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Garland Allen, Thomas Hunt Morgan, and Development

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Abstract. Garland E. Allen's 1978 biography of the Nobel Prize winning biologist Thomas Hunt Morgan provides an excellent study of the man and his science. Allen presents Morgan as an opportunistic scientist who follows where his observations take him, leading him to his foundational work in *Drosophila* genetics. The book was rightfully hailed as an important achievement and it introduced generations of readers to Morgan. Yet, in hindsight, Allen's book largely misses an equally important part of Morgan's work – his study of development and regeneration. It is worth returning to this part of Morgan, exploring what Morgan contributed and also why he has been seen by contemporaries and historians such as Allen as having set aside some of the most important developmental problems. A closer look shows how Morgan's view of cells and development that was different from that of his most noted contemporaries led to interpretation of his important contributions in favor of genetics. This essay is part of a special issue, revisiting Garland Allen's views on the history of life sciences in the twentieth century.

Keywords: Garland E. Allen, Thomas Hunt Morgan, Embryology, Genetics, Regeneration

It is an honor to write in recognition of Garland Allen's long and distinguished career as an historian of biology. This paper, like the others in this special issue of the *Journal of the History of Biology* that Gar and I had the privilege to edit from 1998 to 2006, began as an informal talk at a ''Gar Fest'' at Washington University in St. Louis in 2014. The spirit is one of recognizing what is special about Gar Allen's contributions to the history of biology, and in this case particularly about his understanding of Thomas Hunt Morgan. For decades, Gar and I have enjoyed arguing about how important development was to Morgan. This is my chance to make clear what is at issue and why it matters for understanding the history of biological sciences.

When Garland Allen published his masterful biography of Thomas Hunt Morgan in 1978, he made clear that the book was intended as a scientific biography and also a study of the history of genetics. After the first page discussing Gregor Mendel, Allen wrote "the major purpose of the present study is not so much to describe Morgan's personal life for its own sake (though that is, of course, interesting), but to analyze historically some important aspects of the growth of the science of heredity in the early twentieth century" (Allen, 1978, p. x). For Allen, Morgan was primarily a geneticist. Morgan's Nobel Prize in 1933 "for his discoveries concerning the role played by the chromosome in heredity" certainly reinforces the impression that this was the important work by Morgan, and important for Morgan (Nobel Prize, 1933). And Allen's book's reviewers have picked up on the genetics theme since the book's publication.

The reviewers likely focused on genetics in part because that's what they were invited to do in 1978 given both Allen's own and the publisher's emphasis on Morgan the geneticist and given the general enthusiasm about genetics at the time. It also is not surprising that historians of biology have continued to emphasize Morgan's genetics work because the history of biology of the early twentieth century has until quite recently focused more on heredity and genetics. Furthermore, excellent work like Robert Kohler's *Lords of the Fly* galvanized attention on Morgan as a fly man working in the fly room (Kohler, 1994).

Yet Morgan himself might have been disappointed by so much focus on genetics. Allen did recognize that Morgan had wide-ranging interests even though he focused on genetics in his biography. Whereas Allen saw Morgan as precursor to our current interest in genetics, when I look at Morgan's work I see development and regeneration, as discussed more extensively in my study of Morgan and his colleagues Edmund Beecher Wilson, Edwin Grant Conklin, and Ross Granville Harrison (Maienschein, 1991). When I received my Ph.D. degree, my advisor Fred Churchill gave me a copy of a treasured book. This was Morgan's first book, his 1897 study of *Development of the Frog's Egg* (Morgan, 1897). A signed copy of this book recently sold for $2500, which attests to its continued interest and suggests that Morgan the developmental biologist is also worth serious study.

That first book of Morgan's was intended as a textbook that summarized his own work starting with his graduate study under William Keith Brooks at Johns Hopkins, work that explored fundamental issues of egg development. Morgan sought to place those studies in the larger context of contemporary study of frog development.

