



Two new species of semiaquatic *Anolis* (Squamata: Dactyloidae) from Costa Rica

GERARDO CHAVES^{1,7}, MASON J. RYAN^{2,3}, FEDERICO BOLAÑOS^{1,6,8}, CRUZ MÁRQUEZ⁴, GUNTHER KÖHLER^{5,*} & STEVEN POE²

¹Centro de Investigación en Biodiversidad y Ecología Tropical (Museo de Zoología) de la Universidad de Costa Rica

²Department of Biology, University of New Mexico, Albuquerque, NM, 87131, USA

³anolis@unm.edu; <https://orcid.org/0000-0002-7020-4741>

³Arizona Game and Fish Department, 5000 W Carefree Hwy, Phoenix, Arizona 85086

⁴mryan@azgfd.gov; <https://orcid.org/0000-0003-3713-649X>

⁴Dirección, Conservación, Restauración y Desarrollo Sustentable de Ecosistemas Insulares; Parque Nacional Galapagos, Ecuador

⁵cruzcallw@gmail.com; <https://orcid.org/0009-0003-2220-7379>

⁵Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt a.M., Germany

⁶gkoehler@senckenberg.de; <https://orcid.org/0000-0002-2563-5331>

⁶Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica

⁷cachi13@gmail.com; <https://orcid.org/0000-0002-4301-6569>

⁸federico.bolanos@ucr.ac.cr; <https://orcid.org/0000-0002-7935-6418>

*Corresponding Author

Abstract

We describe two new species of *Draconura*-clade semiaquatic anoles from the central Pacific versant of Costa Rica. The two new species are similar to *Anolis aquaticus* in external appearance and ecology but differ from this species in male dewlap coloration and scalation. *Anolis robinsoni* **sp. nov.** and *A. riparius* **sp. nov.** differ from each other mainly in male dewlap color. All three species are distinct according to diagnostic morphological traits and a phylogenetic analysis of mitochondrial DNA sequences (669 bases of COI gene). We discuss the distribution and ecology of *Anolis aquaticus* and the new species.

Key words: Reptilia, anoles, taxonomy, phylogenetics

Resumen

Describimos dos nuevas especies de anolis semiacuáticos del clado *Draconura* de la vertiente del Pacífico Central de Costa Rica. Las dos nuevas especies son similares a *Anolis aquaticus* en apariencia externa y ecología, pero difieren de esa especie en la coloración de la papada del macho y en escamación. *Anolis robinsoni* **sp. nov.** y *A. riparius* **sp. nov.** difieren entre sí principalmente en el color de la papada de los machos. Las tres especies son distintas según los rasgos morfológicos diagnósticos y un análisis filogenético de las secuencias de ADN mitocondrial (669 bases del gen COI). Discutimos la distribución y ecología de *Anolis aquaticus* y las especies nuevas.

Introduction

Lizards of the genus *Anolis* (anoles) form a species rich and ecologically diverse group and occur in almost all habitat types in the Neotropics from sea level to > 2,100 meters (Köhler 2008). Anoles tend to be cryptically colored, diurnal, abundant, usually arboreal, and sexually dimorphic with males possessing large extendable and usually colorful dewlaps (Pianka & Vitt 2003). *Anolis* are popular study subjects in evolutionary and ecological biology and this group of animals has spawned the 'ecomorph' concept of morphology correlating with ecology (Collette 1961; Williams 1983), with six traditional ecomorphological types recognized (*i.e.*, grass-bush, trunk-ground, trunk, twig, trunk-crown, crown-giant).

The ecomorph concept, first and best established in Caribbean *Anolis* (Losos 2009), has been applied to mainland

species with differences and similarities between island ecomorphs (Schaad & Poe 2010). One unusual ecomorph that appears to be shared between the West Indies and the mainland is the semiaquatic type (Leal *et al.* 2002), which tend to have moderate to large bodies, found within 3 m of a stream or water body, dive and swim to escape predators, and sleep on overhanging vegetation or mossy boulders, often in splash zones (Vitt *et al.* 1995; Leal *et al.* 2002; Márquez *et al.* 2005; pers. obs.). There are four species of semiaquatic *Anolis* currently recognized from Middle America, all from the *Draconura* clade of *Anolis* (Poe *et al.* 2017): *Anolis aquaticus* Taylor from Panama and Costa Rica, *A. poecilopus* Cope from Panama and Colombia, *A. barkeri* (Schmidt) from southern Mexico, and *A. lionotus* Cope from Panama, Costa Rica, Nicaragua and Honduras (Köhler 2008). Including Caribbean derivations, the semiaquatic ecomorph has evolved at least four and probably more times within *Anolis* (see Poe *et al.* 2017).

In the 1970s, Dr. Douglas Robinson collected a series of specimens of a semiaquatic anole from Quebrada La Palma, Alto Palma, Puriscal, Costa Rica. The males in this population differed from all known semiaquatic *Anolis* by their dark brown dewlaps, compared with a dominance of orange in other semiaquatic species (Márquez *et al.* 2005). Between 2000 and 2010 we collected additional specimens of this form from Quebrada La Palma and surrounding environs, as well as other areas along the Pacific slope of Costa Rica. During our review of the semiaquatic anoles of southwest Pacific Costa Rica we discovered an additional distinct form of semiaquatic anole similar to *A. aquaticus*. Herein we describe two new species of semiaquatic anoles endemic to the Pacific versant of Costa Rica.

The two new species resemble *Anolis aquaticus* in their semiaquatic life style and a distinctive dorsal color pattern of a dark brown dorsum with light greenish-cream dorsal crossbars and a pair of parallel light greenish longitudinal stripes extending laterally from the level of throat back to the level of hind limbs and from the snout to the nape. Because of their geographic proximity, shared ecology, and similar coloration we hypothesize that *A. aquaticus* and the two new species described herein form a clade. We test this contention, as well as the species status and phylogenetic position of the new species, using DNA sequence data from the mitochondrial COI gene.

Materials and Methods

Species criterion. We adopt the general lineage species concept (de Queiroz 2007) and operationalize this concept by testing for consistent differences between hypothesized independently evolving units. We also emphasize that species should be diagnosable in taxonomic practice. Specimens of putative *Anolis aquaticus* were grouped into testable (phylogenetic and morphological diagnostic) species units using geography, male dewlap color, and size of head scales.

Field work. Specimens analyzed were collected between 1969 and 2010 along streams in Puriscal, Alto Palma, Alfombra, Tres Piedras, and Pérez Zeledón, San José Province, Costa Rica (Fig. 1). All specimens of the new species and comparative material that were used in our analyses are housed at the Museum of Zoology, University of Costa Rica (UCR). Additional paratypes not scored for morphological analysis are at the Museum of Comparative Zoology, Harvard University (MCZ), the Senckenberg Research Institute and Natural History Museum, Frankfurt (SMF), and the Museum of Southwestern Biology, University of New Mexico (MSB); additional non-type specimens and respective institutions are listed in Appendix 1. All georeferenced localities are in geographical coordinate system and WGS 1984 datum.

Morphometric analyses. All measurements were made to the nearest 0.1 mm with dial vernier calipers. Scale counts were made with the aid of a dissecting microscope. We generally follow Williams *et al.* (1995) for scale terminology and characters for anoline lizards, with some additions. Morphometric character definitions with some abbreviations used in the comparative table are as follows: snout–vent length (SVL); head length (HL); head width (HW); ear opening height (EOH); interparietal scale length (IL); length of second largest scale in contact with interparietal (SLS-I); axilla to groin length (AGL); femur length (FL); length of fourth toe (T4L); width of toe fourth pad at broadest point (T4W); tail length (TL) if tail is complete; tail height (TH) measured where knee reaches tail when hind limb is posteriorly adpressed and, tail width (TW) measured where knee reaches tail when hind limb is posteriorly adpressed. Also, we include the proportions: HL/SVL, TL/SVL and; IL/EOH. *Lepidosis.* Characters scored include the following scale counts: scales across the snout between second canthals; scales separating the nasal opening from rostral scale; scales in contact with rostral scale between supralabials; supralabial scales from rostral to level of middle of eye; infralabial scales from mental to level of middle of eye; scales separating supraorbital semicircles; rows of scales separating subocular scales from supralabials; elongate supercilliary scales; scales separating interparietal scale from supraorbital semicircles; enlarged scales in supraocular disk; loreal scales in column just anterior to eye; postmental scales between infralabials; scales in the loreal region; rows and number of scales per row in the dewlap; expanded lamellae under fourth toe (counted in the

manner of Williams *et al.* 1995); dorsal scales in 5% of SVL; ventral scales in 5% of SVL; middorsal scale rows. Also we present conditions for the following: preoccipital scale; small scales in supraocular disc; enlarged infralabial scales; tail crest; middorsal scale crest; small middorsal caudal scales anterior to the first enlarged caudal scale; axillary pocket; postcloacal scales; head scales in the frontal region; rostral scale and relation between rostral and mental scales; ear opening; dorsal edge of ear; mental scale; edge and posterior extension of the dewlap; tail; position of the longest toe of adpressed limb relative to the eye; lateral scales; dorsal scales; ventral scales; relation between dorsal and ventral scales; relative size of enlarged middorsal caudal scales; supradigital scales. Terminology for hemipenial morphology follows Myers *et al.* (1993) and Savage (1997).

