BOOK REVIEWS

Molecular Evolution: A Phylogenetic Approach. R. D. M. PAGE AND E. C. HOLMES. Blackwell Science, Inc., Malden, Massachusetts, 1998. 352 pp., illus. (ISBN 0-865-42889-1 paper, $51.95)

Molecular phylogenetics, devoted to understanding the hierarchical structure of biological diversity through genetic data, is one of the fastest growing fields in biology, propelled by the polymerase chain reaction (PCR) as well as rapidly improving DNA sequencing technologies and other marker detection systems. One important outgrowth of the phylogenetic revolution is the recognition that evolutionary trees provide an important and appropriate context to address questions in a diversity of disciplines such as evolutionary biology, ecology, and developmental biology. In this book, the authors use the phylogenetic tree as a central metaphor in approaching the study of molecular evolution. Their central aim is to demonstrate what evolutionary information is contained in gene sequences and to show how this information can be recovered. The book is intended for senior undergraduate and graduate students taking courses in molecular evolution and/or phylogenetic reconstruction, or as a supplement for students taking wider courses in evolution. Each chapter begins with a concise table of contents that outlines the subject matter, and ends with a summary and a list of references for further reading. Tables and figures are abundant and extremely clear. Important concepts are discussed in greater detail in gray-shaded boxes. A comprehensive bibliography is included at the end of the book.

Four introductory chapters lay the groundwork for discussions in the rest of the book. After briefly describing the importance of trees in molecular evolution (Chapter 1:10 pages), the phylogenetic lexicon is disentangled in a clear and accessible form in Chapter 2 (26 pp.). Trees come in all shapes, sizes, and configurations, and sorting through the considerable descriptive jargon can be daunting. This chapter alone makes the book an excellent resource for any course in phylogenetic systematics.

Models of the evolution of repetitive sequences, multigene families, and differences in genome size and gene number among organisms are presented Chapter 3 (52 pp.). The authors intentionally emphasize the characteristics of genome function and organization that are most germane to phylogenetic reconstruction. Thus, some readers may be unsatisfied with the level of discussion for some topics. For example, mutation is clearly an important component of molecular evolution, but the authors do not present details about the mechanics of DNA mutation and repair. Instead, they devote more time to the genetic code, which differs not only between the nuclear and mitochondrial genome of an organism, but also between organisms. This knowledge is critical for building an accurate model of molecular evolution that can then be used to estimate a phylogenetic tree. Because the same molecular genetic processes operating within species give rise to the genetic patterns we detect among species, population genetics is a necessary foundation for an understanding of molecular phylogenetics. Population genetics is the focus of chapter 4 (46 pp.), and a good overview of classical Hardy-Weinberg theory is presented. But the biggest impact of a phylogenetic perspective on the molecular evolution of populations has been through coalescent theory, where the histories of extant genes are traced backwards through time. The coalescent receives relatively little treatment in this chapter. More discussion of this important conceptual tool would have been useful.

The analytical problems involved in reconstructing phylogenies from gene sequences are discussed in Chapters 5 (37 pp.) and 6 (56 pp.). A plethora of pairwise genetic distances have been published, and differences in the information content of each of these disparate measures is not always intuitive. Likewise, it is often difficult to decide how best to align divergent sequences containing gaps, and many solutions have been proposed in the primary literature. An exhaustive list of solutions and explanations was beyond the scope of this book. Instead, the authors discuss clearly the central problems involved in alignment and measuring genetic change, and present exemplary solutions. Chapter 6, the longest of the book, explains methods of phylogenetic inference, including distance methods, parsimony, and maximum likelihood. Methods for measuring confidence in trees, such as nonparametric and parametric bootstrapping, are discussed. These two chapters would be invaluable for any course in molecular systematics.

The book ends with two chapters that discuss the application of phylogenies in addressing a variety of evolutionary questions. Phylogenies have been useful in testing the long-standing neutralist-selectionist debate. In Chapter 7 (52 pp.), the ideas from both schools are presented. The final chapter deals with how to estimate an organismal tree from a gene tree, and whether it is best to combine data from different characters in reconstructing a phylogeny. Case studies in host-parasite cospeciation, on estimating the age of taxa, and on molecular epidemiology are then presented, enforcing the thesis of the book that phylogenies can elucidate a diversity of questions in biology.

In summary, I consider the book to be most valuable for its clear discussions of molecular phylogenetics. This authors adherence to the phylogenetic paradigm mean that all topics in molecular evolution do not receive equal treatment. This focus devalues the book somewhat as primary text for a comprehensive course in molecular evolution. However, any course on molecular evolution, or in molecular systemtatics in particular, would benefit from the phylogenetic perspective presented by the authors.

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The Ecology and Evolution of Inducible Defenses. RALPH TOLLRIAN AND C. DREW HARVELL, eds. Princeton University Press, Princeton, 1999. 383 pp., $29.95 US (paperback). ISBN 0-691-00494-3.

