

## A Phylogenetic, Biogeographic, and Taxonomic study of all Extant Species of *Anolis* (Squamata; Iguanidae)

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Received 21 December 2015; reviews returned 9 October 2016; accepted 21 January 2017  
Associate Editor: Robb Brumfield

**Abstract.**—*Anolis* lizards (anoles) are textbook study organisms in evolution and ecology. Although several topics in evolutionary biology have been elucidated by the study of anoles, progress in some areas has been hampered by limited phylogenetic information on this group. Here, we present a phylogenetic analysis of all 379 extant species of *Anolis*, with new phylogenetic data for 139 species including new DNA data for 101 species. We use the resulting estimates as a basis for defining anole clade names under the principles of phylogenetic nomenclature and to examine the biogeographic history of anoles. Our new taxonomic treatment achieves the supposed advantages of recent subdivisions of anoles that employed ranked Linnaean-based nomenclature while avoiding the pitfalls of those approaches regarding artificial constraints imposed by ranks. Our biogeographic analyses demonstrate complexity in the dispersal history of anoles, including multiple crossings of the Isthmus of Panama, two invasions of the Caribbean, single invasions to Jamaica and Cuba, and a single evolutionary dispersal from the Caribbean to the mainland that resulted in substantial anole diversity. Our comprehensive phylogenetic estimate of anoles should prove useful for rigorous testing of many comparative evolutionary hypotheses. [Anoles; biogeography; lizards; Neotropics; phylogeny; taxonomy.]

*Anolis* is a well-studied, ecologically diverse, species-rich clade of Neotropical lizards. Anatomically, *Anolis* lizards (anoles) are characterized by expanded toepads that facilitate an arboreal lifestyle and a throat fan, or dewlap, used mainly in intraspecific signaling. Anoles occupy a diverse range of microhabitats with most species living on trees, bushes, or grasses, but some specializing on rocks, streams, or leaf litter. Communities of anoles range from up to 12 sympatric species (e.g., at Parque Omar Torrijos in Panama; Poe 2012) to solitary species. Behaviorally, all species are diurnal except for a few Caribbean forms that may be nocturnally active around artificial lighting (examples in Schwartz and Henderson 1991). The over 379 species of *Anolis* (see below) natively range from Florida south through Central America and the Caribbean to Bolivia, with naturalized populations as far as Asia.

*Anolis* lizards are model study organisms in ecology and evolution. They have been subjects of classic studies of community ecology (e.g., Williams 1983), ecomorphology (e.g., Collette 1961), communication (e.g., Rand and Williams 1970), character displacement (e.g., Schoener 1970), biogeography (e.g., Lazell 1972), adaptive radiation (e.g., Williams 1972), and competition (e.g., Pacala and Roughgarden 1982), to name just a few textbook examples. Recent authors have incorporated comparative methods and anole phylogeny into studies of these and other important topics in evolution and ecology (e.g., Losos et al. 1998; Nicholson et al. 2005; Ord and Martins 2006). Many evolutionary studies of *Anolis*

would have benefited from better phylogenies based on more comprehensive taxon sampling, particularly of mainland forms, and attempts at a comprehensive taxonomy have also been hampered by limited sampling. For instance, the best-sampled molecular phylogenetic analysis of anoles to date (Gamble et al. 2014) included 216 (<57% of) species, the most recent comparison of mainland and island evolution in *Anolis* (Pinto et al. 2008) included 35 (<17% of) mainland species, and the most recent attempt at a comprehensive taxonomy of anoles (Nicholson et al. 2012) analyzed 240 (<63% of) species.

Etheridge's (1959) landmark study of skeletal morphology was the first large-scale phylogenetic analysis of anoles. This work erected informal groups ranked as "sections" and "series", which were elaborated upon (e.g., by the addition of "species groups") in Williams' (1976a,b) influential taxonomic treatments that were utilized by describers of species seeking pools for taxonomic comparison and evolutionary biologists seeking units for comparative study. Guyer and Savage (1992; preceded by Guyer and Savage 1986) erected new genera within *Anolis* based on a phylogenetic analysis of 27 species. The advent of molecular data brought reorganization of the Etheridge–Williams groups (e.g., Gorman 1973; Shochat and Dessauer 1981; Burnell and Hedges 1990), as well as molecular phylogenetic analyses of many subclades of *Anolis* (e.g., Gorman et al. 1983; Hedges and Burnell 1990; Creer et al. 2001; Schneider et al. 2001; Brandley and de Queiroz 2004; Glor et al. 2004; Castañeda and de Queiroz 2011).

Following the pioneering DNA sequence work of Jackman et al. (1999) and the combined-data study of Poe (2004), the most recent large-scale phylogenetic work (Alföldi et al. 2011; Nicholson et al. 2012; Gamble et al. 2014) has added taxa and data to build on the Etheridge–Williams framework.

Progress in anole phylogeny sometimes has been overshadowed by controversy regarding the taxonomy of anoles (e.g., Guyer and Savage 1986, 1992; Cannatella and de Queiroz 1989; Williams 1989; Nicholson et al. 2012, 2014; Poe 2013). Disagreements in anole taxonomy owe largely to differences among authors concerning the clade or clades to which the Linnaean rank of genus is to be assigned. Because traditional nomenclature is based on taxonomic ranks, those differences have created major discrepancies in the names applied to various anole clades despite considerable agreement regarding their composition and phylogenetic relationships. Consequently, debates have tended to focus on the scientifically meaningless question of how many genera ought to be recognized, thus diverting attention from scientifically germane disagreements concerning the relationships of anole species and the composition of anole clades.

In an attempt to rectify this and similar counterproductive situations in taxonomies throughout the tree of life some systematic biologists have been developing a tree-based approach to biological nomenclature in which taxon names are tied explicitly and directly to clades (e.g., de Queiroz and Gauthier 1990, 1992; Cantino and de Queiroz 2014). By contrast, the traditional, rank-based system does not necessarily tie names to clades, and even when it does, the connection is indirect and tenuous. The tree-focused approach also has the advantage of producing taxonomies with higher information content, because the named clades are not restricted to a particular taxonomic level (in this case, the genus). That is, instead of the names all being applied to mutually exclusive clades (as would be the case with genera), they can be applied to both nested and mutually exclusive clades. Although the tree-based approach has been adopted for some subclades of anoles (Nicholson 2002; Brandley and de Queiroz 2004; Castañeda and de Queiroz 2013), it has not yet been applied across the entire anole clade.

As with taxonomy, rigorous biogeographic treatments of anoles mainly have been confined to subgroups of the clade, with a focus on Caribbean forms (e.g., Brandley and de Queiroz 2004; Glor et al. 2005; Klutsch et al. 2007; Rodríguez-Robles et al. 2007; see Phillips et al. 2015 for a mainland example). Larger-scale treatments have examined general Caribbean patterns (Alföldi et al. 2011; Helmus et al. 2014) or specific biogeographic hypotheses (e.g., the “back-invasion” of the mainland; Nicholson et al. 2005). The one quantitative attempt at describing overall *Anolis* biogeographic history (Nicholson et al. 2012) likely suffers from gross overestimation of the age of the *Anolis* clade (see Townsend et al. 2011; Mulcahy et al. 2012; Prates et al. 2015; and below).

Nevertheless, that work erected testable hypotheses that may be assessed with more realistic dating. Here, we test several biogeographic hypotheses to explain the present-day distribution of *Anolis* in the Neotropics. In particular, we examine the following historical events: timing and ancestral area of the most recent common ancestor of anoles; timing and frequency of transitions of anole lineages between areas (including mainland and islands, and among islands); timing of biotic exchange of anole lineages between Middle America and South America; existence of “sources” or “sinks” for anole diversity.

The goals of this work are to estimate the phylogeny of all 379 species of *Anolis* and use this estimate to describe the biogeographic history of the clade and erect a new phylogenetic taxonomy of anoles.

## MATERIALS AND METHODS

### *Taxon Sampling*

We endeavored to include all valid species of *Anolis* as of 1 June 2014 in our analysis. Supplementary Appendix S1 (available on Dryad at <http://dx.doi.org/10.5061/dryad.s80jq>) lists our judgements of species status for forms included here; this approach resulted in 379 species included for phylogenetic analysis. We included the following outgroups: *Basiliscus plumifrons*, *Polychrus marmoratus*, *Pristidactylus scapulatus*, *Urostrophus gallardoi*. These were selected based on maximizing available data for close relatives of *Anolis* (e.g., Pyron et al. 2013).

### *Data*

We obtained DNA sequence data (varying coverage of mitochondrial genes ND2 and COI and the nuclear exon that codes for endothelin-converting enzyme-like 1 [ECE1]) for 101 species of *Anolis* not previously scored for DNA and combined these with published DNA data (e.g., Jackman et al. 1999; Castañeda and de Queiroz 2011; Alföldi et al. 2011) to produce a matrix with varying taxonomic coverage of 24,879 sites across 50 loci for 317 species. Appendix 1 shows gene coverage for each species. Supplementary Appendix S2 gives specimen vouchers and genes for DNA data new to this article. Sanger sequencing was done in the labs of SP, AN, GK, and OT, and by the Barcode of Life Initiative ([www.barcodeoflife.com](http://www.barcodeoflife.com)). Alignments of our newly generated sequence data (ECE1, ND2, COI) were performed using Muscle in Mega (Tamura et al. 2011) and checked and improved with reference to codon position, previous alignments of these genes in *Anolis* (e.g., Jackman et al. 1999), and the published *Anolis* genome (Alföldi et al. 2011). Alföldi et al.'s (2011) alignment was used for their data, except that we aligned

16S ourselves after adding additional sequences from Genbank.

We collected new morphological data for 144 species not previously scored for morphology and combined these with published data to produce a morphological phylogenetic matrix of 46 characters (Appendix 2) for all 379 species of *Anolis*. Supplemental Appendix S3 describes our codings for species for which we were unable to examine specimens.

### Phylogenetics

Phylogenetic matrices such as ours that include large numbers of terminals and diverse kinds of data are not straightforward to analyze. In particular, the intent to integrate ordered and unordered multistate morphological data with GTR-modeled DNA data greatly restricts the available approaches and computer programs for analysis. Here, we use Bayesian phylogenetic analysis of our combined matrix implemented in MrBayes version 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012; Suchard and Huelsenbeck 2012). This approach allows integration of complex morphological datasets with model-averaging of GTR-class models for DNA datasets (Huelsenbeck et al. 2004).

We used Partitionfinder (Lanfear et al. 2012) to select an optimal partitioning scheme for the DNA data according to the Bayesian Information Criterion under Partitionfinder's "greedy" algorithm. We hypothesized separate models for each codon position for the well-sampled mitochondrial genes (ND2, COI) and for each entire gene for the 48 other analyzed genes. Because MrBayes allows model-averaging across the entire GTR model space ("nst=mixed"), there is little reason to designate particular GTR-class models in comparison of partitioning schemes. Therefore, we compared only GTR versus GTR+G models and ignored GTR-class submodels (e.g., HKY, F81) for each partition in Partitionfinder. We agree with previous authors (e.g., Stamatakis 2006; Moyle et al. 2012) that the assumed benefit of adding an invariant-sites parameter (i.e., "accounting for" gene regions that cannot change) does not outweigh the potential downsides (i.e., duplication of the function of the rate heterogeneity parameter; parameter interaction; overparameterization) and therefore excluded invariant-sites models from consideration.

The 46 morphological characters (Appendix 2) were analyzed with the Standard model for informative characters ("coding=informative") including 42 ordered ("ctype:ordered") and four unordered (the default) characters and allowing gamma-distributed rate variation with six categories ("rates=gamma ngammacat=6"). Topology and branch lengths were linked across partitions and other parameters were unlinked.

Some of our analyses require a timetree so we employed a relaxed-clock approach allowing rate variation across lineages according to the independent

gamma rates model ("brlenspr=clock:uniform clockvarpr=igr") with *Urostrophus gallardoi* constrained as the outgroup in MrBayes.

We experimented extensively with MCMC parameter settings and settled on the following strategy: two concurrent runs of one cold and five heated chains with heating parameter  $T = 0.001$ , for 10 million generations, sampling every 1000 trees. We examined parameter estimates over generations using Tracer (Rambaut and Drummond 2007). We discarded the first 50% of sampled trees as burnin. MrBayes analyses were performed on the computers of the Cyberinfrastructure for Phylogenetic Research (CIPRES) Project. We present a majority-rule consensus of post burnin trees for taxonomic conclusions, and use two fully resolved trees selected from the post burnin sample for biogeographic and dating analyses: a maximum clade credibility tree (hereafter, MCC tree; Rambaut et al. 2014) and the tree with the minimal symmetric distance (Robinson and Foulds 1981) from the 50% majority rule consensus tree (hereafter, MRC tree). The topology of the MRC tree was also analyzed with BEAST (Drummond et al. 2012) to produce a third fully resolved tree for analysis (see below). The MrBayes NEXUS file of DNA and morphological data are in Supplemental Appendix S4.

### Biogeography

*Divergence times*—Divergence-time estimates were generated using a Bayesian approach in BEAST v. 1.8.1 (Drummond et al. 2012). We fixed the tree topology as the MRC tree and pruned species not scored for at least one gene (i.e., species scored only for morphology). We applied an uncorrelated log-normal relaxed-clock model to the DNA data using the same DNA partitioning scheme discussed above and two fossil calibrations. The root of our tree was calibrated with the crown group pleurodont iguanian *Saichangurvel* (Conrad et al. 2007) from the late Campanian (70.6 ± 0.6 Mya) (Townsend et al. 2011). This fossil was used by Townsend et al. (2011) to constrain the crown of the Pleurodonta clade of the iguanian tree. We assigned this fossil point calibration to the root of our tree (anoles + outgroups) using a uniform distribution prior (70–72 mya). The second fossil calibration point was located in the most recent common ancestor (MRCA) of the *Anolis chlorocyanus* group (*A. aliniger*, *A. chlorocyanus*, *A. coelestinus*, *A. singularis*). We used a Dominican amber anole fossil assigned to this group (de Queiroz et al. 1998) with a minimum age of 23 mya. We also used a uniform prior distribution for this node based on stratigraphic information from the fossil (17–23 mya). Both fossil calibration points used in this study were placed conservatively at the crown of each clade. Analyses were performed on the CIPRES cluster, with two independent runs for 50 million generations sampling every 5000. We checked log files to assure stationarity in likelihood values and convergence using Tracer. We used 5 million generations as a burn-in period and generated a maximum clade credibility time

tree (hereafter, MRCT tree). We summarized posterior divergence date estimates for the most recent common ancestor of anoles and for regional trees in order to associate particular historical events (e.g., the uplift of the Andes) with anole divergence times.

*Biogeographic regions.*—We defined a set of 14 areas for biogeographic analyses based on the present-day distribution patterns of *Anolis* lizards and the geological history of the Middle and South American mainland and the Caribbean region (i.e., geological barriers and areas of endemism; Gregory-Wodzicki 2000; Losos 2011; Coates and Obando 1996; Supplementary Fig. S1). We follow previous workers on Middle America, South America and the Caribbean islands (Castoe et al. 2009; Santos et al. 2009; Antonelli et al. 2009; Daza et al. 2010) and use the following regions in our analysis: a) Lesser Antilles; b) Puerto Rico and satellite islands and banks; c) Cuba and satellite islands and banks plus Cayman islands; d) Hispaniola and satellite islands and banks; e) Jamaica; f) the Bahamas; g) small Caribbean islands (i.e., San Andres and Providencia islands and Swan islands); h) Nearctic from the Isthmus of Tehuantepec to the United States; i) Upper Central America from the Nicaraguan depression to the Isthmus of Tehuantepec; j) Lower Central America from the Panama Isthmus to the Nicaraguan depression; k) South American Chocó region encompassing Pacific lowlands from Colombia and Ecuador; l) Caribbean region and inter-Andean valleys in Colombia and northwestern Venezuela; m) Andes region from Venezuela to Bolivia, above 1000 m; n) Amazonia, including Orinoco and Amazon river basins. We assigned each species to one or more regions based on distributional records compiled from several sources (e.g., Nicholson et al. 2012; Velasco et al. 2015).

*Statistical biogeographic methods.*—Biogeographic analyses were performed using the *BioGeoBEARS* R package (Matzke 2013b) on the MCC tree and the MRC tree (i.e., including all taxa) and on the MRCT tree (i.e., on the dated tree including only those taxa scored for molecular data).

We performed two biogeographic reconstructions on the MRC tree and the MCC tree, one focused on the mainland and the other focused on the Caribbean. We performed separate reconstruction analyses rather than a single large analysis due to the computational complexity of performing likelihood reconstructions with a large number of areas as in this case (Matzke 2014). Because our exploratory analyses detected a low number of dispersal events between the mainland and Caribbean islands (see below), this strategy seems unlikely to have had a major effect on ancestral range estimates. For the analysis on the mainland areas, all Caribbean islands were merged into two discrete regions, a) Lesser Antilles and b) Greater Antilles plus the Bahamas and Cayman Islands. Thus, this first analysis was conducted on nine regions, including seven mainland and two Caribbean

regions. For the analysis focused on the Caribbean region, all mainland areas were merged into two regions, Middle America and South America. Thus, this second analysis included seven Caribbean and two mainland regions.

