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A NEW SPECIES OF *ERYTHROLAMPRUS* (SERPENTES: DIPSADIDAE) FROM THE ANDES OF ECUADOR

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ABSTRACT

We describe a new species of *Erythrolamprus* from the eastern slopes of the Tropical Andes in Ecuador. The most similar species in morphology and color patterns are *E. fraseri* and *E. lamonae*. However, this new species differs in dorsal and ventral color patterning, as well as scale count and hemipenial morphology. Previous molecular phylogenies strongly support monophyly of the new species described herein and its sister taxon relationship with *E. fraseri* from the western slopes of the Andes of Ecuador and northern Peru. An identification key for species of Ecuadorian *Erythrolamprus* formerly assigned as subspecies of *E. epinephelus* is provided.

With over 800 species, Dipsadidae Bonaparte, 1838 is the richest Neotropical snake clade traditionally ranked as a family (Zaher et al., 2009). One of the most diverse and widespread clades within Dipsadidae is Xenodontini Bonaparte, 1845, which is diagnosed by lacking hemipenial calyces and capitular grooves, having paired nude hemipenial apical disks and exhibiting a horizontal neck flattening behavior (Myers, 1986; Zaher et al., 2009). Within Xenodontini, *Erythrolamprus* Boie, 1826 (sensu Grazziotin et al., 2012) is the most diverse genus with 55 currently recognized species ranging from Honduras to Argentina, throughout the Andes and Amazon basin and in the Lesser Antilles, between sea level and ~4,000 m in elevation (Dixon, 1989, 2000; Solís et al., 2014). *Erythrolamprus* spp. are diurnal, medium-sized (∼50–150 cm total length) snakes that exhibit a wide range of coloration patterns, ranging from uniform to striped bodies, uniform or checkered venters, and a few species mimic highly venomous coral snakes (Curcio et al., 2009; Dixon, 1989). Members of *Erythrolamprus* are primarily terrestrial, but some species have semi-aquatic and fossorial habits; they occupy many habitats including rainforests, savannas, thorn forests, mountain forests, and páramos (Dixon, 1980).

Until recently, *Erythrolamprus epinephelus* Cope, 1862 was considered one of the most widespread species of *Erythrolamprus*, occurring from Costa Rica to northern Peru and throughout the Andes of Venezuela, Colombia, and Ecuador, with the greatest altitudinal distribution (0–3,400 m) of all congenerics (Dixon, 1983). Dixon (1983) recognized eight subspecies within *E. epinephelus* based on scutellation characters, teeth, and, more importantly, color patterns: *E. e. epinephelus*, *E. e. albiventris* Jan, 1863, *E. e. fraseri* Boulenger, 1894, *E. e. bimaculatus* Cope, 1899, *E. e. opisthotaenius* Boulenger, 1908, *E. e. pseudocobellus* Peracca, 1914, *E. e. juvenalis* Dunn, 1937 and *E. e. lamonae* Dunn, 1944. Subsequently, Bernal-Carlo (1994) described *E. e. kogiorum* from Colombia. However, a recent phylogenetic hypothesis based on maximum likelihood and Bayesian analyses of six genes and 24 species of *Erythrolamprus* showed that *E. epinephelus* was paraphyletic. Consequently, *E. e. albiventris*, *E. e. fraseri*, and *E. e. lamonae* were elevated to distinct species (Torres-Carvajal & Hinojosa, 2020). In the same study, an undescribed species of *Erythrolamprus* from the central Andes of Ecuador was identified as sister taxon to *E. fraseri*. Here we describe this species based on color patterns, external morphology, and hemipenial characters.

MATERIALS AND METHODS

In addition to the type material presented in the results, we examined 20 specimens of *Erythrolamprus* (Appendix 1) housed in three herpetological collections in Quito, Ecuador: Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Museo de Historia Natural Gustavo Orcés, Escuela Politécnica Nacional (EPN), and División de Herpetología del Instituto Nacional de Biodiversidad (DHMECN). We took measurements with a caliper to the nearest 0.1 mm, except for snout-vent length (SVL) and tail length (TL), which were recorded with a tape measure. Terminology for scales followed Dixon (1983); ventral scales were counted as proposed by Dowling (1951). The terminal scale was not included in the subcaudal counts, and paired head scales were counted on the right side. Scutellation data of species of *Erythrolamprus* compared with the new species described herein were taken from Dixon (1983) and examined material (Appendix 1). We determined sex by noting the presence or absence of hemipenes as revealed through a ventral incision at the base of the tail. Left hemipenes of *E. fraseri* (QCAZ 14056), *E. lamonae* (QCAZ 9032), and the new species described herein (QCAZ 9962) were prepared using standard techniques (Pesantes, 1994) and described following the terminology in Dowling and Savage (1960) and Zaher (1999). Data on phylogenetic relationships were taken from Torres-Carvajal and Hinojosa (2020).

