

Phylogenetic Position and Biogeography of Three-Lined Snakes (*Atractus trilineatus*: Squamata, Dipsadidae) in the Eastern Caribbean

JOHN C. MURPHY^{1,6,7}, DANIELE SALVI^{2,3}, ALVIN L. BRASWELL⁴, AND MICHAEL J. JOWERS^{3,5,7}

¹ Science and Education, Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA

² Department of Health, Life, and Environmental Sciences, University of L'Aquila, Via Vetoio snc, 67100 Coppito, Italy

³ CIBIO/InBIO (Centro de Investigação em Biodiversidade e Recursos Genéticos), Universidade do Porto, Campus Agrário De Vairão, 4485-661, Vairão, Portugal

⁴ North Carolina State Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601-1029, USA

⁵ National Institute of Ecology, 1210, Geumgang-ro, Maseo-myeon, Seocheon-gun, Chungcheongnam-do, 33657, Korea

ABSTRACT: The Neotropical dipsadid snake genus *Atractus* contains more species than any other genus of serpents. The type species for the genus, Three-lined Snakes (*Atractus trilineatus*), occurs in northern South America, as well as in the islands of Trinidad and Tobago. Little is known about the phylogenetic position of this fossorial snake. Here, we examine the genetic variation of this species. Phylogenetic analyses suggest that *A. trilineatus* is an early branch within *Atractus*, and is deeply divergent from all of the other 31 species within the genus included in our analyses. Populations of *A. trilineatus* from Trinidad and Tobago show a close genetic affinity with mainland populations from Guyana, and indicate recent vicariance following Late Pleistocene sea-level rises. Overwater dispersal events cannot be ruled out, however, especially for the colonization of Tobago. Our results add to the understanding of the complexity of the phylogeographic events in the eastern Caribbean with this ecologically constrained species.

Key words: DNA; Fossorial; Guyana; Phylogeny; Trinidad and Tobago; Vicariance

THE NEOTROPICAL genus of fossorial snakes, *Atractus* Wagler 1828 (Dipsadidae or Dipsadinae), is one of the most successful extant snake lineages, with 143 currently recognized species (Uetz et al. 2019). The genus is primarily South American with some minor representation in Panama (Myers 2003). Besides the large number of species descriptions (Passos and Lynch 2010; Passos et al. 2019), a comprehensive revision of the genus is lacking. Furthermore, the fact that some species are only known from the type specimens and many others are likely misidentified makes this task challenging. Several species of *Atractus* are known from just the holotype or a small series of specimens from a restricted range (e.g., Passos et al. 2007), fitting the description of microendemics. Others are relatively widespread species such as *A. collaris*, *A. major*, *A. snethlageae*, and *A. torquatus* (Wallach et al. 2014). Among the widely distributed *Atractus* species, Three-lined Snakes, *Atractus trilineatus* (Wagler 1828), occur in Trinidad, Tobago, northern Venezuela, western Guyana (Beebe 1946, 1952; Murphy et al. 2018), and Roraima, Brazil (Martins and Oliveira 1993), and have been reported as far south as Manaus, Brazil (Martins and Oliveira 1998). The origins of the Trinidad and Tobago populations and their relationships with mainland populations have never been investigated. Findings from previous phylogenetic studies on the herpetofauna of the region (eastern Caribbean and northern South America) reflect a pattern of colonization and diversification of species in congruence with their ecological requirements (e.g., if they are habitat specialists vs. habitat generalists), dispersal capability (e.g., dependent on species morphology, such as fossorial or semiaquatic), and the area from where the

founder mainland populations originated (coastal or inland). Such studies have produced contrasting findings on the tempo and mode of speciation in such a complex topographical terrain. All three biogeographic scenarios—vicariance (Jowers et al. 2008, 2011; Murphy et al. 2016a,b), overwater dispersal (Camargo et al. 2009; Murphy et al. 2016a,b), and land bridge connections (Jowers et al. 2015)—have been proposed to explain the herpetological diversity in the eastern Caribbean islands. In addition, recent invasions through anthropogenic actions are likely taking place (Camargo et al. 2009; Smith et al. 2011; Murphy et al. 2016a). Information on *A. trilineatus* life-history could supply valuable information in understanding phylogeographic and phyletic patterns of diversification of the species on the islands; yet, this information is limited.

Atractus trilineatus has a long and tortuous nomenclatural history, with the species having been described six different times (*Coluber brachyurus* Kuhl 1820; *A. trilineatus* Wagler, 1828; *Rhabdosoma lineatum* Duméril et al. 1854; *Rhabdosoma trivirgatum* Jan 1862; *Rhabdosoma punctatovittatum* Jan 1862; *Rhabdosoma lineatum* Garman 1887 [Wallach et al. 2014]). The nomenclatural confusion has been addressed at length by Hoogmoed (1982), and began with the use of the Rijks Museum specimen RMNH 48 (which is *A. trilineatus*) as the type specimen for two different species: *A. trilineatus* and the eastern Indonesian homalopsid, *Brachyorrhos albus*. These two unrelated snakes are separated by 19,000 km, and share a similar but superficial appearance because they live similar life styles. Indeed, morphology-based assessments of evolutionary relationships between *Atractus* lineages are confusing because snakes are often morphologically convergent as the result of similar habitat use, predators, and prey (Erwin 2008; Losos 2010; Ricklefs 2010). Molecular techniques have resolved many of these problems, and provide an accurate method for estimating phylogenetic relationships between snake lineages.

