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A new giant anole (Squamata: Iguanidae: Dactyloinae) from southwestern Ecuador

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Abstract

We describe a new species of *Anolis* lizard from the Pacific slopes of the Andes of southwestern Ecuador at elevations between 372–1,000 m. The new species belongs to the *Dactyloa* clade and may be distinguished from other *Anolis* by size, external anatomy, mitochondrial DNA divergence, and dewlap color. Based on phylogenetic analyses of mitochondrial and nuclear DNA sequence data, we found that the new species is sister to *A. fraseri* in a clade composed primarily of large *Dactyloid* species. The new species is known from a protected area in southern Ecuador, Buenaventura Reserve, which suggests that at least some its populations are well protected.

Key words: Andes, *Anolis*, phylogeny, South America, systematics, taxonomy

Introduction

The Pacific versant of Ecuador and southern Colombia is one of the most herpetologically diverse regions of the world. *Anolis* lizards (anoles) in particular have flourished here, with 28 of the 43 species known from Ecuador restricted to the Pacific versant. This diversity has resulted in large multispecies assemblages such as the 11 species of *Anolis* found sympatrically at Rio Palenque field station in Los Rios province. Cryptic species pairs such as *A. aequatorialis* Werner 1894 and *A. dracula* Yánez-Muñoz, Reyes-Puig, Reyes-Puig, Velasco, Ayala-Varela & Torres-Carvajal 2018, or *A. poei* Ayala-Varela, Troya-Rodríguez, Talero-Rodríguez & Torres-Carvajal 2014 and *A. otongae* Ayala-Varela & Velasco 2010 differentiated in this region, as did mini radiations such as the lineage of *A. peraccae* Boulenger 1898, *A. anchicayae* Poe, Velasco, Miyata & Williams 2009a, *A. fasciatus* Boulenger 1885, *A. festae* Peracca 1904, *A. chloris* Boulenger 1898, and *A. gorgonae* Barbour 1905. The proliferation of Pacific versant anoles has produced striking offshoots such as the rostrally endowed *A. proboscis* Peters & Orcés 1956, the ecologically unusual semiaquatic *A. lynchi* Miyata 1985, and the vibrantly colored giant *A. fraseri* Günther 1859.

Anolis fraseri appears morphologically distinct among anoles due to its large size, brilliant color pattern, short hindlimbs, broad toepads, and variably keeled venter. The evolutionary roots of *A. fraseri* were sufficiently mysterious that ultimate anole expert Ernest Williams (1966) judged its most reasonable systematic comparison to be with *A. biporcatus* Wiegmann 1834, a species that has been shown to be a very distant evolutionary relative (Etheridge 1959; Poe *et al*. 2017). More recent work has grouped *A. fraseri* with two other enigmatic species, *A. parilis* Wil-

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liams 1975 and *A. kunayalae* Hulebak, Poe, Ibáñez & Williams 2007, with the divergence of these three species from other anoles some 12 million years ago (mya; Prates *et al.* 2020). Although *A. parilis* and *A. kunayalae* share large size and a colorful (but distinctly patterned) dorsum with *A. fraseri*, these species nevertheless are quite morphologically distinct from *A. fraseri*. *Anolis parilis* and *A. kunayalae* share a toe morphology that is very unusual in anoles and absent in *A. fraseri*, namely a narrow toepad with few lamellae coupled with a very large claw. Although its evolutionary history has become less obscure, *A. fraseri* has remained a singularly unusual species in Pacific Ecuador.

During exploratory fieldwork in the southern aspect of the Pacific Andes of Ecuador we collected a series of anoles composed of individuals that were both clearly distinct from other anole species and more similar to *Anolis fraseri* than any known species. Subsequent detailed molecular and morphological work confirmed this distinctness, and we here describe this form as a new species.

Material and methods

Data sampling. Voucher specimens of the new species described in this paper were deposited in the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ), Herpetological Collection of Instituto Nacional de Biodiversidad (DHMECN), and Universidad San Francisco de Quito (JMG field numbers). Other specimens examined are listed in Appendix 1. We followed terminology for external characters by Williams *et al.* (1995), Poe (2004) and Köhler (2014), as well as Savage (1997) and D'Angiolella *et al.* (2016) for hemipenial characters. Morphological measurements were taken with digital calipers to the nearest 0.1 mm; tails were measured with a ruler; regenerated or broken tails were not measured. Scale counts were made on the left side if applicable. Sex was determined by the presence of everted hemipenes and dewlap color. The right hemipenis of specimens DHMECN 7687 (*Anolis* sp. nov.) and QCAZ 10212 (*A. fraseri*) were removed with a subcaudal incision and prepared using the method described by Pesantes (1994), with the modifications proposed by Betancourt *et al.* (2018).

In addition to describing color in life, we measured spectral reflectance of the dewlap of seven individuals of the new species (two males, five females) and 14 individuals of *Anolis fraseri* (eight males, six females). We measured reflectance using a bifurcated fiber optic probe connected to a portable Jazz spectrometer (Ocean Optics) following Fleishman *et al.* (2009) and used a tubular holder of 3.5 mm diameter cut at 45 relative to the surface. Measurements were taken in five sections of the dewlap: close to head (DH), close to base of sac (DB), close to abdomen (DA), approximate center of sac (DM), and uttermost edge of sac (DE).

Statistical analyses. Because the new species described herein is very similar in morphology to *Anolis fraseri*, we used the *t*-test for independent samples to evaluate quantitative differences in morphometric characters with normal distributions, as well as the Mann-Whitney *U* test to assess differences in scale counts. We used the Shapiro-Wilk normality test to assess the distribution of the data. Statistical analyses were performed in IBM SPSS Statistics 19.0 (SPSS Inc.).

DNA sequence data and phylogenetic analyses. Muscle or liver tissue samples were mixed with Proteinase K and lysis buffer and digested overnight. Total genomic DNA was extracted using a guanidinium isothiocyanate extraction protocol. DNA samples were quantified using a Nanodrop ND-1000 (NanoDrop Technologies, Inc.), resuspended and diluted to 25 ng/ul in ddH_2O prior to amplification.

We obtained eight new DNA sequences—three individuals each of the new species described below and *A. fraseri*, and two of *A. parilis*,—representing the nuclear recombination-activating gene 1 (*RAG1*, up to 1,092 nucleotides), as well as the mitochondrial genes cytochrome c oxidase I (*COI*, 617) and a continuous fragment of up to 1,392 nucleotides including the NADH dehydrogenase subunit 2 (*ND2*), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, and the origin of the light-strand replication (*Ol*). Primers and amplification protocols were taken from the literature (Folmer *et al.* 1994; Kumazawa & Nishida 1993; Macey *et al.* 1997; Schulte & Cartwright 2009). We added the new sequences to previous datasets of *Dactyloa* (Torres-Carvajal *et al.* 2018; Yánez-Muñoz *et al.* 2018) to produce a matrix of 125 taxa and 3,221 aligned nucleotides. Gene regions of taxa sequenced in this study along with their GenBank accession numbers are shown in Table 1.

Data were assembled and aligned in Geneious Prime 2020.2.2 (https://www.geneious.com) under default settings for MUSCLE 3.8.425 (Edgar 2004). Protein-coding sequences were translated into amino acids for confirmation of alignment. After partitioning the concatenated dataset by codon position for each gene and all *tRNA* genes + *Ol* as a single partition (i.e., 10 partitions total), we chose the best partitioning scheme using PartitionFinder v2 (Guindon *et* *al.* 2010; Lanfear *et al.* 2017) under the Bayesian Information Criterion (BIC). The "greedy algorithm" (Lanfear *et al.* 2012) was used with branch lengths of alternative partitions linked to search for the best-fit scheme.

TABLE 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions sequenced in this study.

Taxon	Voucher and locality	Coordinates		Genbank accession number		
		Lat	Long	*COI*	*ND2*	*RAG1*
Anolis fraseri	**QCAZ 3441**. ECUADOR: Chimborazo: La Victoria, Pallatanga-Bucay road.	-2.098	-78.975	MW514056	MW512710	MW512702
Anolis fraseri	**QCAZ 8025**. ECUADOR: Cotopaxi: San Francisco de Las Pampas.	-0.433	-78.966	MW514057	MW512711	MW512703
Anolis fraseri	**QCAZ 14393**. ECUADOR: Cotopaxi: S of Pucayacu.	-0.755	-79.025	MW514058	MW512712	MW512704
Anolis parilis	**QCAZ 15058**. ECUADOR: Esmeraldas: Reserva Tesoro Escondido.	0.494	-79.136	MW514059	MW512713	MW512705
Anolis parilis	**QCAZ 15386**. ECUADOR: Esmeraldas: Durango, 20 km SE Tundaloma Lodge.	1.034	-78.623	MW514060	MW512714	MW512706
Anolis sp. nov.	**QCAZ 14317**. ECUADOR: El Oro: 13.2 km SW Piñas.	-3.662	-79.760	MW514061	MW512715	MW512707
Anolis sp. nov.	**QCAZ 14431**. ECUADOR: El Oro: 13.2 km SW Piñas.	-3.662	-79.760	MW514062	MW512716	MW512708
Anolis sp. nov.	**QCAZ 14596**. ECUADOR: El Oro: Buenaventura Reserve.	-3.654	-79.777	MW514063	MW512717	MW512709

We used a maximum likelihood inference method to obtain the optimal tree topology of the combined, partitioned dataset using the program RAxML v8.2.10 (Stamatakis 2014). This analysis was performed under separate GTRGAMMA models for each partition, with 1,000 rapid bootstrap inferences (Stamatakis *et al.* 2008) followed by a thorough ML search. In addition, we used MrBayes v3.2.1 (Ronquist *et al.* 2012) to perform a Bayesian analysis with three independent runs, each with four MCMC chains, set for 10^7 generations sampling every 1,000 generations. Results were analyzed in Tracer v1.7 (Rambaut *et al.* 2018) to assess convergence and effective sample sizes (≥ 200) for all parameters. Additionally, we verified that the potential scale reduction factor of all the estimated parameters approached values of 1. Of the 10,000 trees resulting per run, 1,000 were discarded as "burn-in. We used the resulting 27,000 trees to calculate posterior probabilities (PP) for each bipartition on a Maximum Clade Credibility Tree in TreeAnnotator (Rambaut & Drummond 2016). Phylogenetic trees were rooted with *Polychrus marmoratus*, *Pristidactylus scapulatus*, and *Urostrophus gallardoi* as outgroups (Poe *et al.* 2017). Phylogenetic analyses were performed in the CIPRES Science Gateway (Miller *et al.* 2010). Additionally, uncorrected genetic distances among species of the clade *Megaloa* were calculated in PAUP 4.0a (Swofford 2002) for *ND2* and *COI*.

Results

Taxonomy

The taxonomic conclusions of this study are based on the study of external morphological features and color pattern, as well as inferred phylogenetic divergences. We consider this information as species delimitation criteria following the evolutionary species concept (de Queiroz 1998, 2007; Simpson 1951, 1961).

Anolis nemonteae **sp. nov.**
(Figs 1, 2, 3, 4, 5, 6)

Proposed standard English name: Star anoles
Proposed standard Spanish name: Anolis de las estrellas

Holotype. QCAZ 14595 (Figs 1, 2, 3), adult female, Ecuador, El Oro province, Buenaventura Reserve, 3.654 S, 79.777 W, WGS84, 417 m, 30 January 2016, collected by Andrea Narváez, Sebastián Valverde, Keyko Cruz, and David Reyes.

Paratypes (N=12, Figs 3, 4). ECUADOR: El Oro: QCAZ 14317 (adult female), 14318 (juvenile female), 14431 (juvenile female), 14432 (adult female), 13.2 km SW Piñas on highway, 3.662 S, 79.760 W, 754 m, 11 January 2016, collected by Fernando Ayala, Steven Poe, and Chris Anderson; QCAZ 14596 (adult male), same collection data as holotype; QCAZ 14597 (juvenile male), Buenaventura Reserve, 3.650 S, 79.780 W, 372 m; QCAZ 14660 (female hatchling), Buenaventura Reserve, 3.653 S, 79.766 W, 578 m, 30 January 2016; DHMECN 4132 (juvenile male), Buenaventura Reserve, 3.645 S, 79.763 W, 800 m, 7 February 2006, collected by Mery Juiña; DHMECN 7687 (adult male), same collection data as DHMECN 4132, 18 January 2010, collected by Marco Reyes-Puig, and Michael Harvey; DHMECN 11543 (juvenile male), Buenaventura Reserve, 3.667 S, 79.766 W, 1,000 m, 31 December 2014, collected by Juan Carlos Sánchez, Karem López, Luis Oyagata, and Paúl Guerrero; JMG 0484 (adult male), 0485 (adult female), Buenaventura Lodge, 3.653 S, 79.768 W, 520 m, 6 January 2017, collected by Paulina Romero.

