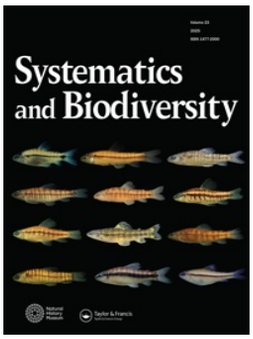

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Research Article

Biogeography and hidden diversity in the coffee snake species complex *Ninia atrata* (Dipsadinae) from South America and the Lesser Antilles

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We used a multilocus sequence molecular dataset, constructed using mitochondrial and nuclear DNA from South American populations of *Ninia atrata* (with its recently described synonyms), to examine its evolutionary history and evaluate the possible existence of cryptic lineages using Bayesian and maximum likelihood criteria. Phylogenetic inferences and species delimitation analyses indicated the existence of at least seven distinct lineages within the former *N. atrata* group. However, only three lineages remain to be described, a trans and a cis Andean lineage from Colombia and another from the oceanic island of Tobago. Additionally, the age of divergence between continental and insular populations of *Ninia* is estimated, providing information on its evolution and biogeography. We find that the uplift of the northern Andes during the Pliocene was possibly the determining factor in the evolution of continental populations of *N. atrata*. At the same time, the presence of this species complex in the island of Trinidad and Tobago suggests the existence of terrestrial corridors that connected the islands with the continent for brief periods during the Pleistocene, corresponding with the drier climates and lower sea levels of the Pleistocene glaciation periods. Subsequent prolonged isolation in Trinidad and Tobago could explain why these *N. atrata* populations are genetically distinct from those on the mainland. On the other hand, reconstructions of ancestral areas suggest a Central American origin and a subsequent expansion towards South America. In conclusion, phylogenetic and species delimitation results indicate that *N. atrata* is a species complex that shows relatively deep divergences at the species level initiated during the Pliocene. Finally, this work provides a first step in delimiting species at a continental level for this species complex and recognizing conservation units for preservation.

Key words: Andes mountains, evolutionary lineages, reptiles, taxonomy, undescribed species

Introduction

Often different species share morphological characteristics that are so similar that they are indistinguishable from each other, allowing them to be erroneously classified as a single species, despite in fact being, a complex

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of cryptic species (Bickford et al., 2007; Jadin et al., 2020; Jowers et al., 2023). The identification of cryptic diversity and understanding of the distribution of individual species is essential to assigning them a conservation status (Funk et al., 2012; Murphy et al., 2016). Furthermore, the formal description of new species drives the adoption of conservation strategies for the ecosystems of which they are part (Ferrão et al., 2022). Molecular-based studies have been used to infer the evolution of genetic lineages between closely related species (Avise et al., 1979; Jowers et al., 2023), but the precise delimitation of species requires the integration of genetic, morphological and ecological data (Padial et al., 2010).

The convergence of morphological characters between different species is frequent in ectothermic organisms that inhabit the Andes Mountain range, such as amphibians and reptiles. For example, the colubrids of the genus *Ninia*, commonly known as coffee snakes, form a lineage made up of 13 species (Angarita-Sierra, 2014; Arteaga & Harris, 2023; Savage, 2002): *Ninia atrata* (Hallowell, 1845), *N. celata* (McCranie & Wilson, 1995), *N. diademata* (Baird & Girard, 1853), *N. spinali* (McCranie & Wilson, 1995), *N. franciscoi*, previously *Ninia atrata* (Angarita-Sierra, 2014), *N. hudsoni* (Parker, 1940), *N. maculata* (Peters, 1861), *N. pavimentata* (Bocourt, 1883), *N. psephota* (Cope, 1875), *N. sebae* (Duméril et al., 1854), *N. teresitae,* previously *Ninia atrata* (Angarita-Sierra & Lynch, 2017), *N. schmidti* (Jan, 1862), previously *Ninia atrata* and *N. guytudori* (Arteaga & Harris, 2023). Snakes of this genus live mainly in leaf litter in most habitats from southern Mexico to northern Peru, at altitudes between sea level and 1800 m (Angarita-Sierra, 2014; Savage, 2002).

Several of these species are morphologically similar and the overlap in their coloration patterns makes it difficult to distinguish them. For example, *N. atrata*, *N. celata*, *N. spinali*, *N. franciscoi*, and *N. maculata* have 19 rows of dorsal scales without reductions, a black or dark brown back, and a cream or white nuchal collar (Angarita-Sierra & Lynch, 2017). Furthermore, given that in most studies both the number of specimens used, and their localities of origin are limited, the data obtained on their counts and morphometric characters are not very representative, and likely to be geographically variable, which constitutes an added difficulty for the characterization and determination of the biological identity of this taxon (Angarita-Sierra, 2009).

One species group, *Ninia atrata*, has recently undergone substantial taxonomic changes (Angarita-Sierra, 2014; Angarita-Sierra & Lynch, 2017; Arteaga & Harris, 2023) and is widely distributed, found on both sides of the Andes Mountains in Colombia at altitudes of at least 1200 m; In Venezuela, most of the records come from the Cordillera de la Costa "within 320 km of Caracas" (the type locality) (Roze, 1958), and to a lesser extent from the Cordillera de Merida (Venezuelan Andes), Sierra de San Luis, with very few from the Venezuelan Guyana, below 1800 meters (Natera-Mumaw et al., 2015; Rivas pers. obs.); in all cis (eastern)-Andean geographical areas in the Pacific lowlands of the extreme east of Panama up to 525 m; in western Ecuador, and in Trinidad (*Ninia franciscoi*) and Tobago up to 980 m (Jaramillo et al., 2010; Murphy, 1997; Murphy et al., 2018; Savage, 2002). This species lives in both humid lowland forests and dry forests, in savannahs, plantations, and rural gardens (Angarita-Sierra, 2015; Jaramillo et al., 2010; Murphy, 1997). The taxonomic history of *N. atrata* is complex due to its morphological similarity with other species of the same genus. Initially it was believed that *N. atrata* was distributed throughout Ecuador, Colombia, Venezuela, Panama, Costa Rica and Trinidad (Dunn, 1935). Later, Wilson and Meyer (1985) recorded the species for Honduras. However, the first comprehensive taxonomic evaluation of *N. atrata*, carried out by McCranie and Wilson (1995), concluded that the South American populations were distinguishable at the species level from both the populations of Costa Rica and western Panama (later described as *N. celata*), as well as from the populations of Honduras and El Salvador (later described as *N. spinali*). Later, Angarita-Sierra (2014) studies on *N. atrata* populations in Trinidad made it possible to describe a new species called *N. franciscoi* (also present in Paria Peninsula in Venezuela), and two Ecuadorian populations are now considered *N. teresitae* (Angarita-Sierra & Lynch, 2017) and *N. schmidti* (Arteaga & Harris, 2023). Therefore, *N. atrata* represents a species complex that requires careful review to clarify the taxonomic composition of the genus and elucidate its evolutionary history (Angarita-Sierra & Lynch, 2017).

