

REVIEWS

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MORPHOGENESIS AND EVOLUTION. By Keith Stewart Thomson. 1988. Oxford University Press, New York, New York 10016. 154 p., \$29.95 (hardcover).—The last few years have witnessed a surge of interest in the relation of developmental processes to evolutionary change. This is reflected in the onslaught of books, beginning with Gould's 1977 volume *Ontogeny and Phylogeny*, with titles involving permutations on a few key words such as evolution, development, and ontogeny (Bonner, 1982; Goodwin et al., 1983; Raff and Raff, 1987). Among the latest of these is *Morphogenesis and Evolution* by Keith Stewart Thomson.

Thomson's focus is on "the mechanisms affecting the expression of variation among individual phenotypes" (p. 3), particularly those responsible for morphogenesis, or the determination of form and pattern. This is reflected in the book's organization. Following introductory chapters which attempt, among other things, to couch the development-evolution relation in the broader context of hierarchical processes in biology, several chapters are concerned with various aspects of morphogenesis, including one devoted exclusively to "early pattern formation" in amphibians (i.e., from unfertilized egg to neurulation). Closing chapters address evolutionary patterns and problems for which development may provide needed insights and understanding.

The book raises some provocative issues, and many of Thomson's points are well taken. For example, he challenges the recent focus on heterochrony as a, if not the, primary developmental factor in evolutionary change, by asserting that "the number of cases in which heterochronic mechanisms are the sole or principal cause of significant innovation, as opposed to within-group diversification, are probably rather small." Instead, he suggests, the appearance of truly novel phenotypes betrays a more fundamental "developmental reprogramming," thereby echoing similar suggestions of de Beer (1958) and, more recently, Roth and Wake (1985).

At the same time, much of the book's promise, set out in early chapters, remains unfulfilled at its end. Despite one of the book's central tenets that developmental processes form an invaluable link between genetic and phenotypic variation and that a more complete theory of evolution must incorporate knowledge of developmental process and pattern, many of the seemingly most relevant developmental phenomena receive scant attention. Two of these are developmental genetics (including gene regulation) and pattern formation (particularly molecular aspects and mathematical modeling), both of which can make important contributions to our understanding of both the rate and pattern of evolutionary change. Moreover, while unabashedly championing a greater place for developmental biology in evolutionary theory, Thomson misses the opportunity to offer (or at least promote) a more rigorous assessment of the potential of developmental processes to provide viable explanations for evolutionary phenomena. One of the areas in which this would have been most helpful is the concept of developmental constraints. While only a few years ago the question of the reality of developmental constraints engendered widespread and often acrimonious debate, I think it is fair to say that today even the most ardent selectionist will concede that developmental mechanisms do limit the spectrum of organic form in some real sense. What is now needed are detailed case studies that: 1) critically evaluate the relative contributions of both intrinsic (i.e., developmental) and extrinsic (natural selection) factors to phenotypic variation in particular lineages; and 2) explore the relation of developmental processes to (including possible constraints on) processes at higher levels of the evolutionary hierarchy, such as taxonomic diversity, rates of speciation, and population size.

These limitations only underscore what is perhaps the most fundamental problem now confronting the field of development and evolution: that those people who may have the most to contribute to its progress—developmental biologists—are demonstrably reluctant to do so. For example, Jonathan Slack (1988) a noted developmentalist who specializes on early am-

phibian development, recently commented that, "we [developmental biologists] don't know enough about the development of any organism to tell the evolutionary biologists anything that they would find interesting." Yet, that this is not the case is readily exemplified by the recent work of Hall (1984, 1987) with vertebrates, and Raff and colleagues (Parks et al., 1988; Raff, 1987) with invertebrates. Until a larger number of developmental biologists come to view evolutionary and comparative biology as a primary and legitimate focus of their work, the commendable and valuable efforts of biologists trained in other disciplines will remain incomplete.

