



A review of the *Cnemidophorus lemniscatus* group in Central America (Squamata: Teiidae), with comments on other species in the group

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Abstract

We provide the results of a morphological and molecular study on the Honduran Bay Island and mainland populations of the *Cnemidophorus lemniscatus* complex for which we resurrect *C. ruatanus* **comb. nov.** as a full species. Morphological comparison of the Honduran populations to *Cnemidophorus* populations from Panama led to the conclusion that the Panamanian population represents an undescribed species named herein. In light of these new results, and considering past morphological studies of several South American populations of the *C. lemniscatus* group, we suggest that three other nominal forms of the group are best treated as valid species: *C. espeuti* (described as a full species, but subsequently treated as a synonym of *C. lemniscatus* or a subspecies of *C. lemniscatus* until this publication), *C. gaigei* **comb. nov.**, and *C. splendidus* **comb. nov.**

Key words: *Cnemidophorus lemniscatus* species group, *Cnemidophorus ruatanus* **comb. nov.**, *Cnemidophorus duellmani* **sp. nov.**, morphology, mtDNA, 12s, cytochrome b, Honduras, Guatemala, Nicaragua, Panama, Colombia

Introduction

Burt (1931) provided a revision of the genus *Cnemidophorus* in which he recognized *C. lemniscatus* (Linnaeus) as a wide-ranging species that occurred from “Guatemala south to Colombia and northern Brazil, often insular” (p. 29). Burt (1931: 29) recognized the subspecies *C. l. nigricolor* Peters as occurring on the “Islands north of Venezuela from the Aves east to Blanquilla, also southward on Margarita Island.” That concept of the geographical distribution of *C. lemniscatus* has existed in the literature to very recently.

McCrystal & Dixon (1979) were the first to divide populations previously consumed under *Cnemidophorus l. lemniscatus* when they described *C. gramivagus* for the *C. lemniscatus* complex populations from the llanos of Venezuela and Colombia. Cole & Dessauer (1993) noted that *C. lemniscatus* actually represented a complex of species and described two new species (*C. cryptus* and *C. pseudolemniscatus*; both unisexual) previously masquerading as *C. lemniscatus* from southeastern Venezuela, Amazonian Brazil, Suriname, and French Guiana. Vanzolini (1970) had first reported the discovery of unisexual populations of *C. lemniscatus* along the eastern portion of the Amazon River in northeastern Brazil. Markezich *et al.* (1997) described the new species (*C. arenivagus*) of the *C. lemniscatus* complex from the Paraguana Peninsula of Venezuela and described the new subspecies *C. l. splendidus* from other populations of the same complex from the same peninsula. Specimens from near the Gulf of Maracaibo, Colombia, were also assigned to *C. arenivagus*. Markezich *et al.* (1997) assigned specimens from Guyana, Suriname, and Bolivar, Venezuela, to *C. l. lemniscatus*, with specimens they examined from other areas of Venezuela and Colombia left unassigned to a subspecies. One of the characters used by Markezich *et al.* (1997) to distinguish *C. l. splendidus* from *C. l. lemniscatus* was that the vertebral stripe was split in the later, whereas that stripe was single or absent in *C. l. splendidus*. Cole & Dessauer (1993) included photographs of a specimen they erroneously designated as the lectotype of *C. lemniscatus* and other specimens of *C. lemniscatus* from Suriname and Guyana that clearly show the split nature of the vertebral stripe. Markezich *et*

al. (1997) provided a photograph of the originally designated lectotype from Suriname (see Hoogmoed 1973: 264, Maslin & Secoy 1986: 25), but the specimen is too dark to verify the nature of the vertebral stripe. However, Markezich *et al.* (1997) did provide photographs of other *C. lemniscatus* from Suriname and Guiana that do show the split nature of the vertebral stripe in eastern *C. l. lemniscatus*. Ugueto *et al.* (2010) continued the splitting of the *C. lemniscatus* complex when they described an additional two species (*C. senectus* and *C. flavissimus*) from islands off the coast of Venezuela. Those authors gave the range of *C. l. lemniscatus* as “Isolated localities in Central America (Guatemala, Honduras, Panama); widespread throughout Colombia, Venezuela, Guyana, Suriname, French Guiana, northern Brazil, Trinidad, Tobago, and several islands of the southern West Indies” (p. 125). Ugueto *et al.* (2010: 125) also gave the range of *C. l. splendidus* as “northwestern Venezuela and probably adjacent Colombia.” Ugueto & Harvey (2011) also presented systematic data on *Cnemidophorus* from islands off the north coast of Venezuela and characterized *C. lemniscatus* as having a divided (split) vertebral stripe. However, populations of the *C. lemniscatus* complex from Honduras have a single vertebral stripe.

Harvey *et al.* (2012) provided a morphological review of the Teiidae and proposed a revised taxonomy that included a revised *Cnemidophorus*. Harvey *et al.* (2012) recognized four species groups in their new concept of *Cnemidophorus*, including a *C. lemniscatus* species group. Their *C. lemniscatus* group contains *C. arenivagus*, *C. arubensis* (Lith de Jeude; considered a subspecies of *C. murinus* [Laurenti] by Burt 1931), *C. cryptus*, *C. flavissimus*, *C. gramivagus*, *C. l. espeuti* Boulenger, *C. l. gaigei* Ruthven, *C. l. lemniscatus*, *C. l. splendidus*, *C. pseudolemniscatus*, *C. senectus*, and a *Cnemidophorus* “sp. B.” The *C. l. nigricolor* recognized by Burt (1931) was placed in a *C. nigricolor* species group by Harvey *et al.* (2012).

Thus, as shown above, the vast majority of the taxonomic studies on the *Cnemidophorus lemniscatus* complex subsequent to Burt (1931) involved South American populations. Populations of *C. lemniscatus* from the north coast of Colombia (described as *C. l. gaigei* by Ruthven 1915), the Colombian islands of Providencia and San Andrés (described as *C. espeuti* by Boulenger 1885), as well as the Caribbean coastal populations from Guatemala to Nicaragua, and the Pacific versant population of Panama have received scant interest by herpetologists since Burt’s (1931) work. Burt (1931) had placed *C. espeuti*, *C. l. gaigei*, and *C. l. ruatanus* Barbour in the synonymy of *C. lemniscatus*. Only Dunn & Saxe (1950), Rand (1954), and Echternacht (1968) had offered brief morphological discussions of any of these northern forms until Harvey *et al.* (2012), without discussion, used the trinomials *C. l. espeuti* and *C. l. gaigei*.

McCranie began an effort during May 2011 to collect tissues of Honduran Bay Island and mainland populations of *Cnemidophorus* in an effort to gain knowledge on their relationships among the *C. lemniscatus* species group. A morphological study of the Honduran, Panamanian, Colombian island and northern mainland Colombian populations was also undertaken by McCranie. The results of that morphological study and those of the available sequence data in the Hedges laboratory are reported herein.

Methods

The morphological data presented herein follow the methods and terms as suggested by Harvey *et al.* (2012), unless otherwise stated. Abbreviations used are: HD (head depth at deepest point); HL (head length; anterior edge of ear to tip of snout); HW (head width; measured at level between orbits); SHL (shank length; includes skin covering outer edges of tibia); SL (snout length; anterior edge of eye to tip of snout); SVL (snout-vent-length); TAL (tail length). Color codes and names used herein follow those of Smithe (1975–1981) and museum acronyms follow those of Leviton *et al.* (1985).

The new molecular data set comprised sequences of three mitochondrial genes (16S rRNA, 12S rRNA, and cytochrome b) from 11 individuals of *Cnemidophorus* collected at diverse localities in Honduras (Appendix I). These new sequences were aligned with 16S and 12S sequences of four species of *Cnemidophorus* from South America, represented in GenBank: *C. arenivagus* (western Venezuela; AY046483, AY046441), *C. gramivagus* (western Venezuela; AY046474, AY046432), *C. lemniscatus lemniscatus* (Guyana; AY046480, AY046438), and *C. l. splendidus* (western Venezuela; AY046482, AY046440). The teiid lizard *Kentropyx borkiana* Peters (AY046499, AY046457) was included as outgroup. All of those GenBank sequences were originally presented in Reeder *et al.* (2002). Localities and accession numbers for the new sequences of the 11 Honduran samples are in Appendix I. The total concatenated alignment for the three genes was 1,564 aligned sites: 16S—434 sites (22 parsimony informative), 12S—394 sites (25 PI), and cytb—736 sites (8 PI).

Methods used for the collection of the new DNA sequences are detailed elsewhere (Heinicke *et al.* 2007, Hedges *et al.* 2008, Hedges & Conn 2012). Alignments were performed with (MUSCLE) in MEGA 5.0 (Tamura *et al.* 2011). A maximum likelihood (ML) analysis was performed using RAxML 7.6.3 (Stamatakis 2006, Stamatakis *et al.* 2008) through the CIPRES Science Gateway (Miller *et al.* 2010), partitioned into four partitions (16S+12S, cytb by codon), using the evolutionary model GTRGAMMA, the maximized available option in RAxML. Gaps were treated as missing data. All parameters for the ML analyses were estimated by the program during the run. Branch support in the trees was provided by bootstrap analysis (2,000 replicates). A Bayesian phylogenetic analysis using MrBayes 3.2.1 (Ronquist *et al.* 2012) also was performed through CIPRES, again using the GTR + Γ model. The Bayesian analysis was set to two parallel runs for ten million generations, sampled every 100 generations, each run employed three heated and one cold chain, with a temperature parameter of 0.10. The first 10% of samples were discarded as burn-in. Convergence was assessed by the standard deviation of split frequencies (< 0.01 in all cases).

