

Book Review

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The Shape of Life: Genes, Development, and the Evolution of Animal Form. By Rudolf A. Raff. Chicago and London: The University of Chicago Press, 1996. Pp. 520. \$29.95.

This is a very readable and important book that illuminates the early stages of the ongoing synthesis of evolutionary and developmental biology. This synthesis, which continues to influence biologists working at all levels of analysis, may be seen as a continuation of the events of the 1930s and 1940s, when population geneticists, systematists, and paleontologists together developed a common vocabulary and intellectual framework for the study of evolution. Embryologists, who at the time were no longer asking evolutionary questions, were excluded from the synthesis. Along with comparative morphologists, embryologists had been at the forefront of evolutionary investigations during the decades immediately following the publication of *The Origin of Species*. However, increasingly ambiguous results from the testing of recapitulation theory had led them to turn from evolutionary investigations and instead to concentrate on the mechanisms of embryonic development. During the early years of the twentieth century, many disenchanted embryologists and morphologists adopted the new science of experimental genetics as a more fruitful program of research. Until the evolutionary synthesis of the 1930s and 1940s, the geneticists followed their own independent lines of research on evolution, which were often at odds with the other research traditions.

Now, the embryologists are back, and they are asking evolutionary questions. The current generation, today's developmental biologists, is equipped with both classical and molecular techniques for identifying genes and unraveling developmental programs. The realization that homologous regulatory genes are involved in organizing the body plans of many disparate phyla had immediate evolutionary implications, with the origins of these genetic programs rooted deep in the phylogenetic tree of animal life. Furthermore, an understanding of developmental constraints on variation in form can be brought to bear on the understanding of macroevolution. A major principle of the neo-Darwinian evolutionary synthesis, that the accumulation of microevolutionary events over geologic time can explain macroevolutionary events, has grown untenable. In other words, changes in allele frequency have become an increasingly unsatisfactory way of explaining the origin of major taxa, but the novel classes of genes studied by developmental biologists are inspiring new ideas about the processes and patterns of evolution. Raff has been a pioneer in this field at his lab at the University of Indiana, where he

and his coworkers have used evidence from 18S rRNA to reconstruct the relationships between the major animal phyla.

In the first chapter of this book, Raff elucidates the historical relationship between evolutionary biology and developmental biology, or, as was the case for a long time, the lack of relationship between the two fields. He manages to convey a lively sense of both the investigators and their investigations, and he maintains this focus throughout the book.

In chapters 2–5, Raff describes the use of the concept of homology, in the comparison of metazoan body plans; the importance of having adequate tools for the testing of phylogenetic hypotheses; the advantages and disadvantages of the use of molecules, to determine phylogenies; and the nature of the evidence used to reconstruct the history of life. Raff is more knowledgeable about molecules and embryos, but he makes frequent reference to the fossil record as the most direct source of information about the form and structure of past organisms.

The remaining chapters are the main strength of the book. In his discussion of the developmental basis of metazoan body plans, Raff emphasizes the importance of the phylotypic stage, the stage during embryonic development when all the genes that control the construction of the body plan characteristic of that particular animal's phylum are expressed. Before and after the phylotypic stage, there is a great deal of flexibility in the development of an organism. Raff describes the evolutionary implications for this pattern. He goes on to describe the various forms of heterochrony, in which changes in the rate of development provide a source of evolutionary variation, although, as Raff stresses, heterochrony is not the only developmental mechanism that can constrain the course of evolution. Raff really hits his stride when he describes the modular nature of developing organisms, the ability of the modules to dissociate from one another, and the co-option of modules during the creation of new developmental patterns. In his summary chapter on the evolution of new body plans, Raff invokes once again the recurring themes of change and constancy.

In *The Shape of Life*, Raff provides a vivid account of current developmental evolutionary thinking, and he backs it up with the basis for that thinking. It is a lively text, enhanced with colorful and pertinent narratives illustrative of the scientific process. This book is recommended to all geneticists and to anyone else interested in the latest thinking about the nature of life.

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