Cambridge University Press
0521806992 - The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo
Ron Amundson
Excerpt
More information

1

Introduction

1.1 EVO–DEVO AS A NEW AND OLD SCIENCE

At the annual meeting of the Society for Integrative and Comparative Biology in January of the year 2000, a new Division was formed: the Division of Evolutionary Developmental Biology. This new organization would serve as a home for a lively field by the same name: evolutionary developmental biology, popularly known as evo–devo. In the minds of many of its practitioners (especially the more junior ones), evo–devo was new. It was a product of the explosive growth in knowledge about molecular developmental genetics during the 1990s. In a sense they were right; evo–devo really was new. Without the new molecular knowledge, evolutionary developmental biology would not have gathered the number of researchers or achieved the remarkable results that it could boast by the year 2000. Nevertheless, the subject is more than 150 years old. The conceptual connection between the development of an individual (ontogeny) and the evolution of a lineage (phylogeny) predates the 1859 publication of Darwin's *Origin of Species*. However, if evolutionary developmental biology is an old study, how could it be thought to be new in the year 2000?

The answer is that for most of the twentieth century only a minority of evolutionary biologists believed that ontogenetic development had *any relevance at all* to evolution. The Evolutionary Synthesis of the 1930s and 1940s established the mainstream of evolutionary biology (Mayr and Provine 1980). Population genetics was regarded as a causally adequate model of the evolutionary process. Natural selection was the sole direct-giving mechanism of evolutionary change, and the phenomena of macroevolution (patterns of evolution above the species level) were simply extrapolated from microevolution (natural selection within populations). The ontogenetic development of individual organisms had no place in this framework.

I am a philosopher and self-styled historian of biology. I am primarily interested in theoretical and methodological debates between scientific views, rather than in scientific theories themselves. I am interested in the recent revival of evolutionary developmental biology for a special reason: The evolutionary irrelevance of developmental biology was argued on the basis of philosophical, methodological, and sometimes even historical grounds during the mid-twentieth to late twentieth century. The basic concepts of evolutionary theory were said to preclude the relevance of development to evolution. These principles were described, examined, and (mostly) approved by philosophers as well as scientists. They were used by historians and scientists in reporting the history of evolutionary biology both before and after Darwin. Narratives of the history of biology depicted the predecessors of today's evo–devo practitioners as metaphysically confused and scientifically regressive. Pre-Darwinian biology was described in ways that detracted from the importance of developmental thinkers and that categorized them, along with almost all other opponents of Darwin, as religious reactionaries.

In other words, many philosophers and historians during the mid-twentieth to late twentieth century produced work that showed neo-Darwinism in a favorable light and developmental evolutionary theories in an unfavorable light. This is perfectly understandable, and I would have it no other way. Philosophers of science ought to take contemporary scientific knowledge as their starting point, and they ought not to feign wisdom that is superior to that of their scientific colleagues. In fact, I intend to do the very same thing in this book. I intend to look at the history and philosophy of biology *from the standpoint* of contemporary science. However, I will take a different standpoint from those who assumed the adequacy of the Evolutionary Synthesis.

Nothing succeeds like success. Evo–devo is a flourishing enterprise, notwithstanding the arguments and historical narratives of earlier days. I climb on this bandwagon here. I conduct my philosophical and historical examination from the standpoint of evo–devo rather than the Evolutionary Synthesis. Thus, the difference between this book and writings associated with the Evolutionary Synthesis is that this book has a *different* vantage point, a vantage point that has gained new legitimacy from recent science.

This book assumes the basic legitimacy of evo–devo. It examines certain traditional narratives of nineteenth-century biology with a view toward identifying and replacing the biases that made neo-Darwinian theory seem inevitable and alternative (especially developmental) theories seem regressive. It then examines the history of the twentieth-century interactions between

CAMBRIDGE

Cambridge University Press
0521806992 - The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo
Ron Amundson
Excerpt
More information

evolutionary and developmental biology. Why was developmental biology absent from the early versions of neo-Darwinism? Why was it not later incorporated? Most importantly, what brought about the historical narratives and philosophical arguments that implied that development was *in principle irrelevant* to evolutionary biology?