We performed an additional set of time-calibrated analyses on the MRCT tree. This tree is better sampled for Caribbean forms relative to mainland forms, so we used the Caribbean-focused coding discussed above. We performed an analysis where dispersal rate is assumed constant between all areas. This scenario constitutes a null biogeographic model that ignores the geological history of Caribbean landmasses and the land connections between islands. We also performed a time-stratified analysis based on the geological model from Iturralde-Vinent and MacPhee (1999; see also Iturralde-Vinent 2006). For this scenario, we penalized strongly against dispersal across water assigning a very low probability of traversal (almost zero;  $d = 0.001$ ) when landmasses were separated and a probability of 1 when landmasses were connected. We built cost dispersal matrices based on paleogeographical scenarios hypothesized by Iturralde-Vinent and MacPhee (1999; see also Iturralde-Vinent 2006) for five time periods as follows: (1) Early Eocene (55 Ma): all Caribbean landmasses were hypothesized to be separated at this time, so we penalized dispersal between islands, assigning dispersal probability of 0.01 for all transitions between land masses; (2) Late Eocene–Early Oligocene (35–33 Ma): during this narrow time frame all Greater Antilles except Jamaica were hypothesized to be connected as a single landmass (GAARlandia), which was connected to South America by the Aves Ridge; thus, we assigned a dispersal probability of 1 for all transitions between regions (Greater Antilles, Lesser Antilles, and South America) except transitions involving Jamaica; (3) Late Oligocene (27–25 Ma): Cuba was hypothesized to be fragmented in three landmasses, Hispaniola was divided into northern and southern islands with Southern Hispaniola being connected to Puerto Rico, and the Lesser Antilles were isolated; for this period, we assigned a dispersal probability of 1 to transitions between connected landmasses and 0.01 between separated landmasses; (4) Middle Miocene (16–14 Ma): Cuba remained fragmented, Hispaniola merged again but remained narrowly connected to Puerto Rico, and the Lesser Antilles were isolated; for this period, we assigned a dispersal probability of 0.01 between all landmasses; (5) Pliocene to present (5–0 Ma): current separation of landmasses is assumed; we set a dispersal probability to 0.01 between all islands. We compared the fit of null and time-stratified biogeographic models using the Akaike information criterion (AIC).

For each set of reconstructions, we conducted Dispersal–Extinction–Cladogenesis (DEC) analyses comparing models with and without a jump dispersal parameter  $J$  (Matzke 2014). We used our ancestral area reconstructions to estimate the number of dispersal events in and out of each biogeographic region. The counts allowed us to establish whether an area was a

relative sink (i.e., areas receiving immigrant lineages from other areas) or source (i.e., areas from which lineages dispersed to other areas) (Sedano and Burns 2010; Castroviejo-Fisher et al. 2014). We use the terms sink and source in a macroevolutionary context, as in Goldberg et al. (2005).

### Taxonomy

In the interest of developing a taxonomy of anoles that is stable with respect to taxonomic ranks but allows for appropriate changes in the hypothesized composition of taxa under new hypotheses about phylogenetic relationships, we apply the methods of phylogenetic nomenclature to the major clades of anoles. Specifically, we apply names to both nested and mutually exclusive anole clades using explicit phylogenetic definitions (e.g., de Queiroz and Gauthier 1990, 1992; Cantino and de Queiroz 2014). Our current selection of anole clades to name is subjective and based on traditionally recognized groups of anoles. We do not name every clade due to space constraints, and we do not name only well-supported clades because some poorly supported clades have recurred in several analyses and seem likely to withstand further scrutiny. In the interest of nomenclatural stability, we apply existing names to the clades with which they have the longest associations. However, because not all of the clades have existing names, and because some names have previously been applied to more than one clade, we resurrect four long-unused name and coin two new ones. For the purpose of assessing traditional use, we adopt a criterion similar to that adopted by the ICZN (1999) for maintaining prevailing use (Art. 23.9.1.2). That is, the name must have been applied to the taxon in question (judged on the basis of composition and diagnostic characters) in at least 25 works, published by at least 10 authors, in the immediately preceding 50 years, and encompassing a span of not less than 10 years. This approach corresponds roughly with treating the (formal) names recognized by Etheridge (1959), who is commonly considered to have initiated the modern era of anole systematics, as those having traditional use. The main exception is *Tropidodactylus*, which was recognized by Etheridge but does not meet all the criteria for traditional use.

### RESULTS

The Partitionfinder analysis suggested a 15-partition scheme for the 50 gene, 54 potential partition molecular data (Table 1). The MrBayes analysis took 138 h on the CIPRES XSEDE cluster (maximum allowed is 168 h). The average standard deviation of split frequencies (ASDSF) was 0.059. The two runs appear to have plateaued and converged on similar likelihoods (Supplementary Fig. S2), and MCC trees calculated separately for each run are nearly identical. These results are consistent with the idea that MCMC mixing was sufficient.

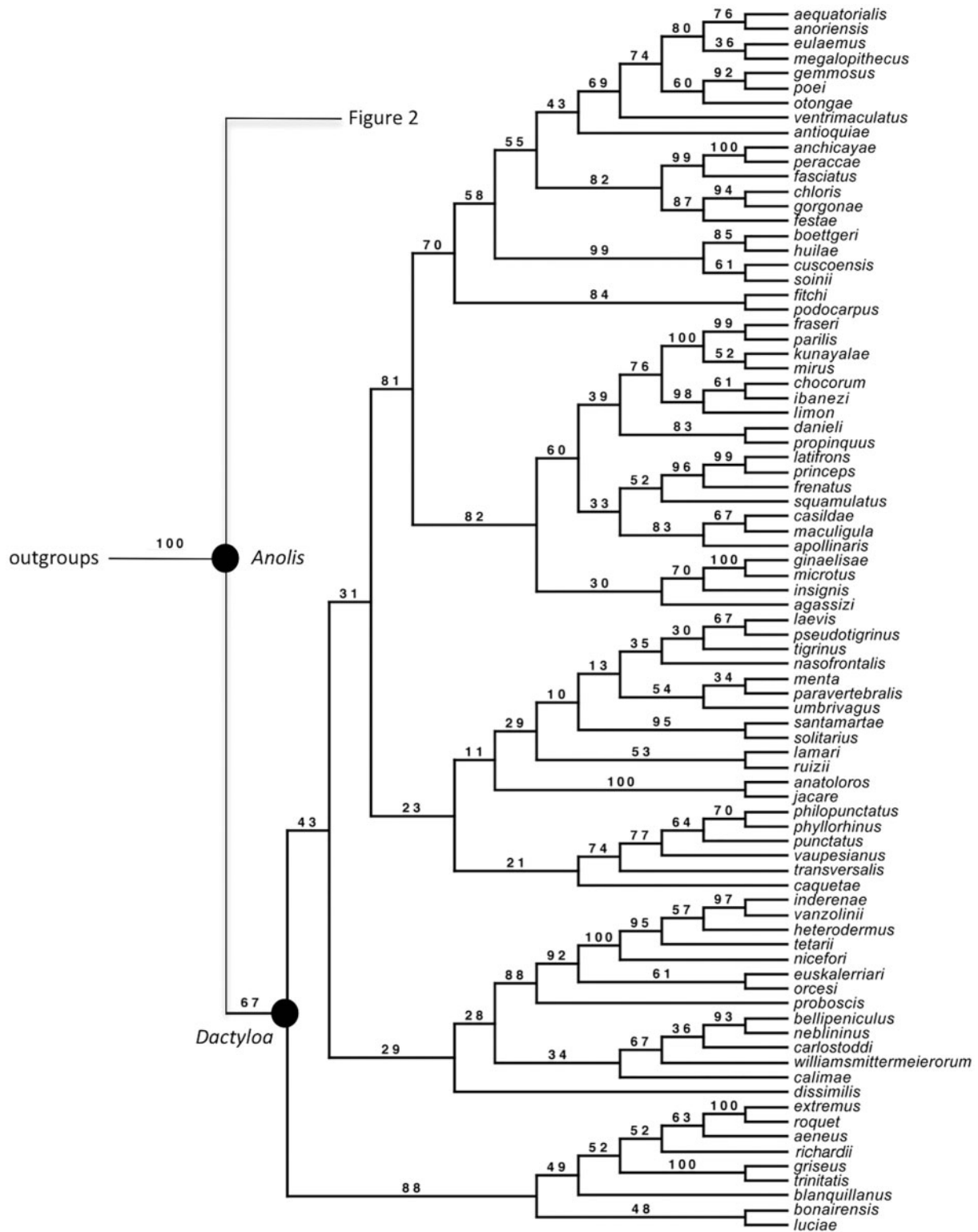
TABLE 1. Partitioning scheme estimated in Partitionfinder analysis

Partition	Model	Genes
1	GTR+G	COI position 1, KCNV2
2	GTR+G	COI position 2, unnamed # 146
3	GTR+G	COI position 3
4	GTR+G	ECEL1, HOXB1, KIF24
5	GTR+G	ND2 position 1
6	GTR+G	ND2 position 2
7	GTR+G	ND2 position 3
8	GTR+G	SOC55 12, PCDH10, FNIP2, KIAA2018, IRS2, RAPGEF2, unnamed # 50, unnamed # 57, TMTC4, RAG1
9	GTR+G	16S
10	GTR+G	unnamed # 127, ENSACAG00000014694, STRN4, PDE4D
11	GTR+G	ENSACAG00000011799, PDS5A, unnamed #183, PPP2R5C, SFRS18, unnamed # 59
12	GTR+G	FRYL, DHX15, KIAA, TLK2, TJP2, ATP2B1, unnamed # 53, TRPA1
13	GTR	unnamed #60
14	GTR+G	ELAVL2, unnamed #10, FBXW7, unnamed #152, GLRB, BNC2, NFIB, PTPRD
15	GTR+G	RXF3, EXPH5, "C10 or F71", BRCA1, unnamed #177

Note: "Unnamed" gene sequences refer to regions listed in Alföldi et al. (2011: Supplementary Table 20).

### Relationships

A majority-rule consensus (including additional compatible groupings) of post-burnin trees from the MrBayes analysis is shown in Figures 1–4. This tree depicts many relationships inferred in previous analyses (e.g., Etheridge 1959; Jackman et al. 1999; Alföldi et al. 2011). In particular, the overall structure of two predominantly mainland radiations, two Lesser Antillean clades, and multiple Greater Antillean radiations is evident. We consider our estimate to supersede previous attempts at reconstructing anole phylogeny due to our greater character and species sampling. Furthermore, comparison with earlier analyses is not straightforward in cases where taxonomic coverage differs. For these reasons, we do not make group-by-group comparisons with all previous studies, but instead mainly discuss previously recognized groups that bear on our formally named clades discussed below. We note that several well-supported small groups recognized by Etheridge (1959) and Williams (1976a,b) and subsequent authors were mostly or completely monophyletic (e.g., Beta anoles, *bimaculatus* series, *roquet* series, *crystalinus* series, *sagrei* series, *grahami* series), and that five of the eight genera of Nicholson et al. (2012) were corroborated as monophyletic. In the summary



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FIGURE 1. Consensus phylogenetic estimate for the *Dactyloa* clade of *Anolis* based on Bayesian analysis of morphological and DNA data. Numbers on clades are posterior probabilities  $\times 100$ .

below, we refer to named groups in Figures 1–4. The names of these groups are defined phylogenetically in Appendix 3.

A large clade of predominantly South American species (approximately equal to Etheridge’s [1959] *latifrons* series and Nicholson et al. [2012] *Dactyloa*) is

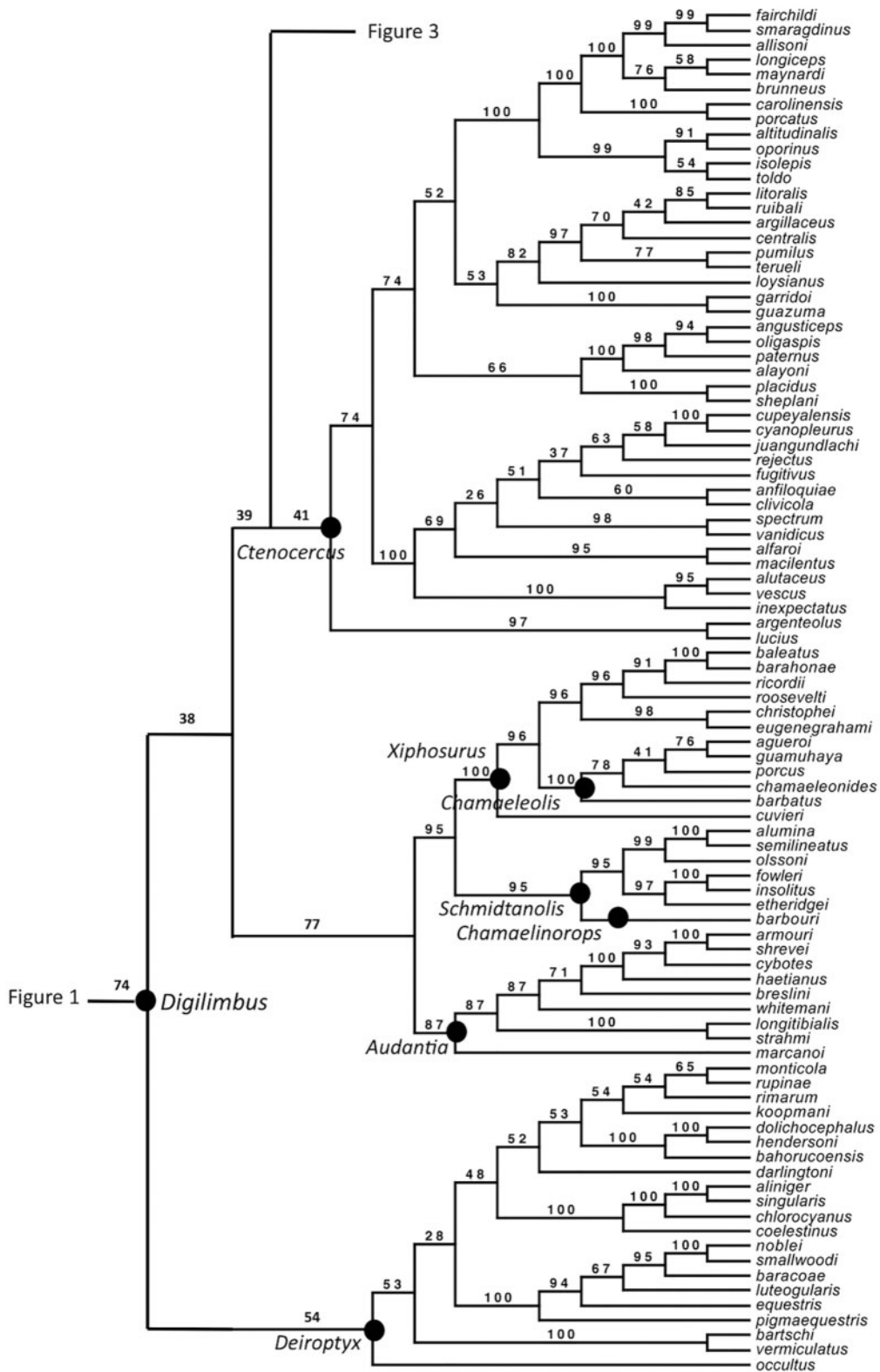


FIGURE 2. Consensus phylogenetic estimate for *Digilimbus* (minus *Ctenonotus* and *Norops*) clade of *Anolis* based on Bayesian analysis of morphological and DNA data. Numbers on clades are posterior probabilities  $\times$  100.

