From Embryology to Evo-Devo: A History of Developmental Evolution

edited by Manfred D. Laubichler and Jane Maienschein

The MIT Press
Cambridge, Massachusetts
London, England

1

Introduction

Manfred D. Laubichler and Jane Maienschein

Ontogeny and Phylogeny of the Volume

Each summer, starting in 1989, the Dibner Institute has offered a seminar in the history of biology at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts. Each year the seminar, founded by Garland Allen and Jane Maienschein, and currently coordinated by John Beatty, James Collins, and Jane Maienschein, is devoted to a different topic in the history of biology. As a rule, the Dibner Seminars in the History of Biology are organized by the coordinators in collaboration with experts in the respective topics and bring together a group of students and faculty for a week of intense discussions. In 2001 the Dibner Seminar "From Embryology to Evo-Devo (Evolutionary Developmental Biology)," organized by Manfred Laubichler and Jane Maienschein, focused on the history of the relations between embryology and evolution. Among the participants exploring the rich and diverse history of the subject were noted historians, philosophers, sociologists, and biologists, including John Tyler Bonner, Evelyn Fox Keller, Rudolf Raff, Sahorta Sarkar, and most of the authors in this volume.

The results of the week-long discussions at the Marine Biological Laboratory encouraged the organizers to convene another meeting with the specific goal of producing a tightly integrated edited volume. The Dibner Institute and its director, George Smith, agreed to continue to fund this project, and in October 2002, Manfred Laubichler and Jane Maienschein convened the Dibner Institute workshop "From Embryology to Evo-Devo." Most of the workshop participants had attended the Woods Hole seminar; a few of the seminar participants were unable to come, and others, such as Everett Mendelsohn and George Smith, joined the group.

The goal of the Dibner Institute workshop was not only further discussion of the work of the participants at the Woods Hole seminar in preparation for the planned volume, but also to have present three of the

leading scientists in the current field of evolutionary developmental biology—Brian Hall, Gerd Müller, and Günter Wagner, all of whom have expressed an interest in the history of their discipline. The rationale for inviting scientists to a workshop devoted to the history of science was to break down disciplinary boundaries and to take advantage of diverse perspectives. This was the first time that scientists had participated in a Dibner Institute workshop other than as the subject for inquiry, and it was, by all accounts, a tremendously successful experience.

Discussions at the workshop benefited greatly from these new perspectives, and when Brian Hall, Gerd Müller, Günter Wagner, and Everett Mendelsohn presented their reflections on the papers and discussions, new avenues for thinking about the history of the relations between development and evolution emerged. The authors subsequently revised their papers in light of these ideas and suggestions, and our commentators graciously agreed to produce additional chapters, which accurately reflect the discussion at the workshop.

The initial seminar's venue at the MBL was a fortuitous match for the topic "From Embryology to Evo-Devo." After its founding in 1888, the MBL had been one of the premier research sites for embryology, physiology, *Entwicklungsmechanik,* and comparative biology and evolutionary biology, as well as a key meeting place for many of the leading scientists of those days. Many discussions about the relations between individual development (ontogeny) and evolutionary transformations (phylogeny) took place in this "marketplace of ideas," where people gathered at the Friday evening lectures to hear about the latest discoveries or theories, and continued their discussion in their labs, during collecting trips, and at (frequent) social events. From the beginning of the MBL, embryology has been one of the core areas of research and education.[1]

The seminar's topic, "From Embryology to Evo-Devo," proved to be extremely timely. The major events in biology during the 1990s, such as the announcement of Dolly, the first cloned mammal; the emerging debates about the therapeutic potential of stem cells (and the resulting regulatory and policy confusions); and the completion of the first sequence of the human genome marked the beginning of a new era in biological research. Development (embryology) clearly was to become a major focus in this "postgenomic" period in the history of biology. Focusing the attention of historians of biology on the largely neglected history of twentieth-century embryology therefore was appropriate, even more so because the seminar emphasized one particular aspect of this history, the discussions about the relations between ontogeny and phylogeny.

