



## Review: The Flowering of Molecular Systematics

Reviewed Work(s):

*Molecular Systematics*. by David M. Hillis; Craig Moritz  
Michael J. Braun

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mental fauna. The mere presence of early Tertiary fossils of mainland taxa (e.g., ungulates, lizards) not now found on the islands would not be "proof positive" for vicariance. Dispersal, on the other hand, according to Perfit and Williams, "... is a fact to be confronted . . ." and "The strength of the dispersal hypothesis is that it may be more often true than not."

Perfit and Williams also seek to undermine a vicariance model of West Indian biogeography by arguing against a continuous land connection between North and South America during the late Cretaceous or Paleocene as proposed by Savage (1983) and Guyer and Savage (1987). They emphatically state, "We are compelled to regard the Cretaceous-Paleocene isthmus as a hypothesis that is not only not demonstrable geologically, but that goes against the weight of the paleontological evidence." The underlining is theirs. This view is to be contrasted to that of the French paleontologist J.-C. Rage (1986), who concluded that the late Cretaceous interchange between North and South America via a terrestrial land connection is an important paleobiological event well supported by the paleontological record and recently obtained geodynamic data.

In the remaining papers of this book having substantial biogeographic content with bearing on general theory, Miller and Miller (butterflies) and Hedges and Joglar (eleutherodactyline frogs) favor a vicariance model for explanation of pattern. Burgess and Franz (freshwater fishes) present a mixed vicariance/dispersal narrative. Strictly dispersalist hypotheses are advocated for bats (Koopman) and rodents (Woods). Hedges and Joglar (eleutherodactyline frogs), Reiskind (a spider genus), Thomas (a snake genus), and Woods (rodents) include cladograms in their papers, but make a minimal or no attempt to evaluate biogeographic hypotheses based on phylogenetic relationships. I did find Thomas's interpretation of the *Typhlops* radiation in the Antilles as part of a lineage fragmented by the separation of North American and African tectonic plates in the early Cretaceous a novel idea meriting further consideration.

If by "synthesis" we imply the combining of often diverse concepts into a meaningful whole, then this book does not meet its stated goal. Williams argues that such a synthesis is premature primarily because crucial fossil evidence is lacking. The diversity of approaches and conclusions by other contributors to this volume tends to support that conclusion. To the extent that this is true, *Biogeography of the West Indies* stands primarily as a status report, a source of data, and a stimulus to future work. Although we still await a synthesis, it should be noted that there are already signs that it may be possible to accomplish (Kluge, 1989; Liebherr, 1989; Rauchenberger, 1989) or at least attempt one.

In conclusion, I ask several questions. At this time in the development of biogeography, how is it that a purported major synthesis does not include clear statements of hypotheses to be tested and the ways in which the distributions of particular taxa do or do not conform to these hypotheses? How can such a work fail to contain even one area cladogram or clado-

gram of areas? Why does not a single author compare a phylogeny to the alternate branching diagrams (geological area cladograms) for the various periods of Caribbean geology provided by Rosen (1986)? Might not these methods elucidate common features of West Indian distributions, explain differences in patterns of distribution among taxa of different ages, and form a basis for a sound theory of biogeography for the region? If the answer to the last question is "yes," it does not seem premature for biogeographers of the West Indies to begin such an undertaking.

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#### THE FLOWERING OF MOLECULAR SYSTEMATICS

**Molecular Systematics.**—David M. Hillis and Craig Moritz (eds.). 1990. Sinauer Associates, Inc., Sunderland, Massachusetts. xvi + 588 pp. \$65.00 (cloth), \$37.95 (paper).

