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Description of two new species similar to *Anolis insignis* (Squamata: Iguanidae) and resurrection of *Anolis* (*Diaphoranolis*) *brooksi*

[1]Steven Poe and [2]Mason J. Ryan

[1,3]*Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA*
[2]*Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85086, USA*

***Abstract.*—The spectacular giant anole lizard *Anolis insignis* is widely distributed but infrequently collected outside of northern Costa Rica. We recently collected several individuals similar to *Anolis insignis* from localities in Panama and southern Costa Rica. These populations differ from type locality *A. insignis* in male dewlap color and morphology. We associate one set of these populations with *Anolis* (*Diaphoranolis*) *brooksi* Barbour from Darién, Panama, and describe two additional populations as new species.**

Keywords. Central America, Costa Rica, lizard, Panama, Reptilia, taxonomy

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Introduction

Costa Rica and Panama contain perhaps the most studied herpetofauna of the Neotropics for ecology and systematics (Savage 2002; Donnelly et al. 2005). The early works of Taylor (e.g., 1956) and then Savage (e.g., 1975), along with the development of the Organization for Tropical Studies (OTS) and the efforts of the University of Costa Rica (UCR), have established Costa Rica as a center of herpetological research. The Smithsonian Tropical Research Institute (STRI) has been instrumental in fostering herpetological work in Panama.

The *Anolis* lizards of Costa Rica and Panama are well studied (Taylor 1956; Savage 2002), but new species continue to be discovered (e.g., Kohler 2011; Poe et al. 2015). As of 28 February 2016 the Reptile Database lists 42 species of *Anolis* from Costa Rica and 45 species from Panama. Relatively unexplored regions such as the southern Cordillera de Talamanca in Costa Rica and the Darién Region of eastern Panama are likely to produce new discoveries, and detailed molecular studies such as those undertaken in frogs (Crawford et al. 2010) are likely to unearth cryptic diversity of *Anolis*.

We have conducted extensive fieldwork on *Anolis* in Costa Rica and Panama since 2006. During this time, we have collected numerous individuals of *Anolis* that might standardly be assigned to the spectacular and rarely collected giant anole species *A. insignis* (Fig. 1). We have noticed numerous differences between populations of this species that are consistent within geographically distinct populations. We now possess enough material to confidently distinguish and recognize three species of *Anolis* similar to *A. insignis*. Herein we resurrect a previously synonymized name and describe two new species.

Materials and Methods

We adopt the evolutionary species concept (Simpson 1961; Wiley 1978) and operationalize this concept by identifying species based on traits that are consistent within hypothesized species but differ among species.

Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm), usually to the nearest 0.1 mm. Specimens are referenced from the Museum of Southwestern Biology (MSB), the Museum of Comparative Zoology (MCZ), the Los Angeles County Museum (LACM), the Museo de Vertebrados, University of Panama (MVUP), and the University of Costa Rica (UCR). Snout–vent length (SVL) was measured from tip of snout to anterior margin of the cloaca. Head length was measured from tip of snout to anterior margin of the ear opening. Head width was measured at

Correspondence. [3]*anolis@unm.edu*

Fig. 1. *Anolis insignis*, male, Pocosol, Alajuela, Costa Rica.

the broadest part of the head, between the posterolateral corners of the orbits. Femoral length was measured perpendicularly from the longitudinal midline of the venter to the knee, with limb bent at a 90° angle. Terminology and characters for qualitative conditions and scale counts follow standards established by Ernest Williams (e.g., Williams et al. 1995).

We tested for the objective identification of hypothesized groups (i.e., species) using the Multiresponse Permutation Procedure (MRPP; Mielke 1984) as described by McCune and Grace (2002). Like the commonly-used discriminant function analysis (DFA), MRPP is among the class of techniques used to test for the distinctiveness of a-priori hypothesized groups. We use this test rather than DFA because we are not confident making distributional assumptions about our data and we suspect the nonparametric nature of this approach will treat our small sample sizes more conservatively. We hypothesized groups based on male dewlap color pattern and geography (see below) and employed the following characters: number of lamellae on 4th toe (counted in the manner of Williams et al. [1995]), number of postmental scales, number of postrostral scales, number of scales across the snout at the second canthals, number of supralabial scales to the center of the eye, number of scales between the supraorbital semicircles, number of scales from the interparietal to the supraorbital semicircles, number of loreal rows. As none of these traits are the basis for our diagnoses (see below), this analysis provides a somewhat independent check of our species inferences. We used Euclidean distances of standardized data (i.e., mean = 0, standard deviation = 1) and present observed and expected Delta (i.e., the test statistic), *P*-value based on 99 randomizations, and Chance Corrected Within Group Agreement (i.e., effect size). Sexual dimorphism, if present, appeared to be less than interspecific dimorphism for the studied traits. Therefore to increase our small sample sizes we analyzed both sexes together. We demonstrate this lack of clustering by sex in two ways. First, we performed the same MRPP analysis but grouped by sex. Second, we performed Principal Component Analysis (PCA) of the above characters and present bivariate graphs of the first two principal components labeled by sex and by hypothesized species. Although PCA may not be appropriate for statistical interpretations and tests given our small sample sizes and high observation-to-variable ratio (see below; although we note that similar PCA results are obtained with subsamples of variables), we believe this technique nevertheless to be useful for the limited purpose of visualizing gross differences in clustering patterns by sex versus by species. Statistical analyses were performed in Stata (2013) and Microsoft Excel.

The hypothesized new species were found to form a well-supported clade with *Anolis insignis*, *A. microtus*, and *A. ginaelisae* (Bayesian Posterior Probability of 100%) by Poe et al. (2015), who included all known *Dactyloa*-clade *Anolis* in their phylogenetic analysis. Terminal taxa NSP.E, NSP.F, NSP.L in Poe et al.'s (2015) Fig. 5 correspond to species described herein. In order to more finely examine the interrelationships of the *insignis*-like anoles, we added new morphological data to the data matrices of Poe et al. (2015) and Poe et al. (2017), and analyzed these data for *A. insignis*, *A. microtus*, *A. ginaelisae*, the three additional species described here, and two *Dactyloa*-clade outgroups (*A. frenatus*, *A. fraseri*). We eliminated characters that did not vary in the ingroup and added characters based on our examination of specimens for the current study. The final matrix includes 18 characters of morphology and 50 genes of DNA sequence data. Additional details of data properties and collection (i.e., gene names, data sources, partitioning) are in Poe et al. (2017). Morphological characters were rescaled differently from Poe et al. (2017) to account for new data and our restricted taxon sample.

