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Evidence for the recognition of two species of *Anolis* formerly referred to as *A. tropidogaster* (Squamata: Dactyloidae)

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Abstract

Based on differences in hemipenial morphology, male dewlap coloration, pholidosis, and 16S mtDNA, we recognize two species of anoles related to what was formerly referred to as *Anolis tropidogaster*: *Anolis tropidogaster* Hallowell 1856 and *A. gaigei* Ruthven 1916. The hemipenis in *A. tropidogaster* is large, bulbous, and bilobed whereas it is small, thin, and unilobed in *A. gaigei*; the male dewlap is almost uniform purplish red, sometimes with a paler orange central area in *A. tropidogaster* versus orange yellow with a darker orange central area in *A. gaigei*; and—aside from more subtle differences in several pholidotic characteristics—in male *A. gaigei* there is a pair of greatly enlarged postcloacal scales which is absent in *A. tropidogaster.* In the western part of its geographic range, *A. gaigei* has been confused with another anole species, *A. polylepis* Peters 1873, from which it can be readily distinguished by its strongly keeled ventral scales (smooth in *A. polylepis*).

Key words: *Anolis albi*, *Anolis cupreus*, *Anolis gaigei*, *Anolis osa*, *Anolis polylepis*, *Anolis stigmosus*, *Anolis tropidogaster*, Central America, Colombia, Dactyloidae, Panama, Reptilia, Squamata, Venezuela

Resumen

Basándonos en las diferencias morfológicas de hemipenes, coloración de la papera gular de los machos, características de escamación y 16S mtDNA reconocemos dos especies de lagartijas relacionadas con lo que hasta ahora ha sido reconocido como *Anolis tropidogaster*: *Anolis tropidogaster* Hallowell 1856 y *A. gaigei* Ruthven 1916. Las dos especies difieren en la morfología de hemipenes (hemipenes grandes, bulbosos y bilobulados en *A. tropidogaster* y pequeños, delgados y unilobulados en *A. gaigei*); en la coloración de la papera gular de los machos (casi rojo púrpura uniforme, a veces con un área central de color naranja más pálido en *A. tropidogaster*, a diferencia de un amarillo anaranjado con un área central de color naranja más oscuro en *A. gaigei*); y—además de varias diferencias más sutiles en características de escamación—machos de *A. gaigei* presentan un par de escamas postcloacales muy agrandadas las cuales están ausentes en *A. tropidogaster.* En la parte occidental de su área de distribución geográfica, *A. gaigei* ha sido confundida con otra especie de lagartija, *A. polylepis* Peters 1873, de la cual se distingue claramente mediante sus escamas ventrales fuertemente aquilladas (lisas en *A. polylepis*).

Introduction

In 1856, Hallowell described *Anolis tropidogaster* based on a single specimen (now ANSP 7618) that originated from "New Grenada," then a republic that contained the territory of today's Colombia and Panama as well as small portions of what is today Ecuador and Venezuela (Aguilera Peña 2002). However, most previous authors have interpreted the type locality of *A. tropidogaster* to be "New Grenada, Colombia" (*e.g.*, Malnate 1971) or merely

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"Colombia" (*e.g.*, Dunn 1930, Barbour 1934, Peters and Donoso-Barros 1970). GK had the privilege of examining ANSP 7618, which constitutes fragments of bone with remains of poorly preserved skin. According to Dunn (1930) and Barbour (1934), the specimen had been in this poor state at least since the early 1930s. Bocourt (1869) established his new species *Anolis stigmosus* based on two specimens (now MNHN 2427 and 2427A) from "la Colombie et ont été recueillis près de la rivière de la Magdeleine". Ruthven (1916) described *Anolis gaigei* based on a holotype (now UMMZ 48304) from "San Lorenzo, Santa Marta Mountains, Colombia, elevation of 2,700 ft." Finally, Barbour (1932) described *Anolis albi* (female holotype MCZ 32301; male paratype MCZ 32302, the latter examined by GK) from "Andagoya, Choco, western Colombia." The nominal species *A. stigmosus, A. gaigei,* and *A. albi* have been considered as synonyms of *A. tropidogaster* for a long time (Barbour 1934; Peters & Donoso-Barros 1970).

In the course of our field work in Panama, we discovered that two distinct and geographically segregated phenotypes are present among the populations currently assigned to *A. tropidogaster.* The two clusters differ most obviously in hemipenial morphology, in the coloration of the male dewlap as well as in several pholidotic characteristics. Here we report upon these results and provide evidence for the recognition of each of these morphological clusters as a distinct species. Because in parts of its geographic range one of these species has frequently been confused with another widespread lowland anole, *A. polylepis* (*e.g.*, Martínez Cortés & Rodriguez 2003, 2005, Ibáñez 2006), we also include the latter species in our comparisons.

Material and methods

In evaluating whether multiple species exist within the *Anolis tropidogaster* complex, we follow the Evolutionary Species Concept (Simpson 1961, Wiley 1978), and operationalize this concept by identifying species based on consistent differences between populations, assuming these differences are the result of different evolutionary histories (Frost & Kluge 1994). Abbreviations for museum collections follow those of Leviton *et al.* (1985) except for MHCH (Museo Herpetológico de Chiriquí, David, Chiriquí, Panama). Nomenclature of scale characters follows that of Köhler (2008). Terminology for dewlap morphology follows that of Fitch and Hillis (1984). Terminology for hemipenial morphology follows that of Myers *et al.* (1993) and Savage (1997). Scale sizes were measured using the ocular micrometer of a stereo microscope (Leica MZ 12) to the nearest 0.01 mm. All other measurements were made using precision calipers to the nearest 0.1 mm. Values are given as minimum–maximum (mean ± standard deviation). Head length was measured from the tip of the snout to the anterior margin of the ear opening. Snout length was measured from the tip of the snout to the anterior border of the orbit. Head width was determined as the distance between the oral ricti. Dorsal and ventral scales were counted at midbody along the midline. Tail height and width were measured at the point reached by the heel of the extended hind leg. Subdigital lamellae were counted on phalanges II to IV of the 4th toe. We considered the scale directly anterior to the circumnasal to be a prenasal. Relative hind leg length was examined in the field by folding the hind leg of the specimen in life towards its head and determining the point reached by the tip of the longest toe. The capitalized colors and color codes (the latter in parentheses) are those of Smithe (1975–1981). Abbreviations used are HL (head length), HW (head width), INL (infralabials), IP (interparietal plate), SO (subocular scales), SPL (supralabial scales), SS (supraorbital semicircles), and SVL (snout–vent length).

For the complementary molecular analysis, we extracted DNA following the protocol of Ivanova *et al.* (2006). To eliminate potential PCR-inhibiting contaminants, the tissue samples were incubated for 14 hours in 200 µL low PBS buffer (20 µL PBS in 180µL of water) before overnight digestion with the vertebrate lysis buffer at 56 °C. After extraction, DNA was eluted in 50 µL TE buffer. A fragment of the mitochondrial 16S rRNA gene was amplified in an Eppendorf Mastercycler® pro using the following program: initial denaturation for 2 min at 94 °C; followed by 40 cycles with denaturation for 35 s at 94 °C, hybridization for 35 s at 48.5 °C, and elongation for 60 s at 72 °C; final elongation for 10 min at 72 °C. Reaction mix for each sample contained 1 µL DNA template, 14 µL water, 2.5 µL PCR-buffer, 1 µL 25 mM $MgCl_2$, 4 µL 2.5 mM dNTPs (Invitrogen), 0.5 µL Taq Polymerase (PeqLab), and 1 µL of each primer (forward: L2510, 5'-CGCCTGTTTATCAAAAACAT-3'; reverse: H3056, 5'-CCGGTCTGAACTCAGATCACGT-3'; eurofins MWG Operon). A total of 7 sequences (one of each Type A and *Anolis polylepis*, two of each Type B and *A. cupreus,* and one *A. kemptoni* as outgroup; see Appendix 2 for examined specimens and GenBank accession numbers) were aligned with MUSCLE (Edgar 2004) using the default settings in Geneious (Drummond *et al.* 2010). The manually refined final alignment contained 542 positions. Using

MEGA5 (Tamura *et al.* 2011), we computed uncorrected pairwise genetic distances, determined the Tamura 3-parameter model as the best-fitting substitution model, and conducted Maximum Likelihood as well as Maximum Parsimony analyses (each with 10000 bootstrap replicates). Using TCSv1.21 (Clement *et al.* 2000), we conducted a statistical parsimony network analysis, with gaps considered as a fifth character state and a connection limit of 95%.

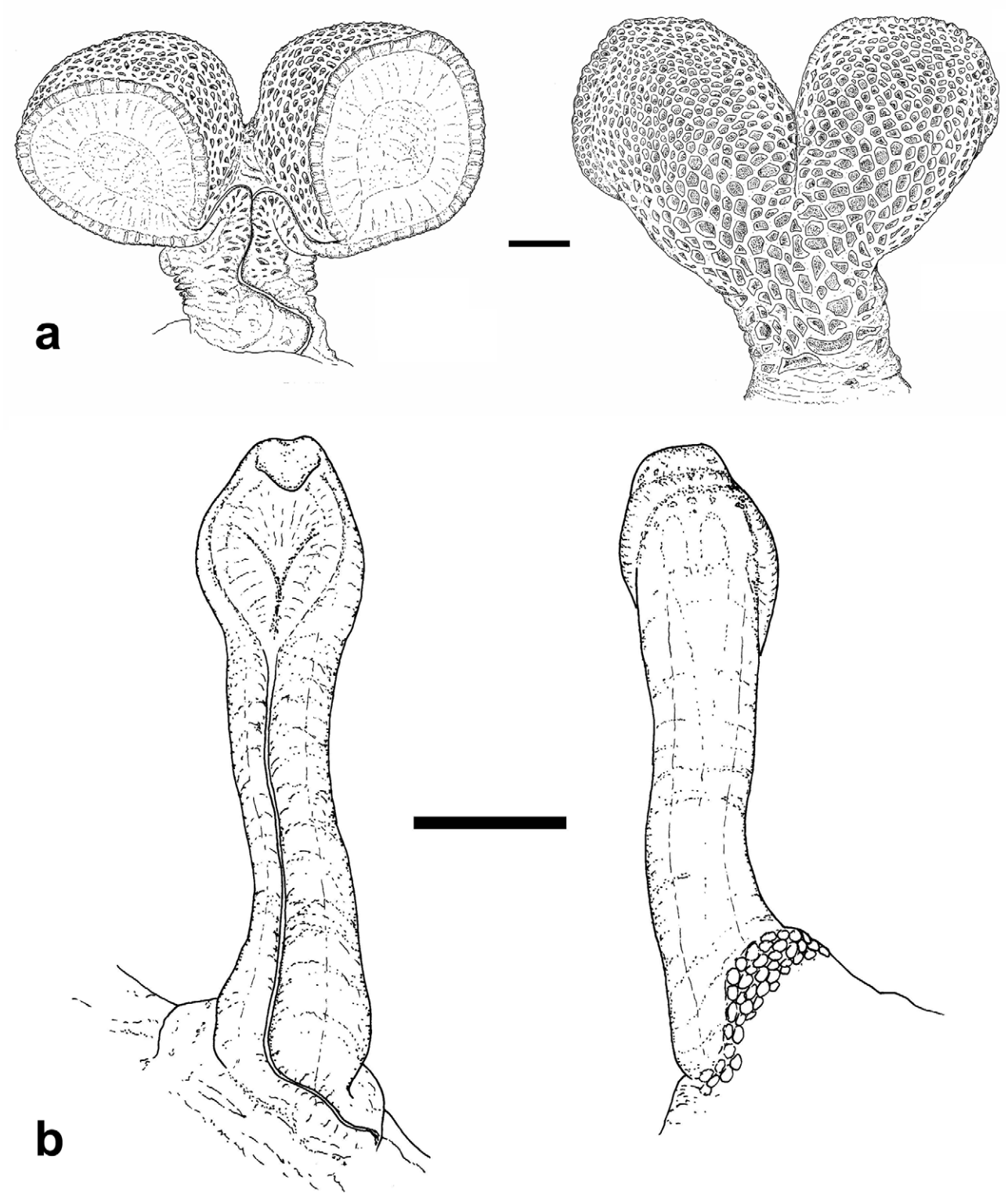

FIGURE 1. (a) Type A hemipenis (SMF 91956); (b) Type B hemipenis (SMF 91902). See text for details. Scale bar = 1.0 mm.