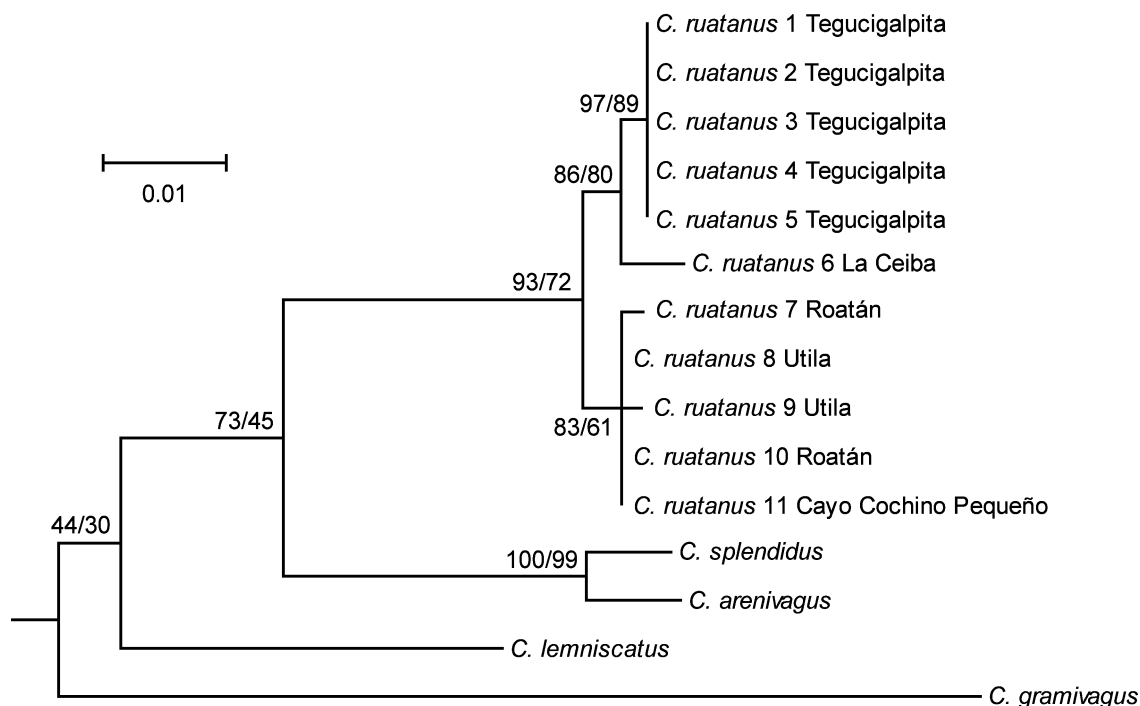


FIGURE 1. Phylogenetic tree of lizards of the *Cnemidophorus lemniscatus* complex from a maximum-likelihood analysis of DNA sequences of three mitochondrial genes (12S rRNA, 16S rRNA, and cytochrome b). A scale bar is indicated. The numbers at nodes are Bayesian posterior probabilities (left) and bootstrap (right) support values. The tree is rooted with the teiid lizard *Kentropyx borkiana* (not shown).

Systematics

Study of the morphological and molecular data demonstrate that the Honduran Bay Island and mainland populations of the *Cnemidophorus lemniscatus* species group are conspecific, but distinct from other nominal forms in the same species group (Fig. 1). Molecular data are not available for the Colombian populations assigned to *C. l. espeuti* and *C. l. gaigei* by Harvey *et al.* (2012), but morphological data support that those two populations are diagnosable from the Honduran populations. The Guatemalan populations of the *C. lemniscatus* species group are from the Caribbean coast and the Río Motagua Valley, a tributary of which extends into Honduras where populations of *Cnemidophorus* also occur. Morphological study of those Honduran Río Motagua tributary specimens indicates they are conspecific with other Honduran populations, thus strongly suggesting that Guatemalan populations are conspecific with the Honduran populations. The Nicaraguan *Cnemidophorus* populations from the Cabo Gracias a Dios reported by Dunn, *in* Dunn & Saxe (1950 and again as a new record for Nicaragua by Sunyer *et al.* 2009) are continuous along the coast with northeastern Honduran populations studied

herein. Thus, we resurrect *Cnemidophorus lemniscatus ruatanus* Barbour as a distinct species for the northern population of the *C. lemniscatus* species group.

***Cnemidophorus ruatanus* new combination**

(Figs. 2, 3)

Cnemidophorus lemniscatus ruatanus Barbour 1928: 60.

Cnemidophorus lemniscatus lemniscatus: Burt 1931: 30 (part).

Cnemidophorus lemniscatus: Echternacht 1968: 152 (part).

Cnemidophorus lemniscatus ruatanus: Wright 1993: 79.

Cnemidophorus lemniscatus: Montgomery *et al.* 2007: 38.

Holotype. MCZ 26759 from Coxen Hole, Isla de Roatán, Islas de la Bahía, Honduras.

Geographic distribution. *Cnemidophorus ruatanus* is known from Isla de Roatán, Isla de Utila, and Cayo Cochino Pequeño in the Islas de la Bahía, Honduras, and from the Río Motagua Valley and adjacent coastal plain of Guatemala eastward across northern Honduras to extreme northeastern Nicaragua. This species is largely a coastal form on the mainland, but does penetrate inland along some river valleys (i.e., Río Motagua in Guatemala into a tributary in adjacent Copán, Honduras; Río Viejo in Atlántida, Honduras; Fig. 4). The record of this species from southeastern Belize reported by Stafford & Meyer (1999) might represent a recent range expansion, or an introduction as thought by Stafford *et al.* (2010).

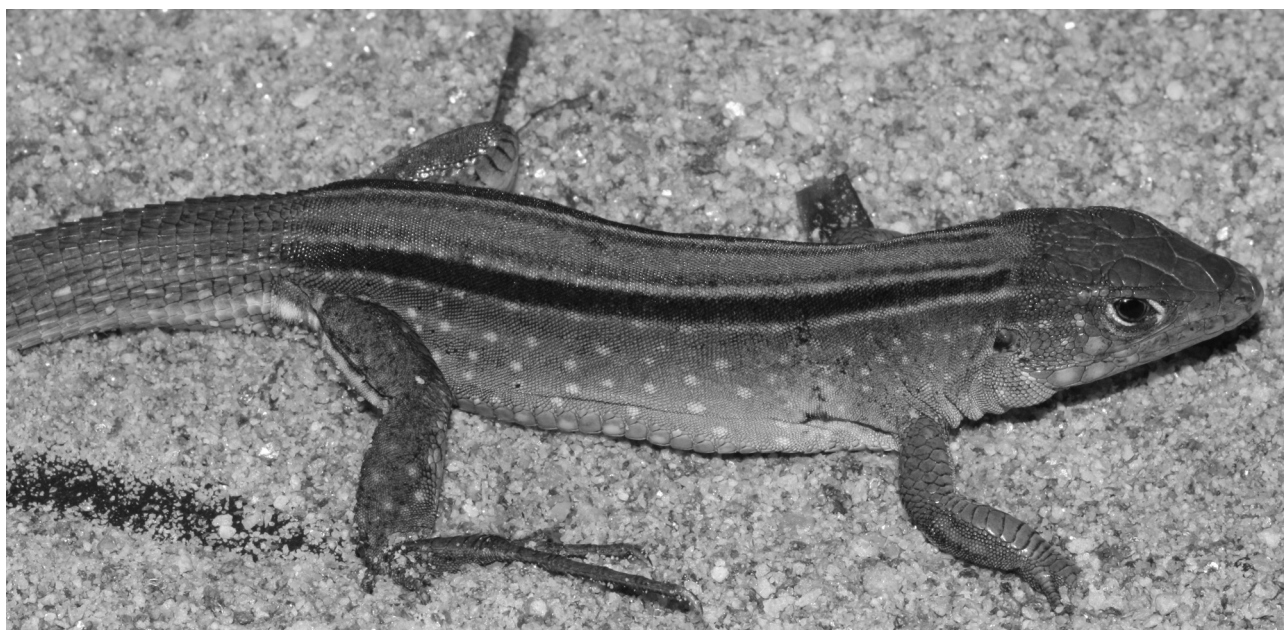


FIGURE 2. Adult male (FMNH 283564) of *Cnemidophorus ruatanus* **comb. nov.** (SVL 76.6 mm).

Diagnosis. *Cnemidophorus ruatanus* can be distinguished from other northern populations of the *C. lemniscatus* species group as follows: from *C. l. espeuti* of Islas de Providencia and San Andrés, Colombia, by having a single and distinct vertebral stripe, 27–32 subdigital lamellae on the fourth toe, and 14–17 subdigital lamellae on the fourth finger (versus vertebral stripe split, 33–35 subdigital lamellae on the fourth toe, and 17–19 subdigital lamellae on the fourth finger in *C. l. espeuti*); from *C. l. gaigei* in having 11–13 in 31, 10 in 5, or 9 in 19 scales surrounding the three enlarged precloacal plates, and in those having only 9 scales the precloacal pair are completely separated by a single scale (Fig. 5A) in 15 or separated by distance of one-third to over one-half in 4 (versus 9–10 scales surrounding the three enlarged precloacal plates in all eight examined and the precloacal pair in broad contact, without a smaller interscale in 6 (Fig. 5B) and a small interscale not separating precloacal pair by more than one-third in 2 in *C. l. gaigei* [see Discussion below]). Burt (1931) synonymized *C. ruatanus* with *C. l. lemniscatus*, but the latter differs most notably from *C. ruatanus* in having a split or divided vertebral stripe (versus

vertebral stripe single in *C. ruatanus*). *Cnemidophorus ruatanus* also differs from *C. l. lemniscatus* in amount of molecular divergence (Fig. 1).