The first description of *N. atrata* was by Hallowell (1845), as a small, dark gray to black snake with a white band extending along the occipital region. This band, also called the nuchal collar, may or may not be present in adult specimens and if present, its degree of prominence is variable (Angarita-Sierra, 2009). Likewise, its color can be white or reddish depending on the locality, as described by Lancini (1979), Pérez-Perez-Santos & Moreno (1988), Savage and Lahanas (1991). Angarita-Sierra (2009) presents the first study on the variation in *N. atrata* populations and its relationship with its geographical distribution in Colombia, based on 128 specimens from more than 24 localities, and considering the trans-(western) Andean and

cis-(eastern) Andean biogeographic regions described by Lynch (1979). These regions are delimited by the Andes Mountain range: the trans-Andean region extends west of the Andes Mountains including inter-Andean Magdalena and Cauca River basins, Caribbean coast and Pacific lowlands, while the cis-Andean region comprises the lowlands east of the Andes, from the Amazon basin to the Colombian-Venezuelan Orinoquia region in the extreme north (Lynch, 1979).

Through the study of *N. atrata* populations in both regions, Angarita-Sierra (2009) found that the coloration of the nuchal collar differed between the cis-Andean and trans-Andean populations: in the cis-Andean the nuchal collar is always white or creamy yellow, while in the trans-Andean populations, the pigmentation of the nuchal collar is variable, prominent white, red, orange or creamy yellow. Furthermore, the shape of the nuchal collar differed between both populations, presenting two states in the trans-Andean populations, one W-shaped and another where the pigmentation of the collar completely covers the parietal scales without exceeding the frontal or postocular scales. On the other hand, in cis-Andean populations, the shape of the nuchal collar presents a very marked pattern of continuous change with six differentiable states, including its absence (for more details see Angarita-Sierra 2009). Therefore, *N. atrata* is considered a polymorphic species with a high level of intraspecific variation both within its populations and throughout its geographical distribution range. This geographic variation could reflect environmental phenotypic plasticity and/or could be due to genetic differences that reflect the divergence of the trans-Andean and cis-Andean populations as independent evolutionary units (Angarita-Sierra, 2009).

Thus, the purpose of this work is to determine if phenotypic variation in the former *N. atrata* (species that have recently been synonymized with different *Ninia* species) and current *N. atrata* populations are correlated with its genetic variation, as well as if the current taxonomy is consistent with molecular phylogenetic data. More specifically we take special interest on newly sequenced populations from Colombian trans and cis Andean populations, and additionally we aim to compare for the first time the oceanic island of Tobago population to its sister island, the continental island of Trinidad (Lesser Antilles), to assess their systematic position and likely taxonomy. We also include for the first time in a phylogenetic study *Ninia franciscoi* from Paria Peninsula (northern Venezuela) to corroborate its phylogenetic position. Furthermore, we intend to investigate the historical biogeography of the species by estimating divergence times and ancestral areas, while also attempting to shed light on the *N. atrata* species complex, clarify its taxonomic and species composition, and elucidate its evolutionary history through phylogenetic analyses.

Materials and methods

Criteria for species recognition

The application of species concepts to recognition, delimitation and description has long been a source of controversy. Following Smart et al. (2021), and as part of a recent trend among molecular systematists and taxonomists to operate under a species delimitation framework, we herein adopt the unified species concept (De Queiroz, 2005, 2007). The unified species concept is broad and compatible with other species concepts, including the biological (Mayr, 1942; Wright, 1940), evolutionary (Simpson, 1951; Wiley, 1978) and general lineage (de Queiroz, 1999, 2005). This unifying species concept complements coalescent species delimitation by emphasizing an integrative framework (De Queiroz, 2007; Fujita et al., 2012; Sukumaran & Knowles, 2017). This concept allows the evaluation of multiple lines of evidence in the face of broad geographic distributions and potential cryptic diversity (Smart et al., 2021). To discover species boundaries and to assess taxonomic richness we followed steps mostly within a Bayesian species delimitation workflow (Grummer et al., 2014). (1) We assigned individuals to lineages using molecular phylogenetic methods, using three independent molecular lines of evidence, haplotypes, mitochondrial and nuclear genes, under both Bayesian and Maximum Likelihood reconstructions; (2) we estimated divergence times to assess the independence of lineages (ca. genetic distance); (3) we utilized three species delimitation models, bPTP (Zhang et al., 2013), the Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2021) and the Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al., 2012), and (4) performed a biogeographic reconstruction using statistical dispersal-vicariance analysis (S-DIVA) (Yu et al., 2010, 2015, 2020), to assess the compatibility of the species identifications with known regional patterns due to associated orographic and biogeographical barriers. Multiple lines of evidence for our candidate species were assumed as validation of independent lineage evolution. Additionally, phylogenetic position and genetic distance is believed to be supportive of reproductive isolation and allopatric isolation, particularly relevant for the islands of Trinidad and Tobago, where many taxa show distinct evolutionary lineages (e.g., Angarita-Sierra, 2014; Avibase, 2025; BES-Net TT Project, 2025;

Jowers et al., 2011; Jowers, Sánchez Ramírez, et al., 2021).

Molecular and phylogenetic analyses

Specimens ($n = 17$) from Colombia, the Republic of Trinidad and Tobago and Venezuela (including Venezuelan samples from the type locality of *Ninia atrata*) were euthanized using pentobarbital following ASIH guidelines (Beaupre et al., 2004). DNA extractions were performed using a Qiagen DNeasy blood and tissue kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The sequenced fragments included mitochondrial 12S and 16S ribosomal RNA, cytochrome b (cytb) and subunit 4 of NADH dehydrogenase (nd4), as well as the nuclear genes for oocyte maturation factor (c-mos) and neurotrophin-3 (nt3). These gene fragments are very informative for interspecific studies in snakes, as shown by Daza et al. (2009) and Salvi et al. (2018). The primers used for the amplification of these genes are shown in the Supplemental Material Table S1. All PCR products were sequenced in forward and reverse directions. Supplementary reads were used to resolve ambiguous base cases in Sequencher v5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). The length of the alignments was: 12S Rrna: 376 base pairs (bp); 16S rRNA: 471 bp; cytb: 1083 bp; nd4: 693 bp; c-mos: 526 bp; nt3: 502 bp. However, not all individuals exhibited the same bp lengths in some alignments.