Morgan's second book was *Regeneration* in 1901, which also has remained in demand and is still cited by those studying regeneration. As with most of Morgan's books, *Regeneration* brought a summary of a considerable array of research, including his own extensive study of regenerative biology with a diversity of species. In his lectures and writings as well as on-line lectures, a leading developmental biologist Alejandro Sánchez Alvarado today frequently points to Morgan's work as having provided the starting point for his own study of planarians and regeneration across diverse types of organisms (Sánchez Alvarado, 2010, see Sánchez Alvarado's websites for more on his work and its relation to Morgan). Morgan was fascinated by the fact that so many organisms could have their heads or tails chopped off and still regenerate to continue living, and he was especially intrigued by the ways they regenerate, often in ways that are not quite "normal."

1903 brought *Evolution and Adaptation*, 1907 *Experimental Zoology*, and only in 1913 did he begin to emphasize inheritance when he published *Heredity and Sex*. Clearly, Morgan was highly versatile as he explored so many different core biological questions. Morgan gave Allen enough so that he could focus his biography of Morgan on the genetics work and find there much to examine and even to admire, while not needing to spend a lot of time on the developmental work as well.

Yet it is important to note that Morgan started his earliest research on development, he maintained that interest throughout his life, and he came back to it with his last book on *Embryology and Genetics* in 1934. Understanding Morgan more fully requires looking at his developmental work in more detail than Allen found it possible to do in his biography. Fortunately, embryologist and historian of embryology Jane Oppenheimer has provided a starting point for a clear look at Morgan as embryologist during Morgan's years at Bryn Mawr College, where she spent her own career. In a symposium for the American Society of Zoologists (now Society for Integrative and Comparative Biology) followed by a special issue of the society's journal, Oppenheimer explained that Morgan "was an embryologist when he came to Bryn Mawr, and remained one during his years there, namely from 1891 until 1904" (Oppenheimer, 1983, p. 845). Oppenheimer points to Morgan's study of widely diverse organisms, on which he observed, described, and especially carried out experimental research to address the many questions about how embryos develop from unformed material into highly structured and functioning whole adult organisms.

Oppenheimer maintained that "It is my belief that Morgan never really abandoned embryology at all, and continued always to think about it" (Oppenheimer, 1983, p. 850). I agree, and enjoyed lively discussions with Oppenheimer when I was a grad student and young faculty member just learning more about Morgan and other notable embryologists. She makes the point in her article and in person that Morgan had significant impact as an embryologist both through his own excellent research and through his support and inspiration for undergraduate and graduate students. At Bryn Mawr, those were young women during the time Morgan was there. Morgan inspired a number of women embryologists at a time when, as Oppenheimer puts it, "he clearly respected the intelligence and abilities of his young woman students and successfully encouraged them to develop as true scientists. No professor can perform a more significant service to science than doing just this for his students" (Oppenheimer, 1983, p. 853). In this case, he performed the service for his embryology students in particular. In the same symposium as Oppenheimer's paper, Allen's paper not surprisingly focused on Morgan and development of the gene concept (Allen, 1983).

After Bryn Mawr, Morgan moved to Columbia and continued his embryological studies. Once again, he asked wide-ranging questions of a broad diversity of organisms. Aside from Oppenheimer, however, most historians of science have emphasized his genetics. I think that historians as well as some of Morgan's contemporaries quickly labeled him as "geneticist" in part because Morgan did not study cells in the same way and with the central emphasis that some of his contemporaries did. This placed him outside the traditional exchanges by his contemporaries about cells in development. In addition, his work in genetics simply overshadowed the study of embryology for those fascinated by that study of heredity. Yet I am sure that Morgan would not have agreed with this emphasis on the genetics alone. I agree with Oppenheimer that he never gave up a primary fascination with embryology and development.

Why, then, did Allen and other historians aside from Oppenheimer see Morgan in terms of genetics, and often exclusively in those terms? His Nobel Prize was for the genetics work, of course, and that is surely an important factor. And as suggested earlier, first biologists and then historians became enchanted with heredity and genetics. Also, I have come to see that Morgan's work on embryology did not fully connect with the work others were doing during his lifetime.

