

Invertebrate Relationships.—P. Willmer. 1990. Cambridge University Press, Cambridge, 400 pp. \$22.95 (paper).

“There is no doubt that cladistic analyses of the whole of invertebrate phylogeny would be greatly welcomed in some quarters. It should therefore be made quite clear at the outset that this book is *not* attempting to fulfil that role.” (*italics original*).

With this salutation, Willmer describes the central theme and methodological bent of her work, *Invertebrate Relationships*, and for the next 359 pages we are treated to convergence narratives, appeals to the functional integrity of ancestors, and denigrations of “rigorous” methods of phylogenetic research. She has achieved her goal handsomely.

Invertebrate Relationships is a bad book and not even the illustrations, which are the crudest line drawings, salvage a purpose for this work. Specific systematic methodology is almost entirely absent and the default reason for the similarity of traits is not history but convergence. In fact, almost every attribute which might be used to support the common history of organisms is said to have had multiple origins. This may well be true, but in absence of evidence to the contrary this can hardly be assumed.

Willmer rejects cladistic analysis for several reasons. She states that “cladistic treatises are generally rather unreadable for the non-specialists.” They are also undesirable because “more informal language and arguments are needed.” The desire to remove scientific gobbledegook is certainly understandable, but there are cases when specific concepts require specific terminology. At any rate, this seems a poor reason to reject a methodology. The criticism of cladistic unreadability is irrelevant; just because the material is difficult does not justify its rejection.

These two criticisms aside, Willmer states that there are two cladistic credos which are “‘inappropriate’ to invertebrate systematics.” These are the avoidance of adaptationist arguments as “story telling” and the assumption that minimization arguments are correct—in that convergence cannot be said to have occurred unless it has been conclusively proven. Willmer seems to think that one can “know” in an absolute sense whether a character has single or multiple origins. Simply because a character “could” arise multiply, does not mean that it has. Basing phylogenetic hypotheses on the plausibility of convergence stories is a dangerous thing. Strangely though, this skepticism does not lead her to question the monophyly of the phyla themselves when she states that the phylum “is probably the most satisfactory taxon after the species.”

Willmer’s second criticism of cladistics—that it assumes that minimization arguments are true—betrays a basic misunderstanding of cladistic thought and the concept of parsimony. Cladists do not believe that most parsimonious hypotheses of relationship are necessarily true, just that they are best supported. A hypothesis

which explains the distribution of a character with a single origin is better supported than another which requires several, in that fewer evolutionary events are required to match the arrangement of taxa. This does not mean that the single origin hypothesis is true, it may well not be, but if you can explain a character distribution with a single change you have no right to propose several.

The fact that cladists do not assume that minimization equals truth is shown in almost every analysis. Unless the data are entirely consistent, some characters will have multiple origins on the most parsimonious cladogram. On other topologies, these same characters would have arisen only once. According to Willmer, this would present a dilemma, because several topologies would be assumed to be true. There is, of course, no dilemma because the arrangement which is most parsimonious overall is the best supported—truth has nothing to do with it.

One result of this world view is that Willmer is exceptionally reluctant to grant monophyletic origin to any grouping of taxa. She states herself that the book is biased towards polyphyly, and that it is. Throughout the entire work appeals are made to functional arguments in the spirit of Manton's work on arthropods. It seems that any number of characters which support a sister group relationship can be overthrown by appeals to the functional integrity of ancestors. The prime example of this is, of course, the case for arthropod monophyly.

Willmer cites sixteen synapomorphies which unite Arthropoda, yet only one (based on developmental fate maps of Anderson) to break up the group. This weight of evidence is overthrown in favor of a polyphyletic origin based on Manton's work in which she states that the method of biting in arthropods is entirely too dissimilar to allow any intermediate to function. On this basis Manton (and Willmer) dismiss the evidence for monophyly. The type of argument involved in stating that these transformations are impossible is really the same as that which asserts similarity as convergence *a priori*. In both cases, appeals are made to knowledge which can only come from phylogeny. More specifically, these statements are the conclusions of phylogenetic analyses, not their origins.

