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## A New Species of *Anolis* Lizard from the Cordillera de Talamanca of Western Panama

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**ABSTRACT.**—We describe a new species of *Anolis* from the highlands of western Panama. The new form is phenetically similar to *lemurinus*-group *Anolis*, especially to *Anolis pachypus* and *Anolis tropidolepis*. It differs from these two species in possessing fewer loreal scale rows, larger middorsal scales, and a solid red dewlap. We present a phylogenetic analysis of the new species and find that it nests within mainland Beta anoles as sister species to *A. tropidolepis*.

**RESUMEN.**—Describimos una especie nueva de *Anolis* de las tierras altas del oeste de Panamá. Esta forma nueva es fenéticamente similar al grupo-*lemurinus* de *Anolis*, especialmente a *Anolis pachypus* y *Anolis tropidolepis*. Ésta difiere de estas dos especies en que posee menos hileras de escamas loreales, escamas medio-dorsales más grandes y un abanico gular rojo uniforme. Presentamos un análisis filogenético de la especie nueva y encontramos que ésta encaja dentro de las anolis Beta de tierra firme como especie hermana de *A. tropidolepis*.

The *lemurinus* species group of *Anolis* is found from northern South America to Mexico. The group is characterized by narrow toepads, moderate adult size (59–79 mm snout–vent length, SVL), imbricate ventrals, a moderate male dewlap (reaching to or just beyond axillae), a dark interorbital bar, some lateral striping, and lack of enlarged postcloacal scales in males (Kohler, 1999, 2003; pers. obs.). The first member of the group, *Gastrotropis* (= *Anolis*) *lemurinus*, was described by Cope in 1861. Soon after that Cope described *Anolis vittigerus* (Cope, 1862) and *Anolis pachypus* (Cope, 1876). *Anolis tropidolepis* was described by Boulenger (1885). More recently, Kohler (1996, 1999; Kohler and Mc Cranie, 2001) has described additional species of *lemurinus*-group *Anolis*, bringing the roster of known forms to seven. Kohler (1999, 2003) has not included *A. pachypus* and *A. tropidolepis* in the *lemurinus* group. We follow Savage (2002) in including these, based on his arguments and personal observation, for purposes of comparison in this paper. This group is a subgroup of Etheridge's (1959) Beta section, sometimes recognized as the genus *Norops* (Guyer and Savage, 1986). We do not recognize this genus because to do so renders the rest of *Anolis* paraphyletic, and the other Guyer and Savage genera have been shown to be non-

monophyletic (Cannatella and de Queiroz, 1989; Jackman et al., 1999; Poe, 2004). The *lemurinus* group may be nonmophyletic (Nicholson, 2002; Poe, 2004). We compare the new species to the members of this informal *lemurinus* group not necessarily as a suggestion of relationship, but because these are the species most likely to be confused with the new form.

Although Myers (e.g., 1971), Williams (e.g., Williams and Duellman, 1967), Ibáñez (e.g., Arosemena and Ibáñez, 1994), and others have made considerable headway in elucidating the diversity of Panamanian *Anolis*, the Panamanian roster of this genus is far from complete (pers. obs.). In this paper, we describe a distinctive population of *lemurinus*-like *Anolis* as a new species.

### 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).

The following description is based on 13 individuals of the new taxon. Comparisons are made with all Panamanian and Costa Rican

