Chapter 13
Evolutionary Developmental Biology: Philosophical Issues

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Abstract Evolutionary developmental biology (Evo-devo) is a loose conglomeration of research programs in the life sciences with two main axes: (a) the evolution of development, or inquiry into the pattern and processes of how ontogeny varies and changes over time; and, (b) the developmental basis of evolution, or inquiry into the causal impact of ontogenetic processes on evolutionary trajectories—both in terms of constraint and facilitation. Philosophical issues are found along both axes surrounding concepts such as evolvability, novelty, and modularity. The developmental basis of evolution has garnered much attention because it speaks to the possibility of revising a standard construal of evolutionary theory, but the evolution of development harbors its own conceptual questions. This article addresses the heterogeneity of Evo-devo's conglomerate structure (including disagreements over its individuation), as well as the concepts and controversies of philosophical interest pertaining to the evolution of development and the developmental basis of evolution. Future research will benefit from a shift away from global theorizing toward the scientific practices of Evo-devo.

Evolutionary developmental biology (Evo-devo) is a loose conglomeration of research programs in the life sciences with two main axes (Raff 2000; Müller 2007): (a) the evolution of development, or inquiry into the pattern and processes of how ontogeny varies and changes over time; and, (b) the developmental basis of evolution, or inquiry into the causal impact of ontogenetic processes on evolutionary trajectories—both in terms of constraint and facilitation. Philosophical issues can be found along both axes, especially surrounding a recurring set of concepts (e.g., evolvability, novelty, modularity). Although the developmental basis of evolution has garnered much philosophical attention because it speaks to the possibility of revising a standard construal of evolutionary theory or Modern Evolutionary Synthesis (Pigliucci and Müller 2010; Laubichler 2010; Minelli 2010), the evolution of development harbors a variety of its own conceptual questions. I begin with Evo-devo's conglomerate structure,

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T. Heams et al. (eds.), *Handbook of Evolutionary Thinking in the Sciences*,
DOI 10.1007/978-94-017-9014-7_13

particularly why its heterogeneity and complex individuations are conceptually intriguing. Next, I survey the evolution of development and the developmental basis of evolution separately, highlighting some concepts and controversies of philosophical interest. I close by suggesting that a move away from global theorizing toward scientific practice will be a productive strategy for future philosophical research.

1 A Fascinating (Philosophical) Question: What is Evo-Devo?

Although Evo-devo is often labeled as if its individuation was uncontroversial, nothing could be further from the truth. Different researchers from different disciplinary backgrounds using an assortment of methods and approaches see themselves as working within Evo-devo, sometimes to the explicit exclusion of one another. Narrow depictions of Evo-devo often revolve around the comparative developmental genetics of metazoans (Carroll 2005; De Robertis 2008), where the focus is on conserved genetic regulatory networks and signaling pathways underlying developmental processes (commonly collected under the concept of ‘the genetic toolkit’). Evolutionary change is understood in terms of processes of gene regulation with a special emphasis on *cis*-regulatory elements (Davidson 2006; Carroll 2008). The majority of this empirical research has been prosecuted using model organisms from mainstream developmental biology (e.g., *Drosophila*), in part because the experimental tools available for these systems are the most powerful and diverse. Since this version of developmental genetics is *comparative*, phylogenetic systematics should play a key role in drawing evolutionary inferences. In practice, things are more complicated (Telford and Budd 2003; Jenner 2006). A diversity of conceptual issues are either implicit or explicit:

(a) How are characters conceptualized (e.g., segmentation), and how does this affect judgments of homology across wide spans of evolutionary time?
(b) How are principles of parsimony applied to developmental aspects of evolutionary change across a phylogenetic tree?
(c) How are we to understand the ontology of ancestral taxa, especially abstract entities that stand in for the suite of characters typical of a common ancestor (e.g., *Urbilateria*)?

Additionally, the historical perspective offered to crystallize a narrow depiction of Evo-devo is problematic in numerous ways. Claims such as, “Evo-devo began in the pre-genomic era when genetic studies in *Drosophila* and gene cloning in *Xenopus* revealed that the Hox genes that control the anterior-posterior (A-P) axis were unexpectedly conserved” (De Robertis 2008, 186), involve the selective exclusion of relevant historical factors and lend false credence to the narrow depiction held by many contemporary biologists (Love 2003a, 2007b).

