

FROM EMBRYOLOGY TO EVO-DEVO:  
A HISTORY OF DEVELOPMENTAL EVOLUTION

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TO EVO-DEVO THROUGH CELLS, EMBRYOS, AND  
MORPHOGENESIS  
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Evo-Devo finally brings us a new synthesis, it is claimed, with evolution of development as the central focus. There is a sense of triumphalism in the declarations that this is a much better synthesis than the so-called evolutionary synthesis before it. Discussion has, naturally enough, centered on the question "Why not before, and why now?"

Fans of the evolutionary synthesis have invoked a variety of explanations for why development was left out of the synthesis of the 1940s and 1950s. Yet we can also ask the question rather differently: Why was evolutionary biology so foolishly distracted by philosophy and theology that it failed to do "real" science and missed the boat of experimental progress? We might, with Yale developmental biologist J. P. Trinkaus (known as Trink), hold that far from feeling left out of some important self-declared "synthesis," those concerned with development actually felt sorry for their evolutionary biology counterparts. As Trink put it, "Hell, no, we didn't feel left out of anything. They were just jealous because they couldn't figure how to get the NIH funding!"<sup>1</sup>

In 1884, Karl Nägeli had already noted the tendency of evolutionists to wander away from what he considered the core biological questions. He emphasized the importance of examining physical and mechanical understanding of organic nature. Nägeli complained that

The theory of evolution touches also philosophy and theology in very sensitive spots and interests the intelligent general public partly for this reason and partly because human vanity has always attached much importance to origin and relationship.

On this account we have seen philosophers, theologians and, in addition, literati of all sorts and conditions take possession of the problem. This too would have been quite in order, if every one had but utilized the established results of scientific investigation for his own field and rendered to his own circle a clarifying and instructive account of them; and if so many had not considered this field of difficult physiological problems to be a free-for-all arena for senseless argumentation.<sup>2</sup>

Citing Nägeli, Ross Harrison echoed this sentiment in 1936, in his address as retiring chairman of the Section on Zoological Science at the American Association for the Advancement of Science meeting in Atlantic City, New Jersey. Discussing "Embryology and Its Relations," Harrison saw evolution as having gone astray because of its engagement with fundamentalist theology and lamented that "The scientific investigation of evolution has suffered severely from this emotional conflict." In particular, he pointed to the failure to achieve scientific—by which he meant experimental—results. He acknowledged that the long time frame required for evolution makes experimental investigation more difficult, but it is nonetheless necessary, for "it can scarcely escape any one accustomed to scientific thinking that the processes of evolution can be elucidated only by painstaking experimental work carried on over a long period of years." Fortunately, Harrison saw "hopeful signs of the applicability of exact methods to the study of evolutionary processes" in the "development of modern genetics, the experimental study of the origin of mutations and the new mathematical theory of natural selection."<sup>3</sup>

Harrison was not alone in his thinking; he represented a community of researchers exploring embryology and its relations to other fields and other processes and patterns of biology. They felt that true science must be experimental and analytical, and must avoid the speculative distractions to which they felt evolution had succumbed.

In the 1920s Harrison had been less sanguine about the prospects for such science and for embryology. In his address as retiring president of the American Society of Zoologists in 1925, he had urged a "Return to Embryology."<sup>4</sup> After a period of quiescence and even depression within the field, he had pointed to what he hoped would soon become a resurgence of embryological study. The concept of the "organizer" had brought promise for analytical approaches to development, and there had been reason to hope that younger researchers would take up the study of embryos again. By 1936, Harrison was clearly pleased to announce, the resurrection had taken place. And even though the organizer theory had given way to concepts of "induction," and to closer and more careful analysis of internal regulation within organisms—and indeed within individual cells within the organisms—this was progress. Embryology had come much farther than scientific study of evolution. For Harrison and his likes, there could be a coming together of evolution and development only if those studying evolution, those studying heredity through genetics, and embryologists all relied on the same experimental scientific approaches.

