A new species of Anolis (Squamata: Iguanidae) from Panama

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Abstract.—We describe Anolis elcopeensis, a new species of anole lizard from low to moderate elevations of the Pacific slope of the Cordillera Central of central Panama. Anolis elcopeensis is a close relative of and resembles the Amazonian species A. fuscoauratus but differs from it and similar species mainly in body size, male dewlap color, and mitochondrial DNA. We estimate the phylogenetic position of the new species relative to all species of Anolis, and analyze variation in the mitochondrial COI gene among some populations of the new species. We also discuss the mythical presence of Anolis fuscoauratus in Panama, document the possible occurrence of A. maculiventris in Panama, and present preliminary evidence for multiple cryptic fuscoauratus-like species in eastern Panama.

Key words. Central America, cryptic species, Darién, lizard, Panama, Reptilia

Introduction

Panama continues to yield new species of lizards and frogs annually despite already displaying one of the highest herpetofaunal diversities in Central America (Kohler 2008, 2011). Thirteen new species of Anolis have been described from Panama since 2007 to bring the number of Anolis species known from Panama to 44. The dynamic biogeographic history of Panama as a land bridge between North and South America has been cited as an explanation for the extraordinary faunal diversity of this country (Savage 1983).

Herpetologists working in Panama have long known of an undescribed species of Anolis similar to A. fuscoauratus from Barro Colorado Island (BCI) and other areas (Myers and Rand 1969; Ibañez et al. 1994; Stan Rand, pers. comm. 2003). This abundant species has remained undescribed probably due to its lack of distinctive characteristics and resemblance to other nondescript anoles in Central and South America. Anolis species similar to A. fuscoauratus frequently are straightforwardly differentiable only by male dewlap color. We have collected numerous examples of this undescribed species from its known localities and several new localities and have confirmed its uniqueness using molecular and morphological data. We describe this form from material collected west of the Panama Canal Zone and provisionally assign the well-known Canal Zone populations to this species. We also present evidence that this form is part of a complex of central and eastern Panamanian species similar to Anolis fuscoauratus.

Materials and Methods

We adopt the evolutionary species concept (Simpson 1961; Wiley 1978) and operationalize this concept by identifying species based on consistent differences between populations. That is, we hypothesize that populations or sets of populations that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species.

Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm), usually to the nearest 0.1 mm. Snout-vent length (SVL) was measured from tip of snout to anterior margin of cloaca. Head length was measured from tip of snout to anterior margin of ear opening. Femoral length was measured...
from midline of venter to knee, with limb bent at a 90° angle. Head width was measured at the broadest part of the head, between the posterolateral corners of the orbits. Scale terminology and characters used mainly follow standards established by Ernest Williams for species descriptions of anole lizards (e.g., Williams et al. 1995). Museum abbreviations follow Sabaj Perez (2014). Type specimens were deposited in the Museum of Southwestern Biology (MSB) of the University of New Mexico.

### Phylogenetic analyses

We first identified a hypothesized undescribed species of *Anolis* based on a discovered population’s all-orange male dewlap, small body size, and morphological and genetic distinctness (see below). In order to determine the phylogenetic position of the new species and identify appropriate species for comparison, we included the putative new species in phylogenetic analyses of all recognized species in the genus *Anolis* as of 01 June 2014 (results not shown). We collected morphological and mitochondrial COI data for the putative species and combined these with existing data for multiple genes (Alfoldi et al. 2012; the informal name “sunni” in supplementary appendices refers to this form but is not listed in the published paper) and additional new collected data. Preliminary phylogenetic analyses of this hypothesized species and all known species of *Anolis* suggested this form to be a member of a strongly supported clade of 14 Central and South American species similar to *A. fuscoauratus* (we henceforth refer to these species as the “fuscoauratus group”). We analyzed this sample of 15 species with two outgroups (*A. carpenteri, A. polylepis*) using a partitioned Bayesian Analysis (Ronquist et al. 2012) with one “mixed” GTR model with rate heterogeneity for the DNA sequence data (24879 sites) and another “standard” model for morphological data (46 characters). We ran the analysis for 2,000,000 generations, sampling every 1,000 trees, and discarded the first 50% of samples as burnin.

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**Fig. 1.** Phylogenetic estimate of placement of *A. elcopeensis* sp. nov. based on Bayesian analysis of morphological and molecular data. Numbers are clade credibility values.
We also performed phylogenetic analysis of the mitochondrial COI gene for multiple individuals of the putative new species and single individuals of close relatives according to the above analysis (Appendix 1). Data were from the Barcode of Life initiative (see wwwbarcode-of-life.org for data collection techniques) and published data. We used Partitionfinder (Lanfear et al. 2012) to identify a best model for this gene and assigned “mixed” GTR models with rate heterogeneity to each partition. We ran the analysis for 2,000,000 generations, sampling every 1,000 trees, and discarded the first 50% of samples as burnin.

