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A new species of *Erythrolamprus* (Serpentes: Dipsadidae: Xenodontini) from the savannas of northern South America

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Abstract. *Erythrolamprus* Boie, 1826 is a highly diverse dipsadid snake genus, ranging from Central America south to Argentina and Uruguay. In this work, we reassess the taxonomic status of specimens previously identified as *Erythrolamprus poecilogyrus schotti* (Schlegel, 1837) from the savannah habitats of Roraima state, northern Brazil, Guyana, and Bolívar state, Venezuela. Based on novel molecular and morphological evidence, we conclude that these specimens represent a distinct, diagnosable and reciprocally monophyletic taxon. We here describe it as a new species. Furthermore, we comment on the taxonomy of other *Erythrolamprus* spp..

Key words. Brazil, *Erythrolamprus* sp. nov., *E. p. schotti,* molecular phylogeny, morphology, open habitats, Squamata, taxonomy, Venezuela.

Introduction

Xenodontini Bonaparte, 1845 is a diverse dipsadid tribe that contains five genera of small- to medium-sized snakes. They are morphologically diagnosed by having bilobate hemipenes with paired nude apical disks, without calyces or capitular grooves, and by displaying horizontal neck-flattening behaviour (Myers 1986, Zaher et al. 2009, Zaher & Prudente 2020). The genera *Baliodryas* Zaher & Prudente, 2020, *Erythrolamprus* Boie, 1862, *Eutrachelophis* Myers & Cadle, 2014, *Lygophis* Fitzinger, 1843, and *Xenodon* Boie, 1826 are widely distributed, ranging from southern Mexico to Argentina and Uruguay, and occurring in most forested and open biomes of the New World (Uetz & Hosek 2020, Zaher & Prudente 2020).

Of these, *Erythrolamprus* is the most diverse genus, with 51 recognized species and 34 subspecies, ranging from Costa Rica and the Lesser Antilles in Central America south to Argentina and Uruguay in southern South America (Dixon 1989, Zaher et al. 2009, Grazziotin et al. 2012, Uetz & Hosek 2020). The taxonomic history and systematic affinities of this genus are highly unstable, and its species have been historically allocated to various other genera, such as *Aporophis* Cope, 1878, *Coluber* Linnaeus, 1758, *Coronella* Laurenti, 1768, *Dromicus* Cocteau & Bibron, 1843, *Elaps* Wagler, 1830, *Liophis* Wagler, 1830, *Leimadophis* Fitzinger, 1843, *Natrix* Laurenti, 1768, *Trigonocephalus* Oppel, 1811, *Rhadinaea* Cope, 1863, and *Umbrivaga* Roze, 1964 (Spix 1824, Wagler 1824, 1830, Duméril, Bibrón & Duméril 1854, Cope 1885, Boulenger 1896, Peters & Orejas-Miranda 1970, Markezich & Dixon 1979, Dixon 1989, Grazziotin et al. 2012). The systematic affinities and definition of *Erythrolamprus* in its current composition are also controversial. Some authors argue for a split between *Liophis* and *Erythrolamprus* (e.g., Curcio et al. 2009, Vidal et al. 2010, Wallach et al. 2014), while others (e.g., Zaher et al. 2009, Grazziotin et al. 2012) propose recognizing both as synonymous. This discussion transcends the scope of the present work, and we will therefore follow the taxonomy proposed by Zaher et al. (2009) and Grazziotin et al. (2012) here.

Seven *Erythrolamprus* taxa are known to occur in the state of Roraima, northern Brazil: *E. aesculapii* (Linnaeus, 1758), *E. breviceps* (Cope, 1860), *E. oligolepis* (Boulenger, 1905), *E. poecilogyrus schotti* (Schlegel, 1837), *E. reginae* (Linnaeus, 1758), *E. trebbaui* (Roze, 1957), and *E. typhlus* (Linnaeus, 1758) (Ascenso et al. 2018, Costa & Bérnils 2018). Despite its being part of the Amazonian realm, Roraima state is composed of highly heterogeneous landscapes of forest and open habitats and its transitions. These habitats can be separated into six major vegetation types: Ombrophilous Dense Forest, Ombrophilous Open Forest, Seasonal Semideciduous Forest, Campinarana, Savanna, and Steppic Savanna (IBGE 2005).

During recent fieldwork in the savannas of Roraima, we collected specimens of *Erythrolamprus* and preliminarily identified them as *Erythrolamprus poecilogyrus* (Wied-Neuwied, 1824). Further investigations based on additional specimens on the variation of external morphology and molecular data then provided evidence for their representing a new species, which we describe here. We also present an in-depth comparison between the new species and available names formerly assigned to *E. poecilogyrus* and *E. reginae*, both being morphologically similar congeners.

Material and methods

Molecular analyses and phylogeny

For molecular analyses, we generated new sequences for *Erythrolamprus* from the Savannas of northern Brazil and from the Caatinga of northeastern Brazil. We pooled the new sequences with available GenBank data of *Erythrolamprus* taxa. Our final data set comprised 94 samples, representing 31 nominal species of *Erythrolamprus* and 9 outgroups (Supplementary Table 1). To generate new sequences, we extracted total genomic deoxyribonucleic acid from liver or muscle tissues using a standard ethanol precipitation method adapted for microcentrifuges (ammonium acetate protocol, Maniatis et al. 1982). We generated sequences from one mitochondrial gene (16S ribosomal ribonucleic acid [rRNA] gene). Primers and protocols followed Klackzko et al. (2014). We purified the amplification products with enzymatic reactions and had them sequenced at Macrogen Inc. (Seoul, South Korea). Chromatograms were checked for quality and trimmed with Geneious v. 6.0 (Biomatters, Ltd., Auckland, New Zealand). All these sequences will be deposited in GenBank. Sequences were aligned using MAFFT v7.245 (Katoh 2013) with default parameters for gap opening and extension. We used these alignments, of up to 432 base pairs, to conduct phylogenetic inferences within a maximum likelihood framework. The maximum likelihood analysis was computed using RaxML software (Stamatakis 2014) in the CIPRES Science Gateway (available at https://www.phylo.org/), and searching the most likely tree 100 times and producing 1,000 nonparametric bootstrap replicates. The run was performed with the GTR þ C model. In order to evaluate genetic distances between congeners, we employed branch lengths and patristic distances (absolute time and mutation rate) as proxies of genetic distance (Supplementary Table 2), following Montingelli et al. (2020). For patristic distances, paraphyletic terminals were treated separately (see Supplementary Table 3). This was evaluated with the package *Ape* for R (R Core Team 2012, Paradis & Schliep 2019). Output analyses are provided as supplementary files (see Supplementary Files 1, 2).

Morphological analyses

We examined 274 specimens of *Erythrolamprus* spp. from South and Central America. A list of examined specimens is given in Appendix I. Collection acronyms follow Sabaj-Pérez (2016), except for the Coleção Herpetológica Universidade Federal de Rio Grande (CHFURG), Rio Grande, Colecíon de Vertebrados Universidad de Los Andes (CVULA), Mérida, and the Miguel Trefaut Rodrigues Collection, Instituto de Biociências, Universidade de São Paulo (MTR), São Paulo. Measurements were taken to the nearest 0.01 mm with a calliper, except for snout–vent (SVL) and tail lengths (TL), which were taken with a flexible ruler. Scale counts follow Dowling (1951). Sexing was done by means of a ventral incision in the base of the tail through which the sexual organs could be examined. Coordinates of localities are given in SIRGAS2000 Datum. Diagnostic, as well as meristic and morphometric, characters were selected based on the nomenclature used by Entiauspe-Neto et al. (2020), and are as follows: head length, measured from centre of rostral to the corner of mouth; head width, measured at the corner of mouth; snout-vent length, ventrally measured from centre of rostral to the posterior margin of cloacal scute; tail length, measured from posterior margin of cloacal scute to terminal caudal scale.

The description of the skull of the new *Erythrolamprus* is based on 3D radiographs obtained of specimen AMNH 60803, using a high-resolution CT scanner (GE phoenix v|tome|x s240) at the American Museum of Natural History (AMNH), New York, USA. We used an X-ray beam with 140 kV source voltage and 140 mA current. Rotations stepped at 0.124° were used to obtain a near-360° scan, resulting in 2901 projections of 1000 ms exposure time each and a total scan duration of 66 min and 14 s. The magnification setup generated data with an isotropic voxel size of 19.62545 µm. The CT-dataset was reconstructed using Phoenix datos reconstruction software and rendered in three dimensions through the aid of Amira visualization software (FEI, Thermo Fisher Scientific). Segmentation to separate and colorize individual bones was also performed with Amira (FEI, Thermo Fisher Scientific).

Osteological terminology follows Bullock & Tanner (1966) and Cundall & Irish (2008). We compared our osteological description with data available for *Erythrolamprus dorsocorallinus* from Souto et al., (2017), and with CT-scan data of a specimen of *E. poecilogyrus* (UMMZ 153016) from the Museum of Zoology (UMMZ), Ann Arbor, USA downloaded from MorphoSource (https://www.morphosource.org/biological_specimens/000S18803). The latter was also rendered in three dimensions, segmented and colorized using Amira software.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclatur (ICZN), and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is:

LSID:urn:lsid:zoobank.org:pub:CCEFE2FC-32C5-4209-A608-D09A9EBCF2A6.

Results

Genetic divergence and monophyly tests

Our molecular phylogeny, as inferred from maximum likelihood (Fig. 1), recovered the specimens of *Erythrolamprus* sp. from the savannas of Roraima as a monophyletic group, distinct from populations of *E. reginae* and *E. poecilogyrus*. These two groups will be referred to as "*Erythrolamprus poecilogyrus* species complex" and "*Erythrolamprus reginae* species complex", respectively, from here on. We also recovered *E. zweifeli* (Roze, 1959) as paraphyletic to *E. reginae*, and *E. ceii* (Dixon, 1991) as paraphyletic to *E. poecilogyrus*. Due to insufficient sample sizes, as well as being beyond the scope of this study, we refrain from making any taxonomic changes to these two species complexes.

Our molecular analysis revealed two monophyletic lineages of specimens formerly assigned to *E. poecilogyrus*; we conducted morphological analyses in order to evaluate the taxonomic status of both entities, which revealed that populations assigned to these clades are allopatric (Fig. 2), and have significant morphological and genetic differences. The genetic distance between both lineages (estimated by patristic distances) is 0.099. This value is considered significant, as Montingelli et al. (2020) reported mean interspecific patristic distances in Xenodontinae of 0.091. In light of these facts, we propose the recognition of the population from the Savannas of northern South America as a distinct species, described below.

***Erythrolamprus aenigma* sp. nov.**

(Figs. 3–5, 8a, 9–11)

ZooBank LSID: urn:lsid:zoobank.org:act:4994764B-8A96-4652-BD5E-72E714C2D6E4

Savannah Racer Snake (English)
Corredeira de Savana (Portuguese)
Guarda-camino de Sabana (Spanish)

Heterochresonymy:
Erythrolamprus poecilogyrus schotti (part.) – Entiauspe-Neto, Rocha & Loebmann 2016: 61.
Erythrolamprus poecilogyrus (non Wied-Neuwied) – Azarak & Farias 2017: 45.

Holotype (Figs 3–4): Adult female (IBSP 90722), col. M. Duarte, F. L. Franco, R. Feltran and W. Azevedo on 03 March 2019, from Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima state, Brazil.

Paratypes: Adult female (INPA-H 34377), col. P. Azarak in 2012, from Rorainópolis (0°50'30" N, 60°40'48" W, 200 m a.s.l.), Roraima, Brazil; adult female (CHFURG 5068), col. D. Loebmann in 2016, from Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; adult female (IBSP 90743), col. M. Duarte, F. L. Franco and W. Azevedo in 2019, dissected head, from Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; adult female (IBSP 90727, Fig. 5E), col. M. Duarte, F. L. Franco and W. Azevedo in 2019, dissected head, from Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; juvenile female (IBSP 90660), col. M. Duarte, F. L. Franco and W. Azevedo in 2019, from Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; juvenile female (AMNH-R 60803), from Kuyuwini (2º12'30" N, 58º28'30" W), Guyana.

Referred specimens: Unsexed adult (MTR 20581), from Fazenda Salvamento, Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; unsexed adult (MTR 20551) from Estação Ecológica Maracá, Amajari (3°39'07" N, 61°22'15" W, 100 m a.s.l.), Roraima, Brazil; unsexed adult (MTR 20546) from Estação Ecológica Maracá, Amajari (3°39'07" N, 61°22'15" W, 100 m a.s.l.), Roraima, Brazil; unsexed adult (MZUSP 10389, field tag LJV 2570), col. L.J. Vitt, from Novo Brasil, Boa Vista (2°49'12" N, 60°40'19" W, 90 m a.s.l.), Roraima, Brazil; unsexed adult (CVULA, voucher unknown, photographic voucher), col. C.B. Amorós, reportedly lost, from "Barinitas" (unknown locality), Bolívar, Venezuela; unsexed adult (CVULA, voucher unknown, photographic voucher), col. C.B. Amorós, reportedly lost, from Santa Elena de Uairen (4º36'8" N, 61º06'36" W, 900 m a.s.l.), Bolívar, Venezuela.

