Cambridge University Press
978-0-521-87500-4 - Evolving Pathways: Key Themes in Evolutionary Developmental Biology
Edited by Alessandro Minelli and Giuseppe Fusco
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Part I Thinking about evolution by taking development on board

What is *evo-devo*? Undoubtedly this is a shorthand for *evolutionary developmental biology*. There, however, agreement stops. Evo-devo has been regarded as either a new discipline within evolutionary biology or simply a new perspective upon it, a lively interdisciplinary field of studies, or even necessary complement to the standard (neo-Darwinian) theory of evolution, which is an obligate step towards an expanded New Synthesis. Whatever the exact nature of evo-devo, its core is a view of the process of evolution in which evolutionary change is the transformation of (developmental) processes rather than (genetic or phenotypic) patterns. Thus our original question could be more profitably rephrased as: What is evo-devo for? This section contributes many-faceted insights into the identity and scope of evo-devo.

According to Gerd Müller (Chapter 1), evo-devo is a discipline in its own right, because it asks a specific set of questions, solves biological problems that could not be solved by other approaches, and affects our understanding of evolutionary theory. After a short reflection on evo-devo history, the chapter examines in detail a set of evo-devo big questions. All these have at their core two interrelated components, namely how evolution affects development, and how the properties of developmental systems affect the course of evolution. Finally the author considers current evo-devo research programs, and discusses the impact of evo-devo on the theory of evolution.

Isaac Salazar-Ciudad (Chapter 2) critically reviews advantages and disadvantages of three ‘schools of thought’ in evolutionary biology that differ with respect to their views on the origin of variation: neo-Darwinism, the developmental constraints school and the developmental genetics school. He then presents a new set of concepts and studies that try to avoid the drawbacks of the three schools and argues that some aspects of the evolution of morphology and development are predictable if information is available about development and about the selective pressures that were operative in previous generations.

Wallace Arthur (Chapter 3) questions whether mega-evolution is more than just a result of the accumulation of micro/macro-evolutionary events, or, alternatively, if evolution is effectively a 'scale-independent' process. This question is approached by comparing magnitude, type and developmental timing of changes involved in high- and low-level divergence of lineages. He discusses three competing hypotheses: that mega-evolutionary changes are something quite apart from everyday changes; that mega-evolutionary divergences are statistically different from their lower-level counterparts; and that all levels of evolution are the same in both the absolute and the statistical sense.

Why do species show the patterns of diversity and disparity they do? Combining an exploration of how phenotypic variation is produced at each generation with an analysis of how this variation is influenced by natural selection and other extrinsic processes can provide the means for a comprehensive understanding of evolutionary patterns. Paul Brakefield (Chapter 4) presents a well-documented case study that illustrates an integrative approach linking the evolution of developmental mechanisms with the role of selection in the evolution of wing eyespots and other traits in *Bicyclus* butterflies.

Evo-devo aims to provide a mechanistic explanation of how developmental mechanisms have changed during evolution, and how these modifications are reflected in changes of organismal form. Thus, in contrast with studies on natural selection, which aim to explain the 'survival of the fittest', the main target of evo-devo is to determine the mechanisms behind the 'arrival of the fittest'. At the most basic level, the mechanistic question about the arrival of the fittest involves changes in the function of genes controlling developmental programs. Thus it is important to reflect on the nature of the elements and systems underlying inheritable developmental modification using an updated molecular background. Claudio Alonso dedicates a chapter (Chapter 5) to precisely this task.

In the search for evo-devo identity, Ronald Jenner (Chapter 6) starts from the perspective of an important, but neglected, epistemological dualism in a science like biology, that is, idiographics vs. nomothetics. Idiographics pertains to the description of unique and historically contingent particulars, while nomothetics pertains to the search for law-like regularities or generalities. Thus, idiographically, evo-devo aims to

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document the unique effects of changes in evolutionary developmental mechanisms on the origin of novelties and the evolution of body plans. Nomothetically, it attempts to establish the general effects of evolutionary developmental mechanisms on determining the overall direction of phenotypic evolution. Recognising the dualism is not only conceptually important, but has also practical consequences, for example in the choice of model organisms.

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Evo-devo as a discipline

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Since its inception in the early 1980s, evo-devo has evolved into a mature discipline. This is manifest in the naming of research groups, scientific journals and books, professional meetings and societies. Despite such formal attributes of a scientific discipline it is often unclear what constitutes its conceptual distinctiveness. Does evo-devo have its own set of specific questions and research methods? Does it solve biological problems that cannot be solved by other approaches? And does it represent a significant change in the theoretical understanding of development and evolution? That is, in which way do the goals, the empirical programs and the theories of evo-devo research differ from those of neighbouring disciplines such as developmental biology or evolutionary biology? The present chapter provides a concise overview of the current status of evo-devo as a discipline. This requires a short reflection on its history.

