

## BOOKS: DEVELOPMENT

# Making Sense of Changing Animal Embryos

Billie J. Swalla

Students and professionals interested in the fields of evolution, development, or genetics as well as those drawn to the interdisciplinary field ("evo-devo") that lies at their intersection will find Adam Wilkins's *The Evolution of Developmental Pathways* a must read. Wilkins, editor of the journal *BioEssays*, admirably attempts to describe the history and basic tenets of evo-devo as well as a few of the field's current model systems. Presenting the emergence of the field in a familiar, story telling fashion, he often sets the stage for discoveries in a historical way and then gradually comes to the latest data. (Many of the case studies include appropriate references up through 2001.)

Setting the tone for the book, the first chapter describes the great split between the fields of evolution and development at the beginning of the 20th century in terms of a martial breakup. This ideological split separated population biologists, who were making mathematical models of evolution, from embryologists, who were interested in developmental processes. Whether or not the analogy is apt, the fields have recently been rejoined with the uncovering and understanding of the genetic pathways that drive embryonic development. Wilkins offers accurate, detailed descriptions of a few of the genetic pathways that are known to be important in development and discusses how they have been implicated in evolutionary processes.

Although I found the historical sections interesting and basically correct, I was disappointed that Wilkins presents the field as simply gradually emerging from the fog in the 1980s rather than resulting from the concerted efforts of creative and talented people. Several leaders in evo-devo were trained simultaneously in developmental biology and evolution and taught students to think in these terms. Comparative embryology was fostered and encouraged at places such as the University of Texas, the University of Washington, Berkeley, Harvard, and the Marine Biological Laboratory

at Woods Hole. At times, one has the feeling that Wilkins is describing evo-devo according to Greg Wray and Rudy Raff (Indiana University). They were and are key players in the field, but there were and are many others who go unmentioned.

I remember the late 1980s as the time when polymerase chain reaction (PCR) changed our way of cloning genes and allowed experiments between evolutionarily closely related species that had previously been impossible. PCR made it relatively easy to move from genetic model systems to evolutionarily interesting model systems, and genomic research is now taking these studies to a sophisticated level thought impossible 20 years ago. Wilkins devotes considerable attention to sea urchins, the model system used by Raff and Wray. He also discusses in some detail

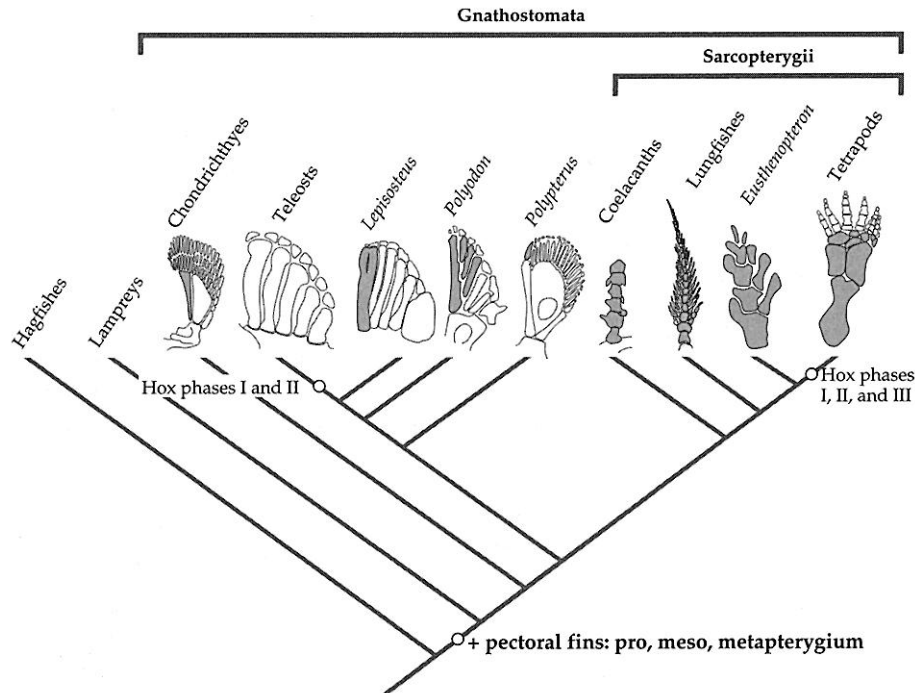
studies by a number of people who examined the expression of *Drosophila* genes in other insects. But he does not cover other important research such as Ann Burke's work with Cliff Tabin on *Hox* gene expression in different vertebrates (1), Mark Martindale and Jon Henry's work on the implications of different cell lineages in different species (2), and my work with William Jeffery on ascidians (3). All of these comparative embryological studies showed the power of examining developmental processes in closely related species with different phenotypes.

Despite the omissions, I enjoyed reading the book from beginning to end. Wilkins touches on almost all of the important issues in the field. For example, the case studies include some that illustrate alternative explanations. The section on *Pax-6* (the gene found in all developing metazoan eyes) carefully describes the exciting initial studies (4, 5) and the later results that uncovered a group of three interacting transcription factors—findings that have somewhat modulated the "master control gene" hypothesis (6). I especially liked the chapter on morphogenesis, because it attempted to conciliate developmental and genetic analyses of the processes that generate organic forms. In our haste to find and characterize genetic pathways that are

## The Evolution of Developmental Pathways

by Adam S. Wilkins

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**Aspects of limb development on a phylogenetic tree.** The distribution of three cartilaginous elements of the pectoral limb among different clades within the Craniata suggests that teleosts have lost the metapterygium (shaded), whereas the sarcopterygians have lost the propterygium and mesopterygium. In addition, teleost limb buds show phases I and II of *Hox* gene expression but not the phase III found in tetrapods. As Paula Mabee points out, these observations and other work with teleosts suggest that the evolution of limb development involved more than simple temporal and spatial extensions of *Hox* gene expression. [Adapted from (10).]

