



Anole classification: A response to Poe

K.E. NICHOLSON¹, B.I. CROTHER², C. GUYER³ & J.M. SAVAGE⁴

¹Department of Biology, Central Michigan University, Mt. Pleasant, MI 48859, USA. E-mail: kirsten.nicholson@cmich.edu

²Department of Biology, Southeastern Louisiana University, Hammond, LA 70402, USA. E-mail: bcrother@selu.edu

³Department of Biological Sciences, Auburn University, Auburn, AL, 36849, USA. E-mail: guyercr@auburn.edu

⁴Department of Biology, San Diego State University, San Diego, CA 92182, USA. E-mail: savy1@cox.net

Introduction

A recent correspondence (Poe 2013; hereafter referred to simply as ‘Poe,’ ‘he,’ or ‘his’) criticized our monographic revision of anole classification (Nicholson *et al.* 2012; hereafter referred to as ‘our’). In tone and content, Poe expresses his distress with the idea that his preferred concept of a single, large genus, containing all living members of the family Dactyloidae, might be divided into eight smaller genera. We acknowledge that science benefits from vigorous, intellectual debate, but would have preferred his commentary to be more constructive, objective, and scientifically accurate. We therefore present this rebuttal to explain how Poe erred in characterizing our work, and missed the opportunity to present an alternative comprehensive taxonomy to replace the one against which he argues so strenuously. In this contribution we explain, and correct, Poe’s errors and misrepresentations, and argue that our taxonomy is likely to be adopted because it 1) eliminates the obvious problem that will arise if the family Dactyloidae contains only a single large genus (i.e., that a single genus obscures the evolution and diversity within the group and misrepresents or cloaks it), 2) conforms with the long historical trend of dissecting large, cumbersome groups into smaller sub-units, 3) is consistent with all recent phylogenetic studies for anoles in membership within clades we recognize as genera, and 4) aids in associating these lizards with the ancient land masses that shaped their history.

Monophyly and Anole Taxonomy

One criticism of our paper appearing in Poe (2013) and Castañeda and de Queiroz (2013), is that we elevated to generic status several groups that are nonmonophyletic. This issue emerges from the very small number of species in our study with unstable relationships (= taxa changing position in trees from different analyses)—which they portray as fatal to the entire enterprise of a reclassification. We wish to point out that our original text explained the issues regarding these problematic taxa in great detail, and that these issues are—not surprisingly—related to conflicts between molecular and morphological characters. We evaluated the available data regarding these taxa, evaluated why there were inconsistencies between the resultant phylogenies, and proposed hypotheses for where we thought these taxa should be placed, both within the phylogeny, and within the classification. We did not always follow one particular analysis or dataset (i.e., only follow the molecular data or only the Bayesian analysis) because, as systematists, we are all aware that there are always shortcomings in both the data and the analyses, especially when considering large, cumbersome groups. We integrated the available information to make these predictions, and these explanations are included in the systematic section for each group. Morphological and molecular data often disagree, and investigators are left to interpret those results. Satisfyingly, these same hypotheses were also supported in the recent paper by Pyron *et al.* (2013), and we discuss some of those details further below. Vences *et al.* (2013) summarize how Linnean taxonomies have dealt with small groups of disruptive taxa, and conclude that such taxa do not force the rejection of groups that are otherwise monophyletic. For the same reason, we do not believe that the community of taxonomists will reject our classification—as Poe advocates—but instead will demand that critics—like Poe—recommend revisions for the disruptive taxa as their relationships become clearer. We could have chosen to treat these taxa as *incertae sedis*, and made our hypothesized placements as footnotes. However, the end result is the same, and highlights our point that the number of problem taxa is remarkably few.

Character Diagnoses for Clades

The diagnoses for clades are discussed in detail in our paper, yet several points made by Poe need to be clarified here. First, Poe overlooks relevant facts to make an unwarranted claim about clade diagnoses:

[pg. 296] “the diagnoses are based on a single tree from a sample of 4999 equally optimal trees. If any other tree had been chosen from this sample, the diagnoses would be different. This fact completely undermines their diagnoses. There is no point in listing detailed clade support for a single tree when there exists an additional 4998 trees that are equally well supported.”

One serious criticism raised by Poe is that our diagnoses were based on one of 4999 equally most parsimonious trees and, therefore, our proposed unambiguous character states are not known to be unambiguous in the sense of uniquely diagnosing single taxa or groups. We see no flaw in our approach for the following reasons. Consensus trees are employed to summarize information among rival phylogenetic hypotheses. In the strict consensus method, only the monophyletic clades found in all the competing hypotheses remain in the consensus tree (Schuh and Polhemus 1980; Sokal and Rohlf 1981). Thus, if Character A State 1 is an unambiguous synapomorphy for a clade inferred in one tree, and that clade is inferred in all the trees, then—by definition—Character A State 1 is a synapomorphy for that clade in every tree. We used these unambiguous synapomorphies to diagnose our genera, and find no error in having done so. We recognize that the status of a given character state can change from unambiguous to homoplastic when comparing a single tree to a strict consensus tree, but even if the status changes, the state remains diagnostic for that same clade. We quote Schuh (2000:149) to close the topic, “The true [=strict] consensus contains only those branches that unambiguously support all possible optimizations of the character data, as was pointed out by Nixon and Carpenter (1996)...Therefore, the [strict] consensus technique is the obvious preference among all techniques proposed because its results are the only ones that receive unequivocal evidential support.” Clearly, extensive conflict among characters remains within each of the eight anole genera, yielding the many equally optimal trees that we recovered. An expanded data set will be required to resolve these conflicts, but a need for additional data within each genus should not prevent us from acknowledging the clear pattern that has emerged for the basal branches used to identify those genera.

Poe takes issue with two additional points in our diagnoses. First, Poe caught a disparity between the diagnosis given by us for the *Ctenonotus distichus* species group and our definition of that group. In the diagnosis, we correctly indicated that all species have two parallel rows of mid-dorsal scales from the level of the second canthals to the nares. However, in our definition, we incorrectly listed this region as having no parallel rows. Second, Poe objects to the fact that our definition of *Dactyloa* lists all possible character states for the size of the angular processes, a detail that appropriately defines the genus for this character, and an occurrence that is common for morphological definitions of large, cumbersome groups. Contrary to Poe’s claim, we conclude that our methods and diagnoses are well within the norm of taxonomic revisions. In fact, a comparison of the characters used by Poe (2004) to diagnose the group that he calls *Anolis*, and that we diagnose as Dactyloidae, will show our uses of morphological data to be virtually identical. Given the scale of our monograph, Poe clearly had to search very hard to find these two minor errors.