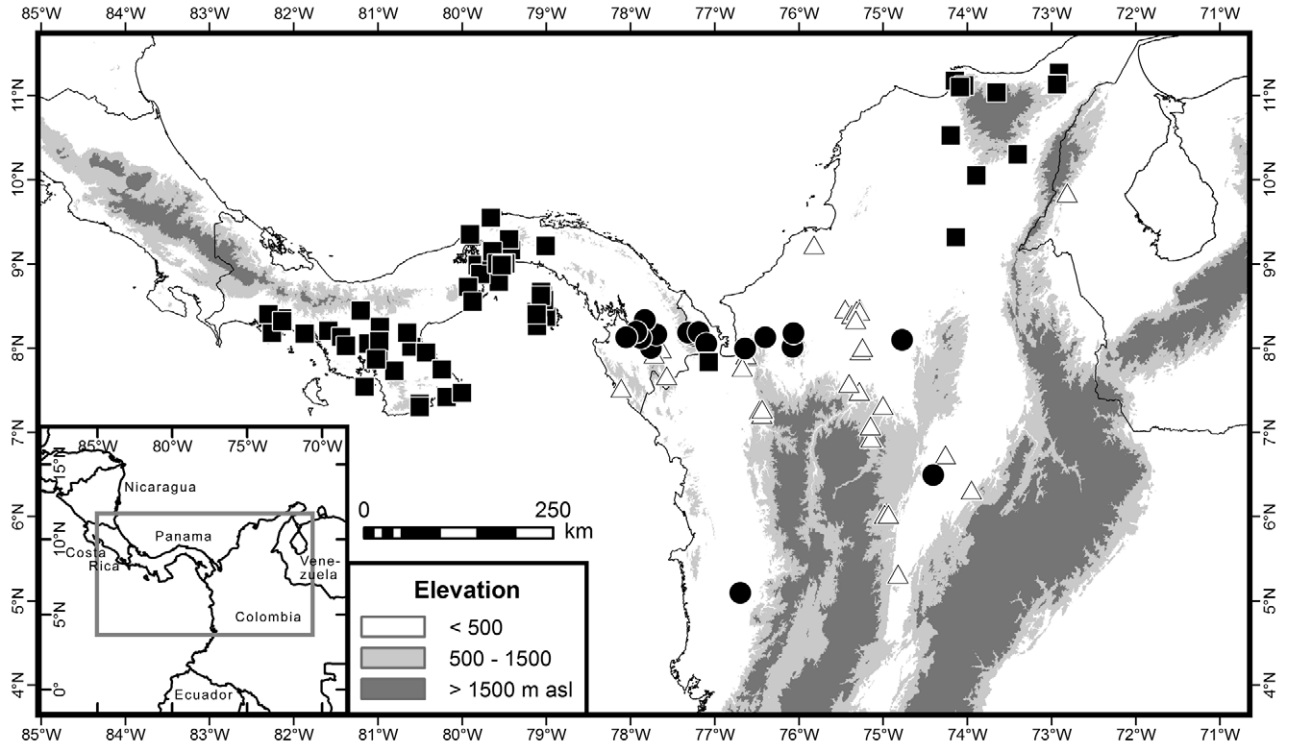

FIGURE 2. Map indicating known collecting sites mentioned in text of anoles formerly referred to as *Anolis tropidogaster*. Each symbol can represent one or more nearby localities. Circles: Type A hemipenes; squares: Type B hemipenes; triangles: localities of *Anolis tropidogaster*-like specimens not verified by authors (sources: MHUA catalogue, Donoso-Barros 1968, Carvajal-Cogollo and Urbina-Cardona 2008). See text for details.

Results

Two distinctly different hemipenial morphotypes are evident in the specimens we examined. In Type A (Fig. 1a; *N* = 5 adult males with everted hemipenes), the hemipenis is a large bilobed organ (length of lobes equal length of truncus); the sulcus spermaticus bifurcates at the base of the apex and the branches open into concave areas, one on each lobe; asulcate side of apex strongly calyculate, truncus with transverse folds. In Type B (Fig. 1b; *N* = 14 adult males with everted hemipenes), the hemipenis is unilobed and smaller and thinner relative to body size as compared to the type A hemipenis; the sulcus spermaticus opens at base of apex into a broad concave area that covers the complete sulcate side of the apex; no discernable surface structure on trunk or apex. The distribution of the two hemipenial morphs is highly correlated geographically (Fig. 2). Furthermore, the two hemipenial morphs differ readily in male dewlap coloration. The dewlap of males with a Type A hemipenis is orange yellow with a darker orange peripheral area (Figs 3a,b). The dewlap of males with a Type B hemipenis is orange yellow with a darker orange central area (Figs. 3c,d). Finally, we observed differences in several scalation characteristics (Fig. 4): (1) in males with a Type A hemipenis the postcloacal scales are usually not, or only slightly enlarged whereas males with a Type B hemipenis always have a very distinct pair of greatly enlarged postcloacal scales; (2) the dorsal head scales, especially in the parietal region: smaller and bearing minute tubercles in Type A versus larger and flat in Type B; (3) middorsal caudal scales: only slightly enlarged and somewhat irregularly arranged in Type A versus distinctly enlarged and forming a regular series in Type B; (4) postmental scales: outer postmental scales only slightly enlarged relative to medial ones in Type A versus outer scales greatly enlarged relative to medial ones in Type B.

The distinctiveness of the hemipenial morphs A and B is further corroborated by the differences in the 16S mitochondrial rRNA gene revealed by our analyses (Fig. 5). In our consensus tree (Fig. 5a), the Type A specimen (MHCH 1634) appears most closely related to the Type B specimens (SMF 91907, 91918), with *Anolis polylepis* and *A. cupreus* forming a sister clade to Type A + Type B. The mean genetic distance between Type A and Type B specimens is 4.1% (4.3 and 3.9%, respectively). This value, although being slightly lower than the genetic distance

of 6.0% observed between *A. polylepis* and both specimens of *A. cupreus*, can be interpreted to indicate a differentiation at species level. This view is supported by the fact that in the haplotype network analysis (Fig. 5b) Type A and B form unconnected subnetworks, just as *A. polylepis* and *A. cupreus* do.

Based on the combined evidence, we recognize the two hemipenial morphotypes defined above as two distinct species with Species A (= our former Type A) being distributed in Colombia and eastern Panama, and Species B (= our former Type B) being distributed from western Panama along northern Colombia, and probably into western Venezuela (Fig. 2). See Table 1 for variation in selected measurements, proportions and scale characters in the two species.

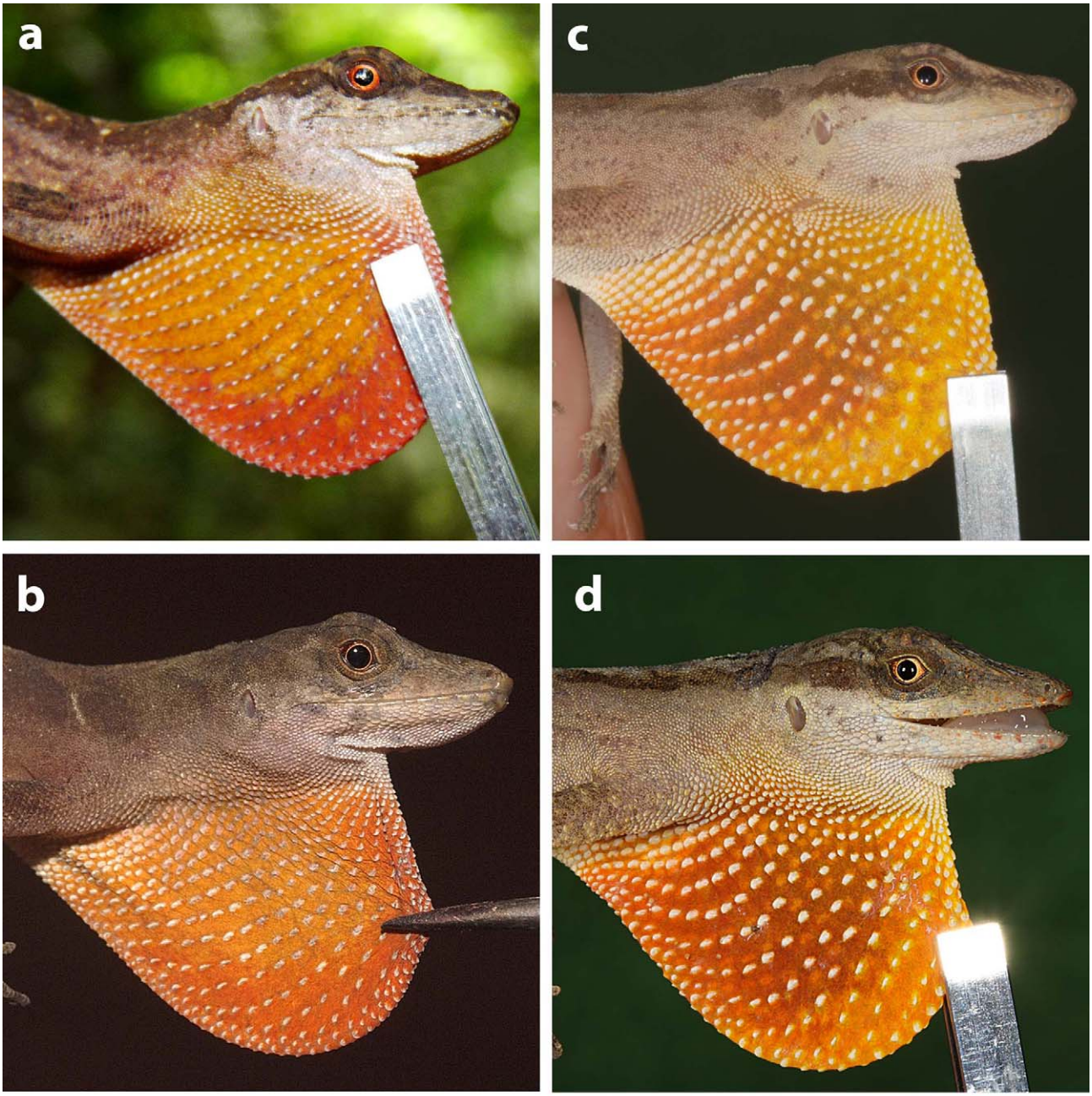

FIGURE 3. Male dewlap in life. Type A hemipenes: (a) SMF 91956; (b) SMF 93598. Type B hemipenes: (c) SMF 91902; (d) SMF 91910.

