




SHORT COMMUNICATION

The enigmatic biogeography of Tobago's marooned relics: The case study of a fossorial snake (Squamata, Dipsadidae)

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Abstract

The islands of Trinidad and Tobago form a southern extension of the Lesser Antilles. Unlike the continental island of Trinidad, the more northerly Tobago formed as an older oceanic island volcanic arc. Their reptile biodiversity reflects colonization events from the South American mainland through land bridge connections at times of glacial maxima. Most of Tobago's herpetofauna has colonized through stepping-stone events from Trinidad. However, the enigmatic presence of a rare and poorly known fossorial snake in Tobago, Western Venezuela and Colombia, but absent in Trinidad and Eastern Venezuela, raises interesting questions regarding its biogeography, mode and timing of colonization of the island. Here, we sequence for the first time gene fragments from three individuals from Western Venezuela and one from Tobago and include them in the largest phylogeny of *Atractus* to date. We validate the monophyly of the species based on morphology and molecular data, with an unexpected low genetic divergence between island and mainland specimens. Despite more than 1000 km separating them, our time tree indicates a mean 550,000 year divergence. We examine alternative scenarios to explain the biogeography and conclude on an ancient corridor of coastal land bridges at times of very low (>100 m) sea-level falls that connected Venezuela to Tobago.

KEYWORDS

biogeography, Caribbean, colonization, South America

Resumen

Las islas de Trinidad y Tobago forman una extensión al sur de las Antillas Menores. A diferencia de la isla continental de Trinidad, la isla de Tobago más al norte se formó mediante un arco volcánico mucho más antiguo. Su biodiversidad de reptiles refleja los eventos de colonización del continente sudamericano a través de conexiones de puentes terrestres en momentos de glaciaciones en su estado máximos. La mayor parte de la herpetofauna de Tobago llegó a través de eventos de colonización en saltos desde Trinidad. Sin embargo, la presencia enigmática de una serpiente fosorial rara y poco conocida en Tobago, en el oeste de Venezuela y Colombia, pero ausente

en Trinidad y el este de Venezuela, plantea preguntas interesantes con respecto a su biogeografía, así como el modo y el momento de colonización de la isla. Aquí, secuenciamos por primera vez fragmentos de genes de tres individuos del occidente de Venezuela y uno de Tobago y los incluimos en la filogenia más grande de *Atractus* hasta la fecha. Validamos la monofilia de la especie basándonos en la morfología y los datos moleculares, con una inesperada baja divergencia genética entre los ejemplares insulares y continentales. A pesar de que los separan más de 1000 km, nuestro árbol del tiempo indica una divergencia media de 550,000 años. Examinamos escenarios alternativos para explicar la biogeografía y concluimos sobre un antiguo corredor de puentes terrestres costeros en momentos de caídas del nivel del mar muy bajas (>100 m) que conectaban a Venezuela con Tobago.

1 | INTRODUCTION

The Trinidad and Tobago archipelago is located on the continental shelf of northern South America, as the two southernmost island extensions of the Lesser Antilles. The more southerly island of Trinidad is located only a few kilometers from the Venezuelan Paria Peninsula to the east and is proximal to the Orinoco Delta to the south. While both islands are considered southern extensions of the Lesser Antilles, they have continental flora and fauna but different geological origins. Trinidad was formerly attached to Venezuela and was subsequently detached by a pull apart basin in the Pliocene when transform faulting separated these two land masses (Erlach & Barrett, 1990; Flinch et al., 1999; Liddle, 1946). Tobago, on the other hand, was formed as a somewhat ancient oceanic island on the front edge of the Caribbean Plate far to the east of its current position (Jowers et al., 2015; Pindell & Kennan, 2007). Trinidad's Northern Range and Tobago's Main Ridge can be considered as eastward extensions of the coastal mountain range complex formed by the Venezuelan coastal ranges (Rivas et al., 2021). Both islands offer a unique opportunity to study the processes of colonization and speciation from the mainland, specifically from Venezuela and the Guianas. Eustatic sea-level changes during the Pliocene-Pleistocene have resulted in prolonged periods of connection between the islands and the mainland (Murphy, 1997), which allowed for both ancient and recent colonization and isolation events. Geologic, geographic, and climatic changes result in three hypotheses to explain the herpetofaunal diversity in these islands: overseas dispersal, landbridge connections, and vicariance (Boos, 1984a, 1984b; Camargo et al., 2009; Jowers et al., 2008, 2011; Manzanilla et al., 2007; Rodriguez & Lopez, 2003).

