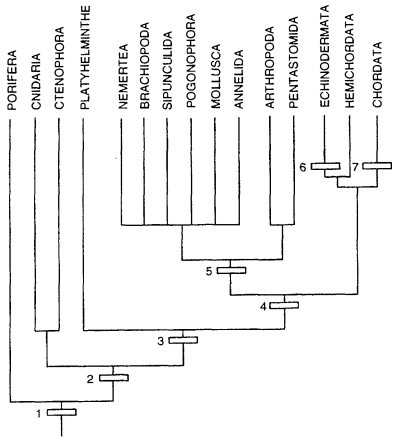
BOOK REVIEWS

Understanding Evolution: The Next Step

The Shape of Life. Genes, Development, and the Evolution of Animal Form. RUDOLF A. RAFF. University of Chicago Press, Chicago, 1996. xxiv, 520 pp., illus. $55 or £43.95; paper, $29.95 or £23.95.

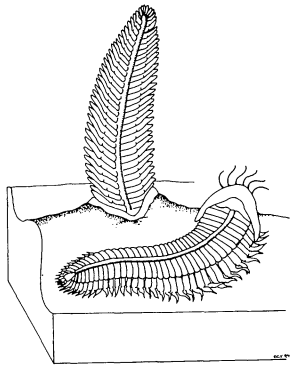
Evolution, as Leigh van Valen once put it, can be viewed as "the control of development by ecology." While this definition obviously omits quite a few details, one could argue that it encapsulates much current thinking in evolutionary biology. It especially captures the emphasis that many workers place on environmental factors as the directional force of evolutionary change. But what about intrinsic factors? Evolutionary biologists have long known that ecology's "control" over development is far from total. The highly contingent nature of the assembling of a complex organism sets major constraints on the amount of developmental tinkering that can be done by evolution.

In this well-written and insightful book, Rudolf Raff helps evolutionary biology take the "next step": to move beyond vague and theoretical discussions of the role of "developmental constraints" in evolution and begin the task of gathering solid empirical data on developmental (and underlying genetic) mechanisms of evolutionary change. This is a tall order that will require serious long-term interdisciplinary investigations among fields, such as developmental biology, paleontology, and anthropology, that have historically had little or no interaction.



"Some important events in regulatory evolution mapped onto a metazoan phylogeny. Significant regulatory innovations include: 1, multi-cellularity; 2, tissues; 3, anterior-posterior axis and central nervous system; 4, Hox gene expression in patterning of the protostome and deuterostome body axes and central nervous systems; 5, metameric segmentation (lost in some phyla); 6, pentameral symmetry; 7, neural crest and amplification of Hox clusters. The tree is based on 18S ribosomal DNA results from several laboratories." [From *The Shape of Life*]

As Raff has taken the time to read deeply and widely among these diverse fields, this book shows that such interactions are not only possible but can be enormously fruitful. It is enlightening, for example, for a paleobiologist like myself to see Raff's expertise in molecular and cellular biology applied to the famous Cambrian "explosion" of complex life. He draws from such diverse lines of evidence as molecular biology, cladistics, genetics, developmental biology, and the fossil record to try to understand why body plans "rigidified" in the early Paleozoic Era, with subsequent evolution consisting largely of relatively minor variations on those more basic developmental themes. In so doing, he shows why many of the simplistic explanations that have traditionally characterized discussions of development and evolution need to be re-examined. Recapitulation, via terminal addition, is one of the best-known misconceptions.



"Two reconstructions of the Ediacaran fossil *Spriggina*, as an annelid and as a vendobiotan frond. The two representations illustrate the range of interpretations that have been made of the fossils by various investigators. [From *The Shape of Life*; drawing by E. C. Raff]

But even many concepts, such as heterochrony and regulatory genes, that are still often used today to relate development and evolution are shown to be widely misunderstood. The discussion of heterochrony (evolution by change in "developmental timing") is especially illustrative in this respect. Heterochrony, as Raff notes, has been the "single most pervasive idea" in evolutionary developmental biology. He argues that heterochrony can sometimes be more productively viewed as a result, not a process, of more fundamental "non-heterochronic" changes such as those that occur in cell-cell interactions.

While showing how the evolution of development is often more complex than we have thought, the book seeks to find hints of basic "laws" of evolutionary developmental biology. Three such basic principles that emerge are modularity, dissociation, and co-option. Development generally consists of modular assembly whereby the modules can be dissociated, duplicated, and co-opted. Genes, also, can be duplicated and co-opted, as illustrated by extensive discussion of homeobox-containing genes.

Stylistically, the book is informal and entertaining, with many personal anecdotes. It is written at a level that makes it accessible to interested readers from many backgrounds. This may explain the omission of the publication year when authors are cited in the text. While this enhances the informal style, it is a serious problem to the scientist who wants to find a reference. When Raff refers to Gould, for instance, in various parts of the book, it is not always clear which one of Gould's 10 works in the reference list is being discussed. On the positive side, the book omits the rhetoric and ideological baggage that have historically hounded discussions of evolution and development. In fact, Raff does an exceptional job of criticizing and clarifying current ideas in a fair-minded way. He discusses, for instance, how scale matters: a paleobiologist may find it useful to define and analyze heterochrony in a way that a developmental biologist does not.

In brief, this is arguably one of the most important books of the decade in evolutionary biology. Its relevance, breadth, scholarship, currency, and key insights make it a substantial contribution toward our efforts to unite disparate fields into a science of "evolutionary developmental biology," to borrow from Brian Hall's 1992 book with that name. It is a nice antidote to John Horgan's apocalyptic *The End of Science* (Addison-Wesley, 1996), which argues that fragmentation of science is producing diminishing returns. This book shows how scientists can overcome the peer and funding pressures promoting specialization and go on to make the interdisciplinary discoveries that may be the future of science.

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