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Notes on Variation in *Anolis boettgeri* Boulenger 1911, Assessment of the Status of *Anolis albimaculatus* Henle and Ehrl 1991, and Description of a New Species of *Anolis* (Squamata: Iguania) Similar to *Anolis boettgeri*

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ABSTRACT.—**We describe a new species of *Anolis* from a high-elevation locality in the Department of Cusco, Peru. This species is similar to *Anolis boettgeri* but differs in characters of scalation and coloration. We reanalyze *Anolis albimaculatus* and find this species to be a synonym of *A. boettgeri*. We describe variation in *A. boettgeri* based on topotypical material, including the first described males of the species. Phylogenetic analysis of the new form places it within the *Dactyloa/latifrons* clade of South American "Alpha" *Anolis*.**

Recent collections in Andean Peru have resulted in descriptions of several new species of reptiles and amphibians (e.g., Lehr et al., 2005), including new species of *Anolis* (e.g., Poe and Yañez-Miranda, 2007). One of us (EL) has collected topotypical specimens of *Anolis boettgeri*, including males. The other authors (SP, CY) have collected specimens of a new *boettgeri*-like *Anolis* in southern Peru. These collections allow reanalysis of *A. boettgeri* and similar Peruvian *Anolis*.

Anolis boettgeri was described by Boulenger (1911) based on four female specimens from Huancabamba, Department of Pasco, Peru. This species was included in a molecular phylogenetic analysis (Hass et al., 1993), but the morphology of this form remains less well known, and museum specimens are rare. *Anolis albimaculatus*, an apparent close relative of *A. boettgeri*, was described by Henle and Ehrl (1991) based on a single female specimen from near the type locality of *A. boettgeri*. Here, we describe variation in male and female *A. boettgeri*, discuss the status of *A. albimaculatus*, and describe a new species of *Anolis* similar to *A. boettgeri*.

MATERIALS AND METHODS

We consider species to be evolutionary lineages (Simpson, 1961; Wiley, 1978) and operationalize this concept by identifying species based on consistent differences between populations (see Frost and Kluge, 1994). That is, we hypothesize that populations that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species (see Wiens and Servedio, 2000).

Specimens were preserved in 10% formalin and stored in 70% ethanol. 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 edge of cloaca. Head length was measured from tip of snout to anterior edge of ear opening. Femoral length (FL) 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. Comparisons were made with preserved material of the putative closest relatives of the new species (Appendix 1). Scale terminology and characters used mainly follow standards established for species descriptions of anoline lizards (e.g., Williams, 1982). Statistical comparisons were made using the Mann-Whitney *U*-test. One specimen was dissected to enable description of the skeleton. Skeletal description is given in terms of Poe's (1998, 2004) and Etheridge's (1959) characters. See those papers for more detailed descriptions of skeletal conditions and alternative conditions in *Anolis*.

We scored the new species for the morphological phylogenetic characters of Poe (2004; 81 of 91 morphological characters scored). We performed a parsimony analysis of the new species and 233 other *Anolis* species and eight outgroups using 1,666 parsimony-informative characters from published sources (Poe, 2004;