Diagnosis. The new species belongs to the *Megaloa* clade of the *latifrons* series of *Dactyloa* (Castañeda & de Queiroz 2013; Prates *et al.* 2020) based on the phylogenetic tree presented in this study. *Anolis nemonteae* sp. nov. differs from most species of the *punctatus*, *heterodermus*, and *nasofrontalis* series (Castañeda & de Queiroz 2013; Prates *et al.* 2020) in having relatively smaller head scales; from the *roquet* series (Castañeda & de Queiroz 2013) in possessing supraorbital semicircles separated from each other and the interparietal separated from the supraorbital semicircles; and from the *aequatorialis* series (Castañeda & de Queiroz 2013; Prates *et al.* 2020) in having wider toepads and larger dorsal head scales.

The new species is most similar in external morphology to the other members of the *latifrons* series (*A. agassizi* Stejneger 1900, *A. apollinaris* Boulenger 1919, *A. brooksi* Barbour 1923, *A. casildae* Arosemena, Ibáñez & de Sousa 1991, *A. danieli* Williams 1988, *A. fraseri, A. frenatus* Cope 1899, *A. ginaelisae* Lotzkat, Hertz, Bienentreu & Köhler 2013, *A. ibanezi* Poe, Latella, Ryan & Schaad 2009b, *A. insignis* Cope 1871, *A. kathydayae* Poe & Ryan 2017, *A. kunayalae*, *A. latifrons* Berthold 1846, *A. limon* Velasco & Hurtado-Gómez 2014, *A. maculigula* Williams 1984a, *A. maia* Batista, Vesely, Mebert, Lotzkat & Köhler 2015, *A. microtus* Cope 1871, *A. mirus* Williams 1963, *A. parilis*, *A. princeps* Boulenger 1902, *A. propinquus* Williams 1984b, *A. purpurescens* Cope 1899, *A. savagei* Poe & Ryan 2017, and *A. squamulatus* Peters 1863). *Anolis nemonteae* can readily be distinguished from *A. agassizi, A. apollinaris, A. casildae, A. frenatus, A. ginaelisae, A. ibanezi, A. latifrons, A. limon, A. maculigula, A. maia, A. princeps, A. purpurescens*, and *A. squamulatus* by having shorter legs not reaching ear when adpressed against body (legs reaching to ear or beyond when adpressed against body); from *A. purpurescens, A. ibanezi, A. maia* and *A. limon* further by having a green-brown dorsal background (green); from *A. danieli* and *A. propinquus* by lacking elongated superciliaries (one elongated superciliary); from *A. brooksi, A. insignis, A. microtus*, *A. savagei,* and *A. kathydayae*, all from Costa Rica and Panama, by possessing weakly keeled ventral scales (smooth); from *A. ginaelisae* (Panama) by lacking enlarged postcloacal scales in males (present); from *A. kunayalae, A. mirus* and *A. parilis* by having a wide toe pad on fourth toe (narrow toe pad), subdigital pad under phalanx III projecting above the proximal end of phalanx IV (subdigital pad continuous or indistinct), 21–23 lamellae under phalanges II and III of fourth toe (11–15 lamellae), and distal phalanx including claw equal or smaller than phalanges II and III combined (longer distal phalanx; see Fig. 1 of Williams 1963).

FIGURE 1. Head of the preserved holotype (QCAZ 14595) of *Anolis nemonteae* **sp. nov.** in dorsal (top), lateral (middle), and ventral (bottom) views. Photographs by M. Masache. Scale bar = 10 mm.

Anolis nemonteae sp. nov. is most similar morphologically to *A. fraseri* in having a large body size (SVL > 85 mm), a green-brown dorsal background, reddish brown iris, smooth head scales, weakly keeled ventral scales, and 21–23 (18–24 in *A. fraseri*) lamellae under phalanges II and III of fourth toe. The new species can be distinguished from *A. fraseri* (character states in parentheses) by having a creamish white dewlap skin with black blotches longitudinally arranged along yellow stripes in females (female dewlap orangish yellow anteriorly, without black blotches); bluish white dewlap skin with yellowish white scales and gold apicogorgetal scales in males (creamish white skin with yellow or greenish white scales; Fig. 5); dark brown dots on neck laterally and dorsally (neck dots absent, large dark blotches might be present; Figs 3 and 5); 7–11, mean = 9.29±1.25 SD scales between second canthals, (6–10, 7.72±1.02, z = 2.737, p = 0.006); 3–4, 3.29±0.49 scales between supraorbital semicircles (2–4, 2.68±0.57, z = -2.281, p = 0.023), 7–10, 8.86±1.07 supralabials counted to a point below center of eye (7–9, 7.69±0.55, z = 2.845, p = 0.004); 21–23, 21.71±0.95 lamellae under phalanges II–III of fourth toe (18–23, 20.32±1.09, z = -2.799, p = 0.005), snout length/SVL, 0.116–0.122, 0.119±0.002 (0.112–0.133, 0.123±0.005, t = 2.664, p = 0.013) interparietal length/SVL, 0.016–0.028, 0.023±0.004 (0.011–0.027, 0.018±0.004, t = -2.750, p = 0.011), humerus length/SVL, 0.131–0.184, 0.159±0.016 (0.155–0.204, 0.171±0.011, t = 2.380, p = 0.025), foot length/SVL 0.259–0.282, 0.272±0.009 (0.262–0.310, 0.287±0.014, t = 2.627, p = 0.014), and fourth toe length/SVL 0.151–0.177, 0.162±0.009 (0.168–0.203, 0.181±0.010, t = 4.287, p < 0.001). Furthermore, *Anolis nemonteae* sp. nov. differs from *A. fraseri* in lacking enlarged postcloacals in males (present, sometimes inconspicuous), and genetic distances between these species range between 0.03–0.05 (*ND2*) and 0.05–0.06 (*COI*). In addition to the above diagnostic traits, the unique male and female dewlap color patterns of *A. nemonteae* sp. nov. distinguish it from all other Ecuadorian *Anolis* of the *Megaloa* clade (Fig. 5).

Description of the holotype (scores for paratypes in parentheses). Snout to vent length 92.4 mm (88.4−115.2 mm); tail length 191.5 mm (200.6−263.1 mm); head length 23.9 mm (23.6−31.3 mm); head width 14.7 mm (14.8−16.9 mm); head height 11.9 mm (12.1−14.4 mm); snout length 11.3 mm (10.4−13.4 mm); interorbital length 4.8 (4.4−5.8 mm); interparietal length 2.3 mm (1.8−2.9 mm); ear height 2.1 mm (1.7−2.5 mm); femur length 22.6 mm (20.5−27.4 mm); tibia length 18.6 mm (17.1−22.7 mm); foot length 25.6 mm (24.2−29.8 mm); humerus length 17.0 mm (13.5−19.2 mm); ulna length 13.3 mm (11.6−16.0 mm); hand length 14.5 mm (13.7−16.5 mm); fourth toe length 16.4 mm (14.3−19.2 mm); fourth toe width 1.8 mm (1.9−2.6 mm); dewlap length 28.8 mm (29.5−49.9 mm); and dewlap height 9.8 mm (6.3−15.2 mm).

Head scales in supraocular disc and frontal region smooth (smooth or rugose); eleven (7−10) scales between second canthals; seven (6−9) scales bordering the rostral posteriorly; circumnasal separated by one (1−2) scale from rostral; supraorbital semicircles separated by three (3−4) scales; supraocular disc with four (3–4) enlarged scales; supraocular edge continuous; superciliaries in two series: first series without rectangular superciliary anteriorly (sometimes present) followed by gradually smaller scales, and second series with squarish scales; five (6−7) loreal rows; >15 loreal scales; midsnout without parallel scale rows (absent or weakly present); rostral with smooth dorsal edge; frontal region of head with a depression; rostral even with mental (even or slight overlapping); interparietal larger (smaller or larger) than ear opening, separated by three (1−3) scales from semicircles; ear oval with normal edge; transparent scales in lower eyelids absent; preoccipital scale absent; suboculars in contact with supralabials; ten (7−9) supralabials counted up to a point below center of eye; six (5−7) postmentals; no enlarged sublabials in contact with infralabials; mental divided partially; mental extending farther back posteriorly than rostral along edge of mouth (even or rostral extending farther than mental or mental extending farther back posteriorly than rostral); and posterior edge of mental straight (straight or slight concave).

Low nuchal crest formed by continuous series of small conical scales; low middorsal crest formed by continuous series of triangular scales (crest present in adults of both sexes); dorsal scales slightly keeled anteriorly and smooth posteriorly (smooth or keeled anteriorly and keeled or smooth posteriorly); two (absent or two) vertebral rows slightly larger than flank scales; eight (9−11) middorsal scales in a longitudinal segment representing 5% of SVL; flank scales smooth (smooth, rugose or weakly keeled), homogeneous in size, and barely separated by skin; ventral scales smaller than dorsals (ventrals larger than dorsals), slightly keeled, subimbricate, with round posterior edge (round or rectangular), and arranged in diagonal rows; ten (7−9) midventral scales in a longitudinal segment representing 5% of SVL; inconspicuous axillary pocket present (present or absent).

Toepads slightly overlapping distal phalanx in all toes; twenty-one (22−23) lamellae under phalanges II and III of fourth toe; supradigitals with multiple keels; tail crest absent; tail round (round or laterally compressed), with a single row of middorsal scales; *insolitus* tail (Poe 2004) absent; enlarged postcloacal scales absent (in males and females); hindlimb reaching posterior to ear when adpressed against body.

Nuchal and dorsal folds present; dewlap large, extending posteriorly behind forelimbs (in males and females), with five (4−6) longitudinal rows of four (3–5) elongate scales each, smaller than ventrals, and separated by naked skin.

