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Knowing your ancestors: themes in the history of evo-devo

Alan C. Love* and Rudolf A. Raff

Department of Biology, Indiana University, Bloomington, IN 47405, USA

*Author for correspondence (email: aclove@indiana.edu)

In his *magnum opus* on the structure of evolutionary theory, Stephen Jay Gould offers the following justification for his extensive attention to the history of evolutionary ideas: "I regard such analysis not as an antiquarian indulgence, but as an optimal path to [a] proper understanding of our *current* commitments, and the underlying reasons for our decisions about them" (Gould 2002). Evolutionary developmental biology ("evo-devo") has become a legitimate research discipline in contemporary biology, and it is time to more adequately trace its origins. A number of articles and conferences have begun an attempt at addressing the historical background to the emergence of evo-devo. The Dibner Institute for the History of Science and Technology has held two workshops entitled "From Embryology to Evo-Devo" (summer 2001 at Marine Biological Laboratories in Woods Hole, MA; fall 2002 at the Dibner Institute in Cambridge, MA), with biologists, historians, and philosophers attempting to seek key contours for a history of evo-devo. Some participants have attempted to highlight the relevance of particular researchers, whereas others have tried to isolate key institutional changes that fostered evo-devo as we now see it. Similar work is also emerging in refereed journals (Guralnick 2002).

Our goal here is to suggest that a different sorting of the intellectual themes that constitute a history of evo-devo is necessary. This requires an examination of assumptions underlying recent discussions. As preliminary evidence for the necessity of this reflective step, it is striking that 20th century work in comparative embryology, which clearly fits into an early history of evo-devo, has yet to be fully explored. For example, in the above-mentioned conferences, most of the presentations were devoted to researchers within the tradition of experimental embryology. Identifying some assumptions found in recent historical work reveals that current histories of evo-devo have overlooked a major intellectual stream. Exposure of this richer history is particularly relevant for biologists involved in evo-devo because it serves to set a perspective for ongoing research efforts in evolution and development.

Much of the attention in discussions of an early history of evo-devo have centered on the 19th century work of Ernst Haeckel, and rightly so (Sander 2002; Hoßfeld and Olsson, in press). Haeckel produced a revolutionary blending of evolutionary (phylogenetic) and developmental themes, most familiar of which is the biogenetic law. Various similar threads of research in comparative embryology and morphology were developed under different individuals (e.g., Gegenbaur, Brooks, and Balfour) with the primary aim of discerning the phylogenetic relationships among various taxa. The emergence of a more experimental approach to organismal development in the 1880s and 1890s by Roux, Driesch, and others (*Entwicklungsmechanik*) gained a large portion of its impetus from dissatisfaction with the stalemate over alternative explanations of these phylogenetic relationships. The blossoming of experimental embryology, with its emphasis on mechanical manipulation as opposed to "mere" description, was connected with an increasingly vocalized expression that comparative embryology and morphology were dead end research programs, poignantly represented in the inability to decide between competing explanations for particular phylogenetic sequences (Nyhart 1995, 2002; Bowler 1996). William Bateson's (1894 [1992], vi) trenchant account of these problems captures the rationale of those turning to developmental mechanics or studies of variation at the time:

> Out of the same facts of anatomy and development men of equal ability and repute have brought the most opposite conclusions. . . . Facts of the same kind will take us no further. The issue turns not on the facts but on the assumptions. Surely we can do better than this. Need we waste more effort in these vain and sophistical disputes?