One philosophical issue lurking in these narrow depictions is how fundamental Evo-devo is with respect to more standard evolutionary genetics. The model of evolution by *cis*-regulatory element alterations has been challenged empirically (Hoekstra and Coyne 2007) and conceptually: “the litmus test for any evolutionary hypothesis must be its consistency with fundamental population genetic principles… population genetics provides an essential framework for understanding how evolution occurs" (Lynch 2007, 8598). These authors argue that the characterization of interspecific differences in developmental mechanisms is not equivalent to identifying the mechanisms of evolution because it ignores the population-genetic processes responsible for evolutionary change. This means that the purported "marriage between developmental biology and Darwinian theory" (De Robertis 2008, 194) is not as close as it might appear. Substantive differences about the place of Evo-devo (narrowly depicted) in evolutionary theory remain. New philosophical models of these disciplinary relationships are needed (Love 2010b).

Broad depictions of Evo-devo include comparative developmental genetics but also draw attention to comparative embryology and morphology, experimental investigations of epigenetic dynamics at different levels of organization, and computational or simulation oriented inquiry (e.g., Müller 2007; Wagner et al. 2000). These depictions are sometimes articulated in terms of disciplinary contributors or methodological approaches: "[Evo-devo] is not merely a fusion of the fields of developmental and evolutionary biology, …[it] 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 joint role of paleontology and systematics is especially notable for supplying a necessary historical-phylogenetic dimension and essential contributions of data from the fossil record (Raff 2007; Hall 2002; Telford and Budd 2003). Examples of these contributions includes character polarity (the direction of evolutionary change) and increased species sampling, which can alter or reverse assessments of evolutionary processes; extinct taxa reveal that the fused palate of lungfish is not homologous to that of tetrapods but rather results from convergence (Raff 2007).

Although the history of biology is supportive of these broader depictions (Laubichler and Maienschein 2007; Love and Raff 2003), the status of this disciplinary mish-mash in contemporary biology raises its own set of questions. Instead of pitting Evo-devo and evolutionary genetics in a battle for fundamentality, questions of disciplinary coordination and relative contributions, both methodologically and explanatorily, come to the fore. Can these different approaches be unified under a coherent explanatory framework? Some argue in the affirmative, appealing to central organizing mechanisms, such as gene regulatory networks (Laubichler 2009), or concepts, such as evolvability (Hendrikse et al. 2007; Minelli 2010), to secure overall coherence. But there are a variety of concepts and themes prevalent in Evo-devo (Arthur 2002), in part because of the different kinds of hierarchical organization in evolution and development (Love 2006; Salthe 1985), including compositional hierarchies (part–whole relationships) and control hierarchies (process dependencies). These are measured and explained differently across many disciplines; insufficient philosophical attention has been given to how they might be synthesized. The (not necessarily stable) constellations of disciplinary approaches may be characterized more accurately in terms of the different problems or complex explanatory projects they represent (Love 2008, 2010b; Brigandt 2010; Brigandt and Love 2010). This suggests that no single theoretical framework based on a small set of principles or restricted set of methods will be fundamental and serve to coordinate or organize all the others within Evo-devo. It also may not be possible to articulate broader relationships to evolutionary genetics and allied disciplines within a single, overarching structure; a pluralist stance on evolutionary theory warrants further investigation (Kellert et al. 2006).

2 Evolution of Development

Much of twentieth century evolutionary biology concentrated on adult phenotypes, whether morphological or behavioral. The structural features and adaptive significance of ontogenetic trajectories, especially those related to larval stages, were relegated to the background of evolutionary theorizing. Life history theory (Stearns 1992) comes closest in touching on these themes, but it offers an explanatory framework in terms of resource investment strategies and parent-offspring conflict rather than in terms of developmental mechanisms, genetic or epigenetic, which have been of more interest to Evo-devo. (A similar divide is manifested between phenotypic plasticity theory, which relies on quantitative genetic methods and phenotypic selection analyses, and developmental studies of the sources of plasticity, which focus on molecular genetic mechanisms that facilitate phenotypic plasticity.)