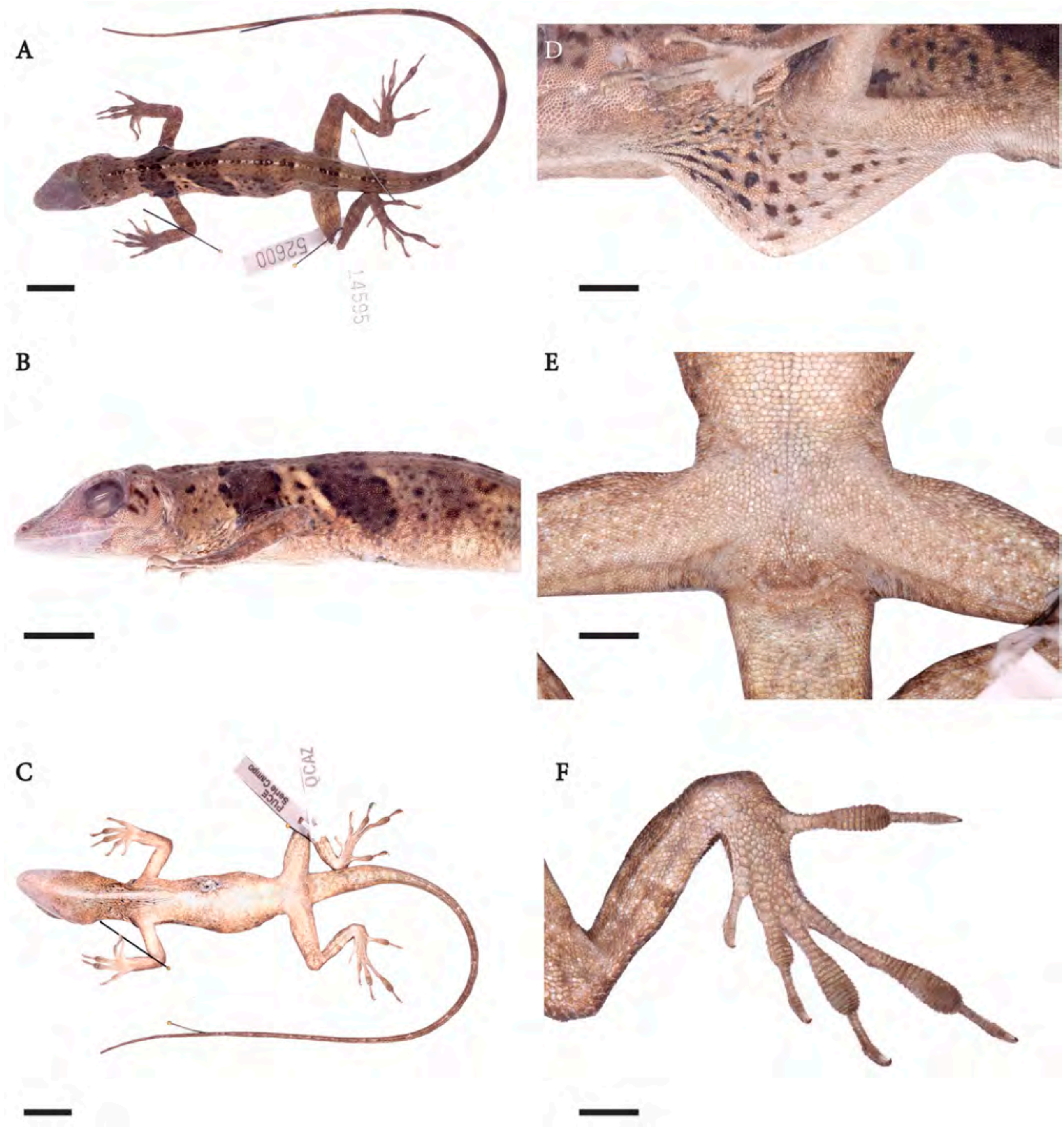

FIGURE 2. Preserved holotype of *Anolis nemonteae* **sp. nov.** (QCAZ 14595) in dorsal (A), lateral (B), and ventral (C) views, with close-ups of dewlap (D), pelvic region (E), and right foot (F). Photographs by M. Masache. Scale bars = 10 mm (A, B, C) and 5 mm (D, E, F).

Inter- and intraspecific variation in morphological characters in *Anolis nemonteae* is presented in Tables 2 and 3, respectively.

Color in life. Holotype, adult female QCAZ 14595 (Fig. 3A, B, C, undisturbed color pattern): dorsum of head, body, limbs and tail pale yellowish green; dorsum of body with three broad, dark brown transverse bands extending onto flanks; dorsal surfaces of limbs and tail with dark brown transverse bands; palpebral scales yellowish green; flanks of neck and body with dark brown spots; ventral aspect of head, body, limbs, and tail cream; iris pale reddish brown; throat lining black; tongue yellow; edge of mouth including jaw hinges white; dewlap skin cream with black blotches, mostly arranged more or less longitudinally along yellow stripes (Fig. 5B); scales of dewlap yellowish white.

TABLE 2. Summary of lepidosis, ratios, measurements (mm) and color patterns of *Anolis nemonteae* sp. nov. and *A. fraseri*. For each quantitative character, the t-value, z-value, and corresponding *p*-values ($p < 0.05$ in bold and *; $p < 0.01$ in bold and **) are given. Range and sample size (N) followed by mean±standard deviation are given.

Character	*A. nemonteae* sp. nov.	*A. fraseri*	t-value	*p*	z-value	*p*
Scales between second canthals	7–11 (7) 9.29±1.25	6–10 (25) 7.72±1.02	-	-	-2.737	0.006**
Postrostrals	6–9 (7) 7.14±1.07	5–9 (22) 7.05±1.05	-	-	-0.027	0.978
Scales between supraorbital semicircles	3–4 (7) 3.29±0.49	2–4 (22) 2.68±0.57	-	-	-2.281	**0.023***
Loreal rows	5–7 (7) 5.57±0.79	4–7 (22) 5.73±0.77	-	-	-0.634	0.526
Scales between interparietal and semicircles	2–3 (7) 2.86±0.38	2–5 (22) 3.36±0.73	-	-	-1.778	0.075
Supralabials to below center of eye	7–10 (7) 8.86±1.07	7–9 (26) 7.69±0.55	-	-	-2.845	**0.004****
Postmentals	5–7 (7) 6.00±0.58	4–8 (26) 5.96±0.82	-	-	-0.151	0.880
Lamellae under phalanges II–III of fourth toe	21–23 (7) 21.71±0.95	18–23 (22) 20.32±1.09	-	-	-2.799	**0.005****
Middorsals in 5% SVL	8–11 (7) 9.71±1.11	8–12 (26) 9.31±1.05	-	-	-0.964	0.335
Midventrals in 5% SVL	7–10 (7) 8.86±1.07	7–10 (26) 8.42±0.86	-	-	-1.172	0.241
Head length/SVL	0.247–0.272 (7) 0.260±0.009	0.246–0.295 (22) 0.272±0.014	1.984	0.057	-	-
Head width/SVL	0.143–0.172 (7) 0.156±0.010	0.142–0.175 (22) 0.155±0.007	-0.092	0.927	-	-
Head height/SVL	0.123–0.148 (7) 0.130±0.009	0.113–0.146 (22) 0.131±0.007	0.302	0.765	-	-
Snout length/SVL	0.116–0.122 (7) 0.119±0.002	0.112–0.133 (22) 0.123±0.005	2.664	**0.013***	-	-
Interorbital length/SVL	0.040–0.061 (7) 0.053±0.007	0.048–0.062 (22) 0.054±0.004	-	-	-0.102	0.919
Interparietal length/SVL	0.016–0.028 (7) 0.023±0.004	0.011–0.027 (22) 0.018±0.004	-2.750	**0.011***	-	-
Ear height/SVL	0.017–0.024 (7) 0.020±0.003	0.012–0.027 (22) 0.020±0.003	-0.182	0.857	-	-
Humerus length/SVL	0.131–0.184 (7) 0.159±0.016	0.155–0.204 (22) 0.171±0.011	2.380	**0.025***	-	-
Ulna length/SVL	0.120–0.144 (7) 0.134±0.009	0.114–0.157 (22) 0.134±0.011	0.152	0.880	-	-
Hand length/SVL	0.135–0.162 (7) 0.146±0.010	0.122–0.165 (22) 0.146±0.011	-0.015	0.988	-	-
Femur length/SVL	0.229–0.245 (7) 0.236±0.006	0.211–0.265 (22) 0.235±0.014	-0.269	0.790	-	-
Tibia length/SVL	0.188–0.216 (7) 0.201±0.009	0.180–0.239 (22) 0.206±0.012	1.012	0.321	-	-
Foot length/SVL	0.259–0.282 (7) 0.272±0.009	0.262–0.310 (22) 0.287±0.014	2.627	**0.014***	-	-
Fourth toe length/SVL	0.151–0.177 (7) 0.162±0.009	0.168–0.203 (22) 0.181±0.010	4.287	**0.000****	-	-
Fourth toe width/SVL	0.019-0.023 (7) 0.021±0.001	0.015–0.025 (22) 0.020±0.002	-0.117	0.908	-	-
Tail length/SVL	2.039–2.515 (7) 2.249±0.189	2.154–2.518 (18) 2.336±0.097	1.156	0.284	-	-
Snout-vent length	88.4–115.2 (7) 100.49±8.72	93.4–120.5 (28) 105.79±8.35	1.49	0.145	-	-
Dewlap color in males	Solid bluish white skin; yellowish white scales; golden apicogorgetals.	Solid creamish white skin; yellowish or greenish white scales.	-	-	-	-
Dewlap color in females	Cream with black blotches longitudinally arranged along yellow stripes; yellowish white scales.	Cream without black blotches, orangish yellow skin anteriorly; greenish yellow scales.	-	-	-	-
Maximum SVL	115	120	-	-	-	-

TABLE 3. Sexual variation in lepidosis, ratios, and measurements (mm) in *Anolis nemonteae* sp. nov.; range followed by mean and standard deviation are given.

Character	Males N = 3	Females N = 4
Scales between second canthals	9, 9.00±0.00	7–11, 9.50±1.73
Postrostrals	6–9, 7.00±1.73	7–8, 7.25±0.50
Scales between supraorbital semicircles	3, 3.00±0.00	3–4, 3.50±0.58
Loreal rows	5–6, 5.33±0.58	5–7, 5.75±0.96
Scales between interparietal and semicircles	3, 3.00±0.00	2–3, 2.75±0.50
Supralabials to below center of eye	8–10, 9.00±1.00	7–10, 8.75±1.26
Postmentals	5–6, 5.67±0.58	6–7, 6.25±0.50
Lamellae under phalanges II–III of fourth toe	21–23, 22.33±1.16	21–22, 21.25±0.50
Middorsals in 5% SVL	10–11, 10.67±0.58	8–10, 9.00±0.82
Midventrals in 5% SVL	9–10, 9.33±0.58	7–10, 8.50±1.29
Head length/SVL	0.250–0.272, 0.263±0.012	0.247–0.267, 0.258±0.008
Head width/SVL	0.143–0.162, 0.153±0.009	0.146–0.172, 0.158±0.011
Head height/SVL	0.123–0.126, 0.125±0.002	0.123–0.148, 0.134±0.011
Snout length/SVL	0.116–0.120, 0.119±0.002	0.118–0.122, 0.120±0.002
Interorbital length/SVL	0.040–0.055, 0.049±0.008	0.052–0.061, 0.056±0.004
Interparietal length/SVL	0.016–0.022, 0.020±0.004	0.023–0.028, 0.026±0.003
Ear height/SVL	0.017–0.024, 0.020±0.004	0.017–0.023, 0.020±0.002
Humerus length/SVL	0.158–0.167, 0.161±0.005	0.131–0.184, 0.158±0.022
Ulna length/SVL	0.120–0.139, 0.128±0.010	0.131–0.144, 0.138±0.006
Hand length/SVL	0.141–0.149, 0.145±0.004	0.135–0.162, 0.147±0.014
Femur length/SVL	0.229–0.238, 0.233±0.004	0.232–0.245, 0.238±0.008
Tibia length/SVL	0.188–0.203, 0.196±0.007	0.193–0.216, 0.205±0.010
Foot length/SVL	0.259–0.276, 0.270±0.010	0.260–0.282, 0.273±0.009
Fourth toe length/SVL	0.151–0.167, 0.159±0.008	0.152–0.177, 0.164±0.011
Fourth toe width/SVL	0.019–0.023, 0.021±0.002	0.019–0.021, 0.020±0.001
Tail length/SVL	2.039–2.515, 2.247±0.244	2.073–2.497, 2.251±0.179
Snout-vent length	98.4–115.2, 106.07±8.49	88.4–102.9, 96.30±7.03
Maximum SVL	115	103
Dewlap color	Solid bluish white skin; yellowish white scales; gold apicogorgetal scales	Creamish white skin with black blotches arranged longitudinally on yellow stripes; yellowish white scales

When stressed, adult females QCAZ 14594 and JMG0485 (Fig. 3D) turned dorsal background of head, body, limbs and tail yellowish brown or dark brown, respectively.

Juvenile female QCAZ 14431 (Fig. 3E, stressed specimen): general color pattern similar to holotype, but dewlap skin dirty white with broad yellow stripes and elongate black blotches; gorgetals, sternals and marginals yellowish white; ventral aspect of head, body, limbs, and tail grayish cream with brown dots.

Hatchling female QCAZ 14660 (Fig. 3F, stressed specimen): general color pattern similar to female QCAZ 14594, but dorsum of head, body, limbs and tail pale brown; dorsum of body with four dark brown transverse bands extending onto flanks.

Adult male QCAZ 14596 (Fig. 3G, H, I, undisturbed color pattern): dorsum of body, limbs, and tail brown; dorsum of head light grayish turquoise with orange and red spots; dorsum of body with four broad, dark brown transverse bands extending onto flanks, of which the two posteriormost merge ventrally; second anteriormost broad band bordered anteriorly by yellowish cream line; dorsum of limbs and tail with dark brown transverse bands; palpebral scales yellow; flanks of neck and body with dark brown spots; ventral aspect of head, body, limbs, and tail cream; iris reddish brown; throat lining black; tongue yellow; edge of mouth including jaw hinges white; dewlap skin solid bluish white with yellowish white scales and golden apicogorgetals (Fig. 5A). When stressed, adult male JMG 0484 (Fig. 3J, K) turned background of body, limbs, and tail light brown.

