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Morphology and Natural History of Three-lined Snakes, *Atractus trilineatus* (Squamata, Dipsadidae), in the Eastern Caribbean

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About 35% of snakes (685 of 1,935 species) are fossorial or cryptozoic-fossorial species that spend much of their life hidden from human view underground or in leaf litter. One genus, *Atractus* Wagler 1828 (Dipsadidae) is the most diverse

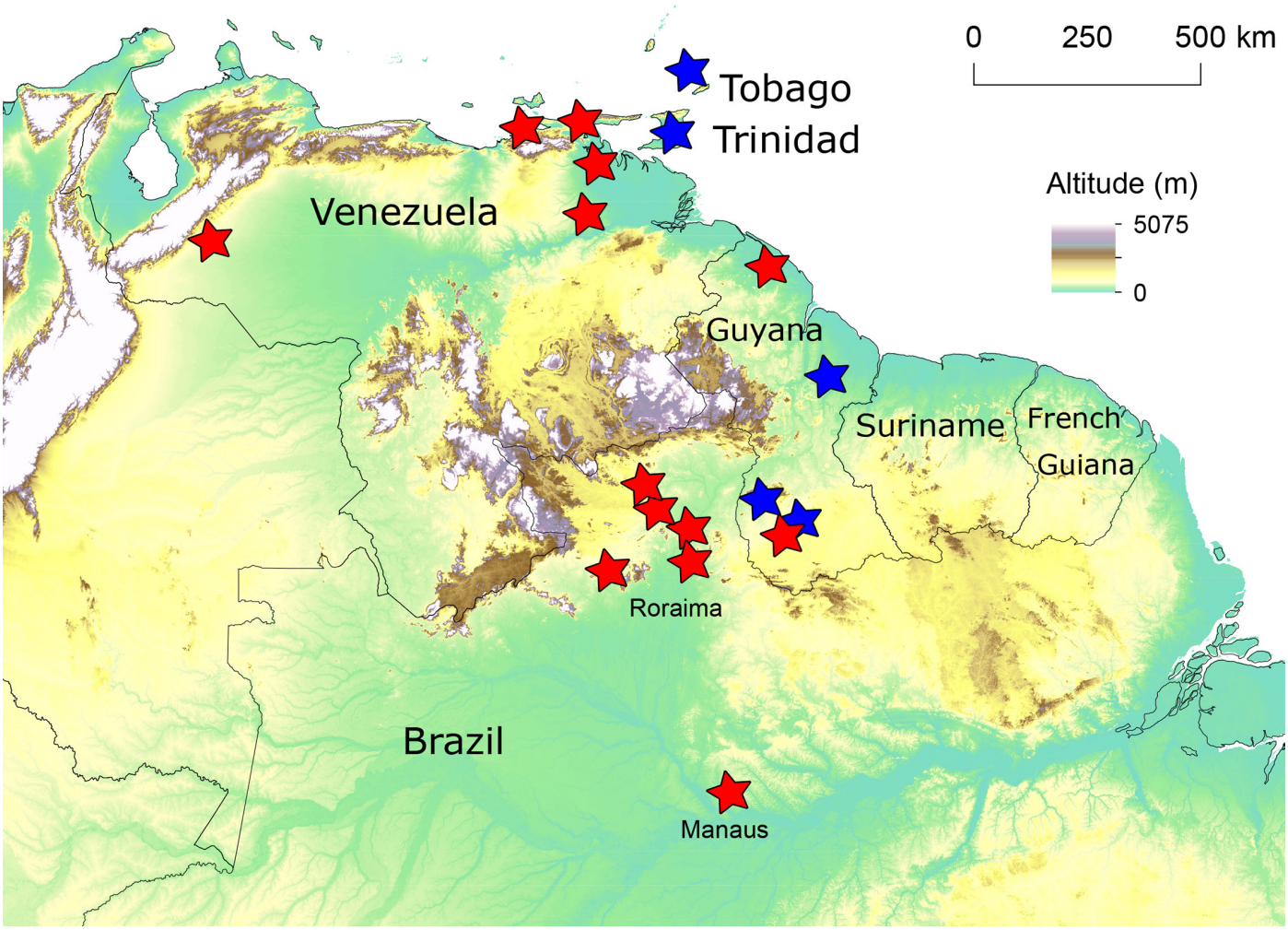

Fig. 1. Known localities for Three-lined Snakes (*Atractus trilineatus*) based on specimens examined and the literature. Blue stars are sequenced specimens from Murphy et al. (2019) and red stars are specimens examined and from the literature.