The fossorial, cryptozoic Hallowell's Ground Snake *Atractus fuliginosus* Hallowell, 1854 is found in Colombia, Venezuela and the Caribbean island of Tobago (Medina-Rangel et al., 2019). Unlike its congener, *Atractus trilineatus*, which occurs on Trinidad and the mainland, the distribution of *A. fuliginosus* remains enigmatic. The frog *Hyalinobatrachium orientale tobagoense*, present in Tobago, has a similar distribution, although in Venezuela it is found much further east, up to the Paria Peninsula. As suggested by Jowers et al. (2015), such relationships indicate a Pliocene "land bridge" connection between Tobago and Venezuela to explain

the presence of the glass frog *Hyalinobatrachium orientale* on Tobago. This land bridge occurred when the island was located circa 60 km further west through 20 km/Myr plate tectonic movement (Weber et al., 2001), on the northwestern side of Trinidad, rather than on its present northeastern side (Jowers et al., 2015). However, the distribution of *A. fuliginosus* and *H. orientale* remain puzzling given that a more intuitive explanation for their presence in Tobago involves stepping stone colonization events from the mainland via Trinidad and then to Tobago. Indeed, many of the species found in Tobago are also found in Trinidad, which suggests prolonged land corridors connecting both islands (Murphy et al., 2018). However, these two species are absent in Trinidad, and if at all present there, would indicate a corridor via Trinidad and subsequent extinctions. Sea-level falls of 120 m would have allowed the colonization of Tobago through land bridge connections and therefore must have also connected Trinidad, since the Paria Gulf has shallower sea depth (~6 m).

Tobago has eight endemic species, three frogs, two lizards, and three snakes (Murphy, Braswell, et al., 2019; Murphy et al., 2018; Murphy, Salvi, Santos, et al., 2019). Most Tobago endemics seem to have their closest living relatives in the Venezuelan Central Coastal Range, as opposed to the more proximal island of Trinidad. For example, the Tobago endemic frog *Mannophryne olmonae* is sister to the coastal range endemic stream frog *M. riveroi* (Manzanilla et al., 2009), and the Tobago endemic *Bachia whitei* seems related to mainland *B. flavescens* (Murphy, Salvi, Santos, et al., 2019). The Tobago Stream Snake, *Erythrolamprus pseudoreginae* is known only from Tobago, but its closest relatives are present in North-Central Venezuela (Murphy, Braswell, et al., 2019). However, other endemics such as the lizard *Gonatodes ocellatus* and the snake *Erythrolamprus ocellatus* seem to have their closest living relatives in both Venezuela and also in Trinidad. Such relationships are likely explained by ancient cladogenic events in the region, but population divergence within species over such distributions remains more enigmatic and their biogeographical explanation remains challenging.

Here, we address for the first time the monophyly of the fossorial snake *A. fuliginosus* from Western Venezuela and from Tobago, by placing DNA sequence data from this species within the most extensive phylogenetic sampling available for the genus. We use the unusual distribution of this species to unravel its biogeography