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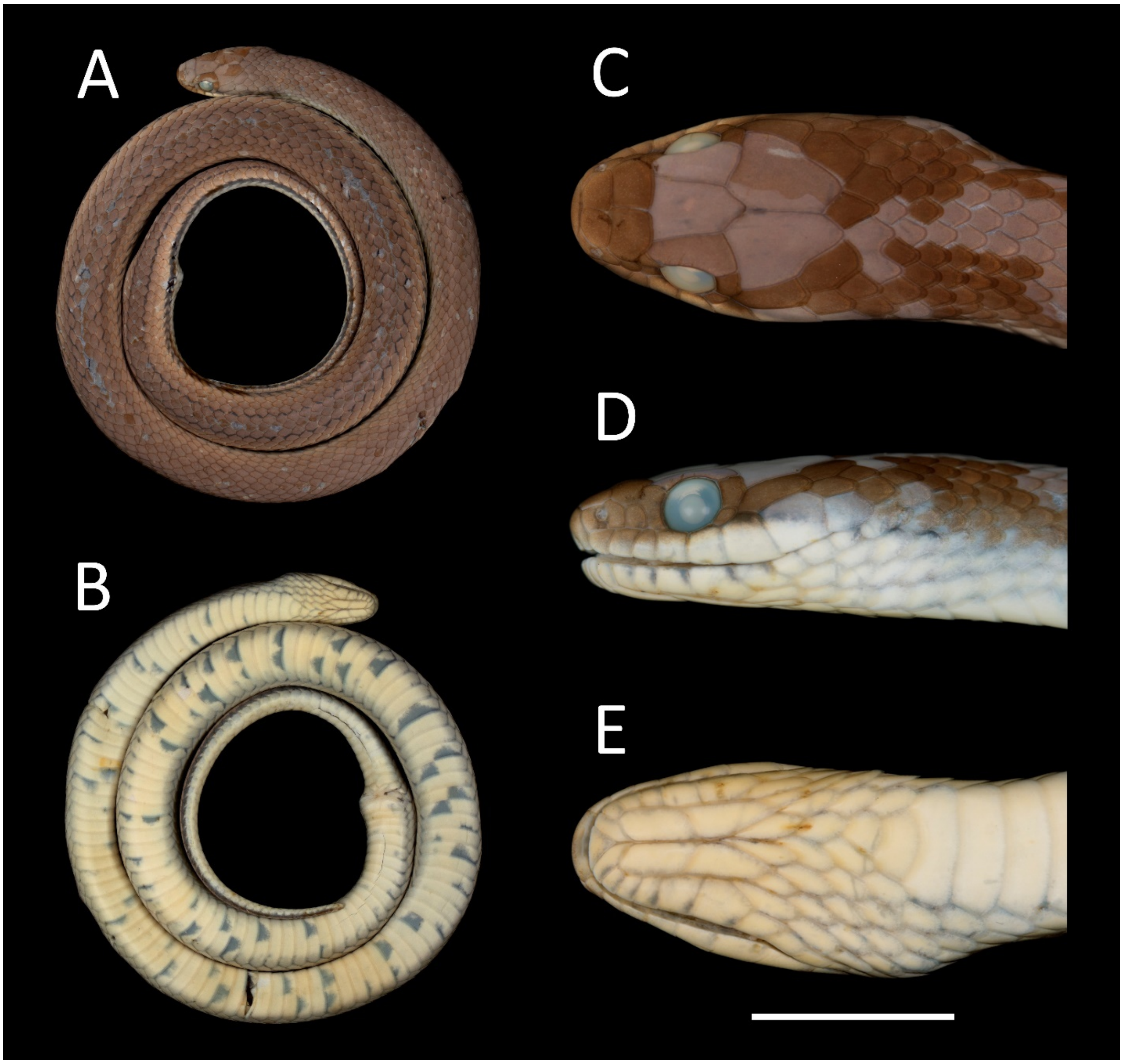

FIGURE 1. Holotype of *E. darwinnunezi* sp. nov. (female, QCAZ 9972) in preservative. Dorsal (A) and ventral (B) views of the body (374 mm SVL), and dorsal (C), lateral (D), and ventral (E) views of the head. Scale bar (C, D, E) = 10 mm.

RESULTS

We followed the general lineage or unified species concept (de Queiroz, 1998, 2007), according to which a highly corroborated hypothesis of existence of a separate species requires multiple lines of evidence. We present phenotypic data (i.e., morphological features, color patterns), which corroborate the hypothesis of a new species of *Erythrolamprus* presented by Torres-Carvajal and Hinojosa (2020) based on phylogenetic relationships and genetic distances.

Erythrolamprus ***darwinnunezi*** sp. nov.

Liophis epinephelus lamonae (Dixon, 1983) in part.

Erythrolamprus epinephelus (Torres-Carvajal et al., 2019) in part.

Erythrolamprus sp. (Entiauspe-Neto et al., 2021; Torres-Carvajal & Hinojosa, 2020).

Holotype.—An adult female, QCAZ 9972 (Fig. 1), collected on 19 October 2009 at 1215 h by S. Aldás at Llanganates National Park, near boundary with Asociación de la Nacionalidad Kichwa Agroecológica Kushillu Urku Community Reserve (1.270°S, 78.056°W, 2,037 m), Pastaza Province, Ecuador.

Paratypes (8).—In Pastaza Province, Ecuador: (1) juvenile male, QCAZ 9962, collected on 15 October 2009 by E. Tapia at Llanganates National Park, near boundary with Asociación de la Nacionalidad Kichwa Agroecológica Kushillu Urku Community Reserve (1.280°S, 78.072°W, 2,000 m); (2) juvenile female, QCAZ 9973, collected on 19 October 2009 by A. Alvarado at type locality. In Tungurahua Province, Ecuador: (3) juvenile male, QCAZ 10001, collected on 20 November 2009 by S. Aldás at Caserío Poatug (1.273°S, 78.491°W, 2,547 m); (4–6) three adult males, EPN 9111, 9112, and 9113, collected by L. Albuja and J. Urgilés in Ambato (1.233°S, 78.617°W, 2,547 m); (7, 8) two juvenile males, QCAZ 18244 and 18245, collected on 23 November 2022 by

