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PHYLOGENY OF THE *DACTYLOA* CLADE OF *ANOLIS* LIZARDS: NEW INSIGHTS FROM COMBINING MORPHOLOGICAL AND MOLECULAR DATA

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NOTE ADDED IN PROOF

Shortly after our paper was accepted, Nicholson and colleagues published a phylogenetic analysis of anoles and a proposal to divide *Anolis* into eight genera (Nicholson, K. E., B. I. Crother, C. Guyer, and J. M. Savage. 2012. It is time for a new classification of anoles (Squamata: Dactyloidae). *Zootaxa* 3477: 1–108). Here, we comment briefly on their study as it pertains to the phylogeny and taxonomy of the *Dactyloa* clade.

Despite not inferring *Dactyloa* to be monophyletic in the tree used for their proposed taxonomy (i.e., the consensus tree from the combined morphological and molecular parsimony analysis; their fig. 5A, note positions of *Anolis bonairensis*, *A. chloris*, *A. peraccae*, and *A. apollinaris*), Nicholson et al. (2012) recognized *Dactyloa* as one of their eight genera without making reference to this inconsistency (although *Dactyloa* was inferred to be monophyletic in their molecular tree, fig. 4A). By contrast, our combined data set supported the monophyly of *Dactyloa* (Figs. 3, 4), and we have chosen to treat *Dactyloa* as a subclade of *Anolis* rather than as a separate genus in the interest of avoiding disruptive and unnecessary name changes.

Some of our informally named series correspond, with some differences in species composition, to the species groups proposed by Nicholson et al. (2012). We describe the differences below.

Our *latifrons* series corresponds to their *latifrons* species group, except that in the tree purportedly used for their taxonomy (fig. 5A), *A. aequatorialis* and *A. ventrimaculatus* were inferred to be part of this species

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group (both species are absent from their molecular tree, fig. 4A), although their classification (appendix III) places both species in their *punctata* species group with no explanation for this inconsistency. We inferred these two species with strong support to be part of a monophyletic *aequatorialis* series that is mutually exclusive with respect to both the *latifrons* and *punctatus* series. Additionally, we have tentatively placed *A. mirus* and *A. parilis* in the *aequatorialis* series based on their previous inclusion in the traditional *aequatorialis* series (Williams, 1975; Ayala-Varela and Velasco, 2010); the tentative assignment reflects the current absence of these species from explicit phylogenetic analyses. By contrast, Nicholson et al. (2012) assigned *A. mirus* and *A. parilis*, neither of which was included in any of their analyses, to their *latifrons* species group without explanation. Finally, we placed *A. propinquus* in the *latifrons* series based on its hypothesized close relationship to *A. apollinaris* (Williams, 1988). By contrast, Nicholson et al. (2012) placed this species, which was not included in any of their phylogenetic analyses, in their *punctata* species group without explanation.

The combination of our *aequatorialis* and *punctatus* series corresponds roughly to the *punctata* species group in the classification of Nicholson et al. (2012, appendix III). We inferred these two series to be mutually exclusive clades (results further supported by molecular data alone; Castañeda and de Queiroz, 2011). Contradicting their own taxonomy, the tree of Nicholson et al. (2012, fig. 5A) supports the separation of the *aequatorialis* series, in that *A. aequatorialis*, *A. ventrimaculatus*, *A. chloris*, and *A. peraccae* are not inferred to be part of their *punctata* species group, despite being referred to that group in their classification (appendix III). Their tree does place *A. fasciatus* in their *punctata* species group, whereas our results indicate that this species is part of the *aequatorialis* series. We have treated *A. calimae* and *A. cuscoensis* as *incertae sedis* within *Dactyloa* based on conflicting results for *A. calimae* (also found by Castañeda and de Queiroz, 2011) and the inferred inclusion of *A. cuscoensis* by Poe et al. (2008) in clades not inferred in our study. By contrast, Nicholson et al. (2012) referred these two species to their *punctata* species group, although neither species was included in any of their phylogenetic analyses. Similarly, we have treated *A. laevis* and *A. phyllorhinus*, species formerly placed in the *laevis* series, as *incertae sedis* based on their current absence from explicit phylogenetic analyses (although we consider it likely that *A. phyllorhinus* belongs to the *punctatus* series). By contrast, Nicholson et al. (2012) assigned both of these species to the *punctata* species group, although neither was included in any of their phylogenetic analyses.

Our *Phenacosaurus* and our *heterodermus* series both correspond approximately to the *heterodema* species group of Nicholson et al. (2012), with the exception that they included *A. carlostoddi, A. bellipeniculus*, and *A. neblininus*. We consider these three species as *incertae sedis* within *Dactyloa* based on conflicting results in our analyses for *A. carlostoddi* and *A. neblininus* and the absence from explicit phylogenetic analyses of *A. bellipeniculus,* as well as its previously inferred close relationship to *A. neblininus* (Myers and Donnelly, 1996).

Our *roquet* series corresponds approximately to their *roquet* species group. However, in the tree purportedly used for their taxonomy (their fig. 5A), their *roquet* species group is not monophyletic: *A. bonairensis* is inferred as sister to *A. occultus* outside of *Dactyloa* (*A. bonairensis* is not included in their molecular-only tree; fig. 4A). By contrast, we inferred *A. bonairensis* to be part of a monophyletic *roquet* series (Figs. 3, 4).

Our combined analyses are based on a sample of 60 of the 83 currently recognized species in the *Dactyloa* clade, 40 of which were sampled for molecular data, whereas the combined analysis of Nicholson et al. (2012) is based on a sample of 31 *Dactyloa* species, 16 of which were sampled for molecular data (three others were sampled for molecular data only). Additionally, our molecular data consists of ~4,950 base positions representing three gene regions and both mitochondrial and nuclear DNA, whereas theirs consists of ~1,500 base positions representing one of the two mitochondrial gene regions used in our study. Because our results are based on larger samples of *Dactyloa* species (for both molecular and morphological data), as well as larger samples of molecular data (with respect to both numbers of bases and numbers of gene fragments, and including both mitochondrial and nuclear genes), and because many of their taxonomic conclusions that differ from ours are either contradicted by their own results or unsubstantiated, we do not consider any of the differences between our phylogenetic results and taxonomic conclusions compared with those in the study by Nicholson et al. (2012) to warrant changes to our proposed taxonomy. In contrast to Nicholson et al. (2012), we refrain from assigning some species to series and treat some taxonomic assignments as tentative because of contradictory results or poorly supported inferences, and we present justifications for all taxonomic decisions pertaining to species not included in our analyses.

Abstract. We present a phylogenetic analysis of the *Dactyloa* clade of *Anolis* lizards, based on morphological (66 characters of external morphology and osteology) and molecular (~4,700 bases of mitochondrial and nuclear DNA) data. Our set of morphological characters includes some that exhibit continuous variation and others that exhibit polymorphism within species; we explored different coding methods for these classes of characters. We performed parsimony and Bayesian analyses on morphology-only and combined data sets. Additionally, we explicitly tested hypotheses of monophyly of: 1) *Dactyloa* including *Phenacosaurus*, 2) *Dactyloa* excluding *Phenacosaurus* (as traditionally circumscribed), 3) taxa previously ranked as series or species groups described based on

morphological characters, and 4) clades inferred from molecular data. The morphological data alone did not yield *Dactyloa* or any of the previously recognized series described based on morphological characters; only the *Phenacosaurus* clade (as delimited based on molecular data) was inferred with the morphological data, and only in the parsimony analysis. In contrast, *Dactyloa* was inferred as monophyletic with the combined data set, although topology tests failed to reject the hypothesis of non-monophyly. Additionally, five clades inferred based on molecular data (eastern, *latifrons*, *Phenacosaurus*, *roquet,* and western) were inferred with the combined data sets with variable support and including additional species for which molecular data were not available and which have geographic distributions that conform to those of the clades in which they were included. Of the previously recognized taxa based on morphological characters, only the *roquet* series, which corresponds in species composition to the *roquet* clade, was inferred with the combined data. Topology tests with the combined data set rejected the monophyly of the *aequatorialis*, *latifrons* (as traditionally circumscribed), and *punctatus* series but not that of the *tigrinus* series and *Phenacosaurus* (as traditionally circumscribed). Our phylogenetic analyses and topology tests indicate that a new taxonomy for *Dactyloa* is warranted; we therefore present a revised taxonomy based on the results our phylogenetic analyses and employing phylogenetic definitions of taxon names.

Key words: *Anolis*, Character coding, *Dactyloa*, Phylogeny, Taxonomy

INTRODUCTION

The *Anolis* clade, one of the most diverse groups of vertebrates traditionally ranked as a genus, is composed of 384 currently recognized species (Uetz, 2012). This group of lizards is primarily Neotropical in distribution. Its members are characterized (with a few exceptions) by the possession of adhesive toe pads formed by laterally expanded subdigital scales, called lamellae, that are covered by microscopic setae, and of extensible and often brightly colored throat fans, called dewlaps, that are supported by elongated second ceratobranchials and occur in males and often in females (Etheridge, 1959).

Based on Etheridge's (1959) seminal work on the phylogeny and taxonomy of anoles, two large groups, traditionally ranked as sections, were informally recognized within *Anolis* based on the absence (alpha section) or presence (beta section) of transverse processes on the anterior autotomic caudal vertebrae. Each section was further subdivided into series and species groups based on morphological characters (Etheridge, 1959; Williams, 1976a,b). Subsequent to the morphological studies of Etheridge (1959) and Williams (1976a,b), a wide variety of data have been brought to bear on the phylogeny and taxonomy of *Anolis*, including albumin immunology (e.g., Gorman et al., 1980b, 1984; Shochat and Dessauer, 1981), allozymes (e.g., Gorman and Kim, 1976; Gorman et al., 1980a; Burnell and Hedges, 1990), behavior (e.g., Gorman, 1968), karyotypes (e.g., Gorman et al., 1968, 1983; Gorman and Stamm, 1975), and DNA sequences (e.g., Jackman et al., 1999; Schneider et al., 2001; Glor et al., 2003). Analyses of these data have provided support for the monophyly of the beta section and of several series and species groups (e.g., Creer et al., 2001; Schneider et al., 2001; Jackman et al., 2002; Nicholson, 2002). However, they have also indicated that other groups, including the alpha section, are not monophyletic. Additionally, the phylogenetic relationships within and among some groups are still disputed (e.g., Jackman et al., 1999; Nicholson, 2002; Poe, 2004).

Within the alpha section, Etheridge (1959) recognized the *latifrons* series for species with at least four postxiphisternal chevrons attached to the bony dorsal ribs and an arrow-shaped interclavicle (in which the lateral processes of the interclavicle are divergent from the proximal parts of the clavicles). Etheridge's (1959) *latifrons* series was composed of all mainland alpha *Anolis* (excluding *Phenacosaurus*; see below) along with the species in the *roquet* series from the southern Lesser Antilles, as well as *Anolis agassizi* and *A. gorgonae* from the Pacific islands of Malpelo and Gorgona, respectively. The *latifrons* series of Etheridge (1959) corresponds to the genus *Dactyloa*, one of five genera recognized by Guyer and Savage (1987 [1986]) based on a proposal to "divide" *Anolis* taxonomically. Although the recognition of those genera is

controversial (Cannatella and de Queiroz, 1989; Williams, 1989; Poe and Ibañez, 2007), some recent authors apply some of the same names to clades within *Anolis* regardless of rank and not necessarily with identical composition (e.g., Nicholson, 2002; Brandley and de Queiroz, 2004; de Queiroz and Reeder, 2008). In the present study, we use the name *Dactyloa* for the clade originating in the most recent common ancestor of the species included in the genus *Dactyloa* by Savage and Guyer (1989), which also includes the anoles formerly assigned to the genus *Phenacosaurus* according to the results of recent phylogenetic analyses (e.g., Jackman et al., 1999; Poe, 2004; Nicholson et al., 2005; Castañeda and de Queiroz, 2011). Currently, there are 83 recognized species in the *Dactyloa* clade, distributed among seven subgroups (based on morphological characters) commonly assigned to the rank of series: *aequatorialis*, *laevis*, *latifrons*, *punctatus*, *Phenacosaurus*, *roquet*, and *tigrinus* (see "Current Taxonomy within *Dactyloa*," below).

Three phylogenetic analyses have included more than 20% of the currently recognized *Dactyloa* species: Poe (2004) included 28 species, Nicholson et al. (2005) included 17 species (13 of which were included in Poe [2004]), and Castañeda and de Queiroz (2011) included 42 species (including 22 of 28 of Poe [2004] and 15 of 17 of Nicholson et al. [2005]). In Poe's (2004) combined analysis of allozyme, karyotype, morphological, and molecular data, *Dactyloa* (as defined in the previous paragraph, the name was not used by Poe) was inferred to be monophyletic based on the arrow shape of the interclavicle and the presence of a splenial in the mandible. However, bootstrap support for the clade (Poe, 2004, fig. 2, node 352) was less than 50% and both morphological characters supporting it are reversals to ancestral conditions. In the analyses of Nicholson et al. (2005, fig. 1) and Castañeda and de Queiroz (2011, fig. 1), based on molecular data, *Dactyloa* was inferred with moderate to strong bootstrap support (≥80%) and Bayesian posterior probabilities (≥0.90).

Of the seven subgroups described within *Dactyloa* based on morphological characters, only the *roquet* series has been consistently inferred by several phylogenetic analyses and has passed explicit statistical tests of monophyly (Jackman et al., 1999; Poe, 2004; Nicholson et al., 2005; Castañeda and de Queiroz, 2011). *Phenacosaurus*, as traditionally circumscribed, was inferred as monophyletic by Poe (2004) and Nicholson et al. (2005), although only two and three species of this group, respectively, were included in their phylogenetic analyses. In the analyses of Castañeda and de Queiroz (2011), which included six species of *Phenacosaurus*, the group was inferred as monophyletic with the exception of *A. neblininus*. The remaining subgroups have not been inferred in phylogenetic analyses or passed explicit statistical tests of monophyly, although the *laevis* series has not been tested (Poe, 2004; Nicholson et al., 2005; Castañeda and de Queiroz, 2011). In contrast to the poor support for the traditional series, Castañeda and de Queiroz (2011) inferred five strongly supported subclades within *Dactyloa*, which they recognized informally as eastern, *latifrons*, *Phenacosaurus*, *roquet*, and western clades. Although some of these clades bear the same names as species groups recognized by Williams (1976b) and series recognized by Savage and Guyer (1989), their composition is not necessarily the same.

In this study, we describe and score 66 morphological characters (external and osteological) for 60 species of *Dactyloa* and 6 outgroup species (including non-*Dactyloa Anolis* and non-*Anolis* Polychrotinae) to resolve the phylogenetic relationships within the *Dactyloa* clade. We analyze the morphological characters alone and in combination with ~4,720 bases of DNA sequence data presented by Castañeda and de Queiroz (2011). We perform parsimony and Bayesian analyses and examine different coding methods for continuous and polymorphic characters. We use tree topology tests to test hypotheses of monophyly of: 1) *Dactyloa* including *Phenacosaurus*, 2)

Dactyloa excluding *Phenacosaurus* (as traditionally circumscribed), 3) the traditionally recognized series delimited based on morphological characters (Williams, 1976b; Savage and Guyer, 1989), and 4) the clades inferred based on molecular data (Castañeda and de Queiroz, 2011). Based on the results of our analyses, we present a revised taxonomy that is consistent with the current knowledge of the phylogenetic relationships within the *Dactyloa* clade.

Current Taxonomy within *Dactyloa*

Based on morphological characters, six subgroups ranked as species groups by Williams (1976b) and as series by Savage and Guyer (1989) have been recognized within *Dactyloa: aequatorialis*, *laevis*, *latifrons*, *punctatus*, *roquet*, and *tigrinus*. In agreement with recent phylogenetic analyses (e.g., Jackman et al., 1999; Poe, 2004; Nicholson et al., 2005; Castañeda and de Queiroz, 2011), we recognize the group of species previously identified as the genus *Phenacosaurus* as an additional subgroup of *Dactyloa*. Some *Dactyloa* species have not been assigned to any of these subgroups; for example, *Anolis agassizi*, *A. anchicayae*, *A. cuscoensis*, and *A. ibanezi* were referred to what is here recognized as the *Dactyloa* clade, but with no series assignment (Etheridge, 1959; Poe et al., 2008, 2009a,b). Other species have been assigned to subgroups, but assignment was inconsistent. For example, *Anolis kunayalae* was described as morphologically similar to *A. mirus* and *A. parilis*, both members of the *aequatorialis* series, but assigned by the describing authors (Hulebak et al., 2007) to the *latifrons* group sensu stricto (= *latifrons* species group of Williams, 1976b) which is equivalent to the *latifrons* series of Savage and Guyer (1989); we therefore consider the series assignment of this species uncertain.

Aequatorialis *series*. The *aequatorialis* series is currently composed of 13 species: *A. aequatorialis*, *A. anoriensis*, *A. antioquiae*, *A. eulaemus*, *A. fitchi*, *A. gemmosus*, *A. maculigula*, *A. megalopithecus*, *A. mirus*, *A. otongae*, *A. parilis*, *A. podocarpus*, and *A. ventrimaculatus*, which are characterized by moderate to large body size (adult male snout-to-vent length [SVL] 66–101 mm), small head scales, smooth ventral scales, uniform dorsal scalation, and in some species narrow toe lamellae (Williams, 1976b; Williams and Acosta, 1996; Ayala-Varela and Torres-Carvajal, 2010; Ayala-Varela and Velasco, 2010; Velasco et al., 2010). The species in the *aequatorialis* series are distributed between 1,300 and 2,500 m above sea level in the Andes of Colombia (western and central cordilleras) and Ecuador (eastern and western slopes) (Williams and Duellman, 1984; Ayala-Varela and Torres-Carvajal, 2010; Velasco et al., 2010; Ayala and Castro, unpublished).

Laevis *series*. The *laevis* series, composed of *A. laevis*, *A. phyllorhinus*, and *A. proboscis*, is characterized by the presence of a soft, median protuberance from the snout, called a proboscis (Williams, 1976b, 1979) or nose leaf (Peters and Orces, 1956). Members of this series have a disjunct geographic distribution: *A. laevis* is distributed in the eastern foothills of the Peruvian Andes, *A. proboscis* is found at mid-elevations on the western slopes of the Ecuadorian Andes, and *A. phyllorhinus* is found in central Amazonia (Williams, 1979; Rodrigues et al., 2002).

Latifrons *series*. The *latifrons* series is composed of 12 species: *A. apollinaris*, *A. casildae*, *A. danieli*, *A. fraseri*, *A. frenatus*, *A. insignis*, *A. latifrons*, *A. microtus*, *A. princeps*, *A. propinquus*, *A. purpurescens*, and *A. squamulatus*, which are characterized by adult SVL $>$ 100 mm, large dewlaps in adult males ($>$500 mm^2), expanded toe lamellae, small head scales, smooth to weakly keeled ventral scales, and uniform dorsal scalation (Williams, 1976b; Savage and Talbot, 1978). These species, also called the giant mainland anoles (Dunn, 1937), are distributed in the lowlands and premontane forests of Costa Rica, western Panama, Colombia (western cordillera), and Ecuador; in the northern central lowlands of Venezuela; and in the inter-Andean valleys of Colombia (Savage

and Talbot, 1978; Arosemena et al., 1991; Ayala and Castro, unpublished).

Punctatus *series*. The *punctatus* series is composed of 21 species: *A. anatoloros*, *A. boettgeri*, *A. calimae*, *A. caquetae*, *A. chloris*, *A. chocorum*, *A. deltae*, *A. dissimilis*, *A. fasciatus*, *A. festae*, *A. gorgonae*, *A. huilae*, *A. jacare*, *A. nigrolineatus*, *A. peraccae*, *A. philopunctatus*, *A. punctatus*, *A. santamartae*, *A. soinii*, *A. transversalis*, and *A. vaupesianus*. The characters used to diagnose this series include adult SVL < 100 mm, wide toe lamellae (compared with the narrow lamellae observed in the *aequatorialis* series), small head scales, smooth to weakly keeled ventral scales (except in *A. punctatus boulengeri*, which has strongly keeled ventrals), uniform dorsal scalation, and in some species a protuberant snout in males (Williams, 1976b, 1982). Species in the *punctatus* series are distributed in the western lowlands of Panama, Colombia, and Ecuador; the mid- to high elevations of the Andes of Colombia (including the Sierra Nevada de Santa Marta), Venezuela, and Peru (eastern slope); the Amazon region and the Orinoco delta (Williams, 1982; Rodrigues, 1988; Poe and Yañez-Miranda, 2008; Poe et al., 2008, 2009a,b; Ayala and Castro, unpublished).

Roquet *series*. The *roquet* series is composed of 9 species: *A. aeneus*, *A. blanquillanus*, *A. bonairensis*, *A. extremus*, *A. griseus*, *A. luciae*, *A. richardii*, *A. roquet*, and *A. trinitatis*. The monophyly of this series is supported by karyological (Gorman and Atkins, 1969), morphological (Lazell, 1972; Poe, 2004), and molecular data (cytochrome *b* sequences, Giannassi et al., 2000; ND2 sequences, Creer et al., 2001). Six morphological synapomorphies support the monophyly of this series: 1) greater sexual size dimorphism, 2) an increase in interparietal scale size relative to surrounding scales, 3) an increase in mean number of postmental scales, 4) a straight (as opposed to concave) posterior border of the mental scale, 5) supraorbital semicircles in contact, and 6) interparietal scale in contact with the supraorbital semicircles (Poe, 2004). The *roquet* series is distributed in the southern Lesser Antilles, from Martinique south to Grenada, and on the islands of La Blanquilla, Bonaire, Tobago, and Trinidad (where *A. aeneus* and *A. trinitatis* have been introduced; Gorman and Dessauer, 1965, 1966) and Guyana (where *A. aeneus* has been introduced; Gorman and Dessauer, 1965; Gorman et al., 1971).

Tigrinus *series*. The *tigrinus* series is composed of 9 species: *A. lamari*, *A. menta*, *A. nasofrontalis*, *A. paravertebralis*, *A. pseudotigrinus*, *A. ruizii*, *A. solitarius*, *A. tigrinus*, and *A. umbrivagus*, and is characterized by small body size (adult male SVL = 40–60 mm), large smooth head scales, a large interparietal scale bordered by large scales and usually in contact with the supraorbital semicircles, and ventral scales smooth and larger than dorsal scales. Some species exhibit a parietal knob (a small projection of the posteriormost end of the central ridge of the Y-shaped parietal crests), externally visible in some species on the occipital area between the post-interparietal scales and nape scales (Williams, 1976b, 1992). Species in the *tigrinus* series are distributed in high elevations of the Sierra Nevada de Santa Marta (Colombia), the Andes of Colombia (eastern cordillera) and Venezuela, and the Atlantic forest of southeastern Brazil (Williams, 1992; Bernal Carlo and Roze, 2005).

Phenacosaurus. *Phenacosaurus* is composed of 11 species: *A. bellipeniculus*, *A. carlostoddi*, *A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. neblininus*, *A. nicefori*, *A. orcesi*, *A. tetarii*, *A. vanzolinii*, and *A. williamsmittermeierorum*. Earlier, *Phenacosaurus* was considered a separate genus from *Anolis* (Barbour, 1920) based on the heterogeneous dorsal scalation (enlarged round flat scales surrounded by smaller scales and granules), the tail structure (probably prehensile), an elevated rim of head plates (casque), digits widely and evenly dilated (such that their sides are parallel), and a "feebly developed" dorsonuchal crest (Lazell, 1969). However, recent phylogenetic analyses (Poe, 1998, 2004; Jackman et al., 1999; Nicholson et al., 2005; Castañeda and de Queiroz, 2011)

inferred these species to be nested within the clades composed of the species assigned to both *Anolis* and *Dactyloa*; therefore, we here consider *Phenacosaurus* another subgroup of *Dactyloa*. *Phenacosaurus* species are distributed in the Andean highlands (between 1,300 and 3,000 m) of Colombia, northern Ecuador, central Peru, and western Venezuela and the isolated tepuis of southeastern Venezuela (Lazell, 1969; Myers et al., 1993; Barros et al., 1996; Myers and Donnelly, 1996; Williams et al., 1996; Poe and Yañez-Miranda, 2007).

MATERIALS AND METHODS

Taxon and Character Sampling

Morphological data were collected for 60 species of *Dactyloa*, representing the subgroups *aequatorialis*, *latifrons*, *laevis*, *Phenacosaurus*, *punctatus*, *roquet*, and *tigrinus*. *Anolis anoriensis* (a recently described species formerly considered part of *A. eulaemus*) was treated as conspecific with *A. eulaemus* given that the description of the former was published after our data analyses were performed. Six species were included as outgroups: one non-*Anolis* Polychrotinae (*Polychrus marmoratus*) and five species representing different series of non-*Dactyloa Anolis* (*Anolis bimaculatus*, *A. cuvieri*, *A. equestris*, *A. occultus*, *A. sagrei*). A total of 643 alcohol-preserved (66 species; 393 males, 250 females), 123 dry (49 species), and 10 cleared and stained (9 species) specimens were examined. Additional data were collected from radiographs of 394 specimens (60 species). External characters were scored for all 66 species, and osteological characters were scored for 63 species (14 of which were only scored from radiographs and thus lack data for all cranial characters). The largest specimens available were examined as a proxy for including adult specimens only. All specimens measured at least 70% of the maximum SVL reported in the literature for the same sex and species (Williams and Acosta, 1996; Savage, 2002). A complete list of specimens examined is given in the Supplementary Appendix 1.[1]

Sixty-six morphological characters were examined, including both continuous characters (those that can be represented by real numbers, e.g., tail length) and discrete characters (those that can only be represented by integer values, including meristic and presence/absence, e.g., number of elongated superciliary scales). This data set includes characters of external morphology and osteology that have been previously used in *Anolis* phylogenetic analyses, have been regarded as diagnostic for *Anolis* subgroups, or have been used historically for species identification (Etheridge, 1959; Williams, 1976b, 1989; de Queiroz, 1987; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Williams et al., 1995; Poe, 1998, 2004; Jackman et al., 1999; Brandley and de Queiroz, 2004). Given that sexual dimorphism occurs in many species of *Anolis* (e.g., Schoener, 1969; Butler et al., 2000, 2007), characters were scored for both males and females and combined only when *t* tests (for continuous characters) or chi-square tests (for discrete characters) revealed no significant difference between the sexes or when tests could not be performed because sample sizes were too small. When significant differences were found, only data from males were used. However, given the small number of specimens available as dry skeletons and the absence of information on sex for roughly one-third of them, data for characters examined on dry specimens were combined without evaluating whether some of the characters exhibit sexual dimorphism. To ensure character independence, we performed correlation tests between characters. To remove the effects of correlation, we estimated residuals by regressing each variable against the correlated variable; residuals were used in subsequent analyses. In cases where a character was correlated with several others (e.g., SVL, head length,

[1] Supplementary material referenced in this paper is available online at www.mcz.harvard.edu/Publications/.

and head width), after residual estimation between two of the variables a second correlation test was performed to ensure that the resulting residuals were not still correlated with the other characters. A list of the characters analyzed, including measurement and coding details, is given in Appendix I.

