congruent to Lee et al. (2016). However, neither of these studies included *M. laticollaris*, increasing the age of the triadal clade significantly. Lastly, the former members of the genus *Leptomicrurus* have been folded into *Micrurus* to make the genus monophyletic. However, *Micrurus laticollaris* is recovered as the sister to the species formerly placed in *Leptomicrurus* and raises the issue of its identity as a true *Micrurus*, or a distinct ancient lineage along with *M. mipartitus* and *M. dissoleucus*.

4.3 | Island colonisation

Several authors have proposed colonisation from Central to South America via island chains or through rafting (Lillegraven, Kraus, & Brown, 1979; Rosen, 1976), but the lack of coral snakes in the Greater Antilles does not seem to support this hypothesis (Gutberlet & Harvey, 2004). *Micrurus circinalis* and *M. psyches* (from Guyana) sister clade relationship, and the unexpected recovery of a common haplotype of *M. diutius* from Trinidad and Guyana suggest recent gene flow. These species are cryptozoic, and *M. diutius* is also semi-aquatic. Both species likely maintained gene flow between Trinidad and the mainland through land-bridge connections at low sea level stands during the Pleistocene (Routledge & Hansen, 2016; Supporting Information Figure S3). Further evidence derives from other *Micrurus* found in islands. In the western Caribbean, two species inhabit islands, *Micrurus nigrocintus* in the Greater Corn Islands and Corn Islands, east of Nicaragua and *M. ruatans* is the islands of Roatán, off the coast of Honduras (Crother, 1999), both these islands were connected to the mainland during the Pleistocene (Petuch, 2013; Woodburne, 2010). In South America, *M. corallinus* inhabits several coastal Brazilian islets (Cicchi, Sena, Peccinini-Seale, & Duarte, 2007), which were connected to the mainland when sea level fell between 10–20 Kya (Bittencourt-Silva & Silva, 2014; Bueno, Schmidt Dias, & Stelle, 2013; Violante & Parker, 2004). Hence, New World coral snakes seem to lack the long-distance dispersal capabilities of other snakes (e.g. Boidae, *Bothrops*) to colonise offshore islands, even though some species have morphological adaptations to swimming and are considered aquatic or semi-aquatic (Silva et al., 2017). The presence of the same *M. diutius* haplotypes in Trinidad and Guyana is somehow surprising as it implies very recent isolation on Trinidad or isolation through sea level rise. However, similar findings on the fossorial snake *Atractus trilineatus* from

Trinidad, Tobago and Guyana suggest dispersal through Pleistocene land bridge formations or rafting (Murphy, Salvi, Braswell, & Jowers, 2019). Furthermore, recent work on the fossorial Trinidad threadsnake, *Epictia tenella*, has shown a remarkable genetic similarity between Guyana and Trinidad, suggesting colonisation by recent dispersal rather than ancient vicariance (Murphy, Rutherford, & Jowers, 2016). The absence of *Micrurus* in Tobago, as well as many other snakes, present in the mainland and Trinidad but not in Tobago (Murphy, 1997), likely relates to lack of suitable land bridge formations between Trinidad and Tobago throughout the Pleistocene. An alternative scenario is the recent colonisation of Trinidad, after the last sea-level fall that connected both islands. However, the presence of snakes on both islands may rely on several factors, such as the timing of colonisation, and the dispersal capabilities of the species. Lack of New World coral snakes in oceanic islands and pre-isthmus colonisation of South America through semi-emergent island chains suggest likely radiations through stepping stone expansions with local island extinctions.

Only six species of Trinidad colubroids may be coral snake mimics. None of them appears to be exact visual mimics of *Micrurus circinalis* although *Erythrolamprus bizona* is quite similar. On Tobago, the endemic *Erythrolamprus ocellatus* is a *Micrurus* mimic. As suggested by Hodson and Lehtinen (2017), the presence of *E. ocellatus* on Tobago suggests a relatively ancient dispersal or vicariance event (Jowers et al., 2015; Lehtinen, Wojtowicz, & Hailey, 2011). The presence of a mimic species in Tobago but the absence of model species may suggest that either *Micrurus* never colonised the island or the population may have become extinction.