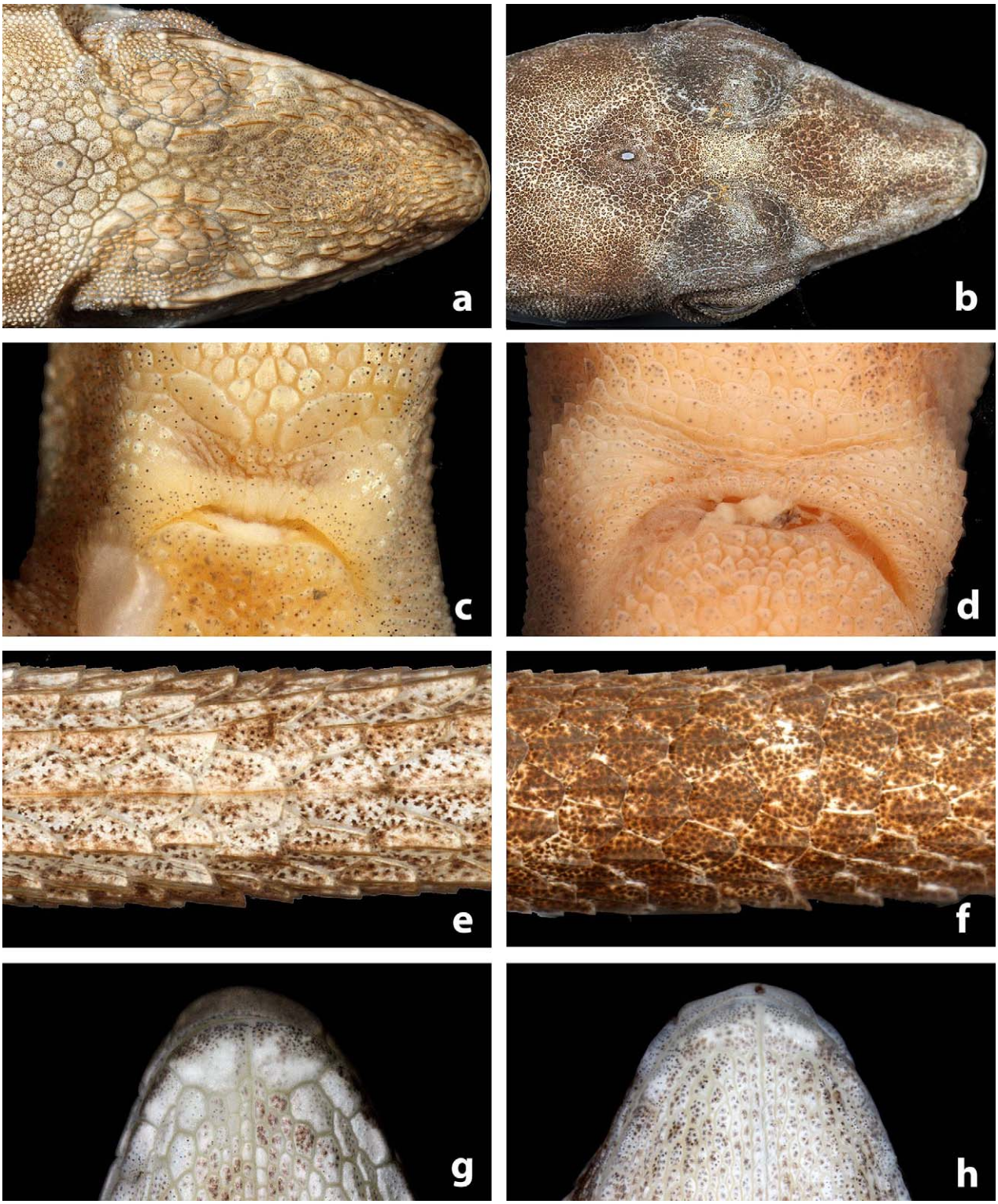

FIGURE 4. Comparison of scalation details in *Anolis gaigei* (left column) and *A. tropidogaster* (right column). Dorsal head in (a) *A. gaigei* SMF 91956 and (b) *A. tropidogaster* MHCH 1701. Cloacal region in (c) *A. gaigei* SMF 82705 and (d) *A. tropidogaster* FMNH 63793. Dorsal tail in (e) *A. gaigei* SMF 91956 and (f) *A. tropidogaster* MHCH 1636. Chin region in (g) *A. gaigei* SMF 91956 and (h) *A. tropidogaster* MHCH 1640.

As mentioned above, the holotype of *Anolis tropidogaster* (ANSP 7618; Fig. 6a) is a macerated skeleton with vague locality data (see above). Fortunately, the original description (Hallowell 1856) provides some clues as for the taxonomic identity of the male holotype (sex as indicated by the presence of "a well developed gular pouch"; Hallowell 1856:225). The information that ANSP 7618 had a "remarkably strong carination of the ventral scales"

and a "color brownish, extremities banded with brown" (Hallowell 1856:224) supports the view that this specimen belongs to the *A. tropidogaster* complex as currently understood. Somewhat odd is the remark that it had "fingers and toes without any dilation whatever" (Hallowell 1856:225), a condition that might be due to desiccation of the specimen although there is no hint for that in the original description. In the light that the original description of *A. tropidogaster* is relatively detailed (at least considering the standard at the time), the lack of mentioning a pair of distinctly enlarged postcloacal scales should be interpreted as the specimen actually lacked this characteristic. Given the distinctness of the enlarged postcloacal scales in our Species B, it seems unlikely that Hallowell simply did not mention this character in spite of being present. Thus, with reasonable confidence, ANSP 7618 can be referred to our Species A. GK has examined the type material of *A. stigmosus* Bocourt (MNHN 2427 and 2427A; Figs. 6b, c) and identified both specimens as belonging to our Species A. The examination of the paratype series of *A. gaigei* Ruthven (UMMZ 48324–30, 48332–33) demonstrated these to belong to our Species B (see also Figs. 6d, f). Furthermore, we have examined two adult males with everted hemipenes (*i.e.*, UMMZ 48322, 54815) from the Santa Marta Mountains, Colombia, and these had a small, thin unilobed organ (our type B hemipenis; Fig. 6e). Finally, GK examined the male paratype of *A. albi* (MCZ 32302; Fig. 6g, h), which can readily be identified as our Species A since it lacks enlarged postcloacal scales and also agrees well with the other diagnostic characters presented above for our Species A.

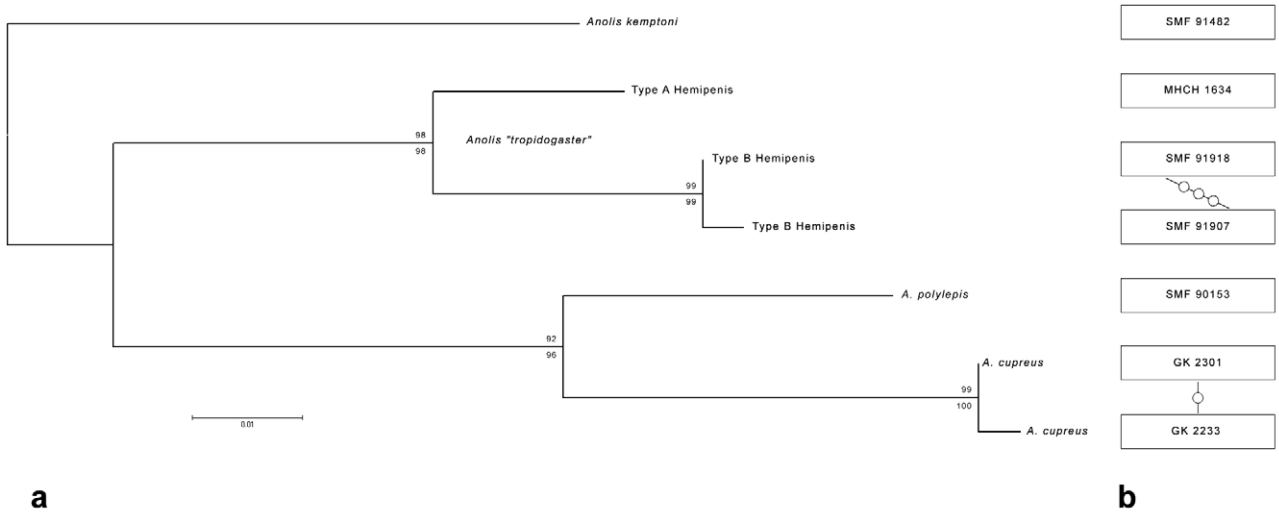

FIGURE 5. Results of 16S mtDNA analysis. a) Consensus tree from Maximum Likelihood analysis. Scale bar refers to substitutions per site. Bootstrap support values above nodes correspond to Maximum Likelihood analysis, those below the nodes to the Maximum Parsimony consensus tree of exactly the same topology. (b) Parsimony network derived from the same alignment, each node representing a unique haplotype.

In conclusion, we refer the following nominal taxa to our Species A: *Anolis tropidogaster* Hallowell, *A. stigmosus* Bocourt, and *A. albi* Barbour. Thus, our Species A has to be referred to as *A. tropidogaster* with *A. stigmosus* Bocourt, and *A. albi* Barbour remaining in its synonymy. The only available name for our Species B is *A. gaigei* Ruthven. In the following we provide standardized descriptions of these two species.

Anolis tropidogaster Hallowell, 1856

Figures 1a; 3a, b; 4b, d, f, h; 6a, b, c, g, h; 7a, b; 8

Anolis tropidogaster Hallowell 1856:224; holotype (ANSP 7618) from "New Grenada". Dunn (1930), Barbour (1934; in part.), Barbour and Loveridge (1946), Breder (1946), Evans (1947), Etheridge (1959), Donoso-Barros (1968), Peters and Donoso-Barros (1970; in part.), Williams (1976), Ayala (1986), Pefaur (1992), Auth (1994; in part.), Williams *et al.* (1995; in part.), Young *et al.* (1999; in part.), Ibáñez *et al.* (2001; in part.), Moreno-Bejarano & Álvarez-León (2003), Poe (2004; in part.), Carvajal-Cogollo and Urbina-Cardona (2008), Moreno-Arias *et al.* (2008), Medina-Rangel (2011).

Anolis albi Barbour 1932:101; holotype (MCZ 32301) from "Andagoya, Choco, western Colombia."

Anolis stigmosus Bocourt 1869:43; syntypes (MNHN 2427 and 2427A) from "la Colombie et ont été recueillis près de la rivière de la Magdeleine." Boulenger (1885).

Norops tropidogaster. Köhler (2003, 2008; in part.)

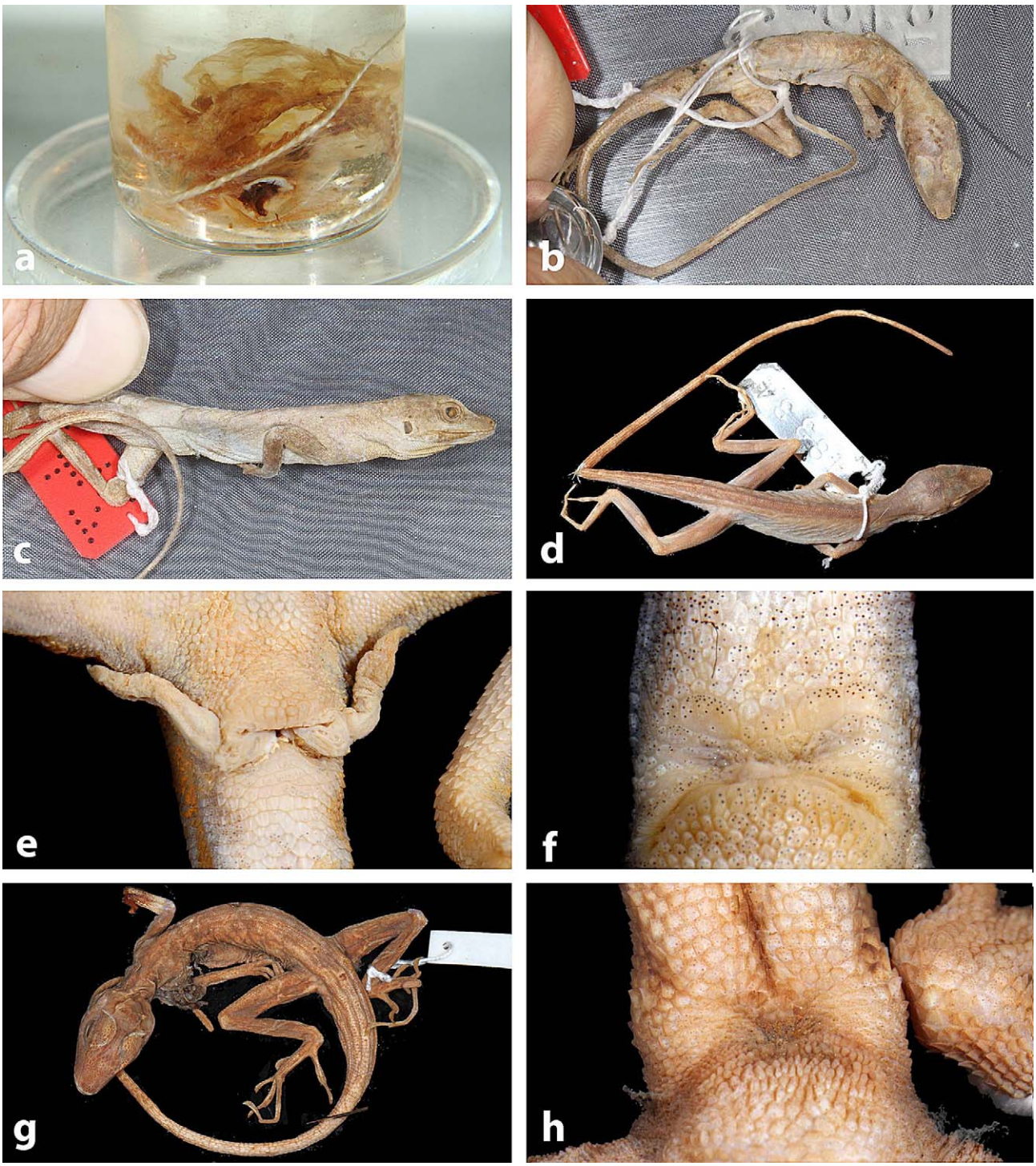

FIGURE 6. (a) Holotype of *Anolis tropidogaster* (ANSP 7618). (b) *Anolis stigmosus* syntype MNHN 2427. (c) *Anolis stigmosus* syntype MNHN 2427a. (d) *Anolis gaigei* paratype (UMMZ 48334) dorsal view. (e) *Anolis gaigei* (UMMZ 48322) hemipenis. (f) *Anolis gaigei* paratype (UMMZ 48334) cloacal region. (g) *Anolis albi* paratype (MCZ 32302) dorsal view. (h) MCZ 32302 cloacal region.