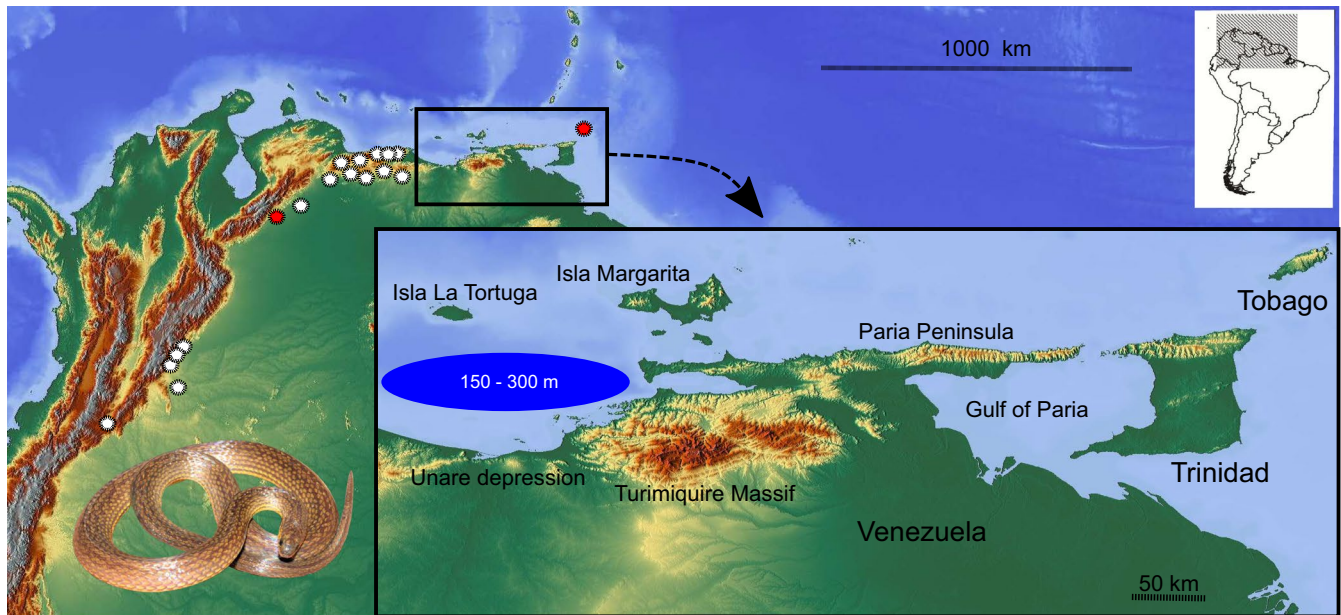


FIGURE 1 *Atractus fuliginosus* sampled localities for this study (red circles) and distribution records (white circles). The insert shows the gap in the distribution from the CCR to Tobago. The blue oval shows modern marine depths in meters. The *A. fuliginosus* pictured is from Tobago, photo by A. L. Braswell

in the Lesser Antilles through the likely timing of colonization from the mainland, and frame it in relation to topographic and climatic conditions in the region. To the best of our knowledge, this is the first study to report on the time and mode of colonization of a reptile that is present in Tobago and in Western Venezuela, but has no population counterparts or sister species inhabiting Trinidad.

2 | MATERIALS AND METHODS

Animals were euthanized following the ASIH guidelines (Beaupre et al., 2004) using pentobarbital. We sequenced parts of genes from a unique specimen of *A. fuliginosus* collected from the island of Tobago ($n = 1$) and from three individuals from North Western Venezuela, in the locality of Barinitas, eastern foothills of the Mérida Mountain range (Figure 1). DNA extraction, purification, and amplification protocols follow Murphy et al. (2020), and primers used are reported in Table S1. We amplified portions of the mitochondrial genes for 12S ribosomal RNA (12S *rRNA*) and 16S ribosomal RNA (16S *rRNA*), cytochrome b (*cytb*) and NADH dehydrogenase 4 (*nd4*), and of the nuclear oocyte maturation factor (*c-mos*) gene. Templates were sequenced on both strands, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v4.9 (Gene Codes Corp., Ann Arbor, MI). The lengths of the alignments were (although not all individuals had the same length in some alignments): 12S *rRNA*, 376 base pairs (bp); 16S *rRNA*, 523 bp; *cytb*, 1083 bp; *nd4*, 669 bp; *c-mos*, 582 bp (Alignment S1–S5). Following Arteaga et al. (2017) and Murphy et al. (2019), we used *Sibon nebulatus* as outgroup. In order to assess the phylogenetic relationships of *A. fuliginosus*, we downloaded all available sequences from Genbank for the targeted loci and concatenated them in an alignment (Table

S2). Sequences were aligned in Seaview v4.2.11 (Gouy et al., 2010) under ClustalW2 default settings (Larkin et al., 2007). The sequences for all five gene fragments were concatenated, resulting in a 3236-bp alignment (Alignment S6). Genetic *p*-distances were calculated using MEGA v7 (Tamura et al., 2011).