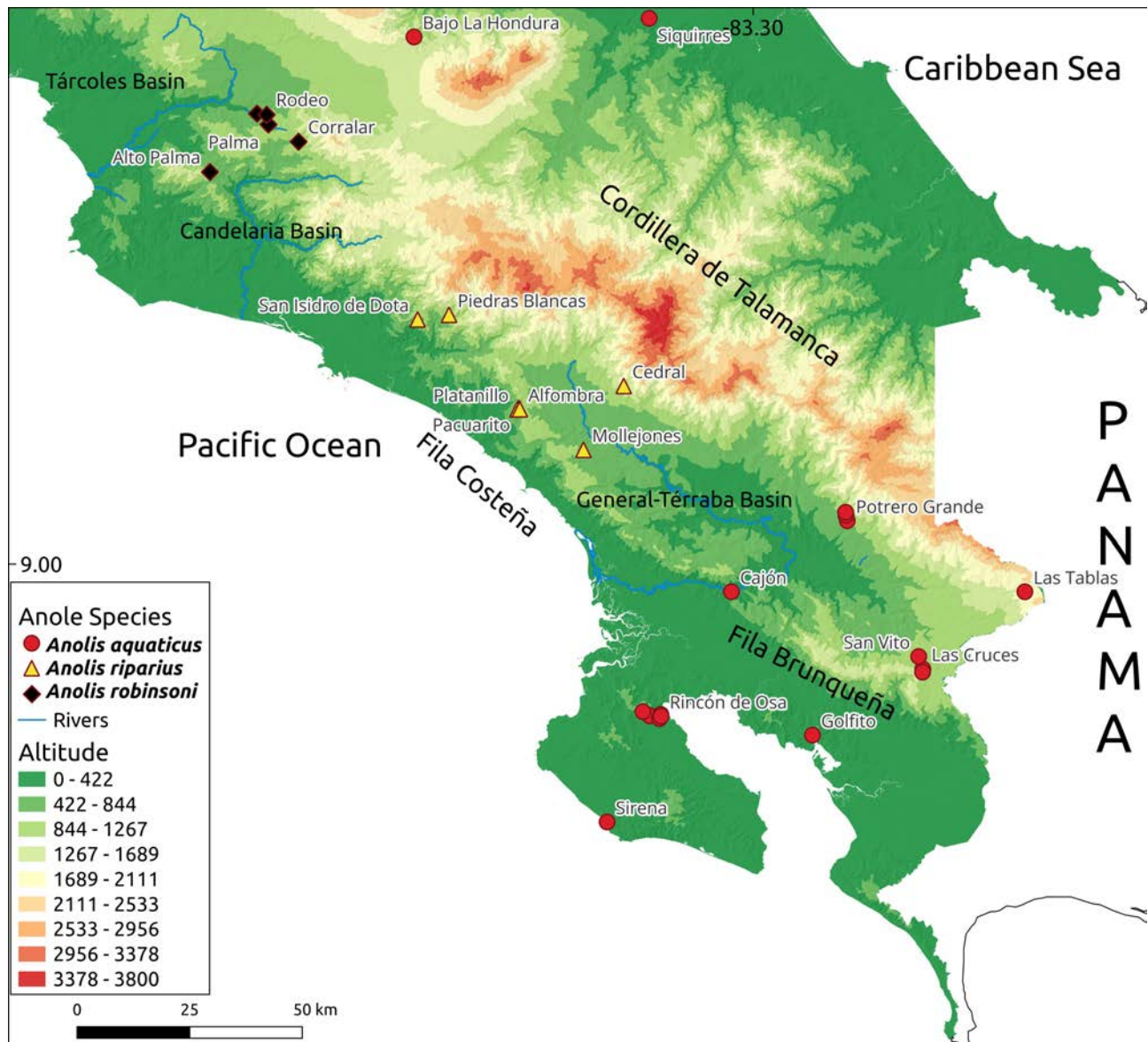


FIGURE 1. Map of Costa Rica showing collecting sites for *Anolis aquaticus* group. Caribbean individuals appear to be *A. aquaticus*, but we consider their status uncertain on geographic grounds.

There do not appear to be differences between sexes in lepidosis. Thus, we pooled male and female data for analyses. All continuous variables were transformed by the allometric transformation (Leonart *et al.* 2000). In this method, a logarithmic transformation is performed on the continuous variables to reduce the effect of extreme values, and then performed linear regression between the dependent variables and the LHA. We used the regression residuals we transformed the data, considering the all population variation through the standardization of the SVL on the residues. We conducted a Principal Component Analysis (PCA) to explore the degree of separation between the species and the ability to distinguish species among the quantitative variables. We calculated the mean, standard deviation, and range for

each morphometric variable using R v3.3.3 (R Development Core Team 2017) and used the Inflation Factor of Variance (VIF) to eliminate the variables with collinearity above 90% of correlation before using them in the analyses below. The following 9 variables were subject to multivariate analyses: HL, HW, number of scales between the second canthals, number of scales separating supraorbital semicircles, number of scales between the interparietal scale and the supraorbital semicircles, number of lamellae under the fourth toe, and number of infralabials. Then we used multivariate analysis of variance (MANOVA) on means for all the selected morphometric variables in order to identify which of them differ between species. Posteriorly the normality was evaluated with a Royston test ($\alpha = 0.05$), and homoscedasticity was tested with BoxM test ($\alpha = 0.05$).

Phylogenetic analyses. We performed phylogenetic analyses of 669 bases of the mitochondrial COI gene for three to seven individuals of *A. aquaticus* and each of the putative new species, 24 Central American *Draconura*-clade *Anolis* species (Poe *et al.* 2017) representing most major groups from this region (Savage & Guyer 1989) and three outgroups (*A. kunayalae*, *A. ibanezi*, *A. sagrei*) using likelihood and Bayesian approaches.

First, we employed Partitionfinder 2 (Lanfear *et al.* 2016) to identify suitable partitions for our data. We hypothesized each codon position for COI as a separate partition and analyzed our alignment using AICc model selection and Partitionfinder's "greedy" algorithm. We performed a partitioned phylogenetic likelihood analysis in RAxML (Stamatakis 2014) using the model partitions decreed in Partitionfinder and the "ML + rapid bootstrap" setting. We also performed a partitioned Bayesian phylogenetic analysis in MrBayes (Ronquist *et al.* 2012). Because MrBayes allows model-averaging across the entire GTR model space ("nst= mixed"), there is no reason to designate particular GTR-class models when comparing partitioning schemes. Therefore, we compared only GTR versus GTR+G models and ignored GTR-class submodels (e.g., HKY, F81) for each partition in Partitionfinder. We agree with previous authors (e.g., Stamatakis 2006; Moyle *et al.* 2012) that the assumed benefit of adding an invariant sites parameter (i.e., "accounting for" gene regions that cannot change) does not outweigh the potential downsides (i.e., duplication of the function of the rate heterogeneity parameter; parameter interaction; overparameterization) and therefore excluded invariant sites models from consideration. We ran the MrBayes analysis for 10000000 generations, sampling every 1000 generations, and discarded the initial 25% of generations as burn-in.

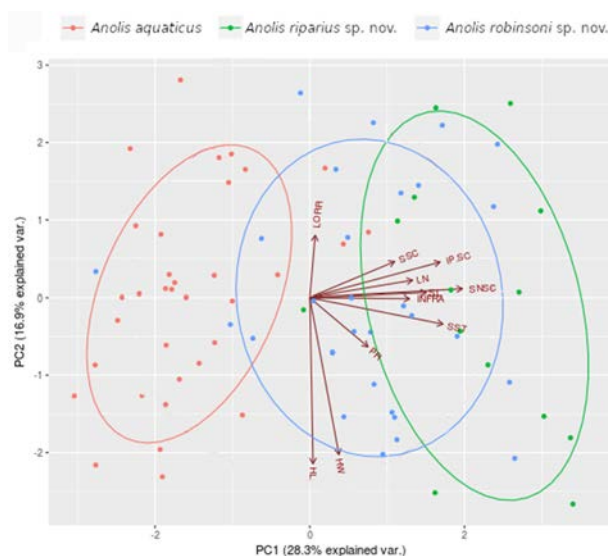


FIGURE 2. Principal component analysis showing as *Anolis aquaticus* populations segregate in three different groups based on morphology.

