

## BOOK REVIEWS

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### COMPREHENSIVE REFERENCE FOR EVO-DEVO OR COLLECTIVE CHALLENGE TO NEO-DARWINISM?<sup>1</sup>

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One way to capture the goals, directions, and vitality of a field of science is to analyze the terminology and concepts that scientists working in that field are using. In this regard, *Keywords and Concepts in Evolutionary Developmental Biology* is an attempt to define the current goals and future directions of the relatively new field of “evo-devo,” which, as the term implies, attempts to unite the disciplines of evolutionary and developmental biology. As John Tyler Bonner points out in the preface, “There has been a remarkable explosion of interest in evolutionary developmental biology in the last twenty years. . . .” This interest has led to many surprising and controversial discoveries that have challenged the way we think about key words and concepts in evolutionary biology. In this timely volume, Brian K. Hall and Wendy M. Olson have brought together more than 60 scientists from a variety of disciplines to document how the meanings of key words and concepts have been impacted by the recent rise of evo-devo.

I expected this book to be similar to its predecessor, *Keywords and Concepts in Evolutionary Biology*, by Evelyn Fox Keller and Elisabeth Lloyd. Both list key words and concepts in alphabetical order, and both are meant to be used by scientists as works of reference. Thus, I was expecting a series of encyclopedia-like entries, in which each author presented a balanced view of each topic, showing the current discourse among researchers currently working in the field of evo-devo. But after examining Hall and Olson’s book more closely, I realized that the goals of these two similarly titled volumes are fundamentally different. The goal of Keller and Lloyd’s book was to provide a philosophical and linguistic analysis of the discourse among working scientists, whereas the goal of Hall and Olson’s book is to reveal something unique about mechanisms of evolutionary change. In fact, Hall and Olson open the introduction with “This book deals with evolutionary change, especially those mechanisms involving embryonic development as the vehicle for evolutionary change.” They claim that the field of evo-devo is just beginning to understand the developmental and evolutionary processes that give rise to what they call “evolutionary developmental mechanisms,” which they define as “the processes of development that mediate descent, whether descent involves modification or stasis.” Thus, this book has a dual identity; on the one hand, it is meant to be used as a com-

prehensive work of reference, but on the other, it is meant to reveal something unique about the evolutionary process.

#### *A comprehensive work of reference?*

A work of reference should in principle attempt to deliver a balanced treatment of each topic it covers. However, this is not the case for *Keywords and Concepts in Evolutionary Developmental Biology*. Hall and Olson have encouraged the authors to present their own perspectives on the current state and future direction of their assigned key word or concept. Needless to say, the authors vary greatly in their approach, style, and depth of coverage. Some authors attempt to bolster the importance of their topic to the mainstream of evolutionary biology or present a new conceptual foundation, while other authors attempt to simply summarize the current state of knowledge or provide a historical framework. A good example of these contrasting approaches is Melanie Stiassny’s essay on “Atavism,” and Anne Burke and Susan Brown’s essay on “Homeotic Genes in Animals.” Stiassny presents a novel framework for the term “atavism,” which is “the reappearance of a character state typical of a remote ancestor in an individual that really shouldn’t have it.” She argues that atavisms, such as the sporadic appearance of hind limb rudiments in modern cetaceans, suggest that there exists latent epigenetic potential in evolving systems. She remarks, however, that the importance of atavism is often sidelined and viewed as irrelevant to the evolutionary process. She then challenges this view by defining phylogenetic character reversal as a type of atavism, which she calls a “taxic atavism.” Taxic atavisms, which are frequent and reappear in taxa over large phylogenetic distances, are relevant to the evolutionary process and can be used to study the mechanisms underlying evolutionary transformation. In contrast, Anne Burke and Susan Brown present a complete summary of the current state of knowledge on Hox genes and their relatives. They detail the classification, distribution, and function of several Hox genes, and highlight their significance for developmental and evolutionary studies.

Although such variation makes this book uneven as a work of reference, it also makes it multifaceted and useful for different purposes and audiences. Entries that summarize the current state of knowledge in a particular field, such as Burke and Brown’s entry on “Homeotic Genes in Animals,” will be most appropriate and useful for undergraduates or scientists unfamiliar with the field of evo-devo. In contrast, those entries that try to present their topic in a new light, such as Stiassny’s entry on “Atavism,” will be more ap-

<sup>1</sup> *Keywords and Concepts in Evolutionary Developmental Biology*. Brian K. Hall and Wendy M. Olson, eds. 2003. Harvard Univ. Press, Cambridge, MA. 496 pp. HB \$59.95, ISBN 0-674-00904-5.

appropriate for debates and discussions in graduate seminars. Still other entries, such as Graham Budd's on "Animal Phyla," are useful for providing directions for future research. Budd suggests, for example, that a critical study of the shared developmental features of living sponges is crucial for elucidating the origins of the Metazoa.