It was not in the 1930s, or even during the next half-century, that evo and devo began to come together in the new and promising ways that have given rise to today's self-proclaimed "Evo-devo" movement. And that has come, as Harrison predicted, because of technical and experimental advances more than because of additional speculation and theory. Some chapters in this volume explore aspects of these recent advances, while others look at episodes of study of devo and earlier attempts at evo-devo syntheses. In this chapter, I concentrate instead on lines of research that lay within what would have been considered embryology and that largely ignored evolution as a factor to be addressed directly. Yet I contend that these studies that focused on exploring embryos and cells really did seek to address fundamental questions about development in the light of evolution.

I look at studies of morphogenesis. This field focused on the proximate or local and immediate causal mechanisms of the emergence of the parts that make up an individual organism's form. Yet attempts to make sense of morphogenesis also bring together the different time scales of individual development and evolutionary history because "morphogenesis" presumes the development of a particular "morph" that conforms to the form of its species. The question, then, was how an individual comes to acquire the particular form of its species, which is a product of the different long-term time scale of evolution.

Therefore, morphogenesis was at its heart one way of bringing together the devo and the evo, respecting the proximate mechanisms of individual development and also the "ultimate" factors brought by evolution and revealed through systematics. In the twentieth century, fundamental questions about morphogenesis found tractability in study of cells and of the whole, interacting, developing embryos of which the cells are the parts. I therefore concentrate on studies at the conjunction of cells, embryos, and morphogenesis. This allows us to get at one set of ways in which researchers thought they could meaningfully bring together development and evolution, and this historical perspective should illuminate current discussions.

#### CELLS AND MORPHOGENESIS IN THE 1890s

In the 1890s, the development of morphological structures was labeled "morphogenesis." At the same time, because of tremendous advances in cytology during the last quarter of the nineteenth century, researchers had begun to focus on cells and on the ways that cells interact to generate

structure. While some researchers moved toward hereditary accounts of development, pointing to the inherited material inside cells as determining what follows, those concentrating on development drew on epigenetic accounts. Cells, embryos, morphogenesis, and epigenesis converged in exciting new research programs.

Years later, the committed agnostic Harrison emphasized the epigenetic outlook that underlay this research by quoting a passage from the Biblical Psalm 139: "And in Thy book all my members were written, which in continuance were fashioned, when as yet there was none of them." Development is not seen as an unfolding of something preexistent, but as a coming into being. Obviously, Harrison agreed and wanted to emphasize that therefore the best approach for understanding the genesis of an individual's life was through embryology as the study of epigenetic emergence, and focused on "Cellular Differentiation and Internal Environment."<sup>5</sup>

The central question was what role cells play in development. Do cells serve as causal agents in morphogenesis, actually bringing about the generation of form and the function that comes with form through the actions and interactions of individual cells? If so, in what way? What is the relative importance of local, proximate, internal environmental factors, and how can the interplay of these factors in shaping each cell give rise to complex, multicellular forms? Or, alternatively, are cells just epiphenomenal results that come only after the real work of development has occurred through other forces? And if they are, what are the forces and how do they do the job of morphogenesis?

One view held that cells do carry significant causal force for development and differentiation. Edmund Beecher Wilson took this view in the first edition of his *The Cell in Development and Inheritance* (1896). He noted that cell theory and evolution provide the two foundations for biology. He asked what cell division does, and how we get from one fertilized egg cell to differentiated cells and eventually to a formed organism. How does development of the form, or morphogenesis, work?

