A review of: *Foundations of Systematics and Biogeography* by Williams and Ebach

In their introductory chapter to *Foundations of Systematics and Biogeography*, Williams and Ebach suggest that, in effect, the wheels are coming off the biological systematics bus. But how can this be? Recent years have seen the rise of phylogenetics as a mainstream discipline in the broader pursuit of knowledge about evolution and, by extension, about most of the rest of biology. The ability to sequence large portions of (even entire) genomes relatively easily and inexpensively has greatly proliferated potential phylogenetic data. New algorithms, methods of analysis, and parallel processing have lent a “sophistication” to phylogenetics impossible not long ago. Phylogenies are dribbled profusely throughout mainstream literature on everything from population genetics to ecosystem science, and major programmatic efforts (e.g. NSF ATOL) are in place to once and for all take up Darwin’s challenge to establish the “Great Tree of Life”. It seems phylogenetic systematics has finally arrived!

Not so, argue Williams and Ebach. According to them, the phylogenetics currently in practice has sold out to process explanations at the expense of a more proper emphasis on patterns inherent in the “natural system.” Going further, they argue that, in fact, the bulk of current phylogenetic practice is nothing more than old-school phenetics dressed up to look fancy. Going even further, they make the case that our current approach is the incarnation of faulty arguments that go way back, at least to Haeckel. What is needed is a return to a critical and careful examination of relationships between taxa (pattern) rather than the “…origin of this or that ‘thing’” (process). It is this thesis that Williams and Ebach explore in a well-crafted and meticulously developed argument in *Foundations of Systematics and Biogeography*.

The text begins with a chapter setting the stage for the argument. The authors ask, “What is cladistics,” and begin to answer by developing their historical and theoretical perspectives on several basic, related terms and concepts. Most of the concepts here are familiar and the way the authors define them are likely to be uncontroversial. They introduce the “cladistic parameter” as a term describing the hierarchical component inherent in any method “…based on specified relationships.” It is upon this concept that much of the remaining argument is centred. Among the (potentially) more controversial concepts they introduce is the distinction between phylogenetic trees and cladograms as “radically different,” which may surprise the casually-reading “modern” phylogeneticist. Phylogenetic trees, they say, are “…based on various speculations concerning the direct ancestral-descendant relationship in an effort to produce a ‘complete’ phylogenetic tree” whereas the cladogram, “simply describes a general statement of relationship.” Regardless of your view on their argument (and this distinction appears to be the crux), one cannot avoid the conclusion that this distinction between “trees” and “cladograms” may involve some subtlety of explanation that may be difficult to impress on many of our contemporary phylogenetically-minded colleagues. Nevertheless, the pattern/process distinction is the common thread through the rest of the book.

Chapter 2 develops the idea of systematics as a discipline seeking to solve a problem, that of determining the interrelationships among organisms…no particular argument there. However, Williams and Ebach make another distinction between “problem solving” versus making “inferences”, “reconstructions”, and “estimations”, as they relate to systematics. They suggest that their approach results in “discovery” of a solution to the problem whereas other approaches instead “impose” a solution. These sorts of arguments generally fail to impress me. At the first, I am not certain that making an inference is, in fact, “imposing a solution”, but I am also not certain “discovery versus inference” is a reasonable distinction to make. From a philosophical standpoint, any human activity is replete with inference, not least the discovery of things (at the extreme—I infer the “existence of things” from sensory input interacting with my “mind”). In his *Treatise*, David Hume successfully undermined even ordinary claims to knowledge by showing the unobservability of
causality and showing that even claims to existence or fact were not rationally defensible (...I still step out of the way of oncoming traffic). However commendable I think it may be to minimize extraneous inference, I do not think it is avoidable, and is often, in fact, desirable depending on one's goals and motivations. The authors eschew "explanation" in favour of "classification", but ultimately, I think they are unrealistic about this. At a minimum, I am not convinced that having a somewhat more "transformational" view of homology imposes undue causal baggage on phylogenetic pursuits. Nevertheless, this chapter does, I think, a good job of making clear another distinction, that between "homologues" (shared parts of organisms) and "homology" (the relationships between those shared parts). This distinction of interest and well articulated and developed by Williams and Ebach, and it forms the basis for their interest in finding the basic "unit" for classification (and, interestingly, phylogeny). The characterization of this "unit" is a main goal of the next several chapters where they detail what they perceive as a continuing historical interconnection between the two central concepts of comparative biology, homologues and homology.

Chapters 3–5 are a shining example of a conceptual historical narrative. The authors begin with Goethe's Archetype in Chapter 3. They move on to Haeckel and Darwin in Chapter 4 and the beginning of the quest for ancestors. Thus also began the emphasis on paleontology as the main source of evidence for phylogeny. I was especially intrigued by the influence of the linguist Schleicher on Haeckel's ideas. Chapter 5 deals mainly with the German systematic morphologists, who sought largely to extend Owen's research within the context of phylogeny. One occasionally has to read carefully to find who are the heroes and villains in the narrative. The chapter culminates with Hennig (hero?) who, the authors contend, introduced the concept of transformation into homology. There is a very fine postscript to Chapter 5 on tests of homology sensu Patterson. This review is among the most complete on the subject.