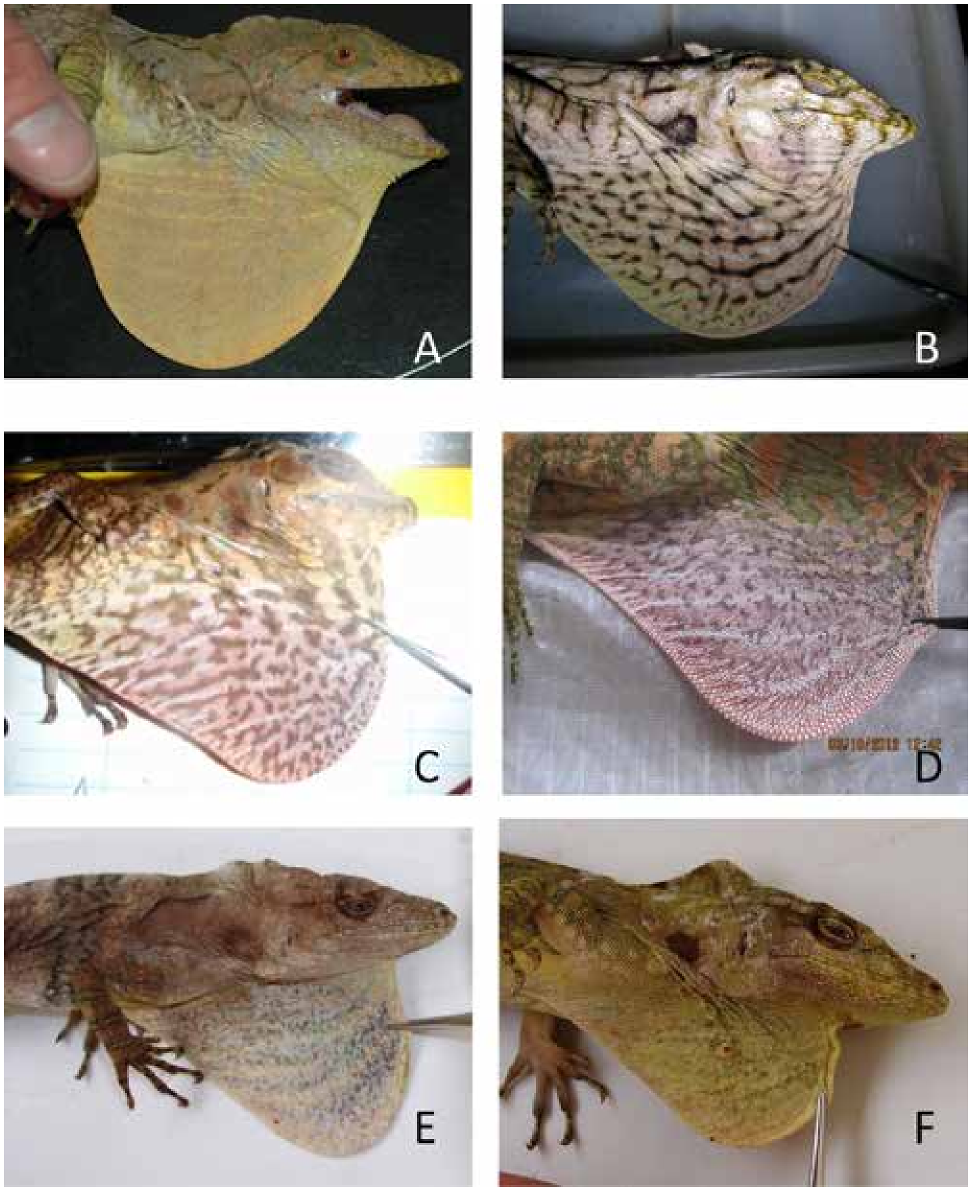

Fig. 2. Dewlaps of **A)** *Anolis brooksi*, male, El Copé, Panama; **B)** *A. brooksi*, female, El Copé, Panama; **C)** *A. savagei*, male, Las Cruces, Costa Rica; **D)** *A. savagei*, female, Las Cruces, Costa Rica; **E)** *A. kathydayae*, male, Fortuna, Panama; **F)** *A. kathydayae*, female, Fortuna, Panama.

Although this data matrix includes 24,897 characters, we note that only the morphological dataset is informative for the interrelationships of *A. insignis* and the other three species discussed in depth in this paper, as only two of the discussed species are scored for some DNA sequence data. The included DNA data are useful for establishing the monophyly of these forms with *A. microtus* and *A. ginaelisae* and examining genetic divergences as they relate to hypothesized species (see below). The phylogenetic matrix analyzed for this paper is available electronically at: stevenpoe.net. The morphological characters and data matrix are in Appendices 1 and 2 respectively.

We analyzed this matrix using a Bayesian phylogenetic approach as implemented in MrBayes (Huelsenbeck and Ronquist 2001) using the model parameters and settings of Poe et al. (2017), except that a heating temperature of 0.01 was used and the analysis was carried out for 2,000,000 generations. That is, we included separate GTR + G models for each of 15 DNA partitions of the 50 genes (including partitions by codon position for the best-sampled protein coding genes COI and ND2) with partitions determined by Partitionfinder (Lanfear et al. 2012) and model-averaging across the entire GTR model space for each gene partition ("nst=mixed" in MrBayes). Morphological character evolution was modeled with the "standard" MrBayes model. We checked for convergence of parameter values by examining estimated sample sizes in Tracer (Rambaut et al. 2014).

Results

Four very different male dewlap types are recognizable (Figs. 1, 2) and correlate with geography. Male specimens from central and northern Costa Rica have orange-

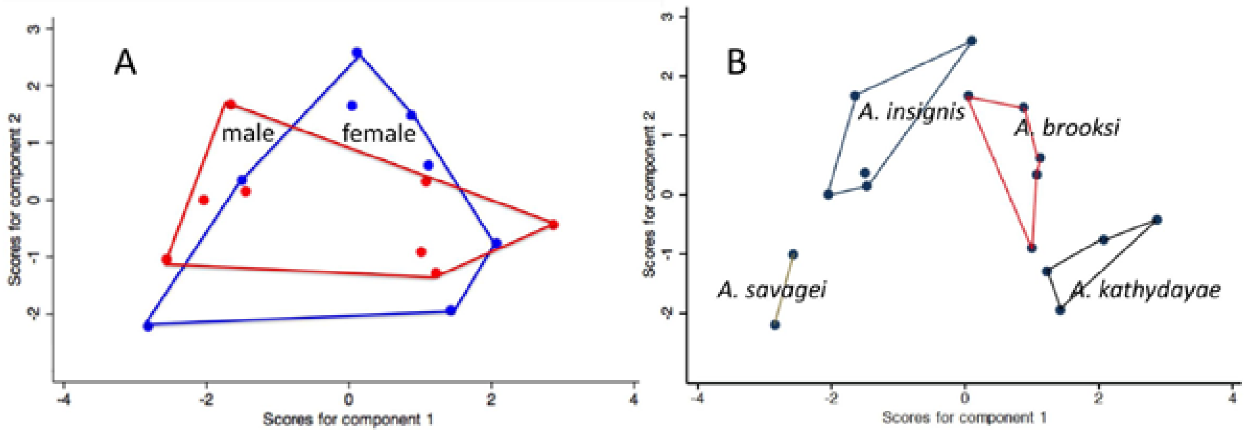

Fig. 3. Graph of principal components 1 and 2 for traits used in MRPP analysis of species of *Anolis* studied here, labeled by **A)** sex and **B)** putative species.

red dewlaps; those from southwestern Costa Rica have pale pink dewlaps with black streaks; those from the Fortuna area in Panama have white dewlaps; and those from eastern Panama (Santa Fé, El Copé, Cerro Azul) have peach-tan dewlaps. We hypothesize that these differences represent inter- rather than intraspecific variation for four reasons. First, we observed at least three adult males within each range, with no significant variation in male dewlap color pattern at any locality or between localities where a particular dewlap type was found. Second, the degree of difference among these male dewlap color patterns would be unprecedented as intraspecific variation in *Anolis*. Third, each male dewlap-group is distinguishable by additional traits (see below). Fourth, groups identified by male dewlap color are different according to MRPP. The MRPP analysis was significant ($P = 0.01$, 99 randomizations; Delta = 3.09, Deltanull = 3.85), rejecting the null hypothesis of random assignment of individuals to groups. The Chance Corrected Within Group Agreement was 0.20, indicating 20% within group agreement above that expected by chance. The MRPP analysis was nonsignificant when individuals were grouped by sex rather than by hypothesized species ($P = 0.24$, 99 randomizations; Delta = 3.75; Deltanull = 3.85), which is compatible with our observation of a lack of sexual dimorphism in these characters. Figure 3 shows that our studied individuals do not cluster morphologically by sex according to PCA of traits used in the MRPP. Based on this evidence, we are comfortable pooling our samples by sex within species for the MRPP analysis.

We associate the Costa Rican specimens examined from near the city of San José with the nominate species *Anolis insignis* Cope 1871 (Type locality: "San José"). Our central Panama specimens from Cerro Azul, Panamá province, and El Copé, Coclé province may be an unrecognized lineage. Alternatively, on geographic and morphologic grounds they may be associated with *Diaphoranolis brooksi* Barbour (holotype MCZ 16297) from the Darién of Panama—an individual previously determined to be "an unquestioned juvenile of *A. insignis*" (Savage and Talbot 1978). As a preserved specimen, the *A.* (= *Diaphoranolis*) *brooksi* holotype specimen appears similar to juveniles we collected at El Copé, and we lack adult dewlap photos and adult specimens for the Darién population. We choose to assign our easternmost form to *A. brooksi* pending future collection of *A. insignis*-like anoles in Darién. The distinctive populations from Fortuna, Chiriquí, Panama, and Las Cruces, Puntarenas, Costa Rica, currently lack names.

Below we redescribe *Anolis insignis* from specimens near the city of San José Costa Rica, and *A. brooksi* from specimens from El Copé and Cerro Azul in Panama. We describe two new species from Las Cruces, Costa Rica, and Fortuna, Panama respectively. We describe variation in *A. insignis* and *A. brooksi* and describe holotype specimens for the two new species. Comparisons among the four species are summarized in Table 1. The results of our phylogenetic analysis of these species are summarized in Fig. 4. We infer that the Markov Chain Monte Carlo analysis was run long enough to sample parameters in proportion to their true posterior probability distributions based on low standard deviation of split frequencies (0.011) and estimated sample sizes well above 200 for all parameters, as recommended by Rambaut et al. (2014).

Systematics

Anolis insignis Cope 1871
(Figures 1, 5)

Holotype
Lost (Savage and Talbot 1978); from "Costa Rica: Provincia de San José: near Ciudad San José; probably from near La Palma," according to Savage and Talbot (1978) and Savage (1974).

