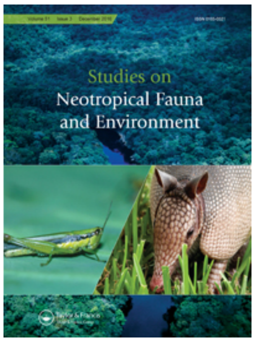

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ORIGINAL ARTICLE

The threadsnake tangle: lack of genetic divergence in *Epictia tenella* (Squamata, Leptotyphlopidae): evidence for introductions or recent rafting to the West Indies

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ABSTRACT

The confusion between the Neotropical threadsnakes *Epictia albifrons* (Wagler) and *Epictia tenella* (Klauber) has been ongoing for decades. The lost holotype of *Stenostoma albifrons*, a poorly detailed original description, and dubious type locality confound the problem. Recently an extant series of nine museum specimen from Belém, state of Pará, Brazil were selected as topotypes for *Epictia albifrons* Wagler. From this series a neotype was designated. Here we compare the morphology of the neotype to specimens from Trinidad and Guyana, confirming that they are *Epictia tenella* (Klauber) not *E. albifrons* (Wagler). We also compare four mitochondrial and one nuclear marker from Trinidad and mainland (Guyana) *Epictia tenella* populations and find *E. tenella* relatively widespread with minimal genetic diversification between island and mainland specimens. Hypotheses that may explain the low divergence for this small, fossorial snake are explored and discussed: over-water rafting, human-mediated dispersal, and avian-mediated dispersal.

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systematics; phylogeny; Neotropics; dispersal; scolecophidian snakes

Introduction

Prior to 2009 the Leptotyphlopidae contained two genera (*Leptotyphlops* and *Rhinoleptus*) with about 116 species found mostly in the Neotropics and Africa, with a few representatives in Arabia and southwest Asia, a distribution that suggests the family evolved in western Gondwana. In a molecular examination of leptotyphlopids Adalsteinsson et al. (2009) found support for increasing the number of genera to 11. This included resurrecting Gray's (1845) genus *Epictia* for about 25 of the Western Hemisphere leptotyphlopids.

The islands of Trinidad and Tobago and their satellites have a South American fauna that includes about 40 species of snakes in six families despite their relatively small geographic area (~5200 km^2) (Murphy 1997). Leptotyphlopids have been known to be present on Trinidad since DeVerteuil (1858) wrote "…another smaller one, provided with a sting at the end of the tail, may possibly be the *Stenostoma Albifrons…*" (sic).

The identity of the Trinidad and Tobago leptotyphlopids has been long confused, with various authors listing one or more species (Table 1). Much of the confusion has centered on the uncertain identity of *Stenostoma albifrons* Wagler in Spix (1824). The lack of morphological detail in the original description, the lost type specimen, and a problematic type locality have been major impediments to defining some members of the genus *Epictia* in northern South America (McCranie & Hedges 2016).

The sequence of events that exacerbated the confusion between *E. albifrons* and *E. tenella* focus on Jan (see Wallach, 2016). Jan (1861, 1864) was the only person to examine the type specimen of *Stenostoma albifrons* after its description and provided a more detailed description. Jan and Sordelli (1860–1866, livr. 2, pl. 5–6, Figure 1) illustrated *S. albifrons* in the 1861 volume of their atlas. Unfortunately, instead of using Wagler's Brazilian type from Munich's ZSM for the illustration, they used a specimen from Lima, Peru in Milan's Museo Civico di Storia Naturale di Milano (MSNM.).

Wallach (2016) concluded that Jan and Sordelli's figure does not depict the type of *S. albifrons*, but represents a different species of the genus *Epictia*.

Stenostoma albifrons was allocated to the genus *Leptotyphlops* by Barbour (1914) who suggested the

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Table 1. Species of leptotyphlopids reported from Trinidad and Tobago by various authors. Note that the confusion between *E. tenella* and *E. albifrons* has resulted in both species being reported from the islands at various times.

