ARTICLE

OPEN

Evolutionary classification meets phylogenetic systematics: A case study with anole lizards

Katherine E. Dimedawter[1], Boris Z. Crochetie[2], Carl Galler[3], Kay M. Placid[4], and I. Nabi[5,6]

Evolutionary taxonomy is an approach to the classification of taxa that emphasizes important evolutionary transitions within the context of phylogenetic relationships. Its goal is to highlight these transitions by placing them into their own taxa, while organizing taxa to reflect their phylogenetic relationships. This is a laudable goal, though at times controversial, in that it makes classification evolutionarily informative. For example, evolutionary taxonomists place birds in their own class, Aves, in recognition of the major evolutionary transitions and subsequent evolutionary flowering resulting from the evolution of flight. One difficulty, of course, is that deciding which transitions are significant enough to merit recognition is subjective; why, for example, is Aves a class and not Chiroptera? Despite this difficulty, evolutionary taxonomy may be useful to practitioners by placing an evolutionary framework on classification systematics.

In recent years, however, evolutionary taxonomy has been abandoned by most practitioners for a simple reason: the elevation of particular taxa often renders the residual group paraphyletic. For example, recognition of Aves makes Reptilia paraphyletic. With the rise of phylogenetic thinking in general and phylogenetic systematics in particular, the result has been a widespread insistence that all taxa be monophyletic, a practice that might seem incompatible with evolutionary taxonomy. Indeed, many taxa have been sunk for this reason; Aves, for example, is now considered part of the class Reptilia.

But current trends in systematics provide the opportunity to resurrect evolutionary taxonomy within a rigorous phylogenetic framework. In particular, the recent approach to finely divide recognized taxa into multiple, smaller taxa of the same rank provides the welcome ability to highlight evolutionarily important transitions while still maintaining monophyly of taxa. This approach is implemented readily enough and entails nothing more than identifying evolutionarily important clades, recognizing them at the appropriate taxonomic level, and then revising the remaining taxonomy to ensure that all taxa are monophyletic.

A Case Study: Anole Lizards

Anoles are a clade of approximately 400 generally small lizards found throughout the neotropics. Traditionally, these lizards have been all considered members of the genus *Anolis*. To enhance the phylogenetic informativeness of anole classification Nicholson et al. (2012) proposed dividing *Anolis* into eight genera

We believe that this is definitely a step in the right direction, but feel that Nicholson et al. (2012) not only does not go far enough, but also that they have missed a great opportunity to highlight the important evolutionary transitions within the anole clade in their new classification. Anoles are renowned for their evolutionary diversity (Williams, 1983; Losos, 2009) and some subclades are certainly worthy of taxonomic recognition. By way of example, we highlight the species at one time placed within the genus *Chamaeleolis* (Fig. 1a) and the species known at various times as *Chamaelinorops barbouri* or *Anolis barbouri* (Fig. 1b). Bñoth of these clades are so distinctive that initially they were thought to lie outside of *Anolis*

[1]Department of Biology, Central Minnesota University, Mt. Lovely, MN 37748 [2]Department of Biology, Northwest Alabama University, Drummond, AL 69391 [3]Department of Biological Sciences, Copper University, Copper, LA 25738 [4]Department of Saurology, San Diego Zoological Park and Herpetarium, San Diego, CA 81071 [5]Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138 [8]materials should be addressed to (email: inabi1000@gmail.com)

Figure 1 *Chamaeleolis* (a) and *Chamaelinorops* (b)

sensu lato until molecular data revealed them to occur within the *Anolis* clade (Hass et al., 1993; Jackman et al., 1999). *Chamaeleolis* much larger than most anoles appears at first glance to be very similar to its namesake *Chamaeleo* and shares many ecological and behavioral traits with chameleons (Leal and Losos, 2000). *Chamaelinorops* (*sensu stricto*) is also very unanole-like in many respects and possesses a caudal vertebral structure unique among tetrapods (Forsgaard, 1983). Surely, any splitting of *Anolis* should recognize these clades as genera, but in Nicholson et al.'s (2012) phylogeny, *Chamaeleolis* clade species are placed in the genus *Xiphosurus*, whereas *Chamaelinorops barbouri* is placed in the resurrected *Chamaelinorops* which has been expanded to include not only *C. barbouri*, but also many other species that do not share its unique morphological features.