Statistical analyses

Among geographically proximal forms, the new species is most similar to Anolis gruuo in external morphology (see below). In order to test the distinctiveness of the hypothesized new species relative to this form, we performed a discriminant function analysis of 14 individuals of the new species and three individuals of A. gruuo using 10 characters of scalation, with a-priori grouping of individuals as either A. gruuo (individuals from Santa Fe, Veraguas, Panama; Lotzkat et al. 2012) or the putative new species (individuals from near El Copé, Penonomé, and El Valle; Cocle; see below; Table 1). Characters incorporated were number of scales across the snout at the second canthals (snc), number of scales between supraorbital semicircles (sosc), number of scales between interparietal and supraorbital semicircles (iposc), number of postrostrals (pr), number of postmentals (pm), number of loreal rows (lorr), number of supralabials from rostral to center of eye (slor), number of expanded lamellae on fourth toe (lm), number of ventral scales counted longitudinally in 5% of snout to vent length (v5), and number of dorsal scales counted longitudinally in 5% of snout to vent length (d5). We observed no consistent differences in these traits between males and females and therefore pooled sexes in the analysis.

Results

The phylogenetic analysis of fuscoauratus group Anolis placed the putative new species with South American species A. fuscoauratus and A. tolimensis with weak support (Fig. 1). There was strong support (probability = 85%) for the new species clustering with a clade separate from species similar to A. altae (i.e., A. altae, A. monteverde, A. tenorioensis) within the fuscoauratus group clade.

The Partitionfinder analysis of the COI dataset suggested two partitions, one for amino acid positions one

\[ \text{elcopeensis Caimito} \]
\[ \text{elcopeensis NW Penonomé} \]
\[ \text{elcopeensis El Valle} \]
\[ \text{elcopeensis El Copé} \]
\[ \text{cf elcopeensis Lake Bayano} \]
\[ \text{fuscoauratus} \]
\[ \text{cf elcopeensis Pipeline Road} \]
\[ \text{gruuo} \]
\[ \text{kemptoni} \]
\[ \text{maculiventris} \]
\[ \text{fortunensis} \]

Fig. 2. Phylogenetic estimate of the mitochondrial COI gene for samples of A. elcopeensis and close relatives based on Bayesian analysis. Numbers are clade credibility values.
Table 1. Specimens and data used in Discriminant Function Analysis (svl listed for reference; not used in dfa). See text for abbreviations.

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A. elcopeensis mean: 12.1 1.9 3.6 6.4 4.9 8.3 5.5 11.4 8.9 14.2 39.6

gruuo

POE 1626 9 1 3 6 4.5 9.5 8 7 8 13.5 45.0

gruuo

POE 1627 9 3 4 6 5 8.5 6 9 9 16 43.1

gruuo

POE 1628 10 2 4 7 4.5 8 6 8 10 14 43.1

A. gruuo mean: 9.3 2.0 3.7 6.3 4.7 8.7 6.7 8.0 9.0 14.5 43.7

and two and a second partition for position three. The resulting tree (Fig. 2) shows substantial divergence of the putative new species. A mitochondrial clade composed of individuals from Parque Omar Torrijos, El Valle, and two localities near Penonomé is minimally divergent among populations (0.2–1.4% p distances) and at least 7.3% divergent from other included Anolis species. We consider these populations, which are uniform in male dewlap color, to inhabit the holotype and paratype localities of our putative new species and we describe this form below. We also discuss the other two samples (from Pipeline Road near the Panama Canal Zone and Lake Bayano) that show substantial divergence from included Anolis.

The discriminant function analysis accurately classified 100% of A. gruuo and 100% of the putative new species.

Systematics

**Anolis elcopeensis sp. Nov**

urn:lsid:zoobank.org:act:9D828BDE-E151-48FE-91E7-E176E693B382

Figs. 3A, 4A–B, 5A, 6.

**Holotype**

MSB 95571, adult male from Parque Nacional G.D. Omar Torrijos H., Cóclea Province, Panama (8.66815, -80.59267, 801 m), collected by Eric Schaad on 13 December 2008 from the trails near the visitor center.