Results

Morphometric variation and comparisons among the populations of the putative species relative to *Anolis aquaticus* are shown in Table 1. The PCA differentiated the populations of *A. aquaticus* from the South Pacific and the populations from the Central Pacific (Fig. 2). The first principal component (PC1) explained 28.30% of the total variance and the second explained 16.90%, however only PC2 efficiently separates the populations. The MANOVA suggested that the

morphological variables were statistically different between populations (Phyllay aprox. 1.40, $F = 15.77$, num-df= 20, den-df= 134, $P < 0.01$). We found that all tested variables except HL, HW, and the number of rostral scales differed between the species. The residuals of the MANOVA were normal ($H = 4.10$, $p = 0.06$) and homoscedastic ($X^2 = 8.18$, $gl = 6$, $p = 0.23$). The variables small caudal scales before the first larger caudal scales and the number of lamellae under fourth toe separated the South Pacific population from the other populations (Table 1). The number of scales between supraocular semicircles, the scales between interparietal and supraoculars semicircle, and the number of labials separates the populations of the Central Pacific from the other populations (Table 1). The northernmost populations of *aquaticus*-like anoles differ from the southern populations in having a much darker, predominantly chocolate brown dewlap (versus orange in the Central and South Pacific).

TABLE 1. Selected measurements and scale characters of *Anolis aquaticus*, *A. riparius*, and *A. robinsoni*. Mean value and one standard deviation are followed by range in parentheses. MANOVA results are for selected variables and all with two degrees of freedom.

| VARIABLES | <i>Anolis aquaticus</i> | <i>Anolis riparius</i> | <i>Anolis robinsoni</i> | MANOVA |
|--|---------------------------|---------------------------|---------------------------|--------------------------|
| Number of individuals | 35 | 8 | 29 | |
| Dewlap coloration | Yellow and red | Yellow and red | Dark brown | |
| SVL (mm) | 57.0 ± 8.5 (30.6–69.5) | 60.8 ± 7.2 (30.6–73.3) | 58.9 ± 9.9 (23.1–73.8) | |
| Extent of dewlap past axilla in males (mm) | 6.4 ± 2.5 (0.1–11.3) | 8.2 ± 3.0 (6.1–10.3) | 8.8 ± 2.7 (3.5–12.2) | |
| HL | 15.6 ± 1.9 (11.4–19.5) | 15.4 ± 2.6 (9.6–20.1) | 15.0 ± 2.6 (8.2–18.8) | $F = 0.35$, $P = 0.35$ |
| HW | 9.2 ± 1.1 (6.4–10.7) | 9.5 ± 1.4 (5.9–12.4) | 9.3 ± 2.2 (4.7–18.2) | $F = 0.07$, $P = 0.92$ |
| Small caudal scales before the first larger scales | 11 ± 1 (9–14) | 18 ± 2 (16–21) | 18 ± 1 (15–20) | $F = 52.05$, $P < 0.01$ |
| Scales between supraocular semicircles | 4 ± 1 (2–7) | 4 ± 0 (4–5) | 6 ± 1 (4–7) | $F = 17.08$, $P < 0.01$ |
| Scales between interparietal and supraoculars semicircle | 6 ± 1 (5–10) | 9 ± 1 (7–11) | 7 ± 1 (5–11) | $F = 30.04$, $P < 0.01$ |
| Supralabials | 9 ± 1 (7–11) | 11 ± 1 (10–12) | 9 ± 1 (7–11) | $F = 12.43$, $P < 0.01$ |
| Infralabials | 9 ± 1 (8–10) | 11 ± 1 (10–12) | 9 ± 1 (8–11) | $F = 7.17$, $P < 0.01$ |
| Lamellae under fourth toe | 14 ± 1 (11–16) | 15 ± 1 (14–17) | 16 ± 1 (15–17) | $F = 12.44$, $P < 0.01$ |
| Loreal scales | 9 ± 1 (7–11) | 9 ± 1 (8–10) | 9 ± 1 (8–11) | |
| Scales between nasal and rostral | 1 ± 0 (0–2) | 1 ± 1 (1–2) | 2 ± 0 (1–3) | |
| SO/LA | 2 ± 0 (1–2) | 1 ± 1 (1–2) | 1 ± 0 (1–2) | |
| Postrostral scales | 9 ± 1 (7–11) | 10 ± 1 (8–11) | 9 ± 1 (7–10) | $F = 0.59$, $P = 0.55$ |

Phylogenetics

The Partitionfinder analysis suggested that each codon position be treated as a separate partition and that a rate heterogeneity parameter was warranted for each partition. Thus, we ran analyses using separate GTR+G models for each codon position in RAxML and MrBayes (with model averaging in MrBayes). Both RAxML and MrBayes analyses found *Anolis aquaticus*, *A. robinsoni* sp. nov., and *A. riparius* sp. nov. to form a strongly supported clade with *A. woodi* (100% Bayesian probability/87% likelihood bootstrap) relative to the other included *Anolis* (Fig. 3). As expected, the three *aquaticus*-

like anoles are nested within *Draconura* clade *Anolis*. *Anolis robinsoni* **sp. nov.** is sister species to *A. riparius* **sp. nov.** with strong support (100% Bayesian probability/100% likelihood bootstrap), and *A. woodi* is sister to this clade, with *A. aquaticus* basal to these three species. The monophyly of *A. robinsoni* **sp. nov.** + *A. riparius* **sp. nov.** and the monophyly of the three *aquaticus*-like anoles with *A. woodi* is insensitive to model assumptions and phylogenetic method applied by us. However, the position of *A. woodi* relative to these species is malleable depending on assumptions employed. Given the overall morphological similarity of these three semiaquatic species, we expect that future phylogenetic analyses including additional (e.g., nuclear) DNA will find them to form a clade, possibly with *A. woodi* as sister species.