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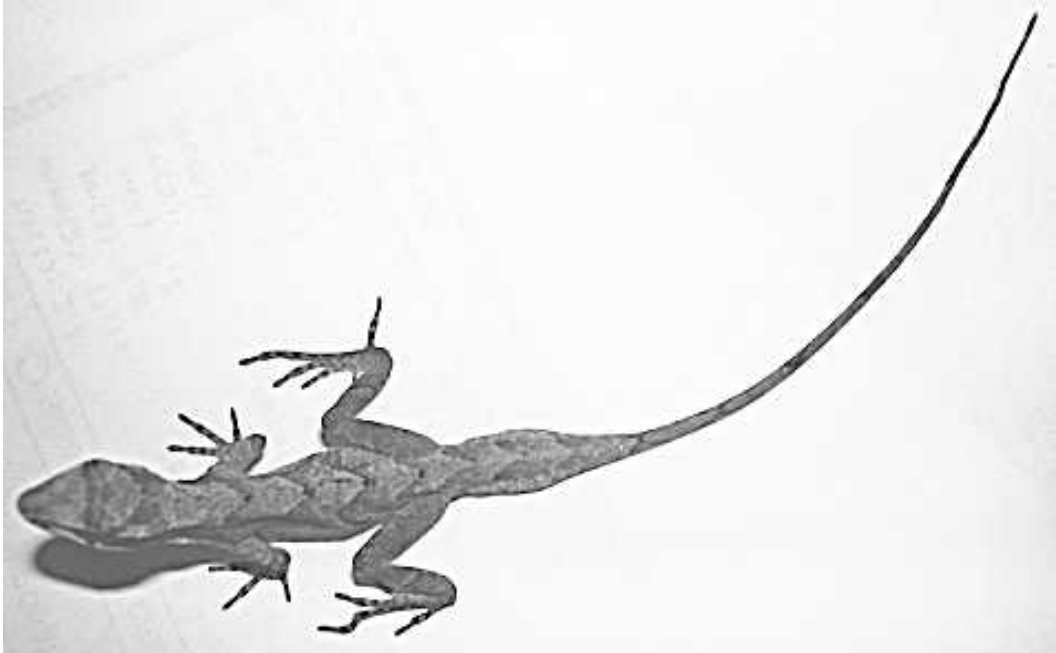


FIG. 1. Male of *Anolis magnaphallus*.

members of the *lemurinus* group: *A. pachypus*, including populations approximately 20 km west of the type locality of the new species; the Costa Rican form *A. tropidolepis*; *A. vittigerus* from eastern Panama; and individuals of *A. lemurinus* from Panama, Costa Rica, and Belize (Appendix 1).

Measurements were made with digital calipers to the nearest 0.1 mm. Snout–vent length (SVL) was measured from the tip of the snout to the anterior of the cloaca. Head length was measured from the tip of snout to the anterior edge of the ear. Head width was measured at the posteroventral corners of the jugal. Femoral length was measured from the midline of the venter to the knee, with the limb bent at a 90° angle.

Scale terminology follows Williams et al. (1995). Hemipenial terminology follows Savage (1997). Skeletal terminology follows Oelrich (1956) and Etheridge (1959). See Poe (2004) for detailed description of skull characters used here.

Museum and collection abbreviations are as follows: CH, Círculo Herpetológico de Panamá; MSB, Museum of Southwestern Biology; MVUP, Museo de Vertebrados de la Universidad de Panamá; POE, field tags of S. Poe.

*Anolis magnaphallus* sp. nov.

Figure 1

*Holotype*.—MSB 72579, an adult male, collected at the eastern entrance to Sendero Quetzales,

8 km North of Boquete, approximately 08°49.0'N, 82°28.6'W, Chiriqui Province, Panama, by S. Poe and C. Hickman on 13 December 2003.

*Paratypes*.—MSB 72577–72578, 72580–72581; MCZ 184540; MVUP 1895: same locality, collectors, and date of collection as holotype; CH 1042: Panamá, Chiriquí, near Boquete, approximately at 1033 m elevation, by L. Bruña, F. Crastz, F. Jaramillo, C. Jaramillo, and R. Ibáñez on 22 April 1982; CH 1046, 1050, 1052, 1055: Panamá, Chiriquí, Horqueta by L. Bruña, F. Crastz, F. Jaramillo, C. Jaramillo, and R. Ibáñez on 22 April 1982; MVUP 1884: road to Palo Alto, approximately at 1490 m elevation, Boquete, Chiriquí Province, Panamá, by C. Jaramillo and R. Ibáñez on 4 September 1982.