The explosive growth of molecular systematics has been perhaps the single most dramatic event in evolutionary biology in the 1980s. Few issues of major

journals in evolutionary biology are published today that do not contain some (or many) papers concerning molecular aspects of evolution. Approximately 40% of recent grant proposals to the U.S. National Science Foundation's Systematic Biology and Population Biology programs have some molecular orientation (J. Edwards, NSF, pers. comm.). The dynamic growth of molecular systematics has created an atmosphere charged with the hope that genetic data will yield new and profound insight into the evolutionary history of virtually all groups of organisms. Yet, this growth has been driven largely by rapid developments in biochemistry and molecular genetics, fields with which many systematic biologists are basically unfamiliar. Thus, there is a lingering air of uneasiness with molecular techniques and molecular data among systematists. *Molecular Systematics* aims to dispel this uneasiness.

This book is intended as a how-to manual for molecular systematics. The editors state "Our hope is that this book can guide beginners all the way through a molecular systematic study, and at the same time provide established investigators with new ideas, techniques and approaches." The need for a single basic reference in the field has been evident for years. Yet, who could have written it? The field is a composite of several complex areas of inquiry: evolutionary biology, biochemistry, molecular biology, population genetics, and phylogenetic inference. Moreover, some of these areas, especially molecular technology and phylogenetic inference, have changed so rapidly that few molecular systematists feel completely current (or even competent!) in all areas at any one time. Hillis and Moritz approached this problem in a logical way, by organizing a multi-authored text (24 contributors) in the hope that a collection of chapters by "masters" would turn out to be a collection of masterful chapters. While some chapters are more masterful than others, the book does succeed at presenting a well-rounded introduction to the field.

The organization and structure of *Molecular Systematics* demonstrates excellent editorial foresight. After an introductory chapter giving an overview of the field and guidelines for use of the book, the 11 remaining chapters are divided into three sections: sampling, molecular techniques, and analysis. These sections represent the three major phases in the execution of a project: experimental design, data collection, and data analysis. Each of the chapters on techniques (Chapters 4-9) is arranged into five sections on (1) principles, assumptions, and comparisons of techniques, (2) applications and limitations, (3) laboratory setup, (4) protocols, and (5) interpretation and troubleshooting. A detailed Table of Contents and Index make it easy to find specific topics within the text, and a Glossary defines specialized terms and many common laboratory abbreviations.

The two chapters on sampling present an introduction on where to begin with a specific project. Baverstock and Moritz give an overview of sampling design that is very general, but will be useful to the beginner. The subject merits more attention from many experienced practitioners as well. One of the most common flaws in molecular systematic research is in-

adequate sampling of something (e.g., individuals, populations, taxa, loci, etc.). Many less-than-conclusive studies have made their way into the literature simply because some new and flashy molecular technique was used. That era is rapidly coming to a close in molecular systematics, and this chapter should hasten its end.

Dessauer, Cole, and Hafner give much practical advice on the collection and storage of tissues for molecular systematic research. Their plea for the development of long-term, well-curated tissue collections should be heeded by all systematists, whether they are of molecular or traditional persuasion. Given the time, effort, and expense required for scientific collecting and the rate at which humans are destroying the biodiversity of the planet, virtually all collecting efforts today should include preservation of tissues, whether or not the collector intends to use them immediately. Similarly, all collecting for molecular systematic purposes should include the preservation of traditionally prepared voucher material.

The section on techniques includes six chapters, each focused on a particular set of methods. These chapters are intended to give a basic introduction to each technique, its applications and limitations, and some proven protocols to get started. The chapters are all written from the perspective of an organismal biologist, and therefore provide useful insight into the applications of the techniques in systematics. However, these chapters are variable in their success at presenting the biochemical foundations of the techniques they describe. Although this topic may engender less interest from systematists, it is no less important to the successful implementation of these techniques. Also, while most protocols are accurate and usable, several are very generalized and sketchy. I doubt that a novice will get far with these, and an experienced person will go to the primary literature before trying.

