A new species of *Erythrolamprus* from the oceanic island of Tobago (Squamata, Dipsadidae)

John C. Murphy¹, Alvin L. Braswell², Stevland P. Charles³, Renoir J. Auguste⁴, Gilson A. Rivas⁵, Amaël Borzée⁶,⁷ Richard M. Lehtinen⁸, Michael J. Jowers⁹,¹⁰

¹ Science and Education, Field Museum of Natural History, 1400 Lake Shore Drive, Chicago, IL 60616 USA  
² North Carolina State Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC USA  
³ Department of Biology, Howard University, 415 College Street NW, Washington, DC 20001 USA  
⁴ Department of Life Science, University of the West Indies, St. Augustine, Trinidad, W rf  
⁵ Museo de Biologia, Facultad Experimental de Ciencias, Universidad del Zulia, Apartado Postal 526, Maracaibo 4011, Venezuela  
⁶ Division of Ewoscience, Ewha Womans University, Seoul, 03760, Republic of Korea  
⁷ Interdisciplinary Program of EcoCreative, Department of Life Science, Ewha Womans University, Seoul, 03760, Republic of Korea  
⁸ Department of Biology, The College of Wooster, Wooster, OH USA 44691 USA  
⁹ CIBIO/InBIO (Centro de Investigação em Biodiversidade e Recursos Genéticos), Universidade do Porto, Campus Agrario De Vairão, 4485-661, Vairão, Portugal  
¹⁰ National Institute of Ecology, 1210, Geumgang-ro, Maseo-myeon, Seocheon-gun, Chungcheongnam-do, 33657, Republic of Korea

Corresponding authors: John C. Murphy (serpentresearch@gmail.com); Michael J. Jowers (michaeljowers@hotmail.com)

Academic editor: Robert Jadin | Received 24 October 2018 | Accepted 8 December 2018 | Published 15 January 2019

Citation: Murphy JC, Braswell AL, Charles SP, Auguste RJ, Rivas GA, Borzée A, Lehtinen RM, Jowers MJ (2019) A new species of *Erythrolamprus* from the oceanic island of Tobago (Squamata, Dipsadidae). ZooKeys 817: 131–157. https://doi.org/10.3897/zookeys.817.30811

Abstract

Tobago is a small island on the southeast edge of the Caribbean Plate with a continental flora and fauna. Using DNA sequences from Genbank, new sequences, and morphological data from the snakes *Erythrolamprus epinephalus*, *E. melanotus*, *E. reginae*, and *E. zweifeli*, the species status of specimens of a Tobago snake previously considered to be *Erythrolamprus reginae* was assessed. *Erythrolamprus zweifeli*, long considered a subspecies of *E. reginae*, was found to be a northern Venezuela-Trinidad endemic and the sister to *E. reginae*. The trans-Andean species *E. epinephalus* is shown to be non-monophyletic while the Costa Rican lineage of *E. epinephalus* is weakly supported as the sister to the Tobago population. The Tobago *Erythrolamprus* is described as a distinct taxon based upon five specimens from four localities in lower montane rainforest. Much of the new species range includes the Main Ridge Forest Reserve of Tobago, the
oldest protected forest in the Western Hemisphere. All known locations fall within a 400-ha area, and its total geographic distribution is likely to be less than 4,566 ha. The restricted distribution of this new snake makes it a likely candidate for threatened status. The new species also becomes another biogeographic link between northern Venezuela and Tobago.

**Keywords**
cryptic species, evolutionary species concept, lowland montane rainforest, sky islands, systematics

**Introduction**

The Cordillera de Costa (CC) is a sky island archipelago that extends 925 km in an east-west orientation from western Venezuela, across the Northern Range of Trinidad to the island of Tobago. The CC is separated from the Andes by the Yaracuy River depression, and in the east, the CC is separated from the Guyana shield by the Llanos grasslands. The Gulf of Paria separates the Peninsula de Paria from Trinidad, and Trinidad is separated by 35 km of open water from Tobago. The CC formed between the late Cretaceous and the Miocene (Sisson et al. 2005). Rising and falling sea levels, marine incursions, changing climates, and tectonic events have continually remodeled the landscape isolating and reconnecting populations of organisms.

Tobago is at the eastern edge of the CC sky island complex and is slightly more than 300 km², and its highest peak is about 576 m above sea level (ASL). The island has two physiographic regions: a flat coastal plain composed of a coral terrace in the southwest and the Main Ridge, a mass of metamorphic and igneous rocks, covered by dense tropical forest. The Main Ridge runs in a northeast-southwest direction.

Tobago’s snake fauna contains 23 species, and eleven of these belong to the Dipsadidae clade. Molecular studies on the Western Hemisphere snake clade Dipsadidae (or Dipsadinae) (Zaher et al. 2009; Vidal et al. 2010; Grazziotin et al. 2012) suggest *Erythrolamprus* Boie 1826 is not monophyletic unless most of the snakes formerly placed in the genera *Liophis* Wagler, 1830, *Leimadophis* Fitzinger, 1843, and *Umbrivaga* Roze, 1964 are included. This action increased the number of *Erythrolamprus* species from six, mostly coral snake mimics, to 50 species (Uetz and Jacob 2018) with a variety of color patterns and habits. Thus, *Erythrolamprus* became one of the most species-rich genera of Neotropical snakes. This arrangement has not been accepted by everyone (Wallach et al. 2014). Here we consider the genus *Erythrolamprus* in the broadest sense, including the species traditionally allocated to *Leimadophis, Liophis, and Umbrivaga*, acknowledging that future taxonomic changes are likely.

There is no known synapomorphy for the genus *Erythrolamprus* (Myers 2011). That said, members of the genus are usually less than 1.6 m in total length; nine scales are normally present on the crown; the number of dorsal scale rows is 15–19 and in some species they are reduced once, in others, they may be reduced twice posteriorly; apical pits may be present or absent on some or all of the scales; ventral counts range from 129–212; subcaudal counts range from 38–106; the temporal formula is usually 1+2; the preocular is usually single; the postoculars are usually two; upper labials are usually eight; lower labials are usually ten, and two pair of enlarged chin shields are present.
Erythrolamprus ranges from Costa Rica southward to Argentina and occurs on both sides of the Andes as well as in the Lesser Antilles. Some taxa reach an elevation of 3,500 m ASL. Members of the genus have life styles that range from fossorial to terrestrial to semi-aquatic in habitats spanning rainforests, savannas, and páramo (Savage 2002).

The genus Erythrolamprus in the Cordillera de la Costa

Eighteen species of Erythrolamprus occur in northern Venezuela, of these, two are Pantepui species: E. trebbaii (Roze 1958a), E. ingeri (Roze 1958b). The remaining 16 species are associated with the CC either as montane species, lowland species, or species that are not restricted by elevation. Eight of the 16 species occur on the Guyana Shield and seven species of Erythrolamprus are recognized on Trinidad and Tobago: E. aesculapii (Linnaeus, 1758); E. bizona Jan 1863; E. cobellus (Linnaeus, 1758); E. melanotus (Shaw, 1802), E. ocellatus Peters, 1868; E. zweifeli (Roze, 1959); and E. reginae (Linnaeus, 1758) (Murphy et al. 2018). Both E. aesculapii and E. bizona are coral snake mimics, and each is known from a single specimen from Trinidad (but better known from elsewhere in their ranges).

Erythrolamprus ocellatus is a Tobago endemic, with a bright red dorsum and black ocelli, and is best considered an imperfect coral snake mimic, keeping in mind that there are no extant species of coral snakes on Tobago (Hodson and Lehtinen 2017). Erythrolamprus cobellus is a semi-aquatic, lowland species; while E. melanotus and E. zweifeli are forest species often associated with stream-edge habitats and mountains from sea level to at least 2,000 m. However, in Venezuela, E. zweifeli is usually associated with montane environments.

Noting significant differences in coloration, as well as distinct ventral and subcaudal counts from E. reginae, Rivas et al. (2012) returned Erythrolamprus reginae zweifeli to species status. They noted E. zweifeli differs from E. reginae in having a salt-and-pepper dorsal pattern or a more uniform olive-green or olive-brown pattern. Wallach et al. (2014) concurred and recognized the elevation of zweifeli to species level. E. reginae has a dorsum with dense pale and dark paravertebral flecking. The two species also differ in subcaudal counts (69–88 in E. zweifeli as opposed to 55–78 in E. reginae) with the ranges overlapping, but different means. Following this arrangement, E. zweifeli occurs throughout the Cordillera de Mérida and the CC in Venezuela, including Trinidad.

Natural history of Trinidad and Tobago’s Erythrolamprus

There are some ecological differences between the Trinidad and Tobago Erythrolamprus. The two poorly known coral snake mimics (E. aesculapii, E. bizona) are forest dwellers and snake predators (Campbell and Lamar 2004). Dietary differences between the two better known forest and forest-edge species are apparent. Erythrolamprus melanotus feeds on the microteiid lizards in the genus Bachia, the rain frog Pristimantis urichi, the puddle frog Engystomops pustulosus and the gecko Gonatodes vittatus, and unidenti-
fied fish have been reported. *Erythrolamprus zweifeli* feeds on stream frogs of the genus *Mannophryne*, hylid frogs, *Leptodactylus validus*, salamanders, lizards of the genus *Ameiva*, and small birds (Michaud and Dixon 1989; Murphy 1997; Esqueda et al. 2009). While the diets overlap the presence of *Bachia*, *Gonatodes*, and *Pristimantis urichi* in the diet of *E. melanotus* suggest it is hunting in more terrestrial situations in forests or at forest edges. *Mannophryne* in the diet of *E. zweifeli* suggests it is hunting along forested stream-edges. It supports the fact that *E. zweifeli* was the most common snake encountered during a study in a canal system used for water collection from a mountain stream located in Naiguatá, Venezuela (Silva et al. 1985; Silva and Valdez 1989).