⁶ PRESENT ADDRESS: 2564 E. Murdoch Court, Green Valley, AZ 85614, USA

⁷ CORRESPONDENCE: email, serpentresearch@gmail.com, michaeljowers@hotmail.com

The fossorial natural history of *A. trilineatus* suggests an a priori constraint to colonize islands, especially an oceanic island such as Tobago. Here, we test the phylogenetic and systematic position of *A. trilineatus*, the type species of the genus *Atractus*. Using molecular data, we assess its placement within *Atractus*, estimate the age of divergence between the islands and mainland populations, and provide additional insight into its evolution and biogeography.

MATERIALS AND METHODS

Molecular Methods

We analyzed DNA sequence data from nine *A. trilineatus* adults from the Republic of Trinidad and Tobago (Trinidad, $n = 1$: University of the West Indies Zoology Museum UWIZM.2015.18.2, St. Augustine; Tobago, $n = 5$, UWIZM.2015.19.8 Roxborough; UWIZM.2015.18.6, UWIZM.2015.19.1, UWIZM.2015.19.6 Charlotteville; UWIZM.2011.19.11 Cambleton); and Guyana ($n = 3$); California Academy of Science CAS257740 and CAS257755 South West Guyana, Upper-Takutu–Upper Essequibo Region, USNM566255 (Dubulay Ranch on the Berbice River at ~200 m ASL, North East of Guyana; see Fig. 1). Throughout, we use Guyana when referring to the country (not restricted to the Guiana Shield).

DNA was extracted from tissue samples, and target gene fragments were amplified by polymerase chain reaction. DNA extraction, purification, and amplification protocols follow Jowers et al. (2015), and primers used are reported in Table S1 (Supplemental Materials available online). We amplified a portion of the mitochondrial small and large ribosomal subunits (12S rDNA, 16S rDNA, respectively), cytochrome b (cytb) and NADH dehydrogenase 4 (nd4), and the nuclear oocyte maturation factor (c-mos). These gene fragments are very informative in interspecific and intraspecific studies on snakes, including colubrids (e.g., Daza et al. 2009; Salvi et al. 2017, 2018). Amplification of the cytb gene fragment was problematic for some specimens, and several primers were used to ultimately concatenate fragments to obtain the desired sequence length.

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 sequences were (although not all individuals had the same length in some alignments): 12S rDNA, 372 base pairs (bp); 16S rDNA, 478 bp; cytb, 1092 bp; nd4, 669 bp; c-mos, 513 bp. Following Arteaga et al. (2017), we used *Sibon nebulatus* as outgroup. Sequences were aligned in Seaview v4.2.11 (Gouy et al. 2010) under ClustalW2 default settings (Larkin et al. 2007). The 12S and 16S rDNA, cytb, nd4, and c-mos sequences (Genbank accession numbers provided in Table S2, in the Supplemental Materials available online) were concatenated, resulting in a 3124-bp alignment. Genetic p -distances and standard error ($\% \pm SE$) were calculated using MEGA v6 (Tamura et al. 2011).

We used BEAST v1.8.4 (Drummond et al. 2012) to simultaneously estimate the phylogeny and divergence times between *Atractus* species. We implemented the most appropriate substitution model for each gene fragment as determined by the Bayesian Information Criterion in jModeltest v2 (Posada 2008). We applied a yule speciation

tree prior, and a relaxed clock model, using a substitution rate of 1.34% substitutions per million yr (0.99–1.7%) for the combined nd4 and cytb gene fragments, as estimated by Daza et al. (2009) for Neotropical colubrids based on four calibration points: (a) the split between Viperidae and Colubridae, ~40 million yr ago, (Mya); (b) the divergence between the New World and Old World Crotalinae to be older than 16 Mya and less than 32 Mya; (c) the origin of *Sistrurus* to be older than 9 Mya and less than 32 Mya; and (d) the origin of Natricinae to be older than 30 Mya. To implement this substitution rate, we set a lognormal prior with mean = 0.013 and standard deviation = 0.15 on the nd4 + cytb ucl.mean parameter (linked clock model). BEAST was run twice with 50 million generations per run, sampling every 5000 steps. Convergence of the runs was verified in Tracer v1.6 (Rambaut et al. 2013), both runs were combined in LogCombiner, and the Maximum Clade Credibility Tree was computed using Tree Annotator (BEAST v1.8.4).

Additionally, phylogenetic analyses were performed using the Bayesian Inference and Maximum Likelihood methods without implementing any clock model. MrBayes v3.2 (Ronquist and Huelsenbeck 2003) was used to construct the Bayesian Inference tree under the best-fitting substitution model for each gene partition. We used default priors and Markov chain settings, and searches were performed with random starting trees. Each run consisted of four chains of 10,000,000 generations, sampled every 1000 generations. Posterior distributions of parameter estimates were visually inspected in Tracer ML, searches were conducted in RAxML v7.0.4 using partition data sets under default settings (Silvestro and Michalak 2010), and support was assessed by using 1000 bootstrapped replicates. All phylogenetic analyses were performed through the CIPRES platform (Miller et al. 2010).

