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It is time for a new classification of anoles (Squamata: Dactyloidae)

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Abstract

In this essay, we review concepts of taxonomic categories of anoles, reanalyze accumulated characteristics of these lizards, use these analyses to summarize the topology of the phylogenetic tree for anoles, and use consistent major branches of this topology to recommend a classification scheme for this large group of squamates. We then use this new taxonomy to draw inferences about the evolution of habitat use, as well as the geologic ages and geographic distribution of anole lineages. Our taxonomy eliminates problems of paraphyly inherent in previous classifications by elevating eight major lineages to generic status (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, *Dactyloa*, *Deiroptyx*, *Norops*, and *Xiphosurus*), providing diagnoses of those genera, and then doing the same for species groups within each genus. With the exception of 19 species, the contents of our generic categories are consistent with all recent phylogenetic reconstructions. Thus, the revised taxonomy appears to provide a stable classification for at least 95% of the 387 species currently recognized and included in our treatment of the group. We argue that these lizards originated in South America ~130 ma, where they were large in size and occupied niches focused on the canopy of rainforest trees. The radiation diverged into eight genera 125–65 ma within a volcanic island arc that connected North and South America. This evolutionary diversification generated three genera (*Deiroptyx*, *Dactyloa*, and *Xiphosurus*) that retained an ancestral large size and canopy niche focus and five genera (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, and *Norops*) that became small, with niches focused toward the ground. The complicated divergence and accretion events that generated the current conformation of the Antillean islands, and eventually closed the Panamanian Portal, transported six island genera to their current centers of diversity (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, *Deiroptyx*, and *Xiphosurus*), leaving two genera on the mainland (*Dactyloa* and *Norops*). Our historical reconstruction makes *Norops* a much older radiation than previous reconstructions, allowing basal diversification of this species-rich lineage to occur on mainland terrains that eventually separated from the mainland to become parts of Cuba and Jamaica. This early diversification extended into northern South America, where a basal lineage of *Norops* coevolved with *Dactyloa* prior to the mainland-island separation.

Key words: Reptilia, lizards, systematics, biogeography, ecomorphology, evolution

Introduction

This monograph is about a group of iguanian lizards popularly referred to as anoles and constituting the family Dactyloidae (Townsend *et al.* 2011). For those who regard the family to be monotypic it is often asserted that *Anolis* (*sensu lato*), with nearly 400 valid species, is the largest genus of terrestrial vertebrates (for the sources of the name anole see Appendix I). That the species involved are among the most studied in an array of ecological, behavioral, and physiological contexts is a vital reason for their evolutionary relationships to be critically reevaluated. Systematic progress in this regard has been delayed by an extremely conservative taxonomic approach to recognizing the diversity within the group and its extraordinarily ancient historical roots.

Our primary objective in this paper is to review the classification of the family Dactyloidae and evaluate the evidence for the existing taxonomy. Our second goal is to determine the monophyly of its formal and informal taxa above the species level (i.e., genera and species groups). In order to attain these goals, we perform a phylogenetic analysis based on morphological, molecular, and karyological features to establish relationships among 231 dactyloid species. The principal result of this analysis leads us to propose a new classification consistent with the inferred history and the goal of recognizing major monophyletic lineages. In addition, we use our phylogeny 1) to examine current ideas on ecologic valence for a wide array of dactyloid species and to develop a hypothesis that provides a historical explanation for the evolution of habitat use, and 2) to propose a bold hypothesis of the biogeographic history of the family within the constraints of the phylogeny inferred here, the latest known fossils, and a paleogeographic interpretation of the deep history of the West Indies, North America, Mesoamerica, and South America.

Current Systematic Status

All reviews of the present classification of anoles must begin with an acknowledgement of the monumental work of Richard E. Etheridge (1960). This highly cited—but never published—monograph was the first to comprehensively investigate anole relationships through a comparison of osteological characters polarized via precursors to modern parsimony methods. On the basis of his comparisons, he proposed a hypothesis of relationships and erected a classification scheme for anoles. His conclusions predated modern phylogenetic methods, but were astute in the proposed relationships, many of which were supported by later authors (e.g., Guyer and Savage, 1986, 1992; Poe, 2004), recent molecular studies (e.g., Glor *et al.* 2005; Mahler *et al.* 2010; Nicholson *et al.* 2005), and the present paper. Etheridge (1960) divided the genus *Anolis* into two groups—termed 'alpha and beta sections'—based upon the condition of their caudal vertebrae. The alpha section lacked the anterolaterally-directed transverse processes that are present on the vertebrae of beta section members. He further subdivided each section into groups termed 'series' on the basis of several combinations of osteological characters. Most important among these characters were interclavicle shape, parasternal rib formulae, number of anterior aseptate vertebrae, presence or absence of a splenial, and presence or absence of caudal autotomy. In this same work, he recognized three additional anole genera (*Chamaeleolis, Chamaelinorops,* and *Phenacosaurus*) and hypothesized that they were nested within *Anolis* (Fig. 1). He postulated that each section was monophyletic, and also recognized a fourth anole genus, *Tropidodactylus* (monotypic for *T. onca*), as being a beta section member, but was unsure where within that section it belonged. The recognition of these other dactyloid genera rendered *Anolis* paraphyletic, but he did not propose a resolution to this problem.

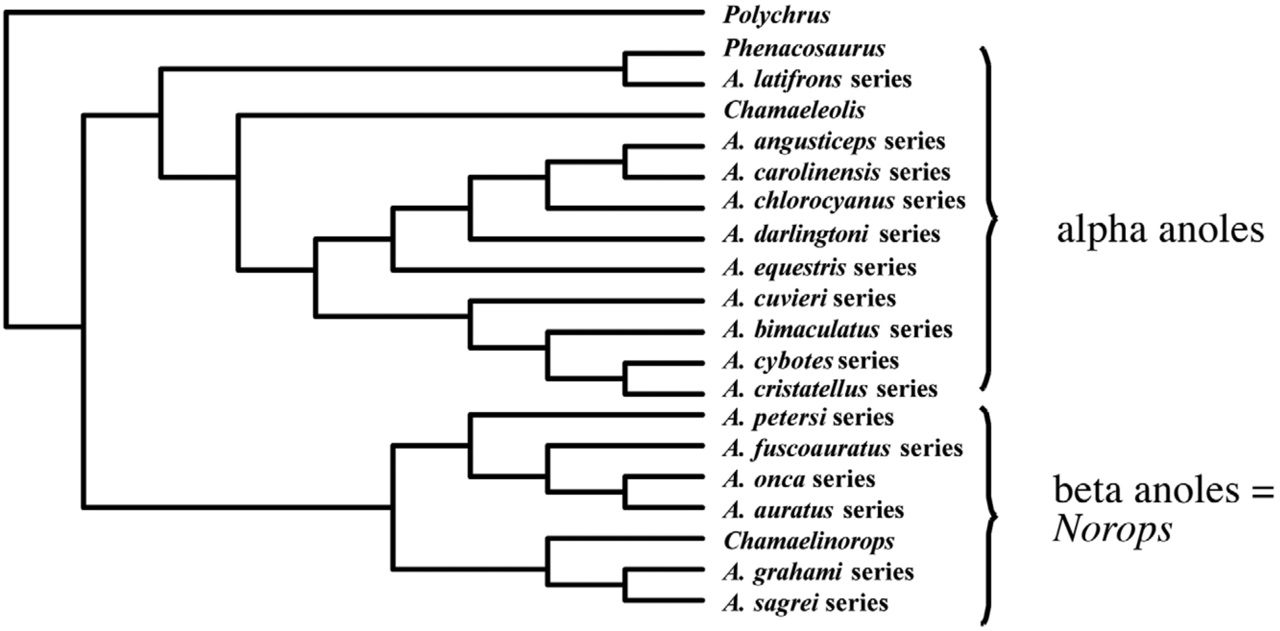


FIGURE 1. Representation of Etheridge's (1960) hypothesis of relationships for dactyloid lizards.

Williams (1976a, 1976b) expanded upon Etheridge's (1960) classification by incorporating additional morphological and some ecological characters. In contrast to Etheridge's evolutionary approach, Williams employed a phenetic approach and recognized several informal groups. He subdivided several of Etheridge's series into subseries and erected several new species groups within series. Williams separated *Phenacosaurus*, *Chamaeleolis*, and *Chamaelinorops* from the rest of the anoles because he thought they were ancestral to his concept of *Anolis*.

A major advance of great promise for aiding in tracing evolution within the Dactyloidae were the detailed studies of karyology by George C. Gorman and associates summarized by him in 1973. In the 1980s additional karyological data generated by the Gorman group were coupled often with papers examining immunological distances to investigate the relationships within subgroups of dactyloids. The most notable of these are Gorman *et al.* (1980), Lieb (1981), and Wyles and Gorman (1981). Shochat and Dessauer (1981) also contributed an important albumin-based analysis of West Indian anoles. These studies raised questions regarding the relationships among several of the Etheridge/Williams infrageneric groupings. As pointed out by Guyer and Savage (1986), however, the albumin-protein data in most of these papers were analyzed phenetically, and only in the Gorman *et al.* (1980) study was a cladistic approach used for a subset of karyological data. Gorman *et al*. (1983) combined allozyme and karyotype data, and none of their trees was congruent with the groupings of Williams (1972). Unfortunately, there have been few advances in karyotype studies for most lizard groups, including dactyloids, in the interim.

The first phylogenetic analysis of relationships among the anoles was conducted by Guyer and Savage (1986). Their study incorporated published data, including Etheridge's (1960) osteological characters, and sought to test the anole relationships of Etheridge and Williams. The phylogeny of Guyer and Savage (1986; Fig. 2a) placed *Chamaeleolis, Chamaelinorops*, and *Phenacosaurus* at the base of the tree, supporting a monophyletic *Anolis*. Their analyses also supported the monophyly of Etheridge's (1960) beta section, but the alpha section was not monophyletic. Guyer and Savage (1986) proposed subdivision of the genus *Anolis (sensu lato)* into five separate genera and applied the appropriate senior synonyms to each one: *Anolis* (*sensu stricto*), *Ctenonotus*, *Dactyloa,* *Norops*, and *Semiurus* (later replaced by *Xiphosurus*, its senior synonym). Their results were criticized by Williams (1989) and Cannatella and De Queiroz (1989), but Guyer and Savage (1992) addressed each of the criticisms, reanalyzed their data, and came to the same overall conclusions as in their earlier paper (Fig. 2b). Some herpetologists did adopt this new classification. Others, in an all-or-nothing approach to classification, felt that all proposed genera must be solidly supported clades, and that recognition of any genera that were not fully resolved meant none of the proposed system could be accepted. Most of the proposed genera in Guyer and Savage's (1986, 1992) scheme were demonstrated consistently to be monophyletic, but in some analytical results their concepts of *Anolis* (*sensu stricto*) and *Ctenonotus* formed unresolved groups. All of the above studies were reviewed in detail by Crother (1999).

The first comprehensive molecular approach to dactyloid classification was published by Losos *et al*. (1998) and Jackman *et al*. (1999). They used DNA sequence data from several species across the genus, primarily from the Caribbean, but with some mainland representatives, and employed modern statistical approaches to evaluate anole relationships. Their trees (Fig. 3) showed points of agreement and disagreement with those of Etheridge (1960), Williams (1976a, 1976b), and Guyer and Savage (1986, 1992). The beta section of anoles formed a monophyletic group, but the alpha section did not. In addition, *Chamaeleolis, Chamaelinorops*, and *Phenacosaurus* nested well within *Anolis* (*sensu lato*), as in Etheridge (1960), resulting in informal synonymy of these nominal genera with *Anolis*. While they did not address classification in their papers, nor analyze the subdivisions statistically, both (Jackman *et al*. 1997; Losos *et al*. 1998) showed topological support for most of the genera recognized by Guyer and Savage (1986, 1992).

Burnell and Hedges (1990), in an electrophoretic-based study using slow-evolving protein loci, proposed a new classification of 21 species series and a myriad of species groups and subgroups for West Indian anoles. They dismissed the work of Guyer and Savage on the basis of the critiques of the 1986 paper, an oversight committed by other authors and criticized by Crother (1999) in his review of Caribbean anole phylogeny. They concluded that each series was essentially restricted geographically to one of the four major Greater Antillean blocks (Cuba, Hispaniola, Puerto Rico Bank) or to either the Northern or Southern Lesser Antilles. No subsequent papers adopted their arrangement.

Nicholson (2002) conducted a statistical test of the monophyly of most of the proposed groups within beta section anoles. She found no support for the monophyly of three series (*auratus, fuscoauratus*, and *petersi* series), two subseries (*auratus* and *laeviventris*), or five species groups (*auratus, fuscoauratus, humilis, laeviventris,* and *petersi*). Three series were supported (*sagrei* series from Cuba, *grahami* series from Jamaica, and *onca* series from South America), although one of these, the *onca* series, contains only two species, making it unclear whether this group warrants its own series designation. Two species groups (*crassulus* and *lemurinus*) were equivocal in terms of their support from the molecular data, and their status remains uncertain. Several groups endemic to Mexico were not examined because sufficient samples were not available. Subsequent studies (Nicholson, 2005; Nicholson *et al*. 2005, 2007) with greater taxon sampling and molecular data were consistent with Nicholson (2002), Losos *et al*. (1998), and Jackman *et al*. (1999), in terms of support (or lack of support) for the several taxonomic groups.

A major advance in understanding dactyloid evolution is the total evidence phylogenetic analysis of Poe (2004) based on 174 species, 91 morphological characteristics, and additional characters from the literature for allozyme, ribosomal RNA, chromosomes, immunological distances, mitochondrial DNA, and nuclear DNA data sets. In Poe's optimal tree, with few exceptions, there are many clearly diagnosable monophyletic groups. In spite of the well-supported structure of his tree, Poe chose the conservative route by placing all species-level taxa in the single genus *Anolis* (*sensu lato*) and made no changes in taxonomy except to implicitly synonymize *Chamaeleolis* with *Anolis. Chamaelinorops* and *Phenacosaurus* had been placed previously in the synonymy of *Anolis* by Hass *et al*. (1993) and Poe (1998), respectively. For convenience, Poe used the Savage and Guyer (1989) treatment of species series and groups, many of which he found to be non-monophyletic; he noted that none of Williams' (1976a, 1976b) series or groups are monophyletic either. As a result he did not propose any system of infrageneric groupings. We were disappointed by his conclusions because they did so little to enhance the systematics of Dactyloidae, and therefore obscured the vast biodiversity of the family by making it monotypic. Additionally, these conclusions inhibited detailed treatment of ecological and biogeographic questions because they failed to eliminate non-monophyletic taxa. We regard Poe's decisions as a missed opportunity to capitalize on a seminal and—in every other aspect—magnificent opus. It is because of these concerns that we undertook the preparation of this paper.

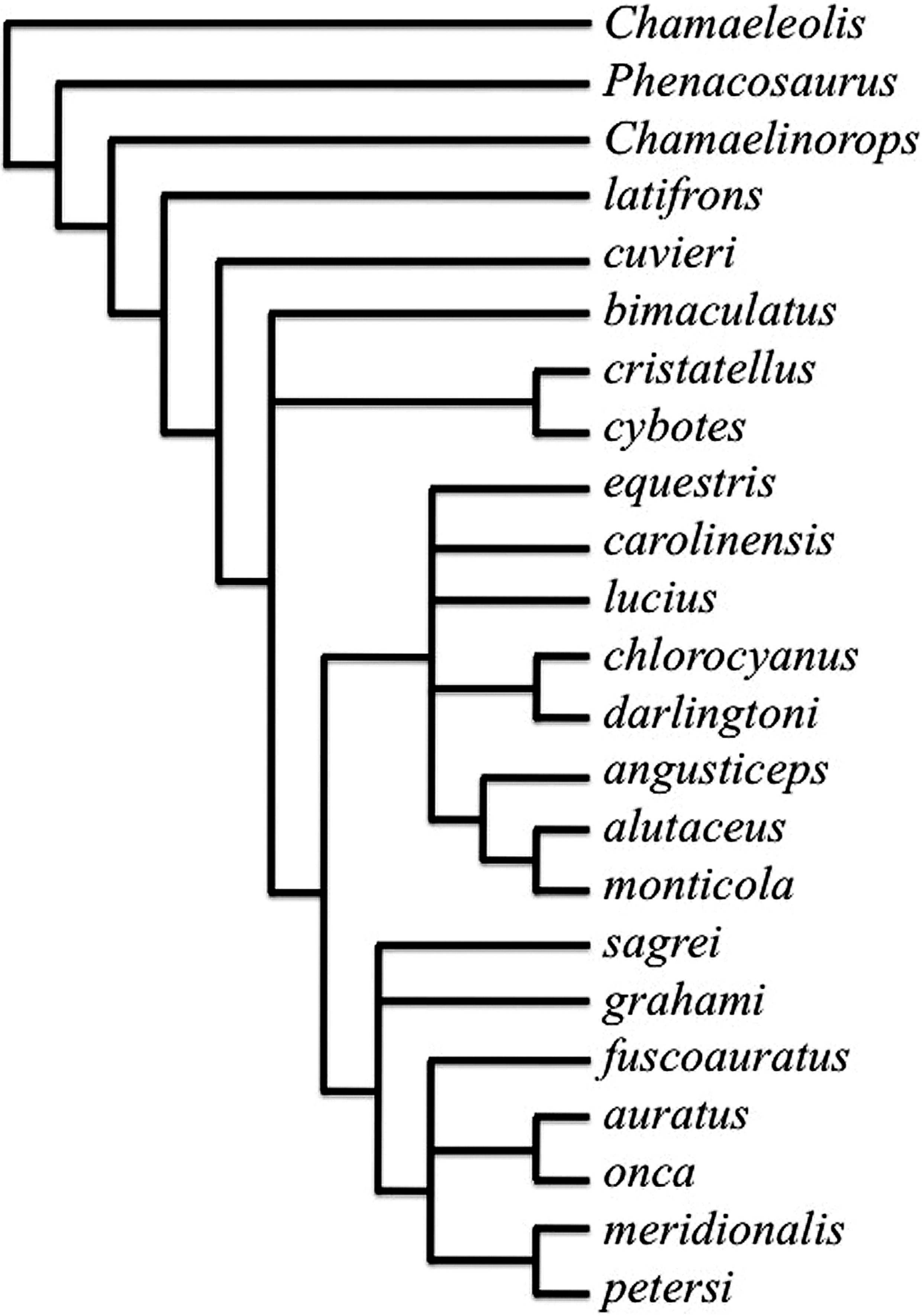


FIGURE 2a. Representation of the hypothesis of relationships for dactyloid anoles by Guyer & Savage (1986).

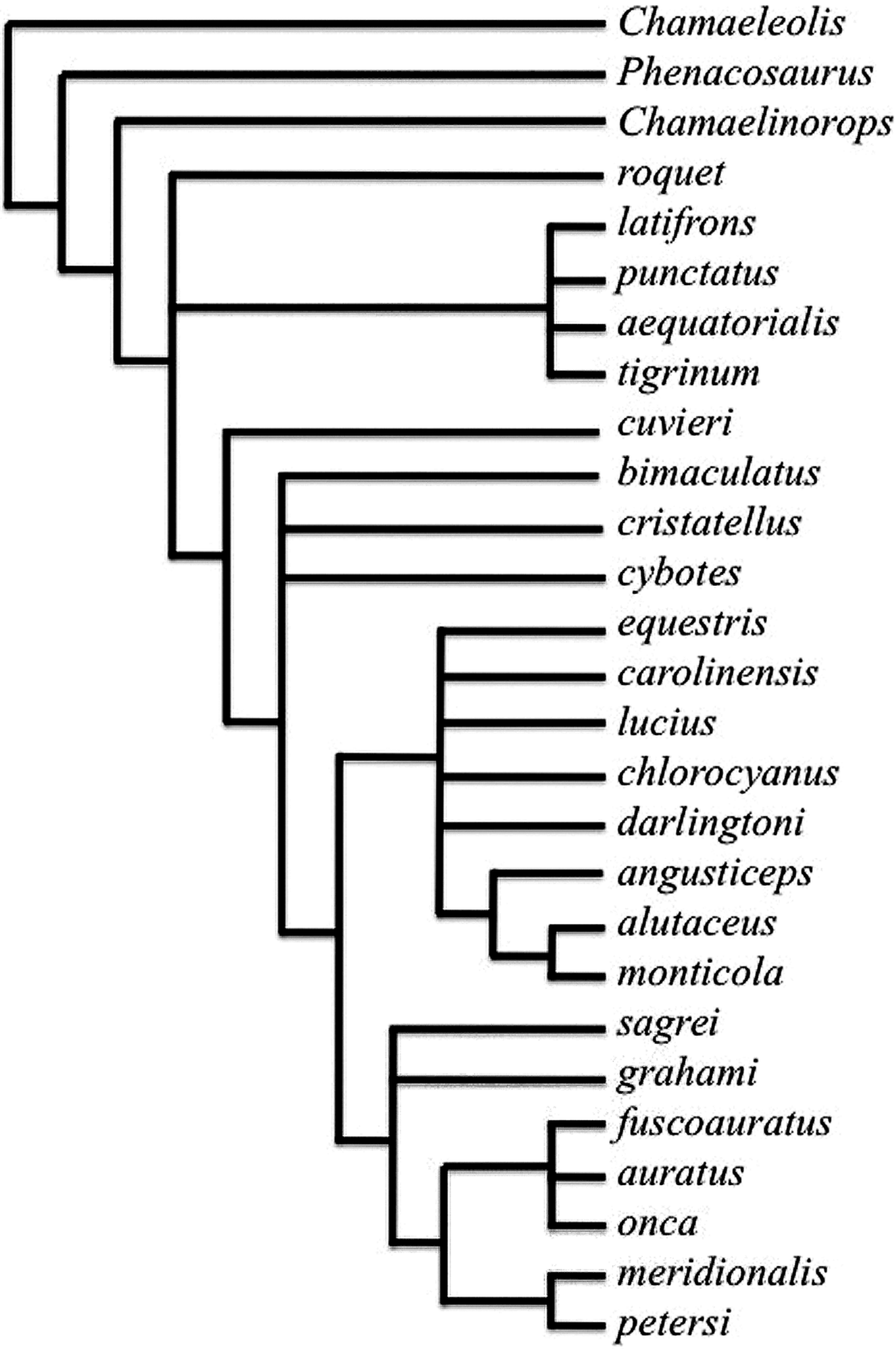


FIGURE 2b. Representation of the hypothesis of relationships for dactyloid anoles by Guyer & Savage (1992).

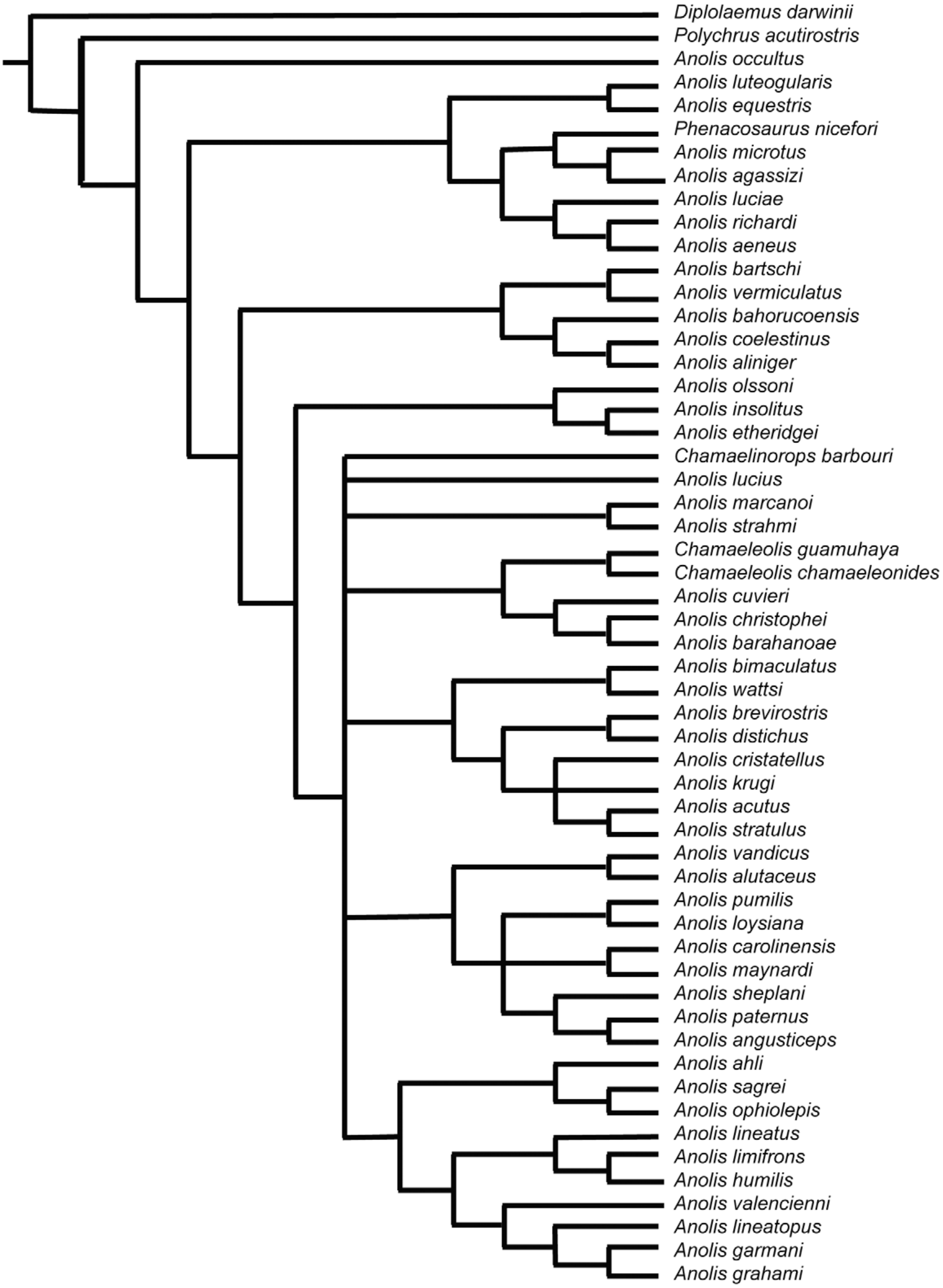


FIGURE 3. Representation of the hypothesis of relationships among dactyloid anoles by Losos *et al*. 1998 and Jackman *et al*. 1999. While figures from both studies are virtually identical, our representation is derived largely from Jackman *et al.* (1999) because the taxon names are not visible in Losos *et al.* (1998).

Phylogenetic Analyses

We investigated phylogenetic relationships among species of *Anolis* (*sensu lato*) by conducting two complementary sets of analyses. The first was a reanalysis of molecular characters from Nicholson *et al.* (2005)

supplemented with previously unpublished molecular data (*Norops medemi, N. townsendi, Dactyloa gorgonae,* and *D. princeps*). In these analyses *Basiliscus plumifrons* and *Polychrus acutirostris* were used as outgroups.

A partitioned Bayesian analysis was performed using the program Mr. Bayes v 3.0 (Huelsenbeck *et al*. 2001; Ronquist and Huelsenbeck, 2003). Eight partitions were recognized, corresponding to each of the gene/gene regions within the dataset (*ND2* gene, *tRNA*^{Trp}, *tRNA*^{Ala}, *tRNA*^{Asn}, *tRNA*^{Cys}, *tRNA*^{Tyr}, the origin of light-strand replication, and a portion of the *CO1* gene). The model of nucleotide evolution for each partition was selected using the program ModelTest (Posada and Crandall, 1998). AIC criteria were used to select the models of evolution and were as follows: GTR+I+G for *ND2, tRNA*^{Trp}, *tRNA*^{Ala}, and *tRNA*^{Asn}; SYM+G for *tRNA*^{Cys} and *CO1*; TVMef+I+G for the origin of light strand replication; and TVMef+G for *tRNA*^{Tyr}. Flat priors were employed. An initial run was conducted for 10 billion generations to determine when parameters converged. Subsequently, three additional independent runs were conducted for 20 million generations and analyzed for convergence using Tracer v 1.5 (Rambaut and Drummond, 2007) and AWTY (Wilgenbusch *et al*. 2004). Node support was evaluated via posterior probabilities.

The second analysis combined data from several studies for a more comprehensive approach. Morphological and molecular data from Poe (2004) and molecular data from Nicholson *et al*. (2005, including the new data presented above) were combined and reanalyzed under the Maximum Parsimony criterion using the program PAUP* v4.0b10 (Swofford, 2000)**.** Nine outgroup OTUs were used in the combined data analyses: *Anisolepis undulatus*, *Basiliscus plumifrons*, *Enyalius iheringii*, *Leiocephalus schreibersii*, *Polychrus acutirostris*, *P. marmoratus*, *Urostrophus melanochlorus*, and *U. vautieri*. Unlike Poe (2004), these data were analyzed with equal character weights because—also unlike Poe—we do not think one can, *a priori*, determine the evolutionary value of a character. A heuristic search was conducted with TBR branchswapping. Because of the length of the dataset and number of included characters, the most parsimonious tree (mpt) search strategy was as follows: 1) used CLOSEST addition option to get starting random addition tree length and 2) 1000 repetition random addition searches with 1000 mpts saved. Only trees shorter than the starting tree length were saved, and this was repeated each time the tree length was reduced. The searches continued until five searches in a row failed to infer a shorter tree. Bootstrap proportions were estimated (Felsenstein, 1985) with 1000 replicates of the equally weighted data set.

Phylogenetic Inference

The molecular dataset consisted of 1482 characters for 189 taxa. All datasets converged at approximately 105,000 generations, and a conservative burnin of trees post-120,000 generations was used. Trees were sampled every 1000 generations for a total of 9,880 trees from each run. Majority rule consensus trees were generated for each run and all were identical (see Figs. 4a and 4b). Node support was high throughout the tree with posterior probabilities 90% or greater for most nodes (posterior probabilities of 80–89% is indicated by numbers, less than 80% is indicated by an "*").

The combined morphological and molecular dataset consisted of 1580 characters for 240 taxa. Of these characters, 1198 were parsimony informative. The most parsimonious trees were 29,797 steps with a consistency index of 0.12 and a retention index of 0.48. Parsimony analysis of these data resulted in 4999 most parsimonious trees, the strict consensus of which is depicted in Figures 5a and 5b. Topological relationships among the taxa are overall similar to those from the Bayesian analysis of molecular characters with a few clades placed in alternative locations. Eight major clades appear that are also observed in the Bayesian analysis, and the contents of these clades are almost identical for taxa overlapping in the two data sets. The incongruent taxa are *occulta*, *darlingtoni*, and the sister taxa *argenteolus* + *lucius*. We discuss the details and consequences of the alternative placements below in the systematic section. Many upper nodes are supported by bootstrap values of 80% or more, while deeper nodes possess bootstraps of less that 50% (nodes with greater than 80% bootstrap support show no value, between 50–80% the value is shown, and less than 50% = *). Apomorphies used to diagnose the clades were derived from one of the most parsimonious trees (Appendix II; tree not shown).

Below we discuss the contents of the major clades retrieved, their correspondence with previous studies, and our taxonomic conclusions based upon this combined evidence.

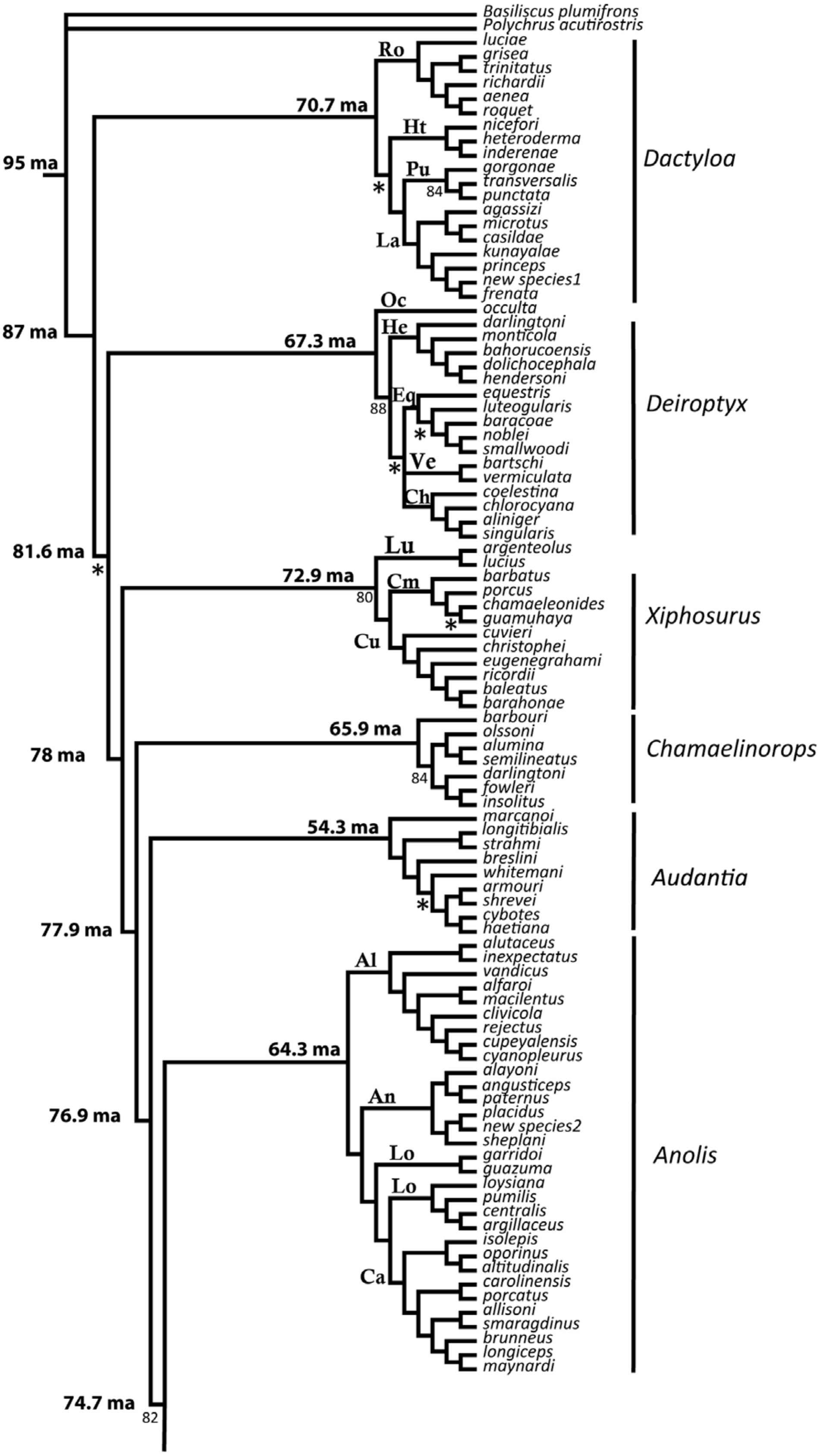


FIGURE 4a. Results of the Bayesian phylogenetic analysis of molecular data from this study. The tree is split in half to accommodate its size. Outgroups are *Basiliscus plumifrons* and *Polychrus acutitrostris*. Nodes with greater than 90% posterior probability have no symbol; posterior probabilities of 80–90% are indicated; less than 80% = *. Names and vertical lines to the right indicate genera we propose to recognize in this study. Two letter abbreviations at nodes indicate species groups we recognize. Dates at major nodes are estimates from our BEAST analysis.

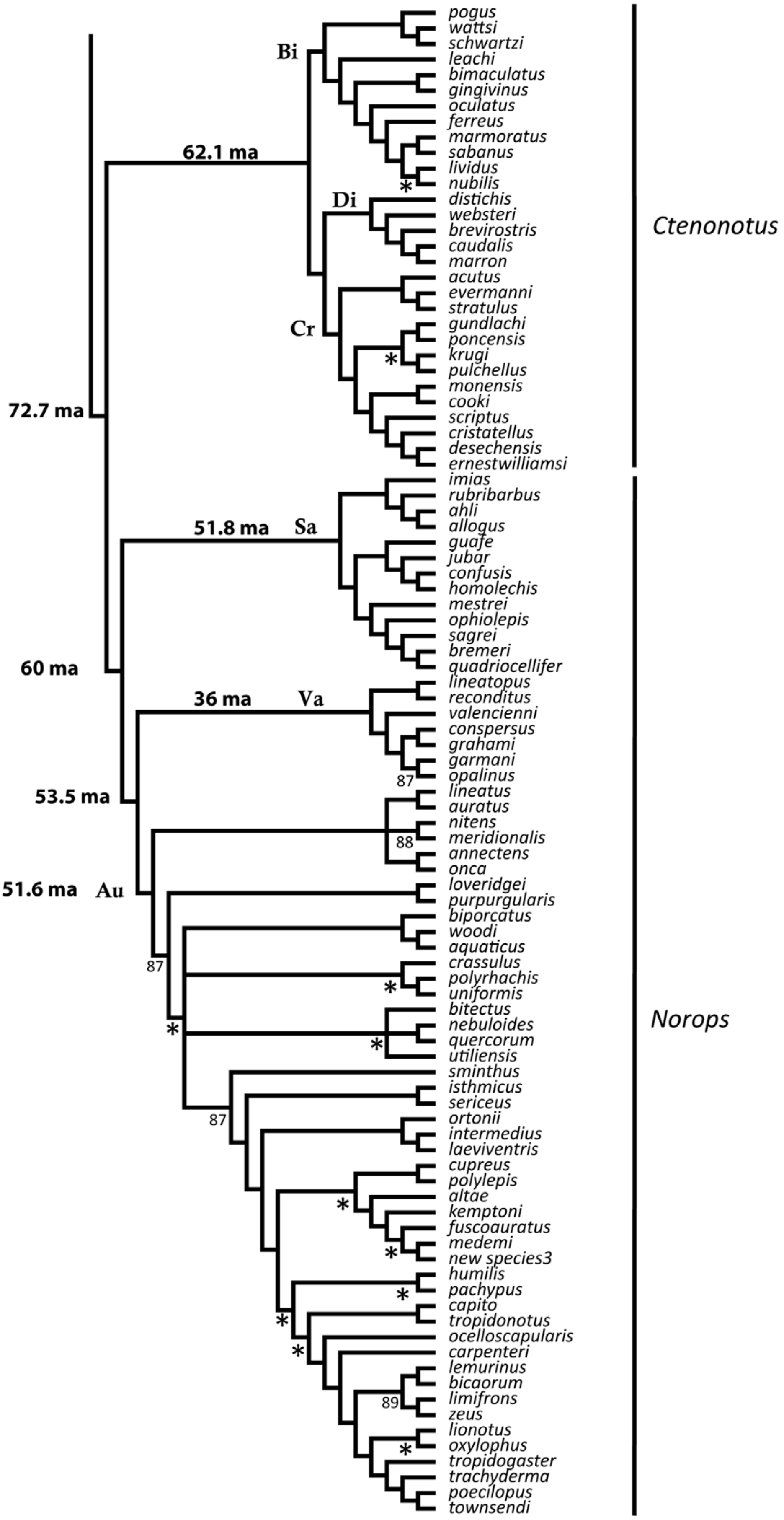


FIGURE 4b. Continued from 4a.

Systematic Accounts

The role of systematics is to advance our understanding of biological diversity in the natural world. Its practitioners are the guardians of the knowledge produced by past generations and responsible for the rational interpretation of new data and their implications. Within this framework, phylogenetic inference has consequences that we think bind its practitioners to produce a systematic classification of the studied organisms. Such a classification must be founded on the inferred evolutionary relationships and dictated by the canon of monophyly. Following the above precepts, in conjunction with our phylogenetic analyses, we recognize eight major evolutionary units (genera) and twenty-two subunits (species groups) of dactyloid lizards (Figs. 4–5). The current practice (following Poe, 2004) of treating all dactyloids as comprising a single genus underemphasizes the evolutionary diversity within the family (as currently recognized) and obfuscates major biological differences among clades. In addition, simply because of the large size of the family (nearly 400 valid species), the single genus concept can be a hindrance to scientific communication regarding evolutionary events and directions of future research. In the following section we describe the principles followed in the adopted classification.

In our classification—and Appendix III—genera and species groups are presented in phylogenetic order, but within these categories species and subspecies are listed alphabetically. Although not advocates of the subspecies concept we list all currently recognized subspecies. We do so because no published analyses have shown them to be invalid and a number are likely to be accorded specific status on further study. We use the informal species group in preference to subdividing genera into formal subgenera. The names of species groups are based on the oldest species-group name among the included taxa. Although genus-group names are available for some of the informal categories, a number of new names would need to be proposed for others if recognized as subgenera. Because most of the species groups contain relatively modest numbers of species, except the *Norops auratus* group, we decided to maintain the informal group convention. Each genus and species group account contains two principal sections: 1) a diagnosis of the taxon based on apomorphies found in our molecular and combined trees; 2) a definition of the taxon based on morphological and karyological features. The unequivocal morphological apomorphies included in the diagnoses below and cited in Appendix II are numbered (1–91) and the character states are defined and coded following Poe (2004: 41–47). His account should be consulted for additional detail. All higher taxa, whether formal or informal, are based on the phylogenetic results (i.e., are thought to be monophyletic). In a few cases the status of some species was equivocal because they appeared on different branches in our two trees. In these cases, a decision regarding their allocation was generally based on the molecular tree. A rationale for each problematic assignment to a higher taxon is presented in the Remarks section, and each represents a candidate for further study. To further increase the utility of the new classification we provide an alphabetical listing of all valid species and subspecies (Appendix IV), indicating their placement by genus and species group.

In the treatment of nomenclatural matters, our use of the term the Code refers to the International Code of Zoological Nomenclature, and the abbreviation ICZN stands for the International Commission on Zoological Nomenclature.

Family Status of Anolis (sensu lato)

For most of the 19th and 20th centuries, although various separate genera were sometimes recognized (e.g., Fitzinger, 1843), lizards currently placed in *Anolis* (*sensu lato*) were usually referred to the family Iguanidae (e.g., Boulenger, 1885; Camp, 1923; Etheridge and de Queiroz, 1989). In a thorough cladistic analysis of morphology, Frost and Etheridge (1989) concluded that no synapomorphy diagnosed the Iguanidae, and consequently recognized eight monophyletic families of pleurodont Iguania. In this system *Anolis* (*sensu lato*) was placed in the family Polychridae Fitzinger, 1843 (later corrected to Polychrotidae by Böhme, 1990).

Subsequently, Macey *et al*. (1997) and Schulte *et al*. (1998) found statistical support for a monophyletic Iguanidae and used plesiomorphic molecular features to justify the reduction of the Frost and Etheridge (1989) families to subfamily status. Frost *et al*. (2001) further analyzed the Iguanidae (*sensu lato*) using morphological and sequence data to propose a system of eleven families of Pleurodonta as a major subdivision of Iguania. Although Schulte *et al*. (2003) disagreed with this scheme, we accept the basic arrangement of Frost *et al*. (2001) for the reasons expressed in the latter paper (pp. 12–13).

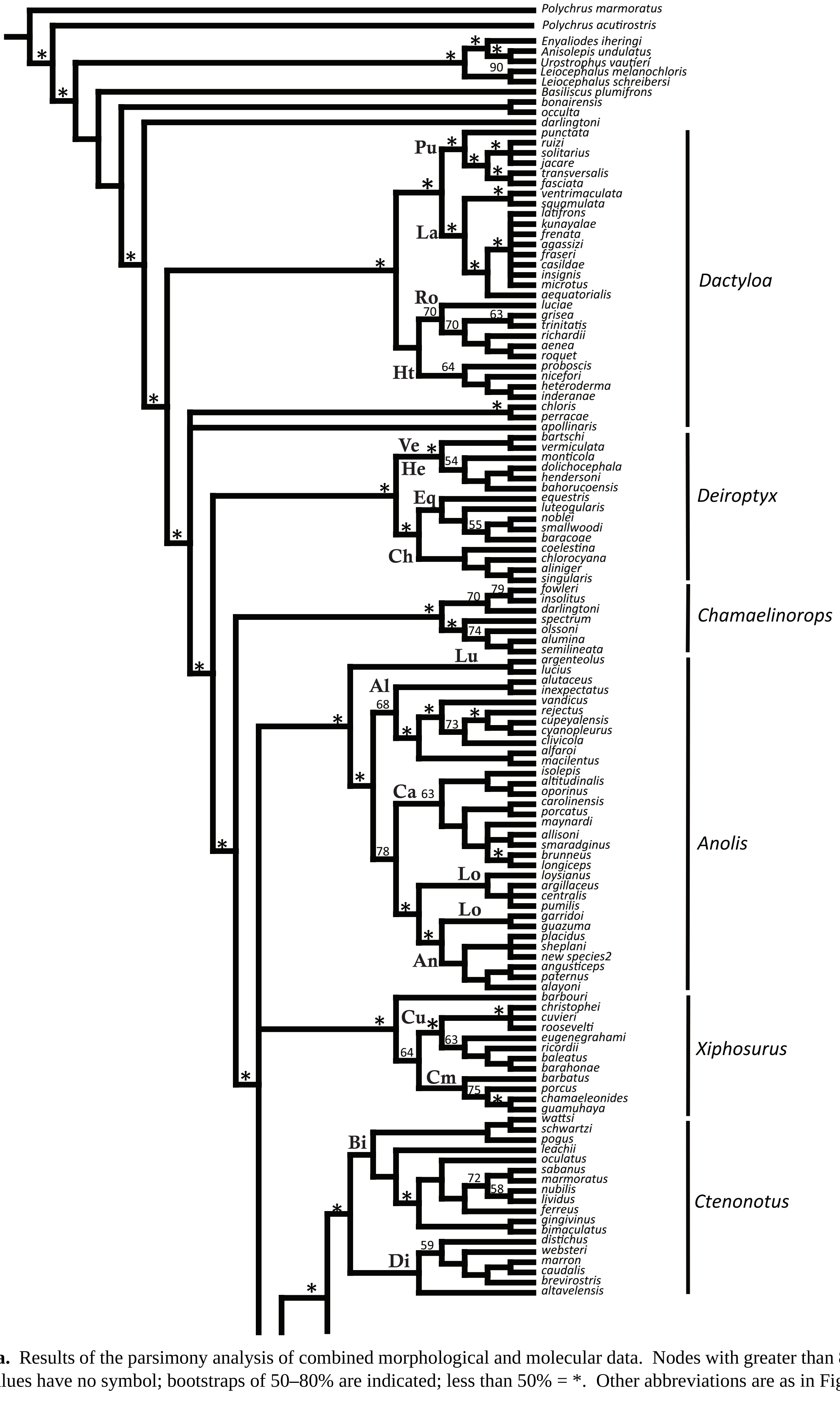


FIGURE 5a. Results of the parsimony analysis of combined morphological and molecular data. Nodes with greater than 80% bootstrap values have no symbol; bootstraps of 50–80% are indicated; less than 50% = *. Other abbreviations are as in Fig. 4.

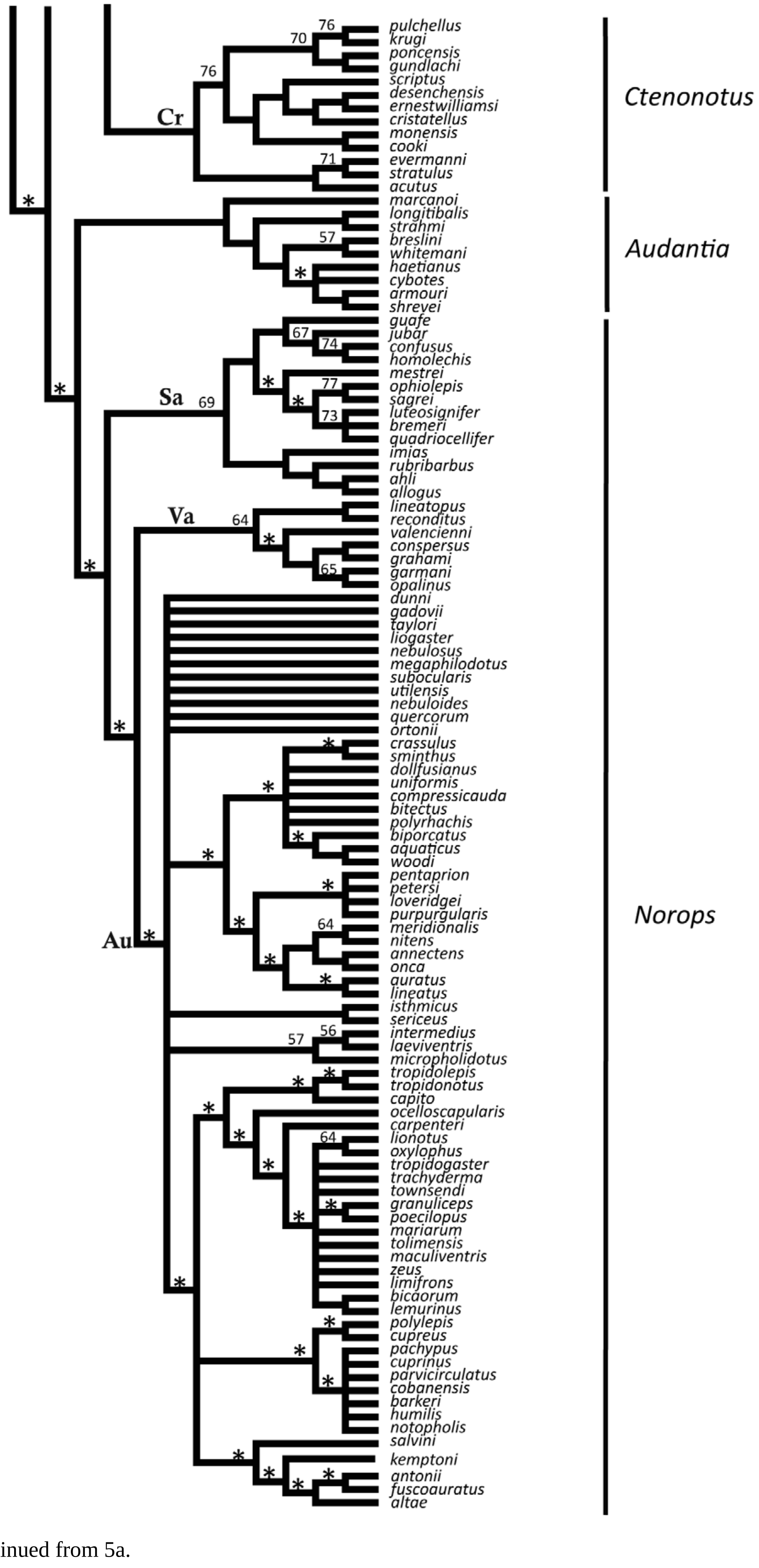


FIGURE 5b. Continued from 5a.

Recently, Townsend *et al*. (2011) found strong support for the monophyly of all but one of the Pleurodonta families and for the two families of acrodont iguanians, Agamidae and Chamaelonidae. They further provided convincing evidence that the Polychrotidae, as previously constituted, is non-monophyletic if *Anolis* is included with *Polychrus*. Their analysis indicates that *Anolis* (*sensu lato*) is the sister group to the family Corytophanidae and consequently should be recognized as a separate family-group taxon.

Inasmuch as, if one followed Poe (2004), only the genus *Anolis* would belong to this family, it would seem intuitive that the correct family name would be Anolidae Cope, 1863. However, under Article 40 of the Code (ICZN, 1999), the name Dactyloidae Fitzinger, 1843 has priority over Anolidae and cannot be replaced by the latter, even if *Dactyloa* is considered a synonym of *Anolis* (Townsend *et al.* 2011).

The following section constitutes our description of the family and the genera of dactyloids. For a more complete taxonomic treatment of all species see Appendix III. For an alphabetical species list see Appendix IV.

Family Dactyloidae Fitzinger, 1843

Dactyloae Fitzinger, 1843: 17, 63. Type genus: *Dactyloa* Wagler, 1830.
Draconturae Fitzinger, 1843: 17, 68. Type genus *Dracontura*, an incorrect subsequent spelling
of *Draconura* Wagler, 1830 (= *Norops* Wagler, 1830).
Anolidae Cope, 1864, 16: 227. Type genus: *Anolis* Daudin, 1802.