Diagnosis: The new species is assigned to *Erythrolamprus* based on molecular evidence, considering that until now, no unambiguous morphological synapomorphy is known for this genus [see Zaher et al. (2009) and Grazziotin et al. (2012)]. The new species can be differentiated from all other *Erythrolamprus* species by the following combination of characters: (1) 19/19/15 dorsal scales; (2) preocular present, contacting loreal, supraocular, 3rd and 4th supralabials; (3) loreal present; (4) temporals 1+2 (1+1+2 in a single specimen); (5) supralabials eight, 4th–5th in contact with orbit; (6) infralabials 10/10 (11/10 in a single specimen), 1st–5th in contact with anterior chinshields; (7) ventrals 149–154 in females; (8) subcaudals 45–50 in females; (9) dorsal background coloration light grey, scales reticulated, with black margins and diffuse light blue lateral edges; (10) ventral and subcaudal coloration white with conspicuous diffuse and irregular small black blotches or dots; (11) black and white nuchal collars present, arrow-shaped, black nuchal collar over parietals, temporals and occipitals, up to one and a half scales wide; white nuchal collar over interoccipitals and dorsals, up to two scales wide, with outer black margins; (12) SVL 167–476 mm, TL 40–114 mm.

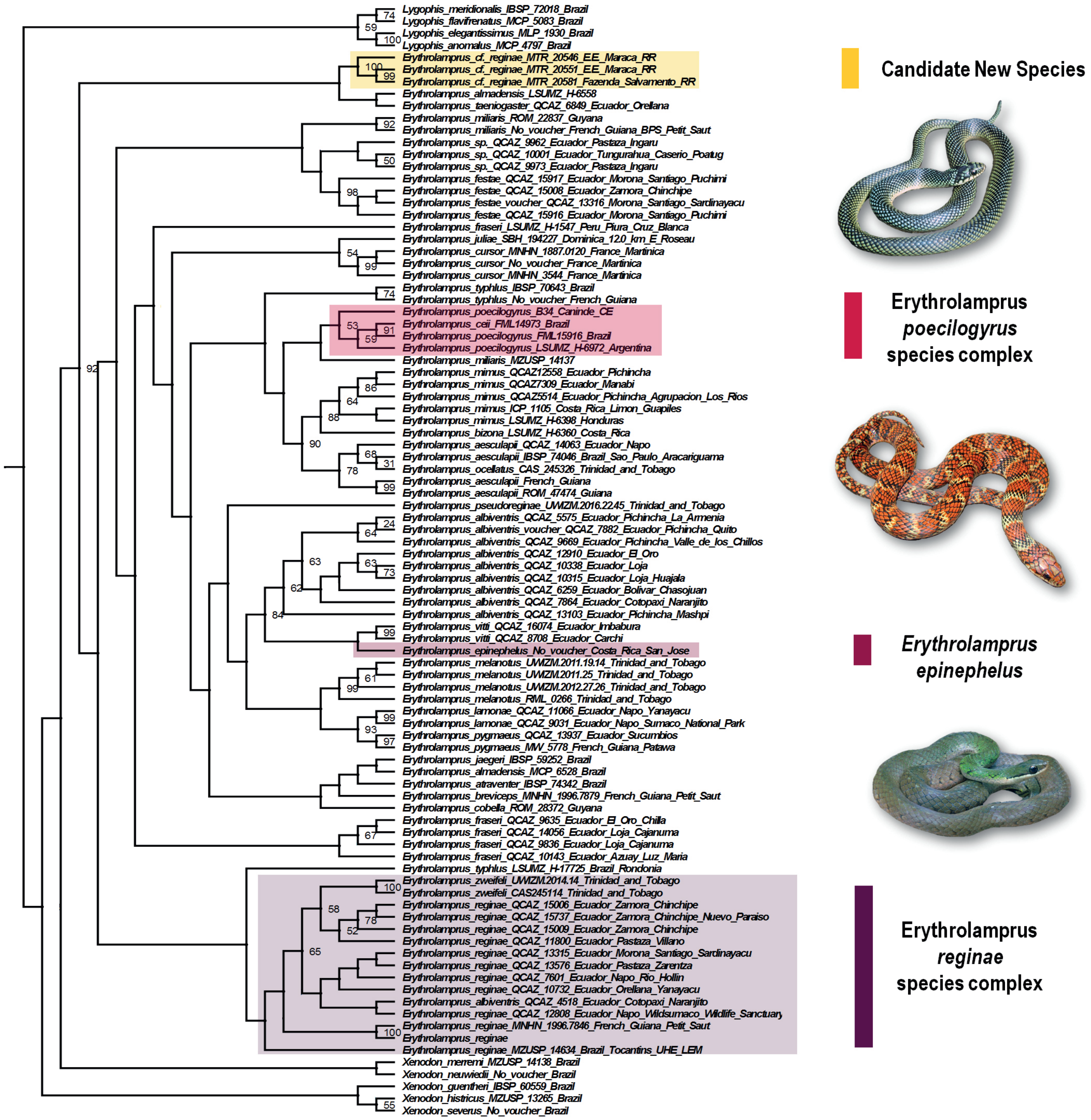

Figure 1. Maximum likelihood phylogeny for *Erythrolamprus*, based on mitochondrial DNA, with bootstrap node values > 50 indicated, cladogram visualization. Inset photographs: *Erythrolamprus aenigma*, top, L. J. Vitt; *Erythrolamprus poecilogyrus poecilogyrus*, middle, M. Freitas; *Erythrolamprus reginae*, bottom, D. Loebmann. Raw file and genetic distance outputs are available as supplementary material (Supplementary Files 1, 2).

Description of holotype: Adult female; total length 473.5 mm; SVL 390.5 mm; TL 83 mm (17.5 % of total length, 21.2 % of SVL); head length 18.02 mm (3.8 % of total length, 4.6 % of SVL); head width 12.5 mm (69.3 % of head length); interocular distance 5.05 mm; rostro–orbital distance 4.05 mm; naso–orbital distance 3.80 mm; cervical constriction slightly distinct; head well distinct from neck, triangular in dorsal view, narrow anteriorly, arched in lateral view; pupil rounded; rostral rounded, 2.5 mm long, 4 mm wide, slightly projected over lower jaw, length of portion visible in dorsal view slightly smaller than its distance to external edge of frontal; internasals present, paired, square shaped, 1.5 mm long, 3 mm wide, anterior edges contacting rostral and anterior nasal, lateral edges contacting posterior nasal, posterior edges contacting prefrontals; prefrontals paired, 3 mm long, 3.5 mm wide, anterior edges contacting internasals and posterior nasal, lateral edges contacting posterior nasal and loreal, lateroposterior edges contacting preocular, posterior edges contacting supraocular and frontal; frontal pentagonal shaped, 4.5 mm long, 3.5 wide, anterior edge contacting prefrontals, lateral edge contacting supraoculars, posterior edges contacting parietals; supraocu-

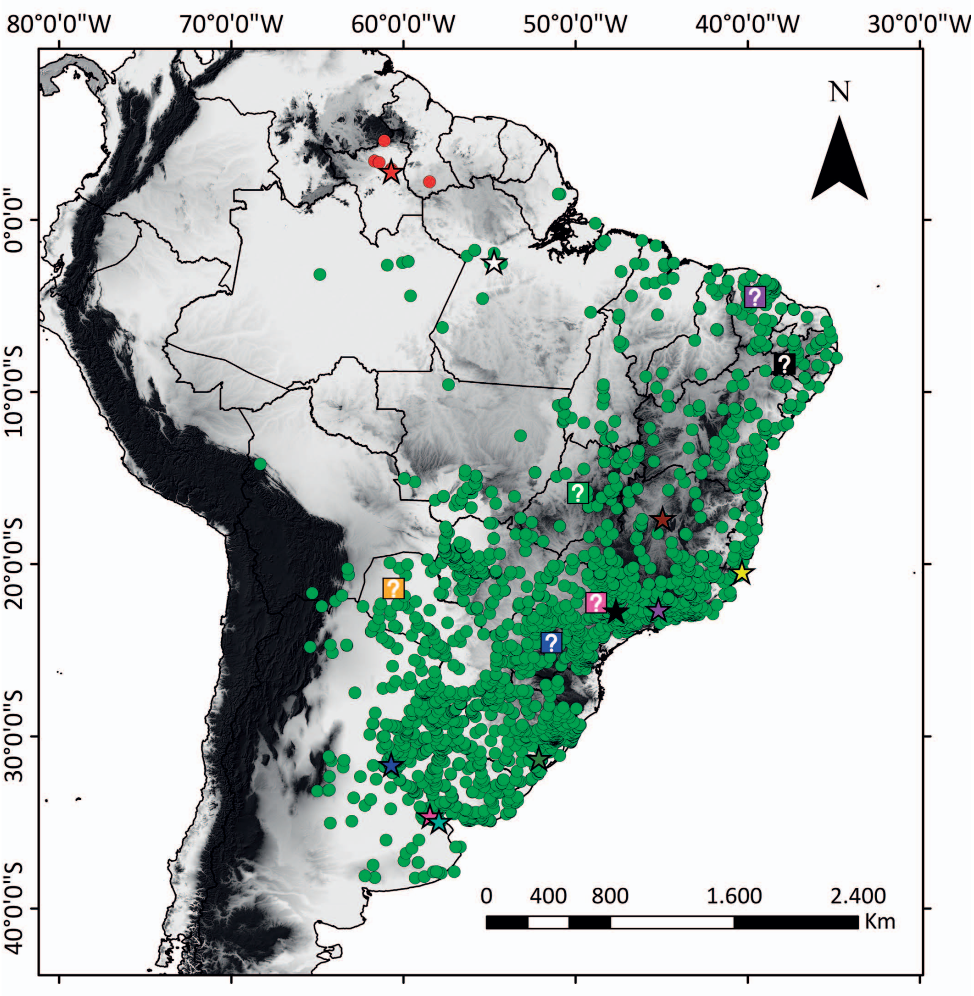

Figure 2. Geographic distribution of populations formerly assigned to *Erythrolamprus poecilogyrus*, based on Dixon & Markezich (1992), Nogueira et al. (2019), and examined specimens. Red star: type locality of *Erythrolamprus aenigma*; Red circles: localities of specimens of *E. aenigma*; Yellow star: type locality of *Coluber poecilogyrus*; White star: type locality of *Leimadophis poecilogyrus amazonicus* and *Dromicus poecilogyrus lancinii*; Brown star: type locality of *Leimadophis poecilogyrus franciscanus*; Purple star: *Leimadophis poecilogyrus montanus*; Black star: type locality of *Leimadophis poecilogyrus albadspersus*; Green star: type locality of *Leimadophis poecilogyrus pictostriatus*; Pink star: type locality of *Liophis merremii* var. *sublineatus*; Dark blue star: type locality of *Opheomorphus doliatus* var. *caesius*; Cyan star: type locality of *Leimadophis poecilogyrus platensis*; Pink interrogation: approximate type locality of *E. poecilogyrus schotti*; Orange interrogation: approximate type locality of *Leimadophis poecilogyrus reticulatus* and *Liophis subfasciatus*; Dark blue interrogation: approximate type locality of *Liophis reginae viridicyanea*, *Leimadophis poecilogyrus montanus*, and *Leimadophis poecilogyrus pinetincola*; Black interrogation: approximate type locality of *Liophis typhlus gastrosticta* and *Liophis typhlus olivacea*; Green interrogation: approximate type locality of *Leimadophis poecilogyrus intermedius*; Purple interrogation: approximate type locality of *Leimadophis poecilogyrus xerophilus*.

lar trapezoidal, 4 mm long, 2 mm wide, anterior edge in contact with posterior edge of prefrontals and preocular, lateral edge contacting frontal, lateroposterior edge contacting upper postocular, posterior edge contacting anterior edges of parietal; parietals paired, 6.2 mm long, 4 mm wide, anterior edge contacting posterior edges of frontal, posterior edge of supraocular, and superior edge of upper postocular, lateral edges contacting first temporal and second upper temporal, posterior edges contacting interoccipitals; occipitals 2/2, indistinct from dorsals; interoccipitals three, slightly smaller than vertebral and paravertebral dorsals; nasal triangular shaped, divided; anterior nasal 1 mm long, 1.5 mm high, anterior edge contacting rostral, lower edge contacting first supralabial, upper edge contacting internasal, posterior edge contacting nostril; posterior nasal 1 mm long, 1.2 mm high, anterior edge contacting nostril, lower edge contacting first and second supralabials, upper edge contacting internasal and prefrontal, posterior edge contacting loreal; nostril located between anterior and posterior nasals, slightly visible from above; loreal square shaped, 1 mm long, 1.2 mm high, anterior edge contacting posterior nasal, lower edge contacting second and third supralabials, upper edge contacting prefrontal and preocular; preocular pentagonal, widest in its upper portion, 1.3 mm long at larger section, 2.8 mm high, anterior edge contacting loreal and prefrontal, lower edge contacting third and fourth supralabials, upper edge contacting supraocular, posterior edge contacting orbit; postoculars paired, square shaped; upper postocular 0.9 mm long, 1 mm high, upper edge contacting supraocular and parietal, anterior edge contacting orbit, posterior edge contacting parietal and first temporal, lower edge contacting lower postocular; lower postocular 0.5 mm long, 1.5 mm high, upper edge contacting upper postocular and first temporal, anterior edge contacting orbit, lower edge contacting fifth and sixth supralabials, posterior margin contacting fifth supralabial and first temporal; temporals 1+2; first temporal 4 mm long, 1.5 mm high, anterior edge in contact with preoculars and sixth supralabial, upper edge in contact with parietal, lower edge in contact with sixth and seventh supralabials, posterior edge in contact with sixth supralabial and posterior temporals; upper posterior temporal 3.2 mm long, 1.2 mm high, anterior edge contacting parietal and anterior temporal, lower edge contacting lower posterior temporal, posterior edge contacting occipitals; lower posterior temporal 2 mm long, 1.1 mm high, anterior edge contacting anterior temporal and seventh supralabial, lower edge contacting seventh and eighth supralabials, upper edge contacting upper posterior temporal, posterior edge contacting occipital; eight supralabials, 4–5 in contact with orbit, first contacting rostral and nasals, second contacting loreal

Figure 3. Holotype of *Erythrolamprus aenigma* (IBSP 90722) from Boa Vista, Roraima, Brazil. Scale bar = 20 mm.