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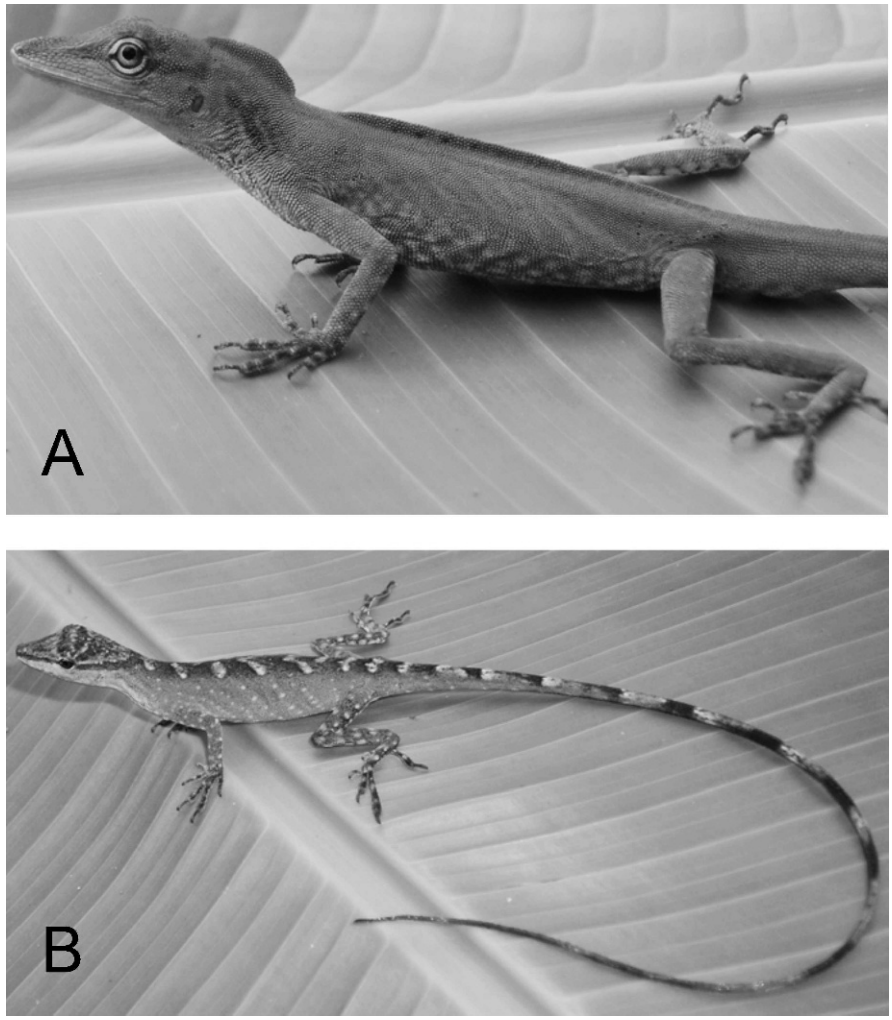

FIG. 1. (A) Adult male of *Anolis cuscoensis*. (B) Adult female of *A cuscoensis*.

Nicholson et al., 2005) and some of our additional unpublished morphological data. This data matrix includes characters of morphology, allozymes, chromosomes, mitochondrial DNA sequences (NADH dehydrogenase subunit 2 and five transfer-RNA genes), and nuclear DNA sequences (internal transcribed spacer region). We used PAUP* version 4.0b10 (D. L. Swofford, Sinauer Associates, Sunderland, MA, 2002) to perform 100 random additions of taxa with tree-bisection-reconnection branch swapping.

Anolis cuscoensis new species
Figure 1

Holotype.—Museo de la Universidad de Amazonía Peruana (MZUNAP) 02.000191, male, Peru, Department of Cusco, 72 km north of Paucartambo on Paucartambo-Itahuania Road, 13°03′30″ S 71°33′54″, 1624 m elevation, collected 28 April 2005 by Steven Poe, Christian Yañez Miranda, and Jenny Hollis.

Paratypes.—Museum of Southwestern Biology (MSB) 72528–72531, MZUNAP 02.000192–02.000194, same locality and collection information as holotype, except that Juan Carlos Chaparro collected paratype 02.000193 and one of the other paratypes was collected on 27 April 2005. Museum of Comparative Zoology (MCZ) 179416, same locality as holotype, collected 24 April 1984 by John Cadle.

Diagnosis.—A distinctive female dorsal pattern of middorsal white chevrons separating dark blotches (Fig. 1B) with white lateral spots distinguishes *A. cuscoensis* from all species of Peruvian, Brazilian, and Bolivian *Anolis* except *A. boettgeri* (this pattern probably distinguishes these species from all *Anolis*, but we are unable