Many of the contemporary *tools* for exploring the evolution of development have arisen by descent through the lineage of an experimental approach to embryology, most notably those from developmental genetics. It is because of the dominance of genetic techniques in contemporary developmental biology that this stream is seen as so crucial to the history of evo-devo. But if we shift our attention away from the tools of investigation to the agenda of problems within contemporary evo-devo, experimental embryology is not the appropriate intellectual ancestor for most of the 20th century. Although overshadowed by the empirical success of experimental embryology and its descendent disciplines, many key issues such as phylogenetic relationships, the

origin of evolutionary innovations, and significance of developmental constraints are the problems of comparative evolutionary embryology. These core agenda items are very much in the tradition of Kowalevsky, Haeckel, Gegenbaur, Balfour, and others that continued long after developmental mechanics constituted a thriving and distinct research program. Gavin de Beer, the most visible and influential theoretician in this tradition during the mid-20th century, has received some attention (Hall 2000). His work primarily emphasized heterochrony, but probably more important was his ability to synthesize empirical studies to make general theoretical points (de Beer 1958 [1st edition, 1930]).

Vigorous programs in comparative embryology were carried out through the 20th century. For example, N. J. Berrill's studies on tunicates led him to explain the origin of vertebrates via a mechanism of size increase by slippage in the number of cell division cycles relative to gastrulation to get a larger basic vertebrate embryo from a tiny ascidian (Berrill 1935, 1955). These studies had a far more integrative role with respect to evolutionary problems at the time than did highly visible and important contemporary studies in experimental embryology, such as Viktor Hamburger's manipulations of the chick embryo (Hamburger 1934) or Spemann's work on the amphibian organizer (Spemann 1938). It is also the case that research programs utilizing comparative developmental data to draw phylogenetic inferences continued, despite a lack of "mainstream" visibility. For example, D. T. Anderson synthesized results from the descriptive embryology literature to prepare presumptive fate maps for a number of taxa, which then provided the raw material for detailed phylogenetic comparisons among annelids and arthropods (Anderson 1973). Again, this approach was ancestral to modern evo-devo in terms of its agenda of research problems. Though the perceived impact of individuals in 20th century comparative evolutionary embryology may appear marginal when compared with the visibility of Haeckelian influences, there are at least two reasons for reconsideration. First, the empirical work of researchers like Berrill was being cited in influential presentations of the relationship between evolution and development (e.g., de Beer 1958, pp. 38–39). Second, the restatement of key problems, such as the origin of the vertebrates, at the beginning of the renewed interest in rejoining evolution and development of the early 1980s explicitly acknowledged these sources (Gans and Northcutt 1983; Northcutt and Gans 1983). (Notably, a recent review of the same topic emphasizing results from developmental genetics did not [Holland and Chen 2001].) Succinctly, we should not confuse the success of a non-evolutionary developmental genetic research program and the tools it provided with an enduring investigative *agenda* that keeps the intersection of evolution and development as its focus.

The overemphasis on experimental embryology is not merely a function of the present success of its manipulative tools. Such a viewpoint has also been fostered by the common perspective that the decisive historical schism relevant for understanding contemporary evo-devo occurred between genetics and embryology before the Modern Synthesis. This has encouraged some contemporary scientists to subscribe to a characterization of evo-devo in terms of developmental genetics as the bridge between genetic accounts of evolution and a molecularized embryology (Arthur 2002; Wilkins 2002; cf. Love, in press). Importantly, our target is not the oft-discussed issue of whether embryology was excluded from the Modern Synthesis. Rather we want to call attention to research questions in embryology during *and* after the period of the Modern Synthesis that provided theoretical and experimental inspiration to those architects of contemporary evo-devo who were all trained before the emergence of any recognizable research program on developmental genetics.

Our criticism and positive proposal can be distilled into two pictorial representations. Figure 1 represents a common view, observable to different degrees and with varying emphasis in the discussions of Wallace Arthur, Sean Carroll, Scott Gilbert, and Adam Wilkins (among others), which sees evo-devo as a merging of themes from the Modern Synthesis with the developmental genetics that emerged from the tradition of