Phylogenetic analyses were performed using the Bayesian Inference and Maximum Likelihood methods without implementing any clock model (see Additional Information S1 for methods, Table S3, Figure S1). Molecular dating analyses were conducted using BEAST v2.6 (Bouckaert et al., 2019). From our original dataset (see Table S2), we chose a single sample per terminal species (unless highly divergent, see Figure S1) keeping a total of 57 sequences (Figure 2). We ran a concatenated analysis by linking the tree prior across gene partitions, while estimating the clock and substitution models separately for each partition in BEAUti. We used bModelTest v1.2 (Bouckaert & Drummond, 2017) to co-estimate the best substitution model, together with the phylogeny, and average best-sampled model parameters. For the clock model, we used a lognormally distributed relaxed clock, and for the tree prior, the two-parameter Birth-Death model. The tree was time-scaled using a *cytb* substitution rate estimated using a uniform prior with a range of 0.0099–0.017 substitutions per million years (Daza et al., 2009). All other free parameters used default distributions. We ran two independent chains of 10 million generations each sampling every 1000 states. Log and tree files were then combined using a resampling rate of 2000 states with LogCombiner. Tracer was used to assess convergence between chains and to quantify parameter mixing ensuring that effective sample sizes were kept above 200. Branch-specific model parameters were summarized on the maximum-clade-credibility (MCC) tree using TreeAnnotator. The final tree was visualized in FigTree v1.4 (Rambaut & Drummond, 2007). In addition,