CONCEPTUAL FOUNDATIONS

The parallels between embryonic stages and the 'scale of beings' had already been contemplated in pre-Darwinian times, and the foundation of a scientific theory of evolution was significantly influenced by embryological arguments. Darwin called embryology 'by far the strongest single class of facts in favour of a change of form', and his first sketches of a phylogenetic tree seem to have been inspired by tree-like renderings of embryological differences between species (Richards 1992). Much of the early work in evolutionary biology focused on the uses of embryonic characters for taxonomical purposes. Francis Balfour, William Brooks, Karl Gegenbaur, Fritz Müller and many others applied the comparative

Evolving Pathways: Key Themes in Evolutionary Developmental Biology, ed. Alessandro Minelli and Giuseppe Fusco. Published by Cambridge University Press.

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method to embryology and could thus discern hitherto unknown phylogenetic relationships. Alexandre Kowalevsky's (1866) discovery, for instance, that larval traits such as a notochord, gill slits and neural folds relate the ascidians to the vertebrates was one of the great successes of this method.

These comparative endeavours were soon followed by more mechanistically oriented and theoretically grounded programs. One sprang from the joining of the concept of recapitulation with a mechanism for effecting developmental change. Recapitulation, a widespread notion in late eighteenth-century Naturphilosophie, was elaborated by Ernst Haeckel into a mechanistic concept of morphological evolution (Haeckel 1866) by uniting it with developmental timing as a key mechanism for embryonic change. Under Haeckel's patronage this approach assumed programmatic and even ideological status. Recapitulation remained the only thinkable way by which ontogeny and phylogeny could be tied together until well into the twentieth century. The rise of experimental embryology on the one hand, and that of genetics on the other, stifled the – by then often exaggerated – recapitulationist claims. Eventually, the new paradigm of genetic variation and differential inheritance eclipsed recapitulation as a general explanatory principle for the progression of organic life. In the subsequent disregard for recapitulation theory it was often overlooked that it had contained a mechanism for evolutionary change, namely the modification of development through heterochrony, a point notably resurrected in the late 1970s (Gould 1977).

The study of environmental influences on embryogenesis, and the maintenance in subsequent generations of the effects thus induced, was another major movement that related ontogeny to phylogeny during the first half of the twentieth century. Most of these endeavours were carried out in a neo-Lamarckian vein, testing the possibility of an inheritance of acquired characters. An extensive amount of data was generated by ingenious modifications of external parameters in the development of insects (Jollos 1934), amphibians (Kammerer 1923), and other taxa (Kammerer 1925, Hämmerling 1929). Entire institutions, such as the Vivarium Institute in Vienna (1902–1945), devoted their efforts to the study of the environment–development–evolution interaction. The conclusiveness of the results was debated heatedly (e.g. E. W. McBride vs. opponents in *Nature* during the 1920s). Eventually the neo-Lamarckian interpretations lost credibility. But these early attempts to combine environmental modification with breeding experiments represent a body of evidence that merits attention independently from their

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Lamarckian interpretations. Recently the importance of 'enduring modification' and 'epigenetic inheritance' has been reconsidered (Rubin 1990, Jablonka and Lamb 1995), and plasticity research actively readdresses the issue of environmental influences on development and evolution (Gilbert and Bolker 2003).

Another conceptual root of evo-devo arose with early attempts to include the genetics of development into evolutionary theory, based on theoretical considerations and experimental quantitative genetics. Among these concepts ranged reaction norms (Wolterek 1909), rate genes (Goldschmidt 1940), assimilation (Waddington 1956) and the whole field of epigenetics (in the Waddingtonian sense). These initiatives took place before the rise of DNA genetics and in the absence of molecular tools for genetic analysis. But the calls for a more prominent role of these mechanisms in evolutionary theory, such as expressed by Goldschmidt and Schmalhausen, and later by Waddington, went largely unheard. Attention concentrated on transmission genetics and quantitative genetics, whereas developmental genetics, and developmental biology for that matter, were left aside.

