The resurrection of recapitulation

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A Theory of the Evolution of Development. By Wallace Arthur. *Wiley: 1988. Pp. 94. £14.95, $34.95.*

LARGELY because of the spectacular success of developmental genetics, the main problems of embryonic development have been well publicized and are seen as central to understanding biology. Yet we are still struggling to incorporate development as a key part of evolutionary theory. This is a curious problem, because even Darwin recognized that development provides information on evolutionary history. Later it was realized that there is a crucial mechanistic connection, in that development translates genotype into phenotype. Why have we not yet managed to build a theory of evolution that satisfactorily incorporates development as well as genetics?

Wallace Arthur suggests that evolution and genetics were readily fused because both fields had powerful unifying laws, whereas development has not been absorbed because it lacks such a unifying theory. *A Theory of the Evolution of Development* is an attempt to provide this missing theory, and to show how it allows an integration of development with evolution — a tall order indeed.

Arthur presents some novel ideas and a coherent point of view, and his book has the great virtue of being concise yet clear. It is divided into five sections. The first presents Arthur's theory of the morphogenetic tree, which constitutes a theoretical model for development. Subsequent sections consider interactions between this model and selection, mechanisms for the principal evolutionary transitions, relationships to other theories, and an application of morphogenetic-tree theory to the evolution of higher taxa.

The morphogenetic tree is a diagrammatic construct that represents ontogeny as a tree, with causal connections between hierarchical levels represented as the branches. The tree has a basal point representing an initial 'morphogenetic heterogeneity'. As the tree forks, along the axis of developmental time, further levels of heterogeneity are added. The entire course of an ontogeny can be depicted in this way, and evolutionary changes of various sorts are readily visualized. This model is extremely simple and understandable, and it allows predictions to be made. But heuristic elegance comes at a high cost. To achieve simplicity, the nature of developmental processes is ignored, and some very static (and demonstrably incorrect) assumptions about development have to be built in.

The most serious explicit assumption is that genes acting early in development have larger effects on adult phenotype than those acting later. Such a view is not new, and it seems to make sense. But it is a gross oversimplification, and it leads to a number of misleading predictions about development and how development must evolve. Thus most evolution by this model must be by addition of new steps near the end of development, a view very much in line with Haeckel's classic concept of recapitulation. Conversely, according to the model, evolution in early development must be much rarer and involve macromutations to other viable states, that is "morphological windows". Arthur presents some thought-provoking ideas on how such events might occur.

The problem with this outlook is that it ignores the ugly fact that early development frequently differs radically in related organisms — early development in direct-developing frogs or sea urchins is quite divergent from that of species with typical larval development. Furthermore, the famous diagram of all vertebrates diverging from a common stage, the pharyngula, with a tail and gills, is true only as far as it goes. Earlier development, including gastrulation, is very different in frogs, birds and mammals. It is the later and much more complex pharyngula stage that is constrained. It may be true that initial states for strictly dependent hierarchical processes will be less likely to evolve, but are we ready to describe early versus late development so confidently in such terms?

Arthur acknowledges that the developmental theory presented in his book lies in the long and honourable tradition of Waddington and other twentieth-century theorists. There is no question but that an integration of development and evolution is vital, but the time for theoretical constructs such as those presented here is either past or not yet with us. Concepts such as the morphogenetic tree, or older ones like the epigenetic landscape, are of heuristic value, but they can never substitute for real experimental data. A detailed analysis of development in specific organisms such as *Drosophila* has been made possible by the application of the tools of molecular genetics. These same tools can also be applied to the variations in developmental controls between organisms, including those not often seen in laboratories. We can now ask experimental questions about the evolution of homoeotic genes, about heterochrony, about developmental constraints. It is a time less for grand theorizing than for empirical studies on how development evolves. □

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