*Erythrolamprus epinephalus* (Cope, 1862) is widespread and polytypic, ranging from Costa Rica to Ecuador, Colombia, and Venezuela and has not been previously associated with Trinidad or Tobago. The examination of a single specimen (USNM 22069) from Tobago led Dixon (1983b) to conclude that it was *Liophis (= Erythrolamprus) reginae* with an atypical color pattern that resembled a *Liophis (= Erythrolamprus) epinephalus* population from eastern Colombia. Dixon’s remark was the only mention of *E. epinephalus* associated with Trinidad and Tobago. He noted the most striking difference in the Tobago animal was a dorsolateral tan stripe not present in the Trinidadian *E. zweifeli*.

Here, we examine the genetic divergence and morphology of a Tobago snake, previously considered part of the *E. reginae* group, in an attempt to understand its phylogenetic relationship to other *Erythrolamprus* and the biogeography in northeastern South America.

**Materials and methods**

Museum material examined (Appendix 1) included 105 specimens of five *Erythrolamprus* species. Snakes were examined for external morphological data; scale nomenclature follows Dixon (1983a, b). Museum acronyms are as follows:

- **AMNH**: American Museum of Natural History
- **FMNH**: Field Museum of Natural History
- **EBRG**: Museo de la Estación Biológica de Rancho Grande
- **UMMZ**: University of Michigan Museum of Zoology
- **USNM**: National Museum of Natural History
- **UWIZM**: University of the West Indies Zoology Museum
- **MBLUZ**: Museo de Biología, Universidad del Zulia
- **MCNC**: Museo de Ciencias Naturales, Caracas

Locality data was converted into coordinates using Google Earth. Measurements of the body and tail lengths were taken to the nearest millimeter; ventral scale count methods follow Dowling (1951). The anal plate and terminal scutes were not included in the number of ventrals or subcaudals. The dorsal scale row counts were made about ten ventrals behind the head, at mid-body, and about ten ventrals anterior to the vent. Values for paired head scales are given in left/right order. Scales were measured to the
A new species of Erythrolamprus from the oceanic island of Tobago...  

nearest 0.1 mm with the aid of a digital caliper and dissection microscope. Total length (TTL) and tail length (TL) measurements were taken to the nearest mm by carefully stretching the specimens along a ruler or placing a measuring tape along the length of the animal (Appendix 2). Statistical analyses were done with Excel-QI Macros (alpha = 0.05). Ventral and subcaudal counts were compared using ANOVA (Appendix 3).

DNA extraction, purification, and amplification protocols follow Jowers et al. (2013). Two mitochondrial gene fragments, 12S rDNA (primers 12Sa and 12Sb; Kocher et al. 1989), 16S rDNA (primers 16SL and 16SH; Palumbi 1996) and a nuclear gene fragment, c-mos (primers G73 and G74; Saint et al. 1998) were amplified. The lengths of the sequences were: 12S rDNA, 343 base pairs (bp); 16S rDNA, 425 bp; c-mos, 564 bp. We sequenced four Erythrolamprus melanotus (GenBank accession numbers are shown in Appendix 4) from Trinidad (n = 1), Tobago (n = 3), two E. zweifeli from Trinidad, and a new undescribed Erythrolamprus sp. from Tobago. We downloaded all Erythrolamprus sequences for the same loci from Genbank and used Xenodon histricus as the outgroup (Hodson and Lehtinen 2017).

Seaview v.4.2.11 (Gouy 2010) was used for preliminary alignments of sequences and were aligned thereafter in MAFFT (Katoh et al. 2002), and phylogenetic analyses were conducted using the concatenated mitochondrial and nuclear (12S+16S rDNA+c-mos) alignment (with a length of 1332 bp) using a partitioned model of substitution by gene fragment. The most appropriate substitution model for each gene partition was determined by the Bayesian Information Criterion (BIC) in PartitionFinder v.2 (Lanfear 2012). The best-fitting models for the ribosomal and c-mos fragments were as follows: 12S rDNA + 16S rDNA (TRN+I+G), c-mos first and second codon positions (TrNef+I) and c-mos third codon position (HKY). Phylogenetic relationships between taxa were inferred using the Bayesian Inference (BI) optimality criterion under the best fitting substitution model for each gene partition. MrBayes Huelsenbeck et al. (2001) was used with default priors and Markov chain settings, and with random starting trees. Each run consisted of four chains of 30 million generations, sampled every 1,000 generations. Runs were evaluated for convergence and mixing by observing and comparing traces of each parameter in Tracer v.1.6 (http://beast.bio.ed.ac.uk/tracer) (Rambaut et al. 2014). We considered effective sampling size (ESS) values > 200 to be good indicators of parameter mixing. Phylogenetic relationships (Figure 1) were also estimated using a Maximum Likelihood (ML) approach, as implemented in the software RAxML v7.0.4 (Silvestro and Michalak 2010), under the best partition scheme under the GTR model. All analyses were performed using the CIPRES platform (Miller et al. 2010). P-uncorrected distances were calculated in MEGA V7 (Kumar et al. 2016) under complete deletion of gaps and missing data.

Molecular results

Runs showed high Effective Sample Size convergence (> 2300), indicating adequate sampling of the posterior distribution. The p-uncorrected distances between L. epinephalus from Costa Rica and E. sp. from Tobago were the highest of all terminal monophyletic
Figure 1. Bayesian inference tree of *Erythrolamprus* species from Genbank MtDNA 12S+16SrDNA+c-mos sequences (1332 bp). Red stars indicate Bayesian inference and ML posterior probabilities (> 95%) and bootstrap (> 70%) support values above and below nodes, respectively. Clade in orange shows *E. zweifeli*, in green *E. melanotus*, and in blue *E. pseudoreginae* sp. n. (*AF158433*) is from French Guiana, and *E. reginae* (*JQ598983*) is from Brazil.

clades (4.69%) indicating the high genetic divergence between both species (Appendix 5). The phylogenetic relationships of *Erythrolamprus* and the paraphyly of some species (*E. typhlus*, *E. poecilogyrus*, *E. epinephalus*, *E. aesculapii*) are similar to past published work (Hodson and Lehtinen 2017), suggesting the need for an in-depth systematic revision of the genus. Furthermore, the results show the paraphyly of *Erythrolamprus reginae*. *Erythrolamprus melanotus* from Trinidad and Tobago are monophyletic, and the Trinidad specimen shows no genetic differentiation from the most common Tobago haplotype. *Erythrolamprus* sp. from Tobago is the sister clade to *E. epinephalus* from Costa Rica. This clade, composed by the three species (*E. melanotus + E. epinephalus + E. sp. Tobago*), is strongly supported in the Bayesian analyses. The Trinidadian *E. zweifeli* form the sister clade to *E. reginae* from Guyana but are a distinct lineage.

**Morphological results**

Figure 2 shows the similarities in the architecture of the scales when *Erythrolamprus* are viewed in profile. They all have a single preocular, two postoculars, and eight upper labials; the second and third upper labials are in contact with the loreal, the fourth and
A new species of Erythrolamprus from the oceanic island of Tobago...

Figure 2. A comparison of the five members of the Erythrolamprus reginae group. A E. reginae for Guyana (FMNH 30959) B E. zweifeli from Venezuela (FMNH 204477) C E. melanotus from Tobago (UWIZM.2012.42.19) D E. pseudoreginae sp. n. from Tobago (FLMNH 91621) E E. epinephalus from Venezuela (MBLUZ 1502).

fifth border the orbit, and the temporal formula is 1+2. Figure 3 compares the crowns and chins of four of these species (including E. zweifeli from three different populations). They all share nine plate-like scales on the crown in similar proportions and two pair of enlarged chin-shields. Figure 4 illustrates the distribution of the five species in northern South America, Trinidad, and Tobago.

Comparisons and summaries of the meristic characters for taxa under consideration are given in Table 1. Ventral counts for all Erythrolamprus taxa under consideration have ranges that overlap, although they have different means, some of which are significantly different. The ranges for the subcaudal counts are similar. The Tobago E. pseudoreginae sp. n. can be separated from E. melanotus but not the other taxa. The
results of single factor ANOVAs are presented in Appendix 2. Some support the separation of *E. zweifeli* from *E. reginae*, *E. zweifeli* from the Tobago *E. pseudoreginae* sp. n., and *E. reginae* from the Tobago *E. pseudoreginae* sp. n.

Substantial genetic differences (0.047) (Appendix 5) and relatively minor morphological differences (different means for ventral counts, distinctive coloration, the absence of apical pits on dorsal scales) and its geographic isolation support the description of the Tobago population as a new species. Figure 5 compares the color morphs of *Erythrolamprus zweifeli* found in Trinidad and Venezuela with *Erythrolamprus reginae* from Guyana. Figure 6 illustrates *E. pseudoreginae* sp. n.