Figure 4. Head views of holotype of *Erythrolamprus aenigma* (IBSP 90722) from Boa Vista, Roraima, Brazil. Scale bar = 10 mm.

and posterior nasal, third contacting preocular and loreal, fourth contacting orbit and preocular, fifth contacting orbit and lower postocular, sixth contacting lower postocular and first temporal, seventh contacting first temporal and second lower temporal, eight in contact with second lower temporal and occipital; mental triangular, as long as wide; two pairs of chinshields, equal in size, longer than wide; infralabials 10/10, 1–5 in contact with anterior chinshields, 5–6 in contact with posterior chinshields, first pair in contact with each other, mental, and anterior chinshields; fifth and sixth supralabials largest, equal in size; 19/19/15 smooth dorsal scale rows, with 1–2 apical pits; cloacal scute divided; 149 ventrals and two preventrals; 45/45 paired subcaudals; terminal scale rounded, acuminate, projected dorsally; head light grey dorsally and laterally, scales with black margins; head uniformly white ventrally; supralabials light grey, with black margins; black and white nuchal collars, arrow-shaped; black nuchal collar over parietals, temporals and occipitals, up to one and a half scales wide; white nuchal collar over interoccipitals and dorsals, up to two scales wide, with black margins; dorsal background coloration light grey, scales reticulated, with black margins and diffuse light blue lateral edges; ventral and subcaudal coloration white with conspicuous diffuse and irregular small black blotches.

Variation: Only female specimens are available. SVL 167–476 mm (365 ± 105.1, n = 5), TL 40–114 mm (85.6 ± 28.5, n = 5), head length 10–18 mm (14 ± 3, n = 5), head width 6–9 mm (8.25 ± 1.5, n = 5). Ventrals 149–154 (152 ± 9, n = 5), subcaudals 45–50 (47 ± 2.5, n = 5). One specimen has 1+1+2 temporals on left side of head (IBSP 90722, holotype); another specimen possesses 10/11 infralabials (IBSP 90727). Largest specimen SVL 478 mm, and TL 105 mm.

Coloration in life: Head uniformly light grey dorsally and laterally, scales with black margins; head uniformly white ventrally; supralabials light grey or light brown, with black margins; black and white nuchal collars, arrow-shaped; black nuchal collar over parietals, temporals and occipitals, up to one and a half scales wide (inconspicuous in IBSP 90743); white nuchal collar over interoccipitals and dorsals, up to two scales wide, with black margins; dorsal background coloration light grey or light brown (Fig. 5), scales reticulated, with black margins (vestigial markings in IBSP 90743) and diffuse light blue lateral edges (white in IBSP 90743); ventral and subcaudal coloration white with conspicuous diffuse and irregular small black blotches.

Geographic distribution and natural history: The new species is known from five localities (Boa Vista, Rorainópolis, Estação Ecológica de Maracá–Amajari, and Novo Brasil) in Roraima state, Brazil, one in Guyana (Kuruwini), and two (Barinitas, Santa Elena de Uairen) in Bolívar state, Venezuela, within open vegetation formations of northern South America. Based on this distribution, it is reasonable to predict that this species lives in open environments and therefore may be more widely distributed throughout this matrix of open habitats of northern Brazil, Guyana, adjacent Venezuela and probably even neighbouring countries, but absent or rare in forested environments. One specimen (IBSP 90743) deposited 7 eggs shortly after being collected. Azarak & Farias (2017) reported the specimen INPA-H 34377 ingesting the spawn of a frog (*Leptodactylus fuscus*) containing eggs and tadpoles. Another specimen (CHFURG 5068) ingested another adult snake (*Leptodeira annulata*) (Entiauspe-Neto et al. 2016). These observations suggest batrachophagous and ophiophagous dietary habits.

Etymology: The specific epithet, *aenigma*, is a Latin singular noun in nominative case, meaning a "mystery" or "riddle", and refers to the noteworthy absence of males in our examined sample of specimens.

Comparisons (data for other species in parenthesis): *Erythrolamprus aenigma* is most likely to be confused with taxa from the *E. poecilogyrus* species complex, since these species share 19/19/17 dorsals.

In order to assure that *E. aenigma* is not allocable to any of the available names (including 'forgotten' synonyms of other taxa), the taxonomic history of *E. poecilogyrus* needs to be briefly summarized here. An overview of the geographic distribution of available valid names associated to *E. poecilogyrus* is also given (Fig. 2), As is an overview of osteological comparisons (Table 1).

Dixon & Markezich (1992) recognized four valid subspecies for *E. poecilogyrus*, and 28 available names associated with this species. The recognized subspecies were: (i) *E. p. poecilogyrus*, described based on specimens from "Rio Jucú", in what is currently the Brazilian state of Espirito Santo, likely in the vicinity of Vitória municipality, in the Atlantic Rainforest of southeastern Brazil; (ii) *E. p. schotti* (Schlegel, 1837), described based on a specimen from São Paulo state, in southeastern Brazil; (iii) *E. p. sublineatus* (Cope, 1860), described based on a specimen from Buenos Aires, Argentina; (iv) *E. p. caesius* (Cope, 1862), described based on a specimen from Santa Fé, Argentina.

Of these names, none were described based on specimens from 'open areas' of northern Brazil, which could possibly represent *E. aenigma.* Three names have unknown or imprecise localities, i.e. *Coluber alternans* Lichtenstein, 1823, described from "Brazil", *Liophis verecundus* Jan, 1863, described from an unknown locality, and *Liophis cobella flaviventris* Jan & Sordelli, 1866, described from "Brazil". *Liophis verecundus* is currently considered a junior synonym of *Erythrolamprus almadensis* (Dixon, 1989). *Liophis cobella flaviventris* is currently considered a junior synonym of *Erythrolamprus p. poecilogyrus* (Wied-Neuwied, 1825) (cf. Dixon & Markezich 1992). The names *Coluber m-nigrum* Raddi, 1820, *Coluber alternans* Lichtenstein, 1823 and *Natrix forsteri* Wagler, 1824 were considered conspecific with, i.e., junior synonyms of, *E. p. poecilogyrus* by Dixon & Markezich (1992).

Erythrolamprus p. poecilogyrus has the following available names associated to it: (i) *Coluber doliatus* Wied, 1825, described from Rio Espírito Santo, Barra do Jucu, Espírito Santo state, southeastern Brazil; (ii) *Liophis verecundus* Jan, 1863, described from "Brazil". Both agree well with the syntypes and description of the nominotypical form, which occurs in Atlantic Rainforest in southeastern Brazil. This form has continuous or alternating bands across its dorsum, extending to the lateral tips of the ventrals, with light pink or yellow scales edged with black (Dixon & Markezich 1992). In light of this, *E. p. poecilogyrus* can

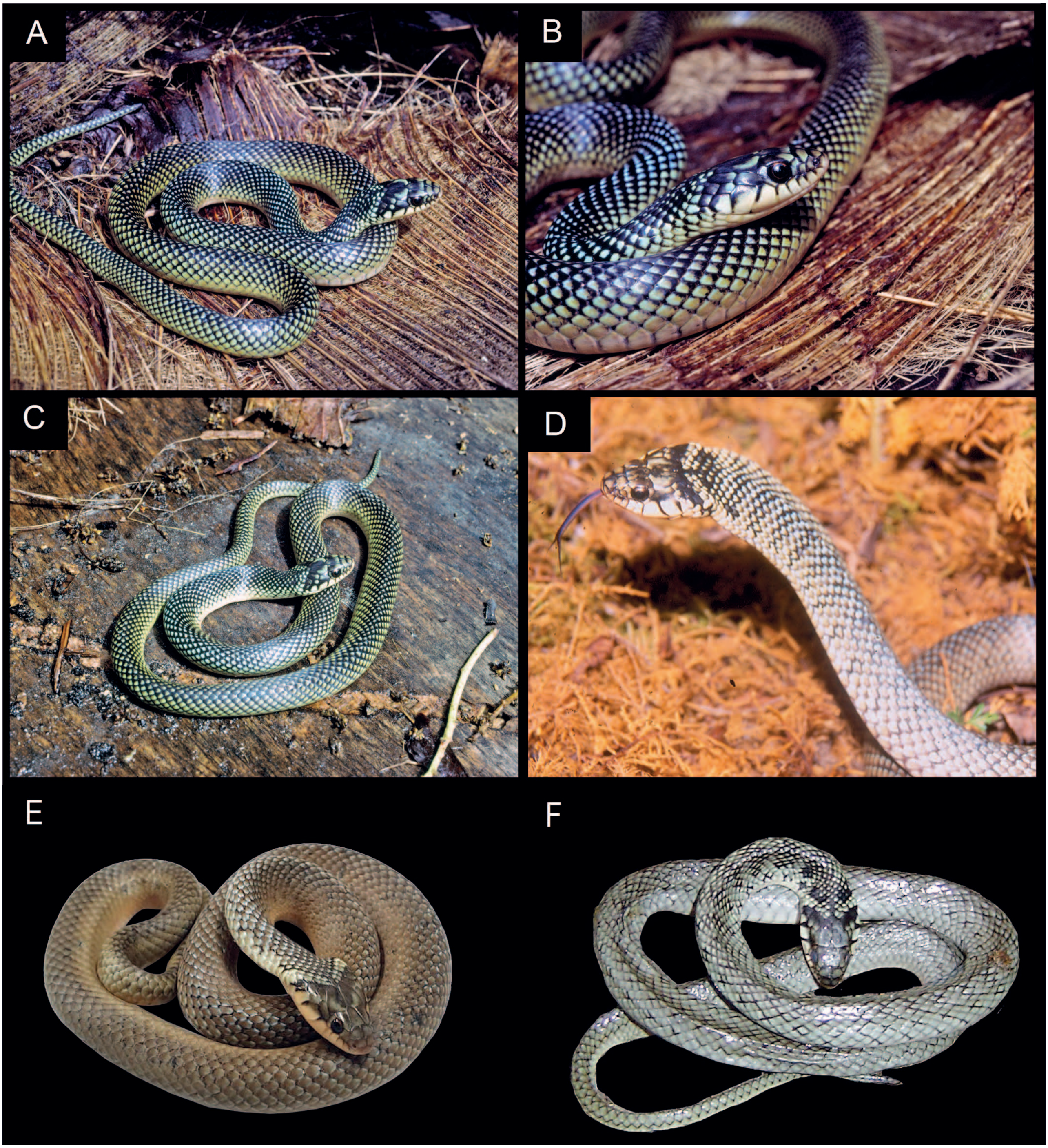

Figure 5. Specimens of *Erythrolamprus aenigma*. (A–B) Unsexed adult (MZUSP 10389, field tag LJV 2570), from Novo Brasil, Roraima, Brazil; (C) Unsexed adult (unvouchered) from Estação Ecológica Maracá, Roraima, Brazil; (D) Unsexed adult (CVULA, voucher unavailable) from Santa Elena de Uairen, Bolívar, Venezuela; (E) Adult female (IBSP 90727) from Boa Vista, Roraima, Brazil; (F) Unsexed adult (CVULA, voucher unavailable) from Barinitas, Bolívar, Venezuela. Photographs: L. J. Vitt (A–C), C. B. Amorós (D, F), E. Marinho (E).

Table 1. Comparison of cranial osteological characters of *Erythrolamprus aenigma* sp. nov. (AMNH 60803), *E. poecilogyrus schotti* (UMMZ 15306), and *E. dorsocorallinus* (UFAC-F 405) based on micro-CT scans. Uncertain or conflicting information is indicated with a question mark, "?".

