

and linkage. The whole is amply illustrated with pertinent binding curves and corresponding three-dimensional structures. In the structure-function analysis, the examples are drawn from systems as varied as respiratory proteins, electron-binding proteins, allosteric enzymes, and nucleic acid-binding processes. This is followed by two chapters in which the general principles of binding equilibria are described. Starting with a simple single-site binding, the authors develop the various types of plots (Scatchard, double-reciprocal, Hill) and the binding isotherm. This analysis is then extended to increasingly complex systems—two independent sites, cooperative binding, allosteric effects. The concepts of the binding partition function and binding polynomial are introduced. The binding polynomial is then developed for various cases of binding interactions. The significance of the Adair constants and the analysis of cooperativity by Hill plots are explained for various cases of linkage. It is shown how electron binding can be treated by the same relations.

The middle of the book includes a discussion of allosteric systems that should be particularly appreciated by biochemists dealing with controlled reactions. This discussion is built upon a historical account of the development of the concept of allosterism since early in this century. The Monod-Wyman-Changeux model and the induced-fit Koshland model, itself a conceptual development of Pauling's early "interaction bonds" model, are seen to be special cases of the parent allosteric model based on Wyman's recognition 40 years ago that the essence of these controlled systems resides in the shifting of preexisting equilibria by the addition of ligands at binding sites. The fifth chapter of the book is devoted to a generalization of the term "binding" to include changes in amounts of heat or volume associated with a reaction, with applications to scanning calorimetry and isothermal titration calorimetry, and effects of pressure on macromolecular reactions. Two chapters are devoted to the complex topics of ligand-controlled aggregation, linkage between ligand binding and macromolecular phases, solubility, the triple point, and phase equilibria. The book closes with a chapter on the thermodynamics of macromolecules.

*Binding and Linkage* not only admirably meets its stated goal, it goes far beyond that. The authors have brought together the fruits of many years of insightful reflection on a central problem in biochemistry with the experience of many years of teaching this subject to first-year graduate students. The result is a short volume that both presents the basics of binding and cooperativity and develops in depth the powerful arsenal that

the linkage concept makes available to experimental biochemists in dissecting interrelations that exist in biological systems. As such, the book can serve as an excellent textbook for the teaching of binding on the elementary level. It is also a must on the desk of any bioscientist dealing with coupled, controlled, interrelated reactions, that is,

with linkages. The publication of this work must be regarded as a major event, and the book will surely find a place among the classics of the scientific literature.

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## The Phylogenetic Perspective

**Phylogeny, Ecology, and Behavior.** A Research Program in Comparative Biology. DANIEL R. BROOKS AND DEBORAH A. McLENNAN. University of Chicago Press, Chicago, IL, 1991. xii, 434 pp., illus. \$45; paper, \$21.

From the human appendix to life's common genetic code (not to mention the panda's thumb), history's indelible mark is ubiquitous. Nonetheless, consideration of historical influences in ecological and ethological studies steadily diminished from the neo-Darwinian synthesis of the 1940s until very recently. Implicit in ahistorical analyses is the assumption that traits are infinitely plastic and molded to their current environment by the omnipotent and omnipresent power of natural selection. Because this assumption in many cases is of dubious validity, recent methods have attempted to incorporate historical information into studies of adaptation and diversity.

