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Another New Species of Green *Anolis* (Squamata: Iguania) from the Eastern Andes of Peru

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ABSTRACT.—We describe a new species of *Anolis* from cloud forest habitat in Department of San Martin, Peru. The new species shares distinctive aspects of color and scalation with *Anolis huilae* from Colombia and *Anolis boettgeri* and *Anolis cuscoensis* from Peru but differs from these species in dewlap color, limb length, and scalation. Phylogenetic analysis places the species among the basal group of ''alpha'' *Anolis* (*latifrons* group sensu lato, ''*Dactyloa*'').

The anoline fauna of Peru is only beginning to be discovered and described. Currently, 14 species of *Anolis* are recognized from Peru. *Anolis nitens*, *Anolis bombiceps*, *Anolis transversalis*, *Anolis punctatus*, *Anolis trachyderma*, and *Anolis ortoni* are widespread Amazonian lowland forms (Carrillo de Espinoza, 1983). *Anolis dissimilis* is a rare, apparently lowland form from southern Department of Madre de Dios. *Anolis boettgeri* is a high-elevation species from northern Department of Pasco. *Anolis laevis* is a distinctive ''proboscis anole'' known only from the type specimen from a mountain trail between Moyobamba and Balsa Puerto in Department of San Martin in central Peru. *Anolis williamsmittermeierorum* is a northeast Andean phenacosaur *Anolis* originally discussed in Williams and Mittermeier (1991) and formally described by Poe and Yañez-Miranda (2007). *Anolis cuscoensis* (Poe et al., 2008) is a southeast Andean form similar to *A. boettgeri*.

Anolis fuscoauratus, the common South American forest anole, occurs up to at least 1,800 m in Peru (pers. obs.). We have observed populations of *fuscoauratus*-like anoles with white (Iquitos area), dull pink (central and southern lowlands), and bicolor orange-pink dewlaps (eastern Andean slope) in Peru (see also Avila-Pires, 1995), the colors of which are constant within populations, and all of these likely represent distinct species. *Anolis bocourti* Cope 1876 is recognized by some authors (e.g., Nicholson, 2002). However, Cope's (1876) description of *A. bocourti* does not suggest any difference from *A. fuscoauratus* D'Orbigny 1837, and the species is said to be ''abundant at Nauta'' (the type locality), nearby where white-dewlapped *A. fuscoauratus* are extremely common (pers. obs.). We have examined syntypes of *A. bocourti* (MCZ 12443, 14942–14945) and are unable to distinguish these from *A. fuscoauratus*. The specific name *bocourti* may eventually be used for the white-dewlapped lowland form of *A. fuscoauratus* once the taxonomy of *A. fuscoauratus* is better understood, or *A. bocourti* may be considered to be a synonym of *A. fuscoauratus*.

Anolis scapularis has been reported from Peru and recognized as valid by some authors (Carrillo de Espinoza and Icochea, 1995) but not others (Henle and Ehrl, 1991). Ernest Williams, the deceased world's expert on *Anolis* taxonomy, considered this form to be a synonym of *A. fuscoauratus* (E. E. Williams, unpubl. data); however, we are unaware of any published synonymization. We have not examined type material of *A. scapularis*, but its description (Boulenger, 1908) does not distinguish it from *A. fuscoauratus* and its type locality is geographically proximate to the type locality of *A. fuscoauratus* in Bolivia. *Anolis scapularis* is likely to be a synonym of *A. fuscoauratus*, and further work is needed.

Carrillo de Espinoza and Icochea (1995), followed by Lehr (2002), list *Anolis leptoscelis* from Peru without comment, but this form is a synonym of *A. trachyderma* (Vanzolini and Williams, 1970). Lehr (2002) also listed *Anolis chrysolepis*, which is a synonym of *A. nitens* (Avila-Pires, 2000), in addition to *A. nitens*. We are unable to verify the presence of *Anolis proboscis* (Carrillo de Espinoza and Icochea, 1995; Lehr, 2002) or *Anolis fraseri* (Lehr, 2002) in Peru, and we suspect these are mistaken records.

Recent fieldwork in Peru has resulted in the discovery of several new species of *Anolis* (e.g., Poe and Yañez-Miranda, 2007). Here, we add to the anoline fauna of Peru a distinctive long-

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legged green anole from the same locality as *A. williamsmittermeierorum*.

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 that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species (see Wiens and Servedio, 2000).

