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Book review

Two hundred years of homology and 50 years of ''Essentialism''

The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. By Ron Amundson. Cambridge University Press (Cambridge Studies in Philosophy of Biology), Cambridge, UK. Hardback, ISBN 0 521 80699 2, 2005, $75.00 £45.00, 294 pp.

If producing a history of science were a straightforward task of translating documents from different languages into a common one, and putting facts and events in chronological order, science would be a simpler enterprise. The history of biology as most people learn it has been told by a small number of biologists, historians and philosophers, who assume the duty of researching the past. This book, recently published by Ron Amundson, a philosopher from the University of Hawaii at Hilo, shows how some of the paradigms previously outlined by some authors can be reinterpreted. The main theme of this book is the paradox of evolution of development (evo-devo) being a new and an old science at the same time. Knowledge and interpretation of research programs pre-dating the New Evolutionary Synthesis are essential to understanding the recently renewed interest in developmental research. This is best done by correcting the biases created by previous explanations about past research methods and philosophies. The book is primarily written for a growing audience of people interested in evo-devo. However, it does not attempt to thoroughly cover recent developments in this field. Amundson's goal instead is to write about the almost 200-year history that justifies the renewal of interest in the field. It does not pretend to be an impartial account of this history—the author presents his personal views, which are many times at odds with what could be called common sense among evolutionary biologists. The result is an opinionated discussion, both illuminating to evo-devo practitioners and researchers of other disciplines, especially systematists.

Ron Amundson is ''primarily interested in theoretical and methodological debates between scientific views, rather than in scientific theories themselves'' (p. 2). This has proven to be an attractive subject to other philosophers interested in the history of biology, most notoriously, David Hull, who chose the controversial field of systematics in the 1970s as an example in his thesis ''Science as a Process'' (Hull, 1988). According to Amundson, our understanding of scientific ideas and paths depends on those who tell us the history of those ideas—seemingly a very sensible proposition. He then goes on to propose that our understanding of the relevant ideas in evolution (following Darwin) and their progress is almost exclusively based on their history as told by the New Synthesis authors, especially Ernst Mayr (e.g., Mayr, 1982). The influence of contextualized historical investigation, in this case, New Synthesis authors, is then named ''Synthesis Historiography.'' Two relevant and interrelated aspects of Synthesis Historiography for twentieth century biology were the underappreciation of morphological and developmental studies for the advancement of evolutionary biology and the denigration of the term ''essentialism''. When history and subjectivity are mixed together they should be called ''story'' rather than history. This is what Amundson does. He borrows the phrase ''Essentialism Story'' from Winsor (2003) to define the historical criticisms of the term ''essentialism''.

In many ways this book is no more than a much-expected step in Amundson's research program focusing on morphology through history. He laid a strong foundation for his book in a previous article (Amundson, 1998), when the distinction between ''structuralists'' and ''functionalists'' was explored. In this scheme, structuralists are represented by the transcendental anatomists, which include Éttiene Geoffroy St.-Hilaire, Richard Owen, and Ernst Haeckel, among others. Of the functionalists, Georges Cuvier and the British Natural Theologians (e.g., Reverend William Paley) are important examples. Amundson does not try to hide his sympathy for the structuralist approach to the study of form, and for the authors who also favored this view, most notably Russell (1916) and Ospovat (1981). He understands this has been a long-standing dichotomy and perceives it as more relevant than other theoretical dichotomies emphasized during the twentieth century: germ–soma, ultimate–proximate, genotype–phenotype, populational–typological. The fourth dichotomy on the list, populational–typological (Mayr, 1959) is built upon the priority of populational over typological (i.e., essentialist) approaches in evolutionary research. This is

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marked by the consistent depreciative use by Mayr and a number of followers of the terms ''essentialist'' and ''typological'', as if they carried intrinsic antievolutionary connotations.

