

Preface

I became aware of what we now call evolutionary developmental biology (“Evo-devo”) in the early 1980s. Many of the contributors to this volume worked in the field earlier than this. They are (mostly) evolutionary biologists; I am a philosopher and historian of science. The three-decade history of the field that is bracketed by the 1981 Dahlem conference (Bonner 1982) and this volume comprises a uniquely exciting episode in the history and philosophy of science. My entry into the study of this field was serendipitous. It was so stimulating that I have devoted almost all of my research efforts to it since that time.

The serendipity occurred because my scholarly interests in 1980 were in the history of methodological debates within the sciences, and not particularly in biology. I was finishing up an extended study of the “cognitive revolution” in psychology of the 1950s and 1960s, in which behaviorism gave way to cognitive psychology. Many people had recognized the formal analogy between the behaviorist principle of trial-and-error learning and Darwinian natural selection. It was my expectation that evolutionary biologists all knew how natural selection worked, so I should learn from them in order to understand the nature of the psychological debate. I arranged a visit in the summer of 1983 to the Harvard Museum of Comparative Zoology (MCZ), and interviews with Ernst Mayr, Stephen Jay Gould, and Richard Lewontin. The reader of this volume can imagine what I stepped into. I had expected some unanimity about natural selection among biologists, but I found myself in the geographical epicenter of a serious, ongoing methodological controversy. Imagine my delight!

Gould invited me to the MCZ, and I spent a sabbatical year (1985–1986) in his lab, next door to Pere Alberch’s office and a short distance from Lewontin and Mayr. Gould had already introduced me to the anthology that had come from the 1981 Dahlem conference (Bonner 1982), a crucial gateway to the debates. One of my first publications on the developmental approach was based on Alberch’s important paper on constraint in that volume (Amundson 1994). This paper showed that developmentalists and adaptationists used divergent concepts of constraint.

It was no wonder that the debates were inconclusive when the central concept at issue was given different interpretations by the two sides.

I also refer to my acquaintance with the field as serendipitous because there was no easy way for a philosopher to identify Evo-devo as an up-and-coming field of science in the 1980s. Most philosophers of biology of that time were concentrating on topics that grew out of the population biology framework of the Evolutionary Synthesis, such as the “units of selection” problem. Notable exceptions included William Wimsatt and Richard Burian. Wimsatt introduced the notion of generative entrenchment to explain developmental constraints (Schank and Wimsatt 1986) and Burian had organized the now-famous conference on developmental constraints (Maynard Smith et al. 1985). Given my geographical isolation and heavy course load, I could bring myself up to speed only by devoting my research to the study of developmental biology and the arguments (pro and con) regarding its relevance to understanding evolution. It was a long shot. If the remarkable explosion of knowledge in developmental genetics, phylogeny, and other related fields had not happened as it did during the subsequent decades, I would have had a rather tedious and mundane academic career. Even so, my research only began to seriously pay off 10 years later.

In those days, it was pretty unclear what would count as the “success” of a developmental approach to evolution. Some advocates (now in a small minority) believed that something like Evo-devo would refute the entire Evolutionary Synthesis and replace natural selection with some other mechanism. More moderate thinkers expected a sort of “Second Synthesis” to integrate development back into mainstream evolutionary theory and create a wider or broader synthesis. My own hope was that the methodological debates would continue, at least long enough to give me a chance to eke out their dynamics. This has happened to a far greater extent than I could have hoped.

Around 1960, the Evolutionary Synthesis biologist Ernst Mayr began to broaden his interests into history and philosophy of biology, and cooperated with several non-scientists to formulate an Evolutionary Synthesis-oriented framework of concepts that set an agenda for most of history and philosophy of biology during the following decades. One outcome of my research was to critique this tradition. I characterized it as “Synthesis Historiography” and argued that it distorted history in a way that made developmental approaches to evolution seem methodologically flawed. Mayr and his associates had introduced a set of dichotomies that came to be seen as logical truths about biology and were particularly useful in arguments that concluded ontogeny was strictly irrelevant to evolution. Among these dichotomies were proximate causation versus ultimate causation and population thinking versus typological thinking, as well as certain ways of formulating the distinction between genotype and phenotype and between germline and soma. Each of these dichotomies was used during the 1980s and 1990s to argue that ontogenetic development was irrelevant to evolution. It was argued, for example, that development concerns proximate causation but evolution is about ultimate causation, and that this was why development is irrelevant to evolution. Prominent thinkers such as Mayr, John Maynard Smith, Bruce Wallace, and George C. Williams offered

these and related critiques. I have come to realize in conversation that many current biologists are skeptical that thinkers of this magnitude could have reasoned in a way that seems so simplistic today. But it is important to recognize how much our perspectives have changed since the 1990s. I have carefully documented these anti-developmental arguments (Amundson 2005, Chap. 11). Views that seem naïve today were in the mainstream not long ago.

