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Evolution of Organismal Complexity

Complex Organismal Functions: Integration and Evolution in Vertebrates.—David B. Wake and Gerhard Roth (eds). 1989. John Wiley and Sons, New York. xiii + 451 pp. $122.00.

One of the most significant contributions made by cladistics to non-systematic biology has been to furnish the conceptual foundation for a modern comparative method. Increasingly, people interested in the evolution of everything from behavior to physiology and community ecology are turning to independently derived phylogenetic hypotheses of their research organisms to explore historical patterns and test evolutionary hypotheses. Nevertheless, the lessons of "historical baggage" and how to choose reference taxa when testing hypothesized adaptation have come hard in functional morphology and comparative physiology. Not everyone is a convert. It is noteworthy, then, that the influence of cladistics can be seen so clearly throughout this book, as nearly all of the contributed chapters cite phylogenetic approaches and several authors explicitly champion the value of a phylogeny. This would have been an unlikely situation just 10 years ago.

The book is the product of a Dahlem conference held to consider the question of how complex, integrated systems evolve. It is probably fair to say that this is the single greatest unifying issue that faces functional morphologists and physiologists as we enter the 1990s. The example that is used repeatedly in the book is that of the vertebrate eye. Given the eye's complexity and the intricate interconnections among its parts what are the principles and mechanisms that govern its transformation during evolution? Leading biologists were divided into four groups to consider the evolution of vertebrate complexity. The first three groups considered the evolution of specific systems; feeding mechanisms, locomotion, and viviparity. The fourth group dealt more generally with the different approaches for studying the evolution of complexity. The backgrounds of Dahlem participants are intentionally diverse and it is abundantly clear from the book that much effort was expended struggling with terminology and other problems that rise from differing perspectives.

The contributed, "background" chapters (which serve as the basis for discussions at the conference) vary in scope from summaries of a particular topic (e.g. Szekeley on the neural anatomy of locomotion) to more conceptually oriented works that propose research programs, some of them quite novel, for addressing problems of special importance (e.g. Emerson and Arnold on contrasting intra- and inter-specific relationships between morphology, behavioral performance, and fitness). This book is not so much a summary of the state of the art on the topic as it is a collection of mostly conceptually focused statements by a broad range of biologists. Indeed, the real strength of the book is that it is simply loaded with interesting discussions of many of the major concepts in this area of evolutionary biology. The popular notion of key innovations is discussed in at least seven chapters. Can a single synapomorphy be shown to underlie the subsequent diversification of a clade? Heterochrony and developmental constraints get knocked about with pleiotropy and genetic correlations in considerations of what avenues are available for changes in ontogeny and what constrains them. Hierarchies are a persistent theme and species selection enters the picture as well. I was struck by how

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differently people used these and other terms and how those differences influence their utility.

One conflict is particularly prevalent and illuminating throughout the book: the internalist-externalist dichotomy. In order to understand how forms evolve it is necessary to know what controls the generation of phenotypic variants as well as the relationship of morphological variation to behavioral performance and fitness. Not coincidentally these are currently two very hot areas of research. Developmental approaches are discussed in interesting chapters by Horder, Presley, Hinchliffe, and Wake and Roth, though the perspectives represented tend to be embryological and theoretical and no chapter considers cellular or molecular mechanisms. From the other end of this spectrum there are several chapters that offer introductory guides to research and different perspectives on the consequences of morphological variation. Chapters by Schluter, Lauder and Liem, Bennett, and Emerson and Arnold advocate research programs that focus on the relationship between morphological variation, performance, and evolutionary or ecological success. Both population level studies and phylogenetic perspectives are presented, sometimes in the same chapter (e.g. Schluter). All four of these chapters make excellent reading and probably foreshadow a major thrust in research on the evolution of complex functional systems.

One novel feature of the Dahlem format is that each group produces a position paper that summarizes the major conclusions reached through discussions by the group and presents a list of areas of particular promise for future research. I enjoyed these chapters, though for different reasons in each case. The group concerned with feeding mechanisms of vertebrates proposed that the pattern of integration and evolution in the feeding mechanism is different from that found in the locomotor apparatus. Citing several possible causes it is claimed that there is greater diversity in vertebrate feeding systems. Notwithstanding the difficulties of quantifying the 'diversity' of feeding and locomotor systems, this is a novel idea that makes use of many of the concepts that surface throughout the book. The idea illustrates much that is interesting about the evolution of complex systems but it also exemplifies key difficulties in studying them. For example, it is likely to be just as challenging to test critically this hypothesis as it has been to test proposed key innovations.

The group report on the evolution of viviparity reveals great difficulty in arriving at a satisfactory definition of their topic, "viviparity". It is made clear that this is due largely to the fact that independent origins of viviparity have been accomplished through different means in different lineages. Reproduction is a very complex phenomenon and it appears that synchronizing the separation of parent from developing offspring with their release from egg or fetal membranes can be accomplished through many different modifications. This appears to be a stellar example of how the same functional "solution" can be arrived at through many different structural alterations in the system.

In summary, the book strikes a nice compromise between reviewing what we have learned about the evolution of specific complex systems, and identifying what lies ahead. Several powerful research programs are literally outlined by way of suggestions for how to proceed with pending challenges. Because the participants of Dahlem workshops are so diverse the book offers few comprehensive guides to single aspects of the issue at hand, but as a collection of viewpoints on how to deal with the general problem of the evolution of complex systems the book strikes admirably at one of the most universal problems faced by organismal biologists.—**Peter C. Wainwright, Department of Biological Sciences, Florida International University, Miami, FL 33199, U.S.A.**