One consequence of the focus on adult phenotypes was a bias in the model organisms upon which evolutionary biology forged its theoretical commitments. Animals exhibiting complex life histories with radically distinct morphologies in their larval stages, such as marine invertebrates, were neglected for direct developing vertebrates and arthropods in evolutionary and developmental studies (Love 2009a). A variety of substantive questions, such as the evolutionary origin of larval forms—literally, novel body plans—were ignored (Raff 2008). Returning to these questions requires taking up model organisms that exhibit the relevant kind of variation in life history to gather molecular and embryological data to test mechanistic hypotheses in the framework of explicit phylogenies (Raff et al. 2003). These models also have the potential to suggest new hypotheses about the evolution of development (e.g., Salinas-Saavedra and Vargas 2011). And yet because the most powerful and diverse experimental manipulations can be accomplished in the more standard developmental model organisms (Ankeny and Leonelli 2011; Slack 2006), some have argued that these—in combination with judiciously chosen, closely related species—have the best potential for integrating development and evolution (Sommer 2009). Because of the known biases affecting the model organisms used in developmental biology (e.g., rapid developmental rate, which correlates with more egg prepatterning, or minimal variation, which correlates with highly canalized ontogenies), there is a worry that the significance of some developmental phenomena for evolution (e.g., phenotypic plasticity) will be underrated (Bolker 1995). A different tactic is to acknowledge the trade-offs when choosing model organisms and instead base the decision on illuminating central themes of Evo-devo, such as modularity or novelty, to balance empirical specificity and theoretical generality (Jenner and Wills 2007). Complete theoretical generality is sacrificed because the capacity to explain particular historical transitions in evolution is paramount.

Another issue that arises surrounding model organisms is that their conceptual and material domestication biases the kinds of data that can be gathered. For example, the study of ontogeny is often executed by establishing a set of stages for ‘normal’ embryonic development that allows researchers in different laboratory contexts to obtain standardized experimental results (Hopwood 2007). The developmental trajectory from fertilized zygote to adult is broken down into distinct temporal periods by reference to the occurrence of major events, such as gastrulation or metamorphosis (Minelli 2003, ch. 4). These stages compose a *periodization* that ignores variation in developmental rate to achieve accuracy in explanatory projects (Kimmel et al. 1995). The variation ignored by staging may be germane to comprehending the evolution of development, including whether there are distinctive phylotypic stages that characterize clades (Hall 1997). Minelli and colleagues argued that the standard periodization for post-embryonic ontogeny in arthropods in terms of molt-to-molt intervals (larva, pupa, and imago for insects) is a barrier to understanding molt-timing evolution. Relevant variation in the timing of molts is intentionally ignored in the conventional staging (Minelli et al. 2006). Staging is a form of idealization (Weisberg 2007)—a representation of developmental phenomena based on concrete observational features and measurement techniques that intentionally sets aside variation in specific parameters to depict a non-abstract typical case for various descriptive and explanatory purposes. Once made explicit, various complementary reasoning strategies (e.g., alternative periodizations) can help to correct for these inherent biases (Love 2010a).

Finally, there are questions about how evidence is evaluated within and between different disciplines when studying the evolution of development. One salient exemplar is the conflicting methodological and explanatory standards between embryology and paleontology/systematics in the controversy over avian digit homology (Wagner 2005). Paleontologists hold that comparative anatomy and phylogenetic reconstructions demonstrate unequivocally that the three manual digits (D) of (extinct) maniraptoran theropods correspond to DI, DII, and DIII (‘thumb’, ‘index’, and ‘middle’). Developmental biologists have argued that the three digits in extant avians (theropods) are conclusively DII, DIII, and DIV (‘index’, ‘middle’, and ‘ring’) because the embryonic origins of the three digits unambiguously correspond to condensations CII, CIII, and CIV. These disciplinary disagreements over the interpretation and weighting of evidence need reconciliation and several possibilities have emerged: (a) a digit identity frame-shift, whereby CII exhibits gene expression characteristic of DI (thus, CII no longer goes together with DII)—digital identity has evolved through developmental dissociation (Wang et al. 2011; Bever et al. 2011; see Fig. 13.1); and, (b) new paleontological finds show mosaic assemblages of reduced DI and a dissociation of phalangeal and metacarpal digit identity correspondences (Xu et al. 2009). Instead of challenging the paleontological or developmental evidence, or questioning the inferences drawn, ongoing research has