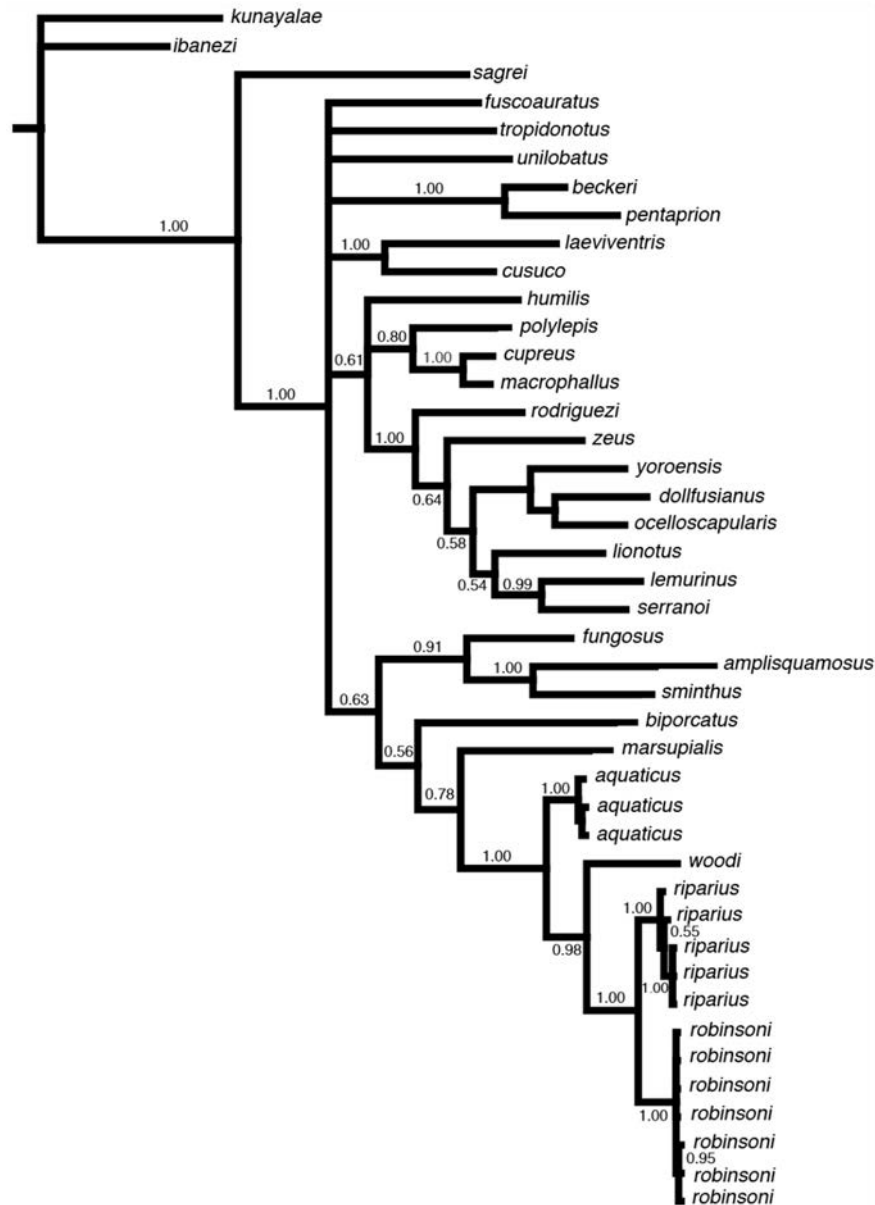


FIGURE 3. Consensus tree resulting from Bayesian phylogenetic analysis of COI sequences. Numbers are posterior probabilities of clades. All species are *Anolis*.

Anolis robinsoni, new species

Holotype. UCR 2463 (Fig. 4) collected 15 March 1969 by Oscar Blanco, an adult male from Palma stream bridge 5.1 km south of Santa Marta de Santiago de Puriscal, 9.79230 N, -84.39530 W, ca. 800 masl, San José Province, Costa Rica.

Paratypes (all from Costa Rica: San José Province). **Adult males:** SMF 92437 (collected 27 March 2010 by Gunther Köhler) from Zona Protectora El Rodeo (Universidad para la Paz), 9.90392 N, -84.28169 W, ca. 825 masl; SMF 92438 (collected 27 March 2010 by Gunther Köhler) from Zona Protectora El Rodeo (Universidad para la Paz), 9.90355 N,

-84.28192 W, ca. 780 masl; UCR 2464 (same data of the holotype); UCR 16048 (collected 28 October 2001 by Mason J Ryan, Robert Puschendorf and Brian Kubicki) from the west slope of the Cerros de Escazú, Río Jaris (9.88460 N, -84.27650 W, 500 ca. masl), close to the Zona Protectora El Rodeo (Universidad para la Paz); MCZ R-186162 (collected 27 December 2007 by Steve Poe and Mason J. Ryan) from Quebrada La Palma in Alto Palma de Puriscal (9.78890 N, -84.39440 W, ca. 1000 masl). **Adult females:** SMF 92439, 92450–51 (collected 27 March 2010 by Gunther Köhler) from Zona Protectora El Rodeo (Universidad para la Paz), 9.90364 N, -84.28182 W, ca. 820 masl; UCR 2558 (collected 15 March 1969 by Oscar Blanco and Douglas Robinson) and MCZ R-186161 (collected 27 December 2007 by Steve Poe and Mason J. Ryan) both of them from Quebrada La Palma in Alto Palma de Puriscal (9.78890 N, -84.39440 W, ca 1000 masl).

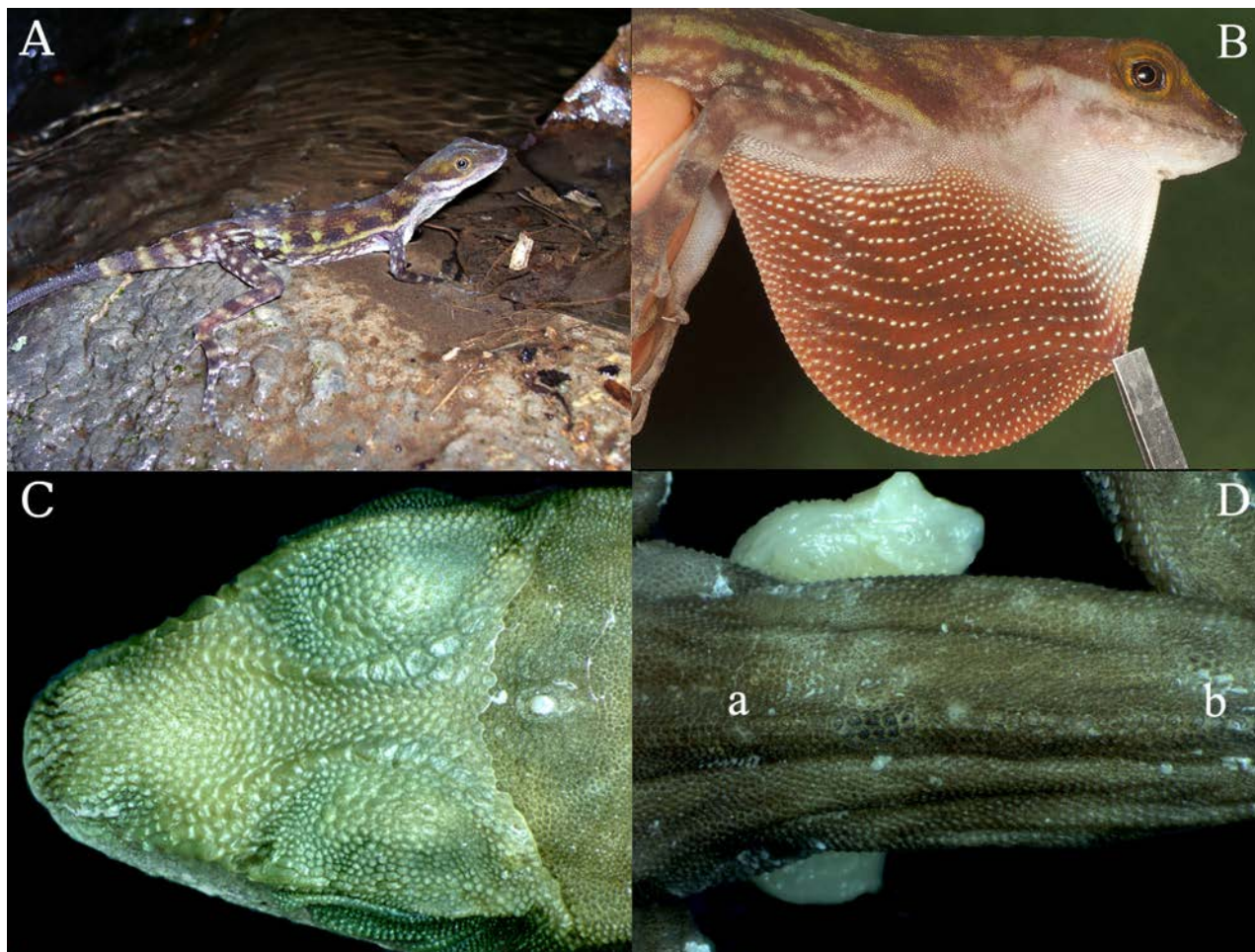


FIGURE 4. A) *Anolis robinsoni* in life; B) Male dewlap of *Anolis robinsoni* (SMF 92437) in life. C) Dorsal view of head and D) Small middorsal scales in the base of the tail of paratype (UCR 2464) of *A. robinsoni* locate between breakpoint (a) and the first enlarge middorsal caudal scale (b). Photo A by Robert Puschendorf, B by Gunther Köhler, and C and D by Gerardo Chaves.