Willmer's overall phylogenetic conclusion is succinctly stated, "With convergence so very prevalent, any attempt to impose a hierarchy of such features and achieve a higher level cladistic type of classification for all these groups would be utterly artificial, if not impossible." However, she never attempts to do this to see if, in fact, it is impossible to discern hierarchy from this supposed jumble of character dissonance.

An analysis of the characters presented in the figures and text present a quite different picture. I was able to extract 55 characters for the 36 "phyla" discussed. Although there was a great deal of missing data, the most parsimonious arrangement of these taxa found by Farris's Hennig86 (see Fitzhugh, K., 1989, J. New York Entomol. Soc. 97:234–241 for review of this program) under the mh* bb* option did contain much structure (Fig. 1). There were over 1,700 equally parsimonious trees found (there were more but my computer overflowed at 1,723 trees) with a length of 113 steps, a consistency index of 52%, and a retention index of 72%. The figure shows the Nelson (strict) consensus of these topologies.

Clearly, there is a great lack of resolution, but approximately one third of the resolvable groups are supported. Additionally, the amount of noise in the data, as shown by the consistency index, is not overwhelming. Many useful analyses have

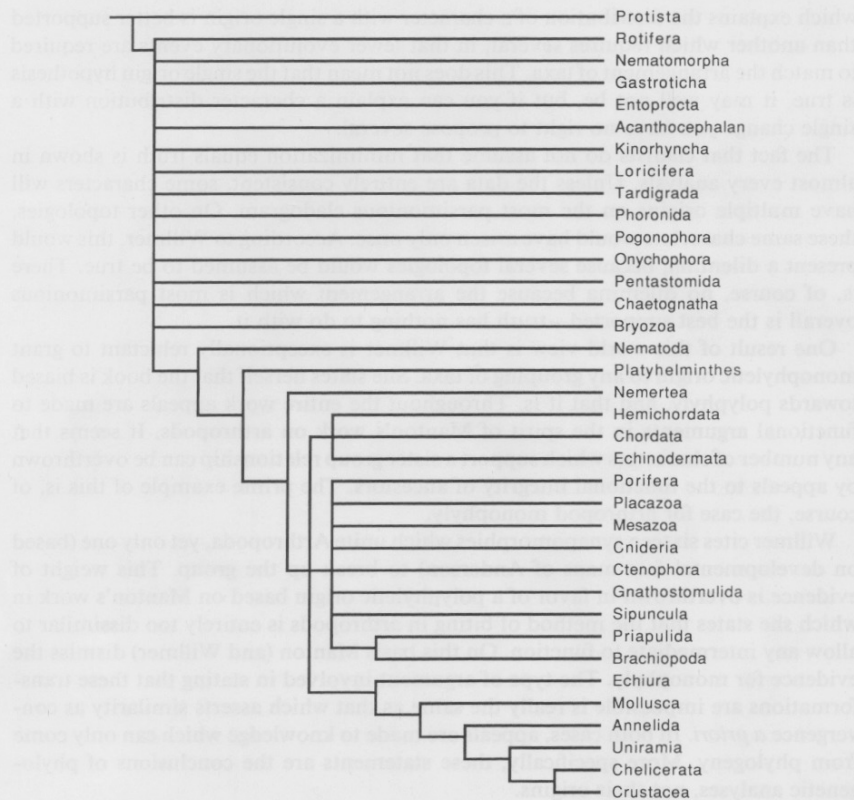


Fig. 1. Reanalysis of Willmer's data, based on 55 characters and using the Hennig86 program. This tree represents a strict consensus cladogram (see text).

much more homoplasy. Some of these groupings seem bizarre, but the point is not that these relationships are "true," but that they are supported by the data as they exist. This is certainly more informative than the analysis of *Invertebrate Relationships*, which is based on "supra-specific ancestors, paraphyletic groups, multiple non-dichotomous branchings, and adaptationist 'story-telling' arguments" (p. 14).—Ward Wheeler, Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

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Ecology and Natural History of Tropical Bees.—David W. Roubik. 1989. Cambridge University Press. x + 514 pp. \$69.50 hardcover.