Recognition of Monophyletic Groups Across Studies

Eight major clades are recovered in *all* studies that have broadly sampled anole taxa (Alföldi *et al.* 2011; Jackman *et al.* 1999; Nicholson *et al.* 2005; Poe 2004), including Pyron *et al.*s (2013) monumental reassessment of the Squamata. We classified these clades as separate genera because clade membership is so remarkably consistent among analyses, as is membership in 21 of 22 subgroups that we recognized within these genera (Figures 1–5). There are 12 species out of the 240 included in our combined molecular and morphological analysis that are unstable with respect to generic designation in our molecular-only tree, or other recent molecular-only phylogenies. Seven of these species have strong molecular support for our placement of them within the genera *Dactyloa* (*apollinaris*, *bonairensis*, *chloris*, and *peraccaae*), *Deiroptyx* (*darlingtoni* and *occulta*), and *Chamaelinorops* (*barbouri*)—we anticipate little disagreement with our placement of these species within those genera. That leaves 5 species that we placed in the genera *Anolis* (*argenteolus*, *cyanopleurus*, *lucius*, and *spectrum*) and *Chamaelinorops* (*christopheii*) that may potentially, eventually, warrant different generic assignments than those we recommended. These remarkably few unstable species are, and—as we noted—*should be*, of particular interest to everyone, for the very reason that they are unstable; clearly something very interesting is going on that should be investigated further. We expect the reassignment of some of these 5 taxa to other genera to emerge from such studies, as is typical for taxonomic schemes of large radiations (Vences *et al.* 2012).

Poe notes that node support for some of the eight major clades of anoles is weak, and concludes that more data are required to justify them. We continue to argue that the consistent recovery of eight dominant clades of anoles in multiple independent studies is sufficient justification for recognizing eight genera. In our view, the pattern is clear; the accumulation of additional data is going to recover these same eight genera. However, we also advocate expanding the database for anoles because the topology characterizing the relationships of the eight genera to each other varies markedly among studies. The fact that no single topology has emerged suggests to us that the basal radiation of anoles likely occurred over a relatively short time interval, a feature that we incorporated into our evaluation of the biogeographic history of the group.

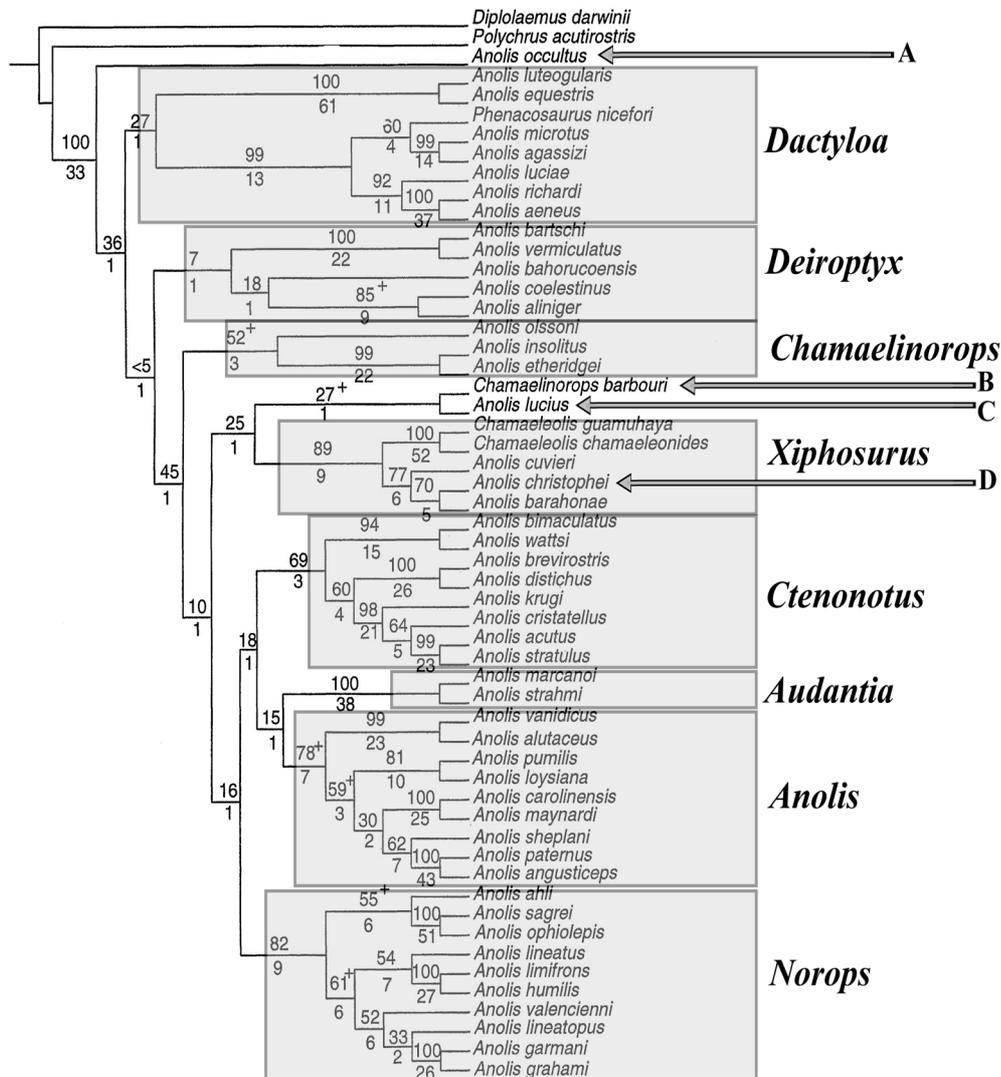
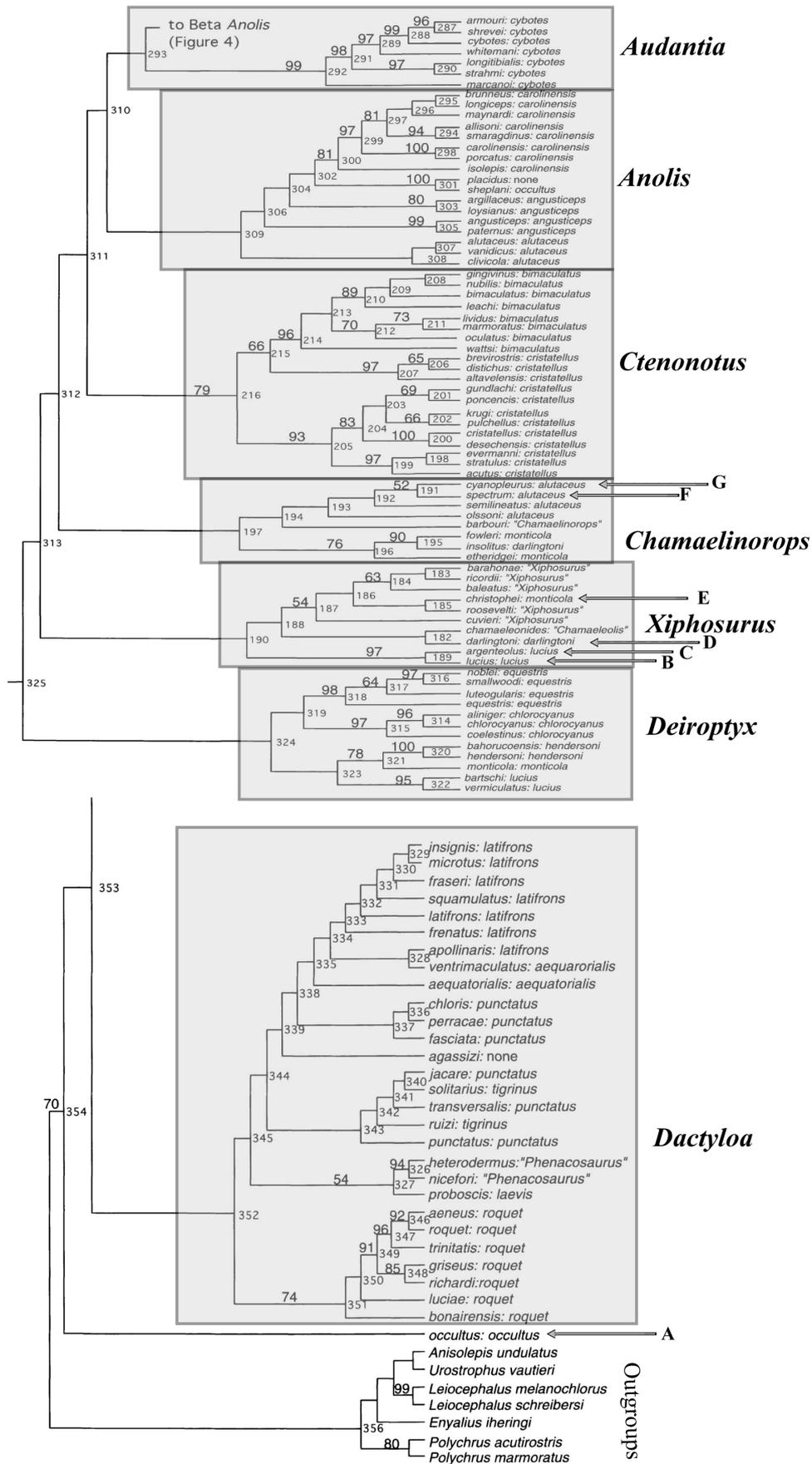


