Chapter 14

Development and Evolution

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1. Introduction

The relation between embryological development and evolution has become a lively topic in recent years. During the 1990s, a wide range of molecular genetic discoveries showed that the basic regulatory genes of virtually all metazoa (multicellular organisms) were shared. Bodies that had seemed to show almost no similarities, like insects and vertebrates, were discovered to be sculpted during their development by shared genes. This was a shocking discovery (for reasons we will soon discuss). It gave rise to the new field of *evolutionary developmental biology* or evo-devo. For most of the twentieth century, most evolutionary biologists (and the philosophers who worked with them) considered development to have little or no relevance to evolutionary biology. These thinkers were neo-Darwinian, in the sense that they regarded natural selection as responsible for the great majority of evolutionary phenomena. Those who insisted on the evolutionary importance of development were often criticized as being *typological thinkers*. The accusation of typology stems from the fact that developmental evolutionists had very little interest in the variation that exists within a species. They concentrated their attention on patterns of commonality at high taxonomic levels. They studied, for example, aspects of body structure that were shared by all mammals, or all vertebrates. These were not just the characters (the backbone, for example) that taxonomists used to group species together. In the early nineteenth century it was discovered that the limbs of bats, horses, porpoises, and humans all have the same internal patterns of bones, even though they looked and functioned very differently. Developmental thinkers hypothesized *archetypes* and *bauplans* (body plans) to represent the common structures within a group. This fondness for abstract types was regarded as unscientific and almost mystical by most mid-twentieth-century evolutionists. The accusation of typological thinking aligned them with pre-Darwinian (and possibly pre-evolutionary) thought. Their lack of interest in within-species variation also justified this label, because variation within populations was the raw material for natural selection. Developmental thinkers were certainly not population thinkers, and population thinking was (and is) held to be the core of modern evolutionary biology by many. Only recently has developmental evolutionary thought shed the stigma of typological thinking. This chapter will first discuss the serpentine history of the relation between

development and evolution up to and including the recent inauguration of evo-devo. It will then discuss the debates that remain concerning the relation between evolutionary and developmental biology.

2. The Nineteenth Century: Evolution Intertwined with Development

Organisms change. Individual organisms change as they develop, from the moment of their first individuality as a zygote through their adult life. Populations of organisms change, as the frequencies of traits in descendent populations vary from those in ancestral populations. On a larger scale, species change. Ancestral species give rise to descendant species, and those to others in a branching pattern. The result, over eons of time, is the current diversity of life. Every metazoon alive today is the result of these two processes of change. The more recent process is the individual organism's own development from a zygote to an adult: its ontogeny. The ancient process is phylogeny: the evolution of the organism's lineage from remote ancestors, through gradual populational change, successive speciation events, and the evolutionary origins of new traits and the losses of old ones.

The tremendous diversity of metazoan life has within it patterns of commonality. Diversity is not chaotic, but patterned. Species with more recent common ancestors are more similar to each other than those with remote common ancestors. Some of the similarities are obvious. Hawks are all similar, and different from other birds; birds are all similar, and different from other vertebrates. However, one set of especially intriguing similarities cannot be seen in adult organisms. We must look at the ontogenies of organisms, the processes of their embryological development. Karl Ernst von Baer in the 1820s showed that the organisms of related species are more similar in their embryonic forms than in their adult forms. This was the beginning of comparative embryology. All embryos begin as a single cell, then proceed through early generalized and homogeneous embryonic forms, until they reach their specialized and heterogeneous adult forms. The early embryo appears to be an unformed lump, but its parts gradually become distinct from each other until they become the various body parts and organs of the juvenile and adult organism. This process is called differentiation. Patterns of differentiation can be compared in different species, and these patterns closely reflect the taxonomic relatedness of the various species. Remotely related embryos begin to diverge from each other with the first patterns of cell division. Closely related organisms share each other's ontogenetic changes until late in embryonic development, when they begin to diverge. The divergence in embryonic form follows a tree-like pattern – a pattern very much like phylogeny itself. In fact, if we look closely at the ontogeny of an individual organism, it can be read as a recapitulation of its ancestors' evolution. In the 1870s Ernst Haeckel proposed this as the *biogenetic law*: ontogeny recapitulates phylogeny. Each organism, during its development, traces the pathway of its ancestors through evolutionary time.

But this picture is too simple. Von Baer's laws of development are only approximately true, and Haeckel's biogenetic law has almost as many exceptions as

confirmations. In fact, von Baer's laws had been invented in order to refute an earlier, pre-evolutionary version of Haeckel's biogenetic law. Von Baer had insisted that embryonic organisms are poorly organized and homogeneous at the start, and become more organized and heterogeneous as they develop. Early embryos only resemble the *generalized embryos* of related organisms. They never resemble the *adult forms* of other species, as the biogenetic law requires. In point of fact, neither von Baer nor Haeckel is wholly correct. The shared patterns of embryological development are far too complex to be captured in such simple models. Some of the early embryonic stages of complex species do resemble the adults of ancestral species, and not merely a generalized version of adults of the same species. The embryological precursors of adult mammalian jaws and inner ears look very much like the gill support structures of our fishy ancestors. As complex as these correspondence patterns were, by the middle of the nineteenth century several people were beginning to see them as evidence for evolution.

One such person was Charles Darwin, whose *Origin of Species* was published in 1859. Darwin used the embryological evidence for evolution in the *Origin*, and considered it his "pet bit" (quoted in Ospovat, 1981, p.165). He convinced the scientific world of the fact of common ancestry, the Tree of Life. Darwin was unsuccessful, however, in convincing most of his contemporaries that natural selection had been the driving force behind evolutionary change. Only a minority of scientists accepted natural selection as the primary evolutionary cause. Selection was often seen as the cause of adaptation within a species, but it was harder to conceive of selection producing new species. In retrospect we can find several reasons why natural selection was disfavored during the nineteenth century. Two of them are of relevance here, because they touch on the complex relation between development and evolution. The first problem for natural selection was heredity. Many theories of heredity were proposed during the nineteenth century; at least thirty have been studied. However, none of these theories could be demonstrated to be consistent with natural selection as a cause of continuous evolutionary change in species. One reason was that almost all of the theories shared one feature: heredity was seen as an aspect of embryological development. The word *heredity* did not just name the similarity between parents and offspring. Instead, heredity was thought to be the construction in the embryo of parent-resembling features. In other words, heredity was a part of embryology. As long as the causes of embryological development were still obscure, evolutionists were not able to explain how natural selection could operate *through* them to yield continuing evolutionary change in a species. The universal acceptance of natural selection would have to wait for a new theory of heredity. It was 1915 before that theory appeared.