	Erythrolamprus aenigma sp. nov. (AMNH 60803)	*E. poecilogyrus schotti* (UMMZ 15306)	*E. dorsocorallinus* (UFAC-F 405)
Ascending process of premaxilla	Ends slightly concave, does not touch nasals	Ends pointed, does not touch nasals	Ends blunt, slightly touches nasals
Vomerine processes of premaxilla	Approaching, but not contacting vomers	Distinctly separated from vomers	Overlapping vomers
Premaxilla and septomaxillae in contact	Yes	No	Yes
Vomer and palatine in contact	Yes	No	Yes
Prefrontal and palatine in contact	Yes	No	Yes
Anteromedial region of frontals	In contact	Separated by a V-shaped notch	Separated by a V-shaped notch
Parietal and supratemporal in contact	Marginally on right side, slightly separated on left side	Separated	Slightly in contact
Supraoccipital	With two posterolaterally orientated oblique ridges	With two posterolaterally orientated oblique ridges	With two anterior and two posterior oblique ridges, forming an "X"
Parasphenoid rostrum	Distinctly surpassing choanal process of palatine	Not surpassing choanal process of palatine	Not surpassing choanal process of palatine
Number of prediastemal tooth loci on maxilla	13	16–17	20
Number of tooth loci on palatine	12–13	12	10–11 (?)
Palatine and pterygoid in contact	Yes	No	NA
Number of tooth loci on pterygoid	25	25	25
Number of tooth loci on dentary	21–22	23	28
Splenial reaching anteriorly to	Level of 10th tooth	Level of 12th tooth	NA
Location of mental foramen of dentary	Level of 10th tooth	Level of 10th or 11th teeth	NA

be readily differentiated from *E. aenigma*, based on its distinctive dorsal (red crossbands) and ventral (black, square-shaped blotches) patterns (Figs 6A–B, 8G).

Erythrolamprus p. caesius was described based on one specimen from Santa Fé in western Argentina. It has one available name associated with it, i.e., *Liophis poecilogyrus reticulatus* Parker, 1931 from the Chaco of Paraguay. Both aforementioned forms agree well with each other morphologically. *E. poecilogyrus caesius* is distributed in open areas of Argentina, Paraguay, and Bolivia. We examined the holotype of *E. poecilogyrus caesius* (USNM 5395), which is similar to our new species in having reticulated scales on its dorsum, but differs from it by lacking arrow-shaped black and white nuchal collars, and by having two lateral white, discolored, stripes. Compared to the new species, this subspecific form also bears a distinct ventral coloration (small square-shaped blotches, restricted to the edges of its ventrals, or uniformly cream), supralabial coloration (scales uniformly yellow or cream, without black edges) and a distinct dorsal pattern (reticulated black and yellow scales and two lateral yellow stripes) (Figs 6C–D, 8F).

Erythrolamprus poecilogyrus schotti has the following available names associated with it: (i) *Liophis subfasciatus* Cope, 1862, described from Paraguay; (ii) *L. ornatissima* Jan, 1863, described from Paraná state, southern Brazil; (iii) *L. typhlus gastrosticta* Jan, 1863, from Pernambuco state, in the Caatinga of northeastern Brazil; (iv) *L. typhlus olivacea* Jan, 1863, from Pernambuco, also in the Caatinga of northeastern Brazil; (v) *L. reginae viridicyanea* Jan & Sordelli, 1866, from Paraná state, southern Brazil; (vi) *Rhadinaea praeornata* Werner, 1909, from "central Brazil"; (vii) *Leimadophis poecilogyrus albadspersus* Amaral, 1944, from Piracicaba, in the Cerrado of São Paulo state, southeastern Brazil; (viii) *L. p. amazonicus* Amaral, 1944, from Santarém, in the Amazon Rainforest of Pará state, northern Brazil; (ix) *L. p. franciscanus* Amaral, 1944, from Pirapora, in the Cerrado of Minas Gerais, southeastern Brazil; (x) *L. p. intermedius* Amaral, 1944, from the Cerrado of Goiás state, central Brazil; (xi) *L. p. pineticola* Amaral, 1944, from "central Paraná", Paraná state, southern Brazil; (xii) *L. p. xerophilus* Amaral, 1944, from the Caatinga of Ceará, northeastern Brazil; (xiii) *L. p. montanus* Amaral, 1944, described from Piquete, in the Atlantic Rainforest of São Paulo state, southeastern Brazil; (xiv) *Dromicus poecilogyrus lancinii* Hoge, Romano, & Cordeiro, 1978, from the Amazon Rainforest of Santarém, Amazon rainforest of Pará state, northern Brazil. *Erythrolamprus poecilogyrus schotti* was diagnosed by Dixon & Markezich (1992) as having frontal and parietal scales without well-defined edges, and stripes or interruption of pattern close to its tail or caudal scale. The aforementioned synonyms agree well with the proposed diagnosis of Dixon & Markezich (1992); this is furthermore corroborated by our examination of specimens from northern, northeastern, southeastern, and southern Brazil (Appendix I). This form ranges into open and forested areas of Brazil, Paraguay and Argentina. However, the morphological variation of *E. aenigma* does not fall within the proposed diagnosis of *E. p. schotti* (Figs 6E–F, 8H). The new species presents well-defined black edges of its head scales, lacks the posterior body stripe, and also has a uniformly reticulated pattern throughout its dorsal body and tail. We also examined

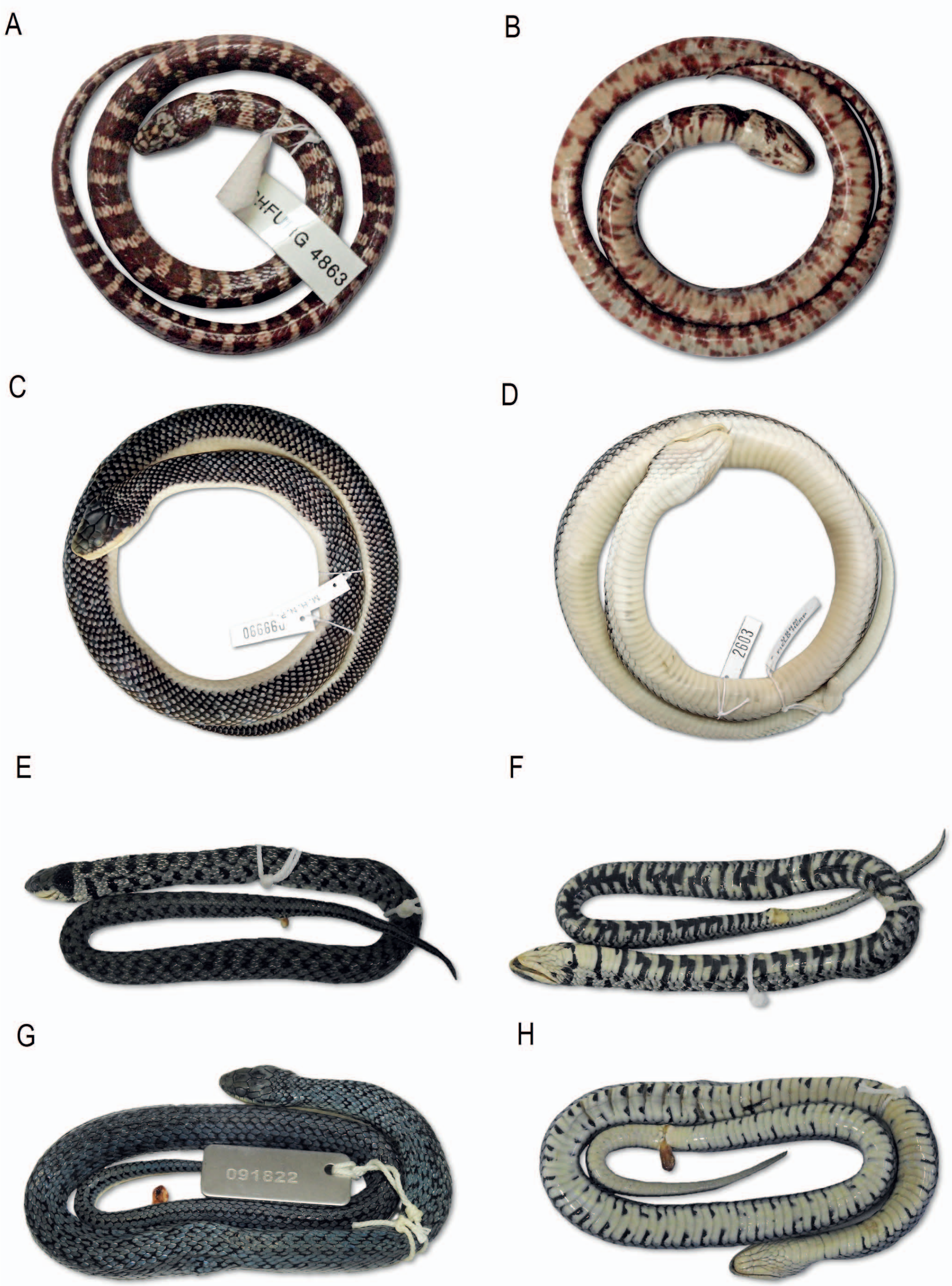

Figure 6. Specimens of the *Erythrolamprus poecilogyrus* species complex, in dorsal (left) and ventral views (right). (A, B) *Erythrolamprus poecilogyrus poecilogyrus* (CHFURG 4863) from Rio de Janeiro, Rio de Janeiro, Brazil; (C, D) *Erythrolamprus poecilogyrus caesius* (MHNP 2603) from San Lorenzo, Paraguay; (E, F) *Erythrolamprus poecilogyrus schotti* (IBSP 91323), topotype, from São Paulo, São Paulo, Brazil; (G, H) *Erythrolamprus poecilogyrus sublineatus* (IBSP 91822) from Rosário do Sul, Rio Grande do Sul, Brazil. Photographs: O. M. Entiauspe-Neto (A–B), P. Cacciali (C–D), A. D. Abegg (E–H).

the syntype of *E. p. schotti*, RMNH 236. The specimen, although discolored from storage in preservative, presents a unvarying grey dorsal pattern, variegated with black, and a white venter with alternating black squares. However, as noted by Dixon & Markezich (1992), populations from northeastern Brazil may have a uniformly white venter. In light of this, it can be readily distinguished from *E. aenigma* based on its dorsal (variegated or with crossbands, and a posterior stripe), head pattern (without well-defined dark edges on scales), absent posterior body stripe (present), and ventral pattern (with alternating black squares or uniformly white). Furthermore, it should also be noted that these species are allopatrically distributed.

Erythrolamprus poecilogyrus sublineatus has the following available names associated with it: (i) *Leimadophis poecilogyrus pictostriatus* Amaral, 1944, described from the Pampas of São Lourenço (São Lourenço do Sul), Rio Grande do Sul state, southern Brazil; (ii) *Leimadophis poecilogyrus platensis* Amaral, 1944, described from the Pampas of La Plata, Argentina. Aside from small differences in their colour patterns, these forms agree well with each other. *Erythrolamprus p. sublineatus* is distributed in open and forested areas of southern Brazil, Uruguay, and Argentina. It can be readily distinguished from the new species based on its ventral coloration (large, square-shaped, alternating blotches). Furthermore, this subspecies also lacks the wide interorbital black stripe and arrow-shaped nuchal black blotch (Figs 6G–H, 8I). In our phylogenetic analysis, *E. ceii* Dixon, 1991, appears nested within the *E. poecilogyrus* complex. This species can be distinguished from *E. aenigma* based on its uniformly green dorsal coloration. In light of this, we conclude that *E. aenigma* cannot be assigned to any taxon of the *Erythrolamprus poecilogyrus* species complex.

Erythrolamprus aenigma might also be confused with species from the *E. reginae* species complex (Fig. 7). Although this group was recently revised by Ascenso et al. (2019), other authors highlighted several inconsistencies in this work (e.g., Torres-Carvajal & Hinojosa 2020), the major ones being: (1) *E. reginae*, in its current sense, is not monophyletic; and (2) *E. zweifeli* appears to be synonymous with *E. reginae*. During examination of type specimens (MPEG 25680, 25681), we also had significant difficulty separating *E. rochai* Ascenso, Costa & Prudente, 2019 from *E. p. schotti*, as both are sympatric and have a large overlap of morphological diagnostic characters. Therefore, we will address these taxa in detail in the following.

Erythrolamprus reginae was described based on specimens from "Indiis" (likely a misspelling of (West) Indies); two specimens are known (NRM 44, 45), one was designated as lectotype (NRM 44) by Andersson (1899), and Dixon (1983a) restricted its type locality to "Surinam". It has the following available names associated with it: (i) *Coluber graphicus* Shaw, 1802, described from "America"; (ii) *Natrix semilineata* Wagler, 1824, described from "Rio Solimões", likely in the Amazon forest, northern Brazil; (iii) *Liophis miliaris intermedius* Henle & Ehrl, 1991, from the Amazon forest of Madre de Dios, Perú. These forms agree well with each other, with minor differences that can be assigned to extremes of morphological variation. *Erythrolamprus reginae* is widely distributed in forested areas of Brazil, Guyana, French Guyana, Surinam, Venezuela, Ecuador, Colombia and Peru. *Erythrolamprus aenigma* can be distinguished from *E. reginae* based on the basis of its dorsal scale counts (17/17/15), ventral pattern (black square-shaped marks), and dorsal pattern in life (uniformly olive green) (Fig. 8E).