FIGURE 3. Adult female (FMNH 283567) of *Cnemidophorus ruatanus* **comb. nov.** (SVL 62.4 mm).

Description. The following is based on 21 males (FMNH 283560–61, 283563–64, 283568; KU 192621, 203160, 220101; USNM 563589–90, 563593–94, 563596, 563598–99, 570397, 570399, 570401, 573206, 573209, 580929) and 14 females (FMNH 283562, 283566; KU 101334, 101340, 192622; USNM 563588, 563592, 563595, 563597, 573207–08, 573211–12, 580928). *Cnemidophorus ruatanus* is a moderately large lizard (maximum recorded SVL 113 mm [FMNH 283561]); dorsal head scales enlarged, smooth, platelike, with paired prenasal scales with short median sutures, a single frontonasal, paired prefrontals, a single frontal, paired frontoparietals, two pairs of parietal scales (occasionally one or two parietals can be partially divided), and a single interparietal scale; rostral not contacting frontonasal; postnasal not contacting prefrontal; prefrontal and first superciliary usually in contact; frontal ridge absent; posterior frontal suture usually aligned near midlength of supraocular 3; scales in frontoparietal region smooth, flat; interparietal varies from slightly narrower than, to slightly broader than, flanking parietals; 1–6 (2.8 ± 1.1) scales between fourth supraocular and inner-most parietal on each side; 1–6 (4.0 ± 1.0) scales between fourth supraocular and outer-most parietal on 34 sides; usually 4 supraoculars per side (occasionally a fifth smaller supraocular present posteriorly, rarely only 3 supraoculars present); median pair of occipital scales distinctly enlarged, much larger than first dorsal scale row; 17–28 (21.4 ± 2.5) occipitals (occipitals of Harvey *et al.* 2012 plus scales bordering frontoparietals); supratemporals moderately enlarged, separated from parietals; short rostral groove present or absent; nostril centered in nasal suture; nostril opening oval; first supraocular contacting second supraocular; 1.0 to 1.5 rows of lateral supraocular granules, 21–52 (29.0 ± 6.4) granules on each side; anterior extent of circumorbital semicircles in single row reaches between midlength and posterior third of supraocular 3, that of double row not reaching seam between supraoculars 3–4; 2–9 (4.2 ± 1.4) circumorbitals; 5–6 (usually 6) superciliaries per side, usually with second (occasionally third) elongated; 4 (rarely 5) suboculars per side, first on each side usually entire (occasionally divided), lower edge (when entire) or lower part (when divided) usually contacting supralabial 3 (rarely contacting both supralabials 3 and 4); subocular keel present; patch of enlarged scales located in front of auditory meatus; no auricular or preauricular flaps or folds; 1–1 loreals; usually 6 (rarely 5 or 7) supralabials and 5 (occasionally 6) infralabials per side; first supralabial straight ventrally, usually longer than second supralabial; lingual sheath absent; moveable eyelids present; pupil rounded; first pair of chinshields contacting infralabials, those chinshields separated only at posterior edge; intergular sulcus absent; 18–26 (22.2 ± 2.2) anterior gulars; 9–18 (14.0 ± 2.5) posterior gulars; gular patch of distinctly enlarged scales absent; intertympanic sulcus absent; sharp transition from anterior gulars to smaller posterior ones; mesoptychial scales moderately enlarged, bordered anteriorly by sharp transition to small scales; edge of gular fold not serrated; dorsal scales conical, 190–230 (212.0 ± 9.0) middorsals between occipitals and first enlarged caudal scale; 97–123 (106.9 ± 6.0) granules around midbody; middorsal scales subequal to lateral scales; chest scales

large, flat; pectoral sulcus absent; ventral body scales large, platelike, squarish, juxtaposed, smooth, in 25–33 (28.9 ± 2.6) longitudinal (long axis of body) rows, in 8 transverse rows at midbody; scales immediately lateral to outside ventral plate on each side small and granular; paired enlarged terminal scales forming precloacal plate; 9–13 (10.6 ± 1.4) scales bordering all three enlarged plates in 55 (those listed above plus FMNH 283565, 283567; KU 101328–30, 101332–33, 101339, 101341–42, 101344–47, 101349–50; USNM 69397–400); males usually with one smaller subtriangular scale flanking paired terminal plates and 1–2 other smaller rounded scales between precloacal plate and small precloacal spur; 4–6 (4.8 ± 0.6) precloacal scales; postcloacal buttons absent; pair of slightly enlarged postcloacal scales present in males, those enlarged scales absent in females; caudal annuli complete, tail lacking crests or dorsolateral row of serrated scales; proximal subcaudals keeled; preaxial and postaxial brachial scales separated by band of continuous moderately enlarged scales; large dorsal brachial and antebrachial scales 1.0–1.5 times as wide as long, both sets of enlarged scales smooth, extending well beyond centers of arm; postaxial brachial scales in continuous enlarged row with preaxial brachial scales; postaxial antebrachial scales slightly enlarged; 29–34 (31.4 ± 1.2) combined subdigital lamellae on fourth finger in 20; subarticular lamellae of Fingers III–IV homogeneous in size, entire; 54–64 (59.7 ± 2.3) subdigital lamellae on fourth toe in 19, distal ones smooth; subarticular lamellae of Toes III–IV divided, each scale smaller than other lamellae; no row of distinctly enlarged scales between Toes IV–V; small scales separating supradigital scales from subdigital lamellae continuous, or nearly continuous; denticulate fringe absent along postaxial edge of outer toes; fifth toe not reduced, claw extending beyond level of articulation of Toes III–IV; 5–11 (7.4 ± 1.4) prefemoral scales on left side; heels without expanded scales; tibiotarsal shields present; tibiotarsal spurs absent; 38–47 (42.4 ± 2.4) total femoral-abdominal pores in males, 33–46 (39.7 ± 3.5) in females; no gap between femoral and abdominal pores; 3–4 (most often 3) scales separating each femoral-abdominal pore series; SVL 61.7–113.4 (79.6 ± 12.2) mm in males, 60.3–75.7 (67.0 ± 4.1) mm in females; TAL/SVL 1.60–2.79 in 13 males, 1.70–2.36 in eight females; HL/SVL 0.23–0.27 in males, 0.21–0.27 in females; HW/SVL 0.13–0.16 in males, 0.12–0.18 in females; HD/SVL 0.13–0.17 in males, 0.11–0.15 in females; HW/HD 0.93–1.13 in males, 1.04–1.23 in females; SL/SVL 0.09–0.11 in males, 0.09–0.12 in females; SHL/SVL 0.19–0.23 in males, 0.18–0.22 in females; foot length/SVL 0.29–0.37 in males, 0.30–0.46 in females; hand length/SVL 0.11–0.16 in males, 0.12–0.16 in females.

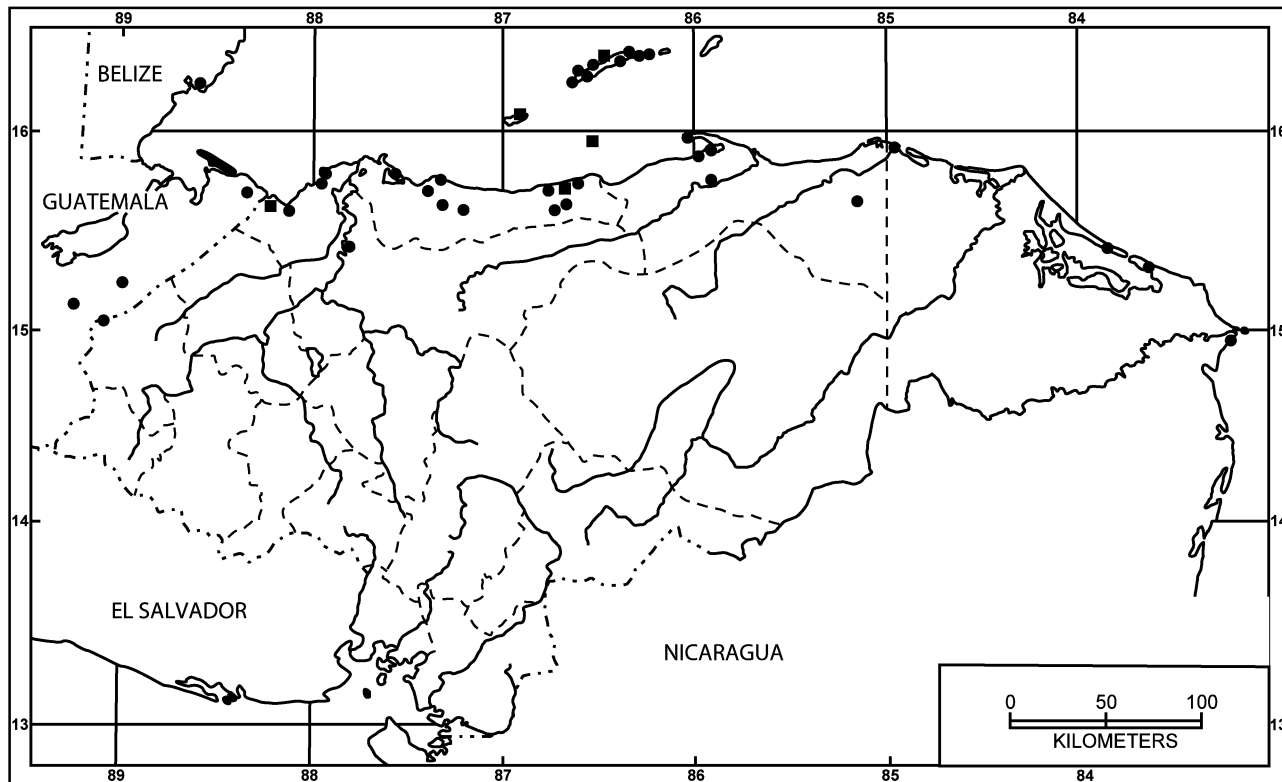


FIGURE 4. Map showing the known localities (circles) for *Cnemidophorus ruatanus* **com. nov.** The squares represent localities from which tissue samples were also sequenced.