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## BOOKS: PHILOSOPHY

# Knowledge and Social Norms

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common to different phyla, we often forget that these genes encode proteins that act within cells; it is the changes in cell shapes and numbers that actually constitute morphogenesis. The chapter on costs and constraints (also well done) wrestles with one of the most difficult problems facing the field: How does one select for a complex developmental process? Exploring the answer to that key question will require studies designed to measure variation and selection on complex traits.

This is the third evo-devo book to appear within a year; it follows volumes by Sean Carroll *et al.* (7) and Eric Davidson (8) [reviewed in *Science* by Wray (9)]. Of the trio, Wilkins's book offers by far the most comprehensive exploration of the field. The other two focus primarily on promoter analyses and the genetic regulatory pathways themselves and, in places, pay little attention to how the processes may be important in evolution. However, unlike Wilkins, they use color illustrations, which are almost imperative for explaining complex patterns of gene expression in space and time. Carroll *et al.*'s text seems the best for teaching undergraduates. It is simple enough to appeal to students who are new to the field, yet it offers enough detail for them to understand the model systems. Wilkins's account should be an easy read for aficionados, but whether it is accessible to undergraduates remains to be seen. (I plan to use the three texts in classes at various levels next year.)

In any case, *The Evolution of Developmental Pathways* would be great to read in a seminar class for graduate students or within a lab meeting. It will certainly generate discussions about data, terminology, and interpretations—matters so important to rigorous science. And it can help train a new generation of students to study how complex morphologies can evolve within the framework of developmental gene networks. If we are to understand how genomes create unique animals from single fertilized eggs, then we will have to grapple with the many complex issues Wilkins raises in this book.

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Philosophers of science and practitioners of the social studies of science have been at loggerheads over how to approach science and how to evaluate it as a knowledge-producing enterprise. Philosophers focus on the evidential grounds and cognitive merits of science. Sociologists highlight the nonevidential considerations that influence science: the professional and ideological interests, the discursive networks, and so forth. Philosophers feel that social studies of science either ignore the question of whether science yields legitimate knowledge or draw unwarranted negative conclusions from their case studies. Sociologists feel that the normative issues raised by philosophers provide little or no purchase on the actual conduct of science. According to Helen Longino, both sides suffer from a misplaced "dichotomizing" drive. They assume that science is either rational and not social or social but not rational; the rational and the social are mutually exclusive. Her mission in *The Fate of Knowledge* is to show how science can be social and produce knowledge.

This is a sensible piece of ecumenism. Longino, however, is not unique in pursuing this course, as she sometimes seems to imply. In recent years, a number of epistemologists and philosophers of science have highlighted the social framework of the epistemic conduct of science and other fact-finding arenas (1). Longino often conflates disagreements with her on other matters with a weakness for dichotomizing. If, by her lights, a philosopher favors an excessively "reductivist" approach to the social, she sees this as perpetuating the dichotomizing tradition. But one can reconcile the rational and the social under many interpretations of the social.

The most important question, though, is how Longino herself effects the reconciliation between the social and the rational. As in earlier work, she proposes social "norms" for social knowledge. These norms require communities to be governed by critical discursive interactions. Publicly recognized fo-

runs for the criticism of evidence and methods must exist. There must be "uptake" of criticisms (beliefs and theories must change in response to critical discourse). There must be publicly recognized standards by reference to which theories are evaluated. Lastly, communities must be characterized by "tempered equality" of intellectual authority (all members must be considered capable of contributing to the dialogue). Insofar as a community satisfies these conditions, Longino says, it is a knowledge-productive community. Because the norms call for social interactions, Longino touts the approach as an emphatically social brand of epistemology. There can be no quarrel there. What is questionable is Longino's claim that

communities satisfying her four conditions will necessarily produce knowledge. It is especially doubtful that these conditions capture what is distinctive about scientific knowledge.

Consider a test case. Members of a religious community form beliefs about the universe by appeal to a sacred text ("evidence"). They often disagree in interpreting the text, so they engage in critical interactions. The criticisms take place in publicly recognized forums. Members are genuinely influenced by the criticisms they receive. There are public standards for interpreting the text. And the community is governed by qualified equality of authority, where greater weight goes to those with more training in the community's seminars. This community satisfies Longino's four conditions, but does it automatically qualify as a knowledge-producing community? Surely not. Still less does it qualify as a community producing scientific knowledge. Longino is not oblivious to such examples; she adduces some of them herself. But how does she answer the worries?

One response is to tighten the requirements. The community must be open to all perspectives: "no claim or belief can be held immune to criticism." The religious community will presumably violate this requirement because it is dogmatic about its standards, e.g., that theories are to be judged by the sacred text. But this move creates a threat from the opposite direction. Instead of excessive looseness, the approach is imperiled by excessive tightness. Isn't science also "dogmatic" in insisting on scientific or statistical methods? Researchers aren't invited to challenge those methods when they submit their research papers. Indeed, general questions of scientific standards are usually relegated to philosophy journals rather than published in scientific journals. Even if a statistical method is challenged, the challenge is assessed by appeal to logic and

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by Helen E. Longino  
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