*Diagnosis*.—*Anolis magnaphallus* is most similar to *A. pachypus* and *A. tropidolepis* of the *lemurinus* group of *Anolis*. In addition to the standard *lemurinus* group characters (see above), it shares with these two forms the conditions of bulging hemipenes (Fig. 1), 3–4 scales separating supraorbital semicircles, multicarinate head scales, and at least 10 scales across the snout between the second canthals. *Anolis magnaphallus* differs from these species in possessing fewer loreal rows ( $\bar{x}$  = 6.2 [5–8] in *A. magnaphallus*;  $\bar{x}$  = 9.2 [7–12] in *A. pachypus*;  $\bar{x}$  = 8.8 [7–10] in *tropidolepis*) and a broader band of larger middorsal scales (6–12 rows of enlarged scales,  $\bar{x}$  = 12.6 [10–15] longitudinal middorsals

TABLE 1. States for selected characters in *lemurinus*-group *Anolis* from Panama and Costa Rica. Values for counts are means with ranges shown in parentheses. Dewlap colors are from observations in life (*Anolis magnaphallus*, *Anolis pachypus*, *Anolis lemurinus*, *Anolis vittigerus*) and a description and photo (*Anolis tropidolepis*; Savage, 2002:plate 266). Maximum SVL for each species is from the *Anolis* Handlist (Williams et al., 1995) or data collected for this paper.

	<i>A. magnaphallus</i>	<i>A. pachypus</i>	<i>A. tropidolepis</i>	<i>A. vittigerus</i>	<i>A. lemurinus</i>
Maximum SVL (mm)	55	54	59	70	79
Male dewlap color	Brick red; white scales	Orange-red with yellow; white and black scales	Purple-red; white scales	Orange-red with dark central spot; white scales	Light orange-red with light center; white and black scales
No. loreal rows	6.2 (5–8)	9.2 (7–12)	8.8 (7–10)	6.7 (5–8)	6.4 (5–8)
Flank scales	Homogeneous	Homogeneous	Homogeneous	Heterogeneous	Homogeneous
No. rows of enlarged middorsal scales	~6–12	~2–5	~2–5	~12–20	~2–4
No. middorsals in 10% SVL	12.6 (10–15)	15.8 (14–17)	16.1 (14–17)	15.3 (12–15)	15.9 (13–20)
No. scales, naris to rostral	2.0 (2)	1.6 (1–2)	2.1 (2–3)	1.8 (1–2)	1.9 (1–2)
No. scales separating supraorbital semicircles	3.0 (2–4)	4.7 (3–7)	4.3 (3–6)	0.9 (0–2)	1.0 (0–2)
No. scale rows separating suboculars and supralabials	0.8 (0–1)	0.9 (0–1)	1.0 (1)	0.5 (0–1)	0.6 (0–1)
No. supralabial scales to center of eye	7.8 (7–9)	6.8 (5–8)	6.8 (6–8)	6.9 (6–8)	6.2 (5–7)
No. scales across snout between second canthals	11.6 (10–13)	14 (10–18)	14.1 (12–17)	8.5 (7–10)	8.1 (7–9)
No. lamellae on phalanges two and three of fourth toe	14.5 (13–16)	14.0 (13–15)	13.8 (13–15)	17.1 (15–19)	17.0 (15–18)
Head scales	Multicarinate	Multicarinate	Multicarinate	Unicarinate	Unicarinate
Hemipenes	Bulging	Bulging	Bulging	Not bulging	Not bulging

in 10% of SVL in *A. magnaphallus*; 2–5 rows of enlarged scales,  $\bar{x}$  = 15.8 [14–17] longitudinal middorsals in 10% of SVL in *A. pachypus*, 2–5 rows of enlarged scales,  $\bar{x}$  = 16.1 [14–17] longitudinal middorsals in 10% of SVL in *A. tropidolepis*, and in dewlap color (solid brick red in *A. magnaphallus*; orange-red with yellow pattern in *A. pachypus*; purple-red in *A. tropidolepis*). Comparisons among Panamanian and Costa Rican members of the *lemurinus* group are summarized in Table 1.

*External description of holotype (paratype variation in parentheses).*—Snout–vent length 52.9 mm (46.5–55.1); head length 13.0 mm (11.6–13.8), width 8.8 mm (7.0–9.5); ear height 1.5 mm (0.9–1.6); femoral length 16.0 mm (12.8–17.1). Tail length approximately 107 mm (67–95 mm).