Citation	*albifrons*	*tenella*	*goudotii*
DeVerteuil (1858)	x		
Garman (1887)	x		
Boulenger (1893)	x		
Mole (1910, 1914, 1924)	x		
Barbour (1914)	x		
Klauber (1939)		x	
Beebe (1946)	x		
Roze (1952)		x	
Underwood (1962)	x		
Boos & Quesnel (1968)	x		
Peters & Oréjas-Miranda (1970)			x
Boos (1975)			x
Emsley (1977)		x	x
Greenhall (1977)			x
Welch (1978)			x
Lancini (1979)			x
Wilson and Meyer (1985)			x
Murphy (1997)	x		x
McDiarmid (1999)	x	x	x
Boos (2001)	x		

species was widespread in the Antilles and South America. Klauber (1939) described *Leptotyphlops tenella* as a species with an entire anal plate, 218–229 dorsal scales, and 15–18 subcaudal scales, a pattern of serrated longitudinal stripes, and a yellow spot on its head and another on the tail tip. *Leptotyphlops tenella* was known from Guyana and Trinidad and believed distinct from Wagler's *E. albifrons*, because *E. tenella* has the supraocular and first upper labial in contact, while *albifrons* has the supraocular and first upper labial separated by the nasal scale (Figure 1). This raises the question of whether this difference is individual variation or species specific. Specimens are relatively consistent in having the supraocular–labial contact with an occasional specimen lacking the character state (McCranie & Hedges 2016, this study). Other authors have found this important, diagnostic character to be conservative in lined Neotropical leptotyphlopids (Francisco et al. 2012).

Adalsteinsson et al. (2009) diagnosed *Epictia* as having 14 mid-body scale rows, 10 (rarely 12) mid-tail scale rows, 155–396 mid-dorsal scale rows, 10–30 subcaudals, two supralabials, a large anterior supralabial, 109–341 mm maximum adult total length, body shapes of 28–90 (total length/width at mid-body), relative tail lengths of 3.3–11.5%, tail shapes of 2.1–6.1, a striped pattern, often with multiple dorsal colors (including reds and yellows), and a pale colored venter.

Using molecular data, Adalsteinsson et al. (2009) split *Leptotyphlops* into several genera including the genus *Epictia* for the Neotropical species with 10 scales around their tail. They also demonstrated the *E. albifrons* group is not closely related to the *Epictia goudotii* group, and a molecular clock divergent date estimates the two groups separated approximately 30 Ma ago in the Oligocene. Despite this ancient divergence, if a specimen of the *E. goudotii* group is placed next to a member of the *E. albifrons* group, the two snakes are remarkably similar in appearance. Convergence in fossorial squamates produces remarkably similar morphology. So, despite the similar morphology and a long history of confusion the two lineages are genetically distinct. In a recent paper McCranie and Hedges (2016) revise the *E. goudotii* species complex and recognize six species within the clade. Noting the problem of the absence of genetic data for *E. goudotii*, McCranie and Hedges (2016) suggested that *E. goudotii* ranges from the Panama Canal Zone to northern Colombia, Venezuela, and Trinidad. They also discussed the confusion over the identity of *E. albifrons* and *E. tenella*. However, Wallach (2016) demonstrates that *E. goudotii* is not present in Central America.

Epictia albifrons and *E. tenella* have both been recognized as valid species (Wallach et al. 2014).

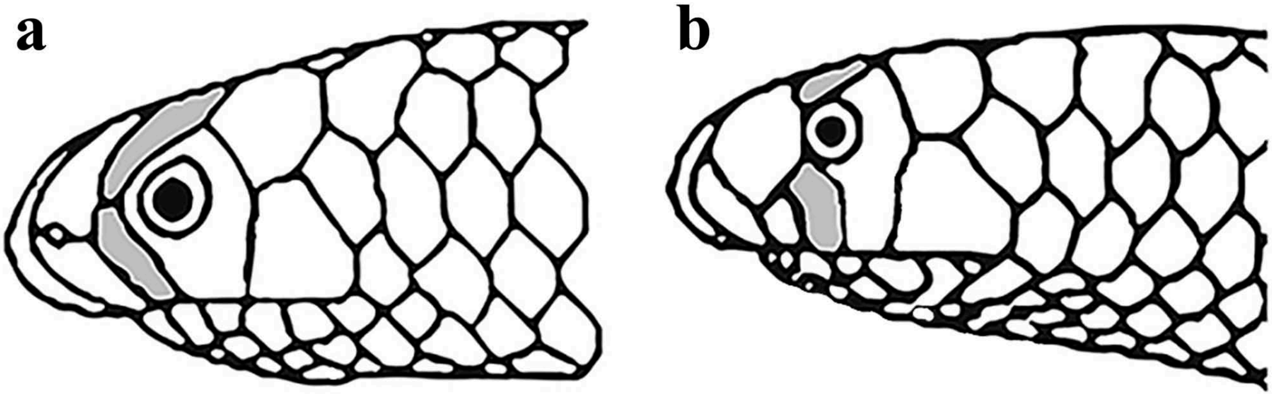

Figure 1. Comparison of the scale arrangements in profiles of (A) *Epictia albifrons* (Wagler) and (B) *Epictia tenella* (Klauber).

