



## Notes on the Feeding Habits of the Caribbean Watersnake, *Tretanorhinus variabilis* (Dipsadidae)

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**Abstract.**—The Caribbean Watersnake, *Tretanorhinus variabilis* (Dipsadidae) is one of two aquatic West Indian snakes. Despite being a relatively common species in Cuba and the Cayman Islands, its feeding habits have been poorly studied. Herein we report several new instances of predation by this species on fishes, frogs, and a freshwater crab. The latter represents the first record of durophagy in this species and the third snake reported as a crab eater in the West Indies.

The Neotropical snake genus *Tretanorhinus* (Dipsadidae) comprises four aquatic species: The Caribbean Watersnake (*T. variabilis* Duméril and Bibron 1854) in the West Indies, the Orange-bellied Swampsnake (*T. nigroluteus*) from southern Mexico to Panama, Mocquard’s Swampsnake (*T. mocquardi*) from Panama to Ecuador, and the Striped Swampsnake (*T. taeniatus*) from Colombia to Ecuador (Uetz et al. 2020). The Caribbean Watersnake (Fig. 1) is one of two aquatic West Indian snakes; the other is the Salt Marsh Snake, *Nerodia clarkii compressicauda* (Natricidae) (Neill 1965; Henderson and Crother 1989; Schwartz and Henderson 1991; Henderson and Powell 2009). Of the five currently recognized subspecies of *T. variabilis*, four are from the

Cuban Archipelago and one occurs on Grand Cayman, the Cayman Islands (Schwartz and Henderson 1991; Henderson and Powell 2009; Estrada 2012; Rodríguez et al. 2013; Fig. 2). The Caribbean Watersnake, which occurs only in aquatic ecosystems, exhibits some morphological adaptations to an aquatic lifestyle. These include dorsally positioned eyes and nostrils (Barbour and Ramsden 1919; Buide 1985; Fig. 1A) and dark markings on a dark olive ground color that blend perfectly with the leaf litter and algae-covered rocks on the bottom of ponds and streams (Fig. 1B). Those characteristics, however, might be considered just a first stage toward the development of more complex adaptations to an aquatic lifestyle (see Lillywhite 2014 for a review).



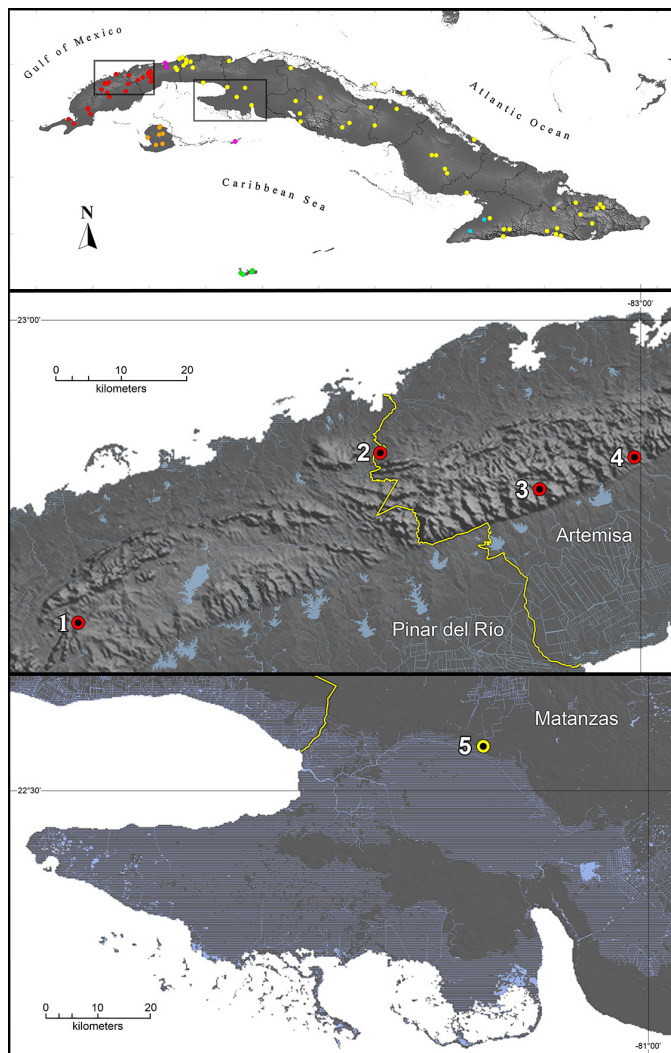
**Fig. 1.** The Caribbean Watersnake (*Tretanorhinus variabilis*) exhibits some adaptations to an aquatic lifestyle, such as the eyes and nostrils on top of the head (A) and a color pattern that blends well with the riparian environments it inhabits (B). Photographs © T.M. Rodríguez-Cabrera.