Examined specimens
LACM 149495 collected by J. Hagnauer and N.J. Scott in January 1975 (no day provided) and LACM 149496 collected by G. Hagnauer and W. Timmerman in April 1974 (no day provided) from Costa Rica, Alajuela, Vicinity of Bijagua (10.7333; -85.1; 425 m); LACM 149500

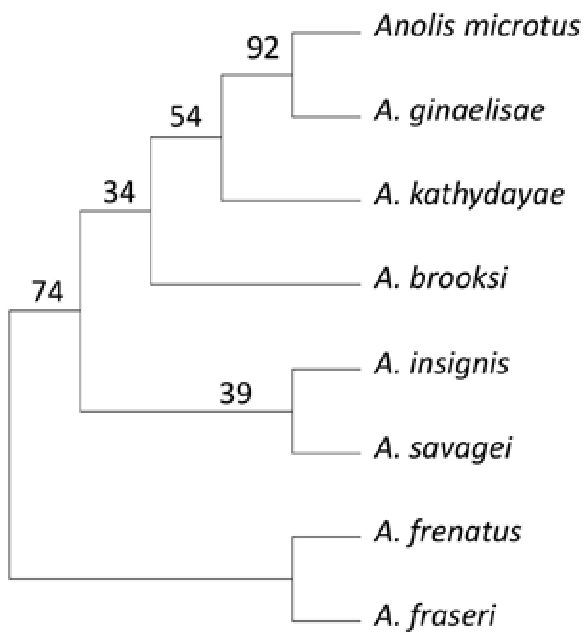

Fig. 4. Bayesian phylogenetic estimate of relationships for *Anolis* species similar to *A. insignis*. Numbers on clades are posterior probabilities.

collected by K. Timmerman 20 June 1984 and LACM 149497 collected by H. Hespenheide and E. Fisher (no date provided) from Costa Rica, Puntarenas, Monteverde (10.3; -84.816667; 1,455 m); LACM 149498 collected by P. Siegfried (no date provided) from Costa Rica, Alajuela, Poco Sol (10.3667; -84.6167; 580 m).

Diagnosis

Anolis insignis and the three species described below are the only Central American *Anolis* to combine large size (> 120.0 mm SVL), smooth scales on the upper thigh, and short limbs (Savage and Talbot 1978). *Anolis insignis* is diagnosed from the three species described below by its orange-red male dewlap (Fig. 1; white, peach-tan, and pink with dark streaks, respectively by species, in the other forms). It further differs from the Southwestern Costa Rican form in its lack of a postorbital blotch (present in the Southwestern Costa Rican form); from the Fortuna form in its prominent postcloacal scales in males (obscure in the Fortuna form); from *A. brooksi* in some scale counts (Table 1; e.g., greater number of postrostrals) and details of color pattern (Savage and Talbot 1978; e.g., absence of narrow black lines dorsally).

External description (in mm)

Snout-vent length (SVL) to 157.0 mm male, 140.0 mm female; head length-SVL ratio 0.24–0.25, head width-SVL ratio 0.14–0.16; ear height-SVL ratio 0.015–0.028; femoral length-SVL ratio 0.24–0.25; tail length-SVL ratio 1.9–2.1. Dorsal head scales mostly smooth, a few with weak keels or rugosity apparently reflecting underlying bone or ossification, pustules present in some specimens; frontal depression present, anterior half of snout raised in two faint parallel rows; rostral overlaps mental anteriorly; lateral edges of mental scales extend farther posteriorly than rostral; 9–11 scales across snout between second canthals; 2–3 scales between supraorbital semicircles; 2–3 scales separating interparietal and supraorbital semicircles; suboculars in contact with supralabials; five loreal rows; no elongate superciliaries, first superciliary is smaller than first canthal; anterior row of small scales following canthals along edge of orbit; circumnasal scale separated from rostral by one scale; interpari-

Table 1. Morphological traits of species similar to *Anolis insignis*. Measurements are in millimeters. Means are given with ranges in parentheses. Measurement characters were scored only for adults.

	Anolis insignis	***A. brooksi***	***A. kathydayae***	***A. savagei***
	n = 2 males, 3 females	*n* = 3 males, 2 females	*n* = 2 males, 2 females	*n* = 1 male, 1 female
Snout to vent length male	154.5	152.7	142.3	141.1
	(152.0–157.0)	(129.5–176.0)	(136.6–148.0)	(141.1)
Snout to vent length female	139.0	134.0	136.1	(juvenile)
	(138.0–140.0)	(134.0)	(136.1)	
Head length male	37.4	36.0	36.4	33.0
	(36.2–38.6)	(30.5–41.4)	(34.8–38)	(33.0)
Head length female	34.6	34.8	33.9	–
	(33.6–35.3)	(34.8)	(33.9)	
Head width male	21.6	21.4	21.6	21.0
	(20.8–22.4)	(18.1–24.7)	(20.7–22.5)	(21.0)
Head width female	21.3	20.8	21.2	–
	(20.4–22.6)	(20.8)	(21.2)	
Ear height male	3.0	3.7	4.2	2.9
	(2.3–3.6)	(3.4–4.1)	(3.9–4.5)	(2.9)
Ear height female	3.5	3.7	4.1	–
	(2.9–3.9)	(3.7)	(4.1)	

Table 1 (continued). Morphological traits of species similar to *Anolis insignis*. Measurements are in millimeters. Means are given with ranges in parentheses. Measurement characters were scored only for adults.

	Anolis insignis *n* = 2 males, 3 females	***A. brooksi*** *n* = 3 males, 2 females	***A. kathydayae*** *n* = 2 males, 2 females	***A. savagei*** *n* = 1 male, 1 female
Femoral length male	37.9 (36.7–39.1)	37.5 (31.6–43.4)	36.3 (34.2–38.5)	30.4 (30.4)
Femoral length female	34.5 (33.5–35.1)	33.4 (33.4)	32.7 (32.7)	–
4th toe length male	25.2 (24.7–25.7)	21.4 (19.1–23.7)	22.4 (20–24.8)	19.9 (19.9)
4th toe length female	23.4 (22.4–24.7)	21.5 (21.5)	20.2 (20.2)	–
Tail length	294.0 (287.0–310.0)	291.6 (240.0–355.0)	284.0 (275.0–292.0)	245.0 (245.0)
Number of dorsal scales in 5% SVL	9.5 (7–11)	11.6 (11.0–12.0)	9.0 (9.0)	8.0 (8.0)
Number of ventral scales in 5% SVL	9.5 (8.0–11.5)	8.5 (8–9)	10.0 (10.0)	8.0 (8.0)
Number of scales across snout at second canthals	10.0 (9.0–11.0)	10.4 (10–11)	10.0 (9.0–11.0)	8.5 (8.0–9.0)
Number of scales between supraorbital semicircles	2.2 (2.0–3.0)	3.4 (3.0–4.0)	3.2 (3.0–4.0)	2.0 (2.0)
Number of scales between interparietal and supraorbital semicircles	2.6 (2.0–3.0)	3.0 (2.0–4.0)	3.2 (3.0–4.0)	1.5 (1.0–2.0)
Number of postrostral scales	7.8 (7.0–10.0)	6.8 (6.0–7.0)	5.7 (5.0–6.0)	6.5 (6.0–7.0)
Number of postmental scales	7.4 (6.0–9.0)	6.0 (5.0–7.0)	5.0 (4.0–5.0)	7.5 (7.0–8.0)
Number of scale rows separating suboculars and supralabials	0	0	0	0
Number of supralabials from rostral to center of eye	8.2 (8.0–9.0)	8.0 (7.0–9.0)	7.2 (7.0–8.0)	7.0 (7.0)
Number of lamellae under phalanges II & III of 4th toe	26.6 (25.0–27.0)	26.4 (25.5–27.5)	25.5 (23.5–27.0)	26.7 (25.0–28.5)
Number of loreal rows	5.0 (5.0)	5.4 (5.0–6.0)	6.0 (6.0)	4.5 (4.0–5.0)
Posterolateral extent of mental	<= rostral	>= rostral	<=rostral	<rostral

etal length-SVL ratio 0.014–0.017; 8–9 supralabials to center of eye; 6–9 postmentals; 7–10 postrostrals; scales in supraocular disc only slightly differing in size; mental partially divided posteriorly, extending posterolaterally equal to or shorter than rostral, with straight posterior border; 0–2 keeled enlarged sublabials.

Dewlap reaches well posterior to axillae in males and females; dewlap scales in rows of multiple scales in both sexes; no axillary pocket; pair of distinct, abruptly enlarged postcloacal scales in males; dorsal scales smooth; zero enlarged middorsal rows, 7–11 longitudinal rows in 5% of SVL; ventral scales in transverse rows, smooth, 8–12 scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 25–27 lamellae under third and fourth phalanges of fourth toe; thigh scales smooth dorsally and ventrally, unicarinate anteriorly, multicarinate at knee; tail with a double row of middorsal scales.

Distribution and habitat

We have no experience with *Anolis insignis* in life. Savage (2002) reports that this is an uncommon canopy species that inhabits undisturbed forests.

