Clade Biology, Phylogenetic Biology, and Systematics

Address of the Incoming BSA president Michael Donoghue, with Erika Edwards

In his incoming BSA presidential address at Botany 2021, Michael introduced the phrase "clade biology." The idea was to draw attention to an approach that the two of us have been thinking needs more attention, and which we think differs importantly from the area now widely referred to as "phylogenetic biology." How do these two differ? Clade biologists are those among us who obsess over some particular group of organisms, wanting to know as much about them as possible. They are fascinated to learn any little thing about these organisms, no matter how inconsequential this may seem to others. They tend to work on their organisms for a long time (often over an entire career), and come at them from multiple angles (functional morphology, development, ecology, biogeography, etc.). Of course, their work tends to be organized phylogenetically, and their knowledge of relationships may eventually yield species delimitations and a phylogenetic classification system, but in our view these are natural outcomes of clade biology, not its primary objectives. Clade biologists tend naturally to build teams of collaborators, drawing in other disciplines as they take deep dives into one aspect or another of the biology of their organisms. If a clade biologist has the good fortune of training students, their students might become engaged in some dimension of the research and might then take that along to their own labs, in which case teams can expand through multiple labs and academic generations. Over the years, the group of organisms might ascend to the level of a "model clade." Like model species (think *Arabidopsis thaliana*), these can then serve as vehicles for testing hypotheses of all sorts, taking full advantage of the wealth of accumulated knowledge. But in this case, they are mostly used to test hypotheses concerning patterns and processes at the level of whole clades.

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Phylogenetic biologists, in our view, take a different approach to understanding clade-level phenomena. They tend to take a hypothesis-testing approach from the outset, focusing on a particular question rather than on a particular clade, such as the evolution of dioecy or shifts in the rate of diversification. They often assemble very large phylogenetic

trees (e.g., harvesting data from sources such as GenBank), with multiple instances of dioecy, for example, scattered throughout. Alternatively, they may assemble and compare phylogenetic trees of multiple individual clades that include dioecious species. In many cases, data on the trait (or traits) under study are gathered not from nature but from surveys of the literature, or perhaps from specialized trait databases. The many other details of the organisms under study—the ones that would fascinate the clade biologist—are mostly viewed as (or assumed to be) irrelevant to the particular phenomenon under investigation. Phylogenetic biologists also have a tendency to move from one problem to another during their careers, switching from one group of organisms to another as appropriate. That is to say, they are not so deeply committed to working on one group of organisms for a long time. They collaborate with clade biologists and experts from other disciplines, as necessary, but these alliances change as they move from one suite of traits or clade to another. And, to the extent that their studies involve students, the threads that pass from one generation to the next tend to revolve around particular methodologies.

Are you a clade biologist or a phylogenetic biologist? Or course, you don't have to be either one—there are plenty of other things to be—and you could certainly be both. We have purposefully set these out as two exclusive categories, but in actuality there's a continuum between them. It's also quite possible to be a clade biologist who occasionally ventures into phylogenetic biology. We think we've done this during our own careers. It's less possible, we think, to go the other direction because, almost by definition, it's hard to dabble in clade biology, or at least to do it very effectively, without pretty complete devotion to a particular clade, or possibly a few different clades over the course of a lifetime.

Where is "systematics" in all of this? We suspect that many BSA members identify as systematists, although this may be less so among younger members—at least, in our recent experience, postdocs and graduate students don't identify as strongly with systematics as they used to. To be sure, they are happy to publish in journals with the word systematics in the title, such as *Systematic Biology,* but they don't really see themselves as systematists.

Traditional systematics doesn't map very neatly onto phylogenetic biology, as we delimit this here, although we suspect that some who identify as systematists would also consider themselves to be (at least partly) phylogenetic biologists. Systematics comes much closer, we think, to clade biology, especially in as much as training in systematics often begins with the choice of a group of organisms on which to become the world's expert. On the other hand, we suspect that our definition of clade biology will seem overly broad to many systematists in the sense that it doesn't specifically highlight species delimitation and classification, which have long been the bread and butter of systematics. In our view, species delimitation and naming are critical elements of clade biology, but our definition puts a greater emphasis on understanding the complete biology of the organisms in question (including work at the intersection of molecular biology, development, physiology, ecology, etc.), whether or not this knowledge bears very directly on species delimitation or classification (although, naturally, it very often will).

Box 1. Where does "systematics" fit in? Of these three options, we prefer number 3.

