Evidence for cryptic diversity in the Neotropical water snake, *Helicops angulatus* (Linnaeus, 1758) (Dipsadidae, Hydropsini), with comments on its ecology, facultative reproductive mode, and conservation

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Abstract.—The neotropical aquatic snake genus *Helicops* contains 19 species, some of which are oviparous, while others are viviparous. Using phylogenetic and morphological relationships, *H. angulatus* from the island of Trinidad (West Indies) is compared to other mainland populations. We recover *H. angulatus* as paraphyletic, suggesting evidence of cryptic diversity within the species, and remove *Helicops cyclops* Cope, 1868 from the synonymy of *Helicops angulatus* (Linnaeus) based on morphology; thus, increasing the number of *Helicops* species to 20. Previous reports suggest some populations of the widespread *Helicops angulatus* are oviparous. In contrast, other populations have been reported as viviparous, and the conflicting reports are discussed based upon recent literature on the evolution of viviparity. Anecdotal evidence suggests Trinidad *Helicops angulatus* are facultatively viviparous. The importance of conserving this unusual population, and its associated aquatic habitats, are discussed.

Keywords. Caribbean, neotropics, ovoviviparous, Reptilia, Squamata, viviparous

Introduction

Most of the 3,700 species of snakes are terrestrial, but a few hundred have become aquatic or semi-aquatic in freshwater and marine environments (Murphy 2012). Two-thirds of 33 family and subfamily level clades contain aquatic species (Murphy 2012). Some clades contain only a single extant species that can be considered semi-aquatic or aquatic (e.g., Viperidae), while others include dozens of species that have radiated into freshwater habitats (e.g., Homalopsidae and the Natricidae). Current knowledge suggests the most diverse aquatic snake communities occur in southeast Asia, but a significant number of radiations into freshwater are present in cis-Andean South America. At least 50 species in 12 genera

can be considered semi-aquatic or aquatic among the species which inhabit the Amazon Basin and adjacent areas (Murphy 2012).

About half of those neotropical species are in the Dipsadidae lineage Hydropsini (Dowling 1975), a clade of 23 freshwater and brackish water snakes in three genera: *Helicops* Wagler, 1828 (19 species), *Hydrops* Wagler, 1830 (three species), and *Pseudoeryx* Fitzinger, 1826 (two species). The relationship of *Helicops*, *Hydrops*, and *Pseudoeryx* was suggested by Roze (1957), while Dowling (1975) provided a name for the clade, and Zaher (1999) hypothesized the three genera formed a clade belonging to the Xenodontinae. Molecular evidence supporting the Hydropsini first came from Vidal et al. (2000), when they recovered *Hydrops* and *Pseudoeryx* as the sister

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to *Helicops*. Kelly et al. (2003) also found Hydropsini to be monophyletic. Since that time, Grazziotin et al. (2012) recovered strong support for the clade with its sister, the terrestrial, Mexican lizard-eating snake *Manolepis*. The Hydropsini was again found to be monophyletic by Zaher et al. (2018). Vidal et al. (2010) also confirmed the Hydropsini clade and presented molecular evidence that *Helicops angulatus* is paraphyletic.

Di Pietro et al. (2014a,b) described what appeared to be synapomorphies in the skull and upper respiratory systems that supported the monophyly of the Hydropsini. They (Di Pietro et al. 2014a) found two nasal features that deviate from the pattern of nasal cartilages known in other alethinophidian and caenophidian snakes: i.e., a cartilaginous connection between the lamina transversalis anterior and the concha of the Jacobson's organ, and a small rostral projection of the planum anteorbital, which probably represents a reduced anterior maxillary process. They (Di Pietro et al. 2014b) later found the unpaired foramen on the parabasisphenoid with an anterior position to be the only skull characteristic shared by all Hydropsini genera.

Viviparity has also been suggested as a synapomorphy for the Hydropsini (Zaher et al. 2009); however, contrary to previous speculation, *Hydrops* is oviparous, and *Pseudoeryx plicatilis* is now known to lay eggs with the female attending the nest (Braz et al. 2016). However, within *Helicops,* some species are oviparous, while others are viviparous (Scartozzoni 2009; Braz et al. 2016).

Rossman (1973) reviewed the early conflicting evidence that suggested *Helicops angulatus* was viviparous. He reported that a female from Leticia (Colombia) laid two atypical eggs with the well-developed embryos visible through the shells. He incubated the eggs, and they hatched 16 and 17 days later. Speculating on the reproductive mode of *H. angulatus,* he wrote, "… there is a remote possibility that even this species may be facultatively ovoviviparous." Continuing, he discussed the advantage of an aquatic snake being viviparous if egg-laying sites were in short supply at times of severe flooding.

Oviparity and viviparity are used to describe the reproductive modes in squamates. The term "ovoviviparity" was used until the mid-20th century with the intention of defining an intermediate strategy between viviparous and oviparous reproductive modes. However, this word was eliminated because of ambiguity caused by the variety of interpretations of its meaning (Blackburn 1994, 2000, 2006). A bipartite classification was proposed by Blackburn (2000) that distinguishes between two parameters: (1) the source of nutrition for embryonic development (lecithotrophy and matrotrophy, as two extremes of a continuum where lecithotrophy indicates the embryo depends entirely on yolk, and matrotrophy indicates the embryo obtains most of its nutrition via a placenta); and (2) the packaging of the embryo (an eggshell or membrane containing the young). While the majority of Squamata are clearly either oviparous or

viviparous, there are reports of some species which use both reproductive modes.

In a review of oviparity and viviparity in squamates, Tinkle and Gibbons (1977) listed 12 species (four lizards and eight snakes) reported in the literature to have bimodal or facultative reproduction. That is, 12 species that use both oviparity and viviparity, including eight snakes (*Typhlops diardi, Boa constrictor, Python regius, Diadophis punctata, Xenodermus javanicus, Cacophis kreffti, Echis carinatus,* and *Trimeresurus okinavensis*). They discuss each of these literature reports and the implications of females retaining embryos in their bodies until they are well developed before secreting an eggshell around the embryo and depositing the eggs in a nest.

Regarding *Helicops,* Rossman (1984) provides an account of *Helicops angulatus* (LSUMZ 27337) from Puerto Maldonado (Peru) collected by Richard Thomas. When Thomas preserved the female, he removed seven full-term young (LSUMZ 27340–46). No eggshells or yolk were present, suggesting that had this female *H. angulatus* carried the embryos to full term, she would have functioned as a viviparous, as opposed to an oviparous, species. In discussing Trinidad *Helicops,* Boos (2001) stated that Rodriguez saw a female giving live birth, citing an unpublished manuscript that was missing pages. Ford and Ford (2002) studied *Helicops angulatus* in Trinidad, and reported two females laid clutches of 11 and 18 eggs in February that required 45 and 39 days of incubation, respectively.