Wilson answered that cell division brings differentiation, and the series of cell divisions leads to the gradual and epigenetic process of morphogenesis. Wilson noted that "for two reasons the cleavage of the egg possesses a higher interest than any other case of cell-division. First, the egg-cell gives rise by division not only to cells like itself, as is the case with most tissue-cells, but also to many other kinds of cells. The operation of cleavage is therefore immediately connected with the process of differentiation, which is the most fundamental phenomenon in development."<sup>6</sup>

Therefore, cleavage and differentiation are connected, with cleavage apparently causing or at least leading to differentiation. There was some "promorphological" arrangement in the segmented egg that brought a sort of "germinal localization," but there was no preformation or even pre-determination in any meaningful sense. The form was not there already. Rather, for Wilson there was some "organization" or prelocalization in the segmented egg that established the starting point for and process that gives rise to an individual organism.<sup>7</sup> Then it was the cell division that brings differentiation, and with it morphogenesis. For Wilson, morphogenesis occurred one cell division at a time, against a background of cytoplasmic differentiation.

Wilhelm Roux took a much more extreme version of this cell-division-as-cause-of-developing-form. His mosaic interpretation involved parceling out differentiated inherited material to each cell, so that every cell division brought specialization and localization of differentiated cells and parts. Again, morphogenesis occurred one cell division at a time, very decidedly *because of* the cell divisions. Yet on this interpretation the cells were little more than containers for the hereditary units. In Roux's case, however, the form was effectively predelineated in the inherited units parceled out to each cell.

Alternatively, a second theory held that cells are epiphenomena that follow rather than cause cell division. In this case, some other causes drive differentiation and morphogenesis. For example, Thomas Henry Huxley saw them this way, for cells "are no more the producers of vital phenomena, than the shells scattered in orderly line[s] along the sea-beach are the instruments by which the gravitational force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted."<sup>8</sup> Instead of cells and cell division, properties of protoplasm and evolutionary factors drove development, according to Huxley; cells were simply secondary, or epiphenomenal.

Charles Otis Whitman agreed with Huxley's view in his essay "The Inadequacy of the Cell-Theory."<sup>9</sup> Whitman insisted that Wilson had it backward. Organization was *not* the product of cell-formation; rather, "organization precedes cell formatting and regulates it."<sup>10</sup> He said that "an organism is an organism from the egg onward," and that cleavage simply followed and divided up the material. He explained morphogenesis and differentiation in terms of a predelineation within the egg that provided the "organization" for the future "organism."

Charles Manning Child agreed with Whitman. It must be "the organism—the individual, which is the unit and not the cell."<sup>11</sup> For Child, morphogenesis was driven by internal gradients set up by inherited nuclear

and cytoplasmic factors, and responding to external and internal environmental considerations.

If this interpretation that cells are secondary effects rather than causes were right, what causes differentiation and morphogenesis? It cannot simply be genes, since, as Thomas Hunt Morgan liked to remind his colleagues, all the genes seem to be the same in every cell. How, then, can we get difference from the inherited sameness? How does morphogenesis—and with it differentiation—occur? It was the failure to address these questions adequately that kept those most seriously committed to explaining development from seeing genetics or evolution as important for understanding embryology.

#### “EMBRYOLOGY AND ITS RELATIONS”

Ross Harrison agreed with Morgan that the answer could not be in the genes, and that this was a central problem of biology. In his 1936 speech to the American Association for the Advancement of Science, Harrison noted: “The prestige of success enjoyed by the gene theory might easily become a hindrance to the understanding of development by directing our attention solely to the genom.” Instead, Harrison insisted that “cell movements, differentiation, and in fact all developmental processes are actually effected by the cytoplasm.”<sup>12</sup> They are effected through the cytoplasm—that is, through local action and particularly through local chemical action—and not through the action of some remote and distance-inherited material or purported information.

Harrison suggested that morphogenesis involves a sort of crystallization process that brings chemical compositions of parts and differentiation through the relations among them.<sup>13</sup> He lamented that excessive enthusiasm about Hans Spemann’s “organizer” had distracted embryologists, as genetics had, and had led them to ignore other important factors in development, especially relations among differentiating parts. Yet embryologists were making great progress by looking at the microstructures of eggs, cells, and developing organic parts. Harrison acknowledged that he had questions with few answers, but that it was very important to work hard—and to continue working hard, using proper scientific experimental analysis—on the hard questions, and not to give in to temptations to unwarranted theorizing or guesswork.

