

mammalian synapsids." Calling them mammal-like reptiles not only fails accurately to reflect the relationships among these groups, but also encourages ladder-of-life thinking, already too prevalent in the general public. The sequence is not fish to amphibian to reptile to mammal. Reptiles are not just advanced amphibians, and mammals did not go through a reptile "stage"; reptiles are a separate branch of the amniotes. Instead, fish gave rise to tetrapods, which were amphibians and amniotes. Amniotes gave rise to reptiles and synapsids. Synapsids included mammals and other lineages—but the other lineages were not reptiles. There is a sequence, but no *scala naturae*. A textbook on evolution should make this distinction clear.

This edition has livelier graphics and a more student-friendly layout, together with marginal outlines of major points for each paragraph. There is also a website keyed to the text (<http://www.blackwellpublishing.com/ridley>), which includes classic articles, illustrations, and a minitutorial of the main ideas of the book. As in the earlier edition, the strength of this volume lies in its detailed presentation of population genetics and microevolutionary processes; anyone searching for the big picture of the history of life should look elsewhere.

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REPRODUCTION & DEVELOPMENT

EMBRYOLOGY, EPIGENESIS, AND EVOLUTION: TAKING DEVELOPMENT SERIOUSLY. *Cambridge Studies in Philosophy and Biology*.

By Jason Scott Robert. Cambridge and New York: Cambridge University Press. \$60.00. xvi + 158 p; ill.; index. ISBN: 0-521-82467-2. 2004.

Philosophy of science, according to Nobel physicist Steven Weinberg, is "at best . . . a pleasing gloss on the history and discoveries of science. But we should not expect it to provide today's scientists with any useful guidance about how to go about their work or about what they are likely to find" (1992. *Dreams of a Final Theory*. New York: Pantheon). Jason Scott Robert, author of *Embryology, Epigenesis, and Evolution: Taking Development Seriously*, begs to differ. There is no reference to Weinberg in Robert's book, and the latter is occupied

with the evolution of development, not with dreams of a final theory of everything. Nonetheless, Robert picks up the challenge that so often scientists launch to philosophers, when the former bother to take any notice at all of the latter: what is philosophy (of science) good for?

An important clue to a reasonable answer is in fact contained in Weinberg's own words. Notice that he is actually stating that philosophers are no good to scientists in *two* realms: one is advice on how to go about their work; the second one is suggestions on what they are likely to discover. It is useful to think of these as the "how-to" and "what-to" questions. It will also help the following discussion if we further finesse our understanding of the "how-to" problem: at a fairly detailed, everyday science level this may mean how to think about a specific problem, design useful experiments or other empirical approaches to solve it, or even simply what sort of data analysis is necessary. At a higher level, however, the "how-to" question is a matter of framing the problem in a general manner, one that is useful to guide scientists toward both the lower-level problem and the "what-to" question. I maintain, and Robert's book is a very good example, that philosophers are not of much use to scientists to solve lower-level "how-to" questions, or in approaching "what-to" sort of problems. Nor are they *expected* to! After all, the philosopher's job is not to solve scientific problems; that is what a scientist ought to do—when was the last time a scientist tried to solve a philosophical problem? Oh, never mind, there are in fact several such cases of rather bloated scientists suddenly discovering easy solutions to life's persistent questions (for example, see E. O. Wilson. 1998. *Consilience: The Unity of Knowledge*. New York: Knopf). What philosophers are supposed to do is to think *about* how science works (or fails to). Scientists, one could argue, should also at least occasionally think about how their profession proceeds, and about how the "big questions" are being framed and tackled. But scientists tend to be pretty busy writing grant proposals (which philosophers by and large do not have to do), so it is ok for a scientist to lean on the insight of philosophers to occasionally raise above the individual trees and take a look at the whole forest (there is an important caveat here: the philosopher has to know quite a bit about science, or risks wasting everyone's time; in my experience, it is not impossible to find an alleged philosopher of science who actually does not understand the science he is supposed to be philosophizing about).

To come down to earth for a moment and be a bit more practical, the problem that Robert poses his readers is deceptively simple: what is develop-

ment? In perfectly philosophical fashion, he maintains—and I think he is right—that once we begin thinking seriously about the sort of process development really is, we will have a guiding light to see what is it that we are doing and is not working, and perhaps even what else we could be doing instead.