The distribution of *Helicops angulatus* is given by Uetz et al. (2020) as "Venezuela (Amazonas, Apure, Bolívar, Monagas, Delta Amacuro, Sucre, Portuguesa, Anzoátegui, Guárico, Cojedes), Colombia, Brazil (Pará, Rondônia, Goias, Mato Grosso, Sergipe, S. Ceará, Acre, Bahia, Piauí, Paraíba, etc.), Bolivia, Peru, Trinidad, Ecuador, French Guiana, Guyana." Many authors writing about the distribution of *H. angulatus* suggest it is widespread in northern South America (Cunha and Nacimiento 1978; Cisneros-Heredia 2006; Roberto et al. 2009; Starace 2013; Cole et al. 2013; Nogueira et al. 2019).

Given the relatively broad distribution of *Helicops angulatus* and the possible bimodal reproduction of this snake, the Trinidad and Venezuelan populations merit further investigation. The Trinidad and Venezuelan *Helicops* is not likely to be an endemic cryptic taxon to the region. *Helicops angulatus* is a mostly lowland aquatic snake present in the Orinoco Delta, the Llanos, and possibly in the low wetlands of the Guiana Shield. Charles (2013) reported finding a juvenile *Helicops* that had washed up on the South coast of Trinidad with a mat of vegetation, suggesting a flood event transported the snake the short distance from the Orinoco Delta to Trinidad.

Here, through phylogenetic analyses, we present evidence that confirms *H. angulatus* is paraphyletic. We compared the morphological data from the literature and

photographs for five type specimens with names that had been placed in the synonymy of *Helicops angulatus*; and based on that information, we reinstate *Helicops cyclops* Cope, 1868 as a valid species. We also further investigate the distribution, ecology, conservation, and the anecdotal story of a Trinidad *H. angulatus* giving live birth.

Materials and Methods

Molecular methods. DNA was extracted from tissue samples, and target gene fragments were amplified by Polymerase Chain Reaction using the DNeasy Blood & Tissue kit (QIAGEN, Hilden, Germany) following the manufacturers' instructions. Primers and specimens sequenced and the GenBank accessions for all species are reported in Supplemental Tables S1 and S2. Portions of the mitochondrial small and large ribosomal subunits (12S rDNA, 16S rDNA, respectively), cytochrome *b* (cytb), and the nuclear oocyte maturation factor (c-mos) were amplified. These gene fragments are highly informative in interspecific and intraspecific studies on snakes, including colubroids (e.g., Daza et al. 2009).

Templates were sequenced on both strands, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The lengths of the sequences were: 12S rDNA, 342 base pairs (bp); 16S rDNA, 436 bp; cytb, 1,060 bp; c-mos, 492 bp, although not all individuals had the exact same length in some alignments. Cytb and c-mos were translated to amino acids to find the presence of stop codons. Following Moraes Da Silva et al. (2019), the analysis included all genera that were sister to *Helicops* and *Pseudoeryx plicatilis* and *Hydrops triangularis* were used as outgroups. Sequences were aligned in Seaview v4.2.11 (Gouy et al. 2010) under MAFFT settings (Katoh et al. 2002). The 12S and 16S rDNA, and c-mos sequences were concatenated, resulting in a 1,271 bp alignment. The cytb sequences were used to assess genetic differentiation within the Trinidad specimens. Because of the lack of cytb for *Helicops*, this gene was not included in the concatenated alignment.

Phylogenetic analyses were performed using the Bayesian Inference and Maximum Likelihood methods. 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. ML searches were conducted in RAxML v7.0.4 (Silvestro and Michalak 2010), using partition data sets under default settings, and support was assessed by using 1,000 bootstrapped replicates. The most appropriate substitution model was implemented for each gene fragment as determined by the Bayesian Information Criterion in PartitionFinder v2 (Lanfear et al. 2012) to choose the optimal partitioning strategy for both phylogenetic analyses. Default priors and Markov chain settings were used, and searches were performed with random starting trees. Each run consisted of four chains of 20,000,000 generations, sampled every 2,000 generations. Posterior distributions of parameter estimates were visually inspected in Tracer. All analyses were performed through the CIPRES platform (Miller et al. 2010).

Distributional analysis methods. The Vertnet and GBIF databases were searched for mappable specimens of *Helicops angulatus*. Additional specimens examined from Trinidad and Venezuela that were not represented in the on-line databases, and specimens reported in Appendix B of Braz et al. (2016), were added. All localities were plotted in ARCView (Fig. 1). Additional localities from the map used in Nogueira et al. (2019) were added to the map using Photoshop, and are indicated by the smallest black markers in Fig. 1. The ARCView layers used for the map were: The World Topographic Map, The World Hydro Reference Overlay Map, and Freshwater Ecoregions of the World.

Morphological methods. Traditional scale count data were collected for 37 specimens from Trinidad and Venezuela; and an additional eight specimens from Brazil, Guyana, and Peru were examined. 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, midbody, and about 10 ventral scales anterior to the vent, and they were all counted on the diagonal. Ventral counts, subcaudal counts, and tail/SVL (snout-vent length) ratios were analyzed for sexual dimorphism. Scale counts and scale measurements were taken under a dissection microscope on small specimens. 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; while those separated by a slash (/) represent data taken from a single individual in the left/right order. *Helicops angulatus* have keeled subcaudal scales; and since this character is unfamiliar to many herpetologists and is easily overlooked, it is illustrated in Fig. 2.

Specimens examined: Brazil (*n* = 4): ANSP 5131–2; CAS-SUR 7436, CAS 49324; Guyana (*n* = 2): FMNH 26647, FMNH 170765; Peru (*n* = 2): FMNH 81527, CAS 8720; Trinidad (*n* = 18): CAS 231757, 231758–60; FMNH 251219; UWIZM 2010.27.2 (*n* = 3), 2010.12.93, 2011.20.30 (*n* = 2), 2013.16.1 (*n* = 7); Venezuela (*n* = 16) MHNLS 1429, 1439, 8444, 9093, 9884, 10953, 11786, 17731, 12082, 13137, 14100, 14426, 15885, 17544–45, 18404.

Results

Molecular results. No stop codons were found in the cytb and c-mos alignments. The best-fitting models and partitions were partition 1 (TRN+G 12s+16S rDNA), partition 2 (JC+I cmos 1st+2nd codon positions), and

Fig. 1. The distribution of *Helicops angulatus* in the Neotropics. Locality data is from the VertNet and GBIF databases, as well as the literature. Diamonds (green oviparous, yellow viviparous): specimens reported in Appendix B of Braz et al. (2016); red stars represent localities where *Helicops* was sampled for DNA; small black markers: localities from *Helicops angulatus* map in Nogueira et al. (2019). As currently defined *Helicops angulatus* occurs in Freshwater Ecoregions: 301 North Andean Pacific Slopes, Rio Atrato; 302 Magdalena, Sinu; 304 South America Caribbean Drainages, Trinidad; 307 Orinoco Llanos; 308 Orinoco Guiana Shield; 311 Guianas; 313 Western Amazon Piedmont; 317 Ucayali, Urubamba Piedmont; 318 Mamore, Madre de Dios Piedmont; 319 Guapore, Itenez; 320 Tapajos, Juruena; 321 Madeira Brazilian Shield; 323 Amazonas Estuary and Coastal Drainages; 324 Tocantins, Araguaia; 325 Parnaiba; and 328 Northeastern Mata Atlantica.

partition 3 (F81+I cmos 3rd codon positions). All six *H. angulatus* from Trinidad recovered the same haplotype for all genes. The two GenBank *H. angulatus* are the sister clade to *H. gomesi*, as shown previously (Moraes Da Silva et al. 2019). However, the inclusion of Trinidad's *H. angulatus* results in paraphyly of the species; the island taxon is ancestral to mainland *Helicops* + *H. gomesi* (Fig. 3). All clades were recovered with high bootstrap and posterior probabilities.