The second reason for the unpopularity of natural selection was that a separate research tradition dominated biological thought in the nineteenth century, a tradition that included both von Baer and Haeckel. This was morphology, the science of organic form. Morphology included embryology, and it had provided Darwin with crucial evidence for the Tree of Life. After 1859 morphologists rapidly converted to evolution, and became what one historian has termed "the first generation of evolutionary biologists" (Bowler, 1996, p.14). The goal of the program was the explanation of organic form, how it arises in ontogeny and how the processes of ontogeny are modified through

phylogenetic time. Natural selection was accepted as a cause of adaptation within species, but adaptation was not an important topic within the morphological research tradition. Haeckel, Carl Gegenbaur, and many others believed that the careful study of comparative embryology would allow both.

(1) a reconstruction of the history of life, and
(2) the causal explanation of how changes in the processes of ontogeny gave rise to changes in the forms of adult organisms.

When morphologists thought about the "mechanism of evolution" they thought of (2), not of natural selection.

The biogenetic law had been the simplest and most dramatic explanation of how evolution worked through embryology. As we saw, Haeckel believed that successive embryological stages of modern species represented the adult forms of their ancestors in phylogenetic time. But the law was known to have exceptions. It would have worked perfectly if evolutionary changes had only occurred in adults. When evolutionary change occurs by the addition of new traits onto adult organisms, the *newest* traits (in evolutionary terms) appear in the *latest* stages of ontogeny, and the oldest traits are in the earliest stages. This is what the biogenetic law says should happen. But not all evolutionary changes happen in adults. Sometimes an evolutionary innovation happens in an embryo, and is inherited by its descendants. When this happens, the descendants of that organism have their *newest* trait (the new innovation) occurring *early* in their ontogenies. The biogenetic record becomes scrambled, and ontogeny no longer represents an accurate phylogenetic history. Because of this possibility, embryologists who observed an early embryological trait of an advanced organism could not be sure how to interpret it. Did it represent an adult trait of a very ancient ancestor, or is it a recent innovation that was inserted into early development? These two origins must be distinguished if the biogenetic law is to be useful in understanding evolution. If the trait we are considering is the mammalian placenta, clearly it must have been an innovation that occurred in early ontogeny, not a trait added onto to an ancestral adult. (The simple reason is that no adult could survive wrapped in a placenta!) Comparative studies revealed more and more ambiguities; embryonic traits simply could not be "sequenced" into a neat phylogenetic order merely by comparing the embryos of different species.

It is important to remember that comparative embryology at this stage was an observational science, not an experimental science. Its data were careful observations of embryological stages in different but related species of organisms. When the problems (ancient adult versus recent insertion) became clear, one possible solution was recognized. If we could discover the internal causes, in the embryo, of the changes it went through, we might be able to decipher which embryonic traits were those of ancient adults and which were recent insertions. (We might be able to tell, for example, how difficult it would be for a particular kind of trait to become inserted in an early embryo.) But how do we discover those internal causes? Gegenbaur had thought that careful observation would lead to the discovery of internal causes, but hope was fading. Others believed that only experimental manipulation would

permit the discovery of the direct, local, proximate causes that propelled the embryo through its successive modifications towards adulthood. Experimentalists such as Wilhelm Roux claimed that experimental embryology could in this way be of service to evolutionary morphology by discovering how proximate causes controlled embryonic development.

Experimental method was rejected by Haeckel, however, and for an intriguing methodological reason. He claimed that proximate developmental causation was irrelevant to evolutionary ("ultimate") origins (Nyhart, 1995, p.189). (The semantic distinction between proximate and ultimate causes was popularized much later by Ernst Mayr, but the distinction applies quite clearly to Haeckel's reasoning; Mayr, 1961.) In effect, Haeckel wanted to black-box ontogenetic causation. He claimed that phylogeny was itself the mechanical cause of ontogeny (Gould, 1977, pp.76–85). It sounds bizarre today to claim that evolutionary history *causes* the growth of an individual embryo. But Haeckel insisted that the complex proximate causes that operate during ontogeny were merely irrelevant details that distracted from the big picture. The big picture was phylogeny (Amundson, 2005, p.121).

It is important to recognize the difference between Haeckel's program and others of his era. Haeckel denied the relevance of proximate embryological causation for the understanding of evolution. Other evolutionary morphologists, such as Gegenbaur, believed that proximate causation must be understood in order to distinguish between embryonic traits of ancient ancestors and those of recent insertion. Roux and other experimentalists expanded Gegenbaur's critique of Haeckel, and urged that proximate causation must underpin any developmental understanding of evolution. Surprisingly, in this sense, Haeckel can thus be seen as an *opponent* of the developmental understanding of evolution – at least of proximate-causal developmental understanding. The biogenetic law declared that embryological *patterns alone* – and not the details of embryological causation – would explain evolution. The failure of the biogenetic law was originally seen not as a refutation of the importance of development to evolution. Instead it was seen as a proof that the proximate causes of embryonic development must be understood before development would shed its light on evolution.

The experimentalists prevailed. The early experimentalists did not directly reject phylogeny. They hoped to contribute to its understanding. Even though the biogenetic law had failed, evolutionary changes in adult form were still seen as products of changes in embryonic development. When the proximate causes of ontogeny were finally understood (it was hoped), the changes in ontogeny that constitute phylogeny could be deciphered. This hope was premature. The proximate causes of ontogeny proved immensely complex. (Indeed we are still working them out, and we are nowhere near a final answer.) Long before embryologists knew enough to return to evolutionary morphology, a new and different evolutionary theory had sprung up. The new theory, called the Evolutionary Synthesis, considered ontogenetic development to be virtually irrelevant to the process of evolution. For the first time in history, development and evolution were seen as completely distinct phenomena, ships passing in the night. Only in the late twentieth century, after radical advances in developmental biology (the successor to experimental embryology), was development again seen as crucial to understanding evolution.