Diagnosis.—The family is unique within the Iguania in sharing the following combination of characters**:** 1) pleurodont dentition; 2) slender clavicles; 3) no ribs on cervical vertebrae 3 and 4; 4) three sternal ribs; 5) no ribs on lumbar vertebrae; 6) jugal in contact with squamosal; 7) well-developed crista prootica that extends ventrolaterally; 8) anterior inferior alveolar foramen bordered by the splenial (when present) and dentary; 9) angular reduced to tiny splint; 10) lamellar subdigital scales form raised pad under phalanges three and four of digits two to five; 11) no femoral pores; 12) no transverse gular fold; 13) three greatly elongate ceratobranchials associated with extensible longitudinal gular fan; 14) scale organs with central filament of twisted spines; 15) subdigital scales with differentiated setae; 16) subocular scales subequal; 17) anole type nasal passage (*sensu* Stebbins, 1948).

Content.—The family is comprised of eight genera, 22 species groups (two genera without subdivisions), 387 species and a total of 499 species and subspecies (see Appendix IV).

Distribution.—The Greater and Lesser Antilles, the Bahamas, the Turk and Caicos Islands, the Cayman Islands, Navassa Island, St. Croix Island, the Virgin Islands; southeastern United States, Mexico, Central America, including Cozumel and Bay Islands, Swan Islands, Corn Islands, San Andres and Providencia Islands; South America and nearby offshore Islands including Malpelo Island, Curaçao, Bonaire, Blanquilla, and Margarita Islands in the Caribbean, from Colombia through Venezuela and the Guayanas to São Paulo State in eastern Brazil, and to Ecuador and northern Peru on the Pacific versant; the basins of the Orinoco and Amazon Rivers in Colombia, Ecuador, Venezuela, Peru, Bolivia, and Brazil to northern Paraguay (Fig. 6).

Introductions.—A number of species have been widely introduced or have successfully colonized areas not included in their historic ranges. See generic and species group sections for details.

Genus *Dactyloa* Wagler, 1830

Dactyloa Wagler, 1830; Natürliches System der Amphibien: 148. Type species: *Anolis gracilis* Wied-Neuwied, 1821; 2: 131 (=*Anolis punctata* Daudin, 1802 (4): 84, by subsequent designation of Savage and Guyer (2004: 304).

Phalangoptyon Wagler and Michahelles, 1833: Isis von Oken 26: 896. Type species: *Lacerta roquet* Bonnaterre, 1789: 54, misidentified as *Anolis bimaculatus* (= *Lacerta bimaculata* Sparrman, 1784: 169) in the subsequent designation by Peters and Donoso-Barros (1970; 297: 43), is herewith selected as the type species of this genus.

Ptychonotus Fitzinger, 1843; Systema Reptilium: 16, 65. Type species: *Anolis alligator* C. Duméril and Bibron, 1837 (4): 134 (= *Lacerta roquet* Bonnaterre, 1789: 54) by original designation.

Eunotus Fitzinger, 1843; Systema Reptilium: 17, 65. Type species: *Anolis gracilis* Wied-Neuwied, 1821 (2): 131 (= *Anolis punctata* Daudin, 1802 (4): 84), by original designation. Proposed as a subgenus of *Ptychonotus*.

Ctenodeira Fitzinger, 1843; Systema Reptilium: 17, 66. Type species: *Anolis richardii* C. Duméril and Bibron, 1837 (4): 141 by original designation. Proposed as a subgenus of *Ptychonotus*.

Eudactylus Fitzinger, 1843; Systema Reptilium: 17, 67. Type species: *Anolis goudotii* C. Duméril and Bibron, 1837 (4): 108 (= *Lacerta roquet*, Bonnaterre, 1789: 54) by monotypy. Proposed as a subgenus of *Dactyloa*.

Rhinosaurus Gray, 1845; Catalogue of the Species of Lizards in the British Museum (Natural History): 199. Type species *Anolis gracilis* Wied-Neuwied, 1821 (2): 131 (= *Anolis punctata* Daudin, 1802 (4): 84), by monotypy.

Scytomycterus Cope, 1875; J. Acad. Nat. Sci. Philadelphia ser. 2, 8: 165. Type species: *Scytomycterus laevis* Cope, 1875; ser. 2, 8: 165, by monotypy.

Diaphoranolis Barbour, 1923; Occ. Paps. Mus. Zool. Univ. Mich. 129. Type species: *Diaphoranolis brooksi* Barbour, 1923; 129: 19 (= *Anolis insignis* Cope, 1871, 23: 213), by monotypy.

Mariguana Dunn, 1939; Not. Nat., Acad. Nat. Sci., Philadelphia: 1. Type species: *Anolis agassizi* Stejneger, 1900; 36: 161, by original designation.

Diagnosis.—Support for this genus is based on 77 apomorphies including four morphological features and 73 molecular ones. Three morphological apomorphies are unequivocal: head decreased in length (4: q to m), size of interparietal scale increased (7: u to h), and modal number of caudal vertebrae anterior to first autotomic vertebra increased (53: 4 to 3). Thirty-three of the molecular features are unequivocal (see Appendix III).

Definition.—Members of the genus *Dactyloa* are defined as dactyloid lizards having: 1) the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the anterior caudal vertebrae are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes and almost always have autotomy septa but are aseptate in *D. agassizi*; 2) interclavicle usually arrow-shaped (Guyer and Savage, 1986, Fig. 2A), T-shaped (Guyer and Savage, 1986, Fig. 2B) in *D. aequatorialis* according to Poe (2004); 3) postfrontal bone present; 4) pineal foramen in suture between frontal and parietal bones; 5) supratemporal processes of the parietal usually leave the supraoccipital bone exposed above but often extend over the supraoccipital; 6) no pterygoid teeth; 7) angular process of articular may be large or reduced or absent; 8) posterior suture of dentary pronged; 9) large splenial present; 10) no lower jaw sculpturing; 11) modal number of lumbar vertebrae 3, 4 or 5; 12) modal number of caudal vertebrae anterior to first without transverse processes usually 8 or more, rarely 7; 13) supraoccipital cresting continuous across supraoccipital with or without distinct lateral processes or single central process; 14) Type I karyotype: 2N usually 36 (12M, 24m), rarely with 20 or 22m; N.F. = 42, 46, 48; no sexual heteromorphism.

Content.—The genus contains four species groups, 83 species and a total of 88 species and subspecies (see Appendix III).

Distribution.—Atlantic and Pacific slopes of Costa Rica and Panama, then south through the Chocó region of Colombia and Ecuador, including Malpelo Island; highlands of Colombia, Ecuador, Peru, and Venezuela; Caribbean slope of Colombia and Venezuela; Bonaire and Blanquilla Islands and the southern Lesser Antilles; south on the Atlantic versant through the Guayanas to Espiritu Santo State in eastern Brazil, and throughout the Orinoco and Amazon Basins in Colombia, Ecuador, Peru, Venezuela, Bolivia, and Brazil (Fig. 7–11).

Introductions.—*Dactyloa aenea* to Trinidad and Guayana; *D. extrema* to St. Lucia, Bermuda, and Caracas, Venezuela; *D. richardii* to Tobago; *D. roquet* to Bermuda; *D. trinitatis* to Trinidad.

Etymology.—The genus name is from the Greek *daktylos* = digit and *oa* = fringe with reference to the characteristic expanded pads on the digits. The name is feminine in gender.

Remarks.—Fitzinger (1843) designated *Anolis punctata* Daudin 1802 as the type species of *Dactyloa*. *Anolis punctata* is ineligible to be selected as the type because it was not included by Wagler (1830) in the original generic description. Guyer and Savage (1986) followed Peters and Donoso-Barros (1970) in regarding this name as available and Savage and Guyer (2004) subsequently designated *Anolis gracilis* Wied-Neuwied, 1821 as the generic type. The content of this genus is essentially unchanged from that presented by Guyer and Savage (1986), with the exception that *Phenacosaurus* is now widely accepted as a member of this genus. *Dactyloa* can be identified as a monophyletic lineage in every published analysis since Guyer and Savage (1986), including Alfoldi *et al*.'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data. In addition, Canstañeda and de Queiroz (2011) presented a molecular based phylogenetic analysis of what they called the *Dactyloa* clade = genus *Dactyloa* of the present account. Their study utilized matrices for a nuclear gene region (RAG1), a mitochondrial region (ND2, 5 tRNA's, COI), and one that combined all three gene regions. They found our concept of the genus *Dactyloa* as detailed herein to be consistently inferred and strongly supported in both Likelihood and Bayesian trees for each of their three data sets.

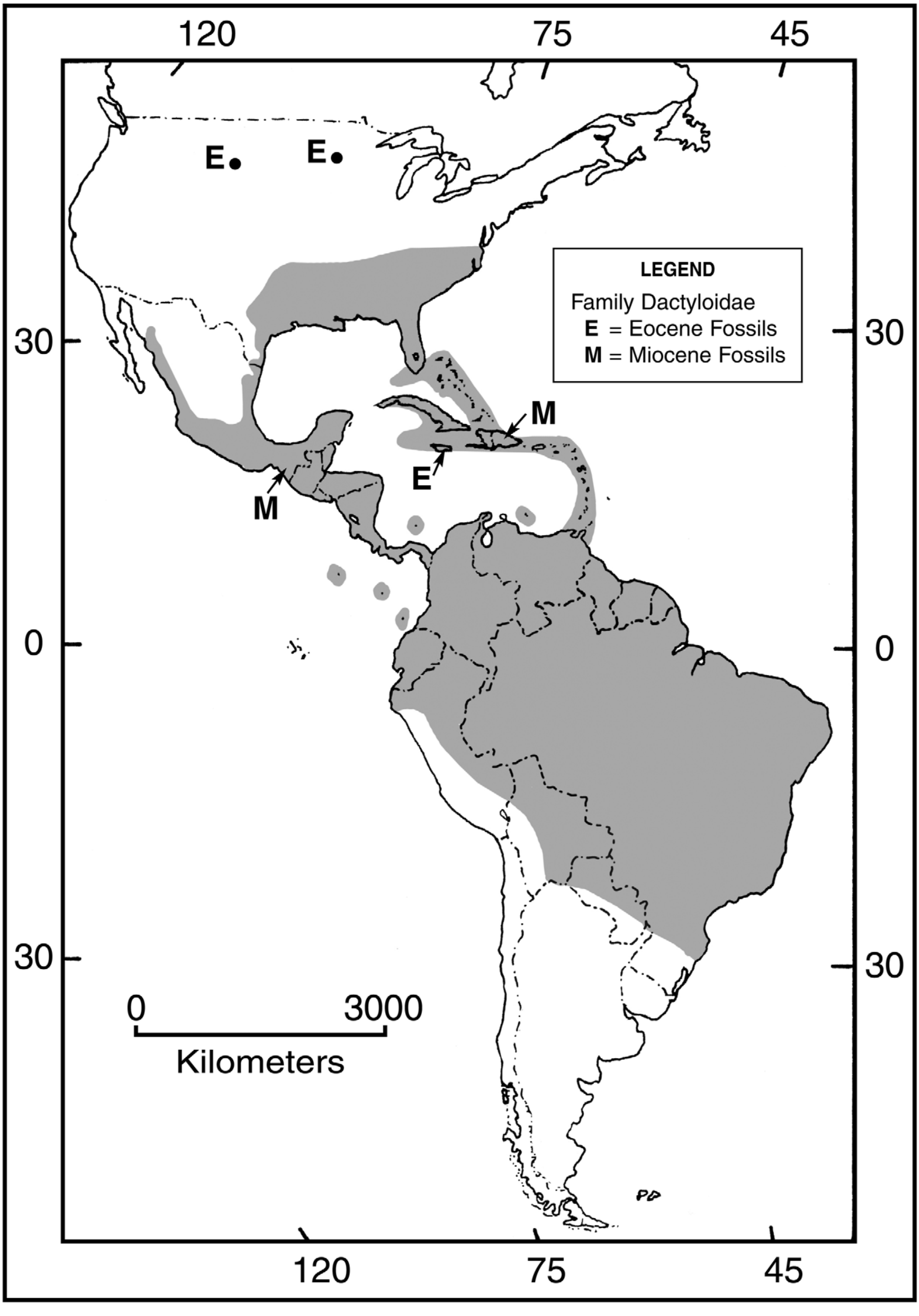


FIGURE 6. Distribution of the lizard family Dactyloidae.

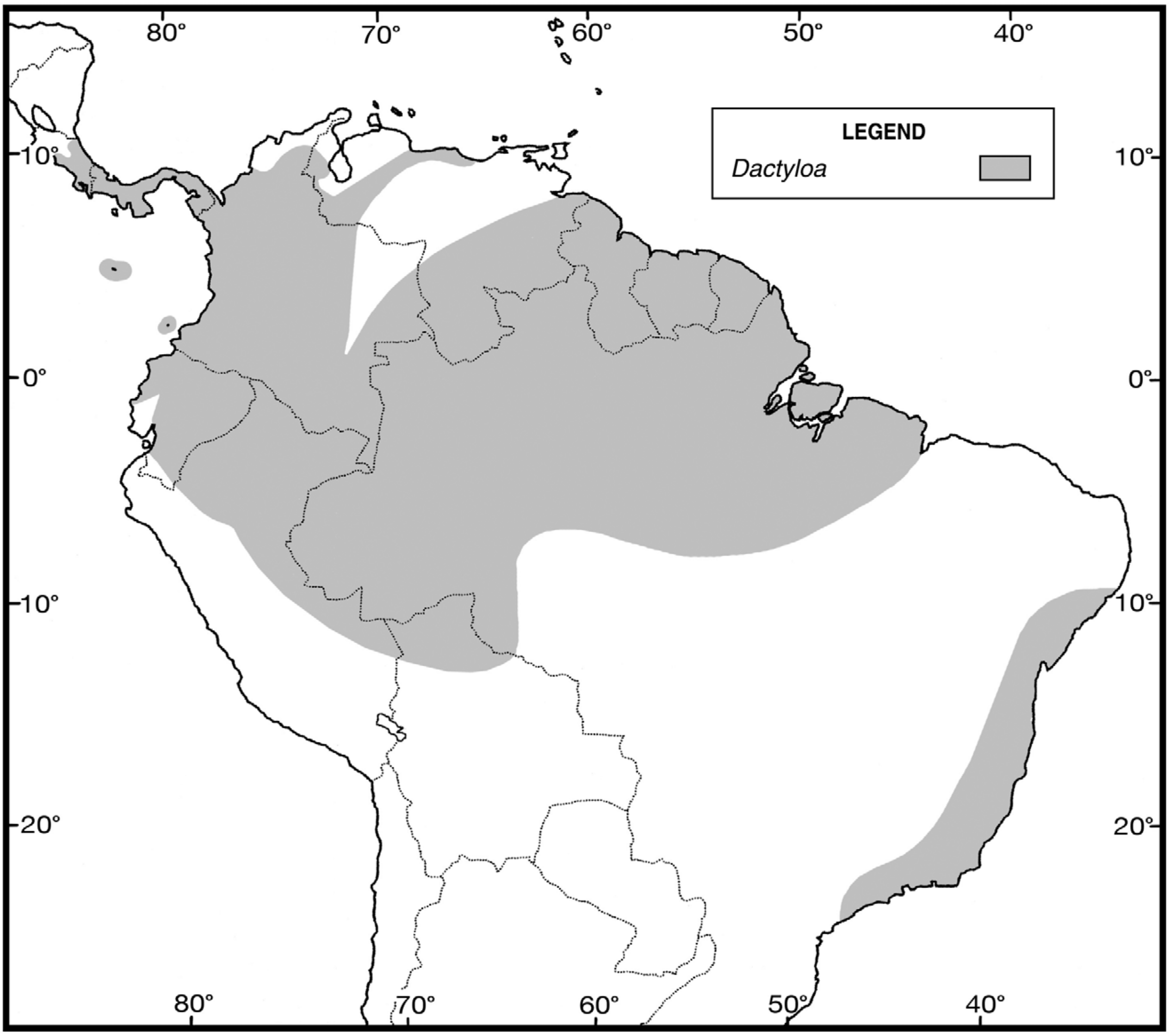


FIGURE 7. Distribution of the genus *Dactyloa* exclusive of the *Dactyloa roquet* Species Group (see Fig. 17).

The generic name *Phalangoptyon* was proposed for illustrations (vol. 1, pl. 87, Figs. 4–5) in Seba (1734). The only originally included species under this generic name is "*Phalangoptyon bimaculatum*?" for *Anolis bimaculatus sensu* Daudin, 1802 (nec *Lacerta bimaculata* Sparrman, 1784). A name questionably included under a new generic name cannot serve as the type of the genus (Art. 67.2.5 of the Code). However, Peters and Donoso-Barros (1970) subsequently designated *Anolis bimaculatus* Daudin, as the type of *Phalangoptyon*. This is a case of a misidentified type species (Art. 70 of the Code) as Duméril and Bibron (1837) pointed out that Seba's figures and Daudin's specimen of "*Anolis bimaculatus*" were representatives of *Anolis alligator* Duméril and Bibron, 1837, not a representative of *Lacerta bimaculata* Sparrman, 1784, as supposed by Daudin. *Anolis alligator* is a junior synonym of *Lacerta roquet* Bonnaterre, 1789. Savage and Guyer (1991) earlier concluded that *A. alligator* (= *A. roquet*) was the type species of this genus. However, their logic is faulty as Art. 67.2.5 of the Code excludes a questionably referred species as the generic type. Consequently, we act to fix *Lacerta roquet* Bonnaterre, 1789, misidentified as *Anolis bimaculatus* (= *Lacerta bimaculata* Sparrman, 1784) in the original designation by Peters and Donoso-Barros (1970) as the type species of *Phalangoptyon.* The name *Lacerta roquet* is often attributed to Lacépède (1788). However, the ICZN (2005) has ruled that Lacépède (1788) is non-binominal (Opinion 2104) and no names published in it are available.

Dactyloa latifrons Species Group

Diagnosis.—Support for this group is provided by 54 apomorphies including seven morphological and 47 molecular ones. Six morphological features are unequivocal: maximum male snout-to-vent length increased (1: k to o); ratio of maximum female snout-to-vent length to maximum male snout-to-vent length decreased (2: a to c); length of thigh increased (3: o to w); length of head decreased (4: m to i); scales on dewlap with at least one double row (21: a to z); mean number of scales across snout increased (29: l to m); and scales in supraorbital disc about equal in size (41: 0 to 4). All of the molecular apomorphies are equivocal (see Appendix II).

Definition.—Species of this group are giant anoles (snout-to-vent length in adult males 100 to 160 mm and 97 to 135 mm in adult females) and have the following combinations of features: 1) inscriptional rib formula 5:0; 2) lack of caudal autotomy septa (present in one species, *D. agassizi*); 3) large splenial present; 4) rows of multiple scales on the dewlap; 5) double row of middorsal caudal scales.

Content.—Eighteen species are referred to this species group (see Appendix III).

Distribution.—Atlantic and Pacific slopes of Costa Rica and Panama, south through the Chocó of Colombia and Ecuador; Malpelo Island; the Caribbean versant of Colombia, including the major river valleys of the Río Atrato, Río Cauca, and Río Magdalena and their adjacent slopes, and the Cordillera de la Costa of Venezuela (Fig. 8).

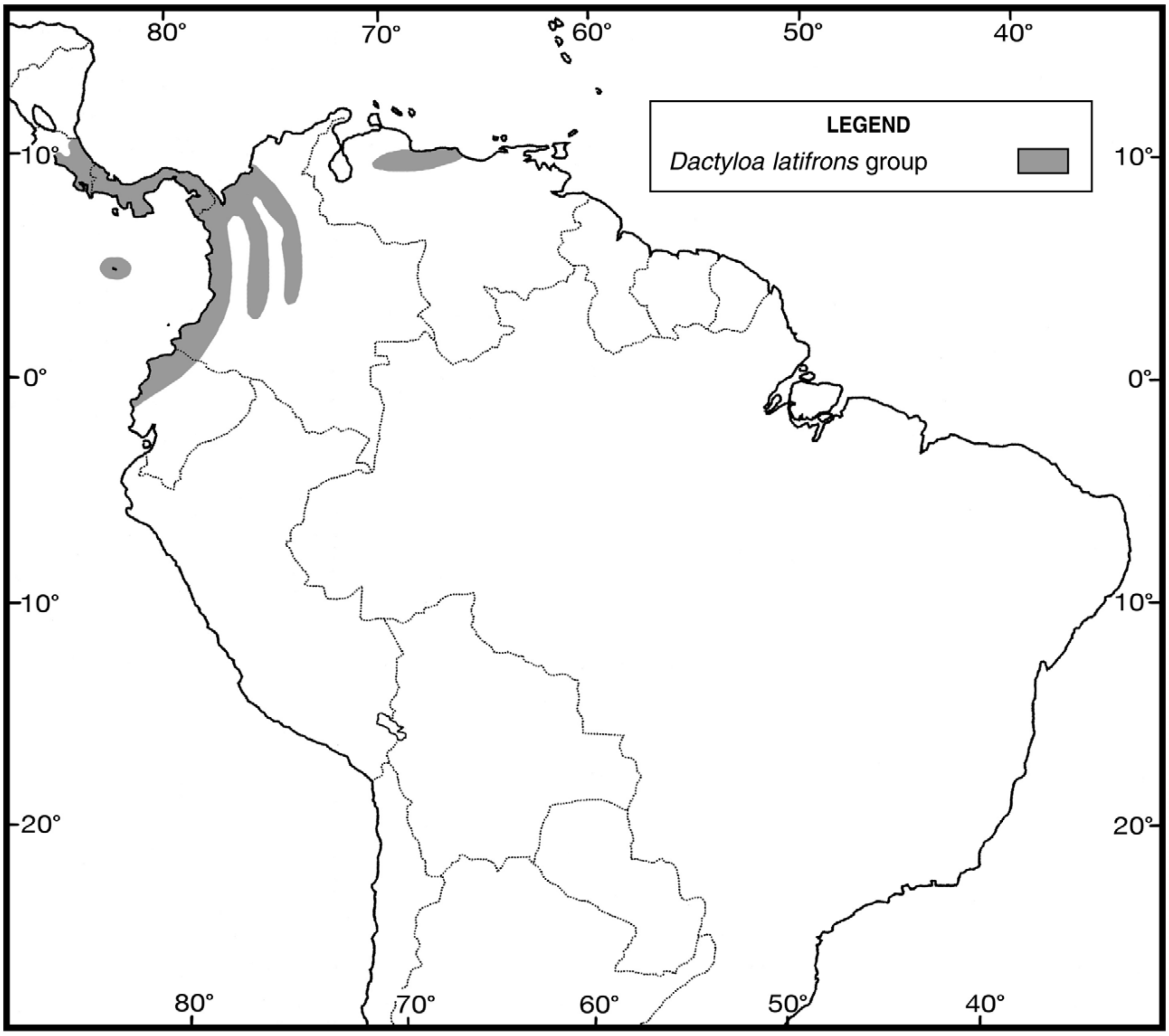


FIGURE 8. Distribution of the *Dactyloa latifrons* Species Group.

Remarks.—Hulebak *et al*. (2007) in the course of describing *Dactyloa kunayalae* suggested that it might be an ally of the Colombian *D. mirus* and *D. parrilis*. They noted that the three taxa share a unique morphology of the fourth toe, including few lamellae, indistinct toe pad, and especially long claw (see Fig. 1 in Williams, 1963).

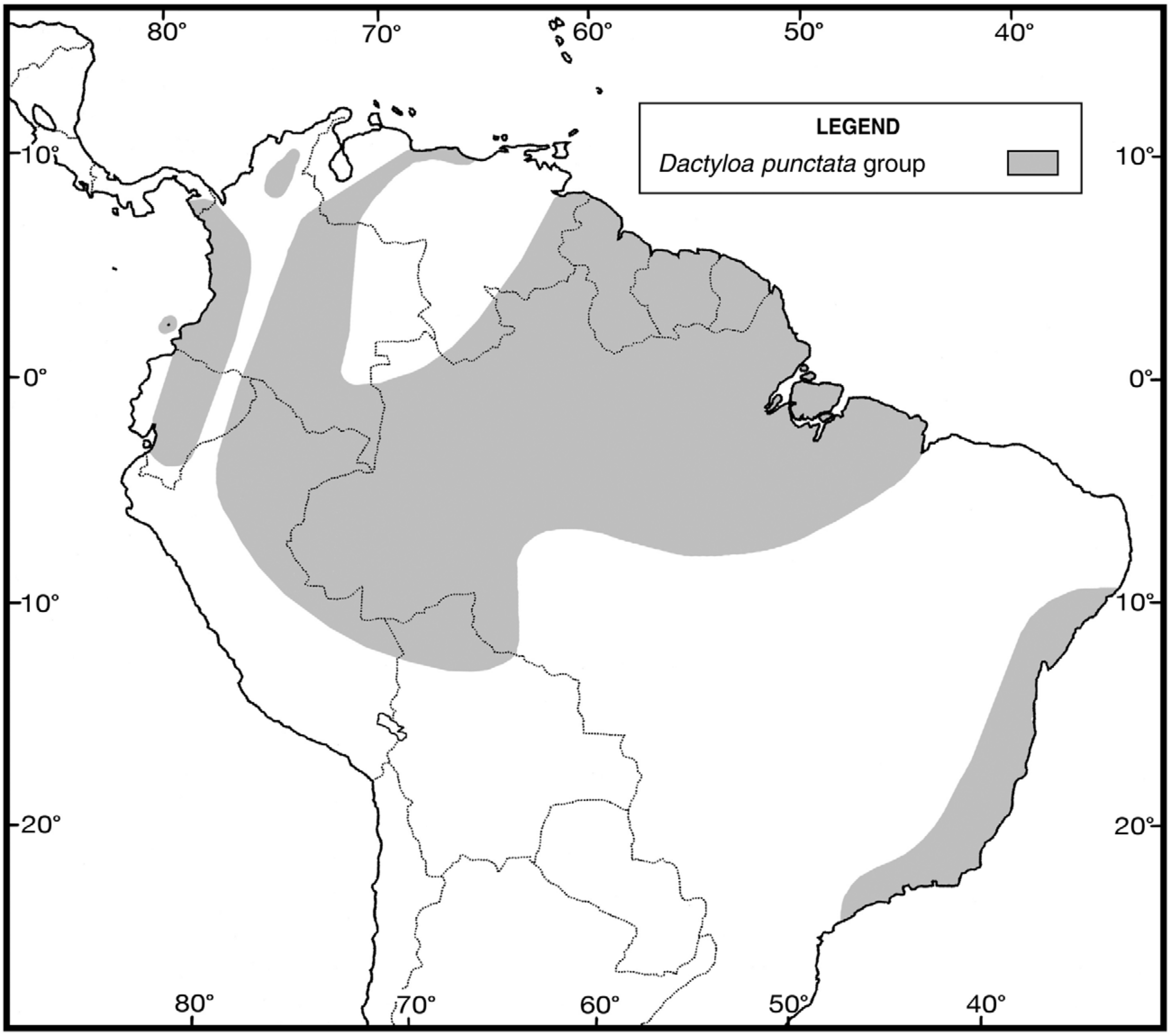


FIGURE 9. Distribution of the *Dactyloa punctata* Species Group.

Dactyloa punctata Species Group

Diagnosis.—Support for this group is provided by 96 apomorphies including eight morphological and 88 molecular ones. Two morphological features are unequivocal: size of interparietal scale decreased (7: h to n) and modal number of presacral vertebrae decreased (51: 0 to 1). Sixty-three molecular apomorphies are unequivocal (see Appendix II).

Definition.—Members of this species group are small to moderate-sized dactyloids (maximum snout-to-vent length in adult males 43 to 96 mm and 53 to 96 mm in adult females) that share the following combination of features: 1) inscriptional rib formula 4:0; 2) caudal autotomy septa present; 3) large splenial; 4) single or multiple rows of scales on the dewlap; 5) usually double rows of middorsal caudal scales.

Content.—Forty-four species are referred to this species group (see Appendix III).

Distribution.—Eastern Panama south through the Chocó of Colombia to Ecuador, including Gorgona Island; Andes of northern Colombia and western Venezuela; upland northern Venezuela; south on the Atlantic versant from eastern Venezuela through the Guayanas to Espiritu Santo State in eastern Brazil, and throughout the Amazon Basin in Colombia, Ecuador, Peru, Venezuela, Bolivia and Brazil; upland eastern Peru (Fig. 9).

Dactyloa heteroderma Species Group

Diagnosis.—Support for this group is provided by 106 apomorphies including 17 morphological and 89 molecular ones. Eight morphological features are unequivocal: height of ear opening decreased (6: v to g); base of tail laterally compressed (15: a to z); modal number of supraciliary scales zero (38: 1 to 0); modal nasal scale type: circumnasal separated from rostral by one scale, not in contact with supralabial (39: 0 to 2); dorsal, ventral, supradigital, and head scales smooth (40: 2 to 1); supraorbital with single narrow central crest (55: 0 to 2); epipterygoid not contacting parietal (70: a to z); and angular process of articular reduced or absent (82: a to z). There are no unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are small (43 mm in snout-to-vent length in adult males), moderate sized (53 to 86 mm in adult males and 55 to 69 mm in adult females) or large dactyloids (maximum snout-to-vent length in adult males 104 to 118 mm and 55 to 118 mm in adult females). Members of the group share the following combination of characters: 1) inscriptional rib formula 4:0, 4:3 or 5:1; 2) caudal autotomy septa present; 3) large splenial; 4) single rows of scales on the dewlap; 5) middorsal caudal scale row single.

Content.—Twelve species are referred to this species group (see Appendix III).

Distribution.—Andes of Colombia, Ecuador, Peru, western Venezuela and Chimantá, Neblina, and Yavi Tepuis of Venezuela (Fig. 10).

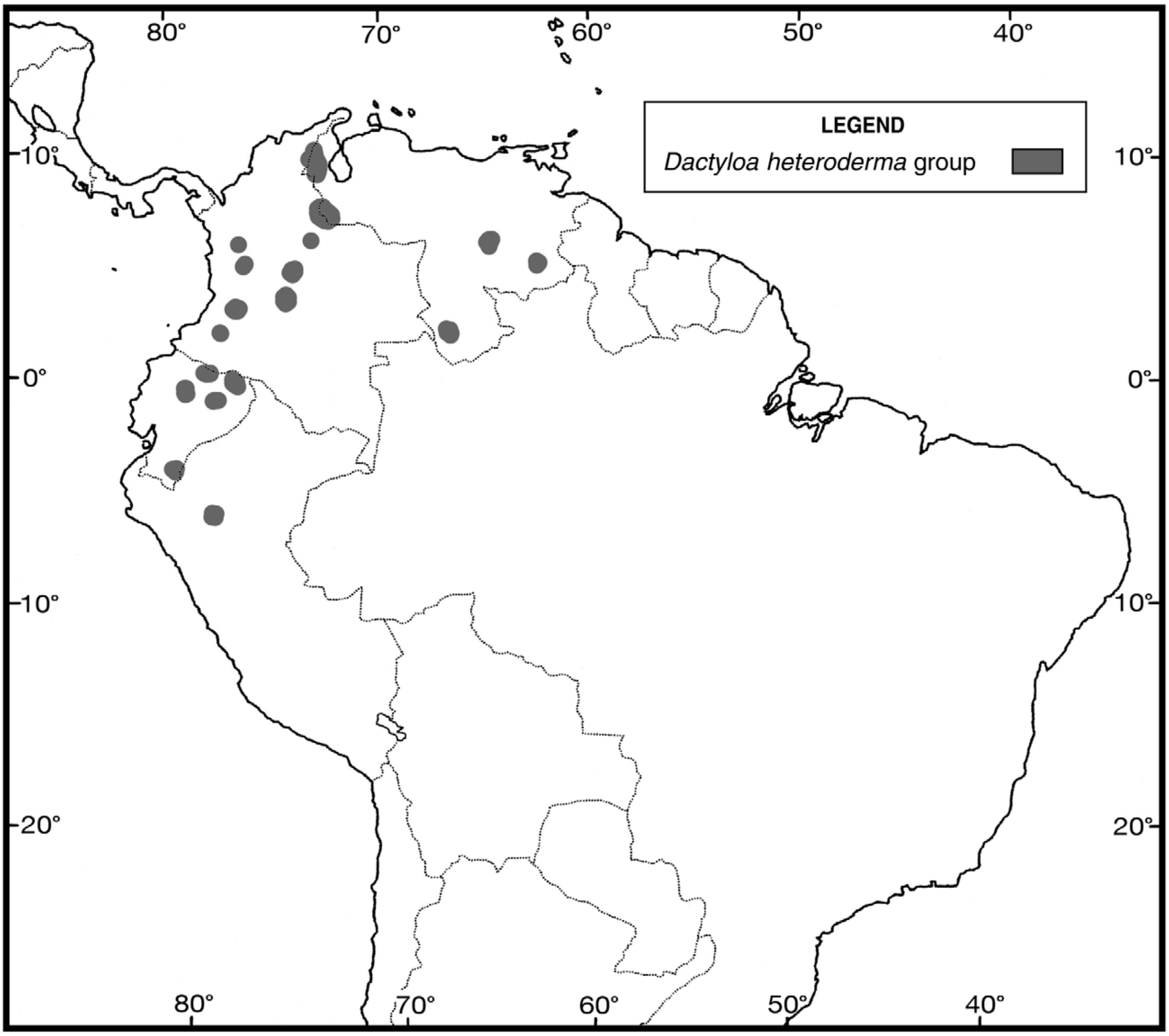


FIGURE 10. Distribution of the *Dactyloa heteroderma* Species Group.

Remarks.—This monophyletic group includes those species frequently described as or referred to the nominal genus *Phenacosaurus*. *Dactyloa proboscis* (Peters and Orces, 1956) clusters with other members of the *heteroderma* group in both Poe (2004) and our combined trees and so is included in this clade. In the *Anolis* (*sensu lato maximo*) of Jackman *et al*. (1999) and Poe (2004), *Phenacosaurus* is considered a junior synonym of the former. If this course is followed *Phenacosaurus nicefori* Dunn, 1944 becomes a junior secondary homonym of *Anolis nicefori* Barbour, 1912, a junior synonym of *Norops tropidogaster* (Hallowell, 1856). As such it requires a new name (Art. 59 of the Code). We recognize *Dactyloa* and *Norops* as distinct genera, however, so no new specific epithet is proposed.

Dactyloa roquet Species Group

Diagnosis.—Support for this group is provided by 83 apomorphies including 12 morphological and 71 molecular ones. Five morphological features are unequivocal: enlarged postanal scales absent in males (10: a to z); increased mean number of ventral scales in 5% of snout-to-vent length (20: m to o); increased modal number of lumbar vertebrae (52: 0 to 1); caudal autotomy septa present (54: z to a); supratemporal process leaves supraoccipital exposed above (61: z to a); prefrontal separated from contact with nasal (63: a to z); and anteriormost aspect of posterior border of dentary anterior to mandibular fossa (84: a–z). There are 35 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are moderate sized to giant anoles (maximum snout-to-vent length in adult males 74 to 140 mm and 55 to 86 mm in adult females) sharing the following combination of characters: 1) inscriptional rib formula usually 4:0, rarely 3:1; 2) caudal autotomy septa present; 3) large splenial present; 4) single rows of scales on the dewlap; 5) single row of middorsal caudal scales.

Content.—This species group contains nine species and a total of 14 species and subspecies (see Appendix III).

Distribution.—Southern Lesser Antilles, Blanquilla Island off northern Venezuela and Bonaire Island (Fig. 11).

Introductions.—*Dactyloa aenea* to Trinidad and Guyana; *D. extrema* to St. Lucia, Bermuda, and Caracas, Venezuela; *D. richardii* to Tobago; *D. roquet* to Bermuda; *D. trinitatis* to Trinidad.

Genus ***Deiroptyx*** Fitzinger, 1843

Deiroptyx Fitzinger, 1843; Systema Reptilium: 17: 66. Type species: *Anolis vermiculatus* Cocteau in Duméril and Bibron, 1837 (4): 28 by original designation. Savage and Guyer (2004: 204) acting as first revisers gave precedence to this name over all other genus-group names proposed by Fitzinger (1843) applicable to dactyloids, except *Ctenonotus*. Proposed as a subgenus of *Ptychonotus*.

Eupristis Fitzinger, 1843: 16, 64. Type species: *Anolis equestris* Merrem, 1820: 45 by original designation. Savage and Guyer (2004: 304) acting as first revisers gave precedence to this name over all other genus-group names proposed by Fitzinger (1843) applicable to dactyloids, except *Ctenonotus* and *Deiroptyx*. Proposed as a subgenus of *Ctenonotus*.

Diagnosis.—Support for this genus is based on 47 apomorphies including five morphological features and 42 molecular ones. There are three unequivocal morphological features: size of interparietal scale increased (7: u to m); decreased mean number of ventral scales in 5% of snout-to-vent length (20: s to n); and pterygoid teeth present (71: z to a). There are 14 unequivocal molecular apomorphies (see Appendix II).

Definition.— Members of the genus *Deiroptyx* are defined as dactyloid lizards having: 1) the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes but have autotomy septa; 2) interclavicle T-shaped (Guyer and Savage, 1986, Fig. 2B); 3) postfrontal bone usually present; 4) pineal foramen usually in the frontal parietal suture; 5) supratemporal processes of parietal bone almost always leave supraoccipital bone exposed above; 6) pterygoid teeth present or absent; 7) angular process of articular usually large; 8) posterior suture of dentary usually pronged, sometimes blunt; 9) splenial usually absent; 10) lower jaw sculpturing of "*Chamaeleolis*" type or wrinkling present in species of some adult males; 11) modal number of lumbar vertebrae 3 or 4; 12) modal number of caudal vertebrae anterior to first autotomic vertebra variable (6 to 10), usually 7; 13) supraoccipital cresting continuous across supraoccipital without single central process, rarely with distinct lateral processes; 14) Karyotypic variation for this genus is summarized by species group in the accounts below. Note that for 2N and N.F. values, even numbers are for females, odd numbers for males. Usually Type I karyotype: 2N = 48; others with Type III karyotype: 2N = 36 to 42 (12–16M, 26m), N.F. = 50–58 or Type VI karyotype: 2N = 44–48 (24I, 20–24m), N.F. = 44–48; no sexual heteromorphism.

Content.—This genus is comprised of five species groups containing 21 species and a total of 49 species and subspecies (see Appendix III).

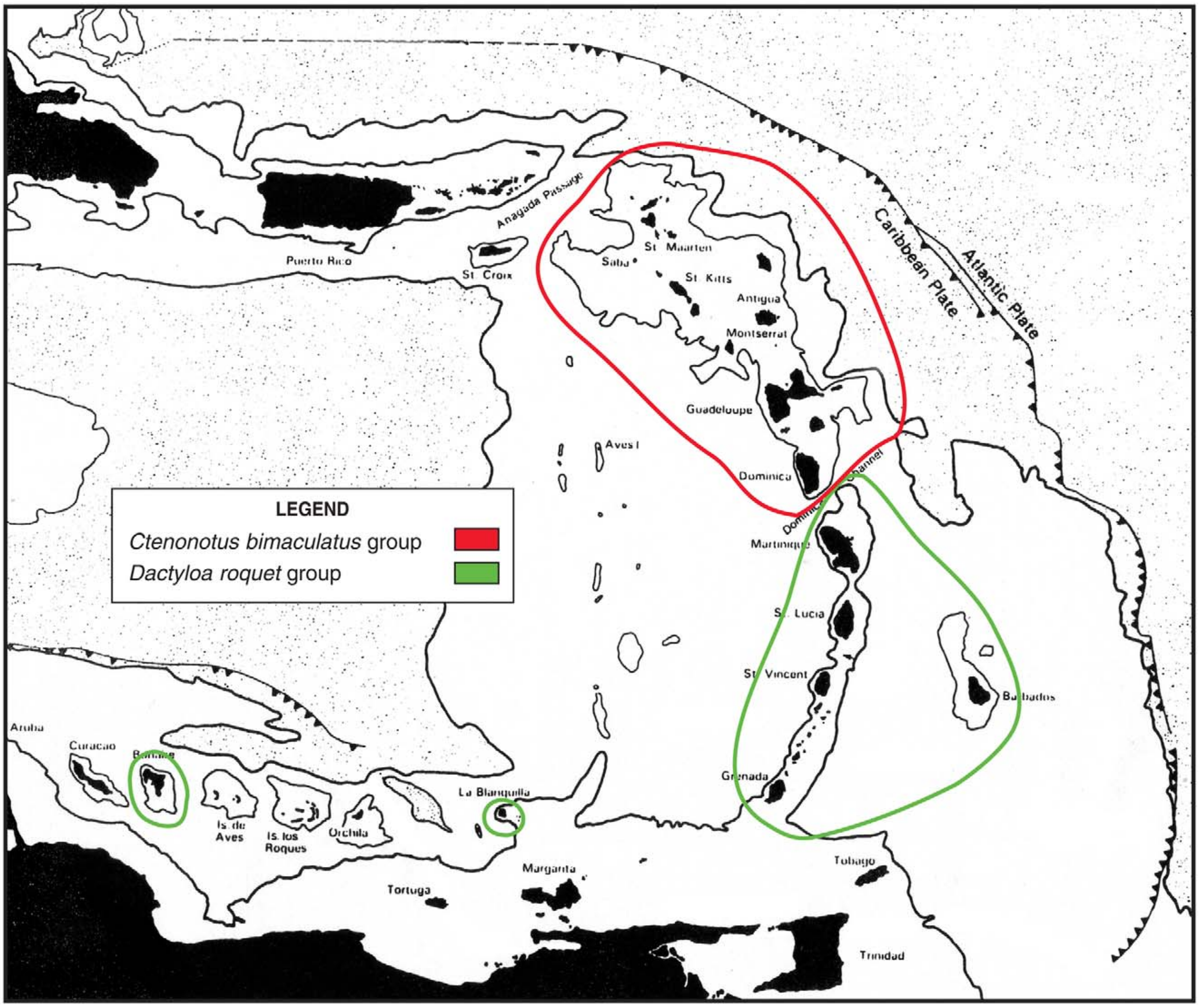


FIGURE 11. Distribution of the *Ctenonotus bimaculatus* and *Dactyloa roquet* Species Groups.

Distribution.—Cuba and Hispaniola, and their satellite islands, and Puerto Rico (Fig. 12).

Introductions.—*Deiroptyx equestris* to Grand Cayman Island, Florida and Hawaii; *D. chlorocyana* to Florida and Suriname.

Etymology.—This generic name is derived from the Greek *deir* = hump and *ptyx* = fold, presumably in reference to the well-developed nuchal crest in males. The name is feminine in gender.

Remarks.—*Deiroptyx* can be identified as a monophyletic lineage in every published analysis since Guyer and Savage (1986), including Alfoldi *et al*.'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

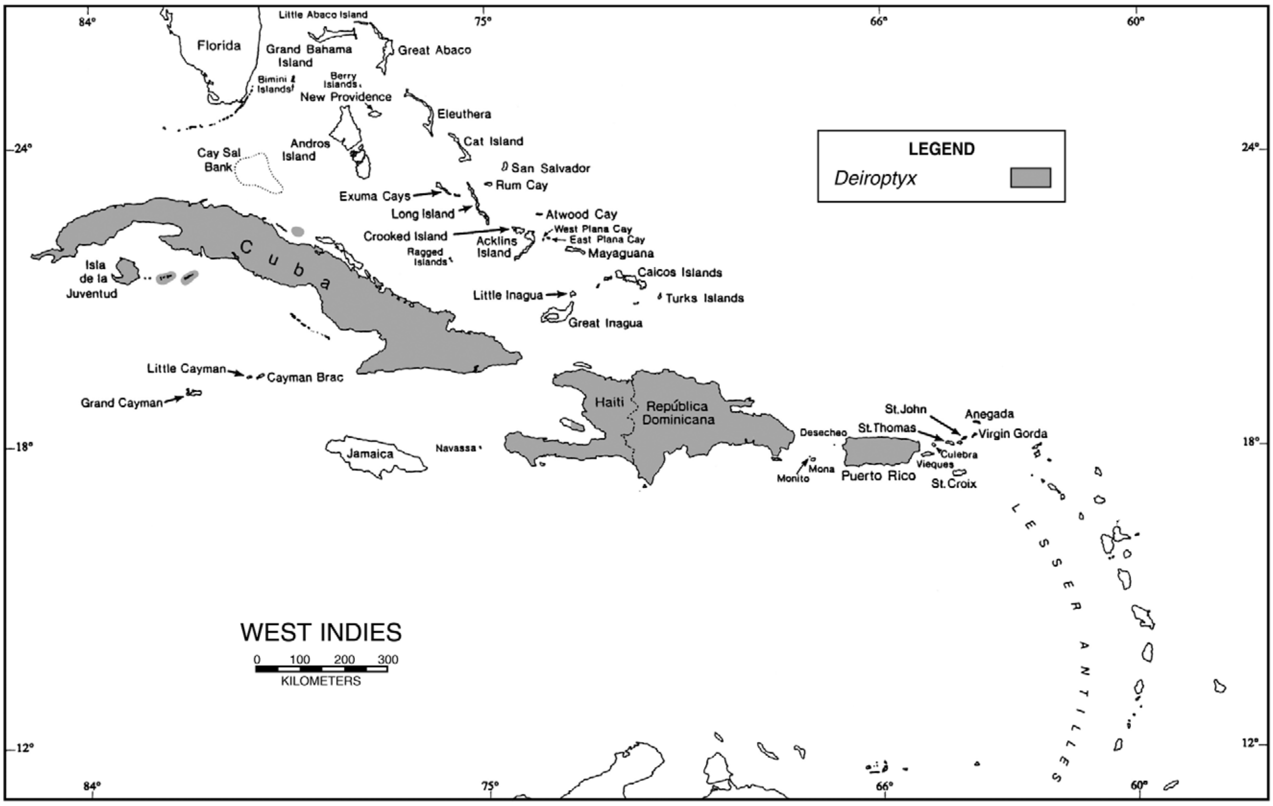


FIGURE 12. Distribution of the genus *Deiroptyx*.

Deiroptyx occulta Species Group

Diagnosis.—Support for this group is provided by 147 apomorphies including 25 morphological and 122 molecular ones. There are 18 unequivocal morphological apomorphies: maximum male snout-to-vent length decreased (1: k to c); head length decreased (4: q to l); preoccipital scales usually absent (33: a to g); scales in supraorbital disk about equal in size (41: 0 to 4); modal number of enlarged sublabial scales zero (44: 2 to 0); modal number of postxiphisternal inscriptional ribs 5:0 (47: 6 to 3); modal number of sternal ribs two (48: 1 to 0); interclavicle T-shaped (50: a to z); modal number of presacral vertebrae 23 (51: 0 to 1); modal number of caudal vertebrae anterior to first autotomic vertebra five (53: 4 to 2); supraoccipital crest with distinct lateral processes (55: 0 to 1); prefrontal usually present (62: a to g); prefrontal separated from nasal by frontal and maxilla (63: a to z); frontal separated from nasal by open gap (64: 0 to 1); epipterygoid usually separated from parietal (70: a to w); posteriormost tooth usually completely anterior to mylohyoid foramen (81: n to x); angular process of articular reduced or absent (82: a to z); anteriormost aspect of posterior border of dentary within mandibular fossa (84: n to z); no splenial (85: 0 to 1); and coronoid labial process absent (88: z to a). There are 70 unequivocal molecular apomorphies (see Appendix II).

Definition.—The single species placed in this species group is a relatively small form (snout-to-vent length in adult males to 42 mm and to 40 mm in adult females) distinctive in the following combination of features: 1) dorsal surface of skull smooth; 2) dewlap large in both sexes, base extending beyond axilla onto venter; 3) no splenial; 4) dorsal scales, small, round, and smooth; 5) ventral scales cycloid, juxtaposed and in transverse rows, larger than dorsal scales; 6) Type I karyotype: 2N = 36 (24M, 24m), N.F. = 48; no sexual heteromorphism.

Content.—A single species, *Deiroptyx occulta*, is referred to this species group (see Appendix III).

Distribution.—Puerto Rico (Fig. 13).

Remarks.—We are accepting the topology of the molecular tree that places *D. occulta* as the basal sister group to all other *Deiroptyx*. We think that its position on the combined tree is an anomaly in which the morphological peculiarities of this lizard overrode the molecular signal.

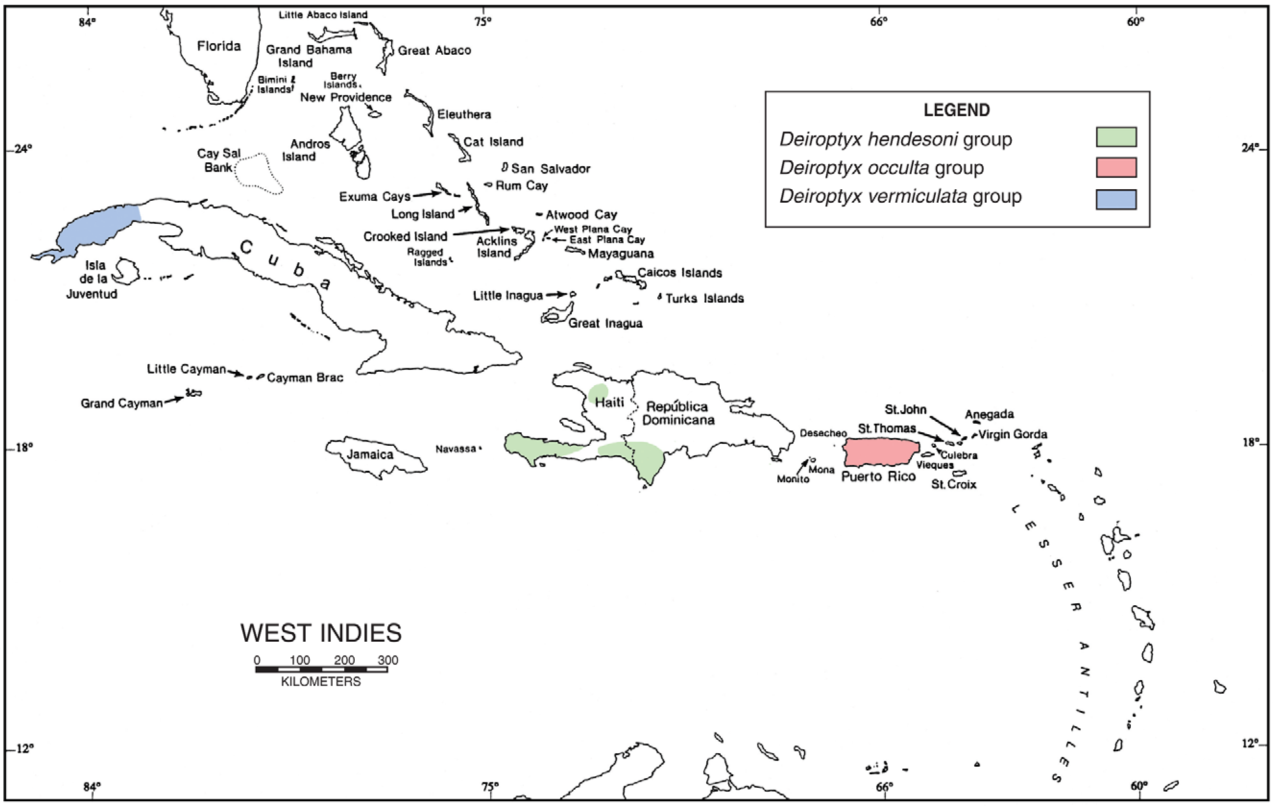


FIGURE 13. Distribution of the *Deirotyx hendersoni*, *Deiroptyx occulta* and *Deiroptyx vermiculata* Species Groups.