**Paratypes scored for traits**

MSB 95570 bears the same data as the holotype. MSB 95550-2 bear the same locality data as the holotype, collected by Steven Poe and Caleb Hickman in December 2003. MSB 95543-9, west of El Valle de Antón, road ending at Chorro Las Mozas, Coclé Province, Panama (8.859476, -80.14686, 570 m), collected by Poe and Hickman in December 2003. MSB 95554-7, 95560-1, same west of El Valle de Antón locality, collected by Poe, Erik Hulebak, and Heather MacInnes during 30 July–4 August 2004. MSB 95559, Hotel Campestre, El Valle de Antón, Coclé Province, Panama (8.6129, -80.1251, 617 m), collected by Poe, Hulebak, and MacInnes on 31 July 2004.

**Additional topotypical paratypes**

MSB 95569, 95572-9 bear the same data as the holotype, collected by Schaad during December 2008.

**Diagnosis**

*Anolis elcopeensis* is a small grayish-brown anole with smooth ventral scales and short limbs. We diagnose this species relative to its 11 closest relatives (Fig. 1). *Anolis elcopeensis* is unlikely to be confused with *A. fuscaura* (Amazon basin; solid pink male dewlap), *A. bo-
A new species of *Anolis* from Panama

**Figure 3.** A) *Anolis elcopeensis* (female, El Copé, Coclé, Panama). B) A. *cf. elcopeensis* (male, south of Gamboa, Panamá, Panama). C) A. *cf. maculiventris* (female, Yaviza, Darién, Panama).
A. elcopeensis is most easily distinguished from the Central American members of its clade by male dewlap color (Fig. 4; except for A. gruuo) and smaller body size (maximum SVL = 45 mm, n = 35): A. gruuo (solid orange male dewlap; maximum SVL = 52 mm); A. pseudokemptoni (red-orange anterior, pink posterior male dewlap; maximum SVL = 55 mm); A. kemptoni (red-orange anterior, pink posterior male dewlap; maximum SVL = 53 mm); A. fortunensis (red anterior, orange posterior male dewlap; maximum SVL = 49 mm).

In the field A. elcopeensis is most likely to be confused with A. gruuo and A. carpenteri, which have similar solid orange male dewlaps (A. altae, which also is similar, does not occur in Panama); and A. limifrons and A. gaigei, with which it is frequently sympatric (Anolis elcopeensis is amply genetically distinct from each of these species; Figs 1, 2; A. gaigei is phylogenetically very distant from the fuscaauratus group, data not shown). In addition to being larger, male A. gruuo display an externally bulging tailbase in our photos, presumably indicating larger hemipenes, which we did not observe in male A. elcopeensis (Fig. 5). Anolis gruuo is found at mid to high elevations (860–1,530 m) of the Serrana Tabasara from Santa Fe west 80 km to just past Hato Chami (Lotzkat et al. 2012). We found Anolis elcopeensis at mid to low elevations (245–801 m) from El Copé east to Altos de Campana and possibly further (see below). Anolis carpenteri has a dorsal greenish tint and we have observed it to become patterned only when stressed. Anolis elcopeensis is never green, and usually displays banding on the tail and a dark interorbital bar regardless of mood. Anolis carpenteri is found on the Caribbean slope at mid to low elevations. All of our collections of A. elcopeensis are on the Pacific slope. Anolis elcopeensis and A. limifrons differ in male dewlap color (solid orange in A. elcopeensis, dirty white with or without basal yellow spot in A. limifrons). Females of these frequently sympatric species may be distinguished by limb length. The adpressed hindlimb of A. elcopeensis usually reaches to the ear, whereas in A. limifrons the hindlimb is longer, reaching anterior to the eye. Anolis elcopeensis and A. gaigei differ in the condition of the ventral scales (strongly keeled in A. gaigei; smooth in A. elcopeensis).

Etymology

The name honors the type locality, Parque Nacional G. D. Omar Torrijos H., and the people who have worked to maintain this wonderful forest. The park previously was named P. N. El Copé. Several new species of Anolis recently have been described from the park (i.e., A. kunayalae, A. ibanezi, A. elcopeensis).