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-degree 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 species that are phenetically similar to the new species (*A. boettgeri*, *A. huilae*, *A. cuscoensis*, *A. punctatus*; Appendix 1). Scale terminology and characters used mainly follow standards established by Ernest Williams for species descriptions of anoline lizards (e.g., Williams, 1982; Williams et al., 1995). One specimen was dissected to describe 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*.

Results

Anolis soinii new species
Figures 1–2

Holotype.—Museo de la Universidad de Amazonía Peruana (MZUNAP) 02.000179, male, Peru, Department of San Martin, Venceremos, approximately 94 km west of Rioja (between old kilometer markers 390–391, near new kilometer marker 380), 05′40.405 S 77′45.310 W, 1,739 m elevation, collected 24 April 2005 by Steven Poe, Christian Yañez-Miranda, and Jenny Hollis.

Paratypes.—Museum of Southwestern Biology (MSB) 72524–72527, MZUNAP 02.000175–02.000178, same locality and collection information as holotype.

Diagnosis.—*Anolis soinii* differs from all other *Anolis* we have examined except one *A. boettgeri* specimen and one *A. huilae* specimen in possessing paired scales immediately anterior to the interparietal, larger than and in contact with the posterior scales of the supraorbital semicircles (the dorsal head scales of the only specimen of *A. huilae* to possess this condition were figured in Williams [1982:fig. 6]). The new species further differs from *A. boettgeri* in adult size (maximum SVL 68.0 in *A. boettgeri*; 82.0 in *A. soinii*) and color of the male dewlap skin (white in *A. soinii*, peach in *A. boettgeri*) and details of scalation (Table 1). *Anolis soinii* differs from *A. huilae* in possessing longer legs (femoral length/SVL mean = 0.29, range = 0.28–0.30 in *A. soinii*; mean = 0.25, range = 0.23–0.26 in *A. huilae*), smaller middorsal scales (mean numbers of scales in 10% of SVL = 22.8, range 21–24 in *A. soinii*; mean = 17.6, range = 14–21 in *A. huilae*), and in dewlap color pattern (white dewlap skin with dispersed dark grey blotching and green and blue scales in *A. soinii*, yellow dewlap skin with cream or blue scales and rows of black dots along scales in *A. huilae*; see below) and details of scalation (Table 1).

Comparisons.—We allocate *A. soinii* to Williams' (1976) large *punctatus* group based on its Alpha-type caudal vertebrae (lacking transverse processes on posterior caudal vertebrae, unlike Beta *Anolis*), moderately sized dorsal head scales (very large in phenacosaur-group *Anolis*, small in *aequatorialis*-group *Anolis*), moderate to large size, and greatly expanded toepads (narrow in *aequatorialis* group). The distinctive color pattern of *A. soinii* is most similar to that of *A. boettgeri*, *A. cuscoensis*, and *A. huilae* of the *punctatus* group. These four forms are the only *Anolis* species to display black or grey spotting or streaking on a light-colored dewlap and irregular yellow spots on a green dorsal ground color in males. Degree and size of dorsal yellow spotting appears to vary between species. *Anolis huilae* displays larger, closer-set spots such that overall dorsum appears light with dark reticulations in some specimens, whereas *A. soinii*, *A. cuscoensis*, and *A. boettgeri* have smaller, more separated spots such that overall dorsum appears dark with scattered light elements (compare Williams [1982:fig. 9] to Fig. 1B). *Anolis huilae* and *A. boettgeri* have black spots along rows of dewlap scales, whereas *A. soinii* has diffuse dark grey spotting along dewlap scales.

In the field, *A. soinii* could be confused only with the other green Peruvian anoles *A. boettgeri*, *A. punctatus*, and *A. cuscoensis* (*A. huilae* is known only from Colombia). Differences from *A. boettgeri* are discussed above. *Anolis soinii* differs from *A. punctatus* in dewlap color (pale yellow or orange in *A. punctatus*), dorsal pattern (absence of yellow spots in *A. punctatus*), limb length (mean femoral length/SVL = 0.26, range = 0.24–0.28 in *A. punctatus*), snout structure (greatly expanded anteriorly and superiorly in males of *A. punctatus*), number of dewlap scales per row (single scales