The best of the technique chapters is the one by Werman, Springer, and Britten on DNA hybridization. This is not surprising, given that Britten was one of the leading pioneers of the method not only in systematics but in molecular biology as well. The chapter by Sessions on cytogenetic methods is also quite good. The treatment of isozyme electrophoresis by Murphy et al. is succinct, but impressively complete and usable. A possible addition to their compilation of stain recipes would be a table indicating those phylogenetic groups in which various isozyme loci are known to occur (e.g., plants, vertebrates, crustaceans, etc.). To my knowledge, no such summary exists, but it would provide valuable guidance to the newcomer attempting to use these recipes. The coverage of some protein techniques by Maxson and Maxson (immunodiffusion, immunoelectrophoresis, and radioimmunoassay) seems superficial. It is true that these techniques are less used today than they were in the 1960s, 1970s, and early 1980s; nevertheless, it would be better either to treat them more fully or simply to refer the reader to previous descriptions of their application.

Although the chapter by Dowling, Moritz, and Palmer on restriction enzyme analyses is generally

well written, I found their description of site mapping sketchy. A neophyte may not realize how complicated this endeavor actually is. Their transfer hybridization protocol gives no guidelines on how much probe to use (the requisite amount varies by several orders of magnitude according to the copy number of the sequence of interest) nor does it describe methods for controlling the stringency of hybridization, a central issue in comparative studies where heterologous probes are used frequently.

The chapter by Hillis et al. on sequencing gives a good overview of applications for the systematist, and certain protocols (e.g., direct sequencing of RNA) are given better treatment than in standard molecular biology manuals. However, the chapter simply covers too much ground to be very useful in the laboratory. In 53 pages, it attempts to cover molecular cloning, the polymerase chain reaction (PCR), and DNA and RNA sequencing. By comparison, a popular comprehensive manual covering these same topics (and, admittedly, many variations upon them) is in three volumes and is over 1,000 pages long (Sambrook et al., 1989). It is easy to imagine the editors' temptation to combine these topics: few molecular systematists actually generate many de novo molecular clones and there was undoubtedly pressure to contain the text in one volume. However, in reality, both cloning and PCR deserve separate chapters devoted to them.

What now seems a cramped combination of topics is also easier to understand when one considers the amazing rapidity of change in molecular technology. In 1987, when the organization of *Molecular Systematics* was laid out, PCR was a simple but interesting innovation with which molecular biologists were just beginning to toy. In 1990, when the book was published, PCR is threatening to become the dominant technique not only in molecular systematics but in all comparative molecular studies. PCR has even spawned new techniques, such as random amplification of polymorphic DNA fragments, that are sure to find wide application in studies of intraspecific variation (Williams et al., 1990).

In the chapters on techniques, there are occasional lapses in description of biochemical or physical processes underlying the protocols (the relevant determinant of sedimentation velocity is not density but molecular weight in the context described on p. 278) and a few protocols contain omissions that will cause them to fail (p. 348, protocol 9, step 9; DNA ligase requires ATP). In another instance, time lag in technology transfer may exist: nick translation is the recommended method for radioactively labeling DNA in three chapters and random priming (Feinberg and Vogelstein, 1983) is only mentioned as an alternative in one. For several years now, random priming has been a popular (often the preferred) method of labeling DNA for applications that require high specific activity, such as probing single-copy sequences in complex genomes. It is simpler to perform and easier to control than nick translation, and yields probes with specific activities up to 10 times as high. It probably deserves more coverage than it received.

Overall, I feel the chapters on techniques represent a good place to start as one tries a new method or

even enters the laboratory for the first time. However, few practitioners will work long in this field without encountering technical issues that are not addressed in this book. *Molecular Systematics* is then best used as a guide to more comprehensive manuals (e.g., Harris and Hopkinson, 1976; Ausubel et al., 1989; Sambrook et al., 1989; Innis et al., 1990). Also, one should never hesitate to contact local molecular biologists. There are some at most universities nowadays, and they are usually quite intrigued by molecular systematics projects.