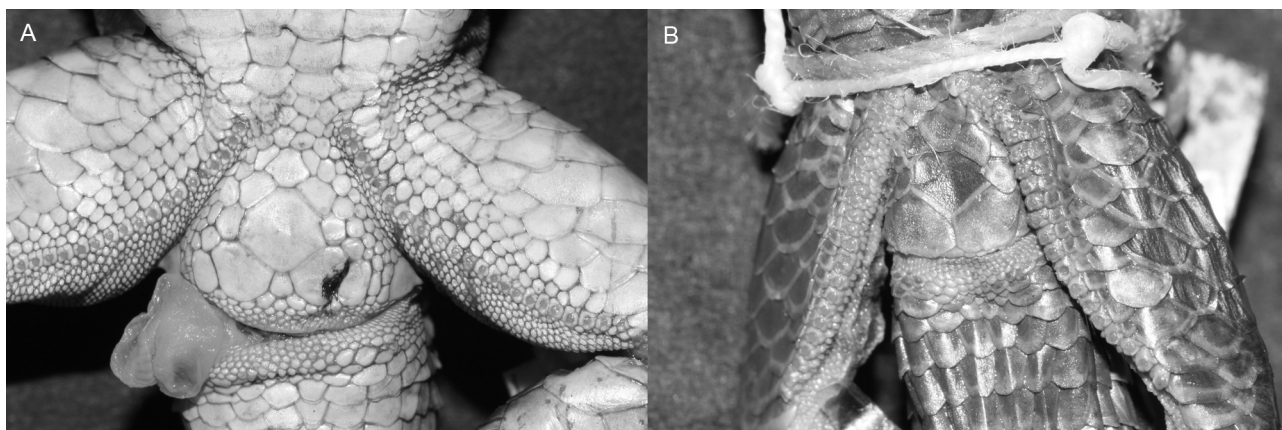


FIGURE 5A. Cloacal plate region of *Cnemidophorus ruatanus* **comb. nov.** (KU 101329) showing the small scale separating the enlarged terminal precloacal plates; **5B** Cloacal plate region of *Cnemidophorus gagei* **comb. nov.** (USNM 117471) showing the enlarged terminal precloacal plates in broad contact medially.

Color in life of an adult male (FMNH 283564): middorsal longitudinal band Ground Cinnamon (239) with two dark brown stripes in dorsolateral field of band; middorsal band bordered by Dark Brownish Olive (129) stripe (about six granules wide), that dark stripe bordered below by narrow Chartreuse (158) dorsolateral stripe; lateral surface of body greenish yellow with scattered brownish green mottling; top of head Emerald Green (163) along outer edges, becoming brown with green tinge medially; anterior surfaces of fore- and hind limbs Opaline Green (162D); ventral surfaces of head, throat, and chest Robin's Egg Blue (93); belly white with pale blue tinge; outer two ventral plates on each side Emerald Green; ventral surfaces of limbs and subcaudal surface pale blue, except palms and soles Robin's Egg Blue. Color in life of another adult male (KU 220101): dorsal surface of head tan; lateral surface of head yellow-green, grading to turquoise blue on lips; outer edge of supraoculars outlined by yellow-green line; middorsal band tan, flanked by dark brown stripe; lateral surfaces yellowish green on neck and near groin, pinkish tan between neck and groin with yellow to white spots; dorsal surfaces of forelimbs olive green; dorsal surfaces of hind limbs tan with white spots; dorsal surface of tail tan; chin turquoise blue; chest pale turquoise blue; belly green with bluish cast; ventral surface of forelimbs white; ventral surface of hind limbs turquoise blue. Color in life of an adult female (UF 150291): middorsum of body Drab-Gray (119D) with slightly paler paramiddorsal stripes; dorsolateral field Hair Brown (119A) bounded by pale tan stripes; lateral and ventrolateral fields Chartreuse (158) bounded by pale tan to white stripes; venter Light Sky Blue (116D) grading to pale bluish green laterally; dorsum of head Grayish Horn Color (91); limbs grayish brown with white spots dorsally, pale grayish blue ventrally; tail Drab-Gray dorsally, pale bluish green ventrally.

Color in alcohol: juveniles have 8 longitudinal white to dirty white stripes dorsally and laterally on a body that is dark brown laterally and slightly paler brown middorsally; adults and juveniles of both sexes have a complete, pale brown middorsal swath extending from posterior edge of head to base of tail; adult females have that middorsal swath bordered laterally by thin paler brown to cream stripe that is in turn bordered below by a broad dark brown stripe that extends to posterior end of body, last mentioned stripe also bordered below by a cream to pale brown, thin stripe, with area below that thin stripe pale brown with or without indistinct cream stripe or cream to pale yellow small spots in adult females; adult males have middorsal swath with or without evidence of paler brown, thin border stripe, but with a dark brown broader border stripe (as in females) extending to posterior end of body, with area below that dark brown border stripe with cream to pale yellow spots in males; ventral surfaces of head and body cream to white with pale bluish gray tinge, or entirely black, except throat region pale blue to pale gray in males. Adults of both sexes from the Bay Islands have pale blue ventral surfaces, whereas those from the mainland can have either pale blue or black ventral surfaces. Adults of both sexes from Isla de Roatán retain the pale stripes to a larger size than do those from the remaining Honduran populations.

Habitat. *Cnemidophorus ruatanus* occurs at low elevations (sea level to 400 m elevation) in the Lowland Moist Forest and Lowland Dry Forest formations of Holdridge (1967). This is a sun loving species that occurs in open areas, such as beach vegetation and along open, gravelly or sandy riverbanks. Both sexes exhibit the habit of pausing while moving about to lift and shake one of its forelegs. It has been collected or seen active during every

month of the year in Honduras. Montgomery *et al.* (2007, 2011) provided studies on the habitats and natural history of a population of *C. ruatanus* on Cayo Cochino Pequeño, Honduras.

Echternacht (1968) compared a series of *Cnemidophorus ruatanus* from the Honduran mainland to a series of *Cnemidophorus lemniscatus* group specimens from El Real, Panama. Echternacht (1968) noted that the El Real specimens frequently had ten ventral plates across the venter at the level of the fifteenth ventral plate. Examination of a series of 15 of the El Real population revealed that all 15 have ten transverse (across the venter) ventrals at the level of the fifteenth ventral or at one or two ventral rows posterior to that point. The Panamanian *C. lemniscatus* group populations are also the only populations of the genus *Cnemidophorus* (sensu Harvey *et al.* 2012) known from the Pacific versant. We herein describe the Panamanian population as a new species of *Cnemidophorus*.

***Cnemidophorus duellmani* sp. nov.**

(Fig. 6)

Cnemidophorus lemniscatus lemniscatus: Burt 1931: 30 (part).

Cnemidophorus lemniscatus lemniscatus: Breder 1946: 428.

Cnemidophorus lemniscatus: Echternacht 1968: 153 (part).

Cnemidophorus lemniscatus: Jaramillo *et al.* 2010: 621.

Holotype. KU 80542, an adult male from El Real de Santa María, Darién Province, Panama, collected 9 January 1964 by William E. Duellman and Charles J. Cole. Anonymous (1969) gave the coordinates 8°08'N, 77°43'W for El Real de Santa María.

Paratypes (14). KU 80552, 80562, 80564, 80566, 80568 (all adult males), KU 80558, 80572, 80574, 80576–77, 80580 (all adult females), KU 80581 (subadult male), KU 80582–83 (both juveniles), all with the same locality data as the holotype, except some collected 10 January 1964.