Diagnosis. *Anolis robinsoni* **sp. nov.** is a semiaquatic anole that is distinguished from all other *Anolis* of Central America by male dewlap coloration (chocolate brown with ill-defined brick red horizontal streaks, Fig. 4B). The only other species with which *A. robinsoni* **sp. nov.** might be confused in the field are the other Middle American semiaquatic anoles *A. aquaticus*, *A. lionotus*, *A. poecilopus*, and *A. barkeri*. *Anolis lionotus* and *A. poecilopus* are easily distinguished from *A. robinsoni* **sp. nov.** by male dewlap color (dull orange-yellow in these species, chocolate brown with ill-defined brick red horizontal streaks in *A. robinsoni* **sp. nov.**), presence of enlarged postcloacal scales in most males (absent in *A. robinsoni* **sp. nov.**), and presence of a longitudinal zone of 10–24 enlarged middorsal scales (0–3 scales enlarged in *A. robinsoni* **sp. nov.**). *Anolis aquaticus* may be distinguished from *A. robinsoni* **sp. nov.** by male dewlap color (orange-red with yellow in *A. aquaticus*, Fig. 5A) and possession of larger dorsal scales of the head and body (e.g., 15–20 scales across the snout between second canthals in *A. robinsoni* **sp. nov.** (Fig. 4C), 7–14 in *A. aquaticus*; Fig. 5B, Table 1) and the size of the middorsal caudal row scales relative to adjacent scales (no more than two times in *A. robinsoni* **sp. nov.** (Fig. 4D),

more than three times in *A. aquaticus* (Fig 5C). *Anolis barkeri* is most easily distinguished from *A. robinsoni* **sp. nov.** by its larger size (maximum SVL 91 mm in *A. barkeri*, 74 mm in *A. robinsoni* **sp. nov.**), lack of distinctly expanded toe pads (ratio width of expanded pads/width of distal phalanx 1.8–2.2 in *A. robinsoni* **sp. nov.** versus 1.4–1.6 in *A. barkeri*), and presence of a double row of middorsal caudal scales (single row in *A. robinsoni* **sp. nov.**).

Description of the holotype (Fig. 4). Adult male as indicated by dewlap and everted hemipenes; SVL 63.9 mm; HL 17.5 mm; HL/SVL 0.28; HW 10.1 mm; EOH 2.36 mm; IL 1.18 mm; IL/EOH 0.50; SLS-I 0.18 mm mm; AGL 23.1 mm; FL 16.6 mm; T4L 15.1 mm; T4W 1.42 mm; TL 10.4 mm, tail complete; TL/SVL 0.38; T4L 15.1 mm and T4W 1.42 mm. 18 scales across the snout between second canthals; two scales separate the nasal opening from rostral scale; nine postrostral scales between supralabials; nine supralabial scales from rostral scale to level of middle of eye; six scales separating supraorbital semicircles; one rows of scales separate subocular scales from supralabials; two slightly elongate superciliary scale; eight scales separating interparietal scale from supraorbital semicircles; 12 enlarged scales in supraocular disk; 11 loreal scales in column just anterior to eye; 11 postmental scales posteriorly in contact with mental scale between infralabials; 16 scales in the loreal region; 19 rows of single scales in the dewlap (10–42 scales per row, rows somewhat irregular); 2 middorsal scale rows slightly larger than adjacent scales; 16 dorsal scales in 5% of SVL; 12 ventral scales in 5% of SVL; 220 scales around midbody; 23 expanded lamellae under fourth toe; 26 small middorsal caudal scales before the first large caudal scale (Fig. 4D). Preoccipital, enlarged infralabial, tail crest, middorsal, and postcloacal scales absent; supraocular disc presents small scales. Frontal region of head concave; scales in supraocular disc unicarinate; rostral scale with weak cleft and overlaps mental scale; ear opening vertically ovoid; dorsal edge of ear lacks ornamentation; mental scale partially divided posteriorly and with its posterior edge convex; dewlap extends well on to chest with anterior insertion at level of anterior portion of the eye and without protruding scales at distal edge; dorsal scales small, keeled with two middorsal scale rows slightly larger than adjacent scales; ventral scales in diagonal rows, keeled and larger than dorsal scales; lateral scales homogeneous; tail is compressed and triangular in cross-section with the base taller than wide; middorsal caudal scales in single row and its size is less than three times than the adjacent scales (Fig. 4D); the longest toe of adpressed limb reaches anterior to eye and, supradigital scales keeled and multicarinate.

Color in life (male based on field notes and color photographs; Fig. 4A and 4B). The dewlap of males in life is chocolate brown with lighter orange-brown bars located centrally. The dorsal ground color is olive to chestnut brown with transverse olive–green bars across dorsum down flanks extending to tail. The head is uniformly dark or light brown. A cream-colored line extends posteriorly from the labial scales down the side of the body. Scattered small greenish spots are present on the dorsum. Scales on the tip of the snout with black pigmentation. The dorsum and tail are marked with olive–green transverse bars and the limbs marked with pale green to yellowish transverse bars with small punctuations.

Variation. *Anolis robinsoni* **sp. nov.** showed variation in the SVL of reproductive males (58.6 ± 11.0 , 42.1–73.8 mm). Table 1 shows the variation in lepidosis. The gular region of females is white with brown streaks. Females have a small brown to black dewlap. Transverse, dorsal olive–green bands of males varied between 7–8, with 10–12 tail bands; females had 7–8 olive–green dorsal transverse bars with 9–11 tail bands. In life, the dorsal coloration of both sexes may vary with transverse bands darker when cold or stressed (e.g., when held in hand).

Hemipenis morphology. The almost completely everted hemipenis of SMF 92438 (Fig. 7A) is a stout bilobed organ. The sulcus spermaticus is bordered by well-developed sulcal lips opening into two broad concave areas, one on each lobe. A small asulcate ridge is present. The apex is strongly calyculate, truncus with transverse folds.

Etymology. The specific epithet is a patronym in honor of the late Douglas C. Robinson, who contributed enormously to the herpetological knowledge of Costa Rica through extensive field collections and by inspiring a generation of Costa Rican biologists. He received his Ph.D. from Texas A&M University in 1968 and studied the Mexican semiaquatic anole, *Anolis barkeri*.

Distribution. *Anolis robinsoni* **sp. nov.** is known from the riparian gallery forests of the Río Candelaria basin (Fig. 1), the foothills of the Montañas de Turrubares in the northwestern section of the Cordillera de Talamanca, and Río Jaris along the western border of the Zona Protectora El Rodeo. These areas are within the Tropical Wet and Humid Premontane forest life zones (Holdridge 1967). *Anolis robinsoni* **sp. nov.** has been found at elevations between 500 and 1100 masl.

Ecology. Most of the following observations are from Márquez–Baltán (1994) and Márquez *et al.* (2005) from Quebrada La Palma. During the day this species is found on bare rocks and boulders along streams with dense canopy cover. At night it is found sleeping on moss and vegetation on boulders near the splash zones of small and medium waterfalls. Both sexes and juveniles were found no more than two meters from the edge of a stream. The operational sex ratio is approximately equal proportions of males to females (Márquez *et al.* 2005), and males share territories with one

to three females. The estimated population density varied from 100 to 200 individuals per hectare and population size fluctuated monthly with a peak during the dry season.

Reproduction occurs throughout the year with a lull in the wet season (May to November). Females lay 1 egg per clutch in cracks and interstitial spaces of boulders in streams. Up to 6 eggs have been found together suggesting that this species lays eggs in communal nest sites. Incubation times ranged between 75–82 days, and hatchlings are approximately 25 mm SVL (Márquez *et al.* 2005).