With our recognition of multiple species within what was previously considered *Anolis insignis*, we restrict the range of *A. insignis* sensu stricto to the Cordillera Tilarán and Cordillera Central of Costa Rica. We currently consider the range of *A. insignis* to encompass localities for *A. insignis*-like anoles collected in Northern and Central Costa Rica. Assuming this range, the known elevation of *A. insignis* is 425 m (Bijagua, CRE 3715, UCR 8783) to

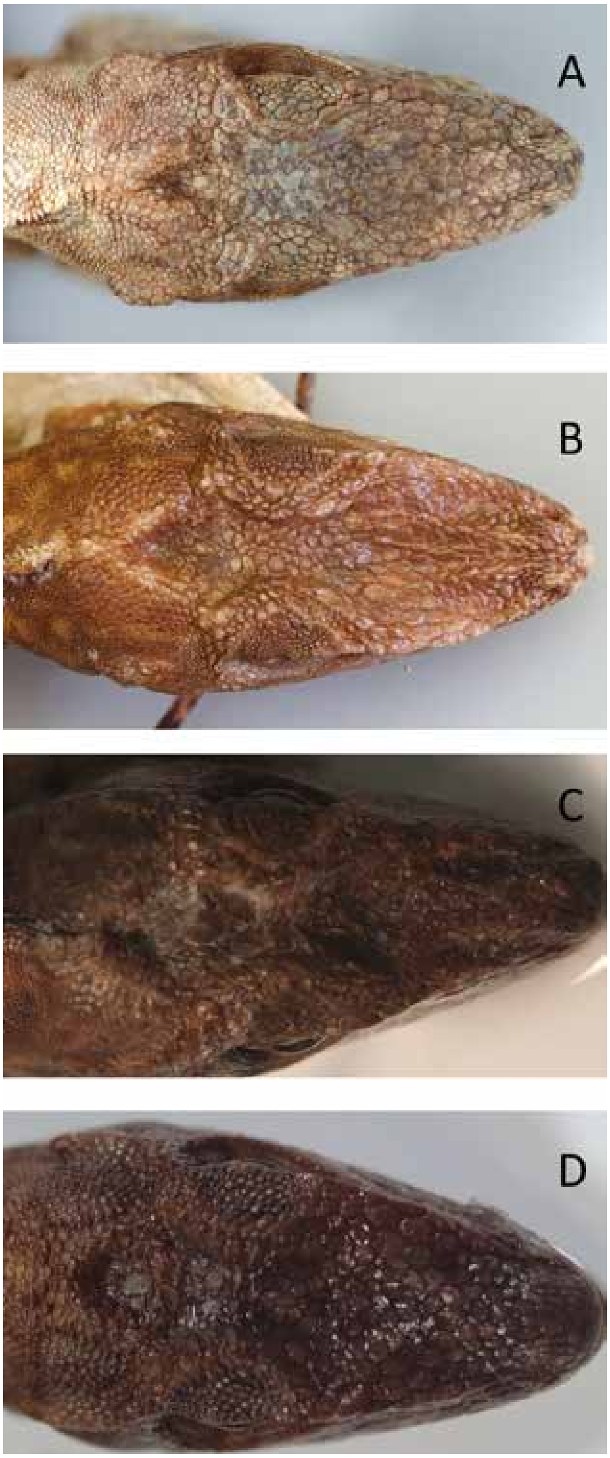

Fig. 5. Dorsal headscales of **A)** *Anolis kathydayae*, MSB 96613; **B)** *A. brooksi*, MSB 75647 **C)** *A. savagei*, MSB 96616; **D)** *A. insignis* LACM 149500.

1,500 m (La Palma, Holotype).

Anolis brooksi Barbour 1923

(Figures 2, 5–7)

Holotype

MCZ 16297 *Diaphoranolis brooksi*, juvenile female, from Mt. Sapo, Darién, Panama, 2,500 feet elevation; collected by Thomas Barbour and Winthrop Brooks, in April, 1922.

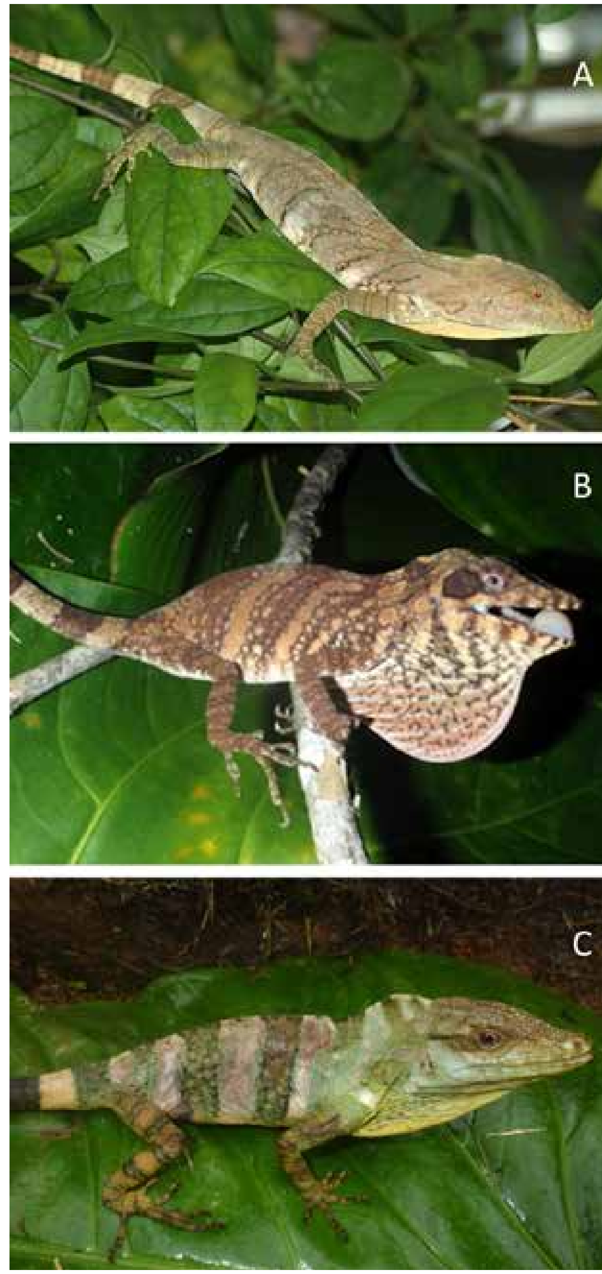

Fig. 6. Adult male individuals of **A)** *Anolis brooksi*, El Copé, Panama; **B)** *A. savagei*, Las Cruces, Costa Rica; **C)** *A. kathydayae*, Fortuna, Panama.

Examined specimens

Parque Nacional G.D. Omar Torrijos H., Coclé Province, Panama; 8.668, -80.593, 775 m: MSB 79924, MSB 79922, MSB 79923, MSB 75647, MSB 79925. Specimens examined but not scored for quantitative analysis: Cerro Azul, Panamá, Panama: MVUP 2007. Mt. Sapo, Darién, Panama: MCZ 16297 (holotype).

Diagnosis

Anolis insignis, *A. brooksi*, and the two species described below are the only Central American *Anolis* to combine

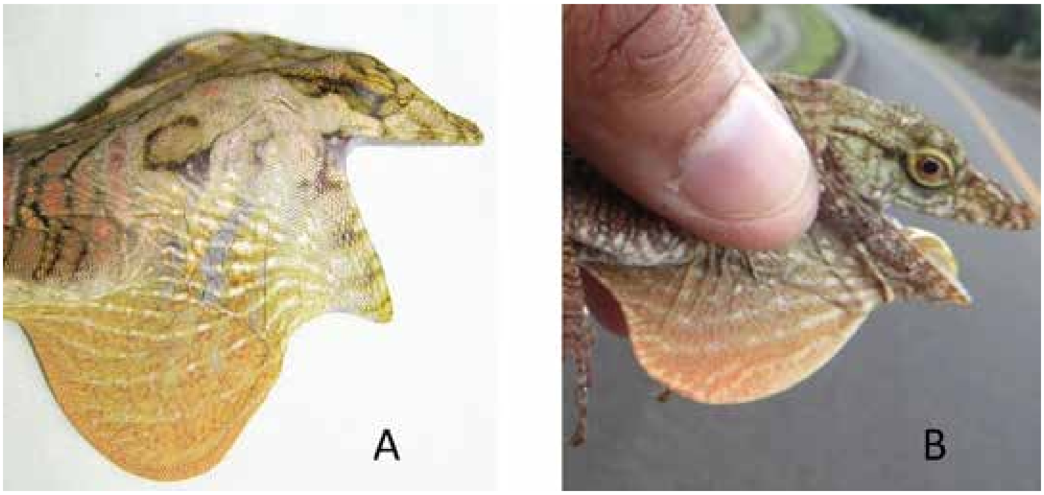

Fig. 7. Dewlaps of males of *Anolis brooksi* from **A)** Cerro Azul, Panama (MVUP 2007); **B)** Santa Fé, Panama (not collected).

large size (> 120.0 mm SVL), smooth scales on the upper thigh, and short limbs (Savage and Talbot 1978). *Anolis brooksi* is diagnosed from the three other *insignis*-like anole species discussed here by its peach-tan male dewlap (Fig. 2; orange-red in *A. insignis*; white, pale pink with dark streaks, respectively by species, in the other two forms). It further differs from the Southwestern Costa Rican form in its lack of a postorbital blotch (present in the Southwestern Costa Rican form) and its female dewlap color pattern (white or brown with dark streaks; pale pink with dark streaks in the Southwestern Costa Rica form); from the Fortuna form in its prominent postcloacal scales in males (obscure in the Fortuna form) and its female dewlap color pattern (white or brown with dark streaks; patternless white in the Fortuna form); from *A. insignis* in some scale counts (Table 1; e.g., fewer postrostrals) and details of color pattern (Savage and Talbot 1978; e.g., presences of narrow black lines dorsally).