The morphological results (Table 1) suggest that animals from Trinidad and Paria, Venezuela, are the same species and are like some other mainland populations in that they have nearly identical meristic traits. Dorsal scale rows, ventral counts, and subcaudal counts are similar for specimens examined and when compared to literature accounts. Boulenger (1893) may have first reported the

keeled subcaudals, which are difficult to detect because they are lateral (Rossman 1973). The Trinidad and Venezuela populations also have the first dorsal scale row lacking keels.

Distribution and ecology. The distribution of *Helicops angulatus* is shown in Fig. 1, and it extends well outside the Amazon Basin. However, there are some records in Colombia that need attention; one of which is a specimen (FLMNH 57235) from the Atlántico Province, which has a locality within 15 km of the coast, west of the Maracaibo Basin. A second is the specimen collected in the Cordillera Central (Sonsón, Antioquia) at 2,300 m (ILS no. 92) and mentioned in Pérez-Santos and Moreno (1988). However, the identification of this specimen requires confirmation. A third specimen (ICN MHN Rep

Fig. 2. Photo showing that *Helicops angulatus* has keeled subcaudal scales, a trait that is easily overlooked because the keels are lateral. *Photo by Renoir J. Auguste.*
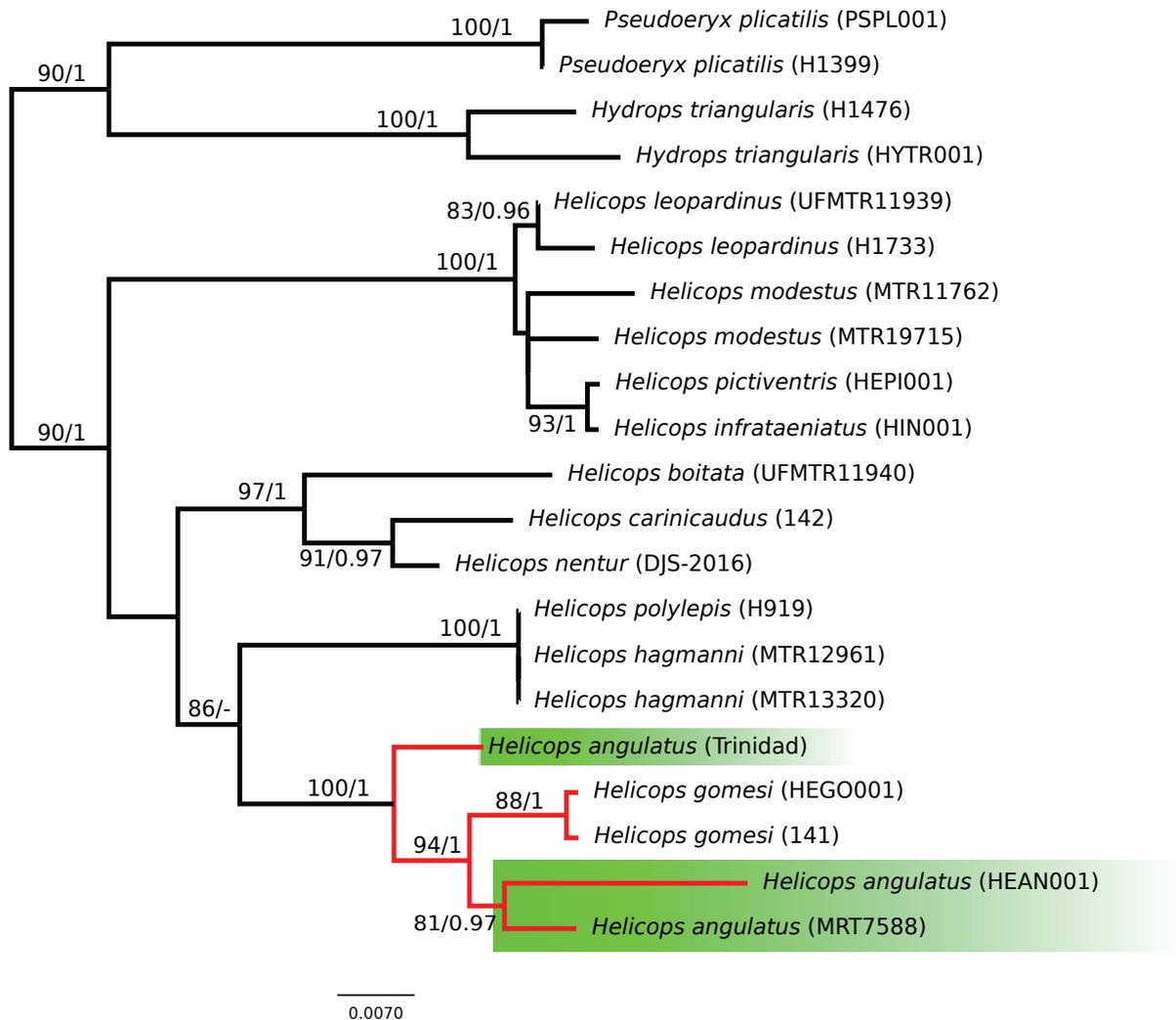
Fig. 3. Best Maximum Likelihood tree based on the data set of concatenated 12S and 16S rDNA, and c-mos sequences. The red clade depicts the *Helicops angulatus* group. On the left and right sides of a slash (/) are values indicated at nodes for Maximum Likelihood bootstraps (> 75%) and Bayesian Posterior probability values (> 95%), respectively. Green clades represent the paraphyly of *Helicops angulatus*. The name *Helicops pictiventris* is currently a junior synonym of *H. infrataeniatus*, but it appears in the tree exactly as the pertinent sequences appear in the GenBank dataset.

