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Systematics and ecology of *Anolis biporcatus* (Squamata: Iguanidae)

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Abstract. *Anolis biporcatus* is a large green anole found in southern Mexico, Central America and northern South America. We examined morphological, molecular, and ecological aspects of specimens from localities throughout the range of *A. biporcatus* and found evidence that warrants elevating *A. biporcatus parvauritus* to species status. *A. parvauritus* differs from *A. biporcatus* in its dewlap colour pattern, overall morphology, and mitochondrial DNA. A deep mitochondrial split exists between northern and central Costa Rican samples of *A. biporcatus*, and substantial morphological variation occurs within this form. These patterns suggest potential species-level splits within currently recognized *A. biporcatus.* More extensive sampling of DNA data is needed to evaluate potential species boundaries within *A. biporcatus.*

Key words. Anole, Central America, lizard, South America, subspecies, taxonomy.

Resumen. *Anolis biporcatus* es un anolis verde y grande que se distribuye al sur de México, América Central y al norte de América del Sur. Examinamos datos morfológicos, moleculares y ecológicos en especímenes a lo largo del rango de *A. biporcatus*, y encontramos evidencia para elevar a *A. biporcatus parvauritus* al estatus de especie. *A. parvauritus* difiere de *A. biporcatus* en el patrón de coloración del pliegue gular, morfología en general y ADN mitocondrial. Existe una división mitocondrial profunda entre las muestras del norte y centro de Costa Rica de *A. biporcatus*, que además presenta una variación morfológica substancial. Estos patrones sugieren divisiones potenciales a nivel de especie dentro de lo que actualmente se reconoce como *A. biporcatus*. Se necesita un mayor muestreo de ADN para evaluar los límites entre especies potenciales en *A. biporcatus*.

Palabras clave. *Anolis*, América Central, lagartija, América del Sur, subespecie, taxonomía.

Introduction

Anolis biporcatus is a large, bright green, arboreal anole found from southern Mexico through Central America, and as far south as Ecuador, Colombia and Venezuela (Williams 1966; Köhler & Vesely 2003; pers. obs.). The species occupies a wide range of forest types and has been recorded to occur from 2 to 1220 meters above sea level (Savage 2002). *Anolis biporcatus* is short-legged and stocky with keeled ventral scales. Both sexes have small dewlaps; the male's dewlap is typically coloured powder-blue proximally with red-orange and yellow at the margin, while that of the female may be white or blue with black speckles. Maximum body size (snout–vent length) reaches 105 mm, and the tail is approximately twice the snout–vent length. The species does not exhibit sexual size dimorphism (Fitch 1976). *Anolis biporcatus* has been found in low densities in disturbed and undisturbed habitats (Lee 1996, Santos-Barrera et al. 2008, Laurencio & Malone 2009).

Wiegmann (1834) described *Dactyloa biporcata* based on a specimen from Mexico. Since its description, *Anolis biporcatus* has experienced a rich and confusing taxonomic history. Bocourt (1873) described *A. copei* based on a specimen from Santa Rosa de Pansos, Guatemala and *A. petersii* from two syntypes from Vera Paz, Guatemala. The following year, Peters (1874) described *A. obtusirostris* from the Chiriquí province of Panama. Boettger (1893) named a population from La Junta, Costa Rica *A. brevipes*. Both *A. obtusirostris* and *A. brevipes* were subsequently determined to be junior synonyms of *A. copei* (Dunn 1930). Ruthven (1916) described *A. solifer* from the Santa Marta Mountains of Colombia, and suggested it was allied with *A. copei*. *Anolis solifer* was later determined to be a junior synonym of *A. biporcatus* (Williams 1966). A subspecies, *A. biporcatus parvauritus* Williams, 1966, with its type locality on Gorgona Island, Cauca, Colombia, was recognized; its range extends from southern Colombia through Ecuador. Recently, the holotype of *A. copei* became the neotype of *A. biporcatus* (see Köhler & Bauer 2001). The holotype of *A. biporcatus* was found to be conspecific with the syntypes of *A. petersii*, and it was argued that use of the name *A. copei* for the lizard commonly known as *A. biporcatus* and the name *A. petersii* for the lizard commonly known as *A. biporcatus* would create taxonomic confusion (Köhler & Bauer 2001).

The relationships of *Anolis biporcatus* have been only slightly less problematic than its taxonomy. Boulenger (1885) considered *A. biporcatus* and *A. fraseri* to be closely related due to similar morphologies (Williams 1966). Etheridge (1959) did not find a close relationship between *A. biporcatus* and *A. fraseri* based on skeletal morphology; instead, his results placed these species in separate lineages: *A. fraseri* with alpha anoles and *A. biporcatus* with beta anoles. Etheridge (1959) placed *A. biporcatus* in the *petersii* series along with *A. capito*, *A. loveridgei*, *A. pentaprion*, and *A. petersii*. Poe (2004) estimated *A. biporcatus* to be sister to a group that included *A. petersii*, *A. vociferans* (= *A. salvini*), *A. pentaprion*, *A. loveridgei*, *A. barkeri*, and *A. aquaticus*. Nicholson et al. (2012) found *A. biporcatus* to be sister to a group consisting of *A. woodi* and *A. aquaticus*.

We have collected and examined museum specimens of *Anolis biporcatus* from throughout most of its range (Appendix 1). Here we assess morphological variation, present molecular and ecological data, and evaluate the taxonomic status of *A. biporcatus parvauritus* relative to these data.