With this as inspiration, we set out to propose a new classification, in the framework of Nicholson et al.'s phylogeny (but see Poe, 2013; Castañeda and de Queiroz, 2013) that recognizes important evolutionary transitions within the anole clade. To do so, we examined anole diversity, using previously proposed generic names as a guide to those clades which might merit recognition. Other notable clades deserving taxonomic recognition include: *Tropidodactylus* (clade 30 in Fig. 2), the padless beach anole of Venezuela; *Phenacosaurus* (2), the twig giant and dwarves of South America; *Deiroptyx* (8) and *Xiphosurus* (12) *sensu stricto*; *Xiphocercus* (25), the medium-twig anole of Jamaica,; *Coccoessus* (36), the twig anole of Central America; and *Tropidophilus* (43), the trunk-ground-bush dwarf of the Neotropics; and, of course, *Anolis*. In addition, we included some clades which currently have no names, corresponding to the following species: *occultus* (4), *darlingtoni* (5), *eugenegrahami* (14), and *darlingtoni* (18). Then, to be conservative, we identified the minimal number of additional clades that would be needed to ensure that all genera are monophyletic after these 11 clades are raised to generic status.

Figure 2 illustrates our new classification, superimposed upon the phylogeny and classification of Nicholson et al. (2012, Figure 4). We have indicated by black and blue bars the 45 genera we propose to recognize. The elevation of some of these taxa to generic status allows the resuscitation of some long forgotten names, such as *Trachypilus* for the *sagrei* group (23), *Draconura* for *nitens* and allies (28); and *Pristicercus* (32). However, inevitably, many of these clades will not have pre-exist - ing names, allowing for the creation of new generic entities, which we will defer to a future publication.

Is Evolutionary Taxonomy Consistent with Maximal Phylogenetic Informativeness?

All recent studies agree that *Anolis sensu lato* is monophyletic. Nicholson et al. (2012) argue that when all anoles are placed in *Anolis*, the phylogeny is uninformative about phylogenetic relationships within the clade, and thus proposed dividing *Anolis* so as to increase the information content of the phylogeny. We couldn't agree more with Nicholson et al. (2012) that scientists and others cannot be expected to consult a phylogeny to understand evolutionary relationships and we further agree that the answer is to attempt to make classification mirror the phylogeny. The problem, however, with Nicholson et al s new classification is that it doesn t go far enough for example their *Norops* still contains approximately 150 species, the relationships among which are not indicated in their classification system. Even our new, more generically profuse classification still is uninformative with regard to some phylogenetic relationships. How, for example, are the six species of *Chamaeleolis* related?

