A Botanical Classification

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adaptation to the environments of Madagascar but largely established before any of their ancestors arrived on the island. His reasons for thinking this stem from his commitment to the "New York cladism" school of phylogenetic reconstruction. Even nonsystematists who have sniffed the fumes of emotion rising from the term "cladism" in the pages of *Science*, or who followed last year's debate in *Nature* over whether cladism is a Marxist plot to grab control of the British Museum's dinosaur exhibit, will have surmised that systematics is currently racked by a doctrinal controversy. This controversy was originally simply over Hennig's contention that classification should be isomorphic with phylogeny. However, the more refined cladists of today have converted Hennig's scheme into a system of principled refusals to look at certain kinds of evidence—geography, stratigraphy, immunology, parallel evolution—in deciphering evolutionary relationships. Adopting these principles, Tattersall concludes from various dental characteristics that the living sportive lemur (*Lepilemur*) of Madagascar is the phylogenetic sister of *Notharctus*, a North American Eocene fossil. No matter that Tattersall's phylogeny implies six or more different waves of lemur immigration into Madagascar, or that his scheme pushes the divergence of the living lemurs back to a time at least 55 million years ago, before the appearance of the earliest known uncontested primates: these problems are not taken very seriously because, in Tattersall's words, "Neither time nor geography has any *necessary* connection with evolutionary relationship." True; but neither do premolar molarization, size of the metastylid, or the other minor (and probably convergent) dental features Tattersall points to in justifying the idiosyncracies of his phylogeny.

Tattersall's phylogenetic machinations, and some related dismissals and omissions of contrary evidence, constitute the only serious flaws in an otherwise authoritative book. But he is so undogmatic and conciliatory about his evolutionary diagrams, and so willing to admit the justice of the opposition's case, that knowledgeable readers will be less outraged than noncladists usually get when they read current cladistic systematics. Traditional systematists will also be gratified to find that Tattersall has returned to the fold on the classificatory issues that spawned cladistic systematics in the first place. "The fatal practical problem with phylogenetic classifications," he writes, "is that they require a potential reordering whenever a new taxon (these days, mostly fossil) is included in the group . . . and a classification changing with every twist in phylogenetic thought, superior though it may be intrinsically, is unfortunately impractical. In any event, there exist far better and simpler ways of expressing phylogeny than through classification." Amen, brother.

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The Monocotyledons. A Comparative Study. ROLF M. T. DAHLGREN and H. TREVOR CLIFFORD. Academic Press, New York, 1982. xiv, 378 pp., illus. $98.50. Botanical Systematics, vol. 2.

Rolf Dahlgren of Copenhagen published a classification of the angiosperms in 1975 and has since developed a distinctive approach to higher-level taxonomy, focusing directly on the distribution of character states. Dahlgren has been working for several years with the Australian botanist Trevor Clifford, a numerical pheneticist and student of the monocotyledons. The book that has resulted from their collaboration is a remarkable compilation of information about the characters of the monocots and a revised classification of the group. It is a reference work that will be of great value to monocot systematists and to angiosperm phylogenists generally. However, in my opinion, there are several fundamental problems with the treatment that render it less useful than it might have been—problems that, unfortunately, characterize most recent efforts to assess relationships among angiosperm families and orders.

Dahlgren and Clifford set out "to investigate the monocotyledons with respect to a wide range of characters and to determine the distribution of these over the whole group" (p. 1). Indeed, 240 pages of the text are devoted to a survey of about 100 characters, including some that are seldom considered, such as root hair development, the host specificity of fungi and insects, and a wide variety of chemical features. Most of the data were assembled from previous literature, but some new information is presented and several sections were contributed by specialists. For each character the authors briefly describe the variation among monocots and often among several groups of presumably related dicotyledons. Character states are generally illustrated with line drawings compiled from a variety of sources. The character discussions also include speculations about function and adaptive significance.

My main criticism of the character treatments is that often the authors have not been sufficiently concerned with homology, a word they seldom use and never define. Clearly homology is difficult to assess and even very similar structures may turn out not to be homologous. However, treating obviously dissimilar conditions as single character states (considering bamboos, palms, and century plants to have the "tree and shrub habit") is apt to lead to confusion in phylogenetic analysis.

The taxonomic distribution of each character state is plotted on a diagram in which orders are depicted as bubbles that are supposed to represent transections through the branches of an imaginary phylogenetic tree. In fact, the bubbles are arrayed so as to indicate overall similarity rather than to specify cladistic relationships. Although it seems useful to superimpose character states on the Dahlgren classification, this unfortunately allows preconceptions of relationship to color the interpretation of the taxonomic significance of the characters. "Good characters," indicators of true relationship, are the ones whose state distributions correspond to the preconceptions of relatedness embodied in the diagram. Conversely, "bad characters" are those that do not conform. In this way the system is continually reinforced by the data rather than tested by them. Thus, it is hardly surprising when the authors conclude that "the supposition on the outset of this study that the Ariflorae are closely connected with the Alismatiflorae has been supported and strengthened in the course of the study" (p. 324). Characters with state distributions that support this preconception are positively weighted even when a state is not unique to the two groups (as in the case of basifixed anthers), and even when only a few members of one or both groups have the state (as in the case of intravaginal squamules). Similar state distributions involving orders or superorders that the authors think are not closely related are usually considered of little taxonomic importance (for example, poricidal anthers).