3. The Twentieth Century: A New Heredity Gives Rise to a New Evolution

Thomas Hunt Morgan began his academic life as an evolutionary morphologist. He and many colleagues abandoned evolutionary morphology in favor of experimental embryology. Early in the twentieth century, while he was studying how the sex of an individual organism was determined during its embryological development, Morgan became convinced that the inherited material substance that controlled the traits of the embryo lay in its chromosomes. In the year 1900 several students of heredity had independently rediscovered the work of one of the rare nineteenth-century heredity theorists who had *not* considered heredity as an aspect of embryonic development. That theorist was Gregor Mendel, who hypothesized unobserved *factors* (later called genes) that somehow carried adult similarities between the parents and offspring (never mind the embryological processes that produced those similarities).[1] Morgan and his colleagues incorporated Mendel's idea of hereditary factors into their theory of the chromosomal location of heredity. The result was the Mendelian chromosomal theory of heredity (MCTH). This was the basis of modern genetics. This theory would have many important influences on twentieth-century biology. One would be to enable, at long last, the construction of a detailed evolutionary theory that had natural selection at its core. Another influence, ironically, would be to prohibit the relevance of embryological development to that new evolutionary theory. Not the failure of the biogenetic law, but the success of the MCTH drove a wedge between evolution and development. To understand this effect, we must appreciate the differences between nineteenth-century concepts of heredity and the new MCTH.

Recall our discussion of nineteenth-century theories of heredity. Almost all of them regarded embryonic development as the action of heredity; to understand heredity we must understand development. To understand why traits are similar between parent and offspring we must first understand how those traits arise in ontogeny. Then we may be able to understand how they arise similarly in parent and in offspring. Heredity named the process by which a parent passed on to an offspring *the ability to develop* its characteristics – its spinal column, its limbs, and eventually the characteristics that made it resemble its parents rather than other members of its species. Development was an expression of heredity. Almost no one except Mendel considered heredity distinct from development, and Mendel's innovative work on heredity was virtually unknown among evolutionary thinkers until 1900. Until at least 1910, Morgan himself accepted this embryological view of heredity. When he developed the MCTH, his views changed. The MCTH made a very radical assertion: development is irrelevant to heredity. Genes are the hereditary causes of the adult traits even though geneticists had no idea how the possession of a gene contributes to the embryological development of the trait in the adult.

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1   Besides Mendel, the only other nineteenth-century non-developmental heredity theorist I am aware of is Karl Pearson. Pearson based his views on the kind of epistemological phenomenalism that will be discussed in Section 3.

Embryologists were horrified at this theory (Lillie, 1927; Hertwig, 1934; Sapp, 1987, pp.17–28; Burian, 2005, pp.183–9; Amundson, 2005, pp.175–88). It was known by this time that (with a few exceptions) all of the cells in the body contained the same genes. One of the most basic facts of embryonic development was differentiation, in which all of the distinct body parts and tissues of the adult organism are produced within an originally formless embryo. This produces a paradox: How can the *same* genes (in each cell) be the causes of *differentiated* body parts (arms and legs, bone and muscle)? The *cause of* an adult character was, to an embryologist, the developmental process that built that character and differentiated it from other characters within the developing embryo. To talk about the cause of an adult trait while ignoring development was to speak nonsense. Did the gene in the zygote magically reach through time and space to insert the trait into the adult? Surely not. Then what sense can it make to speak of hereditary *causes* of traits without taking account of the intervening mechanical steps by which the inherited trait is brought into being?

In reply to this challenge, Morgan and his colleagues distinguished between *transmission genetics* and *developmental genetics*. Transmission genetics was heredity. Heredity was understood as a probabilistic correlation between the traits of adults and offspring, assuming certain facts about the segregation and independent assortment of genes (the carriers of traits) but making no assertions at all about how genes acted within the embryo. Developmental genetics (a study for the future) had the job of explaining how genes acted during development. The important point was this: Transmission genetics *is* heredity, and therefore development is irrelevant to heredity. Morgan had blackboxed embryological causation for the purposes of heredity, just as Haeckel had blackboxed it for the purposes of phylogeny forty years earlier. "The theory of the gene is justified without attempting to explain the nature of the causal processes that connect the gene and the characters. . . . the sorting out of characters in successive generations can be explained at present without reference to the way in which the gene affects the developmental process" (Morgan, 1926, pp.26–7). Embryologists continued to resist this co-option of the term *heredity*, but they gradually lost the battle.

Our discussion at this point will be aided by a distinction between two kinds of scientific methodology, realism and phenomenalism. Although philosophers often interpret the two doctrines as universally applied throughout science, in actual practice the doctrines are selectively applied. A given scientist might be a phenomenalist about some areas of science, but a realist about others. A given scientific theory might receive a phenomenalist interpretation during some period of time, and a realist interpretation later (or earlier). The phenomenalist/realist contrast concerns the proper interpretation of scientific theories. Phenomenalists and realists agree that observation is extremely important to science, but they differ on what can be legitimately inferred from a set of observations. The difference is this: Realists believe that it is proper, appropriate, and productive to infer the existence of entities and processes that are not directly observed by the scientists (entities that are therefore called "theoretical entities"). Phenomenalists do not. Phenomenalists believe that the goal of science (or at least the goal of the particular branch of science under discussion) is to discover the laws that account for variations in the observed phenomena. These so-called phenomenal laws make no reference to unobserved theoretical entities or processes. Once a set of phenomenal laws has been discovered, phenomenalists are satisfied with that achievement and might

turn their attention toward discovering how those laws relate to other known laws. A realist, on the other hand, would ask an additional question: What unobserved processes explain why the phenomenal law operates as it does?

Phenomenalist and realist views are favored under a number of different circumstances. Sometimes a given realistic theory is just too speculative for the phenomenalist to swallow, and no better realist theories are available. At other times, a remarkably good theory may seem to conflict with widely accepted principles of science, or even metaphysics. Phenomenalism can rescue scientists from that uncomfortable position by allowing them to say "The conflict is only apparent; I am not making assertions about reality, but only predictions about observations." This allows a scientist to continue research without worrying about the underlying conflicts. Newton himself made this phenomenalist claim about the law of gravity. Newton's concept of gravity is a force that acts between bodies that have no contact with each other. In his day, this violated the metaphysical principle of "no action at a distance"; it was believed that force could only be conveyed between objects that were in contact. Phenomenalism about gravitation allowed Newton to ignore this problem.