FIGURE 1. Comparison between Jackman *et al.* (1999) and Nicholson *et al.* (2012) for consistency in recognizing monophyletic groups for genera proposed by Nicholson *et al.* (2012). Figure from Jackman *et al.* (1999) used with permission. Shaded boxes show the genera proposed by Nicholson *et al.* (2012). Unless indicated (arrows point to problematic taxa), group membership is identical between the two studies. “A” (*occultus*) nested within other taxa in our (2012) genus, *Deiroptyx*, in our molecular tree, but was located at the base of our combined tree. “B” (*barbouri*) was placed within our (2012) genus *Chamaelinorops* in all analyses. “C” (*lucius*) nested within our (2012) genus, *Anolis*, in our combined tree, but nested within our genus, *Xiphosurus*, in our (2012) molecular tree. “D” (*christopheii*) nested with other taxa in our (2012) genus, *Xiphosurus*, but we provisionally placed it within our (2012) genus *Chamaelinorops* due to several compelling morphological features (see Nicholson *et al.* 2012, systematics section, for further explanation). Note placement of these problematic taxa in Figures 2, 3, 4 and 5. Notice that each genus is consistently monophyletic, with the sole exception of the few problematic taxa.



Poe also observes that 194 described taxa have never been included in any phylogenetic analysis, implying that the real list of unstable taxa must be much larger than we claim. However, 85 of these 194 species are assigned to the genus *Norops*. Because placement of a species into this genus requires the presence of a derived condition of the caudal vertebrae unique among squamates—a synapomorphy corroborated by extensive molecular data—we see no problem with concluding that those taxa were correctly assigned in our original classification. Likewise, 52 of the 194 taxa that have never been included in phylogenetic analyses are assigned to the genus *Dactyloa*. This particular radiation has recently received intensive systematic attention (Castañeda and de Queiroz 2011, 2013). We know of no case in which increased scrutiny has required a species formerly assigned to *Dactyloa* to be reassigned to some other clade. Because of this, we are confident in our assumption that all proposed members of this genus were correctly assigned in our original paper. Of the 56 species that remain, we presume Poe would prefer that we add all of these to the five unstable species. However, given that only about 2% of the 240 species analyzed so far occupy the group of unstable species, a better estimate is that only one of the 56 unassigned species is likely to be unstable in its generic placement.

The last 15 years have revolutionized the field of herpetological classification because of the fantastic rate at which novel molecular data have emerged. Hedges (2013) has observed that scientists need to be emotionally prepared for these changes, lest they suffer from “revision shock.” Within this context, our anole taxonomy is based on a relatively high proportion of all described taxa (ranked fourth of the 11 exemplars listed in Table 1). In the wake of current taxonomic revolutions, large intercontinental genera have consistently been divided into smaller monophyletic units that clarify underlying patterns of ecology, biogeography, and evolution (Table 2). These changes are clearly uncomfortable to some who have published under previous, larger, generic concepts—Poe and his supporters clearly are in this camp. To retain older generic concepts, some have attempted to create taxonomic schemes involving subgenera (e.g., Pauly *et al.* 2009) or nested indented names (Losos 2009). We find no history of the acceptance of such schemes in the herpetological literature. Instead, traditional taxonomies erected under the International Code of Zoological Nomenclature (ICZN) consistently prevail. In short, we argue that our recent contribution meets, or exceeds, current standards in the taxonomic discipline.