Color in preservative. In preservative, the holotype (QCAZ 14595) has a light brown background (Figs 1, 2); otherwise, the color patterns in life (see above) and preservative are similar. Adult male QCAZ 14596 (Fig. 4 A, B, left side): dorsum of body, limbs, and tail brown; dorsum of body with four dark brown transverse broad bands extending onto flanks; dorsum of limbs and tail with dark brown transverse bands; flanks of neck and body with dark brown spots; ventral aspect of head, body, and limbs grayish cream; tail dark brown with cream base; dewlap skin solid white with cream scales.

Adult males JMG 0484 and DHMECN 7687 (Fig. 4 A, B, center and right side): general color pattern similar to male QCAZ 14596, but vertebral region of dorsum with dark brown spots; dorsum of DHMECN 7687 with three brown transverse bands of which the second one is bordered anteriorly by a cream stripe, which is discontinuous medially, where each half projects anteriorly.

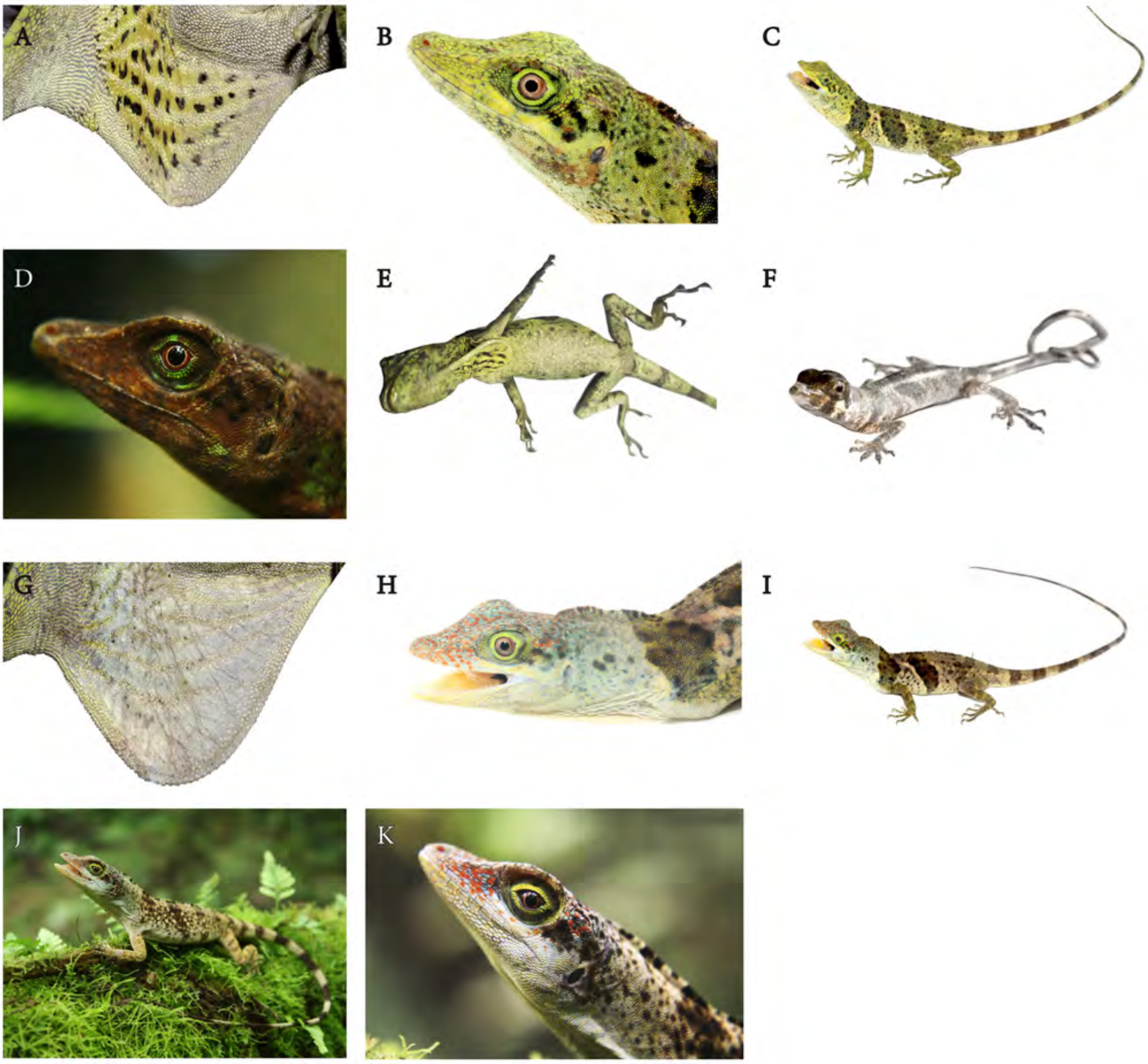

FIGURE 3. Variation of color in life of *Anolis nemonteae* **sp. nov.** Adult female QCAZ 14595 (holotype, A, B, C); adult female JMG 0485 (D); juvenile female QCAZ 14431 (E); hatchling female QCAZ 14660 (F); adult male QCAZ 14596 (G, H, I); adult male JMG 0484 (J, K). Photographs by AEN (A, B, C, G, H, I), FAV (E), P. Pintanel (F) and P. Romero (D, J, K).

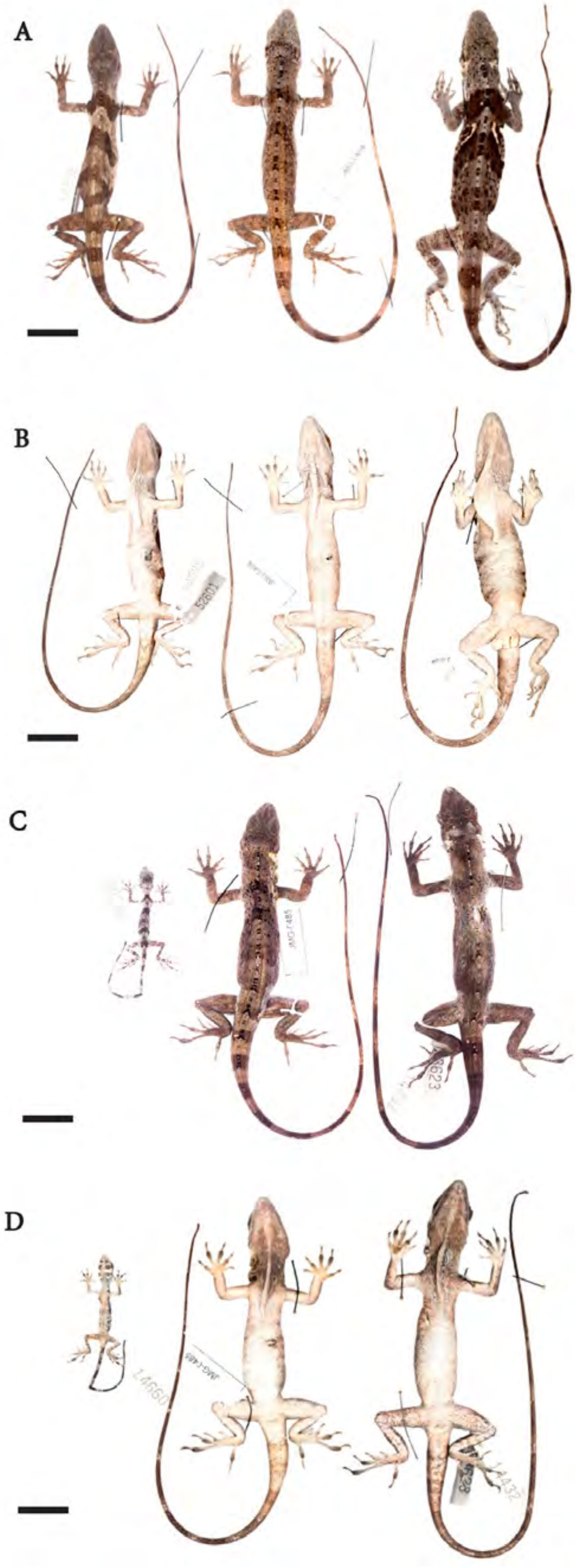

FIGURE 4. Variation of color in preservative of *Anolis nemonteae* **sp. nov.** Dorsal (A) and ventral (B) views of males (SVL = 98.4 mm, QCAZ 14596 left; SVL = 104.6 mm, JMG 0484 center; SVL = 115.2 mm, DHMECN 7687 right); and dorsal (C) and ventral (D) views of females (SVL = 35.5 mm, QCAZ 14660 left; SVL = 88.4 mm, JMG 0485 center; SVL = 101.5 mm, QCAZ 14432 right). Photographs by M. Masache. Scale bars = 10 mm.

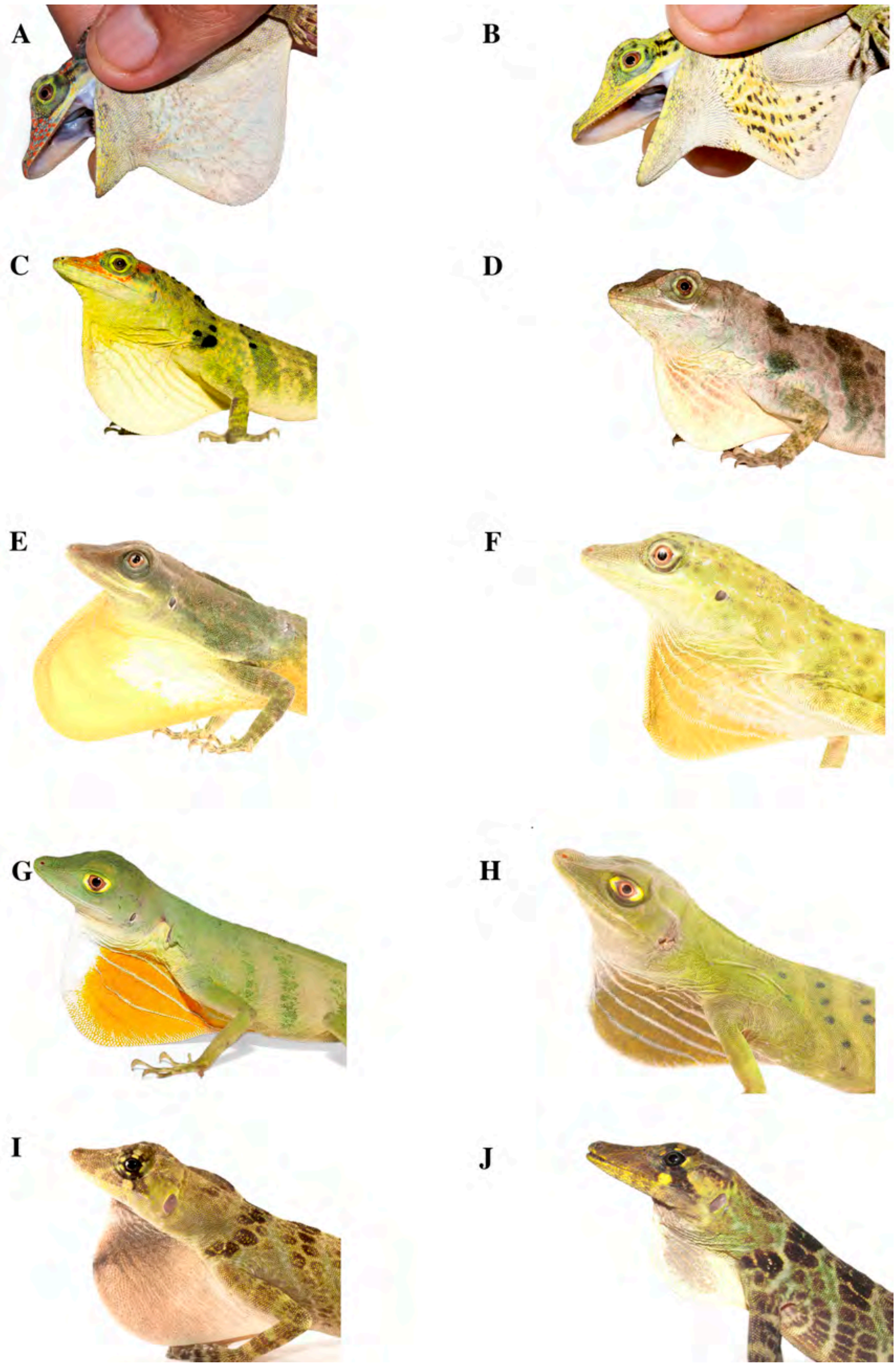

FIGURE 5. Dewlaps of males and females in five species of the *Megaloa* clade from Ecuador. *Anolis nemonteae* **sp. nov.** adult male (QCAZ 14596, A) and adult female (QCAZ 14595, B); *A. fraseri* adult male (QCAZ 6862, C) and adult female (QCAZ 11864, D); *A. parilis* adult male (QCAZ 15047, E) and adult female (QCAZ 15052, F); *A. purpurescens* adult male (QCAZ 4734, G) and adult female (QCAZ 10557, H); *A. princeps* adult male (QCAZ 16895, I) and adult female (QCAZ 6892, J). Photographs by AEN (A, B), FAV (C, J), D. Quirola (D, E, F), OTC (G, H), and D. Núñez (I).