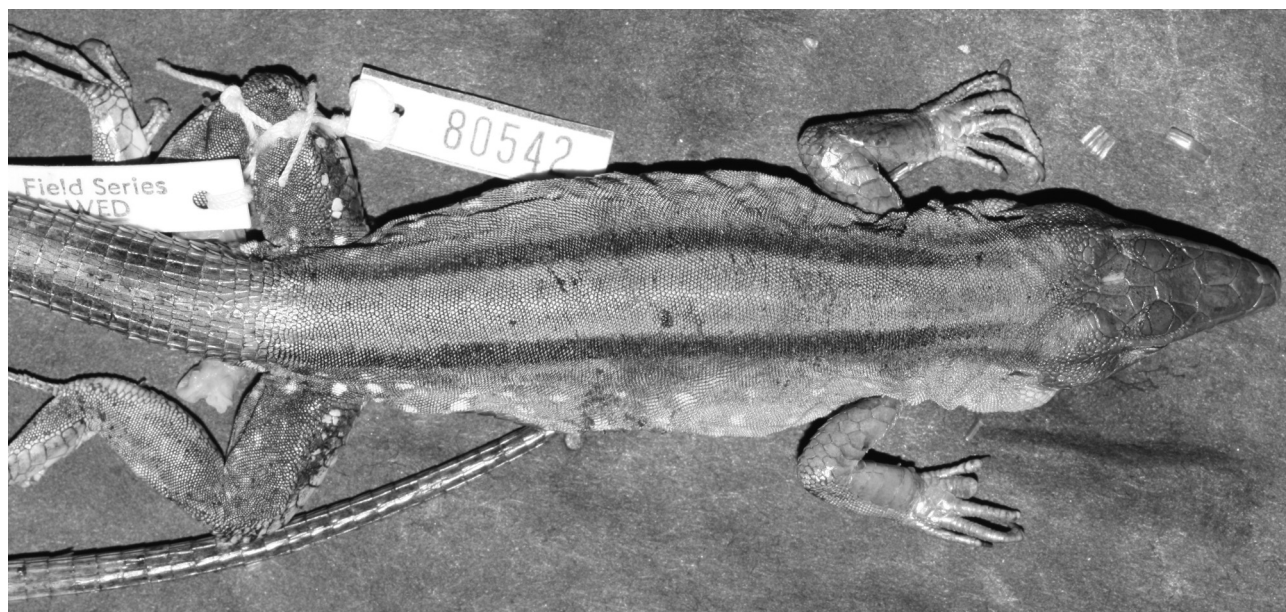


FIGURE 6. Dorsal surfaces of the holotype of *Cnemidophorus duellmani* sp. nov. (KU 80542).

Geographic distribution. *Cnemidophorus duellmani* is known from the environs of the Río Tuirá and its tributaries in Darién Province, on the Pacific versant of eastern Panama (Fig. 7; also see Remarks).

Diagnosis. *Cnemidophorus duellmani* can be distinguished from all other species in the *C. lemniscatus* species group (see Introduction, Harvey *et al.* 2012) by being the only species to have ten transverse ventral plates (Fig. 8) at the level of the fifteenth, sixteenth, and/or seventeenth ventral row (see Harvey *et al.* 2012: 105 who gave eight ventrals for species in the *C. lemniscatus* group). In addition, it differs further from *C. ruatanus*, the only other Central American species of the group, in having broad contact between the precloacal pair of enlarged plates, without a small scale extending anteriorly between those two plates (Fig. 9), in having 8–15 (both sides combined)

small scales bordering the posterior edge of supraocular four, in having a mean of 6.2 scales (both sides combined) between supraocular four and the outer parietal, and 8–15 (11.8 ± 2.0) circumorbitals; (versus paired prelocal plates frequently entirely separated by a small scale [Fig. 5], or separated at least one-third of its distance by a small scale, 4–9 small scales bordering supraocular four, a mean of 4.0 small scales between supraocular four and outer parietal, and 2–9, $x = 4.2 \pm 1.4$ circumorbitals in *C. ruatanus*).

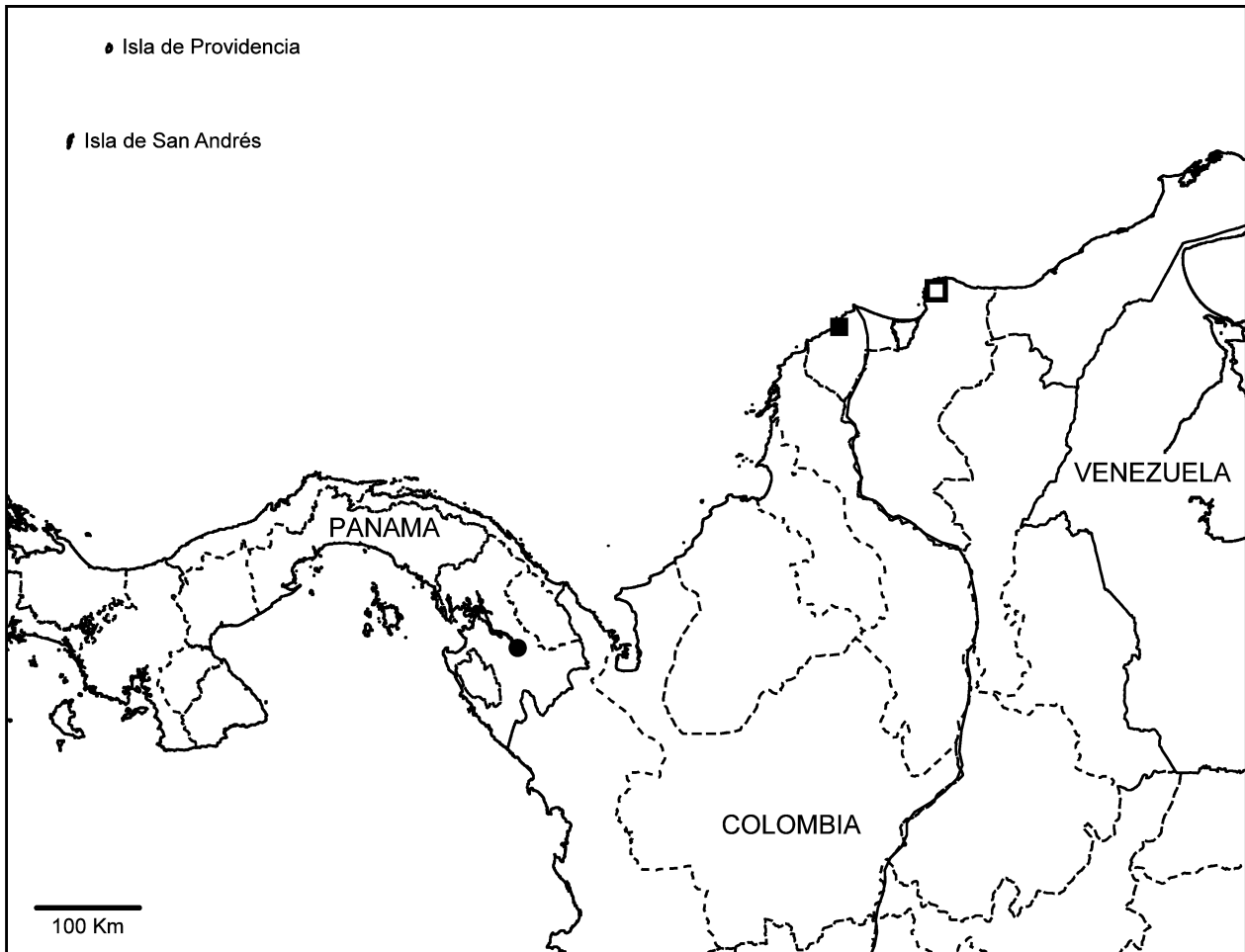


FIGURE 7. Map of eastern Panama and northern Colombia showing the localities for *Cnemidophorus duellmani* **sp. nov.** (circle), *Cnemidophorus gaigei* **comb. nov.** (square = specimens examined, open square = type locality), and the Islas de Providencia and San Andrés (upper left hand corner) where *Cnemidophorus espeuti* occurs.

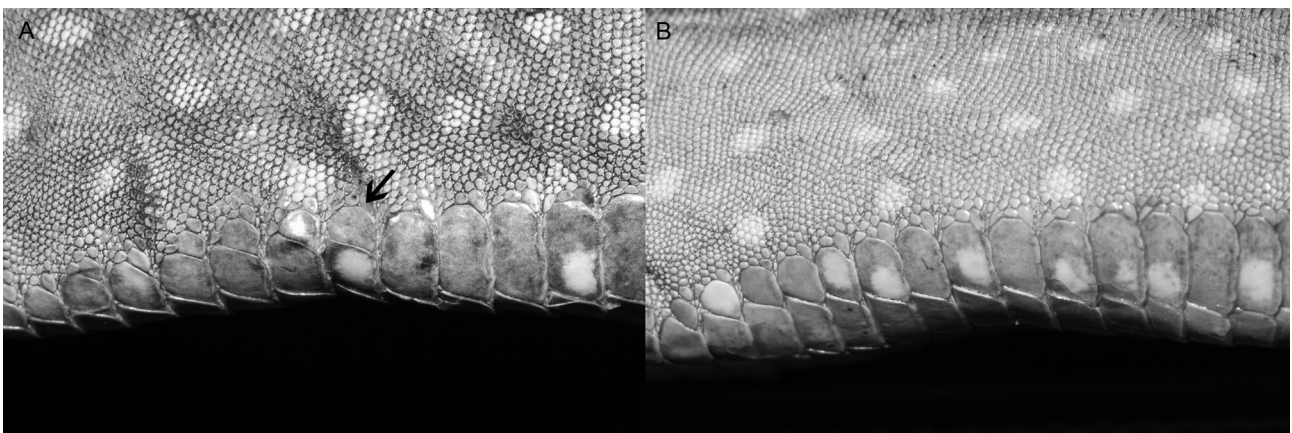


FIGURE 8A. Lateral surface of the holotype of *Cnemidophorus duellmani* **sp. nov.** (KU 80542) showing the extra ventral plate. **8B.** Lateral surface of *Cnemidophorus ruatanus* **comb. nov.** (KU 101329) showing the absence of the extra ventral plate.