Table 1. Data for specimens examined. Museum acronyms follow those listed in the Acknowledgements. Locality abbreviations are: Braz = Brazil, Guy = Guyana, Tob = Tobago, Tri = Trinidad, and Venz = Venezuela. Pattern codes: 1 = stripes on scale rows 4, 5, and 8; 2 = stripes on scale rows other than those in pattern 1 (see text). Sex (S): f = female, m = male. SVL = snout vent length in mm. T = tail length in mm. DSR = dorsal scale rows at midbody. V = number of ventral scales. SC = number of subcaudal scales. IN = number of internasal scales. PO = number of postocular scales. PrO = number of preocular scales. UL = number of upper labial scales. ULO = upper labials bordering the orbit. ULL = upper labials contacting the loreal. LO = loreal single (1 indicates yes). PT = number of primary temporal scales. LL = number of lower labial scales. LLcs = lower labials contacting chin shields. A dash indicates data were not taken. A lower-case d indicates that the structure was damaged. The * indicates that the data for the lecotype were taken from Hoogmoed (1980).

Museum Number	Location	PAT	S	SVL	T	DSR	V	SC	IN	PO	PrO	UL	ULO	ULL	LO	PT	LL	LLcs
*RMNH 48 (lectotype)	"Java"	—	f	194	11	15	142	11	2	2	0	8	45	234	1	1	—	4
AMNH 131798	Braz	1	m	189	20	15	143	19	2	2	0	8	45	234	1	1	7	4
BMNH 1929,7,13.16	Guy	1	f	196	12	15	134	12	2	2	0	8	34	234	1	1	7	4
FMNH 178470	Guy	1	f	208	13	15	147	13	2	2	0	8	45	234	1	1	7	4
AMNH 61536	Guy	2	f	206	10	15	153	14	2	1	0	8	34	234	1	1	7	4
FMNH 178471	Guy	2	f	221	12	15	154	13	2	2	0	8	34/45	23/234	1	1	7	4
USNM 566255	Guy	2	m	177	23	15	148	13	2	2	0	8	45	234	1	1	7	4
FMNH 178469	Guy	1	m	176	19	15	—	21	2	1	0	8	456	234	1	1	7	4
USNM 228048	Tob	1	f	166	12	15	139	12	2	2	0	8	45	234	1	1	7	4
BMNH 1931.10.18.142	Tob	2	f	178	11	15	140	12	2	2	0	8	45	234	1	1	7	4
USNM 228026	Tob	1	f	182	14	15	143	12	2	1	0	8	45	234	1	1	7	4
USNM 228044	Tob	1	f	nd	11	15	143	12	2	2	0	8	45	234	1	1	7	4
USNM 166676	Tob	1	f	175	10	15	144	11	2	2	0	8	45	234	1	1	7	4
USNM 228034	Tob	1	f	209	11	15	144	12	2	2	0	8	45	234	1	1	7	4
USNM 228029	Tob	1	f	255	19	15	145	14	2	2	0	7	45	234	1	1	7	4
USNM 228047	Tob	1	f	221	15	15	145	12	2	2	0	8	45	234	1	1	7	4
BMNH 1931.10.18.141	Tob	2	f	213	12	15	147	12	2	2	0	8	45	234	1	1	7	4
USNM 228030	Tob	1	f	249	17	15	148	15	2	2	0	8	45	234	1	1	7	4
USNM 228037	Tob	1	f	211	13	15	148	13	2	2	0	8	45	234	1	1	7	4
BMNH 1931/10.18.143	Tob	2	f	174	10	15	151	12	2	2	0	8	45	234	1	1	7	4
USNM 228036	Tob	1	f	73	5	15	—	12	2	2	0	—	—	—	—	—	—	—
USNM 228038	Tob	1	f	76	5	15	—	12	2	2	0	—	—	—	—	—	—	—
USNM 228040	Tob	1	f	85	7	15	—	13	2	2	0	8	45	234	1	2	7	4
USNM 228041	Tob	1	f	84	5	15	—	—	2	2	0	—	—	—	—	—	—	—
USNM 228043	Tob	1	m	189	21	15	137	17	2	1	0	7	34	234	1	1	6	3
USNM 228028	Tob	1	m	200	23	15	138	22	2	2	0	8	45	234	1	1	7	4
USNM 228046	Tob	1	m	189	23	15	138	21	2	2	0	7	45	234	1	1	7	4