Dorsal head scales multicarinate; pronounced frontal depression; rostral slightly overlaps

mental; 13 (10–13) scales across snout between second canthals; three (2–4) scales between supraorbital semicircles; two (1–3) elongate supraciliary scales followed by a few enlarged scales; six and seven (5–8) loreal rows; two scales from naris to rostral (sometimes with tiny third scale anterior to narial opening); interparietal length 0.9 mm (0.8–1.0); three (1–4) scales separating interparietal and supraorbital semicircles; seven or eight (7–9) supralabials to center of eye; six (6–8) postmentals; six (5–8) postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in size laterally, bordered medially by a partial row of small scales (or just a few small scales, or a complete row); mental is convex (or straight) posteromedially, partially (or completely) divided, extending posterolaterally beyond rostral; sublabial rows weakly enlarged along

infralabials; dewlap reaches to posterior of axillae in males, with large scales in single rows separated by naked skin, rudimentary in females; no axillary pocket; no enlarged post-cloacal scales in males.

Dorsal scales keeled, with a band of approximately eight (6–12, variable within as well as between individuals) gradually enlarged scales, 12 scales (10–15) counted longitudinally in 10% of SVL; ventral scales imbricate, weakly keeled, 14 scales in 10% of SVL, in diagonal rows (some rows transverse).

Dorsal limb scales multicarinate near the knee, unicarinate medially, larger anteriorly than posteriorly; supradigitals multicarinate; toepads expanded; 14 (13–16) lamellae under second and third phalanges of fourth toe; tail with keeled scales and a single middorsal row.

Hemipenes strongly bilobed in distal third; sulcus spermaticus divided distally; each of the paired distal lobes covered with calyces, appearing honeycombed, except for naked skin around distal terminations of sulci spermaticus; transverse folds on otherwise naked skin of sulcate and asulcate sides of undivided basal aspect; asulcate side with fleshy longitudinal fold extending from between distal lobes to transverse folds of basal part.

*Skeletal description (based on MSB 72578).*—Parietal roof flat, V-shaped, without casque, lacking crenulation on edges, barely extending over supraoccipital, with anterolateral corners flush with edges of frontal; pineal foramen at parietal-frontal suture; some wrinkling on all dorsal skull bones; postfrontal absent on right side, apparently present and partially fused on left; prefrontal separated from nasal by 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; no jugal-squamosal contact; posterior aspect of jugal mostly straight, not concave; epipterygoid contacts parietal; pterygoid and palatine teeth absent; lateral edge of vomer smooth; maxilla extends posteriorly beyond ectopterygoid; no basipterygoid crest; no lateral shelf of quadrate; black pigment present on parietal and posterior aspect of frontal but not on other bones; nasals strongly overlap premaxilla on both sides; posterior of skull slightly inferior to level of parietal-frontal suture; mandibular toothline extends posterior to anterior mylohyoid foramen; no splenial; 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 within 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, large.

Three postxiphisternal ribs attached to dorsal ribs, followed by one unattached rib; three sternal ribs; caudal vertebrae with posterolaterally directed, spatulate transverse processes anteriorly, gradually becoming strongly anterolaterally directed posteriorly (Beta condition); interclavicle T-shaped; 23 presacral vertebrae; three lumbar vertebrae; autotomy septa present anterior to transverse processes on posterior caudal vertebrae.

*Color in life (male, based on field notes and color photographs).*—Dorsum brown, with dark chevrons middorsally pointing posteriorly, separating grayish areas; head brown with dark interorbital bar and dark postoccipital band; lateral head dark dorsally, cream below eye; dark band extends from snout back through eye to shoulder, bordered below by cream band; some blotching on infralabials, darker blotching on posterior supralabials; faint banding on limbs; venter cream; tail with faint chevrons continuing from dorsum; iris bronze; body cavity with black lining.

Other specimens were described in field notes as “Dorsum light green; a lateral line from anterior eye to the shoulder; dorsal color pattern consists of small dark brown spots; dewlap red (magenta-scarlet),” and “Dorsum orange; dewlap red wine; venter yellowish cream with orange dots.” Females were recorded as possessing a small white dewlap.