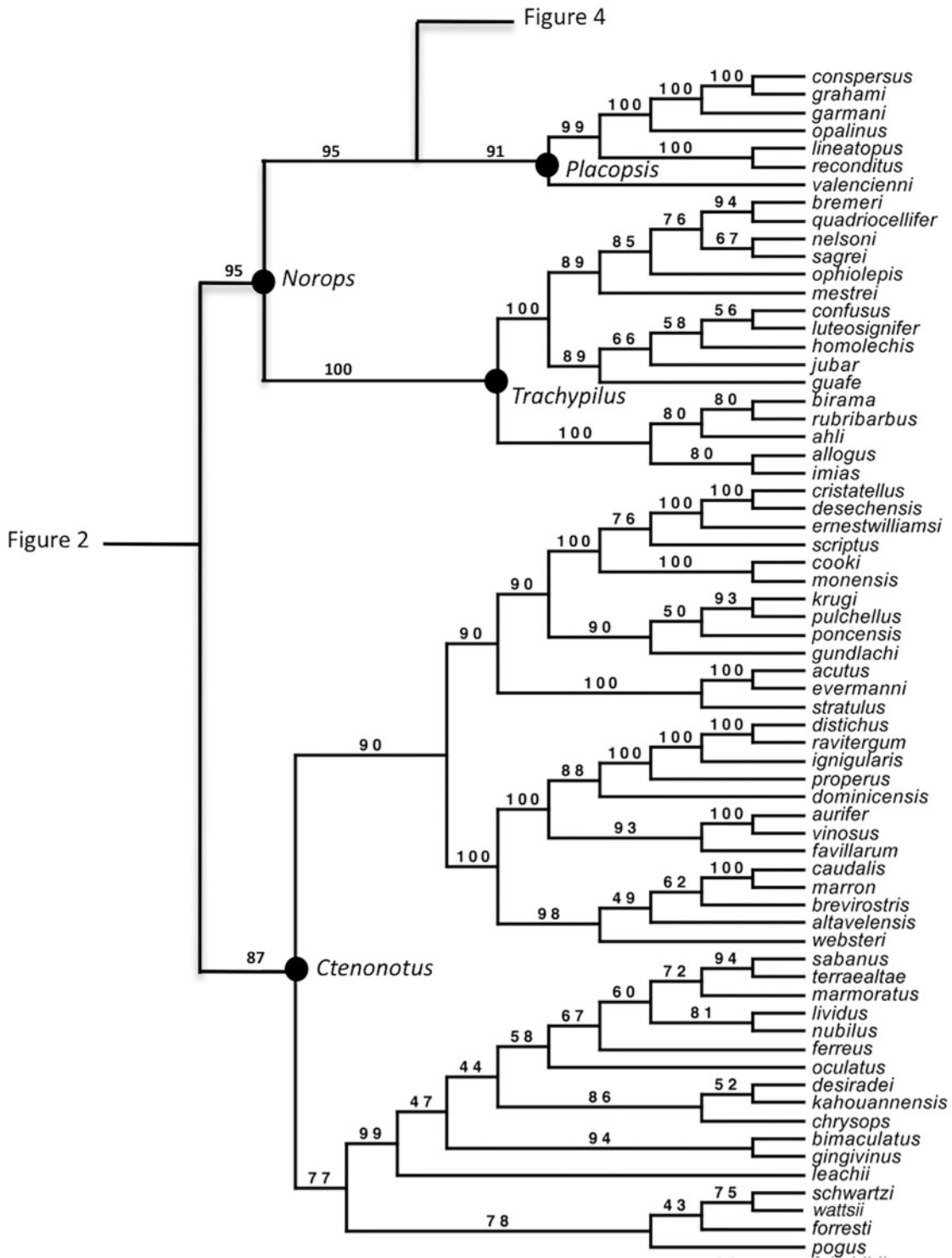


FIGURE 3. Consensus phylogenetic estimate for *Norops* (minus *Draconura*) and *Ctenonotus* clades of *Anolis* based on Bayesian analysis of morphological and DNA data. Numbers on clades are posterior probabilities  $\times 100$ .

sister to the rest of *Anolis* (Fig. 1). This *Dactyloa* clade includes lineages that extend north into the southern Lesser Antilles (members of the *roquet* series) and into Central America. Many of these species are large-bodied

with high numbers of toe lamellae. The clade includes great variation in head scale size with some species (e.g., species formerly recognized as *Phenacosaurus*) displaying as few as two scales across the snout whereas



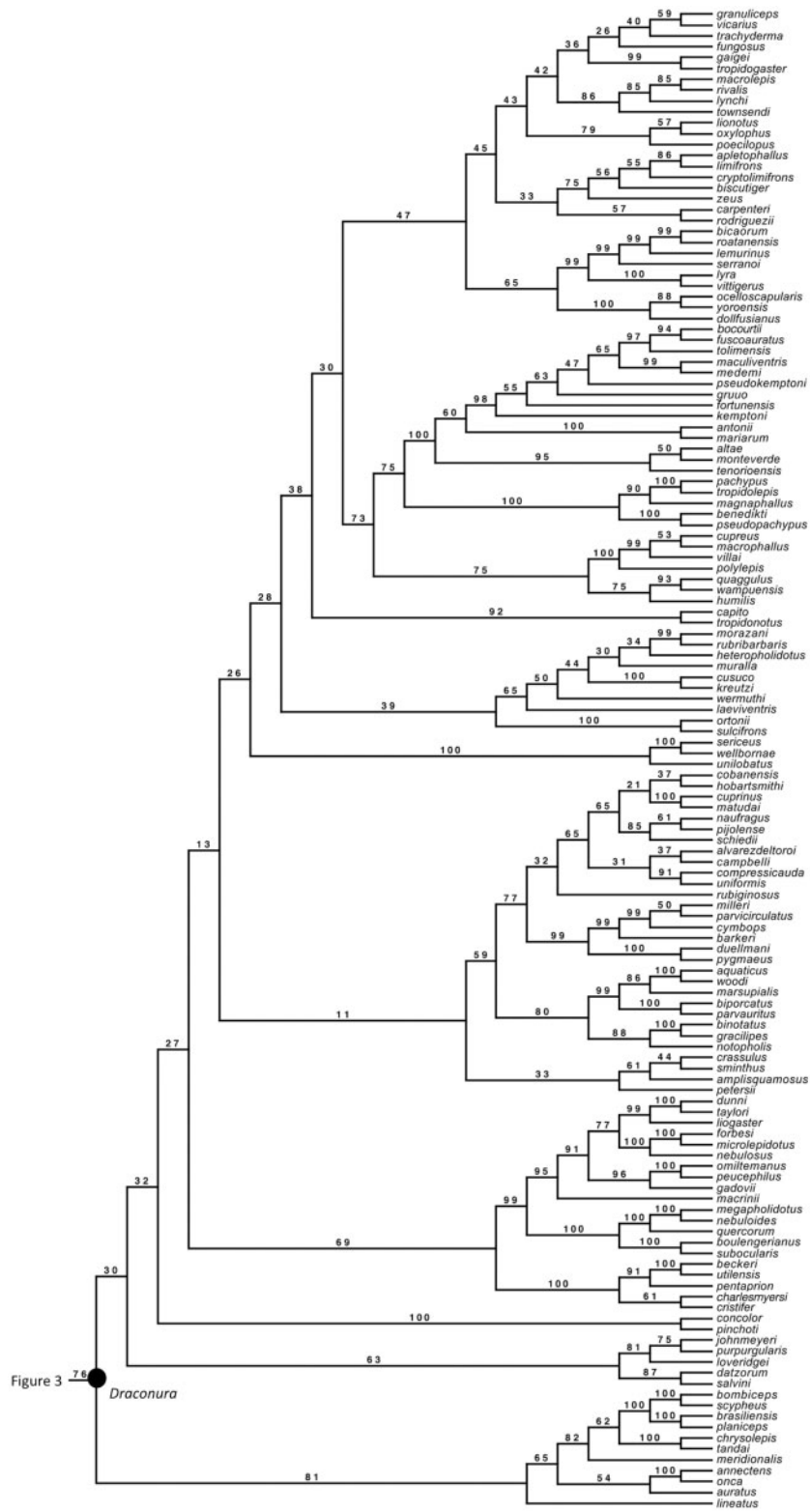


FIGURE 4. Consensus phylogenetic estimate for *Draconura* clade of *Anolis* based on Bayesian analysis of morphological and DNA data. Numbers on clades are posterior probabilities  $\times$  100.

TABLE 2. Comparison of DEC (Dispersal–Extinction–Cladogenesis) and DEC+J (Dispersal–Extinction–Cladogenesis plus jump dispersal) models of historical biogeography of *Anolis* lizards

Tree	Region	Model	LnL	P	d	e	j	AIC	dAICc	Weights
MCC tree	Mainland	DEC	–597.3	2.0	1.2	0.0	0.0	1198.6	38.1	0.0
		<b>DEC+J</b>	<b>–577.3</b>	<b>3.0</b>	<b>1.0</b>	<b>0.0</b>	<b>0.0</b>	<b>1160.5</b>	<b>0.0</b>	<b>1.0</b>
	Caribbean	DEC	–335.6	2.0	0.5	0.0	0.0	675.1	91.0	0.0
		<b>DEC+J</b>	<b>–289.1</b>	<b>3.0</b>	<b>0.3</b>	<b>0.0</b>	<b>0.0</b>	<b>584.1</b>	<b>0.0</b>	<b>1.0</b>
MRC tree	Mainland	DEC	–591.1	2.0	1.3	0.3	0.0	1186.1	36.2	0.0
		<b>DEC+J</b>	<b>–572.0</b>	<b>3.0</b>	<b>1.0</b>	<b>0.2</b>	<b>0.0</b>	<b>1149.9</b>	<b>0.0</b>	<b>1.0</b>
	Caribbean	DEC	–347.4	2.0	0.3	0.0	0.0	698.8	108.5	0.0
		<b>DEC+J</b>	<b>–292.1</b>	<b>3.0</b>	<b>0.3</b>	<b>0.1</b>	<b>0.0</b>	<b>590.3</b>	<b>0.0</b>	<b>1.0</b>

Notes: Ln: Ln likelihood; P: number of parameters; d: dispersal; e: extinction; j: jump-dispersal; AIC: Akaike Information Criterion; dAICc: delta AICc; weights: model weights. MCC tree: Maximum Clade Credibility tree from MrBayes analysis; MRC tree: Consensus-like tree from MrBayes analysis (see text). Mainland: refers to biogeographic analysis focused on continental areas. Caribbean: refers to biogeographic analysis focused on Caribbean areas. Best model in each comparison is highlighted in bold.

others (e.g., Williams' 1976b *aequatorialis* group) have more than 20.

Sister to the *Dactyloa* clade is the *Digilimbus* clade, which includes *Deiropyx* as sister to the remainder of *Anolis* (Fig. 2). *Deiropyx* is composed of the Cuban crown-giant anoles (e.g., *A. equestris*) as sister to a clade of Hispaniolan forms including *A. darlingtoni*, the Hispaniolan green anoles, and the *hendersoni* and *monticola* series of Williams (1976a). The dewlapless Cuban species *A. bartschi* and *A. vermiculatus* are sister to this clade, and the unusual Puerto Rican twig anole *A. occultus* is sister to the rest of *Deiropyx*.

Also within *Digilimbus*, a weakly supported clade includes five named groups as sister to a clade composed of *Ctenocercus*, *Ctenonotus*, and *Norops* (Fig. 2). This clade includes the cybotoid anoles (*Audantia*), the distinctive terrestrial form *Anolis* (*Chamaelinorops*) *barbouri*, and the grass-bush anoles (*Schmidtanolis*) from Hispaniola, as well as a clade of mostly large-bodied Greater Antillean anoles (*Xiphosurus*). The Cuban chamaeleon-like anoles (*Chamaeolis*) form a strongly supported clade within *Xiphosurus*.

*Ctenocercus* is an ecomorphologically diverse clade of predominantly Cuban species that is sister to *Ctenonotus* and the beta anoles (*Norops*) of Etheridge (1959) (Fig. 2). *Ctenocercus* includes mini-radiations of grass anoles (e.g., *Anolis alutaceus*), twig anoles (e.g., *A. angusticeps*), and green trunk-crown anoles (e.g., *A. carolinensis*), as well as the weakly supported placement (posterior probability 0.41) of Cuban *A. argenteolus* and *A. lucius* as sister to the remaining *Ctenocercus*.

*Ctenonotus* is a chromosomally diverse clade (Gorman 1973) that includes well supported Lesser Antillean (Williams' [1976a] *bimaculatus* series), Hispaniolan (*distichus* series), and Puerto Rican Bank (*cratatellus* series) subclades (Fig. 3). *Ctenonotus* anoles tend to be abundant and highly visible, and some are among the best-studied anole species (e.g., Rand 1964; Pacala and Roughgarden 1982; Losos 1990; Dobson et al. 1992; Hertz 1992; Fleishman et al. 1997).

Species of the *Norops* clade of "beta" anoles (Etheridge 1959) share the anatomical trait of anteriorly directed

transverse processes on the posterior caudal vertebrae (Figs. 3 and 4). This well-established clade includes three geographically coherent subclades. *Trachypilus* is a Cuban clade of species mainly belonging to the trunk-ground ecomorph. *Placopsis* is the Jamaican radiation of multiple ecomorphs. *Draconura* is a mainland radiation, with several forms that have become established on offshore islands (e.g., *A. townsendi*, *A. concolor*, *A. villai*). *Trachypilus* and *Placopsis* are very well-studied clades (e.g. Underwood and Williams 1959; Ruibal 1961; Bundy et al. 1987; Losos 1990; Jackman et al. 2002; Vanhooydonck et al. 2005; Knouft et al. 2006; Cádiz et al. 2013), whereas *Draconura* remains the proportionately least-known anole clade (but see, e.g., Andrews 1971; Fitch et al. 1976; Nicholson 2002; Vitt et al. 2002).

### Biogeography

*Biogeographic model selection and anole diversification.*—In all analyses, DEC+J models were favored over DEC models according to both AIC and model weights, suggesting that founder-event diversification has been prevalent during the anole radiation (Table 2). Furthermore, biogeographic models incorporating paleogeographic information were favored (Table 3). These biogeographic models incorporate information about historical connections between Caribbean landmasses by reducing dispersal probabilities between areas that were not connected over time. Several instances of founder-event diversification were inferred during the colonization of the Caribbean (Fig. 5; Supplementary Figs. S3–6). Divergence date estimates in our BEAST analysis (MRCT tree; Supplementary Fig. S6; Fig. 5) provided evidence of an origin of the anole radiation at the Paleocene–Eocene boundary (64.4–46.3 Ma). Posterior density plots summarizing divergence date estimates (Fig. 6) show that most cladogenetic events occurred during the Miocene (20–5 Ma). For South American clades, the majority of cladogenetic events seem not to be associated with Andean uplift (main Andean uplift events occurred between 10–3 Ma

TABLE 3. Comparison of DEC (Dispersal–Extinction–Cladogenesis) and DEC+J (Dispersal–Extinction–Cladogenesis plus jump dispersal) models of historical biogeography of *Anolis* using MRCT tree (BEAST version of MRC, consensus-like tree; see text) with focus on Caribbean areas

Type	Model	LnL	P	d	e	j	AIC	dAICc	Weights
Time stratified	DEC	–290.9	2.0	0.0	0.0	0.0	585.9	78.1	0.0
	<b>DEC+J</b>	<b>–250.9</b>	<b>3.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>507.8</b>	<b>0.0</b>	<b>1.0</b>
Null	DEC	–298.6	2.0	0.0	0.0	0.0	601.3	93.5	0.0
	<b>DEC+J</b>	<b>–260.5</b>	<b>3.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>527.0</b>	<b>19.2</b>	<b>0.0</b>

Notes: Null model assumes equal dispersal probability between islands or landmasses. Time stratified model allows differences in dispersal rates in the model formulation based on Caribbean paleogeographic models (Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2006; see main text for details). LnL: Ln likelihood; P: number of parameters; d: dispersal; e: extinction; j: jump-dispersal; AIC: Akaike Information Criterion; dAICc: delta AICc; weights: model weights. Best model in each comparison is highlighted in bold.

[Antonelli et al. 2009; Horn et al. 2010]). In contrast, most cladogenetic events for Middle American clades appear correlated with intense tectonic activity during the mid-Miocene (15–10 Ma) (Fig. 6; Castoe et al. 2009; Daza et al. 2010).

*Early evolution and mainland-island transitions.*—Analysis of the MRCT tree (Fig. 5) estimated a composite ancestral area for all *Anolis*. This estimate may be interpreted either as ambiguity or that the ancestor of all *Anolis* occupied a large area including Caribbean and South American regions. Other reconstructions using the full complement of taxa (MCC, MRC trees; Supplementary Figs. S3–6) identify South America as the origin of *Anolis*. If the anole ancestor was only present in South America, particularly the Amazonia region (Supplementary Figs. S4, S6), at least two dispersal events are necessary to explain the current distribution of Caribbean clades. The first dispersal event, to the Northern Caribbean, likely occurred during the Paleocene–Eocene boundary (42.4–61.7 Ma; Supplementary Fig. S7; Fig. 5). The timing of this event predates the emergence of the Aves ridge landbridge (Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2006). Thus, under this scenario, an overwater dispersal event likely explains the distribution of all Northern Caribbean clades (i.e., a jump dispersal event promoting founder-event diversification in the Caribbean *Digilimbus* clade). The second dispersal event is the invasion of the *roquet* series to the Lesser Antilles, which likely occurred near the Eocene–Oligocene boundary (23.9–40.1 Ma; Supplementary Fig. S7; Fig. 5) when the Aves Ridge is hypothesized to have been present.

All biogeographic reconstructions indicate a West Indian ancestry for the *Draconura* invasion of Middle America (Nicholson et al. 2005) with later dispersal to South America. One of the ancestral range estimates for *Draconura* inferred a scenario involving a dispersal event from Jamaica to Middle America, which would have occurred during the Eocene–Oligocene boundary (29.9–41 Ma; Fig. 5; Supplementary Fig. S7).

