The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo–Devo

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Evolutionary developmental biology (evo–devo) has become an established field of research, especially since the spectacular results obtained in the 1990s regarding cross-species molecular homologies of (Hox) genes acting early during embryogenesis in insects, vertebrates, and beyond. Amundson summarizes some of these results, which justify a central assertion of evo–devo, namely that one must understand how bodies are built in order to understand how the process of building bodies can be changed, that is, how evolution can occur. But Amundson's book is not about these discoveries, but about the history of evo–devo.

The book consists of two parts: the first part, 'Darwin's century: Beyond the essentialism story', presents a revisionist history of evolutionary biology during the nineteenth century written by a proponent of evo–devo. It is revisionist because it is set against the traditional histories of the same period, which have been written by proponents of the Evolutionary Synthesis. The second part, 'Neo-Darwin's century: Explaining the absence and the reappearance of development in evolutionary thought', includes not only the history of the Evolutionary Synthesis, but also an interesting meta-theoretical discussion of the possibility of a new synthesis between neo-Darwinism and evo–devo.

Darwin's Century

Amundson's history of early evolutionary biology involves important corrections of the traditional histories written by proponents of the Evolutionary Synthesis. The latter are referred to as Synthesis historiography (SH). According to SH, the pre-Darwinian era was characterized by the belief that species are fixed; a belief based on essentialist-typological metaphysics of Platonic origin. Amundson shows, however, that species fixism was an innovation of the 18th century (one of the innovators was Linnaeus), which enabled the construction of a classificatory Natural System, and in that sense was scientifically progressive. Previous to this innovation, the belief in sudden, large mutations was widespread.

For Linnaeus and his early followers, in particular the French systematists Jussieu and Lamarck, the Natural System represented not a system of objectively real relationships, but a convenient labeling system. The taxonomic system of another contemporaneous French systematist, Cuvier, also does not match the SH description of an essentialist system: he used the concept of functionally defined 'embranchements', that is, taxonomic categories, which were chosen because they yielded efficient data management. As Amundson explains, Cuvier also provided a functionalist account of species fixism. As these examples show, essentialism and typology often were not part of the grounds for species fixism, as claimed by SH.

As time passed, the Natural System came more and more to be seen as a description of objectively real relationships. Morphology, the study of organic form, which began as a branch of systematics, and then grew into one of the important biological disciplines in the 19th century, was centrally involved in this change from early nominalism to realism. Amundson discusses the origins of morphology in a separate chapter, starting with Goethe up to the turn from functionalism to structuralism. I find this one of the more complex chapters in the book, addressing several issues: the conceptualization of morphological types, the turn from functionalism to structuralism, and rejection of another claim by SH that pre-Darwinian morphology should be considered to be an idealistic version of the natural theological argument from design.

Chapter 4 of Amundson's book focuses on Owen and Darwin. It contains a very interesting description of Owen's life and work, emphasizing his achievements in strengthening and articulating the morphological type concept and molding it into the Vertebrate Archetype. It also makes clear Owen's difficult position with respect to the conservative British adherents of natural theology, and Owen's strategy to deal with this by using pious language. Of course this has given rise to much misunderstanding, in particular regarding a proper assessment of the importance of Owen's work for Darwin, and Amundson addresses this in a revealing section entitled 'Misunderstanding Darwin on Owen'. Amundson sees Darwin's achievements as consisting of two parts. The first part is Darwin's proof of descent from common ancestry (replacing Owen's archetype), made possible by the availability of a realistically interpreted Natural System and its morphological underpinnings. This part of Darwin's achievements was successful almost immediately. The second part is the argument for natural selection as the force behind evolutionary change. This involved a new explanatory goal for evolutionary biology, namely the explanation of change (instead of the morphologist's goal of explaining form). This was accepted much later, partly because in Darwin's time functionalistic adaptationism was superseded by structuralism.

The last chapter of the book's first part discusses evolutionary morphology, the research program of the first generation of evolutionists. A central aim of evolutionary morphology was phylogenetic reconstruction. Phylogenetic

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reconstruction in evolutionary morphology can be summarized as follows: Identification of an ancestral ontogeny that can be modified into the ontogenies of the descendent groups. Stated more specifically, the causal understanding of ontogeny, as obtained in experimental embryology, will enable the understanding of how ontogenies can change. Amundson explains that 19th century experimental embryology could not provide the required causal understanding of ontogeny, which is why this research program was unsuccessful.

