

Short notes and reviews

Combating footnote status in evolutionary theory

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Review of: Biased Embryos and Evolution, by Wallace Arthur. Cambridge University Press, 2004, xiii + 233 pp. ISBN 0 521 54161 1 (Paperback).

On 11 May 2004, Wallace Arthur presented a characteristically engaging seminar at the Department of Zoology of the University of Cambridge in order to promote his new book *Biased Embryos and Evolution*. After the lecture the speaker and his audience adjourned to the University Museum of Zoology for the official launch of the book. There, amidst wine and canapés, the flocked friends and collected colleagues were given the opportunity to purchase, with a considerable reduction in prize of course, the first copies of Arthur's book, which the author dutifully signed in between his munching of snacks. The festivities included mercifully little speechifying, with the notable exception of Arthur's managing editor at Cambridge University Press, who made a salient point: what set Arthur's book apart for him from most other popular science books was that the entire manuscript of the book was read in just a single sitting. This feat is certainly not the prerogative of merely the most avid bookworms, because Arthur's refreshingly uncluttered prose allows an effortless consumption of the book in one or just a few sessions by any interested reader.

The book's uncomplicated style is well tailored to the intended broad audience of "students and the general reader," but the book is certainly not all style and no content. *Biased Embryos and Evolution* is an enjoyable and instructive read even for dyed-in-the-wool professional biologists. In my view, this book is the best choice currently available for an easy, short, and minimally intimidating introduction to the challenges posed to current evolutionary theory by the accumulating corpus of

empirical and theoretical information generated within the mushrooming discipline of evolutionary development biology, or, in short, evo-devo. Depending on the reader's background, they can then choose to flesh out Arthur's conceptual framework with intellectually more taxing and empirically more dense works such as Gerhart and Kirschner (1997), Davidson (2001), Minelli (2003), and Wilkins (2002).

The core question in Arthur's book is: what determines the direction of evolutionary change? A resounding "natural selection!" will certainly be the most common answer to this question from the educated layman to most professional biologists. However, Arthur labels this expected answer as "overly Darwinian" (p. 10). While not denying the uncontested importance of natural selection as one factor influencing evolutionary change, Arthur considers natural selection to be, at best, only half the answer. Arthur (p.25) writes: "many of us feel that something is missing; that selection is not enough; that the actualization of some creatures, together with the failure of others to emerge from the realm of the possible, requires something else – something internal that interacts with selection in a particular way." Although I would hesitate to label Arthur's more complete answer as "revolutionary," as is dramatically claimed on the back cover of the book, the central ingredients of Arthur's perspective justly merit being called "assaults on the modern synthesis" (p. 74).

The monolithic core of modern Neo-Darwinian theory is the central role assigned to the functional and external mechanism of natural selection, which acts on raw variation between individuals in adapting organisms to changing local environments. Mutations serve as the principal source of variation

between different individuals. These variations, upon which natural selection acts, are generally assumed to be not only copious, but also undirected with respect to the direction of adaptive change and of small phenotypic effect. These presumed characteristics have been taken to imply that natural selection is the most important causative agent underlying significant evolutionary change, and the origin of evolutionary novelties.

Arthur builds a case against this orthodox view by explicitly emphasizing several heretofore neglected internalist themes that require us to focus not just on the interaction between organisms and their external environment, but also on the role of organisms themselves as internal determinants of the direction of evolutionary change. For example, Arthur points out that not all mutations have only very small effects on resulting phenotypes. He also argues that the variation offered to the scrutiny of natural selection is not so unconstrained, or unstructured, as to be essentially inconsequential to the possible directions of evolutionary change. Therefore, in order to understand the direction of evolutionary change, Arthur impels us to study the origin and structure of the variation offered to natural selection. Because evolutionary changes in the phenotype are necessarily effected through changes in development, Arthur focuses on what he calls “developmental bias.” He defines developmental bias as (p. 213) “non-randomness in the variation (both discrete and continuous) in developmental trajectories upon which natural selection acts.” Before the blossoming of evo-devo, such internalist explanations for the direction of evolutionary change were at best awarded the status of footnotes in evolutionary theory. However, the significant revision of evolutionary theory proposed by Arthur necessitates the promotion of these issues from mere acknowledgements in the margins of orthodoxy to fully-fledged focal points of research.

In summary, Arthur proposes that evolutionary change is determined by the interaction of natural selection with the structure of the variation offered to it, played out within an enveloping matrix of historical contingency.

In arguing his case for the importance of development for fully understanding the nature of evolutionary change, Arthur has managed to cram his

sleek book full of insightful introductions to the essential concepts of evo-devo. A partial list includes developmental reprogramming, internal selection and co-adaptation of an organism’s parts, the existence of mutations with phenotypic effects of different magnitudes, gene duplication and functional divergence, co-option, accumulation of hidden genetic variation, heterochrony, the structure of adaptive landscapes, as well as phylogenetic methods, metazoan phylogeny, homeobox genes, comparative study of expression patterns of developmental genes, and homology. In addition, the book is sprinkled with pertinent discussions of the history of biology, and revealing personal reminiscences from Arthur’s own career.

Throughout his book Arthur is refreshingly candid about his intellectual commitments, personal interests and biases, the supposed novelty of his views, and how much they depart from perceived orthodoxy. He clearly shows that a universal consensus about the factors responsible for the direction of evolution is elusive. Arthur’s view is merely one of a variety of different opinions that range from the ultimate reductionism of Davidson (2001), who argues that “the study of the mechanisms by which animal body plans evolve” in time will just “be regarded as a branch of regulatory genomics”, to the expansive view of Vermeij (2004), who argues that the pattern of evolutionary history is largely determined by universally operating economic principles that are equally applicable to humans and the biosphere.

Although the absence of mathematics or the use of a conversational style may not convince all readers of the validity of Arthur’s thesis, it should be noted that his plea for a revision of evolutionary theory is not a lonely cry. In fact, the unquestioned hegemony of natural selection as the sole locus of evolutionary causality, with adaptation signifying the fit of organisms to their external environments, has recently come under attack from several corners. The best-known example is surely Stephen Jay Gould, who argued throughout his career that evolution is not just about natural selection and adaptation. A fuller view should also include a substantial internal component that addresses how organismic structure and development affect the direction of evolutionary change. Gould summarized his views in his massive book, *The Structure*

of *Evolutionary Theory* (2002). Arthur is evidently strongly influenced by Gould, who is one of the dedicatees of Arthur's book. This is demonstrated, for example, by both Gould's and Arthur's choices to represent evolutionary theory with architectural metaphors.

Odling-Smee et al. (2003) recently presented a different perspective that also emphasizes how organisms can affect the direction of their evolution in the book *Niche Construction: The Neglected Process in Evolution*. Where Arthur and Gould argue for a greater role for the organism in providing the raw material for its own evolution by moving away from the interaction of the environment and the organism to produce adaptive evolutionary change, Odling-Smee et al. retain this focus, but would enhance the organism's power to affect its evolution by re-orienting the arrow of cause and effect. Many organisms alter their immediate environments to create their own niches, and thus they can both directly and indirectly affect the selection pressures acting on them, and thereby affect the direction of evolutionary change. Although this perspective is very different from that adopted by Arthur and Gould, it also places the organism in a

more central position in evolutionary biology.

All these efforts attempt to promote "footnotes" in evolutionary theory into fully-fledged research programs.

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