Harrison quoted Max Planck to the effect that “We must never forget that ideas devoid of a clear meaning frequently gave the strongest impulse to further development of science . . . they [can] give rise to

thought, for they show clearly that in science as elsewhere fortune favors the brave."<sup>14</sup> The brave included Joseph Needham, with his ideas about chemical morphogenesis through the internal chemical relations of parts and "morphogenetic hormones,"<sup>15</sup> or those offering the mathematical, mechanical models that Evelyn Fox Keller discusses in her book *Making Sense of Life*.<sup>16</sup>

As J. H. Woodger had pointed out earlier, it is especially important to have some brave theorizers or big thinkers when the data and details pile up and threaten to overwhelm our thinking: "The continual heaping up of data is worse than useless if interpretation does not keep pace with it. In biology, this is all the more deplorable because it leads us to slur over what is characteristically biological in order to reach hypothetical 'causes.'"<sup>17</sup>

#### MORPHOGENESIS

For Harrison, and for many others, biological form and the apparent "organization" of individuals were "characteristically biological" and ought not to be slurred over, no matter how difficult to address. Among the many making scientific sense of the emergence and establishment of form in later decades was another brave man, John Tyler Bonner. Bonner's *Morphogenesis: An Essay on Development* appeared in 1952, roughly a half-century after Wilson's *Cell* and roughly a half-century before our current enthusiasm for Evo-Devo.<sup>18</sup>

Yale biologist John Spangler Nicholas reviewed Bonner's book and wrote that "Bonner deserves our thanks. He makes no pretense of giving the answer to the problem of form. He has, however, placed it succinctly before us and has focused attention on what we do not know but need to know before a more definite answer can be given to the significant factors underlying the formative pattern of development which results in the specific form of the organism."<sup>19</sup>

We still owe Bonner our thanks for keeping a focus on form and pattern, on morphogenesis and internal relations, when so many were rushing to embrace the "modern synthesis" of the evolutionists, or the molecular interpretations brought by DNA and genetics. As they took up other methods and other questions, they set aside and often forgot about scientific efforts to understand these fundamental life processes. Bonner has continued to keep our eye on the "problem of form," especially the question of how form emerges, and, within that problem, on questions about the role of cells and their internal relations in development and



differentiation. Bonner retained his focus on the mechanisms and proximate time frame of individual development, while also remaining mindful of the longer time scale and causal shaping of form by evolution. He sought to bring *devo* and *evo* together through the study of morphogenesis.

Bonner wrote his *Morphogenesis* in Woods Hole, Massachusetts, at the Marine Biological Laboratory. He worked in the library there, and in Edwin Grant Conklin's laboratory, writing the sort of general, problem-oriented, big-picture book that young biologists at places such as Princeton can no longer afford to write if they hope to remain on a normal track toward tenure. Bonner tackled the tough problems and tried to bring order to our thinking about them. He tried to weigh the range of theories, data, and worries without succumbing prematurely to any one interpretation or to giving up trying to address the big questions.

Bonner set out to consider the "problem of form" in terms of three things—growth, morphogenetic movements, and differentiation. He sought to avoid the "treacherously hypothetical" by including a full range of organisms—animals, plants, and microbes: slime molds (especially slime molds), *Hydra*, sponges, frogs, and ants.

First came growth and the patterns of growth. Growth is a basic process and does not bring about any morphogenesis or differentiation by itself, but it makes these processes possible. Next come the patterns of morphogenetic movements. These are like the actions of a sculptor who has already added the clay, through growth, and now shapes it. But it is the cells, rather than the sculptor, doing the shaping in the biological organism. So, yes, cells are inevitably involved, but the movement comes through groups of cells or cell interactions as they move. Morphogenetic movements lead to differentiation, by which Bonner means differences in parts because of the chemical composition and also because of the positions and needs of the whole organism.