Character Coding

Continuous Characters. Continuous characters were coded using two methods: the gap-weighting method of Thiele (1993), and Torres-Carvajal's (2007) modification of Wiens (2001) modification of Thiele's method. In Thiele's (1993) method, continuous characters are coded into discrete values while retaining information about order and relative distance between states. Average values per species were standardized by calculating the natural logarithm (ln, or ln + 1 when zero average values were present) to ensure equal variances; then each standardized average value (x) was range-standardized by applying the formula $x_s = [(x - \min)/(\max - \min)] \times (n - 1)$, where min and max are the minimum and maximum among the standardized average values, respectively, and n is the number of states used. One hundred and one states (0–100, $n = 101$) were used in the parsimony analyses (which allows capturing differences of 0.01 between states) and six states (0–5, $n = 6$) were used in the Bayesian analyses (in that 6 is the maximum number of ordered character states allowed in MrBayes v.3.1.2). Use of the term $(n - 1)$ is a modification of Thiele's (1993) equation, in which n was used incorrectly, because using n will lead to the recognition of an additional state (i.e., the total number of states is one greater than the value of the highest numbered state). Therefore, to ensure a total of 101 (or 6) states (including state "0"), $n - 1$ was used instead. Finally, the resulting values were rounded to the nearest integer and treated as states of a multistate ordered character. Wiens (2001) suggested a modification of Thiele's method using character state (step) matrices to increase the number of character states (then limited in PAUP* v.4.0b10 to 32 states on 32-bit computers). In this method, the term n of Thiele's equation is replaced by 1,000 (the maximum cost in a step matrix in PAUP*), and the difference between range-standardized scores (x_s) determines the cost of transformation between the corresponding states in the step matrix. Given that the default cost of character state transformation in PAUP* is 1, this approach requires weighting non-continuous characters by 1,000 to maintain equal weights among characters. Torres-Carvajal (2007) suggested a modification of Wiens' approach in which the term 1,000 in Wiens' equation is replaced by 1; this practice results in step matrices containing scores between 0 and 1 (rather than 0 and 1,000) and does not involve reweighting the non-continuous characters. Step matrices, in which transformation costs between states are differences between these scores, were generated in PAUP* as described by Torres-Carvajal (2007).

Polymorphic Characters. Polymorphic characters (including presence/absence and meristic) were coded using two different approaches: the MANOB approximation (*Man*hattan distance, *ob*served frequency arrays) of the frequency parsimony method described by Berlocher and Swofford (1997), and the majority or modal condition. Berlocher and Swofford's (1997) method was originally described for allele frequency data (see also Swofford and Berlocher, 1987) but has been applied to polymorphic morphological characters (Wiens, 2000; Brandley and de Queiroz, 2004; Torres-Carvajal, 2007). Under this approach, each taxon with a unique combination of allele (character state) frequencies is assigned a different character state, and changes between states are assigned costs equal to the Manhattan distances between those states using step matrices, which are analyzed under the parsimony criterion. In the MANOB method, the reconstructed hypothetical ancestors are required to have

a state (an array of allele [character state] frequencies) from the pool of states observed in the terminal taxa. Under the alternative majority or modal method, a polymorphic species is assigned the most common state in the individuals examined. The modal coding method was used despite being outperformed by the frequency coding method (Wiens, 1995, 1998; Wiens and Servedio, 1997) to perform Bayesian analyses because, currently, the only models available for morphological characters in MrBayes do not allow unequal rates (analogous to differential parsimony costs) among states. Cases with a 50:50 distribution of states were treated as partial uncertainty; that is, from the subset of states observed in a taxon, the software assigns to the taxon the state that minimizes length on a given tree.

Comparison of Coding Methods. To compare alternative coding methods, we estimated phylogenetic information content using the g_1 statistic (Fisher, 1930; Sokal and Rohlf, 1995; Zar, 1999). The g_1 statistic measures the skewness of a distribution and has been used to test for phylogenetic signal in data sets as part of the tree length distribution skewness test (Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). The test is based on the observation that the shape of the distribution of tree lengths (for all possible trees, or for a random subset when it is not feasible to evaluate the lengths of all possible trees) provides information about the presence of phylogenetic signal in the data (Hillis, 1991). Data sets with phylogenetic signal show a left-skewed distribution of lengths ($g_1 < 0$), which indicates that there are fewer solutions near the best solution than anywhere else in the distribution (Hillis and Huelsenbeck, 1992). We evaluated phylogenetic signal in each of our data sets by comparing the observed g_1 values against a distribution obtained from data with no phylogenetic signal. To construct the null distribution, we used Mesquite v.2.75 (Maddison and Maddison, 2011) to perform 1,000 random permutations (by shuffling states within characters among taxa) of data sets containing only those characters coded with the method being tested. We calculated the g_1 scores for the randomized matrices by evaluating 10,000 random trees in PAUP*. Coding methods whose g_1 scores fell outside the 95% confidence interval were considered to have significant phylogenetic signal.

Besides testing for phylogenetic signal in each data set, we evaluated differences in amounts of phylogenetic signal among data sets based on different coding methods. We did this by directly comparing g_1 values as estimates of the amount of hierarchical information recorded by each coding method. Values were compared between methods for coding continuous characters (Thiele's [1993] gap-weighting method with 101 character states versus Torres-Carvajal's [2007] version of the gap-weighting method versus Thiele's [1993] gap-weighting method with 6 character states) and between methods for coding polymorphic characters (frequency arrays using Manhattan distance step matrices versus using modal conditions). The g_1 values were estimated in PAUP* from data sets containing only those characters coded with the method being tested; g_1 values for each method were estimated from 10 samples of 500,000 random trees, and differences between the g_1 values were evaluated using t tests. To further assess differences (or the lack thereof) between the different coding methods, we performed reciprocal topology tests (Larson, 1998), in which for each data set (or portion thereof), the optimal tree inferred from that data set was compared (using two-tailed Wilcoxon signed-ranks tests) with the optimal trees inferred from data sets based on alternative coding methods.

Morphological Data Sets and Phylogenetic Analyses

Based on the results of the statistical tests comparing g_1 values, we selected Torres-Carvajal's (2007) version of the gap-weight-

ing method for coding continuous characters and the frequency arrays using Manhattan distance step matrices for coding polymorphic characters. This morphology-only data set will be referred to as the Torres-freq data set (See Supplementary Appendix 2) and was used for all subsequent parsimony analyses. A second morphology-only data set was constructed with continuous characters coded using Thiele's (1993) gap-weighting method with six character states and polymorphic characters coded using the modal condition. This data set, hereafter referred to as Thiele6-mode (See Supplementary Appendix 3), was specifically constructed to fulfill the requirements of running analyses in MrBayes (a maximum of six ordered character states and only rates [analogous to costs] of 0 and 1). Both data sets include 66 species and 66 characters (33 external, 33 osteological; 20 continuous, 31 discrete polymorphic, and 15 discrete non-polymorphic; Appendix I).

Parsimony analyses were performed on the Torres-freq data set using PAUP* (Swofford, 2002) with equal costs for state transformations, except for continuous and polymorphic characters (20 and 31 characters, respectively), in which differential costs were implemented with step matrices (see Supplementary Appendix 4), and for discrete (non-continuous, non-polymorphic) multistate ordered characters, which were weighted so that the range of each character equals 1. For each data set, a heuristic search with 1,000 replicates of random stepwise addition was performed, with all additional options left on default settings. Nodal support was assessed with non-parametric bootstrap resampling (BS; Felsenstein, 1985) using 100 bootstrap pseudoreplicates and heuristic searches with 50 replicates of random stepwise addition (remaining options were left on defaults) for each bootstrap pseudoreplicate.

Bayesian analyses were performed on the Thiele6-mode data set in MrBayes (Ronquist and Huelsenbeck, 2003) using the Mkv and Mkv + rate variation (rv) models for morphological data (Lewis, 2001). The Mkv model is analogous to the Jukes Cantor (JC) model of molecular sequence evolution, which assumes equal state frequencies, equal transformation rates between states, and equal rates among characters. The Mkv + rv model allows rate heterogeneity among characters using the symmetric Dirichlet (for multistate characters) and beta (for binary characters) distributions, in which one parameter determines the shape of the distribution of rates. This approach is similar to using the gamma (Γ) distribution to model rate variation among sites in molecular sequence data. Four independent runs—each with four Markov chains, a random starting tree, and default heating settings—were run for 10 million generations. Trees were sampled with a frequency of one every 1,000 generations. The first 25% of the trees were discarded as the "burn-in" phase. Stationarity in the post-burn-in sample was confirmed following the same procedures outlined in Castañeda and de Queiroz (2011). The maximum clade credibility tree (i.e., the tree with the highest product of posterior clade probabilities) was obtained using the TreeAnnotator package of BEAST v.1.6.2 (Drummond and Rambaut, 2007). Bayesian posterior clade probabilities (PP) were calculated based on the post-burn-in sample of trees for all four independent runs combined. Nodes with posterior probabilities greater than 0.95 were considered strongly supported, with the precaution that PP might overestimate clade support, especially in short internodes (Suzuki et al., 2002; Alfaro et al., 2003; Lewis et al., 2005). Bayes Factors (Kass and Raftery, 1995; Pagel and Meade, 2005) were used to compare the results obtained with the Mkv and Mkv + rv models for the morphological characters.

Combined Data Sets and Phylogenetic Analyses

The same two morphological data sets used in the morphology-only analyses were combined with the DNA sequence data (40 species of *Dactyloa* and six outgroup species) from Castañeda and de Queiroz (2011). Two

species for which DNA sequence data were available, *Anolis* sp1 and *A.* sp2, were excluded from our combined data sets because of the absence of morphological data. DNA sequence data included three gene regions: 1) the mitochondrial NADH dehydrogenase subunit II (ND2), five transfer RNAs ($tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$), and the origin for light strand replication (O_L, ~1,500 bases); 2) a fragment of the mitochondrial cytochrome oxidase subunit I (COI, ~650 bases), and 3) the nuclear recombination activating gene (RAG-1, ~2,800 bases). The combined data sets included 60 species of *Dactyloa*, 20 of which were missing molecular data, and 6 outgroup species (for a total of 66 species). Hereafter, the combined data sets will be referred to as CombTorres-freq and CombThiele6-mode, respectively. Parsimony analysis of the combined data set was run under the same conditions used for the morphology-only data sets. For the Bayesian analysis, the data were partitioned into morphological and molecular data. The latter were further partitioned (based on the results of Castañeda and de Queiroz [2011]) by gene region and, within each region, by codon position and tRNAs (ND2: four partitions; COI: three partitions, RAG-1: three partitions). The model of evolution for each molecular partition was selected based on the Akaike Information Criterion (AIC) as implemented in Modeltest (Posada and Crandall, 1998) v.3.7. For the morphological partition, the model of evolution was selected based on the Bayes factor scores from the morphology-only analyses (see above). Bayesian analyses were run under the same conditions used for the morphology-only analyses, except that the number of runs was increased to five and the number of generations was increased to 50 million to ensure that stationarity and convergence between chains were achieved.

Tests of Phylogenetic Hypotheses

We tested hypotheses concerning the monophyly of: 1) *Dactyloa* including *Phenacosaurus*, 2) *Dactyloa* excluding *Phenacosaurus* (as traditionally circumscribed), 3) subgroups described based on morphological characters for which we had adequate taxon samples: *aequatorialis*, *latifrons* (as traditionally circumscribed), *Phenacosaurus* (as traditionally circumscribed), *punctatus*, *roquet*, and *tigrinus*, and 4) the clades inferred by Castañeda and de Queiroz (2011) based on molecular data: eastern, *latifrons*, *Phenacosaurus*, *roquet*, and western. Given that we obtained data for only one species of the *laevis* series, no tests were performed regarding the monophyly of that series.

Phylogenetic hypotheses were tested using parsimony-based (Templeton, 1983) and Bayesian (Larget and Simon, 1999; Huelsenbeck et al., 2001) topological tests. The data sets (morphology-only and combined) with polymorphic characters coded using Torres-Carvajal's (2007) method and continuous characters coded with frequency arrays using Manhattan distance step matrices were selected to perform the parsimony-based tests. For the Bayesian tests, the data sets (morphology-only and combined) with continuous characters coded using Thiele's (1993) method with six character states and polymorphic characters coded using the modal condition were used.

For the parsimony-based tests, optimal trees resulting from parsimony analyses of the morphology-only and combined data sets were compared with optimal trees resulting from parsimony analyses of the same data sets incorporating each hypothesis as a topological constraint (performed using the same search conditions as for the unconstrained analyses). In cases in which the hypothesis of interest (e.g., previously recognized taxa based on morphological data or clades inferred based on molecular data) was obtained in the optimal unconstrained trees, the alternative hypothesis of non-monophyly was tested. Topologies corresponding to the hypotheses of interest were constructed using MacClade (Maddison and Maddison, 2001) v.4.07 and imported into PAUP* as topological constraints. Monophyly constraints were used for the hypotheses of previously recognized

taxa based on morphological characters, because all species included in the tests had been previously assigned to a group. Backbone constraints were used for the hypotheses of clades recognized based on molecular data, because the species for which only morphological data were available had not previously been assigned to any of the clades. Wilcoxon signed-ranks (WSR) tests (Templeton, 1983) were used to determine whether the optimal unconstrained tree is significantly different from the hypothesis corresponding to the constraint (Larson, 1998) and were performed as two-tailed tests in PAUP*. In the Bayesian tests, trees contained in the 95% credible set of trees from the post-burn-in sample for each data set were loaded into PAUP* and filtered based on topological constraints corresponding to each hypothesis. Topologies that were not present within the 95% credible set of trees (i.e., those that resulted in no trees retained under a given topological constraint) were considered rejected by the test.

RESULTS

Comparisons Between Coding Methods

All the methods resulted in characters with significant phylogenetic signal (as assessed by g_1) when compared with randomly permuted data ($P < 0.001$ for all coding methods). Of the methods used to code continuous characters, Torres-Carvajal's (2007) version of the gap-weighting method resulted in the most left-skewed distributions (g_1 values most negative; $\boldsymbol{g_1} = -0.301 \pm 0.004$), indicating that this method yielded characters that contain the most phylogenetic information. The method of Thiele (1993), with 101 character states, followed ($\boldsymbol{g_1} = -0.269 \pm 0.003$), and the same method with 6 character states resulted in the least skewed distributions ($\boldsymbol{g_1} = -0.253 \pm 0.003$). Comparing the coding methods used for polymorphic characters, the frequency arrays using Manhattan distance step matrices resulted in larger negative g_1 values ($\boldsymbol{g_1} = -0.175 \pm 0.004$) than did the modal condition method ($\boldsymbol{g_1} = -0.156 \pm 0.004$). Statistical ($t$) tests indicated significant differences between all coding methods for both continuous ($P < 0.001$ for all comparisons) and polymorphic ($P < 0.001$) characters in the amount of phylogenetic information recorded.

Phylogenetic Analyses

In all Bayesian analyses, the average standard deviation of split frequencies of converging chains reached values lower than 0.06, and the potential scale reduction factor (PSRF) of all runs combined reached 1.0 for most parameters. Bayes factors (BF) favored the Mkv + rv model over the Mkv model (BF = 194.46) in the analyses of morphology-only data sets, although the majority-rule consensus tree inferred using the simpler Mkv model was more resolved and contained more moderately to strongly supported nodes. With the Mkv model, 31 nodes were resolved, 14 of which had moderate (PP $\geq$ 0.75) to strong (PP $\geq$ 0.95) support (PP = 0.77–0.99; tree not shown); with the Mkv + rv model, 24 nodes were resolved, 12 of which had moderate support (PP = 0.76–0.94; tree not shown). In the Bayesian analyses of the combined data set, the five independent runs did not all converge onto the same likelihood values; instead, three runs converged onto a lower negative natural log likelihood score, and the remaining two converged onto a higher score. However, the relationships among species in the majority-rule topologies resulting from the two sets of runs were very similar, differing only in one poorly supported node. Nodal support and substitution model parameter values were also very similar, except for the rate variation among sites (alpha) and the rate multiplier (m) for several partitions. For this reason, two of the five runs were discarded, and only the three with lower negative natural log likelihood scores were used for tree estimation and hypotheses testing.

Morphology-only Data Sets. The parsimony analysis (Torres-freq data set) yielded a single fully resolved most parsimonious tree of 466.63 steps (CI = 0.22, RI = 0.53; Fig. 1). In this tree, *Dactyloa* is not inferred

to be monophyletic, and non-*Dactyloa Anolis* outgroup species are located in three different places (two within *Dactyloa*). These results are poorly supported (BS = 0%), and only two small, deeply nested clades in the entire tree are moderately supported (BS = 75–81%). All species previously placed in the genus *Phenacosaurus* were included in a clade (BS = 0%) that also contained *A. microtus* and *A. proboscis* (traditionally placed in the *latifrons* and *laevis* series, respectively). The *Phenacosaurus* clade, as defined in Castañeda and de Queiroz (2011), which includes all the *Phenacosaurus* species sampled in their study except *A. neblininus*, was inferred with the addition of *A. tetarii* (for which no molecular data are available) with low nodal support (BS = 44%). The Bayesian analysis (Thiele6-mode data set) under the Mkv + rv model, resulted in a fully resolved but poorly supported maximum clade credibility tree (Π PP = 1.497×10^{-12}; Fig. 2). *Dactyloa* was not inferred to be monophyletic, and non-*Dactyloa Anolis* outgroup species were located in four different places in the tree (all within *Dactyloa*). Species previously placed in the genus *Phenacosaurus*, except *A. carlostoddi* and *A. neblininus*, formed a paraphyletic group at the base of the tree. In both parsimony and Bayesian analyses, neither the series based on morphological characters nor the clades based on molecular data (except the *Phenacosaurus* clade in the parsimony analyses) were inferred.

Combined Data Sets. The parsimony analysis (CombTorres-freq data set) yielded a single fully resolved tree of 10,431.86 steps (CI = 0.30, RI = 0.43; Fig. 3). The Bayesian analysis (CombThiele6-mode data set) resulted in a fully resolved maximum clade credibility tree (Π PP = 1.449×10^{-8}; Fig. 4). In both analyses, *Dactyloa* was inferred to be monophyletic with low to moderate support (BS = 51%, PP = 0.81). Eleven unambiguous morphological synapomorphies support the monophyly of *Dactyloa* (Supplementary Appendix 5); however, this interpretation should be made with caution because it is most likely the result of biased outgroup sampling. For example, three out of five outgroup species have very large body sizes (maximum male SVL > 123 mm; Williams and Acosta, 1996) compared with most *Anolis* species, and as a result, a decrease in maximum male SVL is inferred as a synapomorphy of *Dactyloa*. In the parsimony analysis, the major clades inferred by Castañeda and de Queiroz (2011)—that is, eastern, *latifrons*, *Phenacosaurus*, *roquet*, and western—were inferred with weak to strong nodal support (BS = 6–93%). Similarly, in the Bayesian analysis, all five clades were inferred with weak to strong nodal support ($0.15 < PP < 0.97$). For the purpose of assigning species to these clades (eastern, *latifrons*, *roquet*, *Phenacosaurus*, and western), the clades were delimited using nodes bounded by species for which molecular data were available (e.g., the eastern clade is defined as the clade originating with the last common ancestor of a particular set of species inferred from molecular data [Castañeda and de Queiroz, 2011], thus excluding species outside that node that are more closely related to the eastern clade than to any of the other four mutually exclusive clades). In both parsimony and Bayesian analyses, the same sets of additional species, for which only morphological data were available, were included in the western and *Phenacosaurus* clades. In the case of the *latifrons* and eastern clades, different sets of additional species (for which only morphological characters were available) were inferred in the parsimony and Bayesian analyses. No additional species were included in the *roquet* clade in either analysis. In the following paragraphs, the species composition of each clade is detailed, with daggers (†) indicating species lacking molecular data. The synapomorphies that support each clade, inferred based on the parsimony analysis, are given in Supplementary Appendix 5.

The western clade was inferred with weak to moderate support in the parsimony and Bayesian analyses (BS = 25%, PP = 0.82; Figs. 3, 4) and is supported by nine

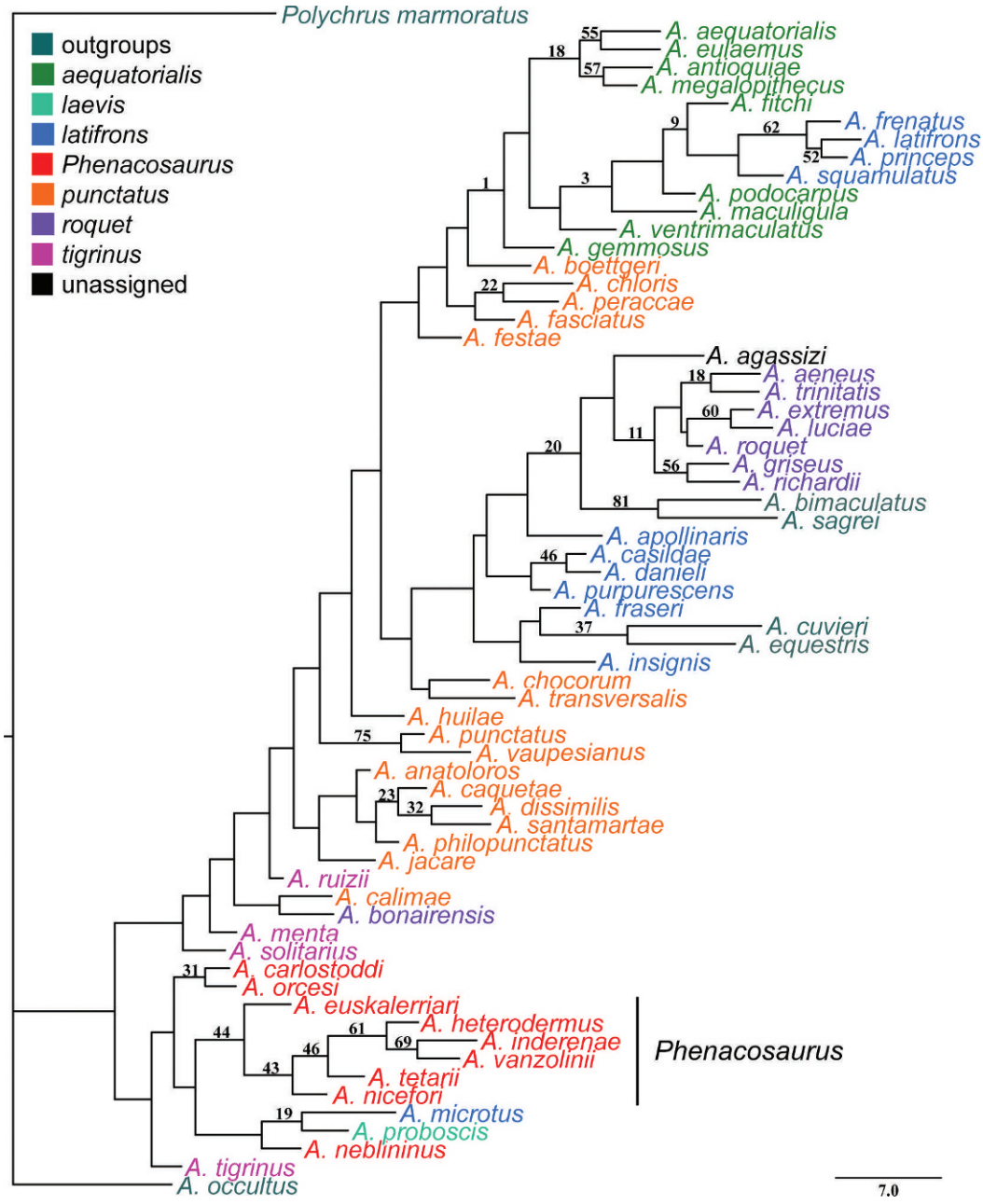

Figure 1. Most parsimonious tree inferred with the Torres-freq morphology-only data set (TL = 466.63, CI = 0.22, RI = 0.53). Bootstrap support (BS) values are shown above branches; missing values above branches indicate BS = 0%. The traditional species groups/series based on morphological characters (see text for details) are differentiated by color. One major *Dactyloa* subclade, of those described based on molecular data (see text for details), is indicated on the right.

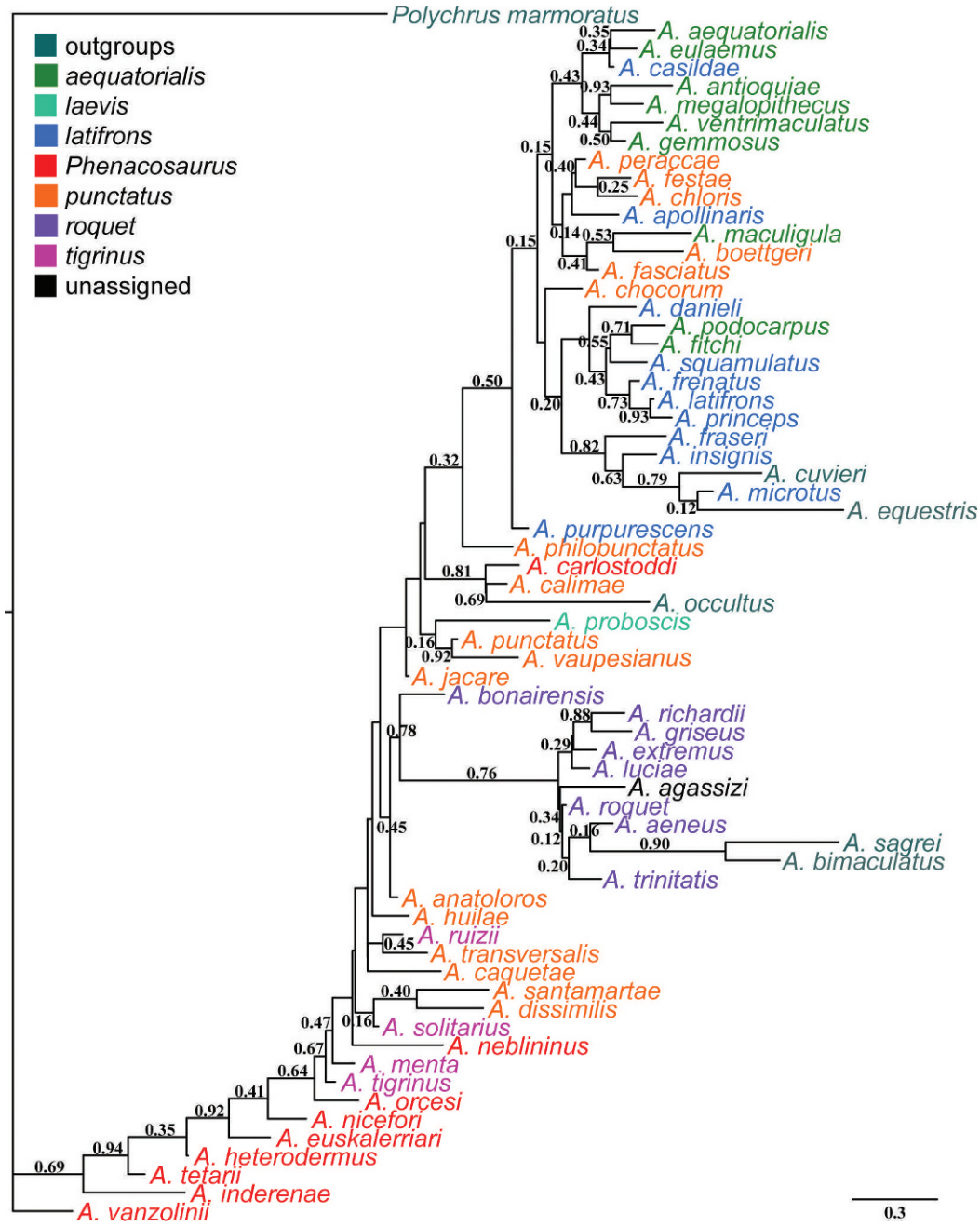

Figure 2. Bayesian maximum clade credibility tree inferred with the Thiele6-mode morphology-only data set using the Mkv + rv model. Bayesian posterior probabilities are shown above branches. The traditional species groups/series based on morphological characters (see text for details) are differentiated by color.