Museum Number	Location	PAT	S	SVL	T	DSR	V	SC	IN	PO	PrO	UL	ULO	ULL	LO	PT	LL	LLcs
USNM 228035	Tob	1	m	184	19	15	139	19	2	2	0	8	45	234	1	1	7	4
USNM 228045	Tob	1	m	195	21	15	141	19	2	2	0	8	45	234	1	1	7	4
USNM 228032	Tob	1	m	180	21	15	143	18	2	2	0	8	45	234	1	1	7	4
USNM 228033	Tob	1	m	193	19	15	146	17	2	2	0	7	45	234	1	1	7	4
USNM 228027	Tob	1	m	174	19	15	—	17	2	2	0	7	34	234	1	1	7	4
USNM 228039	Tob	1	m	74	5	15	—	19	2	2	0	8	45	234	1	2	7	4
USNM 228042	Tob	1	m	85	4	15	—	19	2	2	0	8	45	234	1	1	7	4
FMNH 77901	Tri	2	f	213	12	15	140	12	2	2	0	7	34	23	1	1	7	4
UWIZM 2012.12.142	Tri	1	f	206	13	15	140	13	2	2	0	8	45	234	1	1	7	4
BMNH 65.11.30.11	Tri	2	f	105	8	15	141	13	2	2	0	7	34	23	1	1	7	4
USNM141587	Tri	1	f	168	12	15	141	12	2	2	0	8	45	234	1	1	7	4
FMNH 41679	Tri	d	f	165	10	15	142	12	d	d	0	d	d	d	d	d	d	d
AMNH 101334	Tri	1	f	188	9	15	143	11	2	2	0	7	34	23	1	1	7	4
USNM 523949	Tri	1	f	193	11	15	143	10	2	2	0	7	45	234	1	1	7	4
UWIZM 2010.12.144b	Tri	1	f	233	19	15	144	13	2	2	0	8	45	d	1	1	7	4
FMNH 49971	Tri	2	f	171	—	15	147		2	2	0	8	45	234	1	1	7	4
UWIZM 12.143a	Tri	1	f	234	17	15	147	13	2	2	0	8	45	234/345	1	1	7	4
UWIZM 2010.12.144c	Tri	2	f	197	15	15	147	14	2	2	0	8	45	234	1	1	1	4
UWIZM 2010.12.149	Tri	1	m	180	21	15	129	20	2	2	0	8	45	234	1	1	7	4
AMNH 64470	Tri	1	m	160	15	15	132	17	2	2	0	7	45	23	1	1	7	4
BMNH 1964.1897	Tri	1	m	177	19	15	132	18	—	2	0	8	45	234	1	1	7	4
BMNH 1964.1892	Tri	2	m	116	11	15	133	18	2	1	0	7	34	23	1	1	7	4
UWIZM 2010.12.144a	Tri	2	m	128	12	15	134	19	2	2	0	8	456	234	1	1	7	4
UWIZM 2010.12.147	Tri	1	m	177	19	15	134	21	2	2	0	7	345	23	1	1	6	—
FMNH 35102	Tri	2	m	189	22	15	135	20	2	2	0	8	45	234	1	1	7	4
FMNH 41678	Tri	d	m	154	15	15	137	20	2	2	0	8	45	234	1	1	7	4
UWIZM 12.143b	Tri	1	m	219	22	15	137	21	2	2	0	8	45	234	1	1	7	4
UWIZM 12.143c	Tri	1	m	197	20	15	137	20	2	2	0	8	45	234	1	1	7	4
USNM 523950	Tri	1	m	146	15	15	138	18	2	2	0	8	45	234	1	1	7	4
AMNH 103835	Tri	1	m	217	17	15	146	13	2	2	0	8	45	234	1	1	7	4
UWIZM 10/22	Tri	—	m	—	—	15	148	20	2	2	0	8	45	234	1	1	—	4
BMNH 65.11.30.12	Tri	2	m	83	7	15	—	19	—	2	0	7	34	23	1	1	7	4
USNM 286920	Tri	1	m	167	17	15	—	17	2	2	0	8	45	234	1	1	7	4
USNM 286921	Tri	d	m	156	20	15	—	20	2	2	0	8	45	234	1	1	7	4