Morgan was more driven by deep questions about developmental biology and not so much about embryology per se. That is, it wasn't the embryo itself but the developmental processes and changes that motivated his interest. As the twentieth century continued, studies of animal embryology tended to fall into three groupings. The first was medical, focused on understanding human development and its pathologies. The second looked at the intersections of embryology and evolution, in part using embryology to interpret evolutionary relationships; Walter Garstang, Gavin de Beer, and others contributed notably here. Morgan did not pursue either of those lines of research. The third looked at embryos and sought to understand the processes by which a fertilized egg becomes an organized organism. Morgan did fit here, but not neatly. In the early part of the century, the leaders in this area were focused on cells, then changes that occur in cell lineage, and the role or cells and tissues in determining the morphogenetic "fate" of each part during development and differentiation. Morgan looked at cells and found Boveri's and Wilson's contributions valuable. Yet he did not particularly care about any individual cell so much as about the way the whole structure responded to environmental or internal changes. For Morgan, regeneration involved regeneration of function and structure, not of cells in particular. If I am right about Morgan's lesser role for cells, it is worth examining in a bit more detail just what he did emphasize and why his contemporaries and later historians have come so much to emphasize his work on genetics.

Morgan on Cells and Development

Let's look more closely at Morgan's view of cells, which had become centrally connected with development through the work especially of Oscar Hertwig, Theodor Boveri, and Edmund Beecher Wilson (Hertwig, 1898; Baltzer, 1967; Wilson, 1896). In Morgan's 1927 summary volume *Experimental Embryology*, for example, his 766 pages and 25 chapters include discussion of cleavage in chapter 10 and experimental effects on cleavage in chapter 21, but a great deal more about heredity, chromosomes, fertilization, parthenogenesis, and such topics that he did not present as primarily about cells. This is in contrast to Edmund Beecher Wilson's 1924 third edition of *The Cell in Development and Heredity*, in which the 1232 pages are all about cells. Even the discussion about chromosomes makes clear that Wilson saw them as part of cells, interacting with the cytoplasm and other cell structures.

Their essays in a 1924 volume edited by Edmund Cowdry also make the difference of emphasis very clear. Cowdry had convened a group at the Marine Biological Laboratory in Woods Hole to talk about cells, which led to the edited *General Cytology* (Cowdry, 1924). Wilson provided the Introduction to the volume and pointed to cytology as concerning study of cells as organic units. He noted that the field began when microscopic techniques made it possible really to look inside cells, and that the study of cells grew out of the study of embryology. Wilson pointed to the complex structure of cells, with their nuclei and chromosomes, cytoplasm and apparatus of cell division, and other parts (Wilson, 1924).

In contrast, Morgan contributed the very last chapter on "Mendelian Inheritance and Cytology" (Morgan, 1924). Morgan wrote that, "It is sometimes said that the cytoplasm must be as important as the chromosomes, since no development is known except in the presence of the cytoplasm, and by its activity. Whether the cytoplasm or the chromosomes is or is not equally 'important' is a matter that cannot be determined and is of very little consequence. The statement is an example of obscurantism rather than profundity." In fact, he also noted, since all the chromatin and therefore the "whole genetic complex" (Morgan, 1924, pp. 727, 717) exists in every cell, explaining the changes that take place during development requires more than the presence of genes alone. Morgan certainly understood that the whole cell helps to translate the genetic materials into results, he recognized the importance of the cytoplasm, and he also saw the chromosomes and genes as key in helping to cause developmental processes. It is easy to look with our modern eyes and see the discussion as emphasizing genetics and not looking at the whole cell, even when Morgan included other factors as well. We just do not know yet how the processes work, he reasoned.

It is easy to see how Morgan's words here and in his many, many other articles and books might mislead readers looking with particular genetics-oriented assumptions to miss the emphasis on development. But let's look a little more closely, because other work of Morgan's would lead to a different impression. In many cases, it is important to recall the exact wording that Morgan chose so as not to avoid over-interpreting in light of our own current understanding.

