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The Rediscovery of Hallowell's Ground Snake, *Atractus fuliginosus*, on Tobago with Notes on its Natural History

The Republic of Trinidad and Tobago is composed of two main islands with numerous small satellites and offshore rocks that form an archipelago. The island of Trinidad is considered continental in origin while Tobago had an oceanic origin, but both islands have a continental flora and fauna. Trinidad is an extension of Venezuela's Peninsula de Paria and was formed by a pull-apart basin that separated Trinidad from the mainland. On the other hand, Tobago was formed on the advancing edge of the Caribbean plate and became a terrane, that moved across the edge of the South American plate to its current position northeast of Trinidad,

at one time being accreted onto what is now northcentral Venezuela (Weber 2009; Weber et al. 2015). This history has the potential to explain why some Tobago frogs, lizards, and snakes have their closest relatives in northcentral Venezuela and not in the more proximal Trinidad. Clades exhibiting this Tobago–northcentral Venezuela pattern include the glass frog *Hyalinobatrachium orientale*, the stream frog *Mannophryne olmonae*, the rain frog *Pristimantis charlottevillensis*, the twig anole *Anolis* cf. *tigrinus*, the snake *Erythrolamprus pseudoreginae*, and a species of *Atractus* with 17 dorsal scale rows (Hardy 1982; Murphy 1997; Murphy et al. 2018).

The ground snakes of the genus *Atractus* currently number 143 species (Uetz et al. 2020), making it the most species-rich snake genus. *Atractus* are semi-fossorial and cryptozoic, spending their lives below ground and on the surface in the leaf litter where they forage for food, find mates, and deposit their eggs. Two species of *Atractus* occur in the Trinidad and Tobago Archipelago. The Three-lined Ground Snake, *Atractus trilineatus*, occurs on both islands as well as some of their satellites, and it is in eastern Venezuela, Guyana, and north-central Brazil (Nogueira et al. 2019). It is abundant in gardens, urbanized habitats, agricultural areas, and secondary forests (Murphy et al. 2018). Its presence in Trinidad and Tobago has been recognized since the late 19th century (Garman 1887) as *Rhabdosoma lineatum*. Because it is so abundant in human-modified habitats, we know a bit more about it than most of the other 142 species of *Atractus* (Murphy et al. 2019, 2020). *Atractus trilineatus* has dorsal scales in 15 rows at mid-body, is sexually dichromatic, and feeds primarily on worms, as do many, if not most, species of *Atractus* (Murphy et al. 2019, 2020).

By comparison, the second species of *Atractus* found in the Republic of Trinidad and Tobago is an enigma; it is present on Tobago and absent from Trinidad. However, it is relatively well known from Venezuela and Colombia (Medina-Rangel et al. 2019; Fig. 1). The Tobago population was initially referred to as *A. univittatus* (Hardy 1982; Murphy 1997), and later as *A. fuliginosus* (Murphy et al. 2018). Here, we discuss the discovery, morphology, and natural history of the Tobago *Atractus* with 17 scale rows at mid-body.