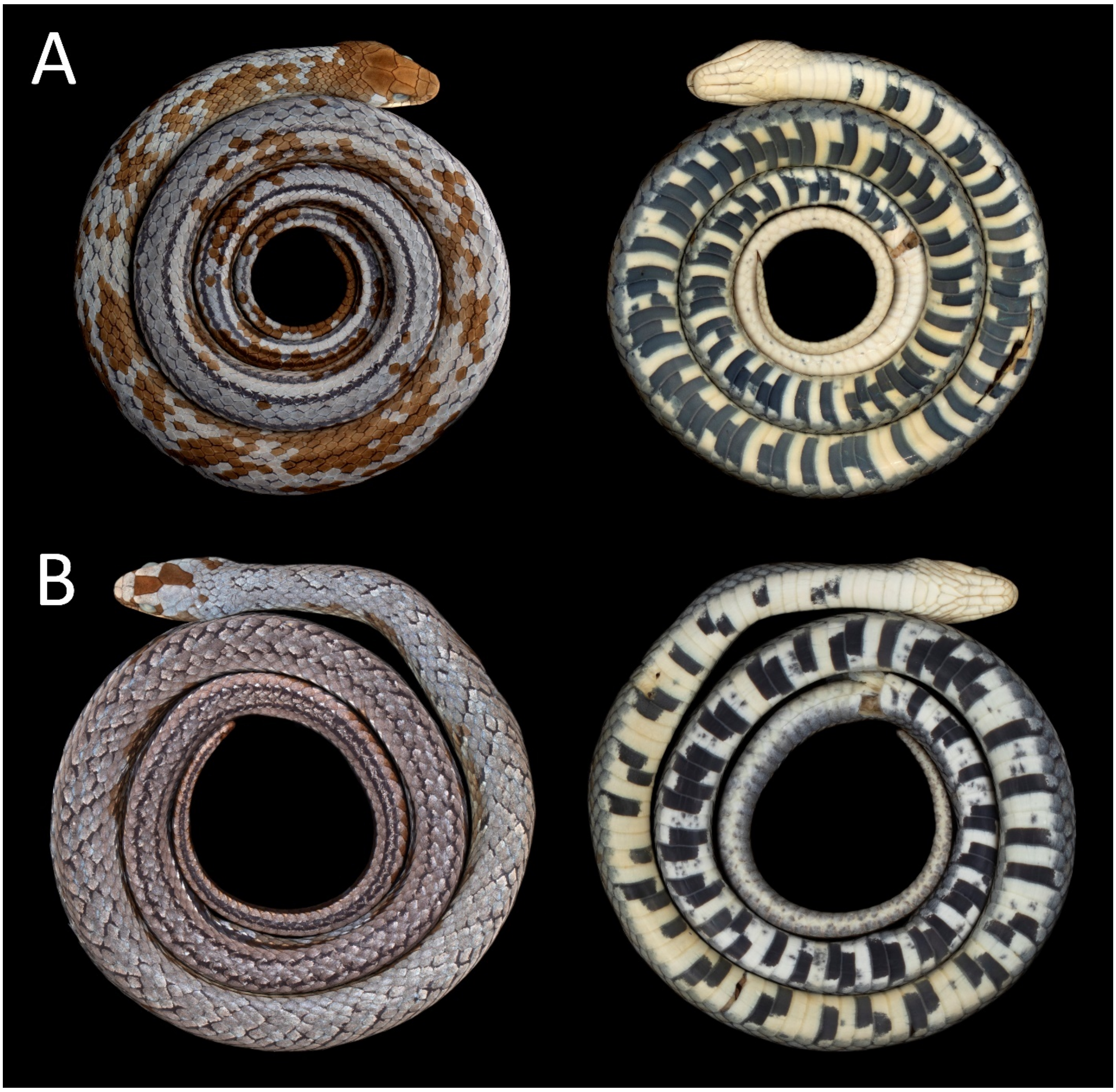

FIGURE 2. Dorsal (left) and ventral (right) views of preserved specimens of *E. fraseri* (A, QCAZ 14056, 390 mm SVL, Loja Province) and *E. lamonae* (B, QCAZ 9032, 405 mm SVL, Napo Province).

D. Núñez at Baquerizo Moreno, 7 km SE of Píllaro (1.228°S, 78.499°W, 2,674 m).

Diagnosis.—E. darwinnunezi sp. nov. differs from all other known congeners by the following combination of characters: (1) dorsal scales in 17–17–15 rows; (2) eight supralabials, with fourth and fifth contacting orbit; (3) 8–10 infralabials, with anterior five or six contacting chinshields; (4) one preocular; (5) two postoculars; (6) 1 + 2 temporals; (7) one or two preventrals; (8) 143–154 ventrals in males, 138–159 in females; (9) 55–66 divided subcaudals in males, 56–66 in females; (10) two pairs of black longitudinal stripes from about midbody to tip of tail, and the ventrolateral stripe is wider, extending over dorsal scale rows II and III, and the dorsal stripe forms a thin line between dorsal rows VI and VII; and (11) yellowish venter, with scattered dark, hill-shaped marks, with the hill base on the proximal border of the ventral scale, except on the tail.

E. darwinnunezi sp. nov. is most similar in morphology and coloration to species previously assigned as subspecies of *E. epinephelus* (Dixon, 1983). Of these, *E. albiventris, E. lamonae, E. fraseri*, and *E. bimaculatus* have been recorded in Ecuador, as *E. epinephelus* sensu stricto was recently restricted to Central America and northwestern Colombia (Torres-Carvajal & Hinojosa, 2020). Both *E. albiventris* and *E. epinephelus* differ from *E. darwinnunezi* sp. nov. in having an immaculate venter (Dixon, 1983, 1989). The number of ventrals is higher in *E. bimaculatus* (162–191, mean = 174.9 ± 1.0 SE: Dixon, 1983) than in *E. darwinnunezi* sp. nov. (138–159, mean = 149.1 ± 2.43 SE). From *E. lamonae* and *E. fraseri*, *E. darwinnunezi* sp. nov. can be readily distinguished by having (1) a venter with fewer and smaller dark marks that are hill-shaped instead of rectangular (Figs. 1, 2); and (2) a different pattern of dorsolateral dark stripes (Fig. 3). All three species have a pair of stripes on each side of the posterior half of the body and tail, the ventral stripes being wider than dorsal. The ventrolateral stripe usually extends over dorsal scale rows II and III in *E. darwinnunezi* sp. nov., row III in *E. fraseri* (ventral margin of IV and dorsal margin of II in some specimens), and rows II (dorsal margin), III, and IV in *E. lamonae*, which has the widest ven-