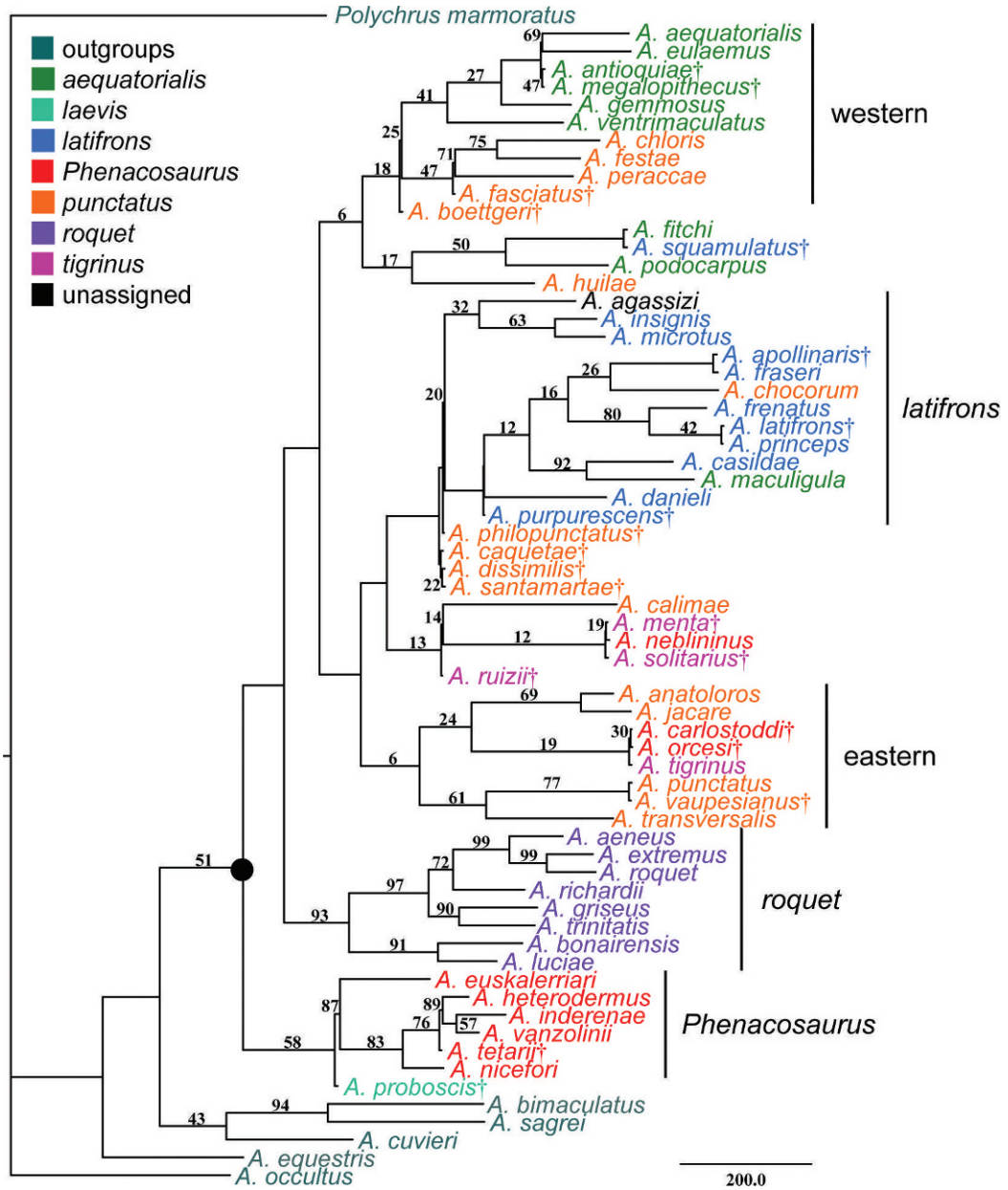

Figure 3. Most parsimonious tree inferred with the CombTorres-freq combined data set (TL = 10,431.86, CI = 0.30, RI = 0.43). Bootstrap support (BS) values are shown above branches; missing values above branches indicate BS = 0%. Daggers (†) following species names indicate the species for which only morphological data were available. The traditional species groups/series based on morphological characters (see text for details) are differentiated by color. Major *Dactyloa* subclades described based on molecular data (see text for details) are indicated on the right. The *Dactyloa* clade is indicated with a black dot on the corresponding node.

morphological characters (Supplementary Appendix 5). In both analyses, this clade is composed of the same 10 species: *A. aequatorialis*, *A. antioquiae*†, *A. chloris*, *A. eulaemus*, *A. fasciatus*†, *A. festae*, *A. gemmosus*, *A. megalopithecus*†, *A. peraccae*, and *A. ventrimaculatus*. Within this clade, the topologies are largely congruent, with the exception of the position of *A. gemmosus* and the internal relationships within the clade composed of *A. chloris*, *A. fasciatus*, *A. festae*, and *A. peraccae*. Additionally, in the parsimony analysis, *A. boettgeri* is inferred with weak support as the sister group of the western clade (BS = 18%), whereas in the Bayesian analysis, the sister taxon of the western clade is the clade (*A. boettgeri*, *A. huilae*) (PP = 0.49).

The *latifrons* clade was inferred in the parsimony analysis with low nodal support (BS = 20%; Fig. 3) and is supported by five morphological characters (Supplementary Appendix 5); it is composed of 13 species: *A. agassizi*, *A. apollinaris*†, *A. casildae*, *A. chocorum*, *A. danieli*, *A. fraseri*, *A. frenatus*, *A. insignis*, *A. maculigula*, *A. microtus*, *A. latifrons*†, *A. princeps*, and *A. purpurescens*†. In the Bayesian analysis, the *latifrons* clade was inferred with low support (PP = 0.46; Fig. 4) and is composed of the same set of species as the parsimony analysis with the addition of *A. squamulatus*. Three mutually exclusive subclades were inferred by both analyses: (*A. agassizi* (*A. microtus*, *A. insiginis*)) (BS = 32%, PP = 0.61), (*A. casildae*, *A. maculigula*) (BS = 92%, PP = 0.62), and (*A. frenatus* (*A. latifrons*, *A. princeps*) (BS = 80%, PP = 0.72). In both analyses, *A. philopunctatus* was inferred as the sister taxon of the *latifrons* clade.

The eastern clade was inferred in the parsimony analysis (Fig. 3) with low nodal support (BS = 6%) and is supported by seven morphological characters (Supplementary Appendix 5); it is composed of eight species: *A. anatoloros*, *A. carlostoddi*†, *A. jacare*, *A. orcesi*†, *A. punctatus*, *A. tigrinus*, *A. transversalis*, and *A. vaupesianus*†. In the Bayesian analysis (Fig. 4), the eastern clade was inferred with low nodal support (PP = 0.15) with 11 species: *A. anatoloros*, *A. dissimilis*†, *A. jacare*, *A. menta*†, *A. punctatus*, *A. ruizii*†, *A. santamartae*†, *A. solitarius*†, *A. tigrinus*, *A. transversalis*, and *A. vaupesianus*†. Despite the differences in species composition, two subclades were inferred in both analyses (Figs. 3, 4): (*A. transversalis* (*A. punctatus*, *A. vaupesianus*)) (BS = 61%, PP = 0.71) and (*A. anatoloros*, *A. jacare*) (BS = 69%, PP = 0.94).

The *roquet* clade was inferred with strong support in both parsimony and Bayesian analyses (BS = 93%, PP = 0.97; Figs. 3, 4) and is supported by 16 morphological characters (Supplementary Appendix 5). In both analyses, this clade is composed of the same eight species: *A. aeneus*, *A. bonairensis*, *A. extremus*, *A. griseus*, *A. luciae*, *A. richardii*, *A. roquet*, and *A. trinitatis*. The topology within this clade is identical for both phylogenetic analyses, with all nodes moderately to strongly supported (BS ≥ 72%, PP ≥ 0.96).

The *Phenacosaurus* clade was inferred with moderate support in both parsimony and Bayesian analyses (BS = 87%; PP = 0.84; Figs. 3, 4) and is supported by 19 morphological characters (Supplementary Appendix 5). In both analyses, this clade is composed of the same six species, *A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. nicefori*, *A. tetarii*†, and *A. vanzolinii*, all previously placed in the genus *Phenacosaurus*. The relationships within this clade are identical between parsimony and Bayesian analyses; however, in the parsimony analysis, *A. proboscis* is inferred as its sister group (BS = 58%), whereas in the Bayesian analysis, *A. orcesi* is inferred as its sister group with moderate support (PP = 0.87), and *A. proboscis* is the sister group to that (*A. orcesi*, *Phenacosaurus*) clade (PP = 0.43).

In both parsimony and Bayesian analyses, nine species, *A. boettgeri*†, *A. calimae*, *A. caquetae*†, *A. fitchi*, *A. huilae*, *A. neblininus*, *A. philopunctatus*†, *A. podocarpus*, and *A. proboscis*†, were not included in any of the five major clades within *Dactyloa* when those clades are treated as originating in the last

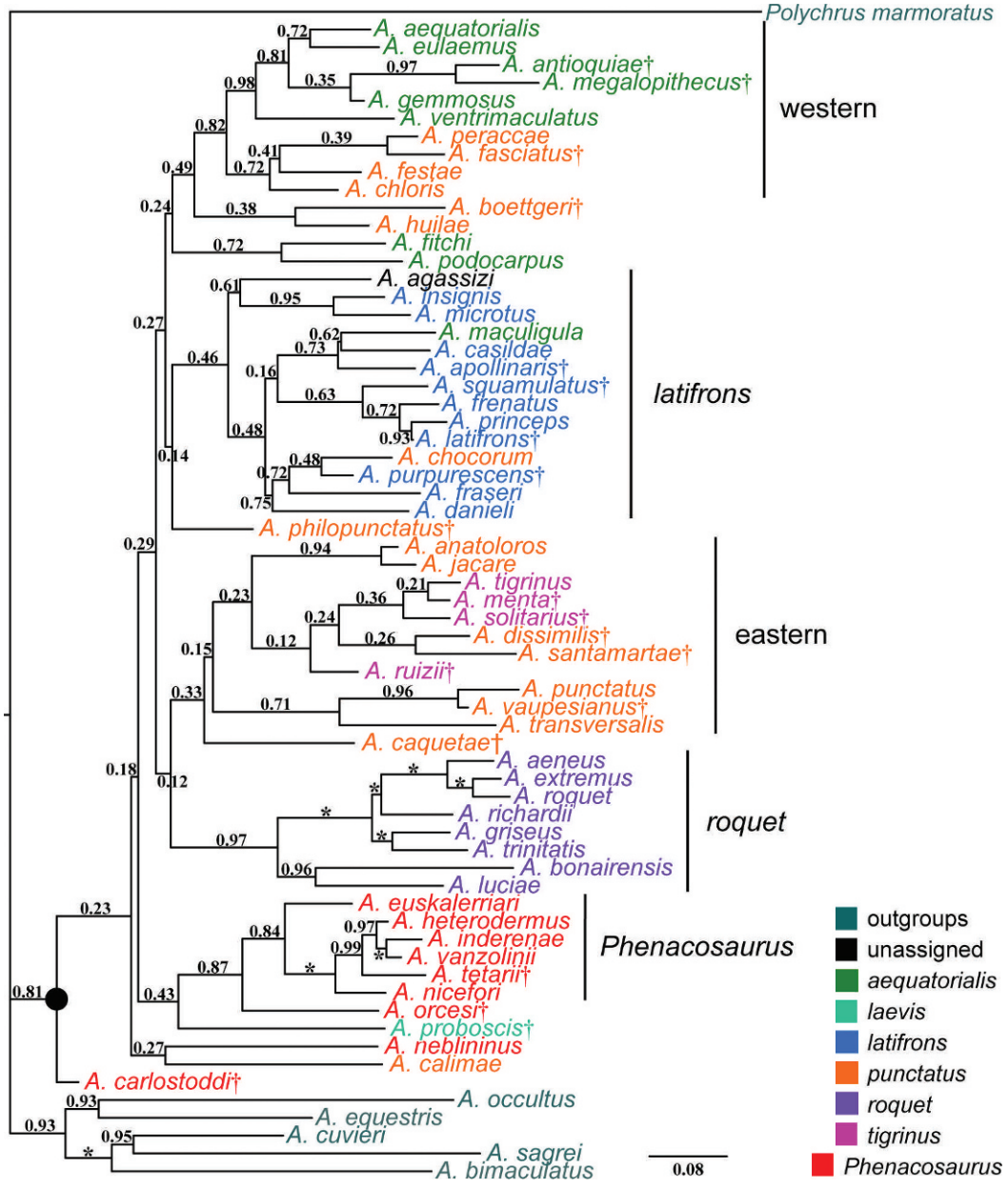

Figure 4. Bayesian maximum clade credibility tree inferred with the CombThiele6-mode combined data set. Bayesian posterior probabilities (PP) are shown above branches; asterisks (*) indicate PP = 1.0. Daggers (†) following species names indicate the species for which only morphological data were available. The traditional species groups/series based on morphological characters (see text for details) are differentiated by color. Major *Dactyloa* subclades described based on molecular data (see text for details) are indicated on the right. The *Dactyloa* clade is indicated with a black dot on the corresponding node.

TABLE 1. RESULTS OF THE WILCOXON SIGNED RANKS (WSR) AND BAYESIAN (B) TESTS OF PHYLOGENETIC HYPOTHESES OF PREVIOUSLY RECOGNIZED TAXA BASED ON MORPHOLOGICAL CHARACTERS (TOP) AND OF CLADES INFERRED BASED ON MOLECULAR DATA (BOTTOM) ON THE BASIS OF MORPHOLOGICAL DATA ONLY (TORRES-FREQ, THIELE6-MODE). FOR THE TORRES-FREQ DATA SET, DIFFERENCES BETWEEN TREE LENGTHS OF UNCONSTRAINED ANALYSES AND THOSE CONSTRAINED TO CORRESPOND TO EACH TESTED HYPOTHESIS (ΔTL) AND WSR *P*-VALUES ARE GIVEN. FOR THE BAYESIAN TESTS OF THE THIELE6-MODE DATA SET, THE PRESENCE (+) OR ABSENCE (−) OF THE ALTERNATIVE TOPOLOGY IN THE 95% CREDIBLE SET OF TREES IS SHOWN. SIGNIFICANT RESULTS ARE INDICATED WITH AN ASTERISK (*).

	Dataset		
	Torres-freq		Thiele6-mode
Test Hypothesis	ΔTL	WSR *P*-Value	B
Traditional groups			
Dactyloa	6.86	0.280	−*
Dactyloa excluding *Phenacosaurus*[a]	13.44	0.001*	−*
aequatorialis series	0.99	0.697	−*
latifrons series[b]	7.33	0.131	−*
punctatus series	9.32	0.332	−*
roquet series	0.84	0.851	+
tigrinus series	2.89	0.175	−*
Phenacosaurus[a]	2.33	0.629	−*
Groups based on molecular data			
Eastern clade	2.58	0.468	−*
latifrons clade	8.42	0.145	−*
Phenacosaurus clade	n/a[c]	n/a[c]	+
Phenacosaurus clade not monophyletic	0.44	0.827	n/a[c]
roquet clade	0.84	0.851	+
Western clade	1.05	0.969	−*

[a] As traditionally circumscribed, which includes (of the species sampled) *A. carlostoddi*, *A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. neblininus*, *A. nicefori*, *A. orcesi*, *A. tetarii*, and *A. vanzolinii*.

[b] As traditionally circumscribed, which includes (of the species sampled) *A. apollinaris*, *A. casildae*, *A. danieli*, *A. fraseri*, *A. frenatus*, *A. insignis*, *A. latifrons*, *A. microtus*, *A. princeps*, *A. purpurescens*, and *A. squamulatus*.

[c] Not applicable: the hypothesis in question was present in the optimal (unconstrained) tree(s), so the alternative hypothesis (monophyly or non-monophyly) was tested instead.

common ancestors of the species for which molecular data were available (see above). However, *A. boettgeri*†, *A. fitchi*, *A. huilae*, and *A. podocarpus* were consistently placed closer to the western clade than to any of the four other major clades; *A. philopunctatus*† was consistently placed closer to the *latifrons* clade, and *A. proboscis*† was consistenty placed closer to *Phenacosaurus*. Additionally, the positions of *A. carlostoddi*†, *A. dissimilis*†, *A. menta*†, *A. orcesi*†, *A*, *ruizii*†, *A. santamartae*†, *A. solitarius*†, and *A. squamulatus*† were inconsistent (particularly relative to the five major clades) between parsimony and Bayesian analyses.

Tests of Phylogenetic Hypotheses

The WSR and Bayesian tests performed on the morphology-only data sets (Torres-freq and Thiele6-mode, respectively) yielded very different results (Table 1): the WSR test failed to reject the monophyly of *Dactyloa* and each of the subgroups previously described based on morphological characters: *aequatorialis*, *latifrons*, *punctatus*, *roquet*, *tigrinus*, and *Phenacosaurus*; in contrast, the Bayesian test rejected the monophyly of *Dactyloa* and all of the previously recognized subgroups except the *roquet* series. Of the hypotheses tested, only the monophyly of *Dactyloa* excluding *Phenacosaurus* was rejected by both the WSR and Bayesian tests. When testing the clades inferred based on molecular data (Castañeda and de Queiroz, 2011) with the morphological data, contradictory results between the parsimony and Bayesian approaches were found again (Table 1): monophyly of the eastern, *latifrons*, *roquet*, and western clades was not rejected with the

TABLE 2. RESULTS OF THE WILCOXON SIGN RANKS (WSR) AND BAYESIAN (B) TESTS OF PHYLOGENETIC HYPOTHESES OF PREVIOUSLY RECOGNIZED TAXA BASED ON MORPHOLOGICAL CHARACTERS (TOP) AND OF CLADES INFERRED BASED ON MOLECULAR DATA (BOTTOM) ON THE BASIS OF COMBINED MORPHOLOGICAL AND MOLECULAR DATA (COMBTORRES-FREQ, COMBTHIELE6-MODE). FOR THE COMBTORRES-FREQ DATA SET, DIFFERENCES BETWEEN TREE LENGTHS OF UNCONSTRAINED ANALYSES AND THOSE CONSTRAINED TO CORRESPOND TO EACH TESTED HYPOTHESIS (ΔTL) AND WSR *P*-VALUES ARE GIVEN. FOR THE BAYESIAN TESTS OF THE COMBTHIELE6-MODE DATA SET, THE PRESENCE (+) OR ABSENCE (−) OF THE ALTERNATIVE TOPOLOGY IN THE 95% OF CREDIBLE SET OF TREES IS SHOWN. SIGNIFICANT RESULTS ARE INDICATED WITH AN ASTERISK (*).

	Dataset		
	CombTorres-freq		CombThiele6-mode
Test Hypothesis	ΔTL	WSR *P*-Value	B
Groups based on morphological data			
Dactyloa not monophyletic	1.47	0.712	+
Dactyloa excluding *Phenacosaurus*[a]	44.83	0.003*	−*
aequatorialis series	135.33	<0.001*	−*
latifrons series[b]	83.91	<0.001*	−*
punctatus series	170.43	<0.001*	−*
roquet series not monophyletic	35.09	0.016*	+
tigrinus series	4.82	0.336	+
Phenacosaurus group[a]	21.35	0.253	+
Groups based on molecular data			
Eastern clade not monophyletic	17.63	0.366	−*
latifrons clade not monophyletic	25.56	0.054	−*
Phenacosaurus clade not monophyletic	59.81	<0.001*	−*
roquet clade not monophyletic	25.11	0.077	−*
Western clade not monophyletic	9.90	0.687	−*

[a] As traditionally circumscribed, which includes (of the species sampled) *A. carlostoddi*, *A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. neblininus*, *A. nicefori*, *A. orcesi*, *A. tetarii*, and *A. vanzolinii*.

[b] As traditionally circumscribed, which includes (of the species sampled) *A. apollinaris*, *A. casildae*, *A. danieli*, *A. fraseri*, *A. frenatus*, *A. insignis*, *A. latifrons*, *A. microtus*, *A. princeps*, *A. purpurescens*, and *A. squamulatus*.

WSR test, but it was rejected—except in the case of the *roquet* series—with the Bayesian test. The parsimony analysis indicated monophyly of the *Phenacosaurus* clade, but the WSR test failed to reject its non-monophyly; conversely, the Bayesian analysis indicated non-monophyly of the group, but the Bayesian test failed to reject its monophyly.

With the combined data sets, the WSR and Bayesian tests yielded mostly congruent results concerning taxa recognized previously on the basis of morphological characters (Table 2). The non-monophyly of *Dactyloa* (given that this hypothesis was inferred in the optimal tree) and the monophyly of the *tigrinus* series and *Phenacosaurus* were not rejected by either test. In contrast, both tests rejected the monophyly of the *aequatorialis*, *latifrons*, and *punctatus* series. The non-monophyly of the *roquet* series (a clade inferred in both parsimony and Bayesian optimal trees), was rejected by the WSR test, but not by the Bayesian test. The monophyly of *Dactyloa* excluding *Phenacosaurus* was rejected by both the WSR and Bayesian tests.

The clades inferred based on molecular data (Castañeda and de Queiroz, 2011) were also present in the parsimony and Bayesian optimal trees of the combined data sets; therefore, the non-monophyly of these groups was tested. Results obtained with the WSR and Bayesian tests differed in most cases (Table 2): the WSR test rejected the hypothesis of non-monophyly of the *Phenacosaurus* clade and failed to reject the non-monophyly of the eastern, *latifrons*, *roquet*, and western clades. In contrast, the Bayesian tests rejected the non-monophyly of all these clades.

DISCUSSION

The objectives of this study were to reconstruct the phylogeny of the *Dactyloa* clade based on morphological characters alone and in combination with molecular data, to explore different coding methods for continuous and polymorphic characters that

were part of our data set, and to test hypotheses of monophyly of previously described taxa. In the following paragraphs, we discuss the advantages and disadvantages of the different coding methods used, the phylogenetic relationships inferred, and their implications regarding previously recognized taxa. Finally, based on our findings, we propose a new taxonomy that recognizes only monophyletic taxa and in which names are defined following the rules of PhyloCode.

Differences Among Coding Methods

For continuous characters, the coding method of Torres-Carvajal (2007) resulted in characters containing the largest amount of phylogenetic signal, followed by Thiele's (1993) method using 101 character states. The main disadvantage of Torres-Carvajal's (2007) method is that it results in a significant increase of computation time compared with Thiele's (1993) method (MRC, personal observation), presumably because it uses step matrices. Although Thiele's (1993) method discretizes continuous characters, it maintains information on order and magnitude of change between states. Therefore, its implementation using 101 character states (i.e., allowing a 0.01 resolution between states) might be sufficient to approximate a continuous distribution (particularly if the values from the continuous distribution are estimated at a similar level of precision). Despite significant differences in g_1 values, reciprocal WSR tests (Larson, 1998) indicate that phylogenetic inferences between the two methods (at least for the *Dactyloa* data set) are not strongly in conflict: tests for differences between the optimal trees resulting from only continuous characters under each of the two coding methods (i.e., Thiele's [1993] gap-weighting method with 101 character states or Torres-Carvajal's [2007] step matrix modification of it) using the data sets produced by each of the coding methods were not statistically significant ($P = 0.872$ using the Thiele-coded data set; $P = 0.391$ using the Torres-coded data set). In contrast, reciprocal tests between the optimal trees resulting from only continuous characters coded with Thiele's (1993) method using 101 states compared with using 6 states were statistically significant ($P = 0.036$ using the data set with 101 states; $P = 0.023$ using the data set with 6 states). Similarly, reciprocal tests between the optimal trees resulting from only continuous characters coded with Torres-Carvajal's method versus Thiele's (1993) method using six states were also statistically different ($P = 0.040$ using the Torres-coded data set; $P = 0.046$ using the Thiele-coded data set). These results combined with the results based on the g_1 statistic indicate that a larger number of character states significantly increases the amount of phylogenetic information recorded by Thiele's coding method. Moreover, these findings suggest that Thiele's (1993) method, when implemented using a large number of character states, may be an effective alternative to fully continuous coding methods. Despite performing more poorly according to g_1 values, it did not yield a significantly different tree according to reciprocal tests. At least in this case, the loss of information appears to be small and is compensated by lesser computational requirements.

The polymorphic characters coded as frequency arrays using Manhattan distance step matrices were found, based on g_1 values, to contain significantly more phylogenetic signal than those coded as standard binary or multistate characters and scored using modal conditions. Reciprocal tests indicate that there are significant differences between the optimal trees resulting from data sets including only polymorphic characters coded using these two methods ($P < 0.001$ using the frequency arrays–coded data set; $P < 0.001$ using the standard coding with modes data set). This result further supports previous studies on empirical (Wiens, 1995, 1998) and simulated (Wiens and Servedio, 1997) data, showing that methods that incorporate frequency information outperform, based on accuracy measurements, other methods for analyzing polymorphic characters (including scoring

modal conditions). The advantages of frequency methods include making use of more phylogenetic information and reducing the effects of sampling errors, in that the probability of being mislead by the presence or absence of states occurring at low frequencies is reduced, which is particularly important with small sample sizes (Swofford and Berlocher, 1987; Wiens, 1995; Wiens and Servedio, 1997). The main disadvantage of some of the methods incorporating frequency information is that they significantly increase the computation time required because of the use of step matrices (e.g., Wiens, 2000; MRC, personal observation).

Phylogeny of *Dactyloa*

This study presents the phylogenetic relationships of *Dactyloa* based on molecular data for 40 species and morphological data for the same 40 species and 20 additional ones (for a total of 60 species). This represents a substantial improvement upon previous studies, which included a maximum of 42 species (Castañeda and de Queiroz, 2011), 2 of which were not included in the current study (see "Materials and Methods") for molecular data only, or a maximum of 28 species (Poe, 2004) for multiple data sources. For the combined data sets, *Dactyloa* was inferred to be monophyletic, provided that it includes the *Phenacosaurus* species, in agreement with previous studies (Poe, 1998, 2004; Jackman et al., 1999; Nicholson et al., 2005; Castañeda and de Queiroz, 2011), although its monophyly was not strongly supported according to topology tests employing constraint trees (the hypothesis of non-monophyly was not rejected, though monophyly of *Dactyloa* excluding *Phenacosaurus* was rejected). Previous analyses of the entire *Anolis* clade based on combined data, with a similar set of characters and coding methods, inferred a fully resolved but poorly supported *Dactyloa* (Poe, 2004, fig. 2), although the analysis of only the morphological component of this data set did not infer *Dactyloa* (Poe, 2004, fig. 5). In contrast, previous analyses based solely on molecular data strongly supported the monophyly of *Dactyloa* (Nicholson et al., 2005; Castañeda and de Queiroz, 2011).

The considerable difference in nodal support between the combined (morphological and molecular) and molecular-only analyses could derive from intrinsic characteristics of the morphological characters. For example, the morphological characters might be highly homoplastic, introducing support for conflicting groupings within the morphological data set, or they might have low phylogenetic information content, allowing multiple placements of taxa for which only morphological data are available. Additionally, it is possible that conflicts between the phylogenetic signal of the morphological and molecular data sets result in a reduction in nodal support. In our analyses, we excluded characters commonly used in studies of morphological convergence (e.g., limb and tail length) to avoid this potential bias (but see de Queiroz [1996, 2000] and Poe [2005] for the advantages of including these characters in phylogenetic reconstruction). Trees inferred with the morphology-only data set showed a general lack of support for any particular topology (regardless of the coding method used), which suggests that the morphological data might not have sufficient phylogenetic signal to produce any strong conflict with the molecular data (and therefore strongly affect nodal support). However, reciprocal WSR topology tests comparing the tree inferred from morphological data (Fig. 1) with that inferred based on molecular data (Castañeda and de Queiroz, 2011, fig. 1A) indicated strong disagreement between the two data sets ($P \leq 0.0001$ for each case). Therefore, the difference in nodal support between the molecular and combined analyses would seem to result, in this case, from multiple placements of at least some of the species that were scored for morphological characters only, as well as the larger total number of species within the *Dactyloa* clade (so that support is distributed among a larger number of nodes).

Castañeda and de Queiroz (2011) inferred, based on molecular data, five strongly supported clades (informally named eastern, *latifrons*, *Phenacosaurus*, *roquet*, and western) with coherent geographic distributions. Based on the combined data, we inferred those same five clades with the inclusion of additional species for which only morphological data are available. In agreement with the inferred relationships of those species, in all cases, their geographic distributions lie within or on the periphery of the clades in which they were placed. The discussion that follows concerns the composition and internal relationships of the five clades and is based exclusively on the results obtained with the combined analyses. Following Castañeda and de Queiroz (2011), we also adopt (in the following discussion) delimitations of the clades based on the species for which molecular data were available.

