EVOLUTION, EMBRYOLOGY, AND ERNST

JANE MAIENSCHEIN

Ernst Mayr is known as the premier champion for Darwinian evolution, and his career has centered on working out the biological causes of speciation and in extending and updating Darwin's "long argument" while showing that there really is "grandeur in this view of life." Mayr himself will say that he has given little attention to embryology. In part this is because embryological explanation appeals to what Mayr has long called "proximate causation". In part it is because he sees embryology as supporting rather than in any way calling into question or demanding interpretation within an evolutionary framework. Yet, with the rise of evo-devo research programs, it is worth reflecting on the role of embryology and individual development in relationship to evolution. This paper explores Mayr's reflections on that relationship.

Ernst Mayr's career has been devoted to exploring, explaining, extending, and expounding upon Darwin's theory of evolution of species through natural selection and adaptation. Mayr acknowledges that "I am not a developmental guy," yet, as he willingly agreed in a letter responding to an invitation in 2001, "I am always ready to answer questions about the evolutionary aspects of evo-devo." That occasion was one in a series of summer seminars on the history of biology organized by the Dibner Institute for the History of Science and Technology in conjunction with the Marine Biological Laboratory in Woods Hole. As co-organizers for that summer's topic on "From Embryology to Evo-Devo," Manfred Laubichler and I had invited Mayr to join us. He insisted that since development isn't his field, he should not make a formal presentation but should only answer some questions for a short time. In fact, of course, he gave generously his time and revealed a fine understanding of aspects of embryology and its relations to evolution. He regaled the group with stories, analyses of ideas, and suggested connections among seemingly disparate topics, enthralling the graduate students who had never met him before and reassuring the rest of us that here was Ernst, going strong as one of the most intellectually

School of Life Sciences, Arizona State University, Temple, AZ 85287, USA.
maienschein@asu.edu

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powerful minds around, despite his protestations of age and lack of the same energy he had shown throughout his long and distinguished career.

The same thing had happened when I visited Harvard in 1983-1984. Mayr set me up in office space at the Museum of Comparative Zoology were philosopher of biology Michael Ruse and I shared the back of a huge storage area, equipped with old wooden desks and an ancient telephone that looked as though they had all been there almost as long as the dusty boxes of brachiopods that filled the metal shelves behind us. Mayr was, of course, retired by then and was deeply engaged in his historical and philosophical study of biology. He welcomed me into his office for discussions, always starting with the caveat that he knew little about the history of embryology on which I was focused. Then he would pull out reprints, articles, books, and even his old notes about all the important works and ideas in the history of study of individual development. Study of individual development is not irrelevant to understanding evolutionary development, and Mayr was fully aware of that. He was a generous and invaluable source of ideas during my year as a new assistant professor, working on my first major projects in the then-neglected history of embryology. His weekly evening discussion sessions provoked lively exchanges covering all topics related to evolution, including developmental and genetics questions. He was always the one bringing in new ideas, wanting to discuss a book he had just read, or enticing us to think about deeper issues.

That he has read so much of what has ever been written in biology, and furthermore has actually understood and remembered it, makes Mayr an invaluable resource. As Stephen Jay Gould noted in an essay on Mayr's Balzan Prize in 1984, Mayr's impressive *The Growth of Biological Thought* "is a grand and curious work, not an objective history in the term's usual sense, but an embodiment of Mayr's personal vision extended through time. It is, as one historian remarked, not a secondary source, but a primary one. I say this not as a criticism, but as a tribute to the finest kind of inspired writing" (Gould 1984). Indeed, that work reveals Mayr's worldview at the same time that it presents those of others. The book is thus doubly important. So was my visit that year at Harvard. Mayr introduced me to historical figures I had not met before, who had been engaged in studying development with different problems in mind or working in different traditions. And he presented familiar figures like Oscar and Richard Hertwig or August Weismann in different ways. He therefore was casting light on the historical figures and ideas while also illuminating his own, just as Gould noted.