Epictia albifrons was considered a *nomen dubium* (Wilson & Hahn 1973; Franco & Pinto 2009). Alternatively, *E. tenella* was considered a junior synonym of *E. albifrons* (Hoogmoed & Gruber 1983).

Orejas-Miranda (1967) considered both *Epictia albifrons* and *E. tenella* to have large geographical distributions that included Guyana and noted the absence versus presence of the supraocular–anterior supralabial contact in those two species, but he failed to find any museum specimens representing the scale arrangement found in *E. albifrons*. Peters and Orejas-Miranda (1970) recognized both *E. albifrons* and *E. tenella* as valid species, citing the presence (*E. tenella*) or absence (*E. albifrons*) of the supraocular–anterior supralabial contact. However they included only *E. tenella* in the Guyana fauna, leaving *E. albifrons* out of the fauna. Hoogmoed (1977) came to a similar conclusion regarding the specimens from Suriname.

During an examination of mainland specimens of the *albifrons* group Thomas (1965) implied multiple species were present within this group. In an attempt to resolve the nomenclatural confusion, Hoogmoed and Gruber (1983) suggested relegating *E. tenella* to the synonymy of *E. albifrons* so that *E. albifrons* could be diagnosed. Esqueda et al. (2015) also considered *E. albifrons–tenella* to represent a species complex, noting that one form is present north of the Amazon, and another form present south of the Amazon. They selected a neotype for *Stenostoma albifrons* Wagler, MCZ R-2885, an adult, of unknown of sex, collected in Pará, Brazil. The specimen clearly shows the characteristics of *E. tenella*.

Wallach (2016) rejected MCZ R-2885 as a neotype and designate BYU 11490, a 154 mm female topotype from the vicinity of Belém, Pará State, Brazil, as the neotype of *Stenostoma albifrons*. He diagnoses the two species, *E. tenella* having the supraocular contacting the first upper labial; the rostral apex rounded; and the nasal suture horizontal, while *E. albifrons* has the supraocular isolated from the first supralabial; the rostral apex truncated; and the nasal suture inclined 45°. He views *E. albifrons* as restricted to the vicinity of the topotype series, an area in northeastern Brazil. While, *E. tenella* is a relatively widespread species in cis-Andean South America. This resolves the long standing confusion over the identity of *E. albifrons* and *E. tenella*.

Using tissue from three Trinidad specimens of *Epictia tenella* and extant sequences in Genbank labeled *Epictia albifrons* (in error, these are actually from *E. tenella*) from Guyana we look for evidence that *E. tenella* may be a complex of cryptic species or a single, widespread species.

Materials and methods

DNA extraction, purification and amplification protocols follow Jowers et al. (2014). DNA was extracted from tissue samples of *Epictia tenella* adults from Trinidad (Republic of Trinidad and Tobago, UWIZM.2011.20.21, Tucker Valley; UWIZM.2012.27.57, Arima Valley; UWIZM.2012.37, Pointe-a-Pierre). The primers used were: 12S rDNA: 12SA 5′-AAACTGGGATTAGATACCCCACTAT-3′, 12SB 5′-GAGGG TGACGGGCGGTGTGT-3′ Kocher et al. (1989) and 16SL rDNA: 16SL 5′-GCCTGTTTAT CAAAAACAT-3′, 16SH 5′-CCGGTCTGAACTCAGAT CACGT-3′ Palumbi (1996), CYTB: L14841 (Kocher et al. 1989) 5′-AAAAAGCTTCCATCCAACATCTCAGCAT GATGAAA-3′ and Epic Alb Rev (this study) 5′-TATCATTCTGGTTTGATGTGTGG-3′, ND4: ND4 (Arevalo et al. 1994) 5′-CACCTATGACTACCAAAA GCTCATGTAGAAGC-3′, LEU 5′-CATTACTTTTACTT GGATTTGCACCA-3′, C-MOS S77 5′-CATGGACTGGG ATCAGTTATG-3′, C-MOS S78 5′-CCTTGGGTGTGA TTTTCTCACCT-3′ (Lawson et al. 2005).

