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Alan C. Love *Editor*

Conceptual Change in Biology

Scientific and Philosophical Perspectives on Evolution and Development

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Preface

I became aware of what we now call evolutionary developmental biology ("Evo-devo") in the early 1980s. Many of the contributors to this volume worked in the field earlier than this. They are (mostly) evolutionary biologists; I am a philosopher and historian of science. The three-decade history of the field that is bracketed by the 1981 Dahlem conference (Bonner 1982) and this volume comprises a uniquely exciting episode in the history and philosophy of science. My entry into the study of this field was serendipitous. It was so stimulating that I have devoted almost all of my research efforts to it since that time.

The serendipity occurred because my scholarly interests in 1980 were in the history of methodological debates within the sciences, and not particularly in biology. I was finishing up an extended study of the "cognitive revolution" in psychology of the 1950s and 1960s, in which behaviorism gave way to cognitive psychology. Many people had recognized the formal analogy between the behaviorist principle of trial-and-error learning and Darwinian natural selection. It was my expectation that evolutionary biologists all knew how natural selection worked, so I should learn from them in order to understand the nature of the psychological debate. I arranged a visit in the summer of 1983 to the Harvard Museum of Comparative Zoology (MCZ), and interviews with Ernst Mayr, Stephen Jay Gould, and Richard Lewontin. The reader of this volume can imagine what I stepped into. I had expected some unanimity about natural selection among biologists, but I found myself in the geographical epicenter of a serious, ongoing methodological controversy. Imagine my delight!

Gould invited me to the MCZ, and I spent a sabbatical year (1985–1986) in his lab, next door to Pere Alberch's office and a short distance from Lewontin and Mayr. Gould had already introduced me to the anthology that had come from the 1981 Dahlem conference (Bonner 1982), a crucial gateway to the debates. One of my first publications on the developmental approach was based on Alberch's important paper on constraint in that volume (Amundson 1994). This paper showed that developmentalists and adaptationists used divergent concepts of constraint.

It was no wonder that the debates were inconclusive when the central concept at issue was given different interpretations by the two sides.

I also refer to my acquaintance with the field as serendipitous because there was no easy way for a philosopher to identify Evo-devo as an up-and-coming field of science in the 1980s. Most philosophers of biology of that time were concentrating on topics that grew out of the population biology framework of the Evolutionary Synthesis, such as the "units of selection" problem. Notable exceptions included William Wimsatt and Richard Burian. Wimsatt introduced the notion of generative entrenchment to explain developmental constraints (Schank and Wimsatt 1986) and Burian had organized the now-famous conference on developmental constraints (Maynard Smith et al. 1985). Given my geographical isolation and heavy course load, I could bring myself up to speed only by devoting my research to the study of developmental biology and the arguments (pro and con) regarding its relevance to understanding evolution. It was a long shot. If the remarkable explosion of knowledge in developmental genetics, phylogeny, and other related fields had not happened as it did during the subsequent decades, I would have had a rather tedious and mundane academic career. Even so, my research only began to seriously pay off 10 years later.

In those days, it was pretty unclear what would count as the "success" of a developmental approach to evolution. Some advocates (now in a small minority) believed that something like Evo-devo would refute the entire Evolutionary Synthesis and replace natural selection with some other mechanism. More moderate thinkers expected a sort of "Second Synthesis" to integrate development back into mainstream evolutionary theory and create a wider or broader synthesis. My own hope was that the methodological debates would continue, at least long enough to give me a chance to eke out their dynamics. This has happened to a far greater extent than I could have hoped.

Around 1960, the Evolutionary Synthesis biologist Ernst Mayr began to broaden his interests into history and philosophy of biology, and cooperated with several non-scientists to formulate an Evolutionary Synthesis-oriented framework of concepts that set an agenda for most of history and philosophy of biology during the following decades. One outcome of my research was to critique this tradition. I characterized it as "Synthesis Historiography" and argued that it distorted history in a way that made developmental approaches to evolution seem methodologically flawed. Mayr and his associates had introduced a set of dichotomies that came to be seen as logical truths about biology and were particularly useful in arguments that concluded ontogeny was strictly irrelevant to evolution. Among these dichotomies were proximate causation versus ultimate causation and population thinking versus typological thinking, as well as certain ways of formulating the distinction between genotype and phenotype and between germline and soma. Each of these dichotomies was used during the 1980s and 1990s to argue that ontogenetic development was irrelevant to evolution. It was argued, for example, that development concerns proximate causation but evolution is about ultimate causation, and that this was why development is irrelevant to evolution. Prominent thinkers such as Mayr, John Maynard Smith, Bruce Wallace, and George C. Williams offered these and related critiques. I have come to realize in conversation that many current biologists are skeptical that thinkers of this magnitude could have reasoned in a way that seems so simplistic today. But it is important to recognize how much our perspectives have changed since the 1990s. I have carefully documented these anti-developmentalist arguments (Amundson 2005, Chap. 11). Views that seem naïve today were in the mainstream not long ago.

The present volume offers the reader a wide range of perspectives about how an understanding of development has changed, if not transformed, our understanding of evolution. The radical anti-selectionists are absent, but a range of other views is present. No one believes, as many adaptationists did in the 1980s, that development is literally irrelevant to evolution. But there are many opinions about what exactly must happen before we can integrate our new knowledge of development into our classical knowledge of population genetics and evolutionary theory to yield an integrated perspective on evolution. I must confess that I have been swayed to some extent by the methodological arguments of adaptationists. Evo-devo practitioners who claim that their approach is perfectly consistent with population genetics are overconfident. I agree with the conclusions of Karl Niklas (Chap. 2, this volume); some major, new theoretical advance is necessary before we will have an understanding of population genetics and development that does justice to both. But Niklas's reasons are different from mine. I am more of a pluralist than he is about what counts as an "explanation" in science. The problem I see revolves around the difficulty of integrating population thinking with the mechanistic thinking of developmental biology. Some Evo-devo practitioners seem to think that merely *endorsing* natural selection is sufficient to prove a consistency between Evo-devo and adaptationist population thinking. But it takes more than this. One must understand the objections raised by Mayr and his associates, and explain just how they do not apply to current thinking. To my mind, this has not yet been done. I am delighted with current science, and smugly satisfied about how many mistakes can be seen in earlier thought, but have we shown that population genetics and Evo-devo can be melted into the same pot? I am not yet convinced.

