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Evolutionary Morphology, Innovation, and the Synthesis of Evolutionary and Developmental Biology

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Abstract. One foundational question in contemporary biology is how to 'rejoin' evolution and development. The emerging research program (evolutionary developmental biology or 'evo-devo') requires a meshing of disciplines, concepts, and explanations that have been developed largely in independence over the past century. In the attempt to comprehend the present separation between evolution and development much attention has been paid to the split between genetics and embryology in the early part of the 20th century with its codification in the exclusion of embryology from the Modern Synthesis. This encourages a characterization of evolutionary developmental biology as the marriage of evolutionary theory and embryology via developmental genetics. But there remains a largely untold story about the significance of morphology and comparative anatomy (also minimized in the Modern Synthesis). Functional and evolutionary morphology are critical for understanding the development of a concept central to evolutionary developmental biology, *evolutionary innovation*. Highlighting the discipline of morphology and the concepts of innovation and novelty provides an alternative way of conceptualizing the 'evo' and the 'devo' to be synthesized.

Key words: comparative anatomy, developmental genetics, embryology, evolutionary developmental biology, innovation, morphology, novelty, synthesis, typology

1. Introduction and methodology

> . . . problems concerned with the orderly development of the individual are unrelated to those of the evolution of organisms through time . . . (Wallace 1986)

One foundational question in contemporary biology is how to 'rejoin' evolution and development. The emerging research program (evolutionary developmental biology or 'evo-devo'; hereafter, EDB) requires a meshing of disciplines, concepts, and explanations (*inter alia*) that have been developed largely in independence over the past century.[1] (Raff 2000) The nature of a joint research program of evolution and development is not wholly agreed upon due to divergent viewpoints resulting from this disciplinary independence and, consequently, the mechanics for accomplishing the task are not clearly specified. Although a variety of biologists (Maynard Smith 1998; Mayr 1991; Wallace 1986) and some philosophers (Sterelny 2000) hold that there is no particular conceptual or empirical difficulty in assimilating recent findings in developmental biology into contemporary neo-Darwinism, there are a number of reasons to doubt this confidence. (Arthur 2000a; Robert, in press) The scientists involved in the emerging research program of EDB concur with many of these doubts and therefore I will proceed with an investigation of the nature of the problem of synthesizing evolution and development.

One way to dissect a foundational problem in contemporary science is through history. Jim Lennox has recently articulated a *methodological* strategy utilizing historical investigation for philosophical purposes; he calls it the ‘phylogenetic approach’ (Lennox 2001). This approach advocates the importance of exploring the origins of foundational problems and tracing their historical trajectories in order to understand contemporary conceptual issues, attempting to identify focal points where particular conceptualizations may have led to present difficulties. The formulation of theoretical frameworks in science is highly contingent and subject to local influences of many different kinds. Alternative conceptualizations were available in the early stages of now mature sciences and often clues to understanding contemporary foundational problems are found in those alternatives left by the wayside. The adjective ‘phylogenetic’ indicates that the focus is on pathways, not mechanisms, keeping in view an assumption that the epistemic currency of science (theories, concepts, explanations, etc.) is subject to change over time and exhibits relationships of ‘cognitive descent’.[2] The philosopher of science utilizes his or her knowledge of *and* distance from contemporary science in conjunction with the history of science to isolate the nature of underlying conceptual issues.

