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Essay review

Dissecting developmental biology

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Towards a Theory of Development, Alessandro Minelli, Thomas Pradeu (Eds.). Oxford University Press, Oxford (2014). 304 pp., Price GBP 37.50 paperback, ISBN: 978-0-19-967143-4

1. Introduction

Minelli and Pradeu have assembled a stellar list of authors, including many of the main scientific contributors to evolutionary developmental biology, as well as some of the leading philosophers of science who have written about that field. Whether or not there really is a theory of development, this volume leaves little doubt about the value of theoretical biology in general.

Despite the title of the book there is no consensus among the authors regarding the feasibility and desirability of a general theory of development, or about how to understand the two terms 'theory' and 'development'. Although the editors do a good job of weaving the themes of the several contributions together in their introduction, those contributions are wide-ranging and thought provoking rather than providing elements of a single approach to the question of a theory of development. Our discussion will focus on three themes that can be found in many of the contributions.

1. What is a scientific theory and what is the significance of having a theory for the scientific status of a research area, such as developmental biology? Answers to these questions would seem to be presupposed in asking if developmental biology should want or need an overarching theory? After all, instead of promoting research an overall theory might constrain it, and even be an obstacle to innovative research.
2. A more substantive question concerns the concept of development and what a theory of development should cover. Is there a consensus about what development is? What is development's temporal dimension: when the organism is able to reproduce a new organism, or is it instead the whole life cycle, no matter how simple or how complex and expanded that may be? What does development include spatially: a single organism, a group of organisms, extended 'hybrids' such as an organism including its symbiotic microorganisms or an organism within its developmental environment (such as the mother or parents, a nest or a womb, siblings, extended resources such as sustenance, warmth, protection and stimulation), or any other system imaginable or as yet unimaginable? If we include within the scope of development a whole life cycle unfolding in its developmental environment—its developmental niche (Stotz, 2008, 2010, 2014a, 2014b; West & King, 1987)—then the relationship between two generations and the modes and mechanisms of the transmission of developmental resources would come into focus. Processes of heredity would then appear as deeply coupled to the process of development. This leads to the question of how should we delineate development from other dynamical processes, such as metabolism, self-organisation, regeneration, and even behavior, or the more overarching dynamical processes of heredity and evolution? Minelli asks if only functionally adaptive aspects of change merit the name development, or possibly any changes (pp. 228, 235). Many authors touch on one or more of these issues.
3. Several authors also address a further question, namely the causal structure of development and the kinds of causal processes that we find in development. The role of genetic causation and its relationship to other causes is obviously of particular interest here, but the more general issue of what kind of causal networks we find in development, how to distinguish between causes and whether they can be modeled, is also debated.

Clarifying these more general issues may, as interesting as they are in their own right, at first lead us away from the question

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regarding a theory of development, but on second thoughts may be an important prerequisite for the development of such an elusive theory.

2. A theory of development?

Textbook philosophy of science contrasts two views of what 'theories' are, the syntactic and the semantic conceptions. On the older, syntactic conception a scientific theory is a claim about how the world works, a claim that would ideally be stated as a set of axioms in which all terms would either be defined in terms of observation, or implicitly defined by their role in the axioms. A theory of development would thus be a set of axioms about development from which the development of an individual system could be predicted by specifying the initial conditions of that system. On the alternative, semantic, view a theory is a family of models, which gain empirical content when we add the claim that some real world system is similar enough to the model that we can reasonably use the model to understand that system. Important issues about the nature of scientific representation have been canvassed in these very abstract terms, but it seems clear that the question of a theory of development will not be usefully approached in this way. The idea of an axiomatic approach to developmental biology seems quite hopeless, and the claim that developmental biology contains a set of models that can be used to understand the development of particular organisms, and that it hopes one day to have more and better models, seems true but unhelpful. It seems that a majority of contributors to this volume would endorse a looser, but in this context probably more helpful, conception of a scientific theory as any form of *systematic* representation of scientific knowledge.

