Book Review

How Development Changes Evolution: Conceptual and Historical Issues in Evolutionary Developmental Biology*

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A review of *Integrating Evolution and Development: From Theory to Practice*, edited by Roger Sansom and Robert N. Brandon, MIT Press, Cambridge, MA: 2007 and *From Embryology to Evo-Devo: A History of Developmental Evolution*, edited by Manfred D. Laubichler and Jane Maienschein, MIT Press, Cambridge, MA: 2007.

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Evolution and development are closely connected, being two elements of one process. However, such a connection was not reflected in mainstream biological thought of the major part of the twentieth century, which was dominated by the Modern Synthesis of the 30s and 40s. Indeed, development was considered irrelevant for evolutionary explanations[1].

It was not always so, however. At the end of the 19th century, the likes of Ernst Haeckel, Francis Balfour or Walter Garstang saw the two processes as interrelated: Haeckel's biogenetic law, which stated that ontogeny recapitulates phylogeny, is a well-known example (Hall 2000).

Over the last 25 years this situation has changed. Evolutionary developmental biology (Evo-Devo) is a new and rapidly developing field of biology which focuses on questions in the intersection of evolution and development, revisiting old problems under the light of recent discoveries, most prominently perhaps those of developmental genetics. Evo-Devo has been seen by many as a potential synthesis of evolutionary and developmental biology.

This synthesis is the topic of the books reviewed here. The first, *(Integrating Evolution and Development*, edited by Roger Sansom and Robert Brandon), with contributors from both the fields of biology and philosophy of biology, is a collection of papers on conceptual issues concerning the attempted synthesis, while the second (*From Embryology to Evo-Devo*, edited by Manfred Laubichler and Jane Maienschein) is a history of the problem of the relations between ontogeny and phylogeny.

[1] This attitude has survived until recently among evolutionary biologists: "problems concerned with the orderly development of the individual are unrelated to those of the evolution of organisms through time" (Wallace 1986).

Conceptual Issues

The potential of Evo-Devo to unify diverse disciplines and modify neo-Darwinism has recently aroused much interest among biologists and philosophers of biology. Crucially, such an attempt has to confront conceptual issues: how are the diverse approaches of evolutionary and developmental biologists, developed separately during the major part of the previous century, to be synthesized? In particular, how are concepts like developmental constraints and novelties to be integrated into a neo-Darwinian framework? Is it just a matter of filling in some missing details or will such synthesis require a fundamental modification of the conceptual structure of evolutionary theory?

Although showing signs of a successful research program, Evo-Devo currently lacks a unified conceptual structure and a consensus among its practitioners concerning the problems and the methodology of the field (Hall 2000, Gilbert 2003). This lack of unity is reflected in the diverse views concerning the general question how Evo-Devo changes our view of evolution (Sterelny 2000, Robert 2002). According to some scientists, the answer to this question will have to be radical: "Population genetics is destined to change if it is not to become as irrelevant to evolution as Newtonian mechanics is to contemporary physics" (Gilbert et al. 1996: p. 368).

All chapters of *Integrating Evolution and Development* are attempts to make connections between development and evolution by focusing on various crucial concepts, thus purporting to contribute to the ongoing synthesis. As the title of the book indicates, the focus is on practical matters; indeed, here one can find, among others, a model of the genotype-phenotype map, a practically-oriented discussion of the notion of constraints, suggestions for a developmental evolutionary psychology, and a model of cultural evolution. This does not mean, however, that more theoretical discussions are absent: three of the seven chapters focus primarily on more theoretical issues. In the following I will review the main arguments of the chapters and their contributions to Evo-Devo; my main focus will be on the implications of the papers concerning the general question how Evo-Devo modifies our picture of evolution.