Materials and methods

We examined 82 specimens (71 adults >70 mm SVL), including 67 specimens allocated to *Anolis biporcatus biporcatus* and 15 specimens allocated to *A. biporcatus parvauritus* (including the holotype, MCZ 78935). We preliminarily assigned species to these subspecies using the geographic distribution given in Williams (1966). We collected lepidotic characters and the following measurements according to the procedures established by Williams et al. (1995) and Poe & Yañez-Miranda (2008): snout–vent length (SVL) from tip of snout to anterior edge of cloaca; head length (HL) measured from tip of snout to anterior edge of ear opening; femur length (FL) measured from the midline of the body laterally to the knee; toe length (TOL) measured from the base of the fourth (i.e., longest) toe to the tip of the claw; tail length (TAL) measured from the cloaca to the tip of the tail; and ear height (EH) measured as the vertical diameter of the ear. Measurements were taken with digital callipers to the nearest 0.1 mm and are given in mm throughout this paper. We performed a Principal Component Analysis (PCA) of adult specimens using the following characters: number of scales across the snout at the second canthals, number of scales between supraorbital semicircles, number of scales between interparietal and supraorbital semicircles, number of loreal rows, number of supralabial scales from rostral to centre of eye, number of scales from circumnasal to rostral, number of expanded lamellae on fourth toe of hind foot. We observed no sexual dimorphism in these traits and therefore pooled males and females for analysis. We also tested for group (i.e., subspecies) membership using a discriminant function analysis (DFA) of the above characters with subspecies as hypothesized groups. Statistical analyses were performed in Stata (2013).

We investigated the genetic divergence of *Anolis biporcatus biporcatus* and *A. biporcatus parvauritus* via a phylogenetic analysis of the mitochondrial COI gene. We obtained DNA sequences from three putative *A. biporcatus parvauritus* from Ecuador and five putative *A. biporcatus biporcatus* from throughout its range. We included 16 additional mainland *Norops*-clade *Anolis* and *Polychrus liogaster* as outgroups. We evaluated the suitability of partitioning these data for phylogenetic analysis using Lanfear's (2012) approach and hypothesized partitions based on codon position. Data were analysed using a partitioned Bayesian phylogenetic analysis in MrBayes (Ronquist et al. 2012), with each partition allowing model–averaging across all GTR–class models and rate variation across sites according to a gamma distribution with six rate categories (because MrBayes allows model-averaging across the entire GTR model space ['nst=mixed'], there is little reason to designate particular GTR-class models in comparisons of partitioning schemes). We ran the analysis for 10 million generations, sampling every 1000th generation, and constructed a consensus tree from the last 50% of sampled trees.

Results

The PartitionFinder analysis decreed a single model for COI positions 1 and 2 and a second model for position 3. The specimens of *Anolis biporcatus parvauritus* form a well-supported, deeply divergent clade separate from other *A. biporcatus* (Fig. 1). The degree of divergence between *A. b. biporcatus* and *A. b. parvauritus* (15–17% uncorrected p–distances) is comparable to interspecies divergences among well-established species in the tree (e.g., the p–distances between *A. aquaticus* and *A. biporcatus* are 16–17%).

Specimens of *Anolis biporcatus biporcatus* and *A. b. parvauritus* display non-overlapping distributions for PCs 1 and 2 (Fig. 2). The DFA classified 100% of specimens according to our initial designations as *biporcatus* or *parvauritus*.

We find *Anolis biporcatus biporcatus* and *A. biporcatus parvauritus* to be distinguishable based on DNA sequence data (Fig. 1), overall morphology (Fig. 2), and male dewlap colour (black distal scales in *A. parvauritus*, white in *A. biporcatus*; Fig. 3). Therefore we propose that *A. parvauritus* be elevated to full species status. Our larger samples suggest that the difference in ear shape described by Williams (1966) does not distinguish *A. parvauritus* from *A. biporcatus*; that is, either species may possess an oval ear opening.

