



Review: [untitled]

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Phylogeny, Ecology, and Behavior. A Research Program in Comparative Biology by Daniel R. Brooks ; Deborah A. McLennan

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extensions. As such, it is essentially a field guide, and I question the usefulness of details on stages of development, tadpole morphology, and preservation techniques. These only occupy a few pages, however, and the bulk of the book is very worthwhile, providing less esoteric information for the reader.

The systematic accounts are well done. The descriptions are concise, the sections on habitat and behavior indicate with which species the author is familiar, and the calls are described in words. I particularly appreciate the information on breeding and development. Many frog guides seem to ignore the tadpole stage, although larvae are often more easy to collect and display characteristic behavior. The section on similar species draws attention to like forms which might confuse identification. The keys are simple and will no doubt work as well (or as badly) as more technical keys to the same species.

There are numerous illustrations: line drawings of hands and feet, stippled pencil sketches of tadpoles and larval mouthparts, and, at the end of the book, two dozen color plates of water-color paintings showing dorsal and ventral patterns. Frog patterns are extremely variable, yet form the basis for many identifications in the popular literature. The author printed these plates, so he must take responsibility for the "rubber-stamp" look of many forms, where the outlines of different species are identical on the plates, although the specimens are quite different. The paintings of dorsal patterns are flat, lacking shading and with minimal highlights, often with stereotyped outlines. Although simplified sketches of dorsal views would have been understandable, the effort and expense involved in producing these plates could have been better used on photographs, even if not all of the species were illustrated. Photographs of live animals always show details and postures not captured when dead animals are painted. Despite these shortcomings, the plates are helpful because different color patterns are illustrated.

The distributions of each form are represented by a shaded outline map, positioned opposite the respective plates. I found this arrangement very handy, because the known distribution and the color variations are illustrated side by side. The distribution maps would have been better showing actual localities rather than just shading in part of the country. The reader is never sure how much conjecture is involved.

The glossary is essential reading. How many non-Zimbabweans know the meaning of *dwala* (a large, unbroken dome of granite)? A glossary is always useful in a popular book on frog identification, but why has the author explained the meaning of *forest*, *grassland*, *submerged vegetation*, and *thicket*? Superfluous detail is also evident in the list of selected references, such as Romer's 1966 *Vertebrate Paleontology*. It seems that the references could have been a little more selected. Indices to scientific and common names are provided.

I find the book to be full of contrasts. The pencil sketches of larval mouthparts must have taken a great deal of time and effort yet are not very accurate, because the fine details are represented very coarsely and some sketches are wrong. For example, the accessory buccal plates characteristic of the tadpoles of *Kassina* are not shown.

Overall, the book is well produced and brings together illustrations, life-history details, and the more technical keys and lists of species. As such, it must benefit all herpetologists and others interested in the frogs of this interesting region of Africa.

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PHYLOGENY, ECOLOGY, AND BEHAVIOR. A RESEARCH PROGRAM IN COMPARATIVE BIOLOGY. By Daniel R. Brooks and Deborah A. McLennan. 1991. University of Chicago Press. ISBN 0-226-07572-9. xii + 434 p., \$45.00 (cloth), \$21.00 (paper).—In 1979, Willi Hennig's *Phylogenetic Systematics* (1966) was reprinted in acknowledgement of its key role in

revolutionizing systematics and our approach to studying evolution. In that reprint, D. E. Rosen, G. Nelson, and C. Patterson contributed a foreword which briefly chronicled the systematic revolution and its effect on neo-Darwinian thought, which was slowly losing its stranglehold on evolutionary theory. The last paragraph of that foreword is worth repeating for its prescience: "As we see it, the significance of this reprinting is that the possibilities opened by Hennig's approach to systematics are still being explored, and the full consequences of the application of his concepts in evolutionary biology are yet to be discovered" (Rosen et al., 1979).

Phylogeny, Ecology, and Behavior by Brooks and McLennan is a singular effort that demonstrates through numerous examples some of the consequences of applying Hennig's basic ideas to fields outside of systematics and historical biogeography. In this regard, the book may be considered a landmark publication, although that will be for time and the accumulation of empirical studies to verify. As a handbook for the budding historical ecologist, however, the book has shortcomings, some understandable due to the book's scope, others not. For the audience of *Copeia*, this book is worth the price because of the plethora of empirical examples based on fish, reptiles, and amphibians.