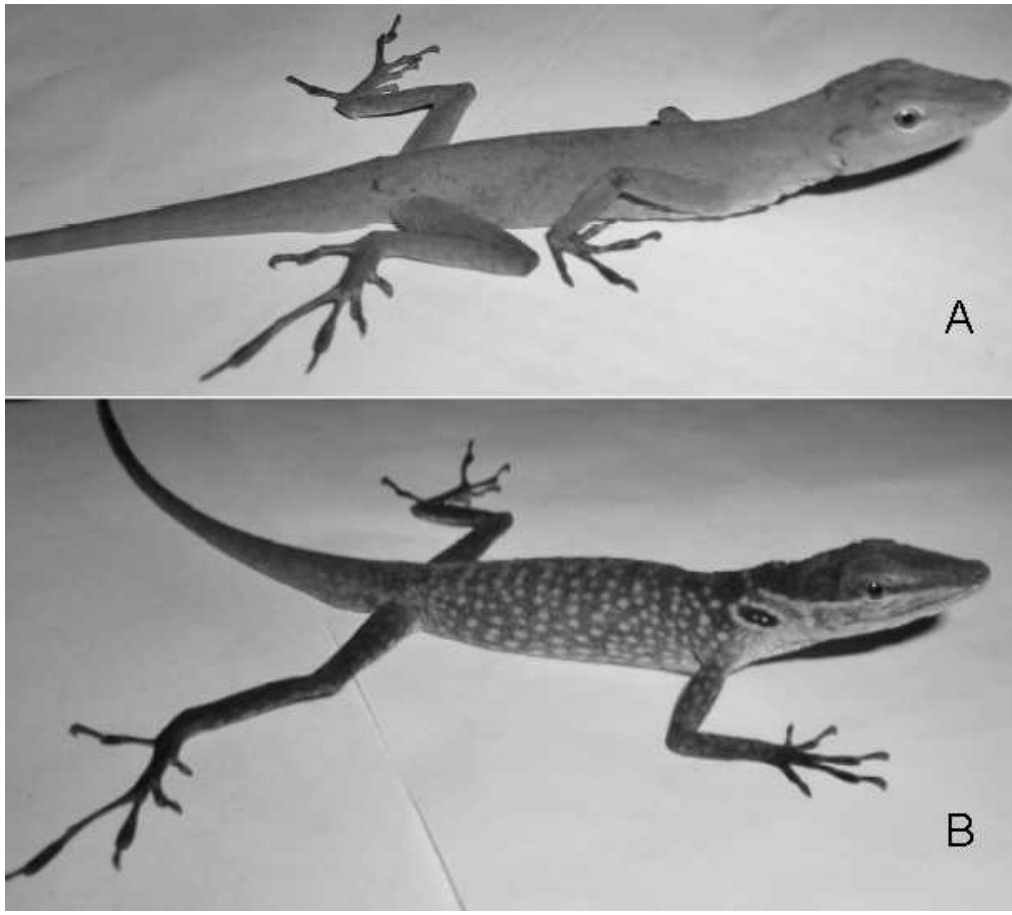

FIG. 1. *Anolis soinii* new species, male, (A) displaying normal green coloration. (B) Same individual in stressed state, displaying brown background and more distinct yellow spotting.

in rows in *A. punctatus*, multiple scales per row in *A. soinii*) and details of scalation (Table 1). *Anolis soinii* differs from *A. cuscoensis* in maximum adult SVL (63 mm in *A. cuscoensis*), limb length (mean femoral length/SVL = 0.25, range = 0.23–0.26 in *A. cuscoensis*), color of dewlap scales (pale blue in *A. cuscoensis*), and details of scalation (Table 1).

External Description of Holotype.—Paratype variation in parentheses; mensural characters scored only on adults. Snout–vent length 73.5 (70.5–82.0); head length 17.2 (18.1–20.9), width 10.8 (10.4–11.4); ear height 1.8 (1.9–2.5); femoral length 21.0 (20.6–23.2); tail length 198 (184–213).