Description (measurements in mm)

Snout–vent length to 176.0 mm male, 134.0 mm female; head length-SVL ratio 0.24–0.26, head width-SVL ratio 0.14–0.16; ear height-SVL ratio 0.023–0.028; femoral length-SVL ratio 0.24–0.25; tail length-SVL ratio 1.9–2.1. Dorsal head scales mostly smooth; frontal depression present, anterior half of snout raised in two faint parallel rows; rostral overlaps mental anteriorly; lateral edges of mental extend farther posteriorly than rostral; 10–11 scales across snout between second canthals; 3–4 scales between supraorbital semicircles; 2–4 scales separating interparietal and supraorbital semicircles; suboculars in contact with supralabials; 5–6 loreal rows; no elongate superciliaries, first superciliary is approximately equal in size to first canthal; row of small scales following canthals along edge of orbit; circumnasal scale separated from rostral by 1–2 scales; interparietal length-SVL ratio 0.014–0.015 (or absent); 7–9 supralabials to center of eye; 5–7 postmentals; 6–7 postrostrals; some enlarged scales present in supraocular disc (or all scales approximately equal), decreasing gradually in size; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border straight or in convex or concave arc; 1–2 keeled enlarged sublabials. Dewlap reaches well posterior to axillae in males and females; dewlap scales in rows of multiple scales in both sexes; no axillary pocket; distinct, abruptly enlarged postcloacal scales present in males; dorsal scales smooth; zero enlarged middorsal rows, 11–12 longitudinal rows in 5% of SVL; pair of middorsal scale rows raised in largest specimen; nuchal crest present with slightly enlarged triangular middorsal scales; ventral scales in transverse rows, smooth, 8–9 scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 25–28 lamellae under third and fourth phalanges of fourth toe; thigh scales smooth dorsally and ventrally, unicarinate anteriorly and multicarinate at knee; tail with a double row of middorsal scales.

Color pattern in life

Adult males from El Copé (MSB 75647) and Cerro Azul (MVUP 2007) appeared mainly tan dorsally, with diffuse banding of white, black, green, peach, and dark brown. The limbs and digits were banded with narrow double lines of black or dark green. The tail was patterned with distinct black and greenish bands. The dewlap was solid peach-tan. An adult female (MSB 79925) appeared similar to the males but possessed scant green dorsally, with a white dewlap with prominent dark streaking. A dark shoulder blotch is evident in individuals in some of our photos of adults, but not in others. The iris is red. The throat is light and the tongue appeared peach in an El Copé specimen but yellow in the specimen from Cerro Azul. Males from Cerro Azul and Santa Fé had dewlaps similar to the El Copé specimen, but slightly paler (Fig. 7). An uncollected specimen from Isla Escudo de Veraguas, Bocas del Toro, that we tentatively allocate to this species had a dewlap similar to those figured here but with a brighter, slightly orange-yellow tint. An adult

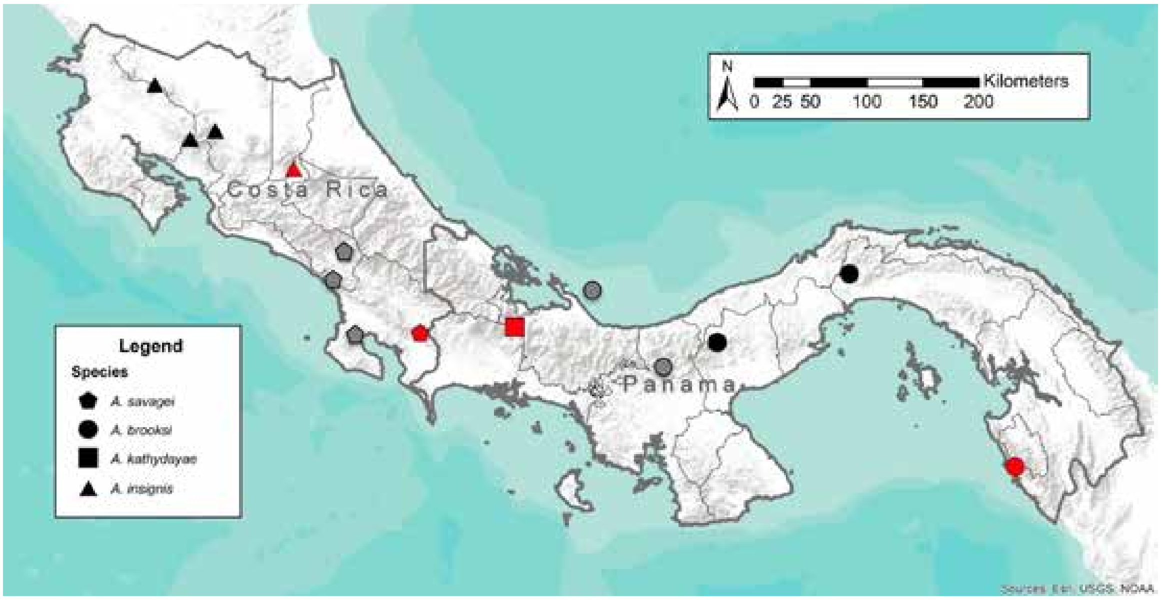

Fig. 8. Map of Panama and Costa Rica, showing localities for specimens referenced in text. Type localities are in red. Black symbols are specimens examined (type locality specimens also were examined for all species). Gray symbols represent unexamined specimens or photographic evidence discussed in text. Each point may represent multiple individuals (see text).

female dewlap figured by Lotzkat et al. (2013) was light brown with dark streaks.

Distribution and habitat

We collected *Anolis brooksi* in El Copé and Cerro Azul sleeping at night on saplings and tree branches from three to five meters above the ground. Specimens were collected in dense secondary forest (El Copé) and in disturbed habitat (Cerro Azul). Photographic evidence of male dewlap color pattern indicates the species is present at Santa Fé, Veraguas (see below) and, potentially, Isla de Escudo, Bocas del Toro (pers. obs.). Thus, *A. brooksi* appears to occur from sea level to 970 m from Darién north to Bocas del Toro.

Anolis savagei, new species

(Figures 2, 5, 6)

urn:lsid:zoobank.org:act:1F0F7528-F3D6-43B3-993D-E7AEBCB5A39C

Holotype

MSB 96616, adult male, collected at Las Cruces, Puntarenas, Costa Rica; 8.78242, -82.95886, 1,127 m; collected by Steven Poe, Eric Schaad, Ian Latella, and Mason Ryan on 20–23 March 2009.

Paratypes

UCR 20635 (not scored; POE 2671); LACM 149499 collected by R.W. McDiarmid on 21 Aug 1971 from Costa Rica, Puntarenas, San Vito de Java, OTS Las Cruces Biological Station (8.816667; -82.966667; 1,100 m).

Diagnosis

Anolis insignis, *A. brooksi*, *A. savagei*, and the species described below are the only Central American *Anolis* to combine large size (> 120.0 mm SVL), smooth scales on the upper thigh, and short limbs (Savage and Talbot 1978). *Anolis savagei* is distinguished from *A. insignis*, *A. brooksi*, and the form described below by its male dewlap color pattern of pale pink with dark streaks (orange-red in *A. insignis*; peach-tan in *A. brooksi*; white in the form described below; Figs. 1, 2) and presence of a prominent postorbital blotch (absent in *A. insignis*, *A. brooksi*, and the form described below).

Etymology

This name is a patronym to honor Dr. Jay M. Savage for his contributions to Neotropical herpetology, especially his seminal works, mentorship, and leadership in tropical biology and conservation in Costa Rica. Dr. Savage helped found the Organization of Tropical Studies (OTS) and the type locality of this species is the Las Cruces OTS field station.

