NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content and cost of new books in the various fields of biology. More books are received by The Quarterly *than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.*

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, *without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works.* Unsigned brief notices, *written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them.* Regular reviews *are more extensive evaluations and are signed by the reviewers. The longer* lead reviews *consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at SUNY Stony Brook or other appropriate recipient.*

The price in each case represents the publisher's suggested list price at the time the book is received for review, and is for purchase directly from the publisher.

Authors and publishers of biological books should bear in mind that The Quarterly *can consider for notice only those books that are sent to The Editors,* The Quarterly Review of Biology, *C-2615 Frank Melville, Jr. Memorial Library, State University of New York, Stony Brook, NY 11794-3349 USA. We welcome prepublication copies as an aid to early preparation of reviews.*

THE NEW EVOLUTIONARY SYNTHESIS: AROUND THE CORNER, OR IMPOSSIBLE CHIMAERA?

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A review of

DEVELOPMENTAL PLASTICITY AND EVOLUTION. *By Mary Jane West-Eberhard. Oxford and New York: Oxford University Press.* $100.00 (hardcover); $49.95 (paper). xx + 794 p; ill.; author, taxonomic, and subject indexes. ISBN: 0–19–512234–8 (hc); 0–19–512235–6 (pb). 2003.

In the fall of 1990 I had just began my doctoral studies at the University of Connecticut. Freshly arrived from Italy, I came to the United States to work with Carl Schlichting on something to do with phenotypic plasticity. I spent most of that semester discussing with other graduate students what I thought was a momentous paper by Mary Jane West-Eberhard (1989) in the *Annual Review of Ecology and Systematics.* That paper, entitled Phenotypic Plasticity and the Origins of Diversity, was a (quite lengthy) forerunner of the (also quite bulky) book I am reviewing now. Like the paper, this volume has the potential to be momentous in the development of our ideas on phenotypic evolution.

In fact, several other authors (including myself, at the cost of sounding a bit self-serving) have recently contributed efforts aiming at crystallizing a much-invoked (or much-derided, depending on the viewpoint) new evolutionary synthesis (Rollo 1995; Raff

1996; Gerhart and Kirschner 1997; Schlichting and Pigliucci 1998; Wolf et al. 2000; Oyama et al. 2001; Pigliucci 2001; Wagner 2001; Wilkins 2002; see also, in a league all its own, for good or for bad, Gould 2002). Like in the case of the previous neo-Darwinian synthesis (see Mayr and Provine 1980), a body of books has appeared over the course of several years, from authors with disparate backgrounds, all converging toward certain ideas about evolutionary processes. The real question is: are we finally witnessing the second synthesis, or is this an interesting side trail that will ultimately not reconnect with the main road? Before discussing West-Eberhard's contribution to this question, it might be useful to ask ourselves what exactly the new synthesis is supposed to be *about* and, in order to do that, we need to briefly remind ourselves of what the previous synthesis was trying to solve.

As it has been well documented, Darwinism spread rapidly during the first few decades of its history, but faced major problems at the beginning of the 20th century (Bowler 1983). These problems lay mostly in the difficulty of reconciling the so-called "Mendelist" and "biometrician" schools in genetics to forge a unified population genetic theory of evolutionary change (Provine 1971). Such reconciliation happened over a fairly long period of time through the publication of books that are now classics in the history of evolutionary thought: from Fisher (1930) to Mayr (1942), and from Dobzhansky (1937) to Simpson (1944).

Other contributions during the period that had a large impact, such as Goldschmidt's (1940) alternative views to the main synthesis, are now considered interesting sidetracks, while publications that were barely noted at the time (e.g., Schmalhausen 1949) are now considered pivotal in the light of further developments. Such are the perils of trying to understand history while it is unfolding.