*Caribbean dispersal events.*—In the biogeographic models that included maximal taxonomic coverage and did not

incorporate geological information (i.e., MCC and MRC analyses) the ancestral range estimated for Caribbean *Anolis* was Hispaniola (Supplementary Figs. S3, S5). However, in the MRCT tree analysis (Fig. 5), the ancestral area was composite including Cuba and Hispaniola. This latter inference is consistent with ancestral Caribbean anole occupation of the composite area known as GAARlandia (Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2006). The MRCT tree indicated at least 18 transitions among Caribbean islands. Many biogeographic movements occurred when islands were connected as either GAARlandia or when Hispaniola was connected to Puerto Rico. Both Cuba and Hispaniola were major sources of Northern Caribbean anole lineages, with at least 12 dispersal events to other islands. Some Caribbean transitions were from Greater Antilles to small Caribbean islands (e.g., Bahamas and Cayman islands) and likely occurred across water. At least three dispersals are inferred to explain the anole diversity in each of Cuba, Hispaniola, and Puerto Rico. Excluding *A. sagrei*, which may not be native to Jamaica (Underwood and Williams 1959), a single overwater dispersal event explains current anole diversity in Jamaica (Supplementary Table S1).

*Faunal exchange through the Isthmus of Panama.*—From 18–20 crossings of the Isthmus of Panama were reconstructed (Supplementary Table S2). Depending on which tree is analyzed, we inferred more dispersal events from Middle America (MA) to South America (SA) than the reverse (MRC, MRCT trees), or an approximately equal number of MA to SA and SA to MA dispersals (MCC tree; Supplementary Table S2). Based on the MRCT tree, at least two dispersal events from MA to SA were very early (~30 Ma; Supplementary Fig. S7; Fig. 5), one for the smallest clade containing *Anolis auratus* and *A. brasiliensis* and another for the smallest clade containing *A. notopholis* and *A. gracilipes*. According to recent geological evidence, the emergence of the South–Middle American landbridge started between 25 and 23 Ma (Farris et al. 2011), and the final closure occurred by 10 Ma (Farris et al. 2011; Bacon et al. 2015). Other dispersal events inferred in the trees involved range expansions during the Miocene.

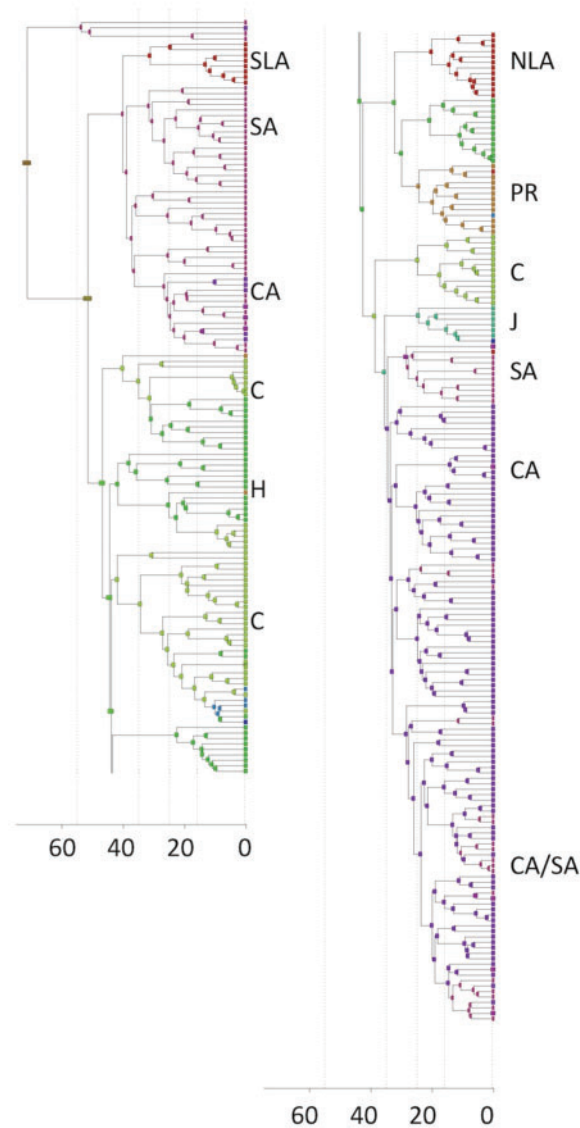


FIGURE 5. Biogeographical reconstruction for *Anolis* lizards with emphasis in Caribbean areas using the dated MRCT tree from MrBayes and BEAST analyses (see text). Vertical dotted lines represents the timing of paleogeographical reconstructions based on [Iturralde-Vinent and MacPhee \(1999\)](#); see also [Iturralde-Vinent 2006](#). Scale is millions of years. SLA = Southern Lesser Antilles; SA = South America; CA = Central America; C = Cuba; H = Hispaniola; NLA = Northern Lesser Antilles; PR = Puerto Rico; J = Jamaica.

*Dispersals among other mainland areas.*—Our mainland analyses estimated at least 77 dispersal events either as range expansions or long-distance events between mainland areas (Supplementary Table S3; Supplementary Figs. S4, S6). Dispersal events were estimated to occur evenly across the timespan of anole history. This result may indicate some constancy of dispersal rates, but we note that some very ancient dispersal events may not be inferred due to lineage extinction, which could bias the overall pattern to underestimate the relative rate of earlier dispersals. Mainland areas with the highest number of immigrations were Nearctic, Upper Central America,

Lower Central America and the Chocó. Invasions to these areas occurred in several instances and involved multiple clades. Upper Central America, Lower Central America, the Chocó and the Andes exhibited the highest number of lineage emigrations. Finally, the Caribbean coast of Colombia and Amazonia exhibited the highest number of dispersals into versus out of the area. In other words, anole diversity in these two areas is a combination of immigration of lineages from nearby regions and *in situ* speciation. In general, mainland areas can be characterized as both source and sink areas of faunal diversity (Supplementary Table S3).

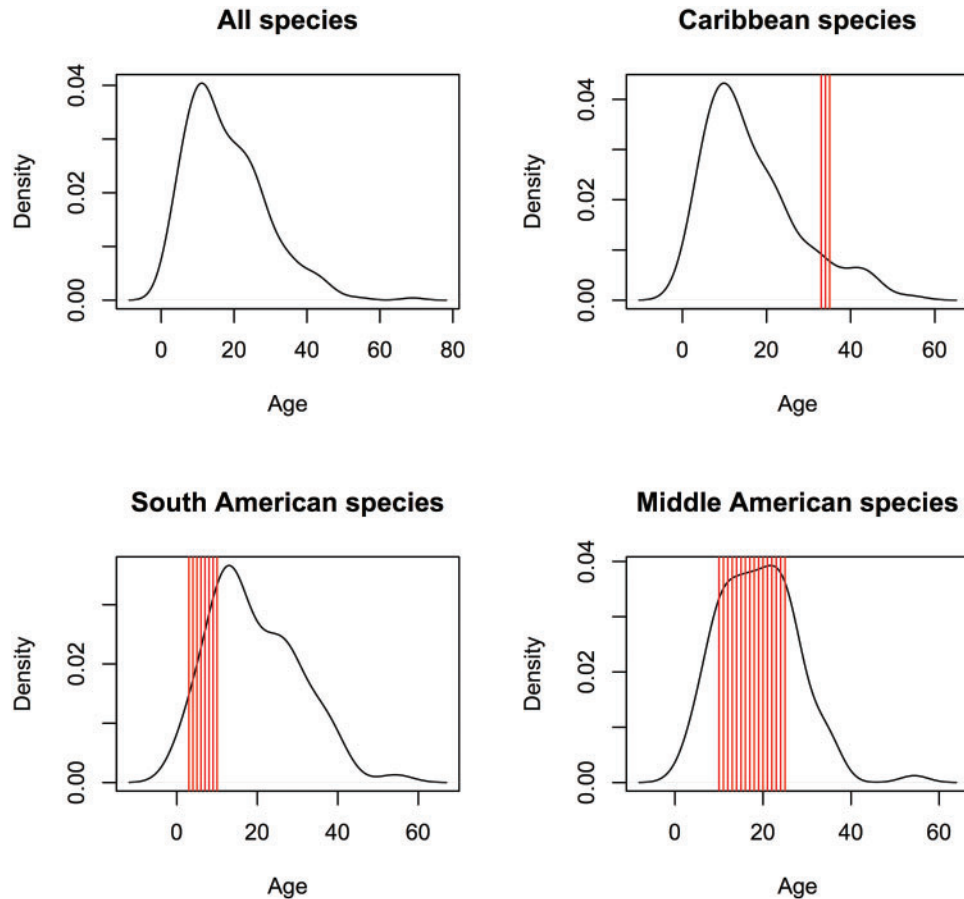


FIGURE 6. Posterior density plots of divergence times for *Anolis* based on the dated MRCT tree from MrBayes and BEAST analysis (see text). a) All species; b) only Caribbean species. The vertical lines represent the timing of the formation of the Aves Ridge; c) South American species. The vertical lines represent the timing of the Andean uplift in South America; d) Middle American species. The vertical lines represent the timing of the formation of the Isthmus of Panama.

## DISCUSSION

*Anolis* lizards are classic study organisms in evolution, physiology, and ecology. The phylogenetic estimate presented here should enable novel and more comprehensive comparative analyses of this well-studied clade. Many subjects that could be addressed only weakly or partially with limited sampling, such as mainland-Caribbean comparisons, comparative community evolution, and rates of speciation, may now be tested rigorously.

The outstanding aspect of our phylogenetic estimates is their completeness. Their principal fault is the weak support for many nodes, especially deep in the trees. Sixty-three percent of clades are supported at less than 95% probability in the comprehensive estimate (Figs. 1–4). We suggest this weak support is due to two factors. First, appropriately evolving nuclear genes have not yet been sufficiently taxonomically sampled to provide support for the deep splits in the anole tree (e.g., Appendix 1). Second, the matrix includes several taxa scored for only a few characters of external morphology (e.g., *Anolis vicarius*, *A. pseudotigrinus*) that are likely to be

weakly placed in the tree. It would be possible to improve support values by removing these taxa, as is sometimes done (e.g., Sanderson and Shaffer 2002; Moyle et al. 2012). For example, a RaxML (v 1.5, Stamatakis 2006) analysis of all DNA data including the 294 species scored for ND2 had only 41% of clades supported at less than 95% bootstrap (same partitioning scheme as above, “ML + thorough bootstrap” command; results not shown). But this practice obviously would result in a less comprehensive estimate of anole phylogeny and taxonomy, and accuracy might be reduced as well (see e.g., Gauthier et al. 1988). Most importantly, such an approach would guarantee an incomplete (i.e., inaccurate) biogeographic reconstruction for the anole clade, as transitions to areas of missing species might not be represented. For example, removal of poorly scored species *A. concolor* and *A. pinchoti* would preclude estimation of an important biogeographic event—the dispersal of the *Draconura* (i.e., mainland *Norops*) clade to oceanic Caribbean islands San Andres and Providencia, where these anoles are solitary endemic species.

Many inferred relationships in Figures 1–4 make sense in light of previous studies and expectations

based on morphology. Our phylogenetic estimates for much of the anole clade are heavily determined by previously published data, and our results for these well-studied forms are largely congruent with previous work on Caribbean (e.g., Jackman et al. 1999) and *Dactyloa* (e.g., Castañeda and de Queiroz 2011) anoles. But relationships of mainland beta anoles (*Draconura*; Fig. 4) were largely unknown before this study (see Nicholson [2002], Poe [2004], and Nicholson et al. [2012] for analyses including a few *Draconura*). *Draconura* relationships that are unsurprising include the monophyly of anoles similar to *Anolis fuscoauratus* (the clade spanning *A. tenorioensis* to *A. bocourtii* in Fig. 4), the monophyly of *tropidolepis*-like anoles (clade spanning *A. pachypus* to *A. pseudopachypus*), the geographic coherence of the Mexican forms (the *A. cobanensis* to *A. pygmaeus* clade and the *A. dunni* to *A. subocularis* clade), and the monophyly of anole species previously referred to or associated with *A. limifrons* (clade spanning *A. apletophallus* to *A. zeus*) and *A. lemurinus* (clade spanning *A. bicaorum* to *A. vittigerus*). Numerous smaller clades likewise reassuringly align with expectation (e.g., geographically proximal island forms *A. concolor*–*A. pinchoti*; South American semiaquatic anoles *A. macrolepis*–*A. rivalis*–*A. lynchi*; Central American semiaquatic anoles *A. lionotus*–*A. oxylophus*–*A. poecilopus*; formerly conspecific species pairs like *A. biporcatus*–*A. parvaauritus*, *A. tropidogaster*–*A. gaigei*, and *A. cupreus*–*A. macrophallus*). In spite of the limited data used to reconstruct these relationships, these groupings seem likely to withstand further scrutiny.

On the other hand, some novel *Draconura* results seem questionable given the degree of morphological convergence they entail. For example, the nonmonophyly of the *humilis* group (*Anolis humilis*, *A. compressicauda*, *A. marsupialis*, *A. notopholis*, *A. quaggulus*, *A. tropidonotus*, *A. uniformis*, *A. wampuensis*) is surprising. These species share a deep axillary pocket, strongly keeled dorsal and ventral scales, an enlarged band of middorsal scales, and leaf-litter habitat niche. Some members of this group that were found to be nonmonophyletic previously have been considered conspecific (e.g., *A. humilis* and *A. marsupialis*). Our data for most of these forms is mainly mitochondrial and morphological, and it is tempting to suspect a misleading mitochondrial signal or mishandled tissue. However, Phillips et al. (2015) found nonmonophyly of this group using greater sampling of individuals and a nuclear gene (ITS-1), so perhaps our estimate is correct. Another seemingly questionable result is the nonmonophyly of the *pentaprion* group (*A. beckeri*, *A. charlesmyersi*, *A. cristifer*, *A. fungosus*, *A. ortonii*, *A. pentaprion*, *A. salvini*, *A. sulcifrons*, *A. utilensis*). These species are distinguished from each other only subtly (e.g., Köhler 2010) and share an unusual pale lichenous coloration, short limbs, and large smooth headscales. The separate monophyly of South (*A. sulcifrons*, *A. ortonii*) and Central American *pentaprion* anoles shown in the tree is geographically reasonable, and *A. fungosus* (which seems out of place, if poorly supported, in a clade of nondescript brown

mainland anoles like *A. trachyderma* and *A. tropidogaster* [Fig. 4]) is unusual enough that few placements within *Draconura* seem completely implausible for this species. But the separation of *A. salvini*, which seems essentially to be a high elevation version of *A. pentaprion* (Myers 1971), from the other Central American *pentaprion* group anoles strains credibility. Similar to the *pentaprion* and *humilis* group anoles, the anoles similar to *A. laeivoventris* (*A. laeivoventris*, *A. cusuco*, *A. kreutzii*) are nearly indistinguishable from each other but they are not monophyletic in our trees. In this case, the result is likely due to limited character information for some “problem” taxa that are similar to the species of the *laeivoventris* group. We lack molecular data and possess only scant morphological data for species such as *A. wermuthi* that disrupt the monophyly of the *laeivoventris*-like forms, and we expect that more comprehensive scoring of these species will render the *laeivoventris*-like species monophyletic. Additional DNA data will illuminate all the unexpected results noted above. It will be interesting to see which of the surprising results in Figures 1–4 are “corrected” with additional data and which, if any, indicate convergence to the degree seen in the anoles of the Greater Antilles (see Losos et al. 1998).

#### Biogeography

In this study, we have provided the most comprehensive biogeographic analysis of anoles to date. Inclusion of all known *Anolis* species allowed elucidation of a complex biogeographic history that involved multiple vicariance and dispersal events. As in other neotropical lineages (Miller et al. 2008; Smith et al. 2014), both simple range expansions and long distance dispersals were found to be important aspects of diversification in anoles. The best supported DEC+J (dispersal–extinction–cladogenesis plus jump dispersal) models incorporated a series of range evolution models (Matzke 2013a, 2014) that allow distinction of biogeographic scenarios based on maximum likelihood. Our analyses allowed us to corroborate or contradict some previous biogeographic hypotheses regarding the present-day distribution of anoles. Below we discuss the origin of the anole clade. More detailed discussion of our results with regard to dispersal within Caribbean and mainland regions and the role of geologic events in anole biogeography is in our Supplementary Appendix 5.