The present volume offers the reader a wide range of perspectives about how an understanding of development has changed, if not transformed, our understanding of evolution. The radical anti-selectionists are absent, but a range of other views is present. No one believes, as many adaptationists did in the 1980s, that development is literally irrelevant to evolution. But there are many opinions about what exactly must happen before we can integrate our new knowledge of development into our classical knowledge of population genetics and evolutionary theory to yield an integrated perspective on evolution. I must confess that I have been swayed to some extent by the methodological arguments of adaptationists. Evo-devo practitioners who claim that their approach is perfectly consistent with population genetics are overconfident. I agree with the conclusions of Karl Niklas (Chap. 2, this volume); some major, new theoretical advance is necessary before we will have an understanding of population genetics and development that does justice to both. But Niklas's reasons are different from mine. I am more of a pluralist than he is about what counts as an "explanation" in science. The problem I see revolves around the difficulty of integrating population thinking with the mechanistic thinking of developmental biology. Some Evo-devo practitioners seem to think that merely *endorsing* natural selection is sufficient to prove a consistency between Evo-devo and adaptationist population thinking. But it takes more than this. One must understand the objections raised by Mayr and his associates, and explain just how they do not apply to current thinking. To my mind, this has not yet been done. I am delighted with current science, and smugly satisfied about how many mistakes can be seen in earlier thought, but have we shown that population genetics and Evo-devo can be melted into the same pot? I am not yet convinced.

Alan Love's Introduction offers a guide to the wide range of views in this volume regarding the changes that have been necessary to bring Evo-devo to its current, favored position. Some of the most obvious examples are the increasing respect paid to phylogenetic systematics and the explosive growth of knowledge in developmental genetics. I was slow to catch on to both of these developments. In the early days, "genetics" simply meant *transmission genetics*, with genes defined abstractly in terms of their relation to phenotypic traits. In that sense, I suspect that many of us still are skeptical about the relevance of "genetics" to development. But the term "genetics" now means something much broader—a form of conceptual change has occurred (see Love, Chap. 1, this volume). We create a false sense of continuity when we fail to distinguish between different kinds of genetics. By the time the term "genetics" became synonymous with molecular genetics, and in particular the regulation of gene expression, Evo-devo was well on its way.

Regarding systematics, I decided when I first reached the MCZ in 1985 to ignore the arguments over cladistics; the debates were too personal and the topic itself hard to comprehend. Armand de Ricqlès (Chap. 12, this volume) reports in this volume how perplexed he was that Gould, otherwise an early hero of Evo-devo, sided with Mayr in opposing phylogenetic systematics (cladistics). I can reassure him that in 1985–1986, Gould was beginning to change, and was encouraging his students to take cladism more seriously. David Hull (1988) has reported on the very personal and nasty nature of the debates during that period. Although Gould had originally opposed cladism, he was softening towards it in 1986. He convinced me to keep an open mind, but it was years before I (and many others) recognized the importance of phylogenetic systematics for the progress of Evo-devo (see Raff, Chap. 11, this volume).

I would like to draw attention to an aspect of the growth of Evo-devo that is distinct from specific methodological issues, although it does indicate an important change in perspective. The difference can be seen in popular narratives about evolution that emerge from mainstream adaptationist evolution theorists as compared to those commonly articulated from the viewpoint of Evo-devo. The mainstream narrative emphasizes adaptations and assumes a sort of autonomous individuality between species. Because true species cannot interbreed, any observed genetic or morphological similarities should be explained in terms of similar selective pressures unless lineages had recently diverged and still displayed a residual conservatism from common ancestry. One would not expect to find homologous genes in species whose phylogenetic separation occurred a long time ago. Only a few dissented from this perspective that was widely held by Synthesis theorists (e.g., de Beer 1971; cf. Raff, Chap. 11, this volume), in part because any causal mechanism that might be used to explain Unity of Type would commit the fallacy of typological thinking. Homologous genes were not only difficult to find (due to their expected rarity and for technical reasons), but even if found they had no bearing on evolution.