Most, if not all, of the relevant key words and concepts of evo-devo are contained within this volume. Although the selection of terms for this kind of book is to some degree arbitrary, terms that abound in the evo-devo literature, like "Homology," "Constraint," "Evolvability," and "Gene Regulation" are present and are discussed elegantly by prominent researchers in the field. It is abundantly clear, however, that Hall and Olson have chosen to include many key words and concepts that emphasize the role and influence of the environment on development and evolution, such as "Inheritance: Extragenomic," "Epigenesis and Epigenetics," "Environment," and "Canalization and Genetic Assimilation." By including such terms, Hall and Olson are sending the message that the role of the environment in influencing developmental and evolutionary processes is a crucial, yet underrepresented part of the growing field of evo-devo.

After having read this book by randomly jumping to different chapters, I realized that the readers are likely to miss this important message, as well as what Hall and Olson mean by the term "evolutionary developmental mechanism." Thus, I decided to go back to the beginning, and read all the entries as one would read a singly authored book. Only then did it become clear that Hall and Olson's concept of an evolutionary developmental mechanism embodies a collective challenge to neo-Darwinism.

#### *A collective challenge to neo-Darwinism?*

Neo-Darwinism can be briefly characterized by the idea that mutation, recombination, natural selection, and other processes operating within species are the principle cause of changes in genes and their corresponding phenotypes, and that these processes account for the major, long-term features of evolution. Hall and Olson have included several entries that appear to challenge this neo-Darwinian paradigm. The following entries: "Behavioral Development and Evolution," "Developmental Systems Theory," "Developmental Processes that Generate Plant Form," "Epigenesis and Epigenetics," "Inheritance: Extragenomic," and "Ontogenetic Integration of Form and Function" are particularly good examples; their authors challenge this paradigm by contemplating the idea that environmental or epigenetic influences during development play a creative role in the evolutionary process.

For example, Gilbert Gottlieb, in his entry on "Behavioral Development and Evolution," revives an old idea, known as the Baldwin effect (Baldwin 1896), to argue that the classical neo-Darwinian view alone is insufficient as an explanation for the origin of new species. The Baldwin effect, which Hall and Olson would consider an evolutionary developmental mechanism, can be described as follows: first, environmental changes during development may potentially induce a shift in behavior that results in the formation of a novel phenotype; second, this novel phenotype is maintained by forming a new

relationship with the environment; and third, after long-term geographic or behavioral isolation from the original population, a change in gene frequencies stabilizes the novel phenotype on an evolutionary timescale. Gottlieb provides several examples in support for this evolutionary developmental mechanism, and notes that, in this case, natural selection is not the principal cause of the new adaptive phenotype, but rather serves as the filter through which novel phenotypes must pass.

Taken together, these and many other entries spread throughout the book, collectively challenge an important tenet of the neo-Darwinian paradigm—that mutation and recombination of genes alone are sufficient as the raw material of evolution. Evolutionary developmental mechanisms primarily focus on the phenotype, and on the underlying developmental processes that produce it. Phenotypes and the developmental processes that produce them are subject to selection. Thus, environmentally induced phenotypes, which are unaffected by genetic differences from the "normal" phenotype, should be considered as much the raw material of evolution as are mutations and recombination in genes. This challenge highlights an important and controversial debate in evolutionary biology between neo-Darwinians, with a genetic perspective on the role of environmental influences during development (e.g., Via et al. 1995; Schlichting and Pigliucci 1999), and evolutionary developmental biologists who believe that the relationship between the genotype and phenotype is too complex to assume a gene-centered view of evolution (e.g., Ho and Saunders 1979; West-Eberhard 2003).

This important and controversial battle will undoubtedly be fought within a new subdiscipline of evo-devo that is becoming known as "ecological developmental biology" or "eco-devo" (Gilbert 2001). Eco-devo, which primarily concerns itself with the role and influence of the environment on development and evolution, has been reinvigorated by the publication of a number of recent books and conference proceedings (e.g., Schlichting and Pigliucci 1999; Gilbert and Bolker 2003; West-Eberhard 2003; Hall et al. 2003). In this context, *Keywords and Concepts in Evolutionary Developmental Biology*, with its emphasis on evolutionary developmental mechanisms, will serve to further define and perhaps even lead this newly emerging subdiscipline.

I highly recommend this multifaceted book, as it will clearly serve many purposes, such as a reference for teaching, source for discussions in graduate seminars, and, in many cases, as ideas for future research. Hall and Olson's concept of an evolutionary developmental mechanism and its importance for evolutionary biology can best be appreciated by reading the book from cover to cover—which might have been avoided if they had chosen to arrange the entries by subject matter rather than alphabetically. The alphabetical ordering scheme also makes it difficult for the reader to draw any links between evolutionary developmental mechanisms at different hierarchical levels, such as those that exist at the level of cells and behavior. Organizational criticisms aside, I recommend that anyone working in the field of evo-devo or who is interested in entering the field should have this book.

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