*The origin of anoles.*—Based on DEC+J analyses using all anole species (Supplementary Figs. S3–S6), we were able to provide an unambiguous ancestral area of the most recent common ancestor (MRCA) of *Anolis* (analysis of the molecular-scored taxa alone produced an ambiguous root state; Fig. 5). We inferred a South American ancestor for *Anolis*. Our hypothesized timing of the origin of *Anolis* (46.3–64.4 Ma; Supplementary Fig. S7, Fig. 5) contradicts previous studies (e.g., Nicholson et al. 2012)

that suggested anoles originated approximately 95 Ma. The results of our study are concordant with recent work by Prates et al. (2015) who found similar divergence dates for the MRCA of *Anolis* using more fossil calibration points. We suspect that Nicholson et al.'s (2012) estimates of divergence times were biased to older dates by an incorrect assignment of the *Anolis electrum* amber fossil (Lazell 1965) to the *fuscoauratus* clade. As Castañeda et al. (2014) showed, this fossil lacks synapomorphies that would allow it to be assigned to any anole clade with confidence. Several studies have found evidence that incorrect fossil assignment may dramatically affect estimates of dating (Magallón 2004, 2010; Mello and Schrago 2014).

### Taxonomy

Based on our results concerning the phylogeny of the *Anolis* clade (Figs. 1–4), we here propose a revised taxonomy of anoles. To promote stability in the associations between names and clades by dissociating the references of names from considerations about taxonomic ranks, clade names are defined following the methods of phylogenetic nomenclature (Cantino and de Queiroz 2014). Listed synonyms are all considered approximate (as they are not phylogenetically defined) and are inferred primarily on the basis of composition. Inferred composition is stated in terms of crown subclades and known, extant species only, although it also includes extinct members of the corresponding total clades. Our phylogenetic taxonomy of anoles is described in Appendix 3.

### SUPPLEMENTARY MATERIAL

Supplementary material, including additional discussion, MrBayes matrix, and online appendices, figures and tables, can be found in the Dryad data repository: <http://dx.doi.org/10.5061/dryad.s80jq>.

### ACKNOWLEDGMENTS

MrBayes analyses were undertaken on the XSEDE cluster of CIPRES ([www.phylo.org](http://www.phylo.org)). Thanks to the International Barcode of Life Project at the Biodiversity Institute of Ontario for performing some of the mtDNA sequencing.

For help in the field and/or the lab we thank Eric Schaad, Norma L. Manríquez-Morán, Uri O. García-Vázquez, Heather MacInnes, Julian Davis, Jenny Hollis, Erik Hulebak, Carlos Vásquez Almazán, Sofia Nuñez, Gustavo Cruz, Federico Bolaños, Roberto Ibañez, Martha Calderon, Andrew Crawford, Andrés Quintero-Angel, Juan Carlos Chaparro, Christian Yañez-Miranda, Carlos Pavón, Devon Graham, Julie Ray, Alvaro Aguilar, James Aparicio, and Liliana Jaramillo.

For loan of specimens, we thank Jose Rosado (MCZ), Jonathan Losos (MCZ), Joe Martinez (MCZ),

Alan Resetar (FMNH), Chris Phillips (INHS), Dan Wylie (INHS), Nefti Camacho (LACM), Greg Pauly (LACM), Toby Hibbits (TCWC), Lee Fitzgerald (TCWC), Rafe Brown (KU), Rob Wilson (USNM), Darrel Frost (AMNH), Margaret Arnold (AMNH), David Kizirian (AMNH), James McCranie, QCAZ, and MSB. We also thank Juan Diego Palacio Mejia and Instituto Alexander von Humboldt and Andrew Crawford and the University of the Andes for use of space and laboratory equipment to conduct molecular work in Colombia.

Permits were provided by the Secretaría de Medio Ambiente y Recursos Naturales, Dirección General de Vida Silvestre (Mexico); Instituto Nacional de Conservación y Desarrollo Forestal, Áreas Protegidas y Vida Silvestre (Honduras); Ministerio de Ambiente y Energía (Costa Rica); Autoridad Nacional del Ambiente (Panama); Instituto Nacional de Recursos Naturales (Peru); Ministerio de Ambiente (Ecuador); Corporación Autónoma Regional de Risaralda – CARDER (Colombia)

### FUNDING

Funding was provided by the National Science Foundation (DEB-0844624 to S.P.); SENESCYT and Pontificia Universidad Católica del Ecuador (to O.T. and F.A.); DGAPA, UNAM (PAPIIT no. 224009) and CONACYT (no. 154093) (to A.N.M.O.).

### APPENDIX 1: SPECIES LIST AND GENE COVERAGE FOR DNA DATA

See Alföldi et al. (2011) for varying coverage of 46 genes (the difference in number of sites between our paper and Alföldi et al.'s [2012]—19,878 versus 19,987—is due to our use of a shorter segment of the 16S gene). Number in parentheses is numbers of species scored for that gene/dataset. og = number of outgroup species. All species were scored for some or all characters of morphology.

### APPENDIX 2. MORPHOLOGICAL CHARACTERS

Continuous quantitative characters were coded using the approach of Thiele (1993). Wiens's (1995) frequency coding was used in cases wherein there appeared to be a morphological break between recognizable states. States were "ordered" if change between morphologically adjacent states seemed evolutionarily more likely than change between nonadjacent states.

1. Maximum snout to vent length (SVL; mm; ordered). 0: <61; 1: 61–86; 2: 87–112; 3: 113–138; 4: 139–164; 5: >165.
2. Maximum female SVL/maximum male SVL (ordered). 0: <0.60; 1: 0.60–0.69; 2: 0.70–0.79; 3: 0.80–0.89; 4: 0.90–0.99; 5: >1.00.

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>acutus</i>		X			X
<i>aeneus</i>	X	X		X	X
<i>aequatorialis</i>	X	X		X	
<i>agassizi</i>	X	X		X	
<i>agueroi</i>		X			
<i>ahli</i>		X			X
<i>alayoni</i>		X			
<i>alfaroi</i>		X			
<i>aliniger</i>		X			X
<i>allisoni</i>	X	X	X		X
<i>allogus</i>		X			X
<i>altae</i>	X	X	X		X
<i>altavelensis</i>					
<i>altitudinalis</i>		X			
<i>alumina</i>		X			
<i>alutaceus</i>		X			X
<i>alvarezdeltoroi</i>	X	X	X		
<i>amplisquamosus</i>	X	X			
<i>anatoloros</i>	X	X		X	
<i>anchicayae</i>		X	X		
<i>anfiloquiae</i>					
<i>angusticeps</i>		X			X
<i>annectens</i>		X			
<i>anoriensis</i>	X	X		X	
<i>antioquiae</i>			X		
<i>antonii</i>		X	X		
<i>apletophallus</i>		X			
<i>apollinaris</i>		X	X		
<i>aquaticus</i>	X	X	X		
<i>argenteolus</i>		X			X
<i>argillaceus</i>		X			
<i>armouri</i>		X			X
<i>auratus</i>	X	X	X		X
<i>aurifer</i>		X			
<i>bahorucoensis</i>		X	X		X
<i>baleatus</i>		X			X
<i>baracoae</i>		X			
<i>barahonae</i>		X			X
<i>barbatus</i>		X			
<i>barbouri</i>		X			X
<i>barkeri</i>	X	X	X		
<i>bartschi</i>		X			X
<i>beckeri</i>	X	X	X		X
<i>bellipeniculus</i>					
<i>benedikti</i>	X		X		
<i>bicaorum</i>	X	X	X		
<i>bimaculatus</i>	X	X		X	
<i>binotatus</i>	X	X			
<i>biporcatus</i>	X	X			X
<i>birama</i>					
<i>biscutiger</i>		X			
<i>blanquillanus</i>					
<i>bocourtii</i>			X		
<i>boettgeri</i>					
<i>bombiceps</i>	X	X			
<i>bonairensis</i>		X			

(continued)



Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>boulengerianus</i>	X	X	X		
<i>brasiliensis</i>		X			
<i>bremeri</i>		X			X
<i>breslini</i>		X			
<i>brevirostris</i>		X			X
<i>brunneus</i>		X			
<i>calimae</i>	X	X		X	
<i>campbelli</i>		X			
<i>capito</i>	X	X	X		X
<i>caquetae</i>					
<i>carlostoddi</i>					
<i>carolinensis</i>	X	X	X	X	X
<i>carpenteri</i>		X			
<i>casildae</i>	X	X	X	X	
<i>caudalis</i>		X			
<i>centralis</i>		X			X
<i>chamaeleonides</i>		X			X
<i>charlesmyersi</i>	X	X	X		
<i>chloris</i>	X	X	X	X	
<i>chlorocyanus</i>		X			X
<i>chocorum</i>	X	X	X	X	
<i>christophei</i>		X			X
<i>chrysolepis</i>		X			
<i>chrysops</i>					
<i>clivicola</i>		X			
<i>cobanensis</i>		X			
<i>coelestinus</i>		X			X
<i>compressicauda</i>		X			
<i>concolor</i>					
<i>confusus</i>		X			
<i>conspersus</i>		X			
<i>cooki</i>		X		X	
<i>crassulus</i>	X	X	X		
<i>crystalinus</i>	X	X	X	X	X
<i>crystalinus</i>	X	X	X		
<i>cryptolimifrons</i>	X	X	X		
<i>cupeyalensis</i>		X			
<i>cupreus</i>	X	X	X	X	
<i>cuprinus</i>		X			
<i>cuscoensis</i>					
<i>cusuco</i>	X		X		
<i>cuvieri</i>	X	X	X	X	X
<i>cyanopleurus</i>		X			
<i>cybotes</i>		X			X
<i>cymbops</i>		X			
<i>danieli</i>	X	X		X	
<i>darlingtoni</i>		X			
<i>datzorum</i>	X		X		
<i>desechensis</i>		X		X	
<i>desiradei</i>					
<i>dissimilis</i>					
<i>distichus</i>		X		X	X
<i>dolichocephalus</i>		X			
<i>dollfusianus</i>	X	X	X		
<i>dominicensis</i>		X			
<i>duellmani</i>		X			

(continued)

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>dunni</i>	X	X	X		
<i>equestris</i>	X	X		X	
<i>ernestwilliamsi</i>		X		X	
<i>etheridgei</i>		X			X
<i>eugenegrahami</i>		X			
<i>eulaemus</i>		X	X		
<i>euskalerruari</i>	X	X		X	
<i>evermanni</i>	X	X		X	X
<i>extremus</i>	X	X	X	X	X
<i>fairchildi</i>					
<i>fasciatus</i>	X	X	X		
<i>favillarum</i>		X			
<i>ferreus</i>		X			
<i>festae</i>	X	X		X	
<i>fitchi</i>	X	X	X	X	
<i>forbesi</i>		X			
<i>forresti</i>					
<i>fortunensis</i>	X		X		
<i>fowleri</i>		X			X
<i>fraseri</i>	X	X	X	X	
<i>frenatus</i>	X	X	X	X	X
<i>fugitivus</i>					
<i>fungosus</i>			X		
<i>fuscoauratus</i>	X	X	X		X
<i>gadovii</i>	X	X	X		
<i>gaigei</i>		X	X		X
<i>garmani</i>		X	X		X
<i>garridoi</i>		X			
<i>gemmosus</i>	X	X		X	
<i>ginaelisae</i>	X		X		
<i>gingivinus</i>		X			X
<i>gorgonae</i>		X			
<i>gracilipes</i>	X	X			
<i>grahami</i>		X			X
<i>granuliceps</i>	X		X		
<i>griseus</i>	X	X		X	
<i>gruuo</i>	X	X	X		
<i>guafe</i>		X			X
<i>guamuhaya</i>		X			
<i>guazuma</i>		X			
<i>gundlachi</i>	X	X		X	X
<i>haetianus</i>		X			
<i>hendersoni</i>		X			
<i>heterodermus</i>	X	X		X	
<i>heteropholidotus</i>					
<i>hobartsmithi</i>		X			
<i>homolechis</i>		X			X
<i>huilae</i>	X	X		X	
<i>humilis</i>	X	X	X		X
<i>ibanezi</i>	X		X		
<i>ignigularis</i>		X			
<i>imias</i>		X			X
<i>inderenae</i>	X	X		X	
<i>inexpectatus</i>		X			
<i>insignis</i>					

(continued)

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>insolitus</i>		X			X
<i>isolepis</i>		X			
<i>jacare</i>	X	X		X	
<i>johnmeyeri</i>	X		X		
<i>juangundlachi</i>					
<i>jubar</i>		X			X
<i>kahouannensis</i>					
<i>kemptoni</i>	X	X			
<i>koopmani</i>		X			
<i>kreutzi</i>					
<i>krugi</i>	X	X	X	X	X
<i>kunayalae</i>	X	X	X		
<i>laevis</i>					
<i>laevisoentris</i>	X	X	X		
<i>lamari</i>					
<i>latifrons</i>	X	X			
<i>leachii</i>		X			X
<i>lemurinus</i>	X	X	X		X
<i>limifrons</i>	X	X	X		X
<i>limon</i>					
<i>lineatopus</i>		X			X
<i>lineatus</i>		X		X	
<i>liogaster</i>	X	X	X		
<i>lionotus</i>	X	X	X		X
<i>litoralis</i>					
<i>lividus</i>		X			
<i>longiceps</i>		X			
<i>longitibialis</i>		X			
<i>loveridgei</i>		X			
<i>loysianus</i>		X			X
<i>luciae</i>	X	X		X	
<i>lucius</i>	X	X		X	
<i>luteogularis</i>		X			
<i>luteosignifer</i>					
<i>lynchi</i>	X	X			
<i>lyra</i>	X	X			
<i>macilentus</i>		X			
<i>macrinii</i>		X	X		
<i>macrolepis</i>		X	X		
<i>macrophallus</i>	X	X	X		
<i>maculigula</i>	X	X		X	
<i>maculivoentris</i>	X	X			
<i>magnaphallus</i>	X				
<i>marcanoi</i>	X	X	X	X	X
<i>mariarum</i>		X	X		
<i>marmoratus</i>		X			X
<i>marron</i>		X			
<i>marsupialis</i>	X	X	X		
<i>matudai</i>		X			
<i>maynardi</i>		X			X
<i>medemi</i>		X			
<i>megalopithecus</i>			X		
<i>megapholidotus</i>	X	X	X		
<i>menta</i>					

(continued)

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>meridionalis</i>		X			
<i>mestrei</i>		X			X
<i>microlepidotus</i>	X	X	X		
<i>microtus</i>		X			
<i>milleri</i>		X	X		
<i>mirus</i>					
<i>monensis</i>		X		X	
<i>monteverde</i>	X	X			
<i>monticola</i>		X			
<i>morazani</i>					
<i>muralla</i>					
<i>nasofrontalis</i>					
<i>naufragus</i>		X			
<i>neblininus</i>	X	X		X	
<i>nebuloides</i>	X	X	X		
<i>nebulosus</i>		X	X		
<i>nelsoni</i>					
<i>nicefori</i>		X			
<i>noblei</i>		X			
<i>notopholis</i>		X	X		
<i>nubilus</i>		X			
<i>occultus</i>	X	X		X	
<i>ocelloscapularis</i>	X	X	X		
<i>oculatus</i>		X			
<i>oligaspis</i>					
<i>olssoni</i>		X			X
<i>omiltemanus</i>	X	X			
<i>onca</i>		X			
<i>opalinus</i>		X			X
<i>ophiolepis</i>		X			X
<i>oporinus</i>		X			
<i>orcesi</i>	X	X			
<i>ortonii</i>	X	X	X		
<i>otongae</i>	X	X		X	
<i>oxylophus</i>		X	X		
<i>pachypus</i>	X	X	X		
<i>paravertebralis</i>					
<i>parilis</i>	X	X	X		
<i>parvaauritus</i>	X	X	X		
<i>parvicirculatus</i>		X	X		
<i>paternus</i>		X		X	X
<i>pentaprion</i>	X	X	X		
<i>peraccae</i>	X	X	X	X	
<i>petersii</i>	X	X	X		
<i>peucephilus</i>		X			
<i>philopunctatus</i>					
<i>phyllorhinus</i>					
<i>pigmaequestris</i>					
<i>pijolense</i>					
<i>pinchoti</i>					
<i>placidus</i>		X	X		
<i>planiceps</i>		X			
<i>podocarpus</i>	X	X			
<i>poecilopus</i>			X		
<i>poei</i>	X	X		X	
<i>pogus</i>		X		X	X

(continued)