Although this species is relatively common and widely distributed in Cuba (Fig. 2), where it has an elevational range from sea level to 1,000 m (Rodríguez et al. 2010, 2013; Estrada 2012), little is known about its natural history (see Henderson and Powell 2009 for a review). This snake appears to consume mostly fishes, amphibians, and aquatic invertebrates. Barbour and Ramsden (1919) mentioned that it preys on fishes, “usually cyprinodonts, called in Cuba Guajacones” (i.e., Poeciliidae). Neill (1965) found a snake that had consumed a small introduced American Bullfrog (*Lithobates catesbeianus*) from a river in Pinar del Río Province, which

is the only previously confirmed prey species of this snake. Schwartz and Ogren (1956) mentioned a snake from Granma Province (*T. v. binghami*) that had captured and swallowed a small unidentified fish. Neill (1965) also observed individuals of this species (*T. v. binghami*) pursuing small fishes by “snapping randomly right and left amidst the darting schools,” in the saltwater of a deep ditch in southern Mayabeque Province. Other authors (Vogel 1965; Henderson and Crother 1989; Seidel and Franz 1994; Sampedro and Rodríguez 2003; Díaz and Cádiz 2008) merely listed aquatic invertebrates, fishes, amphibians and their larvae, and small lizards among the prey of this snake, without providing any additional details. Herein we report four instances of predation and one of foraging behavior by Caribbean Watersnakes (*T. v. wagleri* and *T. v. variabilis*) in western Cuba, including the first case of durophagy in this species.

### Methods

We measured snake snout-vent length (SVL), tail length, and head length to the nearest millimeter using either direct measurements with a measuring tape or a caliper or from photographs using the program ImageJ (v. 1.43; <https://imagej.nih.gov/ij/>). In two instances, we estimated total length. We also measured stomach content volumes to the nearest cubic millimeter by noting liquid displacement of distilled water in a graduated cylinder. Data for all coordinates is WGS 84. Voucher specimens were preserved in ethanol (75%) and deposited in the zoological collections of the Museo de Historia Natural “Tranquilino Sandalio de Noda” (MHN.TSN), Pinar del Río, and the Instituto de Ecología y Sistemática (CZACC), La Habana, Cuba.



**Fig. 2.** Distribution of the Caribbean Watersnake (*Tretanorhinus variabilis*) in Cuba and the Cayman Islands (top): *T. v. variabilis* (yellow dots), *T. v. wagleri* (red dots), *T. v. insulaepinorum* (orange dots), *T. v. binghami* (blue dots), and *T. v. lewisi* (green dots); purple dots represent populations not assigned to subspecies (based largely on Schwartz and Henderson 1991; Estrada 2012; Rodríguez et al. 2013; T.M. Rodríguez-Cabrera, per. obs.). A section of western Cuba (center) depicting the locations where we observed predation events and foraging behavior by *T. v. wagleri*: (1) La Yabita Stream, (2) San Marcos River, (3) Santa Cruz River, and (4) Manantiales River at Soroa. A section of the Zapata Swamp (bottom) showing the location 3 km south of Peralta (5), where we observed a predation event by *T. v. variabilis*.



**Fig. 3.** Juvenile Caribbean Watersnake (*Tretanorhinus variabilis*; MHN.TSN-37-CL) collected at La Yabita Stream, El Moncada, Viñales Municipality, Pinar del Río Province, containing two partially digested Cuban Streamside Frogs (*Eleutherodactylus riparius*) in its stomach. Photograph © L.Y. García-Padrón.