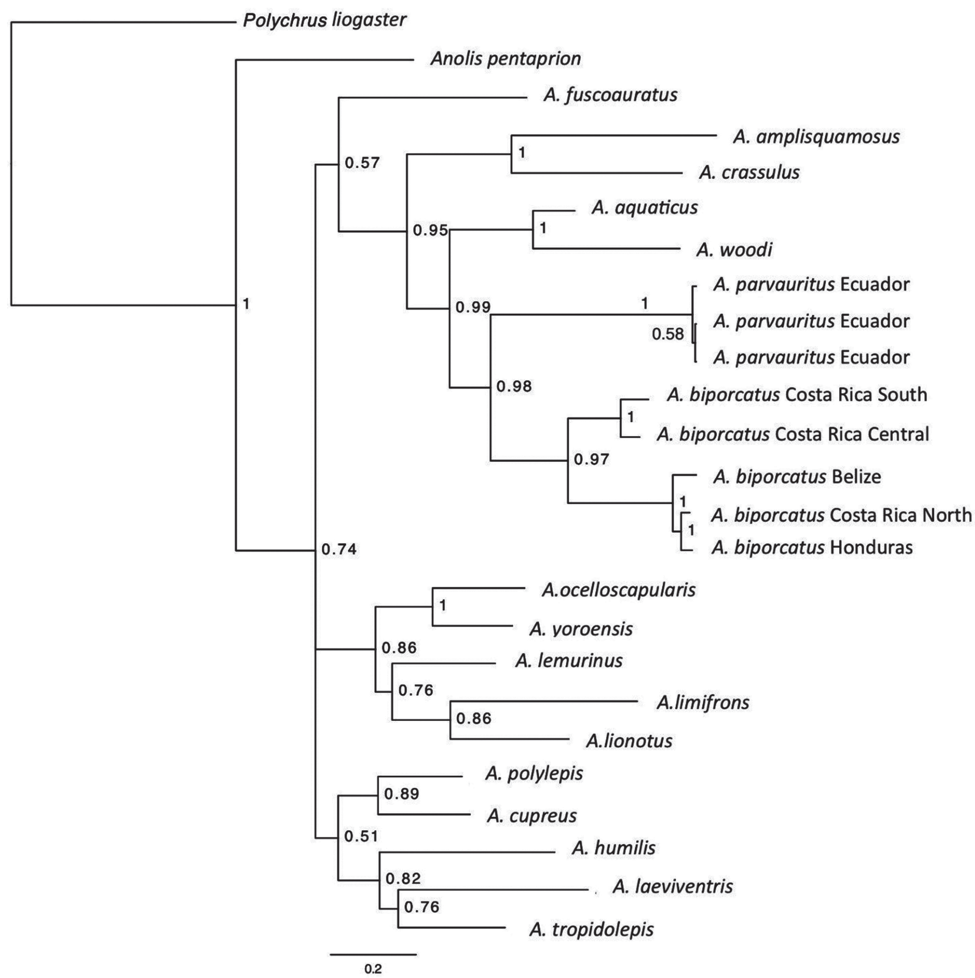

Figure 1. Phylogenetic tree based on Bayesian analysis of mitochondrial COI gene. Numbers on clades are posterior probabilities.

See Table 1 for variation in selected measurements, proportions, and scale characters.

Anolis biporcatus (Wiegmann, 1834)
(Figs 3–5)

Description: Maximum SVL 103.2 mm in males, 107.6 mm in females; TAL/SVL ratio 1.75–2.45; HL/SVL 0.24–0.30; FL/SVL 0.26–0.33; TOL/SVL 0.15–0.25; EH/SVL 0.02–0.04. Dorsal head scales unicarinate or wrinkled; strong frontal depression; rostral overlaps or is even with mental anteriorly; 8–12 scales across snout between second canthals; supraorbital semicircles separated by 1–5 scales or in contact; suboculars in contact with supralabials or separated by 1 row of scales; 1–3 elongate superciliary scales followed by small undifferentiated scales; 4–8 loreal rows; 1–2 scales between circumnasal and rostrum; posterodorsal edge of rostral smooth; interparietal length 0.9–2.8; 2–6 scales between interparietal and supraorbital semicircles; 8–13 supralabials to centre of eye; 5–8 postmentals; some enlarged scales present in supraocular disc, bordered medially by a

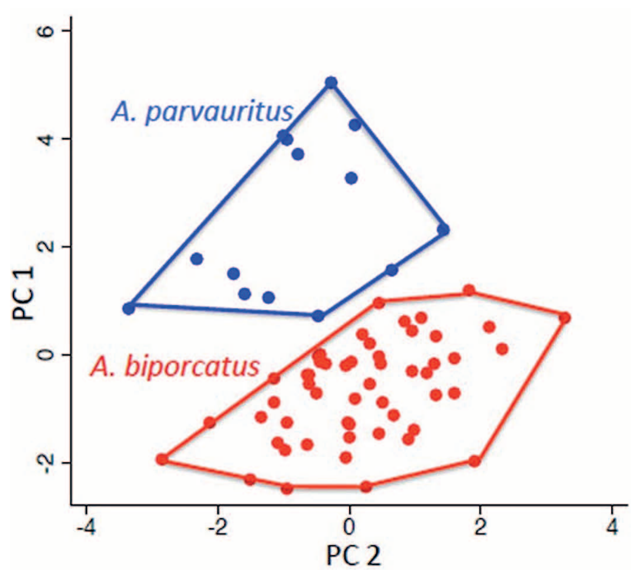

Figure 2. Principal Component Analysis for adult specimens (exclusive of MSB 95847 and MSB 95848).