To evaluate the phylogenetic relationships of *N. atrata*, the sequences obtained in this study were combined with DNA sequences previously generated by Ingrasci (2011) and sequences available in Genbank for the loci analyzed (Supplemental Material Table S2). All of these sequences were aligned in Seaview v.4.2.11 (Gouy et al., 2010) using the default ClustalW2 parameters (Larkin et al., 2007). Finally, the sequences of the six analyzed genes were concatenated into a final alignment of 3651 bp in length. The protein-coding genes cytb, nd4, c-mos and nt3 were translated into amino acids to check for the absence of stop codons.

Outgroup taxa were chosen following Ingrasci (2011), *Dipsas catesbyi*, *Sibon nebulatus*, *Tropidodipsas fischeri* and *Chersodromus* sp. Additionally, other species of the genus *Ninia* were included ($n = 12$, including *Ninia atrata*) in the alignment to evaluate the overall phylogenetic position of *N. atrata.* The most appropriate nucleotide substitution models were determined for each gene fragment using PartitionFinder v.2.1.1 (Lanfear et al., 2017) according to the Corrected Akaike Information Criterion (AICc), in order to choose the optimal partitioning strategy for phylogenetic analyses (Supplemental Material Table S3A,B). To perform this analysis, 14 partitions were established, one for each non-coding gene and three for each protein-coding gene corresponding to each codon position. The search for the optimal partition was carried out under the "greedy" scheme (Lanfear et al., 2012).

In total, 47 taxa were included to construct a phylogenetic tree by the maximum likelihood (ML) method using the RAxML v.8.2.10 program (Stamatakis, 2014), under the GTRGAMMA model, evaluating support through the use of 1000 bootstrap replicates. MrBayes v.3.2.7 program (Ronquist et al., 2012) was used to construct a tree by the Bayesian inference (BI) method under the substitution model that best fits for each gene partition. Two runs of MrBayes were performed, where each run consisted of four chains of 10 million generations, sampled every 1000 generations. 25% of the trees resulting from the analyzes were arbitrarily discarded as "burn in". The remaining trees were used to calculate posterior probabilities (PP) for each bipartition in a consensus tree. Both RAxML and MrBayes were run through the CIPRES platform (Miller et al., 2010). Independent loci ML and BI trees are shown in the Supplemental Material Figs. S1–S6 and selected models are described in the Supplemental Material Table S4. The genetic distances (uncorrected *p*-distances) were calculated with the MEGA v.11.0.13 program (Tamura et al., 2021) using only the fragments of the mitochondrial genes cytb and nd4, as they were the only ones available with sufficient sequences to ensure the reliability of the calculations. PopART (Leigh & Bryant, 2015) was used to build haplotype networks using Median joining networks (Bandelt et al., 1999) (see Supplemental Material Fig. S7).

BEAST v.2.7.5 program (Bouckaert et al., 2019) was used to estimate the phylogeny and divergence times between taxa. Due to the absence of 12S, 16S and c-mos gene sequences in all Ingrasci (2011) samples, these fragments could not be included in the BEAST analysis. Therefore, the partitions used were the sequence of the nt3 gene and the concatenated fragments of the mitochondrial genes cytb and nd4. A concatenated analysis was performed by linking the tree between gene partitions, and separately estimating the clock model and substitution models for each partition in BEAUti. bModelTest v.1.2 (Bouckaert & Drummond, 2017) was used to estimate the most appropriate nucleotide substitution model for each partition, selecting "transitionTransversionSplit" as a parameter of the models to be tested. For the clock model, a strict clock was established using a substitution rate of 1.34% substitutions per million years for the cytb and nd4 gene fragments, and 0.14% substitutions per million years for the

nt3 gene fragment, as estimated by Daza et al. (2009) for Neotropical colubrids based on four calibration points. As for the tree model, a Yule model of speciation was applied. The BEAST program was run twice with 20 million generations per run, sampling every 10,000 steps.

Tracer v.1.7.2 (Rambaut et al., 2018) was used to evaluate convergence between chains and quantify parameter mixing. Effective sampling size (ESS) values greater than 200 are considered to be good indicators of the parameter combination. The log files and tree files were then combined in LogCombiner (BEAST v.2.7.5). A total of 10% of the resulting trees were discarded as "burn in" and the rest were summarized in the maximum clade credibility (MCC) tree using TreeAnnotator (BEAST v.2.7.5) with the "common ancestor heights" option. The final tree was visualized in FigTree v.1.4.3 (Rambaut, 2016) and edited in Inkscape v.1.2.2 (Inkscape Project, 2022).

To assess whether branching patterns within *N. atrata* fit intraspecific or interspecific relationships, the Bayesian Poisson tree process (bPTP) model (Zhang et al., 2013) was used on the maximum likelihood tree estimated at from the six gene fragments analyzed (12S, 16S, nd4, cytb, nt3 and c-mos). This species delimitation method models branching events in terms of the number of substitutions (Zhang et al., 2013). The bPTP method implemented on the PTP web server (Zhang et al., 2013) was executed. In parallel, we run the Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2021) with the following parameters: group probability splitting= 0.001, best scores 10, fixed seed value = −1. In addition, we used the Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al., 2012), method to build species partitions from single locus sequence alignments using the following parameters: 10 steps of intraspecific divergence prior from Pmin = 0.001 to Pmax = 0.10, number of bins: 20. These two methods of species delimitation analyses (ABGD and ASAP) rely on substitution models. We employed a Jukes-Cantor (JC69), but the Kimura (K80) and *p*-distances yield the same results. The analyses were run on the loci that was more representative for the *Ninia atrata* species complex and that could give higher confidence and therefore both analyses were run with the cytb and nd4 data sets separately. Both analyses were run through a web-based interface (https://spartexplorer.mnhn.fr/delimitation).

Biogeographic reconstructions were performed using statistical dispersal-vicariance analysis (S-DIVA) (Yu et al., 2010) in RASP v.4.3 (Yu et al., 2015, 2020). The MCC tree from the BEAST concatenated analyzes was used as an input for S-DIVA analysis, sampling 1000 trees at random. Three areas were defined following Turchetto-Zolet et al. (2013) we established biogeographical areas of South America as (a) Andean, (b) Amazonian, and (c) Central American for the rest of *Ninia* species, allowing for all possible overlaps of areas and maintaining a maximum of two areas. We include Tobago as Amazonian due to its similarity in flora and fauna composition to the mainland mostly through multiple connections to Northern Venezuela (Weber et al., 2025) that has facilitated the colonization of the island. Trinidad was part of the continental mass until the Pliocene (Jowers et al., 2024) and therefore it is considered of Amazonian origin.