Diagnosis. A medium-sized species (SVL in largest specimen examined 55 mm) of the genus *Anolis* (sensu Poe 2004) that differs from all other Lower Central American beta anoles (sensu Etheridge 1967) in that it is long-legged (longest toe of adpressed hind leg reaches to at least center of eye, usually to a point between anterior border of eye and nostril); has strongly keeled ventral scales, a large almost uniformly purplish red (in life) colored dewlap in males; postcloacal scales not enlarged in the majority of males, some male with slightly enlarged postcloacal scales; a large bilobed hemipenis in males, and no tube-like axillary pocket. Anole species from Lower Central America that are somewhat similar in appearance to *A. tropidogaster* are *A. cupreus*, *A. gaigei*, *A. osa*, and *A. polylepis*.

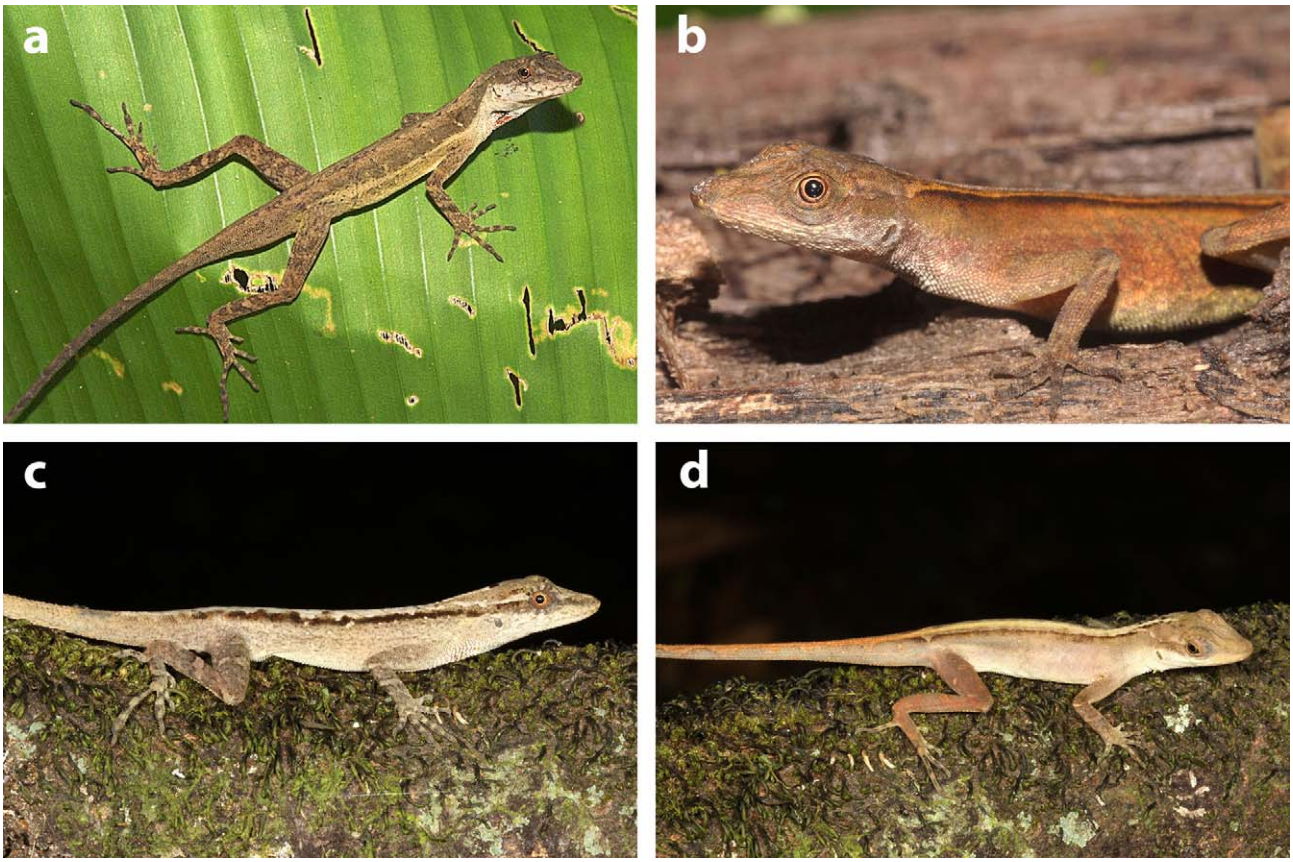

FIGURE 7. Adult individuals in life of (a) *Anolis tropidogaster* (SMF 93598), male from Laguna de Matusagaratí, Darién, Panama. (b) *Anolis tropidogaster* (SMF 93597), male from Cruce de Mono Station at Parque Nacional Darién, Darién, Panama. (c) *Anolis gaigei* (SMF 91918), male from Finca La Providencia, near Ponuga, Veraguas, Panama. (d) *Anolis gaigei* (SMF 91917), female from road from Interamericana to Horconcitos, Chiriquí, Panama.

Anolis gaigei has a small, thin, unilobed hemipenis in males (large, bulbous and bilobed in *A. tropidogaster*); a male dewlap that is orange yellow with a darker orange central area (uniform purplish red, sometimes with a paler orange central area in *A. tropidogaster*); a pair of greatly enlarged postcloacal scales in males (these scales usually not differentiated in *A. tropidogaster*); the dorsal head scales, especially in the parietal region large and flat (smaller and bearing minute tubercles in *A. tropidogaster*); middorsal caudal scales distinctly enlarged and forming a regular series (only slightly enlarged and somewhat irregularly arranged in *A. tropidogaster*); outer postmental scales greatly enlarged relative to medial ones (only slightly enlarged relative to medial ones in *A. tropidogaster*). *Anolis polylepis* and *A. osa* have smooth ventral scales at midbody and a larger, mostly uniform orange male dewlap (in some parts of its range in Costa Rica, considerable variation was observed in male dewlap coloration of *A. polylepis*, see Köhler *et al.* 2010). The male dewlap of *A. cupreus* is brown to pink with an orange margin. For variation in selected morphometric and scalation characters of *A. tropidogaster* see Table 1.

Description. *Anolis tropidogaster* is a medium-sized anole (maximum recorded SVL 54.0 mm in males, 55.0 mm in females); dorsal head scales (Fig. 8) in internasal region keeled, in prefrontal, parietal, and frontal areas rugose to tuberculate; deep frontal depression present, parietal depression absent; 5–8 (6.75 ± 0.69) postrostrals; anterior nasal usually single, occasionally divided, usually in contact with rostral and first supralabial (Fig. 9, Tab. 2); 6–11 (8.97 ± 0.94) internasals; canthal ridge sharply defined; scales comprising supraorbital semicircles weakly keeled, largest scale in semicircles about same size as largest supraocular scale; supraorbital semicircles well defined; 2–4 (3.06 ± 0.58) scales separating supraorbital semicircles at narrowest point; 2–5 (2.95 ± 0.73) scales separating supraorbital semicircles and interparietal at narrowest point; interparietal well defined, greatly enlarged relative to adjacent scales, surrounded by scales of moderate size, longer than wide, usually larger than ear opening; enlarged supraoculars not in contact with supraorbital semicircles; 2 elongate superciliaries, posterior one

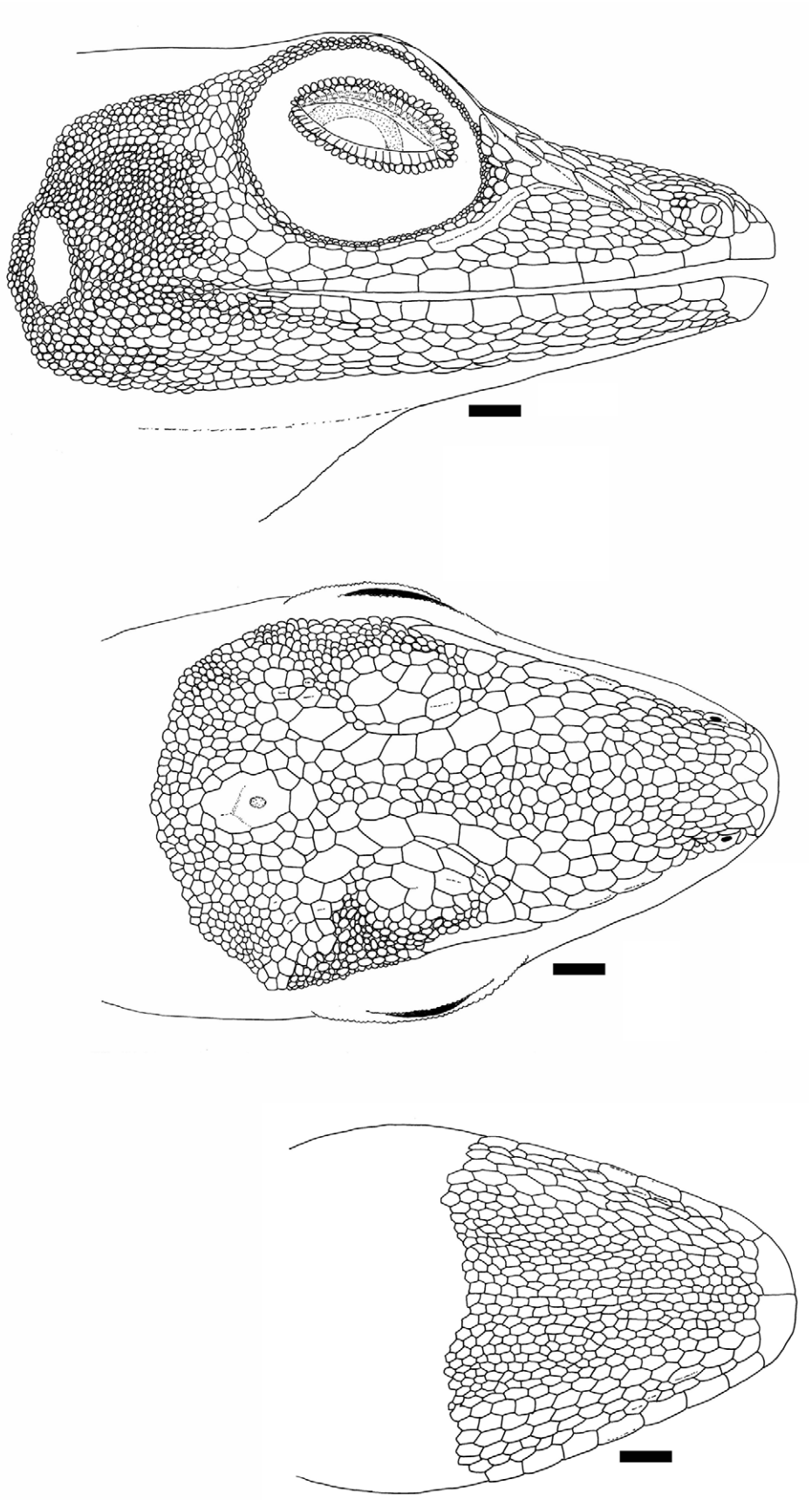

FIGURE 8. Head scalation in *Anolis tropidogaster* (MHCH 1640). Scale bars = 1.0 mm.

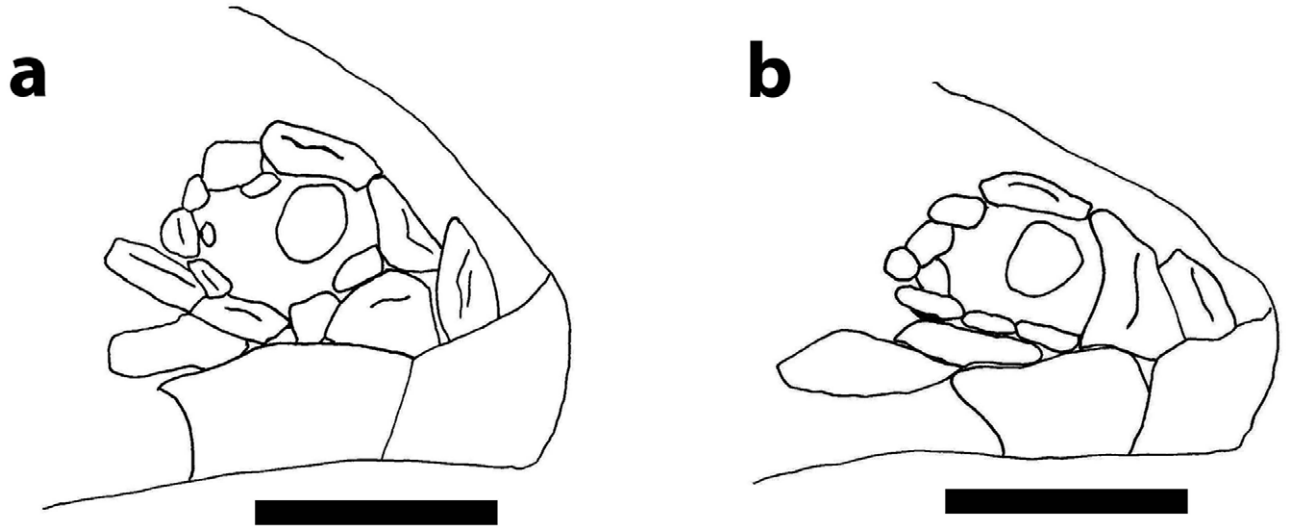

FIGURE 9. Designation of nasal scalation types. (a) Nasal type 1 (MHCH 1636); (b) Nasal type 2 (SMF 91901). Scale bars = 1.0 mm. See Text for details.