Alan Love's Introduction offers a guide to the wide range of views in this volume regarding the changes that have been necessary to bring Evo-devo to its current, favored position. Some of the most obvious examples are the increasing respect paid to phylogenetic systematics and the explosive growth of knowledge in developmental genetics. I was slow to catch on to both of these developments. In the early days, "genetics" simply meant *transmission genetics*, with genes defined abstractly in terms of their relation to phenotypic traits. In that sense, I suspect that many of us still are skeptical about the relevance of "genetics" to development. But the term "genetics" now means something much broader—a form of conceptual change has occurred (see Love, Chap. 1, this volume). We create a false sense of continuity when we fail to distinguish between different kinds of genetics. By the time the term "genetics" became synonymous with molecular genetics, and in particular the regulation of gene expression, Evo-devo was well on its way.

Regarding systematics, I decided when I first reached the MCZ in 1985 to ignore the arguments over cladistics; the debates were too personal and the topic itself hard to comprehend. Armand de Ricqlès (Chap. 12, this volume) reports in this volume how perplexed he was that Gould, otherwise an early hero of Evo-devo, sided with Mayr in opposing phylogenetic systematics (cladistics). I can reassure him that in 1985–1986, Gould was beginning to change, and was encouraging his students to take cladism more seriously. David Hull (1988) has reported on the very personal and nasty nature of the debates during that period. Although Gould had originally opposed cladism, he was softening towards it in 1986. He convinced me to keep an open mind, but it was years before I (and many others) recognized the importance of phylogenetic systematics for the progress of Evo-devo (see Raff, Chap. 11, this volume).

I would like to draw attention to an aspect of the growth of Evo-devo that is distinct from specific methodological issues, although it does indicate an important change in perspective. The difference can be seen in popular narratives about evolution that emerge from mainstream adaptationist evolution theorists as compared to those commonly articulated from the viewpoint of Evo-devo. The mainstream narrative emphasizes adaptations and assumes a sort of autonomous individuality between species. Because true species cannot interbreed, any observed genetic or morphological similarities should be explained in terms of similar selective pressures unless lineages had recently diverged and still displayed a residual conservatism from common ancestry. One would not expect to find homologous genes in species whose phylogenetic separation occurred a long time ago. Only a few dissented from this perspective that was widely held by Synthesis theorists (e.g., de Beer 1971; cf. Raff, Chap. 11, this volume), in part because any causal mechanism that might be used to explain Unity of Type would commit the fallacy of typological thinking. Homologous genes were not only difficult to find (due to their expected rarity and for technical reasons), but even if found they had no bearing on evolution.

Today's evolutionary science is very different. Huge numbers of homologous genes have been identified, and they control some of the most abstract examples of similarities across all metazoan species (e.g., morphological axes of the body). As molecular genetics advances, we find more and more identities among genes in complex organisms and in representatives of their phylogenetically distant and morphologically simpler ancestors. This is most remarkable when those ancestral forms lack the phenotypes produced by the homologous genes in complex organisms. Choanoflagellates possess genes that are homologous to the genes for cell adhesion molecules in metazoa (King et al. 2008). But choanoflagellates are single-celled creatures! What are they doing with (what we call) "cell adhesion molecules"? Simple animals such as jellyfish have no nervous system. Yet they share the genes that are used by metazoans to build nervous systems (Arendt et al. 2008). What need did they have for these genes? Genes involved in the specification and development of the autopod (hands and feet) in terrestrial vertebrates are found in species of fish that have no autopod at all (Schneider et al. 2011).

This unmistakable trend of discovery seems to be one of the most significant developments of recent years. From a historical perspective, the importance of the trend is its conflict with the methodological standards of the critics of Evo-devo during the 1980s and 1990s. But I see an additional complexity. These results greatly magnify the importance of the concept of exaptation (Gould and Vrba 1982), a notion that was earlier referred to as "pre-adaptation" (another form of conceptual change). It is beginning to appear that every gene that performs a biological function today performed different functions in the evolutionary past. This complexity also is manifested in the fact that today's genes perform different functions in different life stages, in different phases of development, and in other sorts of varying contexts (see Piatigorsky 2007). How are we to map population genetic analyses onto such squirming masses of genetic functions?

This observation reflects not only a fact about outside reports regarding evolutionary discoveries, but also a conceptual change in how evolutionists regard the problems facing them. My own research focuses on debates, and so I tend to emphasize conflicts between schools of thought. But even among evolutionists with broadly Evo-devo approaches, things have changed dramatically. Hanken (Chap. 4, this volume) points out how the concept of heterochrony has changed in its explanatory importance from the 1980s until today. Heterochrony and allometry were among the few developmental mechanisms available to theorists of the time, and so received a great deal of attention in earlier days. These mechanisms were applied to observable developmental events, and observations of molecular events were not yet available. Discoveries of gene homologies and re-used mechanisms of regulation changed all that. New developmental mechanisms, with clear evolutionary implications, came into play as gene expression patterns began to be mapped onto the organism and their regulation understood.

A broader change in perspective regards whether or not the observable data of certain evolutionary commonalities actually require *any explanation at all* (again see Amundson 2005, Chap. 11, for details). The mainstream view in the 1980s was that it did not. Bauplans and deep homologies were seen as mere artifacts or historical accidents; it was a typologist's mistake to try to explain them. Today it is broadly assumed that even remote correspondences are likely to reveal deep underlying causes. The very fact that the clade *Bilateria* is commonly discussed shows how radical this change is (e.g., see Freeman, Chap. 10, this volume).