Description of holotype

Snout-vent length 141.0 mm; head length-SVL ratio 0.23, head width-SVL ratio 0.15; ear height-SVL ratio 0.021; femoral length-SVL ratio 0.22; tail length-SVL ratio 1.74. Dorsal head scales smooth, some rugose; frontal depression present, dorsum with weak parallel rows evident anteriorly; rostral overlaps mental anteriorly; eight scales across snout between second canthals; two scales between supraorbital semicircles; one scale separating interparietal and supraorbital semicircles; suboculars in contact with supralabials; five loreal rows; zero elongate superciliaries, first large scale posterior to canthals is slightly smaller than first canthal; row of slightly enlarged scales along anterior aspect of dorsolateral edge of orbit; circumnasal scale separated from rostral by one scale; interparietal length-SVL ratio 0.021; seven supralabials to center of eye; seven postmentals; six postros-

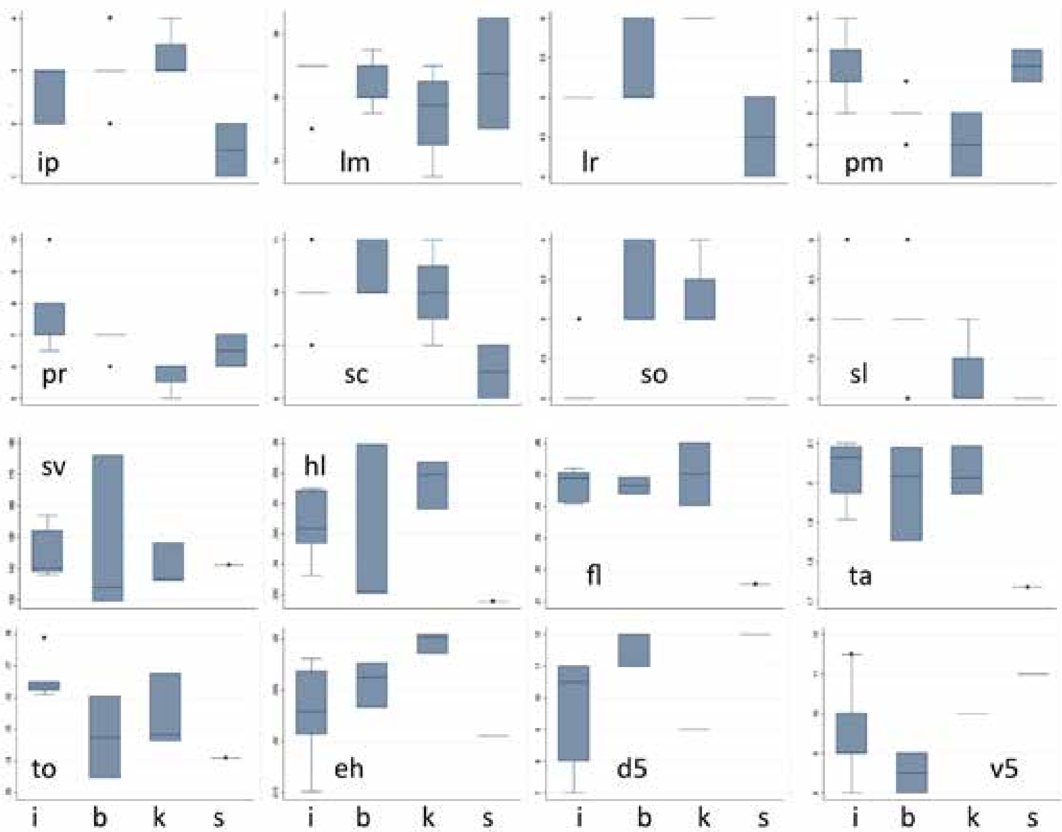

Fig. 9. Box plots showing variation between *Anolis insignis* (i), *A. brooksi* (b), *A. kathydayae* (k), and *A. savagei* (s). Traits are number of scales between interparietal and supraorbital semicircles (ip), number of expanded lamellae on fourth toe (lm), number of loreal rows (lr), number of postmental scales (pm), number of postrostral scales (pr), number of scales across the snout between the second canthals (sc), number of scales between the supraorbital semicircles (so), number of supralabial scales from rostral to center of eye (sl), snout to vent length (sv), head length relative to sv (hl), femoral length relative to sv (fl), tail length relative to sv (ta), toe length relative to sv (to), ear height relative to sv (eh), number of longitudinal dorsal scales in 5% of sv (d5), number of longitudinal ventral scales in 5% of sv (v5).

trals; some enlarged scales present in supraocular disc, decreasing gradually in size; mental partially divided posteriorly, with posterior border in concave arc; lateral edges of rostral extend farther posteriorly than mental; two enlarged smooth sublabials; more posterior lateral throat scales are keeled.

Dewlap reaches well posterior to axillae in males and females; dewlap scales in rows of multiple scales in both sexes; pair of distinct, abruptly enlarged postcloacal scales present; dorsal scales smooth, with no enlarged middorsal rows, 12 longitudinal rows in 5% of SVL; nuchal crest present with slightly enlarged middorsal scales; ventral scales in transverse rows, smooth, 11 scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 28–29 lamellae under third and fourth phalanges of fourth toe; tail with a double row of middorsal scales; thigh scales smooth dorsally and ventrally, mostly smooth anteriorly with a few weakly unicarinate scales.

Color pattern in life

Color patterns of a male (MSB 96616) and female (UCR 20635) specimen were very similar. Dorsal color was generally brown, with alternating tan and dark brown irregular bands, the dark bands with some lighter blotching within them. Photographic evidence (R. Stanley, I. Latella; pers. comms.) indicates some individuals possess green and pale peach-orange dorsally in addition to brown. The dewlap in both sexes was pale pink with black horizontal streaks. No shoulder blotch was observed, but a prominent postorbital blotch was present in all adult specimens examined (*n* = 5).

Distribution and habitat

We found *Anolis savagei* at night sleeping 5–6 m up on narrow tree branches along trails in the closed canopy secondary forest of Las Cruces Biological Station. More work is needed on the ecology of this species. Specimens examined for this paper are from the Cordillera de Talamanca in southwestern Costa Rica at 1,127 m. Two individuals photographed from the western edge of Chirripó National Park at 1,590 m (R. Stanley, pers. comm.) apparently are *A. savagei* based on the presence of a prominent postorbital blotch in each, and the darkly streaked dewlap of the individual for which the dewlap is partially visible. We have not examined the *A. insignis*-like specimens reported from near sea-level by Savage and Talbot (1978; Ballena, BM 1909.7.10.20; Rincón de Osa, UCR 4387), but these are likely to be *A. savagei* based on those authors' emphasis of a postorbital blotch in these specimens. Given these localities, *A. savagei* occurs on the Pacific slope of the Cordillera de Talamanca from sea level to at least 1,590 m, from Chirripó National Park south to Las Cruces (Fig. 8).

Anolis kathydayae, new species

(Figs. 2, 5, 6)

urn:lsid:zoobank.org:act:31E4F176-EA11-4172-A0E1-A9DE3AE65287

Holotype

MSB 96614 adult male from Panama, Chiriquí, trail from paved road near Chiriquí/Bocas del Toro province boundary at Fortuna pass; 8.78533, -82.21434, 1,178 m; collected by Steven Poe and Julian Davis on 13 March 2013.

Paratypes

MVUP 2128, juvenile from Panama, Bocas del Toro, side of Fortuna pass road, just north of Chiriquí/Bocas del Toro boundary; 8.78008, -82.20584, 1,038 m; collected by Steven Poe and Julian Davis on 13 March 2013. MSB 96612, same locality as holotype, collected by Steven Poe and Caleb Hickman, December 2003. MSB 79921, MSB 96613, same locality as holotype, collected by Steven Poe, Erik Hulebak, and Heather MacInnes on 28 July 2005.

Diagnosis

Anolis insignis, *A. brooksi*, *A. savagei*, and *A. kathydayae* are the only Central American *Anolis* to combine large size (> 120.0 mm SVL), smooth scales on the upper thigh, and short limbs (Savage and Talbot 1978). *Anolis kathydayae* is distinguished from these species by male dewlap color pattern (white with light green or dull blue tint in male *A. kathydayae*; orange-red in male *A. insignis*; pale pink with dark streaks in *A. savagei*; peach-tan in *A. brooksi*; Figs. 1, 2). It is further distinguished from *A. savagei* and *A. brooksi* by female dewlap color pattern (solid white with greenish tint in *A. kathydayae*; white or brown with dark streaks in *A. brooksi*; pale pink with dark streaks in *A. savagei*; unknown in *A. insignis*). At least in our samples, *A. kathydayae* is further distinguished from *A. insignis* by several scale characters (Table 1; e.g., fewer postmentals, 4–5 versus 6–9 in *A. insignis*). Additionally, the two male *A. kathydayae* we have examined display obscure, weakly enlarged postcloacal scales, whereas all male individuals of the other *insignis*-like anoles we have examined display large, distinct postcloacal scales.