*Distribution.*—The new species is known only from areas around Boquete and Cerro Horqueta in the Cordillera de Talamanca of Western Panama. We have collected *A. pachypus* west of *A. magnaphallus* approximately 20 km west of the type locality. *Anolis magnaphallus* probably occurs in suitable highland habitats east of the type locality and is replaced by *A. pachypus* to the west.

*Etymology.*—The specific names alludes to the noticeably enlarged genitalia of the males of the new species.

*Ecology.*—The type locality is disturbed forest on the edge of intact forest. Specimens of *A. magnaphallus* were collected there sleeping on vegetation at night. Other *Anolis* collected at the type locality were *Anolis kemptoni* and *Anolis microtus*. Specimens of *A. magnaphallus* collected elsewhere were recorded as “on vegetation,” and “during daytime on the ground near coffee plantations.”

*Relationships.*—The closest relatives of *A. magnaphallus* are likely to be among the *lemurinus* group, specifically with *A. tropidolepis* or *A. pachypus*. However *A. magnaphallus* is sufficiently different (Table 1), and the *lemurinus* group’s

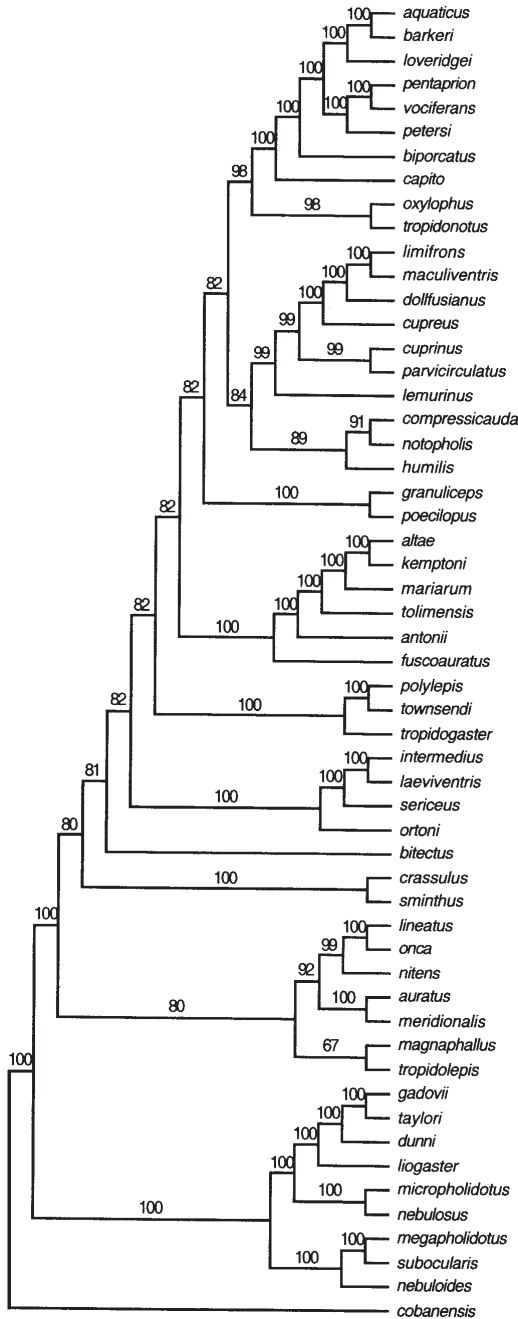


FIG. 2. Most parsimonious placement of *Anolis magnaphallus* on tree of Poe (2004). Numbers are not standard bootstrap values but rather the percentage of replicates each clade was upheld in constrained optimal tree, while the position of *A. magnaphallus* was estimated for each bootstrapped sample of characters.

monophyly and wider relationships sufficiently enigmatic (Nicholson, 2002; Poe, 2004), that close relationship with any of these forms cannot be assured. To assess the phylogenetic relationships of *A. magnaphallus*, we scored this taxon for the 91 morphological characters of Poe (2004) and analyzed the data using PAUP (D. L. Swofford, version 4.01b10, Sinauer Associates, Sunderland, MA, 2002). Codings are listed in Appendix 2. We entered the optimal combined data tree of Poe (2004) as a "backbone" constraint and performed a heuristic parsimony search and 100 replicates of a bootstrap parsimony analysis including data from *A. magnaphallus* and the 174 *Anolis* species in that tree. This analysis results in a tree wherein bootstrap proportions give an estimate of the placement of *A. magnaphallus*, assuming the tree of Poe (2004). Unconstrained searches failed to find shorter trees.