What is the function of a theory? For some of the authors, such as Thomas Pradeu, a scientific theory is a useful thing to have because a systematization of knowledge allows explanation, prediction and understanding, rather than mere local descriptions. The function of theories is foremost to provide "novel, daring, testable, and hence often wrong" statements or hypotheses (p. 23). Such 'how possible' answers therefore "stimulate challenges" (p. 24). Unification—providing a unifying framework for heterogeneous phenomena—is a second function for theories that Pradeu identifies.

For Alan Love, however, scientific theories are valuable because they provide a useful guide for future research. Love denies that a theory of development would or could do that. He argues that what organizes and guides research in developmental biology is not a theory, but a set of core problems or problem agenda; developmental biology is erotetically organized. Developmental biology is not guided in its approach to new questions by an overarching theory that systematizes our understanding of the nature of development. Instead, future research is guided by what has been learnt about the best questions to ask.

Griesemer agrees that a science may not need "a formalized, exact theory to be successful" (p. 200), particularly an inexact science such as developmental biology. While Griesemer does not see the need for a theory of development for the "conduct of inquiry into development per se" (p. 184), he argues that such a theory will be needed for an extended evolutionary theory that integrates developmental biology. He proposes a plurality of theories with the aim of articulating, "a set of core principles, a family of models, and a theoretical perspective" (p. 199). All three ingredients are necessary for a theory for description, explanation and prediction on the one hand and to guide future empirical inquiry on the other. Many contributors seem to agree that a plurality of theoretical perspectives would not be to the detriment of developmental biology.

3. The conceptual boundaries of development

The relationship of development to heredity and evolution, and possibly even to fields like ecology and immunology as some contributors argue, points to another topic touched on by most contributors to the volume: where are the conceptual boundaries of development? There are several reasons for relating a theory of development to a more general theory of "ecological, evolutionary developmental biology" (Griesemer p. 183) or a theory of "developmental evolution" (Moczek p.218). For Moczek the most important reason is "the role of phylogeny in shaping organismal development" (p. 219). An equally important reason would be that understanding phenotypic evolution requires understanding development. But most importantly, we would argue, is that the very existence of the process of evolution relies on there being developing, reproducing systems. Hence Griesemer argues that concepts of development and reproduction, and also of inheritance, should be "conceptually *prior* to a concept and principle of evolution" (p. 190). These key concepts should be able to be defined without reference to the process of evolution to which they give rise.

But how can we delineate development from other dynamical processes such as metabolism or regeneration, or, we argue, even behavior, if the very meaning of development as preformed 'unfolding' is in question? A recent survey article defined behavior, as opposed to development, as the "internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes". They excluded development on the ground that "developmental processes are … generally much slower than phenomena considered as behavior, and are primarily *based on ontogenetic programmes specified by the individual's genetic makeup* (Livitis, Lidicker, & Freund, 2009, 108, emphasis added). We are still a long way from any unbiased characterization of development, but several chapters of this volume provide food for thought about possible avenues in this direction.

The conceptual boundaries of development are contested on at least three axes, temporal, spatial and phylogenetic. The temporal dimension is perhaps the simplest. At what point in the life of an organism, if any, does 'development' end? Developmental biology grew out of embryology, which by definition restricted the temporal dimension of development to the egg and fetus. Developmental biology widened this to include all processes that lead from the fertilized egg to reproductive maturity. Some of the contributors think, as we do, that development must in principle include the entire life-history of an organism. Gilbert and Bard see development as the process which creates the whole life cycle rather than just a sexually mature adult.[1] While the editors acknowledge this as an "extreme position" developmental systems theorists have promoted this view for quite some time.

The phylogenetic and spatial dimensions of development are equally important and equally contested. The editors point out in their introduction that developmental biology has always been "biased by the idiosyncratic properties of the most fashionable model species on which observation and experiments are performed" (p. 2). It is evident how much more challenging it becomes to conceive of a general theory of development if we wish to include plants and fungi as well as animals. But the potential scope of developmental biology is even wider, including microbes and

[1] Interestingly, in *Ecological developmental biology* (Gilbert & Epel, 2009) the authors still distinguish between developmental and phenotypic plasticity, a distinction that would be problematised under the whole life-cycle view.