Erythrolamprus macrosomus (Amaral, 1935) was described based on a series of specimens from Cana Brava, Minaçu, in the Cerrado of Minas Gerais, southeastern Brazil. These specimens could not be examined by us, since they were lost in the Butantan Institute fire accident in 2010 (Ascenso et al. 2019). This species has a single valid available synonym, *Leimadophis reginae maculicauda* Hoge, 1952, from Sarandi, São Paulo, southeastern Brazil. This specimen was also lost in the fire accident (Ascenso et al. 2019). However, both forms can be characterized clearly from their descriptions, and agree well with each other. *Erythrolamprus macrosomus* is distributed in the Pampas, Cerrado, and Atlantic Forest of Argentina, Paraguay, southeastern and central Brazil. It is possible to distinguish it from *E. aenigma* based on its dorsal scale counts (17/17/15), ventral pattern (black square-shaped marks), and dorsal pattern in life (uniformly olive green or greyish brown) (Fig. 8C).

Erythrolamprus zweifeli (Roze, 1959) was described based on a holotype from Rancho Grande, Aragua, Venezuela. Fourteen paratypes were designated, from the states of Aragua, Miranda, Carabobo, and Caracas. It bears no associated synonym. It was considered valid and elevated to species status by Ascenso et al. (2019). Torres-Carvajal & Hinojosa (2020) suggested that this species is not reciprocally monophyletic to *E. reginae*, although these authors did not formally synonymize them; indeed, evidence for the distinction with *E. reginae* is solely based on coloration (see Ascenso et al. 2019). This species occurs in the mountain ranges of the Caribbean versant of Venezuela. Both *E. zweifeli* and *E. reginae* can be differentiated from *E. aenigma* based on the dorsal scale counts (17/17/15), dorsal coloration in life (green, yellow or orange), and ventral pattern (large, black square-shaped marks).

Erythrolamprus dorsocorallinus (Esqueda, Natera, La Marca & Ilija-Fistar, 2007) was described based on a specimen from Andrés Eloy Blanco, Barinas, Venezuela; four paratypes were designated. It bears no synonyms, and occurs in the southwestern lowland Amazon forest of Brazil, Bolivia, and Peru, with a disjunctive population from the Venezuelan Llanos. It should be noted that *E. dorsocorallinus* and *E. reginae* present a near-total overlap of morphological characteristics, except for coloration patterns. Therefore, it is also possible to distinguish *E. dorsocorallinus* from *E. aenigma* based on its dorsal scale counts (17/17/15), dorsal coloration in life (blue, yellow, or orange), ventral pattern (black square-shaped markings), and higher subcaudal counts (62–80).

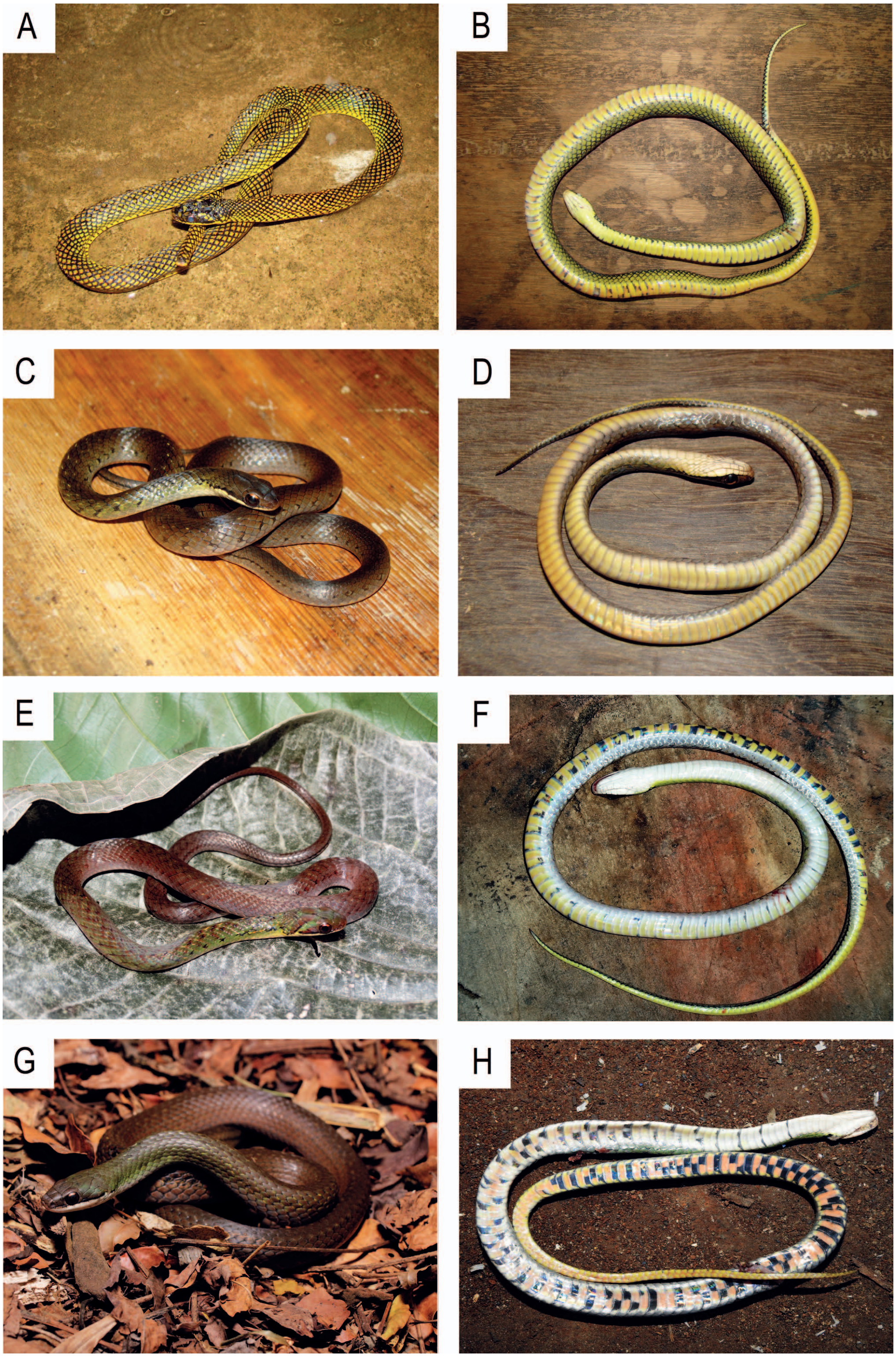

Figure 7. Specimens of the *Erythrolamprus reginae* species complex in life, in dorsal (left) and ventral views (right). (A, B) *Erythrolamprus dorsocorallinus* (CHUPFRE 4378) from Estação Ecológica Rio Acre, Assis Brasil, Acre, Brazil; (C, D) *Erythrolamprus oligolepis* (UFAC 0477) from Estação Ecológica Rio Acre, Assis Brasil, Acre, Brazil; (E, F) *Erythrolamprus reginae* (unvouchered) from Estação Ecológica Rio Acre, Assis Brasil, Acre, Brazil; (G) *Erythrolamprus macrosomus* (MZUSP, voucher unavailable) from Águas de Santa Bárbara, São Paulo, Brazil; (H) *Erythrolamprus macrosomus* (MZUSP, voucher unavailable) from Bahia, Brazil. Photographs: M. A. Freitas (A–F, H) and R. P. Benetti (G).

Erythrolamprus oligolepis (Boulenger, 1905) was described based on a type from Igarapé-Açu, an unknown locality in the Amazon forest of Pará, northern Brazil. Although this species was synonymized in the past, there is compelling evidence for its validity (see Cunha & Nascimento 1993). It bears no synonyms, and occurs in forested areas of northern Brazil and Peru. It can be readily distinguished from *E. aenigma* based on its lower dorsal scale counts (15/15/15), dorsal coloration (uniformly brown or light green), and ventral pattern in life (uniformly cream or white) (Fig. 8D).

Erythrolamprus rochai Ascenso, Costa, & Prudente, 2019 is a recently described species from the state of Amapá, in the Amazon forest of northern Brazil. It is known based solely on two specimens and bears no synonyms. The type specimen has three black bands in its first body third, a variegated dorsal pattern, posterior body stripe, and a uniformly white venter. It agrees well with analyzed specimens of *E. poecilogyrus schotti* from Amapá, differing only by reportedly having 17/17/15 dorsals, whereas in *E. p. schotti* it is 19/19/15 (Ascenso et al. 2019). These two taxa are also sympatric. Further studies, based on integrative evidence, are

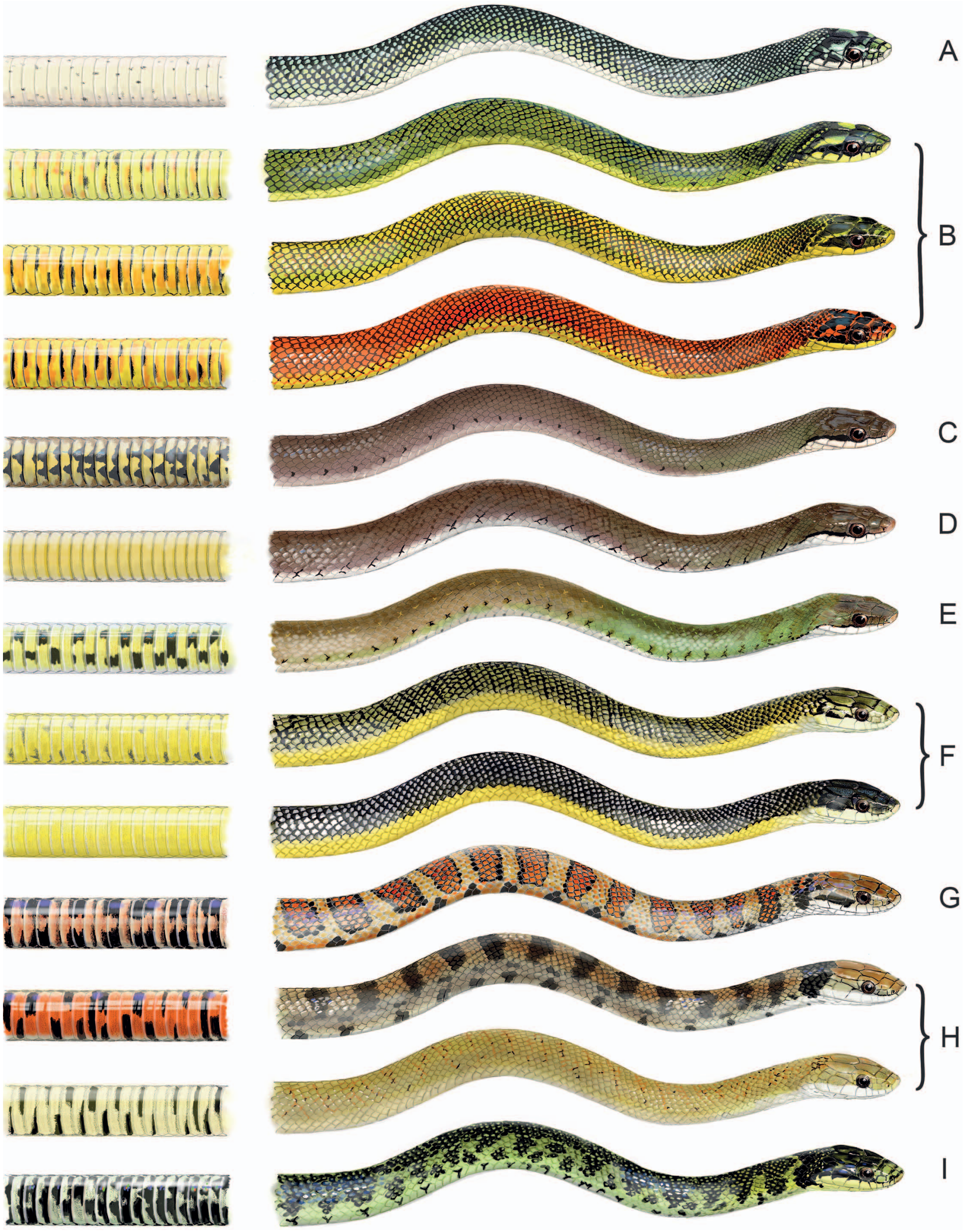

Figure 8. Overview of similar *Erythrolamprus* species, in dorsal and ventral view. A) *Erythrolamprus aenigma*; B) *Erythrolamprus dorsocorallinus*; C) *Erythrolamprus macrosomus*; D) *Erythrolamprus oligolepis*; E) *Erythrolamprus reginae*; F) *Erythrolamprus poecilogyrus caesius*; G) *Erythrolamprus poecilogyrus poecilogyrus*; H) *Erythrolamprus poecilogyrus schotti*; I) *Erythrolamprus poecilogyrus sublineatus*.

needed in order to evaluate its taxonomic validity. From *E. aenigma*, it can be distinguished based on its dorsal pattern (body stripes and variegated) and ventral pattern (uniformly white).