For many (historians as well as biologists), Ernst Haeckel's biogenetic law, "Ontogeny recapitulates phylogeny," still represents the canonical formulation of this relationship. The fact that even though it has long been disproven, at least in its radical form, the biogenetic law still discussed in textbooks is, at the very least, a testament to its intuitive appeal, if not to a more fundamental recognition that these two temporal processes in biology are in some way linked.

Exploring the various connections between ontogeny and phylogeny is also at the heart of a newly emerging discipline, evolutionary developmental biology. The field is often heralded as the new synthesis of developmental and evolutionary biology, especially since developmental biology (embryology) was not prominently featured in the last evolutionary synthesis, which centered more on genetics, systematics, and paleontology.[2] By the late 1990s evolutionary developmental biology had all the markings of a new scientific discipline. Two new journals were specifically devoted to the field: *Evolution & Development* and an independent section of the *Journal of Experimental Zoology, titled Molecular and Developmental Evolution* (now *JEZ Part B: Molecular and Developmental Biology).* In addition, the oldest journal in the field of experimental embryology (*Entwicklungsmechanik*)—*Roux's Archiv für Entwicklungsmechanik der Organismen*, founded in 1890—has been renamed *Genes, Development, and Evolution,* another reflection of the changed focus in developmental biology. Among granting agencies, the National Science Foundation has established a specific panel devoted to the "evolution of developmental mechanisms"; and professional societies, such as the Society for Integrative and Comparative Biology (formerly American Society of Zoologists), now have specific sections for evolutionary developmental biology. In short, by the time of the 2001 Dibner Seminar in the History of Biology, evolutionary developmental biology (Evo-Devo) had arrived, at least institutionally. As a consequence, the focus of developmental biology has been broadened substantially.

This did not happen overnight. Rather, the relations between development and evolution have been the subject of renewed, intense, and controversial discussions since the 1970s. Recognizing that these developments are an interesting episode in the recent history of biology, one that also had the potential to reconfigure the interpretation of the history of twentieth-century biology, the organizers decided to devote a Dibner Seminar in the History of Biology to this topic. It soon became obvious that while quite a bit was known about the late nineteenth-century discussions on the biogenetic law, comparative embryology,

Entwicklungsmechanik, and morphogenesis—and several participants in the recent emergence of evolutionary developmental biology had begun to document these events—next to nothing was known of what happened to these questions in the period between the 1920s and the 1970s. This historiographical vacuum provided the stimulus for expanding the topic of the seminar and focusing on a longer period, taking us "From Embryology to Evo-Devo."

Some readers misread the message and jumped to the conclusion that "from" implied direct causal change. For them, "From Embryology to Evo-Devo" seemed to imply a direct lineage of problems, ignoring the inherent complexity of the history. For others, the title evoked the image of a linear and gradual development, as if embryology had become Evo-Devo. Neither interpretation reflects either the organizers' intentions or the actual discussions at the seminar and the workshop. In these contexts embryology and Evo-Devo are merely historical markers that stand for the late nineteenth and the early twenty-first century, respectively. Exploring what happened in between was the goal of both events. Taken together, the contributions in this volume provide a first map of this extremely rich and fascinating part of the history of twentieth-century biology.

Several common themes emerged in the context of these discussions.

1. Development, as one of the central processes as well as one of the theoretical concepts of biology, has continuously been the focus of both empirical and conceptual attention. This in itself is not surprising. However, throughout the historical period covered here development has been studied and interpreted from different experimental angles and the results of these studies have been incorporated into often radically different conceptual systems, ranging from traditional comparative studies of embryology to molecular genetics and computational analysis. Studying the history "From Embryology to Evo-Devo" thus leads one to appreciate the diversity of conceptual interpretations and experimental strategies that characterizes twentieth century biology.