It may seem that I am starting with a controversial assumption, that evo–devo and neo-Darwinism really are inconsistent. Surely they are not . . . well, probably they are not. Very few evo–devo practitioners doubt that natural selection within populations is responsible for the changes that occur within species. Evo–devo advocates merely believe that additional mechanisms, mechanisms involved with ontogeny rather than population genetics, must contribute to a full understanding of evolution. The problem is that the arguments constructed by neo-Darwinians that imply the irrelevance of development to (neo-Darwinian) evolution are very convincing! They entail that one can accept either evo–devo or neo-Darwinism, but not both; thus it is not my words, but the words of the neo-Darwinian commentators, that entail the inconsistency of evo–devo and neo-Darwinism. I hope, and most evo–devo practitioners believe, that a way can be found to accommodate both evo–devo and neo-Darwinism. There is a genuine tension between these viewpoints. I do not know how to refute the irrelevancy arguments of the neo-Darwinians. It is not yet clear how this dilemma will be resolved.[1]

Some readers will doubt that neo-Darwinians actually argued that development is irrelevant to the understanding of evolution, or that those arguments apply equally well to modern evo–devo. I document both assertions and do my best to explicate the tensions between the two views of evolution. I must leave it to others to resolve the tensions.

---

[1] Frankly, many evo–devo practitioners are not aware of these tensions. Most are aware of the practical barriers between the fields, such as the reliance of evo–devo on a relatively small number of model organisms and the lack of population-level studies. There are a range of opinions within the discipline regarding its relation to neo-Darwinian theory. Some practitioners, such as Brian Hall, consider evo–devo to be a new synthetic field of study that has no particular conflict with neo-Darwinism (Hall 2000). I discuss the contrast between Hall's own approach and that of neo-Darwinism in Chapter 11. Others recognize the conflicts but are optimistic about their resolution (Gilbert 2003b). One valuable approach to the history of evo–devo is to recognize its agenda, the contrast with the agenda of neo-Darwinism, and the various scientific disciplines that kept the evo–devo agenda alive during the twentieth century. These include comparative and experimental embryology, morphology, and paleontology (Love and Raff 2003). In this book I am primarily motivated by the specific methodological arguments that arose around 1980 concerning whether or not development was relevant to the understanding of evolution, and the philosophical and historical doctrines that gave rise to those arguments.

1.2 EVO–DEVO AND THE WINDFALL OF THE 1990s

Most nineteenth-century evolutionists and several twentieth-century evolutionists have argued for the importance of the processes of development in understanding evolution. These early views receive more attention in this book than the stunning molecular discoveries that stimulated the growth of evo–devo in the 1990s. I now briefly report on some of the discoveries of the 1990s to illustrate how new life was breathed into evolutionary developmental biology.

The 1970s and 1980s saw a number of iconoclastic challenges to the well-established Evolutionary Synthesis. Some of the criticisms have since been dropped (e.g., the alleged unfalsifiability of adaptationism), and some have become internal matters within mainstream evolutionary theory (e.g., the punctuation vs. gradualism issue in paleontology). The role of development in evolution is the single persistent dispute. It first took the form of an argument over “adaptation versus developmental constraints” (Maynard Smith et al. 1985; Amundson 1994; Schwenk 1995). That debate will be discussed later. For present purposes, the debate was important because it raised awareness of the significance (for the prodevelopment side) of the concept of homology. This new interest in homology coincided with the discovery by molecular biologists that protein molecules could be sequenced, and the similarity of sequences of different protein molecules could be measured. Like traditional anatomical homology, these molecular “homologies” could be compared in two ways: different forms of a certain category of protein within an individual (e.g., $\alpha -$ and $\beta -$ globin molecules) is similar to anatomical “serial homology,” and comparison between corresponding proteins in two species reveals “special homology.” Like anatomical special homologies, closeness of match of molecular cross-species homologies was correlated with evolutionary relatedness. The serial homologies strongly suggest an evolutionary scenario in which the genetic basis of a single original protein had duplicated in some ancestor’s genome, after which the duplicates independently diverged. Even these early molecular discoveries showed an intriguing similarity between nineteenth-century morphology and modern molecular biology (Gilbert 1980). Nothing radical is implied; both serially and specially homologous proteins merely exhibit evolutionary divergence.[2]

The molecular homologies among globin molecules were not at the time seen as developmental phenomena. The globin genes did not instruct development; rather their activation was seen as the consequence of the

---

[2] The brief narrative in this section follows Gilbert, Opitz, and Raff (1996).