From *Erythrolamprus epinephelus* (Cope, 1862), including its subspecies (*E. e. bimaculatus* (Cope, 1899); *E. e. epinephelus* (Cope, 1862), *E. e. juvenalis* (Dunn, 1937), *E. e. kogiorum* (Bernal-Carlo, 1994), *E. e. opistothaenius* (Boulenger, 1908), and *E. e. pseudocobella* (Peracca, 1914), *E. aenigma* can be distinguished by its dorsal scale counts (17/17/15), dorsal pattern (black crossbands, dark brown stripes or uniformly grey, light brown, red, or green) and ventral pattern (uniformly yellow, cream, or alternating black squares) (Dixon 1983a). The same diagnosis applies to taxa formerly assigned to *E. epinephelus*, these being *E. albiventris* (Jan, 1863), *E. fraseri* (Boulenger, 1894), and *E. lamonae* (Dunn, 1944).

Erythrolamprus aenigma can be furthermore distinguished from other distantly related congenerics, i.e.: (i) *E. aesculapii* (Linnaeus, 1758), based on its dorsal pattern (tricolored coral pattern); (ii) *E. albertguentheri* (Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonatto, 2012), based on its dorsal pattern (variegated green and black), (iii) *E. almadensis* (Wagler, 1824), based on its dorsal pattern (blotched, dark brown marks on a grey background) and ventral pattern (black squares on a red background); (iv) *E. andinus* (Dixon, 1983), based on its dorsal pattern (uniformly green); (v) *E. atraventer* (Dixon & Thomas, 1985), based on its dorsal pattern (uniformly green) and ventral pattern (largely black); (vi) *E. bizona* Jan, 1863, based on its dorsal pattern (tricolored coral pattern); (vii) *E. breviceps* (Cope, 1860), based on its ventral pattern (black squares on a red background); (viii) *E. carajasensis* (Cunha, Nascimento & Avila-Pires, 1985), based on its dorsal pattern (blotched, dark brown marks on a grey background) and ventral pattern (black squares on a red background); (ix) *E. ceii* (Dixon, 1991), based on its dorsal pattern (uniformly green); (x) *E. cobella* (Linnaeus, 1758), based on its ventral pattern (black squares on a red background); (xi) *E. cursor* (Lacépède, 1789), based on its dorsal pattern (blotches on a dark brown background, white stripes in second body third and on tail) and ventral pattern (uniformly white); (xii) *E. festae* (Peracca, 1897), based on its dorsal pattern (large brown blotches on a light grey background) and ventral pattern (large black squares on a white or orange background); (xiii) *E. frenatus* (Werner, 1909), based on its dorsal pattern (black and orange body bands); (xiv) *E. guentheri* Garman, 1883, based on its dorsal pattern (monadal coral pattern, black and red body bands); (xv) *E. ingeri* (Roze, 1958), based on its dorsal pattern (uniformly black) and ventral pattern (large black squares on a white background); (xvi) *E. jaegeri* (Günther, 1858), based on its dorsal pattern (green with brown or black dorsal stripes); (xvii) *E. janaleeae* (Dixon, 2000), based on its dorsal scale counts (17/17/15), dorsal pattern (black bands in first body third, stripes in the other two thirds); (xviii) *E. juliae* (Cope, 1879), based on its dorsal scale counts (17/17/17) and dorsal pattern (white background with diffuse black pigmentation); (xix) *E. maryellenae* (Dixon, 1985), based on its dorsal pattern (uniformly green, or green and brown with stripes); (xx) *E. melanotus* (Shaw, 1802), based on its dorsal pattern (black stripes on a yellow background); (xxi) *E. mertensi* (Roze, 1964), based on its dorsal pattern (black stripes on a grey or dark brown background); (xxii) *E. miliaris* (Linnaeus, 1758), based on its dorsal scale counts (17/17/15) and ventral pattern (ventral scales with black edges, uniformly white, or with black squares); (xxiii) *E. mimus* (Cope, 1868), based on its dorsal pattern (monadal coral pattern, black and red bands); (xxiv) *E. mossoroensis* (Hoge & Lima-Verde, 1973), based on its dorsal scale counts (17/17/15) and dorsal pattern (white reticulations on a white background, with white stripes); (xxv) *E. ocellatus* Peters, 1869, based on its dorsal pattern (black ocelli on a red background); (xxvi) *E. ornatus* (Garman, 1887), based on its dorsal pattern (white blotches on a dark brown background, with light brown body stripes); (xxvii) *E. perfuscus* (Cope, 1862), based on its higher ventral counts (182–200) and dorsal pattern (uniformly brown); (xxviii) *E. pseudocorallus* Roze, 1959, based on its dorsal pattern (monadal coral pattern, with black and red bands); (xxix) *E. pseudoreginae* Murphy, Braswell, Charles, Auguste, Rivas, Borzéé, Lehtinen & Jowers, 2019, based on its dorsal scale counts (17/17/15) and dorsal pattern (green or brown, with black stripes); (xxx) *E. pyburni* (Markezich & Dixon, 1979), based on its dorsal scale counts (15/15/15) and dorsal pattern (large dark brown blotches in first body third, variegated in the other two thirds); (xxxi) *E. pygmaeus* (Cope, 1868), based on its dorsal scale counts (17/17/15) and ventral coloration (uniformly red); (xxxii) *E. sagittifer* (Jan, 1863), based on its dorsal pattern (large dark brown blotches on a light yellow background); (xxxiii) *E. semiaureus* (Cope, 1862), based on its dorsal scale counts (17/17/15) and dorsal pattern (light yellow background with reticulated black scales); (xxxiv) *E. subocularis* (Boulenger, 1902), based on its dorsal scale counts (17/17/17) and dorsal pattern (black and yellow stripes); (xxxv) *E. taeniogaster* (Jan, 1863), based on its ventral pattern (black squares on a red background); (xxxvi) *E. taeniurus* (Tschudi, 1845), based on its dorsal pattern (dark body bands on a light grey background); (xxxvii) *E. torrenicola* (Donnelly & Myers, 1991), based on its dorsal pattern (white nuchal collar, dark brown background coloration with alternating white blotches) and ventral pattern (large brown squares on a white background); (xxxviii) *E. trebbaui* (Roze, 1958), based on its dorsal pattern (uniformly dark brown) and ventral pattern (black squares on a white background); (xxxix) *E. triscalis* (Linnaeus, 1758), based on its dorsal pattern (black stripes on a light yellow background); (xl) *E. typhlus* (Linnaeus, 1758), based on its dorsal pattern (uniformly green, or green with brown blotches); (xli) *E. viridis* (Günther, 1862), based on its dorsal pattern (uniformly green, or green with black crossbands); (xlii) *E. vitti* (Dixon, 2000), based on its dorsal pattern (dark brown body bands on a red background); and (xliii) *E. williamsi* (Roze, 1958), based on its dorsal pattern (dark brown with black stripes) (data adopted from Boulenger 1902, Cunha & Nascimento 1980, Dixon 1981, 1983a, b, c, d, 1985, 1987, 1991, Dixon & Thomas 1982, 1985, Cunha et al.1985, Donnelly & Myers 1991, Fernandes et al. 2002; Curcio et al. 2015; Murphy et al. 2019).

Snout osteology (AMNH 60803, Figs 9–10): Premaxilla triangular in frontal view, with ascending and transverse processes of about the same length; ascending process ends slightly concave, approaching nasals, but still remaining clearly separated from them; transverse processes rela-

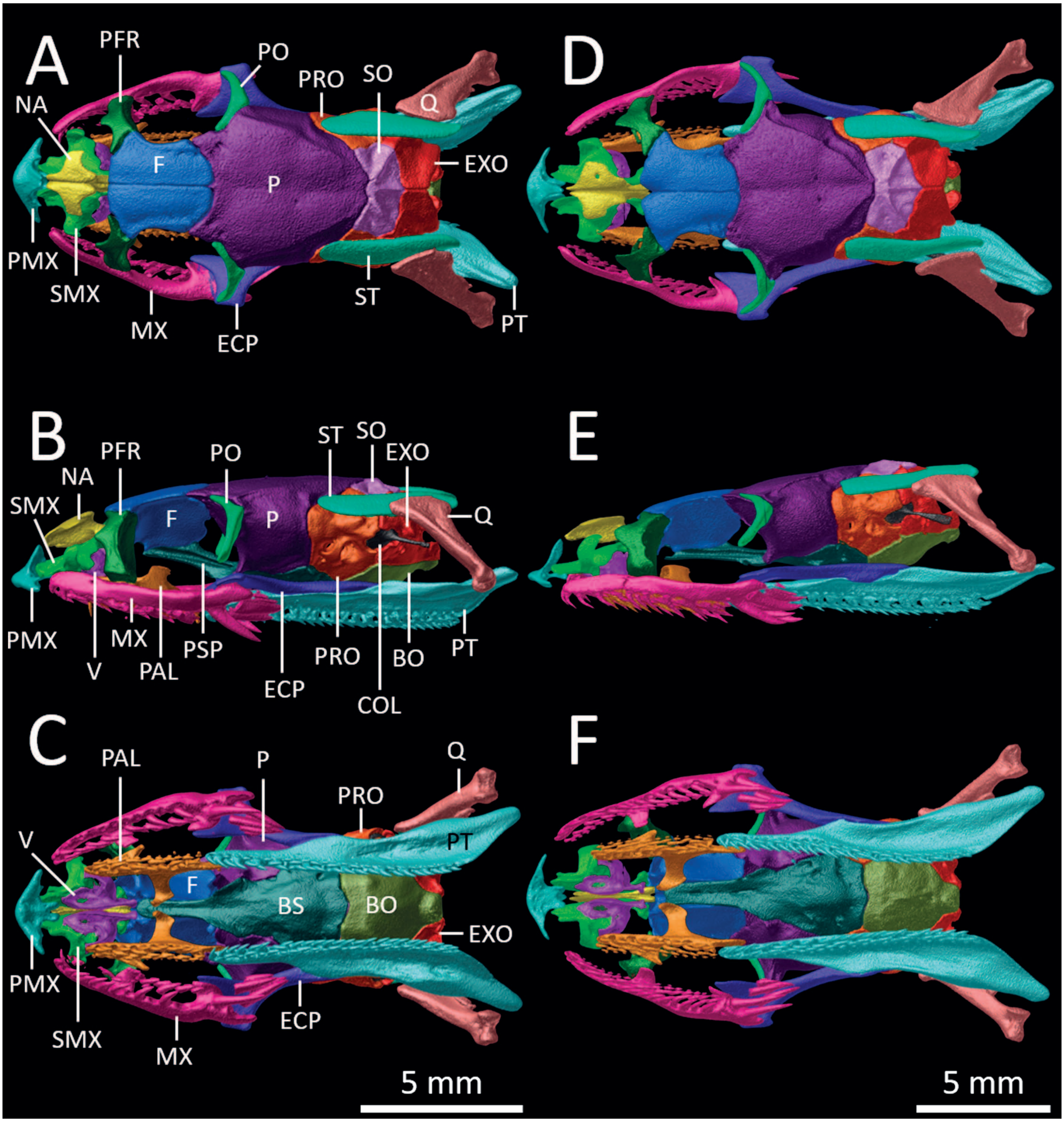

Figure 9. (A, D) Dorsal, (B, E) lateral, and (C, F) ventral views of the skull of *Erythrolamprus aenigma* (A–C; AMNH 60803) and *E. poecilogyrus schotti* (D–F; UMMZ 153016) based on µCT imagery. Different skull elements are digitally colored and the mandible is removed for better visualization. Abbreviations are as follows: BO = basioccipital; BS = basisphenoid; COL = columella; ECP = ectopterygoid; EXO = exoccipital; F = frontal; MX = maxilla; NA = nasal; P = parietal; PAL = palatine; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PRO = prootic; PSP = parasphenoid rostrum; PT = pterygoid; Q = quadrate; SMX = septomaxilla; SO = supraoccipital; ST = supratemporal; V = vomer.

tively pointed in the direction of the first maxillary tooth, but remaining clearly distant from it; vomerine processes short, approaching vomers but remaining distinctly separated from them. Septomaxillae slightly separated from each other; contacting premaxilla anteriorly, anteroventral tip of frontals posteriorly, posterior process of nasals posteromedially, and vomers ventrally; each with short, posterodorsally pointed ascending conchal process, freely extending beyond lateral margins of nasals. Nasals subtriangular in dorsal view, in contact medially, each with a tapered anterior process and a broad, almost rectangular lateral process; posterior process contacting medioventral region of frontals, and approaching, but not contacting anterior tip of parabasisphenoid rostrum. Vomers slightly separated from each other; each with a globular mesoventral portion that laterally contacts the anterior ends of