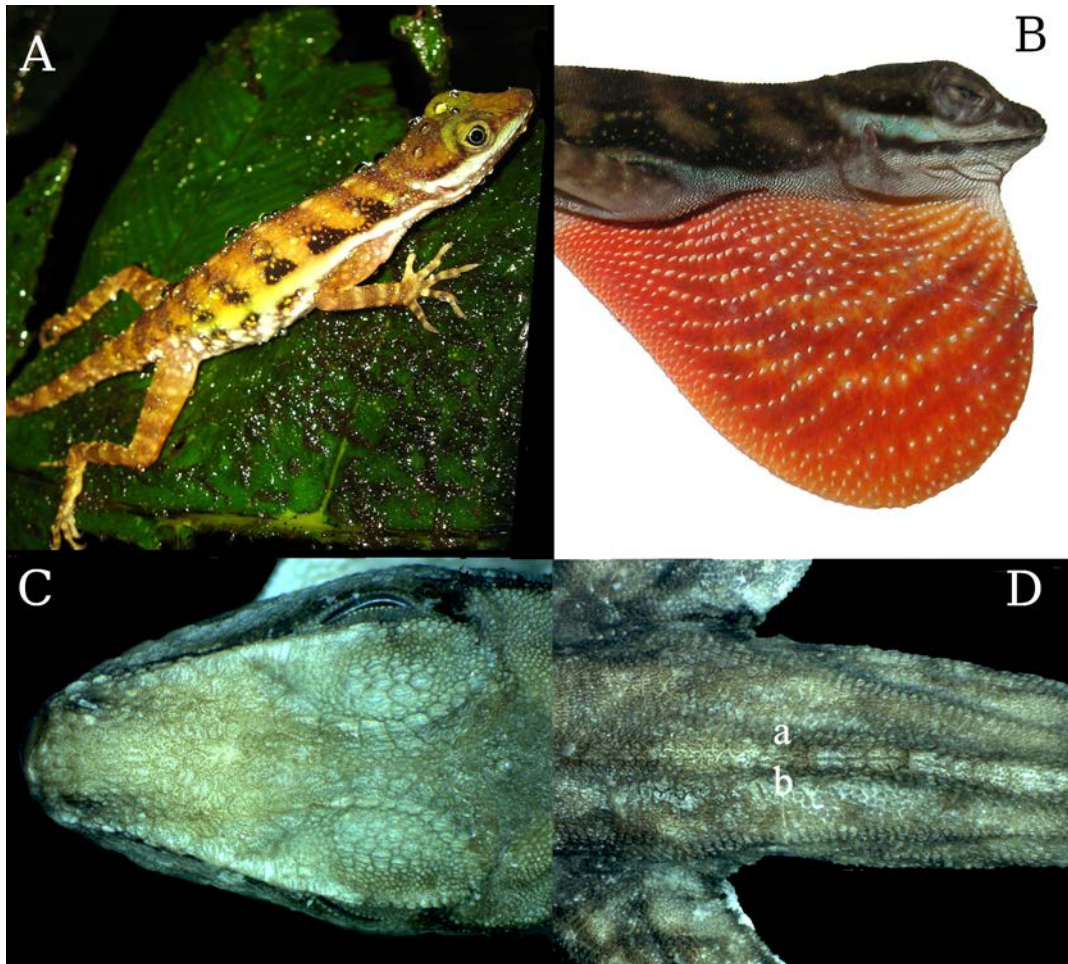


FIGURE 5. A) Lateral and dewlap view of *Anolis aquaticus* in life. B) Dorsal view of head and C) Small middorsal scales in the base of the tail of *A. aquaticus* (UCR 5880) locate between breakpoint (a) and the first enlarge middorsal caudal scale (b). Photo A by Steven Poe and B and C by Gerardo Chaves.

Anolis riparius, new species

Holotype. UCR 5579 (Fig 6) collected on 7 September 2009 by Douglas Robinson and his students; an adult male from Pacuarito river, Pacuarito 10 Km S-SW of Pérez Zeledón, 9.31390 N, -83.77220 W, 880 masl, San José Province, Costa Rica.

Paratypes (all from Costa Rica: San José Province). **Adult males:** SMF 82183–82184 (collected 9 October 2002 by Axel Fläschendräger) from road between Platanillo and San Isidro, 9.31056 N; -83.77500 W, ca. 850 masl; SMF 92428 (collected 15 February 2010 by Gunther Köhler) from 1 km N Cedral 9.35789 N, -83.56094 W, 1425 masl; UCR 7893 (collected 24 August 1979 by Douglas Robinson) from 1.85 Km NE Alfombra, 9.3167 N, -83.7722 W, ca. 930 masl; MCZ-R 18171 (collected 15 December 2007 by Steve Poe and Mason J. Ryan) from Alfombra, 12 Km S-SW of Pérez Zeledón (9.31670 N, -83.77220 W, 930 masl); MSB 95201 (collected on 10 January 2009 by Mason J Ryan and Ian Latella) from Alfombra, 12 Km S-SW of Pérez Zeledón (9.31670 N, -83.77220 W, 930 masl). **Adult females:** SMF 82185–82186 (collected 9 October 2002 by Axel Fläschendräger) from road between Platanillo and San Isidro (ca. 850 masl); SMF 83093–83094 (collected 9 October 2002 by Axel Fläschendräger) from near Platanillo (ca. 850 masl); SMF

92429 (collected 15 February 2010 by Gunther Köhler) from 1 km N Cedral (9.35789 N, -83.56094 W, 1425 masl); UCR 5580 (same data of the holotype); UCR 15959 (collected 3 March 2001 by Mason J Ryan) from Mollejones (9.22930 N, -83.64200 W, 800 masl); UCR 16162 (collected 2 July 2001 by Mason J Ryan) from Alfombra, 12 Km S-SW of Pérez Zeledón (9.31670 N, -83.77220 W, 930 masl); MCZ R-186143 (collected 15 December 2007 by Steve Poe and Mason J Ryan) from Alfombra, 12 Km S-SW of Pérez Zeledón (9.31670 N, -83.77220 W, 930 masl); MSB 95200 (collected 15 December 2007 by Steve Poe and Mason J Ryan) from Alfombra, 12 Km S-SW of Pérez Zeledón (9.31670 N, -83.77220 W, 930 masl); UCR 16638 (collected 15 March 2002 by Franklin Aguilar) from Fila Piedras Blancas area (9.50130 N, -83.91280 W, 900 masl) in the Zona Protectora Los Santos in the Río Savegre basin.



FIGURE 6. A) Dorsal body and B) dewlap views of *Anolis riparius* in life. C) Dorsal view of head and D) Small middorsal scales at the base of the tail of paratype (UCR 5579) of *A. riparius* between breakpoint (a) and the first enlarged middorsal caudal scale (b). Photos A and B by David Laurencio and C and D by Gerardo Chaves.

Diagnosis. *Anolis riparius* **sp. nov.** and *A. aquaticus* are the only semiaquatic Middle American anoles that have a large orange-red dewlap with yellow in males (Fig. 6B). *Anolis riparius* **sp. nov.** differs from *A. aquaticus* in possessing smaller dorsal scales of the head and body (e.g., 15–19 scales across the snout between the second canthals in *A. riparius* **sp. nov.** versus 7–14 in *A. aquaticus*, Fig. 5B), and is phylogenetically distinct (see below). *Anolis riparius* **sp. nov.** is distinguished from the other Middle American semiaquatic anoles as follows: from *A. robinsoni* **sp. nov.** by male dewlap color (chocolate brown with ill-defined brick red horizontal stripes in *A. robinsoni* **sp. nov.**); from *A. lionotus* and *A. poecilopus* by male dewlap color (solid yellow-orange in *A. lionotus* and *A. poecilopus*), lack of postcloacal scales in males (usually present in *A. lionotus* and *A. poecilopus*), and possession of zero to three enlarged rows of middorsal scales (a broadband of 10–24 enlarged middorsal scale rows in *A. poecilopus* and *A. lionotus*); from *A. barkeri* by smaller size (maximum SVL 73 mm in *A. riparius* **sp. nov.**, 91 mm in *A. barkeri*), presence of distinctly expanded toe pads (ratio width of expanded pads / width of distal phalanx 1.8–2.2 in *A. riparius* **sp. nov.** versus 1.4–1.6 in *A. barkeri*), and presence of a single row of middorsal caudal scales (double row in *A. barkeri*).

Description of the holotype (Figure 6). Adult male as indicated by dewlap and everted hemipenes SVL 73.3 mm;

HL 20.1 mm; HL/SVL 0.27; HW 10.7 mm; EOH 1.64 mm; IL 1.45 mm; IL/EOH .88; SLS-I 0.1; AGL 31.26 mm; FL 18.34 mm; T4L 15.95 mm; T4W 1.54 mm; TL 135.00 mm, tail complete; TL/SVL 1.84; TH 5.994 mm and TW 3.42 mm. 18 scales across the snout between second canthals; two scales separate the nasal opening from rostral scale; ten postrostral scales between supralabials; 12 supralabial scales from rostral scale to level of middle of eye; four scales separating supraorbital semicircles; 2 rows of scales separate subocular scales from supralabials; one slightly elongate superciliary scale; nine scales separating interparietal scale from supraorbital semicircles; four enlarged scales in supraocular disk; eight loreal scales in column just anterior to eye; 12 postmental scales posteriorly in contact with mental scale between infralabials; 15 scales in the loreal region; 13 rows of single scales in the dewlap (21–48 scales per row, rows somewhat irregular); seven enlarge middorsal scale row; 16 dorsal scales in 5% of SVL; 12 ventral scales in 5% of SVL; 220 scales around midbody; 15 expanded lamellae under fourth toe; 23 small middorsal caudal scales before the first large caudal scale (Fig. 6D). Preoccipital, enlarged infralabial, tail crest, middorsal, postcloacal scales absent; supraocular disc presents with small scales. Frontal region of head concave; scales in supraocular disc uncarinate; rostral scale with very weak cleft and overlaps mental scale; ear opening vertically ovoid; dorsal edge of ear lacks ornamentation; mental scale completely divided posteriorly and with its posterior edge convex; dewlap extends well on to chest with anterior insertion at level of anterior portion of the eye and without protruding scales at distal edge; dorsal scales strongly keeled and uniform in size; ventral scales in diagonal rows keeled and larger than dorsal scales; lateral scales homogeneous; tail is compressed and triangular in cross-section with the base taller than wide; middorsal caudal scales in single row and its size is less than three times than the adjacent scales (Fig. 6D); the longest toe of adpressed limb reaches anterior to eye and, supradigital scales keeled and multicarinate.