interactions that caused certain cells to become red blood cells. They were the endpoint of differentiation, not its cause. Developmental implications began to take shape when the molecular techniques began to be applied to the genes that controlled the nature of specialized insect segments. The genetic experiments were inspired by homeotic mutations, a class of mutations discovered early in the twentieth century in which an insect segment, together with its ordinary appendages, was transformed into another type of segment; a *Drosophila* haltere could be transformed into a wing, or an antenna into a leg. These had been favorites of developmental evolutionary theorists such as William Bateson and Richard Goldschmidt. It was first discovered that the genes that produced the various homeotic mutations in *Drosophila* were themselves serially homologous. Moreover, they were located tandemly on a small region of a particular chromosome, and they were expressed on that chromosome in the same sequence as along the anterior–posterior axis in a fly's body. Each of these gene sequences contained a certain DNA sequence called the *homeobox*. These homeobox-containing genes came to be called *Hox* genes. So far so good. We were learning about the developmental genetics of *Drosophila* by identifying the genes that encode the proteins that determine segment identity.

The excitement really started when genes homologous to insect *Hox* genes were found in vertebrates. Insects and vertebrates are both segmented, but no one for the past century had seriously argued that segmentation was homologous between the two phyla. Then vertebrate genes similar in sequence to fly *Hox* genes were isolated. They proved to be arranged in the same order on the chromosome, and they were expressed in the same order in the body as the insect genes. "And last, it was shown that the enhancer region of a human homeotic gene, such as *deformed*, can function within *Drosophila* to activate gene expression in the same relative position as in the human embryo – in the head" (Gilbert et al. 1996: 364). Genes that act during development in a human's head can do their usual job in a developing fly's head. This was only the beginning of a sequence of shocking genetic homologies – homologies that firmly demonstrated phylogenetic relationships between groups whose anatomical characters almost no one had been so bold to identify as homologies. For example, the development of both the insect eye and the vertebrate eye is begun by the expression of homologous genes. The same is true with the hearts of insects and vertebrates, and with the limbs not only of insects and vertebrates but almost all other metazoan groups. More and more basic (and often analogous) body parts in diverse groups of organisms were found to be triggered by homologous genes. The implications are very hard to sort out, of course. Anatomical homologies have traditionally been identified either by

Cambridge University Press
0521806992 - The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo
Ron Amundson
Excerpt
More information

their patterns of connections with other body parts or by their embryological origins. These initiating causes do not necessarily make the anatomical structures homologous (although they certainly challenge the traditional concepts of homology). Insect and vertebrate eyes are developed and structured in extremely different ways, even though they are the same with respect to the gene that begins their development. The difficult job for developmental genetics remains to show how the corresponding genes could serve as the original developmental triggers for such structurally distinct body parts. Tracing the genetic pathways and interactions "downstream" toward the eventual adult body part is an ongoing process; surprising new commonalities are revealed at every step.

These discoveries hearken to bygone days, and many developmental biologists knew it. One of the wildest homological speculations in history was put forth by Étienne Geoffroy St.-Hilaire in the 1820s. Geoffroy proposed that arthropods and vertebrates had identical body plans. The obvious problem (to knowledgeable anatomists) was that arthropods have their circulatory (haemal) system on their dorsal side and their neural system on their ventral side. Vertebrates are the reverse, with their neural spine along their back. This forced Geoffroy to suggest that the "identical" body plans were flipped upside -down with respect to the dorsal–ventral axis. Vertebrates travel with their neural spine toward the sun, whereas arthropods travel with their neural spine toward the earth. There was laughter all around. Toby Appel's 1987 book *The Cuvier–Geoffroy Debate* is quite sympathetic to Geoffroy. Still, she describes the arthropod–vertebrate body plan reversal as "preposterous," and she assures the reader that "such comparisons seemed no less fanciful to his contemporaries than they appear to us today" (Appel 1987: 111).

Geoffroy may have had the last laugh. Seven years after Appel's publication, it was discovered that the dorsal–ventral axes of vertebrates and arthropods are determined by homologous genes – but that their expression patterns were reversed in the two groups (De Robertis and Sasai 1996). Indeed, the expression patterns of an entire suite of genes used to specify the dorsal and ventral structures were inverted. These discoveries were not business as usual. Commonalities of animal structure that had previously been regarded as starry-eyed speculation were suddenly being traced to their molecular genetic roots.

