



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.

(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.