Morgan may have found himself in a position somewhat similar to Newton's. Prior to 1910 he believed, with most of his colleagues, that heredity was a matter of embryology. But the causal understanding of embryology was proceeding very slowly. If heredity could be given a phenomenalist interpretation that divorced it from embryology, progress might be faster. By 1915 Morgan was ready to divorce heredity from embryology, and use the MCTH to link parental traits with offspring traits by correlation alone, with no explanation of the development of the offspring's traits. Development was irrelevant to transmission genetics. Morgan's claim about heredity is in fact very similar to Newton's claim about gravity. Transmission-genetic causation is literally *action at a distance*: the genes in the zygote cause traits in the adult, and the intervening embryological processes are black-boxed and ignored.

The phenomenalist nature of transmission genetics is seldom recognized by philosophers (but see Sarkar, 1998, ch. 5), possibly because developmental genetics has always been in the background with the promise of a realistic explanation of *how* genes contribute to the development of traits. Transmission genetics was tremendously successful, but developmental genetics was very slow in producing results. There was scarcely a glimmer of how genes *could* produce embryonic differentiation until the 1960s. Then Francois Jacob and Jacques Monod proposed a simple model of how bacteria could respond to the nutrition in their environment by modifying the expression of their genes. The very concept of the *expression* of genes was beyond the reach of transmission genetics. For most of the twentieth century "genetics" meant transmission genetics, a field of study that was carefully, and phenomenalistically, defined to exclude development from its purview.

The MCTH separated embryological development from heredity. How does that affect the relation between development and evolution? The answer is simple. The Evolutionary Synthesis of the 1930s and 1940s was based on the MCTH, together with a mathematical analysis of the distribution of genes – *transmission* genes of course – in evolving populations of organisms. The MCTH was the very first theory of heredity that was proven to be consistent with natural selection as a cause of long-term evolutionary change. The proof took the form of the equations of mathematical population genetics.

These equations modeled populations of organisms and their genes. As generations passed, the gene frequencies could be shown to be affected by natural selection as well as several other factors such as migration, mutation, and random drift. However – and here is the important thing – embryological development had no place within the models of population genetics. Population genetics was based on transmission genetics, which was *defined* in terms of the Mendelian patterns of correlation of phenotypic traits between generations. Embryological development had been black-boxed by transmission genetics. When transmission genetics was incorporated into the Evolutionary Synthesis, development remained in its black box. Just as in Haeckel's interpretation of the biogenetic law, proximate causes of embryological development were considered irrelevant to the understanding of evolution.

In recent years the advocates of evo-devo have sometimes argued that the resistance of mainstream Evolutionary Synthesis theorists to development was a sort of conspiracy from the start. However, careful study of the historical record reveals no evidence of this. Morgan and his coworkers were actively interested in developmental genetics, although they produced few results. The leaders (the so-called architects) of the Evolutionary Synthesis did react harshly toward some developmentally inclined adversaries such as Richard Goldschmidt, who opposed the Darwinian principle that evolution was a smooth and gradual process. But others were tolerated and sometimes even encouraged. C. H. Waddington and I. I. Schmalhausen were among the developmental advocates who were regarded as relatively friendly to the Synthesis. However, they had no lasting effect on Synthesis theorizing. The importance of development continued to be advocated by a minority of theorists throughout the century, including some comparative anatomists and paleontologists as well as embryologists. The real, open conflicts between mainstream Synthesis evolution and the advocates of development only arose around 1980. [SEE POPULATION GENETICS].

4. The Nature of Developmentalist Explanation: 1920–80

We see that the developmental view of evolution – the view that understanding evolution requires understanding the causal processes of development – was historically confronted with two black boxes. The first was Ernst Haeckel's declaration that the proximate causes of ontogeny were irrelevant because phylogeny itself was the cause of ontogeny. Haeckel is usually remembered as a friend of ontogeny. In fact he was a friend only of ontogenetic *pattern*; not ontogenetic causation. Haeckel's black box died when the biogenetic law died. The proximate causes of ontogeny (for example, the interactions among the developing body parts in the embryo) must be understood in order to decipher the tangled web of evolutionary changes that had occurred at various embryological stages in different lineages. But the task of understanding embryological causation was barely begun when the second black box appeared. It was constructed by the MCTH; development was now irrelevant to heredity. The new theory of heredity was parlayed into a new theory of evolution by the Evolutionary Synthesis. So again the proximate causes of ontogeny were black-boxed with respect to evolution. The logic behind the second black box is one step more complex than the first. Haeckel had said

that because phylogeny is the direct cause of ontogeny, the intervening proximate causes of ontogeny are irrelevant to phylogeny. The later version, due to the Evolutionary Synthesis, states that phylogeny (evolutionary history) is the cause of contemporary genotypes, and contemporary genotypes are the direct cause of phenotypes. Therefore the intervening proximate causes of ontogeny – those that build the phenotype out of the genotype – are irrelevant to phylogeny. As long as genotypes were conceived as the direct causes of phenotypes, evolutionary biology had no causal room, or explanatory need, for ontogeny.

The developmental evolutionist's challenge is the same for either black box. It involves two interrelated tasks. The first task is to argue convincingly that some features of evolution cannot be explained in the absence of a proximate understanding of development. In the case of Haeckel's black box, this was shown by the continued inability to distinguish between traits of ancient adult ancestors and recent insertions. The second task is to show that an understanding of developmental causation can explain those aspects of evolution that non-developmental theories could not explain. Roux, Gegenbaur, and others hoped that this could be accomplished with the aid of knowledge about proximate causation within embryos; we might discover (for example) that certain traits were easy to insert into early embryonic stages, while others could only have gotten there by inheritance from ancient adults. This would allow us to separate the ancient-adult traits from those inserted into early embryology. Unfortunately, the causal structure of ontogeny was far too complex for this program to succeed in the early twentieth century.

These two tasks were the same for the twentieth-century developmentalists who were confronted by the black box produced by the MCTH and the Evolutionary Synthesis. First, find a phenomenon that is unexplained by non-developmental theories of evolution. Second, explain it as a consequence of the facts of development. The twentieth-century developmentalists' intuitions were the same as those of their predecessors: evolutionary changes were changes in ontogeny. But as we have seen, progress was very slow in experimental embryology and its successor developmental biology. The developmentalists were left with few explanatory resources. The problem was exacerbated by the fact that the linked disciplines of transmission genetics and the Evolutionary Synthesis were making great progress. The Evolutionary Synthesis explained evolved traits mostly as adaptations produced by natural selection from genetic variations in ancestral populations. These so-called adaptationist explanations were in competition with any explanation proposed by developmentalists. Some of the adaptationist explanations were extremely well confirmed, both by experiment and by observation of natural populations. But others were quite speculative, at least as seen by developmentalists. The problem for developmentalists was that their understanding of ontogenetic causes lacked the detail needed to offer alternative explanations to the adaptationists. They were forced to construct explanations out of mid-level ontogenetic patterns instead of genuine proximate causes.