The details of modern molecular developmental genetics are much more complex and fast changing than can be described here (Morange 1998). Genes are identified not in terms of the phenotypic effects that they produce in the adult. They are rather defined in terms of their roles in a "genetic toolkit" that

Cambridge University Press
0521806992 - The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo
Ron Amundson
Excerpt
More information

is used, in different ways, in the embryological construction of the bodies of different kinds of organisms. The *Hox* system operates quite differently in insects and in vertebrates, but it operates in largely the same manner within the groups. The basic aspects of organic form are attributed to similar developmental processes, employing homologically similar developmental genes, or to similar "tools" (e.g., genetic processes). The repeated use of not simply genes but also genetic pathways has caused Scott Gilbert to speak of "homologies of process" rather than traditional anatomical homologies (Gilbert and Faber 1996; Gilbert and Bolker 2001). Attempts to understand how identical developmental genes can produce such diversity have led to an interpretation of developmental gene interactions as a kind of circuit, and major evolutionary changes as matters of the "rewiring" of genetic networks (Carroll, Grenier, and Weatherbee 2001; Wray 2001). Diversity is created by different applications of the same old tools. By *applications*, I mean the use of the same genetic systems in the actual building of the individual bodies of organisms of incredible diversity. This diversity is the product of the varying applications of shared developmental processes. Evo–devo itself goes well beyond the discoveries of deep homologies. It constructs evolutionary explanations; it doesn't just discover developmental–genetic causes. Most of the evo–devo explanations are consistent in spirit with developmental theories of past years. The dramatic new genetic homologies count as promises that there is much yet to be discovered. I discuss some of the evo–devo explanations, and their historical predecessors, later in the book. The dramatic new genetic homologies themselves will play no further role. I examine historical arguments, not modern discoveries.

Why are these new discoveries a problem for the neo-Darwinian critique of development? By announcing these dramatic discoveries at the beginning of this book, I may have made it difficult for the reader to imagine how anyone could doubt the importance of development to evolution. However, neo-Darwinism had its origins not in *developmental* genetics but in *transmission* genetics. Transmission genetics identifies individual genes not by their molecular sequence but by tracking phenotypic features through generations of organisms in breeding experiments. Genes are hypothesized on Mendelian principles in order to account for the patterns of the phenotypic features in offspring generations. The genes of transmission genetics are designed to explain the sorting of traits through generations; they expressly do not explain how traits are ontogenetically created within the individual organism. Population genetics, at the core of neo-Darwinian evolutionary theory, requires transmission genetics alone. It has absolutely no need for developmental genetics. This fact, together with the neo-Darwinian evolutionists' dislike for the developmental theorizing of the time, led to the antidevelopmental arguments.

And the arguments made sense. If populational processes are the only "mechanism" of evolutionary change, what difference does it make that human eyes and insect eyes originate from expression of the same gene?

The difference has to do with the significance of homology. As we will see, Darwin and his twentieth-century followers treat homology as a mere by-product of past evolutionary change, the leftover residue of ancestral characters that have not (yet) been selected out of the lineage. Homologies give evidence of past ancestry, but they are causally inert. Developmental evolutionists treat homology as an indicator of underlying causal processes of development that continue to exert their effects in contemporary species. These processes are the constraints in the "adaptation versus constraints" debates. The importance of the discovery of the deep genetic homologies is not just that one more homology has been detected. The discoveries were very special ones. The new deep homologies are causally active in the development of bodies, and that fact cannot be doubted. They are not mere residue. The very different bodies that are built by these genetic processes still show deep commonalities. Even the bilateral symmetry that characterizes such a wide variety of animal groups is no longer regarded as merely an efficient way to build bodies. It is a developmental heritage from an ancient common ancestor: *Urbilateria*.

The widespread sharing of developmentally important genes justifies a central assertion of evo–devo. It is 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. The same arguments have been made since the early nineteenth century. The new genetic homologies offer new evidence that evolution cannot be understood without understanding development.