It's hard not to be impressed by the striking forms that inducible defenses sometimes take in organisms as diverse as protists, plants and animals. Chemical cues from both predators and competitors can induce dramatic and seemingly adaptive changes in morphology, in chemistry, and in behavior. Tollrian and Harvell have responded to the growing interest in these phenomena by assembling an overview of the many taxa in which induced defenses occur and the various factors that might favor their evolution. Given our own interests in predator-induced defenses, we both received this book with anticipation.

Tollrian and Harvell clearly encouraged authors to focus on a common theme. As they note, four criteria must be met for inducible defenses to evolve: i) agents of selection (e.g., predators or competitors) must vary in space or time, ii) cueing mechanisms must be reliable, iii) induced defenses must yield a benefit, and iv) induced defenses must incur a cost, otherwise they should become fixed. Most authors adhere to this theme, but as an unfortunate consequence the later data chapters begin to sound repetitive because, although the taxa and traits change, the script remains more or less the same. Clearly, if inducible defenses *do* exist in a taxon, then all four criteria *must* have been met for them to have evolved. So the only real surprises are how the criteria are met by different organisms, or how unexpected are the forms that costs or trade-offs take.

Chapters fall roughly into five groups. The first few focus on plants. Berenbaum and Zangerl (Ch. 1) detail the multi-faceted work on the biochemistry and genetics of inducible chemical defenses in wild parsnip. Agrawal and Karban (Ch. 3) discuss several thought-provoking alternative benefits—as opposed to costs—to inducibility, such as: lowered reliability of host-finding by specialist herbivores, avoidance of unnecessary defense pathways that might reduce the effectiveness of others, avoidance of autotoxicity, and reduced likelihood of inadvertently deterring pollinators. It seemed to us that some of these phenomena could profitably be explored in animal systems as well. Dicke (Ch. 4) summarizes many striking examples of induced *indirect* defenses in plants: volatile signals that attract predators of the attacking herbivores.

Two of the more fascinating chapters summarize recent discoveries in ''protists.'' Van Donk *et al*. (Ch. 5) describe some wonderful cases of zooplankton-induced changes in phytoplankton morphology (*e.g*., the induction of colonies) and the experimental confirmation that a) chemical signals from the zooplankton are clearly involved, and b) induced forms are less likely to be eaten. Kuhlmann *et al*. (Ch. 8) illustrate some intriguing examples of induced morphological defenses in ciliate protozoans, including changes in cell shape, cell size, locomotory behavior, and the development of defensive spines.

Five chapters examine different groups of invertebrates. Gilbert (Ch. 7) provides a nice summary of his own and others extensive work on induced morphological defenses in rotifers, and offers some sobering and instructive reflections on the difficulties of measuring the ''cost'' of induced defenses. De Meester *et al*. (Ch. 9) outline what is known about predator-induced changes in depth selection and diel vertical migration by zooplankton. Tollrian and Dodson (Ch. 10) review the costs and benefits of induced morphological defenses, behavioral defenses, and life-history shifts in cladocera. Harvell (Ch. 13) enumerates examples of predator- and competitor-induced morphological changes in colonial marine invertebrates. And Lively (Ch. 14) provides a précis of his work on what is perhaps the most fully understood induced morphological defense: the ''bent'' form of the acorn barnacle *Chathamalus anisopoma* induced by contact with predatory snails.

Two chapters outline examples from vertebrates. Brönmark *et al*. (Ch. 11) concisely summarize the costs and benefits of changes in body shape in crucian carp in response to kairomones from piscivorous fish, and Frost (Ch. 6) strives to view the vertebrate immune system from the perspective of an inducible defense, but arrives at few new insights.

The remaining chapters emphasize theory. Jāremo *et al*. (Ch. 2) develop a largely heuristic model of the costs of inducible versus fixed defenses in plants, and conclude that localized defenses should evolve before systemic ones, which in turn should evolve before inter-plant communication. Anholt and Werner (Ch. 12) examine the impact of predator-induced changes in prey behavior on food web dynamics, but this chapter seemed to be a bit out of place between the covers of this book. Lively (Ch. 14), in addition to summarizing his work on barnacles, develops a thought-provoking evolutionarily-stable-strategy (ESS) model suggesting that the conditions permitting a stable genetic dimorphism are considerably more restrictive than those for a stable inducible dimorphism. Adler and Grünbaum (Ch. 15) take an ESS approach that incorporates predator movement between patches, variable emission of cues by the predator, and sensitivity of prey to the predator cues (the coevolutionary ''cues race''), and conclude that changes in the strategy of a predator can greatly alter the outcome of models of inducible defenses; but we wondered why a predator that could restrict its emission of cues would not do so all the time. Similarly, Gabriel (Ch. 16) models the relative merits of reversible versus non-reversible induced changes, and argues that reversible changes may precede irreversible ones evolutionarily.