The western clade, as delimited by Castañeda and de Queiroz (2011), included seven species (*A. aequatorialis*, *A. anoriensis*, *A. chloris*, *A. festae*, *A. gemmosus*, *A. peraccae*, and *A. ventrimaculatus*) distributed in the western and central cordilleras of Colombia, the western slopes of the Ecuadorian Andes, and the pacific lowlands of Colombia and Ecuador. In this study, the western clade was inferred to include three additional species (considering that we treated *A. anoriensis* as conspecific with *A. eulaemus*; see "Materials and Methods"): *A. antioquiae*, *A. fasciatus*, and *A. megalopithecus*, distributed in the northernmost part of the western cordillera in Colombia (*A. antioquiae* and *A. megalopithecus*) and in the Pacific lowlands of central Ecuador (*A. fasciatus*). Two primary subclades were inferred within the western clade. The first includes four species, *A. chloris*, *A. fasciatus*, *A. festae*, and *A. peraccae*, all previously placed in the *punctatus* series (Savage and Guyer, 1989) or species group (Williams, 1976b), that have a humid forest distribution below 1,000 m above sea level and small to moderate body size (max SVL = 62, 72, 55, and 52 mm, respectively [Williams and Acosta, 1996]). The second subclade includes six species, *A. aequatorialis*, *A. antioquiae*, *A. eulaemus*, *A. gemmosus*, *A. megalopithecus*, and *A. ventrimaculatus*, all previously placed in the *aequatorialis* series (Savage and Guyer, 1989) or species group (Williams, 1976b, 1985; Williams and Duellman, 1984; Rueda Almonacid, 1989), distributed from 1,500 to 2,000 m above sea level and with moderate to large body size (max SVL = 92, 72 [MRC, personal observation], 101, 66, 81, and 80 mm, respectively [Williams and Acosta, 1996]). In both parsimony and Bayesian optimal trees (Figs. 3, 4), *Anolis boettgeri*, *A. fitchi*, *A. huilae*, and *A. podocarpus* were inferred closer to the western clade than to any of the other five major clades. Castañeda and de Queiroz (2011) also inferred this close relationship for the last three of those species based on molecular data. *Anolis boettgeri* and *A. huilae* were previously included in the *punctatus* series (Williams, 1976b; Poe et al., 2008), whereas *A. fitchi* and *A. podocarpus* were included in the *aequatorialis* series (Williams, 1976b; Ayala-Varela and Torres-Carvajal, 2010). The geographic distributions of these four species at mid to high elevations in the eastern slopes of the Andes of Colombia (*A. huilae*), Ecuador (*A. fitchi*, *A. podocarpus*), and Peru (*A. boettgeri*), do not correspond with the Pacific lowland and Colombian inter-Andean valley distribution of the western clade and suggest that a dispersal or vicariance event was associated with the branch separating the eastern and western species (i.e., the one at the base of the western clade).

The *latifrons* clade, as delimited by Castañeda and de Queiroz (2011), included 12 species (*A. agassizi*, *A. casildae*, *A. chocorum*, *A. danieli*, *A. fraseri*, *A. frenatus*, *A. insignis*, *A. maculigula*, *A. microtus*, *A. princeps*, *A.* sp1, and *A.* sp2) distributed in the Pacific lowlands of Costa Rica, Panama, Colombia (including Malpelo island), and Ecuador and in the Colombian inter-Andean valleys below 1,000 m above sea level (except *A. danieli*, which ranges from 1,700 to 2,200 m). Most of these species

were previously placed in the *latifrons* species group (Williams, 1976b) or series (Savage and Guyer, 1989), and in all except *A. chocorum*, adult males reach a SVL greater than 100 mm (large size was considered a diagnostic feature of the traditional *latifrons* series [Williams, 1976b], also called the giant mainland anoles [Dunn, 1937]). We inferred the *latifrons* clade (excluding *A.* sp1 and *A.* sp2, which were not included in this study, see "Materials and Methods"), with the inclusion of three additional species in the parsimony analysis, *A. apollinaris*, *A. latifrons*, and *A. purpurescens*, and further including *A. squamulatus* in the Bayesian analysis. All four potentially additional species were previously included in the *latifrons* series or species group (Williams, 1976b; Savage and Guyer, 1989) and have Pacific lowland (*A. latifrons* and *A. purpurescens*) or inter-Andean (*A. apollinaris*) distributions, except *A. squamulatus* (see below). In *A. apollinaris*, *A. latifrons*, and *A. squamulatus* adult male maximum SVL exceeds 100 mm (106, 133, and 122 mm, respectively; Williams and Acosta, 1996; Ugueto et al., 2009); *A. purpurescens*, which is known from a small number of specimens, appears to be smaller (max SVL = 78 mm; Williams and Acosta, 1996). In both analyses, *A. philopunctatus* is inferred as the sister group of the *latifrons* clade. However, this species was not considered as part of the *latifrons* clade based on the delimitation of the clade using species for which molecular data were available (see above). This species was previously included in the *punctatus* series and is distributed in the Brazilian Amazon, and its adult maximum SVL = 73 mm (Rodrigues, 1988). *Anolis squamulatus* was previously placed in the *latifrons* species group of Williams (1976b) and series of Savage and Guyer (1989) based on its large dewlap, small head scales, uniform dorsal scales, and large body size (max adult male SVL > 100 mm; Williams and Acosta, 1996). Although inferred as part of the *latifrons* clade in the Bayesian analysis (Fig. 4), it was not in the parsimony analysis (Fig. 3). Moreover, *A. squamulatus* is the only species, of the sampled taxa, previously placed in the *latifrons* species group or series that was not inferred as part of the *latifrons* clade in the parsimony analysis. However, the geographic distribution of *A. squamulatus*, in the cloud forests of the northern Venezuelan Andes, does not correspond to the Pacific lowland and Colombian inter-Andean valley distribution of the *latifrons* clade or to the Pacific mid and low elevations in Colombia and Ecuador distribution of the western clade (to which it was inferred as being closer in the parsimony analysis). Instead, it corresponds more closely to the geographic distribution of the eastern clade. Either of these alternative relationships of *A. squamulatus* (within or closer to either the western or the eastern clades) would require the convergent evolution of large body size with members of the *latifrons* clade. In agreement with previous studies suggesting the close relationship between *A. frenatus*, *A. latifrons*, and *A. princeps* and including the possibility that those three taxa represent a single species (Savage and Talbot, 1978; Williams, 1988; Castañeda and de Queiroz, 2011), we inferred the clade ((*A. frenatus* (*A. latifrons*, *A. princeps*)) in both parsimony and Bayesian analyses.

The eastern clade, as delimited by Castañeda and de Queiroz (2011), included five species (*A. anatoloros*, *A. jacare*, *A. punctatus*, *A. transversalis*, and *A. tigrinus*) distributed in the northern portion of the eastern cordillera of Colombia into the Venezuelan Andes and the Amazon region. In our parsimony results, the eastern clade was inferred to include three additional species: *A. carlostoddi*, *A. orcesi*, and *A. vaupesianus*, whereas in the Bayesian analysis, it was inferred to include six additional species: *A. dissimilis*, *A. menta*, *A. ruizii*, *A. santamartae*, *A. solitarius*, and *A. vaupesianus*. All of the potential additional species have an eastern Andean and Amazonian distribution. They occur in Amazonia (*A. vaupesianus*, *A. dissimilis*), the eastern slopes of the northern Andes of Ecuador (*A. orcesi*), the eastern cordillera of Colombia (*A. ruizii*), the Sierra Nevada de Santa Marta in Colombia (*A. menta*, *A. santamartae*, *A. solitarius*), and the Chimantá tepui in

Venezuela (*A. carlostoddi*). Within the eastern clade, two subclades were inferred in both analyses: the first includes three species, *A. anatoloros*, *A. jacare*, and *A. tigrinus*, with mostly Andean, high-elevation distributions and smaller body size (max male SVL = 55–68 mm; Williams and Acosta, 1996; Ugueto et al., 2007); the second subclade includes three species, *A. punctatus*, *A. transversalis*, and *A. vaupesianus*, with Amazonian, low-elevation distributions, and larger size (max male SVL = 76–82 mm; Williams and Acosta, 1996). It is not surprising that *A. vaupesianus* (distributed in the Vaupes and Amazonas departments in Colombia and known only from the type series) was consistently inferred as the sister taxon of *A. punctatus* (with a broad Amazonian distribution). These two species were described as close relatives that differ primarily in the size and degree of keeling of the ventral scales (smaller and weakly keeled in *A. vaupesianus* versus larger and strongly keeled in *A. punctatus*), the dewlap coloration in preservative (black skin with white scales in *A. vaupesianus* versus light skin with small dark spots and purplish scales in *A. punctatus*) and the dorsal color pattern of preserved specimens (in *A. vaupesianus*, "brown, strongly blotched with darker, dorsal blotches tending to form transverse series across the back" versus an unpatterned dark dorsum in *A. punctatus*) (Williams, 1982: 8). The unique color pattern of *A. vaupesianus* is only found in one of the paratypes (UTA 6850), whereas the coloration of the other specimens in the type series is not particularly different from that of *A. punctatus* (Williams, 1982: 8–9). Given the small differences separating these two species, a more comprehensive sampling of *A. punctatus* in Colombia (currently <10 specimens are known) and the collection of additional molecular data (particularly for *A. vaupesianus*) could clarify whether these two taxa are conspecific as well as whether the characters used to distinguish them represent extremes in a continuous distribution or are based on an atypical specimen. In contrast to the likely close relationship between *A. punctatus* and *A. vaupesianus*, the relationships of *A. carlostoddi* and *A. orcesi* (parsimony) or *A. dissimilis*, *A. menta*, *A. santamartae*, and *A. solitarius* (Bayesian) to *A. tigrinus* are less clear. The former two species were previously placed in *Phenacosaurus* and thus not considered closely related to *A. tigrinus*. In contrast, two of the latter species, *A. menta* and *A. solitarius*, were placed in the *tigrinus* series (Williams, 1976b; Ayala et al., 1984) (the other two, *A. dissimilis* and *A. santamartae*, were placed in the *punctatus* series). In both cases, the putative clade formed by all three or all six species has low support, and given the low resolving power of the morphological data set and the fact that molecular data are available for neither *A. carlostoddi* and *A. orcesi* nor *A. dissimilis*, *A. menta*, *A. santamartae*, *A. ruizii*, and *A. solitarius*, the inferred relationships are questionable.

The *roquet* clade, as delimited by Castañeda and de Queiroz (2011), included eight species (*A. aeneus*, *A. bonairensis*, *A. extremus*, *A. griseus*, *A. luciae*, *A. richardii*, *A. roquet*, and *A. trinitatis*), distributed in the southern Lesser Antilles, from Martinique to Grenada, as well as the islands of Bonaire and Tobago (with introduced populations in Trinidad and Guyana [Gorman and Dessauer, 1965, 1966; Gorman et al., 1971]). This clade corresponds to the previously described *roquet* species group or series (Underwood, 1959; Gorman and Atkins, 1967, 1969; Lazell, 1972; Williams, 1976a; Savage and Guyer, 1989; Creer et al., 2001). One additional species, *A. blanquillanus*, from the island of La Blanquilla, was previously referred to the *roquet* series (Williams, 1976a) but was not included in our analyses; however, its inclusion in the *roquet* clade is supported by allozyme data (Yang et al., 1974; Creer et al., 2001). Poe (2004) inferred the *roquet* clade (BS = 74%, fig. 2), supported by six morphological characters (see "Current Taxonomy within *Dactyloa*"); two of those, greater sexual size dimorphism and an increase in the number of postmental scales, were also inferred as synapomorphies for the clade in this study.

The *Phenacosaurus* clade, as delimited by Castañeda and de Queiroz (2011), included five species (*A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. nicefori*, and *A. vanzolinii*) distributed in the Andean regions of Colombia, Ecuador, and Venezuela, all of which were previously placed in the genus *Phenacosaurus* (Lazell, 1969; Barros et al., 1996). In this study, the *Phenacosaurus* clade was inferred with the addition of *A. tetarii*, a species that was previously placed in the genus *Phenacosaurus* (Barros et al., 1996) and whose geographic distribution (Venezuelan Andes) conforms to that of the clade. Three other species that were previously referred to *Phenacosaurus*, *A. carlostoddi*, *A. orcesi*, and *A. neblininus*, were not inferred to be part of this clade in the parsimony analysis. However, in the Bayesian analysis, *A. orcesi* was inferred as the sister group of the *Phenacosaurus* clade with moderate support (PP = 0.87; Fig. 4). In contrast, in the parsimony analysis, *A. orcesi* was placed in the eastern clade (as was *A. carlostoddi*), although with weak support (BS = 6%, 24%, and 19%). In both parsimony and Bayesian analyses, *A. proboscis* was inferred as sister group of the *Phenacosaurus* clade (or of the *Phenacosaurs* clade plus *A. orcesi*) with weak support (BS = 58%, PP = 0.43), a relationship also inferred by Poe (2004, fig. 2). A close relationship between *A. proboscis* and species traditionally referred to *Phenacosaurus* was also inferred by Poe et al. (2009b, 2012). The geographic distributions of both species lie on the periphery of that of the *Phenacosaurus* clade: *A. orcesi* is distributed along the eastern slopes of the northern Andes of Ecuador, whereas *A. proboscis* is distributed along the western slopes of the northern Andes of Ecuador. The more deeply nested species within the *Phenacosaurus* clade (*A. heterodermus*, *A. inderenae*, *A. tetarii*, and *A. vanzolinii*) are larger in size (max male SVL=76, 98, 86, and 104 mm, respectively [Williams and Acosta, 1996]) and correspond to the *heterodermus* group of Williams et al. (1996); the two earlier diverging lineages (*A. euskalerriari* and *A. nicefori*) are smaller in size (max male SVL = 53 and 63 mm, respectively [Williams and Acosta, 1996]). Except for *A. euskalerriari*, all of the species in the *Phenacosaurus* clade have heterogeneous dorsal scales, suggesting that this condition originated in the ancestral lineage of *A. heterodermus* and *A. nicefori* after it diverged from that of *A. euskalerriari*. *Anolis carlostoddi*, *A. orcesi*, and *A. neblininus*, which were previously placed in the genus *Phenacosaurus* but were not inferred in this study to be part of the *Phenacosaurus* clade (although *A. orcesi* was inferred to be closely related in the Bayesian analysis), also lack heterogeneous dorsal scales.

Seventeen species (*A. boettgeri, A. calimae*, *A. caquetae*, *A. carlostoddi*, *A. dissimilis, A. fitchi, A. huilae, A. menta, A. neblininus, A. orcesi*, *A. philopunctatus, A. podocarpus, A. proboscis, A. ruizii, A. santamartae, A. solitarius*, and *A. squamulatus*) were not consistently placed in any of the five mutually exclusive clades just discussed, either because their positions did not satisfy the criterion based on the last common ancestor of the species for which molecular data were available or because they differed across phylogenetic methods (and were commonly poorly supported). However, 6 of the 17 species (*A. boettgeri, A. fitchi*, *A. huilae*, *A. philopunctatus*, *A. podocarpus*, and *A. proboscis*) were each consistently placed closer to one of the five clades than to the others. For those species whose relationships differed among analyses (*A. calimae*, *A. caquetae*, *A. carlostoddi*, *A. dissimilis, A. menta, A. neblininus, A. orcesi, A. ruizii, A. santamartae, A. solitarius,* and *A. squamulatus*), 9 out of 11 of which currently lack molecular data (all but *A. calimae* and *A. neblininus*), more data will be necessary to clarify their relationships within *Dactyloa*.

Previously Recognized Taxa

None of the traditionally recognized subgroups of *Dactyloa* based on morphological characters (*aequatorialis*, *latifrons*, *Phenacosaurus*, *punctatus*, *roquet*, and *tigrinus*) were

inferred in the optimal trees inferred from either the morphology-only or the combined data sets except the *roquet* series in the combined analyses. The parsimony-based topology tests (WSR) using the morphology-only data set failed to reject the monophyly of *Dactyloa* or any of the previously described subgroups (Table 1); therefore, despite the morphological data not supporting any of these groups when analyzed under parsimony, it is also unable to reject any of them using parsimony-based tests. In contrast, the Bayesian tests using the morphology-only data set rejected the hypotheses of monophyly of *Dactyloa* and all traditionally recognized series except the *roquet* series. With the combined data sets and both parsimony and Bayesian tests (2), the *aequatorialis*, *latifrons*, and *punctatus* series were also strongly rejected, but the *tigrinus* series and *Phenacosaurus* were not rejected.

Contradictory evidence and absence of support for the series described based on morphological characters is consistent with previous suggestions that morphological characters used for series delimitation might show a high degree of convergence and parallelism (Williams, 1976b: 260) and that some series were described only for convenience (Williams, 1979: 10). Furthermore, traditional series delimitation did not distinguish clearly between ancestral and derived conditions, and the former are not indicative of close phylogenetic relationships. Differences between the results of WSR and Bayesian tests might reflect the conservativeness of the WSR—the requirement of a stronger signal to reject a given hypothesis (Lee, 2000)—because Bayesian tests often rejected hypotheses when WSR tests did not, but WSR tests rarely rejected hypotheses not rejected by Bayesian tests. Differences between the data sets (i.e., resulting from alternative coding methods) do not appear to be the reason for the different results between the two tests. For one thing, the Bayesian tests rejected more of the hypotheses despite using the data set (Thiele6-mode) that contained the least phylogenetic signal. For another, WSR tests performed on the Thiele6-mode data set (the data set used for the Bayesian tests) yielded the same qualitative results as with the Torres-freq data set (results not shown).

Proposed Taxonomy

Our results indicate that a revised taxonomy for *Dactyloa* is warranted. Optimal phylogenetic trees and topology tests indicate that most of the previously recognized taxa within *Dactyloa* based on morphological characters and traditionally ranked as species groups or series are not monophyletic. Moreover, our previously published results based on molecular data (Castañeda and de Queiroz, 2011) indicate the existence of five well-supported major subclades, and the results of the combined analyses of morphological and molecular data in the present study both corroborate the monophyly and clarify the composition of those subclades. Here, we propose a revised taxonomy based on the results of our phylogenetic analyses, including names that are defined explicitly in terms of phylogenetic relationships (de Queiroz and Gauthier, 1990, 1992).

The optimal topologies obtained from the different (parsimony versus Bayesian) methods are in substantial but not complete agreement. We considered it inappropriate to select one topology over the other because each topology has advantages and disadvantages: The parsimony tree is based on a character coding method that incorporates more phylogenetic information, whereas the Bayesian tree is based on more realistic evolutionary models. Therefore, we used a consensus tree as the basis for our proposed taxonomy (Fig. 5). Specifically, we used a pruned and regrafted[2] consensus tree (Gordon, 1980; Finden and Gordon, 1985; Bryant, 2003) derived from the most parsimonious tree (Fig. 3) and the maximum clade credibility tree (Fig. 4) for the combined morphological and molecular

[2] The term "grafted" seems more appropriate here, given that the branch has not been grafted before; however, we use "regrafted" because it has been commonly used in the literature.

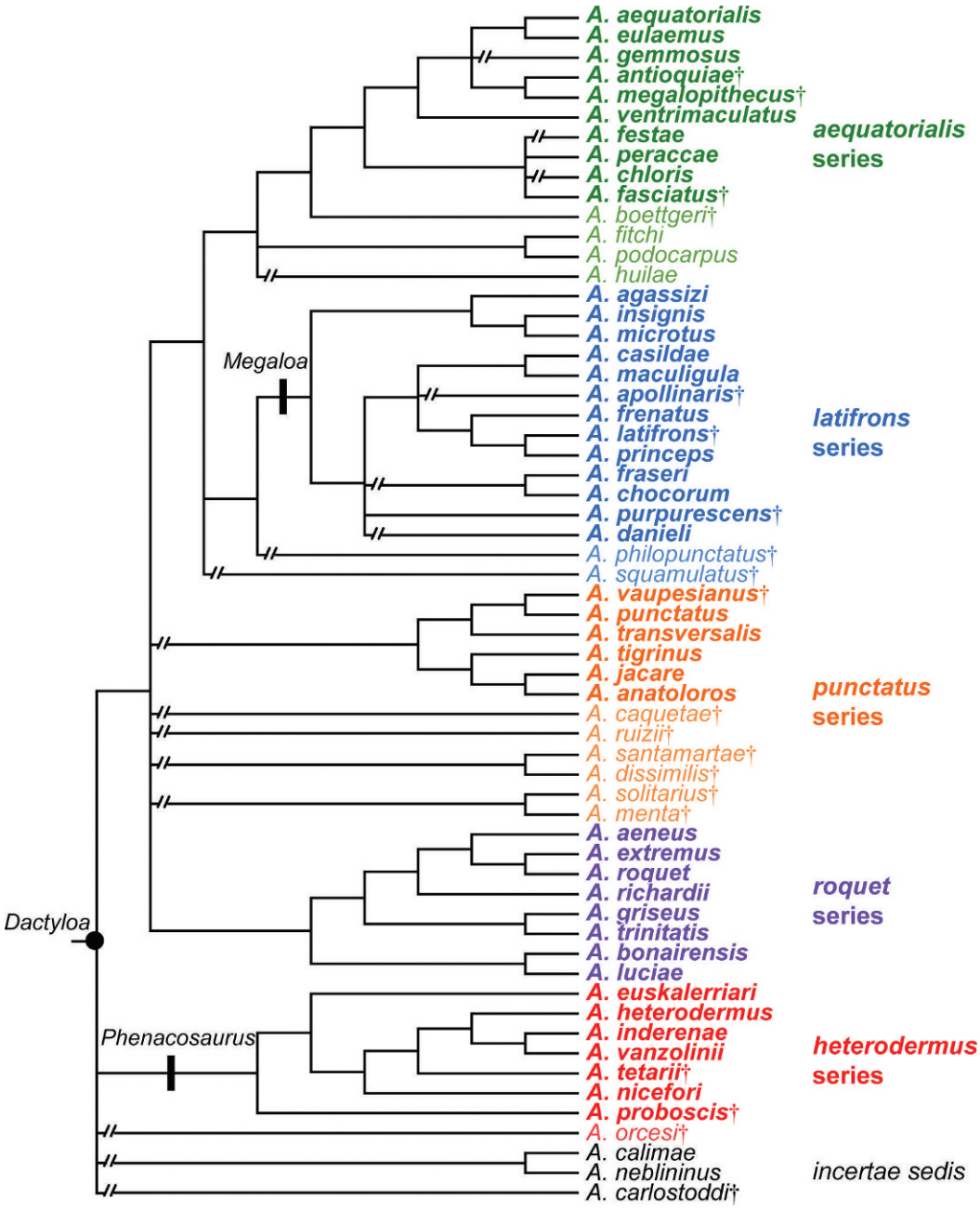

Figure 5. Pruned and regrafted consensus tree based on the most parsimonious tree (inferred with the CombTorres-freq data set; Fig. 3) and the Bayesian Maximum Clade Credibility tree (inferred with the CombThiele6-mode data set; Fig. 4) with the taxonomy proposed in this study. Daggers (†) following species names indicate the species for which only morphological data were available. Regrafted branches are indicated by a break near their bases. See text for details concerning alternative prunings and regraftings 1) within the clade composed of *A. chloris*, *A. fasciatus*, *A. festae*, and *A. peraccae*; 2) of *A. purpurescens* versus *A. danieli*; and 3) of members of the *punctatus* series. The *Dactyloa* clade is indicated with a black dot on the corresponding node. Five mutually exclusive, informally named clades ("series") within *Dactyloa* are distinguished by color, with lighter versions of the

data sets (i.e., CombTorres-freq and CombThiele6-mode matrices).

Because a few of the species (e.g., *A. carlostoddi*, *A. orcesi*, *A. squamulatus*) have very different relationships on the primary trees, the strict and semistrict consensus trees had little resolution, and we therefore originally intended to use an Adams consensus tree (for a review of consensus methods, see Swofford [1991]). However, the Adams consensus tree contained unexpected groups that we felt could not be justified on the basis of the primary trees (e.g., *A. squamulatus* closer to the western clade than to the *latifrons* clade, which is contradicted by the Bayesian tree; Fig. 4), and it turned out that the pruned and regrafted consensus tree exhibited the desired properties we had incorrectly attributed to the Adams consensus method (i.e., placement of species with conflicting relationships within the smallest possible clade in the consensus tree for which there is complete agreement concerning their higher level relationships in the primary trees).

To generate the pruned and regrafted consensus tree, we first produced agreement subtrees (also called common pruned trees; Finden and Gordon, 1985) using PAUP* with identical topologies that result from removing (pruning) the same set of taxa from the primary trees (Finden and Gordon, 1985). We obtained 12 largest agreement subtrees for the 60 *Dactyloa* species (including only one outgroup species, *Polychrus marmoratus*, to root the trees), which differed only in the inclusion of all possible combinations of two species from the clade composed of *A. festae*, *A. chloris*, *A. fasciatus,* and *A. peraccae* (six possible combinations) and the inclusion of either *A. danieli* or *A. purpurescens*. We arbitrarily selected one of the 12 largest agreement subtrees (the one including *A. fasciatus*, *A. peraccae*, and *A. purpurescens*) as the base tree for the regrafting process. In the second step, we manually reattached each previously pruned species or set of species to the node representing the most recent common ancestor of its alternative placements on the primary trees. Because the position of the entire eastern clade and its possible relatives differed between the two primary trees (closer to the *latifrons* clade in the parsimony tree versus closer to the *roquet* clade in the Bayesian tree), all of those species were excluded from the largest agreement subtrees. To determine whether those species should be reattached singly or in sets, we determined the largest agreement subtree for those species (*A. anatoloros*, *A. caquetae*, *A. carlostoddi*, *A. dissimilis*, *A. jacare*, *A. menta*, *A. orcesi*, *A. punctatus*, *A. ruizii*, *A. santamartae*, *A. solitarius*, *A. tigrinus*, *A. transversalis*, *A. vaupesianus*), plus one representative each of the western, *latiforns*, *Phenacosaurus*, and *roquet* clades; we also included *Polychrus marmoratus* to root the trees. We obtained four largest agreement subtrees representing two different topologies for the set of species making up the eastern clade and its possible relatives (the other two topologies differed only in whether the representative of the western or the *roquet* clade was included). Both topologies included (*A. transversalis* (*A. punctatus*, *A. vaupesianus*)), but one included (*A. tigrinus* (*A. anatoloros*, *A. jacare*)) and *A. caquetae*, whereas the other included ((*A. dissimilis*, *A. santamartae*) (*A. menta*, *A. solitarius*)). We selected the former for grafting because those groups were consistent, after pruning, with the primary trees, whereas the latter depended on pruning the representative of the *latifrons* clade, which we intend to be a fixed point of reference (i.e., not a candidate for pruning) in this secondary analysis (given that several members of the *latifrons* clade were present in all of the primary

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same hue indicating tentative assignment to the clade represented by that hue. These informally named clades have the same name as some of the groups traditionally ranked as series within *Anolis*; however, species composition is not necessarily identical. A black bar across a branch indicates an apomorphy used to define the clade name above the bar.

agreement subtrees). The resulting pruned and regrafted consensus tree (Fig. 5) serves as the basis for our taxonomy.