For example, Robert has much praise for the “evo-devo” movement of the last several years, with its stated goal to finally integrate the study of development into the modern neo-Darwinian synthesis (H S Callahan, M Pigliucci, C D Schlichting. 1997. *BioEssays* 19(6):519–525; A S Wilkins. 2002. *The Evolution of Developmental Pathways*. Sunderland (MA): Sinauer Associates). But he also points out that evo-devo is in the grave danger of simply redefining epigenesis and development as a list of what genes are being turned on or off and when. This is surely too simplistic a view of what development is, and yet if one reads the evo-devo literature one cannot escape the feeling that Robert is correct in his assessment of the current state of the field. The author traces this unsatisfactory situation to what he calls the modern consensus between the two ancient intellectual traditions of preformation and epigenesis (see where history of science becomes important?). Aristotle, a philosopher *and* scientist if ever there was one, was probably the first epigeneticist, a position he gained by criticizing (and demonstrating to be empirically wrong!) Hippocrates’s idea of preformation. According to the latter, the bigger parts of the embryo appear earlier because they are easier to see, development being a process of “inflating” to adult size the organs that are already there. Aristotle worked on the chick embryo to demonstrate that its heart appears before its lungs, although the latter are bigger, thereby falsifying (24 centuries before Popper coined the term) Hippocrates’s theory. So, are organs in any sense preformed, ready to go for the adult, so to speak, or are they generated during an epigenetic process? Both, says the modern consensus: the organs themselves appear during epigenesis from simpler structures; what is preformed is the genetic program that makes such epigenesis possible. Hence, the reasonability of the view that reduces epigenesis to switching genes on or off.

But according to Robert, this is not a good way to navigate between the Scylla of preformation and the Charybdis of epigenesis (Chapter 3). That is because such a simplistic compromise misses the point of what sort of thing development really is. What is missing? But the environment, of course! Development does not happen in an environmental vacuum, and recently several other books have attempted to shift the attention from the purely molecular details to a more comprehensive view of

biology (e.g., C D Schlichting, M Pigliucci. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland (MA): Sinauer Associates; M J West-Eberhard. 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press). Robert, however, immediately warns us that here too we have come to a rather unsatisfactory, and rarely questioned, compromise. Today there are very few pure genetic or environmental determinists, and “it seems that everybody is an ‘interactionist’” (p 5). But what does it *mean* to say that phenotypes are the result of genotype-environment interactions? What it does *not* mean is what most people seem to be taking for granted: that we can understand development if we focus on the genes while holding environmental conditions as a constant background (“accounted for,” experimentally or statistically). This will not do for the simple reason that development is a continuous interaction among genes, environments, and supragenetic processes (at the cellular, tissue, and other levels) collectively black-boxed into “epigenesis.”

The problem of development, put quite simply, is to understand how we start with a zygote and end up with a complex adult organism, and taking development seriously means to adopt “a better, less suspect variant of a context simplification heuristic [compared to the one that simply tries to hold the environment constant], a more honest one, one more adequate to investigating biological reality, and one less likely to yield inference to an inappropriate conclusion about development” (p 15). This sounds very good, but I can see the scientist in you rolling his eyes and thinking that this is a lot of fluff that is not going to help you be successful with your next grant proposal. Maybe the latter is true, but Robert does provide a very useful conceptual framework for thinking about alternative approaches to the study of development. Even though I tend to disagree with his specific conclusions, his classification was immensely helpful for me to see why I happen to disagree; indeed, as Ludwig Wittgenstein once said, the whole point of philosophy is “to show the fly the way out of the fly-bottle.” He was not thinking about *Drosophila*, but saying that the chief role of the philosopher is to help clarify the ideas being discussed.