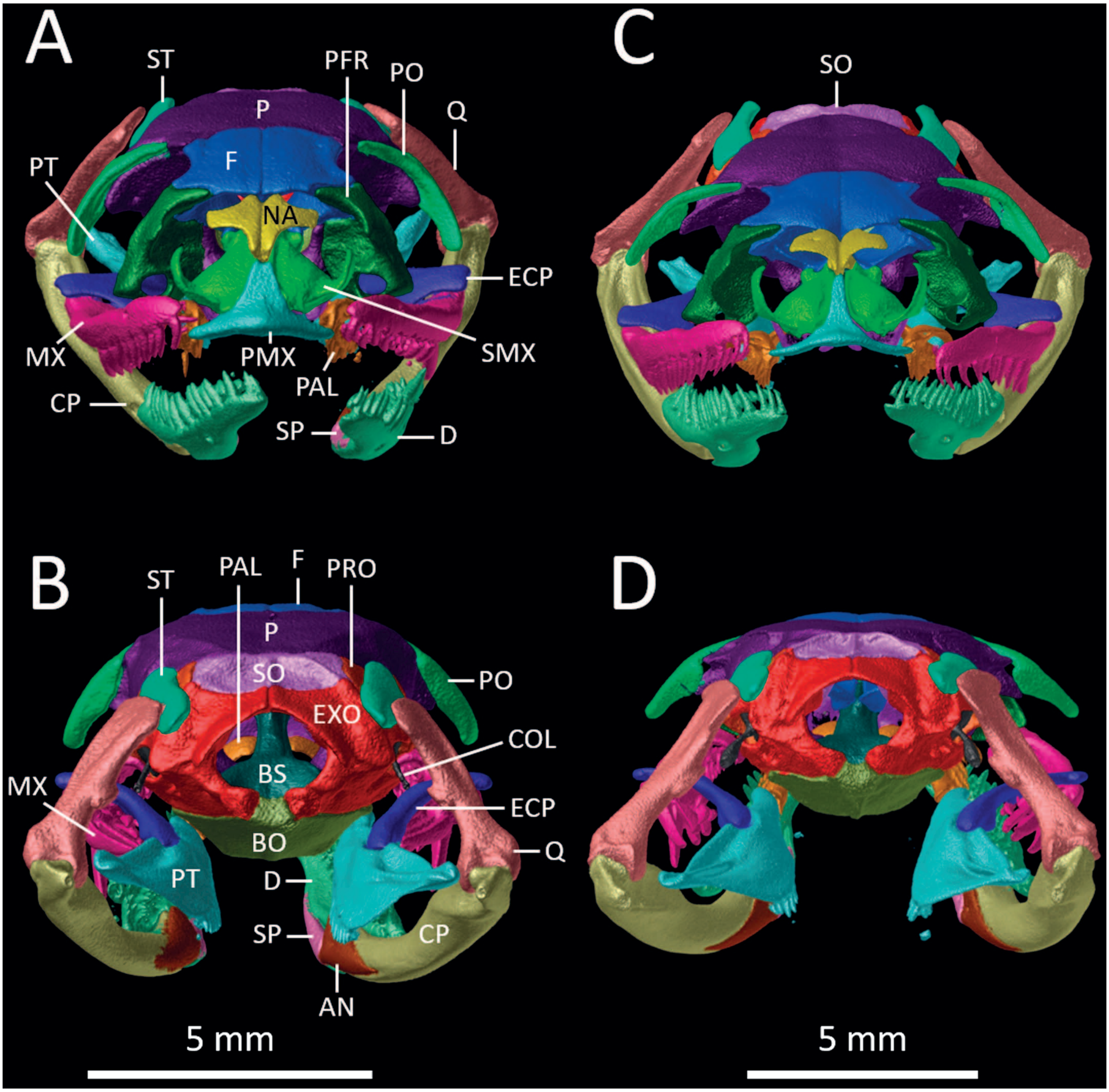

Figure 10. (A, C) Anterior and (B, D) posterior views of the skull and lower jaw of *Erythrolamprus aenigma* (A, B; AMNH 60803) and *E. poecilogyrus schotti* (C, D; UMMZ 153016) based on μCT imagery. Different skull elements are digitally colored to improve visualization. Abbreviations are as follows: AN = angular; BO = basioccipital; BS = basisphenoid; COL = columella; CP = compound bone; D = dentary; ECP = ectopterygoid; EXO = exoccipital; F = frontal; MX = maxilla; NA = nasal; P = parietal; PAL = palatine; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PRO = prootic; PT = pterygoid; Q = quadrate; SMX = septomaxilla; SO = supraoccipital; SP = splenial; ST = supratemporal.

palatines; vertical posteromedial laminae with large circular fenestra.

Braincase osteology (AMNH 60803): Prefrontals forming anterior margins of orbits, with a triangular anterior process in lateral view; in contact with frontals dorsally, and maxillary process of palatines ventromedially; not contacting maxilla ventrally; in anteroposterior view a large lacrimal foramen is visible in the ventral region. Frontals in contact medially with a straight suture, longer than wide; convex anterior and posterior margins and concave lateral margins in dorsal view; forming anterodorsal margin of orbits; posteriorly contacting parietal with a curved suture; ventral edges of vertical laminae of frontals in contact medially, together forming a deep groove which dorsally and laterally encloses the dorsal projection of parabasisphenoid. Parietal single, approximately round in dorsal view; forming posterodorsal margin of orbit; contacting postorbitals anterolaterally, supraoccipital posteriorly, prootics and marginally anterior tip of left supratemporal posterolaterally (right supratemporal slightly separated from parietal), and parabasisphenoid ventrally; dorsolateral oblique ridges extending from region of contact with postorbitals to slightly anterior to region of contact with supraoccipital. Postorbitals long, narrow, slightly crescent-shaped in lateral view; forming the posterolateral margin of the orbit; ventral edge approaching ectopterygoid, but still remaining clearly separated from it. Supraoccipital single, almost rectangular, broader than long, in contact with prootics laterally, and exoccipitals posteriorly; two posterolaterally orientated oblique ridges and a medial posteriorly oriented

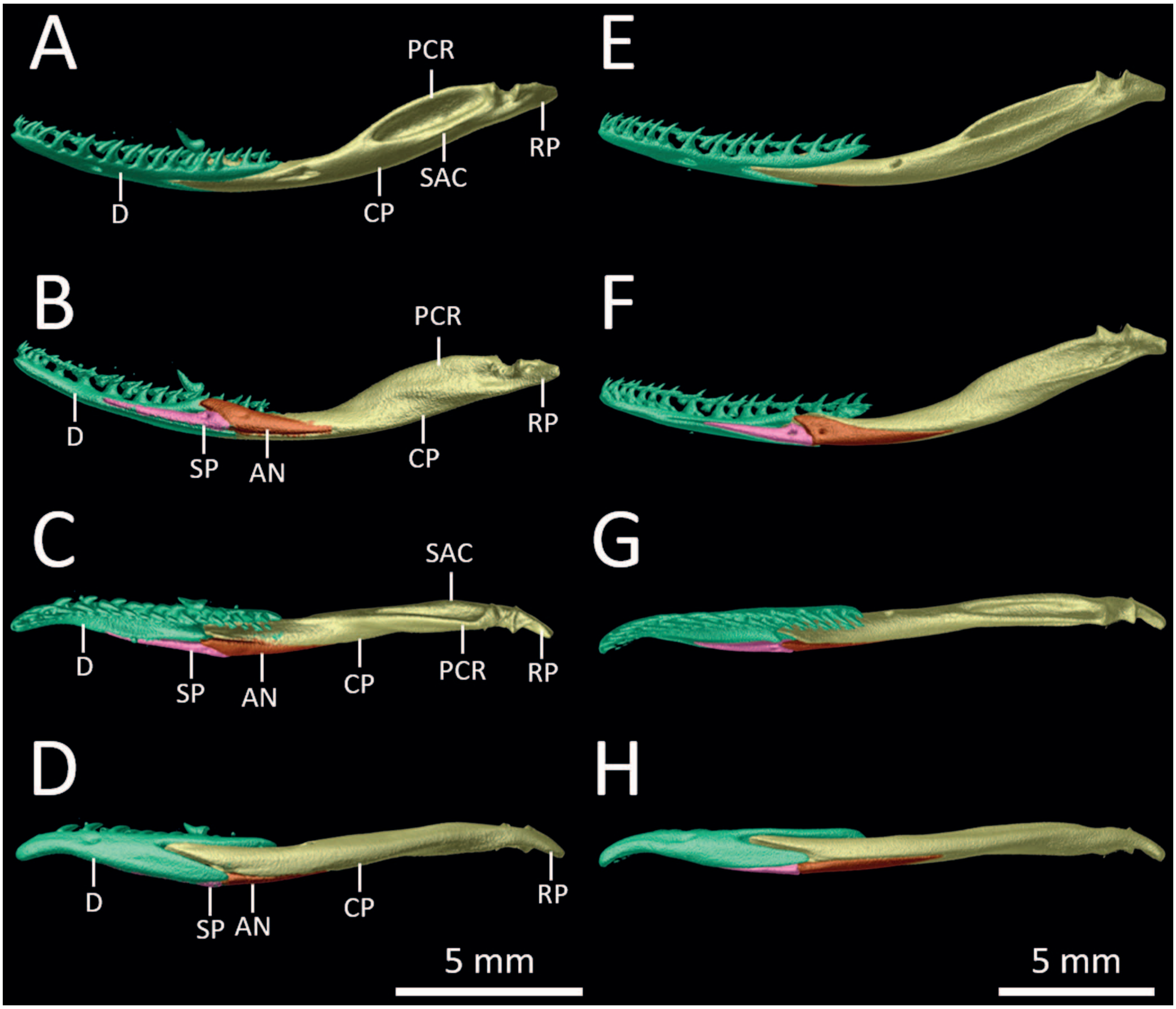

Figure 11. (A, E) Lateral, (B, F) medial, (C, G) dorsal, and (D, H) ventral views of the lower jaw of *Erythrolamprus aenigma* (A–D; AMNH 60803) and *E. poecilogyrus schotti* (E–H; UMMZ 153016) based on µCT imagery. Different skull elements are digitally colored to improve visualization. Abbreviations are as follows: AN = angular; CP = compound bone; D = dentary; PCR = prearticular crest of compound bone; RP = retroarticular process of compound bone; SAC = surangular crest of compound bone; SP = splenial.

ridge emerge from anteromedial region of supraoccipital. Exoccipitals paired, in contact dorsomedially but not ventrally, irregularly shaped, each with a lateral ridge continuous with the posterolateral ridge of the supraoccipital; in contact with prootic anterolaterally, supratemporal dorsolaterally, and basioccipital ventrally; forming the posterior margin of the fenestra ovalis at its suture with the prootic; forming the dorsal, lateral, and lateroventral borders of the foramen magnum. Prootics nearly hexagonal in lateral view, each with a large, a medium-sized, and a small foramen and uneven surface; each dorsally largely overlain by the supratemporal, in contact with parabasisphenoid complex anteroventrally and basioccipital posteroventrally; forming anterior margin of fenestra ovalis at posterior suture with exoccipitals. Columella auris is inserted in fenestra ovalis, with oval footplate firmly contacting prootic anteriorly and exoccipital posteriorly; long, thin shaft extending towards quadrate but remaining distinctly separated from it. Basioccipital nearly pentagonal; in contact with parabasisphenoid complex anteriorly; forming ventral border of foramen magnum posteriorly; medial portion with two dentigerous processes and slight longitudinal medial ridge. Parasphenoid and basisphenoid fused; basisphenoid portion nearly hexagonal, with a small anterolateral and two posterolateral foramina on each side; parasphenoid rostrum distinctly surpassing choanal process of palatine anteriorly, with rounded front end.

Palatomaxillary arch osteology (AMNH 60803, Fig. 11): Maxillae elongate, extending to posterior border of postorbital; posterior region in contact with anterior region of ectopterygoid; slightly arched toward premaxilla; forming the ventral margin of orbit; ventral surface of maxillae with thirteen prediastemal tooth loci and two enlarged and ungrooved postdiastemal teeth; teeth curved and rear-facing, increasing in size posteriorly; palatine process situated at level of seventh to ninth teeth, approaching but not contacting maxillary process of palatine; ectopterygoid process from behind last prediastemal tooth up to and including level of first postdiastemal tooth. Ectopterygoids axe-shaped and flattened, with anterior end bifurcated into a triangular and pointed anteromedial process and a nearly quadrangular anterolateral process; rod-like, almost straight posterior process, posterior part of which in close contact ventrally with dorsal face of lateromedial region of pterygoid. Palatines slender and straight; ventral surface with twelve (left palatine) or thirteen (right palatine) tooth loci; teeth slightly curved and rear-facing; short, triangular, posterolaterally directed maxillary process situated at level of fourth to sixth (left palatine) teeth or seventh (right palatine) tooth; long, about rectangular, strongly curved and medially directed choanal process situated at level of seventh to tenth (left palatine) teeth or eleventh (right palatine) tooth; approaching but not contacting its counterpart anteromedially; posterior end toothless, flattened, and medially in contact with anterior part of pterygoid; a short, posterolaterally directed, thumb-like process behind the last tooth. Pterygoids elongate, corresponding to approximately 60 % length of skull, ventral surface with twenty-five tooth loci; teeth slightly curved and rear-facing; anterior portion up to level of about the eighth tooth slender, broadening posteriorly up to level of the last tooth, and tapering posterolaterally between last tooth and rounded posterior end; both pterygoids nearly parallel along tooth line and laterally apart posterior to tooth line; dorsal surface with a median longitudinal ridge extending from a point posterior to contact zone with ectopterygoid to posterior end.