One concept in particular illustrates the new conceptual breadth in perspective that evolutionists have adopted. The concept of homology is notoriously difficult to account for by means of developmental biology (de Beer 1971). Günter Wagner (Chap. 15, this volume) has taken up this challenge, and (to my modest understanding) has given a uniquely satisfying account of how homology can have the perplexing attributes that it does. The responsibility to even attempt this task shows that today's Evo-devo has duties and goals that go far beyond those of the mainstream of twentieth century evolutionary theory. It is true that Wagner and other Evo-devo thinkers had attempted this task—and failed at it—during the 1980s. But his new analysis shows how it is possible for homologous characters to possess a *sameness* that persists even while the developmental origins of those characters are modified in different groups of descendents. What seemed like metaphysical idealism to the critics of Evo-devo has here received a mechanistic explanation. Achievements like this reveal just how far our goals and abilities have advanced.

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Acknowledgments

This volume has developed and evolved over several years, and many people have contributed substantially to make it finally appear. The original idea surfaced in 2005 when I was transitioning to a new position at the University of California, Santa Cruz, after completing a Ph.D. in History and Philosophy of Science at the University of Pittsburgh. My dissertation had focused on explanations of evolutionary novelty and the conceptual change that occurred surrounding evolution and development from the coalescence of the Modern Synthesis to the early 2000s. I read the 1981 Dahlem conference proceedings as a young graduate student and could grasp then, even if inchoately, that something special had happened there. Given that my dissertation had (in part) tried to isolate key ways in which scientific explanations and theorizing had changed surrounding evolutionary novelty, I started contemplating applying these sorts of considerations to other conceptual elements of evolutionary developmental biology and developmental evolution. The task would be too large for one individual but having original participants from Dahlem 1981 reflect on their own research program's development and evolution could constitute an enduring platform from which others might take up the charge. There was urgency as well due to the age of some potential participants, which was unfortunately reinforced during the invitation stage. (Two weeks after I invited Brian Goodwin, we learned of his accidental death.) Things began to take shape in 2009 after funding for the project materialized and a single semester leave from teaching gave me time to prepare and organize the details. The workshop occurred in 2010 at the Max Planck Institute for the History of Science in Dahlem, Berlin. The reasons for the delay in the volume being published are like many things biological—the result of multiple, distinct (but interacting) causal factors. Some of these involve various contributors; others involve professional obligations or problems; a least one derives from personal and family issues. Rather than attempt to separate out the causal responsibility in fine detail, it is more important to celebrate the fact that the project has now come to fruition. The best and most appropriate way to do so is by thanking those who made it possible.

The research funds and release time from teaching associated with my McKnight Land Grant Professorship (2009–2011), as well as a single semester leave from the College of Liberal Arts (Spring 2009), both at the University of Minnesota, were essential to making the project happen. They provided the catalyst for taking an idea and making it a reality. I owe a special debt to Gerd Müller and the Konrad Lorenz Institute for Evolution and Cognition Research for providing ample financial support for key aspects of the workshop. This made a European location for the workshop possible. Additionally, Gerd and Günter Wagner were extremely helpful at various stages of planning the workshop, all the way back to 2005. Gerd, Rudy Raff, and David Wake played key roles on the Steering Committee for the workshop, and gave me both wise and critical input on who to invite and how. I deeply appreciate all of their assistance from start to finish.

I am very grateful to Hans Jörg-Rheinberger and the Max Planck Institute for the History of Science (MPIWG) for hosting the workshop. It was a special treat to hold a workshop reflecting on conceptual change since the 1981 Dahlem conference *in Dahlem*, making it almost a reunion event, but the MPIWG also provided an ideal meeting space with nearby accommodations, which facilitated many fruitful interactions. I would be remiss not to mention and specially thank Antje Radeck, whose administrative assistance was another essential component to having an academic workshop in Europe when its organizer was in America. She coordinated the local housing arrangements and many other details in Berlin, ensuring a functionally operational endeavor. The Minnesota Center for Philosophy of Science, and Janet McKernan in particular, provided crucial administrative support, specifically with respect to reimbursement processing.

In the preparation of the volume itself, I have had the invaluable assistance of Janet McKernan in reviewing chapter formatting and preparing the index. Additional help on the index came from Matt Spates, an able undergraduate who happily took on the task. Tom Doyle, a graduate student assistant for a portion of time after the workshop, gave me important editorial assistance with respect to all the chapters that yielded stylistic consistency, in both text and bibliography, and improved readability throughout (any remaining mistakes are due to me, not him).

I want to express my special thanks to the contributors for their patience as the volume slowly came into existence. Many of you followed through on deadlines most punctually but have been rewarded with only a wait. I am only sorry that the material could not appear sooner. But I also want to express my gratitude to all of those in attendance at the workshop in 2010 (not all of whom ended up contributing a chapter). As an assistant professor with a dream about bringing together original Dahlem participants and co-travelers alongside of historians and philosophers interested in the intersection of evolution and development, all of you made the experience greater and more stimulating than I could have imagined. It is not that everyone agreed on what was discussed but our conversations showed that the intellectual vigor was alive and well 30 years later and is, in my estimation, an important component of what makes the nexus of evolutionary developmental biology and developmental evolution so fascinating to participate in and analyze. I am confident that these explorations will be of immense value for historians, philosophers, and scientists for years to come because they provide a key bridge between past and present conceptual inventories to display how the architecture of knowledge in biological science has been refined, revised, and transformed. This leads me to note the role that Chris DiTeresi played in audio recording the event for posterity. He flew all the way to Berlin as the "sound guy," but, of course, ended up playing a larger role and offering free (good) advice.

It is fitting that the volume is being published by Springer since they were the publisher of the 1981 Dahlem conference proceedings. I am grateful to Jürgen Renn and the rest of the editorial team of Boston Studies in the Philosophy and History of Science for discerning that this series would be a good home for these contributions. I want to thank Lucy Fleet at Springer for her steadfast and unwavering support, as well as constant prodding to make sure this volume was birthed. It is difficult to say enough good things about Lucy's role in working with me on this project. It sounds trite to remark that it would not have been possible without her, but it is true. I learned a lot about myself as an editor in preparing this volume for publication and a good chunk of it emerged from my cries of frustration to Lucy and her gentle (but firm) nudges to keep the volume on track to completion. To you I owe a special debt of gratitude. Thank you.