Dorsal head scales smooth (or slightly wrinkled, especially posteriorly); strong frontal depression; rostral overlaps mental anteriorly; 11 (9–14) scales across snout between second canthals; supraorbital semicircles in contact (one paratype has two scales separating supraorbital semicircles; others have zero); suboculars in contact with supralabials; one elongate supraciliary scale followed by small undifferentiated scales; six (5–7) loreal rows; anterior nasal scale in contact with sulcus between rostral and first supralabial (or naris separated from rostral by one undifferentiated scale); interparietal length 1.8 (2.3–2.9); large paired scales anterior to interparietal, larger than adjacent supraorbital semicircles, in point contact with interparietal (or separated from interparietal by 1–2 scales); anterior aspect of interparietal forms a smooth border with surrounding scales (or with fragmented anterior border); preoccipital absent (or present); several very small scales at anterior juncture of supraorbital semicircles (similar to *A. huilae* in Williams, 1982:fig. 6); seven (6–8) supralabials to center of eye; five (4–6) postmentals; eight (6–10) 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 beyond rostral, with posterior border in concave arc (or

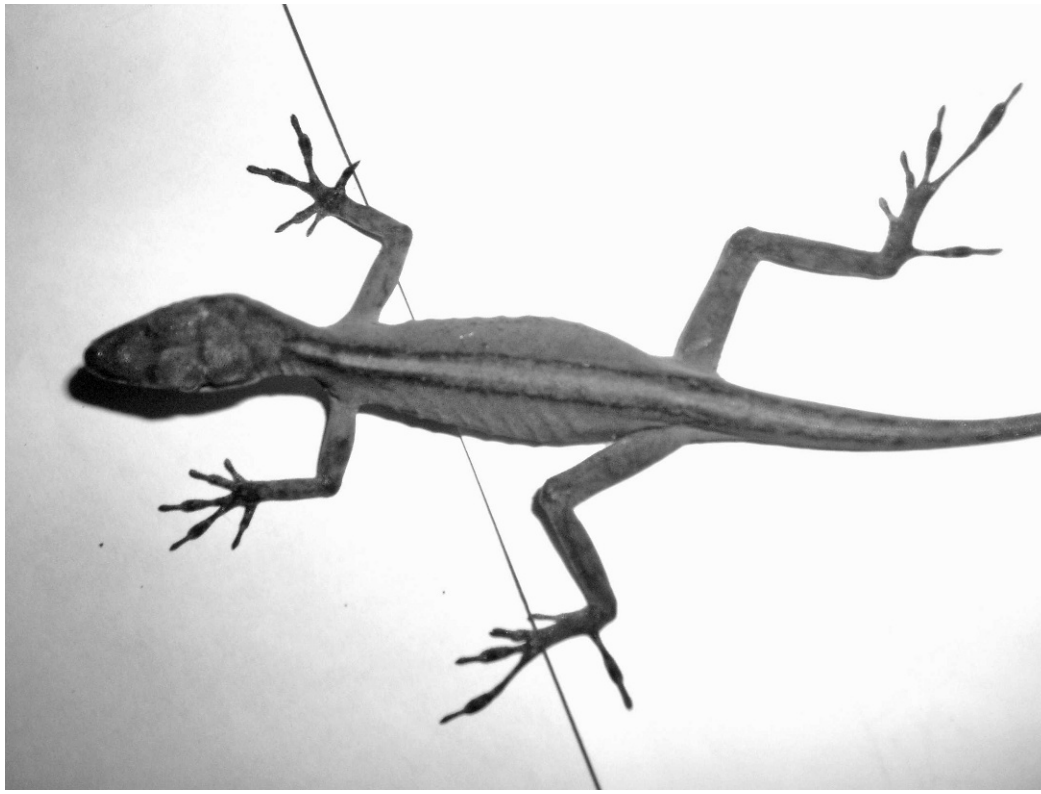

FIG. 2. *Anolis soinii* new species, female.

straight posterior border); four (2–5) enlarged sublabials, with first two (1–3) 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 two to five scales wide; no axillary pocket; pair of enlarged postcloacal scales separated by two small scales (present in male but not female paratypes); nuchal and dorsal crests not evident in preserved specimens; some dorsal scales keeled; zero to three enlarged middorsal rows, 22 (21–24) longitudinal rows in 10% of SVL; ventral scales in transverse rows, smooth, 8 (6–10) scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 20 (17–21) lamellae under third and fourth phalanges of fourth toe; tail with a double row of middorsal scales.

Skeletal Description.—Based on MSB 72525. Parietal roof very slightly convex, with trapezoidal crests with a narrow posterior border, with no casquing, lacking crenulation on edges, barely 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 contacts squamosal; posterodorsal ramus of squamosal approximately equal in size to posteroventral ramus, separated from parietal by supratemporal; posterior aspect of jugal mostly straight; 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 parietal, frontal, nasals, and maxillae, absent on prefrontal and premaxilla; nasals do not overlap premaxilla dorsally; posterior of skull is approximately even with level of parietal-frontal suture; posteriormost mandibular tooth is partially anterior to anterior mylohyoid foramen; large splenial present; 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

TABLE 1. Comparisons of scale counts and measurements for selected characters among *Anolis* species similar to *Anolis soinii* new species. Means are given with ranges in parentheses. Femoral length = FL. Snout–vent length = SVL.