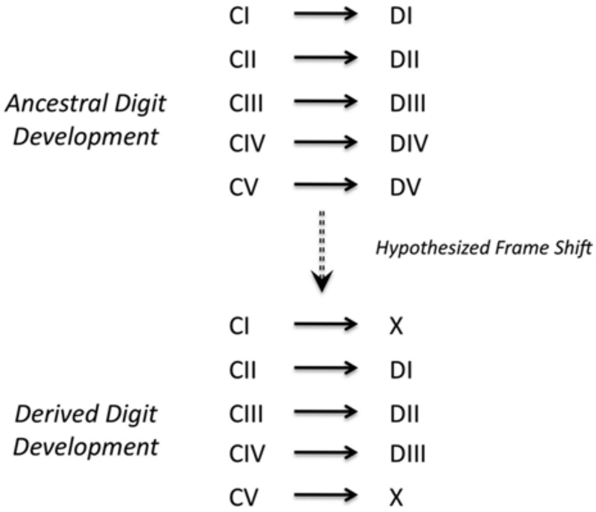

Fig. 13.1 Frame shift hypothesis for avian digital evolution. Evidence from paleontology and comparative anatomy suggest that the three manual digits (D) of (extinct) maniraptoran theropods correspond to DI, DII, and DIII (‘thumb’, ‘index’, and ‘middle’). Developmental biology suggests that the three digits in extant avians (theropods) are DII, DIII, and DIV (‘index’, ‘middle’, and ‘ring’) because they correspond to condensations CII, CIII, and CIV. In order to reconcile the conflicting evidence, a hypothesized frame shift has been proposed whereby a developmental dissociation between condensation and digit identity occurred during evolution. On this proposal, CII now exhibits a gene expression profile characteristic of DI; thus, CII no longer goes together with DII. An ‘X’ indicates that a digit does not result from development (for details, see Wagner 2005; Wang et al. 2011; Bever et al. 2011)

validated a synthetic approach to the problem. One potential lesson from this case is that productive evidential integration across disciplines occurs more readily in the local context of a specific problem (avian digit homology), rather than at a global or theoretical level (evolution of development); progress has emerged through continued negotiations of relative evidential significance in the context of the case. Criteria of adequacy are conceptualized not in terms of a grand theoretical synthesis but with respect to domains of problems in a research agenda.

3 Developmental Basis of Evolution

3.1 Recurring Concepts

The significance of development for evolution can be explored within the context of several recurring Evo-devo concepts: constraints, regulatory evolution, modularity, evolvability, and novelty (Arthur 2002). Instead of simply serving to categorize phenomena, these concepts play roles in delineating the anatomy of research problems

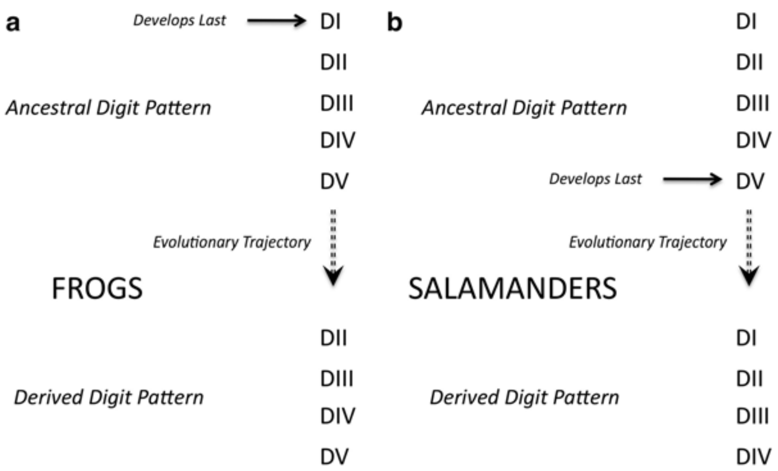

Fig. 13.2 Digital reduction trends in frogs and salamanders. A simplified, schematic representation of how the order of condensation formation in amphibian digit development explains the evolutionary pattern of digital reduction in these two lineages (Alberch and Gale 1985). (**a**) Frogs experiencing hind limb digital reduction lost pre-axial digits ('big toes') because they formed last during ontogeny. (**b**) Salamanders experiencing hind limb digital reduction lost post-axial digits ('pinky toes') because they formed last during ontogeny

and represent key explanatory properties necessary for comprehending evolution. One classic discussion centers on the concept of constraints or biases on the production of phenotypic variation due to characteristic features of developmental processes (Maynard Smith et al. 1985; Wimsatt 1986). The main point of contention was whether these somehow retarded the operation of natural selection (e.g., leading to sustained stasis in the fossil record) or facilitated some evolutionary trajectories over others, thereby diminishing the power of adaptive explanations of phenotypes.[1] For example, the order of condensation formation in amphibian digit development explains the evolutionary pattern of digital reduction in these lineages (Alberch and Gale 1985): frogs experiencing hind limb digital reduction lost pre-axial digits ('big toes') because they formed last during ontogeny; salamanders experiencing hind limb digital reduction lost post-axial digits ('pinky toes') because they formed last during ontogeny (Fig. 13.2). Interdigital webbing that might be explained as an adaptation for arboreality is in some cases a by-product of miniaturization via the retention of juvenile traits or paedomorphosis (Alberch and Alberch 1981).