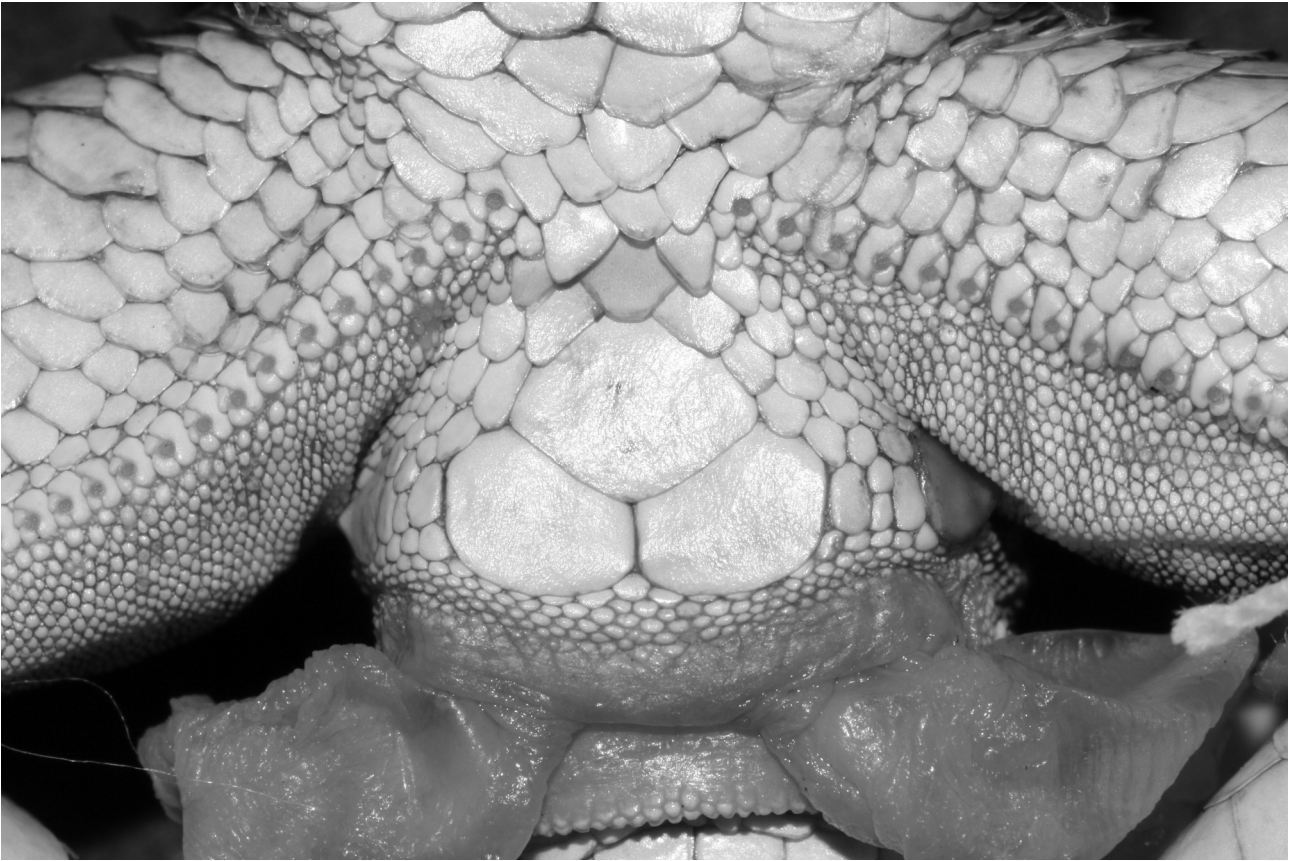


FIGURE 9. Cloacal plate region of the holotype of *Cnemidophorus duellmani* sp. nov. (KU 80542) showing the broad medial contact between the enlarged terminal precloacal plates.

Description of holotype. An adult male with a snout-vent-length (SVL) of 92.2 mm; snout-ear length (head length) 24.2 mm; snout length (snout to anterior border of eye) 11.1 mm; head width 15.0 mm; head depth 15.7 mm; shank length 19.3 mm; foot length 32.7 mm; hand length 13.7 mm; tail length 206.0 mm, tail length/SVL 2.23.

Dorsal head scales enlarged, smooth, platelike, with paired prenasal scales with short median sutures, a single frontonasal, paired prefrontals, a single frontal, paired frontoparietals, two pairs of parietal scales, and a single interparietal scale; rostral not contacting frontonasal; postnasal not contacting prefrontal; prefrontal and first superciliary in narrow contact on one side, separated by posterior extension of loreal on other side; frontal ridge absent; posterior frontal suture aligned near midlength of supraocular 3; scales in frontoparietal region smooth, flat; interparietal narrower than flanking parietals; 2–2 scales between fourth supraocular and inner-most parietal; 3–3 scales between fourth supraocular and outer-most parietal; 4–4 supraoculars plus one smaller supraocular lateral to region of seam between supraoculars 2–3 on each side; median pair of occipital scales distinctly enlarged, much larger than first dorsal scale row; 26 occipitals (occipitals of Harvey *et al.* 2012 plus scales bordering frontoparietals); supratemporals moderately enlarged, separated from parietals; short rostral groove present; nostril centered in nasal suture; nostril opening subtriangular; first supraocular contacting second supraocular; 1.0 to 2.0 rows of lateral supraocular granules, 21–23 granules on each side; anterior extent of circumorbital semicircles in single row reaches posterior third of supraocular 3, that of double row reaching anterior to seam between supraoculars 3–4; 7–8 circumorbitals; 5–5 superciliaries, second elongated; 4–4 suboculars, first on each side entire, upper edge contacting first superciliary, lower edge contacting supralabial 3; subocular keel present; patch of enlarged scales located in front of auditory meatus; no auricular or preauricular flaps or folds; 1–1 loreals; 6–6 supralabials; 6–5 infralabials; first supralabial straight ventrally, longer than second supralabial on one side, both supralabials subequal on other side; lingual sheath absent; moveable eyelids present; pupil rounded; first pair of chinshields contacting infralabials, those chinshields separated only at posterior edge; intergular sulcus absent; 19 anterior gulars; 11 posterior gulars; gular patch of distinctly enlarged scales absent; intertympanic sulcus absent;

sharp transition from anterior gulars to smaller posterior ones; mesoptychial scales moderately enlarged, bordered anteriorly by sharp transition to small scales; edge of gular fold not serrated; dorsal scales conical, 232 middorsals between occipitals and first enlarged, keeled caudal scale; 122 granules around midbody; middorsal scales subequal to lateral scales; chest scales large, flat; pectoral sulcus absent; ventral body scales large, platelike, squarish, juxtaposed, smooth, in 32 longitudinal rows, in 10 transverse rows at midbody; scales immediately lateral to outside ventral plate on each side small and granular; paired enlarged terminal scales forming precloacal plate; paired scales forming precloacal plate in broad contact medially, without small scale making indentation between those two scales; one larger, sub-diamond-shaped, scale anteriorly bordering precloacal terminal pair; 11 scales bordering all three enlarged plates; 3–3 smaller rounded scales between precloacal plate and precloacal spur; 6 precloacal scales; postcloacal buttons absent; pair of slightly enlarged postcloacal scales present; caudal annuli complete, tail lacking crests or dorsolateral row of serrated scales; third row of proximal subcaudal scales keeled; preaxial and postaxial brachial scales separated by band of continuous moderately enlarged scales; largest scales on preaxial and postaxial brachial surfaces 1.5 to over 2 times as wide as long, both sets of enlarged scales smooth, extending well beyond centers of arm; postaxial brachial scales in continuous enlarged row with preaxial brachial scales; postaxial antebrachial scales slightly enlarged; 29 combined subdigital lamellae on fourth finger; subarticular lamellae of Fingers III–IV homogeneous in size, entire; 61 combined subdigital lamellae on fourth toe, distal ones smooth; subarticular lamellae of Toes III–IV divided, each scale smaller than other lamellae; no row of distinctly enlarged scales between Toes IV–V; small scales separating supradigital scales from subdigital lamellae continuous, or nearly continuous; denticulate fringe absent along postaxial edge of outer toes; fifth toe not reduced, claw extending beyond level of articulation of Toes III–IV; 6 prefemoral scales on left side; heels without expanded scales; tibiotarsal shields present; tibiotarsal spurs absent; 41 total femoral-abdominal pores; no gap between femoral and abdominal pores; 4 scales separating each femoral-abdominal pore series; HL/SVL 0.26; HW/SVL 0.16; HD/SVL 0.17; HW/HD 0.96; SL/SVL 0.12; SHL/SVL 0.21; foot length/SVL 0.36; hand length/SVL 0.15.

Color in alcohol: middorsal longitudinal band, single, complete, pale bluish brown, extending from posterior edge of head onto base of tail; middorsal band on each side with a narrow dark brown band located inside middorsal band; dorsolateral ground color pale brown, becoming pale blue on flanks; three rows of about 8–10 white spots per row between axilla and groin; dorsal surface of head brown without distinct markings; anterior supralabials pale blue, those below eye pale blue with brown tinge; infralabials pale blue; dorsal surfaces of forelimbs brown, those of hind limbs bluish black with pale brown spots; middorsal pale band and dark brown band extending onto tail for about one-third of its length, lateral surface of tail in that area blue with scattered white spots, tail becoming brown at about midlength and then pale brown for distal third; all ventral surfaces pale blue, except palms and soles pale brown and subcaudal surface changing to bluish brown at about midlength and then brown on distal third; one row of widely scattered blue to white spots present on some outer ventral plates.