Templates were sequenced on both strands when needed, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v.4.9. The length of the sequences were: 12S rDNA; 372 base pairs (bp), 16S rDNA and 461 bp, Cytb 724 bp, ND4; 844 bp, C-Mos; 540 bp. The 12S and 16S rDNA gene fraction and Cytb were aligned with the larger *Epictia* dataset (3241 bp) to improve support of internal branches. No ND4 sequences are available in Genbank for *Epictia*, but ND4 fragments were sequenced to assess intra genetic variation within the Trinidad samples. Similarly, for the C-Mos gene fragment only three *Epictia* species are available in Genbank (one being *E. albifrons*), and thus this fragment was amplified to rule out the possibility of possible mitochondrial introgression with *E. albifrons*.

Additionally, BLAST searches were conducted in Genbank (Genbank Accessions KX446889-KX446902) and matches with high genetic affinity were downloaded and included in the alignment, including shorter *Epictia* sequences of either the 12S or 16S rDNA gene fragments, but not available for both. Preliminary results including *E. collaris* (a short 16S rDNA fraction section not in common with our targeted region) grouped this taxon with the designated outgroup *Siagonodon septemstriatus* and blast searches matched of this sequence matched closely the outgroup rather than the ingroup. In view of its doubtful affinity to *Siagonodon* and the likely need for further sequencing of other loci for this species we excluded this 16S rDNA sequence from the final analyses. Sequences were aligned in Seaview v.4.2.11 (Gouy et al. 2010) under ClustalW2 (Larkin et al. 2007) default settings. Genetic *p*-distances and standard error (% ± SE) were calculated using MEGA v6 (Tamura et al. 2011). The most appropriate substitution model for the Bayesian inference (BI) analysis was determined by the Bayesian information criterion (BIC) in jModeltest v.2 (Posada 2008). MrBayes v.3.2.6 (Ronquist & Huelsenbeck 2003) was used with default priors and Markov chain settings, and with random starting trees. Each run consisted of four chains of 5,000,000 generations, sampled each 10,000 generations and posterior distributions of parameter estimates were visually inspected in Tracer v1.5 (Rambaut & Drummond 2007). A plateau was reached after few generations with 25% of the trees resulting from the analyses discarded as burn in. Phylogenetic relationships among haplotypes for each locus were estimated using a maximum likelihood (ML) approach, as implemented in the software RAxML v7.0.4 (Silvestro & Michalak 2012), using the default settings. The 50% majority rule consensus tree was built in PAUP 4 (Swofford 2002). All analyses were performed through the CIPRES platform (Miller et al. 2010).

Specimens were examined and measured with a ruler, scale counts and arrangements were made under a stereoscope. Scale count data from the literature follow Wallach (2016).

Material examined: *E. tenella*: Trinidad FMNH42721-22, 49914, 69769, 190745, 200292, 215868, 217237–38; USNM 286926–28; UWIZM.2010.12.239–242. The two Genbank specimens (SBH267110, SBH267111) were from Baramita and Kurupukari, locations south of the Orinoco River and 360 and 720 km respectively from Trinidad.

Results

The three *Epictia* samples from Trinidad recovered three haplotypes with the 12S rDNA gene fraction at two polymorphic sites and only one haplotype from the 16S rDNA gene fraction. The more variable Cytb gene fraction recovered three haplotypes. There was no intraspecies variation in the ND4 and C-Mos loci. Genbank BLAST searches (we here follow the taxonomic nomenclature from Genbank) of the sequences obtained matched *E. albifrons* SBH267111 (12S rDNA: UWIZM.2012.37; 99%, 2 bp, UWIZM.2011.20.21; 100%, 2012.27.57; 99%, 1 bp difference, 16S rDNA: 100% with all three individuals, and the Cytb: UWIZM.2012.37; 99%, 2 bp, UWIZM.2011.20.21; 99%, 1bp, 2012.27.57; 99%, 3 bp difference, C-Mos: 100%).