In the attempt to comprehend the present separation between evolution and development much attention has been paid to the split between genetics and embryology in the early part of the 20th century with its codification in the exclusion of embryology from the Modern Synthesis. This encourages a characterization of EDB in terms of developmental genetics as a bridge between genetic based accounts of evolution and a molecularized embryology (developmental biology). Despite claims to the contrary (Arthur 2002; Wilkins 2002), the emergence of recent discussions about the intersection between evolution and development predate the developmental genetic discoveries of the early 1980s. Morphological and paleontological researchers jointly stimulated vigorous conversation about how results in developmental biology might impinge on the received view of evolutionary theory (‘neo-Darwinism’). Most famous is the Dahlem conference of 1981 (Bonner 1982), as well as work on heterochrony (Alberch et al. 1979; Gould 1977) and systems-analytical approaches (Riedl 1977, 1978). Although there was an early book devoted to the importance of developmental genetics for evolutionary change (Raff and Kaufman 1983), other discussions were quite heterogeneous (Goodwin et al. 1983). Granting that developmental genetics of the past twenty years has played a significant role in reawakening a wider interest in rejoining evolution and development, there remains an untold story about the significance of morphology, also minimized in the Modern Synthesis. I will attempt to reconstruct part of this story, focusing on the rebirth of functional (and evolutionary) morphology from the 1950s onward. Functional morphology is critical for understanding the development of a concept central to EDB, *evolutionary innovation*: “[F]inding answers to what constitutes an evolutionary innovation ... and how developmental mechanisms have changed in order to produce these innovations are major issues in contemporary [EDB]” (Olsson and Hall 1999: 612). The meanings of this concept within morphological research are relevant to the nature of EDB. Understanding part of the story about morphology and innovation reveals a different conception of the foundational problem, providing an alternative way of conceptualizing the ‘evo’ and the ‘devo’ to be synthesized.[3]

2. Synthesis and integration

> Two approaches seem possible: one, in which the structure of one discipline is compared with that of the other, and subsequently bringing both together in one structure, and the other, in which the significance of the concepts of one discipline for the other discipline are considered. (Dullemeijer 1981)

Although Dullemeijer’s comments pertain to the relationship between functional morphology and evolutionary biology, they provide an apt point of departure for characterizing the emerging research program of EDB. The first option, where two disciplines are compared and then brought together, I will call *disciplinary integration* (cf. Bechtel 1986b). This is an appropriate moniker because the result is one disciplinary structure that integrates two previously distinct disciplines. The second strategy, where the significance of concepts in one discipline is evaluated for another (and *vice versa*), I will refer to as *conceptual synthesis*, distinguishing both the level at which the two domains are being compared and the activity that is being engaged in. *Integration* denotes bringing together one or more parts into a new entity where the individuality of the original parts is lost or effaced. *Synthesis* denotes a blending of one or more parts to produce a new entity where the individuality of the original parts is not dissolved, though potentially transformed.

Naturally, a complete taxonomy allows for *disciplinary synthesis* and *conceptual integration*, where the former produces a new discipline without dissolving those from which it was synthesized and the latter refers to how more than one concept can be merged into a single new concept for various purposes. The taxonomy is hierarchically inclusive in that disciplinary integration and synthesis subsume both conceptual integration and synthesis, but the conceptual level can be tackled without necessarily having implications at the disciplinary level.[4] EDB is usually conceived of as a *disciplinary* synthesis, hierarchically inclusive in the above sense.

> For evolutionary developmental biology (EDB or 'evo-devo') is not merely a fusion of the fields of developmental and evolutionary biology, the grafting of a developmental perspective onto evolutionary biology, or the incorporation of an evolutionary perspective into developmental biology. 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)

Analyzing all of these suggested interrelations is beyond the scope of any one essay.[5] A more manageable task is to try to determine the mutual significance of one or more concepts and their disciplinary entanglements for EDB. Ron Amundson has produced an insightful analysis of the concept of constraint in evolutionary and developmental studies, revealing that evolutionary practitioners interpret constraint as 'constraint on adaptation' and researchers in development understand it as 'constraint on form' (Amundson 1994, 2001). Here I utilize the interplay between the conceptual and disciplinary levels as a heuristic tool to approach the issues at stake for EDB, assuming that the conceptual level typically has implications for the disciplinary level.[6]

Given the premise that concepts have a historical lineage, particular concepts must be tracked across time and not just in the present. If concepts important to EDB researchers, such as 'innovation' and 'novelty', are commonly deployed in a discipline not taken to be 'central' to the emergence of EDB, we will have cause to recommend a reconsideration of that discipline and its epistemic currency in the project of synthesizing evolutionary and developmental biology. I am proposing that understanding the historical trajectories of concepts and disciplines within evolutionary and developmental biology is critical to disentangling the problem of synthesizing them in the present.