In their concluding chapter, Tollrian and Harvell (Ch. 17) return to the original four criteria required for inducible defenses to evolve and comment on how convincingly they were demonstrated across the various organismal systems examined: i) variable selection pressures (shown in all systems), ii) reliable chemical cues (shown in most systems), iii) defenses are beneficial (shown in most systems), and iv) defenses incur a cost (may or may not be demonstrable; ''the role of costs . . . continues to be a complex issue'' p. 320). To their credit, they also note how this compilation of examples rejects one of Harvell's earlier predictions: that inducible defenses should be most prevalent among modular as opposed to solitary organisms.

For those unfamiliar with induced defenses, this book offers a convenient overview of the many and varied forms such defenses take and the impressive variety of taxa in which they occur. Both European and North American authors are well represented (20 and 12, respectively), reflecting the editors' geographic affiliations, and many contributors offer up-to-date summaries of what is known about relevant chemical cues: vascular plants (Ch. 1, 3), phytoplankton (Ch. 5), rotifers (Ch. 7), protozoans (Ch. 8), cladocera (Ch. 10), crucian carp (Ch. 11), and bryozoans (Ch. 13). Dicke (Ch. 4) presents a similar summary of the chemicals plants release that attract predators of the attacking herbivores.

Outside of the sometimes fascinating natural history, though, there seems little here to lure new players to the field. With the exception of Agrawal and Karban (Ch. 3), Gilbert (Ch. 7), and Tollrian and Harvell (Ch. 17), few authors acknowledge pressing technical or analytical problems needing to be addressed. One of the major conclusions, that costs are often difficult to demonstrate convincingly, hardly seems an appealing invitation to newcomers. Are there no controversies lurking beneath a patina of perhaps uncomfortable consensus, or exciting new challenges to reigning orthodoxies?

Most disappointing to us is the limited phylogenetic perspective. Few authors compare taxa exhibiting induced defenses to related taxa with similar, but fixed, defenses. In this era of exuberant phylogenetic analysis, the complete absence of cladograms or formal comparative analyses seems a great oversight, particularly given the fine study of spider-mite resistance in cotton plants by Thaler and Karban (1997). As the editors note briefly (Ch. 17), comparative data on the incidence of inducible characters in several related taxa are increasingly available and should permit phylogenetic analyses of inducible characters (*e.g.*, among Cladocera). So why weren't some detailed phylogenetic analyses presented here? Only then can we really begin to understand how often, and under what circumstances, inducibility arises. In many respects, Schlichting and Pigliucci's (1998) book takes a more stimulating approach to the evolution of phenotypic plasticity, including induced defenses.

From a technical perspective, the format of the references and index are not as useful as they might be. All 1000+ references are at the end of the book, even though fewer than 10% were probably cited in more than one chapter. In addition, readers can not, unfortunately, trace references to the pages where they are cited. The index covers seven pages, but in our two tests of its utility, we were disappointed. Under kairomone—''chemicals in interspecific signal transmission which are exclusively advantageous to the receiving organism'' (p. 195)—some relevant pages are identified but a number of others are overlooked. For example, someone wishing to locate such specific information quickly would miss a) the surprising induction of colony formation in the diatom *Scenedesmus* by exudates from the gut flora of *Daphnia* (pp. 95–96), b) the discussion of chemical cues from predators that alter patterns of depth selection behavior and diel vertical migration in *Daphnia* (p. 162), and c) the evidence that carp respond directly to chemical cues released by pike (pp. 209–211). These three examples are also not included under ''cue - chemical.'' Even some pages bearing the word kairomone are not listed (*e.g.*, p. 140, 171, 311). Similarly, ESS models appear three places in the book (pp. 40–44, 249–256, 272–278) but the index indicates only one. Perhaps a bit tongue in cheek, the index does direct inquisitive readers to pages ''1–321'' to find information on ''defenses-inducible.'' Typographical errors are few, but the one in Table 13.1 (p. 235), listing ''predatory'' bryozoans that induce morphological changes in 'prey' bryozoans, certainly made us smile.

This book is probably best read one chapter at a time, maybe over breakfast, to savor the sometimes fascinating twists of natural history without having to rummage through the primary literature. But students will likely find Travis's (1994) fine chapter on adaptive plasticity a more compact and stimulating synthesis of the central issues.

REFERENCES

Schlichting, C. and M. Pigliucci. 1998. *Phenotypic evolution: A reaction-norm perspective*. Sinauer Associates, Sunderland, Massachusetts.

Thaler, J. S. and R. Karban. 1997. A phylogenetic reconstruction of constitutive and induced resistance in *Gossypium*. Am. Nat. 149:1139–1146.

Travis, J. 1994. Evaluating the adaptive role of morphological plasticity. *In* P. C. Wainwright and S. M. Reilly (eds.), *Ecological morphology. Integrative organismal biology*, pp. 99–122. University of Chicago Press, Chicago.

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