TIME FOR A CHANGE?

Beyond Heterochrony: The Evolution of Development. Miriam L. Zelditch, ed. Wiley-Liss, New York, 2001. 371 pp., illus. $99.95 (ISBN 0471379735 cloth).

This book is a collection of 10 studies that aim to move "beyond heterochrony." To understand where the authors might be going, it is necessary to understand where they are coming from.

Heterochrony has a long history. The term, meaning "different timing," is one of many coined by Ernst Haeckel, the great German popularizer of evolution, in the late 19th century (others include ontogeny, phylogeny, and ecology). Haeckel is best remembered among biologists for his biogenetic law, which states that "ontogeny is the brief and rapid recapitulation of phylogeny." In other words, in individual development (ontogeny), the individual passes through all of the stages of evolutionary development (phylogeny). Heterochrony originally described evolutionary changes that did not conform to the biogenetic law—such as the heart developing earlier in mammals (relative to other features) than its phylogenetic appearance would warrant. It is currently defined in broader terms as any evolutionary change in the rate or timing of development.

For Haeckel, heterochrony was an annoyance because it disguised the true record of phylogeny hidden in development. However, in the early 20th century the concept was given a more positive spin, as a mechanism of evolutionary change that resulted in the appearance of novel adult morphologies. In particular, it was recognized that an evolutionary loss of terminal developmental stages could occur, producing a juvenilized descendant (paedomorphosis). Walter Garstang's hypothesis of the origin of vertebrates from a tunicate larva is one well-known example of such a theory. Both change in the relative timing of different processes and truncation of the entire ancestral ontogeny are now generally considered types of heterochrony (local and global, respectively).

The modern phase in the history of the term began in 1977, with the publication of Stephen Jay Gould's *Ontogeny and Phylogeny*. Gould continued the earlier work of Gavin R. de Beer by systematizing the terminology for the ways in which ontogeny could be related to phylogeny. In perhaps his most original contribution, he tied heterochrony to ecological theory by pointing out that paedomorphosis by progenesis (sexual maturation at a small size) would be typical of *r*-selected species, while paedomorphosis by neoteny (retention of juvenile morphology into the adult stage) would be typical of *K*-selected species.

Gould's classification of heterochronic modes was carried further in the seminal paper by Alberch et al. (1979), providing the starting point for most modern work on heterochrony. Since then, a large body of work has been done analyzing the evolution of development from within the framework of heterochrony, and several books on the subject have appeared (e.g., McKinney and McNamara 1991). At the same time, controversy has arisen over the usefulness of heterochrony, and especially the degree to which it can be considered a mechanism of evolutionary change. For some, such as McKinney and McNamara, heterochrony is "the cause of most developmental alterations," whereas

for others (e.g., Raff 1996), it is at best a description of a small subclass of evolutionary changes in ontogeny.

As Brian Hall says in a short foreword, this book truly lives up to its name; each of the authors has attempted to move beyond heterochrony. Four of the chapters (by Ross Nehm; Mark Webster, H. David Sheets, and Nigel Hughes; Robert Guralnick and James Kurpius; and Peter Roopnarine) use morphometric analyses to rigorously test hypotheses of global shape heterochrony. These authors take heterochrony to mean that there is no significant difference in the ontogenetic trajectory for shape between species, only a difference in termination point. Thus heterochrony can be used as a null hypothesis for morphometric analysis. (Roopnarine uses its opposite, "nonheterochrony," as his null hypothesis.) Nehm examines a clade of snails, Webster and colleagues a clade of trilobites, Guralnick and Kurpius ecomorphological variation in the snail *Littorina saxatilis,* and Roopnarine a number of species of the bivalve *Chione.* Only Nehm finds that heterochrony can explain the evolutionary transformations seen; in the other cases, at best only some of the changes seen could be interpreted as heterochronic. An important point made by several authors is that analyses of shape that contain only one dimension (such as an allometric coefficient), as many previous studies have, must necessarily view any change as heterochrony.

The other chapters are very heterogeneous. Two also focus on heterochrony. Michael Shapiro and Timothy Carl show that the reduction in digits seen in the three-digit morph of the skink, *Hemiergis,* cannot be interpreted as a simple truncation of the pattern of limb development in the four-digit morph. David Parichy, examining pigment pattern evolution in ectothermic vertebrates, asks whether heterochrony of cellular behaviors might explain apparently novel morphologies, as has been suggested by previous authors. He finds no convincing evidence of this.

The remaining chapters explore various nonheterochronic models for the evolution of development. Miriam Zelditch, H. David Sheets, and William

Fink examine the evolution of growth gradients, using an example from piranhas, and show that spatial patterns of growth are very complex and are not evolutionarily conserved among species. P. David Polly, Jason Head, and Martin Cohn look for correlation between the number of trunk versus tail vertebrae in snakes to test whether they are separate developmental "modules," which has been suggested to be a necessary prerequisite for ontogenetic dissociation. Larry Hufford examines the evolution of ontogenetic sequences, focusing on an example from the androecial (stamen) ontogeny of the Hydrangeaceae, and shows that his method of analysis provides a powerful way to study changes in these sequences, whether or not they are heterochronic. Finally, Michael Frohlich describes an evolutionary scenario for the origin of the angiosperm flower involving heterotopy (another Haeckelian term), in which the flower derives evolutionarily from an ancestral male flower with ectopic (out of place) ovules grafted on.

Although the contributions are varied, the book doesn't reflect the breadth of current research on the evolution of development, as the subtitle might suggest. For example, none of the recent work on evolutionary developmental genetics, synonymous with "evo-devo" for many, is here. Work on sequence heterochrony (Smith 2001) is also missing. Perhaps a better title might have been *The Limits of Heterochrony,* because most chapters explore areas in which heterochronic explanations are possible, but inadequate.

The common theme that emerges from this volume is that heterochrony provides a restricted framework for studying the evolution of development—many other evolutionary changes in patterns of development are not only theoretically possible but can be shown to occur. The studies herein thus provide little support for the notion that developmental patterns are evolutionarily conserved ("constrained"), with changes in rate or timing (heterochrony) the most common type seen. In one respect, this is heartening, because it suggests that the field of evolutionary developmental biology is becoming more sophisticated and subtle in its analysis.

On the other hand, as we move beyond heterochrony, it is unclear exactly where we are going. The great strength of the heterochronic framework provided by Alberch et al. (1979) was that it suggested that ontogenetic evolution might be governed by relatively simple laws. If the relationships among ontogenies are much more complicated than envisioned in heterochronic models, then what framework should be used to study ontogenetic evolution? Should studies of the evolution of ontogeny focus on the mechanistic changes underlying the divergence of morphologies, or should they characterize the evolution of the ontogenetic patterns, in all their complication? This book doesn't provide definitive answers to these questions, but it does make it clear that the era in which all evolutionary change in ontogeny could casually be ascribed to heterochrony is indeed over.

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