According to Robert, there are three broad categories of approaches to the problem of development (p 110): First, gene-centric research programs, following that all we need to know are the gene frequencies (at the population level) and the patterns of gene expression (at the individual level). In that case, we are currently well on our way to solve the problem of development, all we need is a bit more

genomics (and maybe proteomics). Second, there are genes-in-context approaches, where the focus is still the gene, but this time both the context of expression (internal and external environment) and its evolution play a major (although still secondary) role. This is evo-devo, and the challenge is to identify how much "context" is important, and what constitutes a relevant context to begin with. Finally, there are nongene-centric ways of thinking about development, where genes are considered a crucial, but not primary, player in the evolution of development. The so-called "developmental systems theory" or DST (S Oyama, P E Griffiths, R D Gray. 2001. *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge (MA): MIT Press), where what is inherited by the organism is not just the genes, but also additional information present in the cell, protoplasm, organelles, and the environment itself. West-Eberhard is among the few biologists who approach the question from an almost DST standpoint, as am I and some of my collaborators (e.g., Schlichting and Pigliucci 1998).

If you are still enamored with the gene-centric paradigm, there is not much I can do to help you. But you would do well to read Robert's devastating critique of the whole notion of "genetic program." Robert himself clearly leans toward DST, but admits that—although conceptually useful—it may run short of the quintessentially appealing characteristic for a scientist: it will probably not help very much when it comes to writing grant proposals. In fact, Robert circles around what I think is the best compromise between the second and third alternatives: an enlightened evo-devo. By this I mean an evo-devo that is most emphatically *not* just a matter of listing all the genetic switches we can find, or even of paying lip service to the role of an environment that one then rushes to "keep constant." An enlightened evo-devo would retain the successful approach of molecular biology to the study of development, but would incorporate the *perspective* provided by DST, acknowledging that—as difficult it is to study in practice—the unit of inheritance is in fact a lot more complex and fascinating than a string of DNA. Perhaps we are moving toward the right direction already; as annoying as the string of "omics" is becoming (genomics, proteomics, metabolomics, and phenomics), it is an indication that even former gene-centrists are being forced to admit that there are a lot more layers of complexity in the organism than their philosophy had originally imagined. Welcome back to the study of the whole phenotype!

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ORIGINATION OF ORGANISMAL FORM: BEYOND THE GENE IN DEVELOPMENTAL AND EVOLUTIONARY BIOLOGY. *Based on a workshop held in Vienna, Austria, 1999. The Vienna Series in Theoretical Biology.*

Edited by Gerd B Müller and Stuart A Newman. A Bradford Book. Cambridge (Massachusetts): MIT Press. \$45.00. ix + 332 p; ill.; index. ISBN: 0-262-13419-5. 2003.

In this book, the editors confront one of the most challenging questions in modern biology: how does biological form develop where none existed previously? The goal is not to explain the genetic control of gastrulation during embryogenesis, but instead to explain how a group of cells stuck to each other might organize into a hollow gastrula-like ball for the first time. The editors laudably reintroduce the importance of morphology in evolution. This notion, largely neglected during evolutionary biology's decades-long fixation on genes and their frequencies as almost the only interesting or rigorous aspect of biology, is making a comeback due to new molecular genetic research methods. Even Darwin was unable to address this question, yet development is a key source of the variation that was so crucial to his natural selection. An important message of the book is that the long-entrenched, neo-Darwinian view and its inherent genetic reductionism may not be enough to address questions of this nature.

To that end, Müller and Newman have collected 16 essays separated into four sections, each focused around a set of questions described by the editors: morphological evolution and phylogeny, the relationship between genotype and phenotype, the physics of morphogenesis, and evolvability. These are of digestible length and by an impressive list of contributors covering a broad range of topics that (among others) include Gilbert's discussion on the role of the environment in determining phenotype (Chapter 6), Steinberg's review of his and other's work on the self-organization of cells through differential adhesiveness (Chapter 9), Nijhout's treatment of pattern formation (Chapter 10), Nanjundiah's discussion of plasticity and genetic assimilation (Chapter 14), and Newman's synthesis of many of these ideas (Chapter 13).

To explain the "origination" of form many of the essays return to ideas suggested by James Baldwin, C H Waddington, and others near the beginning of the 20th century that environmentally induced traits that do not reflect a *specific* genetic causal variation can be favorable to reproduction and only later be "assimilated" by more deterministic genetic causation. This falls outside the realm of the standard neo-Darwinian view in which selection can only screen the effects of existing variation.