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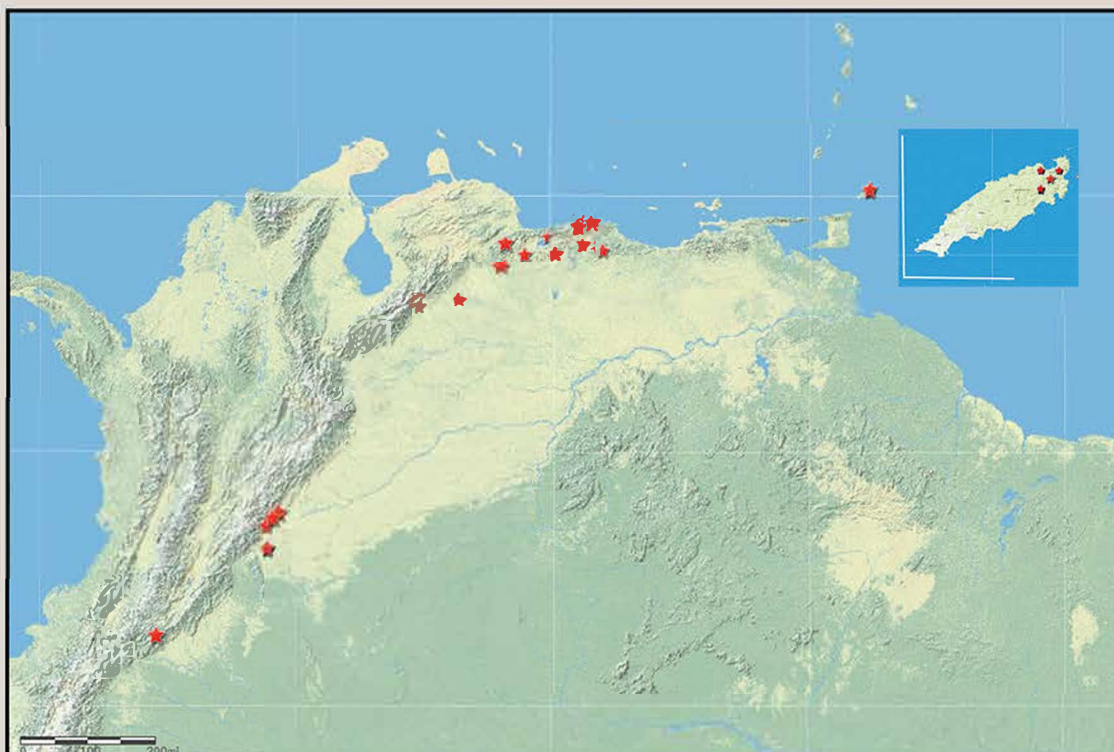


FIG. 1. The distribution of *Atractus fuliginosus*. Stars mark locations of museum specimens examined and those reported in the literature.

MATERIALS AND METHODS

We collected morphological data from the 30 specimens examined. Sex was determined by tail shape, tail length, subcaudal counts, and visual inspection of the hemipenes. Dorsal scales were counted on the anterior body at about the 10th ventral, at midbody, and ca. 10 ventral scales anterior to the vent, and they were counted on the diagonal. Ventral counts and subcaudal counts were made following Dowling (1951). Scale counts and scale measurements were done under a dissection microscope. 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. The specimens examined, and the localities of *Atractus fuliginosus* and *A. univittatus* reported in the literature were placed on a map using ArcView. Specimens examined (N = 30): Colombia, Meta, Lomilinda (UTA 3598–3601, 3642, 3818, 3819, 3865, 3867, 3880, 5172, 5181, 5217); Republic of Trinidad and Tobago, Tobago (USNM 228024; UWIZM 2015.19.9, 2016.22.46, 2017.14–2017.16); Venezuela, Barinas, Barinitas (MCNC 4244); Venezuela, Cojedes, Municipio San Carlos, Potrero Largo, Manrique (MHNLS 13834); Venezuela, La Guaira, Planta Eléctrica de Naiguatá, 730 m (MCNC 3333, 5647, 5663, 5672, 7342, 7360, 7636, 7810); Venezuela, Miranda, Parque Guatopo, 27 km N Altigracia (TCWC 58707). Abbreviations used: TL = total length, SVL = snout–vent length, T/SVL = tail/snout–vent length ratio, r = range, SD = standard deviation. All statistical analysis was done in Excel, Microsoft Office 365.

RESULTS

In December 1978, Dave L. Stephan collected the first specimen of an *Atractus* with 17 dorsal scale rows on Tobago (USNM

228024); it had 154 ventrals and 31 subcaudals plus a tail-tip spine. The specimen was 340 mm in total length with a 44 mm tail; five maxillary teeth on each side; seven upper labials on each side, six lower labials on each side; and a loreal extending from the orbit to the nasal. The snake was found on the trail to Pigeon Peak, a trail that runs off the top of Flagstaff Hill, about 550 m ASL. The specimen was identified as *Atractus univittatus* (Hardy 1982; Murphy 1997), a species otherwise known from Venezuela and Colombia.