In order to assess whether the branching patterns within *A. trilineatus* fit intraspecific or interspecific relationships, we used the Poisson Tree Processes (PTP) model (Zhang et al. 2013) on the ML tree estimated on mitochondrial data (cytb + nd4). This species delimitation method outperforms other methods based on single-locus molecular phylogenies, especially when evolutionary distances between species are small, as expected for the *A. trilineatus* lineages (Zhang et al. 2013). We ran the PTP method as implemented in the PTP web server (Zhang et al. 2013; Kapli et al. 2017).

RESULTS

Phylogeny

The complete data set (3124 base pairs) of the sequenced *A. trilineatus* resulted in nine haplotypes (one haplotype per specimen), with the two individuals from Guyana (CAS257740 and CAS257755) differing by only one substitution in the nd4 gene fragment. The c-mos gene fragment recovered the same haplotype for all individuals. The best-fitting models were as follows: 12S rDNA (TIM2 + G) 16S rDNA (TrN2 + I + G), cytb (TPM2uf + I + G), nd4 (HKY + I + G), and c-mos (K80 + I). For those models that were not implemented in BEAST, we used the most similar and simpler model available (12S: TrN + G; cytb: HKY + I + G).

Genetic divergence of mitochondrial loci combined (uncorrected p -distances) was higher between Guyana samples (CAS257740, CAS257755 vs. USNM566255;

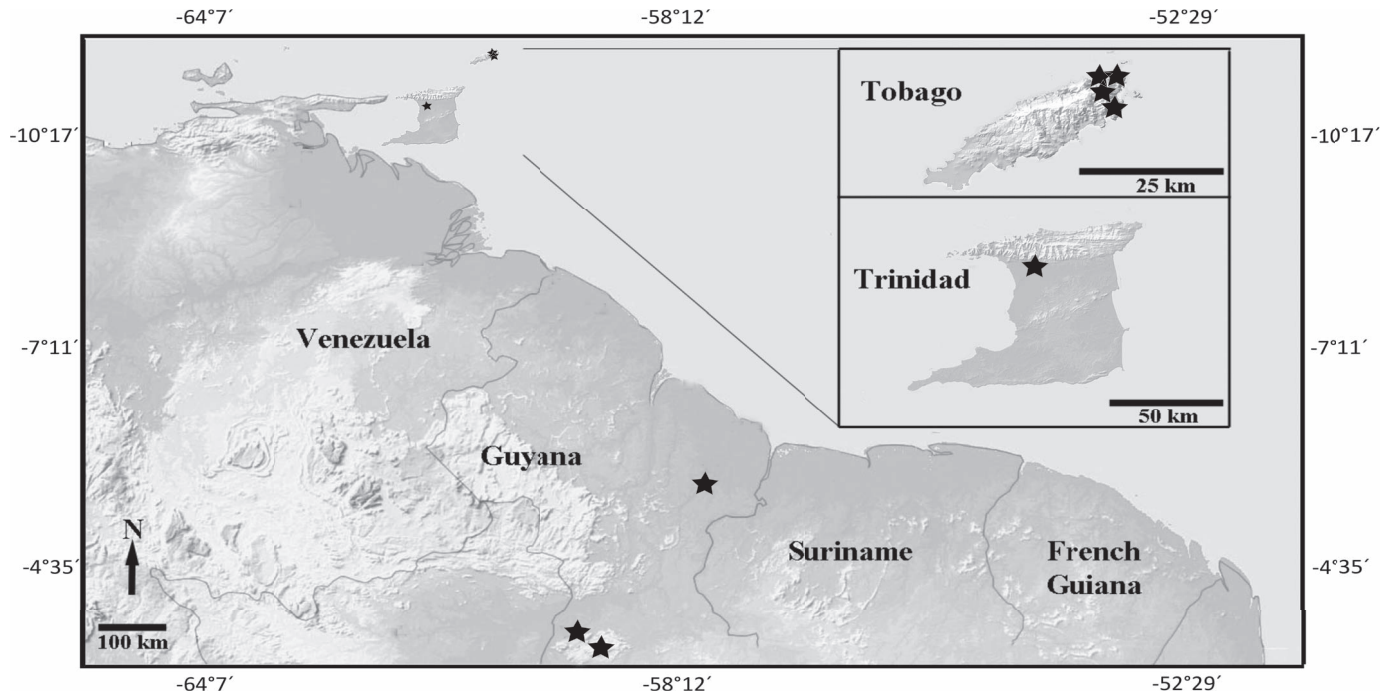


FIG. 1.—Geographic distribution of sequenced *Atractus trilineatus*. Star symbols are sequenced samples included in this study. Specimens from Charlotteville (Tobago) UWIZM.2015.19.6 and UWIZM.2015.19.1 are represented by one star.