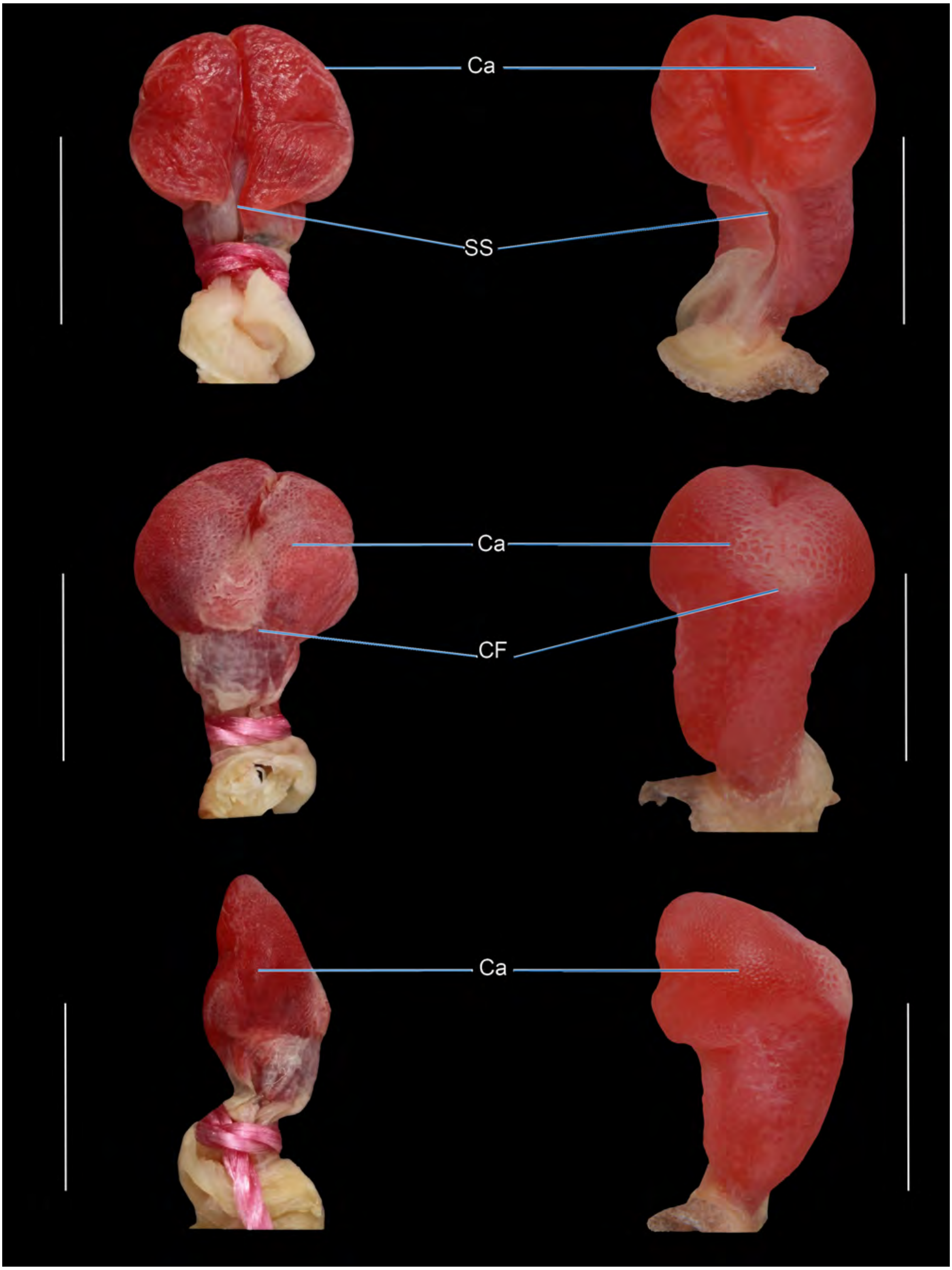

FIGURE 6. Hemipenes of *Anolis nemonteae* **sp. nov.** (DHMECN 7687, SVL = 107.7 mm, left column) and *A. fraseri* (QCAZ 10212, SVL = 111.3 mm, right column) in sulcate (top), asulcate (middle) and lateral (bottom) views. Abbreviations: Ca = calyces, CF = crotch flap, SS = sulcus spermaticus. Photographs by MYM. Scale bars = 5 mm.

Adult female JMG 0485 (Fig. 4 C, D, center): dorsum of head, body, limbs and tail brown; dorsum of body with three broad, dark brown transverse bands extending onto flanks; vertebral region of dorsum with dark brown spots; dorsum of limbs and tail with dark brown transverse bands; flanks of neck and body with dark brown spots; ventral aspect of head, body, limbs, and tail dirty cream; dewlap skin creamish white with black blotches; scales of dewlap creamish white.

Adult female QCAZ 14432 (Fig. 4 C, D, right side) differs from JMG 0485 in having faint dorsal transverse bands and small dark brown spots on limbs ventrally. Female hatchling QCAZ 14660 (Fig. 4 C, D, left side) differs in having four dark brown transverse bands (discontinuous medially) on ventral aspect of head and dark brown transverse bands ventrally on limbs.

Hemipenis. Partially everted hemipenis small (7.3 mm total length, 2.9 mm truncus length) and slightly bilobate; sulcus spermaticus unforked, bordered by well-developed lips and opening into a single, smooth apical area; lobes with small calyces on asulcate side; fleshy projection on lobular crotch (crotch flap) on asulcate surface; truncus with transverse and lateral folds (Fig. 6).

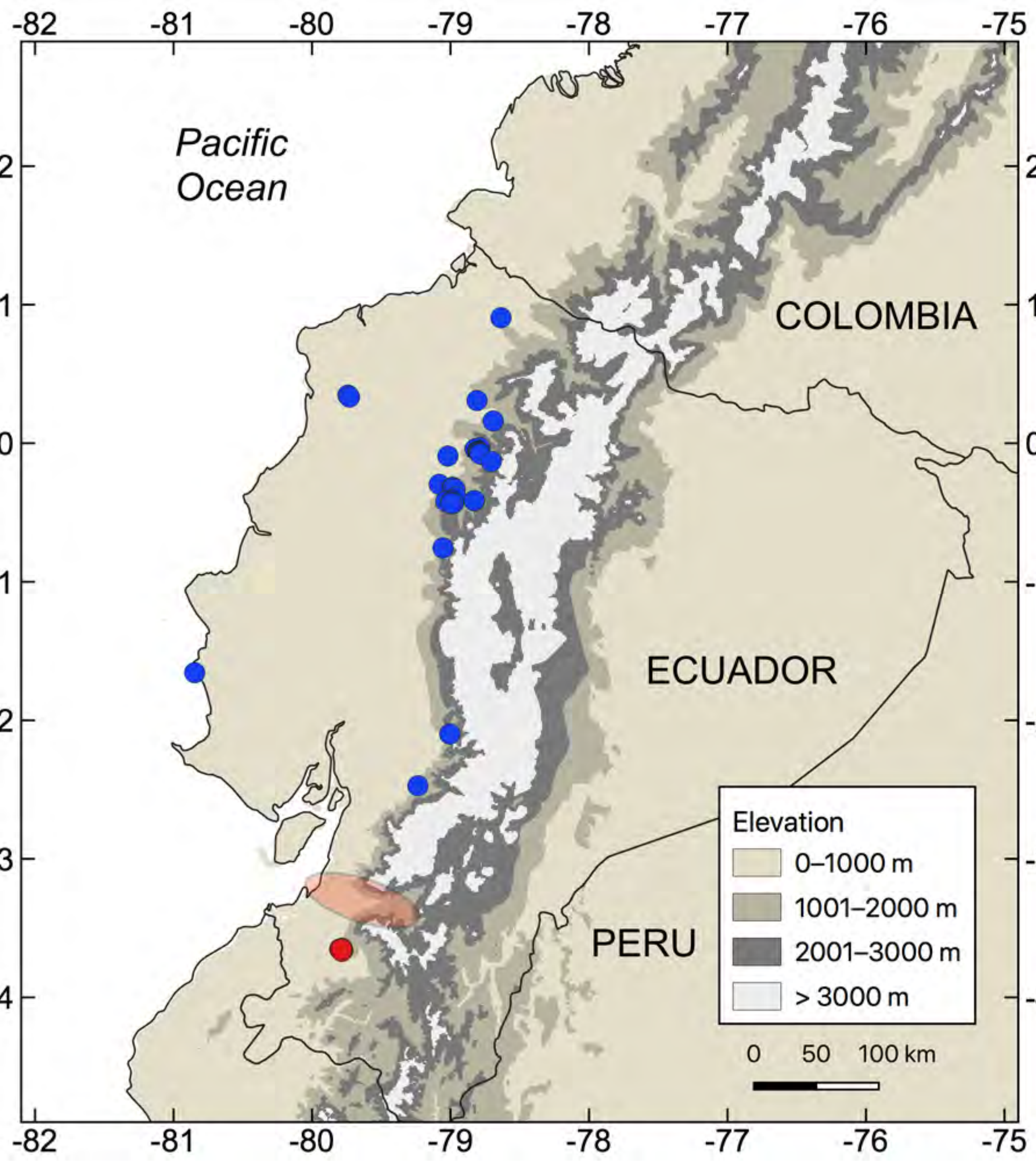

FIGURE 7. Distribution of *Anolis nemonteae* **sp. nov.** (red circles) and *A. fraseri* (blue circles) in Ecuador. The approximate location of the Jubones river basin is marked with a red ellipse.

Distribution and natural history. *Anolis nemonteae* occurs on the Pacific slopes of the Andes in southern Ecuador, El Oro province, between 372−1,000 m (Fig. 7). This species occurs in the Evergreen Foothills Montane Forest of Catamayo-Alamor (Ministerio del Ambiente del Ecuador 2013). Specimens of *Anolis nemonteae* were collected mainly in secondary forest and along the edge of roads (Fig. 8). All individuals were found at night between 20:00 and 01:00 h sleeping horizontally on branches of trees, or leaves of bananas or Panama hat plants, 2.5–6.9 m above ground. A male and a female (JMG 0484, 0485) were found sleeping on banana leaves 10 m away from each other, 2.5 m above the ground. *Anolis nemonteae* occurs in sympatry with *A. binotatus* Peters 1863 and *A. fasciatus* at the type locality (Yánez-Muñoz *et al.* 2013, Garzón *et al.* 2019).

FIGURE 8. Entrance to Buenaventura Reserve, type locality of *Anolis nemonteae* **sp. nov.**, showing its general habitat. Photograph by AEN.

A captive female (QCAZ 14594 [tissue sample], SVL = 93.21 mm) that was subsequently released laid one egg (22.3 x 14.4 mm) on 30 January 2016. The egg was incubated in perlite at 19°C and 85% of relative humidity. After an incubation period of 129 days, a female (Fig. 3F; QCAZ 14660, SVL = 32.9 mm, weight = 2.3 g) hatched.

Conservation. The known distribution area of *Anolis nemonteae* has suffered from dramatic deforestation (Tapia-Armijos *et al.* 2015). However, most individuals of *A. nemonteae* were collected within the Buenaventura Reserve, which suggests that at least some of its populations are well protected. Because of the small known distribution (Fig. 7) and lack of additional data, we suggest assigning *A. nemonteae* to the Data Deficient category according to IUCN (2012) guidelines.

