Beyond Cladistics: The Branching of a Paradigm

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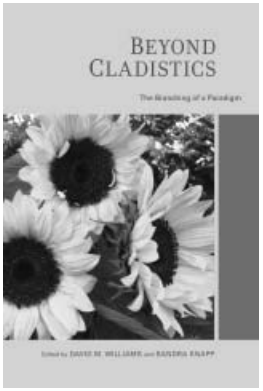
Phylogenetic Systematics by Any Other Name?

Beyond Cladistics: The Branching of a Paradigm. David M. Williams and Sandra Knapp, eds. University of California Press, 2010. 352 pp., illus. $65.00 (ISBN 9780520267725 cloth).

Cladistics is a term, like *species* or *taxon*, that seems to defy coherent definition. The difficulty is that the word invokes divergent connotations that are often at odds with characterization as a subfield of biological systematics, one that was more appropriately termed *phylogenetic systematics* by German entomologist Willi Hennig in his 1966 book of the same title. During the intervening years, phylogenetic systematics qua cladistics has morphed into a peculiar mix, often conflating phylogenetic-, species-, and intraspecific-level systematics, and in some instances, denying the primacy of evolution. This overindulgence in inclusiveness is reflected in the preface to *Beyond Cladistics: The Branching of a Paradigm*, in which editors David Williams and Sandra Knapp state that "this book represents an attempt to document the nature and anticipate the future of cladistics," and explain that their "original intention was to explore the possibilities that lie beyond cladistics, regarding cladistics as the single dominating methodology of systematics" (p. xi). The premise for this work is that it constitutes a tribute to the late Chris Humphries, prominent botanist and systematist in the Department of Botany at the Natural History Museum in London. The 15 essays in *Beyond Cladistics*, including a bibliography of Humphries' publications, are tenuously divided into four sections: "On Chris," "Botany," "Cladistics," and "Biogeography."

The five essays in part 1, "On Chris," cover a mix of topics conveying Humphries' research interests. The first essay, "Chris Humphries, cladistics, and connections" by David M. Williams, Kåre Bremer, and Sandra Knapp, gives an overview of Humphries' professional life. "Ontogeny and systematics revisited: Developmental models and model organisms" by Stephen Blackmore and Alexandra H. Wortley, provides an all-too-brief summary of pollen morphology and ontogeny in relation to plant systematics. "Rooted in cladistics: Chris Humphries, conservation—and beyond?" by Richard I. Vane-Wright recounts Humphries' use of cladistics in service of biodiversity and conservation. Vane-Wright neglects, however, to point out that like its successor, phylogenetic diversity, all of biodiversity cannot be entailed by cladograms. "Do we need to describe, name, and classify all species?" by Quentin D. Wheeler is replete with many of the standard misrepresentations of science that have become a mainstay in systematics. We're repeatedly told that systematists engage in hypothesis testing (e.g., "Every specimen collected in the future may be compared to known specimens to test and corroborate or reject its status as a species; and every newly found character, whether molecular, fossil, developmental, or morphological, is another test," p. 69). In reality, testing is virtually never accomplished, and certainly not in the naive Popperian sense that has fueled much of this rhetoric for over 30 years. In "Floras to phylogenies: Why descriptive taxonomy matters," Sarah Knapp and J. Robert Press echo many of the misconceptions in Wheeler's essay. For anyone versed in the philosophy of science, these two essays will read like a tragicomedy.



Of the three essays in part 2, "Botany," two are irrelevant to the purported cladistic intent of this volume: "Island hot spots: The challenge of climate change" by David Bramwell and "Early British collectors and observers of the Macaronesian flora: From Sloane to Darwin" by Javier Francisco-Ortega, Arnoldo Santos-Guerra, Charlie E. Jarvis, Mark A. Carine, Miguel Menezes de Sequeira, and Mike Maunder. In "Endemism and evolution of the Macaronesian flora," Mark A. Carine, Arnoldo Santos-Guerra, I. Rosana Guma, and J. Alfredo Reyes-Betancott rely on a phylogenetic analysis using internal transcribed spacer (ITS) sequence data to characterize biogeographic patterns, interisland radiations, and growth forms among endemics. Ironically, the substantive aspects of this work are focused on morphology—the very characters not used to infer the phylogenetic hypothesis: "We have not explicitly sought to optimize characters on to cladograms, so no indication of polarity is conveyed in these analyses" (p. 115). In other words, the chapter is an exercise in violating the requirement of total evidence, making the authors' conclusions irrelevant.