Table 1. Morphological comparisons of the type specimens of species that have been synonymized under *Helicops angulatus* to the Trinidad/Venezuela population. The Trinidad and Venezuela animals are sexually dimorphic for body size. Six adult males have SVL 351–560 mm ($\bar{x}$ = 421.6, SD = 65.13), tails 130–219 ($\bar{x}$ = 177.3, SD = 30.85), and tail/SVL ratios 0.37–0.48 ($\bar{x}$ = 0.42, SD = 0.046). Eight adult males had ventral counts 110–118 ($\bar{x}$ = 113.5, SD = 3.27) and subcaudal counts 70–83 ($\bar{x}$ = 75.12, SD = 4.42). Ten adult females have SVL 337–838 ($\bar{x}$ = 575.42, SD = 142.06), tails 98–224 ($\bar{x}$ = 159.80, SD = 36.04), and tail/SVL ratios 0.22–0.36 ($\bar{x}$ = 0.29, SD = 0.04). Female ventral counts for 21 individuals ranged from 113–123 ($\bar{x}$ = 118.48, SD = 2.48); subcaudal counts for 18 females ranged from 59–77 ($\bar{x}$ = 65.33, SD = 5.04); tail/SVL ratios for ten females ranged from 0.22-0.36 ($\bar{x}$ = 0.29, SD = 0.04). nd = no data.

Locality	*alidars* Linnaeus ?	*angulatus* Linnaeus Suriname	*surinamensis* Shaw Suriname	*asper* Wagler Brazil	*fumigatus* Cope Suriname	*cyclops* Cope Brazil	Trinidad/ Eastern Venezuela
Ventral scales	121	120	nd	123	nd	124	109–121
Subcaudal scales	58	61	nd	82	nd	89	59–83
Dorsal pattern extends to venter	nd	yes	yes	yes	no	yes	yes
t/SVL	nd	0.36	nd	0.479	nd	nd	0.37–0.48
Dorsal scale rows	21	19	19	19	19	19	19
Keels on first scale row	nd	no	nd	nd	no	yes	no
Keels on subcaudals	nd	nd	nd	nd	yes	yes	yes
Temporal formula	nd	1+2	nd	2+3	1+2	2+3	1+2
Dorsal transverse bands on midline	nd	36	nd	46	nd	nd	32–43

10735) from Department of Tolima, west of Bogota, was listed in the GIBF database as being from 680 m, but the coordinates given in Google Earth suggest the elevation is quite different, closer to 2,600 m. *Helicops angulatus* is a species restricted in Colombia to the Amazon and Orinoco basin, but the first specimen mentioned above (FLMNH 57235) is almost surely *H. danieli* (Rossman 2002); while the other two individuals most likely represent records with erroneous collection data, and for this reason, they cannot be considered within the geographic distribution of this species. Another specimen (LACM 58898) from near Lima, Peru on the West side of the Andes is likely the result of human transport, as the coordinates suggest it is from a highly urbanized area.

In Trinidad and Venezuela, 37 specimens were found from 26 localities, ranging from sea level in the coastal regions (Trinidad: Caroni Swamp, Nariva Swamp; Venezuela: Orinoco Delta region, Llanos), up to 940 m in forested streams of the Venezuelan Guayana. *Helicops angulatus* occurs in all freshwater systems in Trinidad, while it occurs throughout the Orinoco Basin in Venezuela. Figure 1 documents its presence in 16 freshwater ecoregions.

This species is abundant in slow-moving or stagnant water bodies, such as coastal lagoons, ponds, swamps, grasslands, flooded riparian forest, and mangroves, where the water may be clear, turbid due to high sediment loads, or black with high concentrations of tannic acid (Sioli 1975). It also occurs in bodies of water modified by humans (Ford and Ford 2002; Lasso et al. 2014; Mohammed et al. 2014). Accordingly, Ford and Ford (2002) found it to be abundant in a flooded watermelon field, from which they collected 117 specimens in five days.

Three specimens (MHNLS 17731, 13137, 10943) were collected in the lower Orinoco basin, as well as in an estuary and on two fluvial islands. These localities are on the northern edge of the range and are likely to be influenced by tides. These specimens were captured between March and June, when water flow and precipitation decrease salinity levels (Novoa 2000; Lasso and Sánchez-Duarte 2011). However, the occurrence of *H. angulatus* in mangroves is evidence that it is tolerant of some degree of salinity.

Morphological and systematic results. Linnaeus (1758: 217) described *Coluber angulatus* based on the type NRM 17 (Fig. 4) said to be from Asia (in error). The type specimen has 120 ventral scales and 60 subcaudal scales, and came from King Adolf Fredrik's collection at Ulricsdal Castle, Sweden. After it was examined by Linnaeus, it was transferred to KVA/NRM (Royal Swedish Academy of Science/Swedish Museum of Natural History) in 1801 (Anderson 1899).

Linnaeus appears to have described *C. angulatus* a second time as *Coluber alidras* based upon NRM 18, which originated in the collection of Charles De Geer (= Mus. De Geer) and gave the type locality as "Indiis."

Fig. 4. NRM 17, the holotype for *Helicops angulatus*. *Photo courtesy of NRM.*

Andersson (1899: 34) examined *Coluber alidras* and commented that it is a "…completely discolored specimen of *Helicops angulatus*." However, it differed from *C. angulatus* by having 21 rows of scales on the thickest part of the body instead of 19 (in *Coluber angulatus*). Thus, Andersson considered Linnaeus's *Coluber alidras* a synonym of *Coluber angulatus*. The *C. alidras* specimen had a total length of 720 mm and a 165 mm tail, 121 ventral scales, and 58 subcaudal scales. He (Andersson 1899) added a footnote stating that the tail was somewhat mutilated. NRM 18 contained the remains of the fish *Cichlasoma bimaculatum,* which has a South American distribution that includes the Orinoco River basin, in the Caroni in River Venezuela; Guianas, from the Essequibo River to the Sinnamary River; and the Amazon River

basin, in the upper Branco River basin (Froese and Garilao 2019).