Phylogeny, Ecology, and Behavior is divided into three parts: (1) The Basic Issues, (2) Phylogeny and the Evolution of Diversity, and (3) Phylogeny and the Evolution of Ecological Associations. The first part is concerned with the definition of historical ecology and what one needs to practice it. The second part explores phylogeny and mechanisms of diversity, specifically speciation and adaptation; and finally, in the third section, the authors address ecological associations, especially cospeciation and coadaptation.

What is historical ecology? At its simplest, historical ecology addresses the causes of a trait by way of a phylogeny (i.e., historical information). In contrast, nonhistorical ecology addresses the maintenance rather than the evolution of a trait. In the first section of the book, Brooks and McLennan undertake the task of instructing the novice on how to construct a phylogeny. The attempt is fair but necessarily incomplete in the space of one chapter. Because of this, the book falls short of being a handbook for a non-systematist. However, the authors do

an excellent job of addressing commonly asked questions concerning phylogenetic analysis, such as is outgroup comparison an exercise in circular reasoning, and isn't parsimony an assumption of evolutionary mechanisms? I would add a few more. For example, what is a cladogram? Is it the same as a phylogeny? What is cladistics? Is it the same as phylogenetic systematics? These terms are mysteriously absent in this chapter; I wonder if it is a sociological reaction to other systematists that call themselves cladists, an attempt to get away from the Mayr eponym, or an effort not to scare off ecologists and ethologists because cladistics may have a bad name due to some of its more evangelical and polemical adherents. For whatever reason, the authors' reluctance to use these terms is curious.

In the second part of the book, the authors lay out, in a single sentence (p. 72), the philosophical basis for the methods employed in historical ecology: "We believe that if some aspects of diversity represent persistent ancestral conditions, then the study of diversity is inherently a macroevolutionary research program." Therefore, the program is phylogenetic in scope, which the authors further support by stating that speciation and adaptation are the cornerstones of evolutionary theory. Speciation is the divisive force and adaptation is the cohesive force in evolution; phylogenetic systematics unifies the two. This view might be controversial to some, but the authors do a good job of supporting their position.

The chapter on speciation is confusing, inconsistent, and incomplete. Certainly a majority of the problems are caused by the impossibility of adequately treating speciation in so short a space. With that in mind, it is unfortunate that the authors seem to imply that we completely understand patterns of speciation when, in fact, we do not. Is speciation only the result of cladogenesis? The authors imply as much, yet if that is not their intention, then they fail to elucidate alternatives. Here is where the confusion between phylogeny and cladograms becomes important from an operational perspective. Sister (i.e., cladistic) relationships are a requirement for historical ecology, but as far as I know no one has shown that anagenesis does not or has not occurred. Anagenic relationships are not recoverable through cladistic methods, but that does not preclude their existence. Hence, if the authors defined the difference between a phy-

logeny and a cladogram (see Platnick, 1977), and used the two consistently, perhaps that confusion would have been avoided.

There has been much debate regarding why some clades are more diverse than their sister group. Brooks and McLennan draw the general conclusion that diverse clades result from geologically diverse history and habitat, whereas depauperate clades are relictual. An interesting alternative (other than those discussed in the chapter) based on probability models is that disparity in diversity between sister clades is the norm and that equivalent-sized clades are in fact unusual and require explanation (Slowinski and Guyer, 1989).

Allopatric speciation is divided into three models, essentially following Wiley (1981). However, the discussion by Brooks and McLennan may still leave the reader with a few reservations and questions about just what the different models are. For example, why cannot plesiomorphic constraints maintain persistent ancestral conditions (in the ancestor) in any of the models at any time?

In chapter 5 of the second section the authors address the study of adaptation in historical ecology, solidifying methods for formulating the issues. Basically the chapter is an exercise in Farris Optimization, which the authors explain well, as they do with homoplasy and problems associated with removal of taxa. This chapter is contentious, but empirical examples are bountiful and appropriate. One glaring error that herpetologists would catch is the example of Henderson et al. (1988) on the evolution of foraging behavior and diet of Hispaniolan snakes (p. 163). The prey items are labeled skinks in the figure (fig. 5.26), but are called teiids (they are *Ameiva*) in the text.

At the conclusion of the section on adaptation, the authors leap into what Donn Rosen referred to as the Bridge Principle. In this instance, the bridge spans identification of burdens of history (i.e., the historical ecological approach to adaptation) on one side to making informed decisions about preservation and conservation on the other. The bridge is built on the premise that, because burdens of history can be identified, certain phylogenetic pathways can be rejected in favor of others. This is interesting but difficult to see as practical if, in fact, possible. Conservation biology does not operate on a phylogenetic time scale, but on a recent, far more demanding, influence—that of *Homo sapi-*

ens obsessed with instant gratification while unconcerned with possible extinction or speciation events occurring at a geologic pace. Phylogeneticists would better serve the conservation effort by identifying biodiversity so that bits of genetic diversity can be preserved now (see Vane-Wright et al., 1991).