The optimal parsimony tree is shown in Figure 2, with Alpha *Anolis* and Caribbean Beta *Anolis* (sensu Etheridge, 1959) omitted because *A. magnaphallus* did not occur with any of these species in any bootstrap replicate. *Anolis magnaphallus* is nested within the mainland Beta *Anolis* and sister species to *A. tropidolepis*. The bootstrap proportions on this tree represent the percentage of replicates for which a clade emerged, whereas *A. magnaphallus* was allowed to "float" to different optimal places in the tree during each replicate. Thus, *A. magnaphallus* was a member of the mainland Betas exclusive of some Mexican forms (*Anolis cobanensis*, *Anolis nebuloides*, etc.) in every replicate, was sister species to *A. tropidolepis* in 67% of replicates and clustered with other mainland Beta forms (e.g., *Anolis compressicauda*, *Anolis notopholis*, *Anolis humilis*) in some replicates. Either *A. tropidolepis* or *A. pachypus*, which was not included in this analysis, is likely to be the closest relative of *A. magnaphallus*.

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## APPENDIX 1

### Comparative Material Examined

*Anolis lemurinus* ( $N = 15$ ) POE 1161–1162: Belize, Toledo District, Possum Point field station, N 16 49.85 W 88 17.12; POE 1165–1166, 1168: Belize, Cayo District, Guanacaste Park, N 17 15.677 W 88 47.245; POE 1185: Belize, Cayo District, Five Sisters Lodge, N 17 02.267 W 88 59.125; POE 1200, 1202: Belize, Cayo District, Caracol, N 16 45.756 W 89 06.914; POE 1842: Panama, Bocas del Toro, North end of Fortuna Road on Caribbean coast, 4 km East of turnoff to Almirante, N 08 57.097 W 82.08.906; MCZ 19402: Panama, Chiriqui, Chiriquicito; MCZ 140019: Panama, Bocas del Toro, Almirante; MCZ 140020: Panama, El Valle; MCZ 174174, 174176: Costa Rica: Heredia: Pro Viejo, OTS Finca La Selva; CH 1746: Panamá, Bocas del Toro, east of the PTP camp.

*Anolis pachypus* ( $N = 9$ ) MCZ 100970–100972, 100976–100977: Panama, Bocas del Toro, north slope of Cerro Pando; POE 1491–1492: Panama, Chiriqui, Bambito, across from Cabanas Kucikas; POE 1500–1501: Panama, Chiriqui, 1–2 km East of Las Nubes entrance to Parque Internacional La Amistad.

*Anolis tropidolepis* ( $N = 10$ ) MCZ 110015–110017: Costa Rica, 3 km north of Varablanca on road to summit of Volcan Poas; MCZ 110019–110020, 110023, 110028–110029: Costa Rica, San Jose, La Hondura; MCZ 110457–110458: Costa Rica, San Jose, 1 km above La Hondura.

*Anolis vittigerus* ( $N = 24$ ) POE 1568–1569: Panama, Darien, 7–8 km North of Meteti; POE 1656: Panama, Panama, Embera community along Rio Maje, N 09 02.056 W 78 45.483; 1935–1936: Panama, Darien, Pirre Station, N 08 01.182 W 77 43.952; MCZ 17190–17191: Panama, Darien, Mt. Sapo; CH-0514, 0518: Panamá, Darién, Yaviza-Canglón road; CH-0686: Panamá, Panamá, Parque Nacional Altos de Campana, cerro Campana, RENARE surrounds; CH-1673: Panamá, Coclé, N of El Copé, sawmill; CH-3890: Panamá, Panamá, Cocolí; CH-4172: Panamá, Panamá, Parque Nacional Altos de Campana, cerro Vallolí; CH-4412: Panamá, Panamá, cerro Trinidad surrounds; CH-4511: Panamá, Colón, quebrada Escandalosa on southern slope of cerro Bruja; CH-4643: Panamá, Darién, serranía de Jingurudó, camp at 665 m elevation, 07 39.23 N, 77 59.55 W; CH-4954: Panamá, Coclé, río

Indio, La Mina, Manguesal, approximately 08 56 17 N, 80 08.49 W; CH-5037: Panamá, Panamá, Río Indio Arriba, approximately 08 39.08 N, 80 06.43 W; CH-5160: Panamá, Panamá, Jordanal Arriba, approximately 08 40.30 N, 80 06.52 W.