External description of holotype (paratype variation in parentheses, measurements in mm)

Snout to vent length 43.5 (males to 44.6; females to 44.4); head length 0.23 SVL (0.22–0.26 SVL); head width 0.14 SVL (0.13–0.15 SVL); femoral length 0.25 SVL (0.25–0.28 SVL); ear height 0.03 SVL (0.02–0.03 SVL); tail length 1.7 SVL (1.5–1.7 SVL); fourth toe length 0.17 SVL (0.13–0.17 SVL).
A new species of *Anolis* from Panama

Dorsal head scales multicular in frontal area and unico multicular in nasal area, mostly unico multicular in supranasal disc, some smooth scales between supraorbital semicircles and posterior to orbits (or frontal and supraocular areas nearly smooth); frontal depression present; dorsal surface of rostral scale smooth, not notched; thirteen (10–14) scales across the snout between canthals; supraorbital semicircles distinct, separated by three (1–3) scales; three (2–5) scales separate interparietal and supraorbital semicircles; supraocular disk with some enlarged scales, bordered by a complete row of small scales; one elongate supraciliary scale followed by a series of small scales; seven (4–7) loreal rows; greater than 35 total loreals; elongate anterior nasal scale contacts sulcus between rostral and first supralabial (or nasal not greatly elongate); preoccipital absent; seven (6–9) supralabials to center of eye; six (4–7) postrostrals; 6 (4–8) postmentals; gradually enlarged scales in supranasal disc; mental completely (or partially) divided posteriorly, extends posterolaterally beyond rostral (or nearly even with sulcus), with posterior border in concave arc (or straight line transverse to head); sublabials weakly enlarged, not much larger than medial scales; dewlap large, reaching posterior to axillae (proportionately smaller in small males; variable in females: absent or small, to axillae); six-seven rows of single scales on male dewlap; tubelike axillary pocket absent; enlarged postcloacal scales present (or absent in all females and some males); nuchal, dorsal, and caudal crests absent; dorsal scales keeled; approximately two (0–3) enlarged middorsal rows; twelve (9–15) longitudinal scale rows in 5% of SVL; ventral scales smooth, in transverse rows; eleven (8–11) longitudinal scale rows in 5% of SVL; anterior thigh scales large, keeled, becoming smaller and smooth posteriorly; supradigits multicular; toepads expanded and overlap first phalanx; fifteen (13–16) expanded lamellae under third and fourth phalanges of fourth toe (counted using the approach of Williams et al., [1995]); tail with single row of keeled middorsal scales.

Figure 5. A) Anolis elcopeensis (male, El Copé, Coclé, Panama). B) A. gruuo (male, Hato Chami, Chiriquí, Panama). Note bulging tail base in A. gruuo.
Skeletal description (based on dry skeletons MSB 95560-1)

Parietal roof slightly convex, with Y-shaped parietal crests with a short stem, with no casing, lacking crenulation on edges, with anterolateral corners flush with posterolateral edges of frontal; posterior roof of parietal slopes inferiorly; supraoccipital crests completely visible dorsally (no “half-funnel”); pineal foramen extends posteriorly into parietal, forming a U that opens at the parietal-frontal suture; dorsal skull bones smooth; postfrontal present, appears partially fused; prefrontal separated from nasal by anterior extension of frontal; frontal sutures anteriorly with nasals; no parallel crests on nasals; external nares bordered posteriorly by nasals; premaxilla dorsally nonoverlapping, laterally flush with nasals; dorsal aspect of jugal terminates on lateral or posterior surface of postorbital; posterior aspect of jugal slightly convex; epipterygoid contacts parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer is smooth, without posteriorly directed lateral processes; maxilla extends posteriorly beyond ectopterygoid on ventral surface of skull; crest between basipterygoid processes of basisphenoid absent; lateral shelf of quadrate absent; black pigment is present on parietal only; posteriormost mandibular tooth is posterior to anterior mylohyoid foramen; splenial absent; ventral aspect of anteromedial process of coronoid juts posteriorly or slopes smoothly anteriorly; external opening of surangular foramen bordered by both dentary and surangular; posterior suture of dentary blunt or pronged; anteriormost aspect of posterior border of dentary is well within mandibular fossa; labial process of coronoid present; coronoid does not extend posterolaterally beyond surangular foramen; jaw sculpturing absent; angular absent; teeth unicusp anteriorly, tricuspid posteriorly; angular process of articular present; ten premaxillary tooth positions.

Color in life (adapted from field notes and color photos by SP)

Anolis elcopeensis is a brown or brownish-gray lizard. Its dorsum may be marked with faint lateral banding, rows of spotting, or striations (Fig. 3A) or appear lightly speckled (Fig. 5A), or may be nearly patternless pale gray or dark brown. The tail usually is banded, and there usually is a dark dorsal interorbital bar (Fig. 1A). The ventral body usually displays dark brown markings on white background. The iris is brown. The throat is pale.