If the neo-Darwinian synthesis was a largely successful attempt at reconciling the disparate fields of Mendelian and population genetics, systematics, and paleontology, with the core insights of Darwinism, what is the second synthesis aiming at? According to an almost unanimous consensus of the people involved in it, there are two problems to be addressed: on the one hand, the historical fact that the neo-Darwinian paradigm essentially left embryology and developmental biology out of the main stage. On the other hand, the fact that the spectacular developments of genetics first, and especially molecular biology later, have greatly imbalanced our perception of evolution in favor of a molecule-centered, nonorganismal view of the evolutionary process (surprisingly, a view pushed by evolutionary biologists even more than by their molecular colleagues; see Dawkins 1976).

Calls for the reconciliation of molecular and organismal perspectives on evolution have been made repeatedly (Alberch 1991; Wray 1994; Pigliucci 1996; Carroll 2000; Johnson and Porter 2001), and—together with technical developments and conceptual advancements—have brought to the maturation of two new players on the stage of evolutionary theory: the study of the (molecular) evolution of development (the so-called "evo-devo"; see Wray 1994; Raff 1996; Eizinger et al. 1999; Wilkins 2002), and the study of the genetics, ecology, and evolution of phenotypic plasticity (Schlichting 1986; Sultan 1987; West-Eberhard 1989; Scheiner 1993; Pigliucci 2001). Are recent efforts within the second synthesis succeeding in bringing this all together? West-Eberhard's book is the latest, and perhaps most comprehensive, attempt at an affirmative answer.

Developmental Plasticity and Evolution is clearly a conscious effort at a synthesis along the lines discussed so far. The first part of the book, Framework for a Synthesis, is followed by three additional parts: The Origins of Novelty; Alternative Phenotypes; and Developmental Plasticity and the Major Themes of Evolutionary Biology. The book has been a long time in the making (justified not only by the breadth and complexity of the subject, but by the sheer bulk of the volume), which means that the reference section, despite its comprehensiveness, was already out of date by the time the volume was published. Then again, the role of books in science is not that of up-to-date reviews (which can now be promptly published as short articles and updated electronically), but as lasting con-

ceptual contributions to the evolution of ideas in a given field. In this sense, West-Eberhard's work will make people pay attention and argue long into the next decade and beyond.

Of course, it is impossible to adequately summarize the contents of such book in a relatively brief review, but I have highlighted some of what I think are the most important concepts, in order to give readers a feeling of West-Eberhard's thinking. For example, the second chapter clearly tells us that what the author is looking for is a "unified theory of phenotypic development and evolution," and most of the first part is devoted to a discussion of the basic tools for such synthesis: phenotypic plasticity (Chapter 3), modularity (Chapter 4), and development (Chapter 5). Several important concepts are discussed by West-Eberhard in this part, some of which may be unfamiliar to readers who are not accustomed to the recent literature on phenotypic evolution.

To begin with, there is the idea of phenotypic accommodation, epitomized by the so-called "two-legged goat effect." The latter originates from classic observations by Slijper (1942) of the development of a goat born with stumped front legs (an interesting phenomenon in vertebrates that can be caused by mutations or by environmentally-induced developmental defects). Slijper was struck by the fact that the goat had developed the ability to "hop" bipedally and managed to reach adulthood and sexual maturity (although it did not have progeny). This remarkable recovery from what a priori one could have thought of as a lethal condition was made possible by a substantial rearrangement ("accommodation") of the skeletal and muscular components of most of the goat's body. We now recognize this as a particularly impressive case of the very common phenomenon of developmental plasticity which, for example, allows viable (and fertile) alternative morphs of cichlid fishes (Meyer 1987; Wimberger 1991; Smits et al. 1996) and many other vertebrates to develop from the same or similar genotypes in response to different diets or other environmental conditions.

The two-legged goat effect, together with the more general "equivalence and interchangeability" of genes and environments (something intuited already by Goldschmidt in 1940, with his idea of phenocopy), leads West-Eberhard to claim in the chapter on adaptive evolution that genes can be followers in the evolutionary process—contrary to common, neosynthetic wisdom. In this, the book not only reinforces the move away from gene-centric thinking repeatedly advocated, for example, by Lewontin (1974), but converges with an interesting recent movement originated by an unusual collaboration between organismal biologists and philosophers, known as Developmental Systems Theory (Oyama et al. 2001). The idea is that although genes are obviously fundamental in the process of evolution, they do not "lead" it, because they are not the only elements that need to be inherited from one generation to the next. Rather, genes are one of many crucial—equally important—players, which include also ready-made cellular and subcellular structures and, of course, environmental conditions. To simplify a bit, just as there would be no organism without a genotype, the genotype would be completely inert without the proper environmental and developmental conditions. It is the insistence on the gene's eye view of things—all recent authors involved in the second synthesis agree—that has hampered the development of evolutionary theory after the first synthesis.