Results

Both the Ml and BI phylogenetic analyses recovered similar overall topologies, with major clades having high bootstrap and posterior probability values (Fig. 1). Both analyses supported the monophyly of the *N. atrata* group and revealed the existence of seven divergent lineages: Tobago, Trinidad, trans- and cis-Andean, Venezuela, Ecuador, and Ecuador-Chimborazo, which are highlighted with different colours in Fig. 1. These lineages are grouped into two major clades: one constituted by the lineages of Tobago, Trinidad and cis-Andean, and another clade composed of the lineages of trans-Andean, Venezuela, Ecuador and Ecuador-Chimborazo (Figs. 1 and 2). In comparison to the mitochondrial gene trees and networks, the nuclear data did not resolve some lineages (Supplemental Material S1–S7).

Although the phylogenetic relationships between maximum likelihood and Bayesian inference analyses were generally similar, the location of weakly supported nodes was inconsistent between both analyses. Overall, the relative position of the Colombian trans-Andean, Venezuela, Ecuador, and Ecuador-Chimborazo lineages within the containing clade was weakly supported in the ML and BI analyses. In particular, the maximum likelihood analysis recovered the Venezuela lineage as a sister to the Colombian trans-Andean lineage, while the Bayesian inference analysis recovered the Ecuador lineage as a sister to the Colombian trans-Andean lineage. However, the relative position of these lineages was strongly supported in the BEAST analysis (Fig. 3), coinciding with the topology of the maximum likelihood analysis, with posterior probabilities greater than 0.95 at each node.

The bPTP, ASAP and ABGD species delimitation analyses were congruent, identifying up to nine possible species with 7 lineages within the former *N. atrata* species complex (Fig. 1). Both the ASAP and ABGD recovered the same results for each locus (cytb and nd4). An unexpected delimitation was obtained within

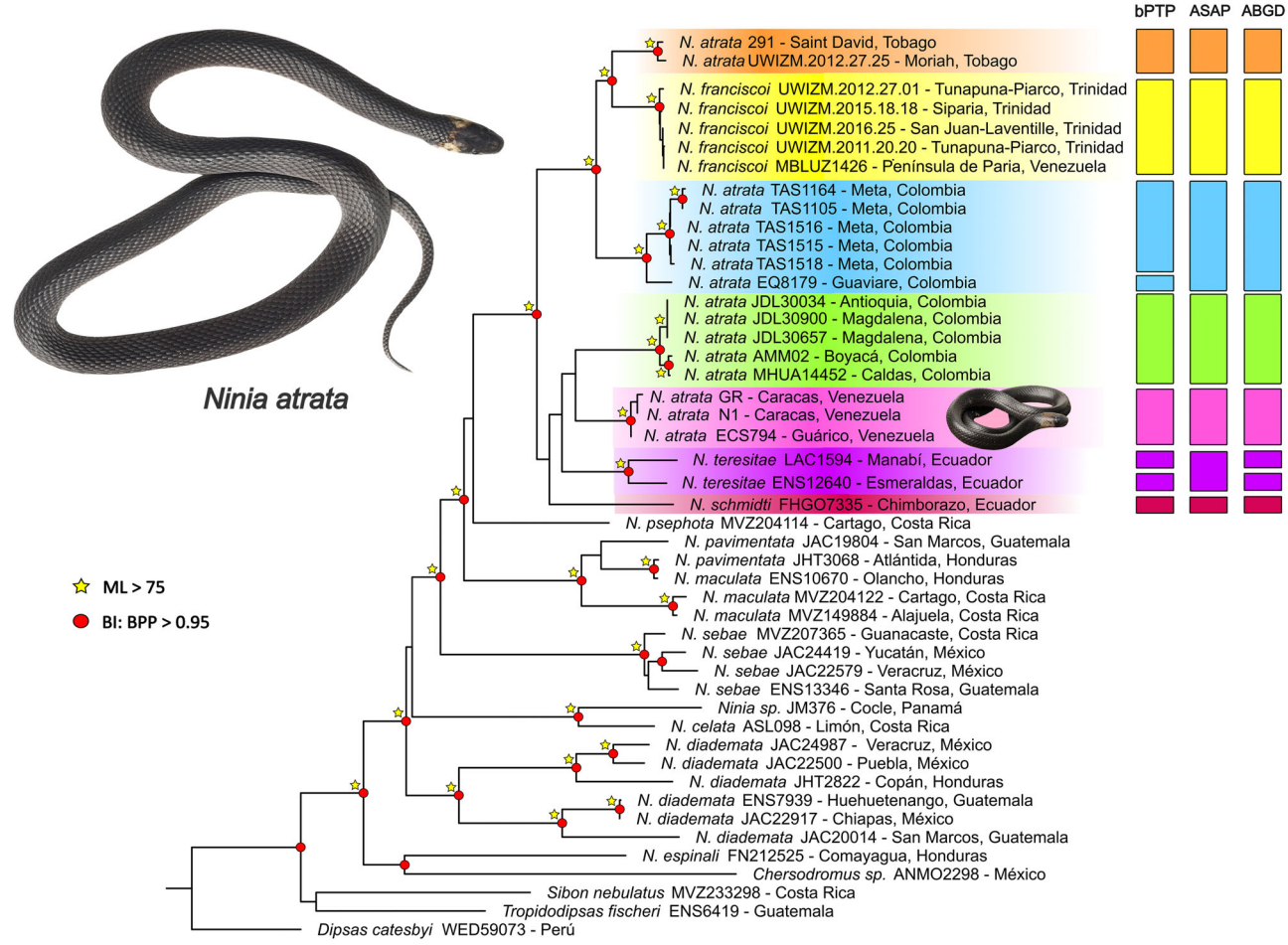

Fig. 1. Maximum likelihood (ML) tree obtained with RAxML and derived from the analysis of DNA fragments of the 12S, 16S, cytb, nd4, c-mos and nt3 genes of specimens of the genus *Ninia*. Red dots on the nodes represent posterior probabilities (BPP) greater than 0.95 obtained from Bayesian inference (BI) analysis. The yellow stars of the nodes indicate bootstrap values greater than 75% obtained from the maximum likelihood analysis. Vertical rectangle bars represent results of species delimitation analyses: Bayesian Poisson tree process model (bPTP), the Assemble Species by Automatic Partitioning (ASAP) and the Automatic Barcode Gap Discovery (ABGD) Lineages are coded by colours; orange: lineage Tobago, yellow: lineage Trinidad and Paria Peninsula; blue: lineage Colombia east; green: lineage Colombia west, pink: lineage Venezuela, purple: lineage Ecuador, plum: lineage Ecuador Chimborazo. The top left photograph of *N. atrata* corresponds to a specimen from Meta, Colombia (Colombian cis-Andean), taken by T.G. Angarita-Sierra. The small *Ninia atrata* picture insert depicts the *atrata sensu stricto* clade, a specimen from the type locality, Caracas, (Venezuela) taken by L. A. Rodríguez.

the Ecuador lineage, separating it into two species with the exception of ASAP. Furthermore, the distinction was reinforced between the Ecuador and Ecuador-Chimborazo lineages as different species.