**Table 1.** A comparison of the meristic and color pattern data for the five taxa in *Erythrolamprus* in the Trinidad and Tobago area. Key: * based on our counts for Venezuelan specimens.

|                  | *E. melanotus* | *E. reginae* | *E. zweifeli* | *E. pseudoreginae* sp. n. | *E. epinephalus* |
|------------------|----------------|--------------|---------------|--------------------------|-----------------|
| Number of specimens | 12             | 14           | 44            | 5                        | 6               |
| stripe on rows    | 4–5            | 3–4          | 3–4           | 3–4–5                    | variable        |
| ventral range     | 139–154        | 129–147      | 134–157       | 143–154                  | 144–157*        |
| mean ventrals ± SD | 146.66 ± 4.36  | 138.35 ± 4.71| 142.54 ± 3.98 | 147.5 ± 3.35             | 151.33 ± 3.38   |
| subcaudal range   | 53–58          | 68–79        | 72–85         | 76–79                    | 65–75*          |
| mean subcaudals ± SD | 55.2 ± 1.4   | 72.0 ± 7.14  | 79.9 ± 4.20   | 77.5 ± 1.5               | 68.2 ± 3.38     |
| postocular stripe | present        | indistinct   | present       | indistinct               | variable        |
| ventral color     | yellow         | yellow to pale orange, usually with black checks | red with black checks, some ventrals solid black | uniform yellow to red with scattered fine speckling | variable |
| apical pit present | yes            | yes          | no            | yes                      | yes             |

**Erythrolamprus pseudoreginae** sp. n.

http://zoobank.org/B5FAE467-C240-4EBB-9DA5-B3D44998757E

Figures 2D, 3A, 6

*Liophis* sp. Hardy 1982: 86.

*Liophis reginae* [ssp.] Dixon 1983b: 12.

**Material.** Holotype. UWIZM.2016.22.45 collected 13 June 2016 by Alvin L. Braswell and Renoir J. Auguste on Gilpin Trace Trail, 8.5 km NNW Roxborough, St. John, Tobago (-11°16’55”N; 60°37’12”W, about 493 m ASL) at 0900 hrs. Paratypes. TOBAGO: St John: FLMNH 91621 Gilpin Trace Trail, 5.3 mi NNW Roxborough, 11°16’N, 60°37’W collected on 17 July by Kurt Auffenberg. USNM 228069 south of Charlotteville, at first creek crossing on Pigeon Peak Trace 11°17’N, 60°36’W collected 12 May 1979 at (14:00 hrs) by Dave Stephens; USNM 325089 NW of Roxborough on Gilpin Trace, ca. 0.5 mi from its junction with Roxborough-Bloody Bay Road, collected 11 November 1992; USNM 539191 approx. 6 km (airline) NNW of Roxborough, 0.5 mi from upper entrance of Gilpin Trace and Roxborough - Parlatuvier Road, 11°17’N, 60°35’W collected 11 July 2000.
A new species of Erythrolamprus from the oceanic island of Tobago...

Figure 3. A comparison of the scale arrangements on the crowns and ventral heads of the Erythrolamprus taxa under discussion. A E. pseudoreginae sp. n. from Tobago B E. epinephalus from Venezuela MBLUZ 1501 (dorsal view) and 1500 (ventral view) C, D Salt and pepper morph of E. zweifeli from Trinidad and Venezuela E An olive-brown morph of E. zweifeli Trinidad, FMNH 215827 F A melanistic morph of E. zweifeli from Venezuela EBRG 2745.

Diagnosis. Ventrals 143–154; subcaudals 76–79; second pair of chin shields longest; some anterior dorsal scales have an apical pit; lateral stripe on scale rows 3–4–5, dark stripe (row 3) and a pale stripe (rows 4–5) on posterior body and tail, the black stripe continues to the forebody as a series of black spots on scale row three; and the ventral surface has scattered flecks of pigment toward mid-body. Otherwise, the belly is uniform cream with fine speckling in preserved material, and red in life, tail uniform cream in preservative, red in life.
Description of the holotype. UWIZM.2016.22.45, an adult male, 525 mm total length, 148 mm tail; tail 28% of SVL. Rostral barely visible from above, broader than tall; internasals paired, shorter than prefrontal; frontal pentagonal; parietals longer than frontal; four post parietals; nasal divided, first lobe does contact the second labial; loreal subrectangular, higher than long, contacts upper labials 2–3; preocular single, T-shaped, contacts upper labials 3–4; postoculars 2/2, upper largest; temporals 1+2, primary temporal contacts upper labials 6–7/6–7; upper labials 8/8; 4–5 in orbit; lower labials 4/5 contact anterior chin shields, total of nine in contact with both pairs; lower labials 9/10; three gular scales; dorsal scales are smooth, some have a single apical pit, they are in 17 rows at mid body and reduced to 15 rows anterior to the cloaca; 146 ventrals; 77 subcaudals.

In life the crown is dark moss green with black spots, the upper labials are cream, with a dark stripe on the upper edge that runs from nasal to orbit, and widens posteriorly onto the temporals. Dorsal spots on scale rows 2–3 about two ventrals apart, start above the 12th ventral, and coalesce into a stripe at about the 96th ventral and extend posteriorly to the tip of the tail; lateral stripe mostly on scale row three on body, goes onto scale row one on tail. About one-third down the body, about ventral 40, scale rows 1–4 blue-gray, row five is brown, row six and above blue-gray; except for the mossy green on the anteriormost dorsal surface for about 40 ventrals. Ventrals surface mostly uniform yellow to orange with light mottling starting about the 50th ventral; tail has a mid-line zigzag stripe.

Variation: The smallest specimen measured 347 mm SVL with a 129 mm tail; the largest specimen 420 mm SVL with a 119 mm damaged tail. Dorsal scale rows 17–17–15. Ventrals range from 143–154 (n = 5, X = 147.5, SD = 3.35); subcaudals 76–79 (n = 2, X = 77.5, SD = 1.5). Upper labials eight or nine, 2–3 contact loreal, 4–5 border the orbit (one specimen has 5–6 bordering the orbit on one side), the tallest can be seventh, (or eight if nine labials are present); the sixth labial is the largest in the area. Loreal is quadrangular to pentagonal. Lower labials 9–10; first four or five contact the anterior chin shields. Longest pair of chin shields is the second. Eye diameter is greater than eye-nostril distance. The dark posterior lateral stripe is usually on scale rows 2–3–4, but one specimen has it on scale rows 2–3 only.

Color in life. The following is based on the holotype (Figure 6) and a color photograph in Brown (2013). Crown and face olive brown, upper labials white, a short black subocular stripe extends from the nasal scale under the eye and posteriorly to the last labial. Immediately behind the head, the interstitial skin is yellow; dorsum brown with an indistinct vertebral stripe and scales partially edged with black pigment most obvious on posterior two-thirds of the body. First three scale rows are blue-gray and separated from brown dorsum by a row of black spots.

Color in alcohol. Head, body, and tail dark blue to brown with a black stripe on the posterior lateral body that becomes a series of dark spots extending anteriorly on the body. The belly is a uniform cream with fine speckling of pigment.

Comparisons. Erythrolamprus pseudoreginae sp. n. differs from E. zweifeli in the presence of apical pits on some dorsal scales, an almost uniform yellow to red venter,
A new species of Erythrolamprus from the oceanic island of Tobago...

and a dark stripe on the posterior body on scale rows 3–4 bordered above by a pale stripe on scale row five. The new species lacks the well-defined postocular stripe that runs from the postocular scales across the temporals to a point just above the rictus in most *E. zweifeli*. In *E. zweifeli* the postocular stripe may also have a pale dorsal border.

*Erythrolamprus pseudoreginae* sp. n. differs from all populations of *E. epinephalus* in having more than 75 subcaudal scales, except for some Venezuelan and Colombian populations. The *E. epinephalus* populations with more than 75 subcaudals have a dorsal or ventral pattern that includes transverse bars, black checks, or a pattern with irregular black spots on the outer edges of the ventral scales that may extend onto the first row of dorsal scales (Dixon 1983a, Escalona 2017).

The new species differs from *Erythrolamprus reginae* in having a uniform venter (*E. reginae*) has yellow to orange venter with black checks, and a dark stripe on the last fourth of the body on scale rows 3–4 which is not bordered by a pale stripe. *Erythrolamprus pseudoreginae* sp. n. has uniform yellow to red ventral surface and a very distinctive, pale posterior lateral stripe on row five above the black stripe on rows 3–4 that extends anteriorly as a row of dark spots. *Erythrolamprus reginae* has fewer ventrals and a lower mean ventral count than *E. pseudoreginae* sp. n.

The pattern will readily distinguish it from the two coral snake mimics (*Erythrolamprus aesculapii* and *E. bizona*) which are on Trinidad but not Tobago. The endemic Tobago Red Snake, *E. ocellatus*, has a bright red dorsum with black ocelli. The semi-aquatic *Erythrolamprus cobellus* has a uniform dark green or black dorsum and is known from Trinidad but not Tobago. The absence of a black stripe five scale rows wide on the vertebral line separates it from Shaw’s Black Back Snake, *E. melanotus*, a species known from both islands.

**Distribution.** It occurs in northeastern Tobago and appears to be restricted to the forested ravines along the crest of the Main Ridge (Fig. 4). Tobago’s Main Ridge is about 16 km long and covered with lower montane rain forest on schist soil above 224 m ASL. The ridge crest reaches elevations of 487–576 m ASL and forms steep terrain with deep gullies and fast-moving streams. The area receives about 318 cm of rainfall per year, and no month receives less than 10 cm (Beard, 1944). Tobago’s Main Ridge Forest Reserve is the oldest protected forest in the Western Hemisphere (since April 1776) and encompasses 3958 hectares. At this writing, five specimens of *Erythrolamprus pseudoreginae* sp. n. are known, all of which came from the northeast end of the Main Ridge. The locality and elevation data available suggest it occurs within an area of about 400 ha at elevations between 430–500 m ASL. Three types of rainforest occur on Tobago: lowland rainforest covers 4,844 ha, lower montane rainforest covers 4,566 ha, and xerophytic rainforest covers 937 ha (Helmer et al. 2012). All of the localities for *E. pseudoreginae* sp. n. fall within the lower montane rainforest, suggesting its maximum area of occupancy may be 4,566 ha, if it is restricted to that forest type.