Here I draw on some of Mayr's own words—words that will be less familiar to his readers who are typically looking at his views on evolution rather than on individual development—to get at his interpretation of

how embryology fits into his interpretation of biology. The widely accepted view is that developmental biology did not fit, that it was even excluded from the modern evolutionary synthesis that Mayr helped to establish. Mayr insists that this is not true. Embryology, or developmental biology as it was labeled later, was not excluded; rather it fit perfectly well but just did not play an important defining role. Evolution and the synthesis were not particularly important for development, or development for the synthesis because they are concerned about different questions and different levels of causation. There was plenty of room for developmental biology, Mayr insists, and he sees the recent rise of work in evo-devo as evidence for how closely evolution and development can work even more closely together. It apparently has just taken longer to discover ways to bring the two studies more obviously and more robustly together. It is therefore worth looking at what role he sees embryology as playing, drawing on the clues he has provided.

In chapter ten of *Growth,* Mayr looks closely at Darwin's evidence for evolution and common descent (though not necessarily for natural selection as the mechanism). Darwin considers a number of types of evidence weighing in favor of evolution, but holds embryology as the strongest evidence of all. Mayr quotes Darwin's emphasis on "the leading factors of embryology, which are second in importance to none in natural history"(Darwin 1859, p. 450). For, as Darwin continued, "Hardly any point gave me so much satisfaction when I was at work on the *Origin*, as the explanation of the wide difference in many classes between the embryo and the adult animal, and of the close resemblance of the embryos within the same class. No notice of this point was taken, as far as I remember, in the early reviews of the *Origin*" (Darwin 1958, p. 125).

Darwin lamented that readers did not appreciate the importance of the embryological evidence in his time. In particular, he saw embryology as providing clear examples of phenomena that could be explained by evolution and common descent and not by the alternative, creation theory. First, if species had been created, then we should expect a direct development from egg to adult. Instead we see "detours." "There is no obvious reason why, for instance, the wing of a bat, or the fin or a porpoise, should not have been sketched out with all the parts in proper proportions, as soon as any structure became visible in the embryo" (Darwin 1859, p. 442). There is no reason for the unused diversions in development we sometimes observe, like the gill-arch stage in land vertebrates, the notochord for higher vertebrates, or many other examples. Such developmental patterns suggest either a rather poor designer or, more obviously, descent with modification from a common ancestor.

On Darwin's account, "the adult differs from its embryo, owing to variations supervening at a not early age, and being inherited at a corre-

sponding age. This process, whilst it leaves the embryo almost unaltered, continually adds, in the course of successive generations, more and more difference to the adults" (Darwin 1859, p. 338). Or, as Mayr notes, Darwin assumed that variations occur late in individual development, leaving the earlier stages more or less intact. Parallels in embryonic stages revealed common descent for Darwin and for Mayr. Embryology should inform the study of phylogeny, as a result.

So far, Mayr is summarizing. But he then asks the question why, assuming Darwin was right as he obviously does, did his contemporaries miss the overriding importance of the embryological evidence? Because, Mayr explains, it was not just the creation interpretation of species that readers had in mind. They were also strongly influenced by the long-standing interpretation of parallelism, according to which individual animals were seen as following the pattern of their species type while those types also followed the patterns of the "animal series" of which they were a part. In other words, the relationships among embryos that Darwin attributed to evolution and common descent, those researchers such as Meckel or Serres explained as common parallel paths of development within a group. As J. F. Meckel put it, "The development of the individual organism obeys the same laws as the development of the whole animal series; that is to say, the higher animal, in its graduate evolution, essentially passes through the same *permanent* organic stages which lie below it," and then tend to rise through the higher stages (Meckel 1821, p. 345). Meckel's interpretation, like that of the other parallelists, fell into that category that Mayr considers unforgivable error, namely "essentialistic thinking."

The idea bears no implications that evolution occurs, since the types do not change but are instead quite fixed. It is, rather, the embryonic steps of an individual organism of a particular type that pass through the stages in question and reveal their parallels. Therefore, a higher vertebrate might have a notochord stage because other animals in the same "series" also had it, or animals might have gill-slits in the embryo not because they needed gill-slits themselves but because gill-slits were part of a particular embryonic type or stage. Not only such thinking did not require or even imply evolution of species by common descent, but it actually reinforced essentialistic and non-evolutionary notions by assuming the existence of defined stages of development and believing that the apparent parallels in embryonic development provided evidence of such stages.

