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Introduction

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The last decade or two has seen a remarkable renewal of interest, especially among developmental biologists, in the project of integrating the divergent models and conceptual resources of developmental and evolutionary biology. While interest in such an integration is not entirely new, having arisen sporadically since the emergence of modern evolutionary theory in the late 1920s and early 1930s, the level of interest that is now being seen is novel, as is evident from the founding of two new specialist journals in 1999: *Evolution and Development* and the *Journal of Experimental Zoology* (*Molecular and Developmental Evolution*). One major reason for the new optimism about integration appears to be a perception among developmental biologists that the techniques of molecular biology had finally become refined and efficient enough that: (i) comparative studies of developmental mechanisms (including genetic mechanisms) can finally be carried out across taxa, making possible the reliable and detailed phylogenetic reconstruction of developmental pathways and processes; and (ii) there is hope for theoretical models of development which can potentially be integrated to theoretical models of evolution which have had a history of success since the early 1920s.

In retrospect, a seminal conference held at Dahlem in 1981 is well regarded as marking the beginning of the relatively continuous history of the current integrative project (Bonner 1982). Shortly after Dahlem, Arthur (1984) published an important attempt to understand morphological evolution simultaneously from a genetic, developmental, and ecological perspective; in 1988 he also published a theory of the evolution of development which,

he claimed, marked a departure from the received neo-Darwinian view of evolution. (This theme, as we shall see and several papers in this issue underscore, of the new field challenging the received view of evolution has been an important rhetorical component in the establishment of the integrative project.) In 1992 Hall produced the first text-book of evolutionary developmental biology, marking the institutional emergence of the field as a focus of class-room instruction. By the mid-to-late 1990s a flurry of new publications, from the new journals mentioned above to some key books (Raff 1996; Arthur 1997; Hall's 1998 second edition of his textbook) strongly suggested that the new field, usually nicknamed 'Evo-Devo', had come of age. (However, 'Evo-Devo' accurately refers to only one of at least three different programs within the integrative project called 'evolutionary developmental biology'. We will not use it any further in this Introduction.) Funding agencies, such as the National Science Foundation in the United States, initiated programs to support research in the general area of evolution and development (Plesset et al. 2000), and the Society for Integrative and Comparative Biology launched a new section on Evolutionary Developmental Biology, with the inaugural symposium held in 2000 (Burian et al. 2000; see also Robert et al. 2001).

Table 1 provides a selective chronology of key events of the past four decades, concentrating primarily on publications, and with the caveat that they did not arise *ex nihilo*, for alternative historiographies are possible. For instance, links may be drawn to the evolutionary embryology of the late nineteenth century (Hall 2000a) or to research in morphology throughout the twentieth century (Love, this issue) or even earlier (Hoßfeld and Olsson, this issue). Identifying every precursor is no small task, and we do not attempt it here. Table 1 also shows that, even if we use the Dahlem conference as the starting point for the present integrative project, there were many important precursors, even in the relatively recent context – that is, not going to the pre-molecular era. John T. Bonner (see, for instance, Bonner 1958) has been advocating integration for decades; N. J. Berrill (1961) also provided important ingredients for integration as early as the 1960s. Most importantly, *Ontogeny and Phylogeny*, Steven Jay Gould's (1977) masterful treatise on heterochrony showed how far integration may be achieved through careful analysis of morphological data without even going down to the molecular level. These texts, however important, are widely scattered in time. What Table 1 shows most clearly is that the period after 1982 has seen continuous sustained interest, not to be derailed even by powerful critiques such as that of Wallace (1986).

Philosophers and historians of biology, especially the latter, have finally begun to pay attention to the new field. During Summer, 2001, there was a Dibner Seminar at Woods Hole, 'From Embryology to Evo-Devo', which