Deiroptyx vermiculata Species Group

Diagnosis.—Support for this group is provided by 62 apomorphies including nine morphological and 54 molecular ones. There is one unequivocal morphological apomorphy: jugal and squamosal in contact (68: 1 to z). There are 30 unequivocal molecular apomorphies (see Appendix II).

Definition.—The two species placed in this species group are moderate-sized to large dactyloids (adult males to 76 or 123 mm in snout-to-vent length and adult females to 62 or 83 mm) with very long legs (about 33% of snout-to-vent length) and a long tail (length more than 2 times snout-to-vent length) that share the following features: 1) no rugose cephalic casque; 2) dewlap absent in both sexes; 3) splenial large (*D. vermiculata*) or absent (*D. bartschi*); 4) dorsal scales small and round, keeled (*D. vermiculata*) or smooth (*D. bartschi*); 5) ventral scales small round, and smooth, same size as dorsals; 6) Type I karyotype: 2N = 34–36 (22–24M, 24m), N.F. = 46–48; no sexual heteromorphism.

Content.—Two species are referred to this species group (see Appendix III).

Distribution.—Cuba (Fig. 13).

Deiroptyx chlorocyana Species Group

Diagnosis.—Support for this group is provided by 81 apomorphies including twelve morphological and 69 molecular ones. Two morphological apomorphies are unequivocal: length of thigh increased (1: 0 to n) and supratemporal processes leave supraocciptal exposed above (61: z to a). There are 26 unequivocal molecular apomorphies (see Appendix II).

Definition.—These are small to moderate-sized anoles (adult males 45 to 84 mm in snout-to-vent length and adult females 45 to 60 mm) that share the following combination of features: 1) no rugose cephalic casque; 2) male and most female dewlaps large, base extending beyond axilla onto venter (dewlap in female *D. alinger* extending only to level of axilla); 3) no splenial; 5) dorsal scales, small, granular, and smooth; 6) ventral scales smooth, slightly imbricate, and larger than dorsals; 7) Type I karyotype: 2N = 36 (24M, 24m), N.F. = 48; no sexual heteromorphism.

Content.—This species group is comprised of five species, four extant and one fossil, and a total of eight species and subspecies (see Appendix III).

Distribution.—Hispaniola and its satellite islands (Fig. 14).

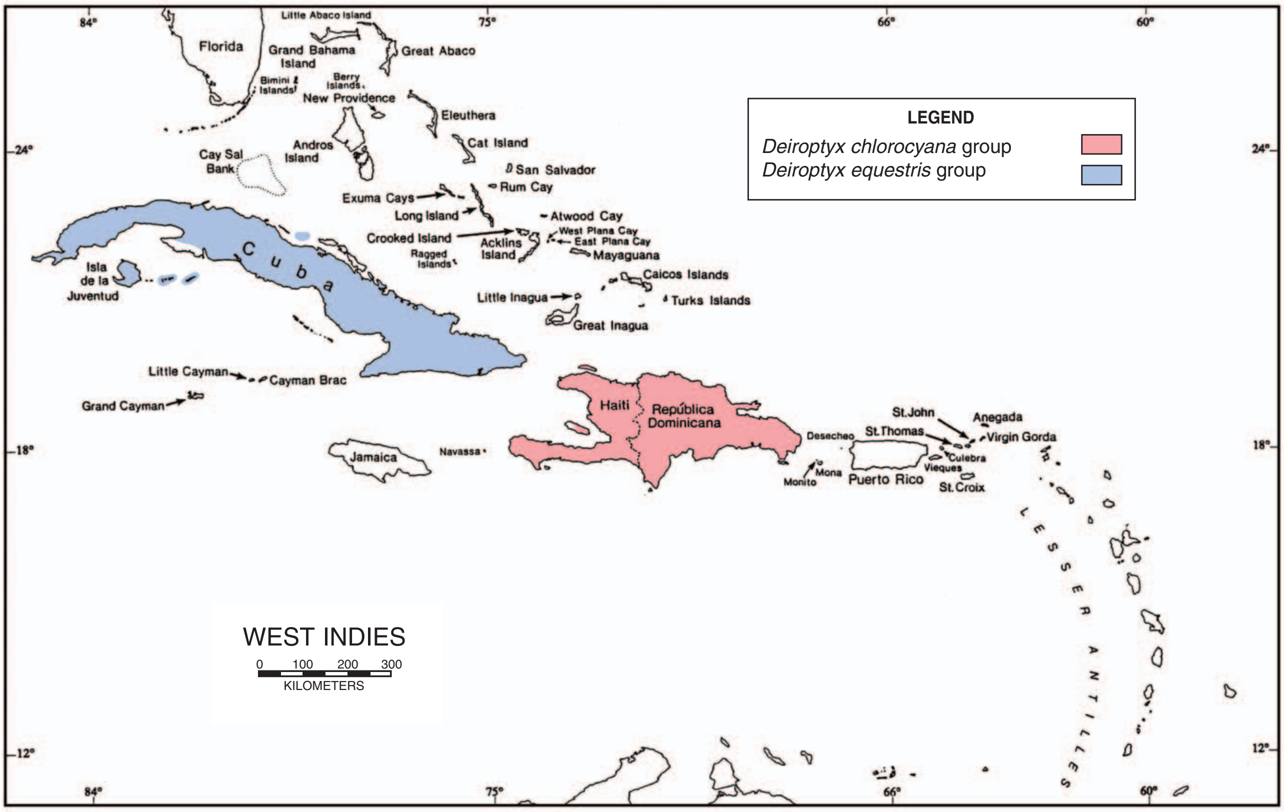


FIGURE 14. Distribution of the *Deiroptyx chlorocyana*, and *Deiroptyx equestris* Species Groups.

Deiroptyx equestris Species Group

Diagnosis.—Support for this group is provided by 120 apomorphies including 23 morphological and 97 molecular ones. There are 15 unequivocal morphological apomorphies: size of interparietal scale decreased (7: m to t); base of tail round (15: z to a); increased mean number of ventral scales in 5% of snout-to-vent length (20: n to p); decreased mean number of scales across snout (29: l to d); modal number of supraciliary scales zero (38: 1 to 0); external naris separated from rostral by two scales, not in contact with supralabial (modal condition) (39: 0 to 3); scales in supraocular disk about equal in size (41: 0 to 4); modal number of lumbar vertebrae three (52: 1 to 0); modal number of caudal vertebrae anterior to first autotomic vertebra ten (53: 4 to 1); dorsal surface of skull rugose with bony tubercles (56: a to z); parietal casque present (59: a to z); anterior edge of nasal does not reach naris (66: a to z); lateral edge of vomer with posteriorly directed lateral processes (72: a to z); anterior-most aspect of posterior border of dentary is anterior to mandibular fossa (84: z to a); and large splenial present (85: 1 to 0). There are 79 unequivocal molecular apomorphies (see Appendix II).

Definition.—Members of this species group are giant anoles (maximum adult male snout-to-vent lengths between 140 to 191 mm, and maximum in adult females 121 to 176 mm) sharing the following combination of features: 1) rugose cephalic casque formed of hard pustulate tubercles; 2) dewlap large in both sexes, its base extending beyond axilla onto venter; 4) splenial present; 5) dorsal scales, small, round, and smooth; 6) ventral scales small, round, and smooth, smaller than dorsals; 7) Type I karyotype: 2N = 36 (24M, 24m), N.F. = 48; no sexual heteromorphism.

Content.—This species group contains six species and a total of 26 species and subspecies (see Appendix III).

Distribution.—Cuba and its satellite islands (Fig. 14).

Introduction.—*Deiroptyx equestris* to Grand Cayman Island, south Florida and Hawaii.

Deiroptyx hendersoni Species Group

Diagnosis.—Support for this group is provided by 44 apomorphies including five morphological and 39 molecular ones. There are no unequivocal morphological apomorphies but there are 17 unequivocal molecular ones (see Appendix II).

Definition.—Lizards of this species group are small to moderate-sized anoles (maximum snout-to-vent-length in adult males 45 to 73 mm and 39 to 44 mm in adult females) sharing the following combination of characters: 1) no rugose cephalic casque, dorsal surface of skull smooth or wrinkled without bony tubercles; 2) male dewlap present, base usually only extending to level of axilla, (large, extending onto venter in *D. darlingtoni*); 3) splenial usually present, (absent in *D. monticola*); 3) dorsal scales, small, round, smooth or keeled; 4) ventral scales usually smooth (keeled in *Deiroptyx hendersoni*), equal to or much larger than dorsals; 5) Type I : 2N = 36 (24M, 12m) N.F. = 36; or type VI 2N = 36–48 (12–24M, 12–13m), N.F. = 39–41; no sexual heteromorphism.

Content.—This species group contains seven species and a total of twelve species and subspecies (see Appendix III).

Distribution.—Hispaniola and its satellite islands (Fig. 13).

Remarks.—The placement of *Deiroptyx darlingtoni* is ambiguous in Poe (2004) and in our trees. Poe has it as sister to *Xiphosurus chamaeleonides*. Its placement in our combined tree is as sister to all of the dactyloids exclusive of *occulta* and *bonairensis*. Our molecular tree clearly supports this species as sister to all other members of the *hendersoni* group. We are further influenced by the morphological data, particularly the occurrence of a T-shaped interclavicle in *D. darlingtoni*, as all *Xiphosurus* have the arrow-shaped condition. Williams (1960) originally proposed that *D. darlingtoni* was related to *D. monticola*, a conclusion supported by the molecular tree.

Genus *Xiphosurus* Fitzinger, 1826

Xiphosurus Fitzinger, 1826; Neue Classificatuin der Reptilien: 17, 48. Type species: *Anolis cuvieri* Merrem, 1820: 45 by subsequent designation of Stejneger (1904:625). Proposed as a subgenus of *Dactyloa.*

Chamaeleolis Cocteau in de la Sagra, 1839; Historia fisica, politica y natural de la Isla de Cuba 4: 90. Type species: *Chamaeleolis fernandina* Cocteau, 1839: 90 (= *Anolis chamaeleonides* 1837; Cocteau in C. Duméril and Bibron,1837 (4): 169) by monotypy.

Pseudochamaeleon Fitzinger, 1843; Systema Reptilium: 16, 63. Type species: *Anolis chamaeleonides* C. Duméril and Bibron: 1837 (4):168 by original designation.

Semiurus Fitzinger, 1843; Systema Reptilium: 16, 64. Type species: *Anolis cuvieri* Merrem, 1820:45 by original designation. Proposed as a subgenus of *Ctenonotus*.

Diagnosis.—Support for this genus is based on 104 molecular apomorphies none of which is unequivocal (see Appendix II).

Definition.—Members of the genus *Xiphosurus* are defined as dactyloid lizards having: 1) the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes but usually have autotomy septa (four species with aseptate ones); 2) interclavicle arrow shaped (Guyer and Savage, 1986, Fig. 2A); 3) postfrontal bone present; 4) pineal foramen in parietal or frontal-parietal suture; 5) supratemporal processes of parietal usually extend over the supraoccipital but sometimes leave supraoccipital exposed above; 6) pterygoid teeth present or absent; 7) angular process of articular large; 8) posterior suture of dentary pronged; 9) large splenial present, reduced to a sliver or absent; 10) lower jaw sculpturing usually absent (sculpturing of the "*Chamaeleolis*" type present in *X. chamaeleonides* and *X. cuvieri*); 11) modal number of lumbar vertebrae 3 or 4; 12) modal number of caudal vertebrae anterior to first autotomic vertebra 6 to 8; 13) supraoccipital cresting continuous across supraoccipital with or without lateral processes; 14) Type I karyotype: 2N = 36 (12M, 24m); no sexual heteromorphism; N.F. = 48.

Content.—This genus is composed of two species groups, eleven species and a total of 26 species and subspecies (see Appendix III).

Distribution.—Cuba, Hispaniola, Puerto Rico, their satellite islands, and the Puerto Rico Bank (Fig. 15).

Introduction.—*Xiphosurus baleatus* to Suriname.

Etymology.—This generic name is derived from the Greek *xiphos* = sword and *oura* = tail, apparently with reference to the high fin-like caudal crest. It was Latinized by Fitzinger (1826) explicitly as a masculine noun.

Remarks.—Fitzinger (1843) designated *Anolis chlorocyanus* Duméril and Bibron, 1837 as the type species of the genus *Xiphosurus*. This designation is invalid as *A. chlorocyanus* was not among the species originally included in the genus. Stejneger (1904) subsequently designated *Anolis cuvieri* Merrem, 1820 as the type species of *Xiphosurus*. *Xiphorsurus* can be identified as a monophyletic lineage in every published analysis since Guyer and Savage (1986), including Alfoldi *et al.*'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

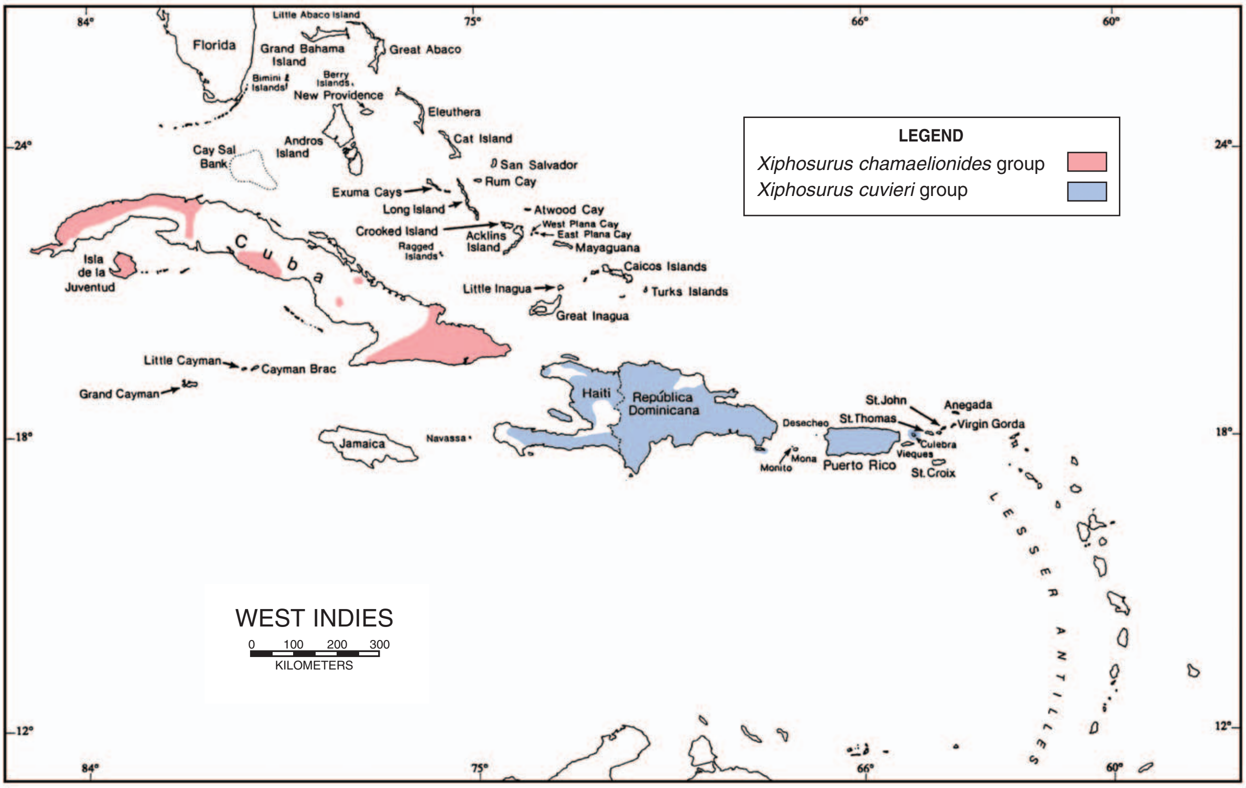


FIGURE 15. Distribution of the *Xiphosurus chamaeleonides* and *Xiphosurus cuvieri* Species Groups**.**

Xiphosurus chamaeleonides Species Group

Diagnosis.—Support for this group is provided by 127 apomorphies including 21 morphological and 106 molecular ones. None of the morphological features is unequivocal. There are 87 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are giant dactyloids (maximum snout-to-vent length in adult males 162 to 177 and 157 to 172 mm in adult females) sharing the following combination of characters: 1) a rugose cephalic casque terminating in a posteriorly raised arch; 2) a small fleshy protuberance in upper border of ear opening; 3) large, circular and flat dorsal scales separated by small granular scales; 4) ventral scales small, smooth granules; 5) large dewlap in both sexes, base extending to venter; 6) free rim of dewlap with conical, filamentous or barbel-like scales; 7) no caudal autotomy septa.

Content.—Five species are referred to this species group (see Appendix III).

Distribution.— Cuba and its satellite islands (Fig. 15).

Xiphosurus cuvieri Species Group

Diagnosis.—Support for this group is provided by 57 apomorphies including four morphological and 53 molecular ones. One morphological feature is unequivocal: mean number of dorsal scales in 5% of snout-to-vent length increased (19: c to l). Twenty-three molecular apomorphies are unequivocal (see Appendix II).

Definition.—The lizards placed in this species group are mostly large or giant anoles (maximum male snout-to-vent lengths 122 to 180 mm and females 87 to 151 mm). *Xiphosurus eugenegrahami* is a moderate-sized species (maximum adult male snout-to-vent length 72 mm and adult female maximum 61 mm). Members of this group share the following combination of characters: 1) dorsal surface of skull rugose with pronounced wrinkling or pustulate tubercles; 2) no small fleshy protuberance in upper border of ear opening; 3) dorsal scales small, keeled; 4) ventral scales small, smooth; 5) large dewlap in both sexes; 6) free rim of dewlap without differentiated scales; 7) caudal autotomy septa present.

Content.—This species group contains six species and a total of 21 species and subspecies (see Appendix III).

Distribution.—Hispaniola, Puerto Rico, their satellite islands, and Isla Culebra (Fig. 15).

Genus *Chamaelinorops* Schmidt, 1919

Chamaelinorops Schmidt, 1919; Bull. Amer. Mus. Nat. Hist. 41: 523. Types pecies: *Chamaelinorops barbouri* Schmidt, 1919, 41: 523 by original designation.

Diagnosis.—Support for this genus consists of 39 apomorphies including two morphologica features and 37 molecular ones. Only one unequivocal morphological apomorphy characterizes the genus: reduced body size (1: f to c). There are sixteen unequivocal molecular apomorphies (see Appendix II).

Definition.—Members of the genus *Chamaelinorops* are mostly small species (maximum snout-to-vent length in adult males 39 to 50 mm, 33 to 55 mm in adult females). *Chamaelinorops fowleri* is moderate sized (maximum snout-to-vent length in adult males to 77 mm and to 75 mm in adult females). Members of this genus share the following combination of characters: 1) usually having the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes but usually have autotomy septa (*C. insolitus* has aseptate ones). *Chamaelinorops barbouri* is unique among dactyloids in having thoracic and lumbar vertebrae with greatly expanded transverse processes and caudal vertebrae that lack autotomic septa but have laterally expanded transverse processes on caudal vertebrae to vertebra 17, followed by vertebrae with nub-like remnants of the transverse processes (Forsgaard, 1983 Fig. 4); 2) interclavicle T-shaped (Guyer and Savage, 1986, Fig. 2C); 3) postfrontal usually present; 4) pineal foramen in parietal or frontal parietal suture; 5) supratemporal processes of parietal may or may not extend over the upper surface of supraoccipital; 6) no pterygoid teeth; 7) angular process of articular usually large, rarely reduced or absent; 8) posterior suture of dentary pronged; 9) splenial absent; 10) usually no lower jaw wrinkling or sculpturing; 11) modal number of lumbar vertebrae 4 or 5; 12) number of caudal vertebrae anterior to first autotomic vertebra 5 to 10; 13) supraoccipital cresting almost always with distinct lateral processes; 14) Type I karyotype: 2N = 36 (12M, 24m); no sexual heteromorphism; N.F. = 48.

Content.—This genus contains nine species and a total of 16 species and subspecies (see Appendix III).

Distribution.—Hispaniola and its satellite islands (Fig. 16).

Etymology.—The name of this genus is derived from the Greek *chamaileôn*, latinized to *chamaeleon* = the Old World chamaeleon lizards and *norops* = bright or gleaming, in reference to its apparent relationship to two other dactyloid genera, *Chamaeleolis* and *Norops*, recognized in 1919. *Norops* is an adjective used as a noun and is in the masculine gender as indicated by the original describer (Wagler, 1830). Thus, *Chamaelinorops* is masculine in gender.

Remarks.—*Chamaelinorops christophei* is tentatively referred to this genus. In both trees it falls out as being allied to members of the genus *Xiphosurus* but differs from them morphologically, particularly in having a T-shaped interclavicle while all *Xiphosurus* have an arrow-shaped one. According to Williams (1962) and Thomas and Schwartz (1967) this form is allied with the species that was described by Cochran (1939) as *Anolis darlingtoni*, here included in *Chamaelinorops*, further supporting our placement of *C. christophei* in the same genus. Cochran (1935) had earlier described a different taxon as *Xiphosurus darlingtoni*. Williams (1962), based on Etheridge's unpublished dissertation (1960), included both *A. darlingtoni* and *X. darlingtoni* in *Anolis*, rendering the 1939 name a secondary homonym of the 1935 one. Williams consequently proposed the name *Anolis etheridgei* as a new name for *Anolis* [not *Xiphosurus*] *darlingtoni*. However, as we place the two species in different genera, the homonymy is resolved and under the Code (Art. 59.4) the correct names are *Deiroptyx darlingtoni* (Cochran, 1935) and *Chamaelinorops darlingtoni* (Cochran, 1939). *Chamaelinorops* can be identified as a monophyletic lineage in every published analysis since Guyer and Savage (1986), including Alfoldi *et al*.'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

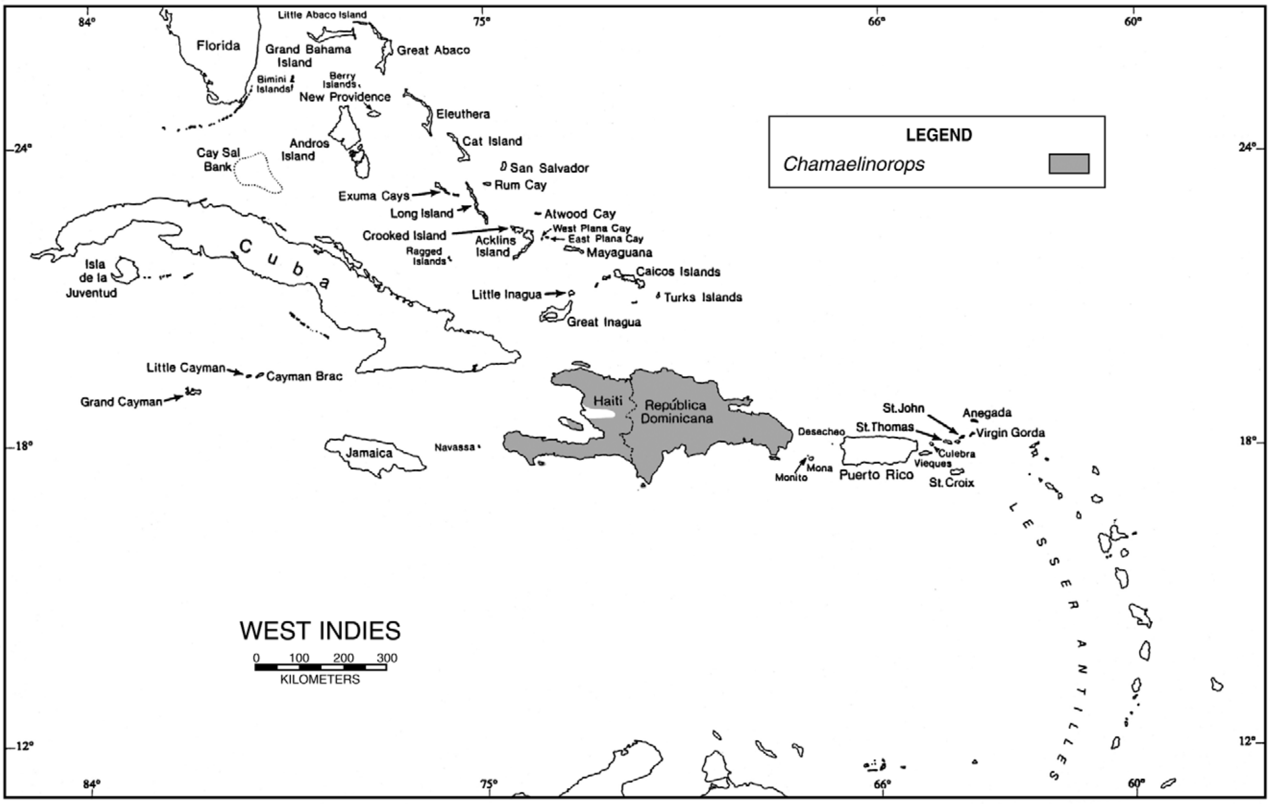


FIGURE 16. Distribution of the genus *Chamaelinorops*.

Genus *Audantia* Cochran, 1934

Audantia Cochran, 1934: 171. Type species: *Audantia armouri* Cochran, 1934: 171 by original designation.

Diagnosis.—Support for this genus is provided by 102 apomorphies including 13 morphological and 89 molecular ones. There are eight unequivocal morphological apomorphies: ratio of maximum female snout-to-vent length to maximum male snout-to-vent length increased (2: h to l); head increased in width (5: o to t), dorsal, ventral, supradigital and head scales smooth (40: 0 to 2); no postfrontal (62: a to z); posteroventral corner of jugal posterior to posterior edge of jugal (69: a to z); pterygoid teeth present (71: z to a); lateral shelf of quadrate present (75: a to z); and jaw wrinkling of *cybotes* type (90: 0 to 4). There are 49 unequivocal molecular apomorphies (see Appendix II).

Definition.—Members of the genus *Audantia* are moderate-sized dactyloids (maximum snout-to-vent length of adult males 57 to 79 mm, 49 to 66 mm in females) that share the following combination of characters: 1) caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes, followed by several autotomic vertebrae with short laterally-directed transverse processes that lie posterior to the autotomy septa and are not bifurcate in the vertical plane and the more posterior autotomic vertebrae which lack transverse processes

(Guyer and Savage, 1986, Fig.1B); 2) interclavicle arrow shaped (Guyer and Savage, 1986, Fig. 2A); 3) postfrontal bone present or absent; 4) pineal foramen in frontal parietal suture; 5) supratemporal processes of parietal extend over upper surface of supraoccipital; 6) pterygoid teeth usually present; 7) angular process of articular reduced or absent; 8) posterior suture of dentary blunt; 9) no splenial; 10) strong semilunar-shaped sculpturing in lower jaw of large adult males (Etheridge, 1969, Fig. 8C); 11) modal number of lumbar vertebrae 3 or 4; 12) modal number of caudal vertebrae anterior to first without transverse processes usually 6 or 7; 13) supraoccipital cresting usually continuous across supraoccipital, rarely with distinct lateral processes; 14) Type I karyotype: 2N = 36 (12M, 24m); no sexual heteromorphism; N.F. = 48.

Content.—This species group contains nine species and a total of 14 species and subspecies (see Appendix III).

Distribution.— Hispaniola and its satellite islands. (Fig. 17).

Introduction.—*Audantia cybotes* to Florida and Suriname.

Etymology.—This generic name is a patronym honoring André Audant, a zoologist at the Government Agricultural School at Damien, Haiti, who first collected the type species of the genus. The name is feminine in gender.

Remarks.— *Audantia* can be identified as a monophyletic lineage in every published analysis since Guyer and Savage (1986), including Alfoldi *et al.*'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

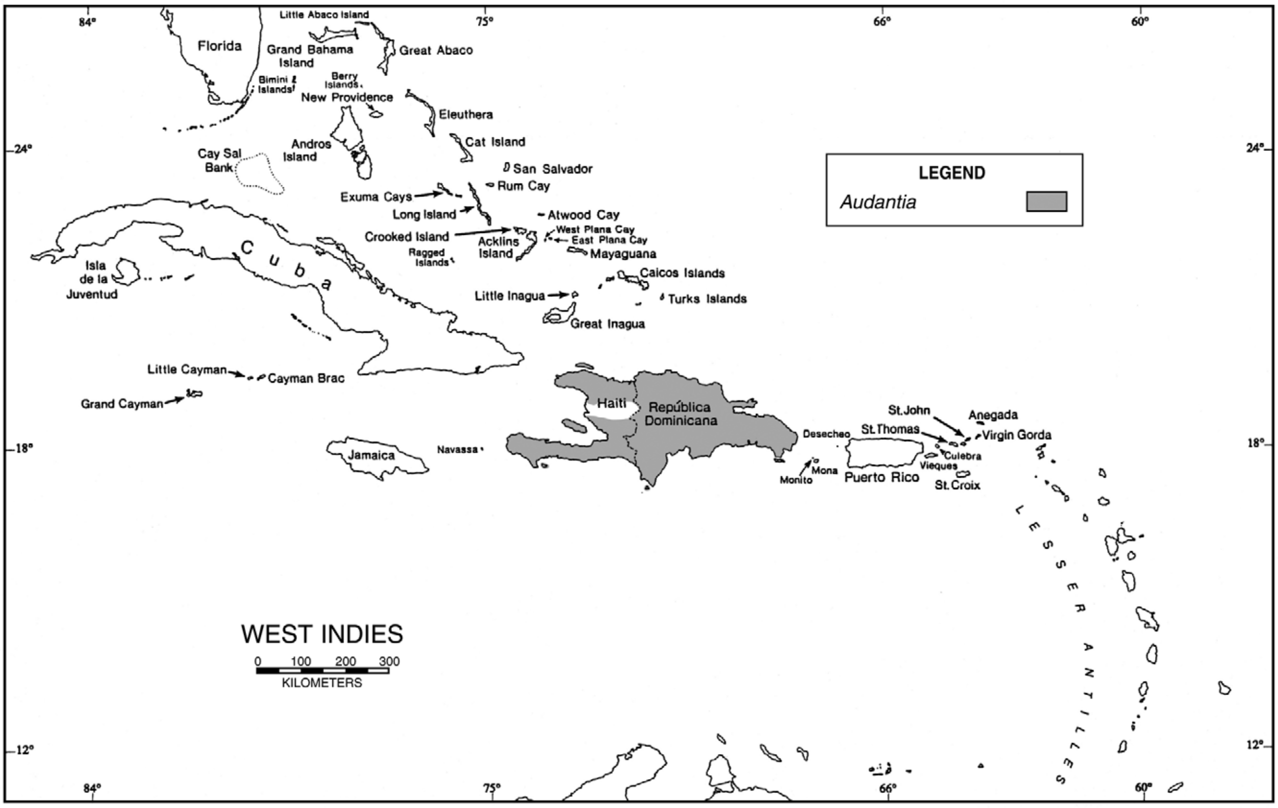


FIGURE 17. Distribution of the genus *Audantia*.

Genus *Anolis* Daudin, 1802

Anolis Daudin, 1802; Histoire Naturelle Gènérale et Particulière des Reptiles 4: 50. Type species: *Anolis carolinensis* Voigt, 1832: 71 by action of the ICZN (1986) (Opinion 1385).

Anolius Cuvier, 1816; Règne Animal (2): 41, an unjustified emendation of *Anolis* Daudin, 1802 (4): 50 that must take same type species as *Anolis*. Type species: *Anolis carolinensis* Voigt, 1832: 71.

Acantholis Cocteau, 1836a; C. R. Hedb. Séanc. Acad. Sci., Paris 3: 226 (*nomen nudum*); 1836b; L'Insitut 4: 287. Type species: *Anolis loysianus*. Cocteau, 1836b; 3: 287 by monotypy.

Microctenus Fitzinger, 1843; Systema Reptilium: 16, 64. Type species: *Anolis edwardsii* Merrem, 1820: 4 (= *Lacerta bimaculata* Sparrman, 1784: 169). Proposed as a subgenus of *Ctenonotus*.

Ctenocercus Fitzinger, 1843; Systema Reptilium: 17, 68. Type species: *Lacerta bullaris* Linné, 1758: 208 [in part] (=*Anolis carolinensis* Voigt, 1832: 71 by original designation. Proposed as a subgenus of *Dactyloa*.

Heteroderma Fitzinger, 1843: 17, 68. Type species: *Anolis loysianus* Cocteau, 1836b; 3: 226 by original designation.

Macroleptura Garrido, 1975; Poeyana 143: 41. Type species: *Anolis cyanopleurus* Cope, 1861; 13: 211 by original designation. Proposed as a subgenus of *Anolis*.

Pseudoequestris Varona, 1985; Doñanna Acta Vert 12: 33.Type species: *Anolis isolepis* Cope: 1861; 13: 214 by original designation. Proposed as a subgenus of *Anolis*.

Gekkoanolis Varona, 1985; Doñanna Acta Vert: 34. Type species: *Anolis lucius* C. Duméril and Bibron, 1837 (94): 105 by original designation. Proposed as a subgenus of *Anolis*.

Brevicaudata Varona, 1985; Doñanna Acta Vert. 12: 35. Type species *Anolis angusticeps* Hallowell, 1856; 8: 228 by original designation. Proposed as a subgenus of *Anolis*.

Diagnosis.—Support for this genus is provided by 47 apomorphies including seven morphological features and 40 molecular ones. There are two unequivocal morphological features: mental scale completely divided (26: a to z); and supratemporal processes leave supraocciptal exposed above (61: z to a). There are 23 unequivocal molecular apomorphies (see Appendix II).

Definition.—Members of the genus *Anolis* are defined as dactyloid lizards having: 1) the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes but have autotomy septa; 2) interclavicle T-shaped (Guyer and Savage, 1986, Fig. 2B); 3) postfrontal bone usually present (absent in *A. sheplani*); 4) pineal foramen in frontal parietal suture or parietal; 5) pterygoid teeth usually absent; 5) supratemporal processes of parietal may or may not extend over upper surface of supraoccipital; 6) pterygoid teeth usually absent; 7) angular process of articular usually large; 8) posterior border of dentary usually pronged; 9) no splenial; 10) no lower jaw sculpturing; 11) modal number of lumbar vertebrae 5; 12) number of caudal vertebrae anterior to first without transverse processes 6–8, modal number 7; 13) supraoccipital cresting with distinct lateral processes; 14) 2N karyotype = 36 (12M, 24m); no sexual heteromorphism; N.F. = 48.

Content.—This genus is comprised of five species groups, 44 species, one a fossil, and a total of 49 species and subspecies (see Appendix III).

Distribution.—The Bahamas, Cuba, and adjacent islands, Navassa Island, Little Cayman island, Hispaniola, and the southeastern United States west to Oklahoma and Texas. One Cuban species (*A. allisoni*) occurs on Isla Cozumel, Mexico and Islas de la Bahía, Honduras, and on coastal islands off Belize (Fig. 18).

Introductions.—*Anolis carolinensis*, to Hawaii, Guam, and Ogasawara Islands; *Anolis maynardi* to Cayman Brac and *A. porcatus* to Hispaniola and Florida.

Etymology.—The generic name is from the French, *l'anole*, derived from the Carib name, *anoli*, *anoali* (Rochefort, 1658) for lizards on Martinique in the Lesser Antilles. It was used in the masculine gender by the original describer, Daudin (1802). It is ironic that the anole of Martinique (*Dactyloa roquet*) is now referred to a different genus. However, see Appendix I on the identities of both *l'anole* and *l'roquet*.

Remarks.—Linné's (1758) *Lacerta bullaris*, the type species of *Ctenocercus*, is based on Catesby's (1754: pl. 66) *Lacerta viridis jamaicensis*. It is not possible to definitely associate Catesby's brief description and plate with any Jamaican dactyloid. Fitzinger (1843) designated *Dactyloa bullaris, sensu* Wagler (1830), as the type species of *Ctenocercus*, but indicated it was a synonym of *Dactyloa (Ctenocercus) carolinensis*.

This genus is basically a Cuban radiation. It seems likely that its establishment in the southeastern United States was by overwater transportation from Cuba. There has been doubt that the presumed mainland form, *Anolis carolinensis*, is actually a species distinct from *Anolis porcatus* of Cuba. However, both species are diagnosed by over 70 apomorphies each in our combined tree. Both the genus *Anolis*, as envisioned by Cannatella and de Quieroz (1989) and the genera *Dactyloa* and *Xiphosurus*, as envisioned by Guyer and Savage (1986), were rendered paraphyletic by the discovery that *Phenacosaurus* is nested within *Dactyloa* and *Chamaeleolis* is nested within *Xiphosurus*. Given this, the widely cited criticism that the genera of Guyer and Savage (1986) are paraphyletic boils down to a single problem of the concept of *Anolis* advocated in that publication. Analyses subsequent to Guyer and Savage (1986) consistently demonstrate that the problem of paraphyly can be eliminated by restricting the content of *Anolis* to the groups described below along with recognition of a genus *Deiroptyx* and expansion of the concepts of *Chamaelinorops* and *Xiphosurus* described above. Identification of this problem and of potential solutions were summarized in Guyer and Savage (1992). The genus described here is also recognized as a clade in Alfoldi *et al*.'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

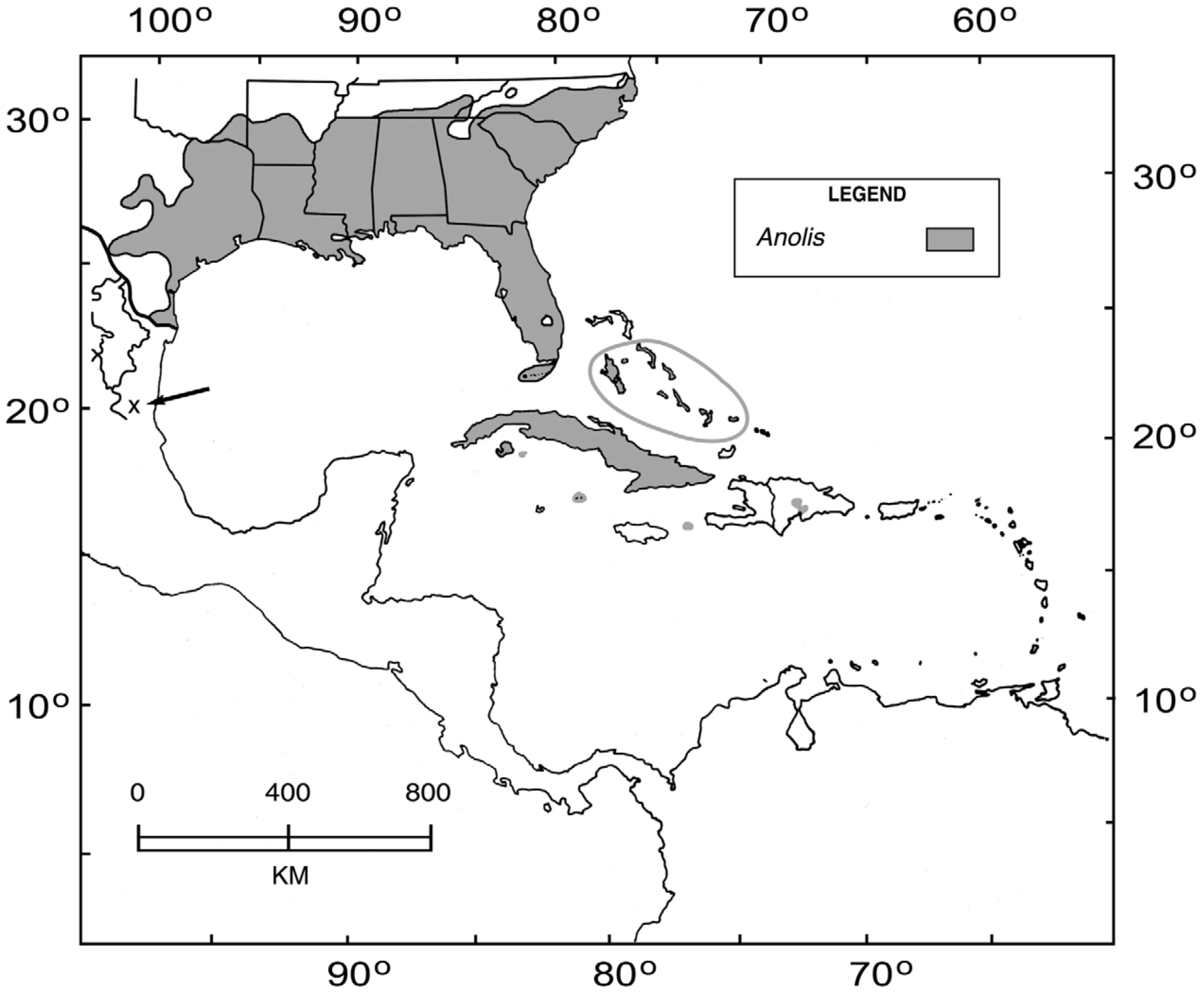


FIGURE 18. Distribution of the genus *Anolis*.

Anolis lucius Species Group

Diagnosis.—Support for this group is provided by 91 apomorphies including 16 morphological and 75 molecular ones. There are nine unequivocal morphological apomorphies: maximum male snout-to-vent length increased (1: f to g); ratio of maximum female snout-to-vent length to maximum male snout-to-vent length increased (2: h to d); scales on dewlap with at least one double row, (21: a to z); transparent scales in lower eyelid (25: a to z); mean number of postmental scales increased (30: m to s); supraorbital semicircles in contact (32: a to z); anteriormost aspect of rostral scale usually even with lower jaw (36: a to g); dorsal, ventral, supradigital, and head scales smooth (40: 0 to 1); and quadrate lateral shelf usually absent (75: a to g). There are 33 unequivocal molecular apomorphies (see Appendix II).

Definition.—The two species placed in this species group are moderate-sized lizards (maximum size of adult males to 66 mm in snout-to-vent length and adult females to 44 mm) that share the following combination of features: 1) two or three transparent scales in lower eyelid; 2) interparietal scale large, several times larger than adjacent scales; 3) head narrow, length much longer than width; 4) arms and legs long; 5) tail long, about 2.5 times snout-to-vent length; 6) no dewlap in females; 7) four lumbar vertebrae; 8) five aseptate caudal vertebrae anterior to first autotomic vertebra.

Content.—Two species are referred to this species group (Appendix III).

Distribution.—Cuba (Fig. 19).

Remarks.—The two species forming the *lucius* group appear at different places on three phylogenetic trees. In Poe (2004) they are sister to a clade consisting of *Xiphosurus chamaeleonides* and *Deiroptyx darlingtoni*. In our molecular tree they are sister to all *Xiphosurus*. In our combined tree they are sister to all *Anolis* (*sensu stricto*). Morphologically, the two taxa in this group appear to be most closely related to *Anolis* (*sensu stricto*) particularly in having a T-shaped interclavicle and lacking the many unique morphological features of the *X. chamaeleonides* group. Members of that group and all other species of *Xiphosurus* most importantly differ from *A. argenteolus* and *A. lucius* in having arrow-shaped interclavicles. One solution to this non-concordant situation would be to recognize a separate genus for these two species, for which the name *Gekkoanolis* Varona, 1985 is available. We eschew that alternative awaiting further study. Only the two species comprising this group, among all dactyloids, have semitransparent scales in the lower eyelid, which separates them most obviously from *Deiroptyx darlingtoni*.

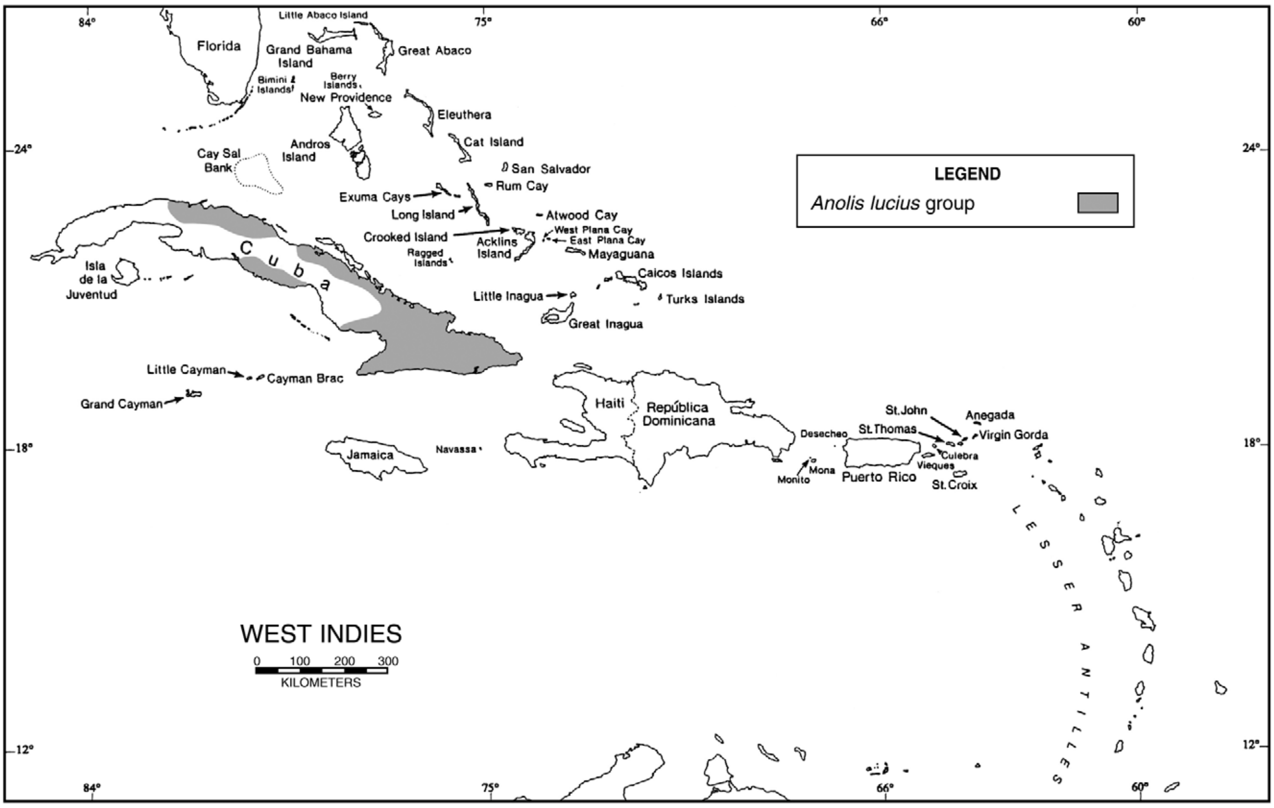


FIGURE 19. Distribution of the *Anolis lucius* Species Group.

Anolis alutaceus Species Group

Diagnosis.—Support for this group is provided by 81 apomorphies including eight morphological and 73 molecular ones. There are six unequivocal morphological apomorphies: maximum male snout-to-vent length decreased (1: f to a); size of ear opening increased (6: m to q); tail length about 2.5 or more times snout-to-vent length (8: s to v); five or more enlarged rows of middorsal scales (13: a to z); modal number of supraciliary scales two (38: 1 to 2); and scales in supraorbital disc vary continuously in size and are bordered medially by an unbroken row of small scales (41: 0 to 1). There are 40 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are very small to small, gracile anoles (maximum snout-to-vent length in adult males 33 to 49 and 31 to 45 mm in adult females) sharing the following combination of characters: 1) no transparent scales in lower eyelid; 2) interparietal scale small, about same size as adjacent scales; 3) head narrow, length much longer than width; 4) legs long and slender; 5) tail long, about 2.5 to 2.7 times snout-to-vent length; 6) dewlap absent in females; 7) five or six lumbar vertebrae; 8) usually seven or more aseptate vertebrae anterior to first autotomic caudal vertebrae, rarely six.

Content.—This species group contains 14 species and a total of 15 species and subspecies (see Appendix III).

Distribution.—Cuba and its satellite islands (Fig. 20).

Remarks.—In the Poe (2004) tree, members of this group form the sister group to *Chamaelinorops barbouri*. In our molecular and combined trees they fall out well within the *Anolis* clade, and are referred to that genus.

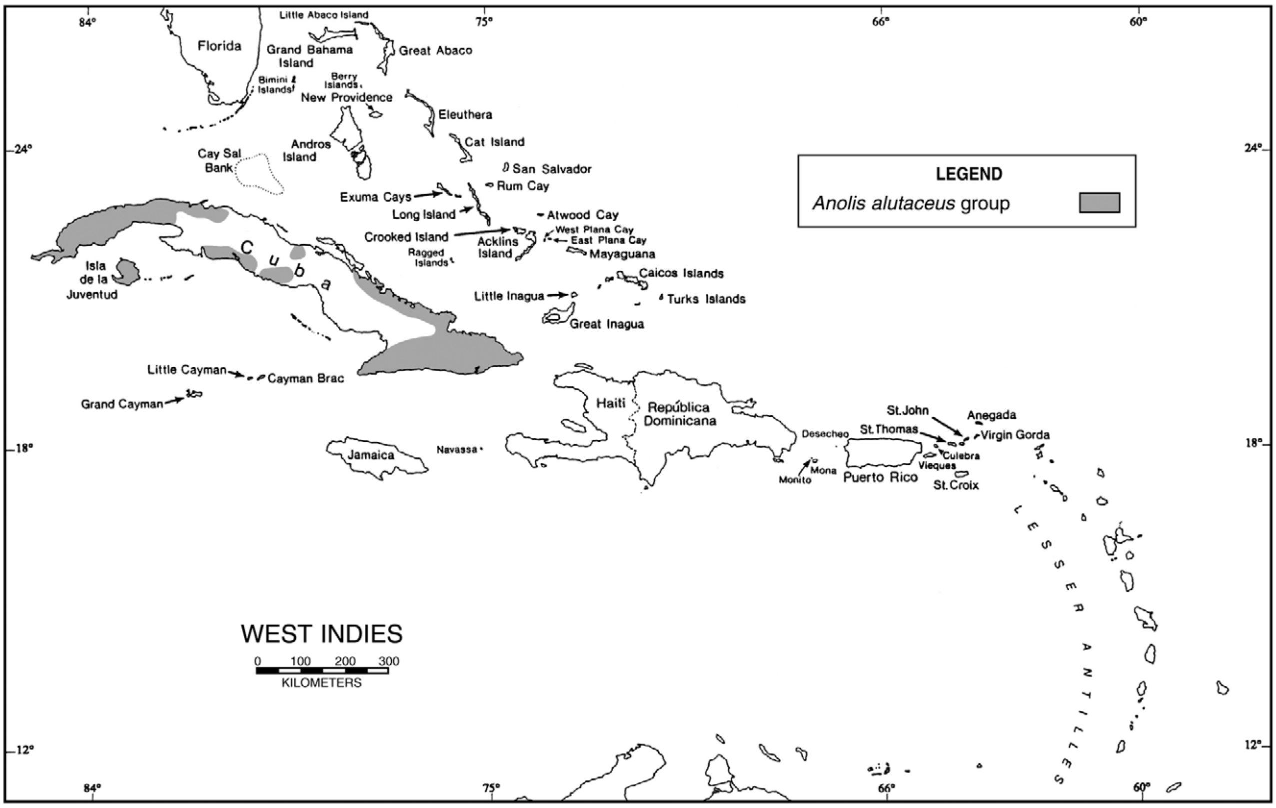


FIGURE 20. Distribution of the *Anolis alutaceus* Species Group.

Anolis angusticeps Species Group

Diagnosis.—Support for this group is provided by 56 apomorphies including zero morphological and 56 molecular ones. Twenty of the latter are unequivocal (see Appendix II).

Definition.—Lizards of this species group are small anoles (maximum snout-to-vent length in adult males 41 to 53 mm and 40 to 47 mm in adult females) sharing the following combination of characters: 1) no transparent scales in lower eyelid; 2) interparietal scale small, about same size as adjacent scales; 3) head elongate, length much longer than width; 4) arms and legs short; 5) tail short, about 2.0 times snout-to-vent length; 6) dewlap present or absent in females; 7) five or six lumbar vertebrae; 8) seven aseptate caudal vertebrae anterior to first autotomic vertebra.

Content.—This species group contains seven species and a total of nine species and subspecies (see Appendix III).