This was a major mistake, Mayr feels. Yet, Darwin was led to this idea because the existing alternative explanation of individual development was even worse. Karl Ernst von Baer's version of essentialism, whereby each individual organism conforms to the archetype and starts from the homogeneous and general, then gradually acquires characteristics of the particular. For von Baer, the anti-evolutionist, every embryo within a

group would have basically the same general beginning, and only later would diverge to seek its proper teleological goals. But then, Mayr asks, why would gill-arches occur in species that did not need them? Were these once general characteristics of the archetype and then lost or discarded somehow? Von Baer's interpretation clearly bothers Mayr. And it bothers him that Darwin came close to accepting it in his early sketches and notebooks. Mayr sees it as fortunate that Louis Agassiz provided an interpretation of the Meckel-Serres view that Darwin found promising and that moved Darwin beyond von Baer's mistakes. Better for Darwin to make the parallelists' mistakes than von Baer's, apparently. Clearly Darwin puzzled over embryology. Mayr sympathizes with Darwin's position. There Darwin was, recognizing the importance of embryological evidence, yet within an interpretation of embryonic development in which he felt confident.

Because of his own lack of a detailed explanation of heredity or of development, Darwin was attracted to ideas of recapitulation. As Mayr puts it, "With Darwin's silent blessing (1872, p. 498) and Haeckel's enthusiasm, the theory of recapitulation was immensely popular and successful in the three or four decades after 1870. It led to the splendid flowering of comparative embryology and was responsible for many spectacular discoveries." Furthermore, "embryology also became an indispensable tool in establishing otherwise uncertain homology. By the end of the century, various excesses as well as a growing interest in proximate causation led to disenchantment and to the eventual rejection of recapitulation, particularly in its extreme form" (Mayr 1982, pp. 474-475).

The idea of recapitulation was turned by Haeckel into an explanatory claim whereby phylogenetic development causes individual, ontogenetic development. This suggested that the individual developmental stages, which are much easier to study than the phylogenetic development, should reveal patterns. Those embryonic stages that look most alike should reveal the most closely related species. That, in turn, should reveal evolutionary relationships. The historical record reveals that, indeed, a number of researchers rushed in the late nineteenth century to descriptive and then comparative embryology in aid of understanding the patterns of evolution.

Mayr reveals his sympathies for this approach, even while he obviously recognizes the problems with such method. Assuming evolution and using embryology to illuminate evolution seemed far preferable nonetheless to falling back on von Baer's essentialist and linear thinking, whereby embryonic development leads from the general to the specific. In this discussion in *Growth,* Mayr recognizes Darwin's problem. Darwin knew little of the mechanisms of heredity or development, yet he sought evidence for close evolutionary relationships. Darwin needed evidence that

species had evolved from a common descent through the gradual accumulation of variations over time. Recapitulation seemed to provide the best available interpretation of the perceived patterns.

This did create some difficulties, Mayr notes, because when Darwin tentatively, and Darwinian followers such as Haeckel enthusiastically, hitched the interpretations of evolution to recapitulation, they had a problem when recapitulation was cast aside. Indeed, as embryologists began to study individual development in a number of species, they found a diversity of patterns instead of neat relationships. Individuals in some species could even develop in different ways depending on the environmental conditions. By the turn of the twentieth century, the strongest version of the recapitulation hypothesis had been set aside.

So, as Mayr noted, this left Darwin's questions unanswered, including: why do gill-arches appear in the ontogeny of animals including mammals? "To be frank—Mayr admitted—until the physiology and biochemistry of developmental systems is better understood, only a tentative answer is possible. One can suggest that the genetic program for development consists of a set of such complex interactions that is can be modified only very slowly." It takes a long time to eliminate the unnecessary variations when they are not harmful. Some vestigial developmental patterns remain. "We do not have a recapitulation of ancestral types, but we do occasionally have in ontogeny the recapitulation of individual ancestral characters and developmental pathways. How they are to be identified and how to explain their developmental physiology are matters of current discussion" (Mayr 1982, pp. 475-476).

Fortunately, by 1994, Mayr had recovered his confidence in the efficacy of evolution to explain embryology. "As Gould (1977) has pointed out so rightly, recapitulation, properly understood, is simply a fact that cannot be eliminated by attacks on it." As he concluded,

> we are dealing here with a not infrequent phenomenon in the history of science. A phenomenon or process is discovered that demands an explanation for which the field does not yet have the required maturity. As a result, an inappropriate, that is erroneous, explanation is offered. When this is subsequently refuted, the baby is thrown out with the bathwater; that is, the legitimate phenomenon (observation) is also denied, as if this were necessitated by the refutation of the erroneous explanation. It documents the maturation of biology that we are now ready to accept recapitulation, but with an explanation derived from other areas in biology (Mayr 1994, p. 231).