3. Exclusion historiographies, 'evo-devo', and morphology[7]

> Curiously, the only group of biologists not participating were the developmental biologists. In Germany, in France, in England (with the exception of Waddington) and in the United States they were opposed to the synthesis on a Darwinian basis. They were all Lamarckians. (Mayr 1997)

It is almost a historical truism that embryology was excluded from the Modern Synthesis (Hamburger 1980), or least that embryologists did not want to participate. (Mayr 1993) This exclusion is usually understood to be the primary source of the foundational problems attending contemporary evolutionary theory that require the synthesis called EDB.[8] The historical trajectories of genetics and embryology, their split, and various interrelations (or lack thereof) have been documented by many historians (Allen 1986; Maienschein 1987; Sapp 1987). Much of this narrative unfolds in the first three decades of the 20th century, as genetics became an autonomous discipline. T.H. Morgan played a prominent role in codifying the division, ironic given his own participation in both areas of research (Morgan 1926a, b). If we assume genetics and embryology were separate by 1935, the tight connection between population genetics and evolutionary theory in the Modern Synthesis helps explain the exclusion of embryology. Although some participants had resources for bringing embryology into the discussion (e.g. Julian Huxley), by and large this simply did not occur.

The genetics and embryology exclusion historiography is not incorrect in its details but a concern arises over how it is put to use.[9] If evolution is cast primarily in terms of genetics (which is not unusual given the conjoining of evolutionary theory and population genetics in the Modern Synthesis and later emergence of molecular genetics), then a synthesis of evolutionary and developmental biology calls for a bridge between 'genetics' and 'embryology'. Recent results pouring forth from studies in developmental genetics are exciting and appear to be the needed materials for constructing a new synthesis, providing the link between genetically based accounts of evolutionary mechanisms and molecularly characterized developmental processes (e.g. Carroll 1995). Tinkering with the developmental genetic toolkit also appears to be central to explaining the origin of morphological novelties in the context of EDB (Carroll et al. 2001; Marshall et al. 1999; Shimeld and Holland 2000). The co-option (or recruitment) of regulatory genes before or after gene duplication appears to be a powerful mechanism for generating novel structures in the evolutionary process (Ganfornina and Sánchez 1999; Raff 1996).

This historiographic premise can be observed in several different places. In a prospective article on the future of EDB, Holland says: "Three main factors have contributed to the emergence and phenomenal growth of [EDB]. Ironically, all three depend on genetics — the discipline that split evolution and development apart 60 years earlier" (Holland 1999: C41). The three genetic factors are conserved regulatory genes that play similar functional roles in ontogeny across widely divergent taxa, molecular phylogenetics, and molecular biological advances in technique that allow for the sophisticated analysis and manipulation of genetic material. The 'radical alteration of genetic systems', such as genome duplication, is marked as critical for dissecting innovations in the history of life. (p. C44) In his textbook on developmental biology, Scott Gilbert concludes his recounting of the dramatic results from recent developmental genetics as follows:

> Such discoveries have converged to form a developmental evolutionary synthesis that incorporates the population genetic approach but which expands evolutionary theory to explain macroevolutionary phenomena as well. ... We are at a remarkable point in our understanding of nature, for a synthesis of developmental genetics with evolutionary biology may transform our appreciation of the mechanisms underlying evolutionary change and animal diversity. (Gilbert 1997: 914)

Gilbert implicitly equates the population genetic approach with traditional evolutionary theory and sees developmental genetics as the key, missing component for the synthesis. "The merging of the population genetics model of evolution with the developmental genetics model of evolution is creating a new evolutionary synthesis that can account for macroevolutionary as well as microevolutionary phenomena" (Gilbert 2000: 706).[10] Morphology is also represented as part of the Modern Synthesis when it is usually understood as having been *excluded* (Gilbert 1997: 915; see below). This portrayal of the EDB synthesis concentrates on only two disciplines, population genetics and developmental genetics, in contrast to the multidisciplinary synthesis described by Brian Hall above.[11] A synthesis between population and developmental genetics fits snugly within the confines of the genetics and embryology exclusion historiography, but does the synthesis of EDB include non-genetic disciplines such as morphology or paleobiology? Reconsidering the role of these disciplines is necessary in part because they formed a sizeable portion of the momentum behind initiatives for rejoining evolutionary and developmental perspectives prior to the explosion of developmental genetic research.