Development of the Frog's Egg

Development of the Frog's Egg from 1897 provides an excellent summary of observations and results of experimental studies of development.

From formation of the egg and sperm cells, to fertilization, to cleavage, to effects of experimental manipulation: Morgan reports on the most current science of the day. Coming shortly after Edmund Beecher Wilson's *Atlas of Fertilization and Karyokinesis* in 1895 and *The Cell in Development and Inheritance* in 1896, Morgan's work moves beyond Wilson's focus on cells to focus on development. The book was clearly intended as a summary, and it just ends with reports on particular experiments and a technical appendix. Morgan did not try to summarize what he had learned from the survey, nor to draw conclusions about development in general. He left the story as one about frog's eggs. Despite the fact that Morgan discussed the work of Wilhelm Roux at length and clearly was intrigued by experimental methods for embryology, he said repeatedly that the results to date were not sufficient to draw conclusions about the causes of development.

Allen's discussion of this period of Morgan's life emphasizes Roux's *Entwickelungsmechanik* and suggests that Morgan was inspired by Jacques Loeb and studies of physiology. Yet the term *Entwickelungsmechanik* does not even appear in the index, and Loeb does not appear in the references to Morgan's book on frog's eggs. This might give a reader the impression that Morgan ignored those topics, when in fact he did not but rather saw these themes as part of the larger approach to understanding developmental processes. Allen's own emphasis on the "revolt" from morphological to the sort of experimental study that Allen sees Roux and Loeb as exemplifying may have led Allen to see Morgan's life and work of the time in particular terms, while looking at Morgan with a different lens might give a different impression.

Regeneration

Morgan's 1901 *Regeneration* was the culmination of years of work on multiple organisms published through dozens of papers. Allen's biography of Morgan spends not quite eight lines of text looking at this volume, but the work was extremely important to Morgan – and has inspired others since. As Morgan explained, the volume was also the outgrowth of a series of lectures he had delivered at Columbia in 1900. Morgan explained in his Preface that "If it should appear that at times I have gone out of my way to attack the hypothesis of preformed nuclear germs, and also the theory of natural selection as applied to regeneration, I trust that the importance of the questions involved may be an excuse for the criticism." And that "we so often fail to realize which problems are really scientific and which methods are legitimate for the solution of these problems.'' He continued that science must avoid ''unverifiable speculation'' and instead bring solid empirical evidence to bear on verifying testable hypotheses (Morgan, 1901, pp. vii, viii).

Morgan then worked through the results of empirical observation and of experimental tests, looking also at the range of theories offered to explain regeneration. This then led to the final chapter of ''General Considerations and Conclusions.'' There he asked what we have learned from all the separate studies, and in particular what we learn about '''organization,' 'polarity,' 'factors,' 'formative forces,' 'vitalistic.' and 'mechanical principles,' 'adaptation,' etc.'' (Morgan, 1901, p. 277). Regeneration raises questions at the core of developmental biology, as well as at the heart of studies of cytology (Sunderland, 2010).

Sometimes when an animal is injured, as seen in the hydra, earthworms, or planarians that Morgan studied, the injured part seems to react as if directed by the whole organism, so that new regenerating tissue seems informed by what is needed to make the organism whole again. ''It can be shown, I think with some probability that the forming organism is of such a kind that we can better understand its action when we consider it as a whole and not simply as the sum of a vast number of smaller parts,'' Morgan wrote (Morgan, 1901, p. 278). Chemical or physical analysis of the materials alone cannot explain the result. Nor can the organism be seen as simply a sum of interacting cells. There is more to an organism, Morgan urged, and he suggested that the whole has some agency and ability to organize the organism. Perhaps this is a sort of ''harmony'' of the whole, as Morgan's friend Hans Driesch had put it.