We are surprised at Poe’s notion that designations of genera “turn on human perception” (page 298); a key feature to his argument that—because genera are human constructs and not inherent to the natural world—retention of the previous concept of *Anolis* is preferred in order to reduce confusion. Despite a few notable exceptions (Pauly *et al.* 2009), we doubt that the community of taxonomists agrees with Poe’s characterization of the field of taxonomy. Each of the eleven exemplars of recent taxonomic change listed in Table 1 involves increasing the number of recognized genera in order to adequately characterize the diversity revealed by expanded phylogenetic information. When new monophyletic structure is revealed in groups for which such structure was previously unrecognizable, taxonomy should change to incorporate that new information. This process does reveal constructs inherent to the natural world and, therefore, forces us to change the way we train future generations of biologists, design future comparative analyses, and interpret new data. We have benefitted from this process in dealing with a skyrocketing number of genera characterizing the herpetofauna of Costa Rica (Savage and Bolaños 2009). For example, all glassfrogs from this region used to be placed in the genus *Centrolenella*, a taxonomic distinction that made identification of the group easy because the characteristics of the family simultaneously allowed identification of the genus. Taxonomic changes emerging from phylogenetic studies of this

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FIGURE 2. Comparison between Poe (2004) and Nicholson *et al.* (2012) for consistency in recognizing monophyletic groups of members for genera proposed by Nicholson *et al.* (2012). Figure from Poe (2004) used with permission. Shaded boxes show the genera proposed by Nicholson *et al.* (2012), and—unless indicated (arrows point to problematic taxa)—group membership is identical between the two studies. To conserve space, the *Norops* portion of Poe’s (2004) tree is not shown, but showed clear monophyly for the group, with no associated problematic taxa. “A” (*occultus*) nested with other taxa in our (2012) genus *Deiropyx* in our molecular tree, but diverged at its base in our combined tree. “B” (*lucius*) nested with our (2012) genus “*Anolis*” in our combined tree, but was nested with our genus “*Xiphosurus*” in our (2012) molecular tree. “C” (*argenteolus*) nested with other *Anolis* taxa in our combined tree, but nested within *Xiphosurus* in our molecular tree. “D” (*darlingtoni*) nested with our (2012) genus *Deiropyx* in our molecular tree, but lay at the base of combined tree—we elected to place it within our genus *Deiropyx* in our classification. “E” (*christopheii*) nested with other taxa in our (2012) genus *Xiphosurus*, but we tentatively placed it within our (2012) genus “*Chamaelinorops*” due to several compelling morphological features (see Nicholson *et al.* 2012, systematics section, for further explanation). “F” (*spectrum*) nested within our (2012) genus “*Chamaelinorops*” in our combined tree, but we lacked molecular data for this taxon. Given that all other *alutaceus* group species nested together, with high support, in molecular analyses, we placed this taxon within our (2012) genus *Anolis*. “G” (*cyanopleurus*) nested with our (2012) genus “*Anolis*” in all analyses. Note placement of these taxa in Figures 1, 3, 4 and 5. Notice that, in each case, each genus is monophyletic at a high level of confidence, with the sole exception of the few problematic taxa.

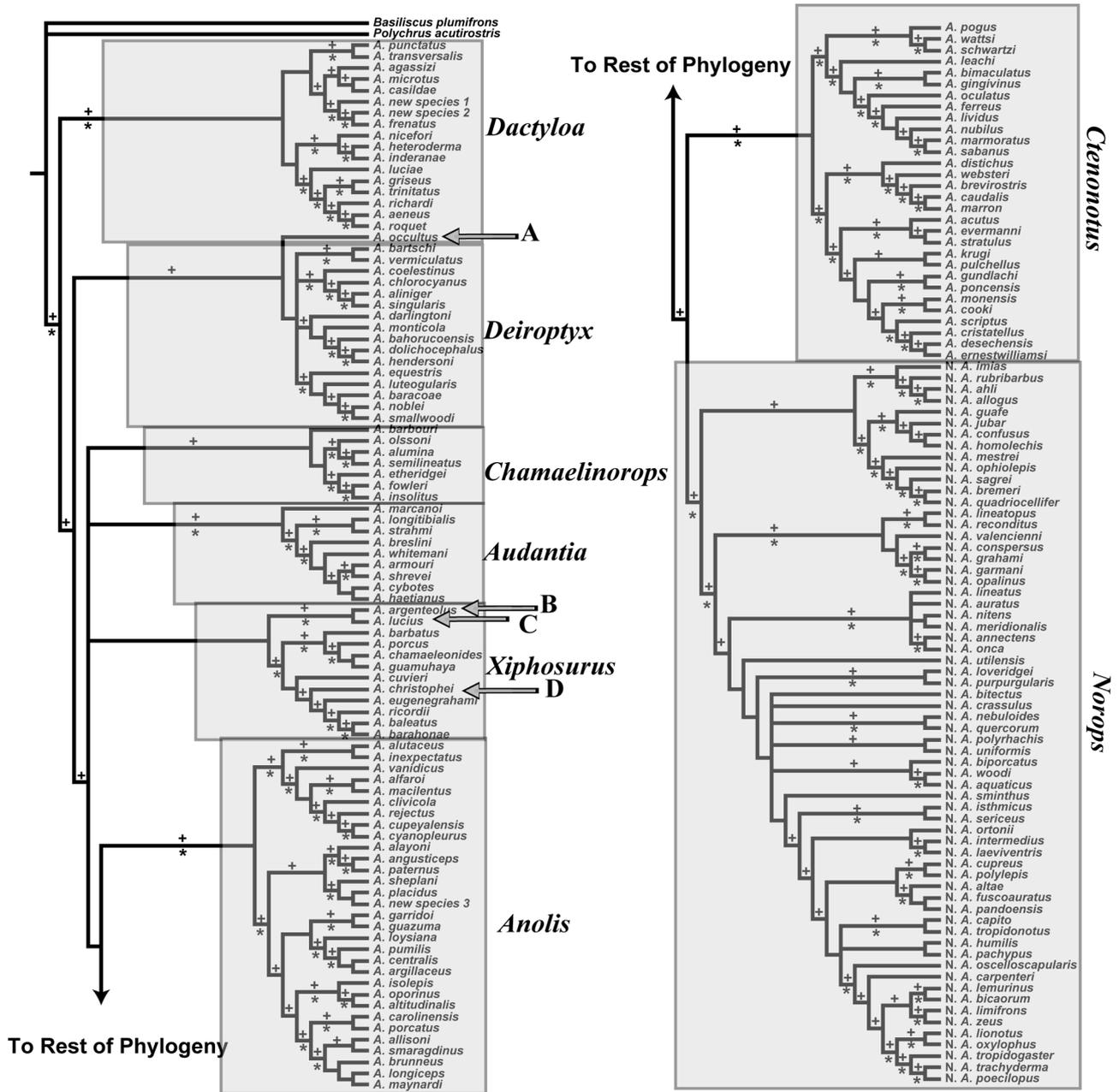


FIGURE 3. Comparison between Nicholson *et al.* (2005) and Nicholson *et al.* (2012) for consistency in recognizing monophyletic groups of members for genera proposed by Nicholson *et al.* (2012). Figures used with permission. Shaded boxes show the genera proposed by Nicholson *et al.* (2012), and—unless otherwise indicated (arrows point to problematic taxa)—group membership is identical between the two studies. “A” (*occultus*) nested with other taxa in our (2012) genus *Deiroptyx* in our molecular tree, but was located at the base of our combined tree. “B” (*argenteolus*) and “C” (*lucius*) nested with our (2012) genus *Xiphosurus* in our molecular tree but nested with our (2012) genus “*Anolis*” in our combined tree; because support was higher in our combined tree and there were several compelling morphological synapomorphies, we placed this taxon in our genus “*Anolis*.” “D” (*christopheii*) nested with other taxa in our (2012) genus “*Xiphosurus*,” but we placed it tentatively in our (2012) genus “*Chamaelinorops*” due to several compelling morphological features (see Nicholson *et al.* 2012, systematics section, for further explanation). Note placement of these taxa in Figures 1, 2, 4 and 5. Note that, in each case, each genus is clearly monophyletic, with the exception of the few problematic taxa.