Implicit in this discussion was a terminological ambiguity about constraints that traded on the conflict over the explanatory power of development versus adaptation (Amundson 1994). Many evolutionary biologists understood it as 'constraint on

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[1] The difference between "diminish" and "complement" can be subtle. Developmental explanations do not necessarily expose adaptive explanations as false and sometimes reveal their incompleteness. But these interpretations turn on whether developmental and adaptive explanations are thought of as belonging to the same type (e.g., *causal* explanation), and whether they are understood to be explaining the same target phenomenon.

adaptation' (constraint$_A$), whereas many developmental researchers understood it as 'constraint on form' (constraint$_F$). Constraint$_A$ revolved around assessments of optimality (*non*-optimal phenotypes are constrained); constraint$_F$ focused on impossible morphologies due to development (independent of their adaptive value). This divergence of meaning signified a deep difference in the explanatory endeavors of neo-Darwinian biology and Evo-devo: functionally oriented biologists explain the process of evolutionary change from one adult phenotype to another via population processes such as natural selection, which sorts genotypes, alters allele frequencies, and yields adaptive outcomes; structurally oriented biologists explain the process of evolutionary change from one ontogeny to another via developmental processes such as morphogenesis, which can be altered in different ways to generate novel morphology (Amundson 2005). But further studies have not necessarily vindicated the empirical significance of a constraint$_F$ interpretation. Niklas (2009) used computer simulation and biomass-partitioning patterns in the context of a model composed of functional tasks (e.g., light interception and water conservation) to show that plant morphospace is governed by the performance requirements of these functions in combination—convergence due to selection seemingly trumps the effects of phylogenetic history and developmental constraints (constraint$_F$).

There remain conceptual issues with distinguishing selective constraints from those associated with development. A recent synoptic treatment argues explicitly that constraints should encompass both selection and development (Schwenk and Wagner 2003; see also Arthur 2011). Constraint is always relative to a context that includes the time frame of interest, an explicit historical pattern, a specific character rather than whole organisms, a particular clade, a focal life history stage, and a null model expectation. Viability ('internal') selection (developmental lethality) will be one type of constraint that can be formulated from a contextual specification, such as the misregulation of increased asynchronous cleavage in gastropods, as will be the more stereotypical variational inaccessibility, such as the inability to generate intermediate forms of chirality in gastropod shell shape. Importantly, this more encompassing perspective on constraint includes developmental considerations that are absent from traditional evolutionary explanations that invoke natural selection (e.g., variational inaccessibility).

Organismal characters are subject to universal physical constraints (e.g., surface-volume ratio), but much of the controversy about constraints has turned on whether and how epigenetic dynamics bias variation in predictable ways (Hallgrímmson and Hall 2011). Thus, knowing the structure of the genotype-phenotype map could help elucidate the importance of development to evolution; instead of constraints, one should more broadly explore the variational properties of ontogeny (Brigandt 2007; Salazar-Ciudad 2006). Subsequent studies have shown pervasive modularity in terms of discrete sets of pleiotropic interactions during development (Wagner and Zhang 2011), which facilitates evolutionary change in lineages (i.e., evolvability). Modules—quasi-autonomous parts—are ubiquitous in biological systems but therefore can be easily confused depending on the hierarchical levels in view (Kuratani 2009) and whether the concern is structural, physiological, or developmental (Winther 2001). Ironically, modularity contributes to evolvability but the origin of modularity (or, more broadly, the evolution of the genotype-phenotype map) is a thorny question of its own (Wimsatt and Schank 2004; Wagner and Mezey 2004; Pavlicev et al. 2011).