Distribution.—Cuba, its satellite islands, Hispaniola, and the Bahamas (Fig. 21).

Remarks.—A pair of sister species, *Anolis garridoi* and *A. guazuma*, form a basal branch to the *loysianus* group in the molecular tree and have a similar relationship to the *angusticeps* group in the combined tree. Rodriguez-Schettino (1999) groups these taxa with other narrow-headed forms in her *carolinensis* species group. Members of the *loysianus* species group, in contrast, have shorter and broader heads. One solution to the incongruence between the trees would be to place the two species at issue into a separate species group but we are influenced by Rodriguez-Schettino's treatment and include them in the *angusticeps* group pending further study.

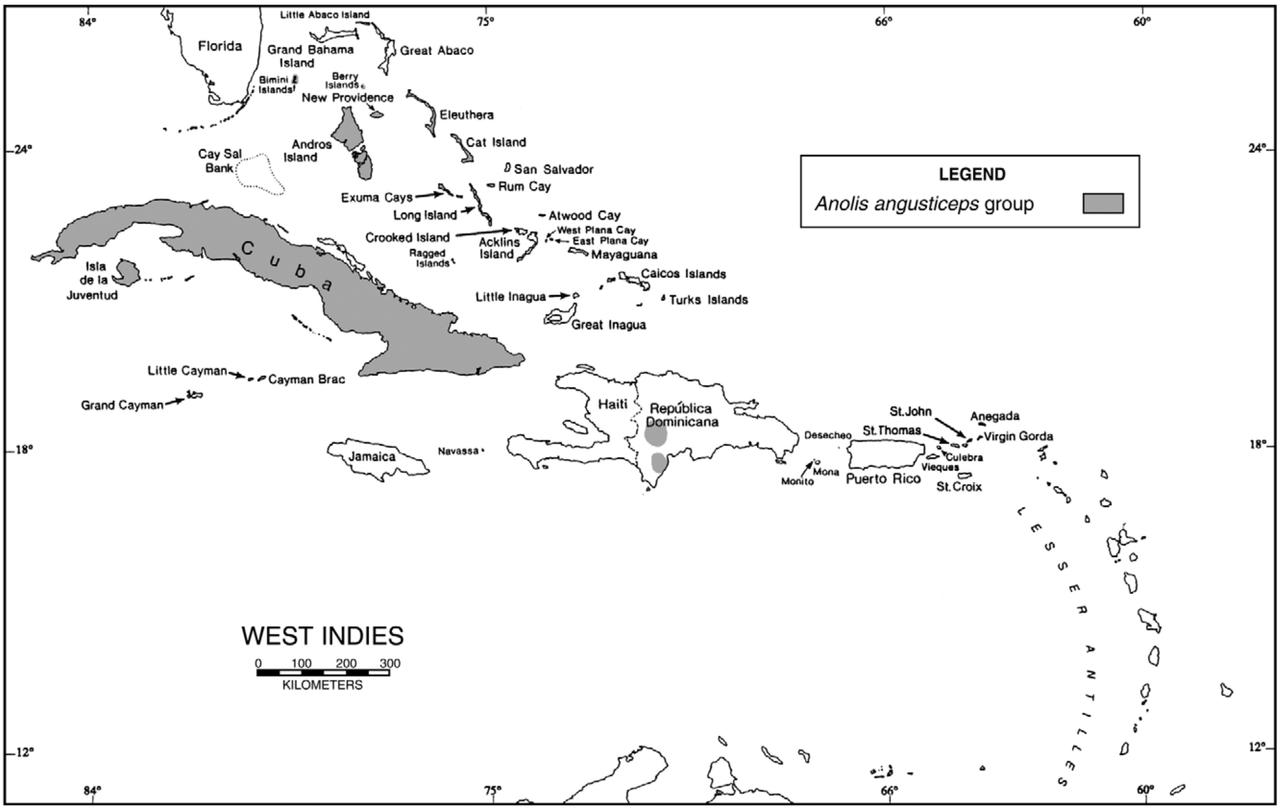


FIGURE 21. Distribution of the *Anolis angusticeps* Species Group.

Anolis loysianus Species Group

Diagnosis.—Support for this group is provided by 68 apomorphies including 13 morphological and 55 molecular ones. There are five unequivocal morphological apomorphies: mean number of scales across the snout decreased (29: e to c); supraorbital semicircles in contact, (32: a to z); circumnasal separated from rostral by one scale, not in contact with supralabial (modal condition) (39: 3 to 2); black pigment over most bones on surface of skull (76: a to z); and posteriormost tooth usually completely anterior to the mylohyoid foramen (81: z to n). There are 29 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are small anoles (maximum snout-to-vent length in adult males 33 to 54 and 36 to 44 mm in adult females) sharing the following combinations of characters: 1) no transparent scales in lower eyelid; 2) interparietal scale small, about same size as adjacent scales; 3) head stubby, length slightly shorter or equal to width; 4) arms and legs short; 5) tail very short, about 1.5 times snout-to-vent length; 6) dewlap absent in females; 7) four or five lumbar vertebrae; 8) six or seven aseptate caudal vertebrae anterior to first autotomic vertebra.

Content.—Six species are referred to this species group (see Appendix III).

Distribution.—Cuba and its satellite islands (Fig. 22).

Anolis carolinensis Species Group

Diagnosis.—Support for this group is provided by 33 apomorphies including seven morphological and 26 molecular ones. There are two unequivocal morphological apomorphies: female dewlap extends to arms or shorter (17: 2 to 1); and mean number of ventral scales in 5% of snout-to-vent length decreased (20: p to o). There are nine unequivocal molecular apomorphies (see Appendix II).

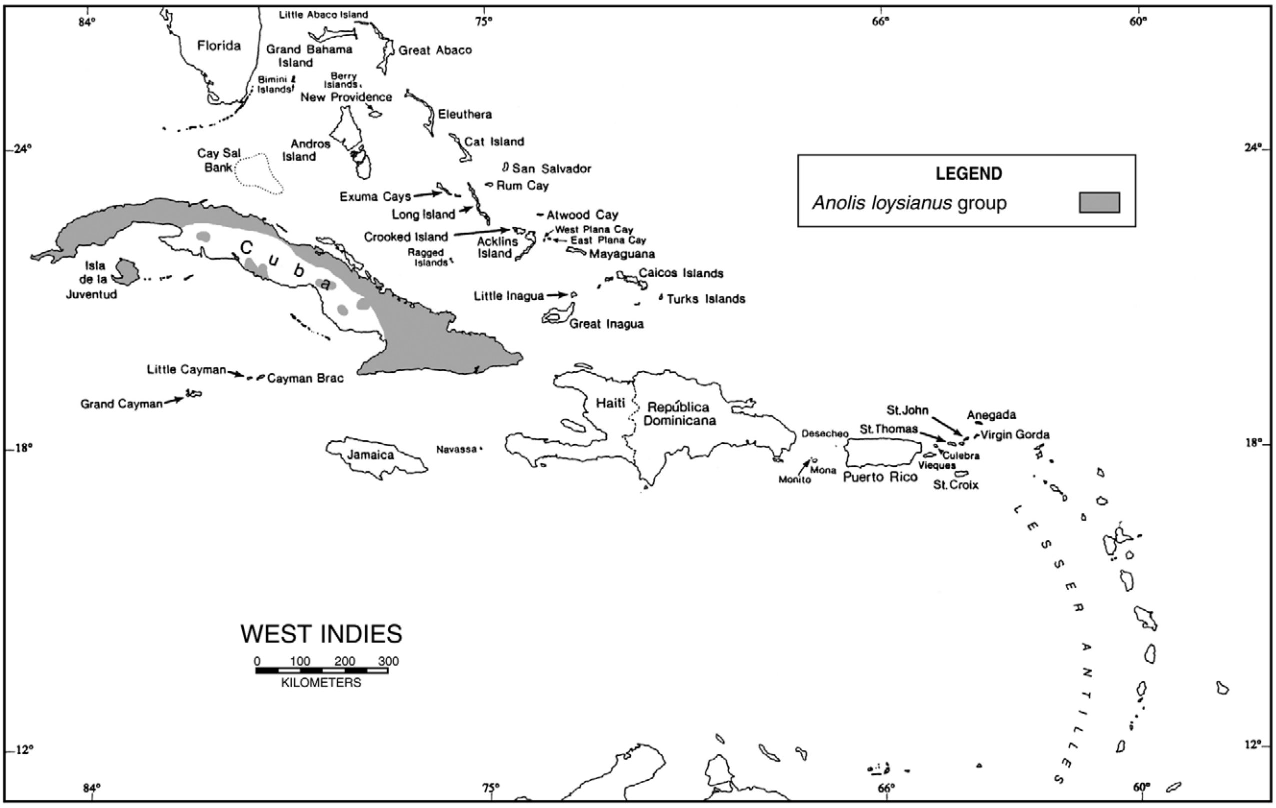


FIGURE 22. Distribution of the *Anolis loysianus* Species Group.

Definition.—Lizards of this species group are moderate-sized anoles (maximum snout-to-vent length 52 to 83 in adult males, 48 to 75 mm in adult females) sharing the following combinations of characters: 1) no transparent scales in lower eyelid; 2) interparietal scale small, about same size as adjacent scales; 3) head elongate, length much longer than width; 4) limbs short; 5) tail long, about 2.3 to 2.5 times snout-to-vent length; 6) dewlap usually absent in females; 7) four lumbar vertebrae; 8) six or seven aseptate caudal vertebrae anterior to first autotomic vertebra.

Content.—This species group contains 14 species and a total of 17 species and subspecies (see Appendix III).

Distribution.—The Bahamas Islands, Cuba, and adjacent islands, Little Cayman Island, Navassa Island (Fig. 23), and the southeastern United States from southeastern Virginia southward to southern Florida and the Florida Keys, westward through eastern and southern North Carolina, South Carolina, Georgia, southern Tennessee, Alabama, Mississippi, Louisiana, southern and central Arkansas and southeastern Oklahoma to central Texas. (Fig. 23).

Introductions.—*Anolis carolinensis* to Hawaii, Guam, and Ogasawara Islands, *Anolis maynardi* to Cayman Brac and *A. porcatus* to Hispaniola and Florida.

Genus *Ctenonotus* Fitzinger, 1843

Ctenonotus Fitzinger, 1843; Systema Reptilium: 16, 64. Type species: *Lacerta bimaculata* Sparrman, 1784: 116 by original designation. Savage and Guyer (2004: 304) as first revisers, gave this name precedence over all other Fitzinger genus-group names applicable to dactyloids.

Istiocercus Fitzinger, 1843; Systema Reptilium: 16, 65. Type species: *Anolis cristatellus* Duméril and Bibron, 1837 (4): 143 by original designation. Proposed as a subgenus of *Ptychonotus*.

Diagnosis.—Support for this genus is from 46 apomorphies including seven morphological and 39 molecular ones. There are two unequivocal morphological features: maximum male snout-to-vent length increased (2: h to m); length of tail about 2.0 to 2.5 times snout-to-vent length (8: h to m). There are 21 unequivocal molecular apomorphies (see Appendix II).

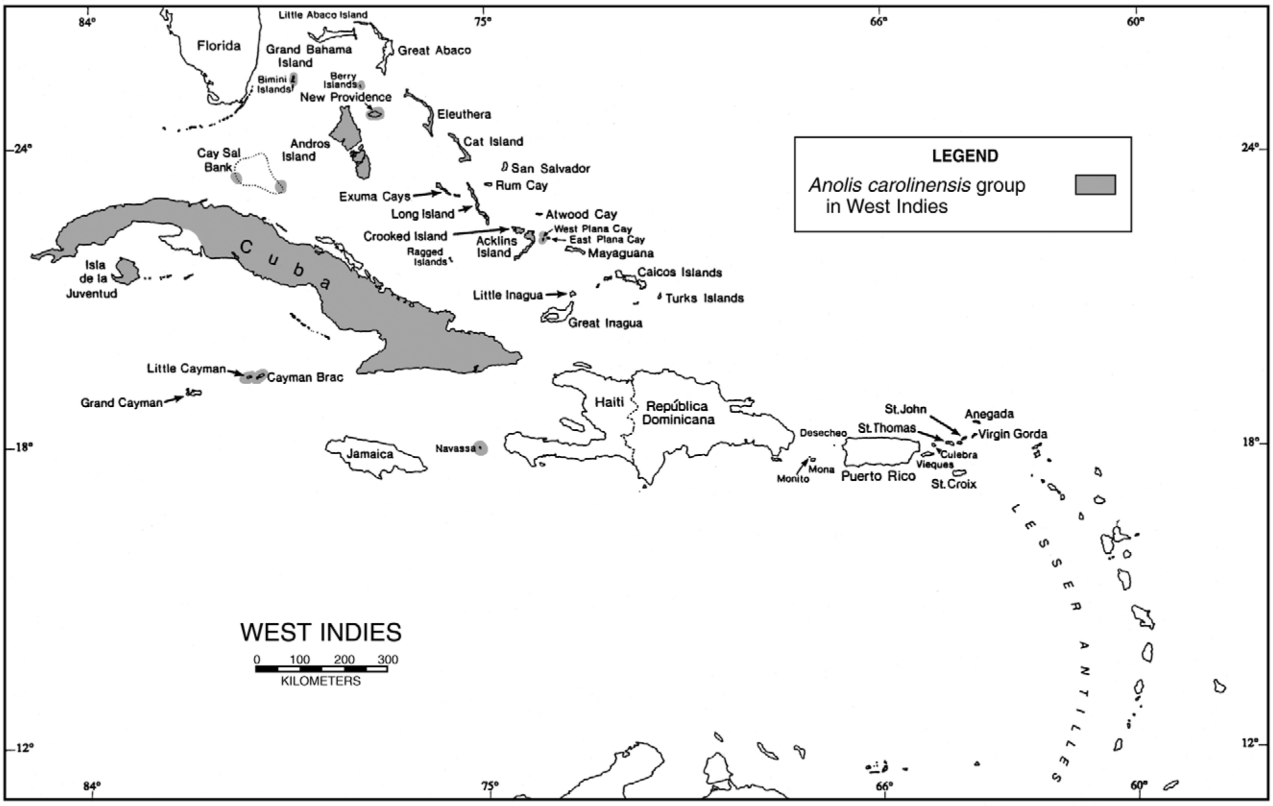


FIGURE 23. Distribution of the *Anolis carolinensis* Species Group in the West Indies.

Definition.—Members of the genus *Ctenonotus* are defined as dactyloid lizards having: 1) the alpha condition of the caudal vertebrae (Etheridge, 1967, Fig. 2C) in which the caudal vertebrae anterior to the first autotomic vertebra are aseptate and have transverse processes and the posterior caudal vertebrae lack transverse processes but have autotomy septa; 2) interclavicle arrow-shaped; 3) postfrontal bone usually present; 4) pineal foramen usually in frontal-parietal suture; 5) supratemporal processes of parietal leave supraoccipital exposed above; 6) pterygoid teeth present or absent; 7) angular process usually large; 8) posterior suture of dentary blunt; 9) splenial present or absent; 10) usually slight to extensive lower jaw sculpturing in large males (Etheridge, 1969, Figs. 8a, b) or not; 11) modal number of lumbar vertebrae 3 or 4; 12) modal number of aseptate caudal vertebrae anterior to first autotomic vertebra usually 6, sometimes 7; 13) supraoccipital cresting continuous across supraoccipital, rarely with distinct lateral processes; 14) karyotypic variation for this genus is summarized by species group in the accounts below. Note that for 2N and N.F. values, even numbers are for females, odd numbers for males.

Content.—This genus is comprised of three species groups, thirty-six species and a total of 67 species and subspecies (see Appendix III).

Distribution.—Bahama Bank, Turks and Caicos Islands, Hispaniola, Puerto Rico and their satellite islands, Mona and Desecheo Islands, Puerto Rico and St. Croix Banks, the Virgin Islands, and the Lesser Antilles, north of the Dominica Channel (Fig. 24).

Introductions.—*Ctenonotus cristatellus* to Dominican Republic, Yucatan, Costa Rica and south Florida; *C. distichus* to Florida; *C. ferreus* to Florida; *C. leachii* to Bermuda; *C. wattsi* to St. Lucia and Trinidad.

Etymology.—The generic name is derived from the Greek *kteis* = comb and *noton* = back, latinized to *Ctenonotus*, in allusion to the large nuchal crest in males of the type species. The name is masculine in gender.

Remarks.—Fitzinger (1843) lists *Anolis bimaculatus* Daudin (1802) as the type species (p. 16) of *Ctenonotus*. As noted above Daudin's specimen was actually of a different species than the type of Sparrman's (1784) *Lacerta bimaculata*. Daudin's specimen was later made the type of C. Duméril and Bibron's *Anolis alligator* (= *Anolis roquet* Bonnaterre, 1789). However, Fitzinger indicated (p. 64) that he considered both Daudin's specimen and Duméril and Bibron's *Anolis alligator* to be synonyms of *Lacerta bimaculata* Sparrman. It is clear that Fitzinger's intent was to designate the last named species (as *Ctenonotus bimaculatus*) as the generic type because it is the only taxon included in his subgenus *Ctenonotus*. Guyer and Savage (1992) anticipated the action that we now take of restricting *Ctenonotus* to the three groups listed below and recognizing *Audantia* as a separate genus. The genus described here is also recognized as a clade in Alfoldi *et al*.'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

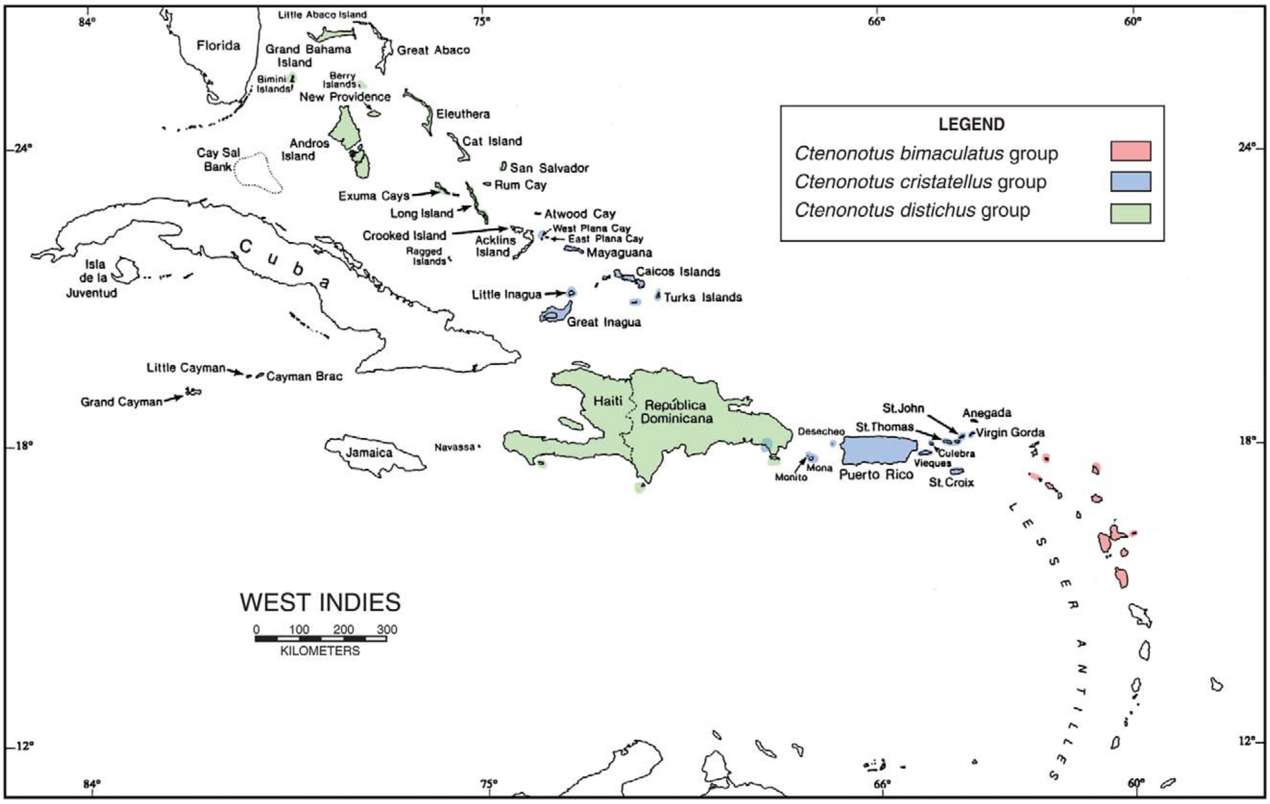


FIGURE 24. Distribution of the genus *Ctenonotus*: *Ctenonotus bimaculatus* Species Group (see also Fig. 17), *Ctenonotus distichus* Species Group, and *Ctenonotus cristatellus* Species Group.

Ctenonotus bimaculatus Species Group

Diagnosis.—Support for this group is provided by 84 apomorphies including six morphological and 68 molecular ones. There is one unequivocal morphological apomorphy: posterior suture of dentary blunt (83: a to z). There are 27 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are mostly moderate-sized anoles (maximum snout-to-vent length in adult males 58 to 96 mm, in adult females 46 to 64 mm). *Ctenonotus bimaculatus* and *C. ferreus* are large forms with maxima of 123 and 119 mm in males and 70 and 65 mm in females, respectively. Members of this group share the following combination of characters: 1) posterior suture of dentary blunt; 2) middorsal scales on snout arranged in two parallel rows that extend from the level of the second canthal to the nares; 3) prefrontal separated from nasal by frontal and nasal; 4) quadrate lateral shelf present or absent; 5) slight, wrinkled lower jaw sculpturing often present in large adult males; 6) N.F. = 43 or 44; Type III karyotype: 2N = 29/30 (8V + 4v, 6sT, 11 or 12m) in nine species or 31/32 (6V + 4sv, 6sT, 4T, 11 or12m) in *C. oculatus*; xxy heteromorphism; N.F. = 47/48.

Content.—This species group contains seventeen species and a total of 26 species and subspecies (see Appendix III).

Distribution.—Northern Lesser Antilles (Fig. 24).

Introduction.—*C. leachii* to Bermuda; *C. wattsi* to St. Lucia.

Ctenonotus distichus Species Group

Diagnosis.—Support for this group is provided by 93 apomorphies including 15 morphological and 78 molecular ones. There are six unequivocal morphological apomorphies: maximum male snout-to-vent length decreased (1: m to j); length of head decreased (4: s to m); mean number of scales across the snout decreased (29: e to d); middorsal scale of the snout arranged in two parallel rows that extend from the level of the second canthals to nares (34: a to z); dorsal, ventral, supradigital, and head scales smooth (40: 0 to 1); and quadrate lateral shelf present (75: a to z). There are no unequivocal molecular apomorphies (see Appendix II).

Definition.—Dactyloids of this species group are small lizards (maximum snout-to-vent length in adults males 47 to 51 mm, in adult females 42 to 48 mm), sharing the following combination of features: 1) posterior suture of dentary pronged; 2) middorsal scales on snout not in a regular pattern; 3) prefrontal contacts nasal; 4) quadrate lateral shelf present; 5) no lower jaw sculpturing; 6) Type II karyotype: 2N = 33 (10M, 4 T, 19 or 20m); xxy heteromorphism.

Content.—This species group contains six species and a total of 24 species and subspecies (see Appendix III).

Distribution.—Bahamas and Hispaniola and its satellite islands (Fig. 24).

Introduction.—*C. distichus* to southern Florida.

Ctenonotus cristatellus Species Group

Diagnosis.—Support for this group is provided by 59 apomorphies including six morphological and 53 molecular ones. There is one unequivocal morphological feature: female dewlap to arms or shorter (17: 2 to 1). There are 26 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are small to moderate-sized dactyloids (maximum snout-to-vent length in adult males 44 to 82 mm, in females 36 to 73 mm) sharing the following combinations of characters: 1) posterior suture of dentary variable, blunt or pronged; 2) middorsal scales on snout not in a regular pattern; 3) prefrontal usually in contact with nasal; 4) quadrate lateral shelf usually absent; 5) usually some lower jaw sculpturing in large adult males, absent in *C. evermanni*; 6) Type II karyotype: 2N = 26 (12M, 2v, 12m), xy heteromorphism, N.F. = 44 in *C. evermanni*; 27/28 (12M, 4v, 11 or 12m), 29/30 (12M, 2v or 4v, 13/14 or 15/16m), 31/32 (12M, 2v, 17/18m), N.F. = 43/44 or 45/46, xxy sexual heteromorphism in nine other species.

Content.—This species group contains thirteen species and a total of 17 species and subspecies (see Appendix III).

Distribution.—Turk and Caicos Islands, Puerto Rico and its satellite islands, Mona Island, and the Virgin Islands (Fig. 24).

Introductions.—*Ctenonotus cristatellus* to Dominican Republic, Cozumel Island off the Yucatan, Costa Rica and southern Florida.

Genus *Norops*

Genus *Norops* Wagler, 1830

Norops Wagler, 1830; Natürliches System der Amphibien: 149. Type species: *Lacertaaurata* Bonnaterre, 1789: 52 by monotypy. Selected as the senior synonym over *Draconura* Wagler, 1833 by Savage and Guyer (1991:303).

Draconura Wagler, 1830; Natürliches System der Amphibien: 149. Type species: *Draconura nitens* Wagler, 1830: 149 by monotypy.

Trachycoelia Fitzinger, 1843; Systema Reptilium: 17, 66. Type species: *Anolis lineatus* Daudin,1804 (4): 66 (= *Lacerta strumosa* Linné, 1758:208) by original designation. Proposed as a subgenus of *Ptychonotus*.

Tropidopilus Fitzinger, 1843; Systema Reptilium: 17, 66. Type species: *Anolis fuscoauratus* D'Orbigny in Duméril and Bibron, 1837 (4): 110 by original designation. Proposed as a subgenus of *Dactyloa*.

Xiphocercus Fitzinger, 1843; Systema Reptilium: 17, 67. Type species: *Anolis valencienni* C. Duméril and Bibron, 1837 (4): 131 by original designation. Proposed as a subgenus of *Dactyloa*.

Trachypilus Fitzinger, 1843; Systema Reptilium: 17, 67. Type species: *Anolis sagre*i Cocteau in Duméril and Bibron, 1837(4): 149 by original designation. Proposed as a subgenus of *Dactyloa*.

Pristicercus Fitzinger, 1843; Systema Reptilium: 17, 67. Type species: *Dactyloa biporcata* Wiegmann, 1834: 47 by original designation. Proposed as a subgenus of *Dactyloa*.

Gastrotropsis Fitzinger, 1843; Systema Reptilium: 17, 68. Type species: *Dactyloa nebulosa* Wiegmann, 1834: 47 by original designation. Proposed as a subgenus of *Dactyloa*.

Dracontura Fitzinger. 1843: 17, 69. Unjustified emendation of *Draconura* Wagler (1830) that must take same type species as *Draconura*. Type species: *Draconura nitens* Wagler, 1830: 149.

Dracontopsis Fitzinger, 1843: 17, 69. Type species: *Draconura nitzschii* Wiegmann, 1834: 16 (= *Lacerta aurata,* Bonnaterre, 1789: 52) by original designation. Proposed as a subgenus of *Dracontura*.

Placopsis Gosse, 1850; Ann. Mag. Nat Hist. ser. 2, 6: 346: type species: *Placopsis ocellata* Gosse, 1850: 346 (= *Anolis valencienni* Duméril and Bibron, 1837 (4): 13) by monotypy.

Coccoessus Cope, 1862; Proc. Acad. Nat. Sci, Philadelphia 14:178. Type species: *Anolis* (*Coccoessus*) *pentaprion* Cope, 1862: 178 by monotypy. Proposed as a subgenus of *Anolis*.

Tropidodactylus Boulenger, 1885; Catalogue of the lizards in the British Musuem (Natural History) 2: 97. Type species: *Norops onca* O'Shaughnessey, 1875; ser. 4, 15: 280 by monotypy.

Diagnosis.—Support for this genus is from 57 apomorphies including nine morphological and 48 molecular ones. There are four unequivocal morphological apomorphies: mean number of ventral scales in 5% of snout-to-vent length increased (20: q to r); anterolaterally directed transverse processes on autotomic caudal vertebrae (beta condition) (49: 0 to 1); nasal overlaps lateral edge of premaxilla (77: a to z); and posterior suture of dentary usually pronged (83: a to n). There are 28 unequivocal molecular apomorphies (see Appendix II).

Definition.—Members of the genus *Norops* can be defined as dactyloid lizards having: 1) the beta condition of autotomous caudal vertebrae (Etheridge, 1969, Fig. 3A) in which all caudal vertebrae have elongate transverse processes with those on the autotomic vertebrae bifurcate in the vertical plane and directed anterolaterally with their base located posterior to the septum; 2) interclavicle T-shaped (Guyer and Savage, 1986, Fig. 2B); 3) postfrontal bone present or absent; 4) pineal foramen in parietal; 5) supratemporal processes of parietal may or may not cover upper surface of supraoccipital; 6) pterygoid teeth absent; 7) angular process of articular large; 8) posterior suture of dentary pronged or blunt; 9) usually no splenial; 10) no lower jaw sculpturing in males; 11) modal number of lumbar vertebrae 3 or 4; 12) modal number of caudal vertebrae anterior to first autotomic vertebra usually 6 or 7, sometimes 8; 13) supraoccipital cresting continuous across supraoccipital or with distinct lateral processes; 14) karyotypes IV or V, no sexual heteromorphism in many species, xy heteromorphism in many species, and xxy heteromorphism in one species. The extensive variation in this genus is summarized by species group below (Appendix 7).

Content.—This genus is comprised of three species groups, 175 species, one which is a fossil, and a total of 190 species and subspecies (see Appendix III).

Distribution.—Cuba, Jamaica, Bahamas, Grand and Little Cayman, Cayman Brac, Mexico, Central America, and many adjacent islands, including Cozumel, the Bay Islands, the Corn Islands, Swan Island, San Andres and Providencia (Caribbean) and Isla del Cocos (Pacific); south to western Ecuador, northern South America (Colombia and Venezuela), including Isla Gorgona (Pacific), the islands of Aruba, Curaçao, and Margarita (Caribbean), Trinidad and Tobago; then south through the Guyanas to southeastern and southern Brazil, and Paraguay, and throughout the Orinoco and Amazon Basins (Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia) (Fig. 25).

Introductions.—*Norops garmani* to Grand Cayman Island, Florida, *N. grahami* to Bermuda; *N. maynardi* to Cayman Brac; *N. sagrei* to Jamaica, Caribbean coast from Mexico to Belize, including Bay Islands and Cozumel, also Grenada and St. Vincent and Little and Grand Cayman Islands and Cayman Brac, the southern United States from Florida to Texas; Hawaii.

Etymology.—The generic name is from the Greek *norops* = brilliant or gleaming with reference to the bright color of the type species and is a translation of the Latin specific name of that species. In this case, *Norops* is an adjective used as a noun and is in the masculine gender as indicated by the original describer (Wagler, 1830). *Norops* is masculine in gender.

Remarks.—The species name, *Anolis auratus*, is usually attributed to Daudin (1802). However, the name *Lacerta aurata* was established on the same basis (a description in Lacépède, 1788) by Bonnaterre (1789).

Linné's (1758) *Lacerta strumosa*, the type species of *Trachycoelia* Fitzinger (1843), is based on Seba (1735, pl. 20, Fig. 4). The specimen (MNHNP 795) that was the model for Seba's portrait is also the type specimen of *Anolis lineatus* Daudin, 1802. It was part of the Seba cabinet at the Paris Museum and at one time was on exhibit in

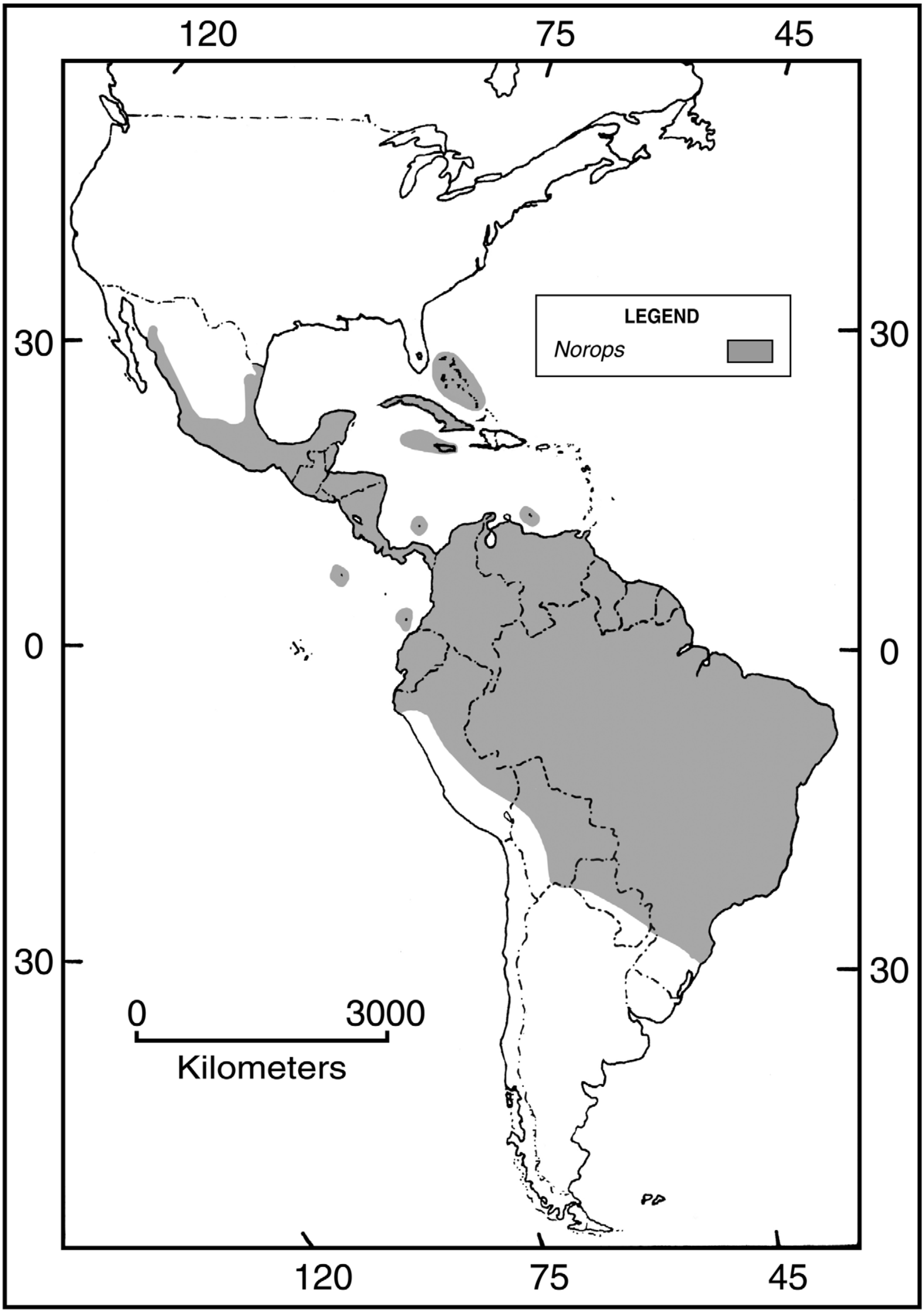


FIGURE 25. Distribution of the genus *Norops*.

the Museum's gallery (Duméril and Bibron, 1837). The name *strumosa* has not been used as a valid name since 1837 and we regard it as a *nomen oblitum* under the Code (Art. 23.9.1.1-2.). The junior synonym, as *Anolis lineatus*, is in prevailing usage and meets the requirements to be treated as a *nomen protectum* under Art. 23.9.2 of the Code, based on a review of the citations in the Zoological Record (1918–2008).

Variation in karyotypes in this nominal genus is extensive. It is especially substantial in the *auratus* group. A limited number of species in the *valencienni* and *auratus* species groups have xy sexual heteromorphism and one species in the latter group has xxy sexual heteromorphism.

The genus described here has long been recognized as a monophyletic group and is supported as such in nearly all published accounts that include species from this group. It is also recognized as a clade in Alfoldi *et al.*'s (2011) analysis of the genome of *Anolis carolinensis* that includes a molecular phylogeny for 96 anole taxa based upon 46 loci and 20,000 bp of sequence data.

Norops sagrei Species Group

Diagnosis.—Support for this group is provided by seven morphological apomorphies and 58 molecular ones. There are three unequivocal morphological apomorphies: ratio of maximum female snout-to-vent length to maximum male snout to-vent-length decreased (2: h to p); tail crest present in largest adult males (12: a to z); and basipterygoid crest present (74: a to z). There are twenty unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are mostly moderate-sized anoles (maximum snout-to-vent length in adult males 55 to 88 mm, in females 40 to 52 mm, but *N. ophiolepis* is a notably small species with maxima of 35 and 30 mm for males and females, respectively). Members of this group share the following combination of characters: 1) basipterygoid crest present; tail crest usually present in large males; 2) tail base usually round in cross section; 3) modal postxiphisternal inscriptional rib formula 2:2; 4) parietal foramen in parietal; 5) supratemporal processes usually leave supraoccipital exposed; 6) prefrontal usually is separated from the nasal by frontal and maxilla; 7) lower jaw sculpturing in large adult males usually absent, some with wrinkling; Type IV karyotype: 2N = 28 (14V, 14m); no sexual heteromorphism; N.F. = 40.

Content.—This species group contains eighteen species and a total of 29 species and subspecies (see Appendix III).

Distribution.—Cuba and its satellite islands, Bahamas and Swan Island (Fig. 26).

Introduction.— *Norops sagrei* to Jamaica, Caribbean coast from Mexico to Belize, including Bay Islands and Cozumel, also Grenada and St. Vincent, Little and Grand Cayman Islands and Cayman Brac, the southern United States from Florida to Texas, and Hawaii.

Norops valencienni Species Group

Diagnosis.—Support for this group is provided by 57 apomorphies including nine morphological and 48 molecular ones. There are two unequivocal morphological apomorphies: mean number of scales across the snout increased (29: f to i); and jaw sculpturing in large adults wrinkled (90: 0 to 5). There are 20 unequivocal molecular apomorphies (see Appendix II).

Definition.—Lizards of this species group are mostly small to moderate-sized anoles (maximum snout-to-vent length in adult males 53 to 80 mm, 44 to 65 mm in adult females; *Norops garmani* and *N. reconditus* are much larger forms with maxima of 131 and 100 mm in males and 80 and 84 mm in females, respectively). Members of this group share the following combinations of characters: 1) basipterygoid crest absent; tail crest present or absent in large males; 2) tail base usually round in cross section; 3) modal postxiphisternal inscriptional rib formula 3:1; 4) parietal foramen in parietal; 5) supratemporal processes leave supraoccipital exposed or not; 6) prefrontal usually contacts nasal; 7) lower jaw sculpturing in large adult males usually absent, some with wrinkling; 8) most species with Type V karyotypes: 2N = 30–37 with variable numbers of metacentric macrochromosomes, small biarmed ones, and telocentrics and 16 m, no sexual heteromorphism, N.F. = 44–43; two species (*N. conspersus*, *N. opalinus*) with type IV karyotype: N = 30 (14V, 16m), xy sexual heteromorphism, and N.F. = 44.

Content.—This species group contains seven species and a total of 11 species and subspecies (see Appendix III).

Distribution.—Jamaica and its satellite islands and Grand Cayman Island (Fig. 26).

Introduction.—*Norops garmani* to Grand Cayman Island and Florida; *N. grahami* to Bermuda.

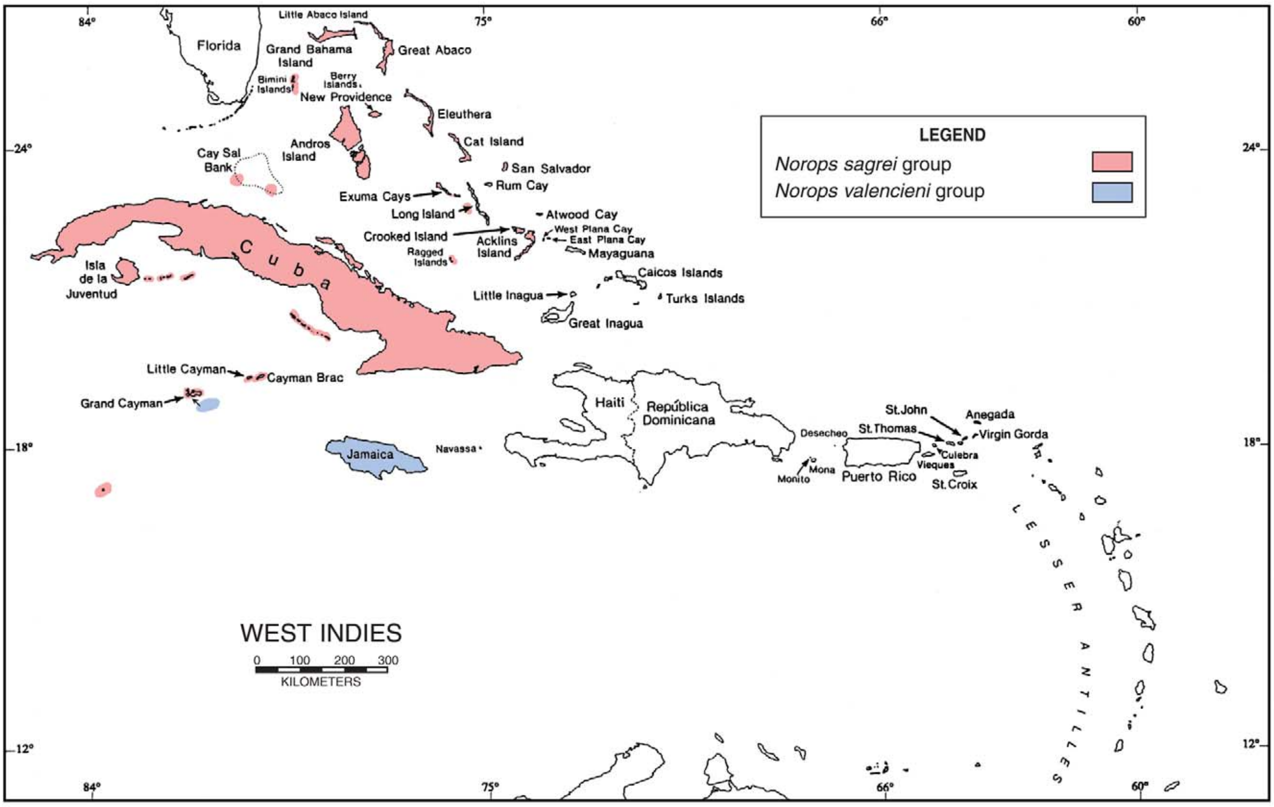


FIGURE 26. Distribution of the *Norops sagrei* and *Norops valencienni* Species Groups.

Norops auratus Species Group

Diagnosis.—Support for this group is provided by 39 apomorphies including six morphological and thirty-three molecular ones. There are two unequivocal morphological apomorphies: base of tail laterally compressed (15: a to z); and supratemporal processes extend over supraoccipital (61: n to z). There are 11 unequivocal molecular apomorphies (see Appendix II).

Definition.—Species of this group are mostly moderate-sized anoles (maximum snout-to-vent lengths of 41 to 102 mm in adult males and 35 to 108 mm in adult females) sharing the following combination of features: 1) basipterygoid crest absent; 2) tail crest usually absent in large males; 2) tail base usually compressed in cross section; 3) modal postxiphisternal inscriptional rib formula 3:1; 4) parietal foramen in parietal; 5) supratemporal processes leave supraoccipital exposed; 6) prefrontal separated from the nasal by frontal and maxilla; 7) lower jaw sculpturing in large adult males usually absent, some with wrinkling; 8) Type IV or V karyotypes: 2N = 28, 29, 30, 32, 36, 38, 40, 42 with various combinations of biarmed and microchromosomes but lacking sexual heteromorphism, divisible into two subgroups: one with 2N = 28–32 and N.F. = 40–44, another with 2N = 36–42, N.F. = 38–40; xy heteromorphism reported in 12 species, 2N = 30, 32, 36, 38 (N.F. = 40–56); xxy heteromorphism is one species (*N. biporcatus*), 2N = 29/30 (12M, 17 or 18 m); N.F. = 41/42 .

Content.—This species group contains 150 species, one of which is known only as a fossil (see Appendix III).

Distribution.—Mexico, Central America, and many adjacent islands, including Cozumel, the Bay Islands, the Corn Islands, San Andres and Providencia Islands (Caribbean) and Cocos Island (Pacific); south to western Ecuador, northern South America (Colombia and Venezuela), including Isla Gorgona (Pacific), the islands of Aruba, Curaçao, and Margarita (Caribbean), Trinidad and Tobago; then south through the Guyanas to southeastern and southern Brazil, and Paraguay, and throughout the Orinoco and Amazon Basins (Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia) (Fig. 27).

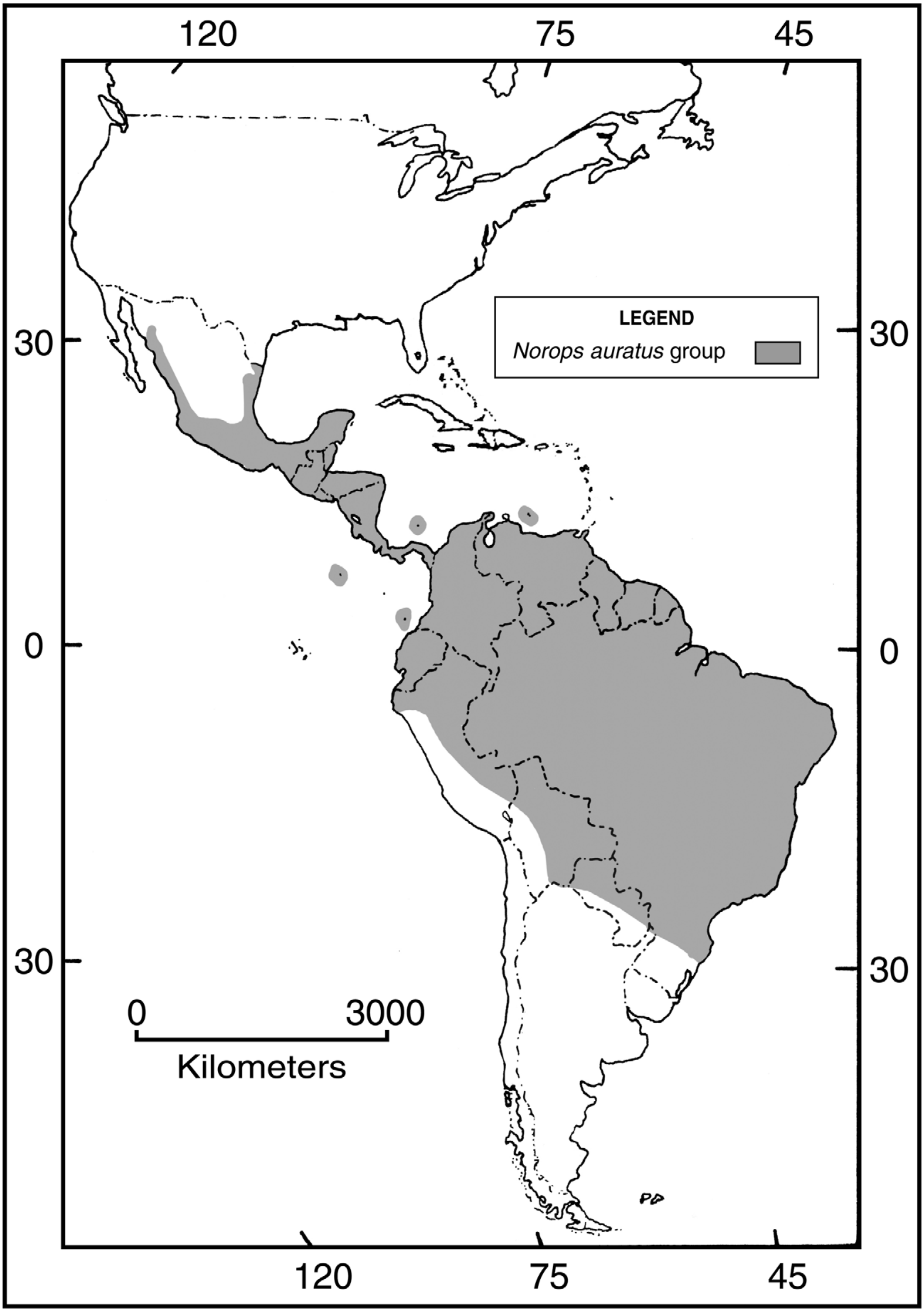


FIGURE 27. Distribution of the *Norops auratus* Species Group.

Remarks.—We have not attempted at this time to further dissect the relationships or propose additional species groups within the large mainland radiation referred to here as the *Norops auratus* species group. However, it is clear that there are two primary clades within this taxon. One, which may be called the southern clade, is basal and restricted to South America and extreme Lower Central America (Table 1). The second is a Mesoamerican clade that is widespread from Mexico southward and has invaded South America after the re-connection of the two regions by the Isthmian Link in the Pliocene (see Fig. 28).

TABLE 1. South American species within subclades of the *Norops auratus* species group. Asterisk (*) indicates species used in our molecular analysis.

Southern Clade:
*annectens**
*auratus**
bombiceps
brasiliensis
chrysolepis
eewi
*lineatus**
*meridionalis**
*nitens**
*onca**
scypheus
tandai

MesoAmerican Clade:
albi
antonii
*biporcatus**
*bitectus**
*fuscoauratus**
gibbiceps
gracilipes
granuliceps
ibague
lemniscatus
lynchi
lyra
macrolepis
maculiventris
mariarum
*medemi**
nigrolineatus
notopholis
*ortonii**
palmeri
*pentaprion**
*poecilopus**
rivalis
scapularis
sulcifrons
tolimensis
*trachyderma**
*tropidogaster**
vicarius
williamsi

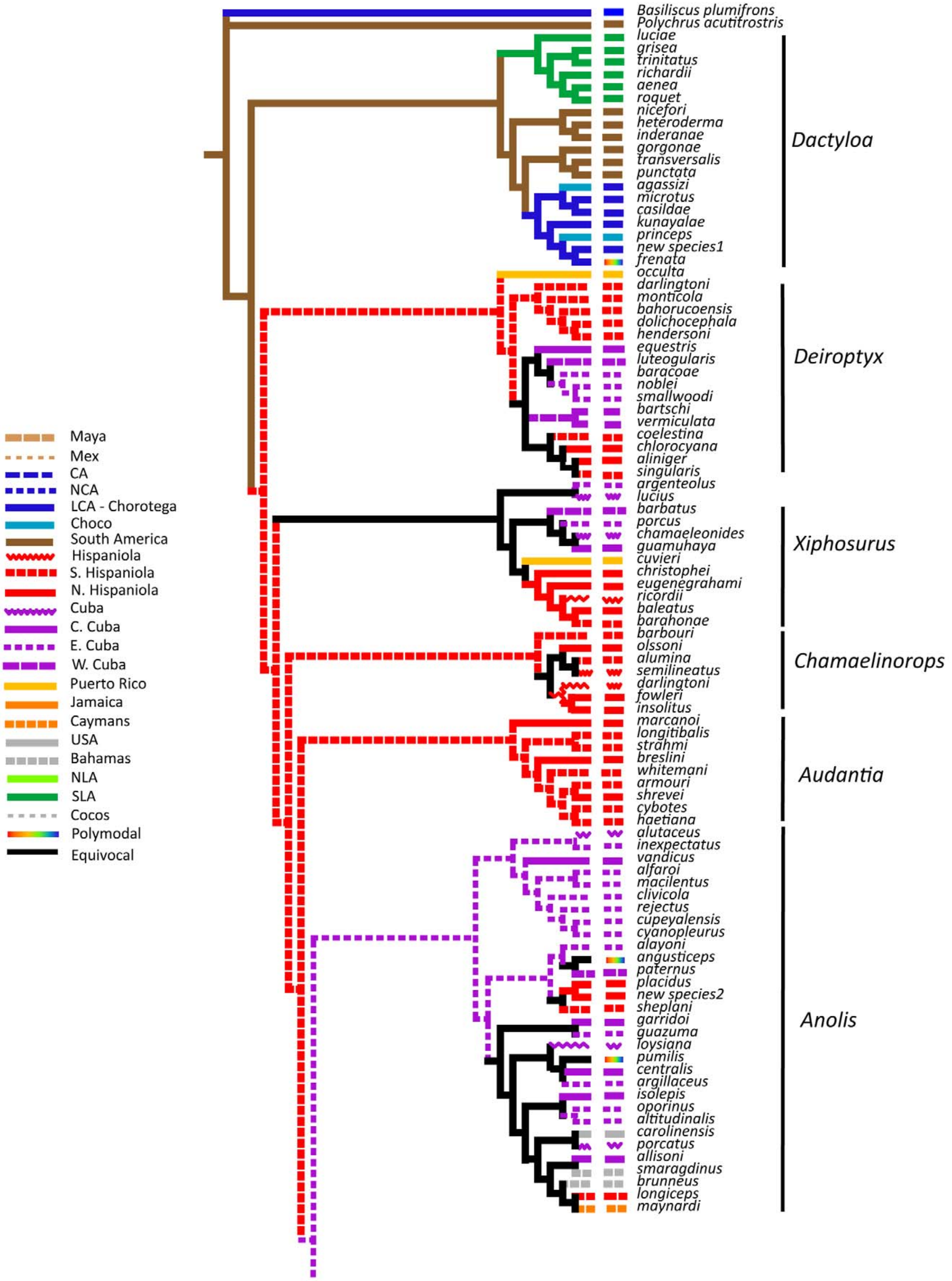


FIGURE 28a. Ancestral state reconstruction of biogeographic areas on the molecular tree (see Fig. 4). Branches are color coded and patterned to reflect the areas those species or clades currently inhabit (see legend to left for reference).