Nor is regeneration the result of adaptations to special circumstances, Morgan insisted. He outright rejected August Weismann's interpretation, which hypothesized that those parts most liable to be injured are those with the special capacity to regenerate. Over the long sequence of generations through evolution, Weismann and other contemporary evolutionary thinkers argued that the capacity has become adapted. This explains why some organisms can regenerate some parts, while others cannot, Weismann concluded. Morgan spelled out the arguments against this view in his Chapter 5.

Throughout his discussion, Morgan did not talk about chromosomes and only mentioned the nucleus briefly. He noted that cells seem to require a nucleus in order to regenerate, and he noted that Jacques Loeb hypothesized that this might be because non-nucleated cells lack the oxidation required. Morgan remained unconvinced by any of the claims about the importance of nuclei and uncertain what causes cells to regenerate, concluding that the nucleus and cytoplasm both seemed to be involved with regeneration in some ways that were not yet understood (Morgan, 1901, p. 258). This was not the side of Morgan that Garland Allen saw in writing his biography, focused as Allen was on chromosomes and heredity. Yet this Morgan of regeneration was working to sort out the central problems of development – of both normal and regenerating organisms, through an attempt to understand the complexities of organization and interacting cellular parts.

Experimental Embryology

This work of 1927 followed a series of books more directly focused on genetics and heredity. Here again, Morgan summarized work to date and provided a sort of textbook for advances students. Allen gives us just a few sentences on p. 298 that point to Morgan's "monumental treatise" that "surveyed a number of topics in the modern experimental approach to embryology." Allen saw the book as signaling a revival of Morgan's youthful interest in embryology rather than as a continuation in the way that Morgan himself seems to have seen it.

In his volume, Morgan noted the significant advances in thinking about development since his earliest study of frog's eggs and other embryological problems. In his preface Morgan noted that "A transparent egg as it develops is one of the most fascinating objects in the world of living beings. The continuous change in form that takes place from hour to hour puzzles us by its very simplicity." The predictability and order of the events as they unfold provides a "pageant" with "irresistible appeal to the emotional and artistic sides of our nature" (Morgan, 1927, p. vii). Studying embryology, Morgan makes clear, is tremendously fascinating and downright fun. It also calls for careful attention not to get caught up in the beauty of the developmental process itself. His 100 pages of references demonstrate that Morgan himself took very seriously the call for close study of what we have learned from experimental embryology and what questions remain.

Embryology and Genetics

In looking at this book of Morgan's, Allen spends a longer time looking at Morgan's contribution, a full two pages, but still is so much looking with eyes filled with chromosomes that he misses some of what is most important about the cells and development. The fact that Morgan doesn't quite fit the traditional pattern of his contemporaries may have contributed to misleading his twentieth century reader. After a lifetime filled with rich study of genetics, evolution, and embryology, Morgan said in this last book he published that he was looking at two interlocking areas of biology, embryology and genetics. "In the following pages," he wrote, "I have attempted to point out in a simple way their interrelations. That much remains to be done will be only too obvious, but with the openings furnished by experimental investigation of heredity and embryology there is promise that a great deal more is within our reach" (Morgan, 1934, p. vii).

This important book of Morgan's is relatively short, just 258 pages to cover both genetics and embryology. Chapter 1 provides an introduction, which is easy to read too fast and for which it is all too tempting to read interpretations into the words. In fact, the way Morgan set up this book is fascinating. He noted that "The common meeting point of embryology and genetics is found in the relation between the hereditary units in the chromosomes, the genes, and the protoplasm of the cell where the influence of the genes comes to visible expression" (Morgan, 1934, p. 9). It is very easy to misread this in twenty-first century terms and to see Morgan as writing about gene expression in our sense. But he was not doing that.

In fact, he recognized three possible interpretations of how genes and development work. First is the idea that "all the genes are acting all the time in the same way." Yet this view is problematic in that it fails to explain development and differentiation: how can cells become different if the hereditary causes are all the same? An alternative view is that "different batteries of genes come into action as development proceeds." While this might seem to parallel our current view, Morgan concluded that it is inconsistent with the development of parts in a normal way even when they are experimentally manipulated, as with compression studies: if there is a normal sequential process, how can it work under altered conditions?