LITERATURE CITED

- DE BEER, G. R. 1958. Embryos and ancestors, 3rd ed. Oxford University Press (Clarendon), London, England.
- BONNER, J. T., ED. 1982. Evolution and development. Springer-Verlag, Berlin, West Germany.
- GOODWIN, B. C., N. HOLDER AND C. G. WYLIE (EDS.). 1983. Development and evolution. Cambridge University Press, Cambridge, England.
- HALL, B. K. 1984. Developmental processes underlying heterochrony as an evolutionary mechanism. *Can. J. Zool.* 62:1-6.
- . 1987. Tissue interactions in the development and evolution of the vertebrate head, p. 215-259. *In: Developmental and evolutionary aspects of the neural crest.* P. F. A. Maderson (ed.). John Wiley & Sons, New York, New York.
- PARKS, A. L., B. A. PARR, J.-E. CHIN, D. S. LEAF AND R. A. RAFF. 1988. Molecular analysis of heterochronic changes in the evolution of direct developing sea urchins. *J. Evol. Biol.* 1:27-44.
- RAFF, R. A. 1987. Constraint, flexibility, and phylogenetic history in the evolution of direct development in sea urchins. *Devel. Biol.* 119:6-19.
- , AND E. C. RAFF (EDS.). 1987. Development as an evolutionary process. A. R. Liss, Inc., New York, New York.
- ROTH, G., AND D. B. WAKE. 1985. Trends in the functional morphology and sensorimotor control of feeding behavior in salamanders: an example of the role of internal dynamics in evolution. *Acta Biotheor.* 34:175-192.
- SLACK, J. 1988. Review of *A Theory of the Evolution of Development*, by W. Arthur. *British Society for Developmental Biology Newsletter*, no. 18:12-13.
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- ALTERNATIVE LIFE-HISTORY STYLES OF ANIMALS. Michael N. Bruton (ed.). 1989. Kluwer Academic Publishers, 101 Philip Drive, Norwell, Massachusetts 02061. 616 p., \$215.00 (hardcover).—This collection of 24 papers had its origin at a conference in Grahamstown, South Africa, in June 1987. As stated in the preface the motivation for the conference arose out of the fascination of the editor, Michael Bruton, for the ideas of Eugene Balon. Thus, the overall intellectual drive of this volume is skewed to the views of a particularly radical ichthyologist. Balon, in turn, is enamored with the ideas of the "epigeneticist," Søren Løvtrup, who has also contributed a paper. If you believe that all there is to evolution is natural selection, you'll hate this book. You may also not like it because these several dominating figures use this opportunity to further develop their personal vocabulary of evolution while seeming to ignore much of what is relevant in the current literature. This fractures the volume into two parts which I'll call the normal and the radical.
- Fifteen of the 24 papers are written by South African ecologists. Six papers deal with fishes, two with frogs, and one with reptiles. Of the remaining 15, five deal with mammals, five with invertebrates, two with birds, and three are not taxon specific. The majority of the papers are normal descriptive studies of inter-specific differences in life-history features of a particular group. Among these are Christine Flegler-Balon's thoughtful review of direct and indirect development in fishes which has a good discussion of Eugene Balon's interesting views on altricial and precocial development, and Bill Duellman's solid review of reproductive modes in anuran amphibians. William Branch produces an overly ambitious review of inter-specific clutch size variation, neoteny, hermaphroditism, parthenogenesis, sex determination, parental care, and viviparity in reptiles and for the most part simply documents that there is a lot going on in the group. Most of the authors interpreted the concept of "alternative life-histories" as meaning that there are differences in life-histories among species. The term "alternative" could easily be dropped from the title.
- One of the most surprising features of this collection is that many authors invoke r- and K-selection as a post hoc explanation for the variation observed in their group in a fashion reminiscent of the 1970s. For example, Ward states in his paper on plovers that "clutch sizes of temperate-zone birds are often larger (and