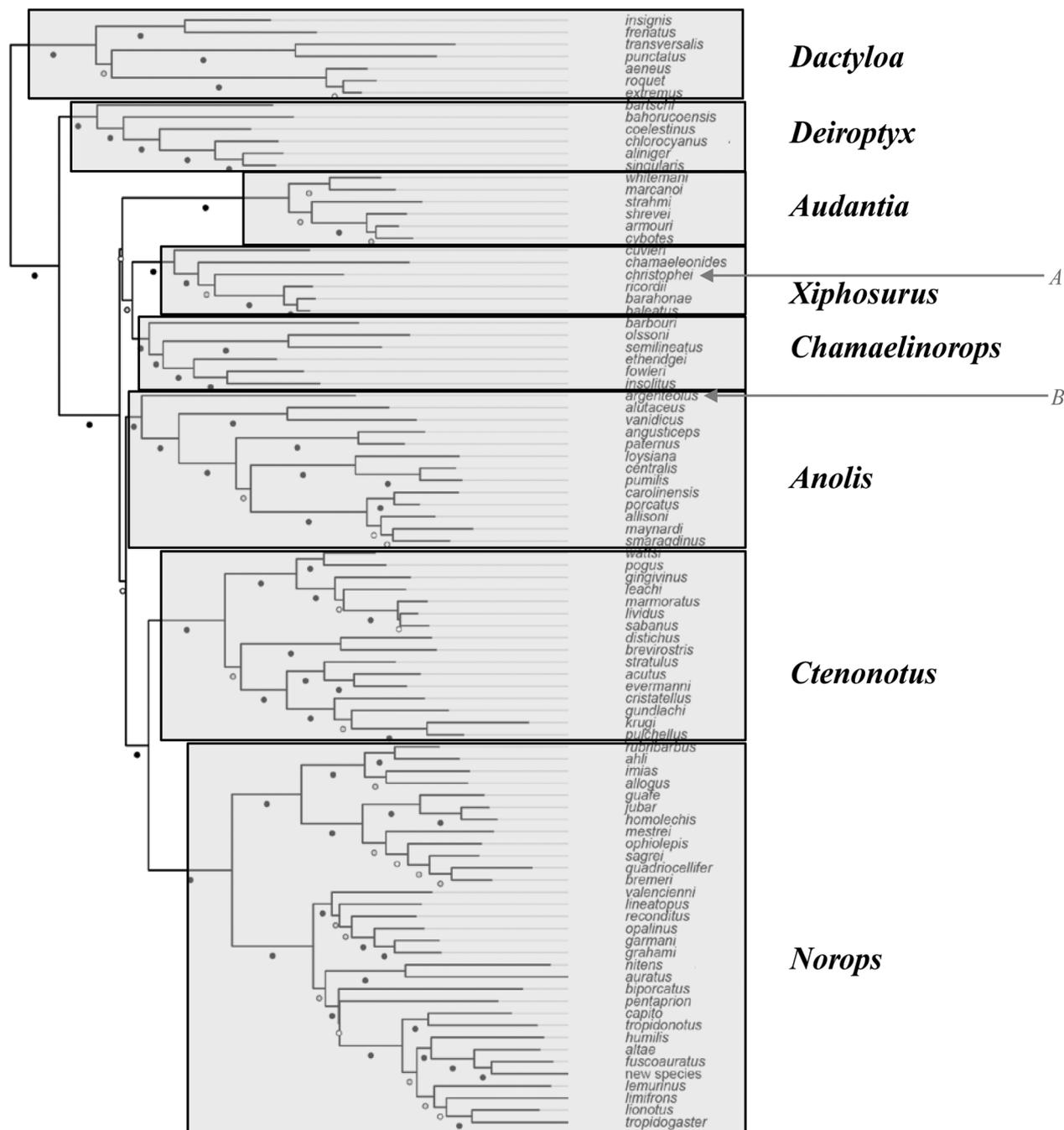


FIGURE 4. Comparison between Alföldi *et al.* (2011) and Nicholson *et al.* (2012) for consistency in recognizing monophyletic groups of members for genera proposed by Nicholson *et al.* (2012). Figure used with permission. Shaded boxes show the genera proposed by Nicholson *et al.* (2012), and—unless indicated otherwise (arrows point to problematic taxa)—group membership is identical between the two studies. “A” (*christophei*) nested with other taxa within our (2012) genus “*Xiphosurus*,” but we provisionally placed it within our (2012) genus “*Chamaelinorops*,” due to several compelling morphological features (see Nicholson *et al.* 2012, systematics section, for further explanation). “B” (*argenteolus*) nested with other “*Anolis*” taxa in our combined tree, but nested within “*Xiphosurus*” in our molecular tree. Note placement of these taxa in Figures 1, 2, 3 and 5. Notice that, in each case, each genus is monophyletic, with the exception of the few problematic taxa.

