Journal of Insect Behavior, Vol. 5, No. 1, 1992

Book Review

The Long March of History

Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology. By Daniel R. Brooks and Deborah A. McLennan. University of Chicago Press, Chicago, 1991, xii + 434 pages, $21.00 paper, $45.00 cloth.

In their mythology the ancient Greeks deified time, Cronos, placing him near the beginning of order out of Chaos. In our evolutionary representation time is likewise given a special role in explaining the origins of organic diversity and adaptive change. This is Darwin's legacy—the idea that life evolves via interactions among genealogy ("phylogeny") and environmental processes ("ecology"). *Phylogeny, Ecology, and Behavior* (PEB) begins with the premise that panglossian adaptationist followers of "The Modern Synthesis" have lost sight of Darwin's sophisticated view and, due to the dissociation of ecological and genealogical studies, have put blinders on their evolutionary worldview through a neglect of history. Brooks and McLennan aim to recapture Darwin's wholistic views by budding off an academic discipline, "historical ecology," whose objectives are "to integrate ecological, behavioral, and historical information to produce a more robust picture of evolution" (p. 5). To a considerable extent they succeed in their task. The methods used to reach this goal involve the application of phylogenetic systematics to problems of comparative biology. The underlying assumption is that knowledge of evolutionary patterns (history) is often necessary for a rational understanding of processes producing those patterns.

This book forces the reader to confront history at every turn, at least the kind of history that can be represented in branching diagrams. The organization of the book is excellent for provoking thought. Major points are usually well illustrated with numerous examples, including enough entomological examples (slightly less than 10% of over 700 bibliographic citations) to make the book interesting to readers of *Journal of Insect Behavior;* there are numerous other examples from a wide variety of taxa. Case studies are illustrated with relevant figures, although most of them consist of phylogenetic trees which are given without the distributions of informative characters (synapomorphies). As such, unfortunately it is impossible for readers to judge the evidence supporting a

0892-7553/92/0100-0141$06.50/0

particular phylogenetic hypothesis without consulting original publications. The prose is usually clear and the text is nearly free of typographical errors; some pages of my paperback review copy are already coming unglued.

PEB consists of three parts. Part One (Chapters 1 and 2) deals with "The Basic Issues." Chapter 1 sets the stage by giving a brief history of the "eclipse of history" in ecology and ethology. This section is something of a caricature, and systematists might read a book such as that by Thorpe (1979) for another point of view. For example, Brooks and McLennan cite with approval a statement by C. O. Whitman that "instincts . . . are to be studied from the common viewpoint of phyletic descent." For Whitman and some subsequent ethologists, however, this viewpoint was a starting point rather than an objective in itself (e.g., Hinde and Tinbergen, 1958). Whitman (1895) also wrote that

> We have no longer any use for the "*Ahnengalleries*" [ancestor portrait galleries] of phylogeny . . . we are no better off for knowing that we have eyes because our ancestor had eyes. If our eyes resemble theirs it is not on account of genealogical connections, but because the molecular germinal basis is developed under similar conditions.

I do not agree with Whitman that *Ahnengalleries* are no longer useful, but his emphasis on exploring the genic and epigenic mechanisms which maintain homology is important. In other words, what are the proximate mechanisms which produce patterns that can be described as "historically constrained"? Brooks and McLennan view a "phylogenetic constraint" as a causal process, apparently ignoring the fact that these constraints must be manifested during the development of individual organisms. Schmalhausen's (1949) long-neglected *Factors of Evolution* would nicely complement *PEB* (also e.g., Waddington, 1975) since long ago he recognized that evolution results from a dialectic tension between the creative and the conservative facets of natural selection, between a tendency to change and a tendency to resist change, all "involved in the transformation of the individual organism during its historical development" (Schmalhausen, 1949, p. xxi).

Chapter 2 continues the basic issues by briefly describing the "tools of the trade." The authors correctly assert that phylogenetic systematics is "the best method currently available for reconstructing phylogenies" (p. x). This commendable approach allows them to push their methodology to its limits (and beyond), which serves to highlight both the strengths and the weaknesses of their approach. The former are thoroughly discussed and the latter are not. Brooks and McLennan's approach involves a more rigorous methodology for comparative biology. Phylogenetic relationships among taxa are proposed on the basis of shared derived homologous characters (synapomorphies), and a phylogenetic tree is a composite hypothesis of inferred historical relationships among multiple taxa. The preferred hypothesis is the one which minimizes the number of postulated evolutionary changes in character states (assuming parsimony). Characters of ethological or ecological interest are then mapped onto

this tree to ascertain their patterns of evolution, again minimizing the number of postulated evolutionary changes (character optimization—assuming parsimony). Brooks and McLennan emphasize repeatedly that the suite of characters under consideration should *not* be included among those characters used to reconstruct the phylogeny, since doing so would violate an assumption of independence. A reduced data matrix might result in a less parsimonious tree, so other phylogeneticists stress the importance of including "total evidence" to produce the most robust phylogenetic hypothesis (e.g., Kluge, 1989). The authors rarely discuss such controversial issues, and they omit any serious discussion of related philosophical issues: e.g., What are the consequences of multiple applications of parsimony? Why are optimality arguments appropriate for character evolution, yet they are criticized when applied to studies of adaptation?