to confirm this). *Anolis cuscoensis* differs from *A. boettgeri* in possessing fewer postrostrals (mean = 8.1, range = 7–9; mean = 9.3, range = 8–11 in *A. boettgeri*; $P = 0.0095$), shorter hind limbs (mean FL/SVL = 0.25, range = 0.23–0.26; mean = 0.28, range = 0.26–0.29 in *A. boettgeri*; $P = 0.004$), smoother headscales (almost all head scales smooth; *A. boettgeri* displays several multicarinate scales anteriorly and almost all head scales keeled), different male dewlap color (white with blue scales; yellowish with white scales in *A. boettgeri*), and in the structure of the occipital scales. *Anolis boettgeri* has a narrow, elongate interparietal in contact with the supraorbital semicircles or separated by one scale (12 specimens) or with paired large scales anterior to the elongate interparietal (one specimen); *A. cuscoensis* displays two to four small scales separating the supraorbital semicircles from a more rounded (i.e., not elongate) interparietal (mean width of interparietal divided by length in *A. cuscoensis* = 0.62; *A. boettgeri*: 0.43; $P = 0.003$).

Comparisons.—In the field, *A. cuscoensis* could be confused only with the other green Peruvian anoles *A. boettgeri* and *Anolis punctatus*. Differences from *A. boettgeri* are discussed above. *Anolis cuscoensis* differs from *A. punctatus* in dewlap color (pale yellow or orange in *A. punctatus*; white with blue scales in *A. cuscoensis*), snout structure (greatly expanded anteriorly and superiorly in males of *A. punctatus*; not expanded in *A. cuscoensis*), and number of dewlap scales per row (single scales in rows in *A. punctatus*, multiple scales per row in *A. cuscoensis*).

External Description of Holotype (Paratype Variation in Parentheses; Mensural Characters Scored Only on Adults).—Snout–vent length 58.0 (55.0–61.0); head length 14.6 (13.8–14.4), width 8.4 (8.1–9.0); ear height 1.6 (1.3–1.8); femoral length 15.3 (13.0–16.3); tail length 154 (130–178).

Dorsal head scales smooth (or unicarinate); weak (or absent) frontal depression; rostral overlaps mental anteriorly; 10 (9–11) scales across snout between second canthals; supraorbital semicircles in contact (one paratype has one row of scales separating supraorbital semicircles; others have zero); suboculars in contact with supralabials; one elongate supraciliary scale followed by small undifferentiated scales (one paratype has three slightly enlarged scales along supraciliary ridge; others have one elongate supraciliary); seven (4–6) loreal rows; anterior nasal scale in contact with rostral, separated from supralabial-rostral sulcus by one scale (Williams et al.'s [1995] ''inferior'' nasal); interparietal length 1.8 (1.1–1.9); eight (6–8) supralabials to center of eye; six (4–6) postmentals; nine (7–9) postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in size, bordered medially by a partial (or complete) row of small scales medially; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border in concave arc (or straight posterior border); two (2–5) enlarged sublabials, with first two (1–4) scales in contact with infralabials, gradually decreasing in size posteriorly; dewlap reaches well posterior to axillae in males, absent in females; approximately five rows of scales on dewlap, each row one to three scales wide; no axillary pocket; pair of enlarged postcloacal scales separated by one (or two) small scales (present in male but not female paratypes); nuchal and dorsal crests not evident in preserved specimens, both clear in life in a male specimen (Fig. 1A); some dorsal scales keeled; zero to two enlarged middorsal rows, 20 (17–21) longitudinal rows in 10% of SVL; ventral scales in transverse rows, smooth, seven (6–7) scales in 5% of SVL; supradigitals multicarinate; toe pads expanded; 18 (16–18) lamellae under second and third phalanges of fourth toe; tail with a double row of middorsal scales.

Skeletal Description (Based on MSB 72529).—Parietal roof very slightly convex, with V-shaped crests, with very slight lateral casquing, lacking crenulation on edges, not extending posteriorly over supraoccipital, with anterolateral corners flush with posterolateral edges of frontal; pineal foramen at parietal-frontal suture; dorsal skull bones smooth; postfrontal present; prefrontal in contact with nasal; frontal sutures anteriorly with nasals; no parallel crests on nasals; external nares bordered posteriorly by nasals; dorsal aspect of jugal terminates on lateral surface of postorbital; jugal nearly contacts squamosal; posterodorsal ramus of squamosal smaller than posteroventral ramus, separated from parietal by supratemporal; posterior aspect of jugal mostly straight, slightly concave; epipterygoid contacts parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer is smooth, without posteriorly directed lateral processes; maxilla barely extends posteriorly beyond ectopterygoid on ventral surface of skull; no crest between basipterygoid processes of basisphenoid; no lateral shelf of quadrate; black pigment is present on all dorsal skull bones, very weakly on central aspect of frontal; nasals do not overlap premaxilla dorsally; posterior of skull is approximately even with level of parietal-frontal suture (appears slightly inferior in some unskeletonized specimens); posteriormost mandibular tooth is partially anterior to anterior mylohyoid foramen; large splenial present, extending from lingual to venral surfaces of mandible; ventral aspect of anteromedial process of coronoid extends pos-