Finally, I am thankful for the nurture and support of my family over the past several years, and especially my wife Lolene. I am constantly reminded that I do not exist in a vacuum and am utterly dependent on those immediately around me (whether they want me around or not). I could not ask for a better environment in which to work and certainly do not deserve it. *Transit umbra, lux permanet*.

Contents

Chapter 1
Conceptual Change and Evolutionary Developmental Biology

Alan C. Love

1.1 The 1981 Dahlem Conference: A Catalyst for Evolutionary Developmental Biology

The year was 1978. A very promising graduate student at UC-Berkeley, Pere Alberch, was at home in Barcelona, Spain, and wrote a letter to his advisor, David Wake, describing some of his recent intellectual interactions with biologists at a Gordon Conference on Theoretical Biology.

> So far, these days have been excellent. The Gordon Conference on Theoretical Biology was very interesting since I had the opportunity to meet a lot of people in a field that is new for me. The most important event was to meet Lewis Wolpert. He was very interested in our paper and we had a long discussion about the role of development in evolution. He also believes that "the next major breakthrough in biology will involve the integration of development in evolutionary theory", the product of this discussion is that we put him in contact to Gould to organize a small meeting, probably in Germany, where the topic will be evolution and development. We will try to bring together developmental biologists that like Wolpert are interested in general principles, with evolutionists and comparative anatomists. A small list of people that will be invited has been elaborated and it certainly includes you. Other people considered are Kauffman, Lovtrup, A.C. Wilson, etc... we have included even Pierre Grasse. George Oster is coming to Berkeley next week and he will give you more information about it (personal letter from Alberch to Wake, 8 July 1978).

In retrospect, Alberch's missive was prescient. Within 5 years there would be a veritable explosion of interest in the connections between development and evolution (e.g., Raff and Kaufman 1983; Alberch et al. 1979; Goodwin et al. 1983), following on the heels of Gould's seminal book-length treatment (Gould 1977), which included the profound discovery of homeobox gene conservation across metazoans (Scott and Weiner 1984; McGinnis et al. 1984). A fountainhead of

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that interest stemmed from the 1981 Dahlem conference that grew out of the "small list of people" referred to by Alberch. It, and the resulting edited volume (Bonner 1982), proved to be a catalyst for evolutionary developmental biology (Evo-devo) over the next three decades. Many of the participants were already well established (e.g., Eric Davidson); others were just starting out but would go on to become central figures in contemporary Evo-devo (e.g., Günter Wagner).

The goal of the original Dahlem conference on evolution and development was "*to examine how changes in the course of development can alter the course of evolution and to examine how evolutionary processes mold development*." In addition to attempts at producing answers to these "how" questions, the 1981 Dahlem conference encouraged renewed efforts to explore these research themes empirically and theoretically. The examination itself did not yield a consensus about how development evolves or how development structures the evolution of organismal traits. What it did yield was the crystallization of a growing *zeitgeist* that these questions had been ignored by population genetic conceptions of evolution undergirding the Modern Synthesis and required multidisciplinary attention, which remains an enduring aspect of Evo-devo (see Gerson, Chap. 20, this volume; Winther, Chap. 21, this volume). This multidisciplinarity was manifested at the conference and an intentional component of its structure.

> the integration of ideas from different fields is important . . . there is suddenly a general consensus that this is precisely what is needed at this time. There is an sentiment that a knowledge of development will give us greater insight into the mechanisms of evolution and that a knowledge of evolution will give us corresponding insight into mechanisms of development. (Bonner 1982, 4)[1]

Bonner saw the effort in terms of synthesis, "bringing the ideas of different fields together," and interpreted the Modern Synthesis as allied in spirit if lacking in substance with respect to evolution and development: "only by such integration can we obtain a perspective and fully appreciate the meaning of advances in any one specialized field." The conference participants (48 total) were drawn from a variety of disciplinary approaches (e.g., mathematical biology, paleontology, morphology, molecular biology, evolutionary genetics, developmental genetics, and experimental embryology) and taxonomic specialties (lower eukaryotes, marine invertebrates, terrestrial arthropods, and vertebrates).[2] The self-described fields of research are

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[1] Some philosophers have turned their attention to "integration" as an important relation between scientific concepts, explanations, and theories that is distinct from the traditionally discussed relation of "reduction" (Brigandt and Love 2012b). For a representative sample of articles, including integrative relationships between concepts relevant to Evo-devo, see *Studies in History and Philosophy of Biological and Biomedical Sciences*, Vol. 44, December 2013 (Brigandt 2013).

[2] "We wanted to assemble as large a variety of different kinds of biologists as possible. We had molecular biologists, especially molecular geneticists, developmental geneticists, developmental biologists of different skills including neurobiology, development of invertebrates in general, of insects, and even of slime molds. We had invertebrate zoologists, including a specialist in their bioengineering, and population biologists who are concerned with the strategies of life history. We had vertebrate comparative anatomists with deep interests in evolution and development shared by a group of paleontologists, both vertebrate and invertebrate. As icing on this rather remarkable mixture we had a group of theoretical and mathematical biologists interested in these subjects at all levels" (Bonner 1982, 4–5). But not everyone was included; Bonner acknowledges that the planning committee intentionally left out botanists and behavioral biologists (14).

sometimes predictable (e.g., David Wake: "Evolutionary and developmental morphology of amphibians"), sometimes unexpected (e.g., Stuart Kauffman: "Developmental genetics—*Drosophila*"),[3] and sometimes unconventional (e.g., Günter Wagner: "Self-organization and typogenetic evolution").

The Dahlem Conference series was highly structured, if not rigid (Stearns, Chap. 6, this volume; D. Wake, Chap. 5, this volume). Each conference, whether focused on life sciences or physical and chemical sciences, followed a pre-specified outline and made very concrete demands on the attendees (Appendix 1.1). These demands were especially taxing for the rapporteurs, who often stayed awake through the night typing up the input from members of their groups (Gerhart, personal communication). With the individual papers prepared in advance and the group report completed on site, a rapid publication of the entire volume ensued (even by today's standards). The rigor of the conference did not wholly exclude extracurricular activities, including time set aside for enjoying both food and drink at the end of the day's discussions and for touring the sites of Berlin, such as Potsdam or the Natural History Museum (Fig. 1.1).