The best-fitting model for the rDNA and Cytb alignment were the TIM2 + I + G (-lnL = 9219.94212, BIC = 18891.936187) and TrN+G (-lnL = 3870.49372, BIC = 8076.146946), respectively. The effective sample size (ESS) values for all runs were over 3000, thus confirming good convergence mixing of all Markov chain Monte Carlo runs. All analyses recovered a well-resolved monophyletic clade (Bayesian posterior probability: 1, ML bootstrap 100%) with *Epictia* from Trinidad and *E. tenella* (SBH267111 and SBH267110) from Guyana. Our tree topology (Figure 2) is fully concordant to Adalsteinsson et al. (2009) and McCranie and Hedges (2016) showing the basal position of *E. tenella* to the rest of the genus.

There was no genetic divergence between *E. tenella* SBH267111 and UWIZM.2011.20.21 from Tucker Valley (Northwest Trinidad) based on the 12S and 16S rDNA, and only 0.27% for the Cytb gene fragment. The overall genetic divergence between the two Guyana individuals and Trinidad was 0.94%±0.34 (12S rDNA), 0.43%±0.21 (16S rDNA) and 1.76%±0.59 (Cytb). Population *p*-distances at Guyana and within Trinidad were: 1.34% and 0.44%±0.1, respectively for the 12S rDNA, 0.87% and 0%, respectively for the 16S rDNA and 2.78% and 0.37%±0.1, respectively for the Cytb.

A comparison of the head scales of the Pará, Brazil, neotype, specimens from Trinidad, and specimens from Guyana, including the specimens represented with gene sequences, indicates that they are remarkably similar to each other (Figure 3), agreeing with the molecular results.

Discussion

The Trinidad specimens of *Epictia* that we have examined are all morphologically similar to *E. tenella*, with the exception of a specimen from the satellite island of Chacachacare, and two USNM specimens without specific locality data. These three specimens belong to another, or possibly two, undescribed species. Thus Trinidad has at least two species of *Epictia*.

The designation of a neotype for *E. albifrons* by Wallach (2016) resolves the *E. albifrons–tenella* issue. Clearly, *E. tenella* has been present in Trinidad and Tobago since at least the mid-nineteenth century based upon DeVerteuil's (1858) comment; and the low genetic divergence between the mainland and island populations is indicative of relatively recent gene flow.

Scolecophidian snakes usually do not have large distributions (Broadley & Wallach 2007a, 2007b). The exception is the Brahminy Blind Snake, *Ramphotyphlops braminus* (Typhlopidae), an all-female