Two examples of mid-level patterns are allometry and heterochrony. Allometry refers to correlations, sometimes expressed in complex equations, in the relative sizes of body parts during growth. These correlations are presumed to be produced by the mechanisms of development. When the modifications in relative size of two body parts during the growth of an individual are seen to correspond to size comparisons between

two related species, the phylogenetic ratios between the species are said to reflect the same developmental causes as the ontogenetic ratios during development. It has been argued, for example, that body size increases faster than tooth size in the growth of individual mammals, and that therefore the relatively small teeth of gorillas as compared to chimpanzees is to be explained by the mere fact that gorillas are larger, as adults, than chimpanzees. This is allometry. The problem is that adaptationists could easily claim that natural selection caused the smaller tooth size, and so argued in opposition to the allometric explanation.

Heterochrony is a modification in the relative timing of different developmental events during embryogenesis. For example, if sexual maturation were selected to occur earlier than the maturation of body form within a lineage, the adult forms of descendants might retain juvenile bodily traits. This is *paedomorphosis*, one particular heterochronic pattern. The process is often said to have been involved in the evolution of humans, because juvenile chimpanzees show greater similarity to human adults than do adult chimpanzees. Even though natural selection is invoked in the paedomorphosis explanation, the traits that are explained developmentally are not directly selected for. Instead they are linked by developmental mechanisms to the selected-for traits. The adaptationist alternative is to argue that the juvenile traits of the descendant population were individually selected for – they did not piggy-back along, because of developmental linkage, on the single selected-for trait of early sexual maturity.

Heterochrony and allometry both refer to proximate causation during embryonic development: how form is generated in the body. However, proximate causation is inferred from observable morphological patterns rather than studied directly through experiment. Because embryological causation was so difficult to trace, many developmental evolutionists of the mid-twentieth century were comparative morphologists and paleontologists, rather than embryologists. Morphologists and paleontologists had the data necessary to do heterochronic and allometric analyses, but not to directly study the proximate causes of ontogeny. Direct knowledge of developmental causation began to come into the picture in the 1980s. Before we discuss the results, let us consider the resistance to developmentalist evolutionary views that came from the adaptationism of the Evolutionary Synthesis.

5. Adaptationism and the Synthesis

From the discussion of allometry and heterochrony it might seem that the developmentalist and the adaptationist explanations were on equal footing. They were not. Adaptationist explanations, even in the absence of direct evidence, possessed much more prestige and scientific plausibility than developmentalist ones during mid-century. Although developmentalists often describe this as an unfair prejudice, it followed upon genuine successes of the adaptationist research program during the middle of the century. Adaptationism was not particularly dominant during the early years of the Synthesis. Genetic drift was considered by many Synthesis thinkers to be the cause of the traits that differentiated between related species. But careful adaptationist studies had revealed that examples of these traits were, surprisingly, adaptive to the species (Cain & Sheppard, 1950). The prestige of adaptationism was well-earned. Nevertheless,

it was based on limited data. Adaptationist over-enthusiasm led to conclusions that are now seen as unjustified. Two examples will illustrate the exuberance of adaptationism during this period.

First, it was believed by many adaptationists during the 1950s that major taxonomic groups, such as mammals and birds, were not monophyletic (that is, descended from a single evolutionary ancestor), but polyphyletic (descended from two or more originally distinct ancestors). This means that diverse ancestors had adaptively converged on the common characteristics by which mammals and birds are identified. It was suggested, for example, that all of the anatomical properties that characterized mammals (such as hair, mammary glands, and placental gestation) were coincidental adaptive consequences of the independent evolution of homeothermy (warm-bloodedness) among several pre-mammalian lineages. The power of natural selection to produce adaptive convergence was so highly regarded that it was considered hazardous to infer common ancestry from any degree of anatomical similarity. Extremists were willing to hypothesize that virtually every trait of an organism was there because it served an adaptive purpose to that species. This means that no traits at all should be ascribed to common ancestry (let alone common embryological causation), at least until it was conclusively proven that the traits were not adaptive to that species. Because traits shared between species are assumed to be selectively produced in each species, those who wish to use developmental explanations have virtually nothing to explain.

A second illustration of the consequences of mid-century adaptationism relates to the concept of homologous genes. Mendelian genetics is based on crosses between individuals that have different heritable traits. For practical purposes this means that it is impossible to identify the genetic basis of similar traits within distinct species, simply because it is impossible to crossbreed between species. Given this lack of data, it would seem to be an open question whether or not traits shared between species had the same (or "homologous") genetic causes. Nevertheless, even in the absence of direct genetic evidence, the commitment to adaptationism inclined evolutionists to believe that shared genes were *most likely not* the causes of shared traits. Shared traits were believed to have been independently sculpted in each species in which they appeared. The common commitment of leading evolutionists such as Ernst Mayr and Theodosius Dobzhansky in the 1950s and 1960s was that "If there is only one efficient solution for a certain functional demand, very different gene complexes [in different species] will come up with the same solution, no matter how different the pathway by which it is achieved" (Mayr, 1966, p.609). As we shall see, the adaptationist commitment to convergent rather than conserved similarities was a spectacularly hasty conclusion.

Additional barriers to developmentalist thought came from the articulation of several philosophical and methodological concepts in the form of binary distinctions between classes of phenomena. These were invented to express basic concepts of the MCTH and Synthesis theory, and give the appearance of basic conceptual truths. Nevertheless, they can be taken to imply the irrelevance of development to evolution. We have already used one of these binaries, the distinction between proximate and ultimate causation. Ernst Mayr, the popularizer of this distinction, has used it to argue against developmental evolutionists on the grounds that development is a proximate process while evolution is an ultimate process. Another important but biased binary is the

genotype versus phenotype distinction.[2] This distinction predated the MCTH, but was modified from its original meaning in order to reflect the ontological commitments of the MCTH. The updated version is often taken to exhaustively label all organismic factors that are relevant to evolution. If understood in this way, it expresses the black-boxing of embryological development. The genotype is held to "cause" the phenotype, with no reference to the causal activities that take place within the black box of development. If the genotype and the phenotype together provide a complete and adequate account of evolutionary processes, then ontogeny is irrelevant to that account [SEE GENE CONCEPTS] Population genetics deals with the sorting of the traits of populations through evolutionary time. This sorting can be seen in terms of genes or of phenotypic traits, depending on whether one is a gene-selectionist or an individual selectionist. But it cannot be seen as the sorting of ontogenies (or elements of ontogenies), because ontogeny is conceived to be irrelevant to the hereditary causation of traits.