	A. soinii (N = 9)	*A. huilae* (N = 9)	*A. boettgeri* (N = 6)	*A. cuscoensis* (N = 8)	*A. punctatus* (N = 8)
Maximum SVL (male/female)	82/78	80/69	69/66	58/63	83/82
FL/SVL	0.29 (0.28–0.30)	0.25 (0.23–0.26)	0.28 (0.26–0.29)	0.25 (0.23–0.26)	0.26 (0.24–0.28)
No. middorsals in 10% SVL	22.8 (21–24)	17.6 (14–21)	20.7 (19–22)	19.7 (17–21)	22.3 (19–25)
No. scales across snout	11.4 (9–14)	9.1 (7–11)	9.8 (8–11)	9.8 (9–11)	9.8 (8–11)
No. supralabials to center of eye	6.7 (6–8)	6.1 (5–7)	8.0 (7–9)	6.9 (6–8)	7.6 (7–9)
No. postmentals	4.8 (4–6)	4.1 (4–5)	6.2 (5–7)	5.3 (4–6)	6 (5–8)
No. scales separating supraorbital semicircles	0.2 (one specimen with 2; eight with 0)	0	0	0	1.3 (0–2)
No. postrostrals	8.1 (6–10)	8.1 (7–9)	9.5 (9–10)	8.0 (7–9)	9.5 (8–11)
Scales between interparietal (ip) and supraorbital semicircles (sosc)	Paired scales anterior to ip, larger than and in contact with sosc	ip and sosc in contact (8 of 9)	ip and sosc in contact (5 of 6)	2.8 (2–4) small scales separate round ip, sosc	2.3 (1–3) small scales separate ip, sosc

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; five premaxillary teeth.

Three sternal and two xiphisternal ribs; four postxiphisternal ribs attached to dorsal ribs, none unattached (4 : 0 rib formula); transverse processes on anterior caudal vertebrae, gradually lost posteriorly (Alpha condition); distal portions of interclavicles not in contact with clavicles (arrow-shaped condition); 23 presacral vertebrae; three lumbar vertebrae; autotomy septa not evident.

Color in Life.—Adapted from field notes and color photos. Male is bright green dorsally with faint yellow spots most visible on lower flanks, spots becoming absent dorsally; blue wash ventrolaterally; venter yellowish with blue, spots present only laterally; ventral aspects of forelimbs and especially hind limbs with reticulating blue-brown on tan-yellow background; reticulations also present under base of tail; iris brown; tongue yellow; throat light grey.

When stressed, a male turned dark brown, and the yellow spots became more intense, especially dorsally (Fig. 1B). A dark line bordered below by a light line became evident from near the naris through the eye and joining midnuchally. A dark blotch with white center appeared on the shoulder; this blotch is clearly evident on one of the nine preserved specimens and weakly developed on another. Female specimens (N = 2) were bright green dorsally with a broad brown stripe bordered by black middorsally (Fig. 2). Dorsal aspects of limbs and head were darker green than flanks.

Dewlap skin in males white with dark grey irregular spotting and streaking; within each row of two to five dewlap scales, central two rows pale green and lateral rows turquoise (sharp demarcation between colors).

Etymology.—We name this form in honor of Pekka Soini, for his outstanding contributions to Peruvian herpetology.

Distribution and Natural History.—*Anolis soinii* currently is known only from the type locality on the eastern Andean slope in Department of San Martin. This area has been mapped and described by Williams and Mittermeier (1991) and figured in Poe and Yañez-Miranda (2007). Habitat there is partially cleared cloud forest. All specimens were collected sleeping at night on leaves or ferns.

DISCUSSION

Anolis soinii appears most similar to the Colombian form *A. huilae*. Consistent differences

(Table 1), geography (to our knowledge, *A. huilae* has not been found in intervening Ecuador), and phylogeny (see below) suggest that these forms are not conspecific. Although the dewlap color of *A. huilae* has been recorded as displaying some intraspecific or interobserver variability (Williams, 1982:13–15), the distinctive dewlap colors of *A. soinii* have never been recorded for *A. huilae*.