The book starts with the historically oriented discussion by Manfred Maienschein and Jane Laubichler, which serves as a good introduction to the conceptual problems of the developmental synthesis. Through brief historical case studies of such central figures as

Ernst Haeckel, August Weismann and T. H. Morgan, the authors describe the rise, at the turn of the century, of independent research programs within biology that led to the break of the nineteenth century conceptual framework in which evolution, development, and inheritance were unified. This process led to the current 'conceptual topology' which separates development from evolution. In the second part of this review we will have the opportunity to see in more detail various aspects of that historical process. For now, note Maienschein's and Laubichler's conclusion that, in order to achieve a unity similar to the 19th century biological thought, a novel conceptual framework is required.

The subsequent chapters attempt to answer to this challenge; they can be divided into two groups: chapters 2 to 5 focus on evo-devo itself, while the two last papers apply evo-devo ideas to other areas, namely evolutionary psychology (chapter 6) and cultural evolution (chapter 7). Here I will be mainly concerned with the former group, leaving for the end some comments on the last chapters.

Is there, then, a challenge posed to neo-Darwinism by attempts at synthesizing development and evolution as discussed in the present book? Much turns, of course, on what we identify as the central features of neo-Darwinian explanations, a task not without difficulties, in view of the changes that Modern Synthesis has undergone since its inception in the 30s. However, a characterization according to which neo-Darwinism is a theory that –given variation, heredity, and differential reproduction- takes natural selection as the most important cause of the fit of organisms to their environments (adaptationism) and defines evolutionary change as changes in gene frequencies in populations[2], is, I think, correct (Robert 2002). Given this general characterization, a variety of unifying scenaria are possible, with varying degrees of divergence from neo-Darwinian theory. Thus, proposed scenaria can be assessed by focusing on the roles of genes as well as on the possible supplementation of selection with other factors affecting evolutionary change.

Opinions vary among scientists about the position of genes in Evo-Devo; some focus on the importance of developmental genetics in the new discipline and argue that genes continue to play a fundamental role, while others disagree, stressing the developmental relevance of, e.g., morphogenetic fields or the self-organizing properties of living tissues.

[2] Although concepts such as genetic drift and developmental constraints have become part and parcel of evolutionary biological research, this does not change this general characterization of neo-Darwinism.

As to adaptationism, some argue that laws of form should be regarded, together with natural selection, an explanation of organismal form. Process structuralism, for example, is a radical position which downplays the role of selection in favor of ahistorical laws of form (Webster and Goodwin 1996). A relevant notion here are *constraints*, which are taken by some to complement natural selection in effecting evolutionary change.

In the second chapter, *The Organismic Systems Approach: Streamlining the Naturalistic Agenda*, biologists Gerd Mueller and Stuart Newman and philosopher Werner Callebaut argue both of these points. In doing so, they develop their own *Organismic Systems Approach* (OSA) to Evo-Devo, contrasting it to neo-Darwinism. Like above, they identify *adaptationism* and *gene-centrism* as the two most central aspects of neo-Darwinian theory. However, they understand gene-centrism rather narrowly, interpreting it along the lines of gene selectionism (Williams 1966, Dawkins 1976). But neo-Darwinism does not have to be interpreted along these lines. A hierarchical view of evolution, for example, as the authors themselves agree, is compatible with neo-Darwinism. So, in asking about the relation between Evo-Devo and neo-Darwinism, it is more interesting to construe neo-Darwinism more broadly, as has been done above.

As the name implies, OSA focuses on the organism as a *complex system*: the authors criticize the notion of a genetic program that guides ontogeny and urge for a causal analysis that takes into consideration epigenetic and environmental interactions, in addition to genetic ones. Such a focus on causal-mechanical processes, the authors argue, will enable us to better understand selection processes, but also explain phenomena of the evolutionary process, such as biased variation, non-adaptive traits and the existence of higher-level organization (body plans), that neo-Darwinism leaves unexplained.