Shaw (1802: 460) described *Coluber surinamensis,* stating that it was thought to be from Suriname and listed the holotype as a drawing (Sebae, 1735, Vol. 2, Pl. 59, Fig. 2) [Fig. 5]. The specimen used for that illustration survives to the present day. Bauer and Wahlgren (2013) examined some of the snake specimens from the 18th century Linck family collection that are in the Naturalienkabinett Waldenburg in Saxony, Germany. Specimens in that collection served as types of species described by Linnaeus and Blasius Merrem, and are thus of taxonomic importance. For example, specimen 502 is the basis for the illustration holotype of Shaw's *Coluber surinamensis*.
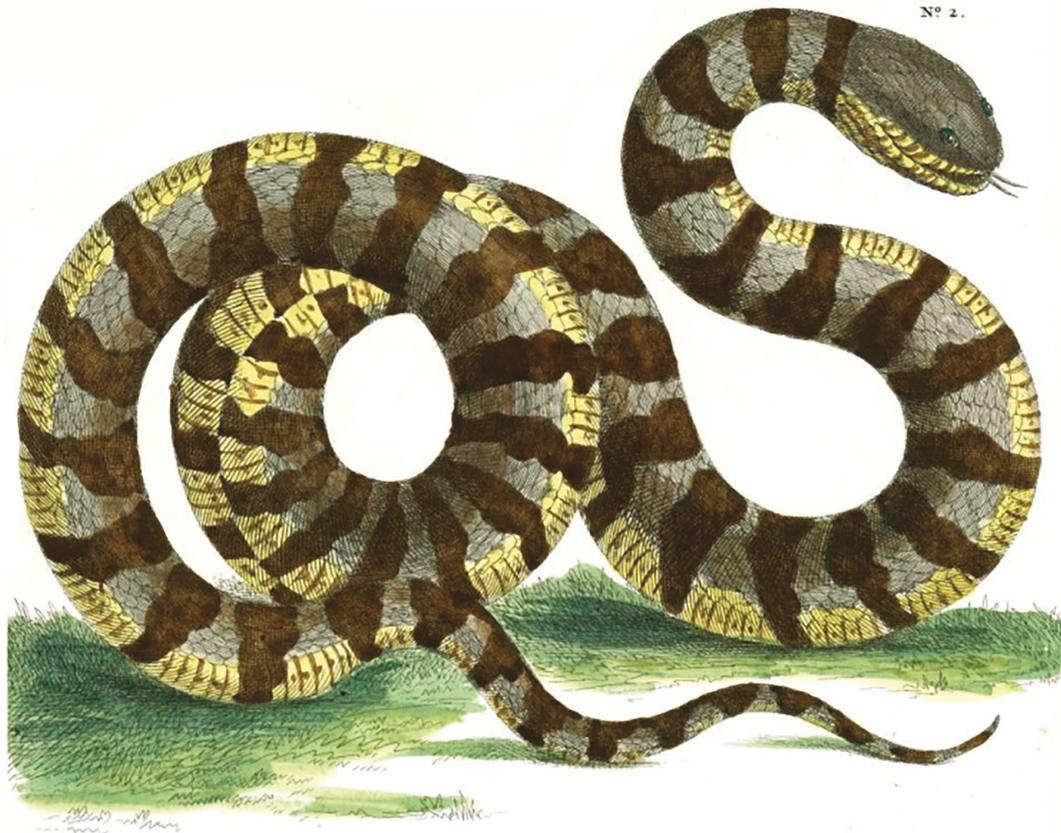
Fig. 5. Illustration of the holotype of *Coluber surinamensis* Shaw. From Sebae (1735, Vol. 2, pl. 59, Fig. 2).

Eighteenth century collectors sent many animals (alive and preserved) from Suriname to the Netherlands. The preserved specimens found their way into private collections and Linnaeus undoubtedly saw many Suriname specimens because the collectors C.G. Dahlberg and D. Rolander were sending Suriname specimens to Sweden (Husson 1978). Thomas (1911) wrote that it would not be unjustified to regard all South American animals in *Seba's Thesaurus* as originating in Suriname. Therefore, we consider it likely that NRM 17, NRM 18, and the Linck family collection specimen 502 used in Seba's drawing and Shaw's description all originated in Suriname.

Wagler (1824: 37) described *Natrix aspera* which is now represented by the lectotype (ZSM 1528/0). Hoogmoed and Gruber (1983) commented that the original Spix collection contained adults and juveniles, and gave scale counts for two specimens (123 and 118 ventral scales and 82 and 100 subcaudals, respectively). However, they found that only one Brazilian specimen collected by Spix was still present in the Munich collection and selected it as the lectotype of *Natrix aspera* Wagler. The lectotype (Fig. 6), is a female which has 123 ventrals, a divided cloacal plate, 82 subcaudals, and dorsal scales in 19-19-17 rows. The SVL is 690 mm, the tail length is 331 mm (t/SVL = 0.479), the head length is 38.8 mm, and it has maxillary teeth (± 14). The specimen agrees well with Wagler's description except for the pattern. Subsequently, Wagler (1830: 171) erected the genus

Helicops for *Coluber angulatus* and used the combination *Helicops angulatus*.

Cope (1868: 308) described *Helicops fumigatus* based on the holotype: ANSP 5132 from Suriname, stating that it has keeled scales that are in 19 rows and provided no other information on scale characters. However, he described this snake on the basis of the ventral pattern, writing, "Belly with a broad brownish gray band from throat to vent, the ends of the gastrosteges yellow, forming two bands; a median longitudinal brown line on the tail." We have not seen any *Helicops angulatus* with this ventral pattern nor a mid-ventral stripe on the tail (Fig. 7).

In the same paper, immediately following the *H. fumigatus* description, Cope (1868: 309) described *Helicops cyclops* based on the holotype ANSP 5131 from Bahia, Brazil. The specimen has 19 dorsal scale rows, 124 ventral scales, and 89 subcaudals, and it has 26 dark brown transverse bands. Boulenger (1893: 279) placed both of Cope's species into the synonymy of *Helicops angulatus* without comment.

Helicops cyclops has a remarkably short head and more ventral scales than have been reported for *Helicops angulatus*. Its subcaudal scales are keeled. It also has chin shields that are short and plate-like, and dorsal transverse bands which extend around the body and across the ventral surface. There is also a distinctive band between the eyes, a trait not seen in members of the *Helicops angulatus* group. Dorsal head plates are also imbricate,

more so than those seen in members of the *H. angulatus* group. Based on this morphology, we remove *Helicops cyclops* Cope from the synonymy of *H. angulatus*.

Helicops cyclops Cope (1868)
Fig. 8

Helicops cyclops Cope 1868: 309. Holotype ANSP 5133, Type locality Bahia, Brazil.
Helicops angulatus – Boulenger 1893, 2: 287.

Cope's description of this species is as follows:

Helicops cyclops Cope, sp. nov.
Scales in nineteen rows, strongly keeled everywhere, including the first row. Two pairs genials; occipitals short and wide, long as frontal. Head exceedingly short, mouth wide as the length of the rounded lip margin Superior labials eight, fourth scarcely entering orbit by its upper corner (by its whole extremity in *H. angulatus*), the fifth, sixth and seventh narrow and high. Prefrontals broad as long (much broader than long in *H. angulatus*). Orbitals 1–2, nearly meeting below orbit. Temporals 2 |1 | 3 (1 | I | 3 in *H. angulatus*). Loreal plate wide as high, (higher than wide in *H. angulatus*). Tail 0.33 total length, slender (less than 0.25, *H. angulatus*). Gastrosteges 124, anal 1-1; urosteges 89. Light yellowish brown, with twenty-six transverse deep brown rhombs across the back which terminate at the second row of scales, being separated from the back ventral cross-bar, which is opposite each, by a longitudinal yellow band. This band is not distinct between the spots. Belly strong yellow with jet black cross bars, which are on more than two gastrosteges. Tail black spotted below. A brown cross-band between the eyes Length 27.5 inches. From Bahia, Brazil. Mus. Academy, from Dr. Otho Wucherer. This species is at first sight much like the *H. angulatus* but differs variously as above. In coloration the spots in the latter are always continued into the ventral cross-bars, and not interrupted as in *H. cyclops*.