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>polylepis</i>	X	X	X		
<i>poncensis</i>		X		X	
<i>porcatus</i>	X	X	X		X
<i>porcus</i>		X			
<i>princeps</i>	X	X	X	X	
<i>proboscis</i>	X	X	X		
<i>properus</i>		X			
<i>propinquus</i>					
<i>pseudokemptoni</i>	X		X		
<i>pseudopachypus</i>	X				
<i>pseudotigrinus</i>					
<i>pulchellus</i>	X	X		X	X
<i>pumilus</i>		X			X
<i>punctatus</i>	X	X		X	X
<i>purpurgularis</i>		X			
<i>pygmaeus</i>		X			
<i>quadriocellifer</i>		X			X
<i>quaggulus</i>	X		X		
<i>quercorum</i>	X	X	X		
<i>ravitergum</i>		X			
<i>reconditus</i>		X			X
<i>rejectus</i>		X			
<i>richardii</i>	X	X		X	
<i>ricordii</i>		X			X
<i>rimarum</i>					
<i>rivalis</i>					
<i>roatanensis</i>	X		X		
<i>rodriguezii</i>	X	X	X		
<i>roosevelti</i>					
<i>roquet</i>	X	X		X	X
<i>rubiginosus</i>	X	X			
<i>rubribarbaris</i>					
<i>rubribarbus</i>		X			X
<i>ruibali</i>					
<i>ruizii</i>					
<i>rupinae</i>		X			X
<i>sabanus</i>		X			X
<i>sagrei</i>	X	X		X	
<i>salvini</i>	X		X		
<i>santamartae</i>					
<i>schiedii</i>		X			
<i>schwartzii</i>		X			
<i>scriptus</i>		X		X	
<i>scypheus</i>	X	X			
<i>semilineatus</i>		X			X
<i>sericeus</i>		X			
<i>serranoi</i>	X	X	X		
<i>sheplani</i>		X			
<i>shrevei</i>		X			X
<i>singularis</i>		X			X
<i>smallwoodi</i>		X			
<i>smaragdinus</i>	X	X		X	X
<i>sminthus</i>	X	X	X		
<i>soinii</i>	X	X	X		
<i>solitarius</i>					
<i>spectrum</i>					

(continued)

Species	CO1 (142 + 1 og) 734 sites	ND2 (294 + 4 og) 1039 sites	ECEL1 (111) 474 sites	RAG1 (62 + 4 og) 2754 sites	Alfoldi et al. (89 + 1 og) 19878 sites
<i>squamulatus</i>					
<i>strahmi</i>		X			X
<i>stratulus</i>		X		X	X
<i>subocularis</i>	X	X	X		
<i>sulcifrons</i>		X	X		
<i>tandai</i>		X			X
<i>taylori</i>	X	X	X		
<i>tenorioensis</i>					
<i>terraealtae</i>					
<i>terueli</i>					
<i>tetarii</i>					
<i>tigrinus</i>	X	X		X	
<i>toldo</i>					
<i>tolimensis</i>		X	X		
<i>townsendi</i>		X			
<i>trachyderma</i>		X			
<i>transversalis</i>	X	X		X	X
<i>trinitatis</i>	X	X		X	
<i>tropidogaster</i>			X		
<i>tropidolepis</i>	X	X			
<i>tropidonotus</i>	X	X	X		X
<i>umbrivagus</i>					
<i>uniformis</i>	X	X	X		
<i>unilobatus</i>	X	X	X		
<i>utilensis</i>	X	X	X		
<i>valencienni</i>		X			X
<i>vanidicus</i>		X			X
<i>vanzolinii</i>	X	X			
<i>vaupesianus</i>					
<i>ventrimaculatus</i>	X	X		X	
<i>vermiculatus</i>		X			
<i>vescus</i>					
<i>vicarius</i>					
<i>villai</i>					
<i>vinosus</i>		X			
<i>vittigerus</i>	X	X	X		
<i>wampuensis</i>					
<i>wattsii</i>		X			X
<i>websteri</i>		X			
<i>wellbornae</i>	X		X		
<i>weruthi</i>					
<i>whitemani</i>		X			X
<i>williamsmittermeierorum</i>	X	X	X		
<i>woodi</i>	X	X	X		
<i>yoroensis</i>	X	X	X		
<i>zeus</i>	X	X	X		
<i>B. plumifrons</i>		X		X	
<i>P. marmoratus</i>	X	X		X	X
<i>P. scapulatus</i>		X		X	
<i>U. gallardoi</i>		X		X	

3. Femoral length/SVL (ordered). 0: <0.20; 1: 0.20–0.22; 2: 0.23–0.25; 3: 0.26–0.28; 4: 0.29–0.31; 5: >0.32.
4. Head length/SVL (ordered). 0: <0.23; 1: 0.23–0.24; 2: 0.25–0.26; 3: 0.27–0.28; 4: 0.29–0.30; 5: 0.31+.
5. Ear height/SVL (ordered). 0: <.018; 1: 0.018–0.025; 2: 0.026–0.033; 3: 0.034–0.041; 4: 0.042–0.048; >: 0.049.
6. Toe length/SVL (ordered). 0: <0.14; 1: 0.14–0.16; 2: 0.17–0.19; 3: 0.20–0.22; 4: 0.23–0.25; 5: >0.26.
7. Tail length/SVL (ordered). 0: <1.30; 1: 1.30–1.59; 2: 1.60–1.89; 3: 1.90–2.19; 4: 2.20–2.49; 5: >2.50.
8. Mean number of longitudinal ventral scales in 5% of SVL (ordered). 0: <4.5; 1: 4.5–5.9; 2: 6.0–7.4; 3: 7.5–8.9; 4: 9.0–10.4; 5: >10.5.
9. Mean number of longitudinal dorsal scales in 5% of SVL (ordered). 0: <5.0; 1: 5.0–7.4; 2: 7.5–9.9; 3: 10.0–12.4; 4: 12.5–14.9; 5: >15.0.
10. Mean number of expanded lamellae on toe IV (ordered). 0: <15.0; 1: 15.0–20.9; 2: 21.0–26.9; 3: 27.0–32.9; 4: 33.0–38.9; 5: >39.0.
11. Male dewlap (ordered). 0: extends posteriorly past arms; 1: to arms or shorter; 2: absent.
12. Female dewlap (ordered). 0: extends posteriorly past arms; 1: to arms or shorter; 2: absent.
13. Head scales (frequency-coded). 0: keeled; 5: smooth.
14. Subocular scales (frequency-coded). 0: in contact with supralabials; 5: separated from supralabials by a row of scales.
15. Mean number of scales across the snout at the second canthals (ordered). 0: <5; 1: 5–7; 2: 8–10; 3: 11–13; 4: 14–16; 5: >17.
16. Mean number of supralabial scales from rostral to center of eye (ordered). 0: <6; 1: 6; 2: 7; 3: 8; 4: 9; 5: >10.
17. Supraorbital semicircles (frequency-coded). 0: separated by one or more rows of scales; 5: in contact.
18. Interparietal scale (frequency-coded). 0: separated from supraorbital semicircles by at least one scale; 1: in contact with supraorbital semicircles.
19. Length of interparietal scale/length of scale lateral to interparietal (ordered). 0: <1.25; 1: 1.25–2.24; 2: 2.25–3.24; 3: 3.25–4.24; 4: 4.25–5.24; 5: >5.25.
20. Modal number of elongate superciliary scales (ordered). 0: none; 1: one; 2: two; 3: three.
21. Scales in supraocular disc (frequency-coded). 0: some enlarged, gradually decreasing in size, or all scale equal; 5: 2–4 abruptly enlarged, at least 2 × larger than other supraocular scales.
22. Differentiated scales in lower eyelid (frequency-coded). 0: absent; 5: present.
23. Mental (frequency-coded). 0: partially divided; 5: completely divided.
24. Mental (frequency coded). 0: extends along mouth posteriorly past rostral; 5: rostral extends posteriorly past mental.
25. Mean number of postmental scales (ordered). 0: <4.5; 1: 4.5–5.4; 2: 5.5–6.4; 3: 6.5–7.4; 4: 7.5–8.4; 5: >8.5.
26. Posterior border of mental (frequency-coded). 0: convex or straight; 5: concave.
27. Dorsal surface of rostral (frequency-coded). 0: smooth; 5: cleft.
28. Preoccipital scale (frequency-coded). 0: absent; 5: present.
29. Dorsal snout scales (frequency-coded). 0: not in regular rows; 5: in longitudinal parallel rows.
30. Scales around naris (unordered). 0: anterior nasal in contact with rostral; 1: circumnasal separated from rostral by one scale, not in contact with supralabial; 2: external naris separated from rostral by two scales, not in contact with supralabial; 3: external naris separated from rostral by three or more scales, not in contact with supralabial; 4: circumnasal in contact with rostral; 5: circumnasal in contact with supralabial, separated from rostral by 1–2 scales.
31. Modal number of abruptly enlarged sublabial scales (ordered). 0: zero; 1: one; 2: two or more.
32. Ventral scales (frequency coded). 0: keeled; 5: smooth.
33. Middorsal scales (frequency-coded). 0: 0–4 enlarged; 5: >5 enlarged.
34. Middorsal crest (frequency coded). 0: absent; 5: present.
35. Deep tubelike axillary pocket (frequency-coded) 0: absent; 5: present.
36. Lateral scales (frequency-coded). 0: homogeneous; 5: heterogeneous.
37. Middorsal caudal scales (frequency-coded). 0: single row; 5: double row.
38. Tail fin (frequency-coded). 0: absent in large males; 5: present in large males.

39. Scales on dewlap (frequency-coded). 0: in rows of single scales; 5: in rows of multiple scales or scattered.
40. Enlarged postcloacal scales (frequency coded). 0: present in males; 5: absent in males.
41. Discrete expanded toepad on toe IV (frequency-coded). 0: present; 5: absent.
42. Modal dominant dorsal color when sleeping (unordered). 0: brown; 1: green; 2: gray/white; 3: blue.
43. Modal lateral pattern when sleeping (unordered). 0: solid; 1: lateral stripe along body; 2: bands; 3: ocelli/spots; 4: speckled; 5: jumbled, lichenous.
44. Interorbital bar (frequency-coded). 0: absent; 5: present.
45. Throat color (frequency-coded). 0: light; 5: dark.
46. Color of iris (unordered). 0: brown; 1: yellow; 2: blue or gray; 3: green; 4: red.

#### APPENDIX 3. PHYLOGENETIC TAXONOMY OF ANOLES

##### *Anolis* Daudin 1802 [nobis], converted clade name

**Synonyms:** *Anolius* of Cuvier (1817), *Anolidae?* of Cope (1864), *Anolidae* of O'Shaughnessy (1875), *Anolinae* (except for the inclusion of *Polychrus*) of Cope (1900), *Anolinae* of Varnoa (1985), and *Dactyloidae* of Townsend et al. (2011). *Dactyloa* of Wagler (1830) and Fitzinger (1843), *Dactyloae* of Fitzinger (1843), *Anolini* and *Anolina* of Varona (1985), alpha section (informal) of Etheridge (1959) and *punctatus* subsection (informal) of Williams (1976b) are partial synonyms that refer to paraphyletic groups originating in approximately the same ancestor.

**Definition:** The crown clade for which both adhesive toe pads and an extensible throat fan (dewlap), as inherited by *Anolis carolinensis* Voigt 1832, are apomorphies relative to other crown clades.

**Reference phylogeny:** Figure 1 of this study.

**Comments:** Daudin (1802) originally coined the name *Anolis* for the group of saurian reptiles diagnosed by toe pads and an extensible dewlap. Later 19th century authors, most notably Wagler (1830, 1833) and Fitzinger (1826, 1843) named several mutually exclusive taxa (ranked as genera and subgenera) for species possessing those characters; however, Boulenger (1885) treated all but three of those names as synonyms of *Anolis*. Additional "genera" were named during the first half of the 20th century (Schmidt 1919; Barbour 1920, 1923; Cochran 1934; Dunn 1939). The modern era of anole systematics is commonly considered to have begun

with the work of Etheridge (1959), who recognized five "genera" of anoles: *Anolis*, including the vast majority of the species, and four other small, segregate "genera." The last of these, *Tropidodactylus*, which differed from *Anolis* in having lost the toepads, was eliminated when a morphologically intermediate species was discovered (Williams 1974). Subsequent phylogenetic analyses revealed that the other three "genera"—*Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus*—were also derived from within *Anolis*, leading the authors of those studies either to reject those taxa (Hass et al. 1993; Poe 2004) or to treat them as unranked subclades of *Anolis* (Jackman et al. 1999). Thus, the name *Anolis* was applied to the smallest clade containing all species possessing adhesive toe pads and an extensible dewlap, including some species lacking one or the other of those characters (through secondary loss) that were inferred to be part of that clade (e.g., Poe 2004; Nicholson et al. 2005; Losos 2011).

Etheridge (1959; see also Williams 1976a,b) also recognized various informally named subgroups of anoles associated with the ranks of section and series. The two sections that he recognized, designated the alpha and beta sections, were recognized formally as the "genera" *Anolis* and *Norops* by Savage and Talbot (1978). However, the finding that the alpha section (*Anolis* sensu Savage and Talbot) is paraphyletic (Shochat and Dessauer 1981; Gorman et al. 1984; Guyer and Savage 1986), led authors following Savage and Talbot (1978) to partition their paraphyletic version of *Anolis* into multiple genera and to shift the name *Anolis* to smaller and smaller clades (Guyer and Savage 1986, 1992; Nicholson et al. 2012).

In the interest of historical continuity, the name *Anolis* is here applied to the crown clade for which adhesive toe pads and an extensible dewlap are apomorphies relative to other non-nested crown clades. Applying the name to this clade associates it with the most recent common ancestor of the species originally included in *Anolis* by Daudin (1802); except that he included a gecko, O'Shaughnessy (1875), Boulenger (1885), Schmidt (1919), Cochran (1934), Dunn (1939), Barbour (1920, 1923), Etheridge (1959), and Williams (1976a,b), whose paraphyletic versions of *Anolis* excluded various small, deeply nested, segregate "genera," as well as by Savage and Talbot (1978; see also Savage (1980, 1982), whose paraphyletic version of *Anolis* also excluded an expanded version of *Norops* (=beta section of Etheridge 1959). It also associates the name *Anolis* with the clade to which it has been applied by authors who did not recognize Etheridge's beta section as a separate "genus" subsequent to the finding that *Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus* are nested within that clade (e.g., Hass et al. 1993; Jackman et al. 1999; Poe 2004; Nicholson et al. 2005; Losos 2011).

**Inferred composition:** *Dactyloa* and *Digilimbus* (see below).



**Etymology:** According to [Daudin \(1802\)](#), the name is that given in the French colonies in the Americas to lizards of this kind.

***Dactyloa* Wagler 1830** [[Castañeda and de Queiroz 2013](#)]

**Synonyms:** *latifrons* series (informal) ([Etheridge 1959](#)).

**Definition:** The most inclusive crown clade containing *Anolis punctatus* [Daudin 1802](#) but not *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](#) ([Castañeda and de Queiroz 2013](#)).

**Reference Phylogeny:** Figure 1 of this study.

**Comments:** Early divergence between the members of this clade and all other anoles, with the exception of some distinctive groups that were treated as separate “genera”, was inferred in several early studies of anole phylogeny ([Etheridge 1959](#); [Guyer and Savage 1986, 1992](#); [Cannatella and de Queiroz 1989](#)), but evidence for the monophyly of this group, including species formerly placed in the “genus” *Phenacosaurus*, emerged later (e.g., [Jackman et al. 1999](#); [Poe 2004](#); [Nicholson et al. 2005, 2012](#); [Alföldi et al. 2011](#); [Castañeda and de Queiroz 2011, 2013](#), this study). Although originally proposed as a substitute name for *Anolis* [Daudin 1802](#), the name *Dactyloa* [Wagler 1830](#) has been applied to the clade of mainland alpha anoles (*latifrons* series of [Etheridge 1960](#)) by [Guyer and Savage \(1986\)](#) and various subsequent authors (e.g., [Savage and Guyer 1989](#); [Guyer and Savage 1992](#); [Castañeda and de Queiroz 2011](#); [Castañeda and de Queiroz 2013](#); [Nicholson et al. 2012](#); [Prates et al. 2015](#)), and was defined phylogenetically as applying to that clade by [Castañeda and de Queiroz \(2013\)](#). We have adopted an equivalent definition with a more concise wording.

**Inferred Composition:** The following five (informally named) non-nested crown clades: *aequatorialis* series, *latifrons* series, *punctatus* series, *heterodermus* series, *roquet* series ([Castañeda and de Queiroz 2013](#)). The compositions of these clades as inferred in the present study are largely congruent with those proposed by [Castañeda and de Queiroz \(2013\)](#), with the following exceptions: *Anolis bellipeniculus*, *A. calimae*, *A. carlostoddi*, and *A. neblininus* were considered *incertae sedis* within *Dactyloa*, and *A. dissimilis* was tentatively referred to the *punctatus* series; all of these species are here referred to the *heterodermus* series. *Anolis laevis* and *A. phyllorhinus* were considered *incertae sedis* within *Dactyloa*, and *A. philopunctatus* was tentatively referred to the *latifrons* series; all of these species are referred to the *punctatus* series. *Anolis parilis* and *A. mirus* were tentatively referred to the *aequatorialis* series, and *A. limon* had not been described; all of these species are referred to the *latifrons* series. *Anolis cuscoensis* was considered *incertae sedis* within *Dactyloa*, *A. soini* and *A. gorgonae* were tentatively referred to the *punctatus*

series, and *A. poei* had not been described; all of these species are referred to the *aequatorialis* series. The series assignments (including tentative ones) of all other *Dactyloa* species discussed by [Castañeda and de Queiroz \(2013\)](#) that were included in the present study are corroborated by our results. In addition, [Castañeda and de Queiroz \(2013\)](#) defined the (formal) names *Megaloa* [Castañeda and de Queiroz 2013](#) and *Phenacosaurus* [Barbour 1920](#) for clades corresponding roughly to, but potentially less inclusive than, the *latifrons* series and the *heterodermus* series, respectively. According to the results of the present study, *Megaloa* corresponds precisely to the *latifrons* series in terms of known composition, but *Phenacosaurus* may correspond to the largest subclade of the *heterodermus* series that includes *A. heterodermus* but not *A. neblininus* and *A. calimae*, which are not twig anoles ([Castañeda et al.](#), manuscript in preparation), although the ecomorph assignments of some critical species are currently unknown. [Poe et al. \(2015\)](#) defined *Continenteloa* to include the non-*roquet* series *Dactyloa*, a clade that is weakly corroborated here.