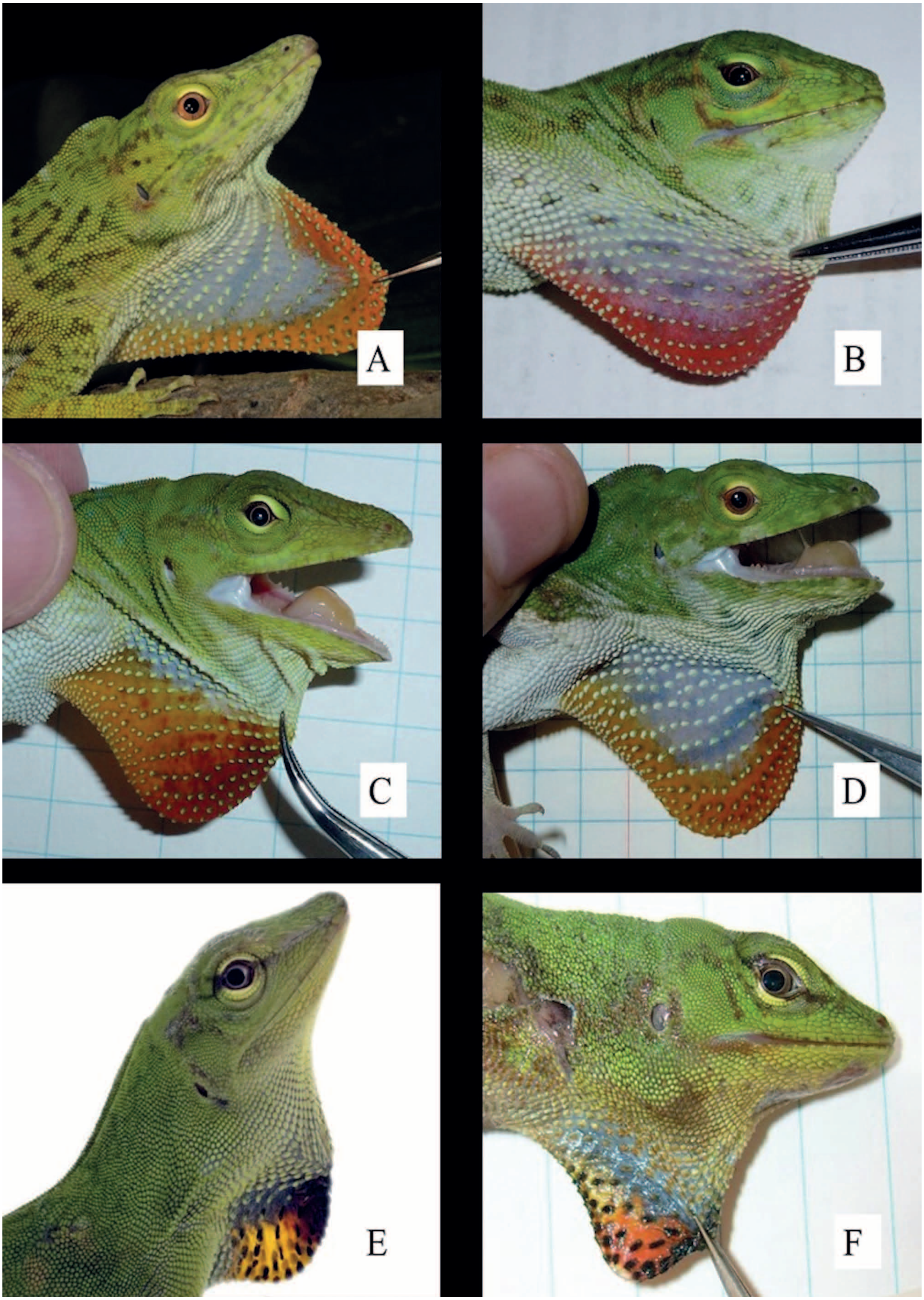

Figure 3. Dewlap variation in males of *Anolis biporcatus*; (A) MSB 95919, Honduras (Santa Barbara); (B) MSB 79880, Panama (Cocle); (C) POE 2458, Panama (Chiriqui); (D) MSB 95916, Mexico (Oaxaca); and *A. parvauritus*: (E) QCAZ 9807, Ecuador (Los Rios); (F) POE 2039, Colombia (Valle de Cauca).

continuous or broken row of small scales; no abruptly enlarged sublabial rows; mental partially or completely divided, extending posterolaterally beyond rostral or even with rostral, with posterior border straight or convex; dewlap extends posteriorly to axillae, or just anterior to axillae; no axillary pocket; 0–2 enlarged postcloacal scales in males, none in females; nuchal and dorsal crests not evident in preserved specimens; 2–3 enlarged middorsal rows; dorsal scales keeled with 6–11 scales in 5% of SVL; ventral scales in transverse or diagonal rows, keeled, 4–7 scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 20–25 lamellae under third and fourth phalanges of fourth toe; tail with a single row of middorsal scales; tail weakly laterally compressed.

Geographic distribution: The distribution of *Anolis biporcatus* extends from southern Mexico, throughout Central America, and into Colombia and Venezuela in South America (Fig. 6). The neotype locality is Santa Rosa de Pansos, Guatemala. The vertical range of our examined specimens is 13 to 1,145 metres a.s.l.; Köhler (2008) mentioned an altitudinal range from sea level to 2,000 metres.

Natural history: We have observed *Anolis biporcatus* in several forest types, from primary to highly disturbed, and found the species to be moderately common in disturbed and secondary forest. During the day, we observed individuals on large understorey leaves (palms and *Heliconia* spp.), branches, and tree boles up to 3 metres high. Individuals were observed to flee upwards on tree trunks when approached (maximum observed climb was to 10 metres up). Four individuals were observed pouncing on prey in the leaf litter from vertical, head-down positions on tree trunks. At night, we observed individuals sleeping