Etymology. The specific epithet *nemonteae* is a noun in the genitive case and is a patronym for Nemonte Nenquimo, indigenous activist who led a successful campaign and legal action that protected 500,000 acres of Amazonian rainforest and Waorani territory from oil extraction in Ecuador. Nemonte means 'many stars' in Wao Tereo language. Nemonte Nenquimo's work has been recognized worldwide. In 2020, she was awarded the prestigious Goldman Prize and was listed among the 100 most influential people of the year by the Time Magazine. Here we honor Nemonte Nenquimo for her braveness and determination to protect natural forests and their inhabitants.

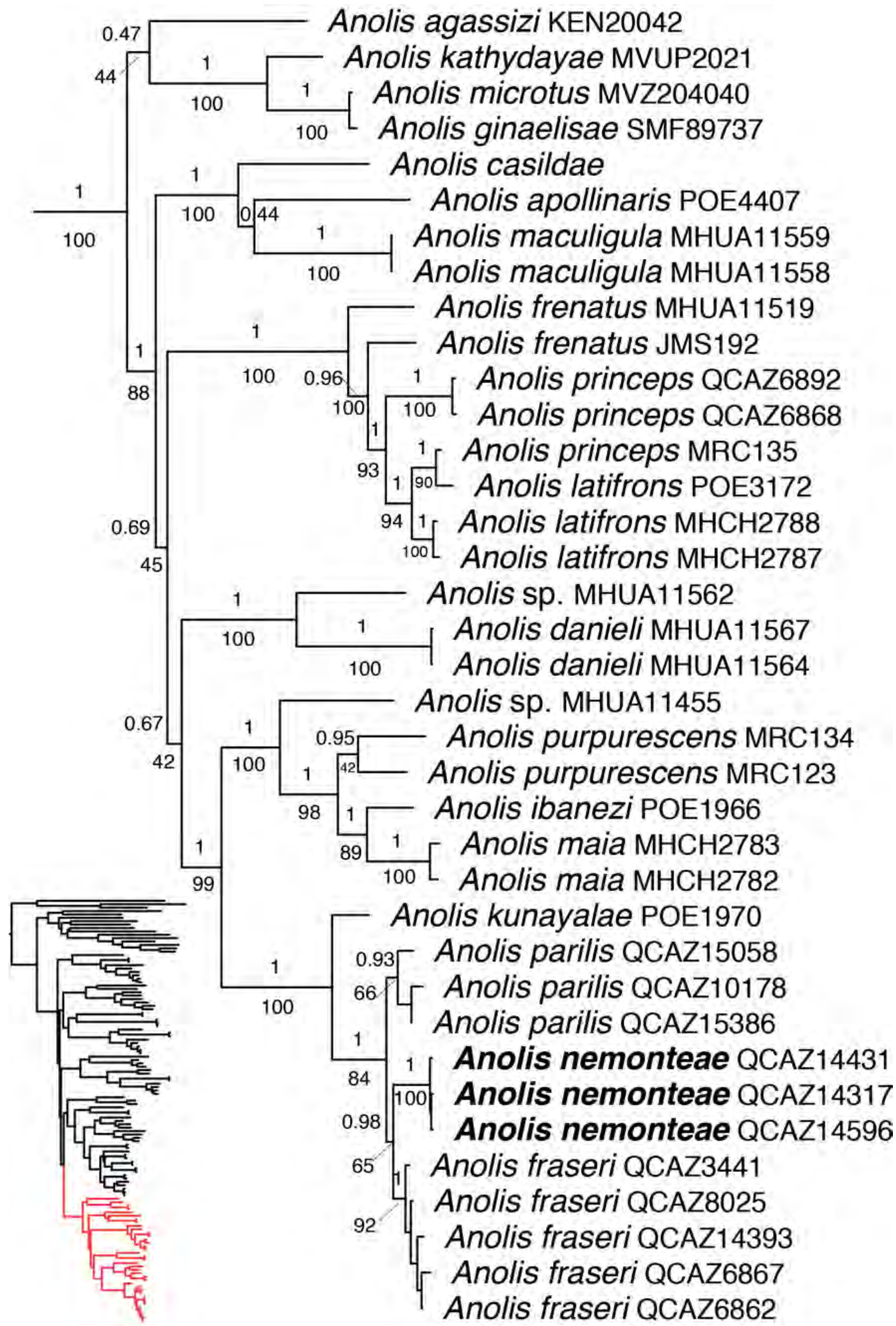

FIGURE 9. Phylogeny of the clade *Dactyloa*, with a close-up of the *latifrons* series as defined by Castañeda & de Queiroz (2013) and Prates *et al.* (2020). Maximum clade credibility tree obtained from a Bayesian analysis of 125 taxa and 3,221 characters. Numbers above branches are Bayesian posterior probability (PP) values and those below branches are ML bootstrap support (BS) values. GenBank accession numbers along with locality data are presented in Table 1 for newly sequenced specimens.

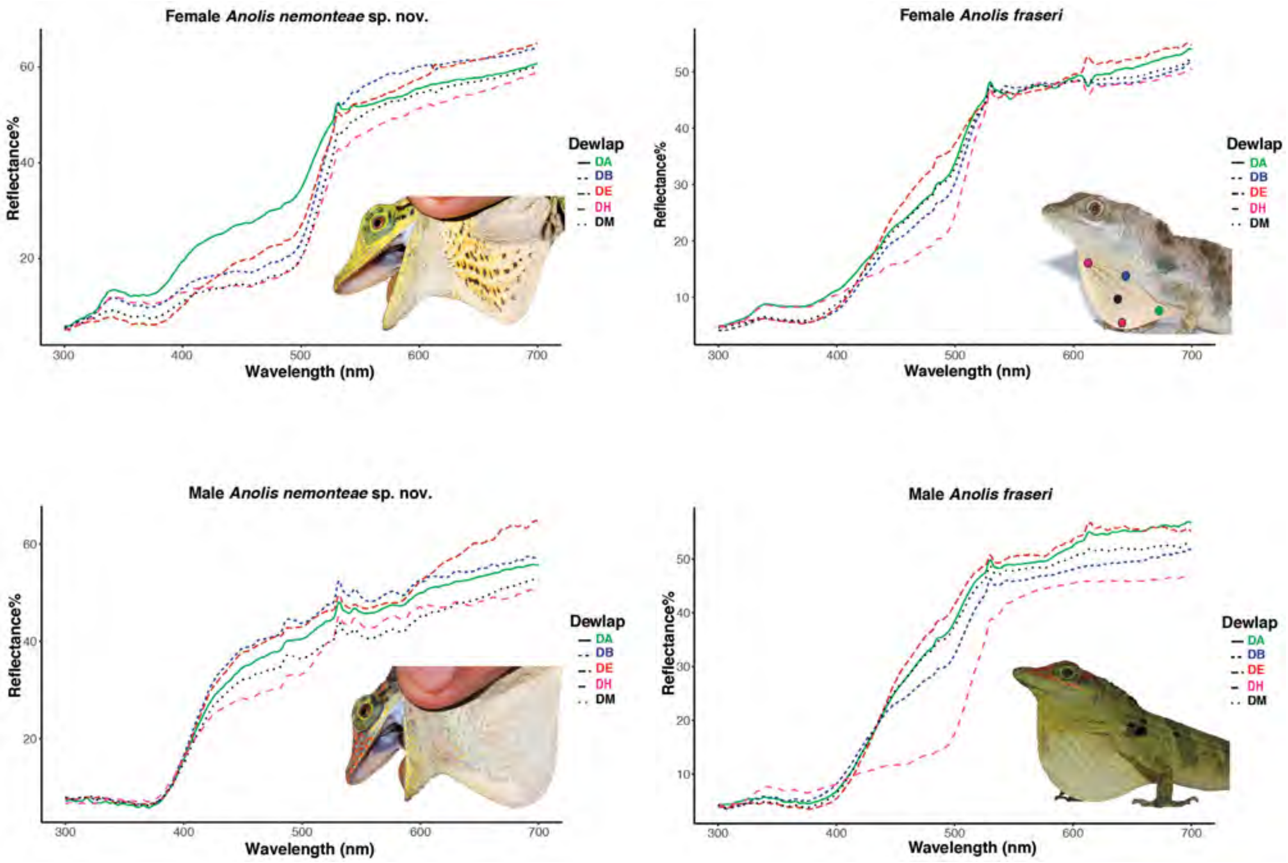

FIGURE 10. Reflectance of the gular sac in males and females of *Anolis nemonteae* **sp. nov.** and *A. fraseri*. Measured regions are gular sac base 'DB', center 'DM', and edge 'DE', as well as regions close to the head 'DH' and the abdomen 'DA'. Photographs by AEN (male and female of *A. nemonteae* sp. nov.), D. Quirola (female of *A. fraseri*) and FAV (male of *A. fraseri*).

Phylogenetic relationships. Data partitions and models of evolution are presented in Table 4. Both ML and Bayesian analyses positioned *Anolis nemonteae* sp. nov. within a clade highly congruent with the *Megaloa* clade of Castañeda & de Queiroz (2013) with maximum support (Fig. 9). The difference to the *Megaloa* clade as originally defined is that *Anolis ibanezi*, *A. kunayalae*, and *A. parilis* were also included (Fig. 9). As expected, *A. ginaelisae* and *A. maia*, both described more recently, were also included in this clade (Lotzkat *et al.* 2013, Batista *et al.* 2015). Both ML and Bayesian tree topologies for the *Megaloa* clade are identical, except for the sister species of *A. maculigula* (*A. casildae* and *A. apollinaris*, respectively). The sister species of *A. nemonteae* sp. nov. is *A. fraseri* (PP = 0.98, BS = 65), and together they form a clade sister to *A. parilis* (PP = 1, BS = 84).

Interspecific genetic distances among sampled species of the *Megaloa* clade range from 0.02 (*A. fraseri*/*A. parilis*, *A. latifrons*/*A. princeps*) to 0.23 (*A. latifrons*/*A. microtus*, *A. microtus*/*A. princeps*) for *ND2* and from 0.02 (*A. latifrons*/*A. princeps*) to 0.19 (*A. kathydayae*/*A. fraseri*, *A. maculigula*/*A. nemonteae*, *A. parilis*/*A. maculigula*) for *COI*. Genetic distances between *Anolis nemonteae* and *A. fraseri* are 0.03–0.05 (*ND2*) and 0.05–0.06 (*COI*).

Dewlap reflectance. The dewlap of *Anolis nemonteae* reflects light in the visible spectrum in both sexes (Fig. 10). Reflectance starts increasing significantly at around 400 nm in males and 500 nm in females, and it reaches a peak (~50%) at ~530 nm. Light is also reflected near the ultraviolet spectrum (~15% at 320 nm) in females.

Remarks. *Anolis nemonteae* is most similar in morphology to its sister species *A. fraseri*. Even their hemipenes only seem to differ in relative size (smaller in *A. nemonteae*) and in having more pronounced calyces on the asulcate side in *A. fraseri* (Fig. 6), although the variation of these characters should be analyzed with a larger sample size. However, in addition to the differences presented above, the dewlap of males of the new species is different from both sexes of *A. fraseri* in lacking reflectance within the ultraviolet spectrum (Fig. 10). The dewlap of both sexes of *A. fraseri* reflects light with a peak near the ultraviolet spectrum (~10% at 350 nm). Although it has been reported in only a few species of anoles (e.g., Fleishman *et al*. 2009; Torres-Carvajal *et al*. 2018), data on reflectance spectroscopy of dewlaps seems to be informative for species delimitation and should be explored in more detail.

TABLE 4. Data partitions used in phylogenetic analyses. Numbers in parentheses indicate codon position. Number of sites, selected model, number of unique site patterns (USP), variable sites (VS) and parsimony-informative sites (PIS) are indicated.