4.4 | Phylogenetic relationships of *Micrurus circinalis*

Our results confirm the status of *Micrurus circinalis* as a full species (Roze, 1996), as it was formerly considered a subspecies of *M. psyches circinalis* (Roze, 1967; Schmidt, 1936, 1957). The MCC tree recovered a strongly supported monophyletic clade composed by *M. circinalis*, *M. psyches* (Guyana) and *M. dumerilii transandinus* (Colombia) with a time since the most recent common ancestor for this group at a mean 3.2 Mya (2.3–4.3 Mya, 95% HPD), in contrast to the low divergence found between Trinidad and Guyana *M. diutius*. The presence of both tail colour polymorphism in *M. circinalis* and *M. dumerilii* and their sister clade relationship begs for further investigation to understand the selection pressures acting on populations. It is interesting to note that within the several species of *Micrurus* found in Venezuela, *M. dissoleucus* occurs in the Paria Peninsula region (Rivas et al., 2012), an extension of Trinidad's Northern Range, but it is absent on the island.

4.5 | Systematic implications for the *Micrurus lemniscatus* Group

A comparison of CAS257629 morphology to descriptions of the *Micrurus lemniscatus* group in Roze (1996) suggests it is in fact the real *M. lemniscatus*. The scale counts and the pattern description are similar to *M. lemniscatus*. The only trait described by Roze (1996) not represented in this specimen is black pigmentation in the gular area, but it does have black anterior lower labials and a black mental (Supporting Information Figure S4).

Linnaeus (1758) described *Micrurus lemniscatus* and gave the type locality as “Asia,” in error. Schmidt and Walker (1943) restricted the type locality to Belem, Brazil. However, Roze (1967) proposed the northern Guianas as a more likely point origin after he examined the syntypes. He observed a high number of black triads, ventral scales and subcaudal scales, and the general colouration of the animals used in the description. In an unpublished dissertation, Pires (2011) provided evidence that the subspecies of *M. lemniscatus* should be given full species status based on morphology, an action supported by our molecular results.

Five species (formerly subspecies) of the *Micrurus lemniscatus* have been recognised. *M. lemniscatus* is distributed in Brazil (Amapa, Para) and the northern Guianas and is syntopic and sympatric with *M. diutius* at some locations (Pires, 2011). In our tree (Figure 2), *M. carvalhoi* Roze, 1967 has one branch significantly longer than the other, but the low *p*-distances (Table 2) suggest that they are the same species. *M. carvalhoi* has a broad distribution, inhabiting northeastern and central Brazil. Werner's *M. frontifasciatus* was found to be a composite of several species. It was raised to species level (Wallach, Williams, & Boundy, 2014). *Micrurus diutius* Burger has a type locality on Trinidad and has been reported from Venezuela (as far West as the eastern versant of the Andes), and the Guianas (as far East as French Guiana) and in Amazonas Brazil. Our molecular results confirm its presence in Guyana. However, the second lineage from southern Guyana reinforces the species status of *M. diutius* and demonstrates that it is not monophyletic and is composed of at least one other cryptic species. The specimen sequenced from Upper Takutu-Upper Essequibo River of Guyana (CAS 257629) was labelled *M. lemniscatus* and was the sister of another specimen labelled *M. l. diutius* from Brazil (JF308706).

4.6 | Conclusions

This is the first study to address the phylogenetic relationships of New World coral snakes about monadal and triadal banding body and tail patterns. We recovered a sister clade relationship between the Central and South

American Late Miocene monadal and bicolour tail pattern clade and the South American Early Miocene triadal and tricolour tail pattern clade. We found that the colonisation of South America dates to before the closure of the Panama isthmus. The correlation between mitochondrial loci and banding and tail patterns points to a genetic linkage mechanism maintaining such variation, but further data are needed to address this scenario. It is apparent that additional sequencing of other nuclear markers will be necessary to assess monadal vs. triadal and tail patterns from nuclear-derived markers. Trinidad's two sympatric coral snake species *Micrurus diutius* and *M. circinalis* belong to the triadal and monadal clades, respectively. Another lineage similar to *M. diutius* from Guyana is confirmed as *M. lemniscatus* and is assigned as a voucher and type locality for *M. lemniscatus*. Further sampling of *M. lemniscatus* throughout its wide distributional range is needed to assess the cryptic diversity of this group.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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