Chapter 6 is a continuation of the historical narrative dealing with the development of Cladistics beginning with Hennig (1950, 1966) and Brundin (1966) (but not, of course, Sokal and Sneath (1963) sensu Hull, 1988; Felsenstein, 2003). The authors clearly state their aim is to clarify the history of this development in marked contrast to other, less reliable sources (specifically Hull, 1988; Felsenstein, 2003 and others). This is admirable and needed, and the authors are to be thanked for setting the record straight. Hennig's and Brundin's work met headlong with the New Synthesis crowd as well as the paleontologists, and what emerged from the resulting "cladistic revolution", they contend, were "two cladistics", "Process Cladistics" and "Pattern Cladistics". But, they conclude that process cladistics is simply a codification of the paleontological method (specifically, optimization = the progression rule).

Chapters 7–10 discuss the historical and conceptual development of homology to homologues to data matrices to transformation, all amid some historical context and a wealth of other terminology. A challenge in reading these sections is the authors' use of the term "phenetics" to refer to a particular view of character evidence rather than as a method of treating characters. As they explain, data can be phenetic, not just the commonly understood clustering algorithm. This seems to reflect their view that the standard application of parsimony to a matrix, or any other application that uses a matrix of data including the coding of plesiomorphies as information, necessarily uses plesiomorphies as grouping information and is, thus, phenetic. Their main argument from this viewpoint appears to be that plesiomorphies contain no information of use to an understanding of relationships and that construction of a typical matrix (e.g. with character states coded as alternatives 0 and 1) abuses this logic. This is the crescendo of their argument that the pursuit of relationships should rely on information that is applicable to a particular level in the hierarchy. Relationships should be based on "positive occurrences only", and negative occurrences (i.e. plesiomorphy) do not contain information about relationships.

Once they establish this view, Chapters 11 and 12 are then used to explain how to deal with the realities of data analysis (e.g. character conflict). They return to the idea that, ultimately, "homology = taxon" within the context of the cladistic parameter. I like this articulation. That taxa are characters clarifies greatly the human understanding of the diversity of life. If living things all looked the same, there would be nothing to talk about. Chapter 12 culminates in the development of three-item analysis as the method of choice for getting at the relationships the authors seek. This method, in fact, codes plesiomorphy as inapplicable and, so, succeeds in defining the data more precisely than other "phenetic" methods in terms of relationship, at least according to Williams and Ebach. It does, however, require the determination of the derived state a priori, which, they say, can be done using the outgroup method. As one who was carefully trained that polarity is (only) the result of rooting an unrooted tree, my gut reaction is to balk at this. But also as a morphologist who regularly (ahem!) polarizes characters a priori in his mind, I am sympathetic to this clearly Hennigian viewpoint.

The final chapter reviews biogeography in a historical and conceptual perspective. This biological discipline is closely tied to systematics and has a close associated history. They contend that the process arguments underlying "vicariance versus dispersal" is a distraction from what we really seek, which is "unification of classification and explanation,"...pattern, again.
The book is well-written, heavily footnoted, and well-figured (though some of these could have been reproduced more clearly). There are quite a number of errors in wording, syntax, and numbering of figures and tables that I am hesitant to even mention for fear someone will be as critical of the errors in my own works. Nevertheless, these are numerous and rise to the point of being distracting.

There is much that can be gained by reading this book. I suspect that many in the readership of Cladistics will be highly sympathetic to the appeal to emphasize patterns of relationships rather than the processes that underlie them, and students will find cogent arguments for doing so (much needed today). The contention regarding character states and their information content relative to grouping (i.e. what information do the 0's actually contain in my matrix) is an unsettled argument that needs to be investigated further. The advocacy of three-item analysis could spur discussion about methods for dealing with relationship “discovery” and character distributions more effectively. But I think the greatest strength, by far, of this volume is the incredible mastery of the historical context for the conceptual framework of systematics. I learned (and relearned) a great deal of information. Many of my non-taxonomic colleagues (including those with a phylogenetic bent) have little or no appreciation for historical literature (does literature exist more than 5 years ago, except, of course, for Darwin?). Fortunately, in empirical taxonomy we are at least aware that scientists went before us and are not dismissive when Williams and Ebach refer to “recent”(!) publications from the late 1980s and early 1990s.

As I read this book, I tried to think how I will be making some of my arguments with colleagues, most of whom (including me, apparently) have intellectual commitments to the modern “phenetics” derided by Williams and Ebach. As a pragmatist, I am not so concerned for me, but my students will need to be taken seriously by the greater community as they seek jobs and grants in these difficult times. Many of Williams’ and Ebach’s arguments, however well justified, seem reactionary, or, at least, will probably be interpreted as so. Are we shaping up for a new revolution in systematics? Maybe...I hope so. In the meantime, as I monitor the “underground”, I suspect I will continue teaching within the current consensus. There are other battles that may be more pressing (barcoding and the PhyloCode, to name a couple). Systematics has weathered a lot of change, and historical trends suggest it will continue to develop. But perhaps for the time being we will simply have to take the bad with the Goethe.

References


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