In all but two cases, we have selected preexisting names that have been applied traditionally to groups of species approximating, to one degree or another, the clades to which we apply them. Three of the selected names are similar in appearance to genus names; however, they are here tied to clades rather than to the rank of genus and are implicitly ranked below the genus level (given that we use the name *Anolis* in the binomina of all of the species included in the named clades). Five of the selected names combine the species name (epithet) of the first described species (e.g., "*roquet*") with the name of a rank (i.e., "series"). Because those names violate the rule stating that clade names must be single words beginning with a capital letter (ICPN, Article 17.1), they are treated here as informal names. They are nevertheless given explicit phylogenetic definitions as guides for applying the names in the context of future phylogenetic hypotheses. Despite being given explicit phylogenetic definitions, the names in question are compatible with traditional nomenclature, in that they have been defined so as to ensure that they will always refer to mutually exclusive taxa (see de Queiroz and Donoghue, 2013), as would names associated with the rank of series under traditional nomenclature. As a consequence, the "series" names are applied to clades that are more inclusive than the five clades based on the species for which molecular data were available that formed the basis of our discussion in the "Phylogeny of *Dactyloa*" section (above), though those five less inclusive clades form the cores of the "series" clades. The number of *Dactyloa* subclades named in our taxonomy exceeds five, the number of well-supported clades based on molecular data (Castañeda and de Queiroz, 2011) and corroborated in this study, because in two cases, we considered it useful to name additional clades associated with the origins of distinctive apomorphies.

Dactyloa Wagler 1830, converted clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *Anolis punctatus* Daudin 1802 and all extant species that share a more recent common ancestor with *A. punctatus* than with *A. bimaculatus* (Sparrman 1784), *A. cuvieri* Merrem 1820, *A. equestris* Merrem 1820, *A. occultus* Williams and Rivero 1965, and *A. sagrei* Duméril and Bibron 1837. **Reference phylogeny:** Figure 5, this study (see also Poe, 2004, figs. 2–4). **Inferred composition:** *Anolis aeneus* Gray 1840, *A. aequatorialis* Werner 1894, *A. agassizi* Stejneger 1900, *A. anatoloros* Ugueto, Rivas, Barros, Sánchez-Pacheco and García-Pérez 2007, *A. anchicayae* Poe, Velasco, Miyata and Williams 2009 (inclusion based on inferred close relationship to *A. peraccae* following Poe et al., 2009b), *A. anoriensis* Velasco, Gutiérrez-Cárdenas and Quintero-Angel 2010 (inclusion based on inferred close relationship to *A. aequatorialis* following Castañeda and de Queiroz, 2011), *A. antioquiae* Williams 1985, *A. apollinaris* Boulenger 1919, *A. bellipeniculus* (Myers and Donnelly 1996) (inclusion based on inferred close relationship to *A. neblininus* following Myers and Donnelly, 1996), *A. blanquillanus* Hummelinck 1940 (inclusion based on inferred close relationship to *A. bonairensis* following Yang et al., 1974), *A. boettgeri* Boulenger 1911, *A. bonairensis* Ruthven 1923, *A. calimae* Ayala, Harris and Williams 1983, *A. caquetae* Williams 1974, *A. carlostoddi* (Williams, Praderio and Gorzula 1996), *A. casildae* Arosemena, Ibáñez, and de Sousa 1991, *A. chloris* Boulenger 1898, *A. chocorum* Williams and Duellman 1967, *A. cuscoensis* Poe, Yañez-Miranda and Lehr 2008 (inclusion based on the results of Poe et al., 2008), *A. danieli* Williams 1988, *A. deltae* Williams 1974 (inclusion based on inferred close relationship to *A. dissimilis* following Williams, 1974), *A. dissimilis* Williams 1965, *A. eulaemus* Boulenger 1908, *A. euskalerriari* (Barros, Williams, and Viloria 1996), *A.*

extremus Garman 1887, *A. fasciatus* Boulenger 1885, *A. festae* Peracca 1904, *A. fitchi* Williams and Duellman 1984, *A. fraseri* Günther 1859, *A. frenatus* Cope 1899, *A. gemmosus* O'Shaughnessy 1875, *A. gorgonae* Barbour 1905 (inclusion based on inferred close relationship to *A. andianus* [a synonym of *A. gemmosus* according to Williams and Duellman (1984)] following Barbour, 1905), *A. griseus* Garman 1887, *A. heterodermus* Duméril 1851, *A. huilae* Williams 1982, *A. ibanezi* Poe, Latella, Ryan and Schaad 2009 (inclusion based on inferred close relationship to *A. chocorum* following Poe et al., 2009a), *A. inderenae* (Rueda and Hernández-Camacho 1988), *A. insignis* Cope 1871, *A. jacare* Boulenger 1903, *A. kunayalae* Hulebak, Poe, Ibáñez and Williams 2007 (inclusion based on inferred close relationship to *A. mirus* following Hulebak et al., 2007), *A. laevis* (Cope 1876) (inclusion based on inferred close relationship to *A. proboscis* following Williams, 1979), *A. lamari* Williams 1992 (inclusion based on inferred close relationship to *A. tigrinus* following Williams, 1992), *A. latifrons* Berthold 1846, *A. luciae* Garman 1887, *A. maculigula* Williams 1984, *A. megalopithecus* Rueda Almonacid 1989, *A. menta* Ayala, Harris and Williams 1984, *A. microtus* Cope 1871, *A. mirus* Williams 1963 (inclusion based on inferred close relationship to *A. fraseri* following Williams, 1963), *A. nasofrontalis* Amaral 1933 (inclusion based on inferred close relationship to *A. tigrinus* following Amaral, 1933), *A. neblininus* (Myers, Williams and McDiarmid 1993), *A. nicefori* (Dunn 1944), *A. nigrolineatus* Williams 1965, *A. orcesi* (Lazell 1969), *A. otongae* Ayala-Varela and Velasco 2010 (inclusion based on inferred close relationship to *A. gemmosus* following Ayala-Varela and Velasco, 2010), *A. paravertebralis* Bernal Carlo and Roze 2005 (inclusion based on inferred close relationship to *A. solitarius* following Bernal Carlo and Roze, 2005), *A. parilis* Williams 1975 (inclusion based on inferred close relationship to *A. mirus* following Williams, 1975), *A. peraccae* Boulenger 1898, *A. philopunctatus* Rodrigues 1988, *A. phyllorhinus* Myers and Carvalho 1945 (inclusion based on inferred close relationship to *A. punctatus* following Myers and Carvalho, 1945), *A. podocarpus* Ayala-Varela and Torres-Carvajal 2010, *A. princeps* Boulenger 1902, *A. proboscis* Peters and Orcés 1956, *A. propinquus* Williams 1984 (inclusion based on inferred close relationship to *A. apollinaris* following Williams, 1988), *A. pseudotigrinus* Amaral 1933 (inclusion based on inferred close relationship to *A. tigrinus* following Amaral, 1933), *A. punctatus* Daudin 1802, *A. purpurescens* Cope 1899, *A. richardii* Duméril and Bibron 1837, *A. roquet* (Bonnaterre 1789), *A. ruizii* Rueda and Williams 1986, *A. santamartae* Williams 1982, *A. soinii* Poe and Yañez-Miranda 2008 (inclusion based on inferred close relationship to *A. transversalis* following Poe and Yañez-Miranda, 2008), *A. solitarius* Ruthven 1916, *A.squamulatus* Peters 1863, *A. tetarii* (Barros, Williams, and Viloria 1996), *A. tigrinus* Peters 1863, *A. transversalis* Duméril 1851, *A. trinitatis* Reinhardt and Lütken 1862, *A. umbrivagus* Bernal Carlo and Roze 2005 (inclusion based on inferred close relationship to *A. solitarius* following Bernal Carlo and Roze, 2005), *A. vanzolinii* (Williams, Orcés, Matheus, and Bleiweiss 1996), *A. vaupesianus* Williams 1982, *A. ventrimaculatus* Boulenger 1911, and *A. williamsmittermeierorum* Poe and Yañez-Miranda 2007 (inclusion based on inferred close relationship to *A. orcesi* following Poe and Yañez-Miranda, 2007). **Comments:** The name *Dactyloa* was previously used by Savage and Guyer (1989) for a taxon ranked as a genus containing all species referred to the *Dactyloa* clade in this study except those species formerly assigned to the genus *Phenacosaurus* Barbour 1920 (*A. bellipeniculus*, *A. carlostoddi*, *A. euskalerriari*, *A. heterodermus*, *A. inderenae*, *A. neblininus*, *A. nicefori*, *A. orcesi*, *A. tetarii*, *A. vanzolinii*). Here, the name *Dactyloa* is not associated with the rank of genus (it is implicitly associated with a lower rank) so that the binomina of the included species retain the prenomen (genus name) *Anolis*.

The following named clades are subclades of *Dactyloa*.

***aequatorialis* series** Savage and Guyer 1989, informal clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *Anolis aequatorialis* Werner 1894 and all extant species that share a more recent common ancestor with *A. aequatorialis* than with *A. latifrons* Berthold 1846, *A. punctatus* Daudin 1802, *A. roquet* (Bonnaterre 1789), and *A. heterodermus* Duméril 1851. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis aequatorialis* Werner 1894, *A. anoriensis* Velasco, Gutiérrez-Cárdenas and Quintero-Angel 2010 (see "Comments"), *A. antioquiae* Williams 1985, *A. boettgeri* Boulenger 1911 (see "Comments"), *A. chloris* Boulenger 1898, *A. eulaemus* Boulenger 1908, *A. fasciatus* Boulenger 1885, *A. festae* Peracca 1904, *A. fitchi* Williams and Duellman 1984 (see "Comments"), *A. gemmosus* O'Shaughnessy 1875, *A. huilae* Williams 1982 (see "Comments"), *A. megalopithecus* Rueda Almonacid 1989, *A. peraccae* Boulenger 1898, *A. podocarpus* Ayala-Varela and Torres-Carvajal 2010 (see "Comments"), and *A. ventrimaculatus* Boulenger 1911. Other species that may belong to the *aequatorialis* series are *A. anchicayae* Poe, Velasco, Miyata and Williams 2009, *A. mirus* Williams 1963, *A. otongae* Ayala-Varela and Velasco 2010, and *A. parilis* Williams 1975 (see "Comments"). **Comments:** Referral of *A. anoriensis* to this clade is based on the results of Castañeda and de Queiroz (2011). In the context of the reference phylogeny, six species not traditionally included in the *aequatorialis* series (e.g., Savage and Guyer, 1989) are included in the *aequatorialis* series as conceptualized here: *A. boettgeri*, *A. chloris*, *A. fasciatus*, *A. festae*, *A. huilae*, and *A. peraccae*. There is strong evidence supporting inclusion of *A. chloris*, *A. festae*, and *A. peraccae* (Castañeda and de Queiroz, 2011), and *A. fasciatus* is placed consistently in a subclade with those three species (Figs. 3, 4). In contrast, because of inconsistent placement of *A. huilae* between analyses (Fig. 3 versus Fig. 4), because of weak support for the inclusion of both *A. boettgeri* and *A. huilae* and because molecular data are currently lacking for *A. boettgeri*, inclusion of those two species in the *aequatorialis* series should be considered tentative. Additionally, *A. maculigula*, a species included in the traditional circumscription of the *aequatorialis* series, is excluded based on strong evidence supporting its inclusion in the *latifrons* series (see below). The inclusion of *A. fitchi* and *A. podocarpus*, traditionally included in the *aequatorialis* series (Savage and Guyer, 1989), should also be considered tentative given the weak support for the relevant relationships (Figs. 3, 4). Although the parsimony analysis (Fig. 3) places *A. squamulatus* in the *aequatorialis* series, we have tentatively retained that species in the *latifrons* series based on the results of the Bayesian analysis (Fig. 4) and its large body size (see "Comments" on the *latifrons* series). The inclusion of *A. mirus*, *A. otongae*, and *A. parilis*, previously considered members of the *aequatorialis* series (Williams, 1975; Ayala-Varela and Velasco, 2010), should also be considered tentative given the current absence of these species from explicit phylogenetic analyses. *Anolis anchicayae*, inferred as closely related to *A. peraccae* in a recent phylogenetic analysis (Poe et al., 2009b), should also be considered tentatively included in the *aequatorialis* series given that in that analysis these two species were not inferred as close relatives of *A. aequatorialis*.

The *aequatorialis* series as conceptualized here corresponds approximately to the western clade of Castañeda and de Queiroz (2011). However, the *aequatorialis* series is more inclusive than the western clade of Castañeda and de Queiroz (2011) in that it appears to include *A. boettgeri*, *A. fitchi, A. huilae*, and *A. podocarpus* and might also include some species currently considered *incertae sedis* within *Dactyloa* or absent from explicit phylogenetic analyses if they

are found to be more closely related to *A. aequatorialis* than to *A. latifrons*, *A. punctatus*, *A. roquet*, and *A. heterodermus*. Additionally, species in the western clade of Castañeda and de Queiroz (2011) are characterized by having a cohesive western Andean geographic distribution, but *A. boettgeri*, *A. fitchi*, *A. huilae*, and *A. podocarpus*, and possibly other species in the more inclusive *aequatorialis* series, do not conform to this geographic pattern (see "Phylogeny of *Dactyloa*" above for more details about the geographic distributions of the four species mentioned).

***latifrons* series** Gorman and Dessauer 1966, informal clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *Anolis latifrons* Berthold 1846 and all extant species that share a more recent common ancestor with *A. latifrons* than with *Anolis aequatorialis* Werner 1894, *A. punctatus* Daudin 1802, *A. roquet* (Bonnaterre 1789), and *A. heterodermus* Duméril 1851. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis agassizi* Stejneger 1900, *A. apollinaris* Boulenger 1919, *A. casildae* Arosemena, Ibáñez, and de Sousa 1991, *A. chocorum* Williams and Duellman 1967, *A. danieli* Williams 1988, *A. fraseri* Günther 1859, *A. frenatus* Cope 1899, *A. insignis* Cope 1871, *A. kunayalae* Hulebak, Poe, Ibáñez and Williams 2007, *A. latifrons* Berthold 1846, *A. maculigula* Williams 1984, *A. microtus* Cope 1871, *A. princeps* Boulenger 1902, *A. philopunctatus* Rodrigues 1988 (see "Comments"), *A. purpurescens* Cope 1899, and *A. squamulatus* Peters 1863 (see "Comments"). Other species that may belong to the *latifrons* series are *A. ibanezi* Poe, Latella, Ryan and Schaad 2009, and *A. propinquus* Williams 1984 (see "Comments"). **Comments:** Referral of *A. kunayalae* to this clade is based on the results of Nicholson et al. (2005, fig. 1, where *A. kunayalae* corresponds to Nicholson et al.'s "New Species 1" [Hulebak et al., 2007]). In the context of the reference phylogeny, four species not traditionally included in the *latifrons* series (e.g., Savage and Guyer, 1989) are included in the *latifrons* series as conceptualized here: *A. agassizi*, *A. chocorum*, *A. maculigula*, and *A. philopunctatus*. There is strong evidence supporting inclusion of the former three species (Castañeda and de Queiroz, 2011). In contrast, because of weak support for the relationship of *A. philopunctatus* (Figs. 3, 4) and because of a current lack of molecular data, its inclusion in the *latifrons* series should be considered tentative. Similarly, the inclusion of *A. squamulatus*, traditionally included in the *latifrons* series (e.g., Savage and Guyer, 1989) should be considered tentative given the weak and inconsistent support for the relevant relationships (Fig. 3 versus Fig. 4) and the current lack of molecular data. We have tentatively included *A. squamulatus* in the *latifrons* series, where it was placed in the Bayesian tree (Fig. 4), rather than in the *aequatorialis* series, where is was placed in the parsimony tree (Fig. 3) or in the *punctatus* series, with which it agrees best in terms of geographic distribution (see "Phylogeny of *Dactyloa*," above) because it shares the derived character of large body size with members of the *latifrons* series. *Anolis propinquus* has traditionally been considered part of the *latifrons* series (Williams, 1988); however, the inclusion of this species should be considered tentative given its current absence from explicit phylogenetic analyses. Inclusion of *Anolis ibanezi*, inferred as closely related to *A. chocorum* in a recent phylogenetic analysis (Poe et al., 2009a), should also be considered tentative given that the phylogenetic tree was not shown by Poe et al. (2009a); thus, the placement of these two species with respect to the *latifrons* series as conceptualized here is uncertain.

The first use of the name "*latifrons* series" appears to have been in Etheridge's (1959) dissertation; however, that use does not qualify as published according to the ICPN (Article 4.2). Moreover, Etheridge used the name for a more inclusive taxon

approximating the clade to which the name *Dactyloa* is applied here. The oldest published use of the name "*latifrons* series" appears to be that of Gorman and Dessauer (1966), who also used the name for the more inclusive clade. As delimited here, the *latifrons* series more closely approximates the taxon called the *laticeps* group by Cope (1899; which appears to be a lapsus because the species is elsewhere [p. 7] referred to by the correct name *A. latifrons*), the giant mainland anoles or *squamulatus-latifrons* group by Dunn (1937), the *latifrons* species group by Williams (1988), the *latifrons* series by Savage and Guyer (1989), and the *latifrons* clade of Castañeda and de Queiroz (2011). However, the *latifrons* series as conceptualized here is potentially more inclusive than the *latifrons* clade of Castañeda and de Queiroz (2011), in that it appears to include *A. philopunctatus* and might also include some species currently considered *incertae sedis* within *Dactyloa* or absent from explicit phylogenetic analyses if they are found to be more closely related to the *A. latifrons* series than to *A. aequatorialis*, *A. punctatus*, *A. roquet*, and *A. heterodermus*.

Megaloa Castañeda and de Queiroz, new clade name

Definition (apomorphy-based): The clade originating in the ancestor in which a maximum SVL > 100 mm in males, synapomorphic with that of *Anolis latifrons* Berthold 1846, originated. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis agassizi* Stejneger 1900, *A. apollinaris* Boulenger 1919, *A. casildae* Arosemena, Ibáñez, and de Sousa 1991, *A. chocorum* Williams and Duellman 1967 (see "Comments"), *A. danieli* Williams 1988, *A. fraseri* Günther 1859, *A. frenatus* Cope 1899, *A. insignis* Cope 1871, *A. latifrons* Berthold 1846, *A. maculigula* Williams 1984, *A. microtus* Cope 1871, *A. princeps* Boulenger 1902, and *A. purpurescens* Cope 1899 (see "Comments"). Another species that might belong to *Megaloa* is *A. squamulatus* Peters 1863 (see "Comments"). **Etymology:** Derived from the Greek *Mega* (large) + *loa* (the last part of the name *Dactyloa*) in reference to the large body size of the members of this subclade of *Dactyloa*.[3] **Comments:** Two supraspecific names are based on species in this clade: *Diaphoranolis* Barbour 1923 (type species = *D. brooksi* = *Anolis insignis* according to Etheridge [1959] and Savage and Talbot [1978]) and *Mariguana* Dunn 1939 (type species = *Anolis agassizi*). These names were applied to taxa ranked as genera and separated from *Anolis* based on differences in dorsal scalation (juxtaposed pavement-like scales in *A. insignis* [Barbour, 1923], and tiny non-imbricating granules interspersed with larger, single, obtusely keeled scales in *A. agassizi* [Dunn, 1939; Etheridge, 1959]) and dewlap morphology (supposedly nonextensible in *A. insignis* [Barbour, 1923] and poorly developed in *A. agassizi* [Dunn, 1939]). Given that we are emphasizing the associations of names with clades, rather than with categorical ranks, and that neither of these names has been associated with the clade of mainland anoles with large body size (if they have been associated with clades at all, those clades are subclades of the large size clade), it is more appropriate to create a new name for this clade than to use either *Diaphoranolis* or *Mariguana* (which remain available for smaller clades including their type species). Therefore, we created a name that refers etymologically to the large size character (see "Etymology").

In the context of the reference phylogeny, *A. chocorum* and *A. purpurescens* are included in *Megaloa* despite not being known to possess the synapomorphy of the clade. In the case of *A. chocorum*, smaller size is parsimoniously interpreted as a reversal. In the case of *A. purpurescens*, the only two known male specimens have

[3] The component *loa* is not intended to have any other meaning beyond reference to *Dactyloa* because it contains parts of both of the Greek words on which the name *Dactyloa* is based (*daktylos*, finger + *oa*, hem, border; in reference to the toe pads).

SVLs of 74 and 78 mm and have been considered juveniles (Williams 1988; MRC, personal observation), which suggests that adults may reach a body size larger than 100 mm.

Megaloa corresponds closely to the *laticeps* group of Cope (1899; which appears to be a lapsus because the species is elsewhere [Cope, 1899: 7] referred to by the correct name, *A. latifrons*), the giant mainland anoles or *squamulatus-latifrons* group of Dunn (1937), the *latifrons* species group of Williams (1988), the *latifrons* series of Savage and Guyer (1989), and the *latifrons* clade of Castañeda and de Queiroz (2011). However, it should be noted that *Megaloa* as conceptualized here is less inclusive than the *latifrons* series as conceptualized here, in excluding species that are more closely related to *A. latifrons* than to *A. aequatorialis*, *A. punctatus*, *A. roquet*, and *A. heterodermus* but branched from the lineage leading to *A. latifrons* before large size evolved (currently, there is only one known species, *A. philopunctatus*, that is considered to belong to the *latifrons* series but not to *Megaloa* [Fig. 5]). If *A. squamulatus* (which exhibits large body size) is part of the *latifrons* series, then it is also likely part of *Megaloa*, although it might not be part of either clade (see "Comments" on the *latifrons* series).

***punctatus* series** Guyer and Savage 1987 ("1986"), informal clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *A. punctatus* Daudin 1802 and all extant species that share a more recent common ancestor with *A. punctatus* than with *Anolis aequatorialis* Werner 1894, *A. latifrons* Berthold 1846, *A. roquet* (Bonnaterre 1789), and *A. heterodermus* Duméril 1851. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis anatoloros* Ugueto, Rivas, Barros, Sánchez-Pacheco and García-Pérez 2007, *A. caquetae* Williams 1974 (see "Comments"), *A. dissimilis* Williams 1965 (see "Comments"), *A. jacare* Boulenger 1903, *A. menta* Ayala, Harris and Williams 1984 (see "Comments"), *A. punctatus* Daudin 1802, *A. ruizii* Rueda and Williams 1986 (see "Comments"), *A. santamartae* Williams 1982 (see "Comments"), *A. solitarius* Ruthven 1916 (see "Comments"), *A. tigrinus* Peters 1863, *A. transversalis* Duméril 1851, and *A. vaupesianus* Williams 1982. Other species that might belong to the *punctatus* series are *A. deltae* Williams 1974, *A. gorgonae* Barbour 1905, *A. lamari* Williams 1992, *A. nasofrontalis* Amaral 1933, *A. paravertebralis* Bernal Carlo and Roze 2005, *A. pseudotigrinus* Amaral 1933, *A. soinii* Poe and Yañez-Miranda 2008, and *A. umbrivagus* Bernal Carlo and Roze 2005 (see "Comments"). **Comments:** In the context of the reference phylogeny, eight species traditionally associated with the *punctatus* series are excluded (*A. boettgeri, A. chloris, A. chocorum, A. fasciatus, A. festae, A huilae, A. peraccae, A. philopunctatus*), and four species not traditionally associated with the *punctatus* series (all placed in the *tigrinus* series, see below) are included (*A. menta*, *A. ruizii*, *A. solitarius*, *A. tigrinus*). *Anolis tigrinus* and its previously hypothesized relatives have traditionally been included in the *tigrinus* series (e.g., Williams, 1976b, 1992; Savage and Guyer, 1989); however, strong evidence supports *A. tigrinus* as nested within the *punctatus* series (Castañeda and de Queiroz, 2011). Williams (1992) noted problems in distinguishing the *punctatus* and *tigrinus* series (referred to by him as species groups) and raised the possibility that the *tigrinus* series is an ecomorphic subgroup of the *punctatus* series (he considered members of the *tigrinus* series to be representatives of the twig ecomorph, whereas he classified at least some members of the *punctatus* series as trunk-crown anoles). Our results support this hypothesis and we therefore consider *A. tigrinus* and its relatives part of the *punctatus* series rather than a separate *tigrinus* series, although a clade containing *A. tigrinus* and all species closer to it than to *A. punctatus* could be recognized as a sub-series or a species group within the *punctatus* series.

Strong evidence also supports the inclusion of *A. chloris*, *A. fasciatus*, *A. festae*, and *A. peraccae* in the *aequatorialis* series and *A. chocorum* in the *latifrons* series (see "Comments" on the *aequatorialis* and the *latifrons* series, above) and therefore the exclusion of those species from the *punctatus* series. In contrast, because of inconsistent placement or weak support for the relevant relationships between analyses (Fig. 3 versus Fig. 4), and because of a current lack of molecular data for most of the species (all except *A. huilae*), exclusion of *A. boettgeri*, *A. huilae*, and *A. philopunctatus* from the *punctatus* series and inclusion of *A. menta*, *A. ruizii*, and *A. solitarius* in that series should be considered tentative. For similar reasons, inclusion of *A. caquetae*, *A. dissimilis*, and *A. santamartae*, all traditionally included in the *punctatus* series (Williams, 1965, 1974, 1982), should also be considered tentative. *Anolis calimae*, another species traditionally referred to the *punctatus* series (Ayala et al., 1983), was inferred as closely related to species that we tentatively refer to the *punctatus* series in the parsimony tree (Fig. 3) but not in the Bayesian tree (Fig. 4); because of this and additional contradictory results regarding the relationship between *A. calimae* and the *punctatus* series (Castañeda and de Queiroz, 2011), *A. calimae* is here considered *incertae sedis* (which does not rule out inclusion in the *punctatus* series). The long branch leading to this species and its ambiguous relationships are consistent with Williams' (1983) conclusion that this species has no evident close relatives. The geographic distribution of *A. calimae* in the central portion of the western Cordillera of Colombia between 1,300 and 1,800 m (Ayala et al., 1983) does not correspond to the eastern distribution of the *punctatus* series but instead corresponds more closely to the distribution of the *aequatorialis* or the *heterodermus* series.

Although *A. carlostoddi* and *A. orcesi* were placed in the *punctatus* series in the parsimony tree (Fig. 3), they were not placed there in the Bayesian tree (Fig. 4). We have considered *A. carlostoddi incertae sedis* within *Dactyloa* based on the deep level of disagreement concerning its placement between analyses (Figs. 3, 4), as indicated by its basal regrafted position on the pruned and regrafted consensus tree (Fig. 5). The eastern distribution of *A. carlostoddi* suggests that it may be part of the *punctatus* series, as does that of *A. neblininus*, another species that we consider *incertae sedis* but which is grouped in the parsimony tree with species that we tentatively refer to the *punctatus* series (*A. menta*, *A. solitarius*, and *A. ruizii*). By contrast, we have tentatively assigned *A. orcesi* to the *heterodermus* series (and *Phenacosaurus*) based on moderate support from the Bayesian analysis for its inclusion (Fig. 4) as well as its possession of characters of the twig ecomorph (Losos, 2009). The distribution of *A. orcesi* on the eastern slopes of the northern Andes of Ecuador is consistent with referral to the *heterodermus* series, although it is also compatible with referral to the *punctatus* series (see "Comments" section on the *heterodermus* series below). The inclusion of *A. deltae*, *A. gorgonae*, and *A. soinii*, traditionally considered members of the *punctatus* series (Williams and Duellman, 1967; Williams, 1974; Poe and Yañez-Miranda, 2008), and *A. lamari, A. nasofrontalis, A. paravertebralis, A. pseudotigrinus,* and *A. umbrivagus*, traditionally considered members of the *tigrinus* series (Williams, 1992; Bernal Carlo and Roze, 2005), should also be considered tentative given their current absence from explicit phylogenetic analyses.

The *punctatus* series as conceptualized here is more inclusive than the eastern clade of Castañeda and de Queiroz (2011) in that it includes species that are more closely related to *A. punctatus* than to *Anolis aequatorialis*, *A. latifrons*, *A. roquet*, and *A. heterodermus*, but that diverged before the last common ancestor of the members of the eastern clade and might also include some species currently considered *incertae sedis* within *Dactyloa* or absent from explicit phylogenetic analyses. Additionally, species in the eastern clade of Castañeda and de Queiroz (2011) are characterized by having a cohesive

eastern Andean and Amazonian geographic distribution, and it is possible that some species in the *punctatus* series do not conform to this geographic pattern. All of the species here tentatively referred to the *punctatus* series (*A. caquetae*, *A. dissimilis*, *A. menta*, *A. ruizii*, *A. santamartae*, *A. solitarius*) are outside of the eastern clade in the parsimony tree (Fig. 3), and one of them (*A. caquetae*) is outside of the eastern clade in the Bayesian tree (Fig. 4), although all have eastern geographic distributions (see "Phylogeny of *Dactyloa*" above for details).