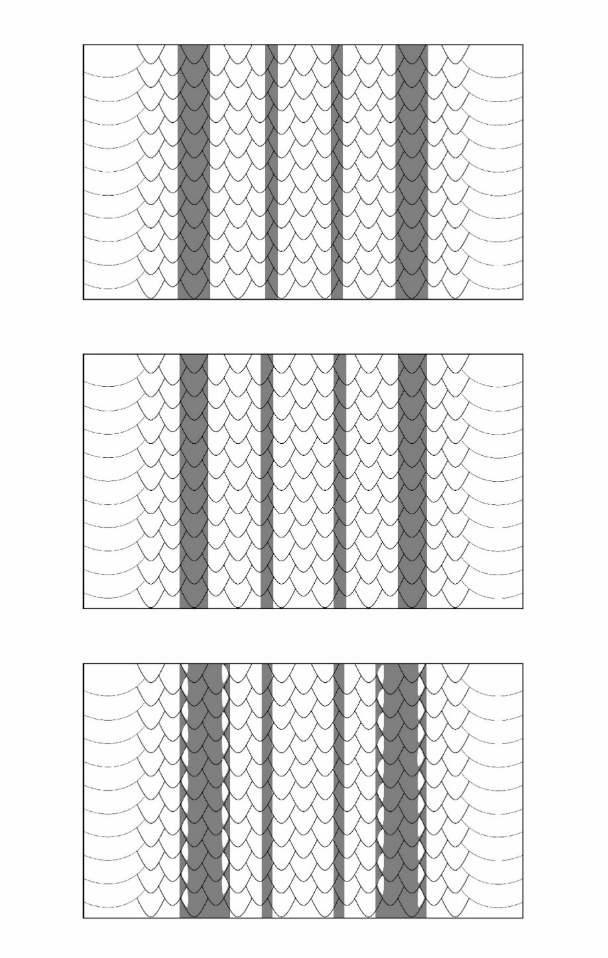

FIGURE 3. Patterns of longitudinal dark stripes on posterior half of body of *E. darwinnunezi* sp. nov. (top, QCAZ 9973, paratype), *E. fraseri* (middle, QCAZ 2873) and *E. lamonae* (bottom, QCAZ 11066).

tral stripes of all three species. Unlike *E. darwinnunezi* sp. nov. and *E. fraseri*, *E. lamonae* bears cream or white spots along the dorsal and ventral margins of the ventral longitudinal stripe. In addition, *E. fraseri* generally has more ventrals (143–164, mean = 153.8 ± 1.3 SE) and subcaudals (51–75, mean = 66.6 ± 0.8 SE) than both *E. lamonae* (ventrals: 141–157, mean 149.7 ± 0.7 SE; subcaudals: 51–67, mean 59.2 ± 0.7) and *E. darwinnunezi* sp. nov. (ventrals: 138–159, mean = 149.1 ± 2.43 SE; subcaudals: 55–66, mean 60.89 ± 1.57 SE). Compared to *E. darwinnunezi* sp. nov., hemipenis of *E. fraseri* bears lobes that are more parallel than divergent, and the spines are smaller and more abundant (especially on the asulcal side), and sulcus spermaticus bifurcates more basally; whereas in *E. lamonae*, the hemipenis bears spines that are smaller and less abundant (especially on lobes), the spines are not longitudinally arranged on the asulcal side, and the sulcus spermaticus is narrower (Fig. 4). Phylogenetic analyses of DNA sequence data and genetic distances also distinguish *E. darwinnunezi* sp. nov. from its congeners (see Phylogenetic Relationships section below).

Description of the Holotype.—QCAZ 9972, adult female (Fig. 1), body cylindrical; 374 mm SVL, 111 mm TL (missing tip). Dorsal head scales slightly overlapping; internasals and prefrontals densely covered with tiny pores; rostral subtriangular in frontal view, barely visible from above, broader than tall; internasals trapezoidal, slightly smaller than prefrontals (which are pentagonal); each nasal divided above and below nostril, in contact with supralabials I and II ventrally, rostral anteriorly, both internasals and prefrontals dorsally, and loreal posteriorly; frontal pentagonal and longer (4.35 mm) than wide (2.53 mm); two parietals longer (4.69 mm long, 3.20 m wide) than frontal; loreal slightly higher (1.38 mm) than wide (1.10 mm), in contact with supralabials II and III ventrally, nasal anteriorly, prefrontal dorsally, and preocular posteriorly; single preocular, subrectangular, more than twice as high as wide, in contact with supralabials III and IV ventrally, loreal anteriorly, prefrontal anterodorsally, and supraocular posterodorsally; maximum eye diameter 3.14 mm, pupil circular; two postoculars, uppermost scale approximately twice the size of lowermost scale; 1 + 2 temporals, rectangular primary temporal (3.86 mm long, 1.65 mm high), in contact with supralabials VI and VII; eight supralabials, with IV and V in orbit, and VI and VII higher and wider than other supralabials; ten infralabials, with the first pair in contact medially, pairs I–V in contact with anterior chinshields, and pairs V and VI in contact with posterior chinshields; triangular mental scale (maximum width 2.33 mm, maximum length 1.78 mm), with apex pointing posteriorly; first pair of chinshields completely in contact medially, second pair only in contact medially along anterior third; smooth dorsal scales, without apical pits, dorsal scales in 17–17–15 rows; one preventral scale; 138 ventrals; and a paired anal plate.