**Etymology:** Derived from the Greek *dactyl* (finger) + *oa* (hem, border), presumably referring to the toepads of the lizards in this clade (the name was originally proposed as a substitute name for *Anolis*).

***Digilimbus nobis*, new clade name**

**Synonyms:** None.

**Definition:** The most inclusive crown clade containing *Anolis carolinensis* [Voigt 1832](#) but not *Anolis punctatus* [Daudin 1802](#).

**Reference Phylogeny:** Figure 2 of this study.

**Comments:** Although a clade composed of all anoles except the “mainland” alpha anoles has been inferred repeatedly and consistently (e.g., [Gorman et al. 1984](#); [Hass et al. 1993](#); [Jackman et al. 1999](#) [with the exception of *A. occultus*]; [Poe 2004](#) [with the exception of *A. occultus*]; [Nicholson et al. 2005, 2012](#); [Alföldi et al. 2011](#); [Castañeda and de Queiroz 2011, 2013](#); this study), and despite the naming of its sister group (*Dactyloa*; see above), an emphasis on ranks has left this highly corroborated clade unnamed. We therefore take this opportunity to name it.

**Inferred Composition:** The following mutually exclusive crown clades: *Deiropyx*, *Audantia*, *Schmidtanolis*, *Xiphosurus*, *Ctenocercus*, *Ctenonotus*, and *Norops* (see below).

**Etymology:** Derived from the Latin *digitus* (finger, toe), truncated for the sake of euphony, and *limbus* (edge, border), referring to the toepads. *Digilimbus* is the Latin equivalent of the Greek *Dactyloa* and thus seems appropriate as the name of the sister group of *Dactyloa*,

given that toepads are present in the vast majority of the lizards in both clades.

***Deiroptyx* Fitzinger 1843 [nobis], converted clade name**

**Synonyms:** None.

**Definition:** The most inclusive crown clade containing *Anolis vermiculatus* Duméril and Bibron 1837 but not *A. auratus* Daudin 1802, *A. bimaculatus* (Sparrman 1784), *A. armouri* (Cochran 1934), *A. carolinensis* Voigt 1832, *A. cuvieri* Merrem 1820, *A. semilineatus* Cope 1864, and *A. punctatus* Daudin 1802.

**Reference Phylogeny:** Figure 2 of this study.

**Comments:** Jackman et al. (1999) inferred a close relationship between the *Anolis vermiculatus* species group and the *A. chlorocyanus* species group (both *sensu* Williams 1976a). Poe (2004; see also Alföldi et al. [2011]) inferred a larger clade composed of those two species groups plus the *A. equestris* species group, the *A. hendersoni* species group, and the *A. monticola* species group (all *sensu* Williams 1976a), and Nicholson et al. (2005) added *A. occultus* and *A. darlingtoni*, which was corroborated by Nicholson et al. (2012) and this study. Nicholson et al. (2012) applied the name *Deiroptyx* Fitzinger (1843) to this clade under rank-based nomenclature. Although *Deiroptyx* was previously applied to a smaller clade composed only of *A. vermiculatus* and *A. bartschi* (e.g., Cochran 1928), with the exception of Varona (1985), that name has not been so applied for more than 50 years and therefore is here considered available to be applied to the larger clade, following Nicholson et al. (2012). However, in the interest of maintaining the association the name with that clade (here conceptualized as the largest crown clade containing *A. vermiculatus* but not certain other species, including *A. auratus*, which seems consistent with the concept of Nicholson et al. 2012), we have provided it with a formal phylogenetic definition.

**Inferred composition:** *Anolis equestris* species group (Williams 1976a; see also Schwartz and Garrido 1972), *Anolis chlorocyanus* species group (Williams 1965, 1976a), *Anolis monticola* species group (Williams 1976a) minus *A. etheridgei*, *Anolis hendersoni* species group (Williams 1976a), *Anolis vermiculatus* species group (Williams 1976a), *Anolis darlingtoni* (Cochran 1935), *Anolis occultus* Williams and Rivero 1965.

**Etymology:** Derived from the Greek *deire* (neck, throat) and *ptyx* (a fold), possibly in reference to the transverse gular fold of *A. vermiculatus*, upon which the name was based.

***Audantia* Cochran (1934) [nobis], converted clade name**

**Synonyms:** *cybotes* subseries, *cybotes* species group, and *cybotes* superspecies (all informal) of Williams (1976a);

*cybotes* series (informal) of Gorman et al. (1980; see also Burnell and Hedges 1990).

**Definition:** The most inclusive crown clade containing *Anolis armouri* (Cochran 1934) but not *A. auratus* Daudin 1802, *A. bimaculatus* (Sparrman 1784), *A. carolinensis* Voigt 1832, *A. cuvieri* Merrem 1820, *A. semilineatus* Cope 1864, *A. vermiculatus* Duméril and Bibron 1837 and *A. punctatus* Daudin 1802.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** *Anolis cybotes* and its relatives were considered close to *Anolis cristatellus* and its relatives by Etheridge (1959), but this relationship was challenged by early molecular studies (e.g., Gorman et al. 1980; Wyles and Gorman 1980). Subsequently, Poe (2004) inferred the cybotoids in a relatively isolated position, as sister to the beta anoles (*Norops*). The relatively isolated position of the cybotoids, but not necessarily a close relationship to the beta anoles, was corroborated by subsequent studies (e.g., Nicholson et al. 2005, 2012; Alföldi et al. 2011; this study). The name *Audantia* Cochran 1934 (type species *A. armouri*) was originally proposed for Hispaniolan anoles with a transverse, as well as a longitudinal, gular fold and came to include *A. armouri* and *A. shrevei* (Cochran 1934, Cochran 1939, 1941). *Audantia* was not recognized by Etheridge (1959), who noted that a transverse gular fold was also present in *Anolis cybotes*, which was not included in *Audantia* but which he considered closely related to the included species. Nicholson et al. (2012) resurrected the name *Audantia* for the cybotoid anoles (*cybotes* subseries of Williams [1976a]; *cybotes* series of Gorman et al. [1980] and Burnell and Hedges [1990]). Because that name was not in use during the previous 50 years, and because the transverse gular fold does not appear to be diagnostic of the clade composed of *A. armouri* and *A. shrevei*, we accept *Audantia* as the name of the cybotoid clade and here provide it with a formal phylogenetic definition.

**Inferred composition:** *cybotes* subseries, species group, and superspecies of Williams (1976a) = *cybotes* series of Gorman et al. (1980) and Burnell and Hedges (1990).

**Etymology:** Named for the collector of the type specimen of the type species, André Audant, zoologist at the Government Agricultural School at Damien, Haiti (Cochran 1934).

***Schmidtanolis nobis*, new clade name**

**Synonyms:** *Chamaelinorops* of Nicholson et al. (2012).

**Definition:** The most inclusive crown clade containing *Anolis semilineatus* Cope 1864 but not *A. auratus* Daudin 1802, *A. bimaculatus* (Sparrman 1784), *A. armouri* (Cochran 1934), *A. carolinensis* Voigt 1832, *A. cuvieri*

Merrem 1820, *A. vermiculatus* Duméril and Bibron 1837, and *A. punctatus* Daudin 1802.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** A monophyletic group approximating this clade was first inferred by Jackman et al. (1999), except that it did not include *Anolis barbouri*, and by Poe (2004), except that it included some now-excluded Cuban grass anoles (*A. cyanopleurus*, *A. spectrum*). A monophyletic group matching this clade more precisely in composition was inferred by Nicholson et al. (2005, 2012: Fig. 4a) and Alföldi et al. (2011). Nicholson et al. (2012) applied the name *Chamaelinorops* Schmidt 1919 to this clade; however, that name was originally proposed for only one of the included species, *Anolis barbouri*, based on its distinctive morphology (Schmidt 1919), a use adopted by Etheridge (1959) and numerous subsequent authors, whether as a “genus” name (e.g., Thomas 1966; Williams 1976a; Schwartz and Insháustegui 1980; Wyles and Gorman 1980; Case and Williams 1987; Guyer and Savage 1986, 1992; Burnell and Hedges 1990; Autumn and Losos 1997) or simply as a clade name (Jackman et al. 1999). Therefore, we have preserved the traditional use of the name *Chamaelinorops* (see below) and propose the name *Schmidtanolis* for the larger clade.

**Inferred composition:** *semilineatus* species group (Hertz 1976; Williams 1976a), *Anolis etheridgei* Williams (1962), *A. insolitus* Williams and Rand (1969), *A. fowleri* Schwartz (1974), and *A. barbouri* Schmidt (1919).

**Etymology:** Named in honor of Karl P. Schmidt (1890–1957), who made important contributions to West Indian herpetology (*Schmidtanolis* is endemic to Hispaniola), including the naming of species in both of the primary subclades of the named clade. The name is a combination of his surname with *Anolis*, the name of a more inclusive clade.

***Chamaelinorops* Schmidt 1919 [nobis], converted clade name**

**Synonyms:** None.

**Definition:** The crown clade for which the presence of both laterally extending zygapophysial plates connecting the pre- and poszygapophyses of the thoracolumbar vertebrae and laterally expanded transverse process of the caudal vertebrae, as inherited by *Anolis barbouri* (Schmidt 1919), are apomorphies relative to other crown clades.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** The name *Chamaelinorops* was proposed by Schmidt (1919) for the single species *C. barbouri* and distinguished from other then-recognized anole “genera” (*Anolis*, *Norops*, *Tropidodactylus*, and

*Chamaeleolis*) based on relatively minor differences. However, the taxon was retained by Etheridge (1960) on the basis of the unique zygapophysial plates of the thoracolumbar vertebrae (possibly related to the extreme compression of the body noted by Schmidt 1919) and the laterally expanded transverse processes of the caudal vertebrae (both characters described in detail by Forsgaard 1983) and was recognized by a number of subsequent authors (e.g., Thomas 1966; Williams 1976a; Schwartz and Insháustegui 1980; Wyles and Gorman 1980; Case and Williams 1987; Guyer and Savage 1986, 1992; Burnell and Hedges 1990; Autumn and Losos 1997). The finding that *Chamaelinorops* was derived from within *Anolis* led Hass et al. (1993) to “synonymize” *Chamaelinorops* with *Anolis* under rank-based nomenclature; however, Jackman et al. (1999) noted that *Chamaelinorops* could be retained for a subclade of *Anolis* under phylogenetic nomenclature. More recently, Nicholson et al. (2012) applied the name *Chamaelinorops* under rank-based nomenclature to a clade including *A. barbouri* and several inferred close relatives, thus changing the reference of that name to a more inclusive clade that is not diagnosed by the distinctive morphological features with which the name had previously been associated. Because of the long-standing association of the name *Chamaelinorops* with *A. barbouri* and its distinctive morphological characters, we here formalize that association by proposing a phylogenetic definition based on the distinctive features (apomorphies) with which that name has come to be associated, and we propose a new name for the clade called *Chamaelinorops* by Nicholson et al. (2012) (see *Schmidtanolis*, above).

**Inferred composition:** *Anolis barbouri* (Schmidt 1919).

**Etymology:** Derived from the Greek *chamai* (ground), *leon* (lion), and *norops* (bright, flashing, gleaming), in reference to “its apparent relations with *Chamaeleolis* and *Norops*” (Schmidt 1919: 523).

***Xiphosurus* Fitzinger 1826 [nobis], converted clade name**

**Synonyms:** *cuvieri* series (informal) of Williams (1976a) and *Xiphosurus cuvieri* species group of Nicholson et al. (2012) are partial synonyms referring to a paraphyletic group originating in approximately the same ancestor in the context of our inferred phylogeny.

**Definition:** The most inclusive crown clade containing *Anolis cuvieri* Merrem 1820 but not *A. auratus* Daudin 1802, *A. bimaculatus* (Sparrman 1784), *A. armouri* (Cochran 1934), *A. carolinensis* Voigt 1832, *Anolis semilineatus* Cope 1864, *A. vermiculatus* Duméril and Bibron 1837, and *A. punctatus* Daudin 1802.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** A clade approximating the one here named *Xiphosurus* was first inferred by Jackman et al. (1999) and has been fully or partially corroborated, with the addition of *Anolis eugenegrahami*, by Poe (2004), Nicholson et al. (2005, 2012), Alföldi et al. (2011), and the present study. The name *Xiphosurus* was proposed by Fitzinger (1826) for *A. cuvieri* but was seldom used after Boulenger (1885) treated it as a synonym of *Anolis Daudin* (1802). Guyer and Savage (1986) applied the name *Semiurus Fitzinger* (1843), a younger name also based on *A. cuvieri*, to the *cuvieri* series of Williams (1976a), a group composed of the giant anoles of Hispaniola and the Puerto Rico Bank, which now appears to be paraphyletic, but they later (Savage and Guyer 1991) replaced *Semiurus* with the older name *Xiphosurus*. Nicholson et al. (2012) applied the name *Xiphosurus* to a larger clade including, in addition to the members of Williams's (1976a) *cuvieri* series, *A. christophei*, *A. eugenegrahami* and the species traditionally included in *Chamaeleolis*. Because the name *Xiphosurus* was not used by Boulenger (1885) and subsequent authors, with the exception of Varona (1985), until it was resurrected by Savage and Guyer (1991), and because the clade to which this name was applied by Nicholson et al. (2012) does not have another name, we here formalize the association of the name *Xiphosurus* with that clade by providing it with a phylogenetic definition. The taxon to which Varona (1985) applied the name *Xiphosurus* (composed of the *equestris*, *ricordii*, and *cuvieri* species groups of Williams (1976a) appears to be polyphyletic.

**Inferred composition:** *ricordii* species group (Schwartz 1974; Williams 1976a), *Anolis christophei* Williams 1960, *A. eugenegrahami* Schwartz 1978, *Chamaeleolis* (Garrido and Schwartz 1967; Rodríguez-Schettino 1999), *A. cuvieri* Merrem 1820.

**Etymology:** Derived from the Greek *xiphos* (sword) and *oura* (tail), presumably in reference to the crested tail of adult *Anolis cuvieri*, upon which the name was based.

***Chamaeleolis* Cochran 1838 [nobis], converted clade name**

**Synonyms:** *Pseudochamaeleon Fitzinger 1843*, *Xiphosurus chamaeleonides* species group of Nicholson et al. (2012).

**Definition:** The crown clade for which both assignment of its members to the twig giant ecomorph (including short limbs and tail and a maximum body size > 100 mm SVL) and possession of a head casque formed by posterolateral extensions of the parietal roof over the upper temporal fenestrae, as inherited by *Anolis chamaeleonides* Duméril and Bibron 1837, are apomorphies relative to other crown clades.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** Recognition of *Chamaeleolis*, a taxon composed of the distinctive Cuban twig giant anoles, has a long history (e.g., Cochran 1838; Cope 1864; O'Shaughnessy 1875; Boulenger 1885; Barbour and Ramsden 1919; Etheridge 1959; Garrido and Schwartz 1968; Williams 1976a; Garrido 1982; Rodríguez-Schettino 1999). Although originally described for a single species, *Anolis chamaeleonides*, that and subsequently described species referred to *Chamaeleolis* appear to form a clade (Hass et al. 1993; Jackman et al. 1999; Nicholson et al. 2005, 2012; this study). The finding that *Chamaeleolis* is nested within *Anolis* and *Xiphosurus* led authors operating in the context of rank-based nomenclature (e.g., Hass et al. 1993; Nicholson et al. 2012) to "synonymize" the names (i.e., to treat them as if they refer to the same taxon and therefore no longer use the younger name *Chamaeleolis*); however, that rank-based practice makes little sense phylogenetically. From a phylogenetic perspective, *Chamaeleolis* is nested within both *Anolis* and *Xiphosurus*, and those nested relationships can be preserved by adopting appropriate phylogenetic definitions of the names. We have emphasized the twig (giant) ecomorph and the skull casque in our definition of the name *Chamaeleolis* because those features give the lizards in this clade a chameleon-like appearance, as implied by the name.

**Inferred composition:** *Anolis chamaeleonides* Duméril and Bibron 1837, *A. porcus* (Cope 1864), *A. barbatus* (Garrido 1982), *A. guamuhaaya* (Garrido et al. 1991), and *A. agueroi* Diaz et al. (1998).