***roquet* series** Williams 1976a, informal clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *Anolis roquet* (Bonnaterre 1789) and all extant species that share a more recent common ancestor with *A. roquet* than with *A. aequatorialis* Werner 1894, *A. latifrons* Berthold 1846, *A. punctatus* Daudin 1802, and *A. heterodermus* Duméril 1851. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis aeneus* Gray 1840, *A. blanquillanus* Hummelinck 1940 (see "Comments"), *A. bonairensis* Ruthven 1923, *A. extremus* Garman 1887, *A. griseus* Garman 1887, *A. luciae* Garman 1887, *A. richardii* Duméril and Bibron 1837, *A. roquet* (Bonnaterre 1789), and *A. trinitatis* Reinhardt and Lutken 1862. **Comments:** Referral of *A. blanquillanus* to this clade is based on the results of Yang et al. (1974) and Creer et al. (2001). The *roquet* series as conceptualized here corresponds exactly in known composition to the *roquet* group, species group, series, and clade of previous authors (Underwood, 1959; Gorman and Atkins, 1967, 1969; Lazell, 1972; Williams, 1976a; Savage and Guyer, 1989; Creer et al., 2001; Castañeda and de Queiroz, 2011). Nevertheless, the *roquet* series as conceptualized here is potentially more inclusive than the *roquet* clade of Castañeda and de Queiroz (2011) in that it could include some species currently considered *incertae sedis* within *Dactyloa* or absent from explicit phylogenetic analyses if they are found to be more closely related to the *roquet* clade than to the four other mutually exclusive *Dactyloa* subclades inferred by Castañeda and de Queiroz (2011).

***heterodermus* series** Castañeda and de Queiroz, new informal clade name

Definition (branch-modified node-based): The crown clade originating in the most recent common ancestor of *Anolis heterodermus* Duméril 1851 and all extant species that share a more recent common ancestor with *A. heterodermus* than with *Anolis aequatorialis* Werner 1894, *A. latifrons* Berthold 1846, *A. punctatus* Daudin 1802, and *A. roquet* (Bonnaterre 1789). **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis euskalerriari* (Barros, Williams, and Viloria 1996), *A. heterodermus* Duméril 1851, *A. inderenae* (Rueda and Hernández-Camacho 1988), *A. nicefori* (Dunn 1944), *A. orcesi* (Lazell 1969) (see "Comments"), *A. proboscis* Peters and Orcés 1956 (see "Comments"), *A. tetarii* (Barros, Williams, and Viloria 1996), and *A. vanzolinii* (Williams, Orcés, Matheus, and Bleiweiss 1996). Another species that might belong to the *heterodermus* series is *A. williamsmittermeierorum* Poe and Yañez-Miranda 2007 (see "Comments"). **Comments:** Inclusion of *A. orcesi*, a species traditionally included in *Phenacosaurus* (Lazell, 1969), should be considered tentative given the inconsistent placement of this species between analyses (Fig. 3 versus Fig. 4) and because molecular data are currently lacking. We have included *A. orcesi* in the *heterodermus* series, where it was placed in the Bayesian tree (Fig. 4), rather than in the *punctatus* series, where it was placed in the parsimony tree (Fig. 3), because of the stronger support obtained for that relationship as well as its sharing of characters of the twig ecomorph with other species traditionally referred to *Phenacosaurus* (Losos, 2009). The geographic distribution of *A. orcesi* along the eastern slopes of the northern Ecuadorean Andes corresponds with the distribution of

the *heterodermus* series, but also with that of the *punctatus* series. *Anolis williamsmittermeierorum*, previously considered closely related to *A. orcesi* (Williams and Mittermeier, 1991; Poe and Yañez-Miranda, 2007), is tentatively referred to *Phenacosaurus* given the current absence of this species from explicit phylogenetic analyses.

Anolis proboscis, *A. laevis*, and *A. phyllorhinus* were previously placed in the *laevis* species group or series, a group characterized by the presence of a nose leaf (Williams, 1979). Here we consider the relationships of *A. laevis* and *A. phyllorhinus* to be uncertain (see "Comments" section on *Phenacosaurus* below). The geographic distribution of *A. laevis* in the eastern foothills of the Peruvian Andes does not suggest a close relationship with *A. proboscis* but is consistent with referral to the *heterodermus* series (as well as the *aequatorialis* and *punctatus* series). In contrast, the geographic distribution of *A. phyllorhinus* in central Amazonia (Williams, 1979; Rodrigues et al., 2002) suggests neither a close relationship to *A. proboscis* nor inclusion in the *heterodermus* series but instead suggests inclusion in the *punctatus* series as proposed by Rodrigues et al. (2002), Yánez-Muñoz et al. (2010), and Poe et al. (2012). If *A. laevis* and one or both other species form a clade within the *heterodermus* series, then that clade could be recognized as the *laevis* species group (see also comments on *Scytomycterus*, below). If *A. laevis* and one or both other species are closely related to members of the *punctatus* series, as has been hypothesized previously (Williams, 1965, 1979), then they should be included within the *punctatus* series (perhaps as the *laevis* species group). However, if *A. laevis* and one or both of the other species lie outside of the five clades whose names incorporate the term "series" as defined here, then it would be appropriate to include them in a separate *laevis* series (defined as the most inclusive crown clade containing *A. laevis* but not *Anolis aequatorialis*, *A. latifrons*, *A. punctatus*, *A. roquet*, and *A. heterodermus*). Regardless of whether a separate *laevis* series is to be recognized, if *A. laevis* forms a clade with either or both *A. phyllorhinus* and *A. proboscis* that can be diagnosed by the nose-leaf synapomorphy (but see Yánez-Muñoz et al., 2010), the name *Scytomycterus* Cope 1876 (derived from the Greek *Skytos*, skin or leather, + *mykteros*, nose; type species = *A. laevis*) would be an appropriate name for that clade. However, if *A. phyllorhinus* or *A. proboscis* form a clade but are not closely related to *A. laevis*, which differs from the other two species in having only a rudimentary nose leaf (Williams, 1979), the name *Scytomycterus* is not appropriate for that clade (given that the type is *A. laevis*); therefore, if that clade is to be named, a new name would be appropriate.

The *heterodermus* series as conceptualized here corresponds closely to the *Phenacosaurus* clade of Castañeda and de Queiroz (2011) and *Phenacosaurus* as conceptualized here. However, it should be noted that the *heterodermus* series as conceptualized here is potentially more inclusive than *Phenacosaurus* as conceptualized here (see below), in that it might include some species currently considered *incertae sedis* within *Dactyloa* or absent from explicit phylogenetic analyses if they are found to be more closely related to *A. heterodermus* than to members of the other four well-supported clades but branched from the lineage leading to *A. heterodermus* before the twig morphology evolved (currently, all species assigned to the *heterodermus* series are also referred to *Phenacosaurus*).

Phenacosaurus Barbour 1920, converted clade name

Definition (apomorphy-based): The clade originating in the ancestor in which the combination of morphological characters of the twig ecomorph (long pointed snout; forelimbs, hindlimbs, and tail short in proportion to body size), synapomorphic with that in *Anolis heterodermus* Duméril 1851, originated. **Reference phylogeny:** Figure 5, this study. **Inferred composition:** *Anolis euskalerriari* (Barros, Williams, and

Viloria 1996), *A. heterodermus* Duméril 1851, *A. inderenae* (Rueda and Hernández-Camacho 1988), *A. nicefori* (Dunn 1944), *A. orcesi* (Lazell 1969) (see "Comments"), *A. proboscis* Peters and Orcés 1956 (see "Comments"), *A. tetarii* (Barros, Williams, and Viloria 1996), and *A. vanzolinii* (Williams, Orcés, Matheus, and Bleiweiss 1996). Another species that might belong to *Phenacosaurus* is *A. williamsmittermeierorum* Poe and Yañez-Miranda 2007 (see "Comments").

Comments: *Phenacosaurus* was originally proposed (Barbour, 1920) as the name of a genus separate from *Anolis*. However, the addition of subsequently discovered species (e.g., Dunn, 1944; Lazell, 1969; Rueda and Hernández-Camacho, 1988; Myers et al., 1993; Barros et al., 1996; Williams et al., 1996) has decreased the morphological gap between the two taxa, and several phylogenetic studies (e.g., Jackman et al., 1999; Poe, 2004; Nicholson et al., 2005; Castañeda and de Queiroz, 2011; this study) have inferred *Phenacosaurus* to be nested within *Anolis*, so that recognizing *Phenacosaurus* as a genus would render *Anolis* paraphyletic. We therefore use the name *Phenacosaurus* for a subclade of *Anolis* that is not associated with the rank of genus (it is implicitly associated with a lower rank). All species in the *Phenacosaurus* clade have been considered twig anoles (Losos, 2009), an ecomorphological category characterized by long pointed snouts, few toepad lamellae, short limbs, and short, often prehensile, tails. Because several of those characters were used in the original diagnosis of *Phenacosaurus* (Barbour, 1920), we have defined that name as referring to the clade of twig anoles that includes its type species (*A. heterodermus*).

In the context of the reference phylogeny, one species not traditionally referred to *Phenacosaurus* is included (*A. proboscis*). Molecular data are currently lacking for *A. proboscis*, but this species was consistently placed with other species referred to *Phenacosaurus* (see also Poe et al., 2009b, 2012). *Anolis proboscis* possesses the morphological features characteristic of the twig ecomorph: long pointed snout, forelimbs, hindlimbs, and tail short in proportion to body size. Moreover, ecological data indicates *A. proboscis* should be classified as a twig anole (Losos et al., 2012; Poe et al., 2012). Two species traditionally referred to *Phenacosaurus*, *Anolis carlostoddi* and *A. neblininus*, were placed inconsistently between analyses (Fig. 3 versus Fig. 4), but in neither case were they placed within *Phenacosaurus*. Because molecular data are currently lacking for *A. carlostoddi* and because some analyses based on molecular data suggest inclusion of *A. neblininus* in *Phenacosaurus* (Castañeda and de Queiroz, 2011, fig. 2C), neither species can be confidently excluded. Both species are here considered *incertae sedis* within *Dactyloa*. Inclusion of *A. orcesi*, a species traditionally included in *Phenacosaurus* (Lazell, 1969), should be considered tentative given the inconsistent placement of this species between analyses (Fig. 3 versus Fig. 4) and because molecular data are currently lacking. We have included *A. orcesi* in *Phenacosaurus*, where it was placed in the Bayesian tree (Fig. 4), rather than in the *punctatus* series, where it was placed in the parsimony tree (Fig. 3), because of the stronger support obtained for that relationship as well as its sharing of characters of the twig ecomorph with other species traditionally referred to *Phenacosaurus* (Losos, 2009). *Anolis williamsmittermeierorum*, previously considered closely related to *A. orcesi* (Williams and Mittermeier, 1991; Poe and Yañez-Miranda, 2007), is tentatively referred to *Phenacosaurus* given the current absence of this species from explicit phylogenetic analyses. *Anolis bellipeniculus* is tentatively excluded from *Phenacosaurus* based on its previously hypothesized close relationship to *A. neblininus* (Myers and Donnelly, 1996) and is here considered to be of uncertain position within *Dactyloa* (see "*Incertae sedis*," below).

Williams (1979) hypothesized that *A. laevis* and *A. phyllorhinus* are closely related to *A. proboscis*, which is here included in *Phenacosaurus*; however, that relationship has been questioned by Yánez-Muñoz et al. (2010) and Poe et al. (2012), and therefore

we consider *A. laevis* and *A. phyllorhinus* to be *incertae sedis* within *Dactyloa*. Little is known about *A. laevis*, which is known only from the type specimen, now in poor condition (Williams, 1979). However, as illustrated in Williams (1979, fig. 1), this specimen does not possess a nose leaf but only a protruding rostral scale, which is questionably homologous with the ample appendages of the other species. Moreover, the geographic distribution of *A. laevis* in the eastern foothills of the Peruvian Andes does not suggest a close relationship with *A. proboscis*, and although it is consistent with referral to the *heterodermus* series, it is also consistent with referral to the *aequatorialis* and *punctatus* series. *Anolis phyllorhinus* is better known, and although it possesses a true nose leaf, which is both similar to and different from that of *A. proboscis*, the information in Williams (1979) and Rodrigues et al. (2002) suggest that *A. phyllorhinus* is a trunk-crown rather than a twig anole (e.g., green coloration, moderate snout and limb lengths, long tail, high lamella counts, relatively large perch diameters, upward flight behavior, and high degree of similarity to *A. punctatus*, which has been classified as a trunk-crown anole [Williams, 1992]). Moreover, the geographic distribution of *A. phyllorhinus* in central Amazonia (Williams, 1979; Rodrigues et al., 2002) suggests neither a close relationship to *A. proboscis* nor inclusion in the *heterodermus* series but instead suggests inclusion in the *punctatus* series. Although we think that Yánez-Muñoz et al. (2010) are likely correct in assigning *A. phyllorhinus* in the *punctatus* series, the inclusion of neither *A. phyllorhinus* nor *A. laevis* in an explicit phylogenetic analysis leads us to treat both species as *incertae sedis* within *Dactyloa*.

Phenacosaurus as conceptualized here is more inclusive than the *Phenacosaurus* clade of Castañeda and de Queiroz (2011) in that it contains species (e.g., *A. proboscis* and possibly *A. orcesi*, see below) that share the twig ecomorph synapomorphy with *A. heterodermus* but lie outside of the smallest clade containing *A. heterodermus* and *A. euskalerriari*. *Phenacosaurus* as conceptualized here is less inclusive than the *heterodermus* series as conceptualized, in excluding species that are more closely related to *A. heterodermus* than to members of the other four clades recognized here whose names include the term "series," but branched from the lineage leading to *A. heterodermus* before the twig morphology evolved (although currently all known species referred to *Phenacosaurus* are also referred to the *heterodermus* series).

Incertae sedis

The placement of the following species could not be resolved because of lack of data or because of conflicting results between analyses, and we therefore defer assigning them to any of the above described clades until more definitive evidence is available: *A. calimae* Ayala, Harris and Williams 1983, *A. carlostoddi* (Williams, Praderio and Gorzula 1996), *A. laevis* (Cope 1876), *A. neblininus* (Myers, Williams and McDiarmid 1993), and *A. phyllorhinus* Myers and Carvalho 1945. Possible relationships of these species have been discussed under "Comments" on the *punctatus* series (*A. calimae, A. carlostoddi, and A. neblininus*), the *heterodermus* series (*A. laevis* and *A. phyllorhinus*), and *Phenacosaurus* (*A. carlostoddi*, *A. laevis, A. neblininus* and *A. phyllorhinus*). We also consider the position of *A. bellipeniculus* (Myers and Donnelly 1996) to be uncertain within *Dactyloa* given its hypothesized close relationship to *A. neblininus* (Myers and Donnelly, 1996) and the uncertain relationships of that species. The eastern distribution of *A. bellipeniculus* on the isolated Cerro Yaví tepui of southeastern Venezuela (Myers and Donnelly, 1996) suggests that it may be part of the *punctatus* series. Similarly, the placement of *A. cuscoensis* Poe, Yañez-Miranda and Lehr 2008 is considered unresolved, because although this species has been included in an explicit phylogenetic analysis (Poe et al., 2008), its hypothesized relationships are incongruent

with the clades recognized here. The geographic distribution of this species along the eastern slopes of the southern Peruvian Andes (Poe et al., 2008) is congruent with the distributions of the *heterodermus*, *punctatus*, and *aequatorialis* series (if extended to the south). Although many species in the *aequatorialis* series have western distributions, the earliest branching species within the clade (including *A. boettgeri*, which was considered closely related to *A. cuscoensis*) inhabit the eastern slopes of the Andes.

According to the definitions presented above, some species might not belong to any of the five clades whose names incorporate the term "series"; specifically, any species or clade that is sister to a clade composed of two or more of the five clades whose names include the term "series" would not be a member of any of those clades. If strong support were to be found for such relationships, new "series" names could be proposed for the corresponding species or clades, although such names might be judged unnecessary for "series" composed of single species. Currently, however, most known species of *Dactyloa* are at least tentatively referable to one of the five mutually exclusive "series" clades, and even those species that are the best candidates for not being members of those clades (i.e., the species that we consider *incertae sedis*) might belong to them.

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APPENDIX I

Morphological Character Descriptions

Description of morphological characters used in phylogenetic analyses. Ranges of species means (for continuous characters) correspond to values before data transformation and coding. Results of correlation tests (R^2 and P values) are shown.

External Characters, Examined on Alcohol-Preserved Specimens

1. Maximum male snout-to-vent length (SVL; Williams et al., 1995, character 35). Measured with a 1-mm precision ruler from the tip of the snout to the anterior lip of the cloacal opening. Continuous character. Range: 41–170 mm.
2. Ratio of maximum female SVL to maximum male SVL (Poe, 1998, character 11), both measured with a 1-mm precision ruler. This character was not correlated with SVL ($R^2 = 0.03$, $P = 0.25$). Continuous character. Range: 0.64–1.35.
3. Length of head (Poe, 2004, character 4), measured with 0.01-mm precision calipers from the tip of the snout to the anterior edge of the ear opening. This character was correlated with SVL ($R^2 = 0.94$, $P < 0.001$) and head width ($R^2 = 0.97$, $P < 0.001$). To correct for size, head length mean values were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 10.68–47.16 mm.

4. Width of head (Poe, 2004, character 5), measured with 0.01-mm precision calipers at the widest part of the head—usually the corners of the mouth. This character was correlated with SVL ($R^2 = 0.94$, $P < 0.001$) and head length ($R^2 = 0.97$, $P < 0.001$). To correct for size, head width mean values were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 5.00–29.46 mm.
5. Height of ear (Poe, 2004, character 6), measured between the internal borders with 0.01-mm precision calipers. This character was correlated with SVL ($R^2 = 0.58$, $P < 0.001$), head length ($R^2 = 0.46$, $P < 0.001$), and head width ($R^2 = 0.56$, $P < 0.001$). To correct for size, ear height mean values were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 0.60–4.84 mm.
6. Interparietal scale length (modified from Poe, 2004, character 7), measured with 0.01-mm precision calipers from the anterior to posterior edges of the scale. The interparietal scale is defined as the scale overlying the parietal foramen (Peters, 1964). Located in the parietal area, this scale is typically of larger size than surrounding scales and exhibits an area of clear skin above the parietal eye. In some species, no clear skin area is observed, but a scale appears to be homologous to the interparietal based on position, shape, and size. These scales were measured as interparietals. When scale edges were not parallel to each other, the distance between the most anterior to the most posterior points on the scale were measured. This character was correlated with SVL ($R^2 = 0.07$, $P = 0.03$), head length ($R^2 = 0.09$, $P = 0.002$), and head width ($R^2 = 0.10$, $P = 0.01$). To correct for size, interparietal length mean values were natural log transformed and regressed on natural log-transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 0.55–3.86 mm.
7. Mean number of dorsal scales in 5% of SVL (Poe, 2004, character 19). The equivalent of 5% of SVL was set on 0.01-mm precision calipers, and the number of scales contained in this length was counted three times (using the average as the final count) lateral to the dorsal midline at the level of the forelimbs. This character is an estimate of dorsal scale size. Continuous character. Range: 4.20–18.27.
8. Mean number of ventral scales in 5% of SVL (Poe, 2004, character 20). The equivalent of 5% of SVL was set on 0.01-mm precision calipers, and the number of scales contained in this length was counted three times (using the average as final count) lateral to the ventral midline in middle and posterior areas of the body. This character is an estimate of ventral scale size. Continuous character. Range: 5.08–13.80.
9. Mean number of scales between the second canthals (Williams et al., 1995, character 2). Minimum count between left and right second canthals, excluding canthal scales. This character was not correlated with SVL ($R^2 = 0.01$, $P = 0.38$), head length ($R^2 < 0.001$, $P = 0.93$), or head width ($R^2 = 0.003$, $P = 0.64$), thus no correction for size was applied. Continuous character. Range: 2.00–17.50.
10. Mean number of postrostral scales (Williams et al., 1995, character 3). Postrostrals are all scales in contact with (posterior to) the rostral scale, between supralabials. This character was correlated with SVL ($R^2 = 0.08$, $P = 0.02$) and head width ($R^2 = 0.07$, $P = 0.03$), but not head length ($R^2 = 0.05$, $P = 0.06$). To correct for size, mean numbers of postrostral scales were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 2.88–8.60.
11. Mean number of scales between supraorbital semicircles (Williams et al., 1995, character 6). Minimum count between left and right supraorbital seimicircles. This character was correlated with SVL ($R^2 = 0.20$, $P < 0.001$), head length ($R^2 = 0.16$, $P < 0.001$), and head width ($R^2 = 0.18$, $P < 0.001$). To correct for size, the mean numbers of scales between supraorbital semicircles were $\ln(x + 1)$ transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. The $\ln(x + 1)$ transformation was used because this character contains mean zero values. Continuous character. Range: 0–5.50.
12. Mean number of loreal rows (Williams et al., 1995, character 10). Loreal scales cover the area between canthals, supralabials, and subocular scales. Rows were counted as the minimum number of scales, in a straight line, from the first or second canthal to the sublabial scales on the right side of the head, unless the area was damaged, and then the left side was scored. This character was correlated with SVL ($R^2 = 0.12$, $P = 0.01$), head length ($R^2 = 0.06$, $P = 0.05$), and head width ($R^2 = 0.10$, $P = 0.01$). To correct for size, mean numbers of loreal rows were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 1.00–10.20.
13. Mean number of supralabial scales to below the center of the eye (Williams et al., 1995, character 16), counted from the rostral (not included) to the midpoint of the eye. More than half the scale had to be anterior to the center of the eye to be included in the count. This character was correlated with SVL ($R^2 = 0.12$, $P = 0.01$), head length ($R^2 = 0.15$, $P < 0.001$), and head width ($R^2 = 0.09$, $P = 0.02$). To correct for size, mean numbers of supralabial scales were natural log

transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 5.00–11.00.

14. Mean number of postmental scales (Williams et al., 1995, character 17). Postmentals are all scales in contact with (posterior to) the mental scale between the infralabials (i.e., including the anteriormost sublabial scale on left and right sides). This character was correlated with SVL ($R^2 = 0.06$, $P = 0.04$) and head width ($R^2 = 0.07$, $P = 0.03$), but not head length ($R^2 = 0.03$, $P = 0.21$). To correct for size, mean number of postmental scales were natural log transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. Continuous character. Range: 2.63–10.13.
15. Mean number of sublabial scales (Williams et al., 1995, character 18; Poe, 2004, character 44). Sublabial scales are abruptly enlarged scales (more than twice the size) located medial and parallel to the infralabials and posterior to the mental. This character was correlated with SVL ($R^2 = 0.13$, $P < 0.001$), head length ($R^2 = 0.07$, $P = 0.03$), and head width ($R^2 = 0.11$, $P = 0.01$). To correct for size, the mean number of sublabial scales were $\ln(x + 1)$ transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. The $\ln(x + 1)$ transformation was used because this character contains mean zero values. Continuous character. Range: 0–7.00.
16. Mean number of scales between the interparietal scale and the supraorbital semicircles (Williams et al., 1995, character 13; Poe, 2004, character 46). The minimum number of scales between the interparietal scale and the supraorbital semicircles was counted. This character was correlated with SVL ($R^2 = 0.11$, $P = 0.01$), head length ($R^2 = 0.07$, $P = 0.03$), and head width ($R^2 = 0.09$, $P = 0.02$). To correct for size, the mean number of scales between interparietal and supraorbital semicircles were $\ln(x + 1)$ transformed and regressed on natural log–transformed SVL mean values. Residuals were subsequently used. The $\ln(x + 1)$ transformation was used because this character contains mean zero values. Continuous character. Range: 0–7.25.
17. Number of elongated superciliary scales (Williams et al., 1995, character 8). Superciliaries are scales along the dorsal rim of the orbit, and elongation occurs toward the posterior end of the orbit. Left and right sides were scored separately. States: (0) 0, (1) 1, (2) 2, (3) 3. Polymorphic character. Ordered.
18. Number of scales between subocular and supralabial scales (Williams et al., 1995, character 15; Poe, 2004, character. 28). The minimum number of scales was recorded for each specimen. States: (0) 0, (1) 1, (2) 2. Polymorphic character. Ordered.
19. Number of ventral scales posteriorly bordering one scale (modified from Poe, 2004, character 14). Middle and posterior ventral areas were examined. Ventral scales may be bordered posteriorly by two scales (0), by two and three scales (1), or by three scales (2). Polymorphic character. Ordered.
20. Shape of the base of the tail (modified from Williams et al., 1995, character 30; Poe, 2004, character 15). On each specimen, at the point where the knee would reach the tail if the leg were folded back, the height and width of the tail was measured, and then the ratio of width/height was calculated. States: (0) tail round, for ratios larger than 1; (1) tail laterally compressed, for ratios smaller than 1. Polymorphic character.
21. Toepad overlap (Williams et al., 1995, character 27; Poe, 2004, character 9). The toepad under phalanges III and IV may project distally under phalanx II (0) or not project distally (1), or the toepad may be completely absent (2). Polymorphic character. Ordered.
22. Male dewlap extension (Williams et al., 1995, character 33; Poe, 2004, character 16). On the ventral side, the posterior extension of the unfolded dewlap is examined. Four states were considered: posterior extension past the arm insertion (0), posterior extension to arm insertion (1), shorter than arm extension (2), dewlap absent (3). Polymorphic character. Ordered.
23. Female dewlap extension (Williams et al., 1995, character 34; Poe, 2004, character 17). Measurement and coding as in male dewlap extension. This character is not correlated with male dewlap extension ($R^2 = 0.210$, $P = 0.136$); therefore, it was considered a separate character. Polymorphic character. Ordered.
24. Size of scales in supraocular discs (modified from Poe, 2004, character 41). Three different states were considered: (0) scales vary continuously in size, in which a few scales are slightly larger (less than twice the size) than the others, showing gradual reduction in size; (1) one to three abruptly enlarged scales (more than twice the size) with all other scales of smaller size; and (2) all scales about equal in size. Polymorphic character. Unordered.
25. Dewlap scales (modified from Poe, 2004, character 21). The scales on the dewlap may be in rows of single scales (0); in double rows (1) or have scattered scales covering the entire dewlap (2). In some specimens, most rows were either single or double, with a few rows exhibiting the alternative condition. In such cases, the most common condition was scored for the specimen. Polymorphic character. Unordered.
26. Width of mental relative to rostral (modified from Poe, 2004, character 27). In ventral view, the mental scale may be broader than the rostral (0), the rostral scale may be broader than the mental (1), or both

scales may show the same width (2). Polymorphic character. Unordered.