FIGURE 10. Habitat of *Anolis tropidogaster* at Cruce de Mono Station, Darién, Panama.

much shorter than anterior one; 2–3 enlarged canthals; 10–17 (13.44 ± 1.71) scales between second canthals; 12–20 (15.11 ± 1.86) scales present between posterior canthals; loreal region slightly concave, 33–64 (44.77 ± 8.80) mostly keeled (some smooth or rugose) loreal scales in a maximum of 5–8 (6.22 ± 0.83) horizontal rows; 6–9 (7.00 ± 0.93) supralabials to level below center of eye; suboculars keeled, separated from supralabials by one scale row; ear opening vertically oval; scales anterior to ear opening granular, similar in size to those posterior to ear opening; 6–10 (7.75 ± 0.97) postmentals, outer pair usually largest; keeled granular scales present on chin and throat; male

dewlap large, extending onto chest; 6–8 horizontal gorgetal-sternal rows with 26–38 scales per row, rows somewhat irregular, some of them with pairs or triplets of scales, apical portion of dewlap between marginal pairs and last gorgetal-sternal row free of scales; modal number of marginal pairs 4–5; female dewlap small or absent; no nuchal crest or dorsal ridge; 2 middorsal scale rows slightly enlarged, weakly keeled, dorsal scales lateral to middorsal series gradually larger than granular lateral scales; no enlarged scales scattered among granular laterals; 42–73 (57.0 ± 7.53) dorsal scales along vertebral midline between levels of axilla and groin in males, 53–78 (61.8 ± 10.35) in females; 29–46 (37.6 ± 4.39) dorsal scales along vertebral midline contained in one head length in males, 30–42 (35.3 ± 4.12) in females; ventral scales on midsection about the same size as largest dorsal scales; ventral body scales moderately to strongly keeled, subimbricate to imbricate; 40–65 (51.9 ± 5.50) ventral scales along midventral line between levels of axilla and groin in males, 40–64 (49.0 ± 8.60) in females; 28–46 (36.0 ± 4.52) ventral scales contained in one head length in males, 27–36 (31.6 ± 2.92) in females; 112–144 (124.7 ± 7.90) scales around midbody in males, 122–162 (133.3 ± 12.6) in females; tubelike axillary pocket absent; preanal scales not keeled; postcloacal scales usually not enlarged, or, if differentiated, then only slightly enlarged; tail laterally compressed in cross section, tail height/tail width 1.07–1.53 (1.29 ± 0.11); basal subcaudal scales smooth; lateral caudal scales keeled, homogeneous; dorsal medial caudal scale row slightly enlarged, keeled, not forming a crest; most scales on lateral surface of antebrachium weakly keeled, unicarinate; 23–29 (25.78 ± 1.46) subdigital lamellae on Phalanges II–IV of Toe IV of hind limbs; SVL 42.0–54.0 (48.9 ± 2.96) mm in males, 40.0–55.0 (47.0 ± 5.20) mm in females; HL 11.3–14.6 (12.9 ± 0.72) mm in males, 11.1–14.1 (12.5 ± 1.00) mm in females; tail length 65.0–97.0 (83.9 ± 10.70) mm in males, 69.0–87.0 (80.0 ± 6.54) mm in females; shank length 12.2–15.9 (14.0 ± 1.06) mm in males, 11.2–16.0 (13.1 ± 1.65) mm in females; tail length/SVL 1.35–1.94 (1.75 ± 0.20) in males, 1.28–1.88 (1.68 ± 0.24) in females; HL/SVL 11.3–14.6 (12.9 ± 0.72) in males, 11.1–14.1 (12.5 ± 1.00) in females; shank length/SVL 0.25–0.33 (0.29 ± 0.02) in males, 0.25–0.30 (0.28 ± 0.01) in females; shank length/HL 0.94–1.22 (1.09 ± 0.07) in males, 0.90–1.16 (1.05 ± 0.08) in females. Of 45 specimens examined, the longest toe of the adpressed hind leg reaches to mid-eye in 3 individuals (6.7%), to anterior margin of eye in 29 individuals (64.4%), and to a point between eye and snout in 13 individuals (28.9%).

Coloration in life of an adult male (MHCH 2375) was recorded as follows: Dorsal ground color Drab (27) with Olive Brown (28) vertebral band, postorbital band Dark Drab (119B) extending to level of midbody; a longitudinal level Buff (124) stripe from tympanum to insertion of hind legs; dorsal surface of head Dark Drab (119B), with a medially interrupted Dark Brownish Olive (129) interorbital bar; forelegs and hind legs Drab (27) suffused with Olive Brown (28); dorsal surface of tail Drab (27) with indistinct Olive Brown (28) bands; ventral surfaces of head, body, and limbs Straw Yellow (57); dewlap Chrome Orange (16), grading into Spectrum Orange (17) at center; gorgetals dirty white; iris Sepia (119).

Natural history notes. At the evergreen forest sites (Fig. 10) in the Darién Province, Panama, visited by AB, *Anolis tropidogaster* was an uncommon species. AB and MP encountered it within the forest on low vegetation between 0.5 and 2.0 m above the ground. Occasionally, individuals were observed on the ground. At night, these animals sleep in the usual anole-like fashion on twigs or the upper surface of leaves. One adult male was collected at a forest edge at Matusagaratí Lake, a thin forest belt between the lake and pasture areas. Another individual was captured at the base of a mangrove tree (MHCH 1636) at a riverside at Caserete, Chepigana, Darién, Panama; in the same region three individuals were seen in a cativo (*Prioria copaifera*) forest on low vegetation. Another individual (MHCH 1701) was captured during night sampling in a semideciduous forest on a bush at 1.5 m above ground at Sol Poniente, Chepigana, Darién, Panama. Some ecological observations on *A. tropidogaster* were published by Sexton *et al.* (1964).

Geographic Distribution. *Anolis tropidogaster* is distributed widely in Colombia and in eastern Panama (Figs. 2, 13). The claim that this species occurs in Ecuador seems to go back to Donoso-Barros (1968), who based this view on the holotype of *A. lemniscatus* (from "Puente del Chimbo", see Boulenger 1898), a taxon then placed in the synonymy of *A. tropidogaster.* We were unable to find additional evidence for the occurrence of *A. tropidogaster* in Ecuador and therefore remove this species from the list of known reptiles from this country. The documented vertical range of the species is from near sea level to about 1100 m.

TABLE 1. Selected measurements, proportions and scale characters of *Anolis gaigei* and *A. tropidogaster.* Range is followed by mean value and standard deviation in parentheses. For abbreviations see text.

		A. gaigei ♂ 49, ♀ 30	*A. tropidogaster* ♂ 27, ♀ 9
SVL	♂	36.0–52.5 (45.6 ± 3.40)	42.0–54.0 (48.9 ± 2.96)
	♀	37.0–52.0 (44.7 ± 4.75)	40.0–55.0 (47.0 ± 5.20)
Tail length	♂	59.0–115.0 (95.0 ± 11.63)	65.0–97.0 (83.9 ± 10.70)
	♀	82.0–100.7 (92.3 ± 8.33)	69.0–87.0 (80.0 ± 6.54)
HL	♂	10.5–13.2 (12.1 ± 0.65)	11.3–14.6 (12.9 ± 0.72)
	♀	10.6–12.1 (11.5 ± 0.48)	11.1–14.1 (12.5 ± 1.00)
HW	♂	6.5–7.9 (7.3 ± 0.37)	6.6–9.0 (7.8 ± 0.46)
	♀	6.5–7.7 (7.1 ± 0.37)	6.4–8.7 (7.5 ± 0.66)
Shank length	♂	11.2–15.6 (13.6 ± 0.85)	12.2–15.9 (14.0 ± 1.06)
	♀	10.5–14.0 (12.4 ± 0.82)	11.2–16.0 (13.1 ± 1.65)
Axilla–groin distance	♂	11.2–19.5 (17.0 ± 1.90)	16.9–24.5 (19.9 ± 1.57)
	♀	13.6–24.0 (17.9 ± 2.64)	18.3–24.9 (20.1 ± 2.12)
Tail length / SVL	♂	1.37–2.34 (2.09 ± 0.21)	1.35–1.94 (1.75 ± 0.20)
	♀	1.75–2.27 (2.10 ± 0.13)	1.28–1.88 (1.68 ± 0.24)
Tail diameter vertical / horizontal	♂	1.05–1.47 (1.23 ± 0.10)	1.07–1.53 (1.29 ± 0.12)
	♀	1.06–1.31 (1.17 ± 0.07)	1.13–1.36 (1.26 ± 0.08)
HL / SVL	♂	0.26–0.30 (0.27 ± 0.01)	0.24–0.29 (0.26 ± 0.01)
	♀	0.24–0.29 (0.26 ± 0.02)	0.24– 0.32 (0.27 ± 0.02)
HL / HW	♂	1.56–1.75 (1.66 ± 0.06)	1.49–1.89 (1.73 ± 0.09)
	♀	1.51–1.75 (1.63 ± 0.06)	1.60–1.75 (1.67 ± 0.05)
Shank length / SVL	♂	0.28–0.32 (0.30 ± 0.01)	0.25–0.33 (0.29 ± 0.02)
	♀	0.23–0.33 (0.29 ± 0.02)	0.25–0.30 (0.28 ± 0.01)
Axilla–groin distance / SVL	♂	0.24–0.43 (0.38 ± 0.04)	0.34–0.46 (0.41 ± 0.03)
	♀	0.36–0.48 (0.40 ± 0.03)	0.41–0.46 (0.44 ± 0.02)
Subdigital lamellae of 4th toe		20–28 (25.45 ± 1.65)	23–29 (25.78 ± 1.46)
Number of scales between SS		1–4 (2.10 ± 0.62)	2–4 (3.06 ± 0.58)
Number of scales between IP and SS		2–5 (3.03 ± 0.65)	2–5 (2.95 ± 0.73)
Number of scales between SO and SPL		0–1 (0.69 ± 0.47)	1–1 (1.00 ± 0.00)
Number of SPL to level below center of eye		6–9 (7.31 ± 0.65)	6–9 (7.00 ± 0.93)
Number of INL to level below center of eye		6–9 (7.33 ± 0.61)	5–9 (7.11 ± 0.85)
Total number of loreals		22–59 (40.25 ± 5.79)	33–64 (44.77 ± 8.80)
Number of horizontal loreal scale rows		5–8 (6.31 ± 0.60)	5–8 (6.22 ± 0.83)
Number of postrostrals		5–7 (6.06 ± 0.54)	5–8 (6.75 ± 0.69)
Number of postmentals		5–9 (6.35 ± 0.80)	6–10 (7.75 ± 0.97)
Number of scales between nasals		5–9 (7.03 ± 1.01)	6–11 (8.97 ± 0.94)
Number of scales between 2nd canthals		8–14 (10.93 ± 1.14)	10–17 (13.44 ± 1.71)
Number of scales between posterior canthals		10–16 (13.10 ± 1.32)	12–20 (15.11 ± 1.86)
Number of medial dorsal scales in one head length		28–56 (37.95 ± 6.09)	29–46 (37.03 ± 4.38)
Number of medial ventral scales in one head length		25–48 (33.21 ± 4.87)	27–46 (34.89 ± 4.58)
Number of scales around midbody		94–138 (117.60 ± 8.74)	112–162 (126.63 ± 9.67)
Numbers of medial dorsal scales between axilla and groin		53–83 (62.72 ± 5.92)	42–78 (58.06 ± 8.34)
Numbers of medial ventral scales between axilla and groin		40–58 (48.88 ± 4.01)	40–65 (51.26 ± 6.32)

TABLE 2. Frequency distribution of nasal region and dorsal pattern types in *Anolis gaigei* and *A. tropidogaster.*

	Anolis gaigei	*A. tropidogaster*
	35	9
Nasal region Type A	3 (8.6%)	7 (20.6%)
Nasal region Type B	32 (91.4%)	27 (79.4%)

Anolis gaigei **Ruthven, 1916**

Figures 1b; 3c, d; 4 a, c, e, g; 6 d, e, f; 7 c, d; 11

Anolis gaigei Ruthven 1916:6; holotype (UMMZ 48304) from "San Lorenzo, Santa Marta Mountains, Colombia, elevation of 2, 700 ft." Ruthven (1922).