Variation. The 12 adult specimens of the type series have the following measurements and proportions and scale counts (bilateral counts combined, unless otherwise stated): SVL 61.3–92.2 (81.4 ± 11.4) mm in males, 56.2–74.9 (70.2 ± 7.3) in females; TAL/SVL 2.23–2.61 in five males, 2.33–2.53 in three females; HL/SVL 0.24–0.27 in males, 0.22–0.24 in females; SHL/SVL 0.21–0.23 in males, 0.18–0.23 in females; foot length/SVL 0.34–0.38 in males, 0.32–0.37 in females; hand length/SVL 0.13–0.15 in males, 0.12–0.14 in females; SL/SVL 0.10–0.12 in males, 0.10–0.11 in females; HW/SVL 0.13–0.16 in males, 0.12–0.15 in females; HD/SVL 0.13–0.17 in males, 0.11–0.13 in females; HW/HD 1.10–1.13 in males, 1.03–1.12 in females; femoral pores 41–44 (43.0 ± 1.3) in males, 36–44 (41.0 ± 3.0) in females; 104–132 (116.3 ± 10.4) granules around midbody; 27–32 (30.5 ± 1.4) longitudinal ventrals; 210–236 (222.2 ± 10.1) middorsal scales between interparietal and first enlarged and keeled scale at base of tail; 25–44 (31.5 ± 5.7) lateral supraoculars; 55–63 (59.7 ± 2.9) combined subdigital lamellae on fourth toe in 11; 27–37 (32.2 ± 2.7) combined subdigital lamellae on fourth finger; 25–29 (26.6 ± 1.4) occipitals (including scales bordering frontoparietals); 8–15 (11.5 ± 2.0) circumorbitals; 5–7 (6.2 ± 0.6) scales between supraocular 4 and outer parietal; 4–5 (4.1 ± 0.3) scales between supraocular 4 and inner parietal; 5–7 (5.8 ± 0.6) prefemoral scales on right side only; 4–5 (4.1 ± 0.3) precloacals; 17–22 (19.1 ± 1.8) anterior gulars; 8–14 (11.8 ± 1.7) posterior gulars; 9–11 (9.7 ± 0.7) scales around three enlarged precloacal plates.

Color in life: Duellman recorded in his field notes the following about a series of *Cnemidophorus duellmani*: “Adult male: throat, chin, and anterior surfaces of forearms blue; yellowish green dorsolateral stripe bordered above by dark brown stripe; middorsum buffy tan; flanks orange-tan; tail green laterally, blue below, brown above.”

Color in alcohol of the male paratypes is similar to that recorded for the holotype. However, *Cnemidophorus duellmani* is sexually dichromatic, thus female color in alcohol is described as follows: middorsal band pale brown with two slightly darker brown stripes placed laterally inside large band, middorsal band bordered laterally by black, broad stripe, middorsal band and bordering stripes extending from posterior end of head onto tail, both continuous; two white dorsolateral stripes on each side, those pale stripes separated by broader dark brown to black stripe; lateral field with dark brown to black stripe bordering lowest of paired dorsolateral white stripes, lateral field below that dark stripe pale brown, with or without 1–3 rows of pale spots; two most lateral ventral plates dark blue; dorsal surfaces of forelimbs bluish brown without distinct markings; dorsal surfaces of hind limbs bluish brown, usually with indistinct pale spots; tail bluish gray anteriorly, becoming some shade of brown on distal third; belly paler blue than outer ventral plates; remainder of color in alcohol similar to that of adult males. KU 80583 (SVL 33.3 mm), a juvenile, has eight longitudinal white stripes present; middorsal longitudinal band pale brown, complete, extending from posterior edge of head onto tail; throat and chin white; belly very pale blue; under surfaces of forelimbs pale brown, those of hind limbs dirty white; subcaudal surface pale brown on anterior third, becoming dark brown for posterior half. Another juvenile (KU 80582; SVL 33.1 mm) was similar to that described for KU 80583, whereas that of a subadult male (KU 80581; SVL 48.2 mm) is also similar to KU 80583, except that the ventral surfaces are pale brown.

Habitat. Duellman recorded in his field notes that the type series of *Cnemidophorus duellmani* was “found in open areas.” Breder (1946: 428) recorded the species was “Common along the lower reaches [of the Río Chucunaque and Río Chico valleys] in open fields.” Sexton *et al.* (1964: 293) studied this species at a site along the Río Chucunaque and stated that the “*Cnemidophorus* is commonly associated with areas having a low percentage of vegetation coverage as well as plants low in height.”

Breder (1946: 382) recorded the region encompassing the Panamanian Río Tuira and Río Chucunaque region and tributaries where *Cnemidophorus duellmani* occurs as in the “Lower Arid Zone,” whereas Jaramillo *et al.* (2010: 621) considered *C. duellmani* as occurring in the “Lowland Wet/Moist Forest.” Curiously, none of the authors who presented ecological data on this species mentioned the presence or absence of “foot waving,” which is usually present in members of the *C. lemniscatus* group.

Conservation notes. Jaramillo *et al.* (2010: 621) characterized *Cnemidophorus duellmani* (as *C. lemniscatus*) as a species of medium vulnerability because of the former perceived wide geographic distribution of *C. lemniscatus*. With our study, *C. duellmani* is now a Panamanian endemic species with vulnerability score of 13, thus placing the species in the high vulnerability category. However, in this case, that score is misleading since *C. duellmani* is a species that benefits from human disturbance of habitat (see Sexton *et al.* 1964, Heatwole 1966). Thus, *C. duellmani* appears to not be threatened in the foreseeable future, and in fact will likely benefit from continued clearing of lands along the river valleys in the region where it occurs.

Remarks. Burt (1931) recorded *Cnemidophorus l. lemniscatus* from two localities in the Panamanian Canal Zone (MCZ specimens from Ancón and Obispo Station), otherwise all of Burt’s localities for this species are from the vicinities of the Río Tuira and tributaries in Darién Province. The occurrence of *Cnemidophorus* in the Canal Zone needs to be investigated, but Ibáñez *et al.* (1995) did not list it as occurring in the Canal Zone. It is also possible that Burt (1931) misidentified specimens of *Holcosus undulatus* (Wiegmann) in the MCZ from Ancón, Panama as *Cnemidophorus* since there is a series of *H. undulatus* in the MCZ from Ancón (Echternacht 1971).

Etymology. We take pleasure in naming this new species after William E. Duellman of the University of Kansas. Bill was not only one of the collectors of the type series, but has also produced two significant studies of Mexican and Guatemalan species groups of lizards, which at those times were considered to be members of the genus *Cnemidophorus* (now *Aspidoscelis*).

Discussion

Whereas this study was primarily designed to study the Central American populations of the *Cnemidophorus lemniscatus* species group, we offer some taxonomic suggestions on three South American populations considered subspecies of *C. lemniscatus* by Harvey *et al.* (2012). Markezich *et al.* (1997) described *C. l. splendidus*, which they diagnosed from their concept of *C. l. lemniscatus*, as having a blue ground color in adult males and a black, blue, or dark brown ground color in adult females, dark blue venters in preserved adults, a single or absent

vertebral stripe in adults, and a single vertebral stripe in juveniles (versus ground color green or brown in adult males and females, pale blue venters in alcohol, and a split vertebral stripes in adults and juveniles in *C. l. lemniscatus*). Markezich *et al.* (1997) considered *C. l. lemniscatus* to occur in Guyana, Suriname, and eastern Venezuela, whereas their *C. l. splendidus* occurs on the Paraguana Peninsula of northwestern Venezuela. Markezich *et al.* (1997) also speculated that *C. l. splendidus* might also occur elsewhere in northern Venezuela and adjacent Colombia. Reeder *et al.* (2002) performed a molecular analysis that included four South American nominal forms of the *C. lemniscatus* species group. That study recovered a clade containing *C. l. splendidus* and *C. arenivagus* that was sister to a clade containing *C. l. lemniscatus*, which was in turn a sister clade to *C. gramivagus*. That molecular study, thus, suggested that *C. l. splendidus* might represent a full species, more closely related to *C. arenivagus* of the Paraguana Peninsula, than to the eastern populations assigned to *C. l. lemniscatus*. Our molecular analysis (Fig. 1) with 11 samples of *C. ruatanus* added recovered similar results to the Reeder *et al.* (2002) study, except that the *C. l. splendidus*-*C. arenivagus* clade shows a more distal relationship to *C. l. lemniscatus* than it does to *C. ruatanus*. Thus, we suggest elevating *C. l. splendidus* to a full species, *C. splendidus* **comb. nov.** Markezich, Cole & Dessauer.