Other properties besides modularity have been cited as undergirding evolvability (i.e., the capacity to generate heritable, selectable phenotypic variation), including the versatility of cell components, weak regulatory linkages, exploratory behavior, and robustness (Kirschner and Gerhart 1998). The conserved cellular machinery generating these properties might facilitate links between random genetic mutation and phenotypic variation so that viable character assemblages are more likely to emerge (Gerhart and Kirschner 2007). Others have argued that more generic properties of living systems, such as neutral spaces, undergird evolvability across diverse hierarchical levels (A. Wagner 2005, 2011). But features extrinsic to developing systems have often been neglected in the conceptualization of evolvability (Sterelny 2007), which may be connected to the fact that accounts of dispositional properties are often biased toward the importance of their intrinsic causal bases (Love 2003b). This highlights a somewhat neglected disciplinary connection in Evo-devo—ecology. Despite the empirical demonstration of phenotypic plasticity due to environmental induction in developing systems (Gilbert and Epel 2009) and the ecological structure of macroevolutionary patterns (Jablonski 2005), the role of ecology and the environment in developmental evolution—inclusive of learning and behavioral plasticity—have been undervalued (but see West-Eberhard 2003; Palmer 2012).

Cis-regulatory element evolution has been well studied (Wittkopp and Kalay 2012; Gordon and Ruvinsky 2012) and gene regulatory networks (GRNs) are central to narrow depictions of Evo-devo: “there is in fact no other way to conceive of the basis of evolutionary change in bilaterian form than by change in the underlying developmental gene regulatory networks” (Davidson 2001, 201); “evolutionary change in animal form cannot be explained except in terms of change in gene regulatory network architecture” (Davidson 2006, 29); “the evolution of development and form is due to changes within GRNs” (Carroll 2008, 30). Despite this conceptual inevitability, there is growing evidence that transcription factor change is also important (Lynch and Wagner 2008; Lynch et al. 2011) and additional questions pertaining to epigenetic inheritance, such as prions, membrane templating, and chromatin marking, demand further scrutiny (Jablonka and Lamb 2005). Because the relative significance of epigenetic inheritance and various kinds of genetic architectures for comprehending evolution is often a function of the risks associated with their incorporation into the existing goals, commitments, and styles of reasoning constitutive of different disciplinary specialties (Griesemer 2011), we again find ourselves requiring models for coordinating diverse inputs from multiple approaches.

3.2 Explaining Evolutionary Novelty

One central explanatory focus of Evo-devo is the origin of novelties—morphological traits that are not homologous to features in an ancestral lineage and represent developmental variation not currently accessible to extant species (Müller and

Newman 2005). This sense of novelty is distinct from what has been traditionally labeled a "key innovation," which picks out traits that permit adaptive radiations and species diversification (Liem 1990). The study of novelty is a signature aspect of Evo-devo because its explanation concerns the developmental generation of phenotypic variation, not its adaptive spread through a population.

> Evolutionary innovations are outside the scope of any current research program. Through its contribution to the solution of that question, [Evo-devo] genuinely expands the explanatory range of evolutionary theory. …This is the one area where [Evo-devo] will have its most lasting impact on evolutionary theory and biology in general (Wagner et al. 2000, 822).

> It is essential to include developmental mechanisms in the explanation of evolutionary innovations. …this is also the reason why development evolution makes an indispensable contribution to evolutionary biology (Wagner 2000, 97).

As expected given the stress on genetic regulatory evolution, most explanations of novelty emphasize developmental genetics: "The evolution of new morphological features is due predominantly to modifications of spatial patterns of gene expression" (Gompel et al. 2005, 481); "ancient regulatory circuits provide a substrate from which novel structures can develop…new structures need not arise from scratch, genetically speaking, but can evolve by deploying regulatory circuits that were first established in early animals" (Shubin et al. 2009, 818, 822). Because these claims about genetic regulatory evolution are historical in nature, and are meant to describe events occurring at particular phylogenetic junctures where the range of developmental variation differed from what we observe today, there are substantive questions about testing these sorts of claims (Wagner et al. 2000; Wagner 2001). In particular, if a causal explanation requires experimental manipulation—"demonstrating that the developmental genetic differences associated with a derived character state are sufficient to produce the derive character state" (Wagner 2001, 305)—then this might be unattainable. It assumes one can show that the introduction of the genetic difference into extant organisms that operate as proxies for the ancestral character state can produce the derived character state. If the probability of transition from the ancestral to descendant character state was only high at a specific phylogenetic juncture due to the (unknown) genetic background (i.e., a rare event), then the causal connection may not be demonstrable experimentally. But laboratory research has shown promising results in this regard, both for closely related species (Stern 2011) and broader phylogenetic comparisons (Hinman et al. 2009).