The bulk of West-Eberhard's book is devoted to several chapters (Part II) that describe the origins of novelty. Here we find discussions of familiar topics, such as duplication and deletion of structures (not just genes), and of less familiar pieces of the puzzle, such as cross-sexual transfer and combinatorial evolution (at both the molecular and phenotypic levels). The interest in cross-sexual transfer stems from the realization—on which West-Eberhard is particularly keen—that although we keep looking for the mysterious answer to macroevolutionary changes in phenotype from one species or order to another, we keep strangely forgetting that some of the most spectacular phenotypic differentiation occurs within species. For example, think of cases of sexual dimorphism, or of the intraspecific "macro-"phenotypic changes known as polyphenisms.

Perhaps a better understanding of the physiological and molecular bases of intraspecific macrovariation would then provide obvious solutions to the more general problem of macrophenotypic evolution.

Combinatorial evolution is another major piece of the puzzle being considered by the second synthesists. This is the idea that a great deal of the astounding variation at the molecular level and, *a fortiori*, at the phenotypic level (i.e., everywhere above the sheer sequence of DNA) found among living organisms does not arise by the evolution of entirely new sequences or structures (one of the major conceptual problems limiting the first synthesis). Rather, it is the result of the continuous shuffling and reshuffling of a relatively small number of basic elements that evolved early on during the history of life (with, of course, the occasional addition of a few true novelties here and there). As François Jacob (1977) eloquently put it, evolution is akin to a process of *bricoleur*, a continuous tinkering with the odd parts already available, creatively rearranged by mutation and natural selection to shape the ongoing dialectical interaction between organisms and environments.

The third part of *Developmental Plasticity and Evolution* is devoted to what the study of "alternative" phenotypes within species (e.g., the sexual dimorphisms and polyphenisms mentioned above) can tell us about macroevolution in the classic sense of phenotypic evolution above the species level. The basic idea—again—is that evolutionary biologists would be well served by thinking how the same or very similar genotypes can produce such divergent morphologies, and how these changes do not necessarily lead to speciation (although they may, of course), *pace* punctuated equilibria.

In the final part of the book, West-Eberhard broadens her aim again, and reexamines some of the major themes in evolutionary biology in light of the phenomena related to developmental plasticity that she has analyzed throughout the book. Readers are treated to alternative views on gradualism, homology, genotype-environment interactions, speciation, adaptive radiation, macroevolution (in the classical sense of the term), and punctuated equilibria. All of this peppered by short (sometimes too short, despite the bulk of the book) sections on topics such as Morphological Stasis Is Not Evolutionary Stasis or Why Molecular Biology Cannot Solve the Macroevolution Problem.

This book is a must read for evolutionary biologists, despite of the fact that it is not groundbreaking. In fact, it could not be, since it builds on extensive work done by the author (and many others) to provide a synthesis of facts and how they fit into an overarching conceptual framework. The book has, however, already generated much controversy, as it should. At the 2003 evolution meetings, Mary Jane West-Eberhard was given the Sewall Wright Award by the American Society of Naturalists but, at the same time, a colleague proposed to hold a symposium devoted to the criticism of the book on the basis that it is "too holistic," and "one good idea pushed too far." The symposium proposal was eventually rejected by the Society for the Study of Evolution.

Perhaps West-Eberhard has indeed pushed her general ideas too far. Only time will tell, depending in large part on how her and the work of other second synthesists will affect research in evolutionary biology during the next decades. But if the second synthesis is here to stay, *Developmental Plasticity and Evolution* will surely be considered a fundamental pillar of its structure.

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