Color in Life (based on field notes and color photographs; Fig. 6A and 6B). Dewlap yellow with orange-red horizontal streaks. Dorsal ground color olive to chestnut brown with transverse olive-green bars across dorsum down flanks extending to tail. A dirty cream-colored line extends posteriorly from the labial scales down the side of the body. Scattered small greenish spots are present on the dorsum. The dorsum and tail are marked with olive-green transverse bars. The limbs are marked with pale green to yellowish transverse bars with small punctuations.

Variation. Size of reproductive males (69.6 ± 5.3 , 65.8–73.3 mm) was larger than females (58.0 ± 6.0 , 49.1–65.1 mm). Table 1 shows variation in the lepidosis characters of *Anolis riparius* **sp. nov.**. Individuals exhibited little variation in coloration. Although some individuals were dark, the amount and distribution of the light bands and dots were similar among all specimens.

Hemipenis morphology. The completely everted hemipenis of SMF 92428 (Fig. 7B) is a stout bilobed organ. The sulcus spermaticus is bordered by well-developed sulcal lips and opens into two broad concave areas, one on each lobe. A small asulcate ridge is present. The apex is strongly calyculate, truncus with transverse folds.

Etymology. The specific epithet is an adjective taken directly from Latin (*riparius* = of stream banks) about the riparian habitat of this species.

Distribution. *Anolis riparius* **sp. nov.** is known from streams in the riparian gallery forests of the Pacuar, Guabo, and Savegre river basins (Fig. 1) from 100 to 1450 masl. This species inhabits lowland and premontane tropical wet forest life zones.

Ecology. Little is known about the ecology and life history of *Anolis riparius* **sp. nov.** but it seems to share life-history traits with *A. aquaticus* and *A. robinsoni* **sp. nov.**. What follows is based mainly on field observations by MJR from Alfombra and additional unnamed streams of the Rio Guabo watershed. This species may be common in small order and headwater streams but absent from some other streams within a watershed. During the day this species may be found perched on rocks and boulders along streams and can jump into the water or crawl into interstitial cracks between rocks and boulders when pursued. At night these lizards are found sleeping on moss mats, fern fronds, and other large leafy riparian vegetation, especially near the splash zone around boulders. We have also found juveniles and adults sleeping on vertical rock walls and boulders in and next to waterfalls. We have observed these lizards sleeping from 0.5 to 2.0 meters above the ground. At Alfombra on 21 December 2007 MJR and SP found a congregation of seven gravid females on the same fern-covered boulder. One meter from the sleeping females was a cluster of 6 loosely aggregated eggs that were stuck to the moss on the same large boulder.

Morphological comparisons of the two new species and *Anolis aquaticus*. *Anolis aquaticus* is the smallest species in this complex. It has fewer scales for all traits except for the number of scales between the suboculars and supralabials (Table 1). *Anolis aquaticus* has relatively larger dorsal scales, whereas *A. robinsoni* **sp. nov.** and *A. riparius* **sp. nov.** have small, granular dorsal scales that result in a higher number of total of scales around the body (more than 160, whereas *A. aquaticus* has 160 or fewer). The number of scales between the second canthals is close to half in number in *A. aquaticus* relative to the other species (Table 1, Fig. 4B, 5B, 6B), indicating the larger size of the scales in *A. aquaticus*. The number

of small middorsal caudal scale varies between 0 to 10 in *A. aquaticus* (Fig. 5C) while the other species has more than 20 small middorsal caudal scales (Fig. 4D and 4D). However, the most striking feature separating one of the three species of this group is the color of the male dewlap. The red and yellow dewlap of *A. aquaticus* and *A. riparius* **sp. nov.** (Fig. 5A and 6B) contrasts with the dark brown dewlap of *A. robinsoni* **sp. nov.** (Fig. 4B). We did not find any difference in hemipenes morphology among *A. aquaticus*, *A. riparius* **sp. nov.**, and *A. robinsoni* **sp. nov.** (Fig. 7).

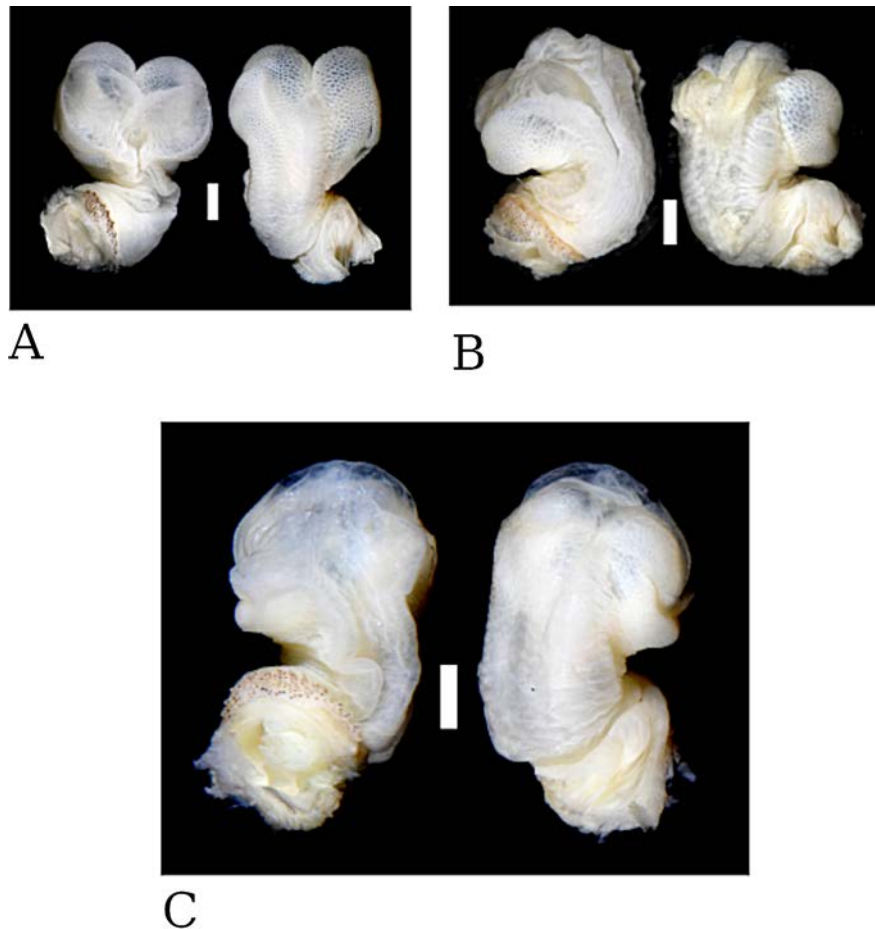


FIGURE 7. Hemipenes of *A. robinsoni* (A), *A. riparius* (B), and *Anolis aquaticus* (C). The notable differences in appearance are due to preservation artifacts (i.e., the hemipenes of *A. riparius* and *A. robinsoni* are not completely everted). Scale bar = 1 mm for all photographs. Photos by Gunther Köhler.

Discussion

The distinctiveness of *Anolis robinsoni* **sp. nov.** and *A. riparius* **sp. nov.** from *A. aquaticus* is reflected in separation according to physiographic and geological provinces. Because *A. aquaticus* was originally described from Palmar Norte and Golfito locations (Taylor 1956), both of them in the South Pacific of Costa Rica, we establish that the range of *A. aquaticus* is herein restricted to the lowland and premontane slopes of southern Pacific Costa Rica and adjacent western Panama, including the Talamancan foothills of the Valle del General (Savage 2002). Two specimens of *A. aquaticus* from the Caribbean slope (Fig. 1) are not morphologically different from the Pacific populations and we suspect that these specimens result from a recent introduction, possibly mediated by human activities.

The two new species of semiaquatic *Anolis* of the Pacific versant of Costa Rica follow a south to north cline in rainfall where *A. riparius* **sp. nov.** occurs in an intermediate moist life zone and *A. robinsoni* **sp. nov.** in a semi-arid life zone (Holdridge 1967). *Anolis robinsoni* **sp. nov.** has the smallest range (Fig. 1) and inhabits the driest and warmest life zone of the three species (Herrera 1985). None of the three *aquaticus*-like species are known to occur sympatrically and of the three species, *Anolis aquaticus* and *A. riparius* **sp. nov.** are the most likely to eventually be found to occur sympatrically, on the southern portion of the Turrubares Mountains near Fila Chonta. These mountains are relatively unexplored and future herpetological work may uncover areas of sympatry or integration in these two species.