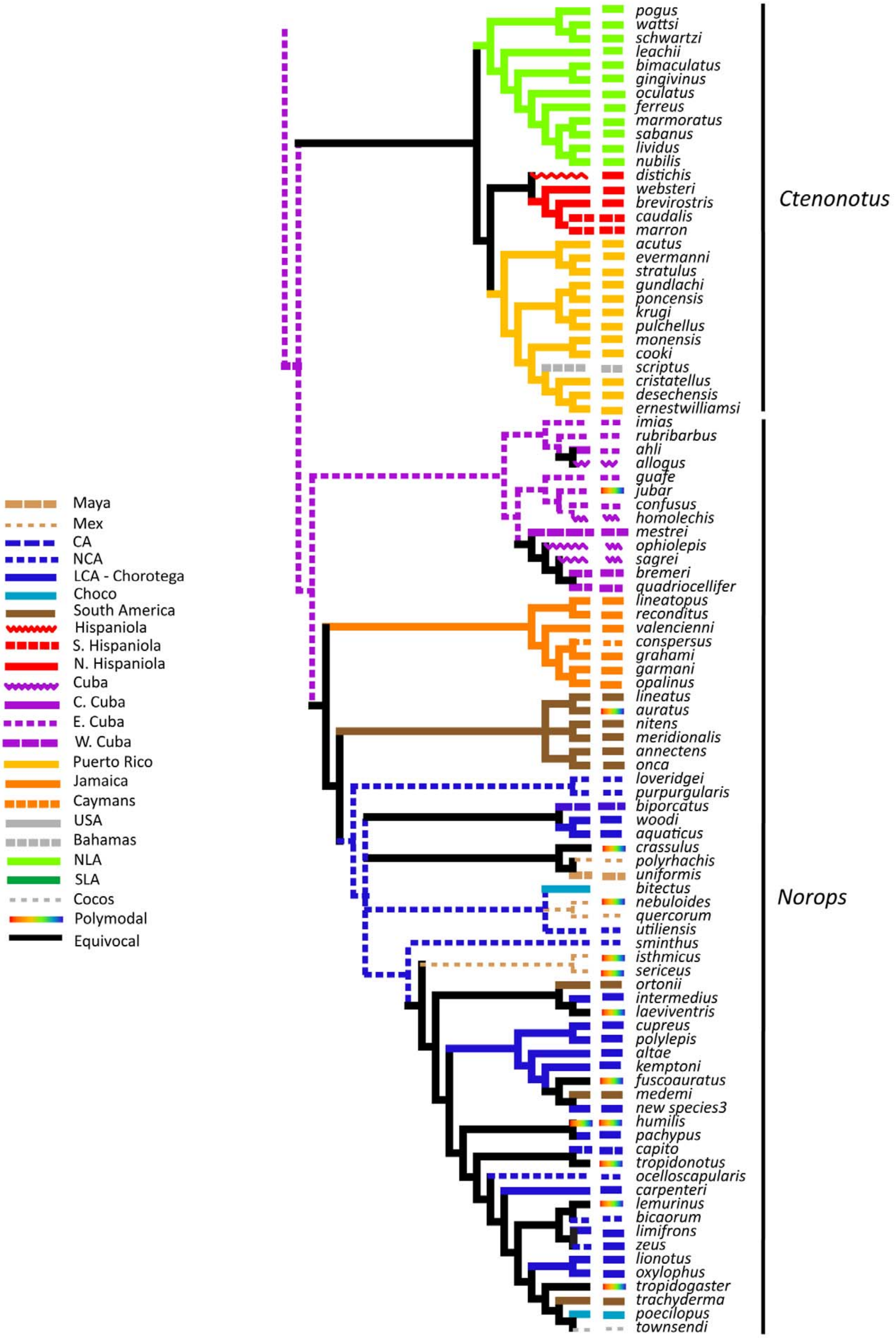


FIGURE 28b. Continued from 28a.

Evolution of ecomodes in the family Dactyloidae

The way that body size and shape correlate with habitat selection in anoles has served as a key example of adaptive evolution within a radiating clade of organisms (Glor, 2011 and references therein). This literature is dominated by the term ecomorph, in reference to assemblages of species that all occupy a particular part of the available habitat, that share a consistent morphology that is demonstrably efficient at activities in that habitat, and that evolved each habitat-specific suite of morphological characters independently (e.g., Losos *et al*. 2006). Although the total number of ecomorphs recognized and their definitions vary, six dominate the literature: crown giant, twig, trunk-crown, trunk, trunk-ground, and grass-bush morphs (Losos, 2009). Anoles on the Greater Antilles are the only species that fit this ecomorph concept fully, despite persistent attempts to broaden it to include other categories of habitat use (e.g., semi-aquatic species) and to include other islands and the mainland (reviewed in Losos, 2009).

Initially, ecomorphs were thought to have evolved on each of the Greater Antillean islands via a consistent pattern of divergence from a generalized ancestral colonist on each island to an assemblage of 4–5 syntopic ecomorphs (Losos, 1992b). Character displacement was thought to be the process that allowed species to evolve while minimizing competition among species (Losos, 1992a). Subsequent analysis of one-species islands of the Lesser Antilles suggested that these initial colonists of the Greater Antilles might be trunk-crown anoles, either because this ecomorph is better at dispersal (Losos and de Queiroz, 1997; Poe *et al*. 2011) or is better at cropping available prey (Roughgarden, 1995). Indeed, if such a consistent historical pattern was shown to have happened independently on the four Greater Antillean islands, this would have demanded some consistent process, such as convergent evolution. Unfortunately, only Jamaica appears to have been colonized by a single species that then diverged to the four sympatric ecomorphs that characterize the current Jamaican anole fauna. Analysis of the only other fauna included in Losos (1992b), the Puerto Rican anoles, suffered from pruning of the phylogeny to include only those taxa present on Puerto Rico. This process generated a misinformative pattern that appeared similar to the pattern for Jamaica only because contradictory evidence from the entire tree had been eliminated via the pruning process. Nevertheless, the observations that sympatric assemblages rarely include more than one member of an ecomorph within Greater Antillean islands is strong evidence that ecomorphs are real biological entities shaped by competition on those islands (Losos, 2009).

Current hypotheses of ecomorph evolution have been generated by scientists whose primary focus has been anoles on Caribbean islands. Those whose primary focus has been anoles at mainland sites have developed a similar jargon for describing habitat preferences of each species because the literature on Caribbean anoles has been so influential. Also, mainland taxa tend to specialize on the same structural features of forests used by the six major Caribbean ecomorphs. Unfortunately, the consistent morphological features of island ecomorphs do not emerge from studies of mainland species (Irschick *et al*. 1997; Pinto *et al*. 2008; Pounds, 1988; Schaad and Poe, 2010). Worse yet, mainland species that conform to morphological definitions of island ecomorphs do not necessarily occupy the forest stratum to which that ecomorph is supposed to be adapted (e.g., *Dactyloa frenatus*, Irschick *et al*. 1997; Losos *et al*. 1991: *Norops altae*, Savage, 2002; Schaad and Poe, 2010). The lack of uniform morphological features suggests that selection pressures associated with particular parts of the environment differ between Greater Antillean islands and mainland forests or other types of islands (Schaad and Poe, 2010).

Because the term ecomorph requires consistent morphological features associated with use of specified portions of the habitat and because this association cannot be demonstrated for mainland anoles, we use the term ‘ecomode’ for the remainder of our discussion. We introduce this term in acknowledgment of the fact that all anole biologists consistently recognize distinctive modal categories of habitat use by anoles, even if these modes do not necessarily display convergent morphology. The major ecomodes that we recognize retain the same names applied to the ecomorph categories described above, again because all anole biologists appear to agree that these general habitat categories are informative about how anoles use available habitat. We retain a category for canopy giant despite the obvious drawback that this category retains a feature of morphology by referring to body size. We do this because of the wide use of this category in past literature and because, as in Caribbean forms, the largest mainland anoles tend to live in the crowns of forest trees. To the basic five categories we add categories for ground (literally on the ground and never perching on vegtation higher than 0.3 m), saxicolous (in rocky habitats), semi-aquatic (within flowing aquatic habitats and never venturing more than 2 m from the water), and ground-bush (on ground or in understory shrubs in forested areas, not grasslands) ecomodes to cover rarer categories of habitat use known for Caribbean and mainland anoles but for which no consistent sets of convergent morphological features have been identified (Losos, 2009); we also recognize a polymodal category for species that fit more than one of these categories. Our view of ecomodes includes two major clusters, one for anoles with niche space that is focused towards the canopy (crown giant, trunk crown, trunk, twig), and one for anoles with niche space focused towards the ground or water (trunk ground, ground, saxicolous, semi-aquatic, grass bush, bush ground).

Ancestral Node Reconstruction—Ecomodes

To examine the evolution of ecomodes, we used published accounts of habitat use and body size to assign species to one of the eleven ecomodes (see Appendix V). We drew inferences about patterns of evolution of these ecomodes across the tree based on molecular data alone (Fig. 4) and the combined molecular and morphological data (Figure 5) by using these trees as the scaffolds for estimating ancestral node reconstruction for ecomodes. The reconstructions were inferred from all the most parsimonious reconstructions (MPRs), as opposed to just delayed or accelerated optimization. The analyses were conducted with MacClade 4.08 (Maddison and Maddison, 2005).

When examined for molecular data alone (Fig. 29), unequivocal most-parsimonious reconstructions of the ancestral ecomode were generated for all genera except *Deiroptyx* and *Xiphosurus*. When based on the combined data sets, only the genera *Chamaelinorops* and *Norops* had unequivocal most-parsimonious ancestral ecomodes; all others were equivocal (Fig. 30). The disparities in outcomes result from convergent morphological characteristics that frequently disrupt groups that otherwise are monophyletic based on molecular information (see Systematic Accounts). Because we generally favored the molecular-only phylogeny in such cases, we focus on this tree in drawing inferences about ecomode evolution.

Our reconstruction of ecomode evolution yielded the crown giant as the most parsimonious ecomode for the ancestral anole (Fig. 29). This result was driven in part by use of the genera *Polychrus*, and *Basiliscus* + *Corytophanes* as the nearest outgroups for anoles. Nevertheless, we infer that the ancestral anole was a large, arboreal lizard in forested environments of South America and whose niche was focused on the canopy. Descendants of this ancestor remain in South America as the *Dactyloa* radiation. Nicholson *et al*. (2005) used alternative analytical tools to reach the same conclusion. The presence of *Dactyloa* on the tepuis of northern South America, the oldest geological formations of the continent (McDiarmid and Donnelly, 2005), suggests that the crown giant and related ecomodes have occupied South America since the split of that continent and Africa in the Cretaceous (see below).

Within mainland *Dactyloa*, a plurality of species (6 of 13 in Fig. 29) have retained the ancestral crown giant ecomode, likely because these species occupy rainforests that are characterized by tall canopy heights and tree community structure in which dominance by any one tree species is limited (Gentry and Terbourgh, 1990). Those forms that occupy the habitat islands composed of dwarf forests on the tops of tepuis (*heteroderma* species group) are the only mainland *Dactyloa* to have evolved an ecomode focused on the ground. Several of these forms are described to inhabit vines and shrubs near the ground (Miyata, 1983), which is the source of our categorization of these as bush-ground anoles (but see Losos, 2009, for an alternative view of the ecomode of this group). A similar progression of change of an ancestral species whose niche is focused towards the canopy diverging to generate derived species whose niche is focused toward the ground characterizes the *roquet* species group, a monophyletic radiation of Lesser Antillean species of *Dactyloa* (Giannasi *et al*. 2000). These species occupy tiny islands of the lower Lesser Antilles on which canopy height is shortened and community structure is characterized by higher dominance of sets of forest trees relative to mainland forests (Dallmeier *et al*. 1998). Our reconstruction suggests that the ancestral *roquet* species group anole was a crown giant, and that two species are of sufficient size to be viewed as retaining this ecomode. However, sister taxa within this series tend to differ in ecomode via multiple independent modifications that result in forms occupying the trunk-ground positions, likely caused by the shorter and open stature of the forest. Our description is compatible with suggestions that a taxon loop (Roughgarden, 1992) or character displacement (Losos, 1992a) then shaped these anoles into the distinctive size categories of current one- and two-species islands of the Lesser Antilles. We simply add to these models the suggestion that the original colonists or participants in vicariance of the lower Lesser Antilles (Roughgarden, 1995) need not have been intermediate in size.

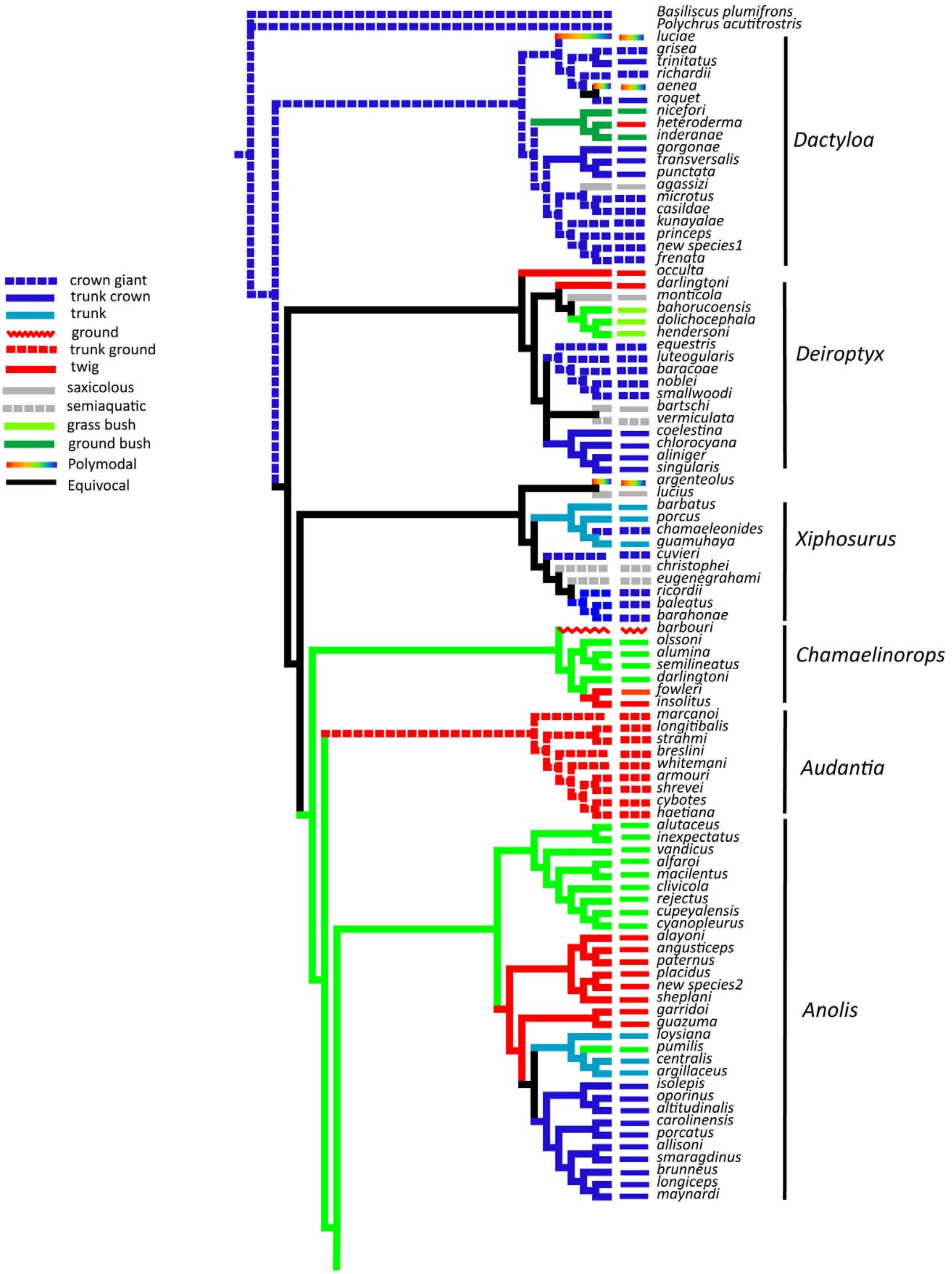


FIGURE 29a. Ancestral state reconstruction of ecomodes on the molecular tree (see Fig. 4). The branches are colored and patterned to indicate the reconstructed ancestral states following the legend to the left.

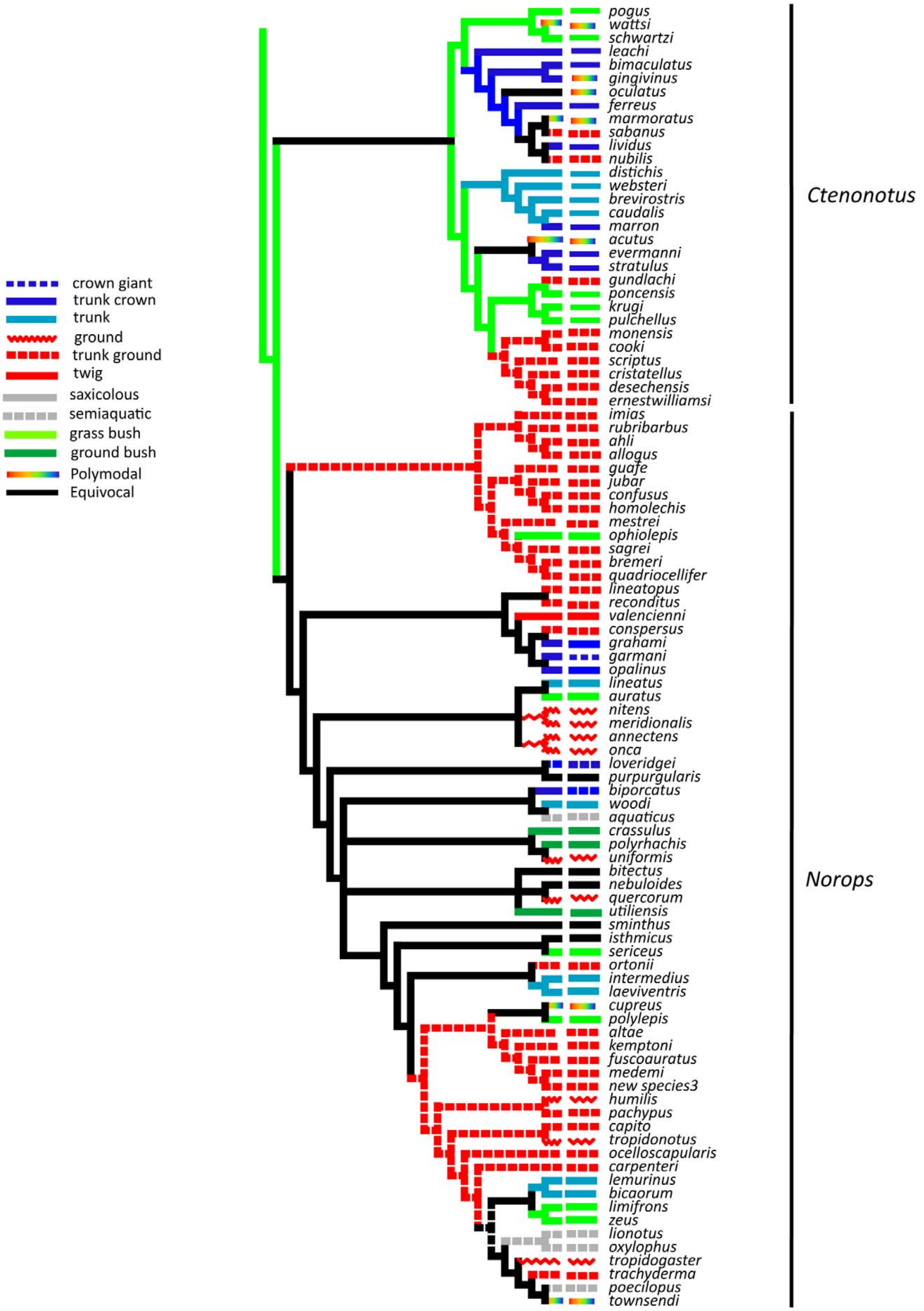


FIGURE 29b. Continued from 29a.

Our phylogeny of anoles indicates that an ancient divergence event separated *Dactyloa* in South America from the ancestor of all other anoles located to the north (hereafter northern ancestor) on ancient lands that eventually created the Greater Antilles and Central America. Our analysis indicates multiple equally parsimonious reconstructions of the ecomode of this northern ancestor. However, this uncertainty is derived from a transition from the crown giant ecomode for the ancestor of all anoles to a grass-bush common ancestor of *Chamaelinorops*, *Audantia*, *Anolis*, *Ctenonotus*, and *Norops* (hereafter derived anoles; Fig. 29). This transition represents a third major revision of the anole niche from one focused towards the canopy to one focused towards the ground and this transition makes the crown giant and grass-bush ecomodes equally parsimonious reconstructions of the northern ancestor as well as the ancestors of *Deiroptyx* and *Xiphosurus*. Because the majority of species of *Deiroptyx* (53%) and *Xiphosurus* (67%) included in our analysis have their habitat focused towards the canopy (crown giant, trunk crown, or trunk ecomorph), we suspect that the ancestors of both lineages, as well as the northern ancestor, were crown giants and not grass-bush anoles. Thus, contrary to arguments by Losos (1992b) that the northern ancestral ecomode was a generalist of intermediate size that dispersed to the Greater Antilles, we argue that the ancestor was a large species focused towards the canopy, possibly associated with tall, complex forests of an ancient connection between Central and South America that included the Greater Antillean Arc (see Revised Anole Biogeography). Our reconstruction agrees with that of Losos (2009) in that the ancestor of the derived anoles became small and moved towards the ground, first as a grass bush ecomode. Descendants of this ancestor became adept at dispersal and rarely (3 times among 114 species in our phylogeny) evolved back into a crown giant. We suspect that this ancestor evolved in areas likely to be covered by dry forest in which canopy height was much reduced and dominance by sets of tree species was increased. We envision this forest structure to provide the selective pressure to cause a crown giant ancestor to orient its niche towards the ground.

The ecomode of the ancestor of *Norops* is equivocal in our reconstruction based on molecular data alone, but, as in Losos (2009), is inferred to have been a trunk-ground ecomode for the reconstruction based on combined data. The difference likely originates from the 25 species of *Norops* included in the combined tree for which no molecular data are available. Therefore, the likely ancestral ecomode for this genus is the trunk-ground mode, indicating that this widespread radiation of anoles occupies niches that are largely focused toward the ground. Of particular note is the near-uniform occurrence of this ecomode for Cuban *Norops*, on an island where they occur in communities with potential competitors belonging to several other genera, as compared to Jamaican and mainland *Norops*, which evolved all other ecomodes in communities with competition from members of no other genera. The one exception to this generalization is associated with the basal split within mainland *Norops* that documents an early occupation of South America by *Norops* soon after the origin of that genus. The South American clade of *Norops* has invaded all of the area occupied by mainland *Dactyloa*, perhaps because that radiation had evolved no competing trunk-ground anoles. However, neither mainland *Dactyloa* nor the South American clade of *Norops* penetrates very far into Central America. We infer that this pattern emerges because the Central American radiation has filled ecomode space so completely, including the crown giant form (*Norops biporcatus*; Irschick *et al*. 1997), that they restricted the ability of *Dactyloa* and *Norops* of the South American lineage to move north when the Panamanian Portal became complete (see below). Similarly, the more recent Central American radiations of *Norops* have had a difficult time penetrating South America, perhaps because an earlier radiation of *Norops* was present in South America and filled available unoccupied ecomode space (see below). We view this standoff as being similar to the sharp line of demarcation in habitat use between species of *Ctenonotus* (restricted to northern islands) and *Dactyloa* (restricted to southern islands) on one- and two-species islands of the Lesser Antilles (Losos, 2009).

In discussing differences between island and mainland anoles, Losos (2009) considered, but dismissed, forest structure as a driving factor in shaping anole assemblages, suggesting that, to anoles, a tree is a tree. Borrowing from earlier arguments by Andrews (1979), Losos (2009) instead advocated differences in food (more limiting for island compared to mainland anoles) and predation (more limiting for mainland compared to island anoles) as the most likely features causing island and mainland anole communities to differ. Schaad and Poe (2010) also failed to list differences in forest structure as being among the primary causes of differences in assemblage structure between mainland and island radiations of anoles. We recommend that much more serious consideration be given to forest structure in addition to food (see Guyer, 1988a,b, for evidence that food can be limiting for mainland anoles) and predation (see Schoener *et al*. 2005 for evidence that predation can be limiting for island anoles). We make these recommendations because we are impressed with the complex nature of the moist, wet, and rain forests of Central and South America (Solé *et al*. 2005) that are home to the majority of anole species. The heavily fluted bark of Neotropical rainforest canopy trees such as *Lecythis* must require substantially different limb and toe pad shapes in anoles that use these trees than those that use the smooth bark of canopy trees such as *Pterocarpus*. The facts that bark texture is likely to be much more diverse in mainland than island forests, and that trees with appropriate bark texture are likely to be so much more widely dispersed in mainland than island forests, must play an important role in making morphology of mainland anoles so much less predictable than it is for island anoles. The fact that island forests are dominated by a relatively few short, smooth-barked tree species must limit the number of morphs that anoles can attain, must increase the density that anole populations can maintain, and must increase the interactions among sympatric species above that experienced by mainland anoles. Additionally, the differences in the structure of understory shrubs associated with mainland areas possessing an ancestral fauna that includes grazing mammals, compared to island areas that lacked such grazers (Dirzo and Miranda, 1990), must affect habitat available for adaptive radiation in anoles. In short, we see little evidence that the assembly rules proposed for anole communities on Caribbean islands will ever be discovered as applicable to mainland anoles, because the factors shaping vegetation structure are so different between island and mainland forests. Therefore, attempts to force mainland anoles into ecomorphological categories based on data from island anoles seems pointless to us, especially given that so many Caribbean anoles fail to conform to any ecomorph category (Losos, 2009) and so many mainland anoles that appear to fit the morphological expectations of particular ecomorphs fail to occupy that ecomode (compare mainland species of Schaad and Poe, 2010 with our Appendix V).

Biogeography of the Dactyloidae

The fossil record of Dactyloidae and related families

The dactyloid radiation encompasses a broad range in time and space, with the history of the space particularly complex and the time surprisingly deep. Here we provide a brief summary of the fossil record of the Iguania (see Table 2 for classification), preliminary to our analysis of dactyloid biogeography. The earliest known Acrodonta are from the Late Triassic of India ca. 223 ma. (Datta and Ray, 2006). The first definitive Pleurodonta are now known from the Late Cretaceous ca. 80 ma in the Gobi Desert of Central Asia (Gao and Hou, 1995; Gao and Norell, 2000; Conrad and Norell, 2007). Other pertinent more recent records of pleurodont lizards are summarized by Augé (2007) for Europe (Late Cretaceous and Early to Late Eocene), South America (Late Cretaceous and Paleocene) and North America (Paleocene and Eocene). Most of these lizards have not been assigned to families, extant or otherwise.

TABLE 2. Classification of Iguania followed in this paper.

- Iguania Cope, 1864
  - Acrodonta Cope, 1864
    - Agamidae Spix, 1825
    - Chamaeleonidae Rafinesque-Schmaltz, 1815
  - Pleurodonta Cope, 1864
    - Corytophanidae Fitzinger, 1843
    - Crotophytidae Smith and Brodie, 1982
    - Dactyloidae Fitzinger, 1843
    - Hoplocercidae Frost and Etheridge, 1989
    - Iguanidae Gray, 1827*
    - Leiocephalidae Frost and Etheridge, 1989
    - Leiosauridae Frost, Etheridge, Janies, and Titus, 2001
    - Liolaemidae Frost and Etheridge, 1989
    - Opluridae Moody, 1983
    - Phrynosomatidae Fitzinger, 1843
    - Polychrotidae Fitzinger, 1843
    - Tropiduridae Bell, 1843

* This name is sometimes credited to Oppel, 1811 but his usage, “Iguanoides” is not a Latin noun in the nominative plural as required by the Code (Art. 11.7.1) nor does it qualify under Art. 11.7.2 as generally having been attributed to Oppel.

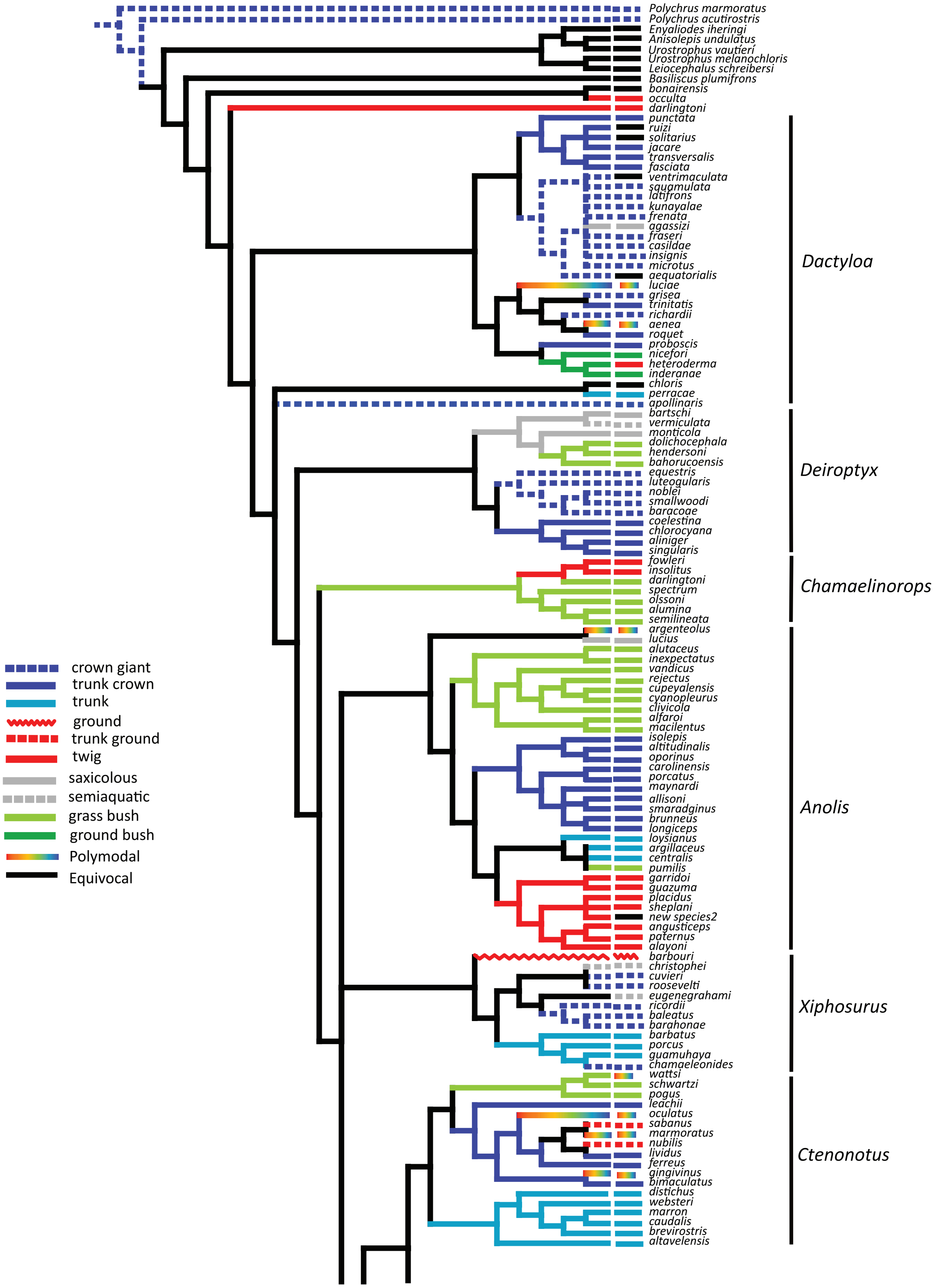


FIGURE 30a. Ancestral state reconstruction of ecomodes on the combined morphological and molecular data tree (see Fig. 4). Ancestral state colors and patterns are as in Fig. 29.

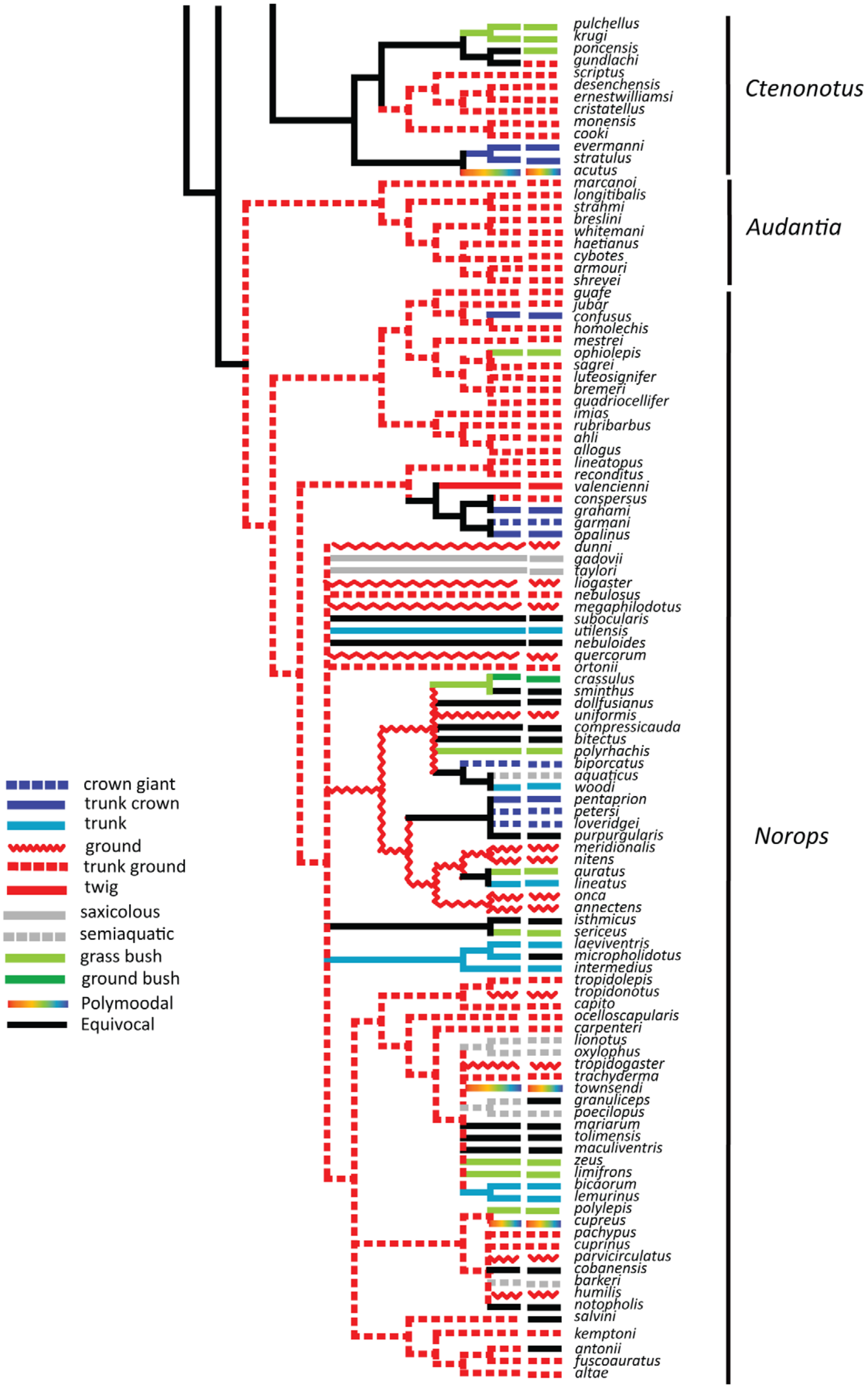


FIGURE 30b. Continued from 30a.

Other recent studies report fossil material referred to Dactyloidae (identified as *Anolis*) from North Dakota and Wyoming (Smith, in prep.) and its sister family Corytophanidae from North Dakota and Wyoming (Smith, 2009, 2011). Definite basal corytophanids are also known from Messel, Germany, ca. 45 ma. (Rossmann, 2000). In addition, lizards of the family Polychrotidae have been documented from Canada ca. 72 ma (Gao and Fox, 1996), North Dakota ca. 55 ma (Smith, 2006, 2011, in prep.), and Wyoming 55–54 ma [Conrad *et al*. (2007); Smith (2009)]. These sites range in age from late Cretaceous to Late Eocene. Conrad *et al*. (2007) indicated an age of ca. 54 ma for their new polychrotid genus, *Afairiguana*, which, according to their analysis, is younger than the age of origin for dactyloids.

Other fossils of significance include the discovery of an early Eocene (49–54.8 ma) anoloid (= dactyloid) fossil on Jamaica (Pregill, 1999), a putative Oligocene–Miocene *Norops* from Chiapas, Mexico (Lazell, 1965), and several definitive *Deiroptyx* from Hispaniola (Rieppel, 1980; de Queiroz *et al*. 1998; Polcyn *et al*. 2002). Ages of these fossils are ca. 16–28 ma for the *Norops* and 15–20 ma for the *Deiroptyx* (Iturralde-Vinent and McPhee, 1996).

The current distribution of dactyloids is principally in the New World tropics and that of all but three other extant pleurodont families (Crotaphytidae, Phrynosomatidae, and Opluridae) is exclusively or mostly Neotropical. Among these are the dactyloid sister taxon Corytophanidae (Townsend *et al*. 2011) and the Polychrotidae. This pattern, and the fact that the earliest pleurodont iguanians where at one time known only from Brazil and Argentina (Augé, 2007), led to the intuitive notion that these families all had a South American origin. It was further thought that the Pleurodonta must have been of Gondwanan origin as one small family (the Opluridae) occurs only on Madagascar. However, the extensive fossil record of pleurodonts in Central Asia in the Cretaceous, the presence of both corytophanids and polychrotids in Europe in the Eocene, and the occurrence of these two families and the Dactyloidae in northern North America in the Cretaceous–Eocene, suggest other interpretations. These data led Townsend *et al*. (2011) to posit that the Iguania originated in the Northern Hemisphere. Whatever hypothesis for the geographic origin of iguanians is favored, it is clear, from the presence of Acrodonta in the Late Triassic and the diversity of pleurodonts from the Cretaceous, that current ideas on biogeography are in need of re-evaluation.

In that regard, the evidence demonstrates that dactyloids, corytophanids, and polychrotids have had a long history with the opportunity to move between continents as far back as the Late Cretaceous but probably earlier. The Dactyloidae is essentially Neotropical in its current distribution (Middle and South America and the West Indies) but was definitely present in what is now non-tropical North America in the Paleocene–Eocene. Its sister, Corytophanidae, today occurs only in tropical Middle America and extreme northwestern South America, but is known from the Paleocene–Eocene boundary of north-central North America and the Eocene of Europe. The Polychrotidae is currently distributed in tropical South America and Lower Central America but is also known from the Cretaceous on north-central North America and Europe. The data of Smith (2006, 2009, 2011, in prep.) strongly suggest that the dactyloid/corytophanid and polychrotid radiations were ancient enough to have participated in distributional changes via vicariance (contra Hedges, 2006 and others). Phylogenetic pattern suggests that dactyloids and polychrotids evolved in South America; therefore, both groups must have crossed over into North America in the Cretaceous when a landbridge existed between the two continents (Hoernle *et al*. 2002; Pindell and Kennan, 2009). Further evidence for the antiquity of dactyloids is provided by the Jamaican, Hispaniolan, and Mexican fossils previously mentioned.

The above discussion demonstrates that corytophanids and dactyloids are ancient lineages, and this view sets the stage for our historical biogeographic hypothesis. Consideration of these clades as at least Cretaceous in origin goes against the orthodoxy that regards dactyloids as young, no older than Oligocene or late Eocene (e.g., Polcyn *et al*. 2002; Hedges, 2006).

A Revised biogeographic hypothesis to explain the current distribution of the Dactyloidae

As we did for ecomode evolution, we used published accounts of geographic location to assign species to one of 22 biogeographic units; to these we added a polymodal category for species distributed across more than one unit (see Appendix VI). We drew inferences about patterns of geographic distribution across the tree based on molecular data alone (Fig. 4) and the combined molecular and morphological data (Fig. 5). These trees were used as the scaffolds for estimating ancestral node reconstruction for biogeography. The reconstructions were inferred from all most parsimonious reconstructions (MPRs), as opposed to just delayed or accelerated optimization. The analyses were conducted with MacClade 4.08 (Maddison and Maddison, 2005).

Ancestral Node Reconstruction

The biogeographic distribution optimization results (Figs. 28 & 31) differed in resolution where the molecular tree inferred ancestral areas of the interior branches for almost the entire tree except for *Norops*. The combined tree inferred a South American origin for dactyloids but beyond that all the interior branches were equivocal (see Appendix VI for all possible MPRs). The molecular tree also inferred a South American origin for dactyloids and a southern Hispaniola (SH) ancestral area for *Deiroptyx*, *Chamaelinorops*, and *Audantia* (*Xiphosurus* is equivocal). Eastern Cuba is the inferred ancestral area for *Anolis* and basal *Norops* (*Ctenonotus* is equivocal).

Southern Hispaniola as an ancestral area requires explanation because it was submerged for probably the entire Oligocene. Southern Hispaniola has representatives of six genera (*Deiroptyx*, *Chamaelinorops*, *Audantia*, *Xiphosurus*, *Anolis*, *Ctenonotus*). We hypothesize that, unlike other Antillean islands, the newly emergent southern Hispaniola had no dactyloids and so was wide open for colonization and was so colonized as evidenced by the eclectic collection of taxa. What does this mean for the optimization procedure? We think because of the distribution of southern Hispaniola across the phylogeny (except *Dactyloa* and *Norops*), the optimization analysis inferred southern Hispaniola as the ancestral condition. While this may be the correct outcome operationally, our knowledge of the history of southern Hispaniola indicates that result is incorrect. As described in the section below, the history of the areas is so complex with multiple reticulations because of repeated fragmentations, accretions, submergence, and emergence, a simple optimization procedure could not possibly capture the detailed biogeographic history of dactyloids. As such, our biogeographic interpretation (below) relies less on the interior branch ancestral area reconstructions than the simple constraint of phylogenetic relationships and the distributions of the genera.

Node Dating

Ages of divergences were estimated by analyzing the molecular-only dataset using BEAST v.1.5.3 (Drummond and Rambaut, 2007). The Yule speciation process option was employed as well as an uncorrelated lognormal distribution for evolutionary rates along branches. Adequate effective sample sizes were not achieved with a partitioned analysis (ESS ^{3} 200), but were achieved with a non-partitioned analysis with GTR+I+G as the model of evolution. Three independent runs, each for 100,000,000 generations, were performed, sampling every 1,000 generations. Each run was examined in Tracer (Rambaut and Drummond, 2007) to determine whether sufficient mixing and convergence of parameters occurred. Once confirmed, all runs were combined using LogCombiner (within BEAST), and maximum credibility trees with node dates and 95% HPD's were produced in Tree Annotator (within BEAST).

Calibration of dates was difficult because fossil evidence is largely lacking for anoles, but several amber fossils were used as proxies for minimum dates of origin for extant species. *Anolis electrum* (Lazell, 1965), a fossil dated to 28 mya, is believed to be a member of the previously recognized *fuscoauratus* group and most likely is related to *A. limifrons* or *A. zeus* (members of our *Norops auratus* group) based upon the description of the fossil; this date was used as a minimum age for the branch leading to these two sister species. Two papers report anole fossils in Dominican amber that appear to be closely related to species within the *A. chlorocyanus* group (an alpha group); one, referred to as *Anolis domincanus*, is dated to 21.5 mya (Rieppel, 1980), and another unnamed fossil dated at between 17–23 mya (de Queiroz *et al*. 1998). Given the possibility that these fossils might represent extant species within the *chlorocyanus* group, we used the oldest age (23 ma) as the minimum age for the stem to that group. For both fossil calibrations, divergence time was estimated by using translated-lognormal age distributions.

Dates resulting from the BEAST analysis are indicated at major clades of interest in Figs. 4–5. The estimated age for the root of anoles was calculated as 95 ma. All of the major genera of anoles are estimated to have diversified during the subsequent 23 million years, from approximately 87–72.7 ma. From 60–51.6 ma the *Norops* clade diversified giving rise to the mainland *Norops* clade around 51.6 ma, a clade that subsequently diversified into nearly half of the species in the Family Dactyloidae.

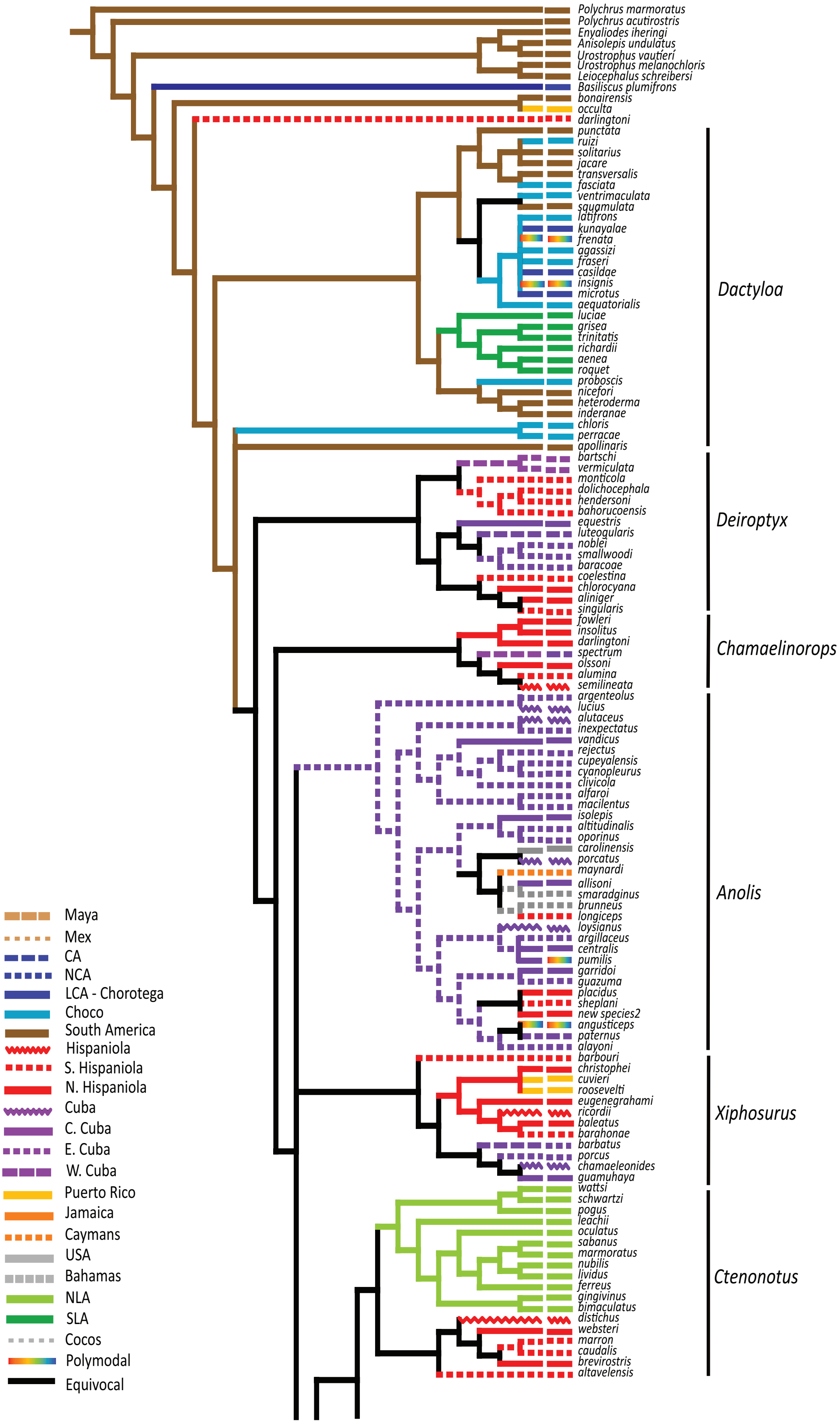


FIGURE 31a. Ancestral state reconstruction of biogeographic areas on the combined morphological and molecular dataset (see Fig. 5). Branch colors and patterns are as in Fig. 28.