The third view, which Morgan preferred, gives the cytoplasm an active role. He acknowledged that the cytoplasm already has structure and differences within the egg itself from the beginning, and the differences become greater as the cells divide and materials move around. In Morgan's words, "From the protoplasm are derived the materials for the growth of the chromatin and for the substances manufactured by the genes. The initial differences in the protoplasmic regions may be supposed to affect the activity of the genes. The genes will then in turn affect the protoplasm, which will start a new series of reciprocal reactions. In this way we can picture to ourselves the gradual elaboration and differentiation of the various regions of the embryo'' (Morgan, 1934, p. 10).

The following chapters present the basics of genetics and development of the time, looking at fertilization, cleavage, gastrulation, induction, and experimental results. Morgan added discussion of parthenogenesis, regeneration, and sex, as well as physiological factors in embryology. It is only in this last chapter that he returned to the intersection of genetics and embryology. Here he concluded that the egg cell is an individual in a unique way that then connects with the resulting organism.

Morgan noted that it is during the process of development that differentiation of cells takes place. Yet it was commonly assumed that the genes remain the same in all cells and over time. Yet Morgan saw other possibilities. It is worth repeating Morgan's exact words on this point, the last words the book:

> It is, however, conceivable that the genes are building up more and more, or are changing in some way, as development proceeds in response to that part of the protoplasm in which they come to lie, and that these changes have a reciprocal influence on the protoplasm. It may be objected that this view is incompatible with the evidence that by changing the location of cells, as in grafting experiments and in regeneration, the cells may come to differentiate in another direction. But the objection is not so serious as it may appear if the basic constitution of the gene remains always the same, the postulated additions or changes in the genes being of the same order as those that take place in the protoplasm. If the latter can change its differentiation in a new environment without losing its fundamental properties, why may not the genes also? This question is clearly beyond the range of present evidence, but as a possibility it need not be rejected. The answer, for or against such an assumption, will have to wait until evidence can be obtained from experimental investigation. (Morgan, 1934, p. 234)

This passage is extremely instructive. Morgan was suggesting that the genes and cytoplasm interact in a dynamic way, such that both may change in response to changing conditions. The parts of each cell interact, and they apparently also respond to the other cells and to the whole organism on this view. As with Morgan's earlier work on regeneration, the whole organism has some agency and causal influence in bringing organization of the organism. Genetics is just part of the story.

How Garland Allen Missed Morgan's Development

Garland Allen seems to have missed this point, partly because Morgan misled him – though not intentionally, of course. Allen points to Morgan's *Embryology and Genetics* as a failed effort. Allen points to Morgan's discussion of "successively triggered batteries of genes" as accounting for differentiation, and suggests that this was Morgan's developmental hypothesis. Yet we have seen that Morgan rejected that idea. Allen sees Morgan as having put forth a theory, having found that it didn't quite work, and having acknowledged failure. He recounts the story that colleagues complained to Morgan that Morgan had not, in fact, told the story of embryology and genetics. Yet Morgan supposedly responded "After all, I did exactly what I said I would do in the title: I talked about embryology, and I talked about genetics" (Allen, 1983, p. 300, fn 32). Allen and other historians since, including me when I first read Allen's biography and Morgan's other books, have seen this as Morgan's acknowledging his failure to unite two fields. I think this interpretation misses important points about what Morgan was actually doing.

Allen suggests that Morgan was unsuccessful in uniting the fields because the relations of genetics and development are complex and because of "the lack of experimental techniques to answer questions about biochemical changes within cells." Yet this suggests that Morgan was looking for biochemical explanations and that he was disappointed by his failure to "integrate genetic and embryological theory." Allen concludes his section with the words "Small wonder that Morgan did not achieve his goal; his hopes were undoubtedly too high for his day. Much more gratifying and successful were his attempts to apply the new Mendelian theory to the problem of evolution by natural selection" (Allen, 1983, p. 301).