Two of the most important such phenomena are the *origination* of primordial forms and body plans and the generation of *innovations*. According to OSA, much morphological plasticity of organisms derives from the properties of living tissues. It postulates the existence of a pre-mendelian world with no ‘fixed matching’ between genotype and phenotype, where the inherent properties of organisms were enough to produce a variety of forms of multicellular aggregates. By focusing on such generic mechanisms of form generation and the non-linear properties of development they give rise to, OSA attempts to explain incidents of rapid change of form, such as the Cambrian

explosion, which are difficult to explain in a neo-Darwinian framework. Phenotypic polymorphisms (the phenomenon that some organisms, depending on the environment, are able to switch among different forms) are also explained in the same way: they are not evolved adaptations, but due to properties inherent in organisms –they are 'primitive and inevitable' (p. 46).

Except the mechanisms of variation that produce adaptation, OSA recognizes another process, *innovation*, which produces morphological *novelty*[3]. The mechanisms of innovation are different than those of variation: mechanisms responsible for generating novelty include 'new developmental interactions' and the 'redeployment of existing developmental modules at a new location in the embryo' (p. 51). These and other *epigenetic processes* are, according to the authors, the major source of evolutionary novelty.

To sum up, then, the 'self-organizing capacities' and 'reactive potential' (p. 57) of cell and tissue masses have implications on how organisms develop. By focusing on such properties inherent in living matter, OSA can explain various aspects of macroevolution. So, to the extent that biological form has as its cause properties inherent to organisms (prime examples being evolutionary innovations), the "external selectionism paradigm of neo-Darwinism" (ibid.) is complemented by an intrinsic one.

Mueller, Newman and Callebaut provide a good presentation of various Evo-Devo ideas and of its potential to change our picture of the evolutionary process. Moreover, the author's own approach is connected to Newman's and Mueller's own research, and the reader is referred to other work for concrete examples and further theoretical work (for example the evolution of the vertebrate limb in Newman and Mueller (2005)).Yet, they do not specify the exact nature of the synthesis, leaving the kind of the relationship between extrinsic explanations, where the properties of organisms are explained by focusing on their environments, and intrinsic ones, where the most important part of the explanans are properties inherent in organisms, an open question[4]. Two cases can be distinguished here: either the two kinds of explanations have the same explananda, or not. In the latter case,

[3] The authors define a novelty as "a structure that is neither homologous to any structure in the ancestral species nor homonomous to any other structure of the same organism" (p. 50).

[4] I borrow the distinction between extrinsic and intrinsic explanations, which the discussion of the present authors implies, from Godfrey-Smith (1996).

for example, whereas natural selection explains complex adaptation, intrinsic approaches to evolution can take the "order and unity of organic systems" as their prime explananda (Godfrey-Smith 1996: p. 47). The former case, where we have competing explanations, seems more problematic, since one has to decide to what extent each holds.

The discussion in chapter two suggests that the second picture is the true one: OSA, as we have seen, explains phenomena that neo-Darwinism presupposes: the origination of 'mendelian' organisms, as well as the origination of novel traits[5]; it focuses on issues such as integration (the integration of novelties in a functional whole) (p. 56). What this shows, is, I think, that there is no prima facie difficulty for the inclusion of development in evolutionary theory; evo-devo approaches to evolution, to the extent that they focus on questions different than the explanation of complex adaptation, do not require a fundamental modification of neo-Darwinism. However, this proliferation of explananda results in a richer evolutionary theory. Moreover, the possibility that genetic modification follows, rather than being synchronous with, phenotypic evolution -a phenomenon that turns out to be much more common than neo-Darwinists have supposed (West-Eberhard 2003)- suggests that in this Extended Synthesis the role of genes will be not as central as it used to be. This is perhaps a more modest conclusion than the discussion of Mueller, Newman and Callebaut implies, yet it is one that is confirmed also by subsequent chapters.

Frederik Nijhout's chapter is a concrete example that illustrates the above points. Nijhout, a developmental biologist with research in evo-devo problems, shows in a clear and accessible manner how a map between genotype and phenotype can be constructed that does more justice to the non-linear interactions among genes in order to produce a complex trait. His model, with its focus on (some) of the epigenetic interactions taken place in organisms, can be seen as a concrete example within the framework proposed by Mueller, Newman and Callebaut.