At this writing, there are too many unknowns to make further taxonomic adjustments. As further molecular and morphological information becomes available on the type specimens (Table 1) of the species which has been placed in the synonymy of *Helicops angulatus,* the species and nomenclature will undoubtedly change again.

Facultative reproduction. The Trinidad and Venezuela populations are known to be oviparous (Mole 1924; Gorzula and Señaris 1998; Boos 2002; Ford and Ford 2002; Natera et al. 2015). One of the authors (JCM) collected a clutch of eight eggs laid in a terrestrial nest under pieces of wood and tin in November 2013. The eggs contained near full-term embryos. When combined with the February oviposition dates reported by Ford and Ford (2002), it seems likely this species reproduces year-round in Trinidad.

Fig. 6. The lectotype of *Natrix asper* Wagler. *Photos by Michael Franzen.*

We also followed up on Boos' (2001) story of viviparity in a Trinidad specimen. Boos (recently deceased) attributed the story to Alan Rodriguez, an avid Trinidad snake enthusiast. One of the authors (RJA) interviewed him, but Rodriguez did not remember much about the incident related to Boos (2001), which took place about 1980. However, he reported that while searching for snakes on 15 March 2011, he observed a female *Helicops angulatus* giving birth in a drain with about 20 cm of water. The observations were made in a semi-urbanized area of Sangre Grande, Trinidad. He observed actively moving young dispersing, but several others present in the drain were stillborn. Thus, he saw this phenomenon twice (once in ~1980 and in 2011).

Curiously, Cunha and Nascimento (1981) found eggs (7–20) in 12 females from Brazil (Leste do Pará), but these authors also state that embryos were present in a single specimen. A comment in Martins and Oliveira (1998) by L.J. Vitt suggested this could be an error. Yet, according to the new evidence, it is plausible that the female examined by Cunha and Nascimento (1981) had fully developed embryos.

A related observation in the viviparous *Helicops scalaris* from the Lake Maracaibo basin (Barros et al. 2001) involved post-partum females depositing what appeared to be shell remains (Barros, pers. comm. 2020).

Table 2. A comparison of the 20 described species of *Helicops,* including some specimens placed in the synonymy of *H. angulatus* and the Trinidad populations. Scalation: AD = anterior dorsal scale rows, MD = midbody dorsal scale rows, PD = posterior body dorsal scales rows, V m/f = ventrals in males and females, sc m/f = subcaudal scales males/females; sck = subcaudal scales keeled; UL = upper labials; ULO in orbit = upper labials bordering the orbit. Reproductive modes: v = viviparity, o = oviparity, o/v both oviparity and viviparity known; ? = reproductive mode unknown. Data are based on our counts and those published in Kawashita-Ribeiro et al. (2013), Costa et al. (2016), and Moraes-Da-Silva (2019). nd = no data.

Species or population	AD	MD	PD	V = m/f	sc m/f	sck	UL	ULO	o/v
Trinidad/Paria	18–19	19	17	109–118/113–123	70–83/59–77	Yes	8	4 or 4–5	o/v?
angulatus	19–21	19–20	17–19	105–123/109–123	74–96/66–84	Yes	7–9	4 or 4–5	o/v
cyclops	nd	19	nd	124	89	Yes	8	4	?
fumigatus	nd	nd	nd	nd	nd	Yes	8	4	?
apiaka	21–24	21–22	17–19	118–127/124–132	79–103/80–84	Yes	7–9	3 or 4	?
boitata	25	25	21	113/nd	68/nd	No	10	34	v
carinicaudus	19	19	17	130–141/135–148	48–69/48–73	No	7–8	3–4, 4,4–5	v
danieli	19–21	19–20	16–19	125–135/130–141	76–86/61–70	No	8–9	4	nd
gomesi	19	19	19	125–132/128–132	71–86/67–73	Yes	8–9	4 or 5	o
hagmanni	23–27	21–29	19–23	117–127/130–134	55–67/51–53	No	8	4	o
infrataeniatus	17–19	17–19	15–19	115–138/117–138	52–88/50–83	No	7–9	3–4, 4	v
leopardinus	15–22	19–22	17–19	108–126/108–130	64–89/53–76	No	8–10	3–4,4, 3–5	v
modestus	19	19	17–19	112–125/116–122	54–70/53–64	No	8	3–4,4	v
nentur	17	17	15	115/111–117	56/41–52	No	8	34	?
pastazae	23	23–25	19	121–134/130–145	93–117/72–97	No	8–10	4	?
petersi	21	21–23	16	135–142/137–150	85–91/67–73	No	8	4	?
polylepis	23–25	23–25	19	112–131/121–133	70–102/71–81	No	8–9	1–4,1–5,1–6	v
scalaris	21–25	19–21	16–19	110–119/113–125	83–95/67–81	Yes	8–9	4, 4–5	v
tapajonicus	19	19	17	118/121–123	79/67–76	No	8	4	?
trivittatus	21–25	20–23	16–19	114–128/115–129	67–80/56–66	No	8–10	4,5	v
yacu	25–29	25–28	18–20	124/129–136	?/85–96	?	8–9	4,5	?

In discussing the reproduction mode in this species, Natera et al. (2015) stated it is "vivipara lecitotrófica" (i.e., embryos receive nutrients from the yolk); and they also mentioned two females which gave birth to 21 and 22 young, in addition to a female with nine eggs in mid-development (probably referring to developing embryos). Table 2 compares the 20 known species of *Helicops* for basic meristic traits and reproductive modes.

Discussion

Helicops angulatus shows considerable intrapopulation variation in coloration and morphology (Murphy 1997; Ford and Ford 2001). Some snakes have keels on the first dorsal row of scales, and others lack them (Cope 1868). The Trinidad and Venezuela specimens we have examined all have keeled subcaudal scales. It is also clear that some *H. angulatus* have 21 dorsal scale rows at midbody, although none of the Trinidad and Venezuela specimens examined had 21 dorsal rows. Thus, Linnaeus' *Coluber aliodras* may be the original description for a valid taxon that has 21 dorsal scale rows at mid-body. *Coluber*

surinamensis Shaw*, Natrix asper* Wagler, and *Helicops fumigatus* Cope are likely conspecific with *H. angulatus*. However, without access to the type specimens, this cannot be confirmed.

Evidence of facultative reproduction in *Helicops angulatus* was reported by Braz et al. (2016). They examined 27 gravid females, and 19 had oviductal eggs surrounded by thick, opaque, and leathery shells, indicating oviparity. The eggshell has a thick fibrous layer overlain by a thinner inorganic layer. Developing embryos were found in the eggs of five oviparous *H. angulatus* females and were visible only after eggshells were removed. They also reported six undisputable records of oviparity in *H. angulatus* that are available in the literature and another six female *H. angulatus* that were viviparous. The viviparous females had thin, transparent membranes surrounding yolk masses and embryos, and developing embryos or fully-developed young were readily visible through the extra-embryonic membranes. Embryos were partially developed in three females and near-term in a female from Colombia. Two other females contained fully-developed young. They also found two likely records of viviparity in *H. angulatus*. Two females

Fig. 7. The holotype of *Helicops fumigatus* Cope, 1868. *Photo by Ned Gilmore.*

Fig. 8. The holotype for *Helicops cyclops* Cope. *Photo by Ned Gilmore.*

had thin and transparent membranes surrounding the yolk masses, but no discernible developing embryos. Another reliable record of viviparity was obtained from a literature report of fully-developed young found in the uterus of a preserved female (Braz et al. 2016).