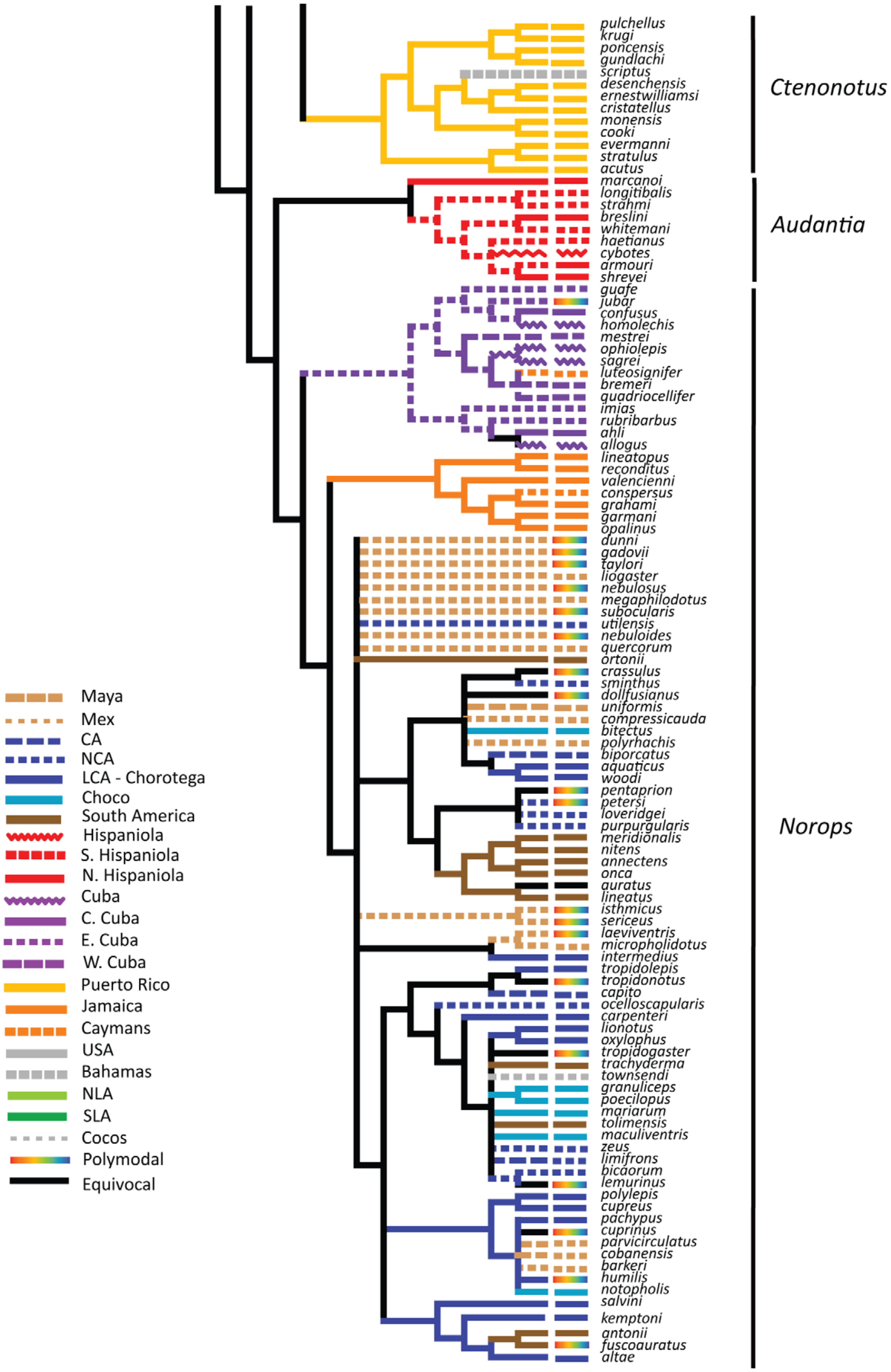


FIGURE 31b. Continued from 31a.

Constraints on biogeographic conclusions

Our hypothesis is constrained by phylogenetic pattern, dates (which we regard as minimum ages) and distributions of fossils, molecular clock estimates presented here, and by the geologic history of the Caribbean basin and Middle American region. The early (e.g., Pindell and Dewey, 1982) broad outlines of Caribbean and Middle American tectonic evolution remain similar to the most current hypotheses (e.g., Hoernle *et al*. 2002; Pindell and Kennan, 2009). Crother and Guyer (1996), Iturralde-Vinent and MacPhee (1999), and Iturralde (2006) provided reviews of earlier work. Briefly and generally, the evolution of the Caribbean Basin and Middle America is hypothesized to have occurred as follows. After the Jurassic breakup of Pangea, North America and South America then separated, initiating the opening of a broad seaway between the two continents. A volcanic island arc (variously called the Great Arc or Caribbean Arc = GAA) rose in the eastern Pacific, west of southern North America (Mexico) and extending southward off northwestern South America (Fig. 32a, top). The arc was carried eastward relative to North and South America on the leading margin of the Caribbean Plate from about 125 ma to 46 ma, when the Cuba–Hispaniola–Puerto Rico block collided with the Bahamas Platform. For most of that time the arc islands were intermittently and sporadically subaerial, but in the Late Cretaceous (75–70 ma) the arc may have consolidated to form a continuous landbridge (the Greater Antilles Landbridge = GAL) that connected North and South America (Fig. 32a, bottom). The GAL laid at this time between northwestern South America and the southern margin of North America (Mexico). As the Caribbean Plate continued its relative motion eastward, the GAL experienced a series of fragmentation and accretion events to create a series of islands. These islands were transported on the Caribbean Plate enroute to its collision with the North American Plate and later its oblique collision with northern South America (Fig. 32b, top). The western Jamaica fragment was the last to separate from a connection to North America ca. 55 ma.

Subsequently, the remnants of the GAA suffered substantial subsidence and submergence during Paleocene to Eocene so that the fragments of the GAL became reduced in number and extent (Fig. 33). However, as shown by Pindell and Kennan (2009), pieces of the future Greater Antillean Islands were present and subaerial throughout the remainder of Paleocene into Middle Eocene (60–40 ma). Over time, accretions to these fragments began to form the components of today’s Greater Antilles. We note that the figures in Pindell and Kennan exaggerate the area of the different island fragments that constitute relatively small components of the total island masses of today's Greater Antilles, but indicate the relative positions at different timeframes between the Cretaceous and the present.

Pindell and Kennan's (2009) and Iturralde-Vincent's (2006) reconstructions suggest the following as major geologic blocks involved in the development of the current Greater Antilles – Cuba: Western, West Central, East Central, and Eastern Blocks; Hispaniola: Northern, Cordillera Central, Central, and Southwestern blocks; a greater Puerto Rican (PR) block. By Middle Eocene in a period of regional tectonic uplift and lowered sea levels, the eastern Cuban blocks, most of the Hispaniola blocks and the Puerto Rican block accreted into a single unit to form the Mega Antillean Island (MAI) that existed ca. 40–32 ma (Fig. 32b, bottom). At the time of the MAI the Western Jamaica block and the Blue Mountains Block were united to form an emergent Jamaica. Also apparently forming a separate island was the Southwestern Hispaniola block.

Subsidence and rising sea levels in the Oligocene led to a renewed episode of fragmentation of the earlier MAI (another vicariance event) into at least the following major fragments: west central Cuba (WCC), east central Cuba (ECC), eastern Cuba (EC), northern Hispaniola (NH), central Hispaniola (CH), Cordillera Central of Hispaniola (CCH), and PR Bank and led to the submergence of southwestern Hispaniola (SWH) and western Jamaica (WJ). However, the Blue Mountain block appears to have remained subaerial through the rest of the Cenozoic. The Cuban blocks began to fragment about 32 ma and the EC-Hispaniola-Puerto Rico block somewhat later around 28 ma. At the same time the still emergent Hispaniola blocks and Puerto Rico (plus the northern Lesser Antilles) were moving southeastward toward their current positions (Fig. 32c, top). Puerto Rico then became separated from the Hispaniola blocks at about 7 ma and re-emergent SWH and CH terranes reconnected with the rest of Hispaniola at about this same time.

The Aves Ridge began to arise in early Eocene with a southern Lesser Antilles following soon thereafter. As the Caribbean arc moved eastward, the Chortis block was translated from its position on the western edge of southwestern North America (basically across from the Yucatan) to its current location sutured to the southern border of the Mayan block. It is thought that the Chorotega block (essentially Costa Rica and the western part of Panama) was sutured with the Chortis block by 33 ma. By the late Cretaceous, southern Panama and the Choco began accreting to northwestern South America from south to north. The final closure of the Panamanian Portal around 3–3.5 ma again separated the Caribbean Sea from the Pacific, and re-established a landbridge between North and South America (Fig. 32c, bottom).

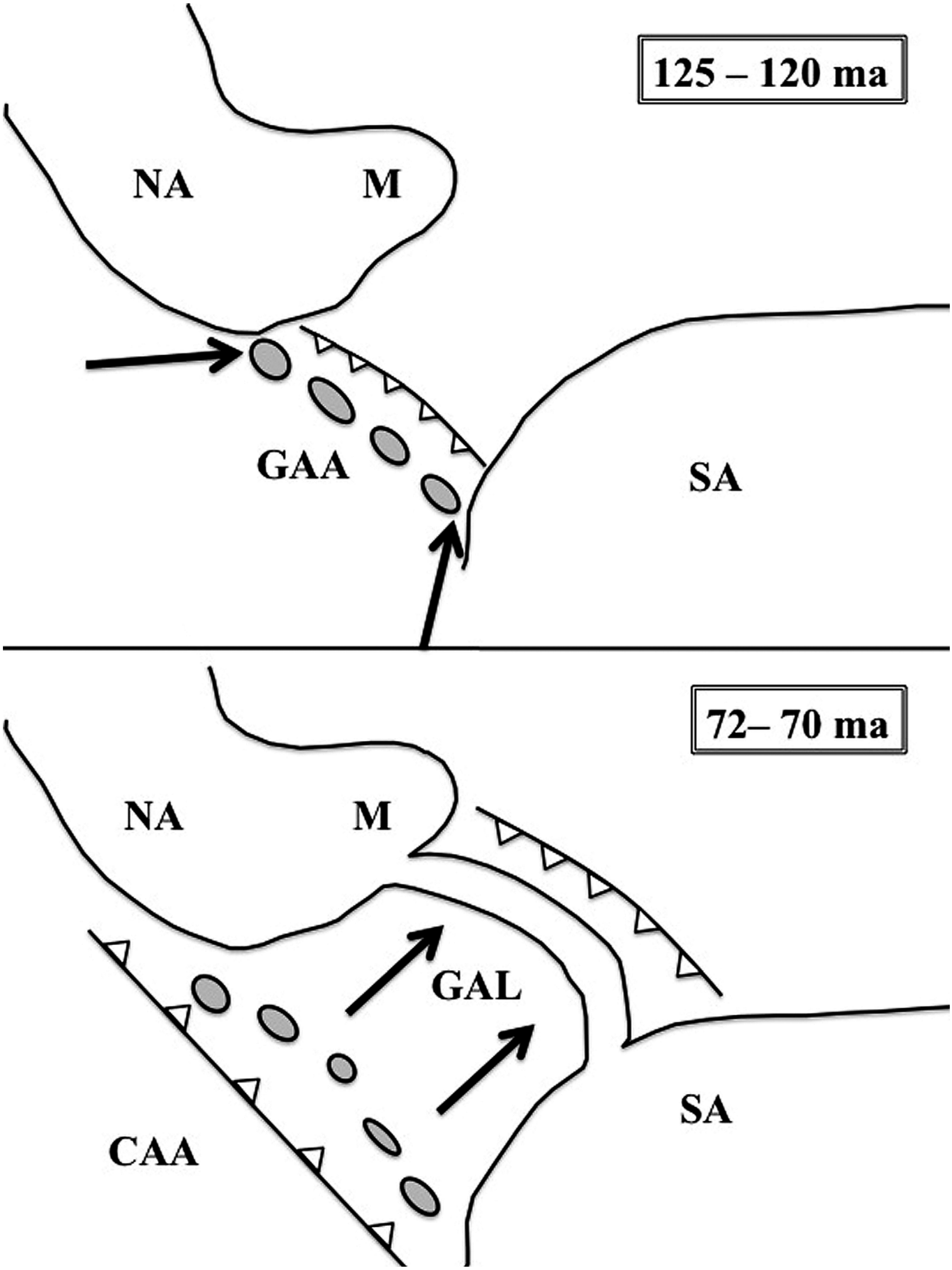


FIGURE 32a. Top: Hypothesized position of early Greater Antillean Archipelago (GAA) at 125–120 ma. The black arrows show the direction of the archipelago motion. The saw tooth line depicts an active boundary. Bottom: Hypothesized position of early Greater Antillean Landbridge (GAL) at 72–70 ma. NA = North America, M = Maya block, SA = South America.

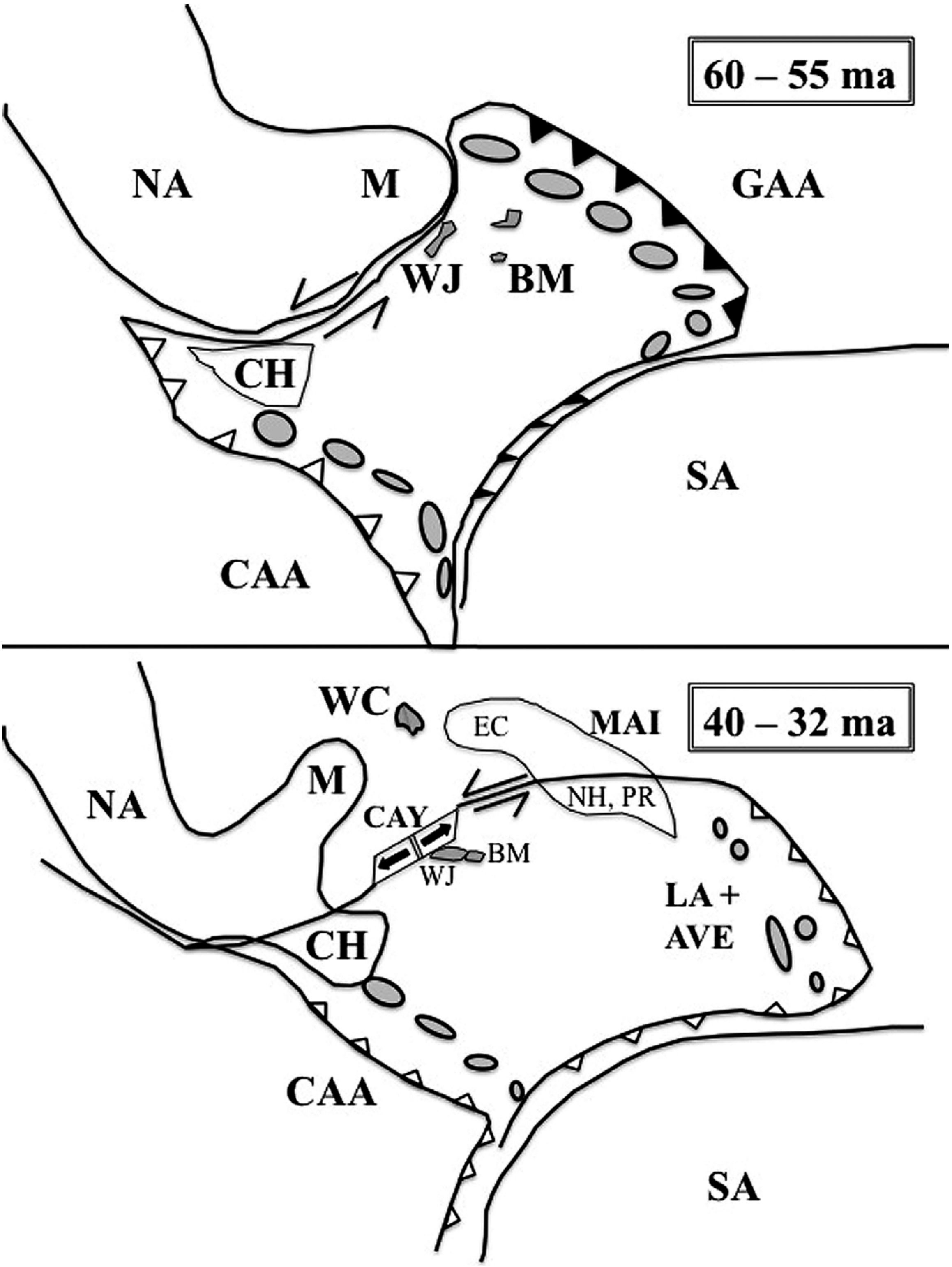


FIGURE 32b. Top: Hypothesized position of early Greater Antillean Archipelago (GAA), Aves Ridge/Lesser Antillean elements, and the Central American Archipelago (CAA) at 60–55 ma. The Caribbean plate is developing and moving east relative to North and South America. The closed saw tooth lines represent convergent boundaries (with Bahamas Platform and South America). The open saw tooth line depicts the active western boundary of the Caribbean plate. The half arrows along the northern boundary depict the relative motion along the transform fault. Bottom: Hypothesized organization of proto-Greater Antilles, Aves Ridge/Lesser Antillean elements, and the Central American Archipelago (CAA) at 40–32 ma. Eastern Cuba (EC), northern Hispaniola (NH), and Puerto Rico (PR) have accreted and form the Mega Antilles Island (MAI). The Chortis block (CH) is in place and western Jamaica has accreted to eastern Jamaica (Blue Mountains, BM). The Cayman spreading center (CAY) is opening, forming the Cayman Ridge. The open saw tooth lines are active plate boundaries. NA = North America, M = Maya block, SA = South America, WC = western Cuba, LAA = Lesser Antillean Archipelago, AVE = Aves Ridge.

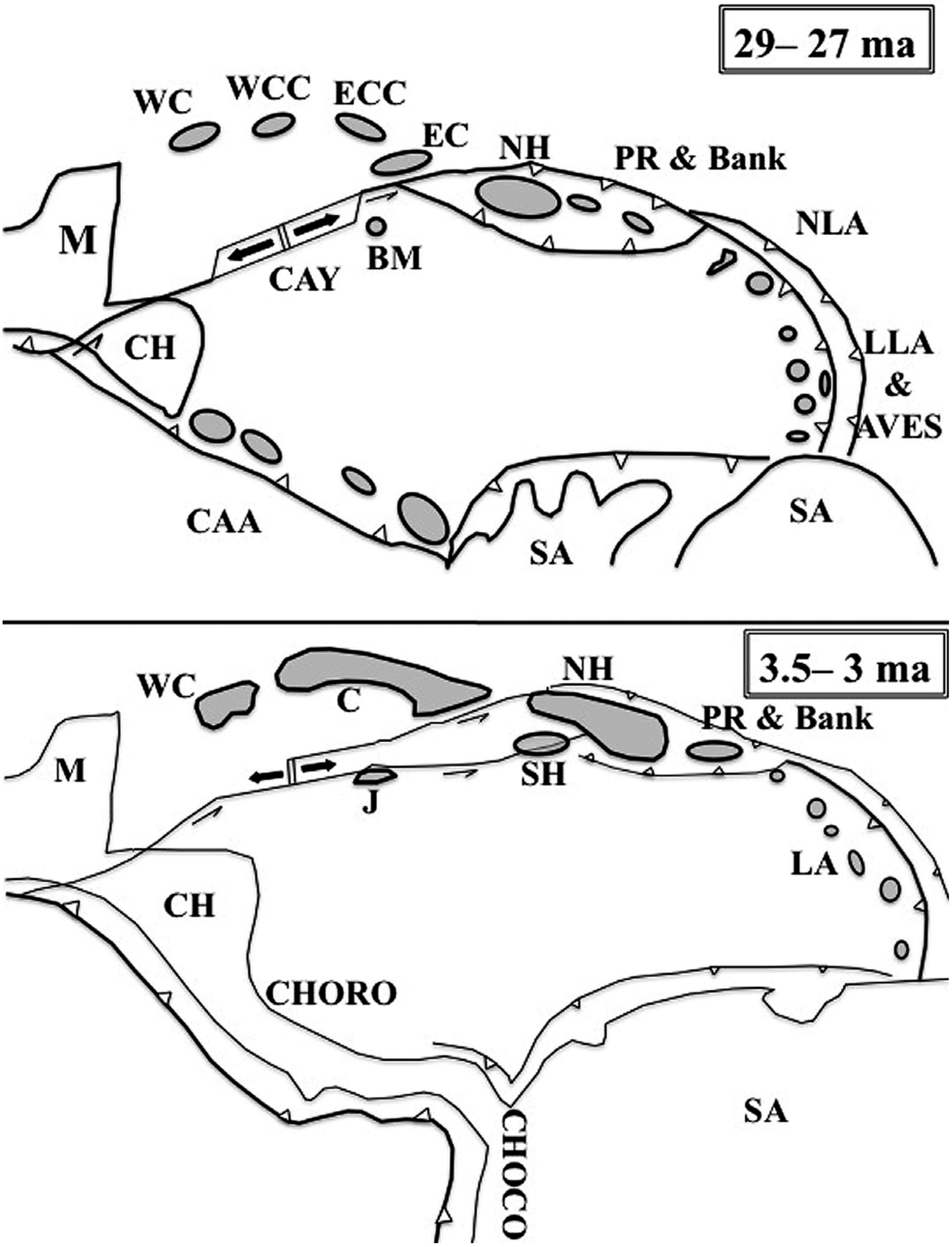


FIGURE 32c. Top: Hypothesized organization of Greater Antilles, Aves Ridge/Lesser Antillean elements, and the Central American Archipelago (CAA) at 29–27 ma. This was a time of elevated sea levels that resulted in submergence and inundation across the entire Caribbean basin. Cuba exists as a series of islands, as does Central America. Western Jamaica and southern Hispaniola are submerged. The open saw tooth line depicts the active boundaries of the Caribbean plate. The half arrows along the northern boundary depict the relative motion along the transform fault. Bottom: Hypothesized organization of Greater Antilles, Aves Ridge/Lesser Antillean elements, and the Central American Archipelago (CAA) at 3.5–3 ma. The Chorotega block (CHORO) is continuous with the closure of the Panamanian Portal. Western Cuba (WC) remains separated from the rest of Cuba, and southern Hispaniola (SH) is separated from northern Hispaniola (NH). The open saw tooth lines depict the active boundaries of the Caribbean plate. The half arrows along the northern boundary depict the relative motion along the boundary. M = Maya block, CH = Chortis block, SA = South America, WC = western Cuba, WCC = west central Cuba, ECC = east central Cuba, EC = eastern Cuba, PR&Bank = Puerto Rican bank, NLA = northern Lesser Antilles, LA = Lesser Antilles, LAA = Lesser Antillean Archipelago, AVE = Aves Ridge, BM = Blue Mts., J = Jamaica, CAY = Cayman Ridge, CHOCO = Choco.

Biogeographical interpretations

The dactyloid radiation is very old and, based on our phylogeny, probably originated in South America. With 55 ma old fossils in North Dakota and Wyoming, the dispersal there must have been intercontinental given that South America and North America were well separated by that time and the proto-Greater Antilles had already disconnected from the Mayan block. We conclude that the initial movement into North America occurred in Cretaceous times, but probably not before the continents began separating at around 140–130 ma. The GAA closed off the Colombian Marginal Seaway that temporarily separated North and South America and acted as an inter-American arc from about 125–75 ma. We follow Hoernle *et al*. (2002) in recognizing a subaerial GAL from 75–65 ma that allowed expedited faunal movement from South America north into North America (and vice versa). By the time the GAA separated from North America, moved east into the Caribbean Basin, and fragmented, ancestors of all extant Antillean dactyloid genera appear to have been on the arc islands. Based on the node dates, all the Greater Antilles dactyloid genera (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, *Deiroptyx*, *Norops*, *Xiphosurus*) evolved during that extended period of occupation of what must have been a dynamic arc system with fragmentations, accretions, submergences, and the emergence of new subaerial components.

Iturralde-Vinent and McPhee (1999) and Iturralde-Vinent (2006) favor varying numbers of evanescent islands in the period between the time that the GAL broke up and the Late Eocene. They thought that none of these islands lasted long enough as subaerial entities to be incorporated into the emergent Greater Antilles. Our phylogenetic analyses (Figs. 28 &31) strongly support a different conclusion, that these fragments carried components of the GAL biota to populate the emerging larger islands. Other endemic groups with similar ages of divergence of around 75 ma include freshwater fishes, the Hispaniolan cichlids (Chakrabarty, 2006) and Cuban poeciliids (Doadrio *et al*. 2009), the Cuban and Hispaniolan solenodons, and the Cuban xantusiid lizard, *Cricosaura* (Roca *et al*. 2004). Because of the overland dispersal events of the Late Eocene–early Oligocene described below, it is not possible to pinpoint with any certainty which fragments of the GAL were populated by the various ancestral dactyloid lineages. However, our phylogeny suggests that the basal *Deiroptyx* and *Audantia* were on a future Hispaniola fragment, basal *Xiphosurus* on a fragment that became part of central Cuba, basal *Chamaelinorops* on a CCH nucleus, basal *Anolis* on the EC component, and *Ctenonotus* on a possible Northern Lesser Antilles (NLA) component. All of these major clades have node dates of late Cretaceous providing support to the hypothesis.

The next major event was the creation of the MAI that existed from the Late Eocene to Early Oligocene. Accretions of various terranes and a period of tectonic uplift and lowered sea levels united most of the major blocks from ECC to the NLA into a single island mass from 40–32 ma. During this period overland dispersal was responsible for the spread of the various genera (e.g. *Deiroptyx* and *Xiphosurus* to Cuba and PR; *Ctenonotus* to PR and H). This laid the foundation for current distribution patterns.

Later in the Oligocene the MAI was fragmented by subsidence and rising sea level to again create a series of separate islands, the main ones being EC, ECC, WCC, CH, and CCH. Further submergence in the Miocene separated the Puerto Rico Bank, Virgin Islands, and NLA. It was during this period that the various subclades (species groups) appear to have undergone major diversification.

In the Pliocene another period of uplift and lowered sea levels led to the creation of essentially present day Cuba including WC by its fusion with EC, ECC and WCC. Additional contributors to the Antillean radiation were the continuing subaerial Blue Mountains island of Jamaica (from 35 ma) that fused with an emergent WJ in the Pliocene (8 ma). Similarly, present day Hispaniola was formed about this time by fusion of formerly separate major components CCH and CH, including a newly re-emergent SWH and possibly NH. These events were followed by a new cycle of dispersal across the major island masses. However, during both the Pliocene and Pleistocene, marine incursions seem to have temporarily fragmented Cuba and Hispaniola into separate islands several times. Thus each of these two island masses is best thought of as an island of islands.

The genus *Norops* presents special problems because it is the most widespread mainland dactyloid (Mexico to South America) and is present on Cuba and Jamaica. Indeed this may be the clade represented by the Jamaican Eocene "anoloid" of Pregill (1999) and the North American Eocene "*Anolis*" (*sensu* Smith, in prep). Most hypotheses argue that the Jamaican clade is recent and derived from a Miocene dispersal event (e.g., Crother and Guyer, 1996; Jackman *et al*. 2002; Nicholson *et al*. 2007). It also has been argued that the mainland radiation of *Norops* is possibly composed of an ancient group and a young group that dispersed from the Antilles to the mainland on two different occasions (Crother and Guyer, 1996). Finally, *Norops* is thought to have evolved in

Cuba, post-separation from Hispaniola-Puerto Rico. Based on our phylogeny and estimated divergence dates, we reject these hypotheses.

Our phylogeny infers a (Cuba (Jamaica (SA, MCA))) (SA = South America, MCA = Mexico-Central America) relationship. The node for this clade is ca. 72 ma, late Cretaceous, and the node for (Jamaica, SA-MCA) is ca. 65 ma. The phylogeny has no evidence of a late dispersal event from Cuba or Jamaica to the mainland. Based on this information, we argue that an already widespread *Norops* radiation was in place in the late Cretaceous across the elements that become Cuba, Jamaica, and Mexico. The initial vicariant event split Cuba from Jamaica-Mexico around 72 ma, and the timing of this geologic event coincides with the clock estimate (e.g., Pindell and Kennan, 2009). The inferred timing of the split of Jamaica and the Mayan block (southern Mexico), 65–50 ma, also coincides with the clock estimate. This rejects a later dispersal from the Antilles to the mainland. If such a later dispersal had occurred we would expect internested Antillean and mainland lineages in *Norops*, but this pattern is not inferred.

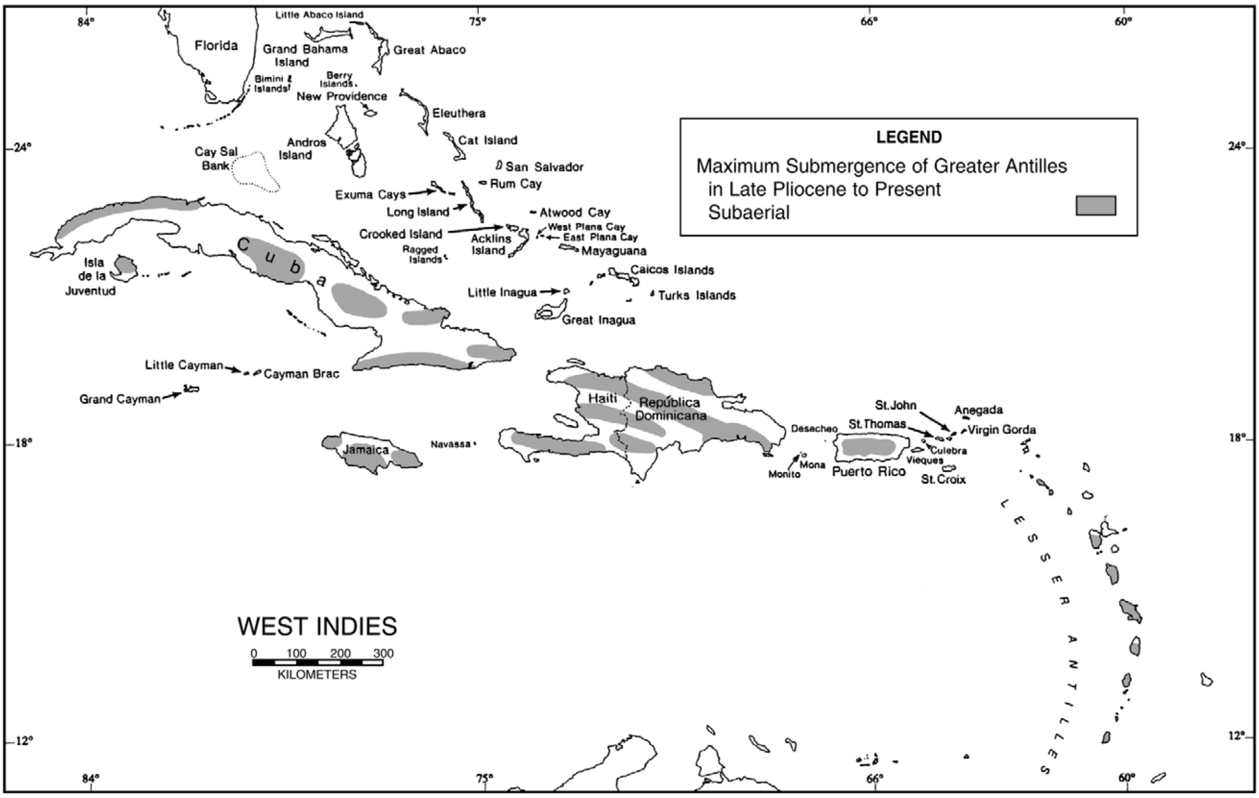


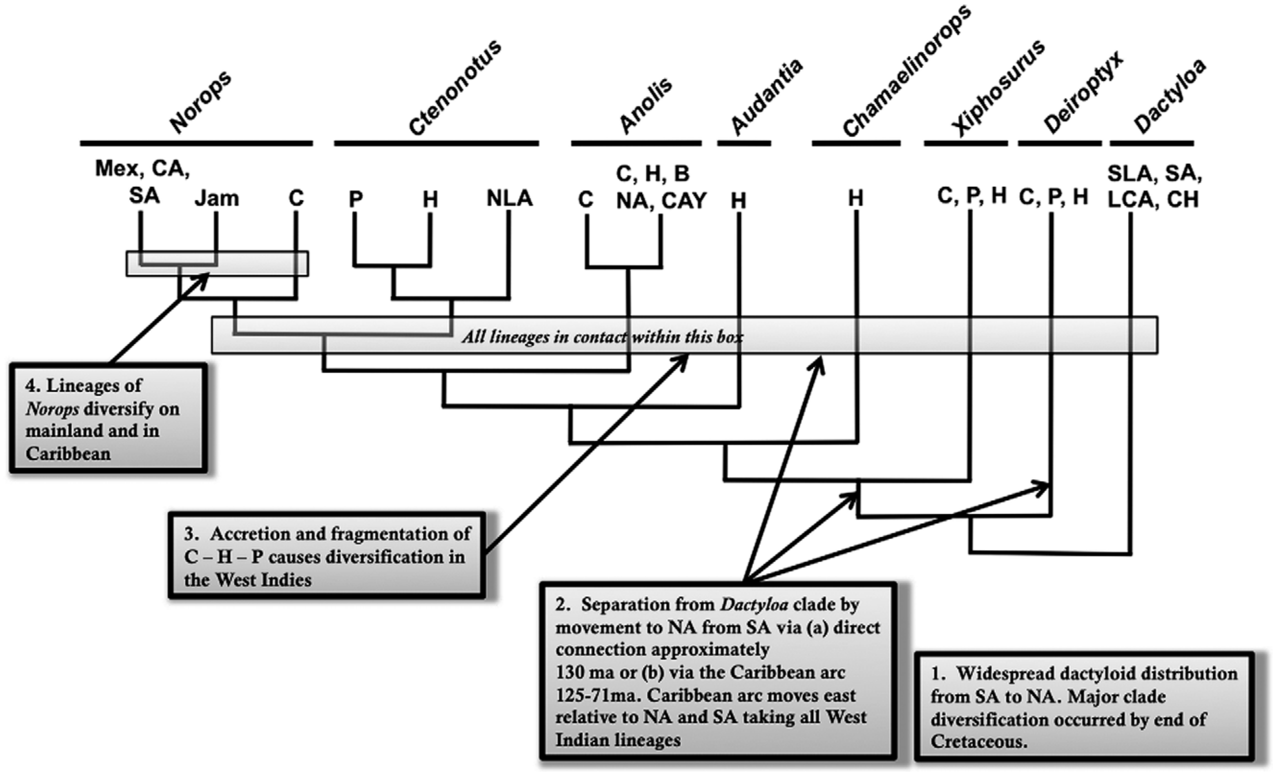
FIGURE 33. Maximum submergence of Greater Antilles in Late Pliocene to Recent.

The node for the mainland *Norops* has an estimated date of 65 ma, with the SA node at 61 ma and the CA-Mexico node at 64 ma. As we argued above, *Norops* was already widespread, from SA, through the arc, and into southern NA. The additional split is between the SA and the arc-Mexico radiations, and this occurred in the Paleocene. Again, the estimated date coincides with the inferred geological history. After the GAA moved into the Caribbean Basin, and the Chortis and Chorotega blocks sequentially became emplaced, the northern component spread southward, but only entered northern South America after the Isthmian Link was re-established in the Pliocene. A single representative of the ancient SA *Norops* radiation, *N. auratus,* has moved northward across the Isthmus.

The southern Lesser Antilles *Dactyloa* are part of a South American radiation, forming a monophyletic group. It appears that the southern Lesser Antilles may have been available for colonization as early as the Eocene, but probably later and possibly initially through the Aves Ridge if it were subaerial. Molecular clock data of southern Lesser Antillean anoles suggest much older dates for colonization than predicted by geological hypotheses of island emergence (Thorpe *et al*. 2005), but are still only late Miocene. Interestingly, those dates are for movement from the islands north to south to Barabados. This suggests that a dactyloid radiation was in place on the southern Lesser Antilles well before the Miocene movement to Barbados. Our dates for the SLA *Dactyloa* are older yet, at ca. 51 ma, and support the hypothesis of an older dactyloid radiation in the SLA. The northern Lesser Antillean radiation, *Ctenonotus*, is unsurprisingly tied to Puerto Rico and Hispaniola.

In summary, there are nine major events to the biogeographic history of dactyloids (see Fig. 34):

1. NA-SA connected: evolution of corytophanid-dactyloid clade that disperses to NA from SA.
2. NA-SA separate at 130 ma: evolution of Dactyloidae in SA.
3. GAA 125–65 ma: Widespread dactyloid radiation from SA through the landbridge and into NA. Major clades (genera recognized in this paper) diverge.
4. Fragmented GAL translation into Caribbean Basin (65–42 ma): all the West Indian genera evolved on fragments of GAL. SA *Norops* (*auratus* subclade) and *Dactyloa* isolated on SA. NA *Norops* isolated in tropical NA; *sagrei* and *grahami* clades of *Norops* isolated on WC and WJ, respectively.
5. Late Eocene-Early Oligocene uplift and lowered sea levels lead to formation of MAI followed by expansion of generic ranges by overland dispersal among the future major Antillean islands. SA lineage moves into southern Lesser Antilles; *Dactyloa* enters Caribbean.
6. New period of subsidence and higher sea levels in Oligocene lead to fragmentation of MAI: Dactyloidae diversification in full swing.
7. Middle American blocks emplaced in Oligocene (33 ma): Southward dispersal of NA *Norops* begins as the northern extent of NA tropical zone is compressed southward.
8. Early Pliocene (8 ma) uplift and sea level lowering reunites various Antillean blocks to form nucleus of present day Cuba, Hispaniola, Puerto Rica, accretion of W Cuba to rest of Cuba, SWH to the rest of Hispaniola, and newly re-emergent WJ to the Blue Mountains block, and separation of Puerto Rican bank and Northern Lesser Antilles from Hispaniola. Expansion of ranges of Antillean genera and further diversification.
9. Panamanian Isthmian Link completed (3–3.5 ma): minimal exchange between NA and SA of *Dactyloa* and *Norops*.



4. Lineages of *Norops* diversify on mainland and in Caribbean

3. Accretion and fragmentation of C – H – P causes diversification in the West Indies

2. Separation from *Dactyloa* clade by movement to NA from SA via (a) direct connection approximately 130 ma or (b) via the Caribbean arc 125-71ma. Caribbean arc moves east relative to NA and SA taking all West Indian lineages

1. Widespread dactyloid distribution from SA to NA. Major clade diversification occurred by end of Cretaceous.

FIGURE 34. Biogeographic area cladogram interpreted on the molecular data only tree (see Fig. 4). Branches are trimmed to reflect only the genera and the areas to which they belong. See text for area abbreviations.

Summary

In summary, we alter the orthodoxy of dactyloid lizard evolution in three key ways. One, to understand the remarkable diversity and phylogenetic relationships within the Dactyloidae, we propose a new classification that follows, in part, the earlier effort of reclassification by Guyer and Savage (1986). Two, we reject the ecomorph concept as currently recognized, largely because the pattern of ecomorph evolution documented so well for Jamaica by Losos (1992b) appears to be found nowhere else in anole evolution, and because a high proportion of island—and especially the mainland—anoles fail to fit any ecomorph class, despite exhibiting clear habitat selection. We replace the term *ecomorph* with the term *ecomode*, a more inclusive concept that appropriately describes habitat use for both Caribbean and mainland species. We note that evolution of ecomodes appears to be widely constrained within anoles and does not necessarily lead to constrained morphology within an ecomode because variation in forest structure across the geographic range of anoles is so great. Third, we reshape the biogeographic history of dactyloids by demonstrating that they are of Cretaceous origin, thereby rejecting the overwater dispersal hypotheses to explain West Indian distributions and especially used to explain the origin of mainland *Norops*. Instead, we argue that our classification appropriately redirects hypotheses towards deep phylogenetic patterns and away from a focus on relatively recent dispersal. We accept the argument that vicariance (and accretion) is the appropriate null hypothesis, and that dispersal is the *ad hoc* explanation invoked for exceptional cases (Nelson, 1974). We continue to be concerned that overexposure of data that document recent dispersal has diverted attention from extensive data that are consistent with vicariant (and accretion) events in anole evolution (Crother and Guyer, 1996).

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APPENDIX I. Source of the name *Anolis* and a bit of history

The first mention of the name *anaoli* or *anolis* is by Du Tertre (1654, p.352). A little later an anonymous author (1658) published the first illustration. The book containing this illustration is usually credited to Charles de Rochefort because later editions of the same work listed him as the author. The 1658 edition is apparently based on Rochefort seeing the manuscripts of Breton's (1665) Carib/French dictionary and Du Tertre's Natural History (1658)[1]. The name is said to be taken directly from the Carib language. It is clear from the illustrations in Rochefort (1658, p. 135) and Du Tertre (1667b, p. 308) that the name was originally used for an *Ameiva* (family Teiidae). In these two works recognizable illustrations of anoles (on the same cited pages) were labeled *gobe-mouche* (Fr. = fly-catcher) and the Carib name was stated to be *oulléouma* the same name in Breton's dictionary. There followed a strange chain of circumstances that led to *Anolis* being applied to dactyloid lizards (Breuil, 2002); read on.

In 1724, Sloane described and illustrated (pl. 273, fig. 4) an anole from Jamaica under the name *Lacertus cinereus minor.* Nicholson (1776) provided a description and illustration (pl. viii, fig. 1) of an anole from Hispaniola that he called *l'anolis* and thought to be the same as Sloane's species. Catesby (1754) illustrated and named two anoles, *Lacerta viridis carolinensis* (pl. 65) and *Lacertus viridis jamaicensis* (pl. 66). Sloane's and Catesby's names are not available as they appeared prior to 1758 (i.e., are pre-Linnean).

The first available names for any species now referred to as anoles are by Linné (1758) for *Lacerta bullaris*, *Lacerta principalis,* and *L. strumosa*. The first is based on the figure (pl. 66) of the unidentifiable *Norops* from Jamaica in Catesby (1754). *Lacerta principalis* is an unidentifiable species from the "Indiis". *Lacerta strumosa* also is based on a figure (Seba, 1735, pl. 20, fig. 4). The figured specimen is also the basis for the currently used name *Anolis lineatus* Daudin (1802).

In 1788 Lacépède, reported that the Cabinet du Roi had received a lizard from Martinique under the name "*d'anolis & lézard de jardin*" which "was not the true anolis of Rochefort and Ray" [translation]. He realized that the name *d' anolis* was based on a species of *Ameiva*. However, he thought that the name *l'roquet* of Rochefort (1658) applied to the lizard in hand and named it *Lacerta roquet.* In this he was in error as Rochefort and Du Tertre in their text and figures had originally applied the French name, meaning pug-nose, to an entirely different lizard, a species of *Leiocephalus* (family Leiocephalidae). Lacépède (1788) and all subsequent editions of that publication have been placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature (ICZN, 2005, Opinion 2104). Consequently, the name *Lacerta roquet* for what is now regarded as a West Indian dactyloid dates from Bonnaterre (1789). Daudin (1802) compounded the confusion by following Nicholson and Lacépède in their use of the name for the Jamaican and Martinique lizards and proposing the new generic name *Anolis*. He states (p. 81) that the name *anolis* is used for several small species of saurians from diverse colonies of South America. As originally conceived the genus contained ten species that resembled *l'anolis roqut (*now *Dactyloa roquet*). Unfortunately, it was not customary at that time to designate a type species for a new genus leading to some taxonomic difficulties later.

Thereafter, *Anolis* was the generic name favored by French herpetologists (especially C. Duméril and Bibron, 1837) for the species of dactyloid lizards recognized at that time. Fitzinger (1826, 1843) and Wagler (1830) presumably did not think the name appropriate and coined new generic names for various clusters of species placed in *Anolis* by others (see synonymies in Systematic Accounts). Nevertheless, by the end of the 19th century, the name *Anolis* had become firmly entrenched in the literature (e.g., Boulenger, 1885) as the generic name for the majority of anoles. Nonetheless, no one designated a type species for the genus until Stejneger (1904) in a synonymy listed (type: *A. bullaris*) in association with the generic name. Brown (1908) disagreed because he considered *A. bullaris* to be unidentifiable, and proposed *Anolis carolinensis,* incorrectly credited to C. Duméril and Bibron, 1837, as the generic type.

In later years, in the checklists of North American amphibians and reptiles by Stejneger and Barbour, starting in 1917 and in all subsequent editions, the type species of *Anolis* was listed as "TYPE: *bullaris = carolinensis*". Unfortunately, *Anolis carolinensis,* actually of Voigt (1832), was ineligible for selection as the type as it was not among the taxa originally included in Daudin's genus. The latter issue was finally raised by Smith *et al.* (1963), who petitioned the ICZN to set aside all previous type designations for *Anolis* and designate *Anolis carolinensis* as the generic type. After considerable delay and a healthy debate regarding whether *Anolis bullaris* was identifiable the Commission finally designated *A. carolinensis* as the generic type in 1986 (ICZN, Opinion 1385).

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[1] This matter is further confused by the fact that the preface to the 1658 Rochefort book has the authorship attributed to C. D. P., thought by some authors to stand for Charles de Poincy. A.A. Barbier (1806–1809) thought that Louis de Poincy was the actual author. Barbier's authority may have influenced others to similarly credit the Rochefort book to L. de Poincy even though Rochefort's name is indicated as the author in all later editions. Further confusion is added by some authors citing César de Rochefort, a totally different person than Charles de Rochefort as the author. However, as pointed out by Rich (1832), Du Tertre indicated in the preface to the 1667 *Histoire* that while he was printing the first edition, General Phillippe de Longvilliers de Poincy, who was Lieutenant Governor of the Isles of America, had begged Pere Raimond Breton to give his vocabulary and some memoirs to a young clergyman, who was collecting materials for a Relation of the Indies. Afterwards he discovered that that person was Charles de Rochefort, a protestant minister from Rotterdam, who had visited the French West Indies on two occasions. Apparently, du Tertre had loaned or left a portion or draft of his manuscript with the General who turned over it and his own notes to Rochefort.