2. Throughout the twentieth century, multiple traditions of developmental biology coexisted; some of them are defined by their experimental strategies, others by their explanatory reference frames. In addition, different local and national traditions have persisted until the present day. These traditions are also reflected in different emphases within current evolutionary developmental biology.

3. Technology played an important role in the history of twentieth-century developmental biology, as it did in the emergence of *Entwicklungsmechanik* in the late nineteenth century (see especially Hall and Gilbert, this volume). In particular with respect to the question of ontogeny and phylogeny, the lack

of an adequate experimental approach is notable during several decades of the twentieth century.

4. Development, even more than physiology, has provided the foundation for an organism-centered perspective in biology. Even the most successful and in a sense most radical, molecular explanations of development, such as reaction diffusion models, lead to a concept, such as positional information, that implicitly refers to the three- and four-dimensional properties of organisms.

5. While the explanatory reference frames for development and evolution are different, roughly reflecting what Ernst Mayr calls proximate and ultimate explanations, at several times since the mid-1850s development has been considered essential to explanations of the patterns of phenotypic evolution. For example, in the context of evolutionary morphology, embryology provided a possible inference about genealogical connections between species (phylogeny); and in the context of developmental physiology and physiological genetics, the developmental and cellular context was considered essential to any mechanistic explanation of the evolution of phenotypes; and currently developmental mechanisms are implicated in discussions about the genotype-phenotype map, the limits of adaptation, and the origin of evolutionary novelties, among other things (see also chapters 15 and 16 in this volume).

6. All these observations contribute to a growing skepticism about what the current emphasis on a "synthesis" of evolutionary and developmental biology actually entails. On the one hand, current evolutionary developmental biology includes more than just developmental and evolutionary biology; on the other hand, it is still unclear whether the Evo-Devo focus can succeed in providing new perspectives that go beyond what would be possible within other explanatory schemata (see especially chapters 15 and 16 in this volume).

Of late, writing the history of science with a long-range perspective in order to get at the underlying persisting traditions, and thereby to be able to recognize and interpret significant patterns of change, has become unfashionable. Recent historiography of science has focused more on the local, immediate, contingent, and particular aspects of the scientific enterprise. The history of science has also matured as an academic discipline in its own right, and no longer sees its primary function as contributing to commemorative occasions and providing a "grand narrative of scientific progress" suitable for the first few pages of introductory textbooks. This new orientation in the historiography of science has led to important new insights, but it has also contributed to a growing alienation between the communities of historians of science and scientists.

In this volume with its long perspectives, we hope to bridge this unfortunate gap by including biologists as well as philosophers and

sociologists. Our focus on a period of almost 150 years and our emphasis on a specific scientific problem—the relationship between ontogeny and phylogeny—allow us to analyze simultaneously continuities and transformations as well as discontinuities and novelties. Indeed, one would not be possible without the other, especially in areas of the history of biology where we do not have a commonly known, detailed historical narrative of their development. The chapters in this volume thus emphasize both the continuity of the general problem of defining the relationship between ontogeny and phylogeny, and the diversity of approaches, technologies, and concepts as well as the continuous transformation of the both the question and the scientific disciplines.

Finally, we want to mention one (tongue-in-cheek) observation that emerged during the workshop discussions: that the history of embryology and developmental biology has certain structural affinities with the individual and the phylogenetic history of organisms, and maybe this explains, in part, why among biologists, evolutionary and developmental biologists show the greatest interest in the history of their profession.

STRUCTURE OF THIS VOLUME

This volume collects the papers that were discussed at the 2002 Dibner Institute workshop. In addition, it includes a paper by Scott Gilbert that was presented at the 2001 Dibner Seminar in the History of Biology but not discussed at the workshop and a paper by Stuart Newman that the editors solicited after hearing a version presented at an international meeting.