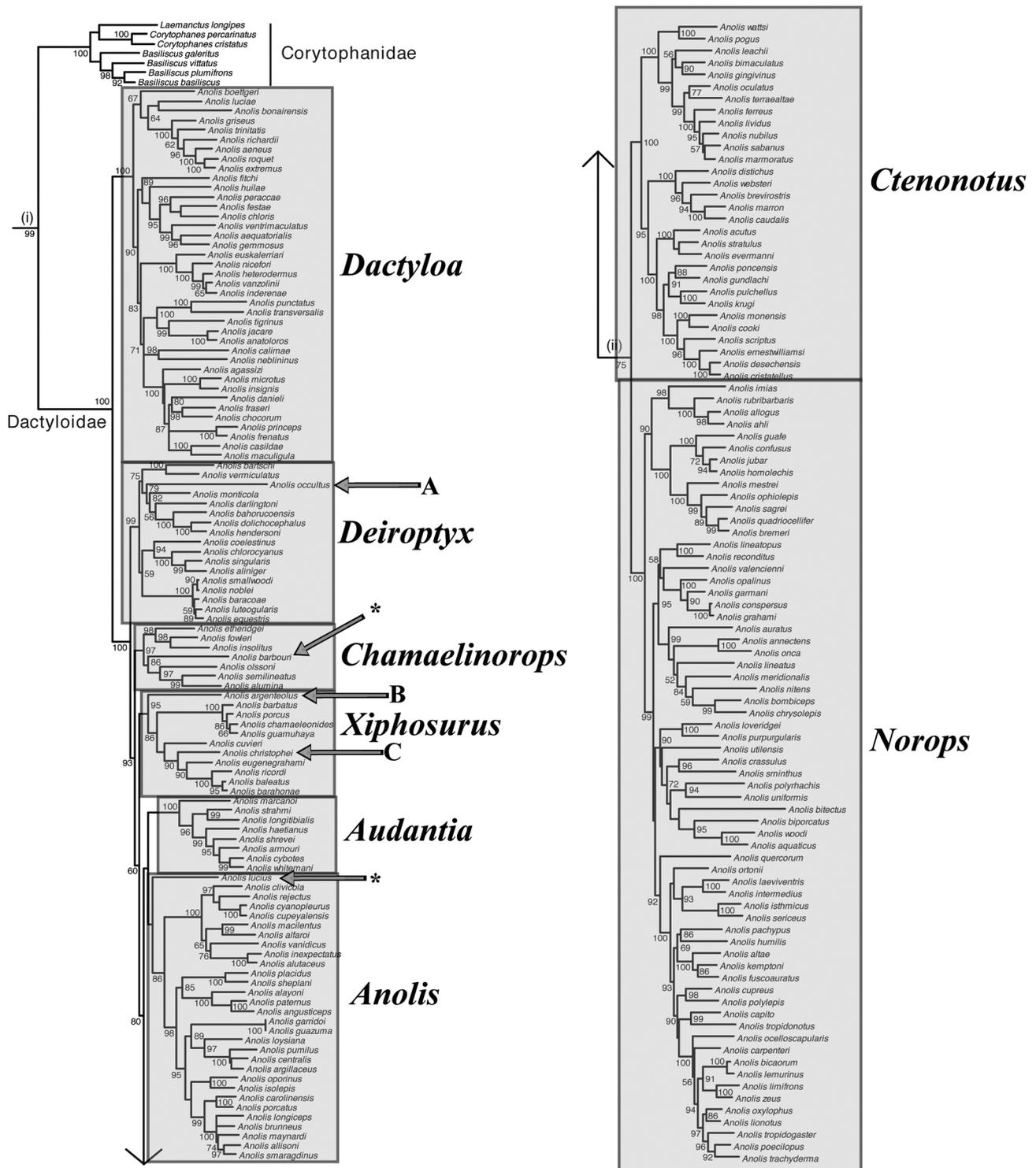


FIGURE 5. Comparison between Pyron *et al.* (2013) and Nicholson *et al.* (2012) for consistency in recognizing monophyletic groups of members for genera proposed by Nicholson *et al.* (2012). Figure used with permission. Shaded boxes show the genera proposed in Nicholson *et al.* (2012), and—unless otherwise indicated (arrows point to problematic taxa)—group membership is identical between both studies. “A” (*occultus*) nested with other taxa in our (2012) genus “*Deiroptyx*” in our molecular tree, but was located at the base of our combined tree. “B” (*argenteolus*) nested with other “*Anolis*” taxa in our combined tree, but nested within “*Xiphosurus*” in our molecular tree. “C” (*christopheii*) nested with other taxa in our (2012) genus “*Xiphosurus*,” but we provisionally placed it within our (2012) genus “*Chamaelinorops*” due to several compelling morphological features (see Nicholson *et al.* 2012, systematics section, for further explanation). Asterisks (*) indicate two taxa that moved around in other analyses but are placed within this tree consistent with our generic designations. Note placement of these taxa in Figures 1, 2, 3, and 4. Notice that each genus is monophyletic, with the exception of the few problematic taxa.

group have caused us to integrate information from osteology (humeral hooks), physiology (causes of green vs white bones), and behavior (patterns of male-male aggression; Guayasamin *et al.* 2009) in order to train students how to properly identify the five genera of glassfrogs now recognized for Costa Rica. This process enhanced our understanding of biological diversity because it forced us to look at old data in newly revealed ways. We see the revision of anole taxonomy as leading to a similar deepening of the understanding of diversity within this group. In introducing students to *Norops* from Costa Rica we have frequently been challenged by those trained in the older taxonomy for anoles. We always recommend that those challenging us read Etheridge (1967)—the seminal paper on caudal autotomy in squamates. Anyone who has caused a squamate’s tail to separate from its body, and has read Etheridge’s paper, understands immediately why we conclude that the beta condition within anoles is as important to understanding the diversity of that group as the toe lamellae of anoles is to understanding the evolution of Dactyloidae. Building on arguments first articulated by Savage and Talbot (1978), our monograph suggests that patterns of habitat use, as well as traditional morphological characters, when examined with accumulating molecular data, make distinguishing female *Audantia cybotes*, *Ctenonotus cristatellus*, and *Norops sagrei* a much less daunting task than Poe suggests.

TABLE 1. Number of sampled taxa (species or genera) and total richness for representative recent major taxonomic revisions.

Taxon	Original number of genera	Current number of genera	Number of new genera	Number of resurrected genera	Number of species sampled	Number of species classified	Species per genus	Reference (# of papers citing this reference)
Dactyloidae	1	8	0	7	189	387 (.48)	48	Nicholson <i>et al.</i> 2012
<i>Eleutherodactylus</i>	1	24	6	15	362	842 (.42)	35	Hedges <i>et al.</i> 2008 (236)
Centrolenidae	4	12	7	1	79	147 (.54)	12	Guayasamin <i>et al.</i> 2009 (75)
Dendrobatidae	7	16	4	1	156	244 (.64)	15	Grant <i>et al.</i> 2006 (329)
Hylinae	27	36	9	4	86	590 (.15)	16	Faivovich <i>et al.</i> 2005 (561)
Leptotyphlopidae	2	12	5	5	38	116 (.33)	10	Adalsteinsson <i>et al.</i> 2009 (47)
<i>Eumeces</i>	1	4	0	3	10	55 (.18)	14	Brandley <i>et al.</i> 2005 (531)
<i>Liophis</i>	1	3	1	1	5	60 (.08)	20	Zaher <i>et al.</i> 2009 (124)
Teiidae	6	13	4	3	87	138 (.63)	11	Harvey <i>et al.</i> 2012
Lacertini	3	19	9	7	56	108 (.52)	6	Arnold <i>et al.</i> 2007 (147)
<i>Mabuya</i>	1	4	0	3	21	168 (.12)	42	Mausfeld <i>et al.</i> 2002 (80)