Anolis limifrons: Martínez Cortés & Rodriguez (2005; in part.: Fig. 22B)

Anolis polylepis: Martínez Cortés and Rodriguez (2003, 2005), Rodríguez *et al.* (2004), Ibáñez (2006; in part.).

Anolis tropidogaster: Swanson (1945), Evans (1947), Donoso-Barros (1968), Myers and Rand (1969), Peters and Donoso-Barros (1970; in part.), Campbell (1971), Sexton *et al.* (1964, 1971), Kiester (1979), Kourany & Telford (1981), Rand and Myers (1990), Quintero and Cambra (1993), Auth (1994; in part.), Williams *et al.* (1995; in part.), Telford (1996), Ibáñez *et al.* (1996), Ibáñez *et al.* (1997 "1995"), Young *et al.* (1999; in part.), Ibáñez *et al.* (2001; in part.), Poe (2004, in part.), Pinto *et al.* (2008), Jaramillo *et al.* (2010; in part.).

Norops tropidogaster: Villa *et al.* (1988), Köhler (2000; in part.), Nicholson (2002), Köhler (2003; in part.), Nicholson *et. al.* (2005), Köhler (2008; in part.), Steffen (2009).

Diagnosis. A medium-sized species (SVL in largest specimen examined 52.5 mm) of the genus *Anolis* (sensu Poe 2004) that differs from all other Lower Central American beta anoles (sensu Etheridge 1967) in that it is long-legged (longest toe of adpressed hind leg reaches to at least center of eye, usually to a point between anterior border of eye and nostril), has strongly keeled mucronate imbricate ventral scales, a large almost orange red (in life) colored dewlap with a yellowish margin in males, a pair of greatly enlarged postcloacal scales in males, a small unilobed hemipenis in males, and no tube-like axillary pocket. Anole species from Lower Central America that are somewhat similar in appearance to *A. gaigei* are *A. tropidogaster, A. polylepis*, and *A. cupreus*. The males of *A. tropidogaster* have a mostly uniform purplish red dewlap, a bilobed hemipenis, and lack a pair of greatly enlarged postcloacal scales. For a more detailed comparison of *A. gaigei* and *A. tropidogaster* see the Diagnosis section for the latter species. *Anolis polylepis* and *A. osa* have smooth ventral scales at midbody and a larger, mostly uniform orange male dewlap (in some parts of its range in Costa Rica, considerable variation was observed in male dewlap coloration of *A. polylepis*, see Köhler *et al.* 2010). Also, male *A. polylepis* have a bilobate hemipenis. The males of *Anolis cupreus* lack a pair of greatly enlarged postcloacal scales, have a brown to pink dewlap with an orange margin, and a bilobate hemipenis.

Description. *Anolis gaigei* is a medium-sized anole (maximum recorded SVL 52.5 mm in males, 52.0 mm in females); dorsal head scales (Fig. 11) in internasal region keeled, in prefrontal, parietal, and frontal areas rugose to tuberculate; scales in distinct prefrontal depression slightly wrinkled, parietal depression absent; 5–7 (6.06 ± 0.54) postrostrals; anterior nasal usually single, occasionally divided, usually in contact with rostral and first supralabial (Fig. 9, Tab. 2); 5–9 (7.03 ± 1.01) internasals; canthal ridge sharply defined; scales comprising supraorbital semicircles weakly keeled, largest scale in semicircles about same size as largest supraocular scale; supraorbital semicircles well defined; 1–4 (2.10 ± 0.62) scales separating supraorbital semicircles at narrowest point; 2–5 (3.03 ± 0.65) scales separating supraorbital semicircles and interparietal at narrowest point; interparietal well defined, greatly enlarged relative to adjacent scales, surrounded by scales of moderate size, longer than wide, usually larger than ear opening; supraorbital disc composed of 6–12 distinctly enlarged keeled scales; enlarged supraoculars not in contact with supraorbital semicircles; usually a single elongated superciliary, or, if 2 elongate superciliaries, posterior one much shorter than anterior one; 2–3 enlarged canthals; 8–14 (10.93 ± 1.14) scales between second canthals; 10–16 (13.10 ± 1.32) scales present between posterior canthals; loreal region slightly concave, 22–59 (40.25 ± 5.79) mostly keeled (some smooth or rugose) loreal scales in a maximum of 5–8 (6.31 ± 0.60) horizontal rows; 6–9 (7.31 ± 0.65) supralabials to level below center of eye; suboculars keeled, suboculars separated from supralabials by 0–1 (0.69 ± 0.47) scale row; ear opening vertically oval; scales anterior to ear opening granular, similar in size to those posterior to ear opening; 5–9 (6.35 ± 0.80) postmentals, outer pair largest; keeled granular scales pres-

ent on chin and throat; male dewlap extending well onto chest, anterior insertion at level of center of eye, posterior insertion about 3.0 mm beyond level of axilla; 8–9 horizontal gorgetal-sternal rows with 11–15 scales per row, rows somewhat irregular; female dewlap small or absent; no nuchal crest or dorsal ridge; 2 middorsal scale rows slightly enlarged, weakly keeled, dorsal scales lateral to middorsal series gradually larger than granular lateral scales; no enlarged scales scattered among granular laterals; 53–75 (62.7 ± 5.57) dorsal scales along vertebral midline between levels of axilla and groin in males, 55–83 (62.7 ± 6.45) in females; 31–56 (38.5 ± 5.35) dorsal scales along vertebral midline contained in one head length in males, 28–52 (37.1 ± 7.10) in females; ventral scales on midsection about the same size as largest dorsal scales; ventral body scales strongly keeled, imbricate; 43–58 (50.0 ± 3.94) ventral scales along midventral line between levels of axilla and groin in males, 40–54 (47.6 ± 3.79) in females; 29–48 (35.0 ± 4.31) ventral scales contained in one head length in males, 25–38 (30.5 ± 4.44) in females; 94–138 (119.0 ± 9.68) scales around midbody in males, 101–128 (116.1 ± 7.5) in females; tubelike axillary pocket absent; preanal scales not keeled; males with a pair of greatly enlarged postcloacal scales; tail laterally compressed in cross section, tail height/tail width 1.05–1.47 (1.20 ± 0.09); basal subcaudal scales smooth; lateral caudal scales keeled, homogeneous; dorsal medial caudal scale row slightly enlarged, keeled, not forming a crest; most scales on lateral surface of antebrachium weakly keeled, unicarinate; 20–28 (25.45 ± 1.65) subdigital lamellae on Phalanges II–IV of Toe IV of hind limbs; SVL 36.0–52.5 (45.6 ± 3.40) mm in males, 37.0–52.0 (44.7 ± 4.75) mm in females; HL 10.5–13.2 (12.1 ± 0.65) mm in males, 10.6–12.1 (11.5 ± 0.48) mm in females; tail length 59.0–115.0 (95.0 ± 11.63) mm in males, 82.0–100.7 (92.3 ± 8.33) mm in females; shank length 11.2–15.6 (13.6 ± 0.85) mm in males, 10.5–14.0 (12.4 ± 0.82) mm in females; tail length/SVL 1.37–2.34 (2.09 ± 0.21) in males, 1.75–2.27 (2.10 ± 0.13) in females; HL/SVL 0.26–0.30 (0.27 ± 0.01) in males, 0.24–0.29 (0.26 ± 0.02) in females; shank length/SVL 0.28–0.32 (0.30 ± 0.01) in males, 0.23–0.33 (0.29 ± 0.02) in females; shank length/HL 1.04–1.24 (1.12 ± 1.04) in males, 0.94–1.18 (1.08 ± 0.05) in females. Of 20 specimens examined, the longest toe of the adpressed hind leg reached to mid-eye in 2 individuals (10%), to anterior margin of eye in 4 individuals (20%), and to a point between eye and nostril in 14 individuals (70%).

Coloration in life of an adult male (SMF 91918) was recorded as follows: Dorsal ground color Sayal Brown (223C) with a Beige (219D) vertebral band, edged by Raw Umber (223) pigment; Raw Umber (223) line continuing anteriorly through eye to tip of snout; dorsum of head Clay Color (26) with a medially interrupted Dark Brownish Olive (129) interorbital bar and a Sepia (219) nuchal spot, followed posteriorly by a Beige (219D) longitudinal line; forelegs Sayal Brown (223C); hind legs Cinnamon-Brown (33) with Raw Umber (23) crossbars; dorsal surface of tail Raw Umber (23) grading into Buff (24) distally and with indistinct Cinnamon-Rufous (40) bands; ventral surfaces of head, body, and limbs Pale Horn Color (92); ventral surface of tail suffused with Orange-Rufous (132C); dewlap Chrome Orange (16), grading into Orange Yellow (18) on anterior and distal margins; gorgetals dirty white; iris Kingfisher Rufous (240). Coloration in life of another adult male (SMF 91529) was recorded as follows: Dorsal and lateral surfaces of body and forelimbs Tawny Olive (223D); two broad Natal Brown (219A) longitudinal stripes extending from eye paravertebrally to base of tail, suffused with Walnut Brown (221B); a series of Sepia (119) blotches between occipital region and base of tail; dorsal surface of head Raw Umber (123), laterally grading into Tawny Olive (223D); ventral ground color Pale Horn Color (92), suffused with Orange-Rufous (132C) beneath tail; dorsal and lateral surfaces of tail and hind limbs Sayal Brown (223C) with the suggestion of diffuse Orange-Rufous (132C) crossbars; iris Robin Rufous (340); dewlap Burnt Orange (116), especially anterior portions suffused with Grayish Olive (43); anterior base of dewlap Warm Buff (118), posterior base Pale Horn Color (92); dewlap scales dirty white. Coloration in life of an adult female (SMF 91917) was recorded as follows: Dorsal ground color Tawny Olive (223D) with a Clay Color (123B) vertebral stripe, edged by Verona Brown (223B) pigment; dorsum of head Cinnamon Brown (33); forelegs Tawny Olive (223D); hind legs True Cinnamon (139) with Orange-Rufous (132C) spots and crossbars; dorsal surface of tail Tawny Olive (223D) with faint Orange Rufous (132C) crossbars; chin dirty white; venter Pale Pinkish Buff (121D); ventral surface of tail suffused with Orange-Rufous (132C); gular region Spectrum Orange (17) grading into Orange Yellow (18) on anterior margin; gorgetals Pale Pinkish Buff (121D); iris Robin Rufous (340). The coloration of an adult male from the Canal Zone (SMF 85304) was recorded as follows: Middorsum Army Brown (219B) bordered by a Burnt Umber (22) dorsolateral stripe; flanks Dark Drab (119B) with Drab-Gray (119D) punctuations; venter Drab-Gray (119D) suffused with Dark Drab (119B); dewlap Chrome Orange (16) with Orange Yellow (18) anterior border.