This interpretation goes astray in two ways. First, in assuming that Morgan was particularly disappointed in his so-called failure. Second, in assuming that Morgan was looking for theories and saw Mendelian theory and evolution as more successful than the developmental work. There is no question that Allen gives us a rich and detailed biography of Morgan and his scientific approaches. Nor that Allen's biography of Morgan sheds much light on the history of biology in the first half of the twentieth century. Yet in Allen's concentration on Morgan's books and many articles on genetics while not looking as closely at Morgan's many studies of development itself, especially those discussed here, he missed parts of what was important in Morgan's approach.

In fact, Morgan's strategy seems always to have been brilliantly opportunistic. He studied the organisms and used the techniques and asked the questions before him. Allen shows that in other parts of Morgan's work. But Allen does not see how often Morgan says, seemingly with satisfaction, that the current research had reached its limits for now. As he said at the end of *Embryology and Genetics*, "The answer, for or against such an assumption, will have to wait until evidence can be obtained from experimental investigation." This was not admission of failure to achieve a theoretical interpretation. It was not a "disappointment." This was Morgan's standard response, and indeed a standard response of his respected senior colleagues such as E. B. Wilson. A good scientist knows just how far the evidence will carry him, and he does not attempt to draw conclusions that go beyond his results. Indeed, this is how great science works: each discovery leads to new questions, which then cannot be answered without new evidence, and so on. Morgan understood how science works.

Morgan's *Embryology and Genetics* was surely not a failure or disappointment for Morgan. And it should not be for us now. Allen notes in his 1978 biography that "As fascinating as the problem of embryonic differentiation has always been, we are not much closer to knowing its precise mechanism in the 1970s than in the 1930s. Much interesting work has emerged in the areas of tissue induction, nuclear transplantation, biochemistry of genetic control, and other topics that bear on differentiation. But none has demonstrated the exact method of functioning in a full-fledged differentiating system" (Morgan, 1934, p. 301).

Yet Allen is surely wrong here. Considerable progress toward understanding the complexities of development and differentiation had been made by the 1930s, and even more by the 1970s, and even more by 2015. Yes, much remained then and still remains to be discovered. We are even now only beginning to understand how the organism as a whole acts as a complex dynamic system, guided by gene regulatory networks, epigenetics, and other factors. As always, we have to wait for answers to newly articulated questions through new and additional experimental and theoretical approaches. Yes, there is much to learn. But Morgan understood the epistemological needs of scientific research, and he had the imagination to raise the questions and suggest interpretations, always weighing them in the light of the best available evidence.

Allen missed Morgan's excitement about and emphasis on development. Because of the way Morgan wrote his articles and books, it is easy to pick up some of the work and see a thread and emphases, as Allen did. Allen saw genetics and Mendelism. He saw an emphasis on heredity and evolution at a time that those fields dominated biology. Morgan did not talk a lot about cells and cytoplasm, and he did not develop interpretations or analyses of the internal workings of cells. Allen could easily have missed the fact that Morgan was learning about cytology from his colleague Wilson at Columbia and his colleagues at the Marine Biological Laboratory each summer.

It is worth returning to the 1924 group project on *General Cytology*, edited by Edmund Cowdry. There Morgan had noted that we do not know enough about the cytoplasm. Perhaps, he suggested, cytoplasm in different organisms is different, or in different types of organisms. Surely the cytoplasm plays an important role in development, as do the genes; whether they play equal roles remained unclear. He concluded that, "The questions must be kept entirely free from predilections until we have found out more about the physiological processes that take place in the chromosomes and in the cytoplasm" (Cowdry, 1924, p. 728). We could conclude the same today. We need to know a lot more about the relevant phenomenon, and about the complex of factors that influence the physiological processes that connect heredity and development in the context of evolution. Morgan was working hard to make those connections, and he probably would have enjoyed the efforts of those exploring developmental evolution today.

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