Harvey *et al.* (2012) treated the isolated *Cnemidophorus* populations on the Colombian islands of Providencia and San Andrés as a subspecies of *C. lemniscatus*. Dunn & Saxe (1950) had suggested that the *Cnemidophorus* populations of Providencia and San Andrés (described as *C. espeuti* by Boulenger 1885) first reached Providencia from the Cabo Gracias a Dios of Nicaragua and adjacent Honduras by trade between English colonies at the Cape and on Providencia “during the decade 1630–1640, [as] there was much traffic back and forth between the two areas.” However, *C. l. espeuti* differs significantly from the Honduran mainland populations (*C. ruatanus*) in having a split vertebral stripe (versus stripe continuous in *C. ruatanus*). It now seems more likely that *C. l. espeuti* occurs naturally on Isla de Providencia, but it was transported by humans to Isla de San Andrés sometime prior to 1931 (see Dunn & Saxe 1950: 157). *Cnemidophorus l. espeuti* also differs from *C. l. lemniscatus* in having a fewer number of circumorbital scales (4–10, $x = 6.4 \pm 1.8$ in *C. l. espeuti* versus 8–17, $x = 12.0 \pm 4.0$ in *C. l. lemniscatus*; data from Harvey *et al.* 2012: 106, and specimens examined listed in Appendix I). Thus, we suggest elevating *C. l. espeuti* to a full species, *C. espeuti* Boulenger (described as a full species, but subsequent to Burt 1931 until now treated as a synonym of *C. lemniscatus* or as a subspecies of *C. lemniscatus*). It would be preferable to have molecular data to test this suggestion, but Colombia does not allow the export of tissues from their country. It is also unfortunate that Boulenger named this species for W. B. Espeut, the person who first successfully introduced the Small Asian Mongoose (*Herpestes javanicus* [Geoffroy Saint-Hilaire]) to the New World (initially on Jamaica), which caused the extinction of many West Indian reptile species. See Fig. 7 for the location of the Islas de Providencia and San Andrés where *C. espeuti* occurs.

One other subspecies of *Cnemidophorus lemniscatus* (*C. l. gaigei*) recognized by Harvey *et al.* (2012) requires comment. Ruthven (1915) described that nominal form for the *Cnemidophorus* populations in the Santa Marta region of northern Colombia. Burt (1931) placed *C. l. gaigei* in the synonymy of *C. l. lemniscatus*, but Harvey *et al.* (2012) resurrected *C. l. gaigei* for those populations. *Cnemidophorus l. gaigei* has a continuous vertebral stripe, thus differing from *C. l. lemniscatus*, which has a split vertebral stripe. In addition, the geographic distribution of *C. l. gaigei* appears to be separated from *C. l. lemniscatus* by *C. splendidus* along the north coast of Venezuela. *Cnemidophorus splendidus* resembles *C. l. gaigei* in having the vertebral stripe continuous when present (but, see Markezich *et al.* 1997: 40). Harvey *et al.* (2012: 106) presented a table with meristic data on various nominal forms of the *C. lemniscatus* group they examined, including *C. l. gaigei* and *C. splendidus*. Although Harvey *et al.* (2012) only examined two *C. splendidus* and 11 *C. l. gaigei*, they recorded 13–14 total supralabials (both sides combined) for *C. splendidus* and 12 (both sides combined) for all 11 *C. l. gaigei*. We examined an additional nine specimens of *C. l. gaigei* from west of its type locality (see Appendix I and Fig. 7) and all have 12 supralabials (both sides combined). Also, the nine specimens are all more similar to the Harvey *et al.* (2012) data for *C. l. gaigei* than to *C. splendidus* in having fewer circumorbitals (4–6, $x = 5.4 \pm 0.7$ in *C. l. gaigei* versus 12–13 in *C. splendidus*). Morphologically, *C. l. gaigei* appears to be more closely related to *C. ruatanus* than it does to *C. splendidus*, its nearest geographic relative, in having fewer circumorbitals and supralabials. Given that *C. l. gaigei* appears to be geographically isolated from other populations of *C. lemniscatus* that molecular data suggest are best treated as full species (*C. gramivagus* to the south and southeast and *C. splendidus* to the east; Fig. 1), we suggest elevating *C. l. gaigei* to a full species, *C. gaigei* **comb. nov.** Ruthven (see Fig. 7 for the location of the *C. gaigei* specimens examined for this work and the location of its type locality). Following our suggested taxonomy would mean that

C. lemniscatus has no subspecies. We suggest the new taxonomy with the caveat that molecular studies are needed for the Colombian species recognized herein, as well as other South American populations left unassigned to a subspecies by Markezich *et al.* (1997). Since Colombia does not allow tissues to leave the country, Colombian colleagues will likely have to perform any forthcoming molecular analyses on endemic Colombian members of the *C. lemniscatus* group.

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APPENDIX I. Comparative specimens examined. GenBank accession numbers are listed, in parenthesis, for the genetic samples (16SrRNA, 12SrRNA, cytochrome b).

Cnemidophorus espeuti. COLOMBIA: SAN ANDRÉS Y PROVIDENCIA-Isla de Providencia, USNM 76948–55, 239415–16.

Cnemidophorus gaigei. COLOMBIA: ATLÁNTICO-Colonia Agrícola de Caracolcito, USNM 117466–74.

Cnemidophorus ruatanus. HONDURAS: ATLÁNTIDA-Agua Chiquito, USNM 580928; Corozal, LACM 48067, LSUMZ 21693–95; Barra de Colorado, USNM 580929; 14.5 km E of La Ceiba, LACM 48070; 1 km W of La Ceiba, KU 101328–40; 2 km SE of La Ceiba, KU 101341; about 12 km SSE of La Ceiba, KU 101351; La Ceiba, CM 29008, INHS 4486, LACM 48051–62, LSUMZ 21677–88, USNM 62973–79, 117608; Lancetilla, AMNH 69640, 70449–54, 70455 (15), UMMZ 72412 (10); Piedra Pintada, LACM 48071; Punta Sal, USNM 580930–31; Río Cangrejal near La Ceiba, FMNH 283561 (genetic sample 6: KF667254, KF667265, KF667274); along Río Viejo, KU 200584, USNM 563588; San Marcos, USNM 570397–402; about 80 km ESE of Tela, FMNH 13007; Tela, AMNH 46917–19, 157317–41, MCZ R-21117–49, 21757–67, 27570–75 (+ 12 untagged), UMMZ 69537 (2), 62509 (6). COLÓN-: Balfate, AMNH 58624–26; Barranco, ANSP 28124; Puerto Castilla, LSUMZ 22479–81; Salamá, USNM 242610, 242612–13, 242627–37; 1–3 km W of Trujillo, KU 101342–48, LACM 48068–69; between Trujillo and Santa Fé, CM 65704–18; Trujillo, CM 65719–25, KU 101349–50. COPÁN-La Playona, USNM 563589–90. CORTÉS-El Paraíso, UF 144706–07; Puerto Cortés, AMNH 37864–65, FMNH 5096, 213524–27, 213529–35, TCWC 19201–07, UIMNH 66642, UMMZ 79071, USNM 69395–401; about 0.5 km SSE of Tegucigalpa, SMF 79013–14; Tegucigalpa, FMNH 283560, 283563 (genetic sample 5: KF667253, KF667264), 283565, 283566, 283567 (genetic sample 4: KF667252, KF667263, KF667273), 283569, UNAH 256667 (genetic sample 1: KF667249, KF667260, KF667270), 256668 (genetic sample 2: KF667250, KF667261, KF667271), 256669 (genetic sample 3: KF667251, KF667262, KF667272), USNM 563591–93. GRACIAS A DIOS-Cauquira, UF 150291, 150296, 150298–99; Yahurabila, USNM 573206–12. ISLAS DE LA BAHÍA-Cayo Cochino Pequeño, near Bonkes Nose Point, KU 220101; Cayo Cochino Pequeño (voucher not examined; genetic sample 11: KF667259, KF667269); Isla de Roatán, near Coxen Hole, FMNH 34492–538; Isla de Roatán, Flowers Bay, USNM 563594–97, 563599–600; Isla de Roatán, about 3.2 km W of French Harbor, LSUMZ 22384, UF 28554–56; Isla de Roatán, W of Oak Ridge, UTA R-10677–80; Isla de Roatán, near Oak Ridge, MCZ R-150947–49, TCWC 52419–21; Isla de Roatán, Oak Ridge, KU 192621–22; Isla de Roatán, Palmetto Bay, FMNH 283562 (genetic sample 10: KF667258, KF667268), 283564 (genetic sample 7: KF667255, KF667266, KF667275); Isla de Roatán, between Port Royal Harbor and Calabash Bight, UTA R-10674–75; Isla de Roatán, Port Royal Harbor, LSUMZ 33781; Isla de Roatán, about 3.2 km W of Roatán, CM 65699–700, LSUMZ 29632–33, 29669, 46595, 46601–02, 50770; Isla de Roatán, 0.5–1.0 km W of Roatán, LACM 48063–64, LSUMZ 21689–90; Isla de Roatán, about 4.8 km N of Roatán, CM 65701–02, LSUMZ 29631, 46597, 46599–600, 50771; Isla de Roatán, about 1.6 km N of Roatán, LSUMZ 29634, 46596, 46598; Isla de Roatán, 0.5–4.0 km N of Roatán, LACM 48065–66, LSUMZ 21691–92, UF 28485; Isla de Roatán, about 4.8 km W of Roatán, UF 28509–13, 28534; Isla de Roatán, near Roatán, CM 65703, LSUMZ 29629–30, 46603; Isla de Roatán, Sandy Bay, KU 203160–62; Isla de Roatán, Santa Elena, UTA R-10676; Isla de Roatán, West End Town, USNM 563598; “Isla de Roatán,” MVZ 160192; Isla de Utila, east coast near Trade Winds, FMNH 283568 (genetic sample 9: KF667257, KF667267), UNAH 20288 (genetic sample 8: KF667256, KF667276); Isla de Utila, Jake’s Bight, SMF 77111; Isla de Utila, Pumpkin Hill, UNAH 5289–90; Isla de Utila, Utila, CM 28999–9001, LSUMZ 22278–86, UF 28366–88, 28430–36, 28444. YORO-: 17 km NE of El Progreso, AMNH 157312–16, 157342, LSUMZ 24625–27. “HONDURAS”: UF 76231, 90901–08, 99331, 99433, 99662.