The main idea is to describe mathematically the interactions of genes by focusing on gene's products: proteins. For his mathematical model, Nijhout uses *phenotypic surfaces*, a "multidimensional graph of phenotype as a function of genotype" (p. 97). His model is

[5] There are, however, a few cases where OSA and neo-Darwinism offer different explanations, as in the case of polymorphisms or the explanation of the Cambrian explosion mentioned above.

able to illustrate the context-dependency of the effect of a gene on a complex trait and has general application: among the systems with non-linear phenotypic surfaces are biochemical pathways, genetic regulatory networks, and developmental, physiological, or morphological systems in general.

Nijhout uses his model to distinguish between two different modes of evolution, what he calls 'fisherian' and 'waddingtonian' microevolution (both of which can be gradualistic or salutatory). The first involves a change in gene activity and such a mutation is represented by moving to another point on the phenotypic surface. The second corresponds to a change in a developmental mechanism and involves a change in the shape of the surface itself. The second case is the case with the most interest to evo-devo, as it is a way to generate novelty. The model also allows Nijhout to distinguish between *genetic* and *developmental* constraints: due to limited genetic variation, the population is limited on a small region of the surface; developmental constraints arise because, without mutations that change the shape of the surface, the population is constrained by its shape. Thus, 'waddingtonian microevolution' needs to break developmental constraints.

The importance of the chapter lies in that it illustrates a promising way to construct a more realistic genotype-phenotype mapping and mathematically describe such concepts as developmental constraints. However, genes continue here to play a central role, as it is the properties of genes that are of importance. Nijhout's model agrees with what was said earlier about how developmental considerations inform evolutionary explanations: development is used to explain the origin of and limitation on variation, upon which selection acts. The model is thus an instance of an extended evolutionary process, without abandoning radically the neo-Darwinian framework.

As mentioned earlier, developmental constraints provide a reason why development is important for evolution. So, developmental constraints are taken to explain such phenomena as "long-term evolutionary trends, rapid evolutionary change, parallel and convergent evolution, and the origins of higher taxa" (Amundson 1994: p. 573). Constraints bias the course of evolution, limiting the variation available to natural selection. However, a more detailed account of what constraints are and how to test hypotheses about them is a controversial issue among biologists; this uncertainty is reflected in the debate about the relative importance of constraints over natural selection

in affecting evolutionary change. In chapter 4, Gerhard Schlosser attempts to provide answers to these issues.

A difficulty here is whether there can be a clear distinction between constraints and natural selection. Constraints are commonly thought of as focusing on internal factors, whereas natural selection focuses on external ones. But, natural selection has sometimes been thought of as itself a constraint (internal selection). Schlosser's idea is to develop a concept of constraints that allows for external and functional constraints, together with internal and developmental ones, while retaining the distinction between constraints and natural selection.

Schlosser distinguishes between *generative* and *stability* constraints. The former have to do with the states that are reachable for a system after perturbation: for living systems these are the *developmental* constraints, constraints on variation on development that can be generated by existing developmental processes. Some perturbations result in unstable states. Constraints on nondisruptive transformation are *stability* constraints. Since the basic characteristics of living systems are their self-maintenance and reproduction, stability constraints constrain variation that does not result to organisms with these features. This kind of constraints Schlosser calls *functional*.

The author goes on to provide an account of constraints in terms of couplings of constituents in the organism. Different constituents are generatively and functionally coupled to other constituents in various degrees (e.g. limb bones). Environmental factors are also taken into account: there are constraints on "the coevolution of organisms and their abiotic and biotic environment" (e.g. mimesis, mimicry) (p. 133). Schlosser takes pains to explain how we can quantify the degree to which a constituent is constrained by some other. He uses the notion of modularity to provide an 'architecture of constraints': units of constituents strongly interacting with one another and thus constrained by one another are units of evolution; they form modules of evolutionary transformations that can sometimes coincide with modules of development.