teriorly on one side, anteriorly on other; external opening of surangular foramen is entirely within surangular; posterior suture of dentary is pronged; anteriormost aspect of posterior border of dentary is anterior to mandibular fossa on one side, in mandibular fossa on other side; labial process of coronoid is present; coronoid does not extend posterolaterally beyond surangular foramen; no jaw sculpturing; no angular; angular process of articular present; teeth unicuspid anteriorly, tricuspid posteriorly; six premaxillary teeth.

Two sternal and two xiphisternal ribs; five postxiphisternal ribs attached to dorsal ribs, none unattached (5:0 rib formula); transverse processes on anterior caudal vertebrae, gradually lost posteriorly (Alpha condition; Etheridge, 1959); far distal portions of interclavicles not in contact with clavicles (arrow-shaped); 23 presacral vertebrae

Color in Life (Adapted from Field Notes and Color Photos).—Male dorsum green, darker green middorsally, lighter on flanks; yellow spots on flanks near venter, most evident near axillae, faint near hind limbs; top of head darker green, lighter lateroventrally; venter faintly bluish on white, yellow spots with blue fading to green reticulations laterally (no yellow spots centrally); yellow ring around eye; tongue dull pink; iris copper; limbs with faint yellow spots, digits with light cross-bands; dewlap skin cream with some dark blotching; almost all scales pale blue, a very few green scales basally.

Female dorsum green, with broad dark middorsal stripe, interrupted medially by white middorsal chevrons extending out laterally to edge of stripe, pointing anteriorly; a nuchal blotch and then five chevrons down to sacrum, continued on tail as blotches and then broad bands (tail banded); top of head brown-green, lateral head green; dark line extends back from snout through eye dorsally to nuchal blotch; flanks with regular rows of white spots extending diagonally from chevrons; limbs with light spots, digits with light cross-bands; venter white, laterally with green reticulations and faint yellow and yellow-green on gular area.

Etymology.—The specific name *cuscoensis* refers to the type locality of the new species which is located in the Departamento de Cusco.

Distribution and Natural History.—The type locality of *A. cuscoensis* (Fig. 2) is cloud forest habitat on the eastern Andean slope of southern Peru. A good dirt road travels north along the eastern edge of Manu National Park from Paucartambo at 3,300 m down to Itahuania at 430 m. The spectacular high part of this road is cut out of mountainside and traverses waterfalls and lush vegetation. Along this road at about 1,700 m elevation, we collected *A. cuscoensis*

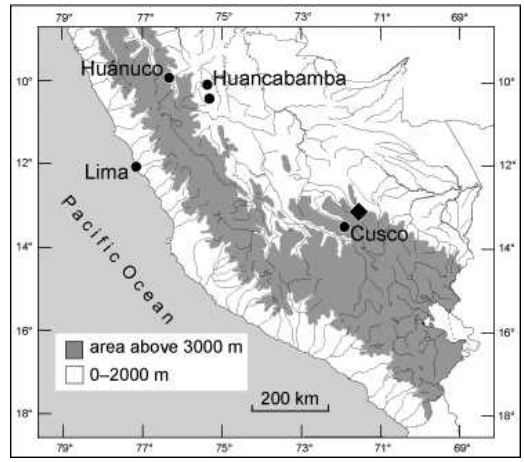

FIG. 2. Map of southern Peru showing type locality of *Anolis cuscoensis* (diamond).

sleeping at night on ferns and leaves from 1–5 m from road level. The only other lizards we collected here were specimens of an undescribed *Anolis* similar to *A. fuscoauratus* that we have collected at similar eastern Andean elevations at numerous sites in Peru and one in Bolivia.