### Results

At about 0900 h on 10 September 2002, we observed an adult female Caribbean Watersnake, *T. v. variabilis* (ca. 700 mm total length) with an obvious abdominal bulge in an area of flooded forest known as “Cantabria” in the northernmost portion of the Zapata Swamp, 3 km south of Peralta, Jagüey Grande Municipality, Matanzas Province (22°35'00"N, 81°18'29"W; ca. 1.5 m asl; Fig. 2). The snake was initially on land before it responded to our presence by attempting to escape into the water. Forced regurgitation revealed a Biajaca, *Nandopsis tetracanthus* (Perciformes: Cichlidae) with a total length of about 100 mm.

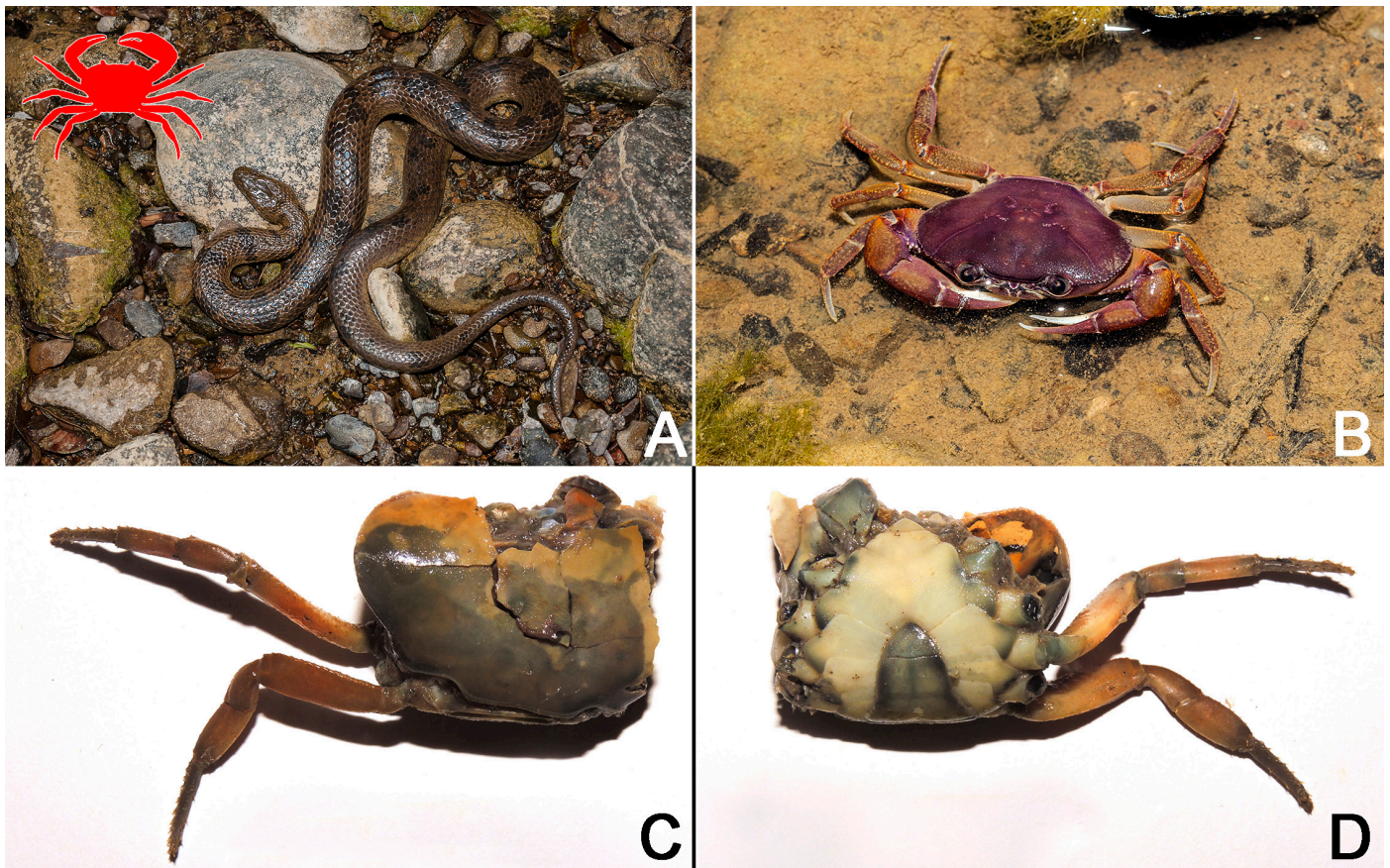
At 1000 h on 8 October 2009, we collected a juvenile Caribbean Watersnake, *T. v. wagleri* (182 mm SVL, 54 mm