Color in Preservative of the Holotype (Fig. 1).—Dorsal background of head, body, and tail is olive-brown, without dorsal spots; lateral head scales are olive-brown, except for supralabials, which are yellowish cream ventrally; dark, faint postocular stripe extending onto upper portion of supralabials VI–VIII; dark pigment on suture between some infralabials; ventral background of head, body, and tail are yellowish cream; venter of body with scattered dark, hill-shaped marks, each restricted to a single ventral scale with rounded "hill-margin" pointing posteriorly; most hill-shaped marks less than half the size of ventral scales; two pairs of longitudinal dark stripes on posterior half of body and tail; the ventrolateral stripe is wider than the dorsal stripe, extending over dorsal rows II and III from midbody to cloaca, and over dorsal row I from cloaca to tip of tail; dorsal stripe extends as a thin line between dorsal rows VI and VII from posterior quarter of the body to the cloaca, and over dorsalmost caudal scales from the cloaca to about the first half of the tail (Fig. 3).

Hemipenes (Fig. 4).—The fully everted left hemipenis (QCAZ 9962, 261 mm SVL) is longer than it is wide, with two short lobes, each bearing a smooth apical disk. Calyces and capitular grooves are absent; lobes are cylindrical, with scattered spines that are less than half the size of body spines; the sulcus spermaticus is conspicuous, bifurcating at less than half the length of the organ, with branches extending onto apical disks; the sulcate surface of the body and lobes are covered with small spines, except for the medial area between the branches of the sulcus spermaticus, which bears seven large spines in two longitudinal rows; lateral and asulcate surfaces are covered with larger spines,

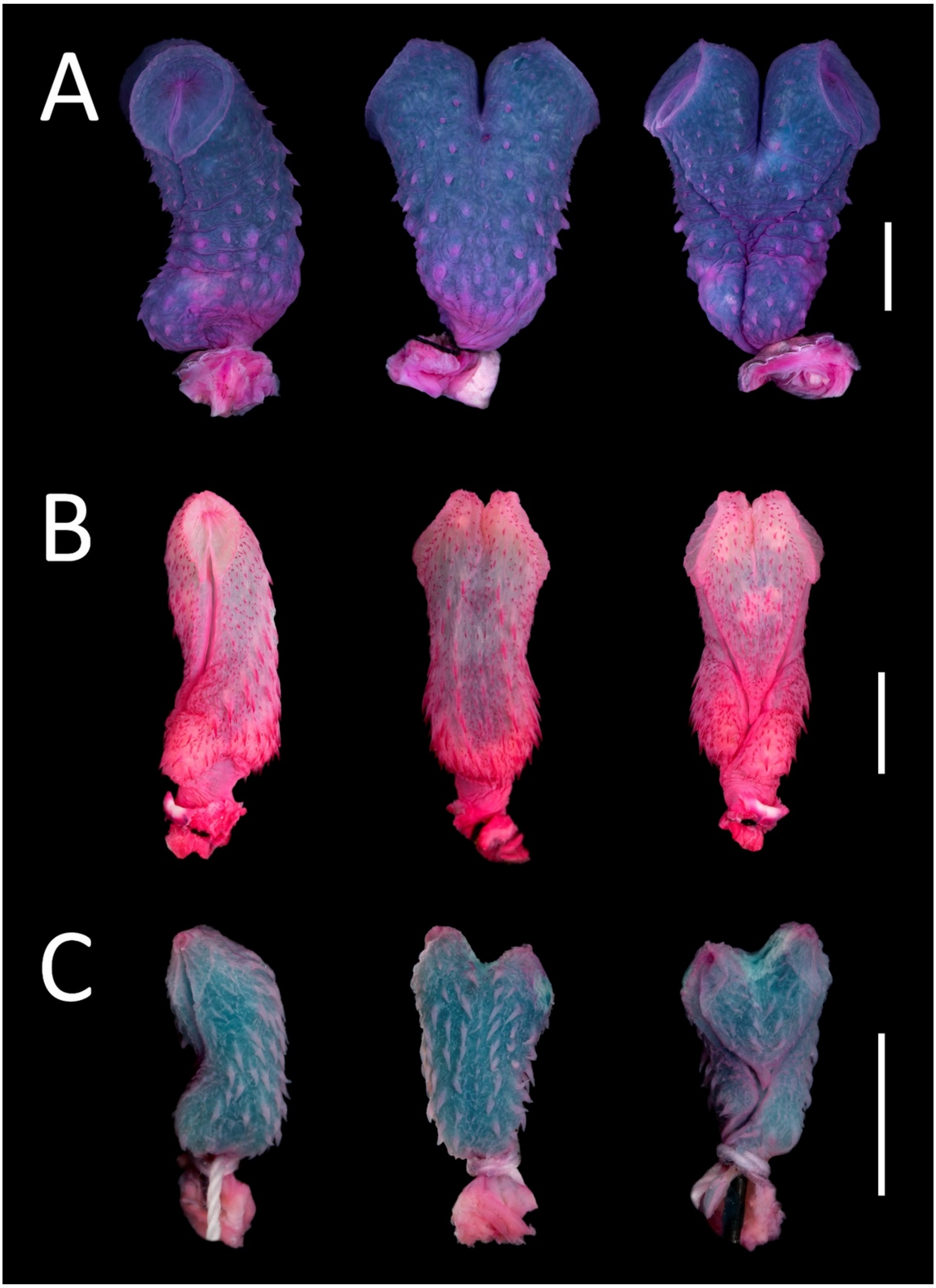

FIGURE 4. Hemipenes (left organ) of *E. lamonae* (A, QCAZ 9032), *E. fraseri* (B, QCAZ 14056), and *E. darwinnunezi* sp. nov. (C, QCAZ 9962, paratype) in lateral, asulcate, and sulcate views from left to right. Scale bars = 5 mm.

with those on the medial aspect of the asulcate side arranged in two longitudinal rows of 8–9 spines bordering a medial row of four smaller (less than half the size) spines.