**Natural History.** *Erythrolamprus pseudoreginae* sp. n. is diurnal, all of the specimens with time of collection data were found in the morning or afternoon. Nothing is known about the diet and reproduction of this snake. Its close relatives have been reported to eat anurans, and it likely preys upon small ground-dwelling frogs.
Figure 4. Geographic distribution of the five species of *Erythrolamprus* under discussion in this paper. 

**A** The distribution of the species of *Erythrolamprus* under discussion in northern Venezuela and Trinidad and Tobago. **B** More detailed view of the distribution on Trinidad and Tobago. **C** Tobago with the known localities for *E. pseudoreginae* sp. n. Note that two of the markers closely overlap. Key: black stars = *E. zweifeli* from Cordillera de Costa in Venezuela and the island of Trinidad; green circles = *E. epinephalus* from the Cordillera de Mérida, Venezuela. Note that these markers denote the closest population to Tobago based on Roze (1966). Specimens examined came from several different locations. Purple stars = *E. reginae* from the Guianas including Orinoco Delta in Venezuela; red stars = *E. melanotus* from Venezuela, Trinidad, and Tobago; blue star = *Erythrolamprus pseudoreginae* sp. n. on Tobago.

**Conservation.** Given the restricted distribution of this snake as well as the fact that most, if not all, of its distribution lies within the oldest protected forests in the Western Hemisphere it may be assumed that it is well protected. However, as the climate changes the microclimate found in the lowland montane rainforest may be expected to change and potentially make the local environment inhospitable for this species and the other endemic taxa found here.

**Etymology.** The epithet *pseudoreginae* was chosen because prior investigators considered this snake to be *Liophis reginae*. We suggest Tobago Stream Snake as the common English name for this snake.
Figure 5. A, B Variations in the olive color morph of *Erythrolamprus zweifeli* from Trinidad (photographs by Michael Patrikeev) C the middle photo shows the “salt and pepper” morph that occurs at higher elevation (photograph by JCM). Both color morphs are included in our molecular sample D *E. zweifeli* Rancho Grande, Parque Nacional Henri Pittier, Luis A. Rodriguez J. E the Royal Snake, *Erythrolamprus reginae* from Kaiteur, Guyana (photograph by P Kok).
Figure 6. *Erythrolamprus pseudoreginae*. A UWIZM 2016.22.45, holotype B–D FLMNH 91621 from Gilpin Trace, on Tobago’s Main Ridge. B Profile. Of the four specimens examined this was the only one that had nine upper labials (on one side only) C The posterior lateral stripe bordered by a dorsal light stripe D Venter mostly uniform with patches of scattered pigment.
Discussion

_Erythrolamprus pseudoreginae_ becomes the fifty-first species in the genus, and the eleventh member of the Tobago herpetofauna closely associated with the Main Ridge. The list of Main Ridge species includes the frogs _Mannophryne olmonae, Pristimantis charlottevillensis_, _P. turpinorum, Hyalinobatrachium orientale_; the lizards _Bachia cf. flavescens, Gonatodes ocellatus, Anolis cf. tigrinus_; and the snakes _Atractus fuliginosus, Erythrolamprus ocellatus_, and _Leptophis haileyi_.

Most of the Main Ridge endemic species seem to have their closest living relatives in the Costal Ranges of Venezuela as opposed to the more proximal island of Trinidad or the Guiana Shield. The Coastal Range endemic _Mannophryne riveroi_ is the sister to _M. olmonae_ (Manzanilla et al. 2009, Lehtinen et al. 2011). Tobago’s _Pristimantis charlottevillensis_ appears to be most closely related to _P. terraebolivaris_ and members of the _Pristimantis conspicillatus_ group (Hedges et al. 2008). Jowers et al. (2015) proposed a Pliocene land bridge connection between Tobago and Venezuela to explain the presence of _Hyalinobatrachium orientale_ on Tobago and northeast Venezuela. An alternative explanation is that Tobago was accreted to Venezuela on its movement to its current position.

With this study, only 21 of the 51 named _Erythrolamprus_ species have been included in molecular studies; thus, the tree contains only 41% of the known species in the genus. Therefore, its topography is likely to change with additional taxa from more locations. _Erythrolamprus reginae_ and _E. epinephalus_ are polytypic and given their distributions and morphological variation they represent a considerable challenge to resolving the lineages found within these taxa. Some of the color patterns have evolved multiple times in the different lineages and when combined with the conserved morphology, separating these taxa by morphology becomes a conundrum. It seems likely that some of the currently recognized subspecies will be found more closely related to lineages other than the one they are currently assigned.

The phylogenetic analyses suggest part of _E. reginae_ is the sister to _E. zweifeli_. The results show for the first time the Trinidadian _E. melanotus_, has no genetic divergence from the most common haplotype from Tobago. This lack of differentiation suggests some recent or ongoing gene flow between islands. The position of _E. ocellatus_ from Tobago suggests that it forms a highly divergent lineage to the remaining Tobago’s _Erythrolamprus_ and may indicate a different time of colonization.

Acknowledgements

We would like to thank all of the institutions and curators who provided us with specimens, work space, and literature resources: American Museum of Natural History (AMNH), David Kizirian; Museo de la Estación Biológica de Rancho Grande (EBRG), Edward Camargo; Florida Museum of Natural History (FLMNH), Max Nickerson, Kenneth Krysto; Field Museum of Natural History (FMNH), Alan Rese-
tar; Milwaukee Public Museum (MPM), Robert W. Henderson; University of Michigan Museum of Zoology (UMMZ), Greg Schneider; National Museum of Natural History (USNM), Jeremy Jacobs, Kevin de Queiroz, Kenneth Tighe, Robert Wilson; Museo de Ciencias Naturales, Caracas (MCNC), Hyram Moreno; University of the West Indies Museum of Zoology (UWIZM) Mike G. Rutherford. Luis A. Rodríguez J. (serpientesdevenezuela.net) provided photos of *E. epinephalus* from Venezuela We would also like to offer our sincerest thanks to Tom Anton and Gabriel Haas for lab and field assistance and Nathalie Aall for Figure 1. The field work and collecting was done under permits from the Wildlife Section Forestry Division in St Joseph, Trinidad issued to John C Murphy, Richard M Lehtinen, and Mike G Rutherford and permits from the Tobago House of Assembly in Scarborough, Tobago issued to Mike G Rutherford and John C Murphy between the years 2010 and 2017.

References

Beard JS (1944) The natural vegetation of the island of Tobago, British West Indies. Ecological Monographs 14: 136–163. https://doi.org/10.2307/1943531

Brown PA (2013) Bird report Tobago and Trinidad 20th February – 6th March 2013. http://www.surfbirds.com/mb/trips/obago-brown-0413.pdf [accessed May 5, 2015]

Campbell JA, Lamar W (2004) The Venomous Reptiles of the Western Hemisphere, Volumes I and II. Comstock Publishing (Cornell University Press), Ithaca, 1–475 [vol. 1], 477–869 [vol. 2].

Cope ED (1862) Synopsis of the species of *Holcosus* and *Ameiva*, with diagnoses of new West Indian and South American Colubridae. Proceedings of the Academy of Natural Sciences of Philadelphia. 1: 60–594. https://www.jstor.org/stable/4059427

Dixon JR (1983a) Systematics of the Latin American snake, *Liophis epinephalus* (Serpentes: Colubridae). In: Rhodin AG, Miyata K (Eds) Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Harvard University, Boston, 132–149.

Dixon JR (1983b) Systematics of *Liophis reginae* and *L. williamsi* (Serpentes, Colubridae), with a description of a new species. Annals of the Carnegie Museum 52: 113–138. https://biodiversitylibrary.org/page/52426132

Dowling HG (1951) A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1: 97–99. https://doi.org/10.2307/1437542

Escalona MD (2017) Range extension for *Erythrolamprus epinephalus bimaculatus* (Cope, 1899) and *E. e. opisthotaenius* (Boulenger, 1908) in Venezuela (Serpentes: Colubridae). Herpetology Notes. 10: 511–5. https://biotaxa.org/hn/article/view/30217/29527

Esqueda LF, Natera-Mumaw M, La Marca E (2009) First record of salamander predation by a *Liophis* (Wagler, 1830) snake in the Venezuelan. Acta Herpetologica 4: 171–175.

Fitzinger L (1843) Systema Reptilium. Fasciculus primus, Amblyglossae, Braumüller et Seidel, Vindobonae. https://doi.org/10.5962/bhl.title.4694

Gouy M, Guindon S, Gascuel O (2010) SeaView version 4. A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27: 221–224. https://doi.org/10.1093/molbev/msp259
Grazziotin FG, Zaher H, Murphy RW, Scrocchi G, Benavides MA, Zhang YP, Bonatto SL (2012) Molecular phylogeny of the new world Dipsadidae (Serpentes: Colubroidea): a reappraisal. Cladistics 28: 437–459. https://doi.org/10.1111/j.1096-0031.2012.00393.x

Hardy JD (1982) Biogeography of Tobago, West Indies, with special reference to amphibians and reptiles, a review. Bulletin of the Maryland Herpetological Society 18: 37–142.