The above is an important part of Schlosser's discussion, as it shows how the notion of constraints can be used in practice. I want here however to focus on the relation between constraints and natural selection. Schlosser takes constraints and selection as complementary: for selection to occur there must be different variants with differences in

fitness. The existence of those variants is not explained by the theory. However, what variants will be generated and what their fitness will be can be explained by taking the two kinds of constraints into account. Thus, the author takes constraints as 'boundary conditions' to evolution dynamics. Constraints "define the space of the permissible and probable transformations" that living systems can undergo (p. 126). Explanations invoking constraints and explanations invoking selection processes, explaining different things, are complementary to each other.

I do not see, however, how the characterization of constraints as boundary conditions is correct given the existence of functional constraints. So, say that an embryo fails to exhibit the required self-maintenance and dies early. This situation can be described both as an instance of viability selection and as functional constraints that reduce variation. This threatens to collapse the distinction between constraints and selection.

It is evident from the above discussion that Evo-Devo can lead to an extended evolutionary synthesis, where many aspects of phenotypic evolution will come under the explanatory scope of evolutionary theory. The present chapters offer some concrete ways how this might be done. While denying radical gene-selectionist or adaptationist positions, the types of unification offered here do not, I think, radically modify the neo-Darwinian framework; rather, evolutionary synthesis is enriched with explanations about phenomena not dealt with by previous theories.

Before ending the first part of the review with some comments on cultural evolution, I will very briefly talk about Roger Sansom's and Paul Griffiths well-argued papers. In chapter 5, Sansom advances some adaptationist hypotheses about the evolution of development. Specifically, he focuses on gradual mutation as an adaptation that enhances evolvability. Differences in ways of mutating are *meta-mutations*, and gradual mutation is a *meta-adaptation*. Since gradual mutation is expressed only through more than one generation, it is a multi-generational trait, and so Sansom argues that there is a multigenerational unit of selection, which he calls a *lineage*. Sansom goes on to argue that selection among lineages will favor the trait of having developmental modules with unitary function.

If Sansom is right that natural selection will favor gradual mutation, then how is innovation possible? Sansom argues that strategies other than mutating gradually may be

favoured by selection, such as a hybrid between gradual and drastic mutation (e.g. producing a 'hopeful monster' in every ten generations). Although this is a plausible view, a complete picture has to include the properties of the genetic mechanisms: arguably, a degree of novelty generation is primitive rather than derived. This is compatible with Sansom's position, as he himself acknowledges at the end of his discussion the existence of meta-constraints on meta-adaptations.

Griffiths's paper is the first of two that apply evo-devo ideas to other fields. He is interested on the relevance of development for evolutionary psychology. Evolutionary psychology assumes the 'functional specialization' of the brain: it postulates that selection has favoured a modular structure of the brain because this is the most efficient way for the brain to deal with problems posed by the environment. Griffiths carefully discusses the difference between the mental modules of evolutionary psychology and the developmental and functional modules of evo-devo. He argues that development determines what environmental problems are relevant to an organism and thus ought to be taken into account; he also argues in favor of homology as opposed to adaptive function as a principle of categorization in evolutionary psychology.

Accounts of the evolution of culture do not in general incorporate individual development. Memetics, to cite one example of a theory that has received much public attention lately, yet not one of the most promising approaches to cultural evolution, 'black-boxes' development in a way similar to neo-Darwinism. In the last chapter (which takes up one third of the book), William Wimsatt and James Griesemer apply evo-devo ideas to the evolution of culture. They focus on the cognitive development of individuals to explain how humans learn and modify 'cultural structures'.

A central idea in Wimsatt's and Griesemer's account is the notion of scaffolding: humans become enculturated with the help of various social structures that help agents acquire the relevant skills, which they could not acquire without them. An example is learning in a simplifying context, but in general any social or material structure that facilitates cultural inheritance acts as scaffolding.