Part Two (Chapters 3–5), on "Phylogeny and the Evolution of Diversity," and Part Three (Chapters 6–9), on "Phylogeny and the Evolution of Ecological Associations," show how phylogenetic methods can throw light on questions relating to patterns and frequencies of different modes of speciation, species diversity, biogeography, coevolution, community ecology, and more. An example of one of the more interesting conclusions is that among some vertebrates the authors support traditional thinking that most cases of lineage divergence involve allopatric speciation. As with other analyses in the book, this example brings out the dubious nature of some underlying assumptions. In speciation studies the idea is that different modes of speciation leave different phylogenetic and biogeographic patterns (although in practice this is not true: e.g., compare stasipatric *versus* allopatric speciation, p. 101). Assumptions of a speciation study are that (i) character evolution provides a sound basis for reconstructing speciation events, (ii) there are no extinctions within the clade, and (iii) the influence of geographic separation during divergence is not obscured by subsequent dispersal of the descendent species. Assumptions ii and iii are biologically doubtful. In fact, the authors give an example from killfishes and note that the assumptions of no dispersal and no extinction "are tenuous at best." The consequences of violating underlying assumptions are rarely discussed.

Another difficulty with the phylogenetic approach to comparative biology concerns character state delineation. The most striking conclusion of the book is that "ecological and behavioral diversification is more conservative than phylogenetic diversification" (p. 345). This conclusion seems possible because of the effective exclusion of anagenesis from historical considerations. Such changes in character states are noninformative to a hennigian systematist, but they are nonetheless historical (genetic). If much behavioral and ecological evolution involves these kinds of changes [see, e.g., West-Eberhard (1986) or Wilson (1990) for evidence], then omitting them will result in an overestimation of

phylogenetic diversification relative to behavioral and ecological diversification at a given level of analysis. Throughout the book Brooks and McLennan are extremely careful to give attention to levels of analysis when dealing with genealogy, yet they are surprisingly loose when the analysis is ecological. The difficulty is that the "evolutionary individuals" (species, genera, etc.) included in the phylogenetic analyses have no known role in the ecological hierarchy—only organisms have both genealogies and ecologies (e.g., Eldridge, 1989). Brooks and McLennan recognize adaptations as derived characters at or above the species level, which potentially introduces a new ecological typology. [See Cracraft (1990) for a brief discussion of the ontological mistake of analyzing evolutionary innovations at hierarchical levels more inclusive than those at which the innovation-producing processes have operated; Łomnicki (1988) critiques population- and community-level ecological studies as too course-grained.] As an example, the authors discuss phylogenetic constraints in oviposition-site preferences at the generic and tribal levels in a group of parasitic wasps (Labeninae). One group (Groteini) is comprised of parasites on the larvae and stored pollen of bees. For the entire tribe the character state for oviposition site is scored as "through lignified plant tissue," which is true for members that parasitize twig-nesting bees; some groteines (e.g., *Labium* spp.), however, have diversified to parasitize soil-nesting bees, and they do not oviposit through lignified plant tissue (e.g., Rayment, 1935; Gauld, 1984). In essence, the problem involves forcing highly variable or complex features into a few "character states" (for discussion see Pogue and Mickevich, 1990), coupled with a failure to specify levels of ecological analyses.

Phylogeny, Ecology, and Behavior details a relatively new approach to some old problems, and it can be strongly recommended to all evolutionary biologists. Ecologists and ethologists will find numerous exciting ideas derived from phylogenetic studies which should enrich their disciplines and help them focus their research programs. Those who study this book will certainly appreciate the indelible mark of history, and this realization, in turn, should help them convince phylogeneticists that history does not end below the species level. A hoped-for synthesis of phylogeny, behavior, and ecology still lies someplace on the horizon, but it is now closer due to Brooks and McLennan's efforts.

REFERENCES

Cracraft, J. (1990). The origin of evolutionary novelties: Pattern and process at different hierarchical levels. In Nitecki, M. H. (ed.), *Evolutionary Innovations*. University of Chicago Press, Chicago, pp. 21–46.

Eldridge, N. (1990). *Macroevolutionary Dynamics*, McGraw Hill, New York.

Hinde, R. A., and Tinbergen, N. (1958). The comparative study of species-specific behavior. In Roe, A., and Simpson, G. C. (eds.), *Behavior and Evolution*, Yale University Press, New Haven, Conn., pp. 251–268.

Gauld, I. (1984). *An Introduction to the Ichneumonidae of Australia, with a Contribution on Metopiinae by M. G. Fitton*, British Museum (Natural History), London, pp. 1–413.
Kluge, A. G. (1989). A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Syst. Zool.* 38: 7–25.
Łomnicki, A. (1988). *Population Ecology of Individuals*, Princeton University Press, Princeton, N.J.
Pogue, M. G., and Mickevich, M. F. (1990). Character definitions and character state delineation: The bête noire of phylogenetic inference. *Cladistics* 6: 319–361.
Rayment, T. (1935). *A Cluster of Bees*, Sydney.
Schmalhausen, I. I. (1949). *Factors of Evolution* (1986 reprint), University of Chicago Press, Chicago.
Thorpe, W. H. (1979). *The Origins and Rise of Ethology*, Heinemann, London.
Waddington, C. H. (1975). *The Evolution of an Evolutionist*, Cornell University Press, Ithaca, N.Y.
West-Eberhard, M. J. (1986). Alternative adaptations, speciation, and phylogeny. A review. *Proc. Natl. Acad. Sci. USA* 83: 1388–1392.
Whitman, C. O. (1895). *Biological Lectures, The Marine Biological Laboratory of Woods Hole, Mass.*, Gin, Boston.
Wilson, D. S. (1989). The diversification of single gene pools by density-and frequency-dependent selection. In Otte, D., and Endler, J. A. (eds.), *Speciation and Its Consequences*, Sinauer Associates, Sunderland, Mass., pp. 366–387.

William T. Wcislo
Center for Insect Sciences
Forbes Building
University of Arizona
Tucson, Arizona 85721