Museum Number	Location	PAT	S	SVL	T	DSR	V	SC	IN	PO	PrO	UL	ULO	ULL	LO	PT	LL	LLcs
AMNH 6562	Tri	2	f	85	6	15	151	10	2	2	0	8	45	234	1	1	7	4
AMNH 81450	Tri	1	m	210	18	15	142	14	2	2	0	7	45	234	1	1	7	4
AMNH 81448	Tri	1	—	—	—	—	—	—	2	2	0	8	45	234	1	1	7	4
AMNH 67868	Venz	2	f	d	7	15	140	11	2	2	0	8	45	234	1	1	7	4
USNM 164839	Venz	1	f	227	16	15	140	13	2	2	0	7	34	234	1	1	6	3
USNM 164841	Venz	1	f	195	10	15	144	9	2	2	0	7	45	234	1	1	7	4
USNM 164834	Venz	1	f	204	13	15	145	11	2	2	0	8	45	234	1	1	7	4
USNM 164835	Venz	1	f	193	14	15	145	10	2	2	0	7	45	234	1	1	7	4
FMNH 178435	Venz	2	f	236	16	15	146	13	2	2	0	8	45	234	1	1	7	4
AMNH 102329	Venz	2	f	210	11	15	148	8	2	2	0	8	45	234	1	1	6	4
USNM 164836	Venz	1	m	199	21	15	139	17	2	2	0	7	34	234	1	1	7	4

of 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). A comprehensive revision of the genus is lacking, and the alpha taxonomy of the clade is in disarray due to some species being known only from the type material, misidentified specimens, and the extraordinarily large number of species descriptions (Passos and Lynch 2010; Passos et al. 2019). Some of these are microendemics and are known only from the holotype or a small series of specimens from restricted ranges (Passos et al. 2007), whereas others are relatively widespread (Wallach et al. 2014). The Three-lined Snake, *Atractus trilineatus* (Wagler 1828), is the type species for the genus.

The Three-lined Snake is found in Trinidad, Tobago, northern Venezuela, western Guyana, and in Brazil from Roraima as far south as Manaus. The origins of the Trinidad and Tobago populations and their relationships with mainland populations were investigated by Murphy et al. (2019). They found *Atractus trilineatus* to be deeply divergent from the other 31 congeners included in their analysis. Populations of *A. trilineatus* from Trinidad and Tobago show a close genetic affinity with mainland populations from Guyana, which suggests recent vicariance following Late Pleistocene sea-level rises, although overwater dispersal events cannot be ruled out, especially for the colonization of Tobago.

Materials and Methods

Terminology for *Atractus* head scalation follows Savage (1960) and ventral and subcaudal count methods follow Dowling (1951). We examined alcohol-preserved specimens from the herpetology collections at the American Museum of Natural History (AMNH), the British Museum of Natural History (NHM), the Field Museum of Natural History (FMNH), National Museum of Natural History (USNM), and the University of the West Indies Museum of Zoology (UWIZM). Specimens examined are listed in Table 1.

Sex was determined by tail shape, tail length, and visual inspection of the hemipenes. Dorsal scales were counted on the neck at about the 10th ventral, at midbody, and about 10 ventral scales anterior to the vent, and they were counted on the diagonal. Ventral counts, subcaudal counts, and tail/SVL ratios were analyzed for sexual dimorphism. Scale counts and scale measurements were done under a dissection microscope. Scale measurements were taken with a metric ruler and dial calipers. Snake sizes are given in millimeters. Scale counts separated by a dash (–) represent a range taken from different individuals. Scale counts separated by a slash (/) represent data taken from a single individual in left/right order. A pattern formula of 45–8 signals a stripe on scale rows four and five and a second stripe on scale row eight.