tail length, 13 mm head length) from under a rock in water about 10 cm deep in La Yabita Stream, El Moncada Town, Viñales Municipality, Pinar del Río Province (22°33'08"N, 83°49'55"W; 150 m asl; Fig. 2). It contained two partially digested Cuban Streamside Frogs, *Eleutherodactylus riparius* (Eleutherodactylidae; ca. 17 mm SVL each; total stomach content volume 690 mm<sup>3</sup>). The snake was preserved and accessioned in the Museo de Historia Natural “Tranquilino Sandalio de Noda,” Pinar del Río (MHN.TSN-37-CL; Fig. 3)

At 0900 h on 10 July 2019, we observed an adult male Caribbean Watersnake, *T. v. wagleri* (ca. 700 mm total length) foraging in the Manantiales River at Soroa, Candelaria Municipality, Artemisa Province (22°47'38"N, 83°00'30"W; 150 m asl; Fig. 2). When first seen the snake



**Fig. 4.** Sequence of photographs of a predation attempt by a Caribbean Watersnake (*Tretanorhinus variabilis*) on an introduced Blue Tilapia (*Oreochromis aureus*) in the San Marcos River: (A) At the moment the snake pulled the fish out of the water; (B–C) holding the fish, notice the disproportionate size of the fish; (D) shifting its hold to the fish’s tail, (E) having moved to the head and started swallowing the fish, and (F) the maximum extent of ingestion attained during the attempt to swallow the fish. Photographs © A. González (A) and Gustavo Blanco (B–F).



**Fig. 5.** An adult female Caribbean Watersnake (*Tretanorhinus variabilis*) (A) in the Santa Cruz River that had ingested a male freshwater crab (*Epilobocera gilmani synoecia*); a living adult conspecific freshwater crab from the same locality (B). The crab-shaped inset in “A” represents the proportional size of the prey compared to the snake. Dorsal (C) and ventral (D) views of the ingested crab (CZACC 4.13400). Photographs © T.M. Rodríguez-Cabrera (A, B) and Raimundo López-Silvero (C, D).

was coiled on a partially submerged dead branch with the anterior portion of its body in the water apparently trying to capture topminnows (Poeciliidae), which were very abundant close to the bank. Poeciliid species inhabiting that river are Cuban Gambusia (*Gambusia punctata*), Creole Topminnow (*Girardinus creolus*), Metallic Girardinus (*Gi. metallicus*), Singlespot Topminnow (*Gi. uninoatus*), and Cuban Limia (*Limia vittata*). Although we did not observe any successful captures, this observation suggests that those fishes likely are components of the snake’s diet.

At 0945 h on 29 October 2019, we observed a predation attempt by an unsexed adult Caribbean Watersnake, *T. v. wagleri* (ca. 750 mm SVL, tail tip missing, unknown head length; Fig. 4) on a Blue Tilapia, *Oreochromis aureus* (Perciformes: Cichlidae; ca. 150 mm total length) in the San Marcos River on the border between La Palma and Bahía Honda Municipalities, Pinar del Río and Artemisa Provinces, respectively (22°48'14"N, 83°23'06"W; 30 m asl; Fig. 2). When we first saw the snake, it was in the water about 2 m from the opposite riverbank and it had captured the fish by the anal fin region. The snake started to swim in reverse, drawing the fish out of the water (Fig. 4A), remaining in the same position (Figs. 4B–C) for about 17 min until the snake

shifted its grip to the fish’s tail (Fig. 4D). Some 3 min later, the snake moved its grip to the head of the fish in an attempt to swallow it (Fig. 4E). Ingestion extended to the edge of the operculum (Fig. 4F) but not beyond that point. The snake continued its attempt to swallow the fish for about 1.5 h before quitting and moving away. At that time, the photographer (G. Blanco) pushed the fish into the water, whereupon it recovered and swam away.