The casting of EDB primarily in terms of developmental genetics is also found in the work of other biological researchers. In a chapter on 'Development and evolution' from a paleobiological textbook, the heading 'Integration of developmental biology with the evolutionary synthesis' discusses only the importance of *Hox* clusters (R. Carroll 1997: 258–262). Under the heading

'Evolutionary developmental biology' in a book on zoological systematics, the following phrase is found: "A completely new approach to animal evolution has grown out of studies of the genetic background of mutations in *Drosophila*. These studies have shown how various genes control the development of axes and domains . . ." (Nielsen 2001: 515). This perspective is also adopted in a major undergraduate textbook where the section on EDB is given the subtitle, 'Genes that control development play a major role in evolution' (Campbell and Reece 2002: 478–480). Additionally, some philosophers have framed the issue in terms of reuniting embryology and genetics (Amundson 2000; Burian 2000).

Consonant with what has already been mentioned, the problem lies in taking the exclusion of embryology and rise of developmental genetics as the *whole* story for understanding the need to rejoin evolution and development. The use of this history as the *primary* narrative for guiding the present construction of EDB is a distortion, implying that the key rapprochement for EDB lies with developmental genetics, while forgetting others excluded from the Modern Synthesis who might be critical to normatively directing and formulating the new synthesis of EDB in the present.[12] Consider the following narrative of exclusion:

> There exists . . . a generally silent group of students engaged in biological pursuits who tend to disagree with much of the current thought [i.e. the Modern Synthesis] but say and write little because they are not particularly interested, do not see that controversy over evolution is of any particular importance, or are so strongly in disagreement that it seems futile to undertake the monumental task of controverting the immense body of information and theory that exists in the formulation of modern thinking. . . . Wrong or right as such opinion may be, its existence is important and cannot be ignored or eliminated as a force in the study of evolution. (Olson 1960)

Given the predominant exclusion historiography concerning genetics and embryology, it may be somewhat surprising that Olson was describing morphologists and paleontologists. Olson went to great lengths in his discussion to create a space for other conceptions of evolutionary theory that were not strictly part of the Modern Synthesis, emphasizing the tendency to consider conceptual frameworks from some disciplines more legitimate by excluding alternative stances from others. He was intensely aware of a lack of 'elasticity' in the synthetic theory of evolution that was connected with its seeming ability to explain everything. The burden of proof was shifted from showing that an alternative explanation for a phenomenon was possible to demonstrating that the phenomenon could not be sufficiently handled by the synthetic theory. "Morphologists and paleontologists feel this, perhaps, more strongly than other students of biology . . . The extent of assumption, interactions of assumptions, and the degrees of extrapolation give a sense of uneasiness when the animals and their structures are foremost in mind" (Olson 1960: 530).

Although an attempt has been made to demonstrate the importance of morphology for the Modern Synthesis in the British context (Waisbren 1988), the key distinction is between the *potential to contribute* and *actual contribution*. Goodrich, Huxley, and de Beer were all potential sources of morphological thinking for the synthetic theory, but none of them can be said to have actually made a significant contribution. Another potential source was Schmalhausen's *The Factors of Evolution* (Schmalhausen 1986 [1949]); but while there is no doubt that this book did attempt to integrate both embryology and morphology, it is also true that Schmalhausen's work was not genuinely part of the synthesis, which may have been due to a perception that it was in conflict with the work of Waddington (Wake 1986). The publication of a translation from the Russian in 1949 with the encouragement and endorsement of Dobzhansky came too late to impact the central core of the synthetic theory, which by this point had effectively passed out of the construction phase and into the realm of application for many biologists. It is possible that the inability to incorporate these more explicit morphological research programs can be attributed to national differences in scientific style that a primarily American context for the synthesis could not overcome. Regardless of the existing resources, those morphologists who *could* have made key contributions to the Modern Synthesis *did not* in fact make them.

A qualitatively stronger thesis is that morphology *could not* have made a contribution to the synthetic theory.