Following the conceptual and epistemological introduction by Manfred Laubichler, the chapters are organized in three sections: part I, Ontogeny and Phylogeny in Early Twentieth-Century Biology; part II, Roots and Problems of Evolutionary Developmental Biology; and part III, Reflections. This structure reflects the course of the discussions at the Dibner Institute workshop and also broadly represents the chronological sequence of events "From Embryology to Evo-Devo." Everett Mendelsohn's observations were helpful in integrating the discussions at the Dibner Institute workshop and are reflected in several of the papers.

In chapter 2, Manfred Laubichler briefly discusses some of the conceptual and historiographic problems associated with writing the history of evolutionary developmental biology. He argues that the many transformations and discontinuities in that history are best understood if they are seen in the context of a specific scientific problem: defining the relations

and connections between ontogeny and phylogeny. As a historical "object" of analysis, or an epistemic thing, this scientific problem has enough continuity that it can serve as a narrative anchor for telling the history "From Embryology to Evo-Devo." The conceptual changes associated with this scientific problem are then used to reconstruct the transformations of the epistemic space associated with the history of evolutionary developmental biology.

The chapters in part I of the volume provide a fresh perspective on events in the history of early twentieth-century embryology and developmental genetics. Fred Churchill discusses the fate of Haeckel's biogenetic law and analyzes several reformulations in major textbooks of embryology during the late nineteenth and early twentieth centuries. The picture that emerges is less black-and-white than many previous characterizations of the biogenetic law, and Churchill opens up new venues for analyzing the "internal critique" and reformulations of the biogenetic law, thus allowing for a careful reconstruction of the epistemic space of early debates about ontogeny and phylogeny. Stuart Newman's chapter focuses on William Bateson and his ideas about the physical determination of organic forms. Newman discusses Bateson's "vibratory theory," an attempt to incorporate physical principles (so-called Chladni patterns) into explanations of segmentation and repetitive pattern formation. Newman situates Bateson's ideas both within turn-of-the-century discussions about the nature of variation and inheritance and within the early twenty-first-century context of system biology. Analyzing the conceptual repertoire of both Bateson and modern system biologists, Newman argues for a broadening of the conceptual (epistemic) framework of explanations of development.

Jane Maienschein's contribution introduces cells and the process of morphogenesis into the discussions about the history of Evo-Devo. She emphasizes the role that cells played as an object of study and, in the form of slime molds in the work of John Tyler Bonner, also as model system for morphogenesis. Maienschein's chapter continues Newman's argument (via Bateson) that the physical and cellular characteristics of developing organisms are an important part of explanations of development.

Where Newman and Maienschein focus on specific objects and morphogenetic processes, Garland Allen takes a more conceptual and dynamic perspective. He presents a detailed account of the dialectics between analytic and synthetic explanations of development. In the interplay between these opposite yet complementary explanations of organic processes, Allen sees the organizing epistemological theme for the history

of evolutionary developmental biology. Far from being abstract, his proposal provides a framework for the inclusion of many of the more detailed historical case studies.

Marsha Richmond's study of Richard Goldschmidt's role in uniting development and evolution concludes part I. During the 1920 and 1930s Goldschmidt, who remains an enigma to many even today, developed his idiosyncratic synthesis of ontogeny and phylogeny. Working with a different model organism (*Lymantria*) and beginning with a physiological and genetic account of sex determination, he developed a theory of the gene as a physiological agent. While during his lifetime many details of gene action remained beyond experimental reach, Goldschmidt nevertheless developed a conceptual framework that connected development, genetics, and evolution during a period when the prevailing attitude in science was to keep these domains apart.

Even though the chapters in part I revisit previously studied territory, each author has discovered new interpretative angles as well as new materials. In light of the theme of this volume, the history of the relations between ontogeny and phylogeny, they provide a fresh perspective on the history of embryology, genetics, and evolutionary biology in the first decades of the twentieth century.