The Tobago and Trinidad lineages are more closely related to each other than to the cis-Andean lineage, which corresponds to the smallest genetic distances, between the Tobago and Trinidad lineages, 4.87% for cytb and 5.69% for nd4 (Supplemental Material Table S5). The genetic distance between these lineages was greater than the genetic distance within each lineage (Supplemental Material Table S6), being 0.08% for nd4 in the Trinidad lineage, 0.87% for cytb, and 0.93% for nd4 in the Tobago lineage. On the other hand, the greatest genetic distances were observed between the two Ecuadorian lineages and those from Trinidad and Tobago, with the maximum genetic distance of 10.61% for cytb between Ecuadorian and Trinidadian lineages. These maximum genetic distances coincide with the greatest geographic distances between *N. atrata* populations (Fig. 2). Furthermore, the Ecuador lineage presented the greatest genetic distance among all lineages, being 4.01% for cytb and 3.24% for nd4 (Supplemental Material Table S5), which contrasts with the values obtained for Trinidad and Tobago, and therefore, the estimated genetic distances show contrasting levels of differentiation within localities. On the other hand, the genetic distance between the trans- and cis-Andean

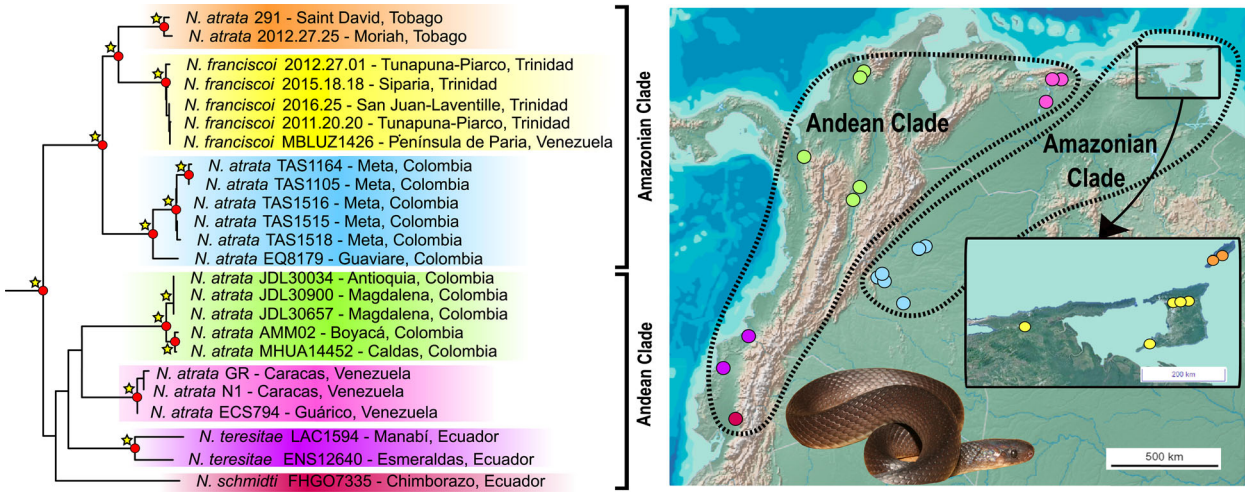

Fig. 2. Left: fragment of the maximum likelihood phylogenetic tree corresponding to the *N. atrata* lineages. Right: map with the location of the 24 *N. atrata* samples analyzed in this work. The colors represent the different lineages obtained in the phylogenetic analyses. The photograph of *N. franciscoi* corresponds to a specimen from Trinidad, taken by J.C. Murphy.

lineages was 8.64% for cytb and 10.09% for nd4; while the genetic distance between the Ecuadorian lineages was 9.58% for cytb and 7.10% for nd4 (Supplemental Material Table S5). Regarding the genetic distance between individuals of the same species, *N. atrata* (the Tobago and trans and cis Colombian linages) was the second species with the highest intraspecific variation among those tested in this study (Supplemental Material Table S7, see Supplemental Material Table S8 for genetic distances).

The MCC tree (Figs. 3 and 4) shows the South American clade *N. atrata* as sister to the more basal Central American species (*N. psephota*+*N. pavimentata*+*N. maculata*). The most recent common ancestor between these clades is estimated to be in the Late Miocene, approximately 6.78 million years ago (Ma) (highest 95% posterior density [95% HPD]: 6.07–7.51 Ma), suggesting a Central American origin, subsequently dispersing towards South America (Fig. 4). Within *N. atrata*, the results suggest an ancient divergence between lineages on either side of the Andes: the split between the lineages of (Trinidad + Tobago + Colombia east lineage) and those of (Colombia west + Venezuela + Ecuador + Ecuador-Chimborazo lineages) It is estimated that it occurred in the Early Pliocene, approximately 5 Ma (95% HDP: 4.42–5.58 Ma). On the other hand, the divergence between the lineages of Trinidad and Tobago and the continent (Colombian east lineage) dates back to 3.02 Ma (95% HDP: 2.54–3.53 Ma). The split between the Tobago and Trinidad lineages is estimated to have occurred 2.26 Ma (95% HDP: 1.84–2.74 Ma), during the Pleistocene; while the time of divergence between the lineage of Ecuador and those of Venezuela and the Colombian west lineage dates to 3.74 Ma (95% HDP: 3.24–4.29 Ma.). These last two lineages (Venezuela-Colombia west lineages) separated 3.06 Ma (95% HDP: 2.53–3.60 Ma).

Discussion

Cryptic species within *Ninia atrata*

Our findings strongly support the existence of a species complex within both current and former *Ninia atrata* populations, distributed from the Lesser Antilles to Ecuador. The combination of genetic distances between these *Ninia* lineages, results from species delimitation analyses, geographical isolation, and previously documented morphological differences suggests these lineages likely represent multiple distinct species.