Hedges SB, Duellman WE, Heinicke MP (2008) New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. Zootaxa (1737): 1–182. http://www.mapress.com/j/zt/article/view/4661

Helmer EH, Ruzycki TS, Benner J, Voggesser SM, Scobie BP, Park C, Fanning DW, Ramnarine S (2012) Detailed maps of tropical forest types are within reach: Forest tree communities for Trinidad and Tobago mapped with multisseason Landsat and multisseason fine-resolution imagery. Forest Ecology and Management 279: 147–166. https://doi.org/10.1016/j.foreco.2012.05.016

Hodson EE, Lehtinen RM (2017) Diverse Evidence for the Decline of an Adaptation in a Coral Snake Mimic. Evolutionary Biology 44: 401–10. https://doi.org/10.1007/s11692-017-9418-7

Huelsenbeck JP, Ronquist F (2001) MrBayes: Bayesian inference of phylogeny. Bioinformatics 17: 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Jan G (1863) Enumerazione sistematica degli ofidi apparteniental gruppo Coronellidae. Archivio per la Zoologia, l’Anatomia, e la Fisiologia 2: 213–330.

Jowers MJ, Caut S, Garcia-Mudarra JL, Alaasad S, Ineich I (2013) Molecular phylogenetics of the possibly extinct Martinique ground snake. Herpetologica 69: 227–236. https://doi.org/10.1655/HERPETOLOGICA-D-12-00085

Jowers MJ, Lehtinen RM, Downie RJ, Georgiadis AP, Murphy JC (2015) Molecular phylogenetics of the glass frog Hyalinobatrachium orientale (Anura: Centrolenidae): evidence for Pliocene connections between mainland Venezuela and the island of Tobago. Mitochondrial DNA (2014): 1–6. https://doi.org/10.3109/19401736.2014.880888

Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059–66. https://doi.org/10.1093/nar/gkf436

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences 86: 6196–200. https://doi.org/10.1073/pnas.86.16.6196

Kumar S, Stecher G, Tamura K (2016) Molecular evolutionary genetics analysis version 7.0. for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lanfear R, Calcott B, Simon YW, Guindon S (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Phylogenetics and Evolution 28: 1695–1701. https://doi.org/10.1093/molbev/msq020

Lehtinen RM, Wojtowicz EA, Hailey A (2011) Male vocalizations, female discrimination, and molecular phylogeny: multiple perspectives on the taxonomic status of a critically endangered Caribbean frog. Journal of Zoology 283: 117–125. https://doi.org/10.1111/j.1469-7998.2010.00752.x
Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, reformata. Laurentii Salvii, Holmiæ (10th edn). https://doi.org/10.5962/bhl.title.542

Manzanilla J, La Marca E, García-París M (2009) Phylogenetic patterns of diversification in a clade of Neotropical frogs (Anura: Aromobatidae: Mannophryne). Biological Journal of the Linnean Society 97: 185–199. https://doi.org/10.1111/j.1095-8312.2009.01074.x

Michaud EJ, Dixon JR (1989) Prey items of 20 species of the neotropical colubrid snake genus Liophis. Herpetological Review 20: 39–41.

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, 1–8. https://doi.org/10.1145/2016741.2016785

Murphy JC (1997) Amphibians and reptiles of Trinidad and Tobago. Krieger Publishing, Malabar, Florida, 245 pp. https://doi.org/10.2307/1447462

Murphy JC, Downie JR, Smith JM, Mohammed RS, Lehtinen RM, Eyre M, Sewlal J, Noriega N, Caspar GS, Anton T, Rutherford MG, Braswell AL, Jowers MJ (2018) A field guide to the amphibians and reptiles of Trinidad and Tobago. Trinidad and Tobago Field Naturalists’ Club, Port of Spain, 336 pp.

Myers CW (2011) A new genus and new tribe for Enicognathus melanachaen Jan, 1863, a neglected South American snake (Colubridae: Xenodontinae), with taxonomic notes on some Dipsadinae. American Museum Novitates 715: 1–33. http://hdl.handle.net/2246/6115

Palumbi S (1996) Nucleic acids II: The polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (Eds) Molecular Systematics. Sinauer, Sunderland, MA, 205–248.

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6. http://beast.bio.edu.ac.uk/Tracer

Rivas GA, Molina CR, Ugueto GN, Barros TR, Barrio-Amorós CL, Kok PJP (2012) Reptiles of Venezuela: an updated and commented checklist. Zootaxa 3211: 1–64.

Roze JA (1958a) Resultados zoologicos de la expedicion de la Universidad Central de Venezuela a la region del Auyante’pui en la Guyana Venezolana, Abril de 1956. 5. Los reptiles del Auyantepui, Venezuela, basandose en las colecciones de las expediciones de Phelps-Ta Acta Biologica Venezuelica 2: 243–270.

Roze JA (1958b) Los reptiles del Chimantá Tepui (Estado Bolívar, Venezuela) colectados por la expedición botánica del Chicago Natural History Museum. Acta Biologica Venezolana 2:299–314.

Roze JA (1959) Taxonomic notes on a collection of Venezuelan reptiles in the American Museum of Natural History. American Museum Novitates (1934): 1–14. http://hdl.handle.net/2246/4351

Roze JA (1964) The snakes of the Leimadophis-Urotheca-Liophis complex from Parque Nacional Henri Pittier (Rancho Grande), Venezuela, with a description of a new genus and species (Reptilia, Colubridae). Senckenbergiana Biologica 45: 533–542.

Roze JA (1966) La Taxonomia y Zoogeographia de los Oftdios de Venezuela. Ediciones de la Biblioteca 28, Caracas, 357 pp.
Saint KM, Austin CC, Donnellan SC, Hutchinson MN (1998) C-mos, a nuclear marker useful for squamate phylogenetic analysis. Molecular Phylogenetics and Evolution 10: 259–263. https://doi.org/10.1006/mpev.1998.0515

Savage JM (2002) The Amphibians and Reptiles of Costa Rica, a herpetofauna between two continents between two seas. The University of Chicago Press, Chicago, 943 pp.

Shaw G (1802) General zoology or systematic natural history. 3, Pt 1. Thomas Davison, London. https://doi.org/10.5962/bhl.title.1593

Silva, JL, Valdez J (1989) Ritmo diario de actividad y periodo de ecolosión de algunos ofidios del Norte de Venezuela. Acta Biológica Venezolica 12: 88–97. https://biblat.unam.mx/fr/revista/acta-biologica-venezuelica/15

Silva, JL, Valdez J, Ojasti O (1985) Algunos aspectos de una comunidad de ofidios del Norte de Venezuela. Biotropica 17: 112–125. https://doi.org/10.2307/2388503

Silvestro D, Michalak I (2010) A user-friendly graphical front-end for phylogenetic analyses using RAxML (Stamatakis, 2006). Organisms Diversity and Evolution 12: 335–337. https://doi.org/10.1007/s13127-011-0056-0

Sisson VB, Avé Lallemant HG, Ostos M, Blythe AE, Snee LW, Copeland P, Wright JE, Donelick RA, Guth LR (2005) Overview of radiometric ages in three allochthonous belts of northern Venezuela: Old ones, new ones, and their impact on regional geology, in Avé Lallemant, HG, Sisson VB (Eds) Caribbean–South American plate interactions, Venezuela: Geological Society of America Special Paper 394: 91–117. https://doi.org/10.1130/0-8137-2394-9.91

Uetz P, Freed P, Hošek J [Eds] (2018) The Reptile Database. http://www.reptile-database.org [accessed June 5, 2018]

Vidal N, Dewynter M, Gower DJ (2010) Dissecting the major American snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). Comptes Rendus Biologies 333: 48–55. https://doi.org/10.1016/j.crvi.2009.11.003

Wallach V, Williams KL, Boundy J (2014) Snakes of the World: A catalogue of living and extinct species. CRC Press, Boca Ratan, 1209 pp. https://doi.org/10.1201/b16901

Zaher H, Grazziotin FG, Cadle JE, Murpht RW, Moura-Leite JCD, Bonatto SL (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. Papéis Avulsos de Zoologi 49: 115–153. http://dx.doi.org/10.1590/S0031-10492009001100001
Appendix 1

Locality data for specimens examined in this study. Coordinates represent georeferencing from Google Earth, variation from the exact collecting locality is expected.