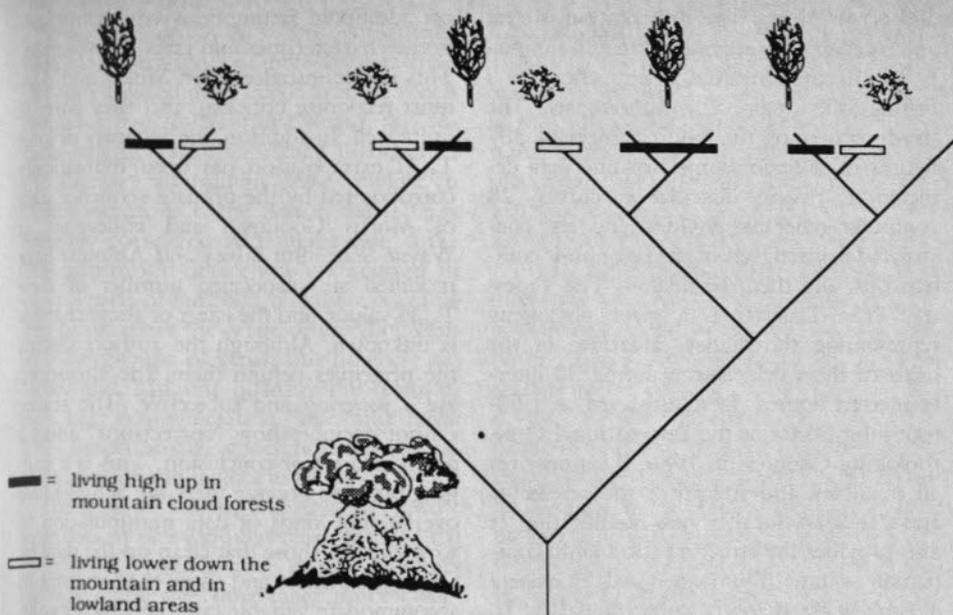
Stemming from these advances, *Phylogeny, Ecology, and Behavior* is the first book devoted exclusively to the use of phylogenetic methods in studies of organismal functions, interactions, and evolution. In an ambitious volume jam-packed with case studies (111 cladograms of real taxa, with 200 more hypothetical examples!), Brooks and McLennan endeavor to demonstrate that the phylogenetic perspective can enlighten our understanding of topics as diverse as biogeography, host-parasite coevolution, speciation, and community ecology. Their method, phylogenetic systematics (in other words, cladistics), has two components. First, phylogenetic relationships are inferred on the basis of the presence of shared derived characters. The favored hypothesis is that tree ("cladogram") which requires the fewest evolutionary changes in character states. Second, evolutionary changes in biological parameters of interest (such as body size, geographic range, or host plant) are mapped onto this tree in such a way that the number of evolutionary changes required

is minimized ("character optimization").

For example, to investigate whether aggressive behavior and ritualized behavior have evolved independently among stickleback fishes, one would first derive a phylogenetic hypothesis and then determine where on the tree each trait evolved. Indeed, in this example, Tinbergen's hypothesis that the two types of behavior have evolved in synchrony is confirmed. The versatility of the cladistic method allows it to be applied in a similar manner to a wide range of questions. To investigate whether the geographic distribution of a particular group of taxa has resulted from geological processes (such as continental drift), one can compare a cladogram of the organisms to a geologically based "area cladogram." Congruence of the cladograms would suggest that the geological splitting of areas has been associated with the evolutionary splitting of taxa. Similarly, the cladograms of hosts and parasites can be compared to test for congruence in their patterns of speciation.

The authors break new ground in their application of the cladistic approach to community ecology, emphasizing that history's mark can be discerned even in studies of contemporary processes such as the role of interspecific interactions in structuring communities: "Much of the confounding data compiled by evolutionary ecologists is due to the inability to distinguish effects stemming from historical background and those stemming from proximal dynamics." Nonetheless, to use phylogenies to test mechanistic hypotheses requires that different processes lead to predictably different outcomes. Unfortunately, as is evident in their discussion of speciation, extrapolating from the phylogenetic pattern to the underlying process is not as straightforward as the authors suggest.