Systematists will only find one of the four chapters in part 3, "Cladistics," remotely interesting: Olivier Rieppel's "Monophyly and the two hierarchies." Although Rieppel examines some historical aspects regarding the notion of monophyly, the critical take-home message is that monophyly is not applicable to species: "Species cannot be monophyletic taxa; species are included in monophyletic taxa" (p. 161). I do, however, take issue with the way Rieppel arrives at his conclusion—by treating species as entities in time and space. This is a popular notion that has impeded the treatment of systematics as a scientific enterprise. The only constructive approach to species—nay, all taxa—is to acknowledge that they are inferential products—explanatory hypotheses—intended to

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causally account for select observations of organismal properties. Contrary to what Rieppel suggests, the term *species* is not just a "theoretical term," wherein "a theory gives relevant meaning to a theoretical term by conveying substantial (and reversible) empirical knowledge about the causal relations in which entities to which the term refers take part. The theory that tells us about the causal roles species engage in is evolutionary theory" (p. 161). Individual organisms, not taxa, have causal relations. We invoke a variety of theories under the rubric of evolutionary biology to infer such relations as the means to causally account for what we observe of those individuals. Those hypotheses are what we refer to as *taxa*. Recognizing the reality that all of systematics is about acquiring (usually vague) causal understanding diminishes the effectiveness of Rieppel's arguments.

Systematics cannot be reduced to mere classification. It is a field of science concerned with systematization*—the act of pursuing causal relationships per the goal of science, which is to pursue causal understanding.*

The essay "Beyond belief: The steady resurrection of phenetics" by David M. Williams, Malte C. Ebach, and Quentin D. Wheeler is one of the more peculiar installments. The authors are fearful that systematics is being distorted into phenetics. Their solution? Stave off the "artificial" relationships of phenetics by looking to eighteenth-century French botanist Augustin Pyramus de Candolle's "real" relationships. But of course, this raises the question of what one means by the term *relationship* in the contexts of science and systematics. Williams and his colleagues want to reduce relationships to instances of sameness: "Classification is meant to make sense of relationships by looking for sameness, which is observable, rather than an event, which is only partially observable. In this sense, relative relationships, in the sense of sameness…, are better ways to classify and summarize overall taxic relationships than inferring genealogies or phylogenies. An inference is purely abstract, whereas relationships are real" (p. 187). This position fails for several fundamental reasons. Relationships, whether they are based on similarity or causality, are by their very nature hypothetical constructs, because they are our inferential reactions to sensory data. Systematics cannot be reduced to mere classification. It is a field of science concerned with *systematization*—the act of pursuing causal relationships in accordance with the goal of science, which is to pursue causal understanding. It is when systematics is accurately framed in the milieu of that causal objective that phenetics, like pattern cladistics, is reduced to the arcane. The last two essays, "Monographic effects on the stratigraphic distribution of brachiopods" by Gordon B. Curry and "The eukaryote Tree of Life" by Diana Lipscomb, offer nothing germane to either this section of the book or to the topic of cladistics.

The final installment, part 4, "Biogeography," contains three essays. In "Tethys and teleosts," Peter L. Forey examines three issues regarding the utility of phylogenetic hypotheses for Cretaceous teleost fishes: filling out causal conditions implied by those trees with actual data on geological events (e.g., vicariance), determining rates of taxon evolution, and determining rates of teleost morphological evolution. Although the first issue is a reasonable action in accordance with systematics' goal of pursuing causal understanding, the remaining two are, at best, dubious. The essay "East–West continental vicariance in *Eucalyptus* subgenus *Eucalyptus*" by Pauline Y. Ladiges, Michael, J. Bayley, and Gareth J. Nelson is a study in methodological folly. Ladiges and her colleagues compiled morphological and DNA (ITS; external transcribed spacer, ETS) sequence data. Phylogenetic analyses were performed with just sequence data sets, both separate and combined. From the ITS + ETS strict consensus tree, nodes with high bootstrap support were converted to binary characters, *sensu* the supertree approach. These "characters" were added to the morphological data matrix to infer cladograms that the authors claim "contributes to the discovery of the biogeographic history of subgenus *Eucalyptus*" (p. 282). Such a claim does not hold. By their very inference (using the term loosely), supertrees are empirically vacuous constructs. Assigning any significance to them for phylogenetic or biogeographic purposes is unacceptable. In "Wallacea deconstructed," Lynne R. Parenti and Malte C. Ebach provide a solid analysis of the empirical validity of the Indo-Australian region known as Wallacea. Relying on areas of endemism, phylogenetic analyses, and area cladograms, Parenti and Ebach show that Wallacea does not form a single, natural unit, but rather spans two biogeographic areas.

Does *Beyond Cladistics* fulfill the editors' intent of documenting the nature and future of cladistics? For the most part, it falls short as a useful systematics reference. As for indicating the future, the book demonstrates that a tremendous amount of work is still required to raise systematics—phylogenetic or otherwise—to the status of a unified, scientific paradigm.

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LIVING TOGETHER: UNITING THE HOW AND THE WHY

Collective Animal Behavior. David J. T. Sumpter. Princeton University Press, 2010. 312 pp., illus. $39.50 (ISBN 9780691148434 paper).

We are social organisms, and we are always fascinated by other social creatures. Yet understanding how and why collective and social