Partition	sites	model	USP	VS	PIS
ND2 (1)	347	GTR+I+G	296	261	227
ND2 (2)	347	GTR+I+G	226	181	149
ND2 (3)	346	GTR+I+G	345	339	329
tRNAs, *Ol*	412	GTR+I+G	300	238	202
COI (1)	218	SYM+I+G	105	68	57
COI (2)	218	F81+I+G	60	13	8
COI (3)	218	GTR+G	218	217	213
RAG1 (3)	372	HKY+G	268	227	164
RAG1 (1,2)	743	HKY+G	300	238	168
All	3,221	—	2,118	1,782	1,517

Discussion

Anolis nemonteae and its sister species *A. fraseri* occur allopatrically along the Pacific slopes of the Andes and adjacent lowlands in western Ecuador. Their distributions are markedly separated by the Jubones river basin (JRB) in southwestern Ecuador (Fig. 7), which extends from sea level to ~4,000 m covering an area of 4,361 km^2 (Ochoa *et al.* 2014). The JRB has been recognized as the northern limit of the Amotape-Huancabamba Zone, an area with high levels of diversity and endemism for plants (Weigend 2002). Intensive herpetological sampling has led to the discovery of five species of reptiles endemic to JRB—*Holcosus orcesi* Peters, *Phyllodactylus leoni* Torres-Carvajal, Carvajal-Campos, Barnes, Nicholls & Pozo-Andrade, *Stenocercus rhodomelas* Boulenger, *Tantilla insulamontana* Wilson & Mena, *Leptodeira misinawui* Torres-Carvajal, Sánchez-Nivicela, Posse, Celi & Koch—and no records of *A. nemonteae* or *A. fraseri*, which supports the idea that the JRB constitutes a geographical barrier separating these species of anoles. Similarly, the JRB geographically separates the gymnophthalmid lizard *Andinosaura kiziriani* Sánchez-Pacheco, Aguirre-Peñafiel & Torres-Carvajal from its sister clade (*A. aurea* Sánchez-Pacheco *et al.*, *A. vespertina* Kizirian) (Sánchez-Pacheco *et al*. 2012, 2017), as well as the dipsadine snake *Dipsas georgejetti* Arteaga, Salazar-Valenzuela, Mebert, Peñafiel, Aguiar, Sánchez-Nivicela, Pyron, Colston, Cisneros-Heredia, Yánez-Muñoz, Venegas, Guayasamin & Torres-Carvajal from its sister clade (*D. oswaldobaezi* Arteaga *et al*., *D. williamsi* Carrillo de Espinoza) (Arteaga *et al*. 2018). On the other hand, the JRB does not disrupt the distribution range of many other species of lizards and snakes, such as *Holcosus septemlineatus* Duméril & Duméril, *Stenocercus iridescens* Günther, *Bothrops asper* Garman, *Dendrophidion brunneum* Günther, and *Erythrolamprus fraseri* Boulenger (Torres-Carvajal *et al*. 2021). We postulate that the JRB has acted both as a center of endemism and a common geographical barrier facilitating the speciation process of a few squamate reptiles from the Pacific slopes of the Andes and adjacent lowlands in Ecuador.

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References

Arosemena, F.A., Ibáñez, D.R. & De Sousa, F. (1991) Una nueva especie de *Anolis* (Squamata: Iguanidae) del grupo *latifrons* de Fortuna, Panam. *Revista de Biología Tropical,* 39 (2), 255–262.

Arteaga, A., Salazar-Valenzuela, D., Mebert, K., Peñafiel, N., Aguiar, G., Sánchez-Nivicela, J., Pyron, R., Colston, T., Cisneros-Heredia, D., Yánez-Muñoz, M., Venegas, P., Guayasamin, J. & Torres-Carvajal, O. (2018) Systematics of South American snail-eating snakes (Serpentes, Dipsadini), with the description of five new species from Ecuador and Peru. *ZooKeys*, 766, 79–147. https://doi.org/10.3897/zookeys.766.24523

Ayala-Varela, F. & Velasco, J. (2010) A new species of dactyloid anole (Squamata: Iguanidae) from the western Andes of Ecuador. *Zootaxa*, 2577 (1), 46–56. https://doi.org/10.11646/zootaxa.2577.1.2

Ayala-Varela, F., Troya-Rodriguez, D., Talero-Rodriguez, X. & Torres-Carvajal, O. (2014) A new Andean anole species of the *Dactyloa* clade (Squamata: Iguanidae) from western Ecuador. *Amphibian & Reptile Conservation*, 8, 8–24.

Barbour, T. (1905) The Vertebrata of Gorgona Island, Colombia. V. Reptilia and Amphibia. Bulletin of the Museum of Comparative Zoology, 46 (5), 98–102.

Barbour,T. (1923) Notes on reptiles and amphibians from Panam. *Occasional Papers of the Museum of Zoology, University of Michigan*, 129, 1–16.

Batista, A., Vesely, M., Mebert. K., Lotzkat, S. & Köhler, G. (2015) A new species of *Dactyloa* from eastern Panama, with comments on other *Dactyloa* species present in the region. *Zootaxa*, 4039 (1), 57–84. https://doi.org/10.11646/zootaxa.4039.1.2

Berthold, A.A. (1846) Über verschiedene neue oder seltene Reptilien aus Neu-Granada und Crustaceen aus China. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen* 3, 3–32. https://doi.org/10.5962/bhl.title.5485

Betancourt, R., Reyes-Puig, C., Lobos, S., Yánez-Muñoz, M. & Torres-Carvajal, O. (2018) Sistemática de los saurios *Anadia* Gray, 1845 (Squamata: Gymnophthalmidae) de Ecuador: límite de especies, distribución geográfica y descripción de una especie nueva. *Neotropical Biodiversity*, 4, 82–101. https://doi.org/10.1080/23766808.2018.1487694

Boulenger, G.A. (1885) Catalogue of the lizards in the British Museum (Natural History). Vol. 2, Second edition. London, xiii+497 pp.

Boulenger, G.A. (1898) An account of the reptiles and batrachians collected by Mr. W. F. H. Rosenberg in western Ecuador. *Proceedings of the Zoological Society of London*, 107–126. https://doi.org/10.1111/j.1096-3642.1898.tb03134.x

Boulenger, G.A. (1902) Descriptions of new batrachians and reptiles from northwestern Ecuador. *Annals and Magazine of Natural History*, Series 7, 9 (49), 51–57. https://doi.org/10.1080/00222930208678538

Boulenger, G.A. (1919) Descriptions of two new lizards and a new frog from the Andes of Colombia. *Procedings of the Zoological Society of London*, 1919, 79–81. https://doi.org/10.1111/j.1096-3642.1919.tb02114.x

Castañeda, M.R. & de Queiroz, K. (2013) Phylogeny of the Dactyloa clade of *Anolis* lizards: new insights from combining morphological and molecular data. *Bulletin of the Museum of Comparative Zoology*, 160, 345–398. https://doi.org/10.3099/0027-4100-160.7.345

Cope, E.D. (1871) Ninth contribution to the herpetology of tropical America. *Proceedings of the Academy of Natural Science of Philadelphia*, 23, 200–224.

Cope, E.D. (1899) Contributions to the herpetology of New Granada and Argentina, with descriptions of new forms. *Philadelphia Museum of Science Bulletin*, 1, 1–19. https://doi.org/10.5962/bhl.title.54674

d'Angiolella, A.B., Klaczko, J., Rodrigues, M.T. & Avila-Pires, T.C.S. (2016) Hemipenial morphology and diversity in South American anoles (Squamata: Dactyloidae). *Canadian Journal of Zoology*, 94 (4), 251–256. https://doi.org/10.1139/cjz-2015-0194

de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation. *In*: *Endless Forms: Species and Speciation.* Oxford University Press, Oxford, pp. 57–75.

de Queiroz, K. (2007) Species concepts and species delimitation. *Systematic Biology*, 56, 879–886. https://doi.org/10.1080/10635150701701083

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797. https://doi.org/10.1093/nar/gkh340

Etheridge, R. (1959) *The relationships of the anoles (Reptilia: Sauria: Iguanidae). An interpretation based on skeletal morphology*. Ph.D. Dissertation. University of Michigan, Ann Arbor, Michigan, 249 pp.

Fleishman, L.J, Leal, M. & Persons, M.H. (2009) Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *Journal of Comparative Physiology A*, 195, 1043–60.
https://doi.org/10.1007/s00359-009-0478-8

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Garzón-Santomaro, C., Sánchez-Nivicela, J., Mena-Valenzuela, P., González-Romero, D. & Mena-Jaén J. (2019) *Anfibios, Reptiles y Aves de la provincia de El Oro. Una guía para la identificación de especies del Páramo al Manglar. Segunda Edición. Publicación Miscelánea No. 11. Serie de Publicaciones GADPEO-INABIO*. GADPEO-INABIO. Available from: https://www.researchgate.net/publication/341342944_Anfibios_Reptiles_y_Aves_de_la_provincia_de_El_Oro_Una_guia_de_identificacion_de_especies_del_paramo_al_manglar (accessed 25 May 2021)

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*, 59, 307–321.
https://doi.org/10.1093/sysbio/syq010

Günther, A. (1859) Second list of cold-blooded vertebrata collected by Mr. Fraser in the Andes of Western Ecuador. *Proceedings of the Zoological Society of London*, 402–422.

Hulebak, E., Poe, S., Ibáñez, R. & Williams, E.E. (2007) A striking new species of *Anolis* lizard (Squamata, Iguania) from Panama. *Phyllomedusa*, 6 (1), 5–10.
https://doi.org/10.11606/issn.2316-9079.v6i1p5-10

IUCN (2012) *IUCN Red List categories and criteria. Version 3.1. 2nd Edition*. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, vi + 34 pp.

Köhler, G. (2014) Characters of external morphology used in *Anolis* taxonomy: Definition of terms, advice on usage, and illustrated examples. *Zootaxa*, 3774 (2), 201–257.
https://doi.org/10.11646/zootaxa.3774.3.1

Kumazawa, Y. & Nishida, M. (1993) Sequence evolution of mitochondrial tRNA genes and deep-branch animal phylogenetics. *Journal of Molecular Evolution*, 37, 380–398.
https://doi.org/10.1007/BF00178868

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) Partition-Finder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
https://doi.org/10.1093/molbev/mss020

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution*, 34, 772–773.
https://doi.org/10.1093/molbev/msw260

Lotzkat, S., Hertz, A., Bienentreu, J.-F. & Köhler, G. (2013) Distribution and variation of the giant alpha anoles (Squamata: Dactyloidae) of the genus *Dactyloa* in the highlands of western Panama, with the description of a new species formerly referred to as *D. microtus*. *Zootaxa*, 3626 (1), 1–54.
https://doi.org/10.11646/zootaxa.3626.1.1

Macey, J.R., Larson, A., Ananjeva, N.B., Fang, Z. & Papenfuss, T.J. (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14, 91–104.
https://doi.org/10.1093/oxfordjournals.molbev.a025706

Miller, M., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Gateway Computing Environments Workshop (GCE), IEEE*, 2010, 1–8.
https://doi.org/10.1109/GCE.2010.5676129

Ministerio del Ambiente del Ecuador (2013) *Sistema de clasificación de los ecosistemas del Ecuador continental*. Subsecretaría de Patrimonio Natural, Quito, Ecuador, 235 pp.

Miyata, K. (1985) A new *Anolis* of the *lionotus* group from northwestern Ecuador and southwestern Colombia (Squamata: Iguanidae). *Breviora*, 481, 1–13.

Ochoa, A., Pineda, L., Crespo, P. & Willems, P. (2014) Evaluation of TRMM 3B42 precipitation estimates and WRF retrospective precipitation simulation over the Pacific–Andean region of Ecuador and Peru. *Hydrology and Earth System Sciences*, 18, 3179–3193.
https://doi.org/10.5194/hess-18-3179-2014

Peracca, M.G. (1904) Viaggia del Dr. Enrico Festa nell' Ecuador e regioni vicine. Rettili ed. Anfibi. *Bolletino dei Musei di Zoologia ed Anatomia Comparata della Reale Universita di Torino*, 19, 1–41.
https://doi.org/10.5962/bhl.part.11596

Pesantes, O. (1994) A method for preparing hemipenis of preserved snakes. *Journal of Herpetology*, 28, 93–95.
https://doi.org/10.2307/1564686

Peters, W.C.H. (1863) Über einige neue Arten der Saurier-Gattung *Anolis*. *Monatsberichte der Königlichen Preussischen Akademie des Wissenschaften zu Berlin*, 1863, 135–149.