Whether developmental biologists were in 1994 or are now really ready to accept recapitulation in any form remains an open question. It is clear that much of the impulse behind the emergence of evo-devo reflects the same sort of thinking Mayr was noting. It is also the case, however, that devel-

opmental biologists very much want to work out the physiology and other processes of development that Mayr finds relatively uninteresting.

In his brief comments on "Theory formation in developmental biology" (1968), Mayr noted that embryologists want to explain individual development from one moment to the next so that differentiation occurs. He cited June Goodfield's observation that the emphasis has changed. Classical embryologists had asked: how the apparently homogeneous and unformed "small ball of yolk-laden cytoplasm, with a nucleus, turn into a large, complicated, highly organized adult with fully functioning organs?" In contrast, the modern embryologist asked "How does the *encoded* structure, compressed into the final developmental stages of a specialized, maternal organ—the egg—become transformed into the *realized* structure of an adult organism?" This modern question assumes that much is predetermined, in the form of coded information, in the inherited material, or that "the complexity is preformed in the blueprint of the genetic program and is only translated into development."

Here, in 1968, Mayr confidently proceeded to suggest that in fact the machinery of genetics provides a "general theory of development" and that development is just a matter of expression. As Mayr put it, "Development, it seems to me, can be compared with the activities of a symphony orchestra. The musical score tells the musicians what to produce and when. The conductor reinforces and synchronizes the 'turning on' and 'turning off' of the activities of the individual musicians." This is very close to the action of gene induction and repression, according to the theory of the day. "The activity of an orchestra, including that of its conductor, is just as much controlled by the score it is playing as the development of an organism is controlled by its genetic program" (Mayr 1968, pp. 378-379). Mayr did admit that this did not mean that development was really understood, but rather than the general theory seemed clear. Mayr's jumping to the big picture in this way very likely infuriated those developmental biologists who were focused on the complexities of differentiation, growth, and morphogenesis that seemed so far from any explanation by genetic action that this particular theory would have carried little direct meaning.

Their probable annoyance would not have bothered Mayr, however. First, because when he is sure that he is right, he has the courage of his convictions and does not much worry what others think. More importantly, he is not particularly concerned about the failure to provide short time frame proximate explanations. The physiological and biochemical details of genetic translation would not have mattered to Mayr. Hand waving was enough to acknowledge that environmental conditions play a role in shaping which of the possible alternative expressions of genes will actually occur, so that a rejection of "beanbag genetics" did not lead

Mayr to concern with the details of individual development or of the interactions of a developing embryo with its environment. Rather, he sees genetics as providing a theory for development, and leaving for developmental biologists the matter of working out the proximate details.

What is remarkable in this short essay is that he did not also hammer home the point that the genetic program is really the product of evolutionary accumulation of adapted sets of genes. Therefore, the explanation of development resides with the genetic program, and that is established by the actions of evolution and natural selection. Therefore, in effect, individual development follows the path laid out for that individual by evolution.

For Mayr, development was not left out of the synthesis or out of modern biology. After all, in his view, embryonic development just followed the program already established. Mayr acknowledged as much in 1988. He asked what on earth developmental biologists want anyway, for "A Darwinian is truly puzzled when he reads in a critique by an embryologist that 'development comes to the fore as a problem unintelligible within neo-Darwinism'." It is worth following Mayr's exact words here:

> What aspect of development is this author talking about? If he is speaking of the translation of the genetic program into molecular chains of events during ontogeny, he is talking about proximate causations. Their study, indeed, has never been the job of the evolutionary biologist. But many other aspects of development do raise questions concerning evolutionary causations that have been of interest to evolutionists from Darwin on (Mayr 1988, p. 537).

It is, of course, precisely the point for embryologists that they believe that the proximate causes matter. Indeed, they matter the most because they turn what would be an inert evolutionary past and genetic program into actual living organisms. For the embryologist and developmental biologist, the embryos very much matter and the developmental processes of growth, differentiation, and morphogenesis lie at the heart of biology. Not, however, for Mayr. Those are details. It is the grandeur in a Darwinian view of life that provides the framework that allows the rest of biology to make sense. And it is this conviction, so assiduously followed, that makes Mayr's own magnificent career "one long argument" of his own.

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