A recurring theme at the nexus of evolution and development connected to the origin of novelty is the potential significance of generic physical mechanisms, such as diffusion, viscoelasticity, and phase separation operating on soft condensed materials (Newman 1994). Newman and colleagues (2006) argue that early in evolution, generic properties of cells and tissues (e.g., self-organization, geometry, and architecture) interacted with environmental forces to yield basic metazoan morphologies with minimal developmental genetic machinery (a 'pre-Mendelian' world). These forms were subsequently stabilized by developmental genetic mechanisms via genetic assimilation, becoming more robust in subsequent generations (the 'Mendelian' world), as we now observe experimentally. This type of epigenetic explanation, reliant on appeals to self-organizing properties of developmental materials and their biomechanical modulation, also has been applied to other innovations, such as the vertebrate limb (Newman and Müller 2005). The explanatory polarization with the developmental genetic approach is stark: "novelty requires the evolution a new gene regulatory network" (Wagner and Lynch 2010, R50); "epigenetic mechanisms, rather than genetic changes, are the major sources of morphological novelty in evolution" (Newman et al. 2006, 290).

Although most Evo-devo researchers favor developmental genetic approaches, and there is more to say about generic physical approaches to development and evolution (Salazar-Ciudad et al. 2001a, b), several philosophical issues can be identified surrounding attempts to explain the origin of novelties. First, even if generic physical mechanisms are ignored, explanations of novelty have an interdisciplinary character involving developmental genetics, paleontology, phylogenetic systematics, and morphology or comparative anatomy (*inter alia*) (Wagner et al. 2000). The subtle interplay of these disciplinary contributions was evinced in a recent *developmental genetic* study of treehoppers claiming to show that their helmet morphology was derived from a wing serial homologue (Prud'homme et al. 2011), which turned out to be incorrect under the scrutiny of more careful *comparative anatomical* investigation (Mikó et al. 2012). One philosophical model for coordinating these disciplines around the explanatory task is through attention to the complex structure of the problem agenda (Love 2008), which exposes where and how different conceptual approaches and methodologies are required via explicit criteria of explanatory adequacy. Second, in conjunction with interdisciplinarity, there is no reason why problem-based explanatory coordination must derive from a global view of the relations between evolution and development; the transient coalescence of disciplines may be quite adequate and differ depending on the problem agenda under consideration (Brigandt 2010). This suggests that an important role for Evo-devo's core concepts is the guiding of research rather than producing strict categorizations (Brigandt and Love 2010, 2012). Third, these types of 'mechanistic' explanations appear to differ from 'population' explanations found in standard evolutionary biology (Laubichler 2010). For example, 'lineage explanations' (Calcott 2009) show how incremental modifications of development yield morphological transformations of individuals through evolutionary time; they detail step-by-step modifications in mechanisms between ancestral states and derived phenotypes. Instead of citing the distribution of traits in a population and changes in their relative frequency due to selection, migration, or drift, these mechanistic explanations cite changes in the development of individuals that are instantiated as a lineage evolves. This distinct explanatory approach has been advanced as a key plank for extended evolutionary syntheses (Pigliucci and Müller 2010).

4 Future Directions: The Importance of Scientific Practice

A large amount of ink has been spilt on articulating wholly general relations between evolution and development (Sterelny 2000), especially as they bear on the possibility of an extended evolutionary synthesis (Müller 2007; Pigliucci 2007; Pigliucci and Müller 2010). These efforts revolve around questions of an integrated theory of evolution or overarching systematic biological framework: “Developing a theory is of utmost importance for [Evo-devo]” (Sommer 2009, 417); “[Evo-devo] is, presently, a largely multidisciplinary field in which there is, yet, not theoretical framework integrating the recent advances in each subfield” (Salazar-Ciudad 2006, 107); “[it] is necessary to bring phenomena pertinent to evolutionary developmental biology under one conceptual umbrella” (Winther 2001; cf. Laubichler 2009; Arthur 2011). Walsh has argued that there are three possible “grades” of ontogenetic involvement—“the space of possible roles for ontogeny in evolutionary biology” (Walsh 2007, 179). These roles (development as constraint; developmental processes as units of selection; development as adaptive) assume relatively monolithic and abstract conceptions of evolutionary biology and Evo-devo (not just a narrow depiction, which is concrete). If we approach these questions from a broad depiction of Evo-devo, then it is unclear whether there is great value in providing philosophical models that attempt to capture every facet of the complex conglomeration of Evo-devo, its potential significance for evolutionary theory, and its wide range of conceptual themes and diversity of problems.

