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Foundations of Systematics and Biogeography.—David M. Williams and Malte C. Ebach, 2008. New York: Springer Science and Business Media. xvii+309 pp. ISBN 978-0-387-72728-8. \$79.95 (Hardcover).

This is a book worth pondering. Its authors begin by suggesting that, in recent years, systematic biology has gone wildly astray: “Today phylogenetic studies are struggling under the weight of their own ingenuity . . . there are now methods dealing with too many data, not enough data, data of the wrong kind, data of the right kind, taxa of the wrong kind, taxa of the right kind, too many trees, not enough trees, trees of the wrong sort, trees of the right sort, no trees at all, *ad nauseam*.” In their view, 40 years of work on statistical, model-based approaches has been (to recall Herb Ross’s sentiments on phenetics) “an excursion into futility.” They cite Felsenstein’s *Inferring Phylogenies* as a good example, noting that he provides no basis whatever for preferring any one of the multitude of methods he discusses over the others. A cynic, observing that acolytes of these approaches seldom (if ever) actually apply the same methods in any 2 consecutive studies, might suspect that in reality those investigators simply keep applying different methods to their data set until they manage to find one which produces results that are not so utterly implausible as to be unpublishable.

Williams and Ebach argue instead for a homology-based approach to systematics and biogeography. They characterize their views as “an amalgamation of the works of several 18th, 19th- and 20th-century comparative biologists, notably Johann Wolfgang von Goethe, Louis Agassiz, Geoffroy St. Hilaire, Richard Owen, Adolf Naef, Rainer Zangerl, and Gareth Nelson.” As such, parts of the book provide a scholarly (but lively) introduction to a largely European, pre-Hennigian literature that is poorly known to most English-speaking systematists (the bibliography alone runs to 43 pages of small print!). Still, Williams and Ebach look to the fu-

ture as much as the past, arguing that it is the concept of relationship, rather than similarity or genealogical hypotheses of descent, that forms the core of comparative biology.

The first 2 chapters set the background of the cladistic revolution of the 1960s and 1970s, but they conclude that we still have no answer to the question: “Is there a ‘unit’ of classification or a ‘unit’ of phylogeny, derivable from our understanding of homologues (the parts of organisms) and, ultimately, of homology (their relationship)?” To frame their answer, they spend 3 chapters examining relevant ideas about archetypes from the writings of Goethe, Haeckel, Heinrich Bronn, the linguist August Schleicher, Spemann, Naef, and other early workers, tracking similarities to, and differences from, the more recent views on homology expressed by Patterson, Rieppel, De Pinna, and others.

Chapter 6 is called “Pattern Cladistics” and avowedly attempts to present a more accurate history of those disputes that can be found, for example, in David Hull’s *Science as a Process*. As an eminent diatom specialist based at the Natural History Museum in London, Williams is well placed to offer a valuable slant on the early development of cladistics, the contributions of Stensiö and Brundin, and especially on “The London Reaction: A Salmon, a Lungfish, a Cow, and the Vertebrate Paleontologists.” Again, these controversies are placed in a historical context, as clashes between a largely Anglo-American paleontological tradition (with roots traced to Haeckel) and the “Stockholm school” (with roots traced to Haeckel’s opponents, particularly Naef). Concluding from these historical analyses that “Cladistics—if not all of systematics—depends almost exclusively on homology,” Williams and Ebach proceed to consider homology and analogy as explicated by Owen, Remane’s criteria for homology, and homologs in phenetics. Here the reader will need to adapt to their use of the term “phenetics”; in their view, after going almost extinct in the 1970s, phenetics “has now reached

something of a crescendo in the early 21st century—albeit disguised as ‘phylogenetics.’” Although they admit that phenetics usually refers just to clustering by overall similarity, they “depart from that convention and discuss the subject in terms of characters, the evidence, rather than the method.” In their view, data (and not just analyses) can be phenetic, and (in particular) “today’s data matrices, regardless of interpretation, include entries that are simply similarities—data that eschew *any* notion of homology (as relationship), beyond the idea that the concept must have some kind of similarity component.”