Perhaps it is inevitable that a reviewer will be most impressed by those subjects she or he knows least about. If so, then it is not surprising that I found the section on data analysis to be the most valuable part of this book. In Chapter 12, Hillis and Moritz give excellent guidance on matching techniques to problems and on predictions of time from molecular data. Weir's chapter on intraspecific differentiation is quite readable. It presents a conceptual framework for the measurement of genetic relatedness within and among populations, and computer programs for the analysis of both haploid and diploid data. Finally, the outstanding chapter in the book by my reckoning was "Phylogeny Reconstruction" by Swofford and Olsen. It gives a balanced and thoughtful overview of current approaches without a trace of the chauvinism or diatribe that has become so tiresome in this field. It recognizes the unique strengths and weaknesses of molecular data, and contains much practical advice for the scientist attempting to analyze real data sets. This may be the best short introduction to phylogenetic inference available today.

Like most science, molecular systematics is a complex enterprise. It is unrealistic to think that one book can prepare the novice to accomplish meaningful research in this field. However, there has been a clear need for a guide to the field that can act as a sourcebook to the literature and get people headed in the right direction. *Molecular Systematics* was an ambitious project that aimed to fill the need, and the final product goes a long way toward accomplishing that goal. It will be a mainstay in the field for some time to come.

Darrilyn Albright, Judy Blake, and Tom Parsons contributed helpful comments on several chapters to this reviewer.

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**Advances in Neotropical Mammalogy.**—Kent H. Redford and John F. Eisenberg (eds.). 1989. Sandhill Crane Press, Gainesville, Florida. \$62.50.

This work, dedicated to Dr. Ralph Martin Wetzel, is a collection of 25 papers concerned with various aspects of Neotropical mammalogy. The book is divided into sections: Part I includes seven papers on "Studies on Neotropical Rodents: Taxonomy and Ecology"; Part II includes four papers on "Studies on the Biology of Neotropical Carnivore Ecology"; Part III includes three papers on "Studies on Relationships and Functional Anatomy of Peccaries"; Part IV includes six papers on "Studies on Distribution and Taxonomy"; and Part V includes five papers on "Studies on Neotropical Mammal Reproduction and Ecology."

As in all cases where books are composed of contributions from various authors, quality, depth of investigation, and length vary tremendously. Overall the quality of work is high. The most interesting advance is presented in the chapter by Eleanor Storrs, H. P. Burchfield, and R. J. W. Rees entitled "Reproduction Delay in the Common Long-Nosed Armadillo, *Dasypus novemcinctus* L.," in which they document a new reproductive strategy for the class Mammalia. In their study, female armadillos experienced an embryological diapause that in some cases lasted over 2 years. The longest birth after isolation from a male was a female that gave birth to four females 24 months after capture; birth was calculated to be 32 months after the estimated breeding date. Additionally, some females produced litters in successive years without exposure to male armadillos between the first and second litter.

The quality of work presented in this book is such that it will prove to be a valuable addition to the library of practicing Neotropical mammalogists. One thing that does concern me is the price of this book. During the last decade, there has been an extraordinary growth in numbers of practicing mammalogists native to and working in Neotropical countries. In visiting with many of these people, it is very apparent that they do not have the resources to purchase a volume that is this expensive. It is unfortunate that a paperback edition or some other mechanism cannot be employed that would make this work available to the growing scientific community that is restricted by limited financial resources available for library growth.

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Molecular Systematics David M. Hillis Craig Moritz Barbara K. Mable. October 1997. The Auk. Shannon J. Hackett. How molecular systematics provides insights into the complexity of urban pest biology nucleotide by January 2010. Tracie Jenkins. Molecular Systematics. Sinauer Assoc, Inc Publishers, Sunderland. 588pp. Google Scholar. Molecular systematics at the species boundary: Exploiting conserved and variable regions of mitochondrial genome of animals via direct sequencing from amplified DNA. In Hewitt, G. M., Johnston, A. W. B. & Young, J. P. W. (eds.), Molecular Techniques in Taxonomy. NATO Advanced Studies Institutes. In Hillis, D. M. & Moritz, C. (eds.). Molecular Systematics. Sinauer Assoc. Inc. Publishers.