The chapters in part II are more diverse. The topics covered here range from the history of comparative embryology in America and morphological and paleontological perspectives in the history of evolutionary developmental biology to a study of how developmental processes have been visually represented, a philosophical-historical analysis of research styles in embryology and genetics, a discussion of recent attempts to integrate development and evolution and the conceptual problems associated with these issues, and, finally, a philosophical-sociological analysis of research styles and conceptual change in biological research during the last few decades of the twentieth century. Most of these chapters focus on events during the period (1920s to the 1970s) that has not received much attention from historians of biology, and all of them provide perspectives that add dimensions to the problem of defining the relations between ontology and phylogeny.

John Wourms's study of comparative embryology in the American context brings to light an almost unknown chapter in the history of biology, especially with regard to the period that he includes. Wourms reminds us that even the most sophisticated conceptual schemata need to be grounded in empirical data, and that in the case of ontogeny and phylogeny, comparative embryology, in both a morphological and a

systematic context, provides many of these data. Since during most periods in the history of biology, comparative embryology was not part of mainstream research, we have to look at different institutional settings (such as fisheries) to find the continuity of the work.

Alan Love's chapter similarly focuses on mostly neglected parts of the history of twentieth-century biology. His discussion of morphological and paleontological research by Dwight Davis and William Gregory is informed by the recognition that present-day evolutionary developmental biology is more than just a "synthesis" of development and evolution; rather, it involves the integration of various research traditions, including morphology and paleontology. As Love argues, it is in these fields which have not been part of mainstream twentieth-century biology that we find a closer continuity of the late nineteenth-century problem of ontogeny and phylogeny. His chapter thus opens an important new perspective on the history of midtwentieth-century biology.

William Wimsatt places attention on areas in the history of biology that have not received much attention from historians of biology, even though they are now becoming part of the canonical history of present-day evolutionary developmental biology. He discusses the problem of so-called internal factors of evolution, the idea that the details of the developing organismal system can have a major impact on the course of evolution. Internal factors of evolution are the prime candidates for a mechanistic integration of developmental processes into a theory of phenotypic evolution, and have received considerable attention since the mid-1970s. Wimsatt focuses specifically on the work of Rupert Riedl and Wallace Arthur, and concludes his historical analysis with a brief discussion of his own work on generative entrenchment, which is one of several attempts to model internal factors of evolution.

Scott Gilbert discusses a current problem in developmental biology that has a long history. Since development is a complex process, visual representations of developmental transformations have always been a major conceptual as well as pedagogical tool. Gilbert argues that there is a conceptual continuity between late nineteenth- and early twentieth-century attempts to trace the fate of cells in the developing embryo and modern approaches designed to establish gene expression patterns. He also states that one important aspect of the mapping program in the context of evolutionary developmental biology is to connect new (molecular) evidence with old (traditional) knowledge in embryology. In ways similar to Goethe's *Faust*, a major problem of current molecular approaches in developmental genetics is to reintegrate new molecular data into an organismal whole.

History, as a repository of knowledge, thus becomes an integral part of cutting-edge research in evolutionary developmental biology.

In his chapter James Griesemer uses a well-documented historical case study, the split between embryology and Morgan-style transmission genetics at the beginning of the twentieth century, to develop a philosophical argument about an important aspect of scientific representations and explanations of complex processes. He argues that in all explanations of complex processes, certain elements will necessarily be foregrounded while other will be relegated to the background. His analysis of the consequences of this dynamic contains several important lessons for all those—historians, philosophers, and biologists—who emphasize the synthetic character of modern evolutionary developmental biology.

The final chapter in part II presents an analytic perspective complementary to the ones proposed by Laubichler and Griesemer. Elihu Gerson focuses on the long-term pattern of relationships among lines of research in comparative biology by providing a framework for the inclusion of institutional and technological factors, what he calls a style of research. These factors cannot be separated from the epistemological concerns raised by Laubichler and Griesemer, so that Gerson's chapter (which includes a discussion of the effects of rationalization of work in both science and society) suggests further explorations of the interplay of contextual and contingent factors with epistemological factors in the history of evolutionary developmental biology.