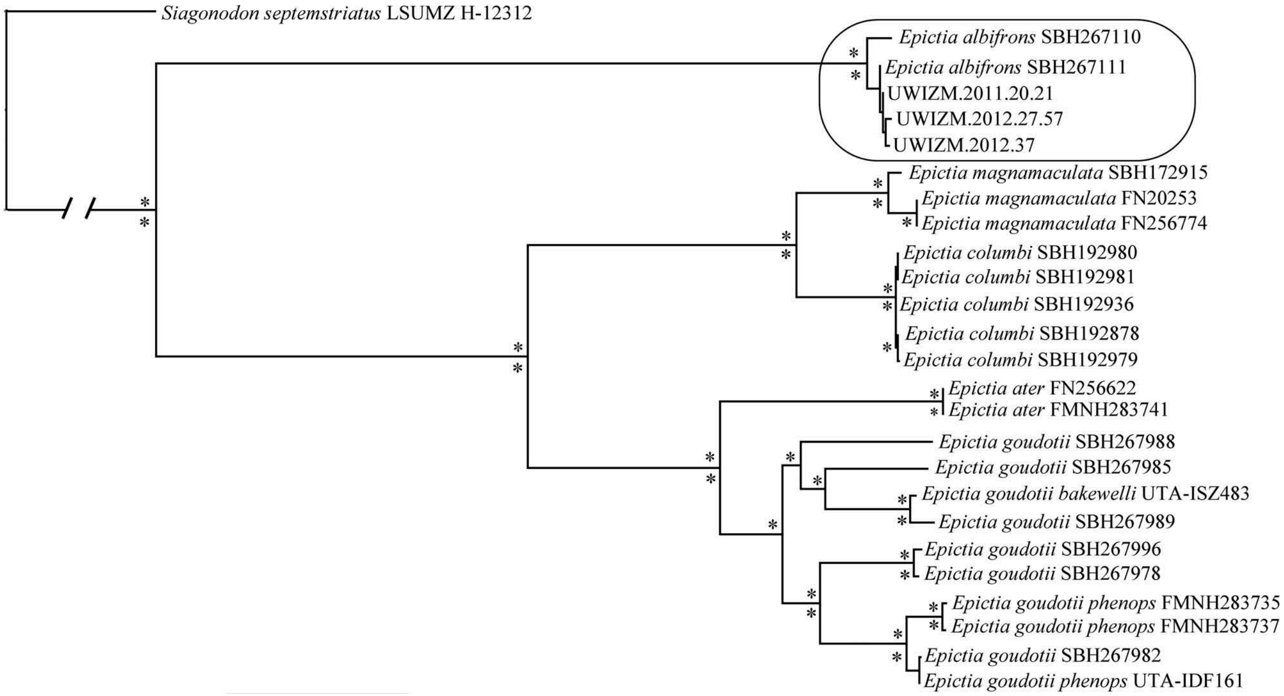

Figure 2. Best ML tree for the 12S, 16S rDNA and Cytb dataset of the *Epictia* genus. Asterisks (*) on and under nodes are posterior probabilities recovered from the Bayesian inference analyses and the ML 50% majority rule consensus tree (95% or above), respectively. The oval delimits the *Epictia tenella* group.

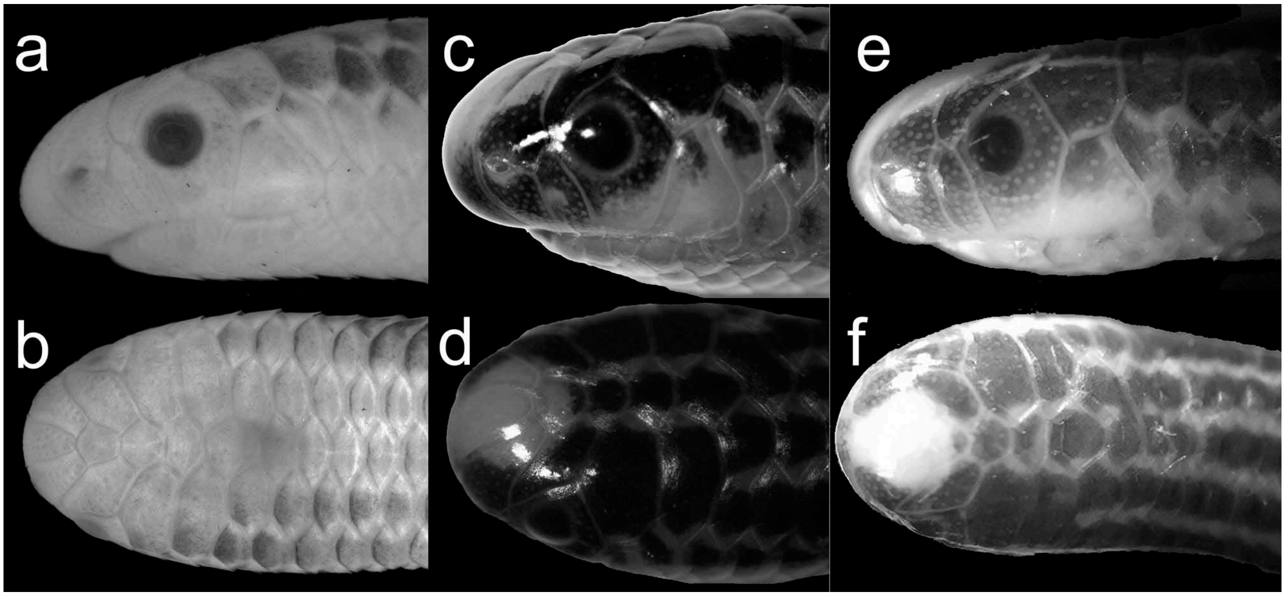

Figure 3. Comparison of the scale pattern on heads and caudal tip between (A, B) neotype of *Epictia albifrons* from Pará, Brazil, chosen by Esqueda et al. (2015) from about 1.45S –48.48333W (MCZ R-2885) (Museum of Comparative Zoology, Harvard University http://mcz.harvard.edu/); (C, D) a Trinidad specimen of the common threadsnake in the *tenella* group (USNM 286928) from the Arima Valley, Trinidad (10.7167–61.2833) JCM; and (E, F) a specimen from Guyana that was sequenced and stored in Genbank (ROM 22487).

species that dispersed in flower pots as people move around the world. Threadsnakes are unlikely candidates for being highly mobile or having a great ability to disperse. They are small, fossorial snakes that feed on social insects and it seems improbable that they would move more than a few hundred meters during their life time and it is unlikely they are capable of long distance swimming.