Variation.—Even though our sample size of females was small (*n* = 2), our data suggest that *E. darwinnunezi* is dimorphic in numbers of ventrals and subcaudals, with males (*n* = 7) having more (143–159, mean 152.14 ± 4.74 SD and 56–66, mean 62.57 ± 3.82 SD, respectively) than females (138–139 and 55, respectively). The largest recorded male (EPN 9113) is 638 mm in length (469 mm SVL, 169 mm TL), whereas the largest female is the holotype.

Color in Life (Fig. 5).—The following description is based on three individuals (QCAZ 10001, QCAZ 18244, and QCAZ 18245). The dorsal background of the head, body, and tail is olive-green, with some body scales having yellow margins; there are faint dark, transverse stripes on the anterior third

FIGURE 5. General view of specimens of *E. darwinnunezi* sp. nov. in life. QCAZ 10001, male, 215 mm SVL (A) and QCAZ 18245, male, 281 mm SVL (B). Photographs by author Diego A. Paucar.

of the body; there is a yellow neck ring, incomplete middorsally; the labials and ventral aspect of the head are whitish cream; there is a dark pigment on the posterior margins of the labials; the ventral background of the body and tail is yellowish cream; there are patterns of ventral dark marks and posterior dorsolateral stripes as there are on the holotype.

Etymology.—The specific epithet *darwinnunezi* is a noun in the genitive case and is a patronym for Darwin Núñez, Ecuadorian herpetologist, in recognition for his extensive field collections that have contributed to science and conservation of the herpetofauna of Ecuador. In addition to the present description, Núñez has collected type specimens of several species of amphibians and reptiles described in recent years, such as *Hyloscirtus hillisi* (Ron et al., 2018), *Pristimantis anaiae* (Ortega et al., 2022), *Pholidobolus condor*, and *P. fascinatus* (Parra et al., 2020).

Distribution and Natural History.—*E. darwinnunezi* occurs in the Amazonian slopes of the Andes in central Ecuador, in the Tungurahua and Pastaza provinces, at elevations between 2,000–2,547 m above sea level (Fig. 6). Known localities lie within Andean Shrub and Eastern Montane Forest ecosystems (Ron et al., 2022). Some localities are within the buffer zone of Llanganates National Park, suggesting that *E. darwinnunezi* also occurs within this park, and thus at least some of its populations are protected. Specimens were found active between 1215 h and 1700 h under leaf litter and under a plastic sheet, as well as on the ground both in forest and pasture. Upon capture, specimens QCAZ 9972 (374 mm SVL), 9962 (261 mm SVL), and 10001 (215 mm SVL) weighed 30.8 g, 11 g, and 5 g, respectively. Specimen QCAZ 10001 exhibited the defensive horizontal neck flattening behavior characteristic of Xenodontini snakes. Specimen QCAZ 18245 regurgitated the remains of an unidentified frog specimen.

Phylogenetic Relationships.—The phylogenetic tree of Torres-Carvajal and Hinojosa (2020) recovered *E. darwinnunezi* as the sister taxon of *E. fraseri* with strong support (Fig. 7). Relationships of this clade with other species of *Erythrolamprus* are ambiguous. Uncorrected genetic distances between *E. darwinnunezi* and other species of *Erythrolamprus* range between 0.054 (with *E. aesculapii*, *E. miliaris*, and *E. reginae*) and 0.104 (*E. breviceps* and *E. taeniogaster*) for 12S, and between 0.005 (*E. fraseri*) and 0.062 (*E. epinephelus*) for 16S (see supplementary material in Torres-Carvajal & Hinojosa, 2020). The distance for 12S between *E. darwinnunezi* and *E. fraseri* is 0.057.

DISCUSSION

The complex orogeny and topography of the Tropical Andes have promoted lineage diversification, especially in organisms with low vagility like amphibians and reptiles, which generally have small distribution ranges. In fact, the Northern Andes and the Andean Yungas are among the most species-rich regions on the planet and have high proportions of small-ranged species (Rahbek et al., 2019). Recent studies based on phenotypic and DNA sequence data

