

## Imaginal discs

*Imaginal Discs. The Genetic and Cellular Logic of Pattern Formation* (2002) Lewis I. Held Cambridge University Press. Price £100 460 pp. ISBN 0-521-58445-0.

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This book is not for the faint of heart. Those familiar with Professor Held's first monograph, "Models for Embryonic Periodicity", might be expecting that "Imaginal Discs" will simply represent a progression to postembryonic development. However, while the new book covers much of the same conceptual ground as the earlier one, that is where the similarity ends. "Models..." was a general synthesis and evaluation of the competing ideas proposed for biological patterning in animals, circa 1991. It cut right to the underlying heart of each model, and at 71 text pages and over 1000 references, it was concise without being superficial. "Imaginal Discs" is not a general overview for newcomers, but an extraordinarily detailed treatment that incorporates a vast amount of new data relevant to an increasingly difficult subject.

The title "Imaginal Discs" is somewhat misleading; *Drosophila* imaginal disc development simply provides the stage where the real subject is played out, as expressed in the subtitle "The Genetic and Cellular Logic of Pattern Formation." Held weaves a tale that intertwines models, cellular behavior, genetic circuitry, and biochemical interactions. These often divergent perspectives of biological patterning are not separated into discrete chapters or even paragraphs, but are integrated into each section of the story. The degree of detail offered is staggering, but Held never loses sight of the bigger picture. Indeed, a major strength of the text is the author's ability to take all bits of data, and present their implications for the various conceptual and molecular models. The reader is continually bombarded with related but different types of information, and this makes for slow going. The data and idea densities are both very high, and I found myself reading many passages twice or more. The narrative text seemed longer than 260 pages, but also had more information than some books twice as long. And, all things considered, I found surprisingly few instances where I might disagree with something approaching a statement of fact, and these were all minor. This is an impressive piece of scholarship.

The book is written so as to be read from beginning to end, although the headings make it relatively easy to find individual sections relating to specific developmental events. To come

away with the broader messages, however, I think it really must be treated as a story. Held writes from an historical perspective throughout; this is valuable in developing ideas, but makes the text less useful as a quick reference. Perhaps the easiest way to use this as a reference work is to just refer to the figures and their legends, which are packed full of more information than most text books. The appendices, especially the compendia of genes affecting particular processes, also are useful. (The appendix on signal transduction pathways needs figures.) In addition, workers in the field will want to own this just for the alphabetical list, with titles, of 4900 references; this could be a life saver at times when the web goes down.

Just as the title "Imaginal Discs" tells only part of the story, some of the chapter titles are also overly modest. Early chapters (for example on bristle determination and patterning) deliver as expected, but the chapter entitled simply "The Leg Disc" provides a detailed treatment of patterning models versus reality, and "The Wing Disc" is a great place to go if one wants to contemplate issues such as gradients and boundaries.

Especially illuminating are the passages dealing with the grand models of pattern formation of the 1960s and 1970s, and their gradual dismantling as the molecular and cellular understanding of the complex events unfolded. (The chronological approach can make the reading somewhat confusing for the uninitiated, for example when data are interpreted with respect to models that are later shown to have little relevance to the particular process.) These models had a major influence on the thinking of a generation of developmental biologists (myself included), and there is no doubt that they guided much experimentation. But, while French flags, polar coordinates, etc. helped to define our concepts regarding mechanistic possibilities, it is debatable how much they actually hastened our enlightenment as to how things really work. I think Held may give them rather too much credit. One undercurrent that runs throughout the book is the whimsical nature of evolution, and the resulting mechanistic complexity that is generated. In the end this means that all the old models are correct to some degree, and none are correct very much. No other result could have been possible.

There are a few things I would definitely change for the second edition. Reading would be eased if there were fewer abbreviations; I suspect that someone relatively new to *Drosophila* patterning would have a very difficult time with these. In addition, while some of the analogies and corresponding names of models, paradoxes, mysteries, etc. are clever, it is a bit much to just refer to the names in later chapters and expect the reader to remember them. I would also recommend a short chapter on standard experimental methods in *Drosophila* development. Finally, the figures want color. They need color. They SCREAM for color.

"Imaginal Discs" would be a useful read for anyone interested in pattern formation generally, and should be required

reading for workers in *Drosophila* patterning. I agree with Held when he says “This field has seen paradigm clashes of Promethean proportions, and those wars must be recounted to do the subject justice. . . . Admitting past mistakes can help in spotting future pitfalls . . . even in the Olympian realm of molecular genetics, which surprisingly has more than a fair share of mortal foibles.” But, in this era of what often appears to be single-minded generation of massive amounts of data, few students seem to have time for historical syntheses of complex ideas and sometimes confusing facts. Alas, I suspect this tome will end up on many bookshelves, only to be used as

a reference book rather than as an instrument of instruction. It would be a loss, as “Imaginal Discs” can be a great antidote for those whose brains have been poisoned to believe that genomics, proteomics, and other -omics are magically going to tell us how life works. This book makes it clear that, in order to really understand how complex biological processes function, we are going to have to roll up our sleeves and get dirty.

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