> To many it has seemed enigmatic that morphology contributed virtually nothing to the synthetic theory of evolution. . . . Morphology has contributed so little primarily because it has had so little to contribute. It is a descriptive science of form, and only when conjoined with other disciplines does it tell us anything about causes. . . . morphology tends to be the sort of discipline that will follow, rather then lead, in the development of evolutionary theory. (Ghiselin 1980: 181)

The Modern Synthesis was focused on the mechanism of evolutionary *processes* and morphology simply could not tackle the causal question (cf. Coleman 1980). Similarities in general characteristics were detailed in order to reconstruct the history of life but population diversity was ignored. Variation was an unimportant phenomenon, signaled by the metaphysical inclinations of many morphologists toward idealistic philosophy. These accusations lead us to another candidate for a contribution to the synthesis from the ranks of morphology in the American context – D. Dwight Davis.

In his report from the 1947 Princeton meeting of the Committee on Common Problems of Genetics, Paleontology, and Systematics, Davis opens with a familiar refrain: “Recent syntheses of current evolutionary thought have, almost without exception, ignored comparative anatomy completely or considered it only very obliquely” (Davis 1949: 64). He did not explicitly challenge the synthetic theory of evolution in this respect and acknowledged that morphologists had not thought in terms of ‘populations’ (p. 76). Davis perceived a remarkable congruence of ideas between population geneticists and evolutionary morphologists, and his article offered a picture of morphological research as *consistent* with the Modern Synthesis. A constructive account of the unique contribution of morphology can be partially recovered from a later discussion (Davis 1960). While delineating the proper goal of comparative anatomy Davis consciously steered clear of idealistic notions found in the phylogenetically oriented morphology of the Gegenbaur School,[13] locating morphology’s absence of contribution to the Modern Synthesis in transnational misunderstanding. He rejected the claim that comparative anatomy could not contribute to questions of evolutionary causality and advocated shifting the focus of morphologists from structural similarity to structural difference. The observed variations in the common structural plan attended to by comparative anatomists are based on the same mechanisms as those minor phenotypic variations described by population geneticists. The contribution of morphology to a causal understanding of evolution occurs at a level inaccessible to laboratory genetic studies, illuminating the mechanism of adaptation at higher levels of structural organization: “we are dealing with adaptation, with functional mechanisms, and differences in structure are meaningless unless they can be correlated with differences in function” (Davis 1960: 49).

Davis’s arguments for a functional approach to morphology hint that it was not just comparative anatomy *per se* that was excluded from the Modern Synthesis but rather a philosophical perspective often associated with morphology. This is evident in an editorial decision made in the early stages of the journal *Evolution*, identified in an analysis of Ernst Mayr’s pivotal role at this juncture (Cain 1994). Rainer Zangerl, a vertebrate anatomist, submitted an article to *Evolution* on the importance of comparative anatomy for evolutionary studies, which drew heavily on German idealist morphologists and argued that concepts such as *morphotype* and *structural plan* were critical for any evolutionary theory.[14] Zangerl illustrated the existence and significance of morphotypes through a study of turtle skulls and proceeded to advocate philosophical holism, with its focus on the organism, as a necessary component of evolutionary biology. “It is in this basic realm where morphology must and can make an important contribution to the future development of ultimate theoretical thinking in biology" (p. 372). After a long editorial process it was finally decided that the paper should be published, but when a rebuttal was submitted a year later it was returned with the explanation that, "the editorial board had agreed it would serve 'no good purpose' to continue with that 'discussion' " (Cain 1994: 420). *Typological* comparative anatomy was not to be a part of the ongoing conversation in the journal *Evolution*, effectively silencing its role as a contributor of theoretical perspectives to evolutionary discussion in the post-Synthesis context. Comparative anatomy and morphology in the service of paleontological studies (Schaeffer 1948), phylogenetic studies (Gregory 1950), and morphometrical analysis (Olson and Miller 1951) were acceptable as long as they were conducted implicitly within the theoretical perspective of the synthetic theory of evolution.[15]

4. Functional and evolutionary morphology

> In 1956 anatomy was moribund; the field of functional and evolutionary morphology barely existed as a scientific discipline. (Wake 1982)