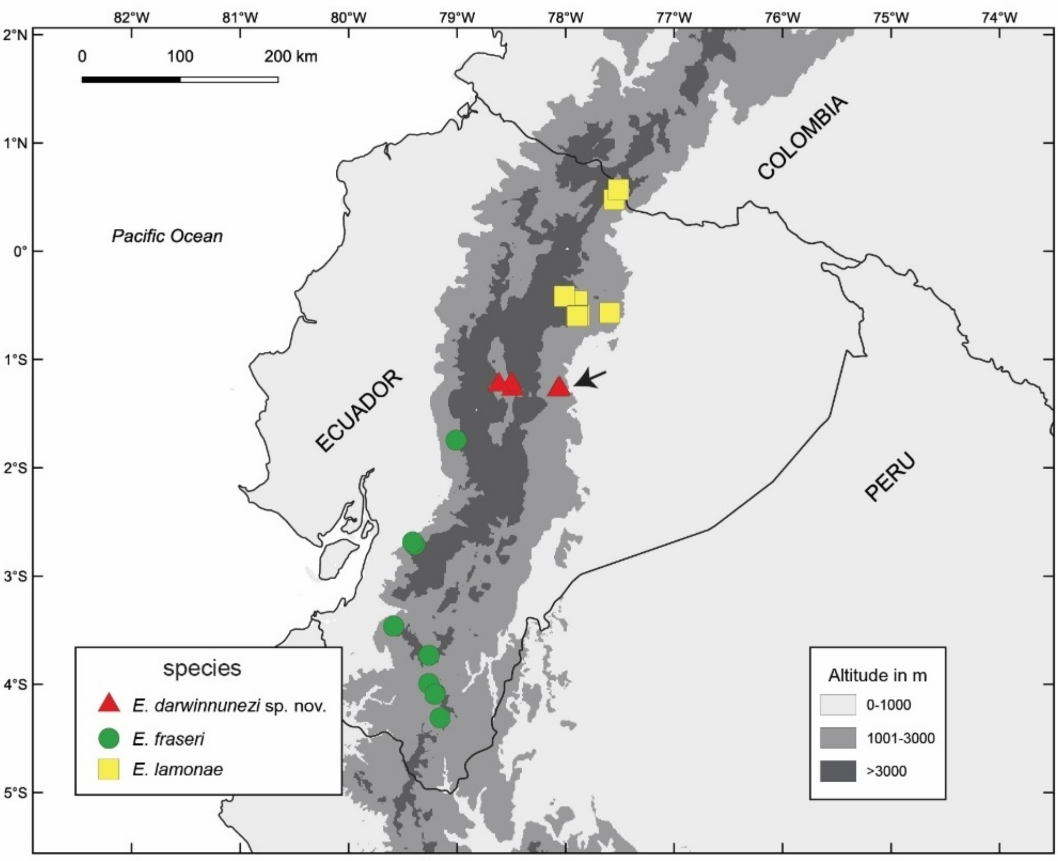

FIGURE 6. Known distribution of *E. darwinnunezi* sp. nov., *E. fraseri*, and *E. lamonae* in Ecuador. Black arrow indicates type locality.

have revealed unexpected levels of diversity within lineages of Andean herpetofauna, such as *Cercosaurinae* lizards, *Stenocercus* lizards, and *Pristimantis* rainfrogs (Fang et al., 2020; Ortega et al., 2022; Parra et al., 2020; Venegas et al., 2022). Among snakes, *E. epinephelus* was considered to be a widespread snake species occurring mostly along the Tropical Andes from Venezuela to Peru, with several subspecies recognized through differences in morphology and color patterns (Dixon, 1983). However, a recent molecular phylogenetic study including some of these subspecies showed that *E. epinephelus* sensu lato was paraphyletic, which led to recognition of some subspecies as valid species with more restricted distribution ranges (Torres-Carvajal & Hinojosa, 2020). Similar to other Andean reptiles, *E. darwinnunezi* sp. nov. seems to have a small distribution range restricted to highlands (~2,000–2,500 m) immediately north of the upper Pastaza River basin in central Ecuador.

The phylogenetic position of *E. darwinnunezi* is controversial. Torres-Carvajal and Hinojosa (2020) recovered it as the sister species of *E. fraseri*, a species from western Ecuador and northwestern Peru, while Entiauspe-Neto et al. (2021) found it to be sister to *E. festae*, a species from southeastern Ecuador and northern Peru. These two hypotheses have different biogeographical implications because a sister taxon relationship with *E. fraseri* suggests that uplift of the Andes probably caused the split between *E. fraseri* and *E. darwinnunezi* by vicariance. We prefer the first hypothesis for two reasons. First, Torres-Carvajal and Hinojosa (2020) analyzed more genes (six genes, with two nuclear genes versus one mitochondrial gene), which makes the dataset underlying this hypothesis more robust (Heath et al., 2008). Second, the sister taxon relationship between *E. darwinnunezi* and *E. fraseri* is strongly supported (bootstrap = 82, posterior probability = 0.91), whereas *E. darwinnunezi* and *E. festae* were recovered as sister taxa with low support (bootstrap < 50). Nonetheless, we recognize that increased geographical and taxon sampling might reveal different topologies in future studies on systematics of *Erythrolamprus*.

Identification Key to Some Species of Erythrolamprus *from Ecuador*.—The following key was modified from Dixon (1989) and only includes species assigned as subspecies of *E. epinephelus* by the same author (Dixon, 1983). A more inclusive key requires further taxonomic work.

1. Ventrals ≤165 ... 2
   Ventrals ≥165 ... *E. bimaculatus*
2. Venter checkered ... 3
   Venter immaculate ... *E. albiventris*
3. Ventral dorsolateral stripe extending over dorsal scale rows II and III or III and IV, without white spots along its dorsal and ventral margins ... 4
   Ventral dorsolateral stripe extending over dorsal scale rows II, III and IV, with conspicuous white spots along its dorsal and ventral margins ... *E. lamonae*
4. 143–164 ventrals (mean = 153.8), 51–75 subcaudals (mean = 66.6), venter checkered with large, rectangular dark marks ... *E. fraseri*