We included *A. soinii* in a phylogenetic analysis of *Anolis* (for details, see Poe et al., 2008). Character states for *A. soinii* are listed in appendix 2, and results of this analysis are shown in Figure 6 of Poe et al. (2008) with *A. soinii* labeled as ''species A.'' According to this analysis, *A. soinii* is sister species to *A. transversalis*, a large Amazonian *punctatus*-group *Anolis*, and this clade is sister to a clade of phenacosaur- and *tigrinus*-group *Anolis*. *Anolis boettgeri* and *A. huilae* are sister species in the sister clade to a group of mostly large *latifrons*-group species. Thus, the external similarity to *A. boettgeri* and *A. huilae* may represent shared ancestral characteristics or convergent evolution (or the phylogenetic estimate may be incorrect). Four unambiguous synapomorphies support the *soinii-transversalis* clade: supraorbital semicircles in contact (character number 32, change from state 0 to 4), presence of ''half funnel'' parietal (61 : 1 to 5), prefrontal separated from nasal by anterior extension of frontal (63 : 2 to 5), and contact between jugal and squamosal (68 : 3 to 5). *Anolis soinii* and *A. transversalis* are easily differentiated, for example by blue eyes, banded tan dorsum, and bright yellow dewlap in *A. transversalis* (reddish-brown eyes, unbanded green dorsum, white dewlap in *A. soinii*).

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APPENDIX 1

Specimens Examined

See Poe (2004) for list of additional specimens examined. Museum of Comparative Zoology, Harvard, USA = MCZ. Museum fur Tierkunde, Dresden, Germany = MTD. Museum Alexander Koenig, Bonn, Germany = ZFMK.

Anolis boettgeri MCZ 8055: Peru, Pasco, Huancabamba; 173311–173312: Peru, Pasco, 0.9 km north of 2.1 km east of Oxapampa; MTD 45684–45685, 45688: Peru, Pasco, Huancabamba; ZFMK 34263 (holotype of *A. albimaculatus*): Peru, Huanuco, Divisoria. *Anolis huilae* MCZ 156305–156306: Colombia, Huila, La Cueva de los Guacheros; 159015: Colombia, Huila, Palestina; 159112–159117: Colombia, Tolima, Cajamarca; 159119–159122: Colombia, Huila, Juntas. *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. *Anolis cuscoensis* MZUNAP 02.000191 (holotype), 02.000192–02.000194 (paratypes), MSB 72528–72531 (paratypes), MCZ 179416 (paratype), Peru, Cusco, 72 km north of Paucartambo on Paucartambo-Itahuania road.

APPENDIX 2

Morphological phylogenetic characters scored for *Anolis soinii*. See Poe (2004) for detailed character descriptions, citations, and justifications for states and Poe and Ibañez (2007) for corrections to character codes (these corrections reverse symbols and do not change results or tree length). Note that codes are changed from a range of *a* to *z* in Poe (2004) to a range of 0 to 5 here. States for *A. soinii* are listed in italics following each character.