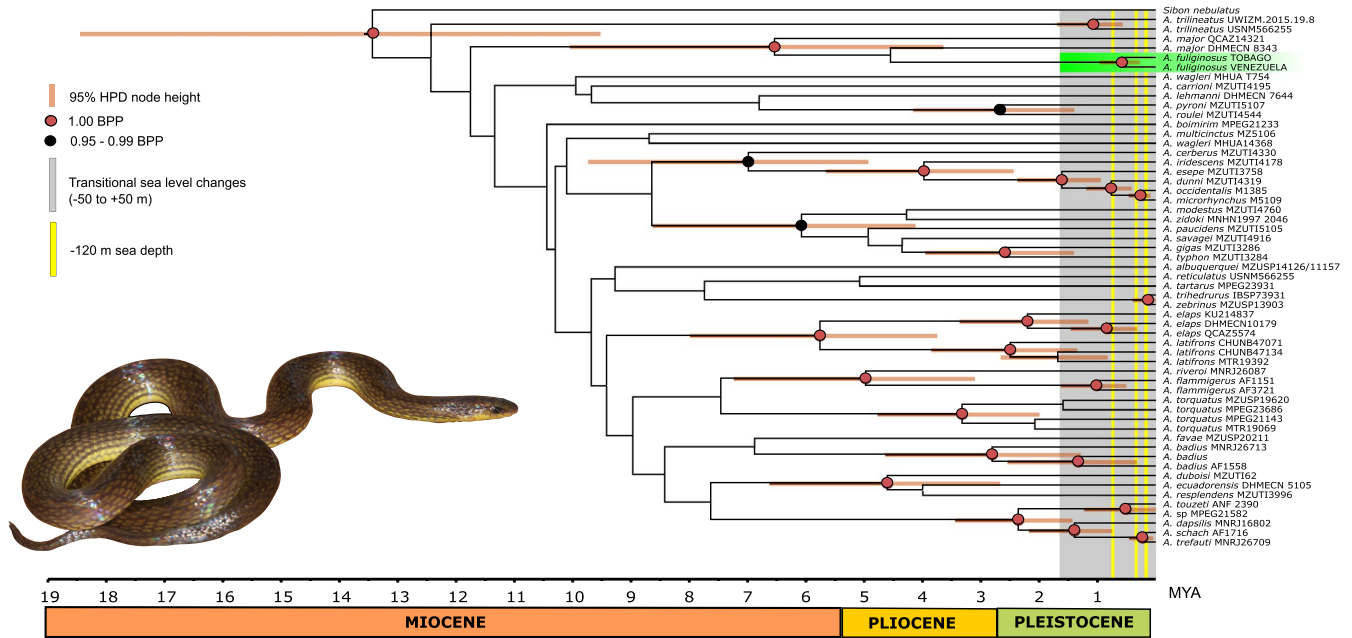


FIGURE 2 Bayesian time tree as inferred by BEAST 2.6 for the dataset of concatenated 12S rRNA and 16S rRNA, cytb, nd4 and c-mos sequences from *Atractus* specimens. Red and black nodes are posterior probabilities (1.00 and >0.95 – 0.99), respectively. Only 95% highest posterior density ranges are shown on well-supported nodes. The *Atractus fuliginosus* pictured is from Tobago, photo by A. L. Braswell

we took morphological measurements of island and mainland specimens. For methods and materials on morphology, see Data S1.

3 | RESULTS

All three individuals from Venezuela recovered the same haplotype for all loci. *Atractus fuliginosus* is monophyletic with low genetic divergence between localities despite the over 1000 km of distance between the Venezuelan locality and Tobago (Figure S1). The genetic distances for the 16S rRNA gene surprisingly revealed no genetic divergence, while the cytb and nd4 genes recovered a 1.7% divergence. *Atractus fuliginosus* is grouped with *A. major* in all analyses rather than with the other *Atractus* species from Tobago, *A. trilineatus*. Overall, our estimates of relationships are highly similar to results from Melo-Sampaio et al. (2019) and Murphy, Salvi, Braswell, et al. (2019) concerning the well-supported clades. Despite weak basal relationships, as in other studies (Melo-Sampaio et al., 2019; Murphy, Salvi, Braswell, et al., 2019), we resolve the tree tips and establish the phylogenetic position of *A. fuliginosus* (Figure 2, Figure S1).

Divergence time estimates between species are also in agreement with those of Murphy, Braswell, et al. (2019). The timing of the most recent common ancestor (TMRCA) between *A. fuliginosus* and *A. major* is estimated at the Late Miocene (6.3 Mya; 95% Highest Posterior Density [95% HPD] 3.6–10 Mya), while the split within *A. fuliginosus* dates at 550,000 years ago (95% HPD 270,000–960,000 years ago). Morphological results confirm our phylogenetic analyses, and suggest that Tobago and Venezuela populations are conspecific, with some population differentiation as well as color patterns (for results on morphology, see Data S1) (Figure 3).

4 | DISCUSSION

Several phylogenetic studies in the region suggest that the frequently changing topography facilitated the connections and colonization events between the mainland (Venezuela and Guyana) and the islands of Trinidad and Tobago (Jowers et al., 2011, 2015, 2020; Murphy, Braswell, et al., 2019; Murphy, Salvi, Santos, et al., 2019). Interestingly, most studies show remarkably low genetic divergence between localities (Jowers et al., 2019; Murphy et al., 2016), suggesting recent colonization of the Lesser Antilles and island extensions plausibly via sea-level drops of 50–120 m (Hansen & Routledge, 2016; Murphy, 1997; Rohling et al., 2014). Most studies have addressed the colonization of Trinidad, as this island has a much greater biodiversity than Tobago, is closer to the mainland, and was historically part of the continental mass. For example, studies on New World Coral snakes (*Micrurus diutius*), and the Black-Headed snake (*Tantilla melanocephala*) from Guyana and Venezuela have shown Pleistocene splits between populations (Jowers et al., 2019, 2020), and genetic similarity in the Trinidad Threadsnake (*Epictia tenella*) indicates possible rafting from Guyana (Murphy et al., 2016). Genetic work on the only other *Atractus* from Trinidad and Tobago, *A. trilineatus*, has likewise revealed recent divergence between Guyana, Trinidad and Tobago, again corresponding to likely low sea-level stands (Murphy, Salvi, Braswell, et al., 2019).