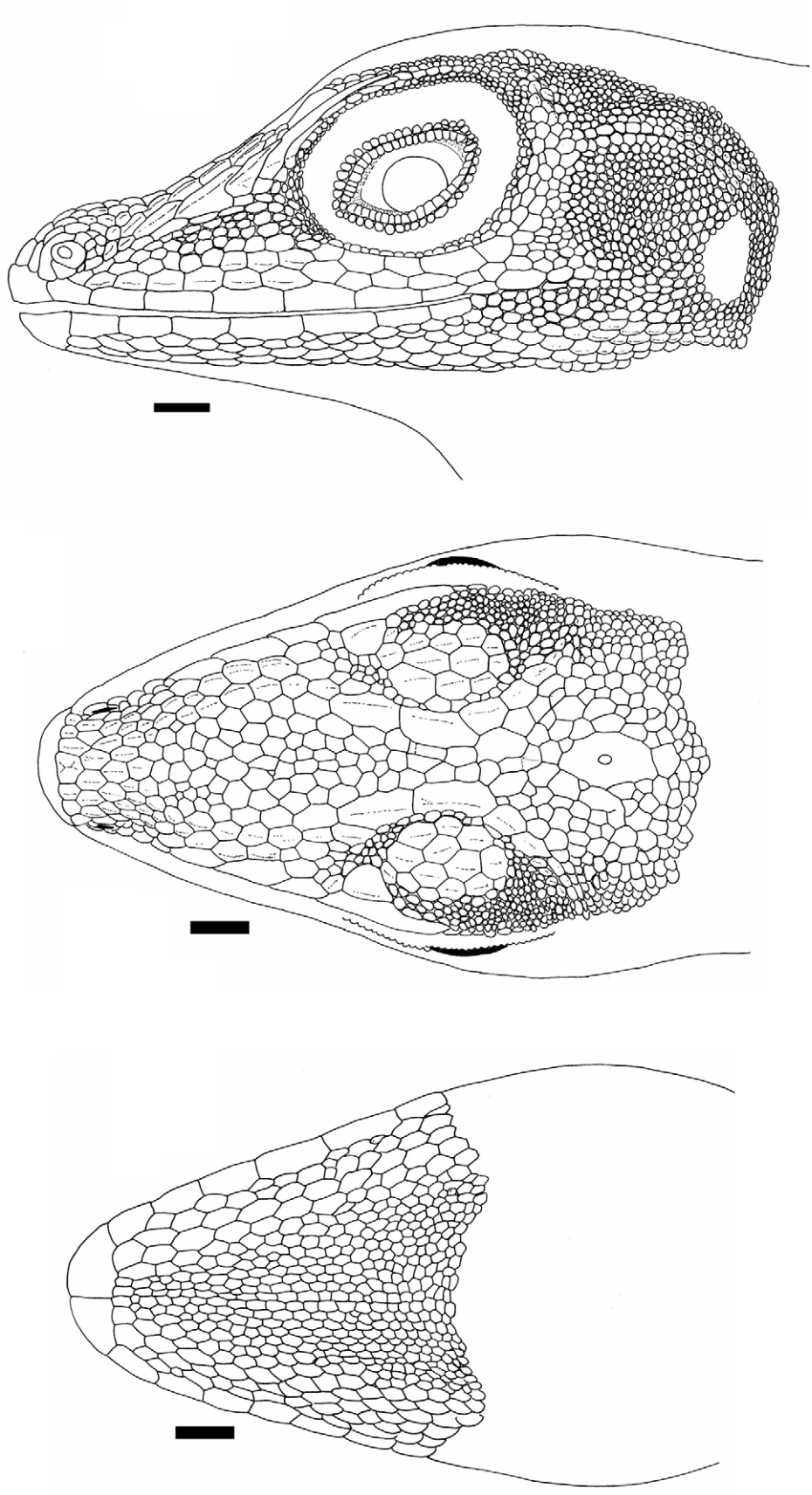

FIGURE 11. Head scalation in *Anolis gaigei* (SMF 91921). Scale bars = 1.0 mm.

FIGURE 12. Habitat of *Anolis gaigei* (a) near Santo Domingo, Los Santos, Panama, 40 masl; (b) at Finca La Providencia, near Ponuga, Veraguas, Panama, 20 masl.

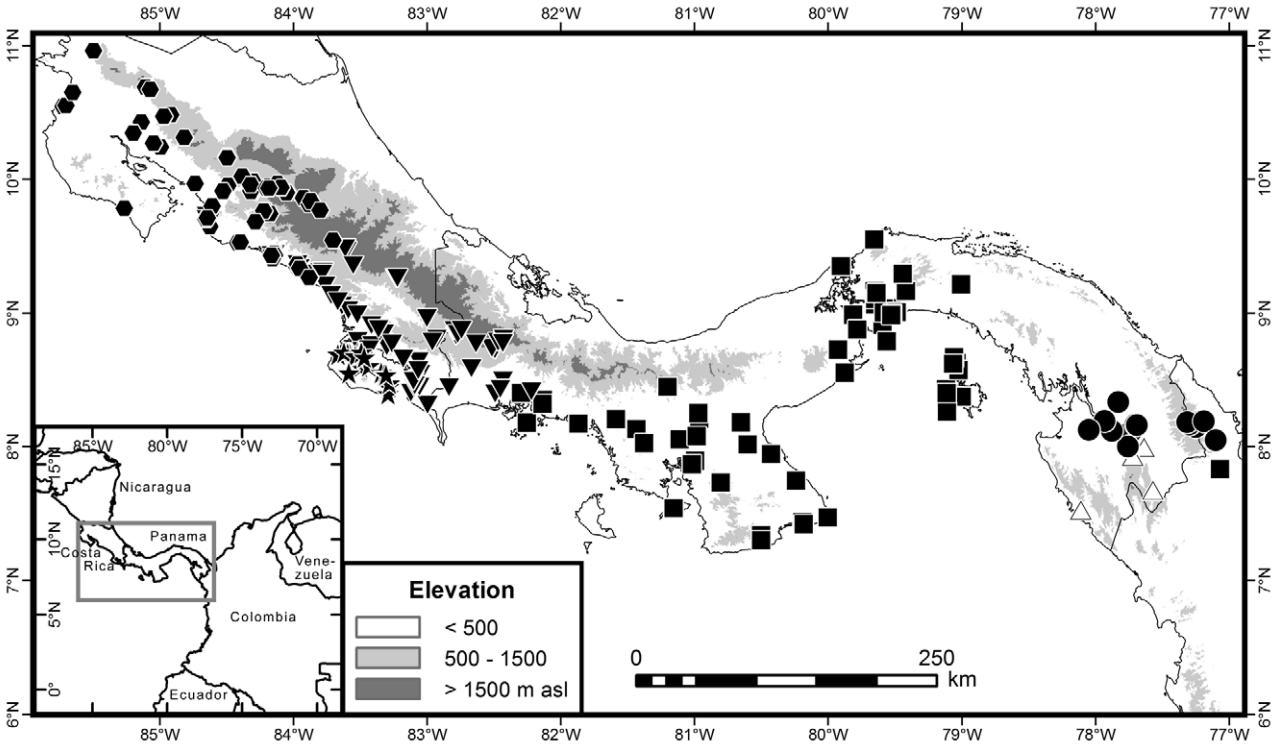

FIGURE 13. Map indicating collecting sites of selected lowland anoles inhabiting the Pacific versant of Panama and Costa Rica. Each symbol can represent one or more nearby localities. Circles: *Anolis tropidogaster;* squares: *A. gaigei;* white triangles: localities of *A. tropidogaster*-like specimens not verified by authors; black inverted triangles: *A. polylepis;* stars: *A. osa;* hexagons: *A. cupreus.* See text for details.

Natural history notes. Wherever we found it in central and western Panama, *Anolis gaigei* is an extremely common anole that reaches high population densities, being the most obvious lizard at many sites where it occurs. It is usually encountered in low vegetation between 0.5 and 2.0 m above the ground. Occasionally, individuals can be observed on the ground. At night, these animals sleep in the usual anole-like fashion on twigs or the upper surface of leaves. Although *A. gaigei* inhabits a wide range of habitats, it seems to be a typical species of the semideciduous forest and of bushy savannahs (Fig. 12). In cattle pasture they depend on the trees along the fences ("living fences," where living trees make up the actual fence posts). Aspects of the ecology of this species were studied by Sexton *et al.* (1971), Campbell (1971), and Quintero and Cambra (1993).

Geographic distribution. As currently known, *Anolis gaigei* is distributed from near the eastern city limit of Davíd, Chiriquí, along the Pacific versant of western and central Panama, including the Azuero Peninsula, to at least the Canal Zone, and widely distributed in the Santa Marta Mountains of Colombia as well as possibly northwestern Venezuela (Figs. 2, 13). The documented vertical range of the species is from near sea level to about 900 m. The elevation stated to be "8, 000 ft." (=2438 m) for a supposed locality of this species (Pueblo Viejo, Santa Marta Mountains, Colombia) by Ruthven (1916: 8) seems to be exceedingly high and therefore unlikely for this species. However, the associated specimens (UMMZ 48322–23) are clearly referable to *A. gaigei*.

Discussion

Four independent lines of evidence, *i.e.*, hemipenial morphology, pholidosis, mitochondrial DNA, and male dewlap coloration, support the recognition of two taxa of anoles formerly referred to *Anolis tropidogaster.* Although male specimens of *A. gaigei* and *A. tropidogaster* exhibit the most obvious differences (hemipenes, postcloacal scales, and dewlap coloration), the doubtless assignation of females to one of the two species is possible in most cases with the help of a little more subtle pholidotic characters. In conclusion, *A. gaigei* and *A. tropidogaster* appear well separated and readily distinguishable from each other, even in preserved material.

Notwithstanding the hiatuses between the known populations of *Anolis gaigei*, the populations which live in the Santa Marta Mountains around the type locality (including the type series) are clearly conspecific with the Panamanian populations considering the pholidotic characters that they share. Yet, the most overwhelming evidence is provided by the unique hemipenis of *A. gaigei*, which is the smallest and most delicate reproductive organ of any anole species documented so far.

Nevertheless, *Anolis gaigei* has long been regarded as a synonym of *A. tropidogaster* all over its range, and several aspects of its life history have been studied at a level of detail remarkable for anole species (Sexton *et al.* 1964, 1971; Campbell 1971; Quintero & Cambra 1993) under the latter name. Moreover, it has been confused with *A. polylepis* in the western part of its range, namely on the Azuero Peninsula and in Veraguas and eastern Chiriquí provinces of western Panama. This documents the fact that the lowland anoles along the Pacific versant of Panama have largely been neglected by herpetologists. It should be emphasized that in this case the taxa in question are not rare highland endemics restricted to a few remote localities, but very common species that abound in areas of high human population density and considerable past collection efforts. Furthermore, these species are not particularly cryptic in respect of their morphology. One only needs to examine the dewlap coloration in life, evert hemipenes, and check a few standard scalation characters to find out that several species are involved.

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APPENDIX I. Specimens Examined.

Anolis cupreus.—**Costa Rica:** Alajuela: 4 km SW San Mateo: SMF 93915–18; 6 km N San Ramón: SMF 93909; ca. 1.3 airline km NNW Angeles Norte: SMF 93910; Garita, La Garita Country Club: SMF 93895–96; Orotina: MCZ 15440; San Miguel de Turrucares: SMF 93897–99; Turrucares: KU 140620, 140622–23, 140625–27, 140629–31, 140637, USNM 37000–01; Volcán Miravalles: SMF 93920; Cartago: Cartago: KU 140665–67, 140676, 140680, 140684, 140707, 140710, 140723, 140735; Navarro: USNM 67338; Paraiso: AMNH 99677; Tapanti, 14 km E, 11.5 km S Cartago: MCZ 141383; Guanacaste: 4.2 km W Cañas, near Río Caribia: CM 117192–95; 4–5 km ENE Tilarán: KU 40758, 40762; Cañas, Tenorio, Las Flores: KU 40747, 40749, 40751; Ojatal, ca. 2 km SW El Coco: KU 66860–61; Parque Nacional Guanacaste: ZFMK 57768–70; Playa del Coco: KU 129246–47; Puerto Culebra: AMNH 62772; Río Bebedero, 2–5 km S Bebedero: KU 66862, 66864; Río Congo, ca. La Irma [Las Juntas de Abangares]: KU 140565, 140568–70, 140578–79, 140582, 140584, 140586, 140591; Río Jabillo: FMNH 167699; Taboga Camp, 20 km SE Cañas: KU 102406–07; Tilarán: ANSP 24437–45, USNM 70657–58; Puntarenas: 1 km E Sta. Elena, near Monteverde Biological Station: CM 117188–89; 2.4 km E Quepos: KU 125695; Boca de Barranca: MCZ 109931–37, 109939–42; Hacienda Barú: SMF 93876–77, 93883–84; Hacienda Barú, road to beach: SMF 93911; Hacienda El Barú, 3 km W Dominical: SMF 89310–17; Hatillo: SMF 93874–75; near Matapalo: SMF 93878–79; near Matapalo, Ecolodge Manuel Espinoso: SMF 93869–70; near Matapalo, Ecolodge Manuel Espinoso: SMF 93872; near Matapalo: SMF 93871; near Portalon: SMF 92728; near Portalon: SMF 93880–82; Neofauna near Jaco: SMF 93885–86; North of Parrita: SMF 93887–94; Parque Nacional Manuel Antonio: SMF 83092; Puente Río Tarcoles: SMF 93873; Punta Leona: SMF 92036; Punta Leona: SMF 93900–04, 93912–14, 93919; Punta Leona, Sendero Gigante: SMF 93906; Quepos: SMF 93905; Quepos: KU 125693–94, 140596–98, 140608, 140612, MCZ 129777–78; San José: 20 km N San Isidro del General: UMMZ 131790; San JoséJosé: UMMZ 70183; Zona Protedora El Rodeo: SMF 93907–08; 1 mi E Cangrejal: LSUMZ 52365–67; 1 mi W Sta. Ana: LSUMZ 52363; 2 mi E Escuadra: LSUMZ 52375; 2 mi N Santa Ana: LSUMZ 52370–71, 52378–80, 52386–87; Cangrejal: LSUMZ 52359, 52372–74, 52377; Caspirola: LSUMZ 52381–83; Finca la Baja, near San José: ZMH 4593; Finca La Pacifica: FMNH 167707, 167711; La Caja: ANSP 24453–54; San José: KU 125619, 125625, 125627, 125635, 125639, 125661, 125671, 125673–75, SMF 10993–94, USNM 74511–12, 75443, 80897–901; Santa Ana: LSUMZ 52325, 152364.