I examine the difference between Darwinian and developmental views of evolution during the course of this book. The book shows how an evo–devo sensibility produces a different narrative of the history of biology than a neo-Darwinian sensibility. I could not have written this book in 1990, prior to the discoveries of deep genetic homologies. The reason is not that my own arguments and historical narratives rely on the molecular discoveries themselves. They do not. The reason is that I intend to *assume* the legitimacy of evo–devo. I do not intend to argue for it. Such an assumption would have been controversial in 1990. The deep genetic discoveries allow me the same luxury that the neo-Darwinian commentators had between 1959 and the 1970s, when the philosophical and historical stage was being set. Like them, I can now reasonably assume that my favorite theory pretty much tells it like it is.

1.3 HOW I CAME TO THIS BOOK

I began studying these debates in the early 1980s, in the midst of the anti-Synthesis criticisms. I was just finishing an extended historical study of methodological conflicts in the history of experimental psychology between behaviorist and early cognitive psychologists (Amundson 1983, 1985, 1986). The two sides often seemed to argue past one another in these debates. However, I found that it was possible to discover hidden methodological conflicts by a close reading of the argumentation. Some features of the evolutionary debates of the 1970s and 1980s seemed very similar to me, especially those centering on development.[3] Adaptation versus developmental constraint was a function-versus-structure debate. The proadaptation side favored function over structure, and the prodevelopmental side favored structure (constraint) over function. I had just worked through a similar debate in psychology: the cognitivists were structuralists and the behaviorists were functionalists (Amundson 1989). I began reading in the history of evolutionary biology to see how deeply the structure–function contrast could be traced. It ran very deep indeed (Russell 1916). It seemed likely that the conflict between adaptation and developmental constraint was not only a phenomenon of the 1970s and 1980s.

My reading in the history of evolutionary biology has been guided by secondary historical sources. As I read through reports about pre-Darwinian British naturalists, I began to get the feeling that the deck had been stacked. Even in the secondary literature I could recognize structure–function debates between pre-Darwinian scientists. Their disagreements paralleled those of the 1980s. However, most historical commentaries failed to take that distinction seriously. They classified all pre-Darwinians into a single category of antievolutionists, and they glossed over the differences between functionalists and structuralists. This was my first hint that an examination of the methodological debates of the 1980s would extend into an examination of how the history of evolutionary biology had been written. Important pre-Darwinian conflicts had been historiographically minimized in a way that obscured the parallel between the pre-Darwinian structure–function debates and those of the 1980s.

---

[3] A sabbatical year in 1985–1986 spent in Stephen Jay Gould's lab, and regular discussions with Pere Alberch and Richard Lewontin, aided these thoughts.

To top it all off, the conceptual errors that were attributed to the (generic) pre-Darwinians were *exactly those conceptual errors* being attributed to the modern-day structuralist critics of the Synthesis!

"The game is afoot," thought I. "Someone is cooking the books!" (though perhaps not in those very words).

This was my first evidence that many histories of evolutionary biology had been written by people who considered the Evolutionary Synthesis to be essentially correct about evolutionary biology, including its opposition to modern alternative theories that involve development. The commitment to a particular modern theory had colored the reportage of historical science. Historical narratives could be read simultaneously as explanations of Darwin's 100-year-old success over his critics, and of the parallel success of the Evolutionary Synthesis over its modern critics. I realized that a historian who took the "constraints" side of the modern adaptation–constraints debate would write a very different history of evolutionary biology.

This is that history. I have cooked my own book.

I have since come to understand that writing the history of science is seldom an objective facts-only report of events. Scientists, especially when writing about the history of their own science, are simultaneously conducting contemporary research and argumentation. This is true of philosophers as well, who often have philosophical as well as scientific theories in the backs of their minds. Historians (especially recently) are somewhat less influenced by modern science, apparently because their discipline has provided them with other frameworks for their studies (e.g., the influence of social institutions or the self-interests of scientists on the practice of science). However, as we will see, historians too have a tendency to provide narratives that "come out right." A narrative *comes out right* when the predecessors of approved modern theories appear (in the narrative) to have made more sense than their contemporaries who turned out to be predecessors of theories that are now regarded as fallacious.

I will not attempt to avoid this problem of bias, but I will try to make it as transparent as possible. We (philosophers especially) do not do history from an abstract love of history. David Hull and I have come to quite different conclusions in our historical writings. In a discussion of our differences, David pointed out to me that my own writing was as biased as I claimed the traditional Synthesis histories to have been. He said that his work of the 1960s and 1970s was "history done in a good cause." He made me realize that mine is exactly the same. But it's now thirty years later. His good cause was won (with his able help), and my good cause is a different cause.