Single factor ANOVAs, principal component analyses, and cluster analyses were performed in Excel with Xlstats and Data Lab with alpha = 0.05. Means are presented ± one stan-

dard deviation. Hatchling measurements were taken before preservation. Individuals with body lengths less than 100 mm were assumed to be immature.

Results

Morphometric and meristic data for males and females from five populations of *Atractus trilineatus* are listed in Table 1 and comparisons are in Table 2. Females are longer, have shorter tails, lower tail/body length ratios, more ventrals, and fewer subcaudals than males. Sexual dimorphism in coloration is readily apparent in this species. Females tend to be red-tan or red-orange in color, whereas males are gray or gray-brown (Fig. 2). Sexual dimorphism data organized by the populations examined are in Table 1 and are graphed in Fig. 3.

The dorsal pattern can have stripes on scale rows 45–8 (common on Tobago and in Venezuela); 4–789 (in one Guyana specimen), 234–8, 2345–8 (common on Trinidad and in Venezuelan specimens), 34–678, 34–78, 345–8, or 45–78. Two postoculars usually are present, but a few specimens have just one. The tallest upper labial is usually the seventh, but it can be six, five, or eight; in six specimens the last upper labial is horizontally divided. Upper labials that contact the loreal are usually 234 but can be 23 or 345. One primary temporal is typical, but two are sometimes present. Lower labials are usually seven, but some specimens have six; the first four usually contact the chin shields, but in one specimen only the first three contact the chin shields. The comparison of morphological traits in mainland and island populations suggests the species is morphologically variable as suggested by Garman (1887).

Natural History

On Trinidad and Tobago, *Atractus trilineatus* occurs in urban gardens, cocoa plantations, secondary forests, and primary forests (Emsley 1977; Mole 1924; Murphy 1997). Martins and Oliveira (1993) reported it from blackwater flooded forest in Brazil.

On Trinidad, we have found this species to be abundant in an experimental cacao plot on the campus of the University of the West Indies, as well as in the secondary forests of the Arima Valley and in some urbanized areas. Adults were found crossing roads at night; during the day they were collected by raking leaf litter and turning ground cover. We also have found specimens in clumps of leaf litter and debris that have been washed into roadside gutters and drains in both urban and forested areas.

The few stomachs we examined contained the remains of annelid setae. Mole (1924) reported that females lay 3–4 large eggs. In Trinidad, egg-laying has been reported for the months of March, April, and August, and eggs are about 18 x 8 mm (Emsley 1977).

One of us (ALB) recovered 12 *Atractus trilineatus* eggs on Tobago from forest leaf litter and logs. On 15 December three eggs were removed from a rotting log on a forested slope behind Charlotteville (Table 3). These were maintained and transported to the United States, where they were kept at 20–22 °C until they hatched on 2–3 April (108 days later). Three eggs were recovered from a rotting log on 16 December; the log was shaded by a large tree and also contained a nest of ants. Two of the eggs were spoiled, the other contained a developing embryo. On 19 December, three eggs were found in vegetation debris and maintained for ten days in some of

Table 2. Morphometric measurements and meristic counts for Three-lined Snakes (*Atractus trilineatus*). Means are presented ± one SD, ranges are in parentheses. m = males; f = females.