Table 1. The integration of evolution and development: A selective chronology

1958	Bonner's lectures on evolution and development at University College, London. These were published in Bonner (1958).
1961	Berrill's *Growth, Development, and Pattern*.
1975	The German publication of Riedl's *Die Ordnung des Lebendigen*. (The English translation is Riedl [1978].)
1977	Gould's *Ontogeny and Phylogeny*.
1980	Hamburger's discussion of the exclusion of embryology from the Modern Synthesis.
1981	Dahlem Conference; proceedings published as Bonner (1982).
1983	Raff and Kauffman's *Embryos*, *Genes*, *and Evolution*.
1984	Arthur's *Mechanisms of Morphological Evolution*.
1986	Wallace's critique, "Can Embryologists Contribute to an Understanding of Evolutionary Mechanisms?".
1987	Buss's *The Evolution of Individuality*.
1988	Arthur's *Theory of the Evolution of Development*.
	Thomson's *Morphogenesis and Evolution*.
1990	A 'round-table discussion group' on the new field of development and evolution (involving 200 participants) at the *Fourth International Congress of Systematic and Evolutionary Biology*, proceedings published as Wake et al. (1991).
1992	Hall's *Evolutionary Developmental Biology*, the first textbook of evolutionary developmental biology.
1994	Rollo's *Phenotypes: Their Epigenetics, Ecology, and Evolution*.
1996	Raff's *Shape of Life*, putting the emergence of morphological structures such as Bauplane at the center of the field.
1997	Arthur's *Origin of Animal Body Plans*, continuing the exploration of Bauplan emergence advocated by Raff (1996).
	Gerhart and Kirschner's *Cells, Embryos, and Evolution*.
	Niklas' *The Evolutionary Biology of Plants*.
1998	Hall's *Evolutionary Developmental Biology*, much expanded 2nd edition.
	Schlichting and Pigliucci's *Phenotypic Evolution: A Reaction-Norm Perspective*.
1999	Inception of *Evolution and Development* and *Journal of Experimental Zoology (Molecular and Developmental Evolution)* as specialist journals devoted to the integrative project.
2000	Society for Integrative and Comparative Biology launches a new section, Evolutionary Developmental Biology, which holds its inaugural session; proceedings published in Burian et al. (2001).
	Hall (2000b) and Wagner (2000) distinguish between evolutionary developmental biology and developmental evolution.
	Arthur (2000) issues an evo-devo-based challenge to Neo-Darwinism.
2001	Carroll et al.'s *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*.
	Davidson's *Genomic Regulatory Systems: Development and Evolution*.
	Wilkins' *The Evolution of Developmental Pathways*.

surveyed the history of developmental biology from the turn of the twentieth century to the present integrative project. In October, 2002 this was followed by a Dibner workshop of the same name. Meanwhile, some philosophers have attempted to elucidate the conceptual structure of the integrative project (Robert 2003; Robert et al. 2001); some have explored the conceptual structure of earlier techniques (Sarkar 1999); and yet others have argued that the integration is not likely to lead to radical conceptual breaks, at least for evolutionary biology (Sterelny 2000). The idea of this issue emerged during the Dibner Seminar at Woods Hole in 2001. Several of the contributers (Gilbert, Love, Olsson, Robert, and Sarkar) were participants at that seminar (Gilbert, Hall, Love, and Robert were participants in the follow-up workshop in 2002). The aim was to promote philosophical interest in the integrative project; the *result* is this issue.

Here, we will note four of the most important sets of philosophical questions raised by the emergence of the new integrative project:

(i) the ongoing attempts to integrate evolution and development are often heralded as a 'synthesis' (e.g., Gilbert et al. 1996; Hall 2000b; Raff 2000; Arthur 2002). But what constitutes a 'synthesis' rather than some other form of disciplinary integration? In particular, are development and evolution entering the integrative discipline with epistemological parity? These questions deserve explicit attention. Otherwise, there is the potential that we will end up in the same situation as philosophers and historians of evolutionary biology who are saddled with the term 'modern synthesis' with no clear idea of what constitutes a 'synthesis' (Sarkar 2003). So as not to pre-judge this issue we have used "evolution and development" interchangeably with "development and evolution" in this Introduction;

(ii) in the new, potentially integrated, discipline, what roles, if any, are left for the sub-disciplines that formed the forefront of developmental biology for the last generation? In particular, what is the status of developmental genetics? Much of the rhetoric of the advocates of the integrative project appears to be derogatory about genetics and genetic reductionism (e.g., Gilbert et al. 1996; Robert 2001, in press). Is this epistemologically justified? Or should this rhetoric be viewed as primarily political, an attempt to co-opt the conceptual and material resources traditionally assigned to developmental genetics?;

(iii) similarly, the integrative project is supposed to present a challenge to the received view of evolutionary theory which is primarily based on population genetics (Arthur 2000, 2002; Robert, in press; see also Love's contribution to this issue). Is this a fair assessment? (For a challenging statement of the contrary position, see Sterelny [2000].)