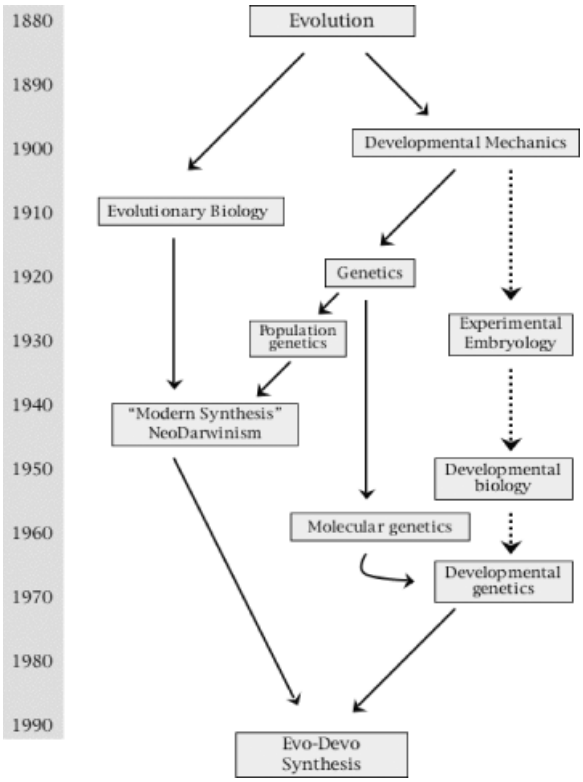

Fig. 1. Common view of the relevant developmental research component (experimental embryology now transformed into developmental genetics, highlighted by thickened dotted arrows) that feeds into contemporary evo-devo.

experimental embryology. The historically important fissure occurs when genetics breaks with embryology and joins the evolutionary intellectual lineage. The investigation of developmental biology, now a multifaceted experimental discipline, remains separate from the evolutionary-genetic lineage. Twentieth century comparative embryology is simply not noticed. Figure 2, our proposed revision, highlights comparative embryology as a strand of research not captured by the common view. Although less popular after the first quarter of the 20th century, it continues throughout (also largely separate from the Modern Synthesis) and includes figures like de Beer, Berrill, and Anderson (among others). The emphasis on the problem of reconstructing phylogenetic relations is probably most distinctive of this lineage, but there was also a strong interest in uncovering developmental mechanisms underlying evolution. The major proposed cause was heterochrony, which was seen as a universal mechanism through much of the 20th century (de Beer 1958; Gould 1977; McKinney and McNamara 1991; Raff 1996; McNamara 1997).

The revised pictorial time line diagrams the existence of two separate tracks of developmental thought and practice in the 20th century. It reconstructs part of the renewed theoretical interest in the intersection between evolution and development that began before the developmental genetic discoveries of the early 1980s (Gould 1977; Alberch et al. 1979; Bonner 1982; Goodwin et al. 1983; Raff and Kaufman 1983). Finally, it illustrates that an evo-devo synthesis arose out of the joining of each developmental stream in the wake of major empirical advances within developmental genetics (e.g., the discovery of the *Hox* genes).