Differentiation very clearly does *not* result from parceling out of genetic information, as Roux and his later genetic determinist followers had suggested. At least for all practical purposes this is true, Bonner was sure. Rather, differentiation can be caused by position in the organism. Bonner cited Henry van Peters Wilson's research on sponges, in which Wilson had separated (disaggregated) cells to discover whether they were all the same or were already differentiated at various points throughout development.<sup>20</sup> That research and other studies on *Hydra*, slime molds, sea urchins, and other organisms showed that cells and groups of cells might be differentiated, but could be redifferentiated by changing position. That

is, the role of the individual cell could be influenced by the needs of the whole organism.

There seemed to be internal diffusion gradients and some organized microstructure that functioned as "ultrastructure" to guide the "regulation" of the whole. Bonner saw this regulation of the whole, with its responsiveness to changing conditions and to the internal and external environments, as an important driver for differentiation. Organisms can have gradients or fields that affect the "patterns of differentiation," and these play out in different ways in different organisms. The differentiation and morphogenetic processes of different organisms can be different not just because the organism started differently, or has different heredity, but also because of the particular interactions within each whole.

Bonner clearly saw differentiation as a problem of the whole, living organism and the way the parts interact. Understanding this is a challenge, however, and Bonner was brave enough to insist that we not ignore it. The question was how to make sense of the "wholeness" or "organization." As Bonner put it, we must not "forget the most important fact that the organism always differentiates as a whole, and that the particular cause of the differentiation of a part is determined by its position with respect to the whole."<sup>21</sup> There is indeed a wholeness that begins with "localization of differences in different parts of the egg or sperm."<sup>22</sup> That is, there is some initial structure that provides a starting point, as E. B. Wilson had suggested, though it is not a "promorphological" delineation in Wilson's sense or any sort of preformation or predetermination of form.

Nonetheless, Bonner cautioned that we should not be "overly impressed by the [special] significance of this wholeness."<sup>23</sup> The wholeness is not mysterious, as some would suggest, but is a product of interactions and microprocesses within the context of the initial germ cell that is itself influenced by natural selection. Organisms inherit the tendency for cells "to migrate and [to] respond to the substances given off by the other cells," through a sort of chemotaxis and interactions among the cells.

Bonner constantly tries to find a balance among microexplanations of chemical and mechanical causation, and also attempts to preserve wholeness and a sense of integrated life—whatever that might mean and even when that might seem vague and mushy. It is precisely this grappling with making sense of form and his unwillingness to fall into reductionistic geneticism or to succumb to mysterious organicism that is appealing. Bonner wrote, "There must be some factor which transcends the cell wall and unifies this cottony mass, but what this factor or factors might be is another matter. Already we have come to the deep-rooted sign of the least

understood problem of this sort of development that makes us say that growth and development is a problem. Really it is many problems; but this one, the unification of great masses of protoplasm into a oneness, a wholeness, has us more mystified than others."<sup>24</sup>

Yet, "More than anything else, this . . . making of a perfect whole from a small bit of a previous whole, is what seems marvelous to us, so much so that we become, I think, psychologically affected and troubled, and cannot believe that a solution to such a problem would be anything but difficult, if not impossible."<sup>25</sup> Yet difficult—or even apparently impossible—as this "problem of development" might seem, Bonner tried, and felt it vitally important to continue trying.

Surely Bonner's drawing on evidence from diverse organisms and trying to bring together different kinds of evidence shaped his thinking in important ways. It kept his focus on the bigger problems, even when they were difficult to solve. Model, select organisms can work to solve particular problems, but would not have served Bonner's purposes unless he made the a priori assumption that all organisms differentiate in the same way. And he did not make that assumption, that the "evo" affects the "devo." This brings us back to cells.