Population	SVL (mm)	Tail (mm)	Tail/SVL	Ventrals	Subcaudals
Brazil (m, n = 1)	189	20	0.11	143	19
Guyana (f, n = 5)	207.17 ± 19.0	13.2 ± 2.79	0.06 ± 0.01	149 ± 7.30	12.83 ± 0.69
	(196–239)	(10–19)	(0.06–0.08)	(134–156)	(12–14)
Guyana (m, n = 1)	176	19	0.11	148	21
Tobago (f, n = 13)	204.92 ± 25.57	14 ± 3.23	0.07 ± 0.01	144.73 ±2.27	12.69 ± 1.73
	(166–249)	(11–23)	(0.05–0.10)	(139–151)	(10–16)
Tobago (m, n = 8)	188.0 ± 7.87	20.75 ± 1.56	0.11 ± 0.01	140.9 ± 3.01	18.75 ± 1.79
	(174–200)	(19–23)	(0.10–0.12)	(137–146)	(17–21)
Trinidad (f, n = 12)	192.55 ± 26.34	12 ± 3.69	0.06 ± 0.01	143 ± 2.58	18.75 ± 1.79
	(165–249)	(10–17)	(0.05–0.07)	(140–147)	(17–21)
Trinidad (m, n = 8)	195.72 ± 16.56	19.75 ± 1.71	0.10 ± 0.01	136.5 ± 5.07	12.09 ±1.24
	(177–219)	(17–22)	(0.08–0.12)	(129–146)	(10–14)
Venezuela (f, n= 6)	210.83 ± 15.87	13.11 ± 2.29	0.06 ± 0.01	144.6 ± 2.34	10.67 ± 1.89
	(195–227)	(11–16)	(0.05–0.07)	(140–148)	(8–13)
Venezuela (m, n = 1)	199	21	0.11	139	17

Fig. 2. Male (A) and female (B) Three-lined Snakes (*Atractus trilineatus*) from Trinidad. Males are gray-brown in colo, whereas females are red-gray. Sexually dimorphic coloration is known from relatively few species of snakes. Photographs by John C. Murphy.

the debris. All hatched on 14 March (85 days later). A second clutch also found on 19 December contained two eggs found in forest leaf litter. On 26 December, one egg was taken from forest litter and maintained until it hatched on 14 February (50 days later). Six hatchlings were measured, total lengths ranged from 84–99 mm (mean = 90.83 ± 6.28 mm). Tails were 5.0–9.5 mm (mean = 7.1 ± 1.2 mm). The mean female SVL from Tobago was 203.75 mm. Thus, hatchlings average 44.5% of average female body length or 35.6% of the largest female measured in this study.

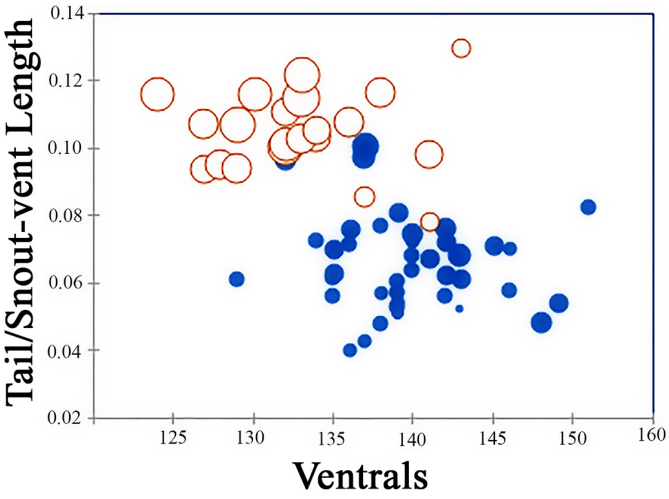

Fig. 3. Sexual dimorphism of tail-SVL ratios in Three-lined Snakes (*Atractus trilineatus*) plotted against ventral scale counts. Blue marks indicate females, brown marks males.

We have removed specimens of this snake from the stomachs of the Red Snake (*Erythrolamprus ocellatus*) and a coral snake (*Micrurus circinalis*).

Discussion

Phylogenetic analyses (Murphy et al. 2019) indicate *Atractus trilineatus* to be the sister lineage of the clade including all other *Atractus* species examined, although with a considerably high genetic divergence from its sisters. *Atractus* is an extremely diverse genus with 143 recognized species, of which the molecular analysis included only 31 (22.4%). Therefore, as more species are added, the topology of the tree can be expected to change.

The island-mainland distribution of *A. trilineatus* is likely the result of sea level changes in the eastern Caribbean. Today the archipelago populations are isolated but were likely continuous with the mainland multiple times during the Pleistocene. Trinidad was connected to the mainland for longer periods than Tobago. The ~410 Kya mean age of divergence reported by Murphy et al. (2019) between the Guyana and Trinidad and Tobago populations suggests that the island populations were isolated from the mainland during sea-level high stands and connected to South American at sea level low stands

Table 3. Data for five clutches of Three-lined Snake (*Atractus trilineatus*) eggs from Tobago.