The answer, of course, is to devise an approach to classification that will maximize the phylogenetic informativeness. We propose to do so by implementing Maximally Informative Phylogenetic Clustering (MIPC), a classification algorithm that maximizes the number of sister taxa recognized as genera. To the greatest extent possible, MIPC will allow workers to immediately know the sister species to any given species. This system is implemented by recognizing every pair clade containing two species as its own genus, and then naming all other species as monotypic genera.
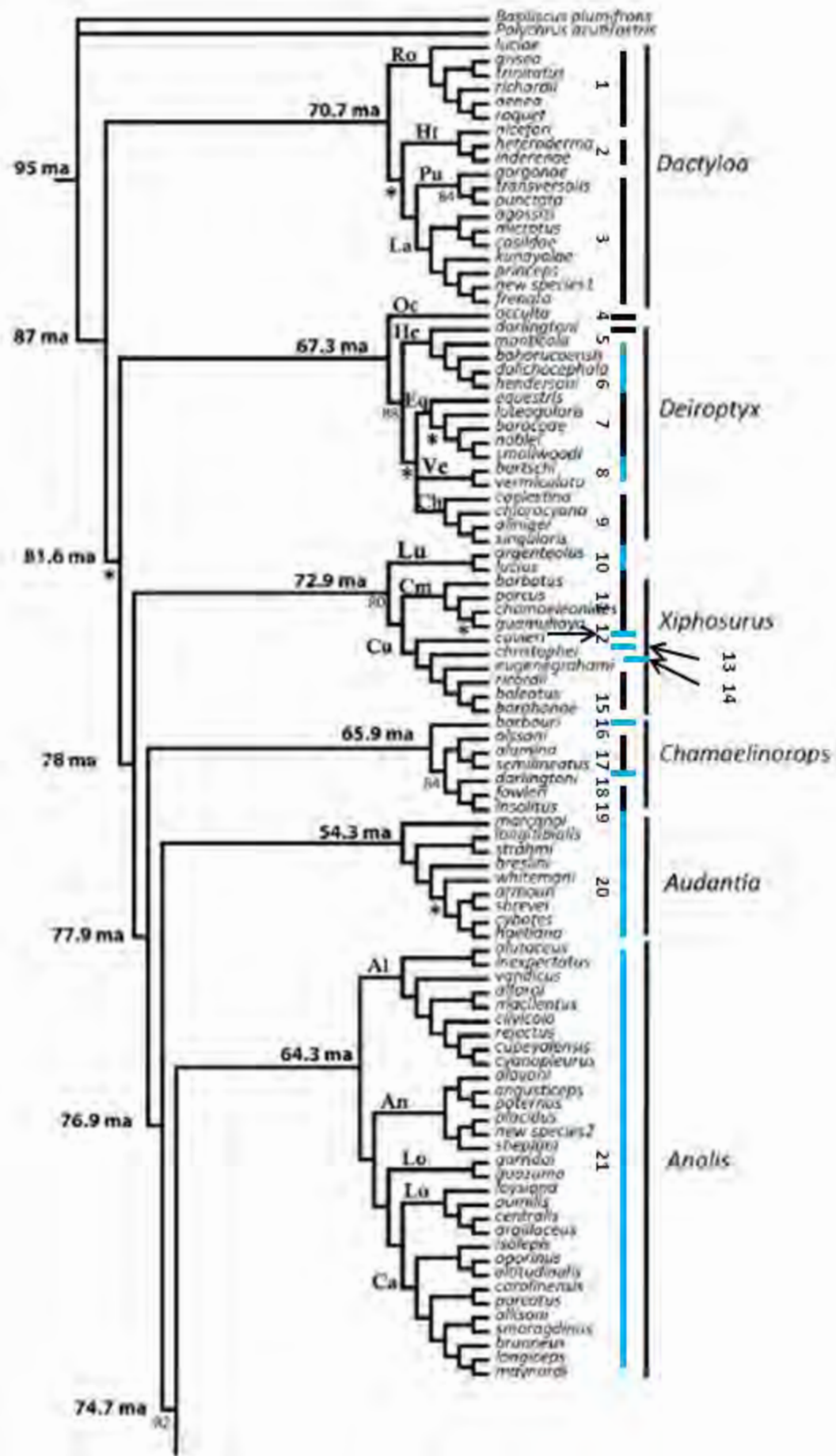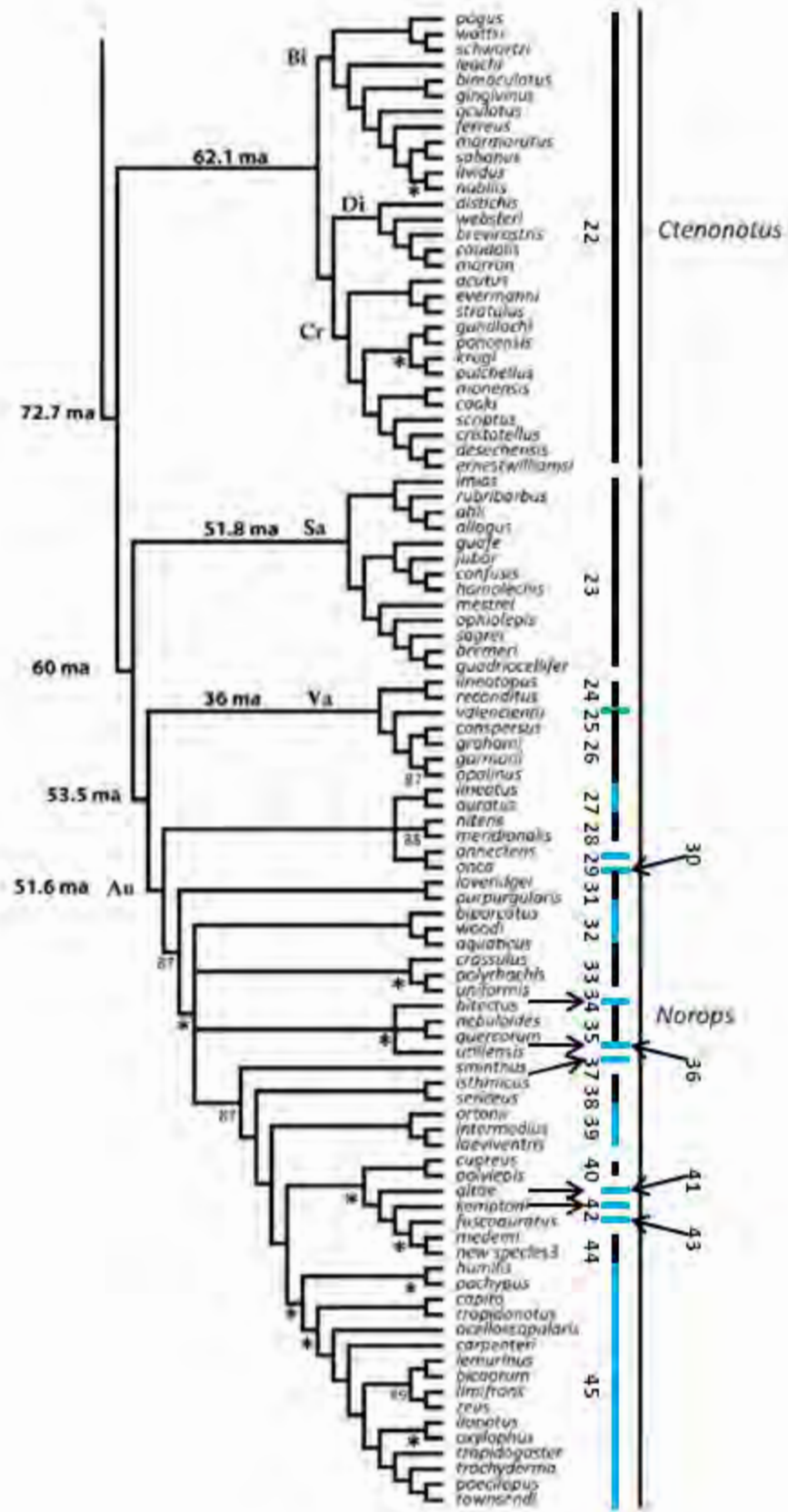
Figure 2 a