Following the character survey, the authors relate the character information to the classification used throughout the survey, and this results in a somewhat modified classification. At the outset of the evaluation section (p. 286) the authors explain that they "estimate the

affinities between groups by using numerous characters in combination" but that since "not all characters are of equal importance" the data were not subjected to "formal numerical analysis." Beyond this there is little mention of general goals, principles, and procedures. There is no discussion of their character weighting procedure, or of the terms "natural group" (often used) or "monophyly" (seldom used). Although the authors seem to recognize (p. 333) the importance of determining which character states are ancestral and which derived, they rarely attempt to do so, and then without appeal to any criterion. No mention is made, for example, of outgroup comparison.

In the absence of any explicit logic it is fortunate that the evaluation sections have a standard format that facilitates an understanding of the approach. Pairwise comparisons are made between selected groups, with similarities and differences listed without regard for polarity. Each such comparison ends with an opinion on whether the similarities outweigh the differences or vice versa, and hence whether the groups are closely or distantly related. These opinions are difficult to evaluate, especially as it is unclear what evidence would compel the authors to reject their views.

In the final sections Dahlgren and Clifford try to determine which group of dicots is most like the hypothetical ancestors of the monocots. They conclude that the similarities between the Magnoliiflorae and some Liliiflorae indicate true relationship and that similarities between the Piperales and Ariflorae and between the Nymphaeales and Alismatiflorae are convergences. Their argument rests on an assumption that they never discuss, namely that the monocots are monophyletic. Perhaps their story is substantially correct, but in this case, as throughout the text, theirs is a plausibility argument that depends heavily on opinions about the weight of the character evidence and takes for granted the monophyly of groups.

Dahlgren and Clifford began their study with a preconception of higher-level relationships (their classification) and evaluated the character data accordingly. This approach seems backwards. It would be better, I think, to begin with lower-level hypotheses about monophyly and homology and then use specified principles to transform these data into a hypothesis of higher-level relationships. One wonders what picture of monocot phylogeny would emerge if "established groups" were abandoned and if the logic of phylogenetic systematics were rigorously applied. In this regard the authors' postscript is promising. Even though they think that "little is added by Hennig's concepts to the classical cladistic methods [sic]" (p. 333), and indeed they violate Hennig's principles repeatedly, they nevertheless confide that "a cladistic analysis of this material will be presented in due course" and might lead to "slightly different conclusions" (p. 345). I will not be too surprised if the results are radically different, but in any case I look forward to an analysis freer of preconceptions and based on an explicit logic for formulating and testing phylogenetic hypotheses.

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Organelles

Mitochondria. ALEXANDER TZAGOLOFF. Plenum, New York, 1982. xvi, 342 pp., illus. Cloth, $42.50; paper, $19.95. Cellular Organelles.

It has been almost 20 years since Lehninger's monograph *The Mitochondrion* first appeared, and now Alexander Tzagoloff has written a book that provides a good account of where the field stands today. A scan of the earlier book subsequent to reading Tzagoloff's is enlightening and indeed points up the remarkable amount of progress that has been made in our understanding of the functioning, organization, and biogenesis of the "powerhouse of the cell" in the interim. For example, the Mitchell chemiosmotic hypothesis, which now stands as the cornerstone upon which the currently conceived mechanism of mitochondrial energy conservation is based, was no more than an idea with no supporting data to speak of in 1964. Progress of a similar magnitude has been made on other subjects, particularly mitochondrial biogenesis and mitochondrial genetics.

Far from simply summing up the current status of a static field, this book serves to point out how fertile an experimental tool mitochondria have been and will continue to be. Add to that Tzagoloff's readable style of writing and the copious, well-done illustrations and you have a book that easily attains its stated goal of providing a thorough introduction for students who want to understand mitochondria in more depth than is provided in advanced cell biology textbooks. Further, the presentation is generally deep and broad-ranging enough that even established "mitochondriacs" should find the book worthwhile reading. One other useful feature is the frequency with which Tzagoloff provides brief explanations (with references) of the theory associated with different techniques when they first appear in the book.

Tzagoloff begins with a brief history of the study of mitochondria and an overview of general mitochondrial structure and terminology. The three chapters that follow consider the oxidative pathways associated with the mitochondrial matrix, the inner membrane, and cytochrome oxidase. Oxidative phosphorylation is the subject of the next two chapters, and all the preceding is brought together in a chapter that considers the resolution and reconstitution of electron transfer and oxidative phosphorylation. The last three chapters cover mitochondrial transport systems, biogenesis, and genetics. Though Tzagoloff has spent his entire career studying some aspect of mitochondria, his most recent interests concern mitochondrial biogenesis and genetics, and the chapters on these subjects are the most up-to-date ones in the book as well as the most insightful. Tzagoloff's tendency to point out unsolved problems becomes most apparent in these chapters.

Although overall the book is well worth recommending, there are two aspects of it that I found disappointing. First, speaking from my own perspective, it would have been helpful to have had a few pages devoted to a discussion of plant mitochondria, particularly the features associated with plant mitochondria that are not commonly found in mitochondria from animal sources (for example, cyanide resistance and the ability to oxidize external reduced pyridine nucleotides). Second, the chapters describing the mitochondrial electron transfer chain present a view that is not as current as that in the chapters on biogenesis and genetics. For example, none of the recent evidence that suggests that some form of protonmotive "Q-cycle" operates in complex III is cited.

The above complaints are relatively minor, however, and do not detract from my overall enthusiastic response to this timely book. It should become required reading for all people interested in mitochondria. Finally, it should be pointed out that the book is the first in a series devoted to cellular organelles. We can only hope that the rest of the series matches the standard it sets.

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