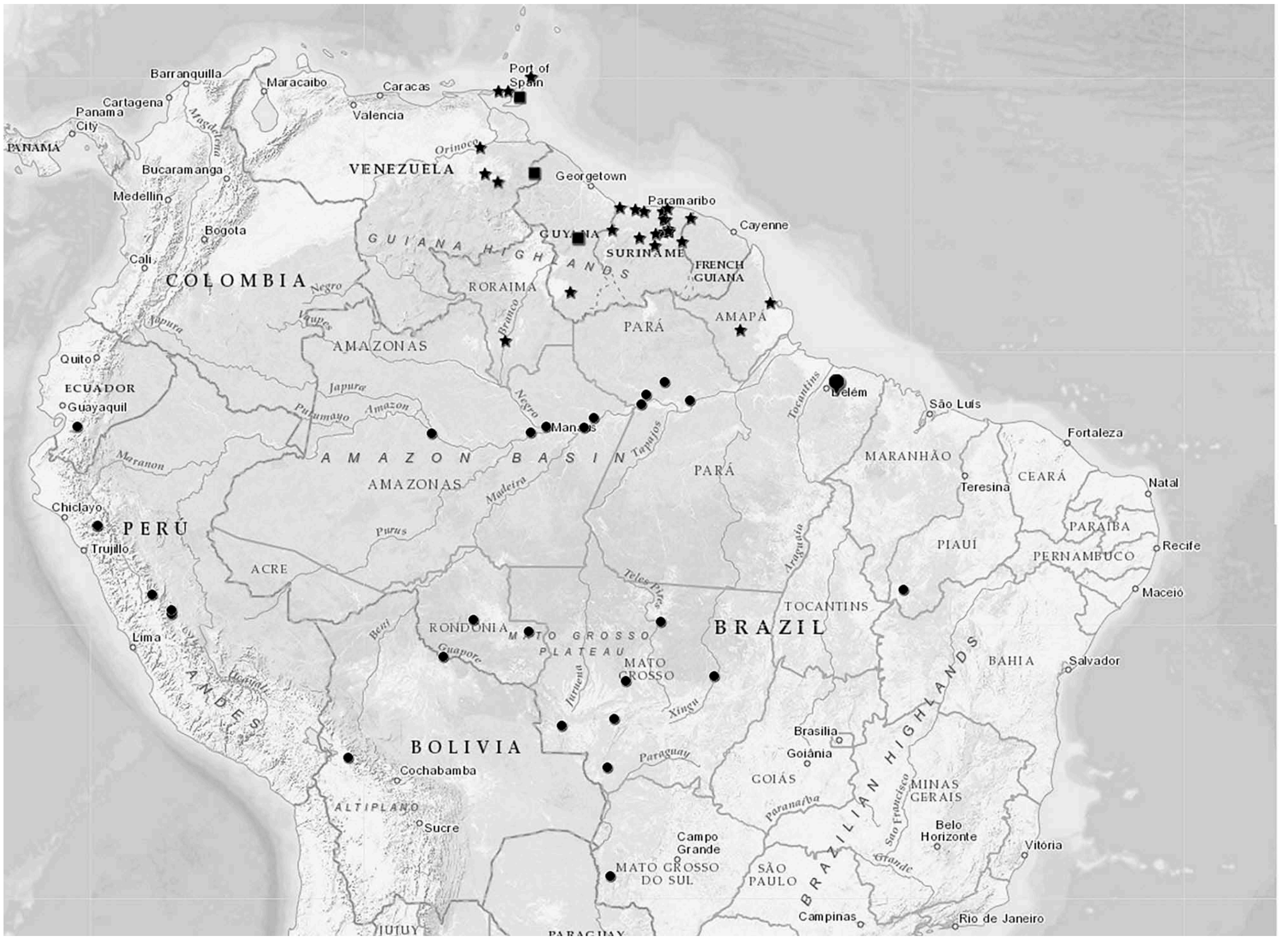

Figure 4. Map showing localities for snakes formerly considered to be *Epictia albifrons* based upon the locations given in Klauber (1939), Hoogmoed (1977), Koch et al. (2015), and Wallach (2016). Localities marked with black squares are those represented by DNA sequences. Localities marked with stars are probably *Epictia tenella*. The type locality of *E. albifrons* is a large balloon marker. Localities marked with black circles are snakes that resemble *E. tenella* or *E. albifrons* but are in fact other species.