2.01% \pm 0.00) than between these and the island populations of Trinidad (0.89% \pm 0.36) and Tobago (1.0% \pm 0.01; Table 1; Table S3 in the Supplemental Material available online). However, genetic divergence between Guyana samples CAS257740, CAS257755, and Trinidad (0.52% \pm 0.0) and Tobago (0.65% \pm 0.01) was three times lower than between USNM566255 and Trinidad (1.64% \pm 0.0) and Tobago (1.77% \pm 0.02). Genetic divergence between Trinidad and Tobago islands (0.28 \pm 0.02) was higher than the divergence recovered within Tobago (0.19 \pm 0.03).

All phylogenetic analyses recovered *A. trilineatus* as the sister taxon to all other *Atractus*, which form a clade strongly supported by Bayesian analyses (Figs. 2, 3). Overall, the phylogenetic relationships between terminal taxa are congruent with Arteaga et al. (2017). *Atractus trilineatus* from Trinidad, Tobago, and Guyana form a well-resolved clade (Bayesian Posterior Probability, BPP = 1.00; ML bootstrap support, BS = 100%). The SW Guyana samples (CAS257740 and CAS257755) are more closely related to *A. trilineatus* from Trinidad than to Tobago (Figs. 2, 3) than

USNM566255 from NE Guyana, which is sister to all other *A. trilineatus*.

The timing of the most recent common ancestor between *A. trilineatus* and the remaining *Atractus* species is estimated at the Middle Miocene (\sim 14 Mya; 95% Highest Posterior Density [HPD95%] = 9.4–19.7 Mya; Fig. 3). Within *A. trilineatus*, the split between samples from Trinidad and Tobago dates to \sim 180,000 yr ago (HPD95% = 60,000–370,000 yr ago). The oldest split between Guyana (USNM566255) and both Trinidad and Tobago *A. trilineatus* dates to \sim 1 Mya (HPD95% = 0.62–1.72 Mya). The most recent split between the mainland (Venezuela/Guyana) and Trinidad and Tobago dates to 410,000 yr ago (HPD95% = 180,000–690,000 yr ago; Fig. 3). The PTP species delimitation analysis identifies a single putative species within *A. trilineatus*, because the branching patterns among *A. trilineatus* sequences fit an intraspecific (coalescent) process.

DISCUSSION

Our phylogenetic analyses indicate that *A. trilineatus* is the sister lineage of the clade including all *Atractus* species examined, although with a considerably high genetic

TABLE 1.—Genetic distance (uncorrected *p*-distances, %) at concatenated mitochondrial genes between *Atractus trilineatus* individuals.

Locality (specimen code)	Guyana1	Guyana2	Guyana3	Trinidad	Tobago1	Tobago2	Tobago3	Tobago4	Tobago5
Guyana1 (USNM566255)									
Guyana2 (CAS257740)	2.01								
Guyana3 (CAS257755)	2.01	0.00							
Trinidad (UWIZM.2015.18.2)	1.64	0.52	0.52						
Tobago1 (UWIZM.2015.19.1)	1.79	0.67	0.67	0.30					
Tobago2 (UWIZM.2015.19.8)	1.72	0.60	0.60	0.22	0.07				
Tobago3 (UWIZM.2011.19.11)	1.79	0.67	0.67	0.30	0.30	0.22			
Tobago4 (UWIZM.2015.19.6)	1.87	0.75	0.75	0.37	0.07	0.15	0.37		
Tobago5 (UWIZM.2015.18.6)	1.72	0.60	0.60	0.22	0.22	0.15	0.07	0.30	



FIG. 2.—Bayesian tree inferred by Mr. Bayes based on the data set of concatenated 12S, 16S rDNA, cytb, nd4, and c-mos sequences. Where they are presented on left and right sides of a slash (/), values indicated at nodes are Bayesian Posterior probabilities (> 0.5) and Maximum Likelihood bootstrap values (>50%), respectively. Scale bar indicates base substitutions per site.