27. Enlarged postanal scales in males (Williams et al., 1995, character 32). Postanal scales may be: (0) absent, (1) present, as a pair of significantly enlarged (more than four times the surrounding scales), (2) present, as a series of more than two scales slightly enlarged (less than twice the size of surrounding scales). Polymorphic character. Unordered.
28. Presence or absence of tail crest in males (Williams et al., 1995, character 31). The tail crest in males may be: (0) absent, (1) present as a series of enlarged, but not elevated, serrated scales, or (2) present as the result of enlarged neural spines. The presence of a crest is associated with sex and age of the specimen; therefore, when intraspecific variation was observed (presence and absence) the species was coded as present. However, states 1 and 2 were never observed in the same species. Unordered.
29. Heterogeneous flank scales (modified from Williams et al., 1995, character 23). Heterogeneous scales may be (0) absent, (1) very large and separated from one another by many scales of much smaller size, (2) a mosaic of scales of different sizes but not very different in size from one another, or (3) of average size surrounded by granular-minute scales. Polymorphic character. Unordered.
30. Mental scale (Poe, 2004, character 26). The mental scale may be partially divided (0), in which a longitudinal split begins from the posterior edge of the mental but does not reach the anterior edge, or completely divided (1), in which the split is complete. Polymorphic character.
31. Frontal depression (Poe, 2004, character 45). A depression around the frontal area may be absent (0), in which case the dorsal surface of the snout is flat, or present (1). Polymorphic character.
32. Presence or absence of an externally visible parietal eye (Estes et al., 1988, character 26). The parietal eye, when visible externally, is located within the interparietal scale (see character 6). States: absent (0), present (1). Polymorphic character.
33. Keeling of dorsal, ventral, supradigital and head scales (Williams et al., 1995, characters 20, 25, 29, 1; Poe 2004, character 40). Dorsal, ventral, and supradigital scales may be smooth (S) or keeled (K); head scales may in addition be rugose (R) or have pustules (P). The four apparently independent characters were combined as one after correlation was found between ventral, supradigital, and head keeling with dorsal keeling ($R^2 = 0.201$, $P < 0.0001$; $R^2 = 0.635$, $P < 0.0001$; $R^2 = 0.456$, $P < 0.0001$, respectively). The condition present in the majority of the scales was reported. Dorsal scale keeling was scored excluding middorsal scales because these often differ from the remaining dorsals (e.g., some species exhibit smooth dorsal scales, but a double row of keeled middorsal scales). Weakly keeled specimens were coded as keeled. Rugose refers to multiple, less pronounced keels or bent ridges (these two conditions were commonly found combined in one scale); with pustules refers to multiple granular projections scattered on the scale. States (for dorsals, ventrals, supradigitals, head scales): KKKK (0), KKKR (1), KKKS (2), KKSP (3), KSKK (4), KSKS (5), SSKR (6), SSKS (7), SSSS (8), SSSR (9). Modal condition coded. Unordered.

Osteological Characters Examined on Dry, Cleared, and Stained Specimens and/or Radiographs.

34. Shape of parietal crests (Etheridge, 1959, fig. 9; Cannatella and de Queiroz, 1989, characters 6, 7; Williams, 1989, character 7, modified from Poe, 1998, character 87). Three different states were considered: (0) trapezoid–shape: lateral borders of the crest reach the occipital crest directly (i.e., do not touch each other before occipital crest contact); (1) V-shape: lateral borders of the crest join at the point of contact with the occipital crest, and there is no extension beyond the point of contact; (2) Y-shape: lateral borders of the crest join before occipital crest contact and extend posteriorly beyond the point of contact (i.e., a unified crest extends toward or beyond the occipital). Etheridge (1959) showed that this character exhibits ontogenetic variation, from a U/trapezoid shape seen in early stages to an intermediate V-shape, to a Y-shaped crest seen in adult stages. To compensate for the absence of sex and SVL information to confirm adulthood in some specimens, the most developed state observed (following Etheridge's ontogenetic sequence) was scored for each species. Ordered.
35. Presence or absence of crenulation along lateral edges of parietal (Poe, 1998, character 88). The parietal may exhibit irregular (crenulated) or smooth lateral edges. States: absent (0), present (1). Polymorphic character.
36. Extension of the parietal roof (modified from Poe, 2004, character 59). In anoles, a parietal casque has been defined as the shelf-like posterolateral extension of the parietal roof over the supratemporal processes of the parietal. Poe (2004) coded the presence or absence of the casque, but we found variation in the length of the extension. The roof extension may be large, almost completely covering the supratemporal processes and sometimes extending beyond the posteriormost margin, or the extension could be small, leaving more of the supratemporal process uncovered and not reaching the posterior margin of the parietal. States: not extended (0; e.g., *A. chocorum*, MCZ 115732); present and small, not reaching posteriormost margin of supratemporal processes (1; e.g., *A. fitchi*, MCZ 178084); present and large, reaching or

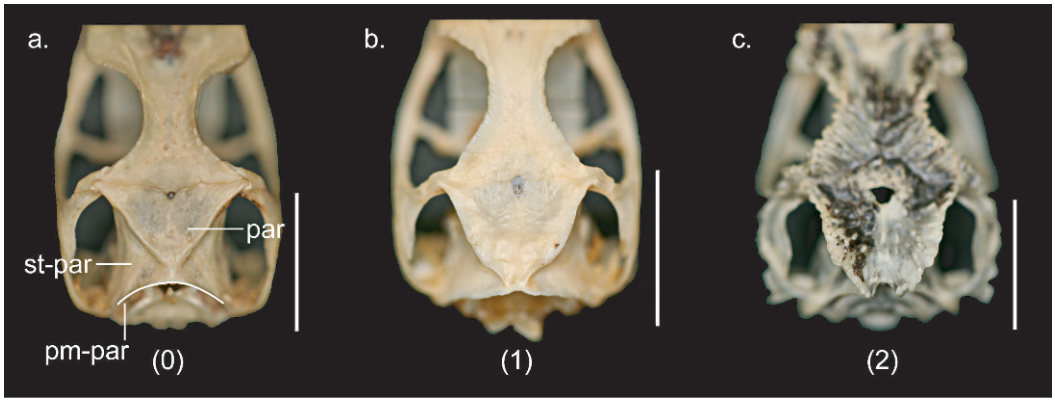

Figure 6. Dorsal views of the skulls of three anoles illustrating differences in the extension of the parietal roof (character 36). (a) *Anolis chocorum*, MCZ 115732 (state 0); (b) *Anolis fitchi,* MCZ 178084 (state 1); (c) *Anolis heterodermus*, MCZ 110138 (state 2). Scale bar = 5 mm. Abbreviations: par, parietal; st-par, supratemporal processes of the parietal; pm-par, posterior margin of parietal.

extending beyond the posteriormost margin of supratemporal processes (2; e.g., *A. heterodermus*, MCZ 110138) (Fig. 6). The largest extension of the parietal roof observed among all individuals was scored for each species. Ordered.

37. Parietal foramen (Etheridge, 1959; Williams, 1989, character 5). The parietal foramen may be located completely within the parietal (0) or may be at the fronto-parietal suture (1). Cases in which the foramen is located within the parietal but connected to the fronto-parietal by a suture were coded as 0. Absence of the parietal foramen was coded as ?, instead of as a third state, given that the information on the presence or absence of an externally visible parietal eye was coded as a separate character (character 32) from alcohol-preserved specimens. Polymorphic character.

38. Fronto-parietal suture (this study). The fronto-parietal suture may form a straight transverse line (i.e., perpendicular to the longitudinal axis of the body) (0; e.g., *A. danieli*, MCZ 164894) or it may exhibit a posteriorly convex curve in the center because of extension of the frontal bone into the parietal bone (1; e.g., *A. eulaemus*, MCZ 158390) (Fig. 7). Significant variation was observed in the latter state (from a slight to a substantial protuberance), but this variation was not quantified. Polymorphic character.

39. Presence or absence of postfrontal (Etheridge and de Queiroz, 1988, character 6; Poe, 1998,

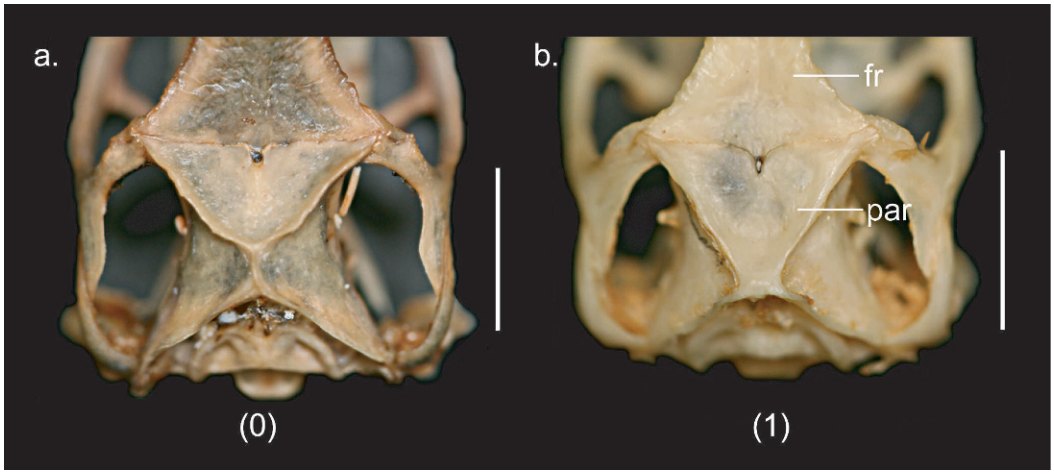

Figure 7. Dorsal views of the skulls of two anoles illustrating differences in the fronto-parietal suture (character 38). (a) *Anolis danieli*, MCZ 164894 (state 0); (b) *Anolis eulaemus*, MCZ 158390 (state 1). Scale bar = 5 mm. Abbreviations: fr, frontal; par, parietal.

character 92; 2004, character 62). The postfrontal bone is located in the posterodorsal margin of the orbit between (or overlapping) the frontal and the postorbital. States: absent (0), present (1). Polymorphic character.

40. Frontal (Poe, 1998, character 94; 2004, character 64). The anterior suture of the frontal may be in contact only with nasals (0), may be separated from nasals by an open gap (1), or may be in contact with both the premaxilla and nasal (2). State 1 includes cases where the gap was along the entire suture or, most commonly, in the center only, allowing partial lateral contact between frontal and nasals. Posterior extension of the premaxilla, sufficient to potentially contact the frontal (i.e., if the gap were absent), was never observed along with the open gap. Polymorphic character. Unordered.
41. Prefrontals (Poe, 1998, character 93, fig. 4). Prefrontals may be in contact with nasals (0) or may be separated from nasals by the contact between frontal and maxilla (1). Any contact between prefrontal and nasal was scored as 0. Differences between left and right sides were observed in some specimens; therefore, each side was treated separately for frequency calculations. Polymorphic character.
42. Posterior extension of maxilla (Poe, 1998, character 103, fig. 8). Different landmarks have been used as boundaries to quantify the posterior extension of the maxilla (e.g., Estes et al., 1988, character 27; Frost and Etheridge, 1989, character 3). Following Poe (1998), the posterior edge of the ectopterygoid was used to delimit two different states: (0) maxilla does not extend posteriorly beyond the posterior edge of ectopterygoid (including cases in which it extends to that level) or (1) maxilla extends beyond the posterior edge of ectopterygoid. Differences between left and right sides were observed in some specimens; therefore, each side was treated independently for frequency calculations. Polymorphic character.
43. Mean number of premaxillary teeth (de Queiroz, 1987, characters 43, 44). This character was not correlated with SVL ($R^2 = 0.01$, $P = 0.46$), head length ($R^2 = 0.013$, $P = 0.39$), or head width ($R^2 = 0.009$, $P = 0.47$); thus, no correction for size was applied. Range: 6–13. Continuous character.
44. Presence or absence of pterygoid teeth (Etheridge, 1959; Poe, 1998, character 101). Pterygoid teeth are found along the edge facing the pyriform recess, either clumped or in a single row. States: absent (0), present (1). Polymorphic character.
45. Presence or absence of contact between jugal and squamosal (Frost and Etheridge, 1989, character 8). The jugal and squamosal bones may be in contact along the ventral edge of the temporal bar, or they may be separated by the postorbital bone. In some specimens, differences between the left and right sides were found; therefore, each side was treated separately for frequency calculations. States: absence (0), presence (1). Polymorphic character.
46. Shape of posteroventral corner of jugal (modified from Poe, 2004, character 69). Poe (2004) recognized two states of this character: posteroventral corner of jugal is anterior to the posterior edge of jugal (in species where the posterior edge of the jugal shows a straight or convex border) or is posterior to the posterior edge of the jugal (in species where the posterior edge of jugal shows a concave border). However, we found these two character states not to be mutually exclusive; therefore, the states were modified as follows: posterior border of the jugal concave, with a sharp (pointed) posteroventral corner (0), or posterior border straight or convex, with a rounded posteroventral corner (1). Differences between left and right sides were observed in some specimens; therefore, each side was treated independently for frequency calculations. Polymorphic character.
47. Presence or absence of contact between parietal and epipterygoid (Poe, 1998, character 99). The epipterygoid extends from the palate toward the skull roof and may or may not reach the parietal. In some species, the most distal portion of the epipterygoid is cartilaginous and often lost during skull preparation, rendering the structure not in contact with the parietal. Cases in which the absence of contact is an artifact of preparation could not be distinguished from those in which the epipterygoid (with or without cartilaginous portion) is short enough not to be in contact with the parietal. All cases with no contact were coded as absence. No intraspecific variation was observed. States: absent (0), present (1).
48. Supraoccipital cresting (Poe, 1998, character 105, fig. 9; 2004, character 55). The supraoccipital may show: (0) a single medial process (called *processus ascendens*; e.g., *A. heterodermus*, MCZ 110133); (1) a medial process in addition to two distinct and smaller lateral processes (not always ossified; e.g., *A. chloris*, MCZ 101290) or (2) a continuous (e.g., *A. agassizi*, MCZ 18088) or partially continuous crest (showing two lateral processes with a distinct crest between them) running along the edge of the osseus labyrinth (Fig. 8). Significant ontogenetic variation was observed within each one of the states, but a sequence linking all three states was not observed; therefore, the modal condition was scored for each species. Unordered.
49. Contact between parietal and supraoccipital (this study). The parietal may be widely separated from the supraoccipital, leaving free space between the two on either side of the processus ascendens (0; e.g., *A. princeps*, MCZ 147444), or may be in contact (or almost in contact) with the supraoccipital, leaving no open space in between (1; e.g., *A. ventrimaculatus*, MCZ 127711) (Fig. 9). Polymorphic character.

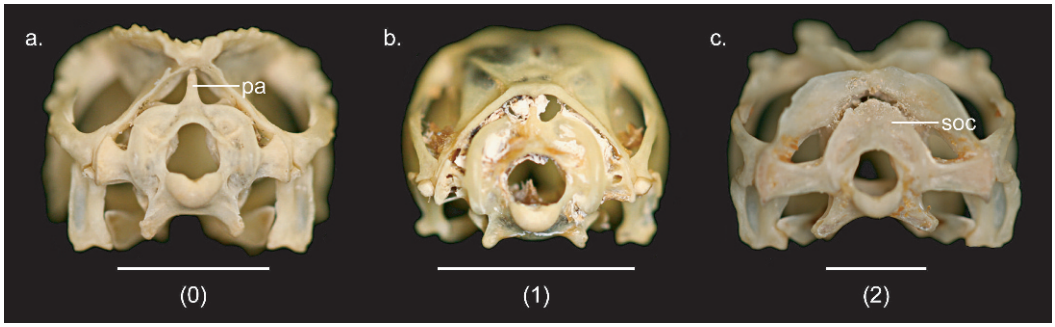

Figure 8. Posterior views of the skulls of three anoles illustrating differences in the supraoccipital cresting (character 48). (a) *Anolis heterodermus*, MCZ 110133 (state 0); (b) *Anolis chloris*, MCZ 101290 (state 1); (c) *Anolis agassizi*, MCZ 18088 (state 2). Scale bar = 5 mm. Abbreviations: pa, processus ascendens; soc, supraoccipital.

50. Extension of the supratemporal processes of the parietal (this study). In some species (e.g., *A. agassizi*, MCZ 27120), the supratemporal processes of the parietal extend dorsally forming a vertical flange (1); in others (e.g., *A. heterodermus*, MCZ 110133), the supratemporal processes of the parietal do not extend (0) (Fig. 10). Significant variation was observed in the height of the extension, but it was not quantified. Additionally, ontogenetic variation was observed within some species; therefore, the most developed state (i.e., supratemporal processes extended) was scored for the species if it was observed in any specimens. States: supratemporal processes of the parietal not extended (0), extended (1).
51. Presence or absence of the quadrate lateral shelf (Poe, 1998, character 106, fig. 10). The quadrate lateral shelf is the lateral extension of the external edge of the quadrate. Ontogenetic variation was observed within some species; thus, the developed state (i.e., presence of quadrate lateral shelf) was scored for the species when observed. States: absent (0), present (1).
52. Presence or absence of angular process of prearticular (de Queiroz, 1987, character 41, fig. 28; Poe, 1998, character 110, fig. 11). This process is located on the medial side of the retroarticular process of the prearticular and has a fin-like or rounded shape. Presence was coded as a significant extension beyond an imaginary line along the medial edge (in dorsal view) of the prearticular. Absent and rudimentary processes were coded as absent. Differences in size of the process were observed, but were not quantified. Poe (1998, 2004) called this structure angular process of the articular, but the articular is an endochondral (rather than dermal) bone that results from the ossification of the posterior end of Meckel's

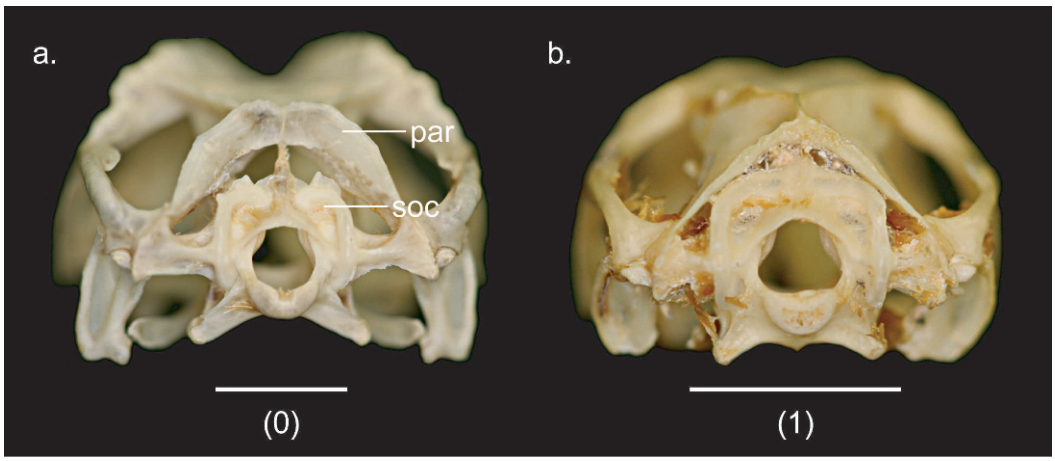

Figure 9. Posterior views of the skulls of two anoles illustrating differences in the contact between the parietal and supraoccipital (character 49). (a) *Anolis princeps*, MCZ 147444 (state 0); (b) *A. ventrimaculatus,* MCZ 127711 (state 1). Scale bar = 5 mm. Abbreviations: par, parietal; soc, supraoccipital.

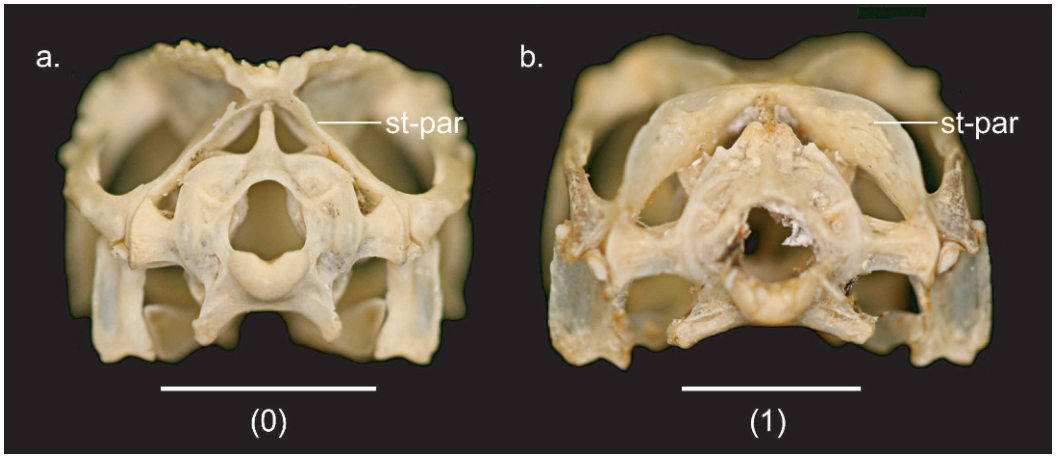

Figure 10. Posterior views of the skulls of two anoles illustrating differences in the extension of the supratemporal processes of the parietal (character 50). (a) *Anolis heterodermus*, MCZ 110133 (state 0); (b) *Anolis agassizi*, MCZ 27120 (state 1). Scale bar = 5 mm. Abbreviations: st-par, supratemporal processes of the parietal.

cartilage and forms the articular condyle, but neither the retroarticular nor the angular process (de Queiroz, 1987). No intraspecific variation was observed. States: absent (0), present (1).

53. Position of posteriormost tooth with respect to the combined alveolar-mylohyoid foramen (camf; modified from de Queiroz, 1987, characters 34, 35; Poe, 1998, character 109; 2004, character 81). Etheridge (1959) reported that in some iguanids (e.g., anoles) the anterior mylohyoid foramen (amf, usually located within the splenial) is united with the anterior inferior alveolar foramen (aiaf, located between the dentary and splenial), resulting in a single foramen. In the present study, the single foramen is called the combined alveolar-mylohyoid foramen (camf). Poe (1998, 2004) compared the position of the posteriormost tooth to the amf, which is the same as this character. We compared the position of the posterior edge of the posteriormost tooth to the camf, and considered three states: posteriormost tooth is anterior to camf (0), overlaps with camf (1), posteriormost tooth is posterior to camf (2). Left and right mandibles were coded separately. Polymorphic character. Unordered.
54. Shape of the posterior suture of dentary (Poe, 1998, character 111, fig. 12). In lateral view, the suture of the dentary with the surangular may have a distinctly pronged (i.e., with two processes) or a blunt, undifferentiated shape. No intraspecific variation was observed. States: pronged (0), blunt (1).
55. Position of posterior suture of dentary, relative to mandibular fossa (Poe, 1998, character 112). Given the possible shape of this suture (blunt or pronged), the anteriormost aspect of the posterior border is the point used for comparison. States: posterior border of dentary is anterior to mandibular fossa (0) or within mandibular fossa (1). Polymorphic character.
56. Position of surangular foramen (Frost and Etheridge, 1988, character 19, fig. 3; Poe, 1998, character 115, fig. 13). The surangular foramen (on the lateral surface of the mandible; same as Poe's [2004] supra-angular foramen) may be located entirely within the surangular (0) or be partially bordered by the dentary (1). Differences between left and right sides were observed in some specimens; therefore, each side was treated separately for frequency calculations. Polymorphic character.
57. Presence or absence of splenial bone (Etheridge, 1959; Poe, 2004, character 85). States: absent (0), present as anteromedial sliver (1), or present and large, as in *Polychrus* and other non-anole iguanids (2). No intraspecific variation was observed. Ordered.
58. Presence or absence of angular bone (Etheridge, 1959). States: absent (0), present (1). No intraspecific variation was observed.
59. Overlap between clavicles and lateral processes of interclavicle (modified from Etheridge, 1959). Etheridge (1959) described two different types of interclavicles in anoles: arrow-shaped (in which the lateral processes of the interclavicle are caudolaterally directed and only medially overlapped by the clavicle) or T-shaped (in which the lateral processes are laterally directed and broadly overlapped by the clavicle). The two components of the interclavicle shape, as described by Etheridge (1959), can vary independently; therefore, this character was divided into two. The first was quantified as

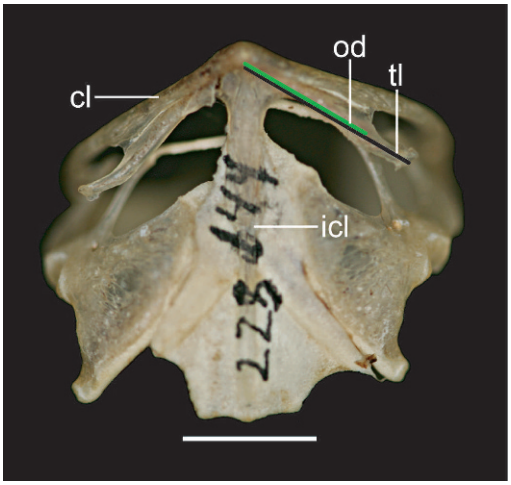

Figure 11. Ventral view of the pectoral girdle illustrating details on measurements of the overlap between clavicles and the lateral processes of the interclavicle (character 59). Scale bar = 5 mm. Abbreviations: cl, clavicle; icl, interclavicle; od, overlapped distance; tl, total length of lateral process of interclavicle.

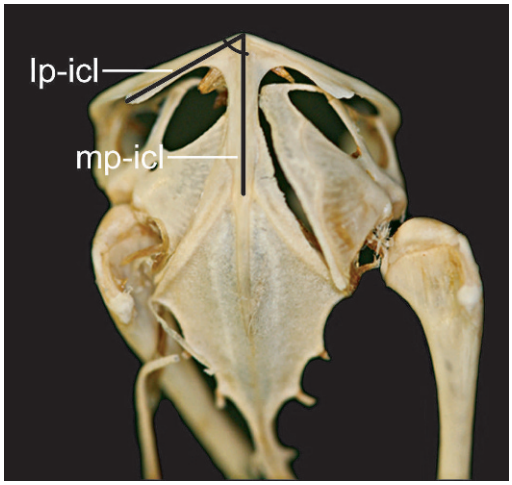

Figure 12. Ventral view of the pectoral girdle illustrating details on measurements of the angle between the median (posterior) process and the lateral process of the interclavicle (character 60). Abbreviations: lp-icl, lateral process of interclavicle; mp-icl, medial process of interclavicle.

the fraction of the length of the lateral process of the interclavicle in direct contact with (i.e., overlapped by) the clavicle. The total length of the lateral process was measured as a straight line from the midline of the interclavicle (an imaginary line along the long axis of the median [posterior] process) to the tip of the lateral process (Fig. 11). The overlapped distance was measured along the same straight line. Length measurements were made on photographs of dry or clear and stained interclavicles using the software MacMorph (Spencer and Spencer, 1993). Two measurements were made on each side (left and right sides separately) and used to calculate the average per species. Continuous character. Range: 0.36–0.96.

60. Angle between the median (posterior) process and the lateral process of the interclavicle (this is the second character derived from the arrow-shaped and T-shaped conditions of Etheridge [1959] described in the previous character). The angle was measured between the long axis of the median process and that of the lateral process (as described in the previous character; Fig. 12) on photographs of dry or cleared and stained interclavicles, using the software MacMorph (Spencer and Spencer, 1993). Two measurements were made on each side (left and right sides separately) and used to calculate the average per species. Continuous character. Range: 44.9–64.5.

61. Postxiphisternal inscriptional rib formula (Etheridge, 1959). The postxiphisternal inscriptional ribs are the cartilaginous ventral rib elements located caudal to the xiphisternum. The first number in the formula refers to the number of such ribs attached to the (ossified) dorsal ribs; the second refers to the number of floating (unattached) postxiphisternal inscriptional ribs caudal to the attached ones. The modal condition was scored for each species. States: (0) 2:2, (1) 3:1, (2) 4:0, (3) 4:1, (4) 5:0, (5) 5:1, (6) 5:2, (7) 8:1. This character was ordered using a step matrix (modified from Jackman et al., 1999), in which the gain or loss of a rib or a connection (from attached to floating or vice versa) costs one step.

62. Number of presacral vertebrae (Etheridge, 1959). The presacral vertebrae are all vertebrate anterior to the sacrum. States: (0) 22, (1) 23, (2) 24, (3) 25, (4) 27. Polymorphic character. Ordered.

63. Number of lumbar vertebrae (Etheridge, 1959). The lumbar vertebrae are post-thoracic vertebrae (i.e., those that are not attached directly or indirectly to the sternum) that bear no ribs. States: (0) 1, (1) 2, (2) 3, (3) 4, (4) 5. Polymorphic character. Ordered.

64. Type of caudal vertebrae (Etheridge, 1959). Caudal vertebrae may be of the alpha type (0), in which the transverse processes are caudolaterally or laterally directed and present only on the most anterior vertebrae (7–15), or the beta type (1), in which transverse processes are present much farther posteriorly in the caudal sequence, where they are directed craniolaterally. No instraspecific variation was observed.