APPENDIX II. Apomorphy lists for all dactyloid genera and species groups

Genus *Dactyloa*—77 (4 Morpho; 73 Molecular)

Morpho

3 unequivocal: head shortens (4: q → m); modal number of caudal vertebrae anterior to first autotomic vertebrae 8 (53: 4 → 3); contact between jugal and squamosal present (68: a → z)

1 equivocal: interparietal scale enlarges (7: u → h)

Molecular

34 unequivocal

39 equivocal

Latifrons group—54 (7 Morpho; 47 Molecular)

Morpho

6 unequivocal: maximum male SVL increases (1: k o); ratio of maximum female SVL to maximum male SVL increases (2: e → c); thigh lengthens; head shortens (4: m → i); scales on dewlap with at least one double row (21: a → z); scales in supraocular disc about equal in size (41: 0 → 4)

1 equivocal: mean number of scales across snout increases (29: l → m)

Molecular

0 unequivocal

47 equivocal

Punctata group—96 (8 Morpho; 88 Molecular)

Morpho

2 unequivocal: interparietal scale reduced in size (7: h → n); modal number of presacral vertebrae decreases to 23 (51: 0 → 1)

6 equivocal: ear size shrinks (6: v → n); posterior border of mental occasionally concave (31: z → t); modal number of caudal vertebrae anterior to first autotomic vertebra nine (53: 3 → 2); prefrontals occasionally separated from nasal by frontal and maxilla (63: a → i); (64: 0 1); frontal occasionally sutures only with nasals anteriorly (86: z → n)

Molecular

62 unequivocal

26 equivocal

Roquet group—83 (12 Morpho; 71 Molecular)

Morpho

5 unequivocal: enlarged postanal scale absent in males (10: a → z); mean number of ventral scales in 5% of SVL increases (20: m → o); modal number of lumbar vertebrae increases to four (52: 0 → 1); caudal autotomy septa revert to being present (54: z a); supratemporal processes revert to leaving supracoccipital exposed above (61: z a)

7 equivocal: maximum male size increases (1: k → o); ratio of maximum female SVL to maximum male SVL decreases (2: g → n); mean number of scales across snout increases (29: a → h); mean number of postmental scales increases (30: c → o); supraorbital semicircles in contact (32: a → z); postfrontal is separated from nasal by frontal and maxilla (63: a z); anteriormost aspect of posterior border of dentary within mandibular fossa (84: a → z)

Molecular

35 unequivocal

36 equivocal

Heteroderma group—18 (18 Morpho; 0 Molecular)

Morpho

2 unequivocal: modal postxiphisternal postscriptional rib formula 5:1 (47: 6 → 1); modal number of sternal ribs decreases to two (48: 1 → 0)

16 equivocal: maximum male size decreases (1: k → i); head widens (5: e → g); interparietal scale decreases in size (7: h → y); mean number of dorsal scales in 5% of SVL decreases (19: s e); mean number of postmental scales increases (30: c → d); interparietal scale frequently in contact with supraorbital semicircles (46: a → t); modal number of presacral vertebrae 23 (51: 0 → 1); dorsal surface of skull occasionally rugose (56: a → g); prefrontal occasionally separated from nasal by frontal and maxilla (63: a → i); dorsal process of jugal terminates on lateral aspect of postorbital (67: a → v); contact between jugal and squamosal occasionally absent (68: z → s); posteroventral corner of jugal posterior to posterior edge of

jugal (69: n → z); crenulation along lateral edges of parietal present (79: a → z); posteriormost tooth occasionally at least partially anterior to anterior mylohyoid foramen (81: a → c); anteriormost aspect of posterior border of dentary occasionally within mandibular fossa (84: a → h); surangular foramen occasionally bordered laterally by dentary (87: a → c)

Molecular

0 unequivocal

0 equivocal

Genus *Deiroptyx*—47 (5 Morpho; 42 Molecular)

Morpho

3 unequivocal: Interparietal scale increases in size (7:u → m); mean number of ventral scales in 5% of SVL decreases (20: s → n); pterygoid teeth changes reverts to being present (71: z → a)

2 equivocal: head lengthens (4: q → s); male dewlap extends to arms or shorter (16: 0 → 1)

Molecular

14 unequivocal

28 equivocal

Chlorocyana group—80 (12 Morpho; 68 Molecular)

Morpho

2 unequivocal: thigh shortens (3: o → n); supratemporal processes leave supraoccipital exposed above (61: z → a)

10 equivocal: ratio of maximum female SVL to maximum male SVL (2: h → g); ear expands (6: h→ k); female dewlap extends posteriorly to arms (17: 0 → 1); mean number of dorsal scales in 5% of SVL increases (19: h → r); posterior border of mental scale reverts to concave (31: z → a); dorsals, head, and supradigital scales keeled and ventrals smooth (40: 1 → 2); parietal crests revert to trapezoid shape (57: 2 → 0); prefrontal occasionally separated from nasal by frontal and maxilla (63: a → g); black pigment occasionally present (76: a → n); jaw sculpturing of large adult males wrinkled (90: 1 → 5)

Molecular

28 unequivocal

40 equivocal:

Equestris group—120 (23 Morpho; 97 Molecular)

Morpho

15 unequivocal: Interparietal scale decreases in size (7:m → t); base of tail reverts to being round (15: z → a); mean number of ventral scales in 5% of SVL increases (20: n → p); mean number of scales across snout decreases (29: l → d); modal number of superciliary scales reverts to none (38: 1 → 0); modal nasal scale type with external naris separated from rostral by two scales and not in contact with supralabials (39: 0 → 3); scales in supraocular disc equal in size (41: 0 → 4); modal number of lumbar vertebrae decreases to three (52: 1 → 0); modal number of caudal vertebrae anterior to first autotomic vertebrae increases to ten (53: 4 → 1); dorsal surface of skull rugose with bony tubercles (56: a → z); parietal casque present (59: a → z); anterior edge of nasal fails to reach naris (66: a → z); lateral edges of vomer possesses laterally directed processes (72: a → z); anteriormost aspect of posterior border of dentary reverts to being anterior to mandibular fossa (84: z → a); splenial changes present and large (85: 1 → 0)

8 equivocal: male size increases (1: m → z); head widens (5: k → o); male dewlap extends posterior past arms (16: 1 → 0); mental scale frequently completely divided (26: a → u); rostral scale frequently broader than mental (27: a → w); contact between jugal and squamosal frequently present (68: a → n); maxilla frequently extends posteriorly beyond ectopterygoid (73: a → u); crenulation along lateral edge of parietal frequently present (79: a → n)

Molecular

79 unequivocal

18 equivocal

Hendersoni group—44 (5 Morpho; 39 Molecular)

Morpho

0 unequivocal

5 equivocal: head lengthens (4: s → q); base of tail occasionally rounded (15: z → m); mean number of scales across snout decreases (29: l → f); supratemporal processes frequently leave supraoccipital exposed above (61: z → c); prefrontal occasionally separated from nasal by frontal and maxilla (63: a → n)

Molecular

19 unequivocal
20 equivocal
Vermiculata group—63 (9 Morpho; 54 Molecular)
Morpho
1 unequivocal: jugal and squamosal in contact (68: a → z)
8 equivocal: maximum adult male size increases (1: f → l); ear increases in size (6: n → w); interparietal scale increases in size (7: m → c); male dewlap absent (16: 1 → 2); mean number of dorsal scale rows in 5% of SVL increases (19: u → w); mean number of ventral scale rows in 5% of SVL increases (20: n → u); mean number of postmentals decreases (30: m → l); maxilla occasionally extends posteriorly beyond ectopterygoid (73: a → n)
Molecular
31 unequivocal
23 equivocal
Genus *Xiphosurus*—106 (0 Morpho; 106 Molecular)
Morpho
0 unequivocal
0 equivocal
Molecular
0 unequivocal
106 equivocal
Chamaeleonides group—127 (21 Morpho; 106 Molecular)
Morpho
0 unequivocal
21 equivocal: maximum male size increases (1: w → y); ratio of maximum female SVL to maximum male SVL increases (2: k → f); length of thigh shortens (3: t → j); head broadens (5: I n); ear becomes smaller (6: s → o); tail shortens (8: s → h); mean number of scale rows in 5% of SVL increases (20: s → z); posterior border of mental occasionally straight or convex (31: a → m); modal nasal scale type external naris separated from rostral by three or more scales, not in contact with supralabials (39: 2 → 4); head scales keeled, dorsals, ventrals and supradigitals smooth (40: 2 → 8); modal postxiphisternal inscriptional rib formula 4:2 (47: 7 → 2); supraoccipital cresting a single narrow central process (55: 0 → 2); parietal casque present (59: a → z); anterior edge of nasal does not reach naris (66: n → z); dorsal process of jugal terminates on lateral aspect of postorbital (67: a → z); epipterygoid does not contact parietal (70: a → z); lateral edges of vomer with posteriorly directed lateral processes (72: a → z); posteriormost tooth occasionally is completely anterior to anterior mylohoid foramen (81: a → n); anteromedial process of coronoid reverts to extending anteriorly (86: z → a); jaw sculpturing of *Chamaeleolis* type (90: 0 → 1); angular bone reverts to present (91: z a)
Molecular
88 unequivocal
18 equivocal
Cuvieri group—57 (4 Morpho; 53 Molecular)
Morpho
1 unequivocal: mean number of dorsal scales in 5% of SVL increases (19: c → l)
3 equivocal: tail crest present in largest males (12: a → z); caudal autotomy septum reverts to being present (54: z → a); splenial present as anteromedial sliver (85: 0 → 2)
Molecular
24 unequivocal
29 equivocal
Genus *Chamaelinorops*—39 (2 Morpho; 37 Molecular)
Morpho
1 unequivocal: maximum male SVL becomes smaller (1: f → c)
1 equivocal: parietal crests V-shaped (57: 2 → 1)
Molecular
16 unequivocal
21 equivocal

Genus *Audantia*—102 (13 Morpho; 89 Molecular)
Morpho
8 unequivocal: sexual size dimorphism becomes more male biased (2: h → l); widened head (5: o → t); ventrals become smooth (40: 0 → 2); postfrontal absent (62: a → z); posteroventral corner of jugal posterior to posterior edge of jugal (69: a → z); pterygoid teeth present (71: z → a); quadrate lateral shelf present (75: a → z); jaw sculpturing of large adult males of cybotes type (90: 0 → 4); Add - unique caudal vertebrae with small projections posterior to autotomic septae
5 equivocal: thigh lengthens (3: q → u); base of tail rounded in most specimens (15: a →g); subocular and supralabial scales in contact in most specimens (28: a → g); mean number of scale rows across snout increased (29: f → g); anterolateral corners of parietal crests generally reach medial to posterolateral corners of frontals (58: a → n)
Molecular
49 unequivocal
40 equivocal
Genus *Anolis*—47 (7 Morpho; 40 Molecular)
Morpho
2 unequivocal: mental fully divided (26: a → z); supratemporal leaves supraoccipital exposed (61: z → a)
5 equivocal: thigh shortens (3: t → k); head lengthens (4: q → t); interparietal scales decrease in size (7: h → p); base of tail laterally compressed (15: a z); modal number of caudal vertebrae anterior to first autotomic vertebrae increases to seven (53: 5 → 4)
Molecular
23 unequivocal
17 equivocal
Alutaceus group—81 (8 Morpho; 73 Molecular)
Morpho
6 unequivocal: Males become smallest size class (1: f → a); ear opening becomes taller (6: m → q); tail lengthens (8: s → v); enlarged middorsal scales > 5 (13: a → z); number of superciliary scales 2 (38: 1 → 2); scales in supraocular disc varying continuously in size and are bordered medially by an incomplete row of small scales (41: 0 → 1)
2 equivocal: thigh lengthens (3: k → r); middorsal scales of snout include some arranged in two parallel rows that extend from level of second canthals to naris (34: a → g)
Molecular
39 unequivocal
34 equivocal
Angusticeps group—56 (0 Morpho; 56 Molecular)
Molecular
20 unequivocal
36 equivocal
Carolinensis group—33 (7 Morpho; 26 Molecular)
Morpho
2 unequivocal: female dewlap extending posterior no further than arms (17: 2 → 1); mean number of ventral scales in 5% of SVL reduced slightly (20: p → o)
5 equivocal: ear opening becomes smaller (6: m → i); frontal depression absent (45: a → z); modal number of lumbar vertebrae reduced to 4 (52: 2 → 1); supraoccipital cresting reverts to being continuous across supraoccipital (55: 1 → 0); posterior suture of dentary blunt (83: a → z)
Molecular
9 unequivocal
17 equivocal
Loysianus group—68 (13 morpho; 55 molecular)
Morpho
5 unequivocal: mean number of scales across snout decreases (29: 3 → c); supraorbital semicircles in contact (32: a → z); circumnasal separated from nasal by one scale and not in contact with supralabials (39: 3 → 2); black pigment present on skull (76: a → z); posteriormost tooth at least partially anterior to anterior mylohyoid foramen (81: z → n)

8 equivocal: thigh lengthens (3: k → m); head broadens (5: k → o); each ventral scale occasionally bordered posteriorly by three scales (14: a → g); base of tail reverts to being round (15: z → a); parietal crests revert to being trapezoidal (57: 2 → 0); maxilla extends posteriorly beyond ectopterygoid (73: a → z); posterior suture of dentary frequently blunt (83: a → r); anteromedial process of coronoid occasionally projects posteriorly (86: a → n)

Molecular

29 unequivocal

26 equivocal

Lucius group—72 (17 Morpho; 55 Molecular)

Morpho

7 unequivocal: ratio of maximum female SVL to maximum male SVL reduced (2: h → j); scales on dewlap with at least one double row (21: a z); transparent scales of lower eyelid present (25: a → z); mean number of postmental scales increases (30: m → s); supraorbital semicircles in contact (32: a → z); keeling of dorsals, ventrals, head, and supradigitals all smooth (40: 0 → 1); quadrate lateral shelf occasionally present (75: a g)

10 equivocal: maximum male size increases (1: f → g); ear opening increases (6: m → w); mean number of dorsal scales in 5% of SVL increases (19: f → w); anteriormost aspect of rostral scale occasionally overlaps lower jaw (36: a → g); color of eye blue (37: 2 → 0); modal number of lumbar vertebrae reduced to four (52: 2 → 1); prefrontal reverts to contacting nasal (63: z → a); contact between jugal and squamosal occasionally present (68: a → g); nasals occasionally overlap edge of premaxilla (77: a → i); posterior suture of dentary occasionally blunt (83: a → n)

Molecular

33 unequivocal

22 equivocal

Genus *Ctenonotus*—46 (7 Morpho; 39 Molecular)

Morpho

2 unequivocal: ratio of female maximum SVL to male maximum SVL decreased (2: h → m); tail length increases to slightly more than 2.5 times SVL (8: s → p)

5 equivocal: thigh lengthens (3: q → s); mean number of scales across snout increases (29: f → e); mean number of postmental scales increases (30: l → r); contact between jugal and squamosal reverts to being absent (68: z → a); splenial present and large (85: 1 → 0)

Molecular

22 unequivocal

17 equivocal

Bimaculatus group—85 (6 Morpho; 69 Molecular)

Morpho

1 unequivocal: posterior suture of dentary blunt (83: a → z)

5 equivocal: maximum male size increases (1: f → h); mean number of ventral scales in 5% of SVL decreases (20: q → m); mental scale completely divided (26: a → z); posteriorventral corner of jugal occasionally posterior to posterior edge of jugal (69: a → n); splenial absent (85: 0 → 1)

Molecular

28 unequivocal

41 equivocal

Cristatellus group—58 (6 Morpho; 52 Molecular)

Morpho

1 unequivocal: female dewlap extending no further than arm (17: 2 → 1)

5 equivocal: head lengthens (4: s → q); interparietal scale enlarges (7: m → h); base of tail occasionally laterally compressed (15: a → g); posterior suture of dentary frequently blunt (83: a → r); jaw sculpturing of cristatellus type (90: 0 → 3)

Molecular

25 unequivocal

27 equivocal

Distichus group—93 (15 Morpho; 78 Molecular)

Morpho

        - 6 unequivocal: ratio of maximum female SVL to maximum male SVL increases (2: m → j); head broadens (5: o → p); mean number of scales across the snout decreases (29: e → d); middorsal scales of snout in two parallel rows that extend from level of second canthals to nares (34: a → z); keeling of dorsals, ventrals, head, and supradigitals smooth (40: 0 → 1); quadrate lateral shelf present (75: a → z)
        - 9 equivocal: head shortens (4: s → m); ear shrinks in size (6: s → r); tail shortens (8: p → h); mean number of postmentals decreases (30: r → l); preoccipital scale occasionally present (33: a → m); posterodorsal edge of rostral frequently cleft (35: a → t); interparietal scale occasionally in contact with suprorbital semicircles (46: a → g); prefrontal reverts to contacting nasal (63: z → a); posterior of skull occasionally slopes inferiorly (78: a → n)
    - Molecular
        - 0 unequivocal
        - 78 equivocal

- **Genus** *Norops*—57 (9 Morpho; 48 Molecular)
    - Morpho
        - 4 unequivocal: mean number of ventral scales in 5% of SVL decreases (20: q → r); caudal vertebrae of beta type (49: 0 → 1); nasal overlaps lateral edge of premaxilla (77: a → z); posterior suture of dentary frequently blunt (83: a → n)
        - 5 equivocal: head shortens (4: s → l); supraorbital semicircles revert to separation by on or more rows of scales (32: z → a); modal number of superciliary scales two (38: 1 → 2); interclavicles T-shaped (50: a → z); pineal foramen in parietal (60: a → z)
    - Molecular
        - 28 unequivocal
        - 20 equivocal
    - *Auratus* group—39 (6 Morpho; 33 Molecular)
        - Morpho
            - 2 unequivocal: tail changes from round to laterally compressed (15: a → z); supratemporal process changes from extending over supraoccipital to leaving supraoccipital exposed (61: z → a)
            - 4 equivocal: maximum male size decreases (1: j → f); lining of throat black (42: a → z); pineal foramen reverts to at parietal/frontal suture (60: z → a); posterior suture of dentary blunt (83: n → z)
        - Molecular
            - 11 unequivocal
            - 22 equivocal
    - *Sagrei* group—65 (7 Morpho; 58 Molecular)
        - Morpho
            - 3 unequivocal: ratio of maximum female SVL to maximum male SVL decreases (2: h → p); tail crest present (12: a → z); basipterygoid crest present (74: a → z)
            - 4 equivocal: maximum male size decreases (1: j → i); head lengthens (4: l → o); tail shortens (8: s → h); color of iris yellow (37: 0 → 1)
        - Molecular
            - 20 unequivocal
            - 38 equivocal
    - *Valencienni* group—57 (9 Morpho; 48 Molecular)
        - Morpho
            - 2 unequivocal: mean number of scales across snout decreases (29: f → i); jaw sculpturing in large adult males wrinkled (90: 0 → 5)
            - 7 equivocal: ratio of maximum female SVL to maximum male SVL decreases (2: h → r); head lengthens (4: l → t); interparietal scale decreases in size (7: m → r); tail shortens (8: s → p); mean number of postmentals decreases (30: l → g); modal postxiphisternal inscriptional rib formula 3:1 (47: 8 → 7); contact between jugal and squamosal frequently absent (68: z → f)
        - Molecular
            - 21 unequivocal
            - 27 equivocal

APPENDIX III. Classification of species of Dactyloidae.

Listed are the 387 recognized species and the 112 additional nominal subspecies as of 15 May 2012. Numbers in parentheses indicate the total number of species and subspecies (e.g., 14–16). New systematic combinations are indicated by asterisks (*). Species used in the two molecular phylogenies (Poe, 2004; Nicholson *et al*. 2005) are indicated in boldface and **P** and **N,** respectively. Where it is unclear as to which putative subspecies was sampled for molecular data, only the genus and species name of the nominate subspecies is given in boldface.

DACTYLOA Wagler, 1830 (83–88)

Dactyloa latifrons **Species Group (18):**

Dactyloa agassizi (Stejneger, 1900)	**P, N**
Dactyloa apollinaris (Boulenger, 1919)	**P**
Dactyloa casildae (Arosemena, Ibáñez, and De-Sousa, 1991)	**N**
Dactyloa chocorum (Williams and Duellman, 1967)	
Dactyloa danieli (Williams, 1988)	
Dactyloa fraseri (Günther, 1859)	**P**
Dactyloa frenata (Cope, 1899)	**P, N**
*_Dactyloa ibanezi_ (Poe, Latella, Ryan, and Schaad, 2010)	
Dactyloa insignis (Cope, 1871)	**P**
Dactyloa kunayalae (Hulebak, Poe, Ibáñez, and Williams, 2007)	**N**
Dactyloa latifrons (Berthold, 1846)	**P**
Dactyloa maculigula (Williams, 1984b)	
Dactyloa microtus (Cope, 1871)	**P, N**
Dactyloa mira (Williams, 1963)	
Dactyloa parilis (Williams, 1975)	
Dactyloa princeps (Boulenger, 1892)	
Dactyloa purpurescens (Cope, 1899)	
Dactyloa squamulata (W. Peters, 1863)	**P**

Dactyloa punctata **Species Group (44)**:

Dactyloa aequatorialis (Werner, 1894)	**P**
*_Dactyloa anatolorus_ (Ugueto, Rivas Fuenmayor, Barros, Sanchez-Pacheco, and García-Peréz, 2007)	
*_Dactyloa anchicayae_ (Poe, Velasco, Miyata, and Williams, 2009)	
*_Dactyloa anoriensis_ (Velasco, Paul, Gutiérrez-Cárdenas, and Quintero-Angel, 2010)	
Dactyloa antioquiae (Williams, 1985)	
Dactyloa boettgeri (Boulenger, 1911)	
Dactyloa calimae (Ayala, Harris, and Williams, 1984)	
Dactyloa caquetae (Williams, 1974)	
Dactyloa chloris (Boulenger, 1898)	**P**
*_Dactyloa cuscoensis_ (Poe, Yanez-Miranda, and Lehr, 2008)	
Dactyloa deltae (Williams, 1974)	
Dactyloa dissimilis (Williams, 1965)	
Dactyloa eulaema (Boulenger, 1908)	
Dactyloa fasciata (Boulenger, 1885)	**P**
Dactyloa festae (Peracca, 1904)	
Dactyloa fitchi (Williams and Duellman, 1984)	
Dactyloa gemmosa (O'Shaughnessey, 1875)	
Dactyloa gorgonae (Barbour, 1905)	
Dactyloa huilae (Williams, 1982)	
Dactyloa jacare (Boulenger, 1903)	**P**
Dactyloa laevis (Cope, 1875)	
*_Dactyloa lamari_ (Williams, 1992)	

**Dactyloa megalopitheca* (Rueda Almonacid, 1989)
Dactyloa menta (Ayala, Harris, and Williams, 1984)
Dactyloa nasofrontalis (Amaral, 1933)
Dactyloa nigrolineata (Williams, 1965)
**Dactyloa otongae* (Ayala-Varela and Velasco, 2010)
**Dactyloa paravertebralis* (Bernal Carlo and Roze, 2005)
Dactyloa peraccae (Boulenger, 1898) **P**
**Dactyloa philopunctata* (Rodrigues, 1988)
Dactyloa phyllorhinus (Myers and Carvalho, 1945)
**Dactyloa podocarpus* (Ayala-Varela and Torres-Carvajal, 2010)
Dactyloa propinqua (Williams, 1984a)
Dactyloa pseudotigrina (Amaral, 1933)
Dactyloa punctata (Daudin, 1802) **P, N**
Dactyloa ruizii (Rueda Almonacid and Williams, 1986) **P**
Dactyloa santamartae (Williams, 1982)
**Dactyloa soinii* (Poe and Yanez-Miranda, 2008)
Dactyloa solitaria (Ruthven, 1916) **P**
Dactyloa tigrina (W. Peters, 1863)
Dactyloa transversalis (A. Duméril, 1851) **P, N**
**Dactyloa umbrivaga* (Bernal Carlo and Roze, 2005)
Dactyloa vaupesiana (Williams, 1982)
Dactyloa ventrimaculata (Boulenger, 1911) **P**

Dactyloa heteroderma **Species Group (12):**
**Dactyloa bellipeniculus* (Myers and Donnnelly, 1996)
**Dactyloa carlostoddi* (Williams, Praderio, and Gorzula, 1996)
**Dactyloa euskalerrari* (Barros, Williams, and Vilario, 1996)
****Dactyloa heteroderma*** (A. Duméril, 1851) **P, N**
****Dactyloa inderenae*** (Rueda Almonacid and Hernández-Camacho, 1988) **P, N**
**Dactyloa neblinina* (Myers, Williams, and McDiarmid, 1993)
****Dactyloa nicefori*** (Dunn, 1944) (preoccupied by *Anolis nicefori* Barbour, 1932)—secondary homonym if in genus *Anolis* **P, N**
**Dactyloa orcesi* (Lazell, 1969)
****Dactyloa proboscis*** (Peters and Orces, 1956) **P**
**Dactyloa tetarii* (Barro, Williams, and Viloria, 1996)
**Dactyloa vanzolinii* (Williams, Orces, Matheus, and Bleiweiss, 1996)
**Dactyloa williamsmittermeierorum* (Poe and Yanez-Miranda, 2007)

Dactyloa roquet **Species Group (9–14):**
Dactyloa aenea (Gray, 1840) **P, N**
Dactyloa blanquillana (Hummelick, 1940)
Dactyloa bonairensis (Ruthven, 1929) **P**
Dactyloa extrema (Garman, 1888)
Dactyloa grisea (Garman, 1888) **P, N**
Dactyloa luciae (Garman, 1888) **P, N**
Dactyloa richardii (C. Duméril and Bibron, 1837) **P, N**
Dactyloa roquet roquet (Bonnaterre, 1789) **P, N**
Dactyloa roquet cracoli (Lazell, 1972)
Dactyloa roquet majogris (Lazell, 1972)
Dactyloa roquet salinei (Lazell, 1972)
Dactyloa roquet summa (Lazell, 1972)
Dactyloa roquet zebrila (Lazell, 1972)

Dactyloa trinitatis (Reinhardt and Lütken, 1863) **P, N**

DEIROPTYX Fitzinger, 1843 (21–49)
Deiroptyx occulta **Species Group (1)**:
*Deiroptyx occulta (Williams and Rivero, 1965) **P, N**

Deiroptyx vermiculata **Species Group (2)**:
*Deiroptyx bartschi Cochran, 1928 **P, N**
Deiroptyx vermiculata **(**Cocteau in C. Duméril and Bibron, 1837) **P, N**

Deiroptyx chlorocyana **Species Group (5–8):**
*_**Deiroptyx aliniger**_ (Mertens, 1939) **P, N**
*Deiroptyx chlorocyana *chlorocyana* (C. Duméril and Bibron, 1837) **P, N**
*_Deiroptyx chlorocyana cyanosticta_ (Mertens, 1939)
*Deiroptyx coelestina *coelestina* (Cope, 1864) **P, N**
*_Deiroptyx coelestina demissa_ (Schwartz, 1969)
*_Deiroptyx coelestina pecuaris_ (Schwartz, 1969)
*_Deiroptyx dominicana_ (Rieppel, 1980) fossil
*Deiroptyx singularis (Williams, 1965) **N**

Deiroptyx equestris **Species Group (6–26):**
*Deiroptyx baracoae (Schwartz, 1964) **N**
*Deiroptyx equestris *equestris* (Merrem, 1820) **P, N**
*_Deiroptyx equestris brujensis_ (Garrido, Moreno, and Estrada 2001)
*_Deiroptyx equestris buidei_ (Schwartz and Garrido, 1972)
*_Deiroptyx equestris cincoleguas_ (Garrido, 1981)
*_Deiroptyx equestris cyanea_ (Garrido, Moreno, and Estrada, 2001)
*_Deiroptyx equestris juraguensis_ (Schwartz and Garrido, 1972)
*_Deiroptyx equestris perspara_ (Schwartz and Garrido, 1972)
*_Deiroptyx equestris potior_ (Schwartz and Thomas, 1975)
*_Deiroptyx equestris sabinalensis_ (Garrido, Moreno, and Estrada 2001)
*_Deiroptyx equestris thomasi_ (Schwartz, 1958)
*_Deiroptyx equestris verreonensis_ (Schwartz and Garrido, 1972)
*Deiroptyx luteogularis *luteogularis* (Noble and Hassler, 1935) **P, N**
*_Deiroptyx luteogularis calcea_ (Schwartz and Garrido 1972)
*_Deiroptyx luteogularis coctilis_ (Schwarz and Garrido, 1972)
*_Deiroptyx luteogularis delacruzi_ (Schwarz and Garrido, 1972)
*_Deiroptyx luteogularis hassleri_ (Barbour and Shreve, 1935)
*_Deiroptyx luteogularis jaumei_ (Schwarz and Garrido, 1972)
*_Deiroptyx luteogularis nivevulta_ (Schwarz and Garrido, 1972)
*_Deiroptyx luteogularis sanfelipiensis_ (Garrido, 1975)
*_Deiroptyx luteogularis sectilis_ (Schwartz and Garrido, 1972)
*Deiroptyx noblei (Barbour and Shreve, 1935) **P, N**
*_Deiroptyx pigmaequestris_ (Garrdo, 1975)
*Deiroptyx smallwoodi *smallwoodi* (Schwartz, 1964) **P, N**
*_Deiroptyx smallwoodi palardis_ (Schwartz and Garrido, 1972)
*_Deiroptyx smallwoodi saxuliceps_ (Schwartz, 1964)

Deiroptyx hendersoni **Species Group (7–12)**:
*Deiroptyx bahorucoensis *bahorucoensis* (Noble and Hassler, 1933**)** **P, N**
*_Deiroptyx bahorucoensis southerlandi_ (Schwartz, 1978)

*___Deiroptyx darlingtoni___ (Cochran, 1935)	**P, N**
*___Deiroptyx dolichocephala___ _dolichocephala_ (Williams, 1963)	**N**
*_Deiroptyx dolichocephala portusala_ (Schwartz, 1978)	
*_Deiroptyx dolichocephala sarmenticola_ (Schwartz, 1978)	
*___Deiroptyx hendersoni___ _hendersoni_ (Cochran, 1923)	**P, N**
*_Deiroptyx hendersoni ravidormitans_ (Schwartz, 1978)	
*___Deiroptyx monticola___ _monticola_ (Shreve, 1936)	**P, N**
*_Deiroptyx monticola quadrisarta_ (Thomas and Schwartz, 1967)	
*_Deiroptyx rimarum_ (Thomas and Schwartz, 1967)	
*_Deiroptyx rupinae_ (Williams and Webster, 1974)	
XIPHOSURUS Fitzinger, 1826 (11–26)	
Xiphosurus chamaeleonides **Species Group (5)**:	
*_Xiphosurus agueroi_ (Díaz, Navarro, and Garrido, 1998)	
*___Xiphosurus barbatus___ (Garrido, 1982)	**N**
*___Xiphosurus chamaeleonides___ (C. Duméril and Bibron, 1837)	**P, N**
*___Xiphosurus guamuhaya___ (Garrido, Peréz-Beato, and Moreno, 1991)	**N**
*___Xiphosurus porcus___ (Cope, 1864)	**N**
Xiphosurus cuvieri **Species Group (6–21)**:	
*___Xiphosurus baleatus___ _baleatus_ (Cope, 1864)	**P, N**
*_Xiphosurus baleatus altager_ (Schwartz, 1975)	
*_Xiphosurus baleatus caeruleolatus_ (Schwartz, 1974)	
*_Xiphosurus baleatus fraudator_ (Schwartz, 1974)	
*_Xiphosurus baleatus lineatacervix_ (Schwartz, 1978)	
*_Xiphosurus baleatus litorisilva_ (Schwartz, 1974)	
*_Xiphosurus baleatus multistruppus_ (Schwartz, 1974)	
*_Xiphosurus baleatus samanae_ (Schwartz, 1974)	
*_Xiphosurus baleatus scelestus_ (Schwartz, 1974)	
*_Xiphosurus baleatus sublimis_ (Schwartz, 1974)	
*___Xiphosurus barahonae___ _barahonae_ (Williams, 1962)	**P, N**
*_Xiphosurus barahonae albocellatus_ (Schwartz, 1974)	
*_Xiphosurus barahonae imiquinatus_ (Cullom and Schwartz, 1980)	
*_Xiphosurus barahonae mulitus_ (Cullom and Schwartz, 1980)	
*___Xiphosurus cuvieri___ (Merrem, 1820)	**P, N**
*___Xiphosurus eugenegrahami___ (Schwartz, 1978)	**N**
*___Xiphosurus ricordii___ _ricordii_ (C. Duméril and Bibron, 1837)	**P, N**
*_Xiphosurus ricordii leberi_ (Williams, 1965)	
*_Xiphosurus ricordii subsolanis_ (Schwartz, 1974)	
*_Xiphosurus ricordii viculus_ (Schwartz, 1974)	
*___Xiphosurus roosevelti___ (Grant, 1931)	**P**
CHAMAELINOROPS K. Schmidt, 1919 (9–16)	
*___Chamaelinorops alumina___ (Hertz, 1976)	**N**
___Chamaelinorops barbouri___ Schmidt, 1919	**P, N**
*___Chamaelinorops christophei___ (Williams, 1960)	**P, N**
*___Chamaelinorops darlingtoni___ (Cochran, 1939)	**P, N**
*___Chamaelinorops fowleri___ (Schwartz, 1973)	**P, N**
*___Chamaelinorops insolitus___ (Williams and Rand, 1969)	**P, N**
*_Chamaelinorops koopmani_ (Rand, 1961)	
*___Chamaelinorops olssoni___ _olssoni_ (Schmidt, 1919)	**P, N**
*_Chamaelinorops olssoni alienus_ (Schwartz, 1981)	

*Chamaelinorops olssoni dominigensis (Schwartz, 1981)	
*Chamaelinorops olssoni extentus (Schwartz, 1981)	
*Chamaelinorops olssoni ferrugicauda (Schwartz, 1981)	
*Chamaelinorops olssoni insulanus (Schwartz, 1981)	
*Chamaelinorops olssoni montivagus (Schwartz, 1981)1	
*Chamaelinorops olssoni palloris (Schwartz, 1981)	
*Chamaelinorops semilineatus (Cope, 1864)	**P, N**

AUDANTIA Cochran, 1934 (9–14)

Audantia armouri Cochran, 1934	**P, N**
*Audantia breslini (Schwartz, 1980)	**N**
*Audantia cybotes cybotes (Cope, 1862)	**P, N**
*Audantia cybotes doris (Barbour, 1925)	
*Audantia cybotes ravifaux (Schwartz and Henderson, 1982)	
_*Audantia haetiana (_Garman, 1888)	**N**
*Audantia longitibialis _longitibialis_ (Noble, 1923)	**P, N**
*Audantia longitibialis specuum (Schwartz, 1979)	
*Audantia marcanoi (Williams, 1975)	**P, N**
Audantia shrevei Cochran, 1939	**P, N**
*Audantia strahmi _strahmi_ (Schwartz, 1979)	**P, N**
*Audantia strahmi abditus (Schwartz, 1979)	
*Audantia whitemani _whitemani_ (Williams, 1963)	**P, N**
*Audantia whitemani lapidosus (Schwartz, 1980)	

ANOLIS Daudin, 1802 (43–49)

Anolis lucius **Species Group (2)**:

Anolis argenteolus (Cope, 1861)	**P, N**
Anolis lucius (C. Duméril and Bibron, 1837)	**P, N**

Anolis alutaceus **Species Group (14–15)**:

Anolis alfaroi Garrido and Hedges, 1992	**N**
Anolis alutaceus Cope, 1861	**P, N**
Anolis anfilioquioi Garrido, 1980	
Anolis clivicola Barbour and Shreve, 1935	**P, N**
Anolis cupeyalensis G. Peters, 1970	**N**
Anolis cyanopleurus _cyanopleurus_ Cope, 1861	**P, N**
Anolis cyanopleurus orientalis Garrido, 1975	
Anolis fugitivus Garrido, 1975	
Anolis inexpectatus Garrido and Estrada, 1989	**N**
Anolis juangundlachi Garrido, 1975	
Anolis macilentus Garrido and Hedges, 1992	**N**
Anolis rejectus Garrido and Schwartz, 1972	**N**
Anolis spectrum W. Peters, 1863	**P**
Anolis vanidicus Garrido and Schwartz, 1972	**P, N**
Anolis vescus Garrido and Hedges, 1992	

Anolis angusticeps **Species Group (7–9)**:

Anolis alayoni Estrada and Hedges, 1995	**N**
Anolis angusticeps _angusticeps_ Hallowell, 1856	**P, N**
Anolis angusticeps oligaspis Cope, “1894”, 1895	
Anolis garridoi Diaz, Estrada, and Moreno, 1999	**N**
Anolis guazuma Garrudo, 1984	**N**

Anolis paternus *paternus* Hardy, 1967	**P, N**
Anolis paternus pinarensis Garrido, 1975	
Anolis placidus Hedges and Thomas, 1989	**P, N**
Anolis sheplani Schwartz, 1974	**P, N**
Anolis loysianus **Species Group (6)**:	
Anolis argillaceus Cope, 1862	**P, N**
Anolis centralis G. Peters, 1970	**N**
Anolis litoralis Garrido, 1975	
Anolis loysianus C. Duméril and Bibron, 1837	**P, N**
***Anolis pumilis* Garrido, 1988**	**N**
Anolis ruibali Navarro and Garrido, 2004	
Anolis carolinensis **Species Group (14–17):**	
Anolis allisoni Barbour, 1928	**P, N**
Anolis altitudinalis Garrido, 1985	**N**
Anolis brunneus Cope, 1875	**P, N**
Anolis carolinensis carolinensis Voigt, 1832	**P, N**
Anolis carolinensis seminolis Vance, 1991	
Anolis fairchildi Barbour and Shreve, 1935	
Anolis incredulus Garrido and Moreno, 1998	
Anolis isolepis Cope, 1861	**P, N**
Anolis longiceps Schmidt, 1919	**P, N**
Anolis maynardi Garman, 1888	**P, N**
Anolis oporinus Garrido and Hedges, 2001	**N**
Anolis porcatus *porcatus* Gray, 1840	**P, N**
Anolis porcatus aracelyae Peréz-Beato, 1997	
Anolis smaragdinus *smaragdinus* Barbour and Shreve, 1935	**P, N**
Anolis smaragdinus lerneri Oliver, 1948	
Anolis terueli Navarro, Fernández, and Garrido, 2001	
Anolis toldo Fong and Garrido, “2000”, 2001	
CTENONOTUS Fitzinger, 1843 (36–67)	
Ctenonotus bimaculatus **Species Group (17–26)**:	
Ctenonotus bimaculatus (Sparrman, 1784)	**P, N**
Ctenonotus chrysops (Lazell, 1964)	
Ctenonotus desiradei (Lazell, 1964)	
Ctenonotus ferreus (Cope, 1864)	**N**
Ctenonotus forresti (Barbour, 1923)	
Ctenonotus gingivinus (Cope, 1864)	**P, N**
Ctenonotus kahouannensis (Lazell, 1964)	
Ctenonotus leachii (C. Duméril and Bibron, 1837)	**P, N**
Ctenonotus lividus (Garman, 1888)	**P, N**
Ctenonotus marmoratus *marmoratus* **(**C. Duméril and Bibron, 1837)	**P, N**
Ctenonotus marmoratus alliaceus (Cope, 1864)	
Ctenonotus marmoratus caryae (Lazell, 1964)	
Ctenonotus marmoratus girafus (Lazell, 1964)	
Ctenonotus marmoratus inornatus (Lazell, 1964)	
Ctenonotus marmoratus setosus (Lazell, 1964)	
Ctenonotus marmoratus specious (Garman, 1887)	
Ctenonotus nubilis (Garman, 1888)	**P, N**
Ctenonotus oculatus *oculatus* (Cope, 1979)	**P, N**

Ctenonotus oculatus cabritensis (Lazell, 1962)	
Ctenonotus oculatus montanus (Lazell, 1962)	
Ctenonotus oculatus winstoni (Lazell, 1962)	
Ctenonotus pogus (Lazell, 1972)	**N**
Ctenonotus sabanus (Garman, 1887)	**N**
Ctenonotus schwartzi (Lazell, 1972)	**N**
Ctenonotus terraealtae (Barbour, 1915)	
Ctenonotus wattsi **(**Boulenger, 1894)	**P, N**
Ctenonotus distichus **Species Group (6–24)**:	
Ctenonotus altavelensis (Noble and Hassler, 1933)	**P**
Ctenonotus brevirostris *brevirostris* (Bocourt, 1870)	**P, N**
Ctenonotus brevirostris deserticola (Arnold, 1980)	
Ctenonotus brevirostris wetmorei (Cochran, 1931)	
Ctenonotus caudalis (Cochran, 1932)	**N**
Ctenonotus distichus *distichus* (Cope, 1861)	**P, N**
Ctenonotus distichus aurifer (Schwartz, 1968)	
Ctenonotus distichus biminiensis (Oliver, 1948)	
Ctenonotus distichus dapsilis (Schwartz, 1968)	
Ctenonotus distichus distichoides (Rosén, 1911)	
Ctenonotus distichus dominicensis (Reinhardt and Lütken, 1863)	
Ctenonotus distichus favillarum (Schwartz, 1968)	
Ctenonotus distichus ignigularis (Mertens, 1939)	
Ctenonotus distichus juliae (Cochran, 1934)	
Ctenonotus distichus ocior (Schwartz, 1968)	
Ctenonotus distichus patruelis Schwartz, 1968	
Ctenonotus distichus properus (Schwartz, 1968)	
Ctenonotus distichus ravitergum (Schwartz, 1968)	
Ctenonotus distichus sejunctus (Schwartz, 1968)	
Ctenonotus distichus suppar (Schwartz, 1968)	
Ctenonotus distichus tostus (Schwartz, 1968)	
Ctenonotus distichus vinosus (Schwartz, 1968)	
Ctenonotus marron (Arnold, 1980)	**N**
Ctenonotus websteri (Arnold, 1980)	**N**
Ctenonotus cristatellus **Species Group (13–17)**:	
Ctenonotus acutus (Hallowell, 1856)	**P, N**
Ctenonotus cooki (Grant, 1931)	**N**
Ctenonotus cristatellus *cristatellus* (C. Duméril and Bibron, 1837)	**P, N**
Ctenonotus cristatellus wileyae (Grant, 1931)	
Ctenonotus desechensis (Heatwole, 1976)	**P, N**
Ctenonotus ernestwilliamsi (Lazell, 1983)	**N**
Ctenonotus evermanni (Stejneger, 1904)	**P, N**
Ctenonotus gundlachi (W. Peters, 1876)	**P, N**
Ctenonotus krugi (W. Peters, 1876)	**P, N**
Ctenonotus monoensis (Stejneger, 1904)	**N**
Ctenonotus poncensis (Stejneger, 1904)	**P, N**
Ctenonotus pulchellus (C. Duméril and Bibron, 1837)	**P, N**
Ctenonotus scriptus *scriptus* (Garman, 1888)	**N**
Ctenonotus scriptus leucophaeus (Garman, 1888)	
Ctenonotus scriptus mariguanae (Cochran, 1931)	
Ctenonotus scriptus sularum (Barbour and Shreve, 1935)	

Ctenonotus stratulus (Cope, 1861)	**P, N**
NOROPS Wagler, 1830 (175–190)	
Norops sagrei **Species Group (18–29)**:	
Norops ahli (Barbour, 1925)	**P, N**
Norops allogus **(**Barbour and Ramsden, 1919)	**P, N**
*_Norops birama_ (Garrido, 1991)	
Norops bremeri (Barbour, 1914)	**N**
*___Norops confusus___ (Estrada and Garrido, 1991)	**N**
Norops delafuentei (Garrido, 1982)	
*___Norops guafe___ (Estrada and Garrido, 1992)	**N**
Norops homolechis *homolechis* (Cope, 1894)	**P, N**
Norops homolechis turquinensis (Garrido, 1973)	
Norops imias (Ruibal and Williams, 1961)	**N**
Norops jubar *jubar* (Schwartz, 1968)	**P, N**
Norops jubar albertschwartzi (Garrido, 1973)	
Norops jubar balaenarium (Schwartz, 1968)	
Norops jubar cocoensis (Estrada and Garrido, 1990)	
Norops jubar cuneus (Schwartz, 1968)	
Norops jubar gibarensis (Garrido, 1973)	
Norops jubar maisiensis (Garrido, 1973)	
Norops jubar oriens (Schwartz, 1968)	
Norops jubar santamariae (Garrido, 1973)	
Norops jubar yaguajensis (Garrido, 1973)	
Norops luteosignifer (Garman, 1887)	**P**
Norops mestrei (Barbour and Ramsden, 1919)	**P, N**
Norops nelsoni (Barbour, 1914)	
Norops ophiolepis (Cope, 1861)	**P, N**
Norops ordinatus (Cope, 1864)	
Norops quadriocellifer (Barbour and Ramsden, 1919)	**P, N**
Norops rubribarbus (Barbour and Ramsden, 1919)	**P, N**
Norops sagrei *sagrei* (Cocteau in C. Duméril and Bibron, 1837)	**P, N**
Norops sagrei greyi (Barbour, 1910)	
Norops valencienni **Species Group (7–11)**:	
Norops conspersus *conspersus* (Garman, 1887)	**P, N**
Norops conspersus lewisi (Grant, 1940)	
Norops garmani (Stejneger, 1899)	**P, N**
Norops grahami *grahami* (Garman, 1888)	**P, N**
Norops grahami aquarum (Underwood and Williams, 1959)	
Norops lineatopus *lineatopus* (Gray, 1840)	**P, N**
Norops lineatopus ahenobarbus (Underwood and Williams, 1959)	
Norops lineatopus merope (Underwood and Williams, 1959)	
Norops opalinus (Goose, 1850)	**P, N**
Norops reconditus (Underwood and Williams, 1859)	**P, N**
Norops valencienni **(**C. Duméril and Bibron, 1837)	**P, N**
Norops auratus **Species Group (150):**	
Norops adleri (H. Smith, 1972)	
Norops altae (Dunn, 1930)	**P, N**
Norops alvarezdeltoroi Nieto Montes de Oca, 1996	
Norops amplisquamosus McCranie, Wilson, and K. Williams, 1992	

Norops anisolepis (H. Smith, Burley, and Fritts, 1968)	
Norops annectens (Williams, 1974)	**N**
Norops antonii (Boulenger, 1908)	**P**
*_Norops apletophallus_ (Köhler and Sunyer, 2008)	
Norops aquaticus (Taylor, 1956)	**P, N**
Norops auratus (Daudin, 1802)	**P, N**
Norops barkeri (Schmidt, 1939)	**P**
Norops beckeri (Boulenger, 1881)	
*_Norops benedikti_ (Lotzkat, Bienentreu, Hertz, and Köhler, 2011)	
Norops bicaorum Köhler, 1996	**N**
Norops biporcatus (Wiegmann, 1834)	**P, N**
Norops bitectus (Cope, 1864)	**P, N**
Norops bocourtii (Cope, 1875)	
Norops bombiceps (Cope, 1875)	
*_Norops brasiliensis_ (Vanzolini and Williams, 1970)	
Norops breedlovei (H. Smith and Paulson, 1968)	
Norops campbelli Köhler and E. Smith, 2008	
Norops capito (W. Peters, 1863)	**P, N**
Norops carpenteri (Echelle, Echelle, and Fitch, 1971)	**N**
*_Norops charlesmyersi_ (Köhler, 2010)	
Norops chrysolepis (C. Duméril and Bibron, 1837)	
Norops cobanensis (Stuart, 1942)	**P**
Norops compressicauda (H. Smith and Kester, 1955)	**P**
Norops concolor (Cope, 1863)	
Norops crassulus (Cope, 1864)	**P, N**
Norops cristifer (Smith, 1968)	
Norops cryptolimifrons (Köhler and Sunyer, 2008)	
Norops cupreus (Hallowell, “1860”, 1861)	**P, N**
Norops cuprinus (H. Smith, 1964)	**P**
Norops cusuco McCranie, Köhler, and Wilson, 2000	
Norops cymbops (Cope, 1864)	
Norops dariense (Fitch and Siegel, 1984)	
Norops datzorum (Köhler, Ponce, Sunyer, and Batista, 2007)	
Norops dollfusianus (Bocourt, 1873)	**P**
Norops duellmani (Fitch and Henderson, 1973)	
Norops dunni (H. Smith, 1936)	**P**
Norops eewi (Roze, 1958)	
Norops electrum (Lazell, 1965) fossil	
Norops forbesi (H. Smith and Van Gelder, 1955)	
Norops fortunensis (Arosemana and Ibáñez, 1993)	
Norops fungosus (Myers, 1971)	
Norops fuscoauratus (D’Orbigny, 1817)	**P, N**
Norops gadovii (Boulenger, 1905)	**P**
Norops gibbiceps (Cope, 1864)	
Norops godmani (Boulenger, 1885)	
Norops gracilipes (Boulenger, 1898)	
Norops granuliceps (Boulenger, 1898)	**P**
Norops gruuo (Köhler, Ponce, Sunyer, and Batista, 2007)	
Norops haguei (Stuart, 1942)	
Norops hobartsmithi (Nieto-Montes de Oca, 2001)	
Norops humilis (W. Peters, 1863)	**P, N**
Norops ibague (Williams, 1975)	

Norops intermedius (W. Peters, 1863)	**P, N**
Norops isthmicus (Fitch, 1978)	**N**
Norops johnmeyeri (Wilson and McCranie, 1982)	
Norops kemptoni (Dunn, 1940)	**P, N**
Norops kreutzi McCranie, Köhler, and Wilson, 2000	
Norops laeviventris (Weigmann, 1834)	**P, N**
Norops lemniscatus (Boulenger, 1898)	
Norops lemurinus (Cope, 1861)	**P, N**
Norops limifrons (Cope, 1862)	**P, N**
Norops lineatus (Daudin, 1802)	**P, N**
Norops liogaster (Boulenger, 1905)	**P**
Norops lionotus (Cope, 1861)	**N**
Norops loveridgei (Schmidt, 1936)	**P, N**
Norops lynchi (Miyata, 1985)	
**Norops lyra* (Poe,Velasco, Miyata, and Williams, 2009)	
Norops macrinii (H. Smith, 1968)	
Norops macrolepis (Boulenger, 1898)	
Norops macrophallus (Werner, 1917)	
Norops maculiventris (Boulenger, 1898)	**P**
**Norops magnaphallus* (Poe and Ibáñez, 2007)	
Norops mariarum (Barbour, 1932)	**P**
**Norops marsupialis* (Taylor, 1956)	
Norops matudai (H. Smith, 1956)	
Norops medemi (Ayala and Williams, 1988)	
Norops megapholidotus (H. Smith, 1933)	**P**
Norops meridionalis (Boettger, 1885)	**P, N**
Norops microlepidotus (Davis, 1954)	**P**
Norops milleri (H. Smith, 1950)	
**Norops monteverde* (Köhler, 2009)	
**Norops morazani* (Townsend and Wilson, 2009)	
Norops muralla Köhler, McCranie, and Wilson, 1999	
Norops naufragus Campbell, Hillis, and Lamar, 1989	
Norops nebuloides (Bocourt, 1873)	**P, N**
Norops nebulosus (Wiegmann, 1834)	**P**
****Norops nitens*** (Wagler, 1830)	**P, N**
Norops notopholis (Boulenger, 1896)	**P**
Norops ocelloscapularis Köhler, McCranie, and Wilson, 2001	**N**
Norops omiltemanus (Davis, 1954)	
Norops onca O'Shaughnessy, 1875	**P, N**
Norops ortonii (Cope, 1868)	**P, N**
**Norops osa* (Köhler, Dehling, and Köhler, 2010)	
Norops oxylophus (Cope, 1875)	**P, N**
Norops pachypus (Cope, 1875)	**N**
Norpos parvicirculatus (Alvarez del Toro and H. Smith, 1956)	**P**
Norops pentaprion (Cope, 1862)	**P**
Norops petersii (Bocourt, 1873)	**P**
Norops pijolense McCranie, Wilson, and K. Williams, 1993	
Norops pinchoti (Cochran, 1931)	
Norops poecilopus (Cope, 1862)	**P, N**
Norops polylepis (W. Peters, "1873", 1874)	**P, N**
Norops polyrhachis (H. Smith, 1968)	**N**
**Norops pseudokemptoni* (Köhler, Ponce, Sunyer, and Batista, 2007)	

*_Norops pseudopachypus_ (Köhler, Ponce, Sunyer, and Batista, 2007)	
Norops purpurgularis McCranie, Cruz, and Holm, 1993	**N**
Norops pygmaeus (Alvarez del Toro and H. Smith, 1956)	
Norops quaggulus (Cope, 1885)	
Norops quercorum (Fitch, 1978)	**N**
Norops rivalis (Williams, 1984)	
Norops roatanensis Köhler and McCranie, 2001	
Norops rodriguezii (Bocourt, 1873)	
Norops rubribarbaris Köhler, McCranie, and Wilson, 1999	
Norops salvini (Boulenger, 1885)	**P**
Norops scapularis (Boulenger, 1908)	
Norops schiedii (Wiegmann, 1834)	
Norops schmidti (Smith, 1939)	
*_Norops scypheus_ (Cope, 1864)	
Norops sericeus (Hallowell, 1856)	**P, N**
Norops serranoi Köhler, 1999	
Norops simmonsi (Holman, 1964)	
Norops sminthus (Dunn and Emlen, 1932)	**P, N**
Norops subocularis (Davis, 1954)	**P**
Norops sulcifrons (Cope, 1899)	
*_Norops tandai_ (Avila-Pires, 1995)	
Norops taylori (H. Smith and Spieler, 1945)	**P**
*_Norops tenorioensis_ (Köhler, 2011)	
Norops tolimensis (Werner, 1916)	**P**
Norops townsendi (Stejneger, 1900)	**P**
Norops trachyderma (Cope, 1875)	**N**
Norops tropidogaster (Hallowell, 1856)	**P, N**
Norops tropidolepis (Boulenger, 1885)	**P**
Norops tropidonotus (Peters, 1863)	**P, N**
Norops uniformis (Cope, “1884”, 1885)	**N**
Norops unilobatus (Köhler and Vesely, 2010)	
Norops utilensis Köhler, 1996	**N**
Norops utowanae (Barbour, 1932)	
Norops vicarius (Williams, 1986)	
Norops villai (Fitch and Henderson, 1976)	
Norops wampuensis McCranie and Köhler, 2001	
Norops wellbornae (Ahl, 1940)	
Norops wermuthi Köhler and Obermeier, 1998	
Norops williamsi (Bocourt, 1870)	
Norops woodi (Dunn, 1940)	**N**
Norops yoroensis McCranie, Nicholson, and Köhler, 2001	
Norops zeus Köhler and McCranie, 2001	
	N

Nomina Dubia

Probably all *Norops auratus* Species Group:
Norops binotatus (W. Peters, 1863) (*nomen dubium*)
Norops cumingii (W. Peters, 1863) (*nomen dubium*)
Norops damulus (Cope, 1864) (*nomen dubium*)
Norops impetigosus (Cope, 1864) (*nomen dubium*)
Norops radulinus (Cope, 1862) (*nomen dubium*)

APPENDIX IV. Alphabetical list of species and subspecies names.

acutus, Ctenonotus (cristatellus)
adleri, Norops (auratus)
aenea, Dactyloa (roquet)
aequatorialis, Dactyloa (punctata)
agassizi, Dactyloa (latifrons)
agueroi, Xiphosurus (chamaeleonides)
ahli, Norops (sagrei)
alayoni, Anolis (angusticeps)
alfaroi, Anolis (alutaceus)
aliniger, Deiroptyx (chlorocyana)
allisoni, Anolis (carolinensis)
allogus, Norops (sagrei)
altae, Norops (auratus)
altavelensis, Ctenonotus (distichus)
altitudinalis, Anolis (carolinensis)
alumina, Chamaelinorops
alutaceus, Anolis (alutaceus)
alvarezdeltoroi, Norops (auratus)
amplisquamosus, Norops (auratus)
anatolorus, Dactyloa (punctata)
anchicayae, Dactyloa (punctata)
anfilioquioi, Anolis (alutaceus)
angusticeps angusticeps, Anolis (angusticeps)
angusticeps oligaspis, Anolis (angusticeps)
anisolepis, Norops (auratus)
annectens, Norops (auratus)
anoriensis, Dactyloa (punctata)
antioquiae, Dactyloa (punctata)
antonii, Norops (auratus)
apletophallus, Norops (auratus)
apollinaris, Dactyloa (latifrons)
aquaticus, Norops (auratus)
argenteolus, Anolis (lucius)
argillaceus, Anolis (loysianus)
armouri, Audantia
auratus, Norops (auratus)
baleatus baleatus, Xiphosurus (cuvieri)
baleatus altager, Xiphosurus (cuvieri)
baleatus caeruleolatus, Xiphosurus (cuvieri)
baleatus fraudator, Xiphosurus (cuvieri)
baleatus lineatacervix, Xiphosurus(cuvieri)
baleatus litorisilva, Xiphosurus (cuvieri)
baleatus multistruppus, Xiphosurus (cuvieri)
baleatus samanae, Xiphosurus (cuvieri)
baleatus scelestus, Xiphosurus (cuvieri)
baleatus sublimis, Xiphosurus (cuvieri)
baracoae, Deiroptyx (equestris)
bahorucoensis bahorucoensis, Deiroptyx (hendersoni)
bahorucoensis southerlandi, Deiroptyx (hendersoni)
barahonae barahonae, Xiphosurus (cuvieri)
barahonae albocellatus, Xiphosurus (cuvieri)
barahonae imiquinatus, Xiphosurus (cuvieri)
barahonae mulitus, Xiphosurus (cuvieri)
barbatus, Xiphosurus (chamaeleonides)
barbouri, Chamaelinorops
bartschi, Deiroptyx (vermiculata)
beckeri, Norops (auratus)
bellipeniculus, Dactyloa (heteroderma)
barkeri, Norops (auratus)
benedikti, Norops (auratus)
bicaorum, Norops (auratus)
bimaculatus, Ctenonotus (bimaculatus)
binotatus, Norops (nomen dubium)
biporcatus, Norops (auratus)
birama, Norops (sagrei)
bitectus, Norops (auratus)
blanquillana, Dactyloa (roquet)
bocourtii, Norops (auratus)
boettgeri, Dactyloa (punctata)
bombiceps, Norops (auratus)
bonairensis, Dactyloa (roquet)
brasiliensis, Norops (auratus)
breedlovei, Norops (auratus)
bremeri, Norops (sagrei)
breslini, Audantia
brevirostris brevirostris, Ctenonotus (distichus)
brevirostris deserticola, Ctenonotus (distichus)
brevirostris wetmorei, Ctenonotus (distichus)
brunneus, Anolis (carolinensis)
calimae, Dactyloa (punctata)
campbelli, Norops (auratus)
capito, Norops (auratus)
caquetae, Dactyloa (punctata)
carlostoddi, Dactyloa (heteroderma)
carolinensis carolinensis, Anolis (carolinensis)
carolinensis seminolis, Anolis (carolinensis)
carpenteri, Norops (auratus)
casildae, Dactyloa (latifrons)
caudalis, Ctenonotus (distichus)
centralis, Anolis (loysianus)
chamaeleonides, Xiphosurus (chamaeleonides)
charlesmyersi, Norops (auratus)
chloris, Dactyloa (punctata)
chlorocyana chlorocyana, Deiroptyx (chlorocyana)
chlorocyana cyanosticta, Deiroptyx (chlorocyana)
chocorum, Dactyloa (latifrons)
christophei, Chamaelinorops
chrysolepis, Norops (auratus)
chrysops, Ctenonotus (bimaculatus)
clivicola, Anolis (alutaceus)
cobanensis, Norops (auratus)
coelestina coelestina, Deiroptyx (chlorocyana)
coelestina demissa, Deiroptyx (chlorocyana)
coelestina pecuaris, Deiroptyx (chlorocyana)
compressicauda, Norops (auratus)