Our molecular results further indicate that the Venezuelan lineage (comprising populations from Caracas and Guárico – both localities falling within the type locality defined by Hallowell, [1845] as “less than 200 miles from Caracas”) represents *Ninia atrata* sensu stricto (see syntype ANSP 3410). This suggests that the Tobago lineage and both eastern and western Andean Colombian lineages remain unnamed, as no available names currently apply to them. However, formal delimitation of these candidate species will require additional supporting data. Furthermore, the validity of *N. franciscoi, N. teseritae* and *N. schmidti* is not disputed, and their divergence times (being conservative at around 3 Ma between clades) suggests that all clades with an older divergence time are candidate species. This would a priori indicate that the populations from Tobago and

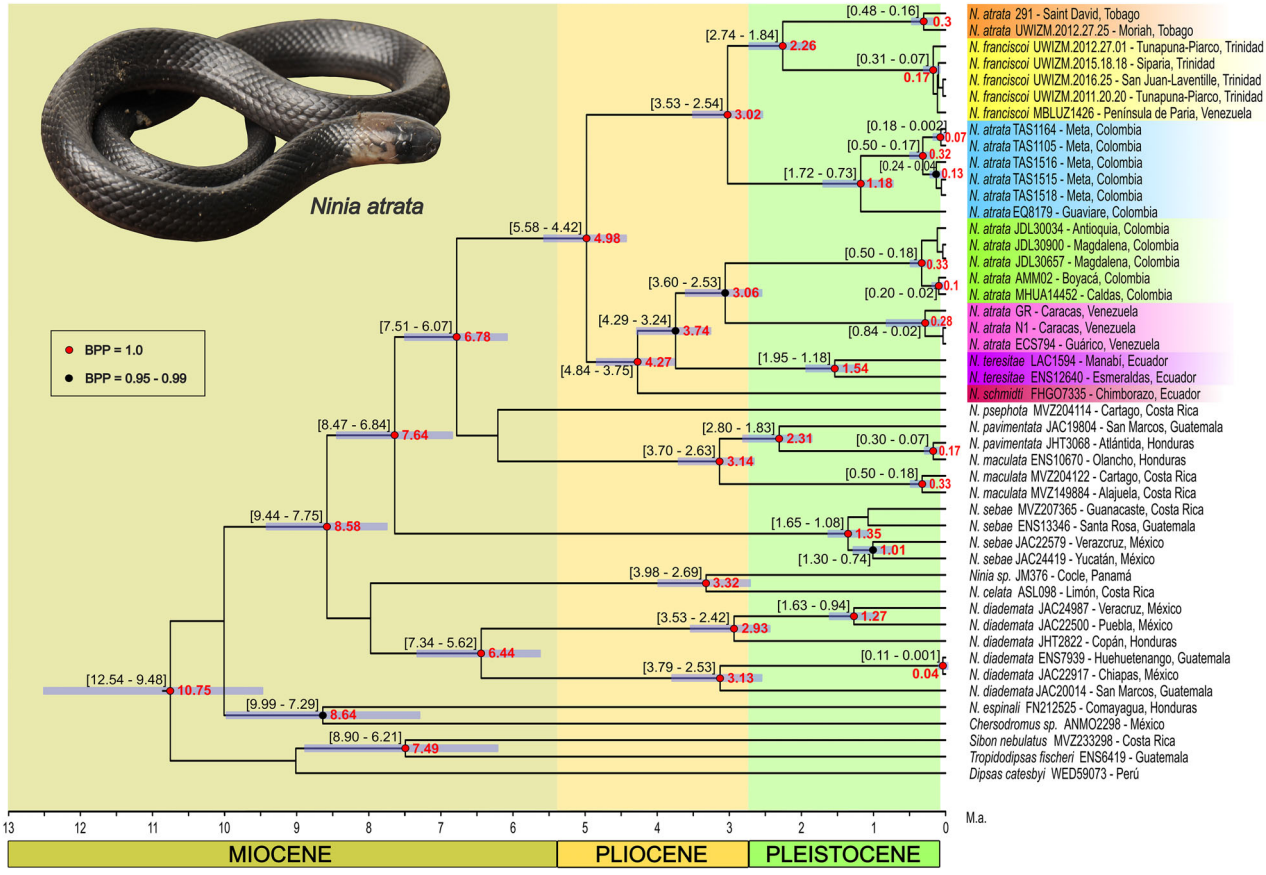

Fig. 3. Bayesian time tree as inferred by BEAST v.2.7.5 for the set of concatenated sequences of the cytb, nd4 and nt3 gene fragments. The red and black dots on the nodes respectively represent posterior probabilities equal to 1.0, or greater than 0.95 but less than 1.0. The red numbers in the nodes indicate mean ages in M.a. (millions of years ago), and the blue bars represent the ranges of the highest 95% posterior density (95% HPD), with their numerical value in brackets. Only 95% HPD is shown on well-supported nodes. The photograph of *N. atrata* corresponds to a specimen from Caracas, Venezuela (the type locality) taken by L. A. Rodríguez.

the trans and cis Andean Colombian populations are likely three distinct species. However, the impossibility of discerning the limits of the species with certainty, in some cases due to their morphological similarity, or simply due to insufficient data, leads to the conclusion that *N. atrata* represents a complex of species that requires greater sampling and in need of a careful review to clarify its taxonomic composition. We follow other studies on hidden snake cryptic diversity (i.e., Jadin et al., 2019, 2024; Jowers et al., 2023) to unravel the presence of lineages that will likely require exhaustive taxonomic arrangements rather than attempting premature taxonomical changes at this point. Furthermore, already preliminary morphological data of populations from the Colombian eastern and western Andean populations suggest significant differences (Angarita-Sierra, 2009) and the likelihood of two distinct species. Indeed, our ongoing preliminary data on morphological data analyses of these lineages show distinctive features between them and to all other described *Ninia*, again suggesting the need for future taxonomical changes (data not shown). The future combination of such data added to genetic differences between the trans-Andean and cis-Andean populations and the geographic isolation between them constitutes additional evidence of the independent evolution of these populations. Unresolved species as inferred from the nuclear data alone suggests that these markers are highly conservative for the short evolutionary times of the studied lineages.

The populations of *N. atrata* from Tobago and Trinidad (now *N. franciscoi* in Trinidad and the Paria Peninsula) present considerable genetic divergence with respect to their presumed ancestral Colombian east lineage, suggesting some level of differentiation. Interestingly, lineages from Trinidad and Tobago were