These initiatives all addressed facets of the ontogeny–phylogeny or development–evolution interface and thus kept the connections between the fields alive even during prolonged periods of their largely separate study in the twentieth century. Except for certain conceptual traces not much of these traditions has survived in modern evo-devo, and none of them can be considered its immediate forerunner. Two developments were more directly responsible. One stimulus was the increasing awareness of explanatory deficits in the prevailing paradigm of evolutionary theory. Neo-Darwinism worked well for the population genetic phenomena it concentrated on, but in the late 1970s and early 1980s concern accumulated about its difficulty to account for many characteristics of phenotypic evolution. Such phenomena included biased variation (Alberch 1982, Maynard Smith *et al.* 1985), rapid changes of form (Eldredge and Gould 1972), the occurrence of non-adaptive traits (Gould and Lewontin 1979), and the origination of higher-level phenotypic organisation such as homology and body plans (Riedl 1978). Most of the criticisms attributed the explanatory deficits of neo-Darwinism to its neglect of the generative processes that relate genotype to phenotype and to the exclusion of developmental theory from the evolutionary synthesis (Hamburger 1980, Reid 2007).

The rising interest in these topics during the early 1980s was reflected in scientific meetings (such as those in Dahlem 1981, Sussex

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1982, Plzen 1984, Columbia 1985 or Woods Hole 1985) and books (Bonner 1982, Goodwin *et al.* 1983, Raff and Kaufman 1983), which began to concentrate on the intersections between development and evolution. Empirical research took up the theme (e.g. Katz *et al.* 1981, Alberch and Gale 1983, 1985, Raff *et al.* 1984, Müller 1986), using classical techniques of comparative and experimental embryology at first, and later, increasingly, the methodologies of molecular biology. This new agenda, which aimed at defining the role of developmental processes in organismal evolution, was initially called 'ontophyletics' (Katz *et al.* 1981, Katz 1983) or 'evolutionary embryology' (Müller 1991), until 'evolutionary developmental biology' (Hall 1992, Wake 1996) became the generally accepted label. Besides heterochrony, developmental constraints were a central topic in this early period of evo-devo (Alberch 1982, Maynard Smith *et al.* 1985).

In the mid 1980s a second major boost for modern evo-devo came from the rise of molecular developmental genetics, which brought the cloning of regulatory genes and the techniques for the visualisation of their activation in the embryo. This created a completely new approach to comparing the development of different taxa and led to the discovery of unexpected similarities in gene regulation among distantly related species (McGinnis *et al.* 1984). During the following years these similarities were found to extend to the spatial and temporal sequences of early gene expression in anatomically very different embryos such as insects and mammals (Duboule and Dollé 1989, Graham *et al.* 1989). In contrast to earlier notions that took the diverse ways in which animals develop to be the result of an equally diverse genetic apparatus, it became increasingly clear that relatively few genetic regulators are implicated in the embryonic foundations of all animal body plans (Akam 1989, Holland 1992, Holland *et al.* 1996). The search for commonalities and differences in gene expression patterns and gene regulation gained rapid momentum and led to a much improved understanding of the molecular underpinnings of development (Carroll *et al.* 2005, Davidson 2006). Today, the evolution of the developmental genome and of gene regulatory networks has become the most popular theme in empirical evo-devo research. High-throughput genomics is adding another methodological level to this comparative developmental genetics.

THE QUESTIONS OF EVO-DEVO

Evo-devo starts from the postulate that a causal-mechanistic interaction must exist between the processes of individual development and the

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processes of evolutionary change. Understanding these interactions and their consequences for organismal evolution represents the central research goal. Hence, the core question of evo-devo has two interrelated components: evolution's influence on development and development's influence on evolution. This reciprocal interrelationship constitutes a genuinely dialectical and systemic research agenda. The following will be a brief characterisation of the major research questions that arise from this general agenda.

How did development originate?

This question relates to the origins of multicellularity and the evolution of life cycles. John Bonner, a major influence in triggering the evo-devo revolution, early on reflected on the relations between organism size, internal complexity, reproductive success and life-cycle selection (Bonner 1965, 1988). Most of these ideas were based on the study of extant colonial or aggregating unicellular organisms such as cellular slime moulds. In early multicellular aggregates competition among cells to become the ones that propagate the next generation was possibly an important factor. The transition between the cell as the unit of selection and the multicellular individual as the unit of selection would have been the key evolutionary event at the origin of development (Buss 1987).