However, all these taxa have representatives in Trinidad, indicating that colonization of Tobago was likely a stepping stone process from southern localities via Trinidad. To the best of our knowledge, the only other study addressing the phylogeography of a species present in Venezuela and Tobago, but not in Trinidad, is the Glass



FIGURE 3 (a) *Atractus fuliginosus* from Tobago photo credit John C. Murphy. (b) *A. fuliginosus* from Guanare, Portuguesa, Venezuela, photo by J. E. García-Pérez

Frog *Hyalinobatrachium orientale*. Jowers et al. (2015) suggest that the divergence between Venezuelan and Tobago populations, estimated at 3.1 Mya, indicates that Trinidad was already detached from the mainland. Nevertheless, they showed the 95% HPD of *H. orientale* falls within that time period of detachment period (Audemard & Audemard, 2002; Moretti et al., 2007; Persad, 2009), and therefore it is not possible to know if Trinidad was fully detached at that time. According to an annual 20 mm (= 20 km/Myr) eastward movement (Weber et al., 2001, 2019), Tobago's position at that time was approximately ~60 km to the west of its current position (Jowers et al., 2015). The shallow marine depths (<50 m) in the region and sea-level falls during the Pliocene (Miller et al., 2005) would have facilitated land-bridge connections between the mainland and the islands. Several Pliocene islands existed between Tobago, the mainland, and Trinidad, connected by shallow, perhaps occasionally emergent, coastal systems (Samlal, 2016). Another frog, the dendrobatid *Mannophryne olmonae* (Jowers et al., 2011), colonized Tobago in the early Miocene, and despite having a congener in Trinidad (*M. trinitatis*), it is more closely related to Venezuelan species, suggesting independent colonization of Trinidad and Tobago by different *Mannophryne* lineages from Northern Venezuela.

The distribution of *A. fuliginosus* resembles an arc shape, reaching from the Colombian Southern Andes in the south-west to Venezuela's coastal mountains in the Cordillera Central in the north-east, where its mainland distribution ends (Figure 1, for localities used in the map see Data S2). Therefore, its continental northernmost distribution is found at Venezuela's CCR (Central Coastal Range), which is still hundreds of kilometers south-west from Tobago. This distribution pattern contrasts with that of *H. orientale*, found in the much closer Cerro del Turimiquire and in the Paria Peninsula to Tobago. Unlike *A. trilineatus* which is found mostly in flooded forests and at low-altitude elevations, while occasionally at higher elevations, the habitat of *A. fuliginosus* is associated with higher altitudes (Murphy et al., 2020). This likely stopped the population from expanding further north-east toward Cerro del Turimiquire through permanent flooding of the coastal region by higher sea levels from about 3 million years ago until present (Hansen & Routledge, 2016), and more recently throughout the Late Pleistocene during interglacial periods (Rohling et al., 2014). These lowlands seem to be a barrier to montane *Atractus*, as only the endemic *A. matthewi* is present in the Turimiquire (Markezich & Barrio-Amorós, 2004). Similarly, the Gulf of the Cariaco pull-apart depression (Schubert, 1985) exhibits sea depths between approximately 150 m and 300 m, suggesting that the colonization of Isla La Tortuga and Isla Margarita could not have taken place throughout the low sea-level falls of the Pliocene-Pleistocene, as these islands were likely never connected in this region. This may explain the absence of the species there.

From a biogeographic perspective, the discontinuous distribution of the species after the CCR and its presence in Tobago remains challenging to interpret. However, several hypotheses may explain the species' presence in the island. The most probable scenario, according to molecular divergence estimates, is the recent vicariance of the Tobago population. A continuous population along a coastal plain from Venezuela to Tobago likely existed in lower lands until the sea level rose during a Glacial Maxima at about 435 ka (Hansen & Routledge, 2016). Accordingly, sea levels were about equally low (> or = -116 m) at 140 ka, 340 ka, and 640 ka (Rohling et al., 2014), and these time estimates mostly fall within the 95% HPD range between the mainland and Tobago specimens. Although this species is mainly associated to high altitude, past populations may have been temporarily associated with lower grounds during warmer periods.