Advocates of developmental evolution are forced to reject the sufficiency of the genotype–phenotype dichotomy. Waddington did so in the 1950s with the proposal to add the *epigenotype* to the genotype/phenotype distinction. The epigenotype is made up of the causal processes in the embryo that mediate between genotype and phenotype. The genotype controls embryological growth (the epigenotype) which in turn builds the phenotype. Waddington was unable to prove to Synthesis evolutionists that his three-part distinction was superior in its explanatory power to the genotype–phenotype binary.

Waddington's situation was typical. An important factor in the persistence of the debates about development is that it was difficult for developmental evolutionists to specify in detail what *they* could explain but population biologists could not. Consider the proposals put forth by developmentalists advocating allometry or heterochrony, for example. Any phenomenon explainable by heterochrony (the similarity between infant chimpanzees and adult humans, for example) was also explainable by adaptation (that infant chimps were subject to different selection pressures than adult chimps, for example – therefore the similarity with adult humans is a mere coincidence). Allometry and heterochrony were too crude to survive a test against the strength of mid-century adaptationism.

6. Direct Debates

During the 1980s the debates began to center around the concept of *constraint*. Developmental evolutionists focused on developmental constraint, but this topic was entangled with several other factors that were also called "constraints." The extreme adaptationism of the 1950s and 1960s had waned somewhat, and adaptationists were now responding to theoretical challenges. Nevertheless, the divergent commitments of the two theoretical orientations resulted in a stalemate in the constraints debates. Let us examine how this happened.

Critics of the Synthesis (including developmentalists) had alleged that adapationists were insensitive to all factors that might limit adaptive perfection, and development

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2   Other binaries include germ-line versus soma, and population thinking versus typology. Each of these was used during the 1980s and 1990s to argue against the legitimacy of developmentalist evolutionary theories (Amundson, 2005).

was merely one of those factors. So the term constraint was often used generically to cover a number of non-adaptive causal factors. From the adaptationists' perspective, the challenge was to demonstrate that they took adequate account of factors that might limit adaptive perfection: constraints on adaptation. The critics had asserted that adaptationists neglected these limits. Adaptationists said that such limits were acknowledged (implicitly or explicitly) in every explanation. The foraging behavior of a particular bird was only optimized *under the constraints* of its eyesight and flight range. The allegation that adaptationists ignored constraints seemed absurd to these authors, and they often said so. To them, constraints are merely the background assumptions that frame the stage on which natural selection takes place. Every selective explanation must have those background assumptions, and so the allegation that adaptationists ignored constraints was simply false.

Unfortunately (for the unity of biology) the adaptationist concept of constraints was quite different from the developmentalists' concept. Developmental constraints were conceived not as mere limiting background assumptions, but as visible manifestations of underlying causal processes. The underlying processes were the processes of ontogeny, the building of bodies during embryological development. Ontogeny, and its modifications through evolutionary time, was the focus of developmental interest. The discovery of constraints was a significant part of the purpose of their study. Developmental constraints were seen to constitute direct evidence about the processes that constituted developmental evolution. They pointed toward a certain kind of positive causal activity underlying evolutionary change: modification of the process of ontogenetic development. Ontogenetic processes are themselves productive. They are not restrictive, as the term "constraint" seems to imply. Ontogeny is productive of functioning phenotypes. Ontogenetic processes can be modified, and certain kinds of modifications are more likely than others. Constraints are the shapes of possible or likely changes in ontogeny (Amundson, 1994). The contours of these possibilities are consequences of the ways in which bodies are, and have been, built. Embryologists and (more recently) developmental biologists have traditionally concentrated on the form, the morphology, of organisms. So developmental constraints were considered to be constraints on form, on the possible morphologies of developmental variants. So conceived, constraints (on form) had no direct implications regarding the study of adaptation. They were involved, instead, in the study of how body form had changed through evolution. The relevance of adaptation to this study was simply not a topic of discussion: that was left to the adaptationists.

So we see that the theoretical role of constraints differs greatly between these groups. Adaptationists were concerned with constraints on adaptation, limitations on adaptive perfection. Developmentalists, in contrast, were interested in constraints on *form* – on the possible configurations that bodies can take.[3] Even if adaptationists were to consider

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3   As an example, consider the universality of four limbs, rather than six or eight, among tetrapods. An adaptationist explanation would concentrate on the relative fitness of variant limb numbers, while a developmentalist would concentrate on the mechanisms by which limbs are constructed in the embryo. The constraints-on-adaptation might be the environmental problems caused by increased limb numbers. The constraints-on-form might be the inflexibility of the embryological processes that produce limb numbers. Although this example is purely imaginary, it illustrates the contrasting interests of the two research orientations.

genuinely developmental constraints (those that are produced by the organization of ontogeny), their relevance would be no different than any other restriction on adaptation, such as a bird's poor eyesight. Constraints would continue to be a background condition for adaptationist explanations, whatever their source. The criteria for success of an adaptationist explanation simply do not require an account of the ontogeny of the trait under consideration; the MCTH made sure of that. Because adaptationist explanations were natural selective explanations, developmentalist accounts of evolution would appear irrelevant to evolution. Developmentalists continued to insist on the importance of constraints. Adaptationists continued to misunderstand this insistence as a complaint against *unconstrained* adaptationism. Adaptationists accepted the need to state the constraining background conditions under which their explanations operated, and saw no point to doing anything further (such as understanding development).