Peters, J.A. & Orcés, G. (1956) A third leaf-nosed species of the lizards genus *Anolis* from South America. *Breviora*, 62, 1–8.

Poe, S. (2004) Phylogeny of Anoles. *Herpetological Monographs*, 18, 37–89.
https://doi.org/10.1655/0733-1347(2004)018[0037:POA]2.0.CO;2

Poe, S. & Ryan, M.J. (2017) Description of two new species similar to *Anolis insignis* (Squamata: Iguanidae) and resurrection of *Anolis* (*Diaphoranolis*) *brooksi*. *Amphibian & Reptile Conservation*, 11 (2), 1–16.

Poe, S., Velasco, J., Miyata, K. & Williams, E.E. (2009a) Descriptions of two nomen nudum species of *Anolis* lizard from northwestern South America. *Breviora*, 516, 1–16.
https://doi.org/10.3099/0006-9698-516.1.1

Poe, S., Latella, I.M., Ryan, M.J. & Schaad, E.W. (2009b) A new species of *Anolis* lizard (Squamata, Iguania) from Panama. *Phyllomedusa*, 8 (2), 81–87.
https://doi.org/10.11606/issn.2316-9079.v8i2p81-87

Poe, S., Nieto-Montes de Oca, A., Torres-Carvajal, O., de Queiroz, K., Velasco, J.A., Truett, B., Gray, L.N., Ryan, M.J., Köhler, G., Ayala-Varela, F. & Latella, I. (2017) A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). *Systematic Biology*, 66 (5), 663–697.
https://doi.org/10.1093/sysbio/syx029

Prates, I., Melo-Sampaio, P., de Queiroz, K., Carnaval, A., Rodrigues, M. & Drummond, L. (2020) Discovery of a new species of *Anolis* lizards from Brazil and its implications for the historical biogeography of montane Atlantic Forest endemics. *Amphibia-Reptilia*, 41 (1), 87–103.
https://doi.org/10.1163/15685381-20191179

Rambaut, A. & Drummond, A.J. (2016) TreeAnnotator version 1.8.3. Available from: http://beast.bio.ed.ac.uk (accessed 25 May 2021)

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Systematic Biology*, 67 (5), 901–904.
https://doi.org/10.1093/sysbio/syy032

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61 (3), 539–542.
https://doi.org/10.1093/sysbio/sys029

Sánchez-Pacheco, S.J., Aguirre-Peñafiel, V. & Torres-Carvajal, O. (2012) Lizards of the genus *Riama* (Squamata: Gymnophthalmidae): the diversity in southern Ecuador revisited. *South American Journal of Herpetology*, 7 (3), 259–275.
https://doi.org/10.2994/057.007.0308

Sánchez-Pacheco, S.J., Torres-Carvajal, O., Aguirre-Peñafiel, V., Nunes, P., Verrastro, L., Rivas, G.A., Trefaut R.M., Grant, T. & Murphy, R.W. (2017) Phylogeny of *Riama* (Squamata: Gymnophthalmidae), impact of phenotypic evidence on molecular datasets, and the origin of the Sierra Nevada de Santa Marta endemic fauna. *Cladistics*, 34 (3), 260–291.
https://doi.org/10.1111/cla.12203

Savage, J.M. (1997) On terminology for the description of the hemipenes of squamate reptiles. *Herpetological Journal*, 7, 23–25.

Schulte, J.A. II & Cartwright, E.M. (2009) Phylogenetic relationships among iguanian lizards using alternative partitioning methods and TSHZ1: A new phylogenetic marker for reptiles. *Molecular Phylogenetics and Evolution*, 50 (2), 391–396.
https://doi.org/10.1016/j.ympev.2008.10.018

Simpson, G.G. (1951) The species concept. *Evolution*, 5, 285–298.
https://doi.org/10.2307/2405675

Simpson, G.G. (1961) *Principles of animal taxonomy*. Columbia University Press, New York, New York, xii + 247 pp.
https://doi.org/10.7312/simp92414

Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology*, 57, 758–771.
https://doi.org/10.1080/10635150802429642

Stejneger, L. (1900) Descriptions of two new lizards of the genus *Anolis* from Cocos and Malpelo Islands. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 36, 161–163.

Swofford, D.L. (2002) *PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland, Massachusetts.

Tapia-Armijos, M.F., Homeier, J., Espinosa, C.I., Leuschner, C. & de la Cruz, M. (2015) Deforestation and forest fragmentation in south Ecuador since the 1970s – Losing a hotspot of biodiversity. *PLoS ONE*, 10 (11), e0142359.
https://doi.org/10.1371/journal.pone.0133701

Torres-Carvajal, O., Ayala-Varela, F., Lobos, S., Poe, S. & Narváez, A. (2018) Two new Andean species of *Anolis* lizard (Iguanidae: Dactyloinae) from southern Ecuador. *Journal of Natural History*, 52, 1067–1089.
https://doi.org/10.1080/00222933.2017.1391343

Torres-Carvajal, O., Pazmiño-Otamendi, G., Ayala-Varela, F. & Salazar-Valenzuela, D. (2021) Reptiles del Ecuador. Versión 2021.0. Museo de Zoología, Pontificia Universidad Católica del Ecuador. Available from: https://bioweb.bio/faunaweb/reptiliaweb (accessed 11 January 2021)

Velasco, J.A. & Hurtado-Gómez, J.P. (2014) A new green anole lizard of the *Dactyloa* clade (Squamata: Dactyloidae) from the Magdalena river valley of Colombia. *Zootaxa*, 3785 (2), 201–216.
https://doi.org/10.11646/zootaxa.3785.2.4

Weigend, M. (2002) Observations on the biogeography of the Amotape–Huancabamba zone in northern Peru. *The Botanical Review*, 68, 38–54.
https://doi.org/10.1663/0006-8101(2002)068[0038:OOTBOT]2.0.CO;2

Werner, F. (1894) Über einige Novitäten der herpetologischen Sammlung des Wiener zoolog. vergl. anatom. Instituts. *Zoologischer Anzeiger*, 17, 155–157.

Wiegmann, A.F.A. (1834) *Herpetologia Mexicana, seu descriptio amphibiorum Novae Hispaniae, quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede im Museum Zoologicum Berolinense pervenerunt. Pars prima, Saurorum species amplectens, adiecto systematis saurorum prodromo, additisque multis in hunc amphibiorum ordinem observationibus*. Lüderitz, Berlin, 54 pp.
https://doi.org/10.5962/bhl.title.119131

Williams, E.E. (1963) Studies on South American anoles. Description of *Anolis mirus*, new species from Rio San Juan, Colombia, with comment on digital dilation and dewlap as generic and specific characters in the anoles. *Bulletin of the Museum of Comparative Zoology at Harvard*, 129, 463–480.

Williams, E.E. (1966) South American anoles: *Anolis biporcatus* and *Anolis fraseri* (Sauria, Iguanidae) compared. *Breviora*, 239, 1–14.

Williams, E.E. (1975) South American *Anolis*: *Anolis parilis*, new species, near *A. mirus* Williams. *Breviora*, 434, 1–8.

Williams, E.E. (1984a) New or problematic *Anolis* from Colombia. III. Two new semiaquatic anoles from Antioquia and Choco, Colombia. *Breviora*, 478, 1–22.

Williams, E.E. (1984b) New or problematic *Anolis* from Colombia. II. *Anolis propinquus*, another new species from the cloud forest of western Colombia. *Breviora*, 477, 1–7.

Williams, E.E. (1988). New or problematic *Anolis* from Colombia. V. *Anolis danieli*, a new species of the *latifrons* species group and a reassessment of *Anolis apollinaris* Boulenger, 1919. *Breviora*, 489, 1–25.

Williams, E.E, Rand, H., Rand, A.S. & O'Hara, R.J. (1995) A computer approach to the comparison and identification of species in difficult taxonomic groups. *Breviora*, 502, 1–47.

Yánez-Muñoz, M.H., Morales, M., Reyes-Puig, M. & Meza-Ramos, P.A. (2013) Reserva Biológica Buenaventura: entre la transición húmeda tropical y la influencia tumbesina. *In*: MECN, Jocotoco & Ecominga (Eds.), *Herpetofauna en áreas prioriotarias para la conservación: El sistema de Reservas Jocotoco y Ecominga.* Serie de Publicaciones del Museo Ecuatoriano de Ciencias Naturales (MECN), Fundación para la Conservación Jocotoco, Fundación Ecominga, Quito-Ecuador, Monografía 6, pp. 62–76.

Yánez-Muñoz, M., Reyes-Puig, C., Reyes-Puig, J., Velasco, J., Ayala-Varela, F., Torres Carvajal, O. (2018) A new cryptic species of *Anolis* lizard from northwestern South America (Iguanidae, Dactyloinae). *ZooKeys*, 794, 135–163.
https://doi.org/10.3897/zookeys.794.26936

APPENDIX 1. Additional specimens examined.

MCZ = Museum of Comparative Zoology, Harvard, United States. QCAZ = Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador, Quito, Ecuador. DHMECN = División de Herpetología, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador. MZUA-RE = Colección de Reptiles, Museo de Zoología, Universidad del Azuay, Cuenca, Ecuador. USNM = Smithsonian National Museum of Natural History, Washington DC, United States.

Anolis fraseri—Ecuador: *Cañar*: Ocaña, 2.472°S, 79.206°W, 1160 m, MZUA-RE 0373. *Chimborazo*: La Victoria (Pallatanga - Bucay), 2.098°S, 78.975°W, 1154 m, QCAZ 3439, 3441. *Cotopaxi*: ca. 30 km E Santo Domingo on road to Reserva de Bosque Integral Otonga, 0.388°S, 78.929°W, 1363 m, QCAZ 9768; Recinto Galápagos, 0.41°S, 78.966°W, 1738 m, QCAZ 1328, 1344; Near San Francisco de Las Pampas, 0.414°S, 79.000°W, 1897 m, QCAZ 3119; Near San Francisco de Las Pampas, 0.423°S, 78.967°W, 1554 m, QCAZ 2114–2116, 2118, 2120; San Francisco de Las Pampas, 0.433°S, 78.966°W, 1604 m, QCAZ 7834, 9223, MCZ 176453–176454; San Francisco de Las Pampas, 0.433°S, 78.95°W, 1600 m, QCAZ 56–59. *Esmeraldas*: Alto Tambo, 5 km by road to Placer, Bosque Integral Otokiki, 0.906°N, 78.605°W, 623 m, QCAZ 8085. *Imbabura*: Plaza Gutiérrez, 0.35°N, 78.500°W, 1753 m, USNM 234610. *Manabí*: Estación Biológica Bilsa, 0.347°N, 79.711°W, 528 m, QCAZ 2724; Río Ayampe, 1.656°S, 80.817°W, 47 m, DHMECN 7682. *Pichincha*: 5 km E Mindo, 0.031°S, 78.760°W, 1566 m, QCAZ 10212; Mindo, 0.041°S, 78.791°W, 1250 m, QCAZ 9755, 9758, 9760; Mindo, on road to Mindo Garden, 0.057°S, 78.774°W, 1256 m, QCAZ 6862; Mindo, 0.061°S, 78.769°W, 1258 m, QCAZ 11864; Mindo, 0.033°S, 78.800°W, 1146 m, USNM 234612; El Cinto-Nambillo, 0.065°S, 78.794°W, 1491 m, QCAZ 11866; Nanegal, 0.131°N, 78.676°W, 1165 m, QCAZ 11905; Near Finca Ecológica Orongo, 0.160°N, 78.662°W, 1478 m, QCAZ 15686; Tandapi, 0.414°S, 78.799°W, 1445 m, QCAZ 94–96; Tandapi, 0.419°S, 78.801°W, 1708 m, MCZ 164608; La Unión del Toachi, Centro de Interpretación Ambiental Otongachi, 0.331°S, 78.938°W, 899 m, QCAZ 7990. *Santo Domingo de los Tsáchilas*: La Unión del Toachi, 0.319°S, 78.958°W, 900 m, QCAZ 6683; Santo Domingo, 0.25°S, 79.150°W, 576 m, MCZ 127689; 12 km E, 13 km S Santo Domingo, mountains south of Tinalandia, 0.296°S, 79.060°W, 650 m, MCZ 147042. *Unknown*: San Rafael (probably in Santo Domingo de los Tsáchilas), USNM 60521.