Secondly, and not mutually exclusive with the previous hypothesis, is the possibility of undiscovered populations in the Turimiquire Massif, Paria Peninsula and Trinidad. Recent species descriptions in the Turimiquire Massif (Markezich & Barrio-Amorós, 2004) and the Paria Peninsula (Kaiser et al., 2015) indicate that these regions are not fully surveyed and biodiversity inventories are still needed. Surveys in these regions have been limited, mostly due to the unstable economic and political situation in Venezuela for the last 20 years (e.g. Rivas et al., 2021). The elusive behavior of *A. fuliginosus* and its fossorial ecology make finding this species challenging. Evidence of this is the poor record of the species in Tobago despite numerous herpetological surveys in its relatively small area, with

only four records for the island. Furthermore, Tobago's Main Ridge forest reserve is the oldest in the New World, and the Main Ridge Forest Reserve has been protected since 1776, which indicates that this region's biodiversity has been well documented. Years of herpetological surveys in Trinidad have never resulted in sightings of *A. fuliginosus*, unlike *A. trilineatus*, which suggests that this species likely never colonized Trinidad. The sunken Gulf of Paria Pliocene-Recent pull-apart, including a ~60 m post-glacial scour in the Bocas de Dragon at the eastern tip of the Paria Peninsula (van Andel, 1967), eliminates the possibility of a recent land-bridge connection through Trinidad. In order to place Tobago in a geographical location next to extant South American populations, it would require 35 Myr at the current plate motion rate of 20 km/Myr; therefore, this hypothesis is not tenable.

Another scenario to account for the absence of *A. fuliginosus* is the extinction of intermediate populations in the mountain ranges of the Turimiquire, Paria and Trinidad. However, the presence of *Atractus trilineatus* in these regions with similar fossorial habitat requirements suggests that this is less likely, although both species are normally found at different elevations. Furthermore, the presence of the species in Tobago suggests that this species should thrive in the similar regions of Trinidad and Paria Peninsula. The role of ecological niche displacement in Tobago, where these two species may be sympatric, merits further investigation. The final more intricate possibility is rafting from the CCR toward Tobago. Although today this species seems constrained to high-altitude terrain, where specimens are less likely to be swept out to sea, possible past distributions throughout lower lands could have aided populations to disperse. Rafting events could suggest the colonization of Tobago using eastern currents, but dispersal events through rafting in the region are documented from the Guianas, more precisely from the Orinoco Delta toward the Lesser Antilles following the northern and western currents and not from Northern Venezuela toward the Eastern Caribbean islands (Iturralde-Vinent & MacPhee, 1999; Murphy et al., 2016; van Andel, 1967). Lastly, the genetic divergence between localities does not favor the possibility of anthropogenic dispersal. In conclusion, despite all evidence and the likelihood of a vicariant event isolating Tobago's population, the observed distribution of this snake remains unique and enigmatic.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Alignment S1. 12S rRNA sequence alignment.

Alignment S2. 16S rRNA sequence alignment.

Alignment S3. *cytb* sequence alignment.

Alignment S4. *nd4* sequence alignment.

Alignment S5. *c-mos* sequence alignment.

Alignment S6. Complete concatenated sequence alignment used for the BI and RaxML analyses.

Table S1. Specimens analyzed in the present study, voucher numbers, and GenBank accession numbers for the various marker sequences.

Table S2. Species used in this study, vouchers, and GenBank accessions.

Table S3. Best partition schemes selected in PartitionFinder for the RaxML and MrBayes analyses

Figure S1. Maximum Likelihood tree based on the complete data set.

Additional Information S1. Bayesian Inference and Maximum Likelihood methods.

Data S1. Morphological Methods and results.

Data S2. Specimen vouchers and localities represented in the map (Figure 1)

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