1.1.1 The 1982 Dahlem Volume

The 1982 Dahlem volume consisted of an introductory chapter written by the Chairman of the Program Advisory Committee (J.T. Bonner) followed by four sections organized in terms of "levels": the Molecular Level, the Cellular Level, the Level of the Life Cycle, and the Level of Evolution (see Appendix 1.2 for lists of the group members). Bonner's introduction began with an anecdote about the fissure that had opened between evolution and embryology, but reminded readers of the many diverse and productive discussions from the twentieth century of how the two relate (Garstang 1928; de Beer 1930, 1941; Waddington 1940, 1957; Schmalhausen 1949). These four section levels did not correspond to spatial or compositional organization, but were articulated as "levels of change." This conception was not well specified and blended together with standard depictions of hierarchical levels: "from molecules to cells to organisms." Bonner then described four themes that he thought were salient, fully acknowledging that other participants might add different themes to this list:

[3] Stuart Kauffmann's self-description sounds like he was doing work similar to Antonio Garcia-Bellido or Peter Lawrence (both developmental geneticists working on *Drosophila*). But the differences are striking. For example, a special issue of *American Zoologist* from 1977 on Gene Regulation and Development in *Drosophila* contains a contribution from Kauffmann that summarizes his model for a binary epigenetic code specifying wing discs as compartments or modules (Kauffman 1977; cf. Kauffman 1973). Instead of a genetic or molecular analysis anchored in experimental methods, which characterized the other papers, Kauffmann provided a mathematical analysis of how standing chemical waves form recurrent patterns, very much in the conceptual lineage of Turing reaction-diffusion mechanisms (Turing 1952).

Fig. 1.1 1981 Dahlem conference snapshots. *Upper left*: dinner in the evening (foreground *left*, David Wake); *upper right*: conferees visiting Potsdam; *lower left*: Level of Evolution Group Photo (Standing, *left* to *right*: Brian Goodwin, Dolf Seilacher, Jim Murray, Pere Alberch, David Raup, Günter Wagner, Paul Maderson; seated, *left* to *right:* Armand de Ricqlès, Tony Hoffman, David Wake, Stephen Gould); *lower right*: *Brachiosaurus* skeleton at the Natural History Museum, which was observed on an adventurous outing to East Berlin during the conference. Picture credits: *upper left, upper right, lower right* (Armand de Ricqlès, personal photos); *lower left* (Bonner 1982, 278)

1. 'How Genes Control Development and How This Control Can Contribute to Changes During the Course of Evolution': "the question is how do genes play their part in different, complex shifts in the phenotype."
2. 'The Physical Basis of Timing Mechanisms which Play such a Key Role in Development and Evolution': "everyone agrees that the most effective way to elicit big phenotypic changes with the least genetic fuss is by heterochrony. . .but how genes control when something starts and stops in a life cycle is far less obvious. . .the wonder is. . .that we should have so little understanding of how these alterations are carried out."
3. 'The Levels of Control Above the Gene Level': "certain events seemed to be occurring in this superstructure that could not have been foreseen in the gene information alone. . .all the control signals do not emerge from the genes, although the gene instructions are the basis of all the higher levels. . .there is a hierarchy of levels of complexity."
4. 'Selection, Constraints, Random Changes, and Rigidity vs. Plasticity in Developmental Pathways': "selection is limited in what changes it can make at one

stage of development by what has occurred at a previous stage. . .developmental constraints are related to the hierarchical levels. . .sometimes rigidity is adaptive and sometimes plasticity is adaptive."

Bonner's four themes pick out issues that arise in each of the four group reports.

The Molecular Level Group Report was entitled "Genomic Change and Morphological Evolution" (I. Dawid, rapporteur) and was supplemented with two individual papers: "Genomic Alterations in Evolution" (R.J. Britten) and "Evolutionary Change in Genomic Regulatory Organization: Speculations on the Origins of Novel Biological Structure" (E.H. Davidson). These discussions review recent findings about gene and chromosomal organization, such as gene families, introns, multigene clusters, repetitive sequences, and transposable elements, with an emphasis on "control" genes. Many of these findings were derived from work in *Drosophila*, but sea urchin studies of mRNA sequence diversity were prominent also (Davidson 1976). The global perspective was pessimistic:

> Present knowledge about genome function is not sufficient to make a large direct contribution. We do not know the mechanisms by which gene activity affects the development of an individual animal, therefore, we cannot come to useful specific conclusions regarding genomic correlates of evolutionary change at the morphological level. (Bonner 1982, 19–20)

But the group argued that what was known provided a "framework of information" relevant to understanding evolutionary change. Davidson's individual contribution encapsulated his theoretical account of hierarchical gene network control (Britten and Davidson 1969, 1971). The non-exclusive alternative was local multigene regulatory units whose organization would be reflected in chromosomal proximity rather than network interactions. Although subsequent history would favor network interactions (Davidson et al. 2002; Davidson 2006), both were offered as substantive hypotheses about how variation and novelty could originate developmentally and take on evolutionary significance.

The Cellular Level Group Report was entitled "The Cellular Basis of Morphogenetic Change" (J.C. Gerhart, rapporteur) and was supplemented by five individual papers: "A Catalogue of Processes Responsible for Metazoan Morphogenesis" (N.K. Wessells), "What does the Comparative Study of Development Tell us about Evolution?" (G.L. Freeman), "Pattern Formation and Change" (L. Wolpert), "Genes That Control High Level Developmental Switches" (T.C. Kaufman and B.T. Wakimoto), and "Ontogenetic Mechanisms: The Middle Ground of Evolution" (M.J. Katz). The group report (and individual paper by Wessells) focused on three properties of cells—shape, division, and locomotion—and three broad mechanisms of cell-cell interaction in morphogenesis—localized mitosis, localized cell death, and mechanical processes (e.g., folding or flattening)—as possible evolutionary constraints but also as contributors to evolutionary potential (see Brigandt, Chap. 14, this volume). Freeman's individual paper approached the issue of how novel features arise in evolution by examining comparative larval biology. He argued that evolutionary changes in features exhibited at larval stages accounted for major differences among animal phyla as a result of the (i) precocious, (ii) differential, (iii) combinatorial manifestation of adult anatomical elements in larval stages of different lineages ('adultation'). Katz emphasized the importance of "ontogenetic buffering mechanisms" to accommodate these novel changes that were distinct from standard variation. Wolpert's positional information model of pattern formation (summarized in his individual paper) received much attention, but was contrasted with mechanochemical models of pattern formation (Odell et al. 1981), which have experienced increased attention recently (e.g., Chirat et al. 2013).