In the original species description, the type locality for the holotype of *Atractus univittatus* (ZMH 2851; 300 mm SVL) was given as “Caracas” which refers to Caracas, Distrito Federal State, Venezuela (Jan 1862). Hallowell (1845:243) had previously described *Coluber fuliginosus* based on the holotype (ANSP 3333; SVL 413 mm) with a type locality reported as the, “Republic of Colombia within 200 miles of Caraccas [sic].” However, Roze (1958) considered this type locality to be located within present-day Venezuela. *Atractus fuliginosus* was later recorded from northeastern Venezuela (Mt. Turimiquire), but that population was subsequently described as *A. matthewi* (Markezich and Barrio-Amorós 2004). Additionally, in the description of *Atractus eriki* (Esqueda and La Marca 2005) mentioned a specimen of *A. fuliginosus* from San Juan de Los Morros, a locality lying in Venezuela’s Central Coastal Range with which they compared the new species.

Rivas et al. (2012) noted the original description of *A. fuliginosus* was based on a single specimen from “within 200 miles of Caracas”, Venezuela and that its status, as well as the precise type locality, remained unclear. Both species (*A. fuliginosus* and *A. univittatus*) possess 17-17-17 dorsal scale rows. The localities provided for the *A. univittatus* specimens they examined (Guanare and Barinitas) are closer to the Venezuelan Andes than to San Juan de Los Morros. It was unclear if Esqueda et al. (2007) considered *univittatus* as a synonym of *fuliginosus*, but if they were, *Coluber fuliginosus* Hallowell 1845 would have priority. Similarly, Rivas et al.

(2012) could not confirm or deny this possibility. However, Natera Mumaw et al. (2015) considered *A. univittatus* Jan as a junior synonym of *Atractus fuliginosus* (Hallowell 1845). So we follow that assignment here.

A second *Atractus* specimen with 17 scale rows from Tobago turned up during the 2015 BioBlitz (UWIZM.2015.19.9). It was found dead in a roadside drain by Nalini Leenoi Rampersad, and it was badly decomposed but clearly represented an individual of this species. The collection locality was again on Tobago's Main Ridge. That specimen had six maxillary teeth on both sides, six mandibular teeth, and each pterygoid bone had 22 teeth. The ventrals were damaged by decomposition; the minimum number present in this specimen is >138. The cloacal plate is single. The specimen is a male (right hemipenes partially everted); the subcaudals were 27/28. A third Tobago specimen (UWIZM.2016.22.46) was found in June of 2016 crossing the Roxborough-Parlatuvier Road by two of us (ALB, RJA); the road traverses Tobago's Main Ridge. This was a female that contained two eggs (Fig. 2A).

On 7 June 2017, three eggs suspected of belonging to this species were collected just off the Roxborough-Parlatuvier Road by JW. The eggs were found in the nest of the trap jaw ant, *Odonotomachus bauri* (Formicidae: Ponerinae) in a cavity under a rock. The eggs were taken to the UWIZM in St. Augustine Trinidad and incubated. They hatched 36 days later on 12 July. The hatchlings were 125–135 mm in total length.

Measurement data from specimens examined. Total length of all undamaged males was 178–449 mm (N = 10), and 159–463 mm (N = 12) for females. SVL for males was 154–390 mm and 142–415 mm for females. Undamaged tail length was 27–53 mm for males and 17–51 mm for females. Tail/SVL ratios in males were 0.15–0.18 (mean = 0.156, SD = 0.009), and 0.11–0.15 (mean = 0.13, SD = 0.01) in females. Ventral scales in males were 149–171 (mean = 161.6, SD 7.45) and 151–175 (mean = 163.1, SD = 6.83) in females. Subcaudal scales were 31–38, (mean = 34.2, SD = 2.52) in males and 27–33 (mean = 29.67, SD = 2.09) in females. A Fisher's F-Test/Two-tailed test was run comparing the ventral and subcaudal counts of the three groups (Colombia, Venezuela, and Tobago) in all of the tests, the null hypothesis could not be rejected ($P > 0.05$).