While this paper was in review, we collected seven specimens of apparent *A. cuscoensis* in the Quillabamba valley, 100.1 km north of Ollantaytambo (12°59.830′ S, 72°32.289′ W, elevation 1,693 m; field numbers POE 2004–2010). Morphology of these specimens matches the above description of *A. cuscoensis*, except that some females possess a complete middorsal brown stripe bordered by black. This condition is not likely to be a diagnostic character for this form; females of *Anolis* are highly variable in pattern, and females of *A. boettgeri* vary in precisely the same way (that is, some females with broad middorsal stripe, others with stripe broken by white chevrons; see below).

Status of Anolis albimaculatus.—*Anolis albimaculatus* was described based on a single female specimen from Divisoria, east of Tingo Maria, Department of Huanuco (Henle and Ehrl, 1991). This locality is approximately 140 km from the type locality of *A. boettgeri* at a comparable elevation in contiguous mountains of the Cordillera Oriental of the eastern Andes. The holotype specimen is in somewhat poor condition; the rostral is mangled, and the body is contorted. The characters used to distinguish *A. albimaculatus* from *A. boettgeri* were number of lamellae on the fourth toe (listed as 18–19 in *A. boettgeri*, 21 in *A. albimaculatus*), size of ear relative to interparietal (larger in *A. albimaculatus*, smaller in *A. boettgeri*), and dorsal pattern (white transverse markings and spots in *A.*

albimaculatus, orange lateral stripes in *A. boettgeri*; Henle and Ehrl, 1991:151). We discuss these characters in turn in reference to states in topotypical *A. boettgeri*.

Anolis albimaculatus was named for its unusual dorsal color pattern (*albi-*, white; *-maculatus*, spotted), and this condition was contrasted with the orange lateral stripes of *A. boettgeri*. However, females of *A. boettgeri* come in two morphs: one with the common *Anolis* condition of a dark middorsal stripe (in this case bordered by orange) and another that fits perfectly with Henle and Ehrl's description of the *A. albimaculatus* pattern (pers. obs.; Fig. 3). We count a range of toe lamellae in *A. boettgeri* from 18–22. In the *A. albimaculatus* type, we count 19 lamellae on the right and 22 on the left toe. Lamellar counts are somewhat subjective, as there may be some question where on the toe the proximal border between lamellar and nonlamellar occurs. However, we were consistent in our method of counting lamellae (following Peterson, 1983) and still found overlap between these putative species. The interparietals of *A. boettgeri* and *A. albimaculatus* are nearly identical: elongate and in contact with the supraorbital semicircles. The *A. albimaculatus* holotype appears to display a rather large ear but is apparently no larger than those seen in *A. boettgeri*. The range of ear heights (EH) in *A. boettgeri* is 1.8–2.3 mm and range of ear widths (EW) 1.3–1.8 mm. The ear sizes of *A. albimaculatus* fall well within these ranges (EH = 1.7 mm, 1.8 mm; EW = 1.1 mm, 1.6 mm). When scaled by head length (HL), the ear of *A. albimaculatus* is proportionately somewhat large but not outside the ranges seen in *A. boettgeri* (EH/HL = 0.12, 0.13; EW/HL = 0.08, 0.12 in *A. albimaculatus*; EH/HL = 0.09–0.14, EW/HL = 0.08–0.13 in *A. boettgeri*). We note that the ear openings of *A. albimaculatus* do appear proportionately large in a qualitative sense, perhaps because of a more rounded ear shape in the *A. albimaculatus* specimen.

In sum, we find that the characters purported to diagnose *A. albimaculatus* are within the range of variation observed in topotypical *A. boettgeri*. Based on this evidence, we consider *A. albimaculatus* and *A. boettgeri* to be conspecific and, thus, that *A. albimaculatus* is a junior synonym of *A. boettgeri*. Additional information on male dewlap color and pattern in *A. boettgeri* from the Tingo Maria area would be useful in reassessing the status of *A. albimaculatus*, as would molecular sequence data.