Anyone with even a glimmer of interest in natural history should find it easy to appreciate the beauty and fascination of bees. To begin with, they are aesthetically appealing. One need not be an entomologist to notice the close association of bees with flowers. Most of us probably learned in elementary school, or perhaps a little later when first exposed to that venerable old analogy for sexual reproduction, that the colors, shapes, and aromas that we find so pleasing in flowers owe their origins to complex interactions that these flowers have with bees (and other pollinators). Furthermore, bees are elegant and beautiful creatures in their own right, some sporting brilliant metallic hues as gaudy as anything in the animal kingdom, others more subtly clothed in elegant plumose vestiture. As with any area of natural history, an interest first sparked by simple aesthetic delight grows deeper and more captivating as one attempts to find explanations for the bewildering diversity of bees.

Consequently, it is rather puzzling that the English-speaking world has so few books dealing in a general way with the natural history of bees other than honey bees and bumblebees (not that there is anything wrong with these two genera, but they are just the tip of the iceberg). Anyone able to read German can enjoy the products of a long tradition of lovingly detailed, beautifully illustrated treatises on the biology of all the bees of central Europe. However, in America there is one publication from the Agricultural Experiment Station of Oregon State University (Stephen et al., 1969), which you will be lucky to find in your library, and Michener's (1974) widely-cited and influential text, which deals only with social bees. So far as I know, even the English, with their unequalled passion for natural history, have been woefully remiss in producing good general books on the natural history and ecology of bees.

Perhaps the editors of the Cambridge Tropical Biology Series sensed this crying need for a book on bees. Or perhaps they were seduced not by the intrinsic appeal of bees themselves, but by the rich and complex interactions between bees and angiosperms. (Complex interactions are an irresistible magnet for tropical biologists.) Whatever the motivation for commissioning a book about the ecology of tropical bees, an obvious choice for the author was David Roubik, who has more than a decade of research experience specifically with tropical bees.

The book that Dr. Roubik has produced is ambitious and comprehensive in scope. After a short introductory chapter that crudely sketches the classification, phylogeny, and geographic distribution of bees and outlines the basic life histories of solitary and social forms, he launches into detailed discussions of foraging behavior and pollination biology, nesting behavior and reproductive biology, and community ecology. No previous author has attempted to synthesize such a broad range of topics for bees. The chapter on foraging and pollination catalogs the types of resources gathered by bees and how they are collected, follows this with theoretical and empirical discussions of foraging ecology, and concludes with a section on pollination ecology that considers the interactions between bees and flowering plants. The next chapter deals with nesting and reproductive biology. It summarizes the wide variety

of nest architectures employed by bees, along with the array of natural enemies and associates that are drawn to these nests. The final section in this chapter discusses mate selection, larval development and nutrition, modes of reproduction in solitary and social bees, and some general aspects of population genetics in bees. The book's final chapter covers several topics in community ecology, including bee seasonality, abundance, and flower preference, ecological (as opposed to historical) biogeography of bees, and the roles of bees in communities.

A major challenge for any author trying to write about a group of organisms as diverse as bees is that he or she cannot possibly avoid discussing many organisms that will be unfamiliar to most of his or her readers. Illustrations are the traditional method for dealing with this problem, and carefully selected illustrations can be extremely effective. In addition to the many graphs and tables that are such an essential (and rarely appreciated) feature of communication among scientists, Roubik's book is filled with numerous excellent drawings and photographs that should help any reader visualize bees as living organisms. The book also contains a unique appendix of black-and-white photographs of museum specimens of tropical bees, which provides a direct visual impression of bee diversity.

Ideally, a general book such as this, which summarizes and synthesizes such a wide range of information, would also be written in a lucid and engaging style that would capture the interest and excite the imagination of any ecologist or evolutionary biologist who picks it up. I found the book to be a disappointment in this respect. I was repeatedly frustrated when the author was discussing an intriguing topic in evolutionary biology, but I lost track of the logic of his argument in a dense thicket of misplaced modifiers within sentences, unrelated sentences within paragraphs, and paragraphs with no obvious relevance to the chapter heading under which they were placed. Perhaps a more patient or persistent reader will not find this as troublesome as I did, and perhaps he or she will discover important new ideas and insights about evolutionary biology where I did not. In any case, Roubik's book is a valuable and unique compendium of information about bees in general, and tropical bees in particular.—*Byron Alexander, Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas 66045.*

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