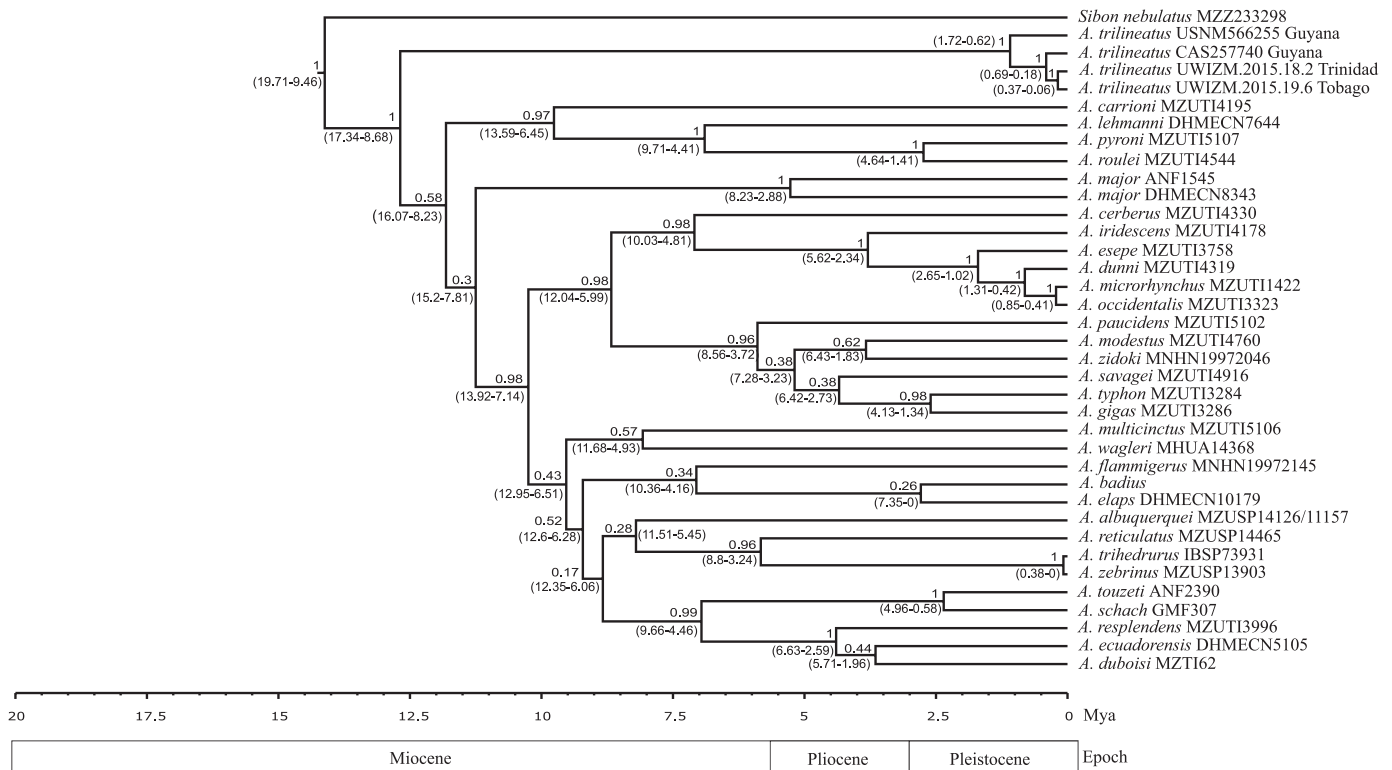


FIG. 3.—Bayesian time tree as inferred by BEAST for the data set of concatenated 12S, 16S rDNA, cytb, nd4, and c-mos sequences from *Atractus* specimens. Values by nodes are Bayesian posterior probabilities, whereas values in parentheses denote 95% Highest Posterior Density ranges.

divergence from this clade. *Atractus* is a diverse genus with 143 recognized species, of which our molecular analysis included only 31 (21.7%). Therefore, as more species are added, the topology of the tree can be expected to change.

The distribution of *A. trilineatus* is likely the result of the changing topographical conditions in the region. The Trinidad and Tobago archipelago was connected to the mainland multiple times with Trinidad connected to the mainland for more prolonged periods than Tobago (Fig. S1 in the Supplemental Materials available online). The mean age of divergence between the southwest lineage in Guyana (CAS257740 and CAS257755) and Trinidad and Tobago, ~410 thousand yr ago (Fig. 3), indicates that the island populations of *A. trilineatus* remained isolated from the mainland during periods of higher sea-levels that were associated with interglacial periods of the Pleistocene. Other examples of recent divergence during the Late Pleistocene are the Robinson's Mouse Opossum (*Marmosa robinsoni*) lineage from Venezuela–Trinidad and Tobago, dating to 0.34 Mya (Gutiérrez et al. 2014), and Trinidad's *Marisora aurulae* and Venezuela's Peninsula de Paria *M. falconensis* skinks, dating to 0.5 Mya (Hedges and Conn 2012). During these stages, sea levels were estimated to be 10–20 m above current levels. At this time, much of the South American continental shelf would have been submerged, and Trinidad and Tobago were isolated from the mainland (Routledge and Hansen 2016). The same scenario might explain the isolation and divergence between populations from Trinidad and Tobago, which we estimate to have taken place circa 180 Kya, in accordance with divergence patterns for other species between the islands (e.g., Camargo et al. 2009).

Given that Trinidad was incorporated in the continental land during sea-level low stands as moderate as –50 m (Fig. S1 in the Supplemental Material available online), a vicariance model of divergence between mainland and Trinidad is more plausible than a scenario of oversea dispersal during interglacial periods. On the other hand, the arrival of the species in Tobago from Trinidad through overwater dispersal cannot be disregarded, as has been suggested for other reptiles in Trinidad and Tobago (e.g., Boos 1984a,b; Camargo et al. 2009; Murphy et al. 2016a). Land-slides following the monsoon rains in the Orinoco Delta and throughout northern Venezuela form rafts of vegetation that could displace a fossorial species via floating mats of vegetation to southern Trinidad. The fact that in Guyana *A. trilineatus* has been found on Kaow Island (~6°25'N, 58°37'W; datum = WGS84), at the mouth of the Mazaruni River (NHM 1977.307), is also compatible with an origin for overwater dispersal during flood stages. Whereas we have no evidence that *A. trilineatus* spends part of its life in the water, populations near sea level are certainly subject to flooding. Two pieces of information in the literature support this view: Martins and Oliveira (1993) report it from the black-water flooded forest in Brazil, and Snyder (2016) found a specimen in the stomach of a Red-bellied Piranha (*Pygocentrus nattereri*), collected in a flooded forest. Both observations indicate that *A. trilineatus* might be spending time in shallow water. Fossorial and aquatic snakes often share similar sets of morphological traits such as valvular nostrils, and means (and ranges) for the number of vertebrae (Jayne 1982; Murphy 2012).