Etymology

The name is a matronym to honor Kathy Day and the Miller Institute for Basic Research in Science. Kathy has contributed greatly to the professional and personal development of scientists and the advancement of basic science through her position running the Miller Institute.

Description of holotype

Snout-vent length 148.0 mm; head length-SVL ratio 0.26, head width-SVL ratio 0.15; ear height-SVL ratio 0.030; femoral length-SVL ratio 0.26; tail length-SVL ratio 2.0. Dorsal head scales mostly smooth, some with weak keels or wrinkling reflecting underlying bone or ossification; frontal depression present, dorsum with weak parallel rows evident anteriorly; rostral overlaps mental anteriorly; 10 scales across snout between second canthals; four scales between supraorbital semicircles; suboculars in contact with supralabials; zero elongate superciliary scales; first scale posterior to canthals is smaller than first canthal; six loreal rows; circumnasal scale separated from rostral by one scale; interparietal length-SVL ratio 0.018; seven supralabials to center of eye; six postmentals; six postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in size, bordered medially by a partial row of small scales; mental partially divided posteriorly, extending posterolaterally approximately even with rostral, with posterior border in concave arc; one-two enlarged keeled sublabials.

Dewlap reaches well posterior to axillae in males and females; dewlap scales in rows of multiple scales in both sexes; no axillary pocket; postcloacal scales slightly enlarged; dorsal scales smooth, pair of middorsal scale rows slightly raised, nine longitudinal rows in 5% of SVL; nuchal crest present with pair of slightly enlarged triangular middorsal scale rows; ventral scales in transverse rows, smooth, 10 scales in 5% of SVL; supradigitals multicarinate; toepads expanded, 27 lamellae under third and fourth phalanges of fourth toe; tail with a double row of middorsal scales; thigh scales smooth to weakly keeled dorsally and ventrally, unicarinate anteriorly, multicarinate at knee.

Color pattern in life

An adult male (MSB 96614) had a tan body with discrete dark green broad bands speckled with light tan. The anterior body to posterior head had a bluish-green wash. Dorsal head scales were greenish-tan, outlined with darker brown. A very faint blotch was present above the shoulder. The iris was brown and the tongue was dark yellow. The limbs and digits were greenish-tan, with darker green bands. The tail was banded with sharply alternating black and tan bands. The dewlap was white, with a yellowish-green tint. Another adult male (MSB 96613) was patterned similarly but mostly lacked green—the anterior bluish-green wash was absent, and the bands were dark brown to black with no greenish tint. The dewlap of this individual was white, with faint blueish tint. One adult female (MSB 79921) appeared dark greenish with diffuse banding of white, darker green, and brown. The dewlap appeared very pale yellow-green. A juvenile female (SVL 87.0 mm; MSB 96612) appeared nearly completely pale green, with faint white lateral bands and some darker green reticulations on the body and darker green bands on the limbs and digits, and white blotches dorsally on the head. This individual had a pale greenish-yellow dewlap with some dark green reticulations. A near-hatchling (MSB 96615) had a cream dewlap with prominent black streaks.

Distribution and habitat

We found adults of *Anolis kathydayae* sleeping horizontally on narrow branches along a trail in secondary forest three to five meters above the ground, and juveniles at roadside habitat four to five meters above the ground on twigs. Elevational range of these two sites is 1,038–1,178 m. Currently known distribution for *A. kathydayae* is the Fortuna pass area of Panama.

Discussion

The four *insignis*-like *Anolis* species discussed here are distinct in male dewlap color (Figs. 1, 2), which usually varies little within species of *Anolis*, and in additional morphological traits (Diagnoses; Table 1; Fig. 9). Below we discuss the status of each species relative to previous discussions on these forms and our own views of the distinctiveness and importance of diagnostic traits for these species, especially in light of our small sample sizes. We also discuss some limited molecular data bearing on these forms.

Savage and Talbot (1978) originally drew attention to differences between Northern Costa Rican (i.e., *Anolis insignis*), southern Costa Rican (i.e., *A. savagei*), and Panamanian (i.e., *A. brooksi*, *A. kathydayae*) "*A. insignis*." The postocular blotch of southern Costa Rican forms discussed by these authors appears to be an autapomorphic diagnostic trait for *A. savagei*. Including photos, preserved specimens, and reports from Savage and Talbot (1978), we are aware of eight specimens that are assignable to *A. savagei* based on male dewlap color of the population and locality. All eight of these specimens possess a postocular blotch, and all *A. insignis*, *A. brooksi*, and *A. kathydayae* examined by us (including photos, $n = 18$) lack a postocular blotch. Additionally, *A. savagei* is quite distinct in overall morphology (Table 1; Diagnoses; Fig. 9).

Anolis kathydayae is striking in its possession of pale, patternless dewlaps in males and females (Fig. 2). Although a few species of *Anolis* display intraspecific variation in male dewlap color pattern, such variation nearly always occurs within populations (e.g., *A. gemmosus* around Mindo, Ecuador; *A. valencienni* in northern Jamaica) or at hybrid zones (e.g., *distichus*-group forms; Glor and LaPort 2012). Thus we note the relative invariance of the distinctive male dewlap of *A. brooksi* across El Copé in Cocle (Fig. 2), Santa Fe in Veraguas (Fig. 7), Cerro Azul in Panama (Fig. 7), and possibly Isla Escudo de Verguas in Bocas del Toro (pers. obs.; see above) as evidence for the species status of this form relative to the other forms discussed here. We note the constancy of the distinctive streaked dewlap of *A. savagei* between Las Cruces and Chirripó (a distance of ~100 km), and the presence of an orange-red male dewlap of *A. insignis* over at least three localities in northern Costa Rica (Poco Sol, La Fortuna, Monteverde; photographic evidence). We know of no intermediate forms between these dewlap types, although some minor variation occurs within each of them. Thus we view the presence of the unusual male and female dewlaps of *A. kathydayae* as strong evidence for the species status of this form, in addition to the molecular evidence presented below and the external morphological patterns shown in Table 1 and Fig. 9.

We observed three of the four species of *insignis*-like anoles to differ consistently in female dewlap color (Fig. 2). Female *Anolis brooksi* have a white or brown dewlap with black streaks, female *A. savagei* have a pale pink dewlap with dark streaks, and female *A. kathydayae* have a pale, patternless dewlap (we have not seen a confirmed female dewlap of true *A. insignis*). We note that there is considerable ontogenetic variation in this trait, with all examined juvenile females in life (*A. kathydayae*, *A. brooksi*) possessing some dark streaking on the dewlap. Our observations of adult female dewlap color pattern suggest some taxonomic utility to this character in this case, but these differences may not be evident in larger sample sizes.

The Northern Costa Rican form (i.e., *Anolis insignis*) and the widespread Panama form (i.e., *A. brooksi*) share similar dorsal color patterns and their male dewlaps are most similar among the species discussed here (Figs. 1, 2). There remains much work to be done on the systematics of these forms. The geographic patterns among the *insignis*-like *Anolis*, including two similar geographically intervening species (i.e., *A. savagei*, *A. kathydayae*; Fig. 8), suggests that conspecificity of *A. brooksi* and *A. insignis* is unlikely. Still, this is a hypothesis that begs continued investigation, as is the potential presence of multiple species within *A. insignis* and *A. brooksi*. In particular, we have little confidence that the populations that we are calling *A. brooksi* are actually conspecific with topotypical *A. brooksi*, for which we have examined only a single preserved juvenile specimen (i.e., the holotype). We elect to use this name because juveniles of the tan-dewlap form (i.e., *A. brooksi* as we are recognizing it) are indistinguishable from the holotype of *A. brooksi*, and the range of the tan dewlap form approaches the *A. brooksi* type locality to the east. To give the tan-dewlap form a new name rather than assume its conspecificity with *A. brooksi* seems unconservative under these circumstances.

The low sample sizes of our analyses (Table 1; supplemented by photographic evidence and observations in Savage and Talbot [1978] and Lotzkat et al. [2013]) are unfortunate but currently unavoidable. The *insignis*-like *Anolis* apparently are difficult to find, or possibly rare. Lotzkat et al. (2013) included just two collected individuals of *insignis*-like anoles in their summary of the giant anoles of Panama. Savage and Talbot (1978) studied all specimens of *insignis*-like anoles collected before 1978, a total of 24 individuals. Vertnet lists just 28 records for *A. insignis* as of 08 August 2016, after decades of intensive herpetological field work in Costa Rica and Panama since Savage and Talbot (1978). Our new sample of eleven collected specimens, plus additional photographic vouchers, warrants a new treatment of these forms and supports recognition of multiple species. However, we recognize that the strength of our inferences is tempered by our necessarily limited sampling. We have little doubt that the taxonomic picture we have painted for these forms, while pragmatic and warranted given the evidence in front of us, is incomplete.