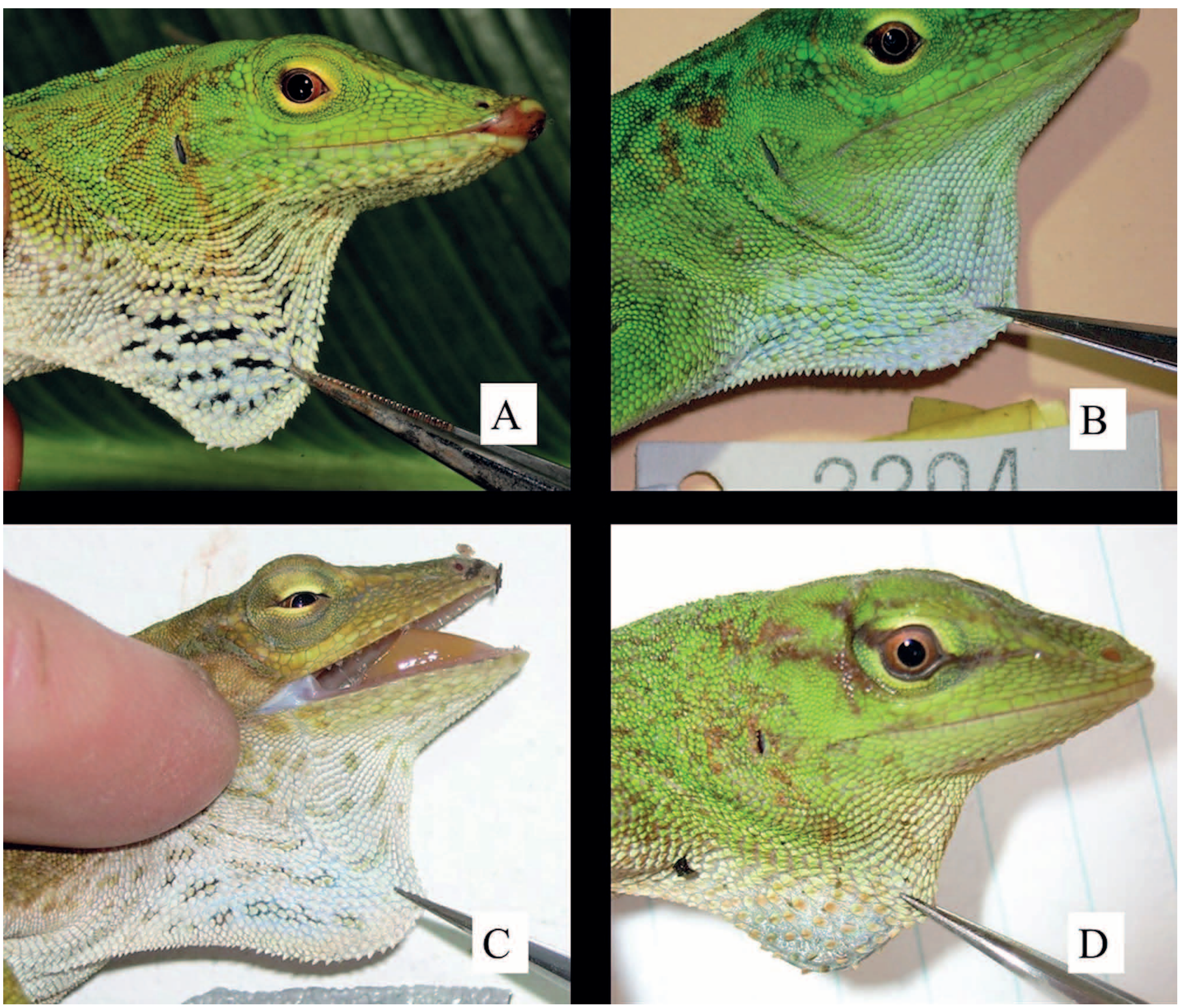

Figure 4. Dewlap variation in females of *Anolis biporcatus*: (A) POE 3423, Honduras (Santa Barbara); (B) POE 2204, Panama (Veraguas); (C) MSB 79874, Panama (Veraguas); and *Anolis parvauritus*: (D) POE 2040, Colombia (Valle de Cauca).

Tab. 1. Selected measurements, proportions and scale characters of *Anolis biporcatus* and *Anolis parvauritus*. Range is followed by mean value and one standard deviation in parentheses, and then by sample size. Abbreviations: SVL = snout–vent length (in mm); HL = head length; SS = supraorbital semicircles; IP = interparietal scale; SPL = supralabial scales; morphometric data were taken only from adults (n=67 + 15).

Character	Sex	*Anolis biporcatus*	*Anolis parvauritus*
SVL	males	70.2–103.2 (87.4±8.2) 30	73.9–88.0 (79.5±5.4) 6
	females	69.9–107.6 (85.7±8.7) 24	77.3–94.5 (88.3±5.6) 9
HL/SVL	males	0.24–0.29 (0.27±0.01) 30	0.26–0.27 (0.27±0.01) 6
	females	0.25–0.30 (0.27±0.06) 24	0.25–0.30 (0.27±0.01) 9
tail length/SVL	males	1.75–2.45 (2.09±0.18) 26	2.16–2.51 (2.36±0.15) 5
	females	1.84–2.42 (2.19±0.16) 21	2.29–2.95 (2.56±0.22) 6
4th toe length/SVL	males	0.15–0.25 (0.18±0.02) 30	0.15–0.22 (0.18±0.03) 6
	females	0.15–0.20 (0.18±0.04) 24	0.16–0.22 (0.18±0.02) 9
number of middorsal scales in 5% of SVL	males	6–11 (8.1±1.2) 30	6–9 (7.7±1.0) 6
	females	6–11 (8.0±1.0) 24	7–9 (8.1±0.8) 9
number of midventral scales in 5% of SVL	males	4–7 (5.3±0.8) 30	4–6 (5.2±0.8) 6
	females	4–7 (5.2±0.8) 24	4–5 (4.8±0.4) 9
number of subdigital lamellae of 4th toe		20–25 (22.1±1.1) 67	20–25 (23.3±1.4) 15
number of scales between SS		0–5 (2.3±0.8) 67	1–3 (1.7±0.7) 15
number of scales between IP and SS		2–6 (3.4±0.7) 67	4–6 (5.0±0.9) 14
number of SPL to level below center of eye		8–13 (10.1±1.0) 67	6–10 (8.4±1.0) 15
number of horizontal loreal scale rows		4–8 (6.3±0.6) 67	6–9 (7.6±1.1) 15
number of scales between second canthals		8–12 (9.9±0.9) 67	9–14 (11.5±1.6) 15
number of postmentals		5–8 (6.4±0.6) 67	6–8 (6.5±0.6) 15

on leaves and slim branches. Sleeping individuals frequently were seen on the upper surface of low canopy vegetation (e.g., at roadsides) among green foliage. Mean sleeping perch height was 4.1 metres (Standard Deviation = 2.3; range 1.0–13.0 m; n=72) in Costa Rica, Mexico, Honduras, and Panama.