Promising avenues for future philosophical research may not derive from further scrutiny of these abstract, wholly general relations (if they exist or what they might look like), but instead from an increased exploration of the heterogeneous practices of Evo-devo biologists—ways of acting or proceeding in the empirical investigation of the natural world—some of which have already been noted (e.g., developmental staging). Both material practices (e.g., animal husbandry) and conceptual practices are germane as they touch on the nature and amount of data gathered and types of classifications generated, as well as the kinds of explanatory generalizations that are derived through abstraction and idealization. Two brief examples of conceptual practice illustrate this future promise: structure versus function reasoning and the utilization of distinct categorizations.

Structure versus function: although noticeable in discussions of constraint, the difference between researchers focused on structure and those focused on function is a critical epistemic fault line. It is often signaled by unintentional errors. Analogies, such as the fusiform morphology of aquatic vertebrates, arise by the action of natural selection; homologies are the same structure under every variation of form or function resulting from common descent. But authors still confuse the two: “Homology refers to two structures arising from an ancestral structure by the action of natural selection on common ancestors” (De Robertis 2008, 193). Part of the confusion surrounding structure and function emerges out of discussions surrounding ‘functional homology’ (Love 2007a) due to the conservation of function in many regulatory genes across wide phylogenetic distances (Carroll 2008). Closer attention to structure/function reasoning has the potential to address aspects of philosophical debates, such as incorrect claims that the identification of homologues involves consideration of selected effect functions or analogues (Rosenberg and Neander 2009; see Love 2011), as well as flag potentially problematic scientific inferences, such as the invocation of *six3* in median brain development across insects and vertebrates (Posnien et al. 2011). They also return us to questions of interdisciplinarity and hierarchy. Combinations of structural, functional, and historical styles of reasoning, when applied to an entire taxon (rather than embedded in a general theory), seem tremendously fruitful (Wake 2009); "conflicts between the different modes of explanation are highlighted and interpreted, not simply argued away or ignored by default" (Wake 1991, 543). Closer attention to how structure and function are individuated across hierarchical levels is essential for a robust understanding of characters as stable results of particular kinds of genotype-phenotype mappings (Wagner 2007; Wagner and Misof 1993).

Distinct categorizations: Evo-devo has been criticized (and lionized) for exhibiting typological thinking. Ernst Mayr linked typological thinking to saltationism and macromutationism, both of which were demonstrably false according to the Modern Synthesis (Mayr 1960). The character of the distinction between population thinking and typology bears important relations to the structure/function dialectic (Amundson 1998). Some of the philosophical discussion has attempted abstract, univocal reconstructions (Lewens 2009), but more attention should be given to the diverse practices of categorization that produce types and their distinct methodological roles in different kinds of inquiry (Love 2009b; DiTeresi 2010). Typologies exhibit variability with respect to the expected stability of types, the number of relevant dimensions in which they are defined, and the scope of their application. Philosophical accounts of these practices should assist in endeavors that attempt to integrate theoretical and empirical results from disciplines utilizing distinct typologies.

The literature discussed herein only touches the tip of the iceberg with respect to both the evolution of development and the developmental basis of evolution. I have concentrated on some central themes in Evo-devo but the range of material available—historical, empirical, theoretical, and philosophical—is vast. Other important questions have been ignored, such as how the evolution of development may violate uniformitarian inferential principles (Erwin 2011). It has been claimed that the "conflicting ménage" of methodological and explanatory standards in the loose conglomeration of Evo-devo research programs is its Achilles' heel (Duboule 2010). Others disagree and see this as the foundation for substantive theoretical, empirical, and conceptual advances on longstanding questions about the origin and evolution of biological characters (Müller 2007). Only time will tell for the science, but one salutary advantage of a philosophical perspective that seizes on the details of scientific practice is the possibility of contributing to ongoing biological inquiry through conceptual clarifications or characterizations of preferred patterns of reasoning. This perspective also represents new vistas of analysis that augment and reorient standard philosophical visions of evolutionary biology.

Acknowledgements Thanks to all of the participants in the graduate seminar on Evolutionary Developmental Biology (University of Minnesota, Fall 2011), where many of these issues were discussed in detail and particular formulations of the philosophical issues were aired (and criticized). Philippe Huneman, Patrick Laine, Molly Paxton, and Jack Powers provided useful feedback on an earlier draft of this essay. This work was supported in part by a grant from the John Templeton Foundation ("Complexity, emergence and reductionism"; ID 24426).

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