1. Maximum male snout–vent length (SVL) 38 mm (0); 188 mm (5); *2*.
2. Ratio of maximum female SVL to maximum male SVL 1.06 (0); 0.57 (5); *3*.
3. Length of thigh short (0); long (5); *?*.
4. Length of head short (0); long (5); *?*.
5. Width of head narrow (0); broad (5); *?*.
6. Height of ear small (0); large (5); *?*.
7. Interparietal scale large (0); about equal to surrounding scales (5); *?*.
8. Length of tail about equal to SVL (0); about 1.5 times SVL (2); about two times SVL (3); about 2.5 times SVL (4); more than 2.8 times SVL (5); *5*.
9. Toepads overlapping first phalanx (0); not distinct from first phalanx (1); absent (2); *0*.
10. Enlarged postcloacal scales present in males (0); absent in males (5); *0*.
11. Row of large spinose middorsal caudal scales separated by smaller smooth scales absent (0); present (5); *0*.
12. Tail crest absent (0); present in largest adult males (5); *0*.
13. Number of rows of enlarged middorsal scales 0–4 (0); 5 or more (5); *0*.
14. Each ventral scale is bordered posteriorly by two scales (0); by three scales (5); *0*.
15. Base of tail laterally compressed (0); round (5); *5*.
16. Male dewlap extends posterior past arms (0); to arms or shorter (1); absent (2); *0*.
17. Female dewlap extends posterior past arms (0); to arms or shorter (1); absent (2); *2*.
18. Tail uniformly patterned (0); base of tail purple, posterior part green or brown (5); *0*.
19. Mean number of dorsal scales in 5% of SVL 2.5 (0); 17 (5); *3*.
20. Mean number of ventral scales in 5% of SVL 2.75 (0); 14.3 (5); *3*.
21. Scales on dewlap in rows of single scales (0); with at least one double row (5); *5*.
22. Middorsal caudal scale rows single (0); double (5); *5*.
23. Axillary pocket absent (0); deep, tubelike (5); *0*.
24. Scales of midnuchal area similar to middorsal scales (0); in continuous row of bulbous scales distinct from dorsal scales (5); *0*.
25. Transparent scales in lower eyelid absent (0); present (5); *0*.
26. Mental scale partially divided (0); completely divided (5); *0*.
27. Mental scale broader than rostral scale (0); rostral broader than mental (5); *0*.
28. Subocular scales and supralabial scales in contact (0); separated by one or more rows of scales (5); *0*.
29. Mean number of scales across the snout 2.5 (0); 19 (5); *3*.
30. Mean number of postmental scales 3.25 (0); 9.75 (5); *1*.
31. Posterior border of mental scale straight or convex (0); concave (5); *4*.
32. Supraorbital semicircles separated by one or more rows of scales (0); in contact (5); *4*.
33. Preoccipital scale absent (0); present (5); *1*.
34. Middorsal scales of the snout not in regular pattern (0); arranged in two parallel rows that extend from the level of the second canthals to the nares (5); *0*.
35. Posterodorsal edge of rostral smooth (0); cleft (5); *0*.
36. Anteromost aspect of rostral scale is even with lower jaw (0); overlaps lower jaw (5); *0*.
37. Color of iris dark brown (0); yellow (1); blue or grey (2); green (3); red (4); *04*.
38. Modal number of supraciliary scales zero (0); one (1); two (2); three (3); *1*.
39. Modal nasal scale type: anterior nasal in contact with rostral (0); divided anterior nasal in contact with rostral (1); circumnasal separated from rostral by one scale, not in contact with supralabial (2); external naris separated from rostral by two scales, not in contact with supralabial (3); external naris separated from rostral by three or more scales, not in contact with supralabial (4); circumnasal in contact with rostral (5); circumnasal in contact with supralabial, separated from rostral by one scale (6); circumnasal in contact with supralabial, separated from rostral by two or more scales (7); *0*.

40. Keeling of dorsals, ventrals, supradigitals, and head scales. The following states are listed in order of whether keels (k) or smooth scales (s) are observed on head scales, ventrals, dorsals, and supradigitals, respectively. For example, ''sssk'' means that all surfaces except supradigitals are smooth. (0) kkkk; (1) ssss; (2) kskk; (3) kksk; (4) kkks; (5) kkss; (6) ksks; (7) kssk; (8) ksss; (9) skkk; (a) skks; (b) sksk; (c) sskk; (d) sssk; (e) ssks; (f) skss; *2*.

41. Scales in supraocular disc vary continuously in size and are bordered medially by an unbroken row of small scales (0); vary continuously in size and are bordered medially by an incomplete row of small scales (1); with one to three abruptly enlarged scales and bordered medially by an unbroken row of small scales (2); with one to three abruptly enlarged scales and bordered medially by an incomplete row of small scales (3); about equal in size (4); *1*.

42. Lining of throat light (0); black (5); *0*.

43. Fold of skin extending over dorsal rim of ear opening absent (0); present (5); *0*.

44. Modal number of enlarged sublabial scales zero (0); one (1); two or more (2); *2*.

45. Frontal depression present (0); absent, top of snout is flat (5); *0*.

46. Interparietal scale separated from supraorbital semicircles by one or more rows of scales (0); in contact with supraorbital semicircles (5); *0*.

47. Modal postxiphisternal inscriptional rib formula 4: 3 (0); 5: 1 (1); 4: 2 (2); 5: 0 (3); 4: 1 (4); 3: 2 (5); 4: 0 (6); 3: 1 (7); 2: 2 (8); 1: 3 (9); 2: 1 (a); 5: 2 (b); *6*.

48. Modal number of sternal ribs two (0); three (1); four (2); *1*.

49. Caudal vertebrae are Alpha type (0); Beta type (1); *Chamaelinorops* type (2); *Basiliscus* type (3); *Sceloporus* type (4); *0*.