One small site where one of us (SP) surveyed and marked individual *Anolis* for 23 consecutive nights (~30 minutes/night) in Boquete, Panama (8.766° N, 82.436° W; WGS84; 1,084 m a.s.l.) was inhabited only by *A. biporcatus* (N=8 observations) and *A. polylepis* (N=17 observations) as far as anoles were concerned. These species slept at significantly different heights (P=0.0001; Mann–Whitney U test), with *A. biporcatus* sleeping on higher perches (mean for *A. biporcatus*: 4.6 m; mean for *A. polylepis*: 0.7 m). For *A. polylepis*, seven recaptures of 10 individuals occurred. None of the eight marked individuals of *A. biporcatus* were recaptured.

Anolis parvauritus Williams, 1966
(Figs 3–5)

Description: Maximum SVL 88.0 mm in males, 94.5 mm in females; TAL/SVL ratio 2.16–2.95; HL/SVL 0.25–0.30; FL/SVL 0.25–0.31; TOL/SVL 0.15–0.22; EH/SVL 0.02–0.04. Dorsal head scales unicarinate or wrinkled; strong frontal depression; rostral overlaps or is even with mental anteriorly; 9–14 scales across snout between second canthals; supraorbital semicircles separated by 1–3 scales; suboculars in contact with supralabials or separated by 1 row of scales; 1–3 elongate superciliary scales followed by small undifferentiated scales; 6–9 loreal rows; 2–3 scales between circumnasal and rostral; posterodorsal edge of rostral

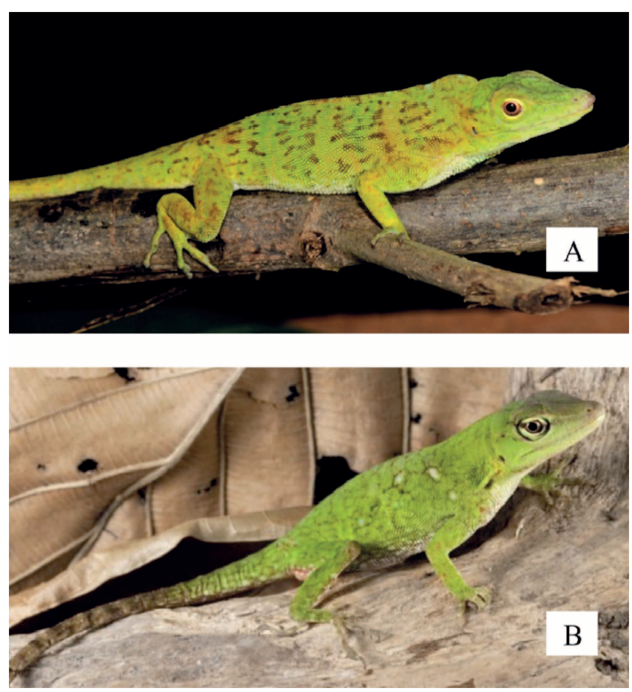

Figure 5. (A) Adult *Anolis biporcatus* MSB 95919, Honduras (Santa Barbara); and (B) *A. parvauritus* QCAZ 8501, Ecuador (Esmeraldas).

smooth; interparietal length 0.9–2.0; 4–6 scales between interparietal and supraorbital semicircles; 6–10 supralabials to centre of eye; 6–8 postmentals; some enlarged scales present in supraocular disc, bordered medially by a continuous or broken row of small scales; no abruptly enlarged sublabial rows; mental partially or completely divided, extending posterolaterally beyond rostral or even with rostral, with posterior border straight or convex; dewlap extends posteriorly to axillae, or just anterior to axillae; no axillary pocket; 0–2 enlarged postcloacal scales in males, none in females; nuchal and dorsal crests not evident in preserved specimens; 2–3 enlarged middorsal rows; dorsal scales keeled with 6–9 scales in 5% of SVL; ventral scales in transverse or diagonal rows, keeled, 4–6 scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 20–25 lamellae under third and fourth phalanges of fourth toe; tail with a single row of middorsal scales; tail rounded.

Geographic distribution: The distribution of *Anolis parvauritus* covers western Ecuador and southwestern Colombia, including the type locality of Gorgona Island in Colombia (Fig. 6). The altitudinal range of our examined specimens is 46 to 401 m a.s.l.

Natural history: As with *Anolis biporcatus*, we have found *A. parvauritus* to be moderately common in disturbed areas and less common but still present in secondary forests. This difference indicates some tolerance of disturbed areas but not, we believe, that its abundance would decrease in denser forest. Rather, the green dorsal colour pattern and high perching (frequently on top of the forest canopy) of these forms renders them difficult to spot in tall dense habitats. We have no quantitative ecological data or daytime observations for *A. parvauritus*. We collected this species from roadside vegetation (several localities), a sap grove (adjacent to the Rio Palenque field station, Ecuador), somewhat denuded trees within 50 m from the ocean (near Juanchaco, Valle de Cauca, Colombia), and in dense secondary forest (several localities).

Discussion

We found significant mitochondrial structuring within *Anolis biporcatus* (Fig. 1). In particular, there is a deep mitochondrial split between northern and central Costa Rican samples with associated genetic divergence (13%) that