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APPENDIX IV. (Continued)

concolor, Norops (auratus)
confusus, Norops (sagrei)
conspersus conspersus, Norops (valencienni)
conspersus lewisi, Norops (valencienni)
cooki, Ctenonotus (cristatellus)
crassulus, Norops (auratus)
cristatellus cristatellus, Ctenonotus (cristatellus)
cristatellus wileyae, Ctenonotus (cristatellus)
cristifer, Norops (auratus)
cryptolimifrons, Norops (auratus)
cumingii, Norops (nomen dubium)
cupeyalensis, Anolis (alutaceus)
cupreus, Norops (auratus)
cuprinus, Norops (auratus)
cuscoensis, Dactyloa (punctata)
cusuco, Norops (auratus)
cuvieri, Xiphosurus (cuvieri)
cyanopleurus cyanopleurus, Anolis (alutaceus)
cyanopleurus orientalis, Anolis (alutaceus)
cybotes cybotes, Audantia
cybotes doris, Audantia
cybotes ravifaux, Audantia
cymbops, Norops (auratus)
damulus, Norops (nomen dubium)
danieli, Dactyloa (latifrons)
dariense, Norops (auratus)
darlingtoni, Chamelionorops
darlingtoni, Deiroptyx (hendersoni)
deltae, Dactyloa (punctata)
datzorum, Norops (auratus)
delafuentei, Norops (sagrei)
desechensis, Ctenonotus (cristatellus)
desiradei, Ctenonotus (bimaculatus)
dissimilis, Dactyloa (punctata)
distichus distichus, Ctenonotus (distichus)
distichus aurifer, Ctenonotus (distichus)
distichus biminiensis, Ctenonotus (distichus)
distichus dapsilis, Ctenonotus (distichus)
distichus distichoides, Ctenonotus(distichus)
distichus dominicensis, Ctenonotus (distichus)
distichus favillarum, Ctenonotus (distichus)
distichus ignigularis, Ctenonotus (distichus)
distichus juliae, Ctenonotus (distichus)
distichus ocior, Ctenonotus (distichus)
distichus patruelis, Ctenonotus (distichus)
distichus properus, Ctenonotus (distichus)
distichus ravitergum, Ctenonotus (distichus)
distichus sejunctus, Ctenonotus (distichus)
distichus suppar, Ctenonotus (distichus)
distichus tostus, Ctenonotus (distichus)
distichus vinosus, Ctenonotus (distichus)
dolichocephala dolichocephala, Deiroptyx (hendersoni)
dolichocephala portusala, Deiroptyx(hendersoni)
dolichocephala sarmenticola, Deiroptyx (hendersoni)
dollfusianus, Norops (auratus)
dominicana, Deiroptyx (chlorocyana)
duellmani, Norops (auratus)
dunni, Norops (auratus)
eewi, Norops (auratus)
electrum, Norops (auratus)
ernestwilliamsi, Ctenonotus (cristatellus)
equestris equestris, Deiroptyx (equestris)
equestris brujensis, Deiroptyx (equestris)
equestris buidei, Deiroptyx (equestris)
equestris cincoleguas, Deiroptyx (equestris)
equestris cyanea, Deiroptyx (equestris)
equestris juraguensis, Deiroptyx (equestris)
equestris perspara, Deiroptyx (equestris)
equestris potior, Deiroptyx (equestris)
equestris sabinalensis, Deiroptyx (equestris)
equestris thomasi, Deiroptyx (equestris)
equestris verreonensis, Deiroptyx (equestris)
eulaema, Dactyloa (punctata)
euskalerrari, Dactyloa (heteroderma)
extrema, Dactyloa (roquet)
eugenegrahami, Xiphosurus (cuvieri)
evermanni, Ctenonotus (cristatellus)
fairchildi, Anolis (carolinensis)
fasciata, Dactyloa (punctata)
ferreus, Ctenonotus (bimaculatus)
festae, Dactyloa (punctata)
fitchi, Dactyloa (punctata)
forbesi, Norops (auratus)
forresti, Ctenonotus (bimaculatus)
fortunensis, Norops (auratus)
fowleri, Chamaelinorops
fraseri, Dactyloa (latifrons)
frenata, Dactyloa (latifrons)
fugitivus, Anolis (alutaceus)
fungosus, Norops (auratus)
fuscoauratus, Norops (auratus)
gadovii, Norops (auratus)
garmani, Norops (valencienni)
garridoi, Anolis (angusticeps)
gemmosa, Dactyloa (punctata)
gibbiceps, Norops (auratus)
gingivinus, Ctenonotus (bimaculatus)
godmani, Norops (auratus)
gorgonae, Dactyloa (punctata)
gracilipes, Norops (auratus)
grahami grahami, Norops (valencienni)
grahami aquarum, Norops (valencienni)
granuliceps, Norops (auratus)
grisea, Dactyloa (roquet)
gruuo, Norops (auratus)
guafe, Norops (sagrei)
guamuhaya, Xiphosurus (chamaeleonides)
guazuma, Anolis (angusticeps)
gundlachi, Ctenonotus (cristatellus)
haetiana, Audantia
haguei, Norops (auratus)
hendersoni hendersoni, Deiroptyx (hendersoni)
hendersoni ravidormitans, Deiroptyx (hendersoni)
heteroderma, Dactyloa (heteroderma)
hobartsmithi, Norops (auratus)
homolechis homolechis, Norops (sagrei)

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APPENDIX IV. (Continued)

homolechis turquinensis, Norops (sagrei)
huilae, Dactyloa (punctata)
humilis, Norops (auratus)
ibague, Norops (auratus)
ibanezi, Dactyloa (latifrons)
imias, Norops (sagrei)
impetigosus, Norops (nomen dubium)
incredulus, Anolis (carolinensis)
inexpectatus, Anolis (alutaceus)
inderenae, Dactyloa (heteroderma)
insignis, Dactyloa (latifrons)
insolitus, Chamaelinorops
intermedius, Norops (auratus)
isolepis, Anolis (carolinensis)
isthmicus, Norops (auratus)
jacare, Dactyloa (punctata)
johnmeyeri, Norops (auratus)
juangundlachi, Anolis (alutaceus)
jubar jubar, Norops (sagrei)
jubar albertschwartzi, Norops (sagrei)
jubar balaenarium, Norops (sagrei)
jubar cocoensis, Norops (sagrei)
jubar cuneus, Norops (sagrei)
jubar gibarensis, Norops (sagrei)
jubar maisiensis, Norops (sagrei)
jubar oriens, Norops (sagrei)
jubar santamariae, Norops (sagrei)
jubar yaguajensis, Norops (sagrei)
kahouannensis, Ctenonotus (bimaculatus)
kemptoni, Norops (auratus)
koopmani, Chamaelinorops
kreutzi, Norops (auratus)
krugi, Ctenonotus (cristatellus)
kunayalae, Dactyloa (latifrons)
laevis, Dactyloa (punctata)
laeviventris, Norops (auratus)
lamari, Dactyloa (punctata)
latifrons, Dactyloa (latifrons)
leachii, Ctenonotus (bimaculatus)
lemniscatus, Norops (auratus)
lemurinus, Norops (auratus)
limifrons, Norops (auratus)
lineatopus lineatopus, Norops (valencienni)
lineatopus ahenobarbus, Norops (valencienni)
lineatopus merope, Norops (valencienni)
lineatus, Norops (auratus)
liogaster, Norops (auratus)
lionotus, Norops (auratus)
litoralis, Anolis (loysianus)
lividus, Ctenonotus (bimaculatus)
longiceps, Anolis (carolinensis)
longitibialis longitibialis, Audantia
longitibialis specuum, Audantia
loveridgei, Norops (auratus)
loysianus, Anolis (loysianus)
luciae, Dactyloa (roquet)
lucius, Anolis (lucius)
luteogularis luteogularis, Deiroptyx (equestris)
luteogularis calcea, Deiroptyx (equestris)
luteogularis coctilis, Deiroptyx (equestris)
luteogularis delacruzi, Deiroptyx (equestris)
luteogularis hassleri, Deiroptyx (equestris)
luteogularis jaumei, Deiroptyx (equestris)
luteogularis nivevulta, Deiroptyx (equestris)
luteogularis sanfelipiensis, Deiroptyx (equestris)
luteogularis sectilis, Deiroptyx (equestris)
luteosignifer, Norops (sagrei)
lynchi, Norops (auratus)
lyra, Norops (auratus)
maclientus, Anolis (alutaceus)
macrinii, Norops (auratus)
macrolepis, Norops (auratus)
macrophallus, Norops (auratus)
maculigula, Dactyloa (latifrons)
maculiventris, Norops (auratus)
magnaphallus, Norops (auratus)
marcanoi, Audantia
mariarum, Norops (auratus)
marmoratus marmoratus, Ctenonotus (bimaculatus)
marmoratus alliaceus, Ctenonotus (bimaculatus)
marmoratus caryae, Ctenonotus (bimaculatus)
marmoratus girafus, Ctenonotus (bimaculatus)
marmoratus inornatus, Ctenonotus (bimaculatus)
marmoratus setosus, Ctenonotus (bimaculatus)
marmoratus specious, Ctenonotus (bimaculatus)
marron, Ctenonotus (distichus)
marsupialis, Norops (auratus)
matudai, Norops (auratus)
maynardi, Anolis (carolinensis)
medemi, Norops (auratus)
megalopitheca, Dactyloa (punctata)
megapholidotus, Norops (auratus)
menta, Dactyloa (punctata)
meridionalis, Norops (auratus)
mestrei, Norops (sagrei)
microlepidotus, Norops (auratus)
microtus, Dactyloa (latifrons)
milleri, Norops (auratus)
mira, Dactyloa (punctata)
monoensis, Ctenonotus (cristatellus)
monteverde, Norops (auratus)
monticola monticola, Deiroptyx (hendersoni)
monticola quadrisarta, Deiroptyx (hendersoni)
morazani, Norops (auratus)
muralla, Norops (auratus)
naufragus, Norops (auratus)
nasofrontalis, Dactyloa (punctata)
neblinina, Dactyloa (heteroderma)
nebuloides, Norops (auratus)
nebulosus, Norops (auratus)
nelsoni, Norops (sagrei)
nicefori, Dactyloa (heteroderma)
nigrolineata, Dactyloa (punctata)
nitens, Norops (auratus)
noblei, Deiroptyx (equestris)
notopholis, Norops (auratus)

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APPENDIX IV. (Continued)

nubilis, Ctenonotus (bimaculatus)
occulta, Deiroptyx (occulta)
ocelloscapularis, Norops (auratus)
oculatus oculatus, Ctenonotus (bimaculatus)
oculatus cabritensis, Ctenonotus (bimaculatus)
oculatus montanus, Ctenonotus (bimaculatus)
oculatus winstoni, Ctenonotus (bimaculatus)
olssoni olssoni, Chamaelinorops
olssoni alienus, Chamaelinorops
olssoni dominigensis, Chamaelinorops
olssoni extentus, Chamaelinorops
olssoni ferrugicauda, Chamaelinorops
olssoni insulanus, Chamaelinorops
olssoni montivagus, Chamaelinorops
olssoni palloris, Chamaelinorops
omiltemanus, Norops (auratus)
onca, Norops (auratus)
opalinus, Norops (valencienni)
ophiolepis, Norops (sagrei)
oporinus, Anolis (carolinensis)
orcesi, Dactyloa (heteroderma)
ordinatus, Norops (sagrei)
otongae, Dactyloa (punctata)
ortonii, Norops (auratus)
osa, Norops (auratus)
oxylophus, Norops (auratus)
pachypus, Norops (auratus)
paravertebralis, Dactyloa (punctata)
parilis, Dactyloa (punctata)
parvicirculatus, Norpos (auratus)
paternus paternus, Anolis (angusticeps)
paternus pinarensis, Anolis (angusticeps)
pentaprion, Norops (auratus)
peraccae, Dactyloa (punctata)
petersii, Norops (auratus)
philopunctata, Dactyloa (punctata)
phyllorhinus, Dactyloa (punctata)
pigmaequestris, Deiroptyx (equestris)
pijolense, Norops (auratus)
pinchoti, Norops (auratus)
placidus, Anolis (angusticeps)
podocarpus, Dactyloa (punctatus)
poecilopus, Norops (auratus)
pogus, Ctenonotus (bimaculatus)
polylepis, Norops (auratus)
polyrhachis, Norops (auratus)
poncensis, Ctenonotus (cristatellus)
porcatus porcatus, Anolis (carolinensis)
porcatus aracelyae, Anolis (carolinensis)
porcus, Xiphosurus (chamaeleonides)
princeps, Dactyloa (latifrons)
proboscis, Dactyloa (heteroderma)
propinqua, Dactyloa (latifrons)
pseudokemptoni, Norops (auratus)
pseudopachypus, Norops (auratus)
pseudotrigrina, Dactyloa (punctata)
pulchellus, Ctenonotus (cristatellus)
pumilis, Anolis (loysianus)
punctata, Dactyloa (punctata)
purpurescens, Dactyloa (latifrons)
purpurgularis, Norops (auratus)
pygmaeus, Norops (auratus)
quadriocellifer, Norops (sagrei)
quaggulus, Norops (auratus)
quercorum, Norops (auratus)
radulinus, Norops (nomen dubium)
reconditus, Norops (valencienni)
rejectus, Anolis (alutaceus)
richardii, Dactyloa (roquet)
ricordii ricordii, Xiphosurus (cuvieri)
ricordii leberi, Xiphosurus (cuvieri)
ricordii subsolanis, Xiphosurus (cuvieri)
ricordii viculus, Xiphosurus (cuvieri)
rimarum, Deiroptyx (hendersoni)
rivalis, Norops (auratus)
roatanensis, Norops (auratus)
rodriguezii, Norops (auratus)
roosevelti, Xiphosurus (cuvieri)
roquet roquet, Dactyloa (roquet)
roquet cracoli, Dactyloa (roquet)
roquet majogris, Dactyloa (roquet)
roquet salinei, Dactyloa (roquet)
roquet summa, Dactyloa (roquet)
roquet zebrila, Dactyloa (roquet)
rubribarbaris, Norops (auratus)
rubribarbus, Norops (sagrei)
ruibali, Anolis (loysianus)
ruizii, Dactyloa (punctata)
rupinae, Deiroptyx (hendersoni)
sabanus, Ctenonotus (bimaculatus)
sagrei sagrei, Norops (sagrei)
sagrei greyi, Norops (sagrei)
salvini, Norops (auratus)
santamartae, Dactyloa (punctata)
scapularis, Norops (auratus)
schiedii, Norops (auratus)
schmidti, Norops (auratus)
schwartzi, Ctenonotus (bimaculatus)
scriptus scriptus, Ctenonotus (cristatellus)
scriptus leucophaeus, Ctenonotus (cristatellus)
scriptus mariguanae, Ctenonotus (cristatellus)
scriptus sularum, Ctenonotus (cristatellus)
scypheus, Norops (auratus)
semilineatus, Chamaelinorops
sericeus, Norops (auratus)
serranoi, Norops (auratus)
sheplani, Anolis (angusticeps)
shrevei, Audantia
simmonsi, Norops (auratus)
singularis, Deiroptyx (chlorocyana)
smallwoodi smallwoodi, Deiroptyx(equestris)
smallwoodi palardis, Deiroptyx (equestris)
smallwoodi saxuliceps, Deiroptyx (equestris)
smaragdinus smaragdinus, Anolis (carolinensis)
smaragdinus lerneri, Anolis (carolinensis)
sminthus, Norops (auratus)

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APPENDIX IV. (Continued)

soinii, Dactyloa (punctata)
solitaria, Dactyloa (punctata)
spectrum, Anolis (alutaceus)
squamulata, Dactyloa (latifrons)
strahmi strahmi, Audantia
strahmi abditus, Audantia
stratulus, Ctenonotus (cristatellus)
subocularis, Norops (auratus)
sulcifrons, Norops (auratus)
tandai, Norops (auratus)
taylori, Norops (auratus)
tenorioensis, Norops (auratus)
terraealtae, Ctenonotus (bimaculatus)
terueli, Anolis (carolinensis)
tetarii, Dactyloa (heteroderma)
tigrina, Dactyloa (punctata)
toldo, Anolis (carolinensis)
tolimensis, Norops (auratus)
townsendi, Norops (auratus)
trachyderma, Norops (auratus)
transversalis, Dactyloa (punctata)
trinitatis, Dactyloa (roquet)
tropidogaster, Norops (auratus)
tropidolepis, Norops (auratus)
tropidonotus, Norops (auratus)
umbrivaga, Dactyloa (punctata)
uniformis, Norops (auratus)
unilobatus, Norops (auratus)
utilensis, Norops (auratus)
utowanae, Norops (auratus)
valencienni, Norops (valencienni)
vanidicus, Anolis (alutaceus)
vanzolinii, Dactyloa (heteroderma)
vaupesiana, Dactyloa (punctata)
ventrimaculata, Dactyloa (punctata)
vermiculata, Deiroptyx (vermiculata)
vescus, Anolis (alutaceus)
vicarius, Norops (auratus)
villai, Norops (auratus)
wampuensis, Norops (auratus)
wattsi, Ctenonotus (bimaculatus)
websteri, Ctenonotus (distichus)
wellbornae, Norops (auratus)
wermuthi, Norops (auratus)
whitemani whitemani, Audantia
whitemani lapidosus, Audantia
williamsi, Norops (auratus)
williamsmittermeierorum, Dactyloa (heteroderma)
woodi, Norops (auratus)
yoroensis, Norops (auratus)

APPENDIX V. Ecomode categories for all species used in the ancestral state reconstruction analysis.

Genus	Species Group	Specific Epithet	Ecomode	Primary Source
Dactyloa	*roquet*	*aenea*	trunk ground/ ground	Henderson and Powell 2009
		grisea	crown giant	Henderson and Powell 2009
		luciae	trunk ground/ ground	Schwartz and Henderson 1991
		richardi	crown giant	Henderson and Powell 2009
		roquet	trunk crown	Henderson and Powell 2009
		trinitatus	trunk crown	Henderson and Powell 2009
	heteroderma	*heteroderma*	twig	Miyata 1983;Torres-Carvajhal et al. 2010
		inderanae	ground bush	Miyata 1983
		nicefori	ground bush	Miyata 1983
	punctata	*gorgonae*	trunk crown	Nicholson, pers. obs.
		punctata	trunk crown	Vitt and de la Torre 1996
		transversalis	trunk crown	Duellman 1978/Vitt and de la Torre
	latifrons	*agassizi*	saxicolous	Losos 2009
		casildae	crown giant	Nicholson et al. 2001
		frenata	crown giant	Savage 2002/Losos 2009
		kunayalae	crown giant	Poe et al. 2007
		microtus	crown giant	Savage 2002
		new species 1	crown giant	Karen Lips, pers. obs.
		princeps	crown giant	Nicholson, pers. obs.
Deiroptyx	*occulta*	*occulta*	twig	Losos 2009/Henderson and Powell 2009
	hendersoni	*bahoucoensis*	grass bush	Losos 2009/Henderson and Powell 2009
		darlingtoni	twig	Losos 2009/Henderson and Powell 2009
		dolichocephala	grass bush	Losos 2009/Henderson and Powell 2009
		hendersoni	grass bush	Losos 2009/Henderson and Powell 2009
		monticola	saxicolous	Schwartz and Henderson 1991
	equestris	*baracoae*	crown giant	Losos 2009/Henderson and Powell 2009
		equestris	crown giant	Losos 2009/Henderson and Powell 2009
		luteogularis	crown giant	Losos 2009/Henderson and Powell 2009
		noblei	crown giant	Losos 2009/Henderson and Powell 2009
		smallwoodi	crown giant	Losos 2009/Henderson and Powell 2009
	vermiculatus	*bartschi*	saxicolous	Henderson and Powell 2009
		vermiculatus	semi-aquatic	Schwartz and Henderson 1991
	chlorocyana	*aliniger*	trunk crown	Losos 2009/Henderson and Powell 2009
		chlorocyana	trunk crown	Losos 2009/Henderson and Powell 2009
		coelestina	trunk crown	Losos 2009/Henderson and Powell 2009
		singularis	trunk crown	Losos 2009/Henderson and Powell 2009
Xiphosurus	*chamaeleonoides*	*barbatus*	trunk	Rodriguez-Schettino 1999
		chamaeleonoides	crown giant	Rodriguez-Schettino 1999

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APPENDIX V. (Continued)

Genus	Species Group	Specific Epithet	Ecomode	Primary Source
		guamuhaya	trunk	Rodriguez-Schettino 1999
		porcus	trunk	Rodriguez-Schettino 1999
	cuvieri	*baleatus*	crown giant	Losos 2009/Henderson and Powell 2009
		barhonae	crown giant	Losos 2009/Henderson and Powell 2009
		christophei	semi-aquatic	Henderson and Powell 2009
		cuvieri	crown giant	Losos 2009/Henderson and Powell 2009
		eugenegrahami	semi-aquatic	Henderson and Powell 2009
		ricordii	crown giant	Losos 2009/Henderson and Powell 2009
Chamaelinorops		*alumina*	grass bush	Losos 2009/Henderson and Powell 2009
		barbouri	ground	Henderson and Powell 2009
		darlingtoni	grass bush	Schwartz and Henderson 1991
		fowleri	twig	Henderson and Powell 2009
		insolitus	twig	Losos 2009/Henderson and Powell 2009
		olssoni	grass bush	Losos 2009/Henderson and Powell 2009
		semilineatus	grass bush	Losos 2009/Henderson and Powell 2009
Audantia		*armouri*	trunk ground	Losos 2009/Henderson and Powell 2009
		breslini	trunk ground	Losos 2009/Henderson and Powell 2009
		cybotes	trunk ground	Losos 2009/Henderson and Powell 2009
		haetiana	trunk ground	Losos 2009/Henderson and Powell 2009
		longitibialis	trunk ground	Losos 2009/Henderson and Powell 2009
		marcanoi	trunk ground	Losos 2009/Henderson and Powell 2009
		shrevei	trunk ground	Losos 2009/Henderson and Powell 2009
		strahmi	trunk ground	Losos 2009/Henderson and Powell 2009
		whitemani	trunk ground	Losos 2009/Henderson and Powell 2009
Anolis	*alutaceus*	*alfaroi*	grass bush	Losos 2009/Henderson and Powell 2009
		alutaceus	grass bush	Losos 2009/Henderson and Powell 2009
		clivicola	grass bush	Losos 2009/Henderson and Powell 2009
		cupeyalensis	grass bush	Losos 2009/Henderson and Powell 2009
		cyanopleurus	grass bush	Losos 2009/Henderson and Powell 2009
		inexpectatus	grass bush	Losos 2009/Henderson and Powell 2009
		macilentus	grass bush	Losos 2009/Henderson and Powell 2009
		rejectus	grass bush	Losos 2009/Henderson and Powell 2009
		vanidicus	grass bush	Losos 2009/Henderson and Powell 2009
	angusticeps	*alayoni*	twig	Losos 2009/Henderson and Powell 2009
		angusticeps	twig	Losos 2009/Henderson and Powell 2009
		new species 2	twig	Blair Hedges, pers. obs.
		paternus	twig	Losos 2009/Henderson and Powell 2009
		placidus	twig	Losos 2009/Henderson and Powell 2009
		sheplani	twig	Losos 2009/Henderson and Powell 2009

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APPENDIX V. (Continued)

Genus	Species Group	Specific Epithet	Ecomode	Primary Source
		garridoi	twig	Losos 2009/Henderson and Powell 2009
		guazuma	twig	Losos 2009/Henderson and Powell 2009
	loysianus	*argillaceus*	trunk	Schwartz and Henderson 1991
		centralis	trunk	Schettino/Henderson and Powell 2009
		loysianus	trunk	Losos 2009/Henderson and Powell 2009
		pumilis	grass bush	Schwartz and Henderson 1991
	carolinensis	*allisoni*	trunk crown	Losos 2009/Henderson and Powell 2009
		altitudinalis	trunk crown	Losos 2009/Henderson and Powell 2009
		brunneus	trunk crown	Losos 2009/Henderson and Powell 2009
		carolinensis	trunk crown	Henderson and Powell 2009
		isolepis	trunk crown	Losos 2009/Henderson and Powell 2009
		longiceps	trunk crown	Losos 2009/Henderson and Powell 2009
		maynardi	trunk crown	Losos 2009/Henderson and Powell 2009
		oporinus	trunk crown	Losos 2009/Henderson and Powell 2009
		porcatus	trunk crown	Losos 2009/Henderson and Powell 2009
		smaragdinus	trunk crown	Losos 2009/Henderson and Powell 2009
	lucius	*argenteolus*	trunk/saxicolous	Schwartz and Henderson 1991
		lucius	saxicolous	Schwartz and Henderson 1991
Ctenonotus	*bimaculatus*	*bimaculatus*	trunk crown	Henderson and Powell 2009
		ferreus	trunk crown	Henderson and Powell 2009
		gingivinus	polymorphic	Henderson and Powell 2009
		leachi	trunk crown	Henderson and Powell 2009
		lividus	trunk crown	Henderson and Powell 2009
		marmoratus	trunk/grass/ ground	Schwartz and Henderson 1991
		nubilis	trunk ground	Schwartz and Henderson 1991
		oculatus	Trunk ground/ saxicolous	Schwartz and Henderson 1991
		pogus	grass bush	Henderson and Powell 2009
		sabanus	trunk ground	Henderson and Powell 2009
		schwartzi	grass bush	Henderson and Powell 2009
		wattsi	Trunk ground/ saxicolous	Henderson and Powell 2009
	distichus	*brevirostris*	trunk	Losos 2009/Henderson and Powell 2009
		caudalis	trunk	Losos 2009/Henderson and Powell 2009
		distichus	trunk	Losos 2009/Henderson and Powell 2009
		marron	trunk	Losos 2009/Henderson and Powell 2009
		websteri	trunk	Losos 2009/Henderson and Powell 2009
	cristatellus	*acutus*	polymorphic	Henderson and Powell 2009; Beuttell and Losos 1999

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APPENDIX V. (Continued)

Genus	Species Group	Specific Epithet	Ecomode	Primary Source
		cooki	trunk ground	Losos 2009/Henderson and Powell 2009
		cristatellus	trunk ground	Losos 2009/Henderson and Powell 2009
		desechensis	trunk ground	Losos 2009/Henderson and Powell 2009
		ernestwilliamsi	trunk ground	Losos 2009/Henderson and Powell 2009
		evermanni	trunk crown	Losos 2009/Henderson and Powell 2009
		gundlachi	trunk ground	Henderson and Powell 2009; Schwartz and Henderson 1991
		krugi	grass bush	Losos 2009/Henderson and Powell 2009
		monensis	trunk ground	Losos 2009/Henderson and Powell 2009
		poncensis	grass bush	Losos 2009/Henderson and Powell 2009
		pulchellus	grass bush	Losos 2009/Henderson and Powell 2009
		scriptus	trunk ground	Losos 2009/Henderson and Powell 2009
		stratulus	trunk crown	Losos 2009/Henderson and Powell 2009
Norops	*sagrei*	*allogus*	trunk ground	Losos 2009/Henderson and Powell 2009
		ahli	trunk ground	Losos 2009/Henderson and Powell 2009
		bremeri	trunk ground	Losos 2009/Henderson and Powell 2009
		confusus	trunk crown	Losos 2009/Henderson and Powell 2009
		guafe	trunk ground	Losos 2009/Henderson and Powell 2009
		homolechis	trunk ground	Losos 2009/Henderson and Powell 2009
		imias	trunk ground	Losos 2009/Henderson and Powell 2009
		jubar	trunk ground	Losos 2009/Henderson and Powell 2009
		mestrei	trunk ground	Losos 2009/Henderson and Powell 2009
		ophiolepis	grass bush	Losos 2009/Henderson and Powell 2009
		quadriocellifer	trunk ground	Losos 2009/Henderson and Powell 2009
		rubribarbus	trunk ground	Losos 2009/Henderson and Powell 2009
		sagrei	trunk ground	Losos 2009/Henderson and Powell 2009
	valencienni	*conspersus*	trunk ground	Losos 2009/Henderson and Powell 2009
		garmani	crown giant	Losos 2009/Henderson and Powell 2009
		grahami	trunk crown	Losos 2009/Henderson and Powell 2009
		lineatopus	trunk ground	Losos 2009/Henderson and Powell 2009
		opalinus	trunk crown	Losos 2009/Henderson and Powell 2009
		reconditus	trunk ground	Henderson and Powell 2009
		valencienni	twig	Losos 2009/Henderson and Powell 2009
	auratus	*altae*	trunk ground	Savage 2002
		annectens	ground	Nicholson, pers. obs.; Williams 1974
		aquaticus	semi-aquatic	Savage 2002/Losos 2009
		auratus	grass bush	Losos 2009
		bicaorum	trunk	McCranie, Wilson, and Kohler 2005
		biporcatus	crown giant	Savage 2002/Losos 2009
		bitectus	?	

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APPENDIX V. (Continued)

Genus	Species Group	Specific Epithet	Ecomode	Primary Source
		capito	trunk ground	Savage 2002; Guyer and Donnelly 2005
		carpenteri	trunk ground	Savage 2002
		crassulus	ground bush	McCranie et al. 1992
		cupreus	polymorphic	Savage 2002
		fuscoauratus	trunk ground	Vitt and de la Torre 1996
		humilis	ground	Savage 2002
		intermedius	trunk	Savage 2002
		isthmicus	saxicolous	Fitch 1978
		kemptoni	trunk ground	Savage 2002
		laeviventris	trunk	Stuart 1955
		lemurinus	trunk	Savage 2002/Guyer and Donnelly 2005
		limifrons	grass bush	Savage 2002
		lineatus	trunk	van Buurt 2005
		lionotus	semi-aquatic	Savage 2002/Losos 2009
		loveridgei	crown giant	McCranie and Cruz 1992
		medemi	trunk ground	Nicholson, pers. obs.
		meridionalis	ground	Langstroth 2006
		nebuloides	trunk ground	Guyer pers. obs.; Ramirez-Bautista and M. Benabib 2001
		new species 3	trunk ground	Nicholson, pers. obs.
		nitens	ground	Vitt and de la Torre 1996
		ocelloscapularis	trunk ground	Kohler, Ponce, Sunyer, and Batista 2007
		onca	ground	Nicholson, pers. Obs, Williams 1974
		ortonii	trunk ground	Vitt and de la Torre 1996
		oxylophus	semi-aquatic	Savage 2002/Losos 2009
		pachypus	trunk ground	Savage 2002
		poecilopus	semi-aquatic	Campbell 1973
		polylepis	grass bush	Savage 2002
		polyrhachis	ground bush	Smith 1968
		purpurgularis	trunk ground	McCranie et al. 1993
		quercorum	ground	Mata-Silva and Oliver-Lopez 2002
		sericeus	grass bush	Campbell 1998
		sminthus	?	
		townsendi	polymorphic	Savage 2002
		trachyderma	trunk ground	Vitt and de la Torre 1996
		tropidogaster	ground	Ballinger et al 1970; Kiester 1979
		tropidonotus	ground	Campbell 1998
		uniformis	ground	Campbell 1998
		utilensis	trunk	McCranie, Wilson, and Kohler 2005
		woodi	trunk	Savage 2002
		zeus	grass bush	Kohler and McCranie 2001

APPENDIX VI. Possible ancestral distributions for the most parsimonious reconstructions of the parsimony optimized molecular data only tree and molecular and morphology combined data tree.

Branch #	Molecular Data Only Tree	Molecular & Morphologic Data Tree
1	WC, SH	SA, CH
2	EC, CC, WC, SH	SA, CH
3	EC, CC, WC, SH	SA, CH
4	WC, SH, NH	SA, CH
5	SH, NH	SA, CH, WC, SH, NH
6	SH, NH	WC, SH, NH
7	C, EC	WC, SH, NH
8	C, EC	WC, SH, NH
9	C, EC	EC, CC, WC, SH, NH
10	C, EC, NH, PR	EC, CC, WC, SH, NH
11	C, EC	WC, SH, NH
12	C, EC	SH, NH
13	C, EC, CC	SH, NH
14	SH, NH	SH, NH
15	SH, NH	SH, NH
16	H, SH, NH	SH, NH
17	EC, SH, NH	SH, NH
18	C, EC, WC, B	SH, NH
19	C, EC, WC, B	SH, NH
20	EC, CC	C, EC, B, US, CAY
21	EC, CC	C, EC, B, US, CAY
22	C, EC, CC	C, EC, B, US, CAY
23	C, EC, CC	EC, SH, NH
24	EC, CC	C, EC, WC, B
25	EC, WC, CC	C, EC, WC, B
26	C, EC, CC	EC, SH, NH
27	C, EC, CC	C, EC, CC, WE, SH, NH
28	C, EC, CC, B. US	C, EC, CC, WE, SH, NH
29	C, EC, CC, B. US	C, EC, CC, WE, SH, NH
30	CC, B	C, EC, CC, WE, SH, NH
Branch #	Molecular Data Only Tree	Molecular & Morphologic Data Tree
31	CC, B	SH, NH
32	CC, B, SH, CAY	SH, NH
33	CC, B, SH, CAY	SH, NH
34	EC, H, NH, PR, NLA	SH, NH
35	EC, H, NH, PR, NLA	H, SH, NH
36	EC, H, NH, PR, NLA	SH, NH
37	C, EC, WC	SH, NH
38	C, WC	SH, NH

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APPENDIX VI. (Continued)

Branch #	Molecular Data Only Tree	Molecular & Morphologic Data Tree
39	C, WC	SH, NH
40	C, EC, CC	SA, NCA, LCA, MEX, EC, SH, NH, J
41	EC, J, NCA	C, EC, CC
42	EC, J, NCA	SA, NCA, LCA, MEX, EC, SH, NH, J
43	LCA, NCA, CAY	SA, NCA, LCA, MEX, EC, SH, NH, J
44	NCA, MAY	NCA, LCA
45	NCA, MAY, MEX	NCA, LCA
46	NCA, MAY	NCA, LCA
47	NCA, LCA, MEX	NCA, LCA, CH
48	NCA, LCA	NCA, LCA
49	NCA, LCA, MEX	NCA, MAY
50	NCA, LCA, MEX	NCA, MAY
51	NCA, LCA, MEX, MAY	MAY, MEX
52	NCA, LCA	CA, NCA, LCA, MAY, MEX
53	LCA, SA	LCA, MEX
54	LCA, SA	SA, NCA, LCA, MEX, EC, SH, NH, J
55	LCA, SA, CH	NCA, LCA
56	NCA, LCA	NCA, LCA
57	NCA, LCA	NCA, LCA
58	NCA, LCA	NCA, LCA, MAY
59	NCA, LCA	NCA, LCA
60	CA, NCA, LCA, CAY	NCA, LCA
61	CA, NCA, LCA, CAY	NCA, LCA
62	NCA, LCA	SA, CH
63	NCA, LCA	CA, NCA, MEX
Branch #	Molecular Data Only Tree	Molecular & Morphologic Data Tree
64	NCA, LCA	MAY, MEX
65	NCA, LCA	---
66	CA, NCA, LCA, MEX	---
67	CA, NCA, LCA, MEX	---
68	NCA, LCA	---
69	NCA, LCA, SA, CH	---
70	SA, CH	---
71	SA, CH	---
72	SA, CH	---
73	SA, CH, CO	---

APPENDIX VII. List of published and unpublished karyotypes for Dactyloidae. Format for the karyotypes below is as follows. Diploid number: number of macrochromosomes (number of biarmed macrochromosomes, number of uniarmed macrochromosomes), number of microchromosomes. N.F. = Nombre Fundamental, calculated by the following formula: 2 x number of biarmed macrochromosomes, plus 1 x number of uniarmed macrochromosomes, plus 1 x number of microchromosomes.

Dactyloa:
Latifrons species group
Dactyloa agassizi **36: 12 (12,0) 24. 48:** Stamm and Gorman. 1975. Smithson. Contr. Zool. 176, 52–54.
Dactyloa frenata **36: 14 (14,0) 22. 50:** Stamm and Gorman. 1975. Smithson. Contr. Zool. 176, 52–54.
Dactyloa squamulata **36: 12 (12,0) 24. 48:** Gorman and Stamm. 1975. J. Herpetol. 9, 197–205.

Punctata species group
No information on species in this group.

Heteroderma species group
Dactyloa heteroderma **36: 12 (12,0) 24: 48.** Gorman et al. 1969. Breviora Mus. Comp. Zool. 316, 1–17

Roquet species group
Dactyloa aenea **34: 12 (12,0) 22. 46:** Gorman and Atkins. 1968. Science 159, 1358–1360; Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.
Dactyloa blanquillana **36: 12 (12,0) 24. 48:** Gorman and Stamm. 1975. J. Herpetol. 9, 197–205.
Dactyloa bonairensis **36: 12 (12,0) 24. 48:** Gorman. 1965. Nature 208: 95–97; Gorman and Atkins.1967. Syst. Zool. 16, 137–143. *Dactyloa extrema* **34: 12 (12,0) 22. 46:** Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.
Dactyloa griseus **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.
Dactyloa luciae **36: 12 (12,0) 24. 48:** Gorman. 1965. Nature 208, 95–97; Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.
Dactyloa roquet **34: 12 (12,0) 22. 46:** Gorman and Atkins.1967. Syst. Zool. 16, 137–143.
Dactyloa trinitatis **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1968. Science 159, 1358–1360; Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.

Deiroptyx:
Occulta species group
Deiroptyx occulta **32 female, 31 male: 24 (16,8) 8: 48; 23 (18,5) 8 X1X2Y: 52.** Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.

Vermiculata species group
Deiroptyx bartschi **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.
Deiroptyx vermiculata **34: 12 (12,0) 22. 46:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Chlorocyana species group
Deiroptyx chlorocyana **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.
Deiroptyx coelestina **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.

Equestris species group
Deiroptyx equestris **36: 12 (12,0) 24. 48:** Gorman. 1965. Nature 208, 95–97; Gorman et al. 1967. Cytogenetics 6, 286–299. **36: 22 (12,10)14. 48:** De Smet. 1981. Acta Zool. Patho. Antverpiensia 76, 35–72.

Hendersoni species group
Deiroptyx hendersoni **36: 12 (12,0) 24. 48: G**orman et al. 1967. Cytogenetics 6, 286–299.*Deiroptyx monticola* **46, 47, 48: 22 (0,22) 24: 46; 23 (1,21) 24: 46; 24 (0,24) 24: 48:** Webster et al. 1972. Science 177, 611–613.

Xiphosurus: *Chamaeleonides* species group
Xiphosurus porcus **36: 12 (12,0) 24. 48:** Gorman et al. 1969. Breviora 316, 1–17.

Cuvieri species group

Xiphosurus cuvieri **36: 12 (12,0) 24. 48:** Gorman & Atkins. 1969. Bull Mus Comp. Zool. 138, 53–80.

Xiphosurus ricordii **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.

Chamaelinorops:

Chamaelinorops barbouri **36: 12 (12,0) 24. 48:** Paull et al. 1976. Breviora 441, 1–31.*Chamaelinorops christophei* **36: 12 (12,0) 24. 48:** Webster et al. 1972. Science 177, 611–613.

Chamaelinorops insolitus **44:** Webster et al. 1972. Science 177, 611–613.

Chamaelinorops koopmani **40:** Webster et al. 1972. Science 177, 611–613.

Chamaelinorops olssoni **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.

Chamaelinorops semilineatus **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.

Audantia:

Audantia cybotes **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1966. Amer. Natur. 100, 579–583.

Anolis:

Lucius species group*Anolis argenteolus* **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Anolis lucius **36: 12 (12,0) 24. 48:** Gorman & Atkins. 1968. Herpetologica 24, 13–21.

Alutaceus species group

No information on species in this group.

Angusticeps species group

Anolis angusticeps **36: 12 (12,0) 24. 48:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Loysianus species group

No information on species in this group.

Carolinensis species group

Anolis allisoni **36: 12 (12,0) 24. 48:** Gorman et al. 1967. Cytogenetics 6, 286–299.

Anolis carolinensis **34:** Painter. 1921. J. Exp. Zool. 34, 281–327; **36: 12 (12,0) 24; 48:** Matthey. 1931. Rev. Suisse Zool. 38, 117–186; Gorman. 1965. Nature 208, 95–97; **36:** Atkins et al. 1965. Chromosoma 17, 1–10; **36 CG banding** Princée and de Boer. 1983. Chrom Inf Serv 34, 3–5; probable XY sex chromosomes but no heteromorphishm: Alfoldi et al. 2011. Nature, 589.

Anolis maynardi **36: 12 (12,0) 24: 48:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Anolis porcatus **36: 12 (12,0) 24:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Ctenonotus:

Bimaculatus species group

Ctenonotus bimaculatus **29 male, 30 female: 18 (18,0) 8+3 sex chromosomes: 47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48**. Gorman. 1965. Nature 208, 95–97; Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus ferreus **29 male, 30 female: 18 (18,0) 8+3 sex chromosomes**; 47; **18 (18,0) 8+4 sex chromosomes X1X2Y: 48.** Gorman & Atkins.1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus gingivinus **29 male, 30 female: 18 (18,0) 8+3 sex chromosomes: 47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48**. Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus leachii **29 male, 30 female: 18 (18,0) 8+3 sex chromosomes**: **47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus lividus **29 male, 30 female: 18 (18,0) 8+3 sex chromosomes: 47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48**. Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus marmoratus 29 male, **30 female: 18 (18,0) 8+3 sex chromosomes: 47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48**: Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus oculatus **32 female, 31 male: 24 (16,8) 8: 48; 23 (18,5) 8 X1X2Y: 52.** Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.*Ctenonotus sabanus* **29 male, 30 female: 18 (18,0) 8+ 3 sex chromosomes:47; 18 (18,0) 8+4 sex chromosomes X1X2Y: 48.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus wattsi **29 male: 18 (18,0) 8+3 sex chromosomes X1X2Y: 47.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Distichus species group

Ctenonotus distichus **34 female, 33 male: 14 (14,0) 16+4 sex chromosomes: 48; 14 (14,0) 16+3 sex chromosomes X1X2Y: 47.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Cristatellus species group

Ctenonotus acutus **31 male: 14 (14,0) 14+3 sex chromosomes X1X2Y: 45.** Gorman & Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus cooki **30 female, 29 male: 16 (16,0) 10+4 sex chromosomes: 46; 16 (16,0) 10+3 sex chromosomes X1X2Y: 45.** Gorman et al. 1968. Breviora Mus. Comp. Zool. 293, 1–13.

Ctenonotus cristatellus **28 female, 27 male: 16 (16,0) 8+4 sex chromosomes:44; 16 (16,0) 8+3 sex chromosomes X1X2Y: 43.** Gorman et al. 1968. Breviora Mus. Comp. Zool. 293, 1–13.

Ctenonotus desechensis **28 female, 27 male: 16 (16,0) 8+4 sex chromosomes: 44; 16 (16,0) 8+3 sex chromosomes X1X2Y: 43.** Brandley, Wynn, and deQuieroz, 2006. J. Herp. 40, 136–139.

Ctenonotus evermanni **26: 16 (14,2) 10 XY: 42.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53-80; Gorman and Atkins. 1968. Copeia 1968, 159–160.

Ctenonotus gundlachi **29 male: 18 (18,0) 8+3 sex chromosomes: 47.** Gorman et al. 1968. Breviora Mus. Comp. Zool 293, 1–13; Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus krugi **29 male: 16 (16,0) 10+3 sex chromosomes: 45.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus monensis **29 male: 18 (18,0) 8+3 sex chromosomes X1X2Y: 47.** Gorman & Stamm. 1975. J. Herpetologica 9, 197–205.

Ctenonotus poncensis **29 male: 16 (16,0) 10+3 sex chromosomes: 45.** Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus pulchellus **29 male: 16 (16,0) 10+3 sex chromosomes X1X2Y: 45.** Gorman et al. 1968. Breviora Mus. Comp. Zool. 293, 1–13; Gorman and Atkins. 1969. Bull. Mus. Comp. Zool. 138, 53–80.

Ctenonotus scriptus **28 female, 27 male 16 (16,0) 8+4 sex chromosomes:44; 16 (16,0) 8+ 3 sex chromosomes X1X2Y: 43.** Gorman et al. 1968. Breviora Mus. Comp. Zool. 293, 1–13.

Ctenonotus stratulus **29 male: 14 (14,0) 12+3 sex chromosomes, X1X2Y: 43.** Gorman and Atkins. 1969. Bull. Mus. Comp.Zool. 138, 53–80.

Norops:

Sagrei species group

Norops homolechis **28: 14 (14,0) 14: 42:** Gorman and Atkins. 1968. Herpetologica 24, 13–21; Porter et al. 1989. Occas. Paps. Mus. Texas Tech. Univ. 130, 1–6 **28: 14 (14,0) 14: 42, rDNA on 2nd or 3rd**: Porter et al. 1991. Herpetologica 47, 271–280; Porter et al. 1994. Copeia 1994, 302–313.

Norops mestrei **28: 14 (14,0) 14: 42:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Norops quadriocellifer **28: 14 (14,0) 14: 42:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Norops rubribarbus **28: 14 (14,0) 14: 42:** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Norops sagrei **28: 14 (14,0) 14: 42:** Gorman and Atkins. 1968. Herpetologica 24, 13–21 **29 male: 20 (20,0) 9 + X1X2Y: 52; scNOR on 1st.**: De Smet. 1981. Acta Zool. Pathol. Antverpiensia 76, 35–72.

Valencienni species group

Norops conspersus **30 male: 14 (13,1) 16: 43: 30 female: 14 (14,0) 16: 44:** Gorman and Atkins. 1968. Copeia 1968, 159–160.

Norops garmani **30: 14 (14,0) 16: 44** Gorman and Atkins. 1968. Herpetologica 24, 13–21.

Norops grahami **32: 16 (12,4) 16: 44:** Gorman. 1965. Nature 208, 95–97; Gorman in Chiarelli and Capanna. 1973. Cytotaxon. Vert. Evol., 349–424; **34: 18 macro 16** micro; 35: 19 macro 16 micro ; 36: 19 macro 17 micro; 37: 19 macro 18 micro; 36: 20 macro 16 micro; 30: 14 macro 16 micro; 31: 15 macro 16 micro; 32: 16 macro 16 micro; 32: 14 macro 18 micro; 34: 16 macro 18 micro; 34: 18 macro 16 micro; 35: 19 macro 16 micro; 36: 18 macro 18 **micro; 32: 16 macro 16 micro C banding**: Blake. 1986. Genetica 69, 3–17.

Norops lineatopus **30: 14 (14,0) 16: 44**: Gorman. 1965. Nature 208, 95–97; Gorman. 1969. Mamm. Chrom. Newslett. 10, 222–224.

Norops opalinus **30: 14 (14,0) 16: 44:** Gorman. 1969. Mamm. Chrom. Newslett. 10, 222–224.

Norops valencienni **30: 14 (14,0) 16: 44:** Gorman and Atkins. 1968. Herpetologica 24: 13–21.

Auratus species group
Basal lineage

Norops onca **30: 14 (14,0) 16+2 sex chromosomes XY: 46:** Gorman. 1969. Mamm. Chrom. Newslett. 10, 222–224.

Norops auratus **30: 14 (14,0) 16: 44:** Gorman et al. 1967. Cytogenetics 6, 286–299. **30: 14 (14,0) 16: 44:** De Smet.1981. Acta Zool. Pathol. Antverpiensia 76, 35–72.

MesoAmerican lineage

Norops aquaticus 28 male: **40: 24 macro 16 micro:** Lieb. 1981. PhD. Dissertation.

Norops biporcatus **29 male: 12 (12,0) 14+3 sex chromosomes X1X2Y: 41; 30 female 12 (12,0) 14+4 sex chromosomes X1X2X3X4: 42:** Gorman and Atkins. 1966. Amer. Natur. 100, 579–583.

Norops capito **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops chrysolepis **30: 14 (14,0) 16: 44:** Gorman. 1965. Nature 208, 95-97; Gorman and Atkins. 1967. Syst Zool 16, 137–143.

Norops compressicaudus **28 male; 28: 14 (12,2) 16, no sex chromosomes: 44:** Lieb. 1981. Ph.D Dissertation.

Norops crassulus **32 male:14 (14,0)16+2 sex chromosomes XY: 46:** Lieb. 1981. Ph.D Dissertation.

Norops cupreus **40: 24 macro 16 micro:** Gorman in Chiarelli and Cytotaxon, Vert. Evol., 349–424.

Norops dunni **42 male: 22 (2,20) 16+2 sex chromosomes XY: 42:** Lieb. 1981. PhD. Dissertation.

Norops fuscoauratus **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops gadovi **36 male: 17 (6,11) 18+2 sex chromosomes XY: 43:** Lieb.1981. PhD. Dissertation.

Norops gracilipes **36: 20 (8,12) 16: 44:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops humilis **40: 24 macro 16 micro:** Gorman. 1967. Gorman in Chiarelli and Capanna (eds). 1973.Cytotaxon, Vert. Evol., 349–424.

Norops isthmicus **36 male: 36: 18 (6,12) 16+2 sex chromosomes XY: 42**:

Norops intermedius **40: 24 macro 16 micro:** Lieb. 1981. PhD. Dissertation.

Norops laeviventris **40 male: 24 macro 16 micro**: Lieb. 1981. PhD. Dissertation.

Norops lemurinus **40 female: 22 (18,4) 16: 56**: Lieb. 1981. PhD. Dissertation.

Norops limifrons **40: 24 macro 16 micro:** Gorman. 1967. Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops lineatus **30: 14 (14,0) 16: 44:** Gorman. 1965. Nature 208, 95–97.

Norops liogaster **38 male: 20 (4,16) 16+2 sex chromsome XY: 42:** Gorman and Atkins. 1967. Syst. Zool. 16, 137–143.

Norops lionotus **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops nebuloides **42 male: 20 (8,12) 20+2 sex chromosomes XY: 50:36: 20 (8,12) 16 + 2: 42; 30 male: 13 (13,0) 17: 43**: Lieb. 1981. PhD. Dissertation.

Norops nebulosus **30 male: 12 (12,0) 16+2 sex chromosomes XY**: **42: 36 male: 8 (4,4) 16 + 2 sex chromosomes XY: 42**: Lieb. 1981. PhD. Dissertation.

Norops omlitemanus **38 female: 38:10 (4.16) 16+2 sex chromsomes XX: 42**: Lieb. 1981. PhD. Dissertation.

Norops pentaprion **28 male: 12 (12,0) 16, no sex chromosomes: 40:** Lieb. 1981. PhD. Dissertation.

Norops polylepis **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops quercorum **30 male: 30: 12 (12,0) 16+2 sex chromosomes XY: 40:** Lieb. 1981. PhD. Dissertation.

Norops sericeus **24 male: 40: 24 macro 16 micro**: Lieb. 1981. PhD. Dissertation.

Norops subocularis **36 male: 18 (6,12) 16+2 sex chromosomes XY: 42**: Lieb. 1981. PhD. Dissertation.

Norops taylori **40 male: 22 (2, 20) 16+2 sex chromosomes: 42:** Lieb. 1981. PhD. Dissertation.

Norops tropidogaster **40: 24 (4,20) 16: 44:** Gorman. 1967. Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops tropidolepis **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops tropidonotus **40: 24 macro 16 micro:** Gorman in Chiarelli and Capanna (eds). 1973. Cytotaxon, Vert. Evol., 349–424.

Norops uniformis **28 male:14 (14,0) 16 no sex chromosomes: 44:** Lieb. 1981. PhD. Dissertation.

Norops woodi **30 or 32: 14 macro 14 or 16 micro:** Lieb. 1981. PhD. Dissertation.