65. Caudal autotomy septa (Etheridge, 1959). Autotomy septa are observed in radiographs as unossi-

fied areas in the vertebrae anterior, posterior, or through the transverse process. The anteriormost autotomy septum usually coincides with a change in the condition of the transverse process (e.g., disappearance, change in direction, or appearance of a second pair; Etheridge, 1959). This character exhibits ontogenetic variation, as in some species, progressive fusion of the septa occurs from caudal to cranial with age (Etheridge, 1959). To account for this variation, three states were recognized: septa absent in all specimens, representing those species that do not have (at any life stage) autotomy (0), septa present in some specimens and absent in others, representing those species that progressively lose autotomy with age (1), or septa present in all specimens, representing those species that retain autotomy throughout life (provided that large individuals were examined) (2). This coding approach is strongly biased by sample size but was the best found to incorporate information on the gradual change of the character. Ordered.

66. Mean number of caudal vertebrae bearing transverse processes (Etheridge, 1959). Transverse processes are always present on the anteriormost caudal vertebrae and progressively decrease in size posteriorly until absent. Continuous character. Range: 6.8–32.2.

LITERATURE CITED

Alfaro, M. E., S. Zoller, and F. Lutzoni. 2003. Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markov chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. *Molecular Biology and Evolution* **20:** 255–266.

Arosemena, F. A., R. Ibañez D., and F. de Sousa. 1991. Una nueva especies de *Anolis* (Squamata: Iguanidae) del grupo *latifrons* de Fortuna, Panamá. *Revista de Biología Tropical* **39:** 255–262.

Ayala, S., D. Harris, and E. E. Williams. 1983. New or problematic *Anolis* from Colombia. I. *Anolis calimae*, new species, from the cloud forest of western Colombia. *Breviora* **475:** 1–11.

Ayala, S. C., and F. Castro. Familia Iguanidae—II Anolinos. *In* S. C. Ayala and F. Castro (eds) *Saurios de Colombia*. Unpublished manuscript.

Ayala, S. C., D. M. Harris, and E. E. Williams. 1984. *Anolis menta,* sp. n. (Sauria, Iguanidae), a new *tigrinus* group anole from the west side of the Santa Marta Mountains, Colombia. *Papéis Avulsos de Zoologia* **35:** 135–145.

Ayala-Varela, F. P., and O. Torres-Carvajal. 2010. A new species of dactyloid anole (Iguanidae, Polychrotinae, *Anolis*) from the southeastern slopes of the Andes of Ecuador. *ZooKeys* **53:** 59–73.

Ayala-Varela, F. P., and J. A. Velasco. 2010. A new species of dactyloid anole (Squamata: Iguanidae) from the western Andes of Ecuador. *Zootaxa* **2577:** 46–56.

Barbour, T. 1920. A note on *Xiphocercus*. *Proceedings of the New England Zoological Club* **7:** 61–63.

Barbour, T. 1923. Notes on reptiles and amphibians from Panamá. *Occasional Papers of the Museum of Zoology, University of Michigan* **129:** 1–16.

Barros, T., E. E. Williams, and A. Viloria. 1996. The genus *Phenacosaurus* (Squamata: Iguania) in western Venezuela: *Phenacosaurus tetarii*, new species, *Phenacosaurus euskalerriari*, new species, and *Phenacosaurus nicefori* Dunn, 1944. *Breviora* **504:** 1–30.

Berlocher, S. H., and D. L. Swofford. 1997. Searching for phylogenetic trees under the frequency parsimony criterion: an approximation using generalized parsimony. *Systematic Biology* **46:** 211–215.

Bernal Carlo, A., and J. A. Roze. 2005. Lizards of the genus *Anolis* (Reptilia: Polychrotidae) from Sierra Nevada de Santa Marta, Colombia, with description of two new species. *Novedades Colombianas* **8:** 9–26.

Brandley, M. C., and K. de Queiroz. 2004. Phylogeny, ecomorphological evolution, and historical biogeography of the *Anolis cristatellus* group. *Herpetological Monographs* **18:** 90–126.

Bryant, D. 2003. A classification of consensus methods for phylogenetics, pp. 1–21. *In* M. Janowitz, F. J. Lapointe, F. McMorris, B. Mirkin, and F. Roberts (eds.), *BioConsensus*. Piscataway, New Jersey: American Mathematical Society Publications–DIMACS Series in Discrete Mathematics and Theoretical Computer Science.

Burnell, K. L., and S. B. Hedges. 1990. Relationships of West Indian *Anolis* (Sauria: Iguanidae): an approach using slow-evolving protein loci. *Caribbean Journal of Sciences* **26:** 7–30.

Butler, M. A., S. A. Sawyer, and J. B. Losos. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* **447:** 202–205.

Butler, M. A., T. W. Schoener, and J. B. Losos. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* **54:** 259–272.

Cannatella, D., and K. de Queiroz. 1989. Phylogenetic systematics of the Anoles: is a new taxonomy warranted? *Systematic Zoology* **38:** 57–69.

Castañeda, M. d. R., and K. de Queiroz. 2011. Phylogenetic relationships of the *Dactyloa* clade of *Anolis* lizards based on nuclear and mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* **61:** 784–800.

Cope, E. D. 1899. Contributions to the herpetology of New Grenada and Argentina, with descriptions of new forms. *Philadelphia Museums Science Bulletin* **1:** 1–21.

Creer, D. A., K. de Queiroz, T. R. Jackman, J. B. Losos, and A. Larson. 2001. Systematics of the *Anolis roquet* series of the southern Lesser Antilles. *Journal of Herpetology* **35:** 428–441.

de Queiroz, K. 1987. Phylogenetic systematics of Iguanine lizards. A comparative osteological study.

University of California Publications in Zoology **118:** 1–203.

DE QUEIROZ, K. 1996. Including the characters of interest during tree reconstruction and the problems of circularity and bias in studies of character evolution. *American Naturalist* **148:** 700–708.

DE QUEIROZ, K. 2000. Logical problems associated with including and excluding characters during tree reconstruction and their implications for the study of morphological character evolution, pp. 192–212. *In* J. J. Wiens (ed.), *Phylogenetic Analysis of Morphological Data*. Washington, DC: Smithsonian Institution Press.

DE QUEIROZ, K., AND M. DONOGHUE. 2013. Phylogenetic nomenclature, hierarchical information, and testability. *Systematic Biology*. doi: 10.1093/sysbio/sys054

DE QUEIROZ, K., AND J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology* **39:** 307–322.

DE QUEIROZ, K., AND J. GAUTHIER. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* **23:** 449–480.

DE QUEIROZ, K., AND T. REEDER. 2008. Squamata—Lizards, pp. 24–45. *In* B. I. Crother (ed.), *Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in Our Understanding*. Society for the Study of Amphibians and Reptiles, *Herpetological Circular* No. 37.

DRUMMOND, A. J., AND A. RAMBAUT. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

DUNN, E. R. 1937. The giant mainland Anoles. *Proceedings of the New England Zoological Club* **16:** 5–9.

DUNN, E. R. 1939. Zoological results of the George Vanderbilt South Pacific Expedition of 1937. Part III—The lizards of Malpelo Island, Colombia. *Notulae Naturae* **4:** 1–3.

DUNN, E. R. 1944. The lizard genus *Phenacosaurus*. *Caldasia* **3:** 57–62.

ESTES, R., K. DE QUEIROZ, AND J. GAUTHIER. 1988. Phylogenetic relationships within Squamata, pp. 119–281. *In* R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families—Essays Commemorating Charles L. Camp*. Stanford, California: Stanford Univ. Press.

ETHERIDGE, R. 1959. The relationships of the Anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. Ph.D. Thesis. Ann Arbor, Michigan: Univ. of Michigan.

ETHERIDGE, R., AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae, pp. 283–367. *In* R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families—Essays Commemorating Charles L. Camp*. Stanford, California: Stanford Univ. Press.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

FINDEN, C. R., AND A. D. GORDON. 1985. Obtaining common pruned trees. *Journal of Classification* **2:** 255–276.

FISHER, R. A. 1930. The moments of the distribution for normal samples of measures of departure from normality. *Proceedings of the Royal Society A*, **130:** 16–28.

FROST, D. R., AND R. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Miscellaneous Publications University of Kansas Natural History Museum* **81:** 1–65.

GIANNASI, N., R. S. THORPE, AND A. MALHOTRA. 2000. A phylogenetic analysis of body size evolution in the *Anolis roquet* group (Sauria: Iguanidae): character displacement or size assortment? *Molecular Ecology* **9:** 193–202.

GLOR, R. E., J. J. KOLBE, R. POWELL, A. LARSON, AND J. B. LOSOS. 2003. Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). *Evolution* **57:** 2383–2397.

GORDON, A. D. 1980. On the assessment and comparison of classifications, pp. 149–160. *In* R. Tomassone (ed.), *Analyse de Donnees et Informatique*. Le Chesnay, France: INRIA.

GORMAN, G. C. 1968. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae). III. Comparative study of display behavior. *Breviora* **284:** 1–31.

GORMAN, G. C., AND L. ATKINS. 1967. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae). II. Comparative chromosome cytology. *Systematic Zoology* **16:** 137–143.

GORMAN, G. C., AND L. ATKINS. 1969. The zoogeography of Lesser Antillean *Anolis* lizards—an analysis based upon chromosomes and lactic dehydrogenases. *Bulletin of the Museum of Comparative Zoology* **138:** 53–80.

GORMAN, G. C., D. G. BUTH, M. SOULÉ, AND S. Y. YANG. 1980a. The relationships of the *Anolis cristatellus* group: electrophoretic analysis. *Journal of Herpetology* **14:** 269–278.

GORMAN, G. C., D. G. BUTH, M. SOULÉ, AND S. Y. YANG. 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies, pp. 626–642. *In* A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology*. Cambridge, Massachusetts: Museum of Comparative Zoology.

GORMAN, G. C., D. G. BUTH, AND J. S. WYLES. 1980b. *Anolis* lizards of the eastern Caribbean: a case study in evolution. III. A cladistic analysis of albumin immunological data, and the definitions of species groups. *Systematic Zoology* **29:** 143–158.

GORMAN, G. C., AND H. C. DESSAUER. 1965. Hemoglobin and transferring electrophoresis and relationships of island populations of *Anolis* lizards. *Science* **150:** 1454–1455.

GORMAN, G. C., AND H. C. DESSAUER. 1966. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae). I. Electrophoretic comparison

of blood proteins. *Comparative Biochemistry and Physiology* **19:** 845–853.

Gorman, G. C., and Y. J. Kim. 1976. *Anolis* lizards of the eastern Caribbean: a case study in evolution. II. Genetic relationships and genetic variation of the *bimaculatus* group. *Systematic Zoology* **20:** 167–185.

Gorman, G. C., P. Licht, H. C. Dessauer, and J. O. Boos. 1971. Reproductive failure among the hybridizing *Anolis* lizards of Trinidad. *Systematic Zoology* **20:** 1–18.

Gorman, G. C., C. S. Lieb, and R. H. Harwood. 1984. The relationships of *Anolis gadovi*: albumin immunological evidence. *Caribbean Journal of Science* **20:** 145–152.

Gorman, G. C., and R. B. Stamm. 1975. The *Anolis* lizards of Mona, Redonda, and La Blanquilla: chromosomes, relationships, and natural history notes. *Journal of Herpetology* **9:** 197–205.

Gorman, G. C., R. Thomas, and L. Atkins. 1968. Intra- and interspecific chromosome variation in *Anolis cristatellus* and its closest relatives. *Breviora* **293:** 1–12.

Guyer, C., and J. M. Savage. 1987 [1986]. Cladistic relationships among anoles (Sauria: Iguanidae). *Systematic Zoology* **35:** 509–531.

Hillis, D. M. 1991. Discriminating between phylogenetic signal and random noise in DNA sequences, pp. 278–294. *In* M. M. Miyamoto and J. Cracraft (eds.), *Phylogenetic Analyses of DNA Sequences*. New York: Oxford Univ. Press.

Hillis, D. M., and J. P. Huelsenbeck. 1992. Signal, noise and reliability in molecular phylogenetic analyses. *Journal of Heredity* **83:** 189–195.

Huelsenbeck, J. P. 1991. Tree-length distribution skewness: an indicator of phylogenetic information. *Systematic Zoology* **40:** 257–270.

Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294:** 2310–2314.

Hulebak, E., S. Poe, R. Ibáñez, and E. E. Williams. 2007. A striking new species of *Anolis* lizard (Squamata, Iguania) from Panama. *Phyllomedusa* **6:** 5–10.

Jackman, T. R., D. J. Irschick, K. de Queiroz, J. B. Losos, and A. Larson. 2002. Molecular phylogenetic perspective on evolution of lizards of the *Anolis grahami* series. *Journal of Experimental Zoology* **294:** 1–16.

Jackman, T. R., A. Larson, K. de Queiroz, and J. B. Losos. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Systematic Biology* **48:** 254–285.

Kass, R. E., and A. E. Raftery. 1995. Bayes factors. *Journal of the American Statistical Association* **90:** 773–795.

Larget, B., and D. L. Simon. 1999. Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution* **16:** 750–759.

Larson, A. 1998. The comparison of morphological and molecular data in phylogenetic systematics, pp. 275–296. *In* R. DeSalle and B. Schierwater (eds.), *Molecular Approaches to Ecology and Evolution*. Basel, Switzerland: Birkhäuser Verlag.

Lazell, J. D., Jr. 1969. The genus *Phenacosaurus* (Sauria: Iguanidae). *Breviora* **325:** 1–24.

Lazell, J. D., Jr. 1972. The anoles (Sauria: Iguanidae) of the Lesser Antilles. *Bulletin of the Museum of Comparative Zoology* **143:** 1–115.

Lee, M. S. Y. 2000. Tree robustness and clade significance. *Systematic Biology* **49:** 829–836.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* **50:** 913–925.

Lewis, P. O., M. T. Holder, and K. E. Holsinger. 2005. Polytomies and Bayesian phylogenetic inference. *Systematic Biology* **54:** 241–253.

Losos, J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley and Los Angeles, California: Univ. of California Press.

Losos, J. B., M. L. Woolley, D. L. Mahler, O. Torres-Carvajal, K. E. Crandell, E. W. Schaad, A. E. Narváez, F. Ayala-Varela, and A. Herrel. 2012. Notes on the natural history of the little-known Ecuadorian horned anole, *Anolis proboscis*. Breviora **531**: 1–17.

Maddison, D. R., and W. P. Maddison. 2001. *MacClade: Analysis of Phylogeny and Character Evolution*. Version 4.03. Sunderland, Massachusetts: Sinauer Associates.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: A Modular System for Evolutionary Analysis. Version 2.75. Available from: http://mesquiteproject.org.

Myers, C. W., and M. A. Donnelly. 1996. A new herpetofauna from Cerro Yaví, Venezuela: first results of the Robert G. Goelet American Museum—TERRAMAR expedition to the northwestern Tepuis. *American Museum Novitates* **3172:** 1–56.

Myers, C. W., E. E. Williams, and R. W. McDiarmid. 1993. A new anoline lizard (*Phenacosaurus*) from the highland of Cerro de la Neblina, southern Venezuela. *American Museum Novitates* **3070:** 1–15.

Nicholson, K. E. 2002. Phylogenetic analysis and a test of the current infrageneric classification of *Norops* (Beta *Anolis*). *Herpetological Monographs* **16:** 93–120.

Nicholson, K. E., R. E. Glor, J. J. Kolbe, A. Larson, S. B. Hedges, and J. B. Losos. 2005. Mainland colonization by island lizards. *Journal of Biogeography* **32:** 929–938.

Pagel, M., and A. Meade. 2005. Mixture models in phylogenetic inference, pp. 121–139. *In* O. Gascuel (ed.), *Mathematics of Evolution and Phylogeny*. Oxford: Oxford Univ. Press.

Peters, J. A. 1964. *Dictionary of Herpetology: A Brief and Meaningful Definition of Words and Terms Used in Herpetology*. New York: Hafner VII.

PETERS, J. A., AND V. G. ORCES. 1956. A third leaf-nosed species of the lizard genus *Anolis* from South America. *Breviora* **62:** 1–8.

POE, S. 1998. Skull characters and the cladistic relationships of the Hispaniolan dwarf twig *Anolis*. *Herpetological Monographs* **12:** 192–236.

POE, S. 2004. Phylogeny of anoles. *Herpetological Monographs* **18:** 37–89.

POE, S. 2005. A study of the utility of convergent characters for phylogeny reconstruction: do ecomorphological characters track evolutionary history in *Anolis* lizards? *Zoology* **108:** 337–343.

POE, S., F. AYALA, I. M. LATELLA, T. L. KENNEDY, J. A. CHRISTENSEN, L. N. GRAY, N. J. BLEA, B. M. ARMIJO, AND E. W. SCHAAD. 2012. Morphology, phylogeny, and behavior of *Anolis proboscis*. *Breviora* **530:** 1–11.

POE, S., AND R. IBÁÑEZ. 2007. A new species of *Anolis* lizard from the cordillera de Talamanca of western Panama. *Journal of Herpetology* **41:** 263–270.

POE, S., I. M. LATELLA, M. J. RYAN, AND E. W. SCHAAD. 2009a. A new species of *Anolis* lizard (Squamata, Iguania) from Panama. *Phyllomedusa* **8:** 81–87.

POE, S., J. VELASCO, K. MIYATA, AND E. E. WILLIAMS. 2009b. Descriptions of two nomen nudum species of *Anolis* lizard from northwestern South America. *Breviora* **516:** 1–16.

POE, S., AND C. YAÑEZ-MIRANDA. 2007. A new species of phenacosaur *Anolis* from Peru. *Herpetologica* **63:** 219–223.

POE, S., AND C. YAÑEZ-MIRANDA. 2008. Another new species of green *Anolis* (Squamata: Iguania) from the eastern Andes of Peru. *Journal of Herpetology* **42:** 564–571.

POE, S., C. YAÑEZ-MIRANDA, AND E. LEHR. 2008. Notes on variation in *Anolis boettgeri* Boulenger 1911, assessment of the status of *Anolis albimaculatus* Henle and Ehlr 1991, and description of a new species of *Anolis* (Squamata: Iguania) similar to *Anolis boettgeri*. *Journal of Herpetology* **42:** 251–259.

POSADA, J. L., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. Version 3.7 (June 2005). *Bioinformatics* **14:** 817–818.

RODRIGUES, M. T. 1988. A new anole of the *punctatus* group from central Amazonia (Sauria: Iguanidae). *Papéis Avulsos de Zoologia* **36:** 333–336.

RODRIGUES, M. T., V. XAVIER, G. SKUK, AND D. PAVAN. 2002. New specimens of *Anolis phyllorhinus* (Squamata, Polychrotidae): the first female of the species and of proboscid anoles. *Papéis Avulsos De Zoologia* **42:** 363–380.

RONQUIST, F., AND J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

RUEDA, J. V., AND J. I. HERNÁNDEZ CAMACHO. 1988. *Phenacosaurus inderenae* (Sauria: Iguanidae), nueva especie gigante, proveniente de la cordillera oriental de Colombia. *Trianea* **2:** 339–350.

RUEDA ALMONACID, J. V. 1989. Un nuevo y extraordinario saurio de color rojo (*Iguanidae: Anolis*) para la Cordillera Occidental de Colombia. *Trianea* **3:** 85–92.

SAVAGE, J. M. 2002. *The Amphibians and Reptiles of Costa Rica. Herpetofauna between Two Continents, between Two Seas*. Chicago: Univ. of Chicago Press.

SAVAGE, J. M., AND C. GUYER. 1989. Infrageneric classification and species composition of the anole genera, *Anolis, Ctenonotus, Dactyloa, Norops,* and *Semiurus* (Sauria: Iguanidae). *Amphibia-Reptilia* **10:** 105–116.

SAVAGE, J. M., AND J. J. TALBOT. 1978. The giant anoline lizards of Costa Rica and western Panama. *Copeia* **1978:** 480–492.

SCHNEIDER, C. J., J. B. LOSOS, AND K. DE QUEIROZ. 2001. Evolutionary relationships of the *Anolis bimaculatus* group from the northern Lesser Antilles. *Journal of Herpetology* **35:** 1–12.

SCHOENER, T. W. 1969. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Systematic Zoology* **18:** 386–401.

SHOCHAT, D., AND H. C. DESSAUER. 1981. Comparative study of albumins of *Anolis* lizards of the Caribbean islands. *Comparative Biochemistry and Physiology* **68A:** 67–73.

SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. 3rd ed. San Francisco: W.H. Freeman.

SPENCER, M. A., AND G. S. SPENCER. 1993. MacMorph Image Analysis Software, Version 2.1. Stony Brook, New York.

SUZUKI, Y., G. V. GLAZKO, AND M. NEI. 2002. Overcredibility of molecular phylogenies obtained by Bayesian phylogenetics. *Proceedings of the National Academy of Science* **99:** 16138–16143.

SWOFFORD, D. L. 1991. When are phylogeny estimates from molecular and morphological data incongruent? pp. 295–333. *In* M. M. Miyamoto and J. Cracraft (eds.), *Phylogenetic Analysis of DNA Sequences*. New York: Oxford Univ. Press.

SWOFFORD, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (* and Other Methods)*. Version 4. Sunderland, Massachusetts: Sinauer Associates.

SWOFFORD, D. L., AND S. H. BERLOCHER. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. *Systematic Zoology* **36:** 293–325.

TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. *Evolution* **37:** 221–244.

THIELE, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* **9:** 275–304.

TORRES-CARVAJAL, O. 2007. Phylogeny and biogeography of a large radiation of Andean lizards (Iguania, *Stenocercus*). *Zoologica Scripta* **36:** 311–326.

UETZ, P. (ED.) [Internet]. The Reptile Database [cited 2012 Mar 10]. Available from: http://www.reptile-database.org/.

UGUETO, G. N., G. RIVAS, T. BARROS, AND E. N. SMITH. 2009. A revision of the Venezuelan anoles II: redescription of *Anolis squamulatus* Peters 1863

and *Anolis tigrinus* Peters 1863 (Reptilia: Polychrotidae). *Caribbean Journal of Science* **45:** 30–51.

Ugueto, G. N., G. Rivas-Fuenmayor, T. Barros, S. J. Sánchez-Pacheco, and J. E. García-Pérez. 2007. A revision of the Venezuelan Anoles I: a new *Anolis* species from the Andes of Venezuela with the redescription of *Anolis jacare* Boulenger 1903 (Reptilia: Polychrotidae) and the clarification of the status of *Anolis nigropunctatus* Williams 1974. *Zootaxa* **1501:** 1–30.

Underwood, G. 1959. The anoles of the eastern Caribbean (Sauria, Iguanidae): revisionary notes. *Bulletin of the Museum of Comparative Zoology* **121(part III):** 191–226.

Velasco, J. A., P. D. A. Gutiérrez-Cárdenas, and A. Quintero-Angel. 2010. A new species of *Anolis* of the *aequatorialis* group (Squamata: Iguania) from the central Andes of Colombia. *Herpetological Journal* **20:** 231–236.

Wiens, J. J. 1995. Polymorphic characters in phylogenetic systematics. *Systematic Biology* **44:** 482–500.

Wiens, J. J. 1998. Testing phylogenetic methods with tree congruence: phylogenetic analysis of polymorphic morphological characters in phrynosomatid lizards. *Systematic Biology* **47:** 427–444.

Wiens, J. J. 2000. Coding morphological variation within species and higher taxa for phylogenetic analysis, pp. 115–145. *In* J. J. Wiens (ed.), *Phylogenetic Analysis of Morphological Data*. Washington, DC: Smithsonian Institution Press.

Wiens, J. J. 2001. Character analysis in morphological phylogenetics: problems and solutions. *Systematic Biology* **50:** 689–699.

Wiens, J. J., and M. R. Servedio. 1997. Accuracy of phylogenetic analysis including and excluding polymorphic characters. *Systematic Biology*, **46:** 332–345.

Williams, E. E. 1965. South American *Anolis* (Sauria, Iguanidae): two new species of the *punctatus* group. *Breviora* **233:** 1–15.

Williams, E. E. 1974. South American *Anolis*: three new species related to *Anolis nigrolineatus* and *A. dissimilis*. *Breviora* **422:** 1–15.

Williams, E. E. 1975. South American *Anolis*: *Anolis parilis*, new species, near *A. mirus* Williams. *Breviora* **434:** 1–8.

Williams, E. E. 1976a. West Indian anoles: a taxonomic and evolutionary summary. 1. Introduction and a species list. *Breviora* **440:** 1–21.

Williams, E. E. 1976b. South American anoles: the species groups. *Papéis Avulsos de Zoologia* **29:** 259–268.

Williams, E. E. 1979. South American anoles: the species groups. 2. The proboscis anoles (*Anolis laevis* group). *Breviora* **449:** 1–19.

Williams, E. E. 1982. Three new species of the *Anolis punctatus* complex from Amazonian and inter-Andean Colombia, with comments on the eastern members of the *punctatus* species group. *Breviora* **467:** 1–38.

Williams, E. E. 1985. New or problematic *Anolis* from Colombia. IV. *Anolis antioquiae*, new species of the *Anolis eulaemus* subgroup from western Colombia. *Breviora* **482:** 1–9.

Williams, E. E. 1988. New or problematic *Anolis* from Colombia. V. *Anolis danieli*, a new species of the *latifrons* species group and a reassessment *Anolis apollinaris* Boulengeri, 1919. *Breviora* **489:** 1–25.

Williams, E. E. 1989. A critique of Guyer and Savage (1986): cladistic relationships among anoles (Sauria: Iguanidae): are the data available to reclassify anoles? pp. 434–478. *In* C. A. Woods (ed.), *Biogeography of the West Indies: Past, Present and Future*. Gainsville, Florida: Sandhill Crane Press.

Williams, E. E. 1992. New or problematic *Anolis* from Colombia. VII. *Anolis lamari*, a new anole from the cordillera oriental of Colombia, with a discussion of *tigrinus* and *punctatus* species groups boundaries. *Breviora* **495:** 1–24.

Williams, E. E., and N. Acosta B. 1996. *The* Anolis *Handlist*. Version 1.0b0. Cambridge, Massachusetts: Museum of Comparative Zoology.

Williams, E. E., and W. E. Duellman. 1967. *Anolis chocorum*, a new *punctatus*-like anole from Darien, Panama (Sauria, Iguanidae). *Breviora* **256:** 1–12.

Williams, E. E., and W. E. Duellman. 1984. *Anolis fitchi*, a new species of the *Anolis aequatorialis* group from Ecuador and Colombia, pp. 257–266. *In* R. A. Siegler, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag (eds.), *Vertebrate Ecology and Systematics—A Tribute to Henry S. Fitch*. Lawrence, Kansas: University of Kansas, Museum of Natural History Special Publication No. 10.

Williams, E. E., and R. Mittermeier. 1991. A Peruvian phenacosaur (Squamata: Iguania). *Breviora* **492:** 1–16.

Williams, E. E., M. J. Praderio, and S. Gorzula. 1996. A phenacosaur from Chimantá Tepui, Venezuela. *Breviora* **506:** 1–15.

Williams, E. E., H. Rand, A. S. Rand, and R. J. O'Hara. 1995. A computer approach to the comparison and identification of species in difficult taxonomic groups. *Breviora* **502:** 1–47.

Yánez-Muñoz, M. H., M. A. Urgilés, M. Altamirano-Benavides, and S. R. Cáceres. 2010. Redescripción de *Anolis proboscis* Peters & Orcés (Reptilia: Polychrotidae), con el descubrimiento de las hembras de la especie y comentarios sobre su distribución y taxonomía. *Avances* **2:** B7–B15.

Yang, S. Y., M. Soulé, and G. C. Gorman. 1974. *Anolis* lizards of the eastern Caribbean: a case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. *Systematic Zoology* **23:** 387–399.

Zar, J. H. 1999. *Biostatistical Analysis*. 4th Ed. Upper Saddle River, New Jersey: Prentice Hall.