The Cladistic Perspective

Phylogenetics. The Theory and Practice of Phylogenetic Systematics. E. O. WILEY. Wiley-Interscience, New York, 1981. xvi, 440 pp., illus. $37.50.

Systematics has had a long and tortuous history. The early period, through the 19th century, was dominated by the search for patterns in organic diversity, with little attention paid to causation. As Darwin's general explanatory theory began to unfold and Mendelian genetics was discovered, the emphasis shifted to the underlying evolutionary processes. That change was responsible for sharply dividing the field into taxonomy and evolutionary systematics, with the latter reaching its zenith in the New Systematics of the 1940's and the neo-Darwinian synthesis of Dobzhansky, Mayr, and Simpson. Preoccupation with genetic mechanisms became so great in the course of the new synthesis that both geographical and historical patterns were claimed to be discoverable only through estimates of genetic similarity. Such a narrow perspective is illustrated today by molecular systematists who argue the importance of molecular data on the grounds of their being "closer to the genes."

The last 20 to 30 years have seen two groups of systematists, pheneticists and cladists, attack the conceptual and methodological weaknesses of evolutionary systematics that pertain to the discovery of historical patterns. The contributions of pheneticists, whose principal concern is operationalism, seem to have been minimal, whereas the cladistic, or phylogenetic, school continues to grow and to be influential. As evidence of this, one need only glance through a journal like *Systematic Zoology* or scan a book like E. O. Wiley's *Phylogenetics*. In my opinion, Wiley's book, although of an introductory nature, is the best single source with which to measure the extent and importance of the revolution that cladists have brought to systematics. It is a reasonably complete description of the goals, assumptions, and methods of cladistics, and the far-reaching nature of its perspective is well illustrated with a variety of animal and plant examples. Wiley clearly states the differences between the three contesting schools, and he evaluates their merits without the acrimony that has sometimes been found in the primary literature.

Wiley begins with a statement of goals and a brief explanation of phylogenetic relationships and the general reference classification, and he summarizes the major tenets of phylogenetic systematics: that patterns of similarity among organisms are due to genealogy; that genealogy can be deduced from certain characteristics of the organisms; and that the best general classification is genealogical. The brief section on philosophy and systematics provides an important perspective for many of the concepts and methodologies treated in later chapters. However, I believe the more advanced student will be disappointed with the treatment of simplicity (the principle of parsimony). The identification of natural groups, diagnostic efficiency, informativeness, severity of testing, avoidance of authoritarianism and a priorism, and avoidance of the impasse created by contradictory evidence are all topics that could have been discussed. It is also at a philosophical level that I believe Wiley makes his biggest mistake, namely claiming that phylogenetic hypotheses are rigorously tested (falsified) with the discovery of incongruent characters.

The second chapter, on species and speciation, clearly documents why phylogenetic systematics is more than the handmaiden of evolutionary systematics. Wiley correctly notes that species, as recognized by most taxonomists, are not necessarily natural, monophyletic groups, and he advocates the evolutionary (Simpsonian), rather than the biological, species concept. Whereas asexual species fit the evolutionary species concept, the biological species concept does not apply to them. Wiley demonstrates that hybridization and introgression depend on phylogenetic position and that the ability to breed successfully is, potentially, a plesiomorphic (primitive) character. He concludes that this ability does not necessarily denote a close phylogenetic relationship. Wiley denounces the successional, paleospecies concept because its application is arbitrary; in fact, the fewer the data the easier the decision. One of the most important features of this chapter is the careful way in which the assumptions and predictions of each of the different models of speciation are examined to see what historical patterns each might generate. I am sure many will disagree with one aspect or another of this chapter, but I believe all will commend the author for a thought-provoking treatment of species and speciation.

It is in the third chapter, on supraspecific taxa, that the major differences between the three schools of systematics are introduced. Wiley argues that higher taxa must be justified by characters (synapomorphies) that demonstrate their status as natural groups. He then goes on to make the point that paraphyletic and polyphyletic groupings are classes, and, as such, are not natural because they cannot be defined in terms of natural processes. Wiley also illustrates the difficulty with using overall similarity, whether phenetic or genetic. Such a measure of similarity cannot discriminate true group characters (synapomorphies) from other characters.

Chapter 4 is largely devoted to making clear the distinction between cladograms and phylogenetic trees. In particular, one must remember that the number of species-level taxa determines the number of possible phylogenetic hypotheses that have to be considered. Wiley also discusses why the outgroup criterion and the distinction between plesiomorphy and apomorphy are so important in phylogenetic inference. The best fit to data (most parsimonious solution) is provided within the context of the higher-level phylogeny when that criterion is used.

Wiley's fifth chapter, on characters and reconstruction of phylogenies, has several shortcomings. His definition of a character ignores independence. The choice among alternative phylogenetic hypotheses rests on weight of evidence, and I see this as related to the number of independent characters involved. For example, character-state correlation due to pleiotropy can bias one's choice of a phylogenetic hypothesis. Also, contrary to Wiley's claim, I believe he does not illustrate the independence of the ontogenetic criterion for estimating primitiveness. All of his arguments and examples seem to reduce to using an outgroup at some level. The description of the Wagner Tree algorithm is disappointing in several regards. The procedure, as presented, is inefficient (that is, hypothetical common ancestors identical to real taxa are recognized, so that unnecessary intervals are added), there is no mention of how to break ties, and the important routine of tree optimization is not discussed, although it is alluded to elsewhere in the book. On the more positive side, Wiley correctly illustrates many of the problems associated with compatibility algorithms. In terms of veracity, compatibility can be no better than the Wagner algorithm, and it is often going to be worse. As convergence and parallelism increase in the data set, compatibility will explain fewer of the data because it will ignore synapomorphies.