| Species     | Voucher | Country  | Coordinates       |
|-------------|---------|----------|-------------------|
| *epinephalus* |         |          |                   |
|            | MBLUZ 1500 | Venezuela | 10°19’N; 72°35’W  |
|            | MBLUZ 1501 | Venezuela | 10°19’N; 72°35’W  |
|            | MBLUZ 1502 | Venezuela | 10°19’N; 72°35’W  |
|            | MBLUZ 1503 | Venezuela | 10°19’N; 72°35’W  |
|            | MCNC 5677 | Venezuela | 07°39’N; 72°21’W  |
|            | MCNC 7875 | Venezuela | 07°29’N; 72°27’W  |
| *melanotus*  |         |          |                   |
|            | FMNH 61669 | Colombia  | 07°09’N; 75°21’W  |
|            | FMNH 61670 | Colombia  | no specific locality |
|            | FMNH 121224 | Colombia | 04°09’N; 73°38’W  |
|            | FMNH 165341 | Colombia | 10°26’N; 75°22’W  |
|            | FMNH 165399-408 | Colombia | 10°26’N; 75°22’W  |
|            | FMNH 165498 | Colombia | 10°26’N; 75°22’W  |
|            | FMNH 165644 | Colombia | 10°26’N; 75°22’W  |
|            | FMNH 165645 | Colombia | 10°26’N; 75°22’W  |
|            | FMNH 217232 | Trinidad | 10°43’N; 61°17’W  |
|            | FMNH 218779 | Trinidad | 10°43’N; 61°17’W  |
|            | FMNH 49947-50 | Trinidad | 10°29’N; 61°28’W  |
|            | FMNH 49945-46 | Trinidad | 10°16’N; 61°1’W   |
|            | FMNH 5674 | Trinidad  | 10°39’N; 61°30’W  |
|            | FMNH 77902-03 | Trinidad | 10°39’N; 61°30’W  |
|            | FMNH 190749 | Trinidad | 10°09’N; 61°30’W  |
|            | FMNH 49938-44 | Trinidad | 10°34’N; 61°15’W  |
|            | FMNH 69778 | Venezuela | 10°28’N; 67°07’W  |
| *reginae*   |         |          |                   |
|            | AMNH 3595 | “Guiana”  | no specific locality |
|            | USNM 164210 | Guyana   | 8°12’N; 59°46’W   |
|            | USNM 164208 | Guyana   | 8°12’N; 59°46’W   |
|            | FMNH 30959 | Guyana    | 10°29’N; 61°28’W  |
|            | FMNH 30962 | Guyana    | no specific locality |
|            | UMMZ 53901 | Guyana    | no specific locality |
|            | UMMZ53912 | Guyana    | no specific locality |
|            | UMMZ 53968 | Guyana    | no specific locality |
|            | UMMZ 53969 | Guyana    | no specific locality |
|            | AMNH 17680 | Guyana    | 6°47’N; 58°09’W   |
|            | FMNH 56149 | Peru      | 4°36’S; 74°10’W   |
|            | FMNH 40234 | Peru      | 11°48’S; 70°48’W  |
|            | AMNH 8132  | Suriname  | 5°51’N; 55°12’W   |
|            | AMNH 4436  | Venezuela | no specific locality |
|            | USNM 539191 | Tobago   | 11°17’N; 60°35’W  |
| *pseudoreginae* |         |          |                   |
|            | UWIZM.2016.22.45 | Tobago | 11°17’N; 60°36’W  |
|            | UWIZM 91621 | Tobago    | 11°16’N; 60°37’W  |
|            | USNM 325089 | Tobago    | 11°17’N; 60°36’W  |
|            | USNM 228069 | Tobago    | 11°17’N; 60°36’W  |
A new species of Erythrolamprus from the oceanic island of Tobago...

| Species            | Voucher      | Country   | Coordinates         |
|--------------------|--------------|-----------|---------------------|
| Erythrolamprus sp. | USNM 549328  | Guyana    | 05°17’N; 60°45’W    |
| zweifeli           | FMNH 215827  | Trinidad  | 10°43’N; 61°17’W    |
| FMNH 217226-27     | FMNH 219615  | Trinidad  | 10°43’N; 61°17’W    |
| USNM 17757-58      | FMNH 49957-58| Trinidad  | 10°28’N; 61°28’W    |
|                    | UWIMZ 2010.12.110 | Trinidad | 10°43’N; 61°25’W |
|                    | UWIMZ 2010.12.201 | Trinidad | 10°45’N; 61°26’W |
|                    | UWIMZ 2010.12.108a, b | Trinidad | 10°16’N; 61°1’W |
|                    | UWIMZ 2010.12.107 | Trinidad | no specific locality |
|                    | UWIMZ 2010.12.109 | Trinidad | no specific locality |
|                    | USNM 252682-83 | Trinidad | 10°45’N; 61°17’W |
|                    | USNM 286922  | Trinidad  | 10°30’N; 61°16’W    |
|                    | AMNH 137503  | Venezuela  | 10°01’N; 67°17’W |
|                    | AMNH 98260   | Venezuela  | 10°06’N; 63°06’W    |
|                    | USNM 217197  | Venezuela  | 02°37’N; 66°19’W    |
|                    | FMNH 120986  | Venezuela  | 10°01’N; 67°17’W    |
|                    | FMNH 204477  | Venezuela  | 10°01’N; 67°17’W    |
|                    | UMMZ 124225  | Venezuela  | 10°01’N; 67°17’W    |
|                    | UMMZ 124227-33 | Venezuela | 10°01’N; 67°17’W |
|                    | UMMZ 128390  | Venezuela  | 10°01’N; 67°17’W    |
|                    | USNM 217198  | Venezuela  | 10°15’N; 68°21’W    |
|                    | USNM 196332  | Venezuela  | 10°13’N; 66°25’W    |
|                    | AMNH 67877   | Venezuela  | 10°06’N; 63°06’W    |
|                    | AMNH 29317   | Venezuela  | 10°09’N; 64°17’W    |
|                    | AMNH 29332   | Venezuela  | 10°29’N; 66°07’W    |
|                    | AMNH 29317   | Venezuela  | 10°22’N; 63°17’W    |
|                    | FMNH 17833-36 | Venezuela | 10°22’N; 63°17’W |
|                    | AMNH 29332   | Venezuela  | 10°09’N; 64°17’W    |
Appendix 2

Morphometric data and sex for specimens of *Erythrolamprus* species examined. Key: m = male, f = female; j = juvenile; SVL = snout vent length mm; tail mm; D1–3 dorsal scale rows at anterior, midbody, and posterior body); V = ventral scales; S = subcaudal scales; nd = no data.

| Museum    | Voucher | Species     | Sex | svl | tail | D1 | D2 | D3 | V | S |
|-----------|---------|-------------|-----|-----|------|----|----|----|---|---|
| MBLUZ     | 1500    | epinephalus | ?   | 335 | 88 d | 17 | 17 | 15 | 153 | 51+|
| MBLUZ     | 1501    | epinephalus | ?   | 330 | 112  | 17 | 17 | 15 | 155 | 75 |
| MBLUZ     | 1502    | epinephalus | ?   | 280 | 95   | 17 | 17 | 15 | 153 | 69 |
| MBLUZ     | 1503    | epinephalus | f   | 340 | 19   | 17 | 17 | 15 | 157 | 67 |
| MCNC      | 5677    | epinephalus | m   | 355 | 112  | 17 | 17 | 15 | 144 | 65 |
| MCNC      | 7875    | epinephalus | m   | 345 | 120  | 17 | 17 | 15 | 146 | 65 |
| FMNH      | 165402  | melanotus   | f   | 332 | 90   | 17 | 17 | 15 | 142 | 54 |
| FMNH      | 49946   | melanotus   | f   | 291 | 61   | 17 | 17 | 15 | 144 | 57 |
| FMNH      | 49947   | melanotus   | f   | 230 | 52   | 17 | 17 | 15 | 139 | 53 |
| FMNH      | 49950   | melanotus   | f   | 307 | 77   | 17 | 17 | 15 | nd  | nd |
| FMNH      | 190749  | melanotus   | f   | 305 | 72   | 17 | 17 | 15 | 142 | 54 |
| FMNH      | 165644  | melanotus   | m   | 358 | 92   | 17 | 17 | 15 | 149 | 55 |
| FMNH      | 165498  | melanotus   | m   | 325 | 97   | 17 | 17 | 15 | 144 | 54 |
| FMNH      | 165407  | melanotus   | m   | 350 | 85   | 17 | 17 | 15 | 147 | 55 |
| FMNH      | 49949   | melanotus   | m   | 271 | 76   | 17 | 17 | 15 | 147 | 56 |
| FMNH      | 77903   | melanotus   | m   | 275 | 76   | 17 | 17 | 15 | 152 | 58 |
| FMNH      | 69778   | melanotus   | m   | 370 | 72+  | 17 | 17 | 15 | 154 | nd |
| FMNH      | 121224  | melanotus   | m   | 282 | 81   | 17 | 17 | 15 | 149 | 57 |
| FMNH      | 61670   | melanotus   | nd  | 310 | 81   | 17 | 17 | 15 | 151 | 55 |
| AMNH      | 4436    | reginae     | f   | 355 | 128  | 17 | 17 | 15 | 144 | 74 |
| UMMZ      | 53912   | reginae     | f   | 420 | 117  | 17 | 17 | 15 | 133 | 79 |
| UMMZ      | 53969   | reginae     | f   | 415 | nd   | 17 | 17 | 15 | 136 | nd |
| USNM      | 164210  | reginae     | f   | 428 | nd   | 17 | 17 | 15 | 139 | nd |
| AMNH      | 3595    | reginae     | f   | 443 | nd   | 17 | 17 | 15 | 136 | nd |
| FMNH      | 40234   | reginae     | j   | 128 | 44   | 17 | 17 | 15 | 147 | 74 |
| AMNH      | 17680   | reginae     | m   | 313 | 120  | 17 | 17 | 15 | 137 | 73 |
| AMNH      | 8132    | reginae     | m   | 445 | nd   | 17 | 17 | 15 | 142 | nd |
| FMNH      | 30959   | reginae     | m   | 443 | d    | 17 | 17 | 15 | 139 | nd |
| FMNH      | 56149   | reginae     | m   | 419 | 117  | 17 | 17 | 15 | 145 | 55 |
| UMMZ      | 53901   | reginae     | m   | 428 | 186  | 17 | 17 | 15 | 139 | 78 |
| UMMZ      | 53968   | reginae     | m   | 474 | 210  | 17 | 17 | 15 | 135 | 75 |
| USNM      | 164208  | reginae     | m   | 308 | nd   | 17 | 17 | 15 | 136 | nd |
| FMNH      | 30962   | reginae     | nd  | nd  | nd   | 17 | 17 | 15 | 129 | 68 |
| USNM      | 539191  | pseudoreginae | f | 408 | nd  | 17 | 17 | 15 | 148 | nd |
| USNM      | 228069  | pseudoreginae | f | 347 | 129  | 17 | 17 | 15 | 143 | 76 |
| USNM      | 539191  | pseudoreginae | f | 408 | nd  | 17 | 17 | 15 | 148 | nd |
| FLMNH     | 91621   | pseudoreginae | m | 420 | 119  | 17 | 17 | 15 | 146 | nd |
| FLMNH     | 91621   | pseudoreginae | m | 420 | 119  | 17 | 17 | 15 | 146 | nd |
| USNM      | 325089  | pseudoreginae | m | 408 | 158  | 17 | 17 | 15 | 154 | 79 |
| USNM      | 549328  | *Erythrolamprus* sp. | m | 361 | 117  | 17 | 17 | 15 | 148 | 64 |
| AMNH      | 137503  | zweifeli    | f   | 456 | 167  | 17 | 17 | 15 | 146 | 83 |
| FMNH      | 17836   | zweifeli    | f   | 380 | 165  | 17 | 17 | 15 | 138 | 82 |
| FMNH      | 204477  | zweifeli    | f   | 454 | 180  | 17 | 17 | 15 | 142 | 85 |
| UMMZ      | 128390  | zweifeli    | f   | nd  | nd   | 17 | 17 | 15 | 141 | nd |
| UMMZ      | 124232  | zweifeli    | f   | 375 | 144  | 17 | 17 | 15 | 144 | nd |
| UMMZ      | 1288390 | zweifeli    | f   | 402 | 162  | 17 | 17 | 15 | 141 | 84 |
### Table: Museum Vouchers of Erythrolamprus zweifeli from Tobago

