Pathways and building blocks

Modularity in Development and Evolution

edited by Gerhard Schlosser & Günter P. Wagner

University of Chicago Press: 2004. 600 pp.
\$90, £63 (hbk); \$35, £24.50 (pbk)

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Modules are relatively independent building blocks. This simple definition suggests that it should be relatively easy to recognize them in the development and evolution of biological organisms. However, there are many degrees of modularity, so any definition is likely to have some ambiguities. One way of identifying developmental modules is the repetitive use of a particular mechanism in different developmental situations. Another characteristic is a tight internal connection between the parts of the module, with fewer, but well defined, connections to the rest of the system in which the module works.

Investigations in development and evolution have been burdened by what Gerhard Schlosser and Günter Wagner refer to as “ugly facts”: a plethora of details that obstruct our view of the underlying principles. Their book is an attempt to overcome this problem by bringing a range of diverse fields together under a common theme. They have assembled more than 20 articles that discuss modularity at different levels: in gene regulation networks, in signalling pathways, in structures such as segments or appendages, and in symbiosis, for example. The authors are authorities in their respective fields and describe their subjects — such as helix-loop-helix proteins, signalling pathways, selector genes or individual versus colonial forms of life — in great detail.

The relevance of these descriptions to the central theme of modularity is not always spelled out, however, with only brief comments at the beginning or end of some of the chapters. To counteract this trend, Wagner and Schlosser have provided an opening introduction that seeks to integrate various themes, as well as separate introductions to each of the four main parts of the book. Promoting communication between different communities is certainly a difficult, but necessary, task.

An archetypal module in higher organisms is the cell. In the book, the transition from single cells to multicellular organisms is illustrated only by a rather specific example, the volvoclean green algae, which exhibits a smooth transition between life as single cells and multicellularity. However, the role of the cell as a module of development can hardly be overestimated. Many of

Poles apart: why do the legs and body of *Drosophila* have different segmentation systems?

the universal capabilities of extant higher organisms that we see in cells presumably evolved before the first multicellular organisms appeared. For example, all cells generate polarity. A pertinent but, at least in the discussion of signalling pathways, often neglected question concerns how modules first arose in evolution. One possibility is that a whole functional unit, including the genes that specified the components of the unit, was re-used in a modified form; the cell is a good example here. Alternatively, a module (such as a signalling system) might be co-opted for a function totally unrelated to its original purpose.

It is still difficult to find the origin of each process that we regard as a module, even with all the data that are now available. For example, the WNT signalling module, mentioned in several chapters of the book, is involved in the formation of the segment polarity network in the fruitfly *Drosophila*, in the generation of the primary anterior-posterior body axis in vertebrates, and in the generation of cell polarity. Do these different functions have a common root? The evolutionary origin of segmentation is still controversial, so we do not know whether there is a direct connection between the polarity of the axis of the whole body and the polarity of individual segments. Likewise, is there a connection between the determination of the axis of a single cell and the axis of a whole body? After all, the development of multicellular organisms starts with the polarization and division of a single cell. The few basic signalling pathways satisfy one criterion of being modules as they are used again and again. It would be interesting to know the

most ancestral organism in which these pathways have been clearly identified, and what their function was.

One chapter that I found particularly interesting deals with the segment polarity network in *Drosophila*, illustrating the importance of, and the difficulties encountered in understanding, the dynamics of a system; this cannot be derived from a list of the parts. The segment polarity network is not a module in the sense of being used repeatedly. The segmentation of the fly's legs is based on the *Notch* system, whereas the segmentation of the body depends on the *engrailed/wingless* pathway. This raises an interesting question for modularity: why was an existing network not redeployed, despite the fact that in both cases segments had to be formed?

The concept of modules spans many disparate fields of biology. This book provides a good introduction to the subject, despite the inevitable heterogeneity of a multi-author volume. Modularity goes to the heart of a central problem in biology: how has such an incredibly complex system as a higher organism evolved? A combinatorial assembly of elementary building blocks is certainly one way of generating complexity, especially if the building blocks were duplicated and modified during evolution. Many of these building blocks are carefully described in this book, which covers a much broader range of topics than most textbooks. Reading it should certainly sharpen your view of what are the interesting questions to ask. ■

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