Neo-Darwin's Century

The book's second part starts with a discussion of heredity, which in the 19th century was conceived as an aspect of embryological development. The epigenetic accounts of inheritance of Barry, Darwin, and Weismann are presented. The account of Weismann's theory is very informative in that it clarifies the role of his distinction between germ line and soma — Weismann proposed a mosaic theory to account for differentiation of the developing embryo and this required sequestering of the germ line. The section discussing Hunt Morgan is in my opinion a high point of Amundson's book. Morgan started his career as an evolutionary morphologist and embryologist, rejecting the Mendelian chromosomal theory of heredity (MCTH) as preformationist — ontogenetic development was a causal process resulting in increasing complexity, and such a process could not be explained by a sequence of particles that were claimed to be associated with adult traits. Then Morgan reversed his views on MCTH.

Amundson is intrigued by this radical change, in particular Morgan's differential concept of the gene. I summarize Amundson's description on pages 149 to 150. Twenty-five factors had been discovered to affect red eye color in drosophila. When one particular factor mutates, the result is a pink eye color. Even when all 24 other nonmutated factors still also affect eye color, the mutated locus is referred to as the cause of the pink color. This differential concept of the gene makes it possible to causally explain adult characteristics without any reference to the embryological processes that actually brought them about. It is the starting point of the split between genetics and embryology. It also is the step, which makes possible the distinction between transmission genetics and the developmental genetics endorsed by embryologists. Rather than genes causing characters (as in developmental genetics), differential genes explain the sorting of characters in a way that requires no attention to development.

Population genetics was based entirely on Morgan's transmission genetics enabled by his differential gene concept. For the first time it was possible to conceive of a theory of heredity, transmission genetics explaining the sorting of characters, which was compatible with natural selection. Amundson describes the origins of the Evolutionary Synthesis as the combination of MCTH, population genetics, and field studies of variation. He also draws attention to the many alternative evolutionary concepts, previously popular, which were explicitly forbidden by the Evolutionary Synthesis (e.g., saltational theories).

The chapter entitled 'Structural reactions to the Synthesis' discusses points of critique by embryological experimentalists. One of these points is based on the causal completeness principle. It asserts that, in order to achieve a modification in adult form, evolution must modify the embryological processes responsible for that form. This principle is violated by the Synthesis. Amundson indicates that this principle is better understood as a statement of theoretical commitment rather than an actual argument. Of course the theoretical commitment of the Synthesis is different: Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute population genetics (Dobzhansky, 1937). Another point of critique refers to Mendelian blind spots: Mendelian breeding experiments cannot study characters that are fixed within a species or that vary only between species. Hence the Mendelian methods ruled out the study of every embryological character that had ever been associated with the basic morphological types. Again the Synthesis reply is as expected: Hereditary factors that are fixed within a breeding population are irrelevant to natural selection. The remainder of this chapter mainly discusses points of contact among developmental biologists and synthesis evolutionists, including Wright, Waddington, Schmalhausen, and Goldschmidt.

Discussion of the maturation of the Synthesis during the1950s mainly focuses on Mayr and his strategic use of four dichotomies: (i) genotype versus phenotype, (ii) germ line versus soma, (iii) proximate versus ultimate, and (iv) typological thinking versus population thinking. Initially these dichotomies are used to safeguard the position of naturalistic studies against the rise of molecular genetics. In the 1980s the same dichotomies are used to argue that development is conceptually irrelevant to evolution.

In the final chapter, Amundson considers recent debates and the continuing tension between the Synthesis and evo–devo. Among many other things, he discusses the importance of the concept of developmental type (e.g., developmental homology) for evo–devo, and points out the fundamental incommensurability of this concept and neo-Darwinian population thinking. On page 256 he summarizes this discussion as follows. According to neo-Darwinism, adaptive radiation is the way of evolution. Once speciation occurs, no causal force can unify distinct populations. Developmental types violate this, in that it involves a unified process that is shared among reproductively isolated groups. Amundson therefore concludes that one or the other (or both) must go before a new synthesis is possible.

Perhaps a less drastic solution is possible. Earlier in this chapter, Amundson approvingly discusses Wagner's account of developmental homology (an instance of developmental type) in terms of homeostatic mechanisms within ontogeny that maintain the integrity of characters. Embryogenesis is a highly nonlinear stochastic process of biological pattern formation. It can be shown that the emergence of biological patterns is not solely the effect of genetic and environmental factors, but in addition is governed by dynamic phase transitions characterizing self-organization of the underlying growth processes. The abstract mathematical

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theory of these growth processes implies that there exist a limited number of canonical forms of phase transitions, irrespective of the details of the stochastic dynamic equations. It is conceivable that these canonical forms of dynamic phase transitions give rise to developmental homologies across reproductively isolated groups.

Amundson has written an impressive and convincing alternative history of evolutionary biology. It is a sophisticated, multi-layered history, of which I only could scratch the surface in this review. One is given an in-depth perspective on the limitations of SH, the program underlying the Synthesis, and on the distant and recent developments leading up to evo–devo. Amundson excels in giving clear descriptions of key concepts, philosophical background, and helpful summaries. An excellent book.

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