Each germ cell has an internal arrangement, and every cell division brings new arrangements. The particularities of growth and morphogenetic movements, with regulatory responses to the conditions and needs of the organism, bring differentiation—and the material basis for the mechanisms of morphogenesis. But each set of opportunities and pattern of responses is shaped by evolution as well, and each represents a set of adaptations. For, as Bonner put it: "In each case, there is a . . . unity which comes with the structure, and this we have related to the advantage of functional wholes, for without being functionally cohesive they would either not live, or at least not withstand the rigors of natural selection. The very fact that they are wholes must be adaptively advantageous, and natural selection, by differential reproduction, would tend to keep them that way."<sup>26</sup> Evolution and development, long and short time scales: all there to be studied in cells through morphogenesis.

## CONCLUSION

In sum, for Bonner cells are not the cause of morphogenesis (as Wilson and Roux had suggested in their very different ways). Nor are they mere epiphenomena (or shells on the shore, as Huxley and Whitman held). Rather, cells and cell interactions are primary players in the processes that

shape organisms, but the processes are also influenced by genetics and by evolutionary adaptations. Bonner just was not sure how, though he felt it important to try to understand.

Bonner ended his book by declaring that if anyone comes up with a microstructural account of the causes of morphogenesis, "the world will acclaim his discovery as a most satisfying explanation and a great advancement in science."<sup>27</sup> But in 1952, it was clear that Bonner did not expect such an account anytime soon.

Compare Bonner's tone with Wilson's ending of his book in 1896, Wilson wrote:

I can only express my conviction that the magnitude of the problem of development . . . has been underestimated. . . . Yet the splendid achievements of cell-research in the past twenty years stand as the promise of its possibilities for the future, and we need set no limits to its advance. . . . We cannot foretell its future triumphs, nor can we repress the hope that step by step the way may yet be opened to our understanding of inheritance and development.<sup>28</sup>

For Bonner a half-century later, the problem of development remained, and would not be solved through cell research alone or even primarily. Today, another half-century later, we are swimming in data, yet the fundamental biological problems of morphogenesis and development of form remain as challenging and exciting as ever—in new ways. It is important not to lose sight of the cells or of morphogenesis as we embrace Evo-Devo enthusiasm for other levels of analysis. Joining evo (and with it molecular genetics) with devo surely offers the greatest promise for achieving the greatest advances in understanding the problem of development that Wilson sought, and also in giving us the microstructural account of development that Bonner would still like to see.

#### NOTES

1. J. P. Trinkaus, personal discussion at the Marine Biological Laboratory, Woods Hole, Massachusetts. He thought this was a silly question that missed the point that, as he saw it, developmental biology had been considered a success even when it was not as much advertised or heralded as genetics or evolution. There is, he noted, no Ernst Mayr for developmental biology, and he clearly did not think that was a bad thing.

2. Nägeli, 1884, translated and quoted by Harrison, 1937, p. 371.

3. Harrison, 1937, p. 371.

4. Harrison, 1925.

5. Harrison, 1940, p. 77.
6. E. B. Wilson, 1896, pp. 264-265.
7. Dröscher.
8. Huxley, 1853, p. 243. For discussion, see Richmond, 2000.
9. Whitman, 1893.
10. See Lillie, 1911.
11. Child, 1900, p. 265. Also see Child, 1915.
12. Harrison, 1937, p. 372.
13. Haraway, 1976.
14. Planck, 1936, p. 112, cited in Harrison, 1937, p. 374.
15. See Haraway, 1976, chap. 4, for further discussion.
16. Keller, 2002.
17. Woodger, 1929, p. 318.
18. Bonner, 1952.
19. Nicholas, 1952, p. 492.
20. H. v. P. Wilson, 1907.
21. Bonner, 1952, p. 260.
22. *Ibid.*, p. 201.
23. *Ibid.*, p. 268.
24. *Ibid.*, p. 100.
25. *Ibid.*, p. 241.
26. *Ibid.*, p. 268.
27. *Ibid.*, p. 276.
28. E. B. Wilson, 1896, p. 330.

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