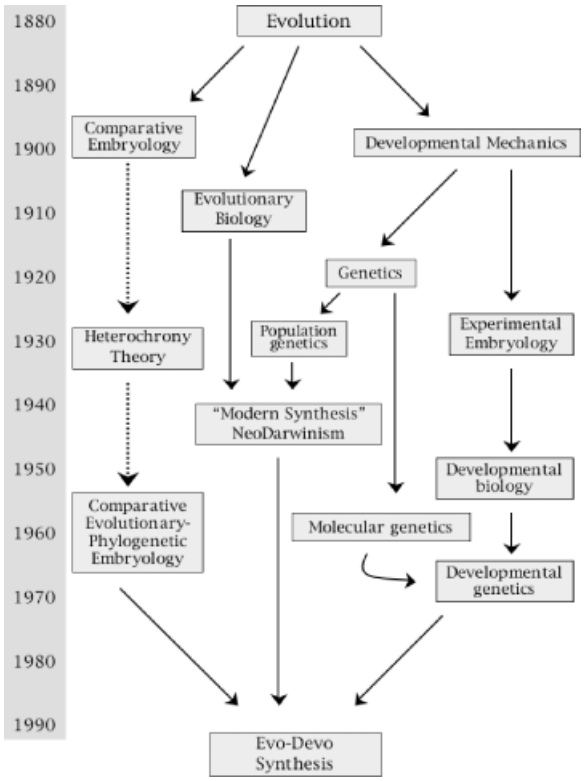

Fig. 2. Revised view of relevant developmental research components that feed into contemporary evo-devo, highlighting the lineage of comparative evolutionary embryology (indicated by thickened dotted arrows) as a key source of the current agenda of research problems that demand an integration of evolution and development.

Drawing attention to the difference between the research problems of comparative evolutionary embryology and the investigative questions and techniques of experimental embryology generates a more accurate vantage point on the roots of the present incarnation of evo-devo. The dramatic success of developmental genetics was important to the evo-devo synthesis in three ways. First, the discovery of widely conserved developmental regulatory genes caught the eye of mainstream developmental biologists. Second, developmental genetics provided powerful experimental methods for a *preexisting* set of biological questions that had interested many others long before. Finally, developmental genetics offers new mechanistic explanations relevant to the evolution of developmental processes. This aspect was visible early, for example, in Lewis' discussion of *Ultrabithorax* in *Drosophila* (Lewis 1978). Incidentally, the evo-devo investigators of the 1980s also reflected the distinctly different trajectories of developmental thought identified here. Some were very much a part of the comparative embryological theme in culture and training. Others were trained in molecular developmental biology and genetics but drew their inspiration and problems from comparative evolutionary embryology.

Once we recognize the centrality of particular research questions connected to the relation between evolution and development, we can more readily recognize the input of other themes. Thus, morphological and paleontological researchers (e.g., D. Dwight Davis or William K. Gregory) who have shared much of the problem agenda with comparative evolutionary embryology are part of the history of evo-devo, as well as its present construction (Love, in press, and submitted). More effort should be expended to see historical developments in systematics during the 1970s–1980s, eventuating in the predominance of cladistics, as a key component of the present structure of evo-devo. It is only a multifaceted history such as this that will match multidisciplinary descriptions of the present evo-devo research program.

> EDB strives to forge a unification of genomic, developmental, organismal, population, and natural selection approaches to evolutionary change. It draws from development, evolution, paleaeontology, molecular and systematic biology, but has its own set of questions, approaches and methods (Hall 1999, xv).

The heterogeneity of disciplinary threads that compose evo-devo, past and present, suggests that sleuthing the

relevant history is going to be complex and demands consideration of a wider swathe of disciplinary contributions. (Our proposed revision in Fig. 2 would thus require the addition of these components to begin moving toward a more adequate representation of intellectual and disciplinary lineages important to contemporary evo-devo.) Recognition of this historical disciplinary heterogeneity is critical to present efforts at forging a multidisciplinary evo-devo capable of offering adequate answers to these research questions.

We conclude that the title of the recent Dibner Institute workshops should be rephrased as a question: "Did embryology contribute to evo-devo?" Instead of providing a direct answer we have rephrased the query: What *kind* of embryology contributed to the emergence of evo-devo, and *how*? If we consider the laboratory tools most commonly deployed today, our attention is drawn to experimental embryology in its most prominent current manifestation—developmental genetics. But if we are interested in a broad set of research problems that evo-devo proponents claim have been ignored within the framework of neo-Darwinism (Arthur 2000; Raff 2000; Wagner et al. 2000), then comparative evolutionary embryology (along with fellow travelers such as morphology and paleontology) is the appropriate place to look. Highlighting this inherited problem agenda from comparative embryology and morphology is a reminder that the recent success of developmental genetics should not be confused with robust answers to the perennial questions of phylogeny, innovation, and constraints in the history of life that provide a continuing impetus to discern the relationship between evolution and development.

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