| Museum | Voucher | Species | Sex | svl | tail | D1 | D2 | D3 | V | S |
|--------|---------|---------|-----|-----|------|----|----|----|----|--|
| USNM   | 17757   | zweifeli| f   | 471 | 187  | 17 | 17 | 15 | 143| 76|
| USNM   | 252683  | zweifeli| f   | 236 | nd   | 17 | 17 | 15 | 140| nd|
| USNM   | 217197  | zweifeli| f   | 434 | 167  | 17 | 17 | 15 | 134| 72|
| USNM   | 252683  | zweifeli| f   | 236 | nd   | 17 | 17 | 15 | 140| nd|
| UWIZM  | 2010.12.109| zweifeli| f  | 245 | nd   | 17 | 17 | 15 | nd | nd|
| UWIZM  | 2010.12.107| zweifeli| f  | 355 | 152  | 17 | 17 | 15 | 139| 79|
| UWIZM  | 2010.12.201| zweifeli| f  | 401 | 158  | 17 | 17 | 15 | 143| 79|
| UWIZM  | 2010.12.109| zweifeli| f  | 245 | nd   | 17 | 17 | 15 | nd | nd|
| FMNH   | 17833   | zweifeli| j   | 172 | 63   | 17 | 16 | 15 | 140| 80|
| FMNH   | 17835   | zweifeli| j   | 152 | 56   | 17 | 17 | 15 | 144| 85|
| UMMZ   | 124229  | zweifeli| j   | 305 | 117  | 17 | 17 | 15 | 139| 83|
| UMMZ   | 124230  | zweifeli| j   | 184 | 67   | 17 | 17 | 15 | 141| 80|
| UMMZ   | 124227  | zweifeli| j   | nd  | nd   | 17 | 17 | 15 | 142| 84|
| UMMZ   | 124231  | zweifeli| j   | 185 | 62   | 17 | 17 | 15 | 145| nd|
| UWIZM  | 2010.12.108b | zweifeli| j | 136 | 45   | 17 | 15 | 15 | 134| 75|
| AMNH   | 29317   | zweifeli| m   | 365 | 152  | 17 | 17 | 15 | 145| 79|
| AMNH   | 29332   | zweifeli| m   | 297 | 114  | 17 | 17 | 15 | 151| 76|
| AMNH   | R-29317 | zweifeli| m   | 369 | 148  | 17 | 17 | 15 | 143| 82|
| AMNH   | 29332   | zweifeli| m   | 322 | 115  | 17 | 17 | 15 | 142| 74|
| AMNH   | 67877   | zweifeli| m   | 361 | 148  | 17 | 17 | 15 | 149| 82|
| FMNH   | 17834   | zweifeli| m   | 384 | 101+ | 17 | 15 | 15 | 141| nd|
| FMNH   | 217226  | zweifeli| m   | 340 | 139  | 17 | 17 | 15 | 138| 77|
| FMNH   | 219615  | zweifeli| m   | 365 | 152  | 17 | 17 | 15 | 145| 79|
| FMNH   | 49957   | zweifeli| m   | 398 | 174  | 17 | 15 | 15 | 145| 79|
| FMNH   | 49958   | zweifeli| m   | 456 | nd   | 17 | 17 | 15 | 145| nd|
| FMNH   | 215827  | zweifeli| m   | 354 | 155  | 17 | 16 | 15 | 140| 78|
| FMNH   | 217227  | zweifeli| m   | 367 | 157  | 17 | 15 | 15 | 141| nd|
| FMNH   | 120986  | zweifeli| m   | 386 | 143  | 17 | 17 | 15 | 142| 83|
| FMNH   | 215827  | zweifeli| m   | 354 | 155  | 17 | 16 | 15 | 140| 78|
| FMNH   | 217227  | zweifeli| m   | 367 | 157  | 17 | 15 | 15 | 141| nd|
| UMMZ   | 124233  | zweifeli| m   | 394 | 163  | 17 | 17 | 15 | 142| 83|
| UMMZ   | 124225  | zweifeli| m   | 363 | 149  | 17 | 17 | 15 | 144| 80|
| UMMZ   | 124228  | zweifeli| m   | 415 | 135+ | 17 | 17 | 15 | 143| nd|
| USNM   | 17758   | zweifeli| m   | 349 | nd   | 17 | 17 | 15 | 142| nd|
| USNM   | 252682  | zweifeli| m   | 370 | 160  | 17 | 17 | 15 | 141| 83|
| USNM   | 286922  | zweifeli| m   | 165 | 55   | 17 | 17 | 15 | 149| 80|
| USNM   | 196332  | zweifeli| m   | 430 | 170  | 17 | 17 | 15 | 145| 78|
| USNM   | 217198  | zweifeli| m   | 509 | 203  | 17 | 17 | 15 | 140| 75|
| USNM   | 252682  | zweifeli| m   | 370 | 160  | 17 | 17 | 15 | 141| 83|
| USNM   | 286922  | zweifeli| m   | 165 | 55   | 17 | 17 | 15 | 149| 80|
| AMNH   | 98260   | zweifeli| nd  | 492 | nd   | 17 | 16 | 15 | 144| nd|
| UWIZM  | 2010.12.108a | zweifeli| nd | 360 | nd   | 17 | 17 | 15 | 146| nd|
| UWIZM  | 2010.12.110| zweifeli| nd | 373 | 157  | 17 | 15 | 15 | 138| 80|
### Appendix 3

(A) compares the single factor ANOVA results for ventral counts and (B) compares the single factor ANOVA results for subcaudal counts. Statistically significant results that resulted in the rejection of the null hypothesis are in bold.

|       | ventrals |                  |                  |
|-------|----------|------------------|------------------|
|       | zweifeli | pseudoreginae    |                  |
| p     |          | p = 0.003        |                  |
| df    |          | df = 53          |                  |
|       | zweifeli |                  | p = 0.00         |
|       |          | df = 59          |                  |
|       | reginae |                  | df = 15          |

|       | subcaudals |                  |                  |
|-------|------------|------------------|------------------|
|       | zweifeli   | pseudoreginae    |                  |
| p     |          | p = 0.350        |                  |
| df    |          | df = 7           |                  |
|       | zweifeli   |                  | p = 0.004        |
|       |          | df = 38          | df = 36          |
|       | reginae   |                  |                  |
A new species of *Erythrolamprus* from the oceanic island of Tobago...

### Appendix 4

Material used for molecular analysis and GenBank numbers. Key: * sequenced in this study.