Brooks and McLennan argue that by considering the geographic ranges of species in the context of their phylogenetic relationships, one can determine how a particular



"Habitat distribution of the tree species of the genus *Montanoa* and their shrubby sister groups. Tree forms only live high in the mountain cloud forests, while the shrub forms are located lower down the mountain sides and into lowland areas." [From *Phylogeny, Ecology, and Behavior*]

speciation event occurred. For example, if two sister taxa (that is, species more closely related to each other than either is to any other) co-occur, then sympatric speciation is implicated, whereas the sympatry of non-sister taxa suggests some other mode of speciation followed by dispersal. Similarly, if the ranges of sister taxa abut, then parapatric speciation is supported, whereas disjunct ranges of sister taxa indicate allopatric speciation. On the basis of this reasoning, the authors endorse a recent analysis that concluded that a surprisingly high 8 to 14 percent of speciation events among a set of vertebrates were sympatric. Certainly, phylogenetic information will bring geographic data into sharper focus, but the reliability of the underlying assumption that the size and location of a species's range are a good indicator of its mode of speciation is suspect. Would one really expect the range of a species that arose by means of peripatric speciation (that is, in a small and isolated peripheral population) to remain restricted forever? Do sympatric sister species indicate sympatric speciation, or might they simply represent species that evolved allopatrically and subsequently expanded into sympatry? Conversely, recent paleoecological studies indicate that species that belonged to the same community in the Pleistocene no longer occur together. Consequently, sister species that are allopatric today could have arisen by sympatric speciation. Although phylogenetic information can render particular scenarios unlikely, within-species studies of speciation in action are the best bet for en-

lightening us about the underlying processes.

A more general concern is the absence of discussion of the underlying tenets of the cladistic philosophy, which is particularly distressing because this book is geared toward workers new to phylogenetics. Given that Brooks and McLennan's method invokes a double dose of parsimony, first in the construction of the phylogenetic tree and then in the optimization of character evolution upon it, the lack of any substantive discussion of the theoretical justification or potential consequences of the reliance upon parsimony is surprising. Indeed, theoretical analyses have made clear that parsimony often will fail to provide the correct phylogenetic tree; the real question is, how far off will it be? Even if the tree is correct, parallelism and reversal in the evolution of characters of interest are likely to be more common than character optimization based on parsimony would suggest. Further, no one has assessed the overall effect of such serial applications of parsimony. Character optimizations that are slightly less parsimonious on the favored tree may be overwhelmingly more parsimonious on slightly less favored trees. These and a host of other questions (for example, what about alternative methods for reconstructing phylogenies and optimizing characters?) need to be addressed before parsimony methodology can be accepted as the best means for incorporating history into comparative biology.

Two promising avenues to extend phylogenetic approaches beyond the mere formulation of historical scenarios are discussed in

the concluding chapter. First is the use of recently proposed statistical methods to test whether particular patterns, be they evolutionary correlation of characters, congruence of taxon and area cladograms, or species-richness of a clade, are more unusual than one would expect from chance. Second is the reciprocal illumination produced between historical and contemporary studies. Brooks and McLennan are at their best when they point out crucial experimental studies suggested by phylogenetic patterns. Conversely, relationships exhibited by extant taxa (such as biomechanical linkages or correlations between phenotypic and ecological features) can be investigated phylogenetically to determine whether they are obligatory and how they arose.

Brooks and McLennan have clearly demonstrated the large contribution historical contingency makes to present-day pattern; failure to consider this historical legacy will critically hinder attempts to understand the diversification of life and will doom many studies to overestimate the power of contemporary processes. Brooks and McLennan's parsimony approach is only one of a number of recently proposed phylogenetic comparative methods, however; new approaches are appearing willy-nilly. Brooks and McLennan have made a strong case for the incorporation of phylogenetic information into studies of all aspects of biological diversity, but only time will tell to what extent the cladistic approach they espouse will be accepted as the method of choice for conducting such studies.

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## The Birds Reclassified

**Phylogeny and Classification of Birds.** A Study in Molecular Evolution. CHARLES G. SIBBLEY and JON E. AHLQUIST. Yale University Press, New Haven, CT, 1991. xxiv, 976 pp., illus. \$100.

Until recently the definition of the relationships among the higher categories of birds (subfamilies, families, and orders) had changed remarkably little since the classification proposed by Hans Gadow a century ago. Ornithologists have debated such issues as whether flamingos are actually modified ducks and whether the seemingly smart ("advanced") crows should be listed last in the linear classification, but the age-old arrangement of taxa based on overall (sometimes clearly convergent) morphological similarity has persisted without substantial