Another central issue for this group was the origin of cell types, such as whether multifunctional cell types have been segregated evolutionarily into more narrowly functioning cell types. This touched on the broader issue of the origin of novelty, including how new organs originate in evolution. These questions were explored via advances in understanding segmented body structure (metamerism) that derived from the genetic analysis of *Drosophila* (reviewed in the individual paper by Kaufman and Wakimoto). This was just prior to the unprecedented discovery of widespread conservation in *Hox* genes underlying the development of segments across metazoans (McGinnis et al. 1984; Scott and Weiner 1984). Other questions included: (a) whether particular developmental events (e.g., gastrulation) are necessary for the formation of particular structures, and therefore a developmental constraint on evolutionary change; (b) the presence and absence of developmental capacities in different lineages (e.g., regeneration); and (c) the cellular basis of changes in developmental timing (heterochrony) and their allometric effects (Hanken, Chap. 4, this volume; Niklas, Chap. 2, this volume). Similar to the Molecular Level Group, there was a studied ambiguity in how much could be concluded ("we could not give solid answers"). The group generally accepted that development may influence evolution ("certain basic constraints may be set on development and evolution by the properties of cells"), but was hesitant to specify how without further experimental inquiry. Suggestions for the latter encompassed investigating metamerism in arthropods or patterns in the vertebrate limb.[4]

The Level of the Life Cycle Group Report was entitled "Adaptive Aspects of Development" (H.S. Horn, rapporteur) and was supplemented by two individual papers: "The Role of Development in the Evolution of Life-Histories" (S.C. Stearns) and "Selection for Size, Shape, and Developmental Timing" (J.T. Bonner and H.S. Horn). This group made the most direct contact with functional considerations predominant in an evolutionary biology oriented around adaptation. Adaptive features exhibited in different animal ontogenies were treated comparatively on the supposition that there is no optimal way to build structures developmentally. The constraints of some particular developmental mechanism usually co-traveled with the facilitation of certain kinds of evolutionary change,

[4] A vigorous discussion of the idea of a "developmental program" occurred at the workshop, which is briefly recapitulated in the Cellular Level Group Report and was covered in a news story about the conference (Lewin 1981). The broad conclusion was that ontogeny is not described accurately as a programmatic phenomenon.

though with a range of potential and many possible combinations: "Patterns of development are in general more conservative than structures of adults. . . .However, there are many counterexamples, in which development is varied and the adult is conservative." Biomechanics (water flow, gas exchange, or muscle force) played a role in thinking about why development displays the features it does and whether evolution is constrained or facilitated as a consequence. As indicated by the title, development was treated in terms of complex life-cycles, which implied that how development constrained or facilitated evolution was related to the time in the life-cycle when particular properties were exhibited and whether the metamorphic transition from one stage to the next was more or less radical morphologically. The Group Report concluded with a yearning for more detailed, comparative empirical studies and systematic reviews of the findings: "our discussions were severely hampered at the outset by a lack of the most basic information." The reviews, in particular, should target a multidisciplinary readership.[5]

The individual paper by Stearns marks a key fault line in how ideas developed post-Dahlem (Stearns, Chap. 6, this volume). Focusing on life history evolution, which he would later write a textbook on (Stearns 1992), Stearns attempted to bridge adaptionist thinking ("what should natural selection favor?") and mechanist thinking ("how does the organism work?") in the context of life history theory. Stearns observed that the meaning of "development" differed for the life history theorist and developmental biologist; the former includes age-specific survival and reproduction patterns of less direct interest to the experimentalist investigating ontogeny. Stearns tried to build a bridge using three concepts—phenotypic plasticity, canalization, and constraint—by exploring how diverse mechanistic phenomena of these kinds can be adaptive. He attended systematically to plasticity and the entire approach was termed "developmental evolutionary ecology." For reasons that still require elucidation, the approach was largely ignored and most Evo-devo biologists were reintroduced to ecology through its physiological effects on ontogeny 20 years later (Gilbert 2001; Gilbert and Epel 2009). If a bridge had been built, no one decided to test its strength or utility; the chasm between population biology and experimental biology remained as Evo-devo, a loosely-knit research program with an emphasis on molecular developmental genetics, waxed in numbers and visibility (Amundson 2005; Love 2006b).

The Level of Evolution Group Report was entitled "The Role of Development in Macroevolutionary Change" (P.F.A. Maderson, rapporteur) and was supplemented by two individual papers: "Developmental Constraints in Evolutionary Processes" (P. Alberch) and "Change in Developmental Timing as a Mechanism of Macroevolution" (S.J. Gould). This was one of the most diverse groups present and contained paleontologists, mathematical biologists, and specialists in the

[5] "The reviews should be written in a style that is mutually intelligible to students of many academic fields. For example, developmental biology and paleontological morphology share little common language, but both must communicate their studies of shells and skeletons before one can fully understand the evolution of "novelties" that actually appear in the fossil record."

organismal and population biology of particular lineages. Their group report was the most far-reaching and conceptual of the four delivered, ranging over philosophical distinctions between universals and particulars, as well as an evaluation of the state of evolutionary theory ("neo-Darwinism"). One central theme was the possibility of predicting macroevolutionary trajectories with knowledge of the constraining features of development, especially the directionality of morphological change observed in the fossil record (e.g., punctuated equilibrium). Analyses of mammalian coat pattern formation in terms of reaction-diffusion mechanisms explained why spots, stripes, and other features are exhibited in particular species (e.g., Murray 1981). Another theme was the distinctness of macroevolutionary questions about the fate of higher taxa or the origin of phenotypic novelty from microevolutionary questions about changes in allele frequencies in populations. Heterochrony was invoked as a source for discontinuous morphological change in evolution, illustrated with multiple examples (e.g., amphibians and the tetrapod limb). Gould's influence on this conversation is palpable (Gould 1977; Gould 1980a, b), and was manifested in his individual paper, but the consensus that development is required to explain particular macroevolutionary phenomena was genuine: "[for] the origin of evolutionary novelties—developmental considerations are indispensable." Alberch's individual paper drove this point home by sharply contrasting natural selection explanations and developmental explanations for the stability of organic form and patterns of morphological variation through evolutionary time (Amundson 1994).