The Guyana sample (USNM566255) shows a much deeper divergence than between individuals from coastal Guyana and Trinidad–Tobago, suggesting an older split, dated at ~1 Mya. Similarly, the frog *Leptodactylus validus* indicates an origin in northern South America (Guyana/Brazil) invading Trinidad ~1 Mya, which the authors attribute to periods of intermittent land connections, or overwater dispersal, throughout the Pleistocene (Camargo et al. 2009). This date also roughly (0.9 Mya) corresponds to a split in the Robinson's Mouse Opossum *Marmosa robinsoni* that produced an eastern Venezuela–Trinidad–Tobago clade and a central Venezuelan clade (Gutiérrez et al. 2014). This likely resulted from habitat changes associated with the presence of a mountain arc and the Pleistocene expansion of humid forests into intermontane areas that blocked gene flow from dry-habitat-adapted species. Likewise, the divergence observed between Trinidad and the northern Guyana coastal population of *A. trilineatus* can be explained by past habitat discontinuity by river systems between northern coastal Guyana and Trinidad, flowing to the Guyana and Orinoco estuaries. In contrast, the southern Guyana populations of *A. trilineatus* might show less restricted population connectivity with northern localities. Our calibration estimates for *A. trilineatus* divergence reject a vicariant event between Trinidad and northern South America in the Late Miocene (when Trinidad detached from the Peninsula de Paria of northern Venezuela ~3.6 Mya), and point to a divergence in the Late Pleistocene, a time of rapid and abrupt topographic change in the eastern Caribbean associated with climate-related sea-level changes.

Savage (1960) proposed three species groups within *Atractus* (*badius*, *elaps*, and *trilineatus*). Since that time, a relatively long list of *Atractus* species have been placed in the *A. trilineatus* group: *A. collaris*, *A. gaigeae*, *A. dunni* (montane), *A. ecuadorensis*, *A. lehmanni*, *A. resplendens* (Savage 1960); *A. favae*, *A. zidoki* (Hoogmoed 1980); *A. taphorni* (Schargel and Garcia-Perez 2002); *A. tamessari* (Kok 2006); *A. dunni* (lowland; Cisneros-Heredia 2005); *A. occipitoalbus* (Passos et al. 2005); and *A. modestus* (Passos et al. 2007). The few of these (*A. dunni*, *A. zidoki*, *A. resplendens*) represented in our tree are not closely related to *A. trilineatus*. Also, the topology of our tree indicates that *A. badius* and *A. elaps* are sister clades, rendering the species groups of Savage (1960) untenable. Martins and Oliveira (1993) noted that the scalation and coloration of *A. trilineatus* specimens from Brazil were similar to other populations, but that these specimens had 11 maxillary teeth as opposed to 7–8 maxillary teeth in Venezuelan specimens reported by Lancini and Kornacker (1989). The few Trinidad and Tobago specimens we checked had six maxillary teeth. The Brazilian populations require further investigation. Whereas the lowland Guyana species have been considered taxonomically stable (Passos et al. 2013), this situation might change once molecular data are available for most or all of the *Atractus* species.

Acknowledgments.—We thank D. Kizirian (American Museum of Natural History), J. Vindum and L. Scheinberg (California Academy of Sciences), and M.G. Rutherford (University of the West Indies) for provided logistical support, access to the museum's collections, and the loan of specimens. Special thanks to C.J. Cole for information regarding the Guyana specimens. All collections were made under permits from The Wildlife

Section of the Forestry Division, Ministry of Housing and the Environment, Trinidad & Tobago; Ministry of the Environment and Water Resources, Trinidad & Tobago; and, the Department of Natural Resources and the Environment, Tobago House of Assembly. DS is currently supported by the program Rita Levi Montalcini (MIUR, Ministero dell'Istruzione dell'Università e della Ricerca) for the recruitment of young researchers at the University of L'Aquila.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-18-00043.S1>.