Anolis gaigei.—**Panama:** Chiriquí: 6 airline km from San Lorenzo: MHCH 1650, SMF 91915; Isla Palenque: MHCH 287–288; Playa Las Lajas: SMF 91914; Río Tabasará: MHCH 1651, SMF 91913; road btw. La Pita and Chiriqui: SMF 91916; road from Interamericana to Horconcitos: SMF 91917; Colón: Quebrada Bonita, ca Buena Vista: KU 100430–31, 113390; Cristóbal: USNM 54263; Portobelo: USNM 48528; Trinidad River: USNM 63995–99; Canal Zone, Juan Mine: AMNH 71742–43; Porto Bello: USNM 65123; Herrera: Porto Bello: USNM 65123; Los Santos: 1–1.5 mi NW Los Santos: CM 47531; Las Palmitas: USNM 148206; near Playa Venao: SMF 92195; Playita Resort: MHCH 1652–54, SMF 91904–08; Pta. Mala: AMNH 71746–49; Santo Domingo: MHCH 1655–57, SMF 91901–02; Panamá: 3 km WSW Chepo: KU 113391; Panama City: KU 117015, USNM 120552, 120564, 120584–610, 120700–01; Isleta Trapiche: USNM 102748–49; Panama City, Barrio San Miguelito: SMF 85302–03; Panama City, Metropolitan National Park: SMF 85304–06; Panamá, Parque Caminos de Cruces: MHCH 158; Pedro González Island: USNM 120695–96; 3 km W El Llano: AMNH 120006; Alto del Jobo Chorrera: UF 124419; Archipiélago de las Perlas: UMMZ 58537; Archipiélago de las Perlas, Isla Chapera: AMNH 108653–58; Archipiélago de las Perlas, Isla Contadora: AMNH 108637–51; Archipiélago de las Perlas, Isla Mogo Mogo: AMNH 108659–62; Archipiélago de las Perlas, Isla Pacheca: AMNH 108652; Archipiélago de las Perlas, Isla Saboga: AMNH 108663–67, UMMZ 51096–105; Archipiélago de las Perlas, Isla San José: AMNH 115897–99; Canal Zone, stream below Casdenas village: UF 124437; Canal Zone, Summit Garden: ANSP 24557, UF 124426; Cerro Azul above Tocumen: UF 124435–36; Chagres River: AMNH 85398; Fort Kobbe: USNM 193369–70, 193454, 532433–40; Isla Taboga: AMNH 103745–47, 107482–89, ANSP 21723–26; UMMZ 181409–10, 181424, 181427; La Chorrera, near Army Post: AMNH 71735, USNM 53821; Madden Forest Preserve: AMNH 107477–81; near Chilibre, twilight zone of Chilibre Cave: USNM 140651; near Fort Clayton Reservation: SMF 82703–07, UIMNH 41896–918; 41992; Nueva Gorgona: AMNH 89974–78; Old Panama: AMNH 71744–45, 107477–81; Panama City, El Cangrejo, Ave. E. Morales: UF 124415–16, 124427–28; Pedro González Island: USNM 120695–96; Veraguas: Finca La Providencia, near Ponuga: MHCH 2294, SMF 91529, 91918, 91956–60; Isla Cebaco: USNM 154243; Mojara: USNM 129858–62; Montuoso Ranger Station: MHCH 1658, SMF 91921; Río Coroba: USNM 148085–90; Río Santa María: SMF 91909; road from Santiago to Soná: MHCH 1659, SMF 91912; road from Soná to El María: SMF 91910–11; San Francisco: SMF 91903; Santiago: AMNH 113567; Sitio Ramsar: 91919–20. **Colombia:** Antioquia: Atrato, Sautata: FMNH 74917; Cesar: Las Pavas, Santa Marta Mountains: UMMZ 54825–30; Valencia, Santa Marta Mountains: UMMZ 54822–24; Guajira: Arroya de Arenas, Santa Marta Mountains: UMMZ 54818–20; Loma Larga, Santa Marta Mountains: UMMZ 54821; Magdalena: Agua Dulce, Santa Marta Mountains: UMMZ 48329–34; Cincinnati, Santa Marta Mountains: UMMZ 54814–15; Fundación, Santa Marta Mountains: UMMZ 48327–28; La Tigrera, Santa Marta Mountains: UMMZ 48324; Minca, Santa Marta Mountains: UMMZ 48325–26; Palomina, Santa Marta Mountains: UMMZ 48321; Pueblo Viejo, Santa Marta Mountains: UMMZ 48322–23; Quebrada, Santa Marta Mountains: UMMZ 54816; Tamocol, Santa Marta Mountains: UMMZ 54817.

Anolis osa.—**Costa Rica:** Puntarenas: ca. 6.5 km SW of Rincón de Osa, Osa Tropical Science Center: USNM 219564; ca. 2.5 km SW of Rincón de Osa, Osa Tropical Science Center: USNM 219561, 219563, 219565–66; ca. 3.5 km WNW of Rincón de Osa, Osa Tropical Science Center: USNM 219562; 5 mi SW Rincón de Osa: CM 41509; Corcovado, National Park: SMF 89260–61; dirt road to Ranger Station "Los Patos": SMF 89187–92, UCR 20731; 2 km NW Cañaza: SMF 89193–97; 4 km W Puerto Jiménez: SMF 89618–20; Puerto Jiménez: SMF 89198–202, UCR 20732, ZFMK 52335; 8, 5 km SW Puerto Jiménez, 25 m after branch to Playa la Colorada: SMF 89205–07, 89621; 11 km SW Puerto Jiménez: SMF 89208; 16.5 km S Puerto Jiménez: SMF 89209–10; 2 km W Rincón de Osa: SMF 89215–21, UCR 20733–35; 9.5 km E Agujitas, Rancho Quemado: SMF 89622–23; 8 km E Agujitas, highest point of road, 8.6945°N, 83.59161°W: SMF 89222–24; Bahía Drake, Agujitas: SMF 89624; Bahía Drake, 3–4 km W Drake: SMF 89625–26; S Rincón de Osa, 1 km after branch of road to Drake: SMF 89225–26; road 6 km SW Rincón de Osa: SMF 89227–32; road 6 km SW Rincón de Osa: SMF 80645; Puerto Escondido: SMF 89628–30; Rincón de Osa: SMF 89233–40, UCR 20740–41.

Anolis polylepis.—**Costa Rica:** Puntarenas: 1 km W Ojochal, Residential Cinco Ventanas: SMF 89607–09, UCR 20708–09, 20736; 12 mi SSW Palmar Sur, 8.7925°N, 83.51917°W: LSUMZ 52362; 2 km N Rincón de Osa, Restaurant Ventanas al Golfo: SMF 89182–86; 2 km W Venecia: SMF 89174–76, UCR 20726–27; 2 km W Villa Colón: SMF 89171–73, UCR 20739; 2.5 km N Platanillo: SMF SMF 89660–65; 2–3 km after branch of road to Rincón de Osa: SMF 89610–17, UCR 20728–29, 20737–38; 3 km E Santa Cecilia: SMF 89177–81, UCR 20730; 3 km N Pavones: SMF 89633, UCR 20743; 5 km W Conte, 8.44919°N, 83.05678°W: SMF 89632, UCR 20742; 7 mi E Golfito: LSUMZ 11866, 30259; 9 km S Zancudo: SMF 89157; Balzar: SMF 89163–65, UCR 20716–19; branch of road to Sierpe: SMF 89168–70, UCR 20720; Fairy Place at Río Cotón: SMF 89631; Golfito, Reserva natural: SMF 89251; Gromaco, 23 mi NNE Golfito, 9.5 mi ESE Potrero Grande, on Río Coto Brus: UF 16377; Las Cruces Biological Station, 6 km (by road) S of San Vito de Java: SMF 89323–24, 89333 ; Manuel Antonio: SMF 81818–20; N Rincón de Osa, suital lodge: SMF 89627; N Uvita, Reserva Oro Verde: SMF 89605; near Quepos: SMF 77658; near Trenzas: SMF 89637–38; Puerto Pilón: SMF 89634–35; Punta Mala: SMF 89639; road halfway between Pilón and Sabalo: SMF 89636; San Buenaventura: SMF 89160–62, UCR 20713–14; Uvita, La Cusinga rainforest lodge: SMF 89606, UCR 20706–07; W Los Mogos: SMF 89642–44; San José: Cedral: SMF 89305–06; 11 mi SW of San Isidro del General, on Dominical Road (Highway 22): USNM 219999–220000; **Panama:** Chiriqui: "Chiriqui": ZMB 7825–26, 7830, 58002–09; Sendero El Pianista: SMF 86384; Boquete: SMF 86383, ZSM 63/1989/1, 4, 5; Cochea, 8.72656°N, 82.49154°W: MHCH 2260–1, SMF 89747–8; El Volcán: USNM 129920; Finca C.A.S.A, 8 km NE Río Sereno, Distrito Renacimiento: SMF 85204–08, 85209–10; Hacienda Café de Eleta: MHCH 2257, SMF 89509–12; headwaters of Río Chevo: SMF 85442; Los Algarrobos: Weg zum Río Majagua: SMF 89513; Meseta de Chorcha: SMF 85211–21, 85287; near El Hato: USNM 129380; Progreso: USNM 120756; Río Chevo: SMF 85441; Santa Clara: MHCH 2262, SMF 89749; Universidad Autonoma de Chiriquí, David: SMF 85202–03; Volante: MHCH 2259, SMF 89514.

Anolis tropidogaster.—**Colombia:** Ont été recueillis près de la rivière de la Magdeleine: MNHN 2427, 2427a; Antioquia: Alto de Quimari, Sinu River side: FMNH 61676–78; Nechi, Cauca River: FMNH 55935–37; Urabá, Río Currulao: FMNH 63794–804; Chocó: Andagoya: MCZ 32302; Golfo de Urabá, Unguia: FMNH 63793; Cordobar: Murrucucu, Sinu River side: FMNH 61658–60; Tierra Alta: FMNH 61666–67, 61702–03; no Provinz: Santander: Puerto Berrio: FMNH 30791; **Panama:** Darién: 7–11 km SW El Real between Río Presencia and Río Morgentese: UMMZ 155803–04; below Río Tupisa on Río Chucunaque: AMNH 42922; Camp Creek, near Yavisa: AMNH 42920–21, 42923–25; Canclones [Canclón]: UMMZ 124957; Caserete–Chepigana: MHCH 1628, 1634, 1640, 1645; Cerro Mali, GML [Gorgas Memorial Laboratory] camp clearing: USNM 151081–83; Cerro Tacarcuna: USNM 151120; Chepigana: MHCH 1636; El Real de Santa María: MHCH 179; Pinogana, El Real: MHCH 209–210; Río Chucunaque, 3 mi W Camp Townsend: AMNH 102560–63; Sol Poniente–Chepigana: MHCH 1701; Tacarcuna Village: USNM 141814; Parque Nacional Darien, mouth of Rio Paca: MHCH 2374; Laguna de Matusagarati, Aguas Calientes, Pinogana: MHCH 2375.

APPENDIX II. Corresponding information of sequenced specimens.

species	collection number	field number	GenBank accession number	country	province	latitude	longitude
Anolis cupreus	SMF 93897	GK 2301	JQ435511	Costa Rica	Alajuela	9.94461	-84.32230
A. cupreus	SMF 93873	GK 2233	JQ435510	Costa Rica	Puntarenas	9.80211	-84.60645
A. gaigei	SMF 91907	GK 3116	JQ435508	Panama	Los Santos	7.42036	-80.18002
A. gaigei	SMF 91918	GK 3202	JQ435509	Panama	Los Santos	7.43513	-80.19132
A. kemptoni	SMF 91482	SL 680	JQ435507	Panama	Bocas del Toro	8.94736	-82.70983
A. polylepis	SMF 90153	JFB 023	JQ435506	Panama	Chiriquí	8.73761	-82.51302
A. tropidogaster	MHCH 1634	MHCH 1634	JQ435505	Panama	Darien	8.11856	-77.87800