## APPENDIX 2

Characters from Poe (2004), with codings for phylogenetic analysis of *A. magnaphallus* in italics. See Poe (2004) for detailed character descriptions, citations, and justifications for codes. States are reversed in character descriptions of characters 15, 31, and 67 of Poe (2004; e.g., "a" should be "z") relative to matrix entries in that paper. These are corrected here. This change serves to match up matrix entries with character descriptions and has no effect on topology or treelength.

1. Maximum male snout-vent length (SVL) 38 mm (a); 188 mm (z); g.
2. Ratio of maximum female SVL to maximum male SVL 1.06 (a); 0.57 (z); d.
3. Length of thigh short (a); long (z); v.
4. Length of head short (a); long (z); l.
5. Width of head narrow (a); broad (z); n.
6. Height of ear small (a); large (z); s.
7. Interparietal scale large (a); about equal to surrounding scales (z); q.
8. Length of tail about equal to SVL (a); about 1.5 times SVL (h); about two times SVL (m); about 2.5 times SVL (s); more than 2.8 times SVL (z); p.
9. Toepads overlapping first phalanx (0); not distinct from first phalanx (1); absent (2); 0.
10. Enlarged postcloacal scales present in males (a); absent in males (z); z.
11. Row of large spinose middorsal caudal scales separated by smaller smooth scales absent (a); present (z); a.
12. Tail crest absent (a); present in largest adult males (z); a.
13. Number of rows of enlarged middorsal scales 0–4 (a); 5 or more (z); z.
14. Each ventral scale is bordered posteriorly by two scales (a); by three scales (z); n.
15. Base of tail laterally compressed (a); round (z); z.
16. Male dewlap extends posterior past arms (0); to arms or shorter (1); absent (2); 1.
17. Female dewlap extends posterior past arms (0); to arms or shorter (1); absent (2); 1.
18. Tail uniformly patterned (a); base of tail purple, posterior part green or brown (z); a.
19. Mean number of dorsal scales in 5% of SVL 2.5 (a); 17 (z); g.
20. Mean number of ventral scales in 5% of SVL 2.75 (a); 14.3 (z); k.
21. Scales on dewlap in rows of single scales (a); with at least one double row (z); a.
22. Middorsal caudal scale rows single (a); double (z); a.
23. Axillary pocket absent (a); deep, tubelike (z); a.
24. Scales of midnuchal area similar to middorsal scales (a); in continuous row of bulbous scales distinct from dorsal scales (z); a.
25. Transparent scales in lower eyelid absent (a); present (z); a.
26. Mental scale partially divided (a); completely divided (z); h.
27. Mental scale broader than rostral scale (a); rostral broader than mental (z); a.
28. Subocular scales and supralabial scales in contact (a); separated by one or more rows of scales (z); s.
29. Mean number of scales across the snout 2.5 (a); 19 (z); p.
30. Mean number of postmental scales 3.25 (a); 9.75 (z); n.
31. Posterior border of mental scale straight or convex (a); concave (z); a.
32. Supraorbital semicircles separated by one or more rows of scales (a); in contact (z); a.
33. Preoccipital scale absent (a); present (z); a.
34. Middorsal scales of the snout not in regular pattern (a); arranged in two parallel rows that extend from the level of the second canthals to the nares (z); a.
35. Posterodorsal edge of rostral smooth (a); cleft (z); a.
36. Antermost aspect of rostral scale is even with lower jaw (a); overlaps lower jaw (z); ?.
37. Color of iris dark brown (0); yellow (1); blue or grey (2); green (3); red (4); 0.
38. Modal number of supraciliary scales zero (0); one (1); two (2); three (3); 2.
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); 3.
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) kksk; (6) kskk; (7) kssk; (8) ksss; (9) skkk; (a) skks; (b) sksk; (c) sskk; (d) sssk; (e) sskk; (f) sksk; 0.
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 (a); black (z); ?.
43. Fold of skin extending over dorsal rim of ear opening absent (a); present (z); a.
44. Modal number of enlarged sublabial scales zero (0); one (1); two or more (2); 0.
45. Frontal depression present (a); absent, top of snout is flat (z); a.
46. Interparietal scale separated from supraorbital semicircles by one or more rows of scales (a); in contact with supraorbital semicircles (z); a.