Distribution and natural history

Anolis elcopeensis is known from Coclé Province in Panama and potentially from Panamá and Darién Provinces (Fig. 7; see below). These provinces have been
well surveyed for herpetofauna, however much of Coclé is difficult to access and remains unexplored. Habitat in this province ranges from lowland rainforest in the Canal Zone up to cool tropical premontane rainforest in Parqué Nacional Omar Torrijos. This range spans an elevation gradient from sea level up to over 1,000 meters. We have collected topotypical and paratopotypical *A. copeensis* from 245 to 801 meters. We have found *A. copeensis* in near-pristine primary and old selectively logged forests (i.e., at the type locality) and in heavily disturbed roadside vegetation.

All of our collections of *A. copeensis* occurred at night when anoles sleep. Among 35 recorded observations at El Copé, mean sleeping perch height was 4.15 m (standard deviation 2.35). Among 30 individuals for which sleeping perch type was recorded, 24 were on twigs, three were on leaves, and three were on vines. Thus, among perches easily surveyable by humans (i.e., excluding high canopy, burrows, etc.), narrow perches that are relatively high seem to be preferred by *A. copeensis*. Diurnally, the species has been observed to be active on the ground and on vegetation at heights up to 1.5 m (Mason Ryan, pers. comm.). On 23 July 2002, Ryan observed a Cocoa Woodcreeper (*Xiphorhynchus susurrans*) catching and consuming an adult male *A. copeensis* that was displaying from a tree buttress.

**Anolis fuscoauratus and *A. maculiventris* in Panama?**

*Anolis copeensis* is more similar to the South American species *A. fuscoauratus* than to any species in Central America. *Anolis fuscoauratus* is a common forest anole in Amazonian South America (Avila-Pires 1995). This nondescript species is difficult to distinguish morphologically from the species described here and from its Andean and Pacific Colombian lowland congeners (*A. antonii, A. mariarum, A. tolimensis, A. maculiventris, A. medemi*), and there are doubtless multiple cryptic species among supposed *A. fuscoauratus* in Amazonia and the eastern Andes (Poe, unpublished). We have collected *A. fuscoauratus* from its type locality in Bolivia, and anoles nearly or completely indistinguishable from topotypical *A. fuscoauratus* in Peru, Colombia, Panama, and Ecuador. Some authors (e.g., Kohler 2008) list *A. fuscoauratus* from Panama, but this occurrence seems unlikely as true *A. fuscoauratus* is replaced in the western lowlands of Colombia by *A. maculiventris*.

We have collected *fuscoauratus*-like *Anolis* in eastern Panama from the Panama Canal to Pirre Station, Darién. The *fuscoauratus*-like anole we have collected along the Pan American highway out to Meteti usually possesses a bicolored orange/yellow dewlap (Fig. 4), although we
have collected specimens near Lake Bayano with solid orange dewlaps (Fig. 4E), as in *A. elcopeensis*. Although our current assignment for these eastern populations is *A. elcopeensis*, we suspect this form may represent one or multiple species distinct from *A. elcopeensis*. The variability in dewlap color (Fig. 4) and mitochondrial DNA (Fig. 2; note positions of samples from Pipeline Road and Lake Bayano) suggests the presence of a species complex of *fuscoauratus*-like anoles in central and eastern Panama. Given the local variation we have observed in limb length and body color pattern, it also is possible that we have failed to recognize multiple sympatric small grayish-brown anole species with orange dewlaps at our study sites. We currently are investigating these issues.

Near Yaviza in Darién, the *fuscoauratus/elcopeensis*-like anoles we have collected possess a bicolor dewlap with pink posteriorly (Fig. 5G), similar to the Pacific Colombian lowland form *A. maculiventris* (Fig. 5H). In addition, some of our collections of this Darién population appeared strongly dorsally patterned (Fig. 3C), as also is common in South American *A. maculiventris* (Fig. 3D; but also occasionally evident in *A. elcopeensis* east of the canal; pers. obs.). This population may represent *A. elcopeensis* or an additional undescribed species, but for now we tentatively assign these to *A. maculiventris*. If this species inference is accurate, the number of recognized anole species in Panama is increased to 46.

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**Literature Cited**


Appendix 1

Samples used in phylogenetic analysis of COI.


Appendix 2

Voucher specimens for referenced localities (all in Panama; see Fig. 7).


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A new species of *Anolis* from Panama

In accordance with the International Code of Zoological Nomenclature new rules and regulations (ICZN 2012), we have deposited this paper in publicly accessible institutional libraries. The new species described herein has been registered in ZooBank (Polaszek 2005a, b), the official online registration system for the ICZN. The ZooBank publication LSID (Life Science Identifier) for the new species described here can be viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/.” The LSID for this publication is: urn:lsid:zoobank.org:pub:22ED2728-2093-46D6-AE9B-A77AC56A7412.

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