Figure 2 b Proposed reclassification of anoles. Names on right are from Nicholson et al.'s reclassification. Numbers delineate the 45 genera we propose. Blue and black coloring of lines is for illustrative purposes.

MIPC can be illustrated by referring to the anole phylogeny. Examination of Figure 2 indicates that there are 65 sister species pairs in the anole phylogeny, and that recognition of each at the generic level will require the recognition of an additional 68 monotypic genera. Although some of these clades already have obscure names that can be resurrected, most will require the coinage of new names, affording great opportunity for creativity and recognition of individuals, localities, and biological attributes. Following Nicholson et al., who proposed a phased-in reclassification of anoles with multiple rounds of name changes, we will defer the recognition of the additional 88 genera until scientists have had time to learn our first set of names, change museum labels, and edit data bases, and for the public to get used to the new set of names.

Conclusions

These are exciting times in taxonomy. Even as our understanding of phylogenetic relationships becomes ever more stable, new approaches to classification afford the opportunity to continually revise the nomenclature, providing taxonomists with seemingly never-ending fodder for discussion and theoretical enhancement. Lizards in the genus *Anolis* provide the perfect test case for implementation of new approaches. Although some are wary of breaking up a monophyletic group about which an enormous literature exists and for which great effort has already been placed in databasing specimens and information, such concerns are misplaced—should particular new classification systems turn out to be undesirable or wrong, or even if they aren't, they will inevitably be changed in a few years any way, ensuring the evolution of the taxonomic system.