The book is structured in a simple and objective way, proceeding primarily in chronological order. The first chapter is an introduction and overview of the book. It warns the reader about Amundson's intentions and his historical revisionist intentions. Two main sections, with distinct characters, treat different historical periods of the biological sciences. Part I is mostly about the nineteenth century and discusses the European natural system and the controversies surrounding idealistic morphology. It discusses the development of Darwinian evolutionary theory and the impacts of morphological research on the conception of Darwin's *The Origin of Species*. Part I ends with a chapter that analyses evolutionary morphological research at the end of the nineteenth century. The ''Interlude'' serves as a summary of the first four chapters of history and bridges the first and the second sections. Part II covers the twentieth century, beginning with the discovery of heredity and proceeding with the New Evolutionary Synthesis. The second half of the book is important as it offers a discussion of the concept of Synthesis Historiography and why the Essentialist Story was created. It shows the reduction of importance and breadth of structuralist research as compared with the nineteenth century. The last chapter of the book outlines some of the recent developments in biology that encouraged the rebirth of evo-devo. Close to the very end, the author offers an appealing discussion about concepts of homology followed by considerations about the needs for a new synthesis of evolution.

Ron Amundson is honest about his game: he takes advantage of the contemporary success of evolutionary developmental biology (evo-devo), and the consequently newly gained ''legitimacy from recent science'', and takes ''a different standpoint from those who assumed the adequacy of the Evolutionary Synthesis'' (p. 2). His disagreements with some New Synthesis authors can be harsh at times, especially with Ernst Mayr and Peter Bowler, but he plays a fair game and includes a substantial number of references and some quotes. Furthermore, it is generally clearer in Amundson's writing, compared with the New Synthesis authors, what constitutes personal interpretations and what does not.

The Changing Role of the Embryo in Evolutionary Thought has goals that leave discussions about species concepts and most systematics-related topics outside the realm of the author's analysis. The divergence in scientific pursuits between morphologists and systematists is the reason why Amundson excluded most of the history of systematics from the book. However, a whole chapter is dedicated to ''Systematics and the Birth of the Natural System'' (Chapter 2). As Amundson explains at the end of this chapter (p. 52), ''[c]lassifications are devised for too many different purposes to unequivocally support the kind of thought that would lead to evolution''. Nineteenth century biology had more of an impact on phylogenetics and systematics than did the modern synthesis of evolution. Amundson (2002) comments on this matter. The explanatory goals attempted by putting forward phylogenetic hypotheses in the late nineteenth century were not the same as the ones in Hennig's mind in the 1950s. As Amundson (2002, p. 685) stated it, in the nineteenth century ''[p]hylogeny then was a means to an end, explaining form'', being thus directly linked to the goals of idealistic morphology. This role of phylogenetic research is not as important now because there is diversity of research programs that make use of trees, but as in its Hennigian and post-Hennigian advances, phylogenies have a more descriptive purpose, being needed for classification purposes. It was primarily due to the work of twentieth century systematists, that comparative biology advanced. Progress was not only in the empirical realm by the collection of large amounts of data for the understanding of relationships. Systematists composed a community of biologists that consistently contributed to discussions about ontological and epistemological aspects of homology for most of the twentieth century. These points could have been further explored in the book.

There is one historical connection of potential interest for systematists. Amundson mentions that the Essentialism Story started with a few papers published around the 100-year anniversary of the publication of *The Origin of Species*, most notably Mayr (1959). Less than a decade later, these views were explicitly translated to meet the standpoint of systematics by Hull (1965), who describes the ''2000 years of stasis'' of taxonomy, due to the long-lasting effects of Greek essentialist philosophies. As a philosophical response to the challenge that systematics fails to assimilate Darwinism, Ghiselin (1966, 1974) proposed that biological entities, such as species, should be viewed as individuals. This was Ghiselin's ''radical solution'' to free systematics from the essentialist notion of set membership. Hull (1976) later adopted the individualist thesis, as did a number of other authors (e.g., Mayr, 1976; De Queiroz and Gauthier, 1990; Ereshefsky, 2001; Kluge, 2005). The most visible consequence of the individualist thesis in current systematics is the proposal of alternative nomenclatural codes to the Linnaean system (see Keller et al., 2003 for discussion). PhyloCode (http://www.ohiou.edu/phylocode/) is the system, among those alternatives, that has attracted the most attention. Its philosophical consistency (Keller et al., 2003) and supposed operational benefits (Nixon et al., 2003, and references therein) have been contested. Its historical justification comes from the need to reject essentialism

in taxonomy. In one of the seminal papers proposing the elaboration of the PhyloCode, De Queiroz and Gauthier (1990, p. 308) stated that "elements of the Aristotelian form of definition have persisted in modern biological taxonomy in that names of taxa continue to be treated as if they were defined by lists of characters." It is critical to ask how much importance should be given to a proposal based on notions built upon the Essentialism Story.