The sixth chapter, on the phylogenetic approach to classification, is excellent. Wiley updates his recently published conventions and rules for an annotated Linnaean system of classification. Unfortunately, his description and example of how to include anagenetic data are difficult to understand because of an incompletely and incorrectly labeled table 6.1 and figure 6.13. I might add that typographical errors are common throughout the book, and careful editing must accompany a second printing.

Wiley treats the alternatives to the phylogenetic system of classification in the next chapter. I agree with him that the fundamental difference remaining between evolutionary systematists and cladists reduces to whether or not paraphyletic groups are recognized. No one has yet identified the discordance between genealogy and genetic similarity that might justify the recognition of paraphyletic groups, and the continued adherence to such unnatural assemblages seems to stem from evolutionary systematists' treatment of higher taxa as artificial entities, their assumption that higher taxa originate from supraspecific taxa of equal or lower rank, and their assumption that lower taxa develop into higher taxa sometime after the origin of the stem species of those higher taxa. Wiley refutes on logical and empirical grounds the pheneticists' assertion that their classifications based on overall similarity are the most stable and natural.

Wiley reviews the relationship between phylogenetic systematics and biogeography in chapter 8. He suggests that primary causal agents for present disjunct distributions must be sought in vicariance events, rather than dispersal. The simplest argument for doing so is that all organisms seem capable of some dispersal, and, in being able to explain any conceivable distribution, dispersal can really explain nothing. Unfortunately, vicariance biogeography is of limited application at this time because there are too few well-corroborated cladograms for a variety of organisms living in a given general region.

The concluding chapters, on specimens and curation, characters and quantitative character analysis, and publication and rules of nomenclature, may seem out of place to more advanced students of systematics. However, I would like to point out that the new systematist, for whom this book is intended, should be apprised of all matters relevant to the discipline. What could be more important than the characters that provide the basic evidence for historical relationships, the care of the specimens that provide those data, and the publication effort itself? Except for some disjointedness in the text of these chapters, Wiley is to be commended for attempting a complete book on phylogenetic systematics.

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Transposons

Movable Genetic Elements. Papers from a symposium, Cold Spring Harbor, N.Y., 1980. Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y., 1981. In two volumes. xxxvi, 1026 pp., illus. $130. Cold Spring Harbor Symposia on Quantitative Biology, vol. 45.

Although chromosomes usually contain stable linear arrays of genes, exceptions to the rules of stability have been known for a long time. Barbara McClintock's genetic crosses in maize provided the first well-studied example of "movable genetic elements." In the late 1960's Shapiro and Starlinger found elements in *Escherichia coli* that caused pleiotropic mutations when inserted within genes.

During the past decade, the development of new technologies to study DNA structure has led to the discovery of movable elements in prokaryotes, eukaryotes, and their viruses. These two volumes present the most up-to-date and comprehensive collection of papers available on the subject. A comparison of this book with a previous compilation of papers (*DNA Insertion Elements, Plasmids, and Episomes*, Bukhari, Shapiro, and Adhya, Eds., Cold Spring Harbor Laboratory, 1977) reveals the rapidity with which this field has expanded during the past few years.

Summarizing the contents of these two volumes in a review is impossible owing to the number (115) of papers included. Two papers are worthy of special mention. The introduction by Allan Campbell puts in perspective our understanding of "movable genetic elements" and DNA rearrangements and its implications for our understanding of the evolution and regulation of gene expression and development. Michael Yarmolinsky's superb summary complements the introduction and serves as a guide to the reading of some of the papers in the book.

The first volume of the book presents detailed genetic and physical analyses of the structure and function of movable genetic elements (transposons) in bacteria. Several papers delineate both host and transposon-coded factors required for the transposition process. The mechanism of transposition is analyzed in depth in two systems: bacteriophage mu and Tn3.

The second volume provides a picture of how widespread these elements are. Papers dealing with their presence in yeast, plants, and *Drosophila* are included. Especially exciting is a group of papers on the structure of integrated retroviruses and the discovery of the structural similarities of such retroviruses and bacterial transposable elements. One section in this volume, although not dealing with movable elements, includes papers on the organization and structure of some eukaryotic genes: globins, collagen, yeast invertases, and histones. This is followed by a comprehensive group of papers on the involvement of controlled DNA rearrangements in the expression of immunoglobulins, antigenic variation in trypanosomes, and mating-type switching in yeast.

The significance of movable genetic elements and DNA rearrangements is just now emerging. By themselves, the elements are able to regulate gene expression in a wide variety of ways. By flanking specific genes, they are able to disseminate antibiotic resistance in bacteria and to determine host specificity and phase variation. Moreover, in the developmental systems that have been examined at the molecular level, for example, immunoglobulins and *Drosophila* homeotic mutants, developmental changes are associated with DNA rearrangements.

Several papers in the book point to the importance of the ends of transposons in the transposition process. It is now clear that there are similarities in structure at the ends of both prokaryotic and eukaryotic transposons that suggest a generality in the mechanism of transposition. In some systems that involve just inversions of the movable sequences, such as the invertons controlling flagellar antigen variation in *Salmonella* and host range specificity in bacteriophages mu and P1, the specific recombination systems are even interchangeable. In spite of these similarities, a single molecular model of transposition cannot explain the wide variety of DNA rearrangements described.