A different approach targets the physical properties of cells and tissues. Single-cell organisms that existed before the emergence of multicellularity possessed liquid-like viscoelasticity, adhesiveness and chemical excitability. Consequently, protometazoan cell aggregates must have had an inherent capacity to self-organise spatial patterns. Development would have arisen at the point when certain cells achieved organisational control over other cells, e.g. by releasing diffusible chemical substances, and this capacity would have resulted in cell aggregates consisting of non-uniformly distributed cell states. In conjunction with differential adhesion (Steinberg 1963) and other generic physical mechanisms (Newman 1994) such simple systems can produce an array of 'generic forms', whose shapes and sizes are much determined by the physico–chemical conditions of the environment in which they form (Newman *et al.* 2006). Because of this strong environmental influence, it is assumed that in early forms of development the close correlation between genotype and phenotype observed in modern organisms would not have existed yet. Rather the genotype–phenotype relation might have been one-to-many

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during what has been called a ‘pre-Mendelian phase’ of evolution (Newman and Müller 2000). Subsequent selectional fixation and genetic routinisation would have resulted in the robust forms of development and the faithful Mendelian kind of inheritance seen in extant organisms.

How did the developmental repertoire evolve?

This question is predominantly approached at the genetic level, e. g. through the study of gene duplications, especially of the regulatory genes (McGinnis and Krumlauf 1992, Holland 1999), and the evolution of gene regulatory networks (Davidson *et al*. 1995, Wray and Lowe 2000). The genetic redundancy generated by such mechanisms can be exploited through the acquisition of new functions for these genes, a process referred to as recruitment (Keys *et al*. 1999) or cooption (True and Carroll 2002). Present summaries of the evolution of developmental pathways rely almost exclusively on genetics (Wilkins 2002, Carroll *et al*. 2005), but the epigenetic mechanisms controlling gene activation also evolve, including the processes of cell and tissue interaction and embryonic induction, which had been considered in earlier treatments of the evolutionary roles of epigenesis (Løvtrup 1974, Hall 1983, Edelman 1988).

Modularity constitutes a principle connecting the genetic and epigenetic facets of evolving developmental repertoires in recognising that developmental systems are decomposable into components that operate according to their own intrinsically determined principles (Schlosser and Wagner 2004, Callebaut and Rasskin-Gutman 2005). Such modules can be characterised as integrated structural and process units that depend on input from other components and, in turn, influence other components by their outputs, represented, for example, by gene signalling pathways or inductive interaction networks. The evolutionary function of developmental modules would be their phenotypic selectability. A selectable developmental module can consist of a set of genes, their products and their developmental interactions, including the resulting character complex and the functional effect of that complex. The genes affecting the modular character complex would be characterised by a high degree of internal integration and a low degree of external connectivity: that is, pleiotropic connections would be largely within-module. Modularity could thus become one of the most productive approaches to the evolving genotype–phenotype relationship (von Dassow and Munro 1999).

How are established processes of development modified through evolution?

The empirical study of changes in developmental gene regulation occupies much of the present research effort (see below and contributions in this volume). A broader concept is heterochrony, i.e. evolutionary changes in the relative timing and rates of developmental processes. This classical idea has been revived by Gould (1977) and Raff and Kaufman (1983) and has since been elaborated into a powerful explanatory framework (McKinney and McNamara 1991, Parichy *et al.* 1992, McNamara 1997). Different forms and mechanisms of heterochrony are associated with different life-history strategies and produce different phenotypic results (Hall 1984, Raff and Wray 1989). Heterochrony has been documented in most groups of organisms, and its study is now taken to molecular and genetic levels (Parks *et al.* 1988, Wray and McClay 1989, Kim *et al.* 2000). Mutations that directly affect developmental timing have been demonstrated in animals (Ruvkun and Giusto 1989) and plants (Dudley and Poethig 1991). A number of genetic mechanisms affecting developmental timing have been tested experimentally (Dollé *et al.* 1993, Zákány *et al.* 1997). Without doubt heterochrony based on gene regulatory changes represents a powerful mode for altering morphological characters and body plans (Duboule 1994). But it remains difficult to distinguish between heterochronic phenomena that are simply a consequence of any change to development and those cases in which heterochrony of a particular process represents the causal mechanism for the evolutionary modification of a trait.

Does development play a role in phenotypic variation?

The extent to which the properties of developmental systems influence the variational and directional dynamics of phenotypic evolution is a question primarily addressed by the concept of developmental constraint. This was one of the themes that triggered evo-devo (Alberch 1982, Maynard Smith *et al.* 1985), and it is still relevant today. The empirical evidence for constraints is extensive, including data from comparative morphology (e.g. Wake 1982, Bell 1987, Vogl and Rienesel 1991, Caldwell 1994), comparative and experimental embryology (e.g. Alberch and Gale 1983, 1985, Müller 1989, Webb 1989, Streicher and Müller 1992), plant biology (e.g. Donoghue and Ree 2000) and quantitative genetics (e.g. Cheverud 1984, Rasmussen 1987, Wagner 1988). Whereas early conceptualisations of constraint concentrated on the limitations of phenotypic