Variation in Anolis boettgeri.—*Anolis boettgeri* was described by Boulenger (1911) based on four female specimens collected by Enrique Boettger. Recent fieldwork around the type locality of *A. boettgeri* combined with historical collections from MCZ present us with a larger sample of specimens than was available to Boulenger, including the first described males. Below we document variation in eight male and five female near-topotypical adult specimens of this species.

FIG. 3. Female of *Anolis boettgeri*, sleeping on leaf.

Snout–vent length 60.6–65.6 in females, 61.5–68.5 in males; head length 14.4–16.1, width 8.5–9.4; ear height 1.8–2.3, width 1.3–1.8; femoral length 17.5–19.1; tail length approximately 150–170.

Dorsal head scales weakly wrinkled to multicarinate, more rugose and carinate anteriorly; frontal depression absent or weak; rostral overlaps mental anteriorly; 8–11 scales across snout between second canthals; supraorbital semicircles in contact; suboculars in contact with supralabials; one elongate supraciliary scale followed by small undifferentiated scales; 5–6 loreal rows; anterior nasal scale in contact with rostral, separated from supralabial-rostral sulcus by one scale (Williams et al.'s [1995] ''inferior'' nasal; two specimens have an anterior scale in contact with the sulcus on one side); interparietal length 1.9–2.9, width 0.7–1.5; 6–9 supralabials to center of eye; 5–7 postmentals; 8–11 postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in

size, bordered medially by a complete or partial row of small scales medially; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border in concave arc; 1–3 enlarged sublabials, at least one in contact with infralabials, gradually decreasing in size posteriorly; dewlap reaches well posterior to axillae in males, absent in females; approximately seven rows of scales on dewlap, each row one to two scales wide; slight axillary pocket; pair of enlarged postcloacal scales separated by one or two small scales in males; dorsal scales unicarinate; middorsal rows raised but not especially enlarged; 9–11 dorsal longitudinal scale rows in 5% of SVL; ventral scales in transverse rows, smooth, 5–9 scales in 5% of SVL; supradigitals multicarinate; toe pads expanded; 18–22 lamellae under second and third phalanges of fourth toe; tail with a double row of middorsal scales.

Skull Description (Based on MCZ 173311).—Parietal roof flat, with convex roughly V-shaped crests, without lateral casquing, lacking crenulation on edges, extending posteriorly over supraoccipital, with anterolateral corners flush with posterolateral edges of frontal; pineal foramen at parietal-frontal suture; dorsal skull bones smooth; postfrontal present; 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; dorsal aspect of jugal terminates on lateral surface of postorbital; jugal does not contact squamosal; posterodorsal ramus of squamosal about equal to posteroventral ramus, separated from parietal by supratemporal; posterior aspect of jugal straight; epipterygoid contacts parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer is smooth, without posteriorly directed lateral processes; posterior maxilla just reaches ectopterygoid on ventral surface of skull; no crest between basipterygoid processes of basisphenoid; no lateral shelf of quadrate; no black pigment on dorsal skull bones; nasals do not overlap premaxilla dorsally; posterior of skull is approximately even with level of parietal-frontal suture; posteriormost mandibular tooth is posterior to anterior mylohyoid foramen; large splenial present, extending from lingual to ventral surfaces of mandible; ventral aspect of anteromedial process of coronoid extends posteriorly; external opening of surangular foramen is entirely within surangular; posterior suture of dentary is pronged; anteriormost aspect of posterior border of dentary is anterior to mandibular fossa; labial process of coronoid is present; coronoid does not extend posterolaterally beyond surangular foramen; no jaw sculpturing; no angular; angular process of articular present; teeth unicuspid anteriorly, tricuspid posteriorly; eight premaxillary teeth.