Part III details methods for addressing cospeciation and coadaptation. Cospeciation here is just another name for historical biogeography: is the present association of two or more species the result of descent, perhaps vicariant in nature, or is it the consequence of dispersal with an ecological twist? Brooks' Parsimony Analysis (BPA; Wiley, 1988) is the authors' tool of choice here which they explain clearly, using numerous examples. At this point cladograms are defined (p. 206) and differentiated from phylogenetic trees: cladograms do not possess any connotation of historical relationships among taxa. Brooks and McLennan hope that this distinction is helpful, not confusing. Examples are numerous, and my guess is that their definition of a cladogram will find the latter more often true than the former.

Like the chapter on cospeciation, that on coadaptation is filled with a variety of empirical examples that demonstrate the usefulness of a historical approach to understanding the evolution of two interacting lineages. Essentially, the method used to examine coevolutionary history is that of congruence, with the null model being agreement between two species' lineages resulting from vicariant events. From that base, the examples expand to resource tracking and the arms race. Later, the authors suggest that genetic distances can be used a posteriori to estimate the influence that two coevolving lineages may have on one another by mapping distances on previously constructed historical frameworks. There is an assumption that equal rates of change, cospeciation, and coadaptation should be correlated, which raises an ambiguity that, if rates of genetic divergence are unequal, then it is possible to deny cospeciation. Last, community evolution is presented as the study of coadaptation and cospeciation on a grand scale. Community ecologists might not readily accept the authors' phylogenetic premise, but it seems to me that teasing out history should be a useful means of understanding community composition.

Overall, this book is well done; the most glaring deficiencies probably result from space lim-

itations. The authors do a good job of expanding Hennig's basic tenets and support their ideas with an exhaustive set of empirical examples. Historical ecology, as outlined by Brooks and McLennan, is provocative and should be required reading for anyone working in comparative biology.

I thank M. White and D. Bolger for their interesting discussion. M. White provided comments on the review.

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FISHES OF THE GREAT BARRIER REEF AND CORAL SEA. By John E. Randall, Gerald R. Allen, and Roger C. Steene. 1991. University of Hawaii Press, Honolulu, Hawaii 96822. 507 p., \$60.00 (hardcover).—The fishes of the Great Barrier Reef are from one of the most intensely studied fish communities in the world. The di-

versity of these fishes in kind, form, and color also places the Great Barrier Reef as one of the best locations for diving and recreational fishing. Despite this, anyone wishing to identify fish in this region has had to rely on general guides to fishes in nearby regions or on specific publications of selected fish families. For years, there existed a gap in every fish-watcher's, diver's, and researcher's library of fish books: a guide to the fishes of the Great Barrier Reef. At long last, this gap has been filled. The authors are to be commended for engaging the mammoth task of providing descriptions and color figures or photographs of over 1100 species found in the Great Barrier Reef region. Few workers would have the knowledge and breadth of experience to successfully complete this task.

The book follows the familiar and popular format used previously by the senior author in guides to the fishes of the Caribbean (Randall, 1968), Hawaii (Randall, 1981), and Red Sea (Randall, 1983). It starts with a pictorial guide to families based on line drawings. This is followed by a brief introduction to the region and a section on how to identify fish. The bulk of the book is composed of species descriptions, covering 1111 species in 111 families. Each family is described briefly and is followed by individual species accounts. A glossary and index are provided at the end.

The format of the species accounts is very clear. Usually a large color photograph is provided with the relevant text immediately adjacent to it. The text provides meristic values, measurements, color notes, distribution, and biological notes. There is usually one photograph per species although, in species where there are distinct sexual or ontogenetic changes in the color patterns, two or three photographs are provided.

The color pictures are generally of good quality and are well reproduced. The majority are underwater photographs, which greatly enhances the value of this book as a guide for divers and researchers.

The identification of sharks and large pelagic species is greatly facilitated by the use of color paintings by Roger Swainston to supplement the color photographs. Seven full-page plates (first published in Allen and Swainston, 1988) are used and enable species to be compared easily.

The book fulfills its stated aim of providing good color plates to the species most likely to be encountered by divers and snorkelers on the