Moreover, beyond the rhetoric, have the proponents of the integrative project produced distinctive models within it? (Garson et al. attempt to do so in this issue, but their models mimic those of received evolutionary theory and, in any case, remain rudimentary.) It is easy enough to castigate the received view of evolution for what it yet cannot do. However, what should always be kept in mind is how much evolutionary biology has already achieved. Moreover, besides adding ammunition to the repertoires of creationists and other miscreants, criticism of the received view with no viable alternative may be of little more than marginal value;

(iv) within the integrative project, there are at least three programs that have been distinguished by its proponents (but *cf.* Gilbert, this issue): (a) most conservatively, there is the 'evolution of development' which attempts to deploy the methods of the received view of evolution to reconstruct the evolutionary history of developmental mechanisms and processes. Is there any reason to doubt that, especially given the molecularization mentioned before, that this program will be successful? However, even if it is successful, what will that show? Will it make us revise any of our usual conceptions of evolution? Or even of development?; (b) there is the program of 'evolutionary developmental biology' (Hall 1992, 1999, 2000b, this issue; Robert et al. 2001). Going beyond the previous program, the aim here is at least to use evolutionary analysis to understand developmental mechanisms and processes, and to understand the developmental basis of evolutionary changes. But, is this, in any sense, a major break with the past or merely the continued and expected expansion of evolutionary studies into new domains?; and (c) most radically, perhaps, there is the program of 'developmental evolution' (Wagner 2000, 2001) which, at the very least, attempts to use the insights of developmental biology to obtain a more complete account of evolution, especially morphological evolution studied in phenotypic space. In particular, it requires exploration of developmental constraints on evolution and, also, what may be called developmental biases on evolutionary futures. But, is this program even coherent? Does it deny the received view of evolution or supplement it? Is it truly as distinctive as it initially seems, especially when compared to evolutionary developmental biology?

This is not intended as a comprehensive list. But it does show, even beyond this issue, there remain many interesting philosophical questions to explore.

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The first paper in this issue is by Hall, one of the architects of modern efforts to integrate evolution and development. Hall traces some of the history of nineteenth-century understandings of the relationships between embryology and evolution, and of twentieth-century work on epigenetics and modularity. He argues that "cell condensations are to evo-devo as genes or species are to evolution and as embryos are to development", and explores the implications of this hierarchical approach to evolutionary developmental biology. In the restricted context of animals (there is no very good analog to condensation in other kingdoms) this is an intriguing approach.

Turning to plants, the second paper, "Plants and the Conceptual Articulation of Evolutionary Developmental Biology", by Vergara-Silva, contends that zoologically oriented evolutionary developmental biologists have much to learn from their counterparts in botany, and so reviews recent findings in plant evolutionary developmental biology that serve to inform conceptual debates within evolutionary developmental biology as a whole. Of particular interest are debates about modularity, character coding in cladistics, the nature of macroevolution, and the role of ecology in the integrative project.

The third paper, Hoßfeld and Olsson's "The Road from Haeckel" explores an earlier period. Besides reconstructing an interesting and generally unknown history, this paper explores what lessons there are for the contemporary integrative project in the largely unsuccessful nineteenth-century attempts to carry out a similar program, particularly with the hope of explaining the biogenetic law.

In the fourth paper, "Evolutionary Morphology, Innovation, and the Synthesis of Evolutionary and Developmental Biology", Love disputes the orthodox historiography of evolutionary developmental biology in which the discipline is seen as the integration of developmental genetics with population genetics. Love argues that this account is incomplete, failing as it does to consider the roles of morphology and comparative anatomy. Love attempts to rectify this omission by detailing potential and actual contributions from these domains. In particular, he argues, morphology and comparative anatomy are critical to understanding the notion of evolutionary innovation – a notion central to the integrative project.

The fifth paper, Scott Gilbert's "Evo-Devo, Devo-Evo, and Devgen-Popgen" focuses particularly on the integration of population genetic and developmental genetics models, and on the context-dependency of gene function, concluding that the name of the field is less important than the work it encompasses.

The sixth paper is more theoretical. Garson, Wang and Sarkar explore a mathematical modeling framework of developmental maps which implicitly model development as a map from genotypic to phenotypic space in a partic-

ular environment. They show that the structure of this map may result in directional evolution with selection playing no role, thus explicitly showing the potential of what was called developmental bias above.

Finally, the issue concludes with reviews of two books of considerable interest to philosophers of biology working in this field. The first review is "Messy Morphogeny and the Allure of Elegant Mathematics", Andrew Reynold's discussion of *First Signals: The Evolution of Multicellular Development* by John T. Bonner. In this slim volume, Bonner explores how the understanding of developmental complexity can be influenced by a focus on simple systems, such as slime molds. Reynolds focuses especially on Bonner's treatment of mathematical modeling as a technique for approaching the 'essence of development'.

The second review is "The Integrative Biology of Phenotypic Plasticity", Trevon Fuller's essay on *Phenotypic Plasticity: Beyond Nature and Nurture* by Massimo Pigliucci. Rounding out Pigliucci's discussion of the historical, conceptual, and empirical aspects of phenotypic plasticity, and the project of visualizing plasticity through norms of reaction, Fuller dwells on the period between Woltereck's introduction of the term *Reaktionsnorm* in 1909 and the publication of *Factors of Evolution* by Schmalhausen in 1949.

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