Braz et al. (2018) suggest eggshell thinning in *Helicops* is associated with the evolution of viviparity. They suggest eggshell reduction occurred independently in the origins of viviparity in *Helicops* and was accomplished by the loss of the mineral layer and thinning of the shell membrane. Viviparous female *H. angulatus* have a shell membrane thickness six times thinner than oviparous congeners. In contrast, the shell membrane of the viviparous *H. infrataeniatus* and *H. carinicaudus* is vestigial and 20–25 times thinner than those of their oviparous congeners. These differences suggest that eggshell reduction is a requirement for the evolution of viviparity, but a nearly complete loss of the shell membrane, as in the viviparous *Helicops*, is not.

We were skeptical of the ability of a population of snakes to contain both oviparous and viviparous females, as suggested by Alan Rodriguez's story. However, recent work on the Australian skink, *Saiphos equalis,* indicates that this ability may be widespread but undocumented in squamates. Laird et al. (2019) reported facultative oviparity by the viviparous skink, *Saiphos equalis*, which is the first report of different parity modes within a single vertebrate clutch. Eggs oviposited facultatively possess shell characteristics of both viviparous and oviparous squamates, demonstrating that the same processes produce egg coverings for both phenotypes.

Foster et al. (2019) followed up on this using transcriptomics to compare uterine gene expression in oviparous and viviparous phenotypes. They provide a molecular model for the genetic control and evolution of reproductive modes. Many genes are differentially expressed throughout the reproductive cycle of both phenotypes. Thus, viviparous and oviparous snakes

have different gene expression profiles. The differential expressions have similar biological functions which are essential for sustaining embryos, including uterine remodeling, respiratory gas and water exchange, and immune regulation. As might be expected, the similarities suggest long egg-retention is an exaptation for viviparity; or it reflects the parallel evolution of similar changes in gene expression needed for long egg-retention oviparous species. In contrast, changes in gene expression across the reproductive cycle of the long egg retaining oviparous *Saiphos equalis* are dramatically different from those of oviparous skinks. This supports the assertion that the oviparous *S. equalis* exhibit a phenotype that is intermediate between true oviparity and viviparity.

The ability of *Saiphos equalis* to change reproductive modes suggests to us that the Trinidad *Helicops angulatus* population (and likely other mainland *H. angulatus* populations) also has this capability. Trinidad *Helicops* likely have two reproductive phenotypes, making this population incredibly valuable to science, for unraveling a better understanding of the evolution of viviparity in Squamata.

Conservation. Given the highly aquatic habits of these snakes, habitat destruction and water pollution are likely the main threats to their survival. They are found in coastal areas as well as inland waters. Coastal mangrove forests are changing in complex ways, with deforestation combined with new growth (Al-Tahir and Baban 2005; Juman and Ramsewak 2013). Trinidad coastal areas have significant oil pollution from the thousands of large vessels that move through Trinidad waters annually (Water Resource Agency 2001).

Freshwater pollutants originate from urban, domestic, and industrial waste, agricultural chemicals, as well as sediments and oil spills. Lowering the water table to a level which exceeds the aquifer's replenishment abilities has resulted in brackish water intrusion into the El Socorro aquifers (Water Resource Agency 2001). Nitrate and bacterial contamination result from the excessive use of agrochemicals, leaking septic tanks, wastes from livestock, and agro-industrial effluents such as pesticides and fertilizers. Specifically, Trinidad has a severe problem with the excessive use of certain fertilizers and pesticides and the release of high concentrations of waste from intensive animal farm operations. Sewage and solid wastes are severe in some areas, such as the Beetham/Laventille swamp (north of the Caroni River). Tires, motor vehicles, major appliances, floating livestock, and an array of consumer disposables are often deposited in the swamp (Water Resource Agency 2001).

Deforestation in the Northern Range removes the protective vegetation layer, resulting in an excessive run-off that exacerbates flooding in the rainy season. Of great concern is the increase in residential development in watershed areas that significantly impacts the run-off rates, sedimentation levels of rivers, and downstream flooding. Silt from quarries has raised the substrates at the lower reaches and mouth of the Caroni River, affecting the hydrology of the river. High concentration rates of siltation affect rivers, such as the North Oropuche and Aripo Rivers in the northeast.

Saaristo et al. (2018) demonstrated how chemical contaminants (e.g., metals, pesticides, and pharmaceuticals) are changing ecosystems by altering animal behavior through physiological changes. Their framework shows how the sublethal behavioral effects of pollutants can have a mixture of negative, and sometimes positive, changes that vary dynamically within the same individuals and populations.

Of less concern are the snakes taken as by-catch by fishers. Hernández-Ruiz et al. (2014) used hoop nets to sample turtle populations in northern Brazil and obtained a by-catch of *Helicops angulatus*. However, through discussions with fishers in Nariva Swamp, we (JCM, RJA) found that they usually release the snakes captured in fishing nets. The loss of the unique *Helicops angulatus* populations on Trinidad and elsewhere would be a wasted significant opportunity to expand our understanding of the evolution of reproductive modes in the Squamata.

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John C. Murphy is a naturalist who focuses on snakes. When he is not hiking in the desert or examining specimens in the lab, John is often writing about reptiles. He is a retired science educator who got serious about his lifelong fascination with lizards and snakes in the early 1980s, when he and his family made their first trip to Trinidad. The work on Trinidad and Tobago provided valuable lessons that shaped his views of nature and evolution. Today he is still working on the eastern Caribbean herpetofauna. In the 1990s he worked on homalopsid snakes in Southeast Asia with other researchers from the Field Museum (Chicago, Illinois, USA). Today John resides in southeastern Arizona (USA) and is involved in multiple projects that concern arid habitats and the impact of climate change on biodiversity. His most recent book, with co-author Tom Crutchfield, is *Giant Snakes, A Natural History*. Born and raised in Joliet, Illinois, he first learned about reptiles on his grandfather's farm by watching Eastern Garter Snakes emerge from their winter dens and Snapping Turtles depositing their eggs at the edge of a cattail marsh.

Antonio Muñoz-Mérida is a bioinformatician with a background in biology and genetics. During his Ph.D. work, Antonio developed several bioinformatics tools and gained computing skills that have been improved during his post-doctoral appointment as the main bioinformatician at the Centro de Investigaçao em Biodiversidade e Recursos Geneticos (CIBIO) research center in Portugal. His expertise ranges across most of the OMICs associated with Next Generation Sequencing and functional annotation of whole genomes.