Color in Life of Anolis boettgeri Male (from EL Field Notes of MTD 45684).—Ground coloration pale green; laterally with yellowish-tan spots in diagonal lines; bluish-green oval fleck on neck with white spots in its center, yellowish-tan surrounded; iris tan, eye surrounded by a tan ringlet; dewlap white to yellowish-orange with white lines bordered on both sides by bluish-grey spots; throat whitish-tan with pale bluish-green reticulations; chest, belly, and tail pale grey with yellowish-tan spots; ventral surfaces of hands and feet grey; ventral surfaces of upper and lower arm, shank and tibia yellowish-green with grey reticulations, posterior surfaces with yellowish-tan spots; beginning of tail ventrally green with yellowish-tan spots (Fig. 4). Under stress, specimens changed coloration to brown; bluish green fleck changes to dark brown.

Color in Life of Anolis boettgeri Female (from EL Field Notes of MTD 4568).—Head brown; pale brown stripe middorsally from neck to tail, bordered on both sides by a narrower, brown stripe which has yellowish-tan spots on its outside; laterally yellowish green with yellowish-tan spots; throat yellowish-tan with greyish-brown reticulations; chest, belly, and tail white and greyish-brown marmorated; extremities pale grey with dark grey reticulations; extremities dorsally green with yellowish-tan spots.

Distribution of Anolis boettgeri.—The type locality of *A. boettgeri* was originally listed as ''Huancabamba, E. Peru, above 3,000 feet'' (Boulenger, 1911), and this is the locality given by W. F. H. Rosenberg in his accession letter. Based on anuran specimens also collected by Enrique Boettger, Boulenger (1912) described *Hyla melanopleura* with the same locality data as for *A. boettgeri* ''Huancabamba, Peru, 3,000 feet.'' Lehr and von May (2004) discussed the possible error in the given elevation of 3,000 feet (= 925 m) that does not fit the elevation of Huancabamba (1,780 m) or its surroundings which are even higher. EL found *H. melanopleura* and *A. boettgeri* around the old Hacienda Yanachaga (nowadays a school for orphans called Prosoya) that family of E. Boettger owned and is about 1 km east of the village Huancabamba. Barbour (1934) later changed the type locality for *A. boettgeri* to ''Oxapampa, Eastern Peru.'' Oxapampa is only about 20 km south of Huancabamba. Barbour apparently made this change based on a letter from Rosenberg that discusses the collector Boettger's localities, which stated ''Boettger appears to have moved in 1911 from Huancabamba to a place called Oxapampa…. It looks to me as though Boettger may have collected that [i.e., the larger] lot at Oxapampa and acciden-

FIG. 4. Adult male of *Anolis boettgeri*.

tally labeled it Huancabamba.'' Rosenberg goes on to reason that Boettger may have confused the names when sending Oxapampa material from Huancabamba. From this letter, it is not clear to us whether the type specimens of *A. boettgeri* collected by Boettger and given by Rosenberg to Boulenger are from Huancabamba or Oxapampa, although Barbour evidently thought Oxapampa was more likely. Our collections, which we consider to be at least roughly topotypical, are from Huancabamba. What seems likely from these and other correspondences is that the American Museum (AMNH) specimen referred to in these letters (assumed to be AMNH 13534) was mapped incorrectly by Carrillo de Espinoza (1983: Fig.1), who listed AMNH material from ''Huancabamba, Piura.'' Piura Huancabamba is some 800 km from Huancabamba in Pasco, on the other (western) side of the Andes. Carrillo de Espinoza apparently was aware that this locality is incorrect, because he cites the distribution of *A. boettgeri* as ''Known only from Huancabamba and Oxapampa of the cis-Andean