1. **Clade Biology** (= Systematic Biology)
   Phylogenetic Biology

2. **Clade Biology**
   Systematic Biology (species delimitation, classification)
   Phylogenetic Biology

3. **Systematic Biology**
   Clade Biology
   Phylogenetic Biology

If one did wish to equate systematic biology with clade biology (i.e., if these were viewed as one and the same; Box 1, option 1), which name would we chose for this field? One might argue that we don't need a new term—we should just stick with systematics for this field. On the other hand, we think that clade biology has a distinct advantage in that it refers unambiguously to the object of study: clades. In this sense it is comparable to terms such as "population biology," "cell biology," etc., where the object of study is clearly named. "Systematics" is ambiguous on this score, as "system" itself is pretty vague and all-encompassing. So, if we had to choose, we think that clade biology would be the better choice.

Another possibility would be to make a hierarchy out of these disciplines (Box 1, options 2 and 3). But does clade biology naturally encompass phylogenetic biology, or vice versa? We think not. As for "systematics," we see two possibilities. One would be to use it to signify the subdiscipline within clade biology focused squarely on species discovery and classification. Another possibility, which we prefer, would be to retain systematics for the more inclusive field that encompasses both clade biology and phylogenetic biology. In any of these cases, we want to emphasize that we see both clade biology and phylogenetic biology as totally worthwhile and necessary endeavors. There's no better or worse here—just alternative approaches to studying clade-level phenomena. Which way you lean just depends on what you find most satisfying.

Of course, it's perfectly okay to not worry at all about where you fit into this schema, and to chart your own path. And, in doing so, you might find yourself flirting with other somewhat ill-defined terms, such as "integrative biology" or "comparative biology." We won't tackle these here, except to note that integrative biology aligns pretty well in some respects with clade biology, although some who identify with this term are not so focused on individual clades. Likewise, comparative biology aligns in some respects with phylogenetic biology in our sense of the word. It's a confusing landscape of terminology, to be sure.

Our main point here is that it's worth recognizing clade biology as a distinct endeavor, with its own peculiar and enduring scientific value. To illustrate this, we'll briefly highlight the work of our recently deceased zoological colleague, David Wake.

Dave, along with his spouse and colleague, Marvalee, both of UC Berkeley, devoted their careers to understanding amphibians, but especially salamanders, and especially lungless salamanders (Plethodontidae). If you haven't followed this work, you should look into it, and you'll find one discovery after another grounded in their deep commitment to, and knowledge of, these organisms, built up over more than five decades (Griesemer, 2013). James Hanken (quoted in Sanders, 2021), long the Director of Harvard's Museum of Comparative Zoology, described Dave Wake in these words:

"He chose a particular lineage of organisms—in this case, the family Plethodontidae—and pursued it in all respects in order to understand how the group diversified and why it did the way it did. It was molecules to morphology to ecology to behavior to development, overlaid by taxonomy—his was a deliberate conviction that in order to really understand the evolution of organisms, you have to focus on a particular group and get to know it extremely well."

This captures perfectly the way that we're thinking about clade biology: complete immersion in a group of organisms, studied from every possible angle. Add to this a team-building mentality and lots of enthusiasm and you're in for a lifetime of pleasure and discovery. And the beauty of such a long-term commitment is that it leads naturally to discoveries of very broad significance. As Michael Nachman (quoted in Sanders, 2021), Director of the UC Berkeley Museum of Vertebrate Zoology, put it: "Salamanders were his love and passion, but he was really a deep thinker who used salamanders as an entry way to thinking about the biggest questions in evolutionary biology."

Clade biology, done well, starts with some organism-of-interest problem, but works its way out to questions and answers in realms that were never anticipated. Wake, for example, was at the epicenter of the formation of the field of evolutionary developmental biology, and of the study of parallel and convergent evolution, and of speciation (e.g., "ring species" in *Ensatina*). He also alerted the world to the global decline of amphibian populations. All of this flowed naturally from his deep knowledge of salamanders.

One last thought concerns the career choices faced by students and early-career scientists, who may consider a long-term commitment to a clade—with uncertain outcomes—to be too risky in this day and age. We certainly understand this worry but would offer the following advice. If you are passionate about a group of organisms, keep that passion alive even as you pursue other things that might lead to more immediate accomplishments. We think you'll find that the deep knowledge that you accumulate will provide you with a special lens through which to view biological phenomena of all sorts, and will serve as an unending source of fresh ideas. Get to know a group of organisms "extremely well," we're certain you won't regret it!

Our overall conclusion is that clade biology is a highly productive way of knowing, which provides a necessary compliment to other approaches, including what we have distinguished here as phylogenetic biology. We are confident that we won't lose this approach so long as at least some people continue to obsess over particular groups of organisms, which seems inevitable. However, what we must do is to properly value, encourage, and support this approach, and consciously improve it not just for or own happiness but for the betterment of science at large.

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