LITERATURE CITED

- Arteaga, A., K. Mebert, J.H. Valencia, D.F. Cisneros-Heredia, N. Peñafiel, C. Reyes-Puig, J.L. Vieira-Fernandes, and J.M. Guayasamim. 2017. Molecular phylogeny of *Atractus* (Serpentes, Dipsadidae), with emphasis on Ecuadorian species and the description of three new taxa. *ZooKeys* 661:661–691.
- Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana and Caripito, Venezuela. *Zoologica* 31:11–51.
- Beebe, W. 1952. Introduction to the ecology of the Arima Valley, Trinidad, BWI. *Zoologica* 37:157–183.
- Boos, H.E.A. 1984a. A consideration of the terrestrial reptile fauna on some offshore islands north west of Trinidad. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club* 1984:19–26.
- Boos, H.E.A. 1984b. Reptiles of Soldado Rock, Trinidad. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club* 1984:12.
- Camargo, A., W.R. Heyer, and R.O. de Sá. 2009. Phylogeography of the frog *Leptodactylus validus* (Amphibia: Anura): Patterns and timing of colonization events in the Lesser Antilles. *Molecular Phylogenetics and Evolution* 53:571–579.
- Cisneros-Heredia, D.F. 2005. Rediscovery of the Ecuadorian snake *Atractus dunnii* Savage, 1955 (Serpentes: Colubridae). *Journal of the National Museum (Prague)*, Natural History Series 174:87–94.
- Daza, J.M., E.N. Smith, V.P. Páez, and C.L. Parkinson. 2009. Complex evolution in the Neotropics: The origin and diversification of the widespread genus *Leptodeira* (Serpentes: Colubridae). *Molecular Phylogenetics and Evolution* 53:653–67.
- Drummond, A.J., M.A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29:1969–1973.
- Duméril, A.M.C., G. Bibron, and A.H.A. Duméril. 1854. *Erpétologie Générale, ou Histoire Naturelle Complète des Reptiles. Comprenant L'histoire des Serpents non Venimeux*. Librairie Encyclopedia de Roret, France.
- Erwin, D.H. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends Ecology and Evolution* 23:304–310.
- Garman, S. 1887. On West Indian reptiles in the Museum of Comparative Zoology at Cambridge, Mass. *Proceedings of the American Philosophical Society* 24:278–286.
- Gouy, M., S. Guindon, and O. Gascuel. 2010. SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27:221–224.
- Gutiérrez, E.E., R.P. Anderson, R.S. Voss, J. Ochoa-G., M. Aguilera, and S.A. Jansa. 2014. Phylogeography of *Marmosa robinsoni*: Insights into the biogeography of dry forests in northern South America. *Journal of Mammalogy* 95:1175–1188.
- Hedges S.B., and C.E. Conn. 2012. A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa* 3288:1–244.
- Hoogmoed, M.S. 1980. Notes on the herpetofauna of Surinam: VII. Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). *Zoologische Verhandlungen* 175:3–47.
- Hoogmoed, M.S. 1982. Nomenclatural problems relating to *Atractus trilineatus* Wagler, 1828. *Zoologische Mededelingen* 56:131–138.
- Jan, G. 1862. Enumerazione sistematica delle specie d'ofidi del gruppo Calamaridae. *Archivio per la Zoologia, l'Anatomie, e la Fisiologia*, Genova 2:1–76.
- Jayne, B.C. 1982. Comparative morphology of the semispinalis–spinalis muscle of snakes and correlations with locomotion and constriction. *Journal of Morphology* 172:83–96.
- Jowers, M.J., J.R. Downie, and B.L. Cohen. 2008. The golden tree frog of Trinidad, *Phyllodytes auratus* (Anura: Hylidae): Systematic and conservation status. *Studies on Neotropical Fauna and Environment* 43:181–188.
- Jowers, M.J., I. Martinez-Solano, B.L. Cohen, J. Manzanilla, and R.J. Downie. 2011. Genetic differentiation in the Trinidad endemic *Mannophryne trinitatis* (Anura: Aromobatidae): Miocene vicariance, in situ diversification and lack of geographical structuring across the island. *Journal of Zoological Systematics and Evolutionary Research* 49:133–140.
- Jowers, M.J., R.M. Lehtinen, R.J. Downie, A.P. Georgiadis, and J.C. Murphy. 2015. Molecular phylogenetics of the glass frog *Hyalinobatrachium orientale* (Anura: Centrolenidae): Evidence for Pliocene connections between mainland Venezuela and the island of Tobago. *Mitochondrial DNA* 26:613–618.
- Kapli, P., S. Lutteropp, J. Zhang, K. Kobert, P. Pavlidis, A. Stamatakis, and T. Flouri. 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* 33:1630–1638.
- Kok, P.J. 2006. A new snake of the genus *Atractus* Wagler, 1828 (Reptilia: Squamata: Colubridae) from Kaieteur National Park, Guyana, northeastern South America. *Zootaxa* 1378:19–35.
- Kuhl, H. 1820. *Beiträge zur Zoologie und vergleichenden Anatomie. Erste Abtheilung. II. Ophidier*. Frankfurt-am-Main, Germany.
- Lancini, A.R., and P.M. Kornacker. 1989. *Die Schlangen von Venezuela*. Armitano Editores C.A., Venezuela.
- Larkin, M.A., G. Blackshields, N.P. Brown, . . . J.D. Thompson. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23:2947–2948.
- Losos, J.B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *American Naturalist* 175:623–639.
- Martins, M., and M.E. Oliveira. 1993. The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazonia, Brazil. *Zoologische Mededelingen* 67:21–40.
- Martins, M., and M.E. Oliveira. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78–150.
- Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA, USA. Institute of Electrical and Electronics Engineers, USA.
- Murphy, J.C. 2012. Marine invasions by non-sea snakes, with thoughts on terrestrial-aquatic-marine transitions. *Integrative and Comparative Biology* 52:217–226.
- Murphy, J.C., M.G. Rutherford, and M.J. Jowers. 2016a. The threadsnake tangle: Lack of genetic divergence in *Epictia tenella* (Squamata, Leptotyphlopidae): Evidence for introductions or recent rafting to the West Indies. *Studies on Neotropical Fauna and Environment* 51:197–205.
- Murphy, J.C., M.J. Jowers, R.M. Lehtinen, S.P. Charles, G.R. Colli, A.K. Peres, Jr., C.R. Hendry, and R.A. Pyron. 2016b. Cryptic, sympatric diversity in tegu lizards of the *Tupinambis teguixin* group (Squamata, Sauria, Teiidae) and the description of three new species. *PLoS One* 11:e0158542.
- Murphy, J.C., J.R. Downie, J.M. Smith, . . . M.J. Jowers. 2018. A Field Guide to the Amphibians and Reptiles of Trinidad and Tobago. Trinidad and Tobago Field Naturalists' Club, Trinidad and Tobago.
- Myers, C.W. 2003. Rare snakes—five new species from eastern Panama: Reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391:1–47.
- Passos, P., and J.D. Lynch. 2010. Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetological Monographs* 24:149–173.
- Passos, P., R. Fernandes, and N.A. Zanella. 2005. A new species of *Atractus* (Serpentes: Colubridae) from southern Brazil. *Herpetologica* 61:209–218.
- Passos, P., D.S. Fernandes, and D.M. Borges-Nojosa. 2007. A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in northeastern Brazil. *Copeia* 2007:788–797.
- Passos, P., L.Y. Echevarría, and P.J. Venegas. 2013. Morphological variation of *Atractus carrioni* (Serpentes: Dipsadidae). *South American Journal of Herpetology* 8:109–120.
- Passos, P., A. Scanferla, P.R. Melo-Sampaio, J. Brito, and A. Almendariz. 2019. A giant on the ground: Another large-bodied *Atractus* (Serpentes: Dipsadinae) from Ecuadorian Andes, with comments on the dietary specializations of the goo-eaters snakes. *Anais da Academia Brasileira de Ciências* 91:1–14.

- Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25:1253–1256.
- Rambaut, A., M.A. Suchard, W. Xie, and A.J. Drummond. 2013. Tracer v.1.6.0: MCMC Trace Analysis Tool. BEAST Developers, UK. Available at <http://beast.bio.ed.ac.uk>.
- Ricklefs, R.E. 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences* 107:1265–1272.
- Ronquist, F., and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- Routledge, R., and J. Hansen. 2016. Sea Level Change During the Last 5 Million Years. Publisher. Available at https://web.archive.org/web/20190703201352/https://serc.carleton.edu/integrate/teaching_materials/coastlines/student_materials/901.
- Salvi, D., D. Lucente, J. Mendes, C. Liuzzi, D.J. Harris, and M.A. Bologna. 2017. Diversity and distribution of the Italian Aesculapian snake *Zamenis lineatus*: A phylogeographic assessment with implications for conservation. *Journal of Zoological Systematics and Evolutionary Research* 55:222–237.
- Salvi, D., J. Mendes, S. Carranza, and D.J. Harris. 2018. Evolution, biogeography and systematics of the western Palaearctic *Zamenis* ratsnakes. *Zoologica Scripta* 47:441–461.
- Savage, J.M. 1960. A revision of the Ecuadorian snakes of the colubrid genus *Atractus*. *Miscellaneous Publications Museum of Zoology, University of Michigan* 112:1–86.
- Schargel, W.E., and J.E. García-Pérez. 2002. A new species and a new record of *Atractus* (Serpentes: Colubridae) from the Andes of Venezuela. *Journal of Herpetology* 36:398–402.
- Silvestro, D., and I. Michalak. 2010. A user friendly graphical front-end for phylogenetic analyses using RAxML (Stamatakis, 2006). *Organisms Diversity and Evolution* 12:335–337.
- Smith, J.M., J.R. Downie, R.F. Dye, V. Ogilvy, D.G. Thornham, M.G. Rutherford, S.P. Charles, and J.C. Murphy. 2011. Amphibia, Anura, Hylidae, *Scarthyla vigilans* (Solano, 1971): Range extension and new country record for Trinidad, West Indies, with notes on tadpoles, habitat, behavior and biogeographical significance. *Check List* 7:574–577.
- Snyder, A. 2016. Natural history notes: *Atractus trilineatus* (predation). *Herpetological Review* 47:308.
- Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28:2731–2739.
- Uetz, P., P. Freed, and J. Hošek (eds.). 2019. The Reptile Database. Available at <http://www.reptile-database.org>. Accessed on 5 May 2019. Archived by WebCite at <http://www.webcitation.org/78F4t29sy> on 9 May 2019.
- Wagler, J. 1828. Auszüge aus seinem Systema Amphibiorum. *Isis von Oken* 21:740–744.
- Wallach, V., K.L. Williams, and J. Boundy. 2014. Snakes of the World: A Catalogue of Living and Extinct Species. CRC Press, USA.
- Zhang, J., P. Kapli, P. Pavlidis, and A. Stamatakis. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29:2869–2876.

Accepted on 2 May 2019
Associate Editor: Christopher Raxworthy