Morphological and molecular phylogenetic analyses support the recognition of *Anolis robinsoni* **sp. nov.** and *A. riparius* **sp. nov.** as distinct species. This work increases the number of species of semiaquatic *Anolis* of Middle America to six and increases the number of Costa Rican *Anolis* to 33 (Bolaños *et al.* 2011; Köhler & Vargas 2019). The subtle morphological differences between these species (i.e., relative scale sizes; dewlap color), supported by molecular data, suggest the possibility of additional cryptic species among semiaquatic *Anolis* in Central America. The stringent ecological requirements of these forms would seem to encourage vicariant speciation in separate river drainage systems in the Talamancas.

Acknowledgements

This is a contribution of the Museo de Zoología of the Universidad de Costa Rica. MJR received support from Tropical Forestry Initiative and Hacienda Baru National Wildlife Refuge, Dominican for financial and logistical; Grove Scholarship from UNM Biology Department; Tinker Foundation Field Research Grant; Idea Wild; the Museum of Comparative Zoology, Harvard University. Thanks to B. Kubicki, I. Latella, R. Puschendorf, E. Schaad, Casey Gillman, and Joseph Vargas for field assistance. I. Latella, R. Puschendorf and D. Laurencio contributed photographs of the new species. Thanks to J. Guevara of MINAE for providing research and collecting permits in Costa Rica.

Appendix 1

Comparative Material Examined

Anolis aquaticus: Costa Rica: Limón: Siquirres UCR 5026. Puntarenas: Osa, Aguabuena, Quebrada Aguabuena UCR 898, UCR 1957, UCR 1959–67; Rincón de Osa UCR 2540, UCR 4568, UCR 18982–83; San Vito 2604; Cajón UCR 7095–96, UCR 7654–55; Las Cruces Jardín Wilson SMF 89331–32, UCR 8580, UCR 10970, UCR 12566–67, Corcovado, Sirena Biological Station UCR 11260–11262, Golfito Naranjal Natural Reserve UCR 11670–75. San José: Bajo La Hondura UCR 1807. Panama: Chiriquí: Quebrada Chevo, 1170 masl SMF 85437–38; 4 km SSE El Hato del Volcán, 1160 masl SMF 89281–83; Chorogo, 380–390 masl SMF 92190–94.

Anolis riparius (additional nontype material): Costa Rica: San José: Alfombra UCR 15967; Mollejones UCR 15934.

Anolis robinsoni (additional nontype material): Costa Rica: San José: Alto Palma, Quebrada La Palma UCR 2459–62, UCR 2465–66, UCR 4651–53, UCR 11590–95; Zona Protectora El Rodeo, Río Jarís UCR 16174–75, Zona Protectora El Rodeo, Quebrada Martilla UCR 20104–08.

Literature cited

- Bolaños, F., Savage, J.M. & Chaves, G. (2011) Amphibians and reptiles of Costa Rica. Listas Zoológicas Actualizadas U.C.R. Museo de Zoología UCR. San Pedro, Costa Rica. Available from: <http://museo.biologia.ucr.ac.cr/Listas/LZAPublicaciones.htm> (accessed 12 June 2023)
- Collette, B.B. (1961) Correlations between ecology and morphology in anoline lizards from Havana, Cuba, and southern Florida. *Bulletin of the Museum of Comparative Zoology*, 125, 137–162.
- De Queiroz, K. (2007) Species concepts and species delimitation. *Systematic Biology*, 56, 879–886. <https://doi.org/10.1080/10635150701701083>
- Herrera, W. (1985) *Clima de Costa Rica*. EUNED, San José, Costa Rica, 118 pp.
- Holdridge, L.R. (1967) *Life zone ecology*. Tropical Science Center, San Jose, Costa Rica, 206 pp.
- Köhler, G. (2008) *Reptiles of Central America*. Herpeton-Verlag Elke Köhler, Offenbach, 400 pp.
- Köhler, G. & Vargas, J. (2019) A new species of anole from Parque Nacional Volcán Arenal, Costa Rica (Reptilia, Squamata, Dactyloidea: *Norops*). *Zootaxa*, 4608 (2): 261–278. <https://doi.org/10.11646/zootaxa.4608.2.4>
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2016) 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>

- Leal, M., Knox, A.K. & Losos, J.B. (2002) Lack of convergence in aquatic *Anolis* lizards. *Evolution*, 56, 785–791.
<https://doi.org/10.1111/j.0014-3820.2002.tb01389.x>
- Lleonart, J., Salat, J. & Torres, G.J. (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205, 85–93.
<https://doi.org/10.1006/jtbi.2000.2043>
- Losos, J.B. (2009) *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, California, 507 pp.
<https://doi.org/10.1525/california/9780520255913.001.0001>
- Márquez-Baltán, C. (1994) *Historia Natural de Anolis aquaticus Taylor 1956 (Sauria:Polychridae) en la Quebrada La Palma, Puriscal, San José, Costa Rica*. Universidad de Costa Rica, San José, Costa Rica, 108 pp.
- Márquez, C., Mora, J.M., Bolaños, F. & Rea, S. (2005) Aspectos de la biología poblacional en el campo de *Anolis aquaticus*, Sauria: Polychridae en Costa Rica. *Ecología Aplicada*, 4, 59–69.
<https://doi.org/10.21704/rea.v4i1-2.299>
- Moyle, R.G., Andersen, M.J., Oliveros, C.H., Steinheimer, F.D. & Reddy, S. (2012) Phylogeny and biogeography of the core babblers (Aves: Timaliidae). *Systematic Biology*, 61, 631–651.
<https://doi.org/10.1093/sysbio/sys027>
- Myers, C.W., Williams, E.E. & McDiarmid, R.W. (1993) A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. *American Museum Novitates*, 3070, 1–15.
- Pianka, E.R. & Vitt, L.J. (2003) *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley, California, 333 pp.
- 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, 663–697.
<https://doi.org/10.1093/sysbio/syx029>
- R Core Team (2017) R: A language and environment for statistical computing. [<https://www.R-project.org/>]
- 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, 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Savage, J.M. (1997) On terminology for the description of the hemipenes of squamate reptiles. *Herpetological Journal*, 7, 23–25.
- Savage, J.M. (2002) *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between two Continents, between two Seas*. University of Chicago Press, Chicago, Illinois, 934 pp.
- Savage, J.M. & Guyer, C. (1989) Infrageneric classification and species composition of the anole genera, *Anolis*, *Ctenonotus*, *Dactyloa*, *Norops* and *Semiurus* (Sauria: Iguanidae). *Amphibia-Reptilia*, 10, 105–116.
<https://doi.org/10.1163/156853889X00142>
- Schaad, E.W. & Poe, S. (2010) Patterns of ecomorphological convergence among mainland and island *Anolis* lizards. *Biological Journal of the Linnean Society*, 101, 852–859.
<https://doi.org/10.1111/j.1095-8312.2010.01538.x>
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
<https://doi.org/10.1093/bioinformatics/btl446>
- Stamatakis, A. (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics*, 2014. Available from: <http://bioinformatics.oxfordjournals.org/content/early/2014/01/21/bioinformatics.btu033.abstract?keytype=ref&ijkey=VTEqgUJYCDf0kP> (accessed 12 June 2023)
- Taylor, E.H. (1956) A review of the Lizards of Costa Rica. *The University of Kansas Science Bulletin*, 38, 1–322.
- Vitt, L.J., Zani, P.A. & Durtsche, R.D. (1995) Ecology of the lizard *Norops oxylophus* (Polychrotidae) in lowland forest of southeastern Nicaragua. *Canadian Journal of Zoology*, 73, 1918–1927.
<https://doi.org/10.1139/z95-225>
- Williams, E.E. (1983) Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In: Huey, R.B., Pianka, E.W. & Schoener, T.W. (Eds.), *Lizard Ecology: Studies of a Model Organism*. Harvard Univ. Press, Cambridge, Massachusetts, pp. 326–370.
<https://doi.org/10.4159/harvard.9780674183384.c18>
- Williams, E.E., Rand, H., Rand, S.A. & O'Hara, R.J. (1995) A computer approach to the comparison and identification of species in difficult taxonomic groups. *Breviora*, 502, 1–47.