| Species                        | Museum voucher | Locality         | 12S    | 16S    | c-mos    |
|-------------------------------|----------------|------------------|--------|--------|----------|
| *Erythrolamprus aesculapii*    | ROM 47474      | Guyana           | -      | KY986512 | KY986488 |
|                               | IBSP 74046     | Brazil           | GQ457795 | GQ457736 | GQ457856 |
|                               | MNHN 1996.7896 | French Guiana    | AF158462 | AF158531 | GQ895814 |
| *Erythrolamprus almadensis*   | LSUMZ H-6558   | Unknown          | -      | KY986517 | KY986497 |
|                               | MCP < BRA > 6528 | Tobago     | JQ598809 | JQ598871 | JQ598979 |
| *Erythrolamprus atraverter*   | IBSP 74342     | Tobago           | JQ598810 | JQ598872 | JQ598980 |
| *Erythrolamprus bizona*       | LSUMZ H-6360   | Costa Rica       | -      | KY986513 | KY986493 |
| *Erythrolamprus breviceps*    | MNHN 1996.7879 | French Guiana    | AF158464 | AF158533 | –        |
| *Erythrolamprus ceii*         | FML 14973      | Tobago           | JQ598810 | JQ598873 | JQ598981 |
| *Erythrolamprus cobella*      | ROM 28372      | Guyana           | KY986514 | KY986489 | –        |
| *Erythrolamprus cursor*       | MNHN 1887.0120 | Martinique       | JX905307 | JX905311 | –        |
| *Erythrolamprus epinephalus*  | LSUMZ H-1547   | Peru             | KY986515 | KY986487 | –        |
|                               | None            | Costa Rica       | GU018158 | GU018176 | –        |
| *Erythrolamprus jaegeri*      | IBSP 59252     | Dominica         | GQ457809 | GQ457749 | GQ457869 |
| *Erythrolamprus juliae*       | SBH 194227     | Tobago           | AF158445 | AF158514 | –        |
| *Erythrolamprus melanotus*    | RML 0266       | Tobago           | KY986510 | KY986492 | –        |
| *Erythrolamprus miliaris*     | ROM 22837      | Guyana           | KY986511 | KY986494 | –        |
|                               | MZUSP 14137    | Tobago           | JQ598811 | JQ598974 | JQ598982 |
|                               | None            | French Guiana    | AF158409 | AF158480 | –        |
| *Erythrolamprus mimus*        | LSUMZ H-6398   | Honduras          | KY986508 | KY986496 | –        |
|                               | ICP 1105       | Costa Rica       | GU018157 | GU018175 | –        |
| *Erythrolamprus ocellatus*    | CAS 245326     | Tobago           | KY986518 | KY986490 | –        |
| *Erythrolamprus poecilogyrus* | LSUMZ H-6972   | Argentina        | KY986516 | KY986491 | –        |
| *Erythrolamrus reginae*       | IBSP 72733     | Tobago           | JQ598813 | JQ598876 | JQ598983 |
|                               | MNHN 1996.7846 | French Guiana    | AF158433 | AF158501 | –        |
| *Erythrolamrus typhlus*       | LSUMZ H-17725  | Brazil           | KY986509 | KY986495 | –        |
|                               | IBSP 70643     | Tobago           | GQ457811 | GQ457751 | GQ457871 |
|                               | None            | French Guiana    | AF158410 | AF158481 | –        |
| *Xenodon histricus*           | MZUSP 13265    |                  | GU018157 | GU018175 | –        |
| *Erythrolamrus pseudoreginae* | UWIZM.2016.22.45 | Tobago     | MK287470 | MK287477 | MK287484 |
|                               | UWIZM.2011.19.14 | Tobago     | MK287471 | MK287481 | –        |
|                               | UWIZM.2011.25  | Trinidad         | MK287472 | MK287478 | MK287485 |
|                               | UWIZM.2016.22.51 | Tobago     | MK287473 | MK287479 | MK287486 |
|                               | UWIZM.2012.27.26 | Tobago     | MK287474 | MK287480 | MK287487 |
| *Erythrolamrus zweifeli*      | CAS245114      | Trinidad         | MK287475 | MK287482 | MK287488 |
|                               | UWIZM.2014.14  | Trinidad         | MK287476 | MK287483 | MK287489 |
### Appendix 5

Table of p-uncorrected distances computed in MEGA7 (under a complete deletion option) of all species shown in Figure 2. The order of specimens from top to bottom follows Figure 2. *Erythrolamprus pseudorreginae* is marked in bold type and the genetic distance of its closest species (*E. epinephelus*) as recovered from the phylogenetic tree is shown in bold type and marker with a square.

|    | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    |
|----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1  | Xenodon hiensis | -     | E. poecilogyrus (Argentina) | 0.053 | -     |       |       |       |       |       |       |       |       |       |       |       |
| 2  | E. epinephelus | 0.059 | E. poecilogyrus (FML 15916) | 0.059 | 0.006 | -     |       |       |       |       |       |       |       |       |       |       |
| 3  | E. epinephelus | 0.059 | E. miliaris (French Guiana) | 0.059 | 0.021 | 0.026 | 0.026 | -     |       |       |       |       |       |       |       |       |
| 4  | E. miliaris (MZUP 14137) | 0.056 | E. miliaris (Guiana) | 0.056 | 0.023 | 0.029 | 0.029 | 0.032 | 0.000 | -     |       |       |       |       |       |       |
| 5  | E. epinephelus (Brazil) | 0.044 | E. reginae (IBSP 72733) | 0.053 | 0.026 | 0.032 | 0.032 | 0.023 | 0.023 | 0.023 | 0.018 | -     |       |       |       |       |
| 6  | E. reginae (French Guiana) | 0.055 | E. zweifeli (CAS245114 Trinidad) | 0.053 | 0.032 | 0.038 | 0.038 | 0.035 | 0.041 | 0.041 | 0.029 | 0.032 | 0.026 | -     |       |       |
| 7  | E. zweifeli (2014.14 Trinidad) | 0.053 | E. epinephelus (Brazil) | 0.055 | 0.023 | 0.032 | 0.029 | 0.026 | 0.035 | 0.035 | 0.032 | 0.032 | 0.038 | 0.041 | 0.041 | 0.021 | 0.015 | 0.047 |
| 8  | E. epinephelus (Peru) | 0.053 | E. epinephelus (Costa Rica) | 0.085 | 0.053 | 0.059 | 0.059 | 0.059 | 0.062 | 0.062 | 0.053 | 0.059 | 0.070 | 0.070 | 0.070 | 0.050 | 0.047 | -     |
| 9  | E. epinephelus | 0.067 | E. pseudorreginae (IBSP 59252) | 0.067 | 0.029 | 0.029 | 0.029 | 0.026 | 0.035 | 0.035 | 0.032 | 0.032 | 0.038 | 0.041 | 0.041 | 0.021 | 0.015 | 0.047 |
| 10 | E. melanotus (IBSP 53432) | 0.056 | E. melanotus (2012.27.26 Tobago) | 0.056 | 0.023 | 0.023 | 0.032 | 0.032 | 0.029 | 0.029 | 0.032 | 0.029 | 0.041 | 0.038 | 0.038 | 0.021 | 0.021 | 0.047 | 0.029 |
| 11 | E. melanotus | 0.056 | E. reginae (IBSP 14137) | 0.056 | 0.023 | 0.023 | 0.032 | 0.029 | 0.029 | 0.032 | 0.029 | 0.041 | 0.038 | 0.038 | 0.038 | 0.021 | 0.021 | 0.047 | 0.029 |
| 12 | E. reginae | 0.056 | E. reginae (IBSP 2014.14 Trinidad) | 0.056 | 0.023 | 0.023 | 0.032 | 0.029 | 0.029 | 0.032 | 0.029 | 0.041 | 0.038 | 0.038 | 0.038 | 0.021 | 0.021 | 0.047 | 0.029 |
| 13 | E. reginae (Brazil) | 0.056 | E. reginae (Brazil) | 0.056 | 0.023 | 0.023 | 0.032 | 0.029 | 0.029 | 0.032 | 0.029 | 0.041 | 0.038 | 0.038 | 0.038 | 0.021 | 0.021 | 0.047 | 0.029 |
| 14 | E. reginae | 0.056 | E. reginae (IBSP 2014.14 Trinidad) | 0.065 | 0.021 | 0.026 | 0.026 | 0.032 | 0.035 | 0.035 | 0.044 | 0.038 | 0.041 | 0.038 | 0.038 | 0.021 | 0.026 | 0.070 | 0.041 |
| 15 | E. reginae | 0.076 | E. reginae | 0.079 | 0.044 | 0.044 | 0.044 | 0.047 | 0.047 | 0.056 | 0.053 | 0.059 | 0.053 | 0.053 | 0.041 | 0.041 | 0.056 | 0.044 |
| 16 | E. reginae (Costa Rica) | 0.076 | E. reginae (Brazil) | 0.066 | 0.021 | 0.026 | 0.026 | 0.026 | 0.026 | 0.026 | 0.029 | 0.029 | 0.035 | 0.041 | 0.041 | 0.018 | 0.012 | 0.047 | 0.021 |
| 17 | E. reginae (Brazil) | 0.059 | E. reginae (Brazil) | 0.059 | 0.016 | 0.021 | 0.021 | 0.023 | 0.032 | 0.032 | 0.029 | 0.029 | 0.035 | 0.035 | 0.035 | 0.012 | 0.012 | 0.050 | 0.026 |
| 18 | E. reginae (Brazil) | 0.062 | E. reginae (Brazil) | 0.062 | 0.032 | 0.038 | 0.038 | 0.041 | 0.044 | 0.044 | 0.041 | 0.047 | 0.041 | 0.041 | 0.041 | 0.029 | 0.029 | 0.065 | 0.032 |
| 19 | E. reginae (Brazil) | 0.065 | E. reginae (Brazil) | 0.065 | 0.032 | 0.035 | 0.035 | 0.041 | 0.038 | 0.038 | 0.041 | 0.047 | 0.053 | 0.029 | 0.029 | 0.073 | 0.038 |
| 20 | E. reginae (Brazil) | 0.062 | E. reginae (Brazil) | 0.059 | 0.018 | 0.023 | 0.023 | 0.032 | 0.035 | 0.035 | 0.032 | 0.032 | 0.038 | 0.038 | 0.038 | 0.015 | 0.021 | 0.065 | 0.035 |
| 21 | E. reginae (Brazil) | 0.059 | E. reginae (Brazil) | 0.059 | 0.018 | 0.023 | 0.023 | 0.032 | 0.035 | 0.035 | 0.032 | 0.032 | 0.038 | 0.038 | 0.038 | 0.015 | 0.021 | 0.065 | 0.035 |

From the phylogenetic tree is shown in bold type and marker with a square.
A new species of *Erythrolamprus* from the oceanic island of Tobago...