50. Interclavicle arrow-shaped (0); T-shaped (5); *0*.

51. Modal number of presacral vertebrae 24 (0); 23 (1); 22 (2); *1*.

52. Modal number of lumbar vertebrae three (0); four (1); five (2); six (3); *0*.

53. Modal number of caudal vertebrae anterior to first autotomic vertebrae 11 (0), 10 (1), nine (2), eight (3), seven (4), six (5), five (6); *?*.

54. Caudal autotomy septa present (0); absent (5); *5*.

55. Supraoccipital cresting continuous across supraoccipital (0); lateral processes distinct from supraoccipital crest (1); single narrow central process (2); *1*.

56. Dorsal surface of skull smooth (0); rugose with bony tubercles (5); *0*.

57. Parietal crests form a trapezoid (0); V (1); Y (2); Y with parietal spur (3); *0*.

58. Anterolateral corners of parietal crests reach posterolateral corners of frontal (0); reach medial to posterolateral corners of frontal (5); *0*.

59. Parietal casque absent (0); present (5); *0*.

60. Pineal foramen at parietal/frontal suture (0); in parietal (5); *0*.

61. Supratemporal processes leave supraoccipital exposed above (0); extend over supraoccipital (5); *5*.

62. Postfrontal present (0); absent (5); *0*.

63. Prefrontal contacts nasal (0); is separated from nasal by frontal and maxilla (5); *5*.

64. Frontal sutures only with nasals anteriorly (0); is separated from nasals by open gap (1); contacts premaxilla and nasals anteriorly (2); *0*.

65. Parallel crests extending longitudinally down nasals from frontal to nares absent (0); present (5); *0*.

66. Anterior edge of nasal forms posterior border of naris (0); does not reach naris (5); *0*.

67. Dorsal process of jugal terminates on lateral aspect of postorbital (0); on posterior or medial aspect of postorbital (5); *0*.

68. Contact between jugal and squamosal absent (0); present (5); *5*.

69. Posteroventral corner of jugal is anterior to posterior edge of jugal (0); posterior to posterior edge of jugal (5); *0*.

70. Epipterygoid long, contacts parietal (0); short, does not reach parietal (5); *0*.

71. Pterygoid teeth present (0); absent (5); *5*.

72. Lateral edges of vomer smooth (0); with posteriorly directed lateral processes (5); *0*.

73. Maxilla extends posteriorly to ectopterygoid (0); beyond ectopterygoid (5); *5*.

74. Basipterygoid crest absent (0); present (5); *0*.

75. Quadrate lateral shelf absent (0); present (5); *0*.

76. Black pigment on skull absent (0); present over most bones on the dorsal surface of the skull (5); *3*.

77. Premaxilla overlaps nasals laterally or is flush with them (0); nasal overlaps lateral edge of premaxilla (5); *0*.

78. Posterior of skull slopes superiorly or is flat (0); slopes inferiorly (5); *0*.

79. Crenulation along lateral edges of parietal absent (0); present (5); *0*.

80. Parietal roof flat (0); convex (5); *1*.

81. Posteriormost tooth is at least partially posterior to anterior mylohyoid foramen (0); posteriormost tooth is at least partially anterior to anterior mylohyoid foramen (3); posteriormost tooth is completely anterior to anterior mylohyoid foramen (5); *2*.

82. Angular process of articular present, large (0); reduced or absent (5); *0*.

83. Posterior suture of dentary pronged (0); blunt (5); *0*.

84. Anteriormost aspect of posterior border of dentary is anterior to mandibular fossa (0); within mandibular fossa (5); *0*.

85. Splenial present, large (0); absent (1); present as anteromedial sliver (2); *0*.

86. Anteromedial process of coronoid extends anteriorly (0); ventral aspect of anteromedial process projects posteriorly (5); *5*.

87. Surangular foramen completely in surangular (0); bordered laterally by dentary (5); *0*.

88. Coronoid labial process absent (0); present (5); *5*.

89. Posterolateral aspect of coronoid terminates anterior to supra-angular foramen (0); extends into or beyond supra-angular foramen (5); *0*.

90. Jaw sculpturing in large adult males absent (0); *Chamaeleolis* type (1); *krugi* type (2); *cristatellus* type (3); *cybotes* type (4); wrinkled (5); *0*.

91. Angular bone present (0); absent (5); *5*.