Contrary to the expectations of the organizers, this four-fold organization may have prevented some of the necessary and anticipated multidisciplinary interaction surrounding the relationship between evolution and development. For example, Strathmann (Chap. 3, this volume) recalls that this structuring partitioned those focused on mechanistic questions ('how' development works and might evolve, such as through gene regulation alterations) from those focused on adaptationist questions ('why' development evolved to exhibit particular features, such as complicated life histories). Subsequent trajectories for research programs were less cross-disciplinary than one might have expected given the productive dynamics of the conference (Stearns, Chap. 6, this volume). The Level of Evolution Group Report closed with a call to tackle evolution and development with the "enormous battery of techniques and thinking capacities" available. Why? "Because, apart from the evolutionary problems, even if a specific exercise fails, it forces a highly desirable interdisciplinary contact between all workers in the Life Sciences." This noble goal has certainly continued to be a hallmark of Evo-devo (Hall 1999; Raff 2000), but biologists are not so easily forced into contact with other disciplines—the desirability of multidisciplinarity is not shared by all. But the participants put their finger on something that continues to be important in present research endeavors: complex scientific problems demand multidisciplinary contributions to generate adequate explanations (Love 2008a; Brigandt and Love 2012a).

1.1.2 Reactions to the 1982 Dahlem Volume

Before the Dahlem volume came off the press, interest in the conference proceedings was notable. Roger Lewin wrote a news story for *Science* emphasizing one of its key themes: developmental constraints are an important factor in the dynamics of evolutionary change (Lewin 1981; see also Miller 1981). Two elements were prevalent in Lewin's recounting of the meeting: (a) natural selection was not the only relevant explanatory factor in evolution; and, (b) the contention that molecular detail is the primary locus of explanatory power. The former comprises part of a competitive narrative between the Dahlem discussion and "the almost exclusively selectionist position that has prevailed for the past several decades," and is most strongly indicated in the Level of Evolution Group. (Reviewers of the volume also detected this element of challenge [de Klerk 1982].) The latter constitutes a division over whether molecular detail was the skeleton key of explanation or whether we require "higher levels of explanation, levels above the genome, for an understanding of evolutionary change," especially the organism as an integral unit (Wagner, Chap. 15, this volume; M. Wake, Chap. 18, this volume). The interview tidbits gleaned by Lewin show just how diverse Dahlem participants were in their thinking: from Eric Davidson's confidence in the explanatory power of molecular detail and genomic organization, to George Oster's computational models of pattern formation based on physical forces; from Brian Goodwin's expectation of a periodic table of morphological forms, to Stephen Jay Gould's elevation of heterochrony to a distinct mechanism of evolutionary change. Lewin observed that many aspects of evolutionary theory were not represented at the meeting although it was held as a "rehabilitation process designed to push a neglected field of evolutionary biology closer to the center of the stage where it can join with other areas of study in shaping a fuller understanding of the origin of morphological novelties." This combining of areas of study did not occur as readily as Lewin's observation suggests (Strathmann, Chap. 3, this volume; Stearns, Chap. 6, this volume), in part because of differences in how core problems were understood across disciplines, such as explaining the origin of morphological novelties (Love 2003, 2007). But the general impression from the meeting was enthusiastic, as reflected in an interview comment by Paul Maderson: "The most important thing we have done is simply being here. The embryo has been expressly invited back into the melee of evolutionary biology" (Miller 1981).

When the Dahlem volume was published in 1982, the reviews recognized that something special was afoot. One reviewer remarked that it "suggest[ed] a lively and vibrant field of study" and prophetically noted that the resulting edited volume "is a harbinger of things to come" (Levinton 1983), a sentiment shared by additional reviewers: "*Evolution and Development* has the spark of disciplined originality" (Schopf 1982). Another saw it as an invigorating discussion of evolutionary theory: "the book is excellent and exciting. It shows that evolutionary theory itself is not in a stasis, but in a process of fascinating evolution" (de Klerk 1982). Some saw the Dahlem volume as an indicator of a broader movement: "Interest has continued to grow in this area, and enough researchers are currently involved that reviews, symposia, and books have started to appear" (Barrowclough 1984).[6] But this broader movement was not always interpreted as the juxtaposition of evolution and development. In a joint review with another volume (Dover and Flavell 1982), Thomas Schopf discerned a different trend:

> These books represent the latest in the relentless surge of molecular biology's incorporation of evolution into its mechanistic world. They specifically focus on the continuing and growing quest for a material basis for genomic organization and genomic change, both in the development of individuals and in the origin of species. (Schopf 1982)

This was consonant with Lewin's report from the meeting, suggesting that the relationship between evolution and development was not the only thing at stake in Dahlem discussions. A growing hegemony of molecular biology's explanatory role in development (and therefore evolution) was being debated as well.