Yet, E. tenella has an unusually large distribution (Figure 4) ranging from Trinidad and Tobago, eastern Venezuela, Guyana, Suriname, French Guiana, and northern Brazil, (Wallach 2016).

Genetic distances between other *Epictia* species (e.g. *E. columbi*, *E. phenops*) show that populations can share the same haplotypes at least 100 km distant. *Epictia tenella* SBH267111 is found in Baramita (Guyana), only 120 km south from the Orinoco Delta. Furthermore because the species and population limit is unknown it is possible that *E. tenella* may well be found in the Orinoco Delta and even further into northwest in Venezuela. Overwater dispersal on rafts of vegetation, dispersal via land bridges during glacial maxima, and human mediated transport in potted plants are all possible methods of dispersal. Throughout the rainy season, the Orinoco River discharges reducing salinity levels in the coast areas and Trinidad's Gulf of Paria (Alkins & De Souza 1984; Read 1987; Kenny 1995) and large rafts of floating vegetation are common between Venezuela and Trinidad. Thus, if *Epictia* can survive several days on vegetation rafts and tolerate moderate levels of salinity, it may explain its recent dispersal in Trinidad.

Many aspects of threadsnake natural history are poorly known and unexpected. One of us (JCM) observed a Trinidad *Epictia tenella* climbing in a tangle of lianas laying against a tree trunk more than 1.5 m above the ground. Birds are known to feed on threadsnakes and bring them to the nest to feed their young. One of us (MGR) recovered a partially digested *Epictia albifrons* at Point-a-Pierre Wildfowl Trust, Trinidad apparently regurgitated by a bird; the specimen was uniform black in color.

In North America, the Eastern Screech Owl (*Otus asio*) has been observed collecting Western Threadsnakes (*Rena dulcis*) and bringing them to their nest to feed on the soft bodied insects that parasitize the nestling birds (Gehlbach & Baldridge 1987). However, the snakes are also eaten. It has been suggested nestling owls that live with threadsnakes grow faster and have a lower mortality rate than broods that were not living with threadsnakes (Gehlbach & Baldridge 1987). Reports of other scolecophidian snakes associated with birds and their nests are known. The Brahminy Blind Snake, *Ramphotyphlops braminus*, and leptotyphlopids are preyed upon by birds and brought to their nests to feed nestlings, rid the nest of pests, or both (Kratter et al. 1993). Live and dead blind snakes in the nest boxes of the Indian Myna (*Acridotheres tristis*, Sturnidae) have been reported (see Jadhav & Parasharya 2003 for a summary).

There is also an account (O'Shea et al. 2013) demonstrating scolecophidian snakes have morphological and physiological adaptations that allow them to survive passage through the digestive system of predators. O'Shea et al. (2013) found a live blind snake emerging from the cloacal opening of a toad, and the same phenomenon cannot be ruled out for birds. Thus, birds could be responsible for moving the snakes a substantial distance from their home range. Given the above observations threadsnakes may have a greater dispersal ability than would otherwise be suspected.

Analyses of *Epictia* sp. *p*-distances from Genbank did not recover the same haplotypes at the geographical distances here reported between (Guyana–Trinidad), which makes this distribution quite enigmatic.

Many authors have suggested *E. tenella* is a complex of cryptic species (Thomas 1965; Orejas-Miranda 1967; Esqueda et al. 2015; McCranie & Hedges 2016). This may be true, but it is in need of further investigation given the results presented here.

Additional population genetic studies are needed to establish the differences between the colonization hypotheses here presented and introduction versus rafting. Some key points to address are as follows. Under the avian-prey introduction scenario: (1) Observations of predators crossing the straits for feeding; (2) presence of *Epictia* sp. in nests in Trinidad; (3) a higher genetic richness of *Epictia* sp. through bird random captures at diverse areas increasing genetic diversity locally (Trinidad); (4) *Epictia* sp. decline in genetic richness with distance from predator nesting areas. Through human introductions: (5) recovery of the same haplotypes in mainland and Trinidad ports through maritime traffic; (6) non-common haplotypes in more human isolated areas. Under the rafting hypotheses: (7) a pattern of coastal genetic diversity with same or similar haplotypes to coastal Venezuela and Guyana throughout Trinidad's western coast, more precisely at the Gulf of Paria; (8) distinct haplotypes or evolutionary lineages to Tobago, influenced by different marine currents in the area.

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