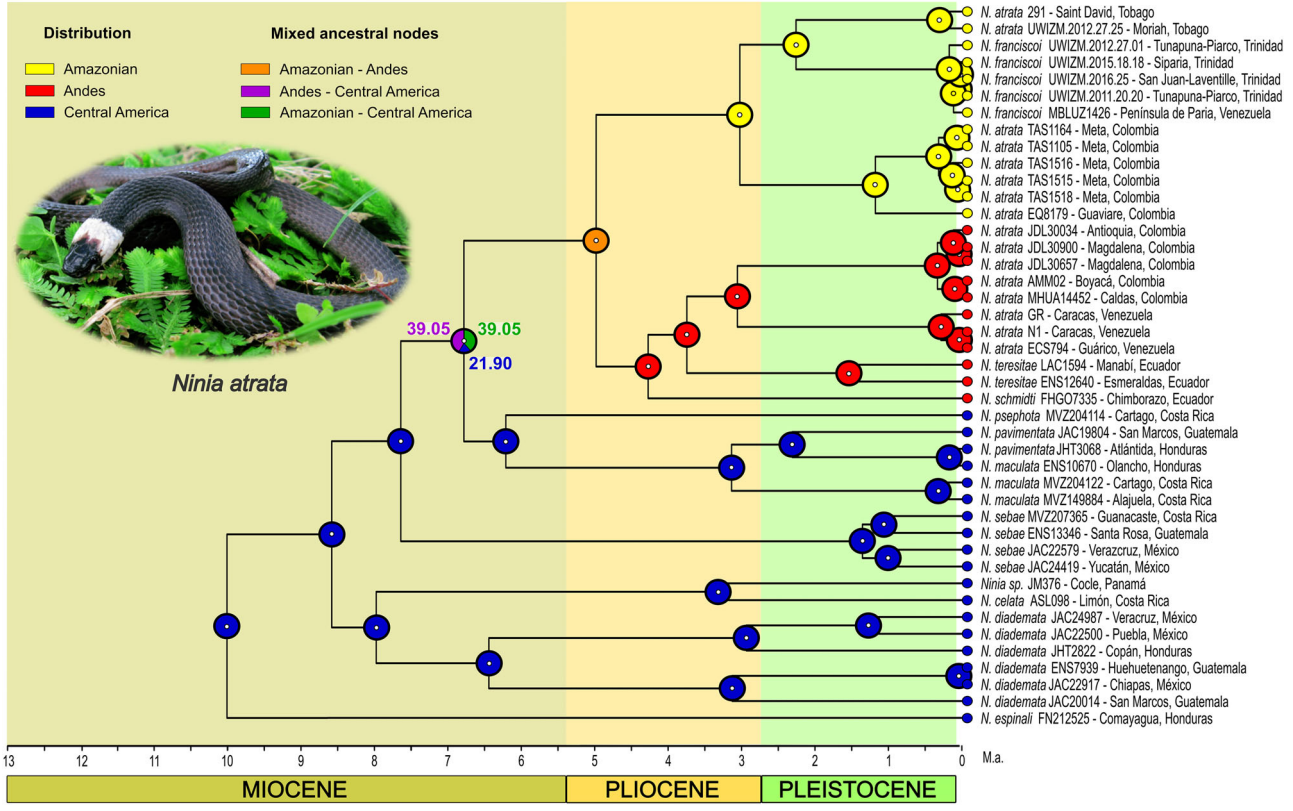

Fig. 4. Statistical dispersion-vicariance analysis (S-DIVA) tree for *N. atrata*. The pie charts on the nodes represent the results of the S-DIVA analysis of the mixed distribution ancestral nodes. All distribution nodes are recovered with a single origin, except for the node with percentages shown. The photograph of *N. atrata* corresponds to a specimen from Antioquia, Colombia (Colombian trans-Andean), taken by T.G. Angarita-Sierra.

more closely genetically to those from the Colombia east lineage than to individuals from Venezuela (Fig. 3). Angarita-Sierra (2009) suggests that the lack of study and knowledge on Venezuelan populations of *N. atrata* has caused different researchers to partially report differences in the pattern of the nuchal collar, from conspicuous to absent, which correspond to the variations in the continuous change of the nuchal collar pattern for populations distributed in the cis-Andean region (e.g., Lancini, 1979; Roze, 1966). This lack of knowledge also suggests the possibility that the topology of the trees obtained in this study changes by increasing the number of samples analyzed per location or by increasing the sampling area, especially in Venezuela.

While species delimitation analyses also identified the Tobago, Trinidad, and Venezuela lineages as three possible distinct species in ASAP and ABGD, the boundaries inferred by bPTP are only approximate (Zhang et al., 2013), so additional data needs to be integrated. Under sampled species or OTUs, compared to over-sampled ones, cannot be correctly delimited, with each individual likely to be identified as a separate species (Zhang et al., 2013).

Biogeography

The South American *Ninia* dates to the Early Pliocene, suggesting a Central American arrival before the closing of the Isthmus of Panama about 2.8 Ma (O'Dea et al., 2016), as has been documented in other snakes (Rojas-Morales, 2012). The existence of two distinct lineages on each side of the Andes Mountains has also been observed in different species (e.g., Dixon, 1979; Murphy et al., 2017; Santos et al., 2009), reflecting the importance of the Andes Mountains as a key factor in the processes of allopatric speciation. Indeed, taking into account that *N. atrata* has a wider altitudinal range (1800 m) whose frequency of encounter decreases as one ascends the altitudinal gradient (Angarita-Sierra, 2009, Natera-Mumaw et al., 2015; Rivas pers. obs), the dates of divergence between some lineages east and west of the mountain range suggest vicariance, where the widely distributed ancestral population would have remained fragmented into isolated subpopulations due to the uplift of the Andes.

Two sister clades were recovered in the *Ninia atrata* species complex. An older Mid-Pliocene clade with an Andean distribution (an environment also associated

with the Choco, Turchetto-Zolet et al., 2013), in Ecuador, Venezuela, and Western Colombia, and a more recent Late Pliocene clade of Amazonian distribution from Trinidad, Tobago, and Eastern Colombia. The distributional pattern of the two groups suggests a first arrival of the Andean clade to South America with likely southern splitting of its most recent common ancestor towards the southern Andean region of Ecuador and an eastern dispersal through the northern region of the Eastern Cordillera of Colombia and Venezuela. Palaeoelevation estimates suggest a 40% reduction in the altitude of the Eastern Cordillera until the Early Pliocene, suggesting a moderate altitude. Our timing estimates indicate that this colonization event towards the east could have occurred before the northern Andes reached their present elevations around 2.7 Ma (Gregory-Wodzicki, 2000) and would have resulted thereafter in an allopatric divergence event between the Venezuela and Colombia West lineages at circa 3 Ma, as suggested by our analysis. To the north, the Mérida Mountain Range would also have served as a barrier isolating the population of Venezuela. Curiously, the species does not appear to be present in the Lake Maracaibo Basin, in the Llanos lowlands of Venezuela (although it is present in the Andean foothills) and in southern Venezuela (Natera-Mumaw et al., 2015, Rivas pers. obs.). The Amazonian clade would have followed an eastern dispersal through the same region, with the most recent common ancestor of the Trinidad and Tobago lineages splitting from the Colombian east lineage at 3 Ma. The Trinidad and Tobago lineages would have reached through the coastal forest region to the Paria Peninsula and most likely stopped in their expansion to the east by the Orinoco Delta. The Colombian west lineage might have used the lower mountain range on the northern Andes for a southern expansion, but it was isolated by the uplift of the Andes thereafter. Rojas-Morales, (2012) discusses a lowland rainforest corridor that existed between the Chocoan and Amazon forest (the Huancabamba Deflection) to account for the presence of *Rhinobothryum* on both sides of the Andes, as did Dixon (1979) to explain the recent geographical connection in *Chironius*, *Leptophis* and *Liophis*. The upper Pliocene rise of the Andes would have isolated populations on both sides of the mountain chain. However, the presence of *Ninia teresitae* found only to the west of the Andes suggests that the species might have arrived from the south only after the closing of the Huancabamba Deflection. In addition, the non-close phylogeographical position of the Colombia West lineage to the Andean clade suggests that this scenario is much less likely to explain the presence of that lineage to the east of the Andes.

