

Forms of Becoming: The Evolutionary Biology of Development

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example. What aspect of nature one chooses to privilege for explanatory purposes may seem insignificant, but it can have consequences for how one comes to understand the evolutionary process and for which problems one deems worthy of serious attention.

Likewise, many problems over which much ink has been spilt (e.g., whether evo-devo is in tension with an adaptationist view of evolution, how Darwinian and Christian worldviews can be reconciled, etc.) are dealt with in a fairly breezy manner; Ruse implies that he doesn't see what all the fuss is about (e.g., p. 216). Early in the book he writes: "Evolution is true and natural selection is its mechanism. No more, but certainly no less" (p. 26). This is shockingly simplistic (presumably deliberately so, since Ruse assuredly understands better than most how dauntingly complicated the issues really are). Ruse's energetic writing style and unbounded enthusiasm for an adaptationist interpretation of Darwin's theory can as easily convey to someone coming to these issues for the first time, or without much training in the history and philosophy of science, that most of the interesting problems arising in connection with Darwin's theory are pretty easy to solve with just a bit of historical investigation and philosophical analysis (hence the tongue-in-cheek title of this review). To achieve the breadth of historical sweep and concise take-home message he is seeking, Ruse has to skim the surface of many topics that could easily be subjects for sustained discussion. This is, however, a minor shortcoming that hardly begins to detract from the great value of this book. Its intended audience is likely to come away with a fresh understanding of Darwin's great theory, and with gratitude to Ruse for being such an engaging and convivial tour guide. *Defining Darwin* is a valuable contribution to the literature emerging from the bicentennial celebration of Darwin's birth. It deserves a wide readership.

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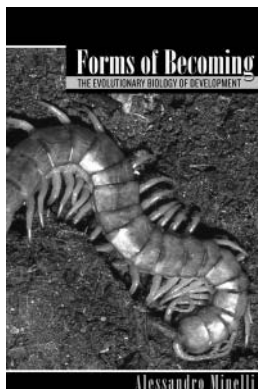
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A MULTIFACETED VIEW OF EVO-DEVO

Forms of Becoming: The Evolutionary Biology of Development. Alessandro Minelli. Princeton University Press, 2009. 242 pp., illus. \$27.95 (ISBN 9780691135687 cloth).

As much as Alessandro Minelli's goal with his latest book, *Forms of Becom-*



ing: The Evolutionary Biology of Development, is to shake up conventional disciplinary-based thinking about the development and evolution of animal form, he succeeds. As in his first book, *The Development of Animal Form: Ontogeny, Morphology, and Evolution* (2003), Minelli engages the reader in considering animal form from unusual points of view by using examples from the development of a broad array of invertebrate taxa (e.g., sipunculids, nemerteans, centipedes) that may be unfamiliar to a comparative vertebrate biologist or model organism-based developmental biologist. These different views are enhanced by his use of thoughtful and creatively worded (translated from Italian) phrases.

One of the central questions posed by *Forms of Becoming* has to do with why some forms occur in nature

while other imaginable forms never do. Thanks to molecular genetics, we understand that similarity of form is due to the high level of gene conservation across animals, but we don't really understand the basis of the differences. The example to which Minelli returns is that many centipede species of the genus *Scolopendra* have 21 segments, and many others have 23, but never has even a single individual with 22 segments been observed in any species. He views this general phenomenon, of phenotypes with "borders," as pointing to developmental rules or laws. Understanding the rules—that is, the developmental mechanics (rather than the set of involved genes)—will enable an understanding of the evolutionary basis for the observed differences and discontinuities in animal form. The analogy is made to the rules of chess: A knight can reach only certain squares by moving from its current position—and these moves are the variation upon which natural selection can act.

As in *The Development of Animal Form*, Minelli warns against finalism in developmental biology; that is, viewing the adult as the end goal of development. The traditional view of segments in adult annelids and arthropods, for example, is that they have been selected because of their usefulness in locomotion. Alternatively, he suggests that one should view segments as the result of a developmental process—a developmental logic that favors the serial repetition of structure. The fact that they are useful in locomotion, and thus are favored by natural selection, is not the primary reason that segments exist. As he says, "development has the first word and natural selection the second" (p. 204). Minelli also usefully reminds the reader that natural selection does not see the genes underlying the developmental mechanisms but rather the phenotypes that take shape throughout the whole of an organism's existence. Thus he warns that

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the relationship between genes and phenotypes is not simple.

Minelli points out the historically different research objectives of the fields of development and evolution. He feels that the comparative spirit was reinvigorated initially by the enormous success of the comparative genetic and developmental studies by the model organism communities, and it now must be kept alive by an evolutionarily oriented view of the development of form. However, the broad coverage of many “evo-devo” fundamentals (e.g., modules, homology, segmentation, and the like), and perhaps the unusual nature of his views, contributed to my sense that Minelli’s coverage of the topics was a bit fragmented and lacked overall coherence. I wasn’t sure exactly what the central message book was intended to be. For example, the concept of morphological modules is raised in chapter 12, but not brought into the discussion of somatic versus visceral components of animals (chapter 9), or gene networks and their relation to phenotypic features (chapter 4), or the competitive situation that most likely exists in the development of larval versus adult organs within an organism (a fascinating chapter). Another example of the book’s discontinuity is promoting a combinatorial (rather than an all-or-nothing) view of homology but not integrating this into some of the other discussions on segmentation. That said, it is a tall order—and we lack the knowledge—to truly integrate the multiple developmental facets and comparative morphological approaches that he describes.

Overall, I enjoyed reading *Forms of Becoming*. It added depth to my knowledge of the historical background of comparative morphological studies, and it regrounded my appreciation of the diversity of evolutionary modifications in development across animals. I recommend this book as entry-level reading for non-“evo-devo” folks as well as the

many developmental and evolutionary biologists whose research involves phenotype. I also recommend this thought-provoking book to graduate students. Minelli suggests several easily tested, high-impact research questions (e.g., figuring out what “anterior” is to a tapeworm by looking at a particular set of genes). In summary, Minelli promotes an integrative view that is timely and immensely valuable.

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