Suspensorium and mandible osteology (AMNH 60803): Supratemporals elongate and laminar; posterolaterally (except the ultimate end) contacting quadrate (left supratemporal) or remaining slightly separated from it (right supratemporal); posterior end freely surpassing the posterior edge of the exoccipital. Quadrate elongate, obliquely orientated, dorsal portion flattened; dorsal portion distinctly broader than ventral portion; medial region at about mid-length with short process in direction of stapedial shaft, but remaining distinctly separated from it; ventral portion straddling glenoid cavity of retroarticular process of compound bone; ventromedial portion approaching but not contacting pterygoid. Dentaries elongate, medially curved anteriorly; dorsal surface with twenty-one (left dentary) or twenty-two (right dentary) tooth loci; teeth slightly curved and rear-facing; mental foramen located at about level of tenth tooth; dentary branching at about level of fifteenth tooth into longer and slenderer tooth-bearing dorsal process, and shorter and broader ventromedial process; dorsal process branching again at level between seventeenth tooth into very short medial process and much longer tooth-bearing dorsal process; contacting splenial medially, compound bone posteriorly, and anterodorsal tip of angular with tip of medial process and anteroventral region of angular with posterior end of ventromedial process. Splenials elongate, triangular, tapering anteriorly and reaching to level of tenth dentary tooth; anterior mylohyoid foramen slightly anterior to summit; posterior edge in contact with anterior edge angular. Angulars elongate, triangular, tapered posteriorly; in contact with compound bone laterally; posterior mylohyoid foramen located centrally, approximately at end of first third of angular. Compound bones elongate, approximately 70 % length of mandible; in ventral view, tapering anteriorly, fitting between dorsal and ventromedial processes of dentary; prearticular crest prominent, distinctly higher than surangular crest, and visible in lateral view; surangular crest not visible in medial view; laterally oriented foramen, approximately at end of first third of compound bone; retroarticular process stout, medially directed.

Additional remarks: Our work raises the number of *Erythrolamprus* species to 52. Of these, 21 nominal taxa were previously known from Brazil (Costa & Bérnils 2018, Nogueira et al. 2019). Our analyses also conclude that populations formerly known as *E. p. schotti* for the open areas of Roraima, northern Brazil, Guyana, and Bolívar, Venezuela, are referable to one reciprocally monophyletic and morphologically distinguishable taxon, distinct from the populations of *E. p. schotti* of southeastern and northeastern Brazil. Therefore, we argue that *E. p. schotti* should be excluded from the list of species of Roraima state. The only two known specimens from Venezuela, from Bolívar province, are now reportedly lost (O.M. Entiauspe-Neto, unpubl. obs.). Populations from Venezuela formerly assigned to *E. p. schotti* likely also refer to our new species; a specimen from Monagas, Anzoátegui province, Venezuela, reported by Natera-Mumaw et al. (2006) fits well the diagnosis of *E. aenigma*, rather than *E. p. schotti*. However, this specimen was not collected, and we refrain from considering it representing *E. aenigma* until further samples from this locality become available for examination.

In its current sense, *E. poecilogyrus* has a wide geographic distribution, ranging from northern Brazil, in Amapá, to southeastern Argentina, in Buenos Aires, and four largely allopatric and diagnosable subspecies (Dixon & Markezich 1992). A taxonomic revision, preferably integrating morphological and molecular evidence, is warranted in order to evaluate the taxonomic status of these subspecies and other proposed names associated with this species.

Our study also highlights the presence of morphologically cryptic, yet evolutionary different lineages within widely distributed species, such as *E. poecilogyrus*. Within Brazil, at least 18 subspecies of *Erythrolamprus* taxa are currently recognized (Costa & Bérnils 2018). Upon closer revision, these entities, which in most cases are allopatric and can be morphologically diagnosed, are likely to be either elevated to specific level or synonymized in further works.

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Appendix I

Material examined

Countries are given in capitals, states in small capitals, followed by municipalities and localities.

Erythrolamprus aesculapii (n = 1). BRAZIL: Minas Gerais: Poço Fundo (MCP 861).

Erythrolamprus almadensis (n = 1). BRAZIL: São Paulo: Oriente (MCP 865).

Erythrolamprus andinus (n = 1). BOLIVIA: Cochabamba: Incachaca (CM-R 2808).

Erythrolamprus atraventer (n = 1). BRAZIL: São Paulo: Oriente (MCP 54001).

Erythrolamprus breviceps (n = 1). BRAZIL: Amazonas: Manaus (MZUSP 8189).

Erythrolamprus cobella (n = 1). BRAZIL: Amapá: Oiapoque (IBSP 24853).

Erythrolamprus epinephelus bimaculatus (n = 2). COLOMBIA: Unknown locality (AMNH 17532, 17604, cotypes of *Liophis bimaculatus*).

Erythrolamprus epinephelus epinephelus (n = 1). COLOMBIA: Chocó: Truando river (ANSP 3688, holotype of *Liophis epinephelus*).

Erythrolamprus epinephelus opisthotaenia (n = 1). VENEZUELA: Mérida: Unknown locality (BMNH 1946.1.4.55, holotype of *Liophis opisthotaenia*).

Erythrolamprus dorsocorallinus (n = 8). BRAZIL: Acre: Estação Ecológica Rio Acre, Assis Brasil (CHUPFRE 4378), Marechal Thaumaturgo (ZUEC 1587, 1971, 1972, 1973), Reserva Extrativista Liberdade, Tarauacá (UFAC 405, 664, 918).

Erythrolamprus festae (n = 1). ECUADOR: Unknown locality, "Valley of Santiago river" (MZUT-R 2108, holotype of *Liophis festae*).

Erythrolamprus fraseri (n = 1). ECUADOR: Unknown locality, "West Ecuador" (BMNH 1946.1.6.63, holotype of *Liophis fraseri*).

Erythrolamprus ingeri (n = 1). VENEZUELA: Bolívar: Chimantá-Tepui (FMNH 74038, holotype of *Liophis ingeri*).

Erythrolamprus jaegeri (n = 7). BRAZIL: Rio Grande do Sul: Rio Grande (CHFURG 4793, 4795, 4806, 4808, 4809, 4839, 4840).

Erythrolamprus janaleeae (n = 1). PERU: San Martín: Moyobamba (BMNH 74.8.4.62, holotype of *Liophis janaleeae*).

Erythrolamprus macrosomus (n = 11). BRAZIL: Goiás: Minaçu (MCP 8326, 8327, 8328, 8329, 13057, 13058, 13059, 13060, 13061, 13062, 13063, topotypes).

Erythrolamprus miliaris merremii (n = 3). BRAZIL: Minas Gerais: Véu da Noiva (CHFURG 4857, 4859); Rio de Janeiro: Guapimirim (CHFURG 4858).

Erythrolamprus oligolepis (n = 1). Acre: Estação Ecológica Rio Acre, Assis Brasil (UFAC 0477).

Erythrolamprus poecilogyrus caesius (n = 12). ARGENTINA: Santa Fé: Santa Fé (USNM 5395, holotype of *Opheomorphus doliatus* var. *caesius);* PARAGUAY: Unknown locality (MHNP 2603, 2258, 7945, 11695); BRAZIL: Mato Grosso do Sul: Porto Murtinho (IBSP 91882, 91883, 91884, 91943, 91944, 91945, 91893).

Erythrolamprus poecilogyrus poecilogyrus (n = 6). BRAZIL: Espírito Santo: Barra do Jucú, near Vitória (AMNH-R 3593, 3594, syntypes of *Coluber poecilogyrus*); Rio de Janeiro: Caxias (CHFURG 4863, 4868), Marangá (CHFURG 4865), Realengo (CHFURG 4864).

Erythrolamprus poecilogyrus schotti (n = 117). BOLIVIA: Santa Cruz: Santa Cruz (UMMZ 153016); BRAZIL: Amapá: Boa Vista (UFAP, Unvouchered); Ceará: Canindé (IBSP 77520, 77521), Ubajara (IBSP 77099, 77104), Viçosa do Ceará (IBSP 77238); Bahia: Correntina (MZUESC 8178), Cruz das Almas (CGBR 6706), Lauro de Freitas (MZUEFS 793); Mucugê (MZUESC 4921, 5132); Juazeiro (MZUEFS 1392); Rio Grande do Sul: Cerro Largo (ZUFSM 2589, 2590), Derrubadas (ZUFSM 2968, 2969, 2970, 2971, 2973), Roque Gonzales (ZUFSM 2615, 2616, 2618, 2620), Santa Maria (ZUFSM 0323, 0350, 0359, 0373, 0379, 0437, 0438, 0439, 0506, 0644, 0540, 0559, 0565, 0568, 0581, 0594, 0601, 0618, 626, 0627, 0629, 0665, 0671, 0775, 0796, 0814, 0828, 0829, 0830, 0864, 0937, 0938, 0941, 0945, 0949, 0953, 0998, 1003, 1008, 1018, 1096, 1097, 1101, 1125, 1127, 1151, 1157, 1170, 1174, 1188, 1191, 1238, 1259, 1276, 1286, 1297, 1322, 1324, 1331, 1349, 1357, 1370, 1374, 1402, 1420, 1439, 1495, 1541, 1594, 1599, 1633, 1656, 1674, 1715, 1717, 1720, 1798, 2186, 2286, 2301, 2321, 2378, 2505, 2506, 2622, 2524, 2527, 2528, 2529, 2530, 2626, 2630, 2915); Pará: Santarém (IBSP 15039, holotype of *Leimadophis poecilogyrus amazonicus* and *Dromicus poecilogyrus lancinii*, lost); São Paulo: Unknown locality (RMNH 236, lectotype of *Xenodon schotti*), São Paulo (IBSP 91323).

Erythrolamprus poecilogyrus sublineatus (n = 49). BRAZIL: Rio Grande do Sul: Pelotas (CHFURG 4775), Rio Grande (CHFURG 959, 960, 961, 962, 963, 964, 965, 966, 967, 968, 969, 970, 971, 972, 973, 974, 975, 978, 979, 980, 981, 982, 983, 984, 985, 986, 987, 988, 989, 990, 991, 992, 993, 994, 995, 996, 997, 998, 999, 1000, 1001, 1002, 1003, 1004, 1005, 1006, 1007), Rosário do Sul (IBSP 91822).

Erythrolamprus reginae (n = 11). BRAZIL: Acre: Estação Ecológica Rio Acre, Assis Brasil (CHUPFRE 4394, 4423, 4929); Amazonas: Tabatinga (MCP 14093, 14115); Ceará: Ubajara (IBSP 77051, 77097, 77100, 77233, 77551, 77552).

Erythrolamprus rochai (n = 2). BRAZIL: Amapá: Urucum, Serra do Navio (MPEG 25680, holotype of *Erythrolamprus rochai*, 25681, paratype of *Erythrolamprus rochai*).

Erythrolamprus typhlus (n = 1). BOLIVIA: Santa Cruz: Santa Cruz de la Sierra (MCZ-R 11860, paratype of *Liophis elaeoides*).

Erythrolamprus torrenicola (n = 1). VENEZUELA: Bolívar: Cerro Guaiquinima (AMNH 136211, holotype of *Liophis torrenicola*).

Erythrolamprus vitti (n = 1). ECUADOR: Unknown locality, "Paramba" (BMNH 1901.3.29.108, paratype of *Liophis vitti*).

Erythrolamprus williamsi (n = 1). VENEZUELA: Distrito Federal: El Junquito, near Caracas (MCZ-R 51329, holotype of *Liophis williamsi*).

Erythrolamprus zweifeli (n = 2). VENEZUELA: Aragua: Rancho Grande (MBUCV 95, holotype of *Leimadophis zweifeli*, MCZ-R 62496, paratype of *Leimadophis zweifeli*).

Supplementary data

The following data are available online:

Supplementary Table 1. GenBank accession numbers for generated and used sequences for molecular phylogeny.

Supplementary Table 2. Patristic distances between the genera *Dipsas*, *Erythrolamprus*, *Lygophis* and *Xenodon*, as inferred in this study.

Supplementary Table 3. Data used for estimation of patristic distances between the genera *Dipsas*, *Erythrolamprus*, *Lygophis* and *Xenodon*, as inferred in this study.

Supplementary File 1. Phylogenetic analysis as per maximum likelihood, raw file, in ".tre" format.

Supplementary File 2. Phylogenetic analysis as per maximum likelihood, branches equal to genetic distance, in ".png" format.