The chapters in part III collect the reflective comments by Brian Hall, Gerd Müller, and Günter Wagner. These papers are expanded versions of the commentaries that these scientists and scholars gave after listening to (and participating in) two days of discussions at the workshop. In his chapter, Brian Hall, author of the first modern textbook of evolutionary developmental biology, who has a "second" career as a historian of developmental biology, reminds us about the many elements that contribute to the Modern Synthesis of Evo-Devo. In Hall's view, Evo-Devo is, and always has been, a model of an interdisciplinary science. To illustrate his point, Hall provides a few historical case studies that demonstrate how the problem of ontogeny and phylogeny has always been approached from a variety of conceptual perspectives and how specific institutions, such as the Naples Zoological Station, and instruments and their associated experimental practices—specifically the Cambridge Instrument Company and the automatic microtome—helped to establish an interdisciplinary environment. Hall's lessons are clear: any reconstruction of the history of evolutionary developmental biology will have to connect questions of

conceptual integration with local issues of institutional and technological changes.

In his chapter, Gerd Müller takes the historical lessons of this workshop and volume and applies them to his analysis of the future of the field. His chapter is also a reflection of what he identifies as a phenomenon peculiar to the Evo-Devo discourse: the emphasis on metatheoretical reflections within Evo-Devo and the close collaboration of philosophers, historians, and biologists in shaping the future agenda of the field. He presents six memos that characterize the distinctiveness the Evo-Devo discipline. These memos, which capture the breadth of the Evo-Devo research agenda, are a fitting conclusion as well as a new beginning for the historical work presented in this volume. They show what happened "From Embryology to Evo-Devo," and they also invite the reader, as they did the workshop participants, to look back at the fascinating complexities of this history and ask: How did we get there? And what does it all mean?

Günter Wagner's comments move us forward by addressing the present state of evolutionary developmental biology, or developmental evolution (Devo-Evo), as he refers to it. This nomenclature reflects the internal disunity of present-day evolutionary developmental biology. Currently, several different questions are pursued in the context of this overarching synthesis. Wagner uses an episode in the history of biology—the decline of evolutionary morphology at the beginning of the twentieth century—to warn of the dire consequences for a field that fails to agree on standards of evidence to evaluate its results and interpretations. He goes on to suggest that if Evo-Devo (Devo-Evo) is currently entering its "academic phase," it will have to establish such evidentiary standards. Wagner then briefly sketches how such standards can be developed for evolutionary innovations.

ACKNOWLEDGMENTS

This project would not have come to fruition without the support of the Dibner Institute. Not only did the project take place through the auspices of the Dibner History of Biology Seminar at the MBL, and through a Dibner workshop at the wonderful Institute building in Cambridge, Massachusetts. In addition, the staff—including Jed Buchwald, Evelyn Simha, George Smith, and Carla Chrisfeld—provided vital support at critical points. The participants in both the seminar and the workshop provided the intellectual substance for the project. And the voices of those who had

been at the seminar but could not join us at the workshop were heard as each participant responded to the substance of the seminar. This was truly a collaborative project, and each participant has an intellectual property interest in the product. Finally, George Smith encouraged us to pursue the publication of the collection and patiently waited for revision after revision during the preparation. His enthusiastic encouragement makes this, as well as other recent Dibner Institute volumes, possible.

NOTES

1. Jane Maienschein and Ruth Davis, *100 Years Exploring Life, 1888–1988. The Marine Biological Laboratory at Woods Hole* (Boston: Jones and Bartlett, 1989); Jane Maienschein, ed., *Defining Biology: Lectures from the 1890s* (Cambridge, Mass.: Harvard University Press, 1986).

2. Ernst Mayr and William B. Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge, Mass.: Harvard University Press, 1980).