Date Collected	Date Hatched	Days of Incubation	Incubation Temperatures	Clutch Size
15 Dec	2–3 April	108	20–22 C	3
16 Dec	none hatched	—	—	3
19 Dec	13 March	85	—	3
19 Dec	none hatched	—	—	2
26 Dec	14 Feb	50	—	1

(Fig. 4). The same explanation can be used for the isolation and divergence of Trinidad and Tobago populations, which according to Murphy et al. (2019) took place about 180 Kya.

Monsoon rains and associated flooding in northern Venezuela are known to form rafts of vegetation that wash up on the southern coastlines of Trinidad (Charles 2013). Murphy et al. (2019) presented two pieces of information that support the view that *A. trilineatus* is spending time in the water as unlikely as it may seem. Martins and Oliveira (1993) reported 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 flooded forest.

Natural History, Dispersal, and Phylogeography

Natural history provides additional insight into the phylogeography of *Atractus trilineatus.* A diet of earthworms and possibly insects (Mole 1924, this study), the elongated incubation time (a minimum of 108 days; see Table 3), year-round reproduction, placement of eggs in vegetative debris and logs, and the relatively large size of offspring all contribute to the ability of *Atractus trilineatus* to disperse via large rafts of floating vegetation. The relationships between natural history, biogeography, and phylogeography are frequently overlooked, which is a mistake – after all natural selection influences the distributions of lineages (Avise 2004).

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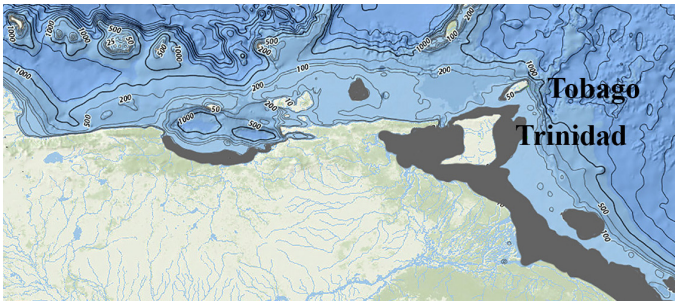

Fig. 4. The coastal plain of northern South America showing bathymetric contour lines. The area shaded in brown would have been exposed land when sea level dropped by 50 m. The map is based on information found at https://maps.ngdc.noaa.gov/viewers/bathymetry.

Literature Cited

Avise, J.C. 2004. *Molecular Markers, Natural History, and Evolution.* 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

Charles, S.C. 2013. An interesting reptile dispersal event from continental South America to Trinidad, Trinidad and Tobago. *Living World, Journal of The Trinidad and Tobago Field Naturalists' Club* 2013: 63.

Dowling, H.G. 1951. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1: 97–99.

Duméril, A.M.C., G. Bibron, and A. Duméril. 1854. *Erpétologie générale ou histoire naturelle complète des reptiles.* Vol. 7. Roret, Paris.

Emsley, M.G. 1977. Snakes, and Trinidad and Tobago. *Bulletin of the Maryland Herpetological Society* 13: 201–304.

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.

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.

Mole, R.R. 1924. The Trinidad Snakes. *Proceedings of the Zoological Society of London* 94: 235–278.

Murphy, J.C., D. Salvi, A.L. Braswell, and M.J. Jowers. 2019. Phylogenetic position and biogeography of Three-Lined Snakes (*Atractus trilineatus*: Squamata, Dipsadidae) in the Eastern Caribbean. *Herpetologica* 75: 247–253.

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.

OLAW (Office of Laboratory Animal Welfare). 2002. *Institutional Animal Care and Use Committee Guidebook, 2nd edition.* National Institutes of Health, Bethesda, Maryland, USA.

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., R. Fernandes, and N.A. Zanella. 2005. A new species of *Atractus* (Serpentes: Colubridae) from southern Brazil. *Herpetologica* 61: 209–218.

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., 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* 19: e20170976.

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.

Snyder, A. 2016. *Atractus trilineatus* (Three-lined Ground Snake). Predation. *Herpetological Review* 47: 308.

Uetz, P., P. Freed, and J. Hošek (eds.). 2019. *The Reptile Database.* <http://www.reptile-database.org>.

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, Boca Raton, Florida.