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); 7.
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); 1.
50. Interclavicle arrow-shaped (a); T-shaped (z); z.
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 (a); absent (z); a.
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 (a); rugose with bony tubercles (z); n.
57. Parietal crests form a trapezoid (0); V (1); Y (2); Y with parietal spur (3); 1.
58. Anterolateral corners of parietal crests reach posterolateral corners of frontal (a); reach medial to posterolateral corners of frontal (z); a.
59. Parietal casque absent (a); present (z); a.
60. Pineal foramen at parietal/frontal suture (a); in parietal (z); a.
61. Supratemporal processes leave supraoccipital exposed above (a); extend over supraoccipital (z); z.
62. Postfrontal present (a); absent (z); n.
63. Prefrontal contacts nasal (a); is separated from nasal by frontal and maxilla (z); z.
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 (a); present (z); a.
66. Anterior edge of nasal forms posterior border of naris (a); does not reach naris (z); a.
67. Dorsal process of jugal terminates on lateral aspect of postorbital (a); on medial or dorsal aspect of postorbital (z); a.
68. Contact between jugal and squamosal absent (a); present (z); a.
69. Posteroventral corner of jugal is anterior to posterior edge of jugal (a); posterior to posterior edge of jugal (z); a.
70. Epipterygoid contacts parietal (a); does not contact parietal (z); a.
71. Pterygoid teeth present (a); absent (z); z.
72. Lateral edges of vomer smooth (a); with posteriorly directed lateral processes (z); a.
73. Maxilla extends posteriorly to ectopterygoid (a); beyond ectopterygoid (z); z.
74. Basipterygoid crest absent (a); present (z); a.
75. Quadrate lateral shelf absent (a); present (z); a.
76. Black pigment on skull absent (a); present over most bones on the dorsal surface of the skull (z); a.
77. Premaxilla overlaps nasals laterally or is flush with them (a); nasal overlaps lateral edge of premaxilla (z); z.
78. Posterior of skull slopes superiorly or is flat (a); slopes inferiorly (z); z.
79. Crenulation along lateral edges of parietal absent (a); present (z); a.
80. Parietal roof flat (a); convex (z); a.
81. Posteriormost tooth is at least partially posterior to anterior mylohyoid foramen (a); posteriormost tooth is at least partially anterior to anterior mylohyoid foramen (m); posteriormost tooth is completely anterior to anterior mylohyoid foramen (z); a.
82. Angular process of articular present, large (a); reduced or absent (z); a.
83. Posterior suture of dentary pronged (a); blunt (z); a.
84. Anteriormost aspect of posterior border of dentary is anterior to mandibular fossa (a); within mandibular fossa (z); z.
85. Splenial present, large (0); absent (1); present as anteromedial sliver (2); 1.
86. Anteromedial process of coronoid extends anteriorly (a); ventral aspect of anteromedial process projects posteriorly (z); z.
87. Surangular foramen completely in surangular (a); bordered laterally by dentary (z); a.
88. Coronoid labial process absent (a); present (z); z.
89. Posterolateral aspect of coronoid terminates anterior to supraangular foramen (a); extends into or beyond supraangular foramen (z); a.
90. Jaw sculpturing in large adult males absent (0); *Chamaeleolis* type (1); *krugi* type (2); *crisatellus* type (3); *cybotes* type (4); wrinkled (5); 0.
91. Angular bone present (a); absent (z); z.