Poe challenged us to explain why, given the many genera that might be carved out of the phylogeny of anoles, we picked only eight, and why we selected the particular eight genera that we did. This is an easy challenge to address. Our approach was made clear first in Guyer and Savage (1986). Starting with that paper and continuing with every phylogeny of anoles published since, the alpha section of Williams’ (1976) influential taxonomy has been demonstrated to be paraphyletic. In our opinion, responsible taxonomy requires revision of the alpha section into the seven monophyletic groups now known to be needed to replace it. Starting with Savage (1973), we have made clear our conclusion that the beta section of Williams (1976) deserves generic status (*Norops*); we note that no published phylogeny since then causes us to question that choice. Therefore, the seven additional genera that we propose as replacements for the alpha section represent the minimum number of genera needed to eliminate the problem of the previous taxonomy. This change is a much more important decision than Poe implies. We have noted how misinformative Williams’ (1976) taxonomy has been to those interested in evolutionary ecology (e.g. van Berkum 1986). We note that at national meetings, and in print, Poe has been remarkably unwilling to relinquish the concept of alpha anoles (see Poe 2004). We suspect his devotion to Williams (1976) prevents him from seeing value in our work in the same way that Williams (1989) was blinded in his criticism of Guyer and Savage (1986; see Guyer and Savage 1992). We are confident that those reading Nicholson *et al.*

(2012) carefully will realize that we did consider recognizing additional genera and presented reasons why we did not do so. We expect that future revisions will continue what we have begun and welcome that process because we recognize such revision will further increase the information content of anole classification within the Linnean system.

Based on what is happening to other taxa all around anoles, we think it is inevitable that Williams' (1976a, b) concept of *Anolis*, as modified and promoted by Losos (2009), will, of necessity, be broken into the smaller units that we proposed (see Vences *et al.* 2013 for support of this conclusion). We remain confident that, once this bridge has been crossed, those who have been so reluctant to accept this change will wonder why they fought so hard to avoid it. As Greene (2001) notes, “[r]ather than hindering biology, increasingly accurate and phylogenetically based taxonomy promotes the study and appreciation of life’s diversity.” We couldn’t agree more.

TABLE 2. Deep patterns of evolutionary history revealed in formerly large, intercontinental genera of amphibians and reptiles after taxonomic revision.

Intercontinental Taxon	Taxonomic Reviser	History Revealed by Revision
<i>Anolis</i>	Nicholson <i>et al.</i> 2012	Vicariant separation of South American <i>Dactyloa</i> from seven Caribbean and Central American genera; vicariant origin of Central American and Caribbean <i>Norops</i>
<i>Bufo</i>	Frost <i>et al.</i> 2006	Single origin of North American <i>Anaxyrus</i>
<i>Elaphe</i>	Utiger <i>et al.</i> 2002	Single origin of North American (<i>Pantherophis</i>)
<i>Eleutherodactylus</i>	Hedges <i>et al.</i> 2008	Dual origin of North American <i>Craugaster</i> and <i>Eleutherodactylus</i>
<i>Eumeces</i>	Schmitz <i>et al.</i> 2004/ Smith 2005	Single origin of North American <i>Plestiodon</i>
<i>Hyla</i>	Faivovich <i>et al.</i> 2005	Single origin of North American <i>Hyla</i> , with dispersal to Asia
<i>Mabuya</i>	Mausfeld <i>et al.</i> 2002	Single origin of New World <i>Mabuya</i>
<i>Natrix</i>	Rossman and Eberle 1977	Single origin of North American <i>Nerodia</i>
<i>Rana</i>	Frost <i>et al.</i> 2006	Dual origin of North American <i>Lithobates</i> and <i>Rana</i>

Literature cited

- Alföldi, J., Palma, F.D., Grabherr, M., Williams, M., Kong, L., Mauceli, E., Russell, P., Lowe, C.B., Glor, R.E., Jaffe, J.D., Ray, D.A., Boissinot, S., Shedlock, A.M., Botka, C., Castoe, T.A., Colbourne, J.K., Fujita, M.K., Moreno, R.G., ten Hallers, B.F., Haussler, D., Heger, A., Heiman, D., Janes, D.E., Johnson, J., de Jong, P.J., Koriabine, M.Y., Lara, M., Novick, P.A., Organ, C.L., Peach, S.E., Poe, S., Pollock, D.D., de Queiroz, K., Sanger, T., Searle, S., Smith, J.D., Smith, Z., Swofford, R., Turner-Maier, J., Wade, J., Young, S., Zadissa, A., Edwards, S.V., Glenn, T.C., Schenider, C.J., Losos, J.B., Lander, E.S., Breen, M., Ponting, C.P. & Lindblad-Toh, K. (2011) The genome of the green anole lizard and a comparative analysis with birds and mammals. *Nature*, 477, 587–591.
<http://dx.doi.org/10.1038/nature10390>
- Adalsteinsson, S.A., Branch, W.R., Trape, S., Vitt, L.J. & Hedges, S.B. (2009) Molecular phylogeny, classification, and biogeography of snakes of the family Leptotyphlopidae (Reptilia: Squamata). *Zootaxa*, 2244, 1–50.
- Arnold, E.N., Arribas, O. & Carranza, S. (2007) Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, 1430, 1–86.
- Brandley, M.C., Schmitz, A. & Reeder, T.W. (2005) Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincoid lizards. *Systematic Biology*, 54, 373–390.
- Castañeda, M. del R. & De Queiroz, K. (2011) Phylogenetic relationships of the *Dactyloa* clade of *Anolis* lizards based on nuclear and mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution*, 61, 784–800.
<http://dx.doi.org/10.1016/j.ympev.2011.07.004>
- Castañeda, M. del R. & De Queiroz, K. (2013) Phylogeny of the *Dactyloa* clade of *Anolis* lizards: new insights from combining morphological and molecular data. *Bulletin of the Museum of Comparative Zoology*, 160, 345–398.
<http://dx.doi.org/10.3099/0027-4100-160.7.345>
- Etheridge, R. (1967) Lizard caudal vertebrae. *Copeia*, 1967, 699–721.
- Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A. & Wheeler, W.C. (2005) Systematic review of the frog family Hyliidae, with special reference to Hyliinae: A phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, 294, 1–240.
[http://dx.doi.org/10.1206/0003-0090\(2005\)294\[0001:srotff\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2005)294[0001:srotff]2.0.co;2)
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M.,