Renoir J. Auguste is a Trinidad and Tobago herpetologist. Renoir received his M.Sc. in Biodiversity Conservation from The University of the West Indies, St. Augustine Campus, Trinidad and Tobago, and is interested in the ecology and conservation of amphibians and reptiles. He has conducted herpetological surveys across Trinidad and Tobago professionally for national baseline surveys aimed at improving protected areas, as part of his academic degrees. He has also conducted surveys as part of his academic degree work and voluntarily with the local environmental NGO Trinidad and Tobago Field Naturalists' Club, in which he held the position as president for three years.

Oscar Miguel Lasso-Alcalá is Curator of the Fish Collection and a Senior Researcher at Museo de Historia Natural La Salle (MHNLS), Fundación La Salle de Ciencias Naturales, Caracas, Venezuela. His undergraduate studies were in Fishing Technology, Aquaculture, and Oceanography, followed by postgraduate work in Agricultural Zoology and Estuary Ecology. He is primarily an ichthyologist, with more than 30 years of experience in the taxonomy, biology, ecology, and fisheries aspects of marine, estuarine, and freshwater fauna. However, during more than 60 research projects and 230 scientific expeditions, he has participated in the study of biodiversity, including amphibians and reptiles. In this way, he has collaborated in several studies of the herpetofauna in the Caribbean, and different regions of Venezuela, where a frog (*Tachiramantis lassoalcalai*) was described in his honor.

Gilson A. Rivas was born in Caracas, Venezuela. He currently serves as co-editor of the scientific journal *Anartia*, and is a collection manager at the Museo de Biología de la Universidad del Zulia, Maracaibo, a Venezuelan centennial university that began academic activities on 11 September 1891. For over two decades, Gilson has devoted his studies to the taxonomy and conservation of the neotropical herpetofauna, and has authored or co-authored more than 100 academic publications, describing over 30 new species of amphibians and reptiles, and a new genus of dipsadine snakes, *Plesiodipsas*. Gilson is the author (with G. Ugueto) of the book *Amphibians and Reptiles of Margarita, Coche, and Cubagua*; and together with M. De Freitas, H. Kaiser, C.L. Barrio-Amorós, and T.R. Barros produced *Amphibians of the Península de Paria: a Pocket Field Guide*. Gilson's research interests are focused on the herpetofauna of the Venezuelan coastal range and insular ecosystems, as well as the influences of invasive species and human development and their impact on the native fauna.

Michael J. Jowers is an evolutionary biologist with broad interests in the processes and timing of speciation. His work focuses on tropical island biogeography, phylogeography, systematics, population genetics, taxonomy, and conservation. Michael is deeply involved in amphibian and reptile studies from the islands of Trinidad and Tobago (Lesser Antilles), but he is also interested in other organisms such as birds, mammals, and insects; and he actively leads studies throughout South America, Africa, Europe, and Asia.

Supplementary Material

Table S1. Primers used in gene fragment amplification.

Gene	Primer name and sequence	Reference
12S rDNA	12SA 5'- AAACTGGGATTAGATACCCCACTAT -3'	Kocher et al. 1989
12S rDNA	12SB 5'- GAGGG TGACGGGCGGTGTGT -3'	Kocher et al. 1989
16S rDNA	16SL 5'- GCCTGTTTATCAAAAACAT -3'	Palumbi et al. 1991
16S rDNA	16SH 5'- CCGGTCTGAACTCAGATCACGT - 3'	Palumbi et al. 1991
cytb	14910 5'- GACCTGTGATMTGAAAAACCAYCG -3'	Burbrink et al. 2000
cytb	H16064 5'- CTTTGGTTTACAAGAACAATGCTT -3'	Burbrink et al. 2000
c-mos	S77 5'- CATGGACTGGGATCAGTTATG - 3'	Lawson et al. 2005
c-mos	S78 5'- CCTTGGGTGTGATTTTCTCACCT - 3'	Lawson et al. 2005

Table S2. GenBank accession numbers of species and specimens of *Helicops* and outgroup taxa included in the molecular phylogenetic reconstructions and genetic divergence analyses. *Helicops angulatus* from this study are all from Trinidad (West Indies): UWIZM.2015.18.32 (Rd. Kernahan to Bush Bush), UWIZM.2011.20.22 (Nariva Swamp), UWIZM.2013.6 (Nariva Swamp), CAS231757 (Nariva Road, Manzanilla Beach), CAS231758 (Nariva Road, Manzanilla Beach), and CAS231760 (Nariva Road, Manzanilla Beach).

Species	12S rDNA	16S rDNA	c-mos	Cyt b
Pseudoeryx plicatilis (PSPL001)	GQ457826	GQ457765	GQ457886	-
Pseudoeryx plicatilis (H1399)	MN038102	MN038115	MN032460	-
Hydrops triangularis (H1476)	MN038103	MN038114	MN032461	-
Hydrops triangularis (HYTR001)	GQ457804	GQ457744	GQ457864	-
Helicops leopardinus (UFMTR11939)	MN038108	MN038121	MN032465	-
Helicops leopardinus (H1733)	-	MN038120	MN032464	-
Helicops modestus (MTR11762)	MN038109	MN038122	MN032468	-
Helicops modestus (MTR19715)	MN038110	MN038123	MN032469	-
Helicops pictiventris (HEPI001)	GQ457800	GQ457741	GQ457860	-
Helicops infrataeniatus (HIN001)	GQ457799	GQ457740	GQ457859	-
Helicops boitata (UFMTR11940)	MN038112	MN038124	MN032471	-
Helicops carinicaudus (142)	MN038104	MN038125	MN032462	-
Helicops nentur (DJS-2016)	-	KT453992	KT453991	-
Helicops polylepis (H919)	MN038111	-	MN032470	-
Helicops hagmanni (MTR12961)	MN038106	MN038118	MN032467	-
Helicops hagmanni (MTR13320)	MN038107	MN038119	MN032466	-
Helicops gomesi (HEGO001)	GQ457798	GQ457739	GQ457858	-
Helicops gomesi (141)	MN038105	MN038117	MN032463	-
Helicops angulatus (HEAN001)	GQ457797	GQ457738	GQ457857	-
Helicops angulatus (MRT7588)	MN038113	MN038116	MN032472	-
Helicops angulatus (CAS231758)	MT951589	MT951597	MT951603	MT951607
Helicops angulatus (CAS231757)	MT951591	MT951599	MT951605	MT951608
Helicops angulatus (CAS231760)	MT951590	MT951600	MT951604	MT951606
Helicops angulatus (UWIZM.2013.6)	MT951592	MT951595	MT951602	-
Helicops angulatus (UWIZM.2015.18.32)	MT951593	MT951598	-	MT951609
Helicops angulatus (UWIZM.2011.20.22)	MT951594	MT951596	MT951601	MT951610