The proximate processes of development began to play a larger role in evolutionary explanations during the 1980s. These studies were based on a detailed understanding of the ontogeny of vertebrate limbs, especially the limbs of the two amphibian groups of urodules (salamanders) and anurans (frogs). David Wake and his colleagues constructed explanations for a number of phylogenetic patterns of limb variation that showed them to result from the mechanisms of limb ontogeny. One was an explanation of a correlation regarding the evolution of digit loss between the two groups. Digit loss occurs frequently, especially in those frogs and salamanders that evolve a miniaturized size. An interesting pattern is that the lost digits differ between anurans and urodeles. Urodeles lose the posterior digits first; anurans lose the anterior digits first. This pattern corresponds with the order in which the digits are ontogenetically produced within the group: urodeles differentiate their digits beginning with the anterior and proceeding to the posterior, and anurans the reverse. So the pattern of digit loss in evolution is the reverse of the pattern of digit differentiation in ontogeny: the last digit developed is the first one lost. Wake and colleagues have argued that a number of similar patterns in the evolution of amphibian limbs can only be understood in terms of the ontogenetic processes by which those limbs are developed (Rienesl & Wagner, 1992; Shubin, Wake, & Crawford, 1995).

These developmentalist explanations of evolutionary patterns conflict with adaptationist standards for a good explanation. Hudson Reeve and Paul Sherman produced an extensive critique of Wake's style of developmentalist explanation from an adaptationist perspective (Reeve & Sherman, 1993). They pointed out that Wake did not examine the ways in which digit loss affected the fitness of the various frog and salamander species. For this reason (they said), Wake had not *explained* the patterns of digit loss, but only re-described them. In order to explain digit loss (by adaptationist standards) one had to demonstrate the effects of fitness on the variant forms. Only if Wake was able to prove that the patterns had not resulted from distinct cases of natural selection for the adaptive benefits of digit loss could he be said to have "explained" digit loss in terms of ontogenetic processes. Adaptationist explanations require an examination of comparative fitnesses of the variants (and do not require an analysis of their comparative ontogenetic sources). From this perspective, developmentalist explanations are no explanations at all.

This is merely one example of the contrast between explanatory standards. From an outsider's point of view, one would think that developmentalists and adaptationists

might be equal players in the explanation game. Adaptive and developmental explanations might compete for legitimacy, but each is a possible contender. For most of the twentieth century this was not true. As we see from the Reeve–Sherman critique, developmentalist explanations were at a disadvantage. Adaptationist explanations had exhibited their power ever since the 1940s. As late as the 1990s, developmentalist explanations had no similar track record. Some of the later developmentalist explanations were more appealing, because they were based on known ontogenetic mechanisms rather than such hypothesized causes as heterochrony and allometry. However, few could definitively rule out adaptation as a possible alternative scenario. For this reason, adaptation retained the upper hand. This was all to change by the end of the century.

7. A Torrent of Homologous Genes

T. H. Morgan had foreseen the genetic study of development in the 1920s. That study was delayed for the greater part of the century. The near-total absence of the genetic understanding of development meant that the phenomenalist science of transmission genetics was left alone to form the basis of evolutionary theory. Certain features of mid-century adaptationism must be seen as byproducts of the absence of developmental genetics during this period. This is certainly true of the opinion of Mayr and Dobzhansky that similar traits were probably not due to homologous genes. These authors are not to blame for their lack of data. Transmission genetic analyses were based on genetic crosses, and so the impossibility of crossbreeding species made homologous genes almost impossible to identify. By the turn of the twenty-first century, however, this commitment to the power of natural selection to sculpt similar traits out of diverse genetic resources is open to serious doubt. What has changed? Our understanding of molecular genetics, and the discoveries of a number of extremely deep genetic homologies.

Consider what the adaptationists of the 1970s might have expected from the advancement of developmental genetics. Natural selection was presumed to be able to sculpt common characters from diverse genetic resources. Most similarities among phylogenetically remote species were due to adaptive convergence rather than developmentally conserved traits. Consider two examples of traits that are shared by widely separated groups of animals: eyes, limbs, and bilateral symmetry. Insects and vertebrates are bilaterally symmetrical, and both have limbs and eyes. But the body plans of the two groups are very different, and their common ancestors are lost in evolutionary time. Eyes, limbs, and bilateral body arrangement have obvious selective advantages – they allow the animal to move forward in a search for food. Surely they must be seen as adaptive convergences, not shared development. (It was believed, for example, that eyes had independently evolved about forty different times.) For these reasons, homologous genes were not to be expected except between very closely related species. Natural selection was the causative force in evolution, and selection produced diversity, not commonality. Developmentalists had claimed that perceived commonalities were attributed to shared developmental causes, but they had never been able to prove that the commonalities had *not* arisen from convergent selection. Given the perceived power of selection, there was no reason to expect surprises from the progress of developmental genetics. But surprises there were.

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By the early 1990s molecular geneticists were beginning to identify genes on the basis of their molecular composition. The first shock was the discovery that certain genes were shared among nearly all animal groups, from mammals to insects to flatworms. The mere fact of widely shared genes was inconsistent with the expectations of major adaptationists. But the nature of those genes was even more surprising. They acted at the deepest and earliest stages of embryonic development. A gene called *Pax-6* was the first to be identified in widely divergent groups. This gene stimulates the development of eyes (and even primitive eye-spots) in all known taxa. A similar gene exists for the developmental origin of limbs. An entire set of genes, called *Hox* genes, sets up the bilateral body axes (front–back and left–right) and specifies the nature of the various body segments from front to back. The bilateral body plan of virtually all complex animals was invented only once in evolutionary history. The hypothetical ancestor of all of these (all of us) animals is named *Bilateria*. The source of this continuing body plan is embodied in a "toolkit" of developmental genes that remain almost identical, after six hundred million years of evolutionary divergence.

The toolkit genes are quite unlike the genes studied by transmission genetics. Because they are shared by virtually all animal species, their discovery under classical methods of crossbreeding was impossible. The protein products of these genes do not directly affect the phenotype. They control the expression of other genes, and do so in the earliest stages of development.

The Evolutionary Synthesis offered a theory that was based on genes that were conceived to vary in populations, and that had direct effects on the phenotype. This allowed population geneticists to imagine that the sorting of genes in a population was conceptually equivalent to the adaptive sorting of traits – the Darwinian process of natural selection. That analysis led them to doubt that development was relevant to evolution, and to doubt that development had any role to play in explaining such commonalities as the bilateral body plan or the existence of legs and eyes. They were right in their recognition of the diversity of life. But they were wrong in their failure to recognize the commonality that underlay that divergence. Developmental evolutionists had been arguing since the late nineteenth century that evolution could not be understood without understanding development. The invention of transmission genetics (via the MCTH) was a serious challenge to that view: exactly what was it that neo-Darwinian evolutionary theory could not explain, but developmental evolution could? Attempts by developmentalists to explain character distribution by heterochrony and allometry were staved off by arguments that the same phenomena could be explained by ordinary selective processes. But now, with the discovery of the deep homologies, developmentalists had a well-confirmed fact about the unity (not the diversity) of life that tied embryological development deeply into the evolutionary process. Adaptationists like Dobzhansky and Mayr had predicted just the opposite – the absence of any important homologous genes. The deep homologies were not *mere* commonalities, but very early and developmentally important commonalities that tied together shockingly diverse life forms. Metazoa all share their deepest developmental mechanisms. To understand the evolution of *this* group of life forms – the ones here on earth – it is necessary to understand their development.