At 2115 h on 13 March 2020, we captured an adult female Caribbean Watersnake, *T. v. wagleri* (710 mm SVL, 150 mm tail length, 35 mm head length; Fig. 5A) in the Santa Cruz River, San Cristóbal Municipality, Pinar del Río Province (22°45'00"N, 83°08'58"W; 140 m asl; Fig. 2). Forced regurgitation revealed a partially digested adult male endemic freshwater crab, *Epilobocera gilmani synoecia* (Pseudothelphusidae; carapace length ca. 22 mm, carapace width ca. 37 mm; total stomach content volume 5,000 mm<sup>3</sup>). We estimated prey size by extrapolating the measurements from other crabs of the same sex and comparable size collected at the same locality (Fig. 5B). The snake was released at the exact site of capture, but the remains of the crab were preserved and accessioned in the Instituto de Ecología y Sistemática, La Habana (CZACC 4.13400).

### Discussion

The feeding ecology of swampsnakes in the genus *Tretanorhinus* from continental areas is little studied. Villa (1970) listed fishes (Poeciliidae, Gobiidae, Eleotridae, Pimelodidae, and Rivulidae [as Cyprinodontidae]) and amphibians (Leptodactylidae, Hylidae, Ranidae, and larval toad [Bufonidae]) among the confirmed prey of Orange-bellied Swampsnakes in nature. He also listed other fishes and frogs that captive snakes readily accepted. The diets of the other species of *Tretanorhinus* remain unknown.

The Cuban Streamside Frog (Fig. 6) taken by the Caribbean Watersnake in La Yabita Stream is the first record of a frog in the genus *Eleutherodactylus* in the diet of a Caribbean Watersnake, which also is the first predator reported for this frog in nature. The Cuban Streamside Frog is a riparian species and is often associated with the same bodies of water as the Caribbean Watersnake (Díaz and Cádiz 2008; Rivalta et al. 2014). The Caribbean Watersnake might be a frequent predator of riparian frogs and other anurans that depend on water to reproduce.

Schwartz and Ogren (1956) mentioned that most of the Caribbean Watersnakes they collected in Granma Province were in quiet areas of streams with their bodies looped around rocks on the bottom close to the banks at night (see also Barbour and Ramsden 1919). In rivers and streams in the Guaniguanico Range in western Cuba and the Guamuhaya Range in central Cuba, we have repeatedly observed this snake patrolling shallow waters (<30 cm deep) close to riverbanks at night. In such situations, poeciliids are frequently motionless on the bottom, especially species of *Girardinus*, as species of *Gambusia* tend to remain close to the surface even at night (T.M. Rodríguez-Cabrera, pers. obs.). Those observations suggest that the species may be an active forager, although apparently it also uses an ambush strategy (see Results).



**Fig. 6.** Adult Cuban Streamside Frog (*Eleutherodactylus riparius*) from the Sierra del Rosario in western Cuba. Photograph © Raimundo López-Silvero.



**Fig. 7.** Comparison of the left maxillae of the four genera of dipsadid snakes present in Cuba. From top to bottom: Cuban Racer (*Cubophis cantherigerus*), Cuban Lesser Racer (*Caraiiba andreae*), Havana Racerlet (*Arrhyton dolichura*), and Caribbean Watersnake (*Tretanorhinus variabilis*). Note the strong opisthognathous condition in all genera except *Tretanorhinus*, which has dentition typical of a piscivorous snake. Scale bars = 1 mm. Photographs © T.M. Rodríguez-Cabrera.