A comparison of the hemipenes between a Tobago specimen (USNM 228024) and a specimen from Venezuela (TCWC 58707) suggested the Tobago and Venezuelan populations were similar in this trait (the hemipenes have five rows of large spines and 22–23 small spines along one branch of the sulcus; when adpressed to the tail, it extended 5.25–5.5 subcaudals; and the base is spineless).

Atractus fuliginosus is distinguished from all congeners with 17 scale rows at the mid-body by the following combination of characters: (1) two postoculars; (2) an elongated loreal that usually borders the orbit (3) a short primary temporal contacting upper labials 4 and 5; (4) seven upper labials, with the third and fourth bordering orbit; (5) five or six lower labials, first three contact the chin shields; (6) six maxillary teeth; (7) one gular scale row; (8) 154 ventrals in two males and 149–171 in females; (9) 27–32 subcaudals; (10) first scale row is yellow and forms a yellow stripe; a second lateral stripe is between scale rows two and three, scale rows four and above each have a scale outlined in brown with a yellow center; (11) the venter is a uniform yellow. In life, the hatchlings were gray above with a pattern of darker grey and yellow. Each dorsal scale in the first two rows has a large, pale pigmented spot. Scales in row four also have a pale-yellow center on most scales. Mid-dorsal rows have an interrupted vertebral stripe composed of two or three scale rows with dark gray pigment. The ventral

