

serve two ends. First, he writes for the non-ciliatologist; and as one of these I find the account an eminently comprehensible introduction, which can be read fast without strain. Frankel's prefatory indication that the book is too long to be read through at a single sitting is unduly modest. It took me a long weekend, but I could have read it in a shorter period.

Second, the entire account addresses the question asked as the title of chapter 11: "Can ciliates help us to find 'nontrivial universals'?" Frankel's thesis is to answer this question affirmatively, and the plan of presentation is to show (in my abbreviation from Frankel's preface): that there exists in ciliates an intracellular hierarchy of qualitatively different systems of spatial control; that these systems can be inherited cytoplasmically; and that the most global level in this hierarchy is analogous to positional information in developing embryos. This thesis denies that global organization of the structures at the cell surface can be accounted for by jigsaw-puzzle-like extension of local self-assembly. It denies also that the credo of the molecular biologist, stated by Frankel as "*omnis forma ex DNA*," can be the whole story of development.

Now I have some difficulty assessing Frankel's establishment of this thesis as critically as many biologists might wish. The importance of hidden global controls of pattern formation, communication between developing units, and the dynamic nature of these processes are to me the preconceptions or paradigms on which I have based my attempts, over 17 years, to apply physico-chemical principles to biological pattern formation. Frankel quotes my 1982 and 1987 reviews in two places in ways that are quite pleasing to me. He does not, however, resort to the mathematical language of change, the calculus, in advocating global dynamic control. (The only mathematical terminology he uses is from the field of topology. It is nicely brought in, and one needs no advance knowledge of it to understand his arguments.) Rather, Frankel addresses the biologist in biologists' language, letting the levels of pattern control emerge from a meticulously detailed account of experimental observations. But, subtly, he subdivides several sections of this account with the subheadings "statics" and "dynamics."

The scholarship of Frankel's account is admirable. The roughly 700 references cover about half a century for detailed experimental work and twice that for concepts. (But in reaching back to Whitman and Bateson in the 1890s he has omitted to go back a decade further and discover that the concept of positional information can be

attributed to Hermann Vöchting.) The section of chapter 11 in which he compares ciliate development to that of *Drosophila* is weaker because, while indicating hierarchy in ciliate controls, he does not give the hierarchical classification of *Drosophila* genes (maternal-effect, gap, pair-rule, and so on).

Chapters 8, 9, and 10 are concerned largely with mirror-image reversals of asymmetry, culminating in a cylindrical coordinate model of positional information on the cell surface. This is very similar to the polar coordinate model discussed by French, Bryant, and Bryant in 1976 for insect and amphibian limb regeneration. The model works quite well, and Frankel, while clearly liking the model, assesses its successes and deficiencies fairly. Its application to ciliates has some fascinating differences from the earlier application to animals. Intercalation of positional values occurs without growth, and these values can even be respecified as an organism shrinks.

The account of ciliates is wrapped up in the questions about universals in chapters 1 and 11. If we are to ask these, we must look outward into each other's fields, where we shall necessarily appear less expert. Thus, I do not count it a fault that there are deficiencies in Frankel's *Drosophila* account. It was important for him to make the comparison. When is any expert drosophilologist going to write a similarly outward-looking book for non-drosophilologists? Frankel has shown how a single-organism specialist can look outward, and see the stars—and wonder.

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