There certainly are alternatives to the individualist thesis, and one whose popularity has grown is an analysis based on the concept of natural kinds (e.g., Boyd, 1999; Wilson, 1999; Wagner, 2001; Keller et al., 2003; Rieppel, 2005). This can be viewed as a modern interpretation of essentialist approaches, in which biological entities receive differential treatment from immutable entities, such as chemical compounds. It is possible to do so by incorporating Richard Boyd's notion of homeostatic property clusters to the definition of natural kind (see Boyd, 1999). Not only can this naturalistic realist thesis be applied to species, but also to parts of organisms (e.g., Griffiths, 1999; Wilson, 1999; Wagner, 2001; Rieppel, 2005). Similarity and group membership are intuitive signatures of natural patterns. The attractiveness of this realist approach is a consequence of its intuitive appeal, favoring "induction and explanation—definitions of natural kinds are reflections of properties of their members that contribute to that aptness" (Keller et al., 2003, p. 102).

Amundson calls the early and mid nineteenth century morphologists "cautious realists". This scientific realist position assumes "a reality underlying a phenomenal law, but they are not yet ready to name it" (p. 15). On another note, Synthesis Historiography depicted pre-Darwinian essentialism as implying a series of metaphysical commitments grounded in species fixism, which ultimately represents a barrier to the development of any sort of evolutionary idea (p. 19). Evolutionary and phylogenetic hypotheses complement the results produced by the early essentialist morphological research. They are theory-dependent *a posteriori* truths that better serve to explain similarity (homology) and complex patterns of morphology (*Baupläne*). O'Hara (1988) discussed the importance of "tree-thinking" to extract explanations and descriptions from phylogenetic hypotheses. According to O'Hara, tree-thinking is the best alternative to Mayr's "population-thinking" when biologists ask historical questions. Population-thinking is neither outdated nor it is wrong, it simply fails to explain phylogenetic patterns. Those were the patterns pre-Darwinians would describe in essentialist ways, e.g., proposing *Baupläne* as abstractions for the morphological diversity observed among taxa.

Homology is the concept that was kept as pivotal to comparative sciences though all theoretical revolutions in biology during the last two centuries. Geoffroy and Owen viewed homology in a way proven to be translatable into contemporary search for patterns in form in both modern systematics and in evo-devo. The interpretations of these observable patterns of similarity have surely changed. If interpretations are so crucial, this should be a reminder that history can completely "change" too, in the way it is told, as it depends on the "(hi)story-teller" we choose to agree with.

According to Amundson, the evolutionary concept of homology, in which a relationship of similarity is due to common ancestry, is insufficient for researchers trying to explain the structural basis for this similarity. Günter Wagner's (1989) biological homology concept tries to offer a counterpoint to the dilemma and inserts the importance of "developmental constraints" into the definition. The application and importance of a homology concept based on developmental properties to systematics is certainly questionable. Nonetheless, the knowledge gained by studying form at the level intended by evo-devo researchers promotes the best delimitation of concepts such as "character" in biology (Wagner, 2001; Freudenstein, 2005). Furthermore, the understanding of phylogenetic relationships favors the answering of questions in the realm of evo-devo (Abouheif, 1997; Bang et al., 2002; Serb and Oakley, 2005).

Even if everything Ron Amundson wrote about essentialism were wrong (which I do not think is the case), it is still refreshing to read such a well-prepared argument for a competing view of the history of biology. New ideas surely arise from disagreement, and disagreement with Amundson can thus be a source for new and fresh ideas.

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