At the same time, not everyone was impressed. Levinton detected key differences between the group reports:

> The book is somewhat schizophrenic. The geneticists and cellular researchers define clearly the tremendous chasm between our knowledge of development and the way in which evolution might fit. The evolutionary biologists state with confidence that development imposes constraints that may be mapped to predict the course of evolution. Is this latter claim a bit premature? (Levinton 1983)

As noted, the fourfold group structure generated conversations within more bounded disciplinary constellations. The tenor of each group report varies. Different reviewers saw similar patterns, such as the promissory note from molecular biology ("while much has been learned about genome organization, details of the mapping between genomic structures and developmental patterns remains unknown" [Barrowclough 1984]) or that the reports were "speculative" (Schopf 1982). There also was concern about the absence of specific constituencies: "My main criticism is that the book is nevertheless too one-sided. Surprisingly, no population geneticist, no botanist, and alas no evolutionist of the synthetic theory were present at the meeting" (de Klerk 1982).[7] While it is untrue that no population geneticists were present (e.g., Günter Wagner had trained in theoretical population genetics), it is the case that botanists and those inured to neo-Darwinism were not in attendance.

But even Levinton's tentative skepticism was won over by the "evolutionary biologists" of the Level of Evolution group: "the group report by Maderson et al. and the articles by Alberch and Gould make a compelling case for the role of developmental programs in directing the course of evolution." And other reviewers concurred:

> The summary and two background papers prepared by the group studying development and macroevolution are definitely worth reading. For it has become clear that a satisfying understanding of macroevolution is going to require a detailed explication of developmental processes. This seems especially true of the origin of morphological novelties. (Barrowclough 1984)

[6] Not everyone noticed: *Nature* received the book but did not review it.

[7] Recall that John Bonner acknowledged some absences explicitly (see footnote 2).

Thus, the reception of the volume was marked by an awareness of something significant with simultaneous caution because what emerged from the meeting was an exciting prospective research agenda rather than a summary of settled empirical findings.

It is crucial to note that the conference participants did not go forth from Dahlem as standard bearers for the necessity of integrating evolution and development. Peter Lawrence, one of the Dahlem 1981 conferees, wrote a scathing review of an edited volume, *Development and Evolution* (Goodwin et al. 1983), which was released shortly after the Dahlem volume and included proceedings of the British Society for Developmental Biology with representatives from the Dahlem conference (e.g., Brian Goodwin). Lawrence pulled no punches—the title of his review was “Unpinioned opinions” (Lawrence 1984). His target was “old-fashioned” researchers whose chapters, “have a curious flavor, redolent of the past, with the gentlemanliness and lack of rigor of the good old days.” The worry was that these researchers were not up-to-speed with the latest methods and results, especially molecular developmental biology, and needed to find a “balance between theory and experiment.”

> To discuss usefully the interface between two subjects—like evolution and development—one depends on a deep understanding of both. Unfortunately, our knowledge of these fields is poor and the result, in the book, is a great deal of pretentious twaddle, much of it dressed up in complex terminology and appeals to defunct authorities. One . . .which, as far as I can understand it, is an attack on modern and reductionist developmental biology with particularly blunt weapons. (Lawrence 1984)

As a developmental geneticist working on *Drosophila* (Lawrence 1992), Lawrence represented those researchers whose confidence was in the growing molecular findings on the genetic control of development. This was a point of tension at the Dahlem meeting, and certainly not a consensus view. These reviews leave us with a reminder that this agitation surrounding the relevance and significance of molecular details for understanding development was just as much an issue as the necessary relationship between development and evolution. Agreement on the latter sometimes obscured disagreement on the former.

1.1.3 Rationale for Revisiting Dahlem

The last 30 years has seen a plethora of empirical and theoretical results from the labor of many researchers working at the juncture of evolution and development (Haag and Lenski 2011; Love 2006b). That labor has come from many quarters and is aptly described as multidisciplinary by both practitioners (Raff 2000, 2007) and philosophers (Love 2008a, 2013a)—the label is well supported by bibliometric evidence (McCain 2010). The contributing disciplines remain heterogeneous and the need for integration is still salient (Wagner and Larsson 2003; Arthur 2004). Numerous concepts relevant to explanations in Evo-devo and other areas were canvassed at Dahlem and subsequently underwent transformations across disciplines. Evo-devo is an ideal place to investigate philosophical questions surrounding conceptual change because the changes are occurring in real time as researchers explore unanswered evolutionary questions with a new set of experimental tools from developmental biology and elsewhere (Love and Raff 2003).

When we look back from the present day, some things have changed, such as an increased emphasis on specific topics or substantial changes in relevant biological sub-disciplines. Not all of those present at Dahlem would now describe themselves as working within Evo-devo. Probing these kinds of conceptual developments in detail offers a novel outlook on questions about how biological research is currently conceptualized and is valuable to historical and philosophical students of biology, as well as biological researchers forging and extending their research programs. These issues provided the motivation for a retrospective workshop that was interdisciplinary in a different sense. Instead of focusing on "a survey of the present state of the art of the topic at hand," a "review [of] new concepts and techniques," or even seeking consensus about these issues in contemporary research, it concentrated on the historical trajectories of diverse biological concepts from the past several decades to understand contemporary research and gain traction on the philosophical issue of conceptual change from a variety of different investigative perspectives. One shared aim remained between the original Dahlem conference and this retrospective workshop: illuminating and advancing biological inquiry ("recommend directions for future research"). Additionally, the hope was to illuminate and advance historical and philosophical inquiry. To put it in parallel with the original Dahlem workshop goals, the aim was to examine changes in how evolution and development have been conceptualized, describe alterations in the trajectories of these research programs, and better comprehend the coalescence of Evo-devo and allied investigations in such a way as to further biological and philosophical inquiry.

To fulfill these goals, the retrospective workshop was held at the Max Planck Institute for the History of Science in Berlin from July 15–18, 2010. It took the 1981 Dahlem conference as a reference point to analyze the diverse historical trajectories of biological research over the past 30 years, and generate scientific and philosophical perspectives that characterize their current status in Evo-devo (and elsewhere). At the 2010 workshop, a combination of complementary and competing perspectives on these concepts and the development of Evo-devo were offered by scientists and philosophers in order to generate a richer picture of how this and other areas of biology have advanced conceptually over several decades. Each scientific participant was asked to present on the changes and developments of conceptual aspects of their scientific research program since the mid-1980s, including connections to different aspects of Evo-devo's increasing prominence during the interim.

– *How did these concepts operate in your research in the 1980s? How do they operate now?*
– *Have these concepts waxed or waned in significance for your ongoing investigations?*