The Late Pliocene divergence between the continental population (Colombia east lineage) and those of Trinidad (Fig. 3) is congruent when the island was already separating from the mainland, but still suitable connections were available (Jowers et al., 2024; Persad, 2009; Weber et al., 2025). Given the shallow sea depths in this region, the island of Trinidad was part of the continent (Paria Peninsula: Rivas et al., 2021) at sea level drops (−50 m), so the existence of land connections between the continent and the island of Trinidad is more plausible than an over-water dispersal scenario (Murphy, Salvi, et al., 2019; Weber et al., 2025). Therefore, the presence of *Ninia franciscoi* on Trinidad and the mainland Paria Peninsula suggests the existence of terrestrial connections that were probably established because of changes in sea level in the eastern Caribbean during the Pleistocene or simply through the connected mountain range of Trinidad′s northern Range and the Paria Peninsula (Jowers et al., 2024; Rivas et al., 2021).

Ninia franciscoi populations from Trinidad and *Ninia* from Tobago would have remained isolated from mainland populations during periods of sea level rises, allowing considerable genetic differences to accumulate between these populations, as has been observed in other species between islands (Jowers et al., 2011, 2015). At the time of the split between the *Ninia* lineages of Trinidad and Tobago, about 2.2 Ma (Fig. 3), the island of Tobago was located north of Trinidad, but west of its current position (Jowers et al., 2015), moving along the edge of the South American plate to its current location to the northeast of Trinidad at a rate of 20 mm per year due to the movement of tectonic plates (Jowers et al., 2015, 2024; Pindell et al., 2007; Weber et al., 2001, 2015, 2025). The sister clade relationship between the Trinidad and Tobago lineages supports the possibility of terrestrial corridors that connected the islands for brief periods (thousands of years) during the Pleistocene, corresponding with the drier climates and lower sea levels (Weber et al., 2025). Sea level rises during the interglacial periods of the Pleistocene may have restricted gene flow between the islands of Trinidad and Tobago, probably allowing the accumulation of genetic differentiation between these populations. This is not the first example of a cryptic snake species in Trinidad and Tobago (Jadin et al., 2024). Few detailed molecular clock estimates report snake divergence between the islands of Trinidad and Tobago (Murphy et al., 2023). Two species, *Tantilla melanocephala* and *Atractus trilineatus*, show younger divergence between islands (180 ka and 1.4 Ma, respectively), suggesting colonization at a later time. Several endemic species in Tobago, such as *Erythrolamprus pseudoreginae* (Murphy, Braswell, et al., 2019), lack molecular dating but likely reflect much earlier colonization periods. The evidence of a high genetic divergence between

Ninia from both islands is a likely indication of their distinct taxonomic status.

Discontinuous biogeographical distribution

As previously explained, the distribution of the *N. atrata* species complex is likely the result of the changing topographical conditions, extending from the slopes of the southern Andes of Ecuador, to the Northern Cordillera of Trinidad and Tobago, the Main Cordillera of Tobago to the northeast, passing through the slopes of the Colombian Andes and the Central Coastal Cordillera in Venezuela (Fig. 2). From a biogeographical perspective, the discontinuous distribution of the species between the Colombian plains east of the Andes and the central plains of Venezuela, as well as after the Central Coast Mountains in Venezuela until its presence again in Tobago and Trinidad, could be explained by several hypotheses. One explanation for the absence of *N. atrata* in the Eastern Coastal Range of Venezuela is that, while conditions for colonization were suitable along the land bridge to Trinidad and Tobago, they may not have been ideal for its survival in the Eastern Coastal Mountain Range. Nevertheless, this is unlikely as there are reports of the species in tropical dry forest on the Caribbean coast (Mesa-Joya, 2015), which is the same habitat as the eastern coast of Venezuela. Based on geography and terrestrial connections throughout the Pliocene, another possible explanation would be that this species colonized both the Eastern Coast of Venezuela and the plains of southwestern Venezuela, but that these populations became locally extinct, possibly as a consequence of the low number of individuals or due to fluctuations in environmental factors in the region (Jowers et al., 2007). Indeed, eastern Andean populations of *N. atrata* are susceptible to dry environments or precipitation fluctuations (Angarita-Sierra & Cesar Alejandro López-Hurtado, 2020; Angarita-Sierra & Lozano-Daza, 2019). Most of the areas inhabited by *Ninia atrata* in the Venezuelan Cordillera de la Costa are characterized by a closed canopy, abundant leaf litter, with very characteristic humidity and rainfall conditions (most records occur between 300 and 1000 m), where they are often found under logs or rocks. However, the presence of the species in the central plains of Venezuela and the Colombian plains suggests that this species should thrive in regions similar to southwestern Venezuela. Furthermore, the elusive behavior of *N. atrata* and its semifossorial ecology constitute an added difficulty for searching and sampling the species. Discontinuous distributions have been found in other studies of reptiles and amphibians in the region, for example, the snake *Atractus fuliginosus* in Tobago and with its closest population in Western Venezuela (Jowers, Schargel, et al., 2021; Murphy et al., 2021). Thus, it is apparent that the biogeography of the region and colonization routes of Ninia are as diverse in snakes (Murphy et al., 2023) as those in frogs of the genera *Elachistocleis* (Jowers, Othman, et al., 2021), *Pristimantis* (Jowers, Sánchez Ramírez, et al., 2021), and the snakes of the genus *Micrurus* (Jowers et al., 2019), suggesting complex scenarios of speciation and changing topography in northern South America.

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Supplemental material

Supplemental material for this article can be accessed online here: https://doi.org/10.1080/14772000.2025.2572760.

Permits

Specimens of *Ninia atrata, Ninia franciscoi* and *Ninia* sp. were collected in different locations in Colombia, Venezuela, Trinidad and Tobago, under collection permit number 1,375 granted to Gilson A. Rivas by the Ministerio del Poder Popular para el Ecosocialismo, and under special hunting licenses from the Wildlife Section of the Government of Trinidad and Tobago granted for scientific purposes in 2015–2016 to Renoir Auguste, John Murphy and Mike Rutherford. Permission for field surveys in Colombia was granted by the National Environmental Licensing Authority (ANLA). Project approval (No. 27212 under resolution No. 0255 of 14 March 2014) was issued by the National Environmental Licensing Authority (ANLA).

Disclosure statement

No potential conflict of interest was reported by the authors.

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