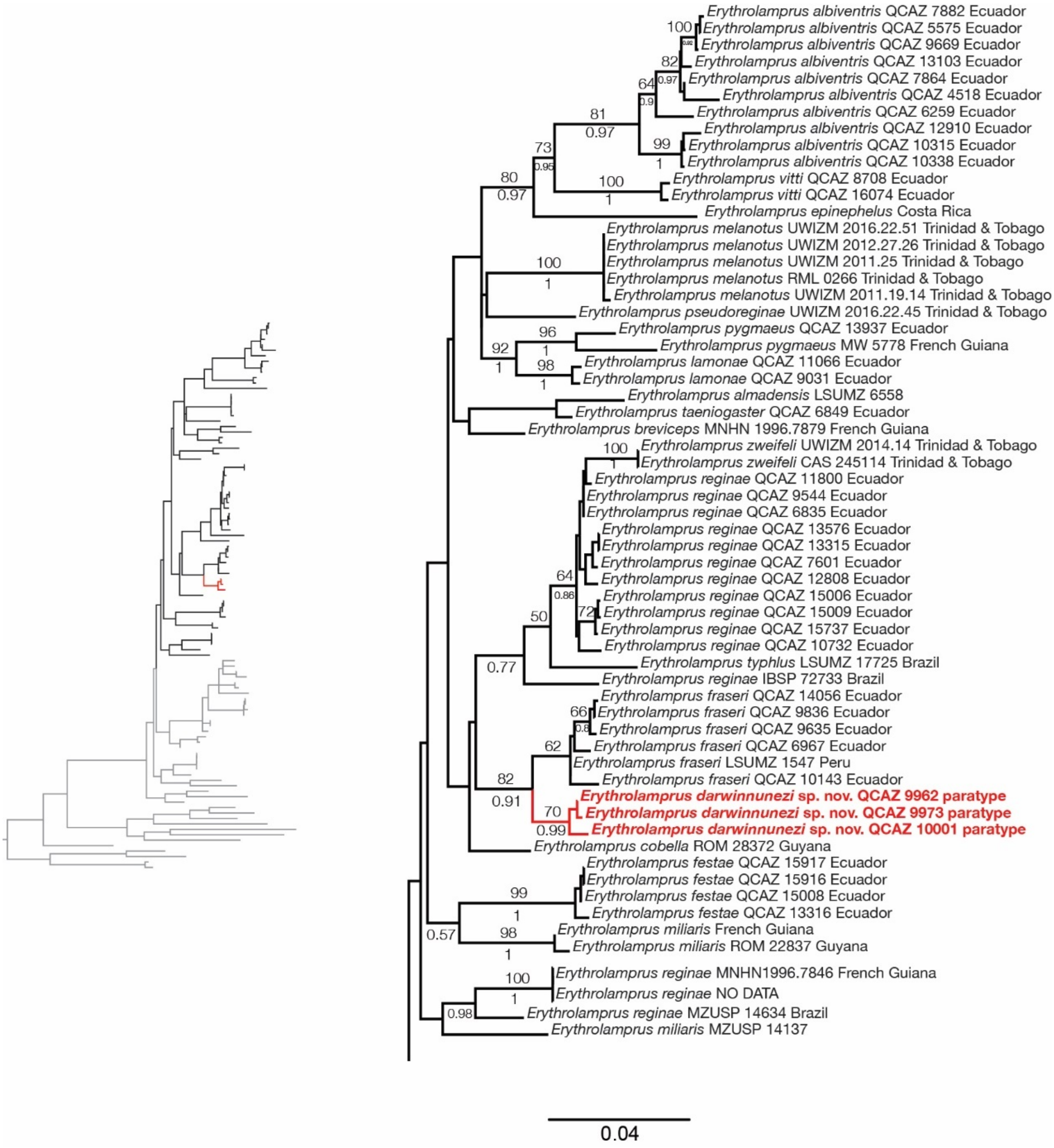

FIGURE 7. Phylogeny of *Erythrolamprus* (modified from Torres-Carvajal & Hinojosa, 2020), with a close-up of a subclade containing *E. darwinnunezi* sp. nov. and its closest relatives. We obtained the maximum likelihood tree from an analysis of 6 genes and 101 terminals. Numbers above branches are bootstrap support values ⩾ 50; numbers below branches are posterior probabilities ⩾ 0.5. For more details on phylogenetic analyses, see Torres-Carvajal and Hinojosa (2020).

138–159 ventrals (mean = 149.1), 55–66 subcaudals (mean 60.89), venter checkered with small, hill-shaped dark marks … *E. darwinnunezi* sp. nov.

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APPENDIX 1

Additional specimens examined. Institutional codes are provided in the methods.

E. lamonae (*n* = 9). Napo Province, Ecuador: (1) QCAZ 11066: Quijos, Cosanga, Yanayacu Biological Reserve (0.5986°S, 77.8902°W, 2,084 m); (2) EPN 15298: El Chaco, Gonzalo Díaz de Pineda (0.1152°S, 77,5736°W, 1,750 m); (3) QCAZ 9031: Sumaco National Park, trail between Mirador and Laguna shelters (0.587°S, 77.590°W, 2,000 m); (4) QCAZ 10566: Quijos, Cosanga, Yanayacu Biological Reserve (0.5942°S, 77.8766°W, 1,986 m); (5) QCAZ 9032: Sumaco National Park, La Laguna Refuge (0.5696°S, 77.5941°W, 2,479 m); (6) QCAZ 1664: 2 km E of Cuyuja (0.4169°S, 78.012°W, 1,829 m); (7) QCAZ 8798: Quijos, Cosanga, Yanayacu Biological Reserve (0.5944°S, 77.89749°W). In Sucumbíos Province, Ecuador: (8, 9) QCAZ 1518 and 1519: La Bonita, (0.4759°S, 77.5537°W 2500 m).

E. fraseri (*n* = 11). Loja Province, Ecuador: (1) QCAZ 6421: Tapichalaca Reserve (4.4841°S, 79.1491°W); (2) QCAZ 816: Curishiro (4.3099°S, 79.1569°W, 2,550m); (3) QCAZ 14056: Cajanuma (4.0925°S, 79.2062°W, 2,230 m); (4) QCAZ 2873: San Lucas (3.7318°S, 79.2605°W, 2,470 m); (5) QCAZ 3603: Virgen de Loja (2,400 m); (6) QCAZ 9836: Cajanuma, Cedro Quemado (4.0853°S, 79.2015°W, 2,523 m); (7) QCAZ 6235: Loja-Catamayo road (3.994°S, 79.262°W, 2,460 m); (8) QCAZ 13925: Huayco Alto, Finca Bioadventures. In Azuay Province, Ecuador: (9) QCAZ 1166: 10-15 km E Luz María (2.7105°S, 79.3922°W, 2,500 m). In El Oro Province, Ecuador: (10) QCAZ 9635: Chilla (3.4643°S, 79.5850°W, 3,246 m); (11) DHMECN 10795: Zaruma, Chivaturco (3.6170°S, 79.4967°W).