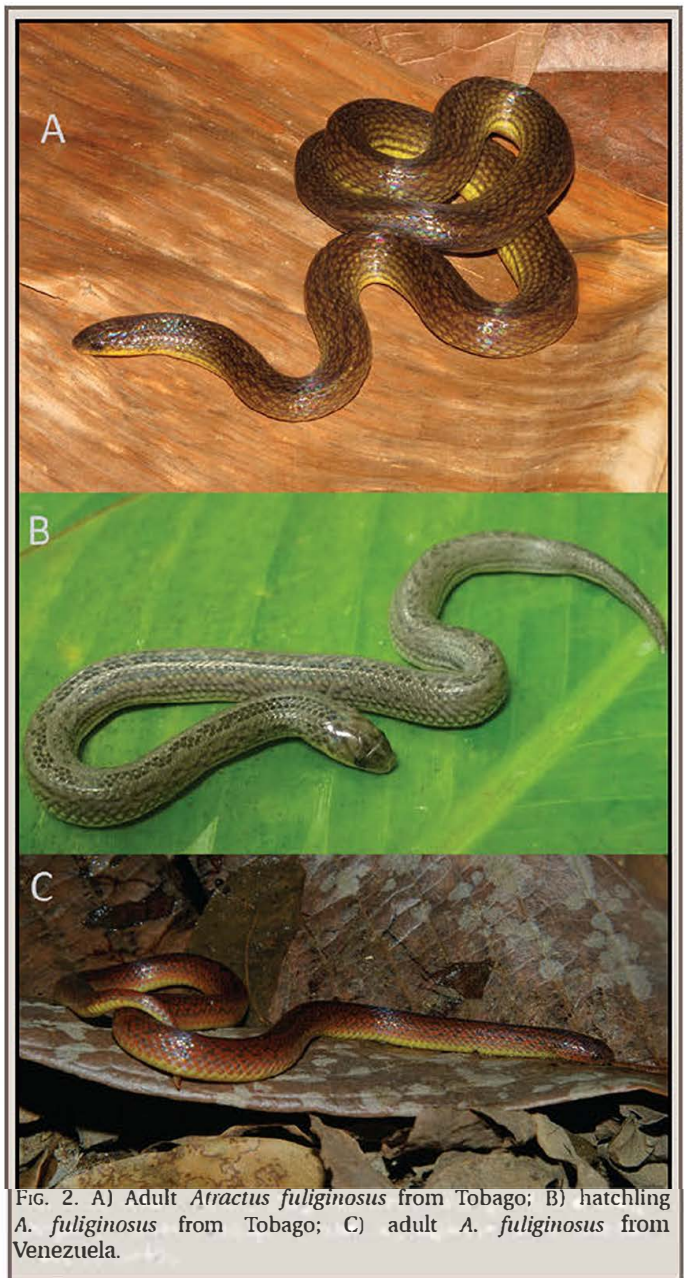


FIG. 2. A) Adult *Atractus fuliginosus* from Tobago; B) hatchling *A. fuliginosus* from Tobago; C) adult *A. fuliginosus* from Venezuela.

surface is mostly immaculate with some scattered melanophores; the scattered pigmentation is slightly denser under the tail.

DISCUSSION

Tobago's Main Ridge is a primarily forest-covered cluster of igneous hills about 29-km long oriented southwest to northeast in the Caribbean Sea and contacts the coral platform on Tobago's southern coast (Arkle et al. 2017). Lower montane rainforest covers most of the area (Beard 1944; Helmer et al. 2012) but some of it has been urbanized. On Tobago, all *Atractus fuliginosus* collected to date have come from the Main Ridge. The Main Ridge Forest Reserve, the oldest protected forest in the western hemisphere, makes up 3958 hectares of the Main Ridge and reaches an elevation of 572 m ASL. Most of the forest reserve is lower montane rainforest and occurs at elevations above 244 m ASL. The Main Ridge receives the most significant rainfall on the island. All three

Atractus fuliginosus specimens and the eggs came from the Main Ridge but were peripheral to the Forest Reserve. The nest was on a roadside that had mowed grass and was ca. 10 m from the forest edge. Esqueda and La Marca (2007) mentioned a Venezuelan specimen of *Atractus fuliginosus* found in a gallery forest surrounded by dry tropical forest. A second specimen also cited by these authors was found under a rock in a grassy area with scattered trees. Both specimens were in the Andean foothills.

Atractus fuliginosus hatchlings are grey, while the adults are brown and yellow. Exactly when this ontogenetic color change occurs is not clear. The difference may reflect hatchlings and subadults being more fossorial and the adults spending more time in the leaf litter. This is not the first report of an *Atractus* depositing their eggs in ant nests. In Corrientes Province, Argentina Sandoval et al. (2009) found four clutches of *Atractus reticulatus* eggs in a *Eucalyptus* woodland. In all cases, the eggs were inside *Odontomachus* ant nests. The humidity recorded in the anthills varied between 40–50%, and the temperature ranged from 27.4–27.8°C, while the ambient temperature was 32°C (Sandoval et al. 2009). Thus, the ant nests create a stable microclimatic that facilitate a warm and humid environment that would likely be more conducive to embryonic development than the external ambient environment. Doan and Lamar (2012) also reported the lizard *Cercosaura hypnoides* (family Gymnophthalmidae) sometimes deposited its eggs in the nests of *Odontomachus* ants. We cannot say that Tobago *A. fuliginosus* usually places its eggs in this ant's nest with a sample size of one clutch or that the snakes have a commensal relationship with the ants. However, the observation suggests that the ants may construct an important microhabitat for the eggs and be important to the life history of *Atractus fuliginosus*.

Ongoing molecular work on the Tobago and Venezuelan population confirm that both populations of *A. fuliginosus* are in fact, the same species (Jowers et al. 2021). A low genetic divergence suggests a recent steppingstone colonization event from Trinidad throughout land bridge connections at low sea levels stands (Murphy 1997) and the possibility of an undiscovered population in Trinidad.

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