**Etymology:** Derived from the Greek *chamae* (on the ground) and *leo* (lion), "que indica sus afinidades con camaleones" (Cochran 1838: 72), plus the termination *-lis*, "que trae[n] á la memoria la del nombre bárbaro de la familia" (Cochran 1838:73).

***Ctenocercus Fitzinger 1843 [nobis], converted clade name***

**Synonyms:** *Anolis* of Nicholson et al. (2012).

**Definition:** The most inclusive crown clade containing *Anolis carolinensis* Voigt 1832 but not *A. auratus* Daudin 1802, *A. bimaculatus* (Sparrman 1784), *A. armouri* (Cochran 1934), *A. cuvieri* Merrem 1820, *A. semilineatus* Cope 1864, *A. vermiculatus* Duméril and Bibron 1837 and *A. punctatus* Daudin 1802.

**Reference phylogeny:** Figure 2 of this study.

**Comments:** A clade corresponding to the core of the one here named *Ctenocercus*, composed of the *carolinensis*, *argillaceus*, and *alutaceus* species groups of Williams (1976a) and *A. sheplani* (but not *A. lucius*), was first inferred by Jackman et al. (1999). This clade was partially corroborated by Poe (2004), who included

some additional species from those groups, except that some of members of the *alutaceus* species group (*A. cyanopleurus*, *A. spectrum*) were excluded. It was fully corroborated by [Nicholson et al. \(2005\)](#); see also [Alföldi et al. 2011](#)), who included still more species of the three species groups. Finally, [Nicholson et al. \(2012; Fig. 5 but not Fig. 4\)](#) and this study placed *A. argenteolus* and *A. lucius* as sister to the above-described clade, although with weak support. [Nicholson et al. \(2012\)](#) applied the name *Anolis* to the larger clade (i.e., the smallest clade containing both *A. carolinensis* and *A. lucius*). However, as we have argued above, that name has a much longer association with the clade of all anoles (lizards descended from the first one possessing adhesive toe pads and a dewlap synapomorphic with those in *A. carolinensis*). Because a fundamental principle of biological nomenclature is that a name is not to be used for more than one taxon (clade), and because the name *Anolis* has a much longer association with the clade of all anoles, we apply the name *Anolis* to that clade and resurrect the name *Ctenocercus* [Fitzinger 1843](#) (based on *A. carolinensis*) for the clade to which the name *Anolis* was applied by [Nicholson et al. \(2012\)](#). Although there is an older name, *Acantholis* [Cocteau 1836](#), that is also based on a member (*A. loysianus*) of the clade here named *Ctenocercus*, that name is more appropriately applied to a smaller clade including *A. loysianus*, such as the *argillaceus* species group (see [Varona 1985](#)). Note also that *Anolis* of [Guyer and Savage \(1986, 1992\)](#) and [Savage and Guyer \(1989\)](#) is not equivalent to *Anolis* of [Nicholson et al. \(2012\)](#) or to our *Ctenocercus*; in the context of our inferred phylogeny, *Anolis* of those earlier studies is a polyphyletic group.

**Inferred composition:** *carolinensis* subgroup of [Williams \(1976a\)](#) = *carolinensis* group of [Burnell and Hedges \(1990\)](#); see [Garrido and Hedges \[2001\]](#) for more recently described species related to *A. isolepis*; the name *Pseudoequestris* [Varona \(1985\)](#) is appropriate for the largest crown clade containing *A. isolepis* but not *A. carolinensis*), *argillaceus* species group of [Williams \(1976a\)](#) = *argillaceus* series of [Burnell and Hedges \(1990\)](#) = *Acantholis* sensu [Varona \(1985\)](#); see [Navarro et al. \[2001\]](#), and [Navarro and Garrido \[2004\]](#), for more recently described members of this group), *angusticeps* subgroup of [Williams \(1976a\)](#) = *angusticeps* group of [Burnell and Hedges \(1990\)](#) = *Brevicaudata* of [Varona \(1985\)](#); see [Estrada and Hedges \[1995\]](#) and [Diaz et al. \[1996\]](#) for more recently described members of this group), *sheplani* series of [Burnell and Hedges \(1990\)](#), *alutaceus* species group of [Williams \(1976a\)](#) = *alutaceus* series of [Burnell and Hedges \(1990\)](#) = *Macroleptura* of [Garrido \(1975\)](#); see [Garrido and Hedges \[1992\]](#) for more recently described members of this group), *lucius* species group of [Williams \(1976a\)](#) = *lucius* group of [Burnell and Hedges \(1990\)](#) = *Gekkoanolis* of [Varona \(1985\)](#).

**Etymology:** Derived from the Greek *ktenos* (a comb) and *kerkos* (tail).

***Ctenonotus* [Fitzinger 1843](#) [nobis], converted clade name**

**Synonyms:** *crstatellus* series (informal) of [Gorman et al. \(1980\)](#).

**Definition:** The least inclusive crown clade containing *Anolis bimaculatus* ([Sparman 1784](#)), *A. cristatellus* [Duméril and Bibron 1837](#) and *A. distichus* [Cope 1861](#).

**Reference phylogeny:** [Figure 3](#) of this study.

**Comments:** A close relationship between the *bimaculatus* series (including *Anolis distichus*) and the *crstatellus* series was hypothesized by [Etheridge \(1959\)](#) and corroborated by subsequent workers (e.g., [Gorman et al. 1980](#); [Jackman et al. 1999](#); [Brandley and de Queiroz 2004](#); [Poe 2004](#); [Nicholson et al. 2005, 2012](#); [Alföldi et al. 2011](#)), who removed *A. cybotes* and its relatives from the *crstatellus* series, placed *A. distichus* and its relatives in their own series (because it was unclear whether they were more closely related to *A. bimaculatus* versus *A. cristatellus*), and transferred *A. acutus*, *A. evermanni*, and *A. stratulus* from the *bimaculatus* series to the *crstatellus* series. The name *Ctenonotus* (based on *Lacerta bimaculata* [Sparman 1784](#)) was originally applied by [Fitzinger \(1843\)](#) to what now appears to be a polyphyletic group. It was resurrected for a questionably monophyletic group composed of the *bimaculatus*, *crstatellus*, and *cybotes* series by [Guyer and Savage \(1986\)](#), and applied explicitly, although informally, to the least inclusive clade containing *A. bimaculatus*, *A. watsii*, *A. distichus*, *A. cristatellus*, and *A. evermanni* by [Brandley and de Queiroz \(2004\)](#); a similar use was adopted by [Nicholson et al. \[2012\]](#) in the context of rank-based nomenclature). We have defined the name formally using a simplified version of the informal definition given by [Brandley and de Queiroz \(2004\)](#).

**Inferred composition:** *bimaculatus* series ([Lazell 1972](#); [Gorman and Kim 1976](#); [Schneider et al. 2001](#)), *crstatellus* series ([Brandley and de Queiroz 2004](#)), *distichus* series [Burnell and Hedges \(1990\)](#).

**Etymology:** Derived from the Greek *ktenos*, comb, and *notos*, back, presumably in reference to the dorsal crest of lizards of the originally included species.

***Norops* [Wagler 1830](#) [nobis], converted clade name**

**Synonyms:** Beta section (informal) of [Etheridge \(1959\)](#), *Noropini* and *Noropina* of [Varona \(1985\)](#).

**Definition:** The crown clade for which the beta type of caudal vertebrae, in which the autotomic caudal vertebrae bear long, anterolaterally directed and distally bifurcated transverse processes that originate posterior to the autotomy septa ([Etheridge 1959](#), [Etheridge 1967](#)),

as inherited by *Anolis auratus* Daudin 1802, is an apomorphy relative to other crown clades.

**Reference phylogeny:** Figure 3 of this study.

**Comments:** Monophyly of the beta anoles was inferred by Etheridge (1959) on the basis of the unique and derived morphology of their caudal vertebrae, and this inference has been corroborated in numerous subsequent studies (e.g., Guyer and Savage 1986; Jackman et al. 1999; Poe 2004; Nicholson et al. 2005, 2012; Alföldi et al. 2011; this study). Wagler (1830) proposed the name *Norops* for the single species *Anolis auratus*. He distinguished *Norops* from other anole “genera” that he recognized (*Dactyloa*, *Draconura*) by, among other things, weakly developed toepads. Boulenger (1885) used *Norops* for anoles with a toepad in which the distal phalanges are not raised above the pad, which is one component of weak pad development, and included only *A. auratus* and *A. ophiolepis* (in retrospect, a polyphyletic group). By the time of Etheridge (1959), *A. meridionalis* had been added, but Etheridge did not consider the included species to be closely related and thus did not recognize *Norops*. Savage and Talbot (1978) applied the name *Norops* to Etheridge’s (1959) beta section, a use that has been followed by some subsequent authors (e.g., Guyer and Savage 1986, 1989; Savage and Guyer 1989; Nicholson 2002; Nicholson et al. 2012). Conveniently, the crown clade diagnosed by the beta type of caudal vertebrae is also the smallest crown clade containing the species previously included in (the polyphyletic) *Norops* (e.g., by Boulenger [1885], and authors just prior to Etheridge [1959]): *A. ophiolepis*, *A. auratus* and *A. meridionalis*. Consequently, we apply the name *Norops* explicitly to that clade by providing it with a phylogenetic definition based on the derived morphology of the caudal vertebrae.

**Inferred composition:** *Trachypilus*, *Placopsis*, and *Draconura* (see below).

**Etymology:** Derived from the Greek *norops* (bright, flashing, gleaming), presumably in reference to the coloration of *Anolis auratus*.

***Trachypilus* Fitzinger 1843 [nobis], converted clade name**

**Synonyms:** *sagrei* species group (informal) of Williams (1976a), *sagrei* series (informal) of Burnell and Hedges (1990) and Nicholson (2002), *Norops sagrei* species group of Nicholson et al. (2012). The *sagrei* series (informal) of Etheridge (1959) refers to a paraphyletic group originating in approximately the same ancestor (see Comments).

**Definition:** The most inclusive crown clade containing *Anolis sagrei* Duméril and Bibron 1837 but not *A.*

*valencienni* Duméril and Bibron 1837 and *A. chrysolepis* Duméril and Bibron 1837.

**Reference phylogeny:** Figure 3 of this study.

**Comments:** Etheridge (1959) recognized the *sagrei* series for *Anolis sagrei* and its close relatives with the exception of *A. ophiolepis*, although he noted that *A. ophiolepis* and *A. valencienni* were not distinguishable from the members of the *sagrei* series in terms of the osteological characters that he studied. Williams (1976a) assigned both *A. ophiolepis* and *A. valencienni* to the *sagrei* series. Chromosomal evidence led Gorman and Atkins (1968) to question the referral of *A. valencienni* to the *sagrei* series, and Gorman (1973) later to remove it (see Comments on *Placopsis* for additional details). Subsequently, except for the addition of newly described species, the composition of the *sagrei* series has been stable (e.g., Burnell and Hedges 1990; Rodriguez-Schettino 1999; Cádiz et al. 2013). Monophyly of the *sagrei* series was inferred by Guyer and Savage 1986 from then available karyological data, and it has subsequently been corroborated repeatedly by DNA sequence data sampled from increasing numbers of species and genes (Hass et al. 1993; Jackman et al. 1999; Nicholson 2002; Poe 2004; Nicholson et al. 2005, 2012; Alföldi et al. 2011; this study). Varona (1985) applied the name *Trachypilus Fitzinger 1843* to the Cuban beta anoles (*sagrei* series or species group) except *A. ophiolepis*—that is, to a paraphyletic group originating in the same ancestor as that of the *sagrei* series of more recent authors (e.g., Burnell and Hedges 1990; Nicholson 2002). Although the name has rarely been used since then, because a clade composed of the members of the *sagrei* series has been inferred repeatedly, consistently and with strong support, we here formalize the application of the name *Trachypilus* to the *sagrei* series by providing it with a phylogenetic definition.

**Inferred composition:** *sagrei* series (Nicholson 2002) or species group (Rodriguez-Schettino 1999).

**Etymology:** Derived from the Greek *trachys* (rough) and *pilos* (hair, cap, ball), presumably in reference to the keeled scales in the parietal region of *Anolis sagrei*.

***Placopsis* Gosse 1850 [nobis], converted clade name**

**Synonyms:** *grahami* series (informal) of Shochat and Dessauer (1981; see also Savage and Guyer 1989; Burnell and Hedges 1990), *Norops valencienni* species group of Nicholson et al. (2012).

**Definition:** The most inclusive crown clade containing *Anolis valencienni* Duméril and Bibron 1837 but not *A. sagrei* Duméril and Bibron 1837 and *A. chrysolepis* Duméril and Bibron 1837.

**Reference phylogeny:** Figure 3 of this study.

**Comments:** Based on skeletal morphology, Etheridge (1959) proposed the *grahami* series for the native beta anoles of Jamaica (including *Anolis conspersus* of the Cayman Islands but not including *A. sagrei*, a species of Cuban origin) with the exception of *A. valencienni*, which he considered more closely related to the *sagrei* series (see also Williams 1976a). When *A. valencienni* was found to have an identical karyotype to members of the *grahami* series, Gorman and Atkins (1968) questioned its relationship to the *sagrei* series, and Gorman (1973) placed it in a series of its own. Based on immunological distances, Shochat and Dessauer (1981) transferred *A. valencienni* to the *grahami* series, and monophyly of the *grahami* series, including *A. valencienni*, has been corroborated by numerous subsequent studies (Hedges and Burnell 1990; Jackman et al. 1999; Jackman et al. 2002; Nicholson 2002; Poe 2004; Nicholson et al. 2005, 2012, this study). Because the monophyly of the *grahami* series has been inferred in numerous studies, and because the group does not have a formal name, we here select such a name for the *grahami* series. There are two preexisting names based on a member of the *grahami* series: *Xiphocercus* Fitzinger 1843 and *Placopsis* Gosse 1850 (both based on *A. valencienni*), neither of which has been used for over 50 years and neither of which has been applied previously to the *grahami* series as a whole. *Xiphocercus* has been used more recently, but it was applied to what is now considered a polyphyletic group composed of *A. valencienni* and either *A. heterodermus* Boulenger (1885) or *A. darlingtoni* (Cochran 1935). Although *Xiphocercus* is older, it is similar in both spelling and etymology to *Xiphosurus*, the name of another anole clade. In order to avoid confusion with that other clade, we have selected the younger name *Placopsis* and applied it to the *grahami* series with a phylogenetic definition.

**Inferred composition:** *grahami* series (Burnell and Hedges 1990; Hedges and Burnell 1990; Jackman et al. 2002).

**Etymology:** Derived from the Greek *plakos* (a broad plate) and *opsis* (the face), presumably in reference to the large, flat scales in the frontal region of *Anolis valencienni*.

***Draconura* Wagler 1830 [nobis], converted clade name**

**Synonyms:** *Norops auratus* species group of Nicholson et al. (2012).

**Definition:** The most inclusive crown clade containing *Anolis chrysolepis* Duméril and Bibron 1837 but not *A. sagrei* Duméril and Bibron 1837 and *A. valencienni* Duméril and Bibron 1837.

**Reference phylogeny:** Figure 4 of this study.

**Comments:** Monophyly of the subclade of *Norops* (beta anoles) composed of all species except the members of the (predominantly) Cuban *Trachypilus* and the Jamaican

*Placopsis* clades was inferred from a limited sample by Jackman et al. (1999) and has been corroborated subsequently with larger samples of both species and characters (Poe 2004; Nicholson et al. 2005, 2012; Alföldi et al. 2011; this study). The members of this species-rich clade are predominantly mainland forms. The oldest pre-existing higher taxon names based on members of this clade are *Draconura* (for *Anolis chrysolepis*) and *Norops* (for *A. auratus*), both proposed by Wagler (1830). *Norops* has come to be associated with the (more inclusive) clade of anoles with the beta type of caudal vertebrae (see above). In contrast, *Draconura* has been little used for over 100 years, since Boulenger (1885) treated it as a synonym of *Anolis* (e.g., Schmidt 1919; Barbour 1923; Dunn 1939; Etheridge 1959; Williams 1976a,b; Guyer and Savage 1986; Savage and Guyer 1989; Nicholson 2002; Poe 2004; Nicholson et al. 2012). The lone exception was Varona (1985), who applied the name *Draconura* to what now appears to be a polyphyletic group composed of (at least) *A. chrysolepis* and Cuban grass anoles of the *alutaceus* species group or series (= *Macroleptura*; see *Ctenocercus*, above). Because the “mainland” clade within the beta anoles has been supported repeatedly but currently lacks a formal name, and because the name *Draconura* Wagler 1830 is based on a member of that clade and does not have a conflicting traditional use, we here establish that name for the clade of all beta anoles that are more closely related to *A. chrysolepis* than to *A. sagrei* and *A. valencienni* by providing it with a phylogenetic definition.

**Inferred composition:** *Norops auratus* species group (Nicholson et al. 2012).

**Etymology:** Derived from the Greek *drakon* (dragon) and *oura* (tail).

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