Strategies used by aquatic snakes for subduing prey vary from constriction and holding with body loops to envenomation, in addition to other more unusual ways (see Lillywhite 2014 for a review). One of the snakes described herein captured a tilapia at least 2 m from the bank of a small river before pulling it out of the water. It subsequently remained in the same position, holding the fish for nearly 20 minutes, before initiating attempts to swallow it. Whether gill desiccation is a previously undescribed strategy to subdue relatively large fish is unknown. One alternative explanation for such behavior might be envenomation. Various dipsadids are opisthognathous (i.e., with enlarged rear maxillary teeth) and have well developed Duvernoy's glands that produce a toxic saliva (e.g., Myers 1974; Rodríguez-Robles 1992; Rodríguez-Robles and Thomas 1992; Rodríguez-Robles and Leal 1993; Weldon and Mackessy 2010; Rodríguez-Cabrera et al. 2016). However, contrary to many other dipsadids, Caribbean Watersnakes are essentially aglyphous (Fig. 7), equipped instead with a high number of sharp, posteriorly curved teeth, dentition comparable to those of other piscivorous snakes (Savitzky 1983; Knox and Jackson 2010). That, combined with powerful jaw muscles, must provide this snake with a strong bite capable of subduing relatively large prey. Because *Tretanorhinus* does not represent a basal colubroid clade (Pyron et al. 2011, 2013; Grazziotin et al. 2012), the aglyphous condition would appear to be a derived secondary character. Nonetheless, we cannot rule out envenomation, since studies are necessary to determine whether Caribbean Watersnakes produce a toxic saliva despite its aglyphous dentition.

The Biajaca is one of two endemic Cuban cichlids (Vergara 1980, 1992b; Froese and Pauly 2019). These medium-sized fish (standard length to 220 mm) are abundant and widely distributed in bodies of water all over the main island and Isla de la Juventud (Vergara 1980, 1992b). Only the Cuban Crocodile (*Crocodylus rhombifer*) and the invasive African Catfish (*Clarias gariepinus*) were previously reported predators of this species (Ramos et al. 1994, 2010; Hurtado et al. 2016). The Caribbean Watersnake reported herein is the third confirmed predator of this fish, although many aquatic birds prey on fish, including cichlids (e.g., Acosta 1998; Acosta and Mugica 2006; see above), and likely consume Biajacas as well. Another potential predator is the Cuban Gaar (*Atractosteus tristoechus*), which is known to consume relatively large fish (Vergara 1992a).

Only a handful of snake species in the world are known as crab eaters (e.g., Savitzky 1983; Shine 1985; Green 1997; Jayne et al. 2002, 2018; Murphy and Voris 2002; Voris and Murphy 2002; Lillywhite 2014), probably due to the hard crustacean exoskeleton and powerful claws, which present an effective defense against many predators. One of the Caribbean Watersnakes reported herein is the sixth confirmed predator of pseudothelphusid crabs in the West Indies. Other natural predators that have been reported for crabs in this family include the Cuban Solenodon (*Solenodon cubanus*), the invasive alien African Catfish, the Yellow-crowned Night-Heron (*Nyctanassa violacea*), the Red-tailed Hawk (*Buteo jamaicensis*; see Rodríguez-Cabrera et al. 2018 for a review; but see also Santana and Temple 1988), and the American Bullfrog (García-Padrón et al. in press). The other two snakes reported as crab eaters (not pseudothelphusids) in the region are the Martinique Lancehead, *Bothrops lanceolatus* (Viperidae; Ruff 1859; De Lalung 1934; B. Raboteau 1968 in Gosner 1987) and the Puerto Rican Boa, *Chilabothrus inornatus* (Boidae; Wiley 2003). The instance of crab predation described herein represents the first report of durophagy by a Caribbean Watersnake. The Crab-eating Snake (*Fordonia leucobalia*) and Gerard's Watersnake (*Gerarda prevostiana*) (Homalopsidae), both from southern Asia, are crab-eating specialists that dismember their prey before ingestion, reducing the impact of constraints imposed by gape size or prey size and morphology (e.g., Jayne et al. 2002, 2018; Murphy and Voris 2002; Voris and Murphy 2002). Although Caribbean Watersnakes are generally considered to be piscivorous and they do not have the adaptations of durophagous snakes (see above; Savitzky 1983), this observation indicates that it is capable of feeding on hard-shelled prey. Since the crab in the stomach of the Caribbean Watersnake was clearly fragmented, we cannot discard the possibility that it used a strategy similar to that of homalopsid snakes, but additional observations are required to corroborate this assumption. In any case, crabs might not be a sufficiently large component of the diet of these snakes to induce morphological adaptations for durophagy.

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