Why is development essential to model cultural evolution? Between biological and cultural evolution there are very important differences. For example, cultural evolution involves multiple channels of inheritance, and the units of culture are inherited in a

sequential fashion, with the first elements in the sequence determining what can follow. The notion of scaffolding is particularly important for describing this process. Thus, as the authors stress, in the case of culture development and heredity, as well as selection, are interacting in complex ways with one another.

The authors try to identify the units of cultural evolution by utilizing the notion of generative entrenchment and Griesemer's work on 'reproducers'. I will not here expand further into the details of Wimsatt's and Griesemer's rich and detailed discussion, which sometimes resembles the entangled nature of its subject matter. Perhaps the most important point of the chapter is the realization of the enormous complexity of cultural processes and the impossibility to account for them by simple-minded theories like memetics, as well as the fruitfulness of a developmental perspective in accounting for the evolution of human culture.

Except from the inclusion of a developmental perspective, there is another similarity between Wimsatt's and Griesemer's account and evo-devo ideas: the focus on development, of individuals as well as of cultural structures, artifacts, institutions, behaviours etc., explains cultural evolution in terms of generative properties of development, leaving less space for explanations of cultural evolution in terms of variation and adaptation. Indeed, although the authors speak about a populational perspective that will justify the application of evolutionary explanations in the case of culture, in view of the blurring of the distinction between evolution and development, this does not seem very promising.

Historical Issues

As mentioned in the beginning of this review, the study of the relations between development and evolution is not only a feature of current research in Evo-Devo. Rather, such explanations were pursued systematically in the context of evolutionary embryology in the last decades of the nineteenth century. According to the received view that many biologists but also historians and philosophers of biology accept, the decline of the program of evolutionary embryology followed a period in which, under the dominance of the Modern Synthesis, the study of evolutionary and developmental problems proceeded independently. Only in the last decade new prospects for a synthesis reappeared in the

form of evolutionary developmental biology. The contributors to *From Embryology to Evo-Devo*, edited by Manfred Laubichler and Jane Maienschein, attempt to describe what happened in between. Contrary to the common view, as it emerges from the papers in the book, research and theorizing in the intersection of evolution and development persisted during the twentieth century.

The papers in the book derive from discussions at a seminar at the Marine Biological Laboratory at Woods Hole, Massachusetts and a workshop, both organized by the Dibner Institute. They include 16 papers by historians, philosophers, as well as, significantly, current practitioners of Evo-Devo. As Laubichler and Maienschein explain in their introductory chapter, the book is not intended as a history of Evo-Devo, as though nineteenth century embryology transformed to twenty first century evolutionary developmental biology. Rather, the object of the historical narrative is the problem of the relations between ontogeny and phylogeny itself.

In his useful contribution, Laubichler discusses in detail the historiographic approach of the book, focusing on the relation of the problem of ontogeny and phylogeny with the experimental practices and social organizations, as well as the theoretical context. Indeed, the contributors illuminate various aspects of this history, focusing on theories and concepts as well as scientific instrumentation, institutional and social factors.

The book is important in that it focuses on a topic of which no detailed historical account exists. Although Haeckel's views and evolutionary embryology in general have been the subject of detailed study, the history of research in the intersection of embryology and development in the twentieth century has been neglected, and so for the history of developmental biology. This is not least because of the focus of history of biology on 'success narratives', the history of Modern Synthesis and molecular biology being prime examples. Thus, writing the history of evo-devo presents the opportunity to reassess twentieth century history of biology.

Except its significance for a revision of twentieth history of biology, a history about how different scientists conceptualized the complex relations between ontogeny and phylogeny has of course relevance for today's discussion. Focusing on theories of scientists whose work has been marginalized by narratives that discuss the success of the Modern Synthesis, is a way to see the possible relevance of developmental considerations

for evolutionary explanations and how to achieve a synthesis between evolution and development. Thus, Evo-Devo is a place where an interdisciplinary approach is beneficial to all participants and the interdisciplinary nature of the book is of itself a very positive sign.