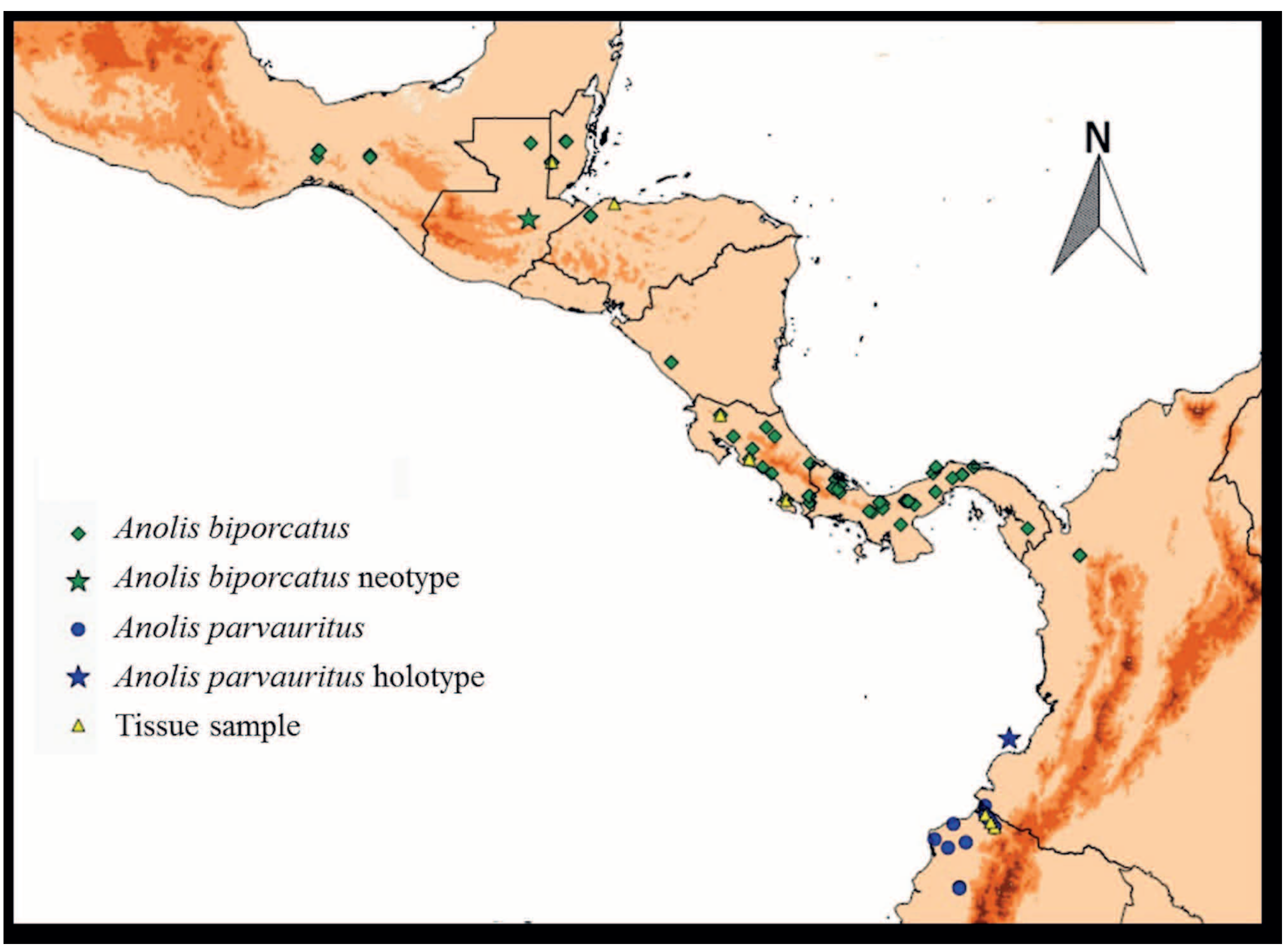

Figure 6. Distribution map of examined specimens, neotype/holotype localities, and tissue samples.

are comparable to some species-level splits in *Anolis* (e.g., divergence between *A. ocelloscapularis* and *A. yoroensis* is 12%). Divergence between the two northern Costa Rican samples is greater than divergences between northernmost Costa Rica and the geographically more distant Belize (4%) or Honduras (2%) samples. However, there are no obvious morphological correlates associated with these DNA patterns. Northern forms tend to be larger, but this discrete split between large northern forms and smaller southern forms does not follow our recovered mitochondrial break. In addition, we emphasize that our DNA sampling was limited. For example, we lacked key samples from Caribbean lowland areas in Panama and Costa Rica near where the mitochondrial split occurs.

There also is some variation in dewlap colour pattern in *Anolis biporcatus*. In particular, individuals from the central mountains of Panama appear to lack yellow-orange in the dewlap (Fig. 3). As above, we observed no obvious morphological or DNA correlates with this pattern and therefore we do not currently consider these forms to represent a separate evolutionary lineage.

Although we have little doubt that more than one species is present within what we are here calling *Anolis biporcatus,* elucidating the boundaries of these forms will require more extensive geographic sampling and gathering additional molecular data.

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Appendix

POE = field numbers of SP; MCZ = Museum of Comparative Zoology; MSB = Museum of Southwestern Biology; QCAZ = Museo de Zoología at Pontificia Universidad Católica del Ecuador; UNAH = Museo de Historia Natural, Universidad Autónoma de Honduras.