Today's evolutionary science is very different. Huge numbers of homologous genes have been identified, and they control some of the most abstract examples of similarities across all metazoan species (e.g., morphological axes of the body). As molecular genetics advances, we find more and more identities among genes in complex organisms and in representatives of their phylogenetically distant and morphologically simpler ancestors. This is most remarkable when those ancestral forms lack the phenotypes produced by the homologous genes in complex organisms. Choanoflagellates possess genes that are homologous to the genes for cell adhesion molecules in metazoa (King et al. 2008). But choanoflagellates are single-celled creatures! What are they doing with (what we call) "cell adhesion molecules"? Simple animals such as jellyfish have no nervous system. Yet they share the genes that are used by metazoans to build nervous systems (Arendt et al. 2008). What need did they have for these genes? Genes involved in the specification and development of the autopod (hands and feet) in terrestrial vertebrates are found in species of fish that have no autopod at all (Schneider et al. 2011).

This unmistakable trend of discovery seems to be one of the most significant developments of recent years. From a historical perspective, the importance of the

trend is its conflict with the methodological standards of the critics of Evo-devo during the 1980s and 1990s. But I see an additional complexity. These results greatly magnify the importance of the concept of exaptation (Gould and Vrba 1982), a notion that was earlier referred to as “pre-adaptation” (another form of conceptual change). It is beginning to appear that every gene that performs a biological function today performed different functions in the evolutionary past. This complexity also is manifested in the fact that today’s genes perform different functions in different life stages, in different phases of development, and in other sorts of varying contexts (see Piatigorsky 2007). How are we to map population genetic analyses onto such squirming masses of genetic functions?

This observation reflects not only a fact about outside reports regarding evolutionary discoveries, but also a conceptual change in how evolutionists regard the problems facing them. My own research focuses on debates, and so I tend to emphasize conflicts between schools of thought. But even among evolutionists with broadly Evo-devo approaches, things have changed dramatically. Hanken (Chap. 4, this volume) points out how the concept of heterochrony has changed in its explanatory importance from the 1980s until today. Heterochrony and allometry were among the few developmental mechanisms available to theorists of the time, and so received a great deal of attention in earlier days. These mechanisms were applied to observable developmental events, and observations of molecular events were not yet available. Discoveries of gene homologies and re-used mechanisms of regulation changed all that. New developmental mechanisms, with clear evolutionary implications, came into play as gene expression patterns began to be mapped onto the organism and their regulation understood.

A broader change in perspective regards whether or not the observable data of certain evolutionary commonalities actually require *any explanation at all* (again see Amundson 2005, Chap. 11, for details). The mainstream view in the 1980s was that it did not. Bauplans and deep homologies were seen as mere artifacts or historical accidents; it was a typologist’s mistake to try to explain them. Today it is broadly assumed that even remote correspondences are likely to reveal deep underlying causes. The very fact that the clade *Bilateria* is commonly discussed shows how radical this change is (e.g., see Freeman, Chap. 10, this volume).

One concept in particular illustrates the new conceptual breadth in perspective that evolutionists have adopted. The concept of homology is notoriously difficult to account for by means of developmental biology (de Beer 1971). Günter Wagner (Chap. 15, this volume) has taken up this challenge, and (to my modest understanding) has given a uniquely satisfying account of how homology can have the perplexing attributes that it does. The responsibility to even attempt this task shows that today’s Evo-devo has duties and goals that go far beyond those of the mainstream of twentieth century evolutionary theory. It is true that Wagner and other Evo-devo thinkers had attempted this task—and failed at it—during the 1980s. But his new analysis shows how it is possible for homologous characters to possess a *sameness* that persists even while the developmental origins of those

characters are modified in different groups of descendents. What seemed like metaphysical idealism to the critics of Evo-devo has here received a mechanistic explanation. Achievements like this reveal just how far our goals and abilities have advanced.

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