They contrast this modern (if surprisingly atheoretical) approach with the search for natural systems via discussions of 19th-century British workers such as MacLeay, Westwood, and Strickland. Another chapter considers transformation (both phylogenetic and ontogenetic) in this context. Chapters 11 and 12, on character conflict and the analyses of relationships, present the crux of their views on “phenetic data.” They point out that methods like parsimony and compatibility can be applied to any character matrix, regardless of whether the entries are regarded as expressions of homology and synapomorphy, so they see no necessary connection between any such methods and Hennig’s synapomorphy schemes. These sections contain some minor errors that may distract the reader: they begin by discussing a matrix (Tables 11.2–11.5) at some length, but the first mention of the matrix erroneously refers to Figure 11.2 (a cladogram) rather than Table 11.2; the references to characters 10–12 on pages 190 and 191 should all read 9–12 instead; and the discussion of the “weight of evidence” therefore gives the groups CD(AB) and D(C(AB)) values of 4 and 8 when those numbers should be 5 and 9, respectively.

The examples nevertheless convey effectively the authors’ views that conventional algorithms merely impose solutions rather than discover actual solutions to the problems presented by apparent character conflict. They pursue instead component analyses, using as an example a putative homology found in taxa C and D but not in A or B, where the component is thus CD, indicating that C and D are more closely related to each other than to A or B, implying perhaps “AB(CD),” or “A(CD) and B(CD),” or even “A(CD) and/or B(CD).” Their point is that “only” the CD part should be considered significant: “Otherwise, the data really imply [AB][CD], as in phenetic characters.” This, of course, leads into discussions of Assumptions 1 and 2, and of 3-item approaches, both in systematics and in biogeography, which they think may “improve understanding of relationships.”

What is the take-home message? Imagine, for example, that taxon C is a jumping spider, D is a crab spider, A is a fruit fly, B is an earthworm, and the character is spinnerets, found only in C and D (and a Hennigian synapomorphy for spiders). The absence of spinnerets in A, or in B, tells us one thing, and one thing only: that A, or B, are not spiders. Any algorithm that presumes otherwise does so at its own peril, and that

peril is readily identifiable (a potentially artifactual result). So the use of the term “phenetic data” by Williams and Ebach may not be as outlandish as it might seem at first glance—conventional algorithms may try to generate grouping information from the shared absence of spinnerets whenever they can, even though the user of the algorithm may have intended no such claims, and only a pheneticist would actually advocate them. In other words, the information provided by spinnerets in taxa A–D is really “– – 1 1” rather than “0 0 1 1.” Hennigian synapomorphies apply at only one level of the hierarchy and are simply inapplicable and irrelevant at all other levels. Conventional algorithms may also fail to handle inapplicables properly (i.e., they are not the same as missing data, as they cannot be interpreted as potential 0s or 1s), but that is a separate issue.

If I understand their argument correctly, the implication is that multistate characters are by definition phenetic, at least to the extent that they are unordered (i.e., do not contain enough homology/synapomorphy hypotheses to be representable instead by a unique set of additive binary characters). They discuss as an example lizard scales and bird feathers, arguing that if we propose “that feathers relate to lizard scales . . . we might discover two taxa, birds (with feathers) and birds + lizards (lizard scales + feathers).” They argue that, at least in the 4-taxon plus outgroup example they discuss, if we do not know “which—feathers or lizard scales—is the subset, the homology relative to the set lizard scales plus feathers,” then the data, although representing real observations, are uninformative unless they are analyzed by a 3-item approach “relating positive occurrences only.”

Perhaps the most telling of their examples is in Table 12.1, which shows, for some simple 4-, 5-, and 6-taxon examples, differences in the numbers of different cladograms produced by Hennig86, NONA (with and without ambiguous optimizations), compatibility methods, and what the authors regard as “the ‘correct’ solution (equivalent to the ‘Assumption 2’ solution in biogeography).” They suggest that: “Such situations help to focus on exactly what data do support nodes in the resulting trees. An appreciation of how three-item analysis deals with increasing resolution with increasing data points again to its greater precision.”

Their conclusions, in any case, are stark: “an exploration of systematic data, as opposed to the creation of a multitude of models, is a more productive way of determining taxon relationships.” They pursue that argument through a final chapter on biogeographic relationships as well, again via a spirited discussion of the early history of the field that leads on to modern considerations of area homology, defining biotic areas and interpreting area monophyly. In a brief epilogue, they discuss conceptual transformation, concluding (like Gary Nelson) that model-based systematics represents a revival of the paleontological approaches of the past and a reversion to phenetics rather than the triumph of cladistics.

Regardless of whether one agrees, Williams and Ebach have produced a book from which almost all of us can learn things we did not know about the history and practice of our field. It should be especially useful for students, who may even discover that there is more to systematics than just choosing a model, running some

software, and varying its parameters until the results seem at least vaguely palatable.

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