- Donnellan, S.C., Razworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
[http://dx.doi.org/10.1206/0003-0090\(2006\)297\[0001:tato\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2006)297[0001:tato]2.0.co;2)
- Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E. & Wheeler, W.C. (2006) Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, 299, 1–262.
[http://dx.doi.org/10.1206/0003-0090\(2006\)299\[1:psodfa\]2.0.co;2](http://dx.doi.org/10.1206/0003-0090(2006)299[1:psodfa]2.0.co;2)
- Greene, H.W. (2001) Improving taxonomy for us and the other fishes. *Nature*, 411, 738.
<http://dx.doi.org/10.1038/35081294>
- Guayasamin, J.M., Castroviejo-Fisher, S., Trueb, L., Ayarzagüena, J., Rada, M. & Vilá, C. (2009) Phylogenetic systematics of glassfrogs (Amphibia: Centrolenidae) and their sister taxon *Allophryne ruthveni*. *Zootaxa*, 2100, 1–97.
- Guyer, C. & Savage, J.M. (1986–1987) Cladistic relationships among anoles (Sauria: Iguanidae). *Systematic Zoology*, 35, 509–531.
- Guyer, C. & Savage, J.M. (1992) Anole systematics revisited. *Systematic Zoology*, 41, 89–110.
- Harvey, M.B., Ugueto, G.N. & Gutberlet, Jr. R.L. (2012) Review of teiid morphology with a revised taxonomy and phylogeny of the Teiidae (Lepidosauria: Squamata). *Zootaxa*, 3459, 1–156.
- Hedges, S.B., Duellman, W.E. & Heinicke, W.P. (2008) New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737, 1–182.
- Hedges, S.B. (2013) Revision shock in taxonomy. *Zootaxa*, 3681 (3), 297–298.
<http://dx.doi.org/10.11646/zootaxa.3681.3.11>
- Jackman, T.R., Larson, A., DeQueiroz, K. & Losos, J.B. (1999) Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Systematic Biology*, 48, 254–285.
- Losos, J.B. (2009) *Lizards in an Evolutionary Tree*. University of California Press, Berkeley, 528 pp.
- Mausfeld, P., Schmitz, A., Bohme, W., Misof, B., Vrcibradic, D. & Rocha, C.F.D. (2002) Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean Archipelago of Fernando de Noronha (Brazil): Necessity of partitioning the genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). *Zoologischer Anzeiger*, 241, 281–293.
<http://dx.doi.org/10.1078/0044-5231-00081>
- Nicholson, K.E., Crother, B.I., Guyer, G. & Savage, J.M. (2012) It is time for a new classification of anoles (Squamata: Dactyloidae). *Zootaxa*, 2477, 1–108.
- Nicholson, K.E., Glor, R.E., Kolbe, J.J., Larson, A., Hedges, S.B. & Losos, J.B. (2005) Mainland colonization by island lizards. *Journal of Biogeography*, 32, 929–938.
- Pauly, G.B., Hillis, D.M. & Cannatella, D.C. (2009) Taxonomic freedom and the role of official lists of species names. *Herpetologica*, 65, 115–128.
- Nixon, K.C. & Carpenter, J.M. (1996) On consensus, collapsibility, and clade concordance. *Cladistics*, 12, 305–321.
- Poe, S. (2004) Phylogeny of anoles. *Herpetological Monographs*, 18, 37–89.
[http://dx.doi.org/10.1655/0733-1347\(2004\)018\[0037:poa\]2.0.co;2](http://dx.doi.org/10.1655/0733-1347(2004)018[0037:poa]2.0.co;2)
- Poe, S. (2013) 1986 Redux: New genera of anoles (Squamata: Dactyloidae) are unwarranted. *Zootaxa*, 3626 (2), 295–299.
<http://dx.doi.org/10.11646/zootaxa.3626.2.7>
- Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 93.
<http://dx.doi.org/10.1186/1471-2148-13-93>
- Rossman, D.R. & Eberle, W.G. (1977) Partition of the genus *Natrix* with preliminary observations on evolutionary trends in natricine snakes. *Herpetologica*, 33, 34–44.
- Savage, J.M. (1973) *A preliminary handlist of the herpetofauna of Costa Rica*. University Graphics, Los Angeles, 17 pp.
- Savage, J.M. & Bolaños, F. (2009) A checklist of the Amphibians and Reptiles of Costa Rica: Additions and nomenclatural revisions. *Zootaxa*, 2005, 1–23.
- Savage, J.M. & Talbot, J.J. (1978) The giant anoline lizards of Costa Rica and western Panama. *Copeia*, 1978, 480–492.
<http://dx.doi.org/10.2307/1443615>
- Schmitz, A., Mausfeld, P. & Embert, D. (2004) Molecular studies on the genus *Eumeces* Wiegmann, 1834: Phylogenetic relationships and taxonomic implications. *Hamadryad*, 28, 73–89.
- Schuh, R.T. (2000) *Biological Systematics: principles and applications*. Cornell University Press, Ithaca, 236 pp.
- Schuh, R.T. & Polhemus, D. (1980) Analysis of taxonomic congruence among morphological, ecological, and biogeographic data sets for the Leptopodomorpha (Hemiptera). *Systematic Zoology*, 29, 1–26.
<http://dx.doi.org/10.2307/2412623>
- Smith, H.M. (2005) Plestiodon: A replacement name for most members of the genus *Eumeces* in North America. *Journal*

of *Kansas Herpetology*, 14, 15–16.

- Sokal, R.R. & Rohlf, F.J. (1981) Taxonomic congruence in the Leptopodomorpha re-examined. *Systematic Zoology*, 30, 309–325.
<http://dx.doi.org/10.2307/2413252>
- Utiger, U., Helfenberger, N., Schatti, B., Schmidt, C., Ruf, M. & Ziswiler, V. (2002) Molecular systematics and phylogeny of Old and New World ratsnakes, *Elaphe* auct., and related genera (Reptilia, Squamata, Colubridae). *Russian Journal of Herpetology*, 9, 105–124.
- van Berkum, F.H. (1986) Evolutionary patterns of thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution*, 40, 594–604.
<http://dx.doi.org/10.2307/2408580>
- Vences, M., Guayasamin, J.M, Miralles, A. & De La Riva, I. (2013) To name or not to name: criteria to promote economy of change in Linnaean classification schemes. *Zootaxa*, 3636, 201–244.
<http://dx.doi.org/10.11646/zootaxa.3636.2.1>
- Williams, E.E. (1976a) West Indian anoles: a taxonomic and evolutionary summary 1. Introduction and a species list. *Breviora, Museum of Comparative Zoology*, 440, 1–21.
- Williams, E.E. (1976b) South American anoles: the species groups. *Papeis Avulsos Zoologia*, 29, 259–268.
- Williams, E.E. (1989) A critique of Guyer and Savage (1986): cladistic relationships among anoles (Sauria: Iguanidae): are the data available to reclassify the anoles? In: Woods, C.A. (Ed.) *Biogeography of the West Indies: Past, Present, Future*. Sandhill Crane Press, Gainesville, FL. pp. 433–477.
- Zaher, H, Grazziotin, F.G., Cadle, J.E., Murphy, R.W. & de Moura-Leite, J.C. (2009) Molecular phylogeny of advanced snakes (Serpentes: Caenophidia) with an emphasis on South American xenodontines: A revised classification and descriptions of new taxa. *Papeis Avulsos de Zoologia*, 49, 115–153.
<http://dx.doi.org/10.1590/s0031-10492009001100001>

Note added in proof

The recent analysis of several large datasets leads us now to recommend placing the species *christophe* into our genus *Xiphosurus* rather than in *Chamaelinorops* as we suggested in our 2012 paper.