Evolutionary developmental biology, evo-devo for short, is the new name for the developmental study of evolution. The momentum of the research program of develop-

mental biology is enormous, and a great deal of it has direct implications for evolution. (For an accessible modern introduction see Carroll, 2005.) So developmental evolution is alive and well. However, the reader may be wondering what became of the constraints debates discussed above. Did the developmentalists refute the adaptationists? The answer is no. The debates remain unresolved. The progress of evo-devo has come by way of an explosion of new information from molecular biology. It has not come by way of philosophical and methodological argumentation. Many of the practitioners of evo-devo are not even aware of the old debates, or the conflicts between adaptationist and developmentalist views of evolution that were exposed in those debates. This leaves the philosophical issues in an odd situation – unresolved. The final section of this chapter will discuss this odd situation, and possible future resolutions.

8. What Now?

Philosophers of biology often claim that their field began around 1960. This period was certainly an evolutionary and philosophical watershed. Ernst Mayr's important work of articulating the philosophical and methodological foundations of neo-Darwinian theory began in 1959, corresponding with centennial celebration of Darwin's *Origin of Species*. Mayr criticized most previous philosophers who wrote on biology for failing to recognize population thinking, and introduced other important philosophical concepts such as proximate versus ultimate causation. Mayr's principles were seen by many as the starting point of philosophy of biology. The preponderance of philosophical writing on biology since then fits within the parameters of Evolutionary Synthesis thought. Problems like units of selection, and the proper scientific definitions of concepts like *adaptation*, *fitness*, and *function* fit perfectly well within this framework. This work has continuing value; no one in the evo-devo camp rejects the importance of population thinking and other neo-Darwinian concepts. However, this work does not help us to understand the role of development in evolution. Something other than adaptation and population thinking must be addressed if we are to establish a philosophical understanding of developmental evolution.

For a developmental understanding of evolution, the most productive area of philosophical inquiry has been genetics. Transmission genetics offered no room for the developmental evolutionist. But molecular genetics, and later developmental genetics, made new understandings possible. Philosophical studies of the changing concepts of the gene provide the strongest philosophical transition between the neo-Darwinian style of philosophy of biology and the kind of understanding that will be necessary in the era of evo-devo. However, most of this work does not directly relate developmental genetics to evolution. This is what is needed for a philosophical understanding of evo-devo.

In recent years, as evo-devo has grown, philosophers have gradually begun to recognize the new field of thought, and attribute more explanatory power to developmental concepts. The relation between natural selection explanations and developmental explanations has been explored, and some of the power formerly attributed to natural selection has been challenged. It has even been argued that certain kinds of genetic systems might make it possible for directional evolution to occur even in the absence of natural selection. This kind of evolution happens *only* because of how development

(and developmental genetics) is structured in the organism. Such a phenomenon is quite inconsistent with traditional neo-Darwinian thought.

Two sorts of philosophical questions still must be addressed before philosophy of biology can be said to include developmental evolutionary thought. The first are relatively pure philosophical questions. The second are questions of the unity of science, and the relation between evo-devo and neo-Darwinian theory.

The first set of questions is the evo-devo analogs to the kinds of topics addressed by earlier philosophers of biology. What additional philosophical analyses are necessary in order to have the kind of understanding of evo-devo that we now have of neo-Darwinian theory? The neo-Darwinian concepts of adaptation and fitness are not enough. Natural selection plays a relatively small role in evo-devo, and so traditional philosophical issues like the units of selection problem would seem irrelevant. But could aspects of ontogeny be seen as new kinds of "units of selection"? The concept of function, another tradition topic of philosophy of biology, may be given a new reading in an evo-devo context. This work has yet to be done. Other core concepts of evo-devo show a contrast – perhaps even an inconsistency – with neo-Darwinian concepts. The concept of the *Bauplan* or body plan is one such concept, seen as illegitimately typological by purely neo-Darwinian thinkers. Evo-devo is filled with such concepts. For example, the *vertebrate limb* is used in reference to an abstract set of developmental possibilities, not merely the set of all limbs of animals that happen to be vertebrates. I have termed these *developmental type concepts*, and argued that they show a continued tension between population thinking and evo-devo (Amundson, 2005). Could philosophers throw the kind of light on the *Bauplan* that they have thrown on adaptation and fitness? Should Waddington's third-choice concept of the epigenotype be added to the genotype/phenotype distinction? What is to come of Mayr's proximate/ultimate distinction, which had seemed such a barrier to the relevance of development to evolution? Do we need a third choice besides proximate and ultimate to account for developmental evolution? Can development itself be understood as somehow ultimate?

The second set of questions concerns the relation between the scientific disciplines of neo-Darwinism and evo-devo. Some (but by no means all) evo-devo practitioners are concerned about the relation between their field and neo-Darwinism. Unlike the constraint debates of the 1980s, no evo-devo practitioner claims that neo-Darwinism will be overthrown. But many of them (especially those whose early career was in evolutionary biology rather than developmental biology) recognize tensions between the two fields. My comments in the previous paragraph about developmental types show that I agree with these concerns. On the other hand, some evo-devo practitioners expect no special problem in giving a natural selective account of developmental types. (As you can see, I am a skeptic.) A third school of thought seems to be that the two fields will naturally coalesce as evo-devo matures. Until recently the two disciplines have concentrated on different characters and even different organisms. When population geneticists and developmental geneticists begin studying the same characters in the same animals, some accommodation will emerge.

The two decades after 1960 were a formative and exciting period for the philosophy of neo-Darwinian evolutionary biology. A new evolutionary paradigm had emerged, and its concepts offered new ways of thinking for a generation of philosophers. Today is exciting for similar reasons. Evo-devo has finally proven that development is relevant

to evolution. The philosophical implications of this new field are only beginning to be addressed.

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