Some DNA sequence data has been generated for *Anolis brooksi* and *A. kathydayae* under the name *A. insignis*, but no molecular data exists for *A. savagei* and true *A. insignis*. Castañeda and de Queiroz (2011) included data from COI, ND2, and RAG1 genes for an "*A. insignis*" sample from Fortuna Reserve, i.e., near the type locality of *A. kathydayae*. Alfoldi et al. (2011) included data for several genes for a sample of *A.* "*insignis*" from Cerro Azul, Panama Province (POE 2154 in their appendix; now MVUP 2007). This individual clearly is assignable to *A. brooksi* (Fig. 7). Lotzkat et al. (2013) collected 16S data for an adult and juvenile female specimen of "*A. insignis*" from Santa Fé, Veraguas, and Willie Mazu, Comarca Ngöbe-Buglé in Panama, respectively. Accurate identification of these specimens is not straightforward because our diagnoses are based mainly on adult male specimens and the species in question generally overlap in scalation (Table 1). However, the adult female specimen of Lotzkat et al. (2013), from Santa Fé, is referable to *A. brooksi* based on female dewlap color pattern (Lotzkat et al. 2013: Fig. 14C) and locality; a subadult male photographed from Santa Fé (Fig. 7) clearly is *A. brooksi*. The juvenile specimen (SMF 91477) may be *A. kathydayae* or *A. brooksi*. The locality of this specimen is proximal to the type and other known locality of *A. kathydayae* but at a lower elevation on the Caribbean slope. This proximity to the *A. kathydayae* type locality suggests *A. kathydayae* as the most likely identification for this population, but reported 16S distances suggest this sample represents *A. brooksi*. The uncorrected 16S distance between the Lotzkat et al. (2013) samples is just 0.004—a 16S distance corroborated by comparison of the Willie Mazu sequence with our Santa Fé sample (MVUP 2007). Perhaps this specimen is *A. kathydayae* and 16S is evolving slowly in one or both of *A. kathydayae* and *A. brooksi*, or perhaps the specimen is *A. brooksi* and this species approaches *A. kathydayae* on the Caribbean slope.

An alternative interpretation of the 16S result is conspecificity of the Fortuna and Santa Fé populations (i.e., of *Anolis brooksi* and *A. kathydayae* as we have recognized them here), with the differences between these populations noted herein attributed to intraspecific variation. This interpretation seems unlikely given the consistent morphological differences between these forms (Fig. 2; Table 1; Fig. 9) and new information on mitochondrial DNA distances for these populations. We sequenced the mitochondrial ND2 gene of the Santa Fé tissue (data included here in the phylogenetic analysis) as part of a larger project (Poe et al. 2017) and found an uncorrected ("p") distance of 12.5% between the Castañeda et al. (2011) "*A. insignis*" sample (i.e., *A. kathydayae*) and the Santa Fé sample (i.e., *A. brooksi*). This distance is similar to pairwise species distances among many distinctive species of *Anolis* (e.g., the *A. microtus*-*A. brooksi* [Santa Fé] ND2 distance is 9.5%). Thus, information from the ND2 gene corroborates our morphological inference of separate species status for Fortuna (*A. kathydayae*) and eastern (*A. brooksi*) populations of anoles similar to *A. insignis*.

The phylogenetic analysis was unable to robustly resolve the relationships of the new forms (Fig. 4). The well-supported clades in the estimated tree—i.e., the ingroup and the sister relationship of *Anolis microtus* and *A. ginaelisae*—were well-established previous to this work (Savage and Talbot 1978; Castañeda and de Queiroz 2011; Lotzkat et al. 2013; Poe et al. 2015). The poor support for the interrelationships of the four species discussed here indicates that external morphological data alone is inadequate to resolve them. Clearly, additional phylogenetic work using DNA sequences is needed on the *insignis*-like *Anolis*. Fresh sampling of known coastal versions of these species in Caribbean Panama and Pacific Costa Rica (Fig. 8; see localities in Savage and Talbot [1978]) and incorporation of material from the type localities of *A. insignis*, *A. savagei* and *A. brooksi* would be especially informative, for questions of species boundaries as well as phylogeny.

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Appendix 1

Morphological characters for phylogenetic analysis.

1. Maximum snout to vent length (SVL; mm; ordered). 0: < 120; 1: 120–129; 2: 130–139; 3: 140–149; 4: 150–159 5: >159.

2. Femoral length/SVL (ordered). 0: < 0.230; 1: 0.230–0.239; 2: 0.230–0.239; 3: 0.240–0.249; 4: 0.25–0.259; 5: >0.259.

3. Ear height/SVL (ordered). 0: < .017; 1: 0.17–0.019; 2:0.020–0.022; 3: 0.023–0.025; 4: 0.026–0.028; 5: >0.28.

4. Toe length/SVL (ordered). 0: < 0.16; 1: 0.16; 2:0.17; 3: 0.18; 4: 0.19; 5: >0.19.

5. Tail length/SVL (ordered). 0: < 1.75; 1: 1.75–1.84; 2: 1.85–1.94; 3: 1.95–2.04; 4: 2.05–2.14; 5: >2.14.

6. Mean number of longitudinal ventral scales in 5% of SVL (ordered). 0: < 8; 1: 8–8.4; 2: 8.5–8.9; 3: 9–9.4; 4: 9.5–9.9; 5: >9.9.

7. Mean number of longitudinal dorsal scales in 5% of SVL (ordered). 0: < 8.5; 1: 8.5–8.9; 2: 9–9.4; 3: 9.5–9.9; 4: 10–10.4; 5: >10.5.

8. Mean number of expanded lamellae on toe IV (ordered). 0: < 23; 1: 23; 2: 24; 3: 25; 4: 26; 5: >26.

9. Mean number of scales across the snout at the second canthals (ordered). 0: < 7; 1: 7-7.9; 2: 8–8.9; 3: 9–9.9; 4: 10–10.9; 5:>11.

10. Mean number of scales between supraorbital semicircles (ordered). 0: 0: < 2; 1: 2; 2: 2.5; 3:3; 4: 3.5; 5:>3.5.

11. Elongate superciliary scale (longer than first canthal; frequency-coded). 0: absent; 5: present.

12. Mental (frequency coded). 0: extends along mouth posteriorly past rostral; 5: rostral extends posteriorly past mental.

13. Mean number of postmental scales (ordered). 0: < 6; 1: 6–6.4; 2: 6.5-6.9; 3: 7–7.4; 4: 7.5-7.9; 5: >7.9.

14. Number of postxiphisternal incriptional ribs (Etheridge 1959; Savage and Talbot 1978; frequency coded). 0:4; 5:5.

15. Number of supralabial scales from rostral to center of eye (ordered). 0: < 6.5; 1: 6.5-6.9; 2: 7.0-7.4; 3: 7.5-7.9; 4: 8.0-8.4; 5: >8.4.

16. Scales on upper surface of thigh (Savage and Talbot 1978; frequency coded). 0: smooth; 5: keeled.

17. Scales in supraocular disc (Savage and Talbot 1978; ordered). 0: small, approximately equal in size; 5: mix of large and granular scales.

18. Male dewlap color (unordered). 0: pink; 1: white; 2: orange-red; 3: tan-peach; 4: pale pink with black streaks; 5: yellow.

Appendix 2

Coding for morphological characters in phylogenetic analysis.

A. fraseri	0	1	3	1	5	1	5	0	2	1	(23)	0	1	0	5	5	0	5
A. frenatus	3	5	4	5	4	5	4	3	5	5	5	0	5	0	5	5	0	1
A. ginaelisae	0	4	0	3	5	2	0	0	1	0	0	0	0	5	3	5	5	0
A. microtus	1	2	0	3	4	0	0	0	0	1	0	0	1	5	2	5	5	0
A. insignis	4	4	3	2	3	4	3	5	4	1	0	4	3	5	4	0	5	2
A. brooksi	5	4	4	0	3	2	5	4	4	3	0	0	1	5	4	0	5	3
A. kathydayae	3	4	5	0	3	5	2	4	4	3	0	4	0	5	2	0	5	1
A. savagei	3	0	2	0	0	5	5	5	2	1	0	5	4	5	2	0	5	4

Steven Poe is Associate Professor in the Department of Biology and Associate Curator in the Division of Amphibians and Reptiles of the Museum of Southwestern Biology at the University of New Mexico, USA. His research focuses on taxonomy, phylogenetics, and comparative ecology and evolution, especially of *Anolis* lizards. He has collected over 250 species of *Anolis* in 15 countries.

Mason J. Ryan is a snake conservation biologist at Arizona Game and Fish Department and Research Associate at the University of New Mexico Museum of Southwestern Biology, USA. His research focuses on tropical and desert amphibians and reptiles with an emphasis on disease, climate change, conservation, and community ecology.