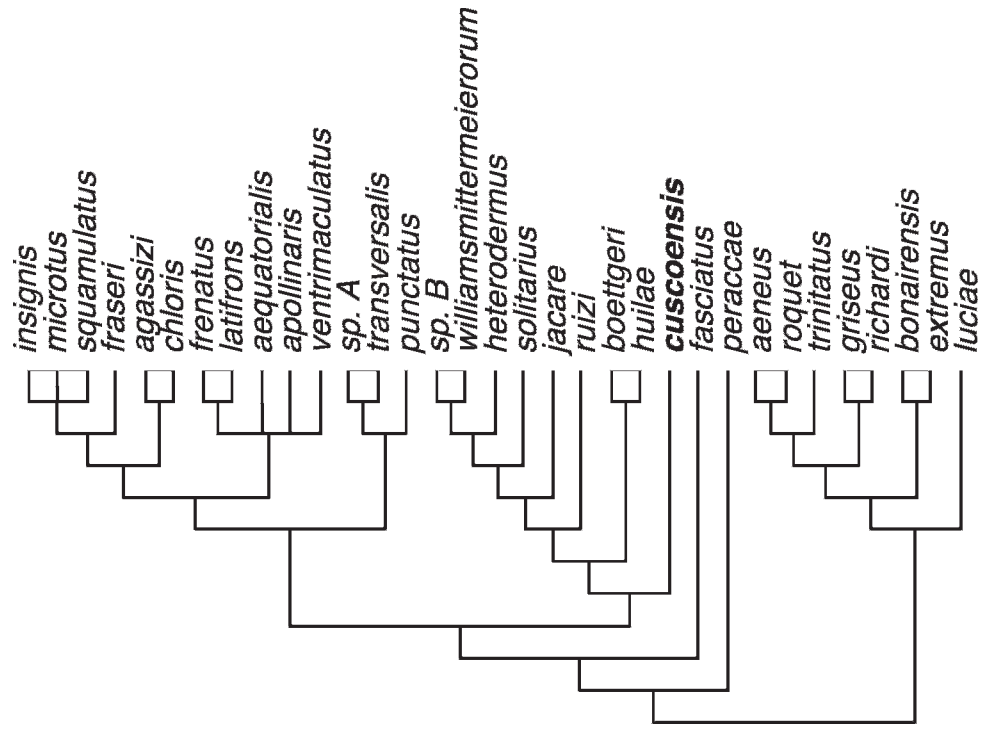

FIG. 5. Phylogenetic estimate of the relationships of *Anolis cuscoensis* based on parsimony analysis of 1,666 parsimony-informative characters (Nicholson et al., 2005; Poe, 2004). All relationships are supported at bootstrap values of less than 50%.

region'' (Carillo de Espinoza, 1983:406). In addition to specimens from Huancabamba or Oxapampa, the species is known from a single specimen from Sira, Department of Huanuco (MHNSM 8604; about equidistant between the type localities of *A. albimaculatus* and *A. boettgeri*). This specimen is indistinguishable from topotypical *A. boettgeri*.

Discussion

The phylogenetic analysis resulted in 320 optimal trees of length 30300. The portion of the strict consensus of optimal trees that includes *A. cuscoensis* and *A. boettgeri* is shown in Figure 5. *Anolis cuscoensis* is a member of a clade of mostly South America ''Alpha'' *Anolis* and is sister species to a clade that includes *A. boettgeri* and phenacosaur- and *tigrinus*-group *Anolis*. This clade (Fig. 5) roughly corresponds to Etheridge's (1959) *latifrons* series and Guyer and Savage's (1986) genus ''*Dactyloa*.'' Bootstrap analyses (Felsenstein, 1985; not shown) supported clades involving *A. cuscoensis* and *A. boettgeri* at less than 50% frequency.

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Appendix 1

Specimens Examined

MCZ = Museum of Comparative Zoology, Harvard, Cambridge, MA, USA. USNM = National Museum of Natural History, Washington, DC., USA. MHNSM = Museo de Historia Natural Universidad Nacional Mayor de San Marcos. MTD = Museum für Tierkunde, Dresden, Germany. ZFMK = Museum Alexander Koenig, Bonn, Germany.

Anolis albimaculatus ZFMK 34263 (holotype): Peru, Huánuco, Divisoria. *Anolis boettgeri* MCZ 8055: Peru, Pasco, Huancabamba; 173311–173312: Peru, Pasco, 0.9 km north 2.1 km east of Oxapampa; MTD 19821–19826, 45684–9, 46286–46288: Peru, Pasco, Huancabamba; MHNSM 8604: Peru, Huánuco, Sira. *Anolis punctatus* MCZ 29326: Bolivia, Santa Cruz, Buenavista; 57389: Peru, Huallaga valley; 65577–65578: Brazil, Para, Cochimbo; 92534: Brazil, Para, Belem; 103676–103677: Peru, Huanuco, Rio Huallaga; 103678: Peru, Huanuco, Universidad Agraria de Selva.