Specimens examined

Anolis biporcatus: Belize: Cayo: Belmopan: Guanacaste Park, along road at turnoff to Belmopan: MSB 79869; Cayo: Caracol: walking paths from parking area: MSB 79860, 79872, 79878, 79883, 79886, 79890, 95922; Five Sisters Lodge, Nature Trail: MSB 79856. Colombia: Antioquia: Villa Arteaga, Region of Turbo Antioquia: MCZ R–79656–7. Costa Rica: Guanacaste: Tenorio: Reserva Ecolodge: MSB 95851, 95915; Heredia: OTS Finca La Selva: MCZ R–174438; Limon: Guapiles: MCZ R–15426; Suretha: MCZ R–19096; Puntarenas: Los Diamentes: MCZ R–56243; Quepos: 8 km NE of Quepos: MSB 95926; San Vito, Las Cruces, Hospital de San Vito, 5 km south: MSB 95848; Jardin Botanico Robert y Catherine Wilson (Las Cruces): MCZ R–174134; Las Cruces OTS Station: MSB 79881, 95927; Rincon de Osa: Fundacion Neotropica: MSB 95850, 95914; San Jose: Mastatal, roadside: MSB 95849; Piedras Negras, Rio Virilla cruzando: MSB 79864; Tres Piedras, Tropical Forestry Initiative: MSB 95847. Guatemala: Tikal: MCZ R–58771. Honduras: Copan: road from Cofradia to Buenos Aires: MSB 95918; Santa Barbara: Cofradia to Buenos Aires, along road: MSB 95919. Mexico: Chiapas: Ocozocoautla, about 24 km north, road to Apic-pac: MSB 95917, 95928; Oaxaca: Chalchijapa: MSB 95920–1; Santa Maria Chimalapa, just west of Santa Maria Chimalapa: MSB 95916. Nicaragua: Managua, 10 miles south of Managua: MCZ R–54966. Panama: Bocas del Toro: between Chiriqui Grande and Almirante: MSB 79854, 79862, 79870; Fortuna Road, 3 km north of Chiriqui Province boundary: MSB 95923; Fortuna Road, 4 km NE of turnoff to Almirante: MSB 79882; Fortuna Road, 4.4 km south of turnoff to Almirante: MSB 79873; Fortuna Road, 13.8 km south of turnoff to Almirante: MSB 79888; Chiriqui: 50–150 km east of David, turnoff to north at bus stop along Pan American highway: MSB 79884–5; Coclé: Parque Omar Torrijos, trails from cabana: MSB 79857, 79865–6, 79880; Penonome, 8.5 km northwest of Penonome, then 0.3 km on gravel road: MSB 79875; Penonome, 12 km northwest of Penonome near bridge: MSB 79855; Pan American highway to Chica, 25 km west of Chorrera, 6.9 km north of intersection, Altos de Campana Park: MSB 79871; Pan Am HWY, 70.5 km west of Penonome, along Pan Am HWY: MSB 79879; Colon: about 1 km south of Sabanitas: MSB 79868; Sherman Forest, 14 km west of Gatun Locks, dirt road/trail to west: MSB 79889; Darien: MSB 79861; Panama: Cerro Azul, 5 km north of Cerro Azul: MSB 79876; Cerro Azul: 10 km north of Cerro Azul, along road: MSB 79867, 79877; El Llano: 11–15 km north of El Llano on El Llano-Carti Road, along road: MSB 79891, 95925; Veraguas: Cerro Plata, 148 km west of west side of Panama Canal along Pan Am HWY: MSB 79859; La Mesa, 135 km west of west side of Panama Canal: MSB 79887; Santa Fe, about 5 km south of Santa Fe: MSB 79863, 79874; Santa Fe, about 20 km south of Santa Fe: MSB 79853; Santa Fe: Altas Piedras, about 10 km northwest of Santa Fe: MSB 79858.

Anolis parvauritus: Colombia: Cauca: northern part Gorgona Island: MCZ R–78935 (holotype); Rio Mataje: MCZ R–79142. Ecuador: Esmeraldas: Barro: QCAZ 6809; Caimito: near Caimito: QCAZ 6731; Canandé: QCAZ 12191; Durango: QCAZ 6810; Durango–San Francisco: QCAZ 4532; Hostería Tundaloma: QCAZ 6927, 6928; Laguna Cube: QCAZ 6767; Lita: Near Lita QCAZ 10204, 10205; Los Rios: Pichincha: Centro Cientifico Rio Palenque: MCZ R–146993; QCAZ 9807; Playón de San Francisco: QCAZ 8501.

Samples used in phylogenetic analysis of COI

Anolis amplisquamosus: POE 3398; *Anolis biporcatus* (specimen names in Fig. 1 are listed in parentheses): Belize: Cayo: Caracol: walking paths from parking area: MSB 79890 ("*biporcatus* Belize"). Costa Rica: Guanacaste: Tenorio: Reserva Ecolodge: MSB 95851 ("*biporcatus* Costa Rica North"); Puntarenas: Rincon de Osa: Fundacion Neotropica: MSB 95850 ("*biporcatus* Costa Rica South"); San Jose: Mastatal, roadside: MSB 95849 ("*biporcatus* Costa Rica Central"). Honduras: Atlantida: Lancetilla Botanical Garden: 5990–UNAH ("*biporcatus* Honduras"); *Anolis parvauritus* (specimen names in Fig. 1 are listed in parentheses): Ecuador: Esmeraldas: Durango–San Francisco: QCAZ 4532 ("*parvauritus* Ecuador"); Lita: near Lita: QCAZ 10205 ("*parvauritus* Ecuador"); San Lorenzo: Bosque privado de Tundaloma Lodge. Km 17 en la vía San Lorenzo–Ibarra: QCAZ 5047 ("*parvauritus* Ecuador"); *Anolis aquaticus*: POE 2371; *Anolis cupreus*: POE 3265; *Anolis laeviventris*: POE 3350; *Anolis crassulus*: POE 3488; *Anolis fuscoauratus*: POE 2761; *Anolis humilis*: POE 1461; *Anolis lemurinus*: POE 3256; *Anolis limifrons*: POE 3355; *Anolis lionotus*: POE 1418; *Anolis ocelloscapularis*: POE 3440; *Anolis pentaprion*: POE 1855; *Anolis polylepis*: POE 2276; *Anolis tropidolepis*: POE 3300; *Anolis woodi:* POE 3357; *Anolis yoroensis*: POE 3395, POE 3626; *Polychrus liogaster*: POE 2756.