How successful is then the book as a whole concerning the above problems? The chapters of the book are clustered in three sections: the first focuses on early twentieth century, whereas the second, which is entitled *Roots and Problems of Evolutionary Developmental Biology*, contains chapters that focus on later decades of the twentieth century and make connections with the current discussions. The final section contains three papers by leading figures in Evo-Devo. Due to space limitations, it is not possible here to refer to all chapters. I will limit the discussion to some representative cases.

A recurrent theme in the book is the realization that the relations between evolution and development continued to be discussed through the twentieth century, even in the decades when the Modern Synthesis had excluded development from its scope. For example, John Wourms describes how comparative evolutionary embryology in America survived during the 20th century in fisheries research stations and marine laboratories and museums, rather than universities. Other chapters which illustrate this point include Stuart Newman's presentation of William Bateson's ideas. Bateson, whom the author describes as being "ahead of his time" (p. 83), although praised for introducing Mendel's ideas in England, has been criticized for his resistance to the emerging evolutionary synthesis. Newman notes the relation of some of his views with current evo-devo ideas (specifically Newman's own research). Marsha Richmond's discussion of Richard Goldschmidt's program of physiological genetics is another case in point, of an early figure that tried to develop a unified theory of heredity, development, and evolution, at a time when the study of these problems proceed independently.

The chapters of Alan Love and William Wimsatt are particularly interesting. The previous papers focus on early twentieth century biology. These discussions consider the period after the middle of the century, a time for which little is known concerning theorizing about the phylogeny and ontogeny problem. Love takes the notions of innovation and novelty as central to current evo-devo, and so looks at morphology and paleontology, areas of biology where these problems where discussed. In this way, he

connects older approaches to present research. Love presents the views of Dwight Davis, a morphologist, and William Gregory, a paleontologist, who both discussed the problem of the origin of evolutionary novelty. William Wimsatt presents Rupert Riedl's notion of burden connecting it with the work of Wallace Arthur and his own notion of generative entrenchment. Jane Maienschein's chapter has a more general focus, discussing various morphogenetic studies, from the end of the 19th century to Bonner's *Morphogenesis* of 1952, all of which aimed at bringing together evolution and development. These chapters, as well as some of those that space does not permit to discuss, all contribute to a reassessment of twentieth century history of biology and to a history of the problem of ontogeny and phylogeny specifically. At the same time, they provide examples of evolutionary explanations that take development processes into account. In general, all the chapters provide useful perspectives on the history of the problem of phylogeny and ontogeny, focusing on case studies or on broader periods, on figures and theories as well as instrumentation and social contexts.

However, although there is much discussion of early twentieth century biology, later decades receive much less attention. This of course is something to be expected, since these problems were more prominent during that period. Indeed, many chapters in the book investigate the reasons that tended to keep the study of development and evolution apart. But, in face of the realization that the problem of ontogeny and phylogeny never ceased to occupy biologists, in spite of the exclusion of embryology (as well as morphology and paleontology) form Modern Synthesis, one would want to see a more detailed account of this history during the years from the early decades of twentieth century to the formation of current Evo-Devo in early 80s. For example, more could be said about twentieth century evolutionary comparative embryology, which, though limited, followed a route parallel to that of experimental embryology (Love and Raff 2003).

To conclude, both of the books reviewed here are valuable additions to the literature on evolutionary developmental biology, making important contributions to better understanding the complex relations between development and evolution. Their interdisciplinary nature is a proof that Evo-Devo unifies not only several scientific fields, but creates connections with both the communities of philosophers and historians of

biology. Biologists, philosophers, and historians alike will find in these books novel accounts of conceptual and historical issues in the developmental synthesis, as well as challenges for the future.

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