The significance of morphology in 19th and early 20th century biological research, including evolutionary theory, has recently been reconsidered by a number of authors (e.g., Bowler 1996; Maienschein 1991; Nyhart 1995). In this section I draw attention to the period after the Modern Synthesis, congruent with David Wake's remarks about the status of comparative anatomy in the mid-1950s. His retrospective comments are somewhat ironic now that there are dense textbooks filled with rich examples of functional anatomical studies in an evolutionary framework (e.g., Walker and Liem 1994). The thread of continuity with the period prior to 1950 is found in individuals like Davis who articulated an agenda for morphology that was distinctly functional in orientation, pulling away from the traditional emphasis on structure apart from function. Wake identifies a reductionist research outlook as one factor in the decline of comparative anatomy in the first half of the 20th century but he also notes that the exclusion of morphology from the Modern Synthesis played a critical role (Wake 1982: 604–605).

The return of functional morphology that began in the 1960s was linked with an increasing emphasis on experimental approaches (Gans 1985; Hanken and Wake 1991; Wake 1982). New techniques such as mechanical and chemical sensors, force plates, and electromyography led to a proliferation of data that were then analyzed using new computer technology. Unsuspected aspects of morphological performance were discerned through studying the unused capacities of functional systems. Terminology was clarified to facilitate the fruitful use of data from descriptive morphology in functional investigations (Gans 1969). Explicit connections were made with phylogenetic considerations (thus leading to 'evolutionary' morphology) as well as developmental studies (Lauder 1990).[16] Because of the renewed emphasis on phylogenetics, there was an erosion of any simplistic equivalence between functional morphology and standard biomechanical studies. This can be seen most clearly in the work of George Lauder who emphasized that a diachronic approach was essential to morphology, cogently arguing for the necessity of historical analysis through the use of phylogenetic systematics (Lauder 1981, 1982a). An important aspect of utilizing an explicit phylogenetic framework is specifying a way to test hypotheses about morphological innovations (Lauder 1990; Lauder and Liem 1989), as well avoid the trap of adaptationism (Fisher 1985). As Gould noted in 1974, "[d]uring the past decade, like a thief in the night, morphology has surreptitiously become interesting again" (Gould 1974: 401)[17]

In addition to the experimental approach, philosophical aspects of the nature of and relations between functional and evolutionary morphology were addressed (e.g., Bock and von Wahlert 1965; Dullemeijer 1974, 1981). At the forefront of these discussions was an articulation of the form-function relation, foundational to all morphological investigation. Bock and von Wahlert redefined several notions of adaptation in terms of selection acting on the 'biological role' of a trait, which is comprised of a form-function complex. They, as well as Dullemeijer, dwelt on conceptually distinguishing form from structure and function from biological role, though subtle disagreements between them are evident. Dullemeijer also takes in broad philosophical themes such as holism/reductionism, idealism/realism, monism/dualism, and vitalism/materialism, as well as discussing inductive versus deductive methodology.[18]

In a review of the state of morphology in 1985, Liem and Wake gave the following definition of evolutionary morphology: "[The] field of biology that studies the evolution of form and function by combining comparative and experimental methods of analysis" (Liem and Wake 1985: 366). They advocated the necessity of including both extrinsic and intrinsic determinants of organismal 'design'. With regard to extrinsic factors, necessary components include structural analysis, functional analysis, and experimental ecological analysis. For intrinsic factors, phylogenetic and historical analysis, analysis of biological repetition, and ontogenetic analysis are essential components. The latter component (ontogenetic analysis) receives the most thorough treatment with special attention to the importance of nonlinear epigenetic processes that generate stable morphological patterns.[19] Heterochrony is invoked as a potential source for the origin of morphological novelties and the research program outlined for morphology seems to be immediately relevant to EDB. Developmental genetics is not explicitly discussed.

Although David Wake did not perceive the integration of morphology into the structure of evolutionary theory in the early 1980s (Wake 1982: 609), its impact was palpable at the fourth meeting of the International Congress of Systematic and Evolutionary Biology where the relation of functional morphology and biomechanics to evolutionary biology was discussed (M. Wake 1991). Shortly thereafter, Marvalee Wake reviewed the breadth and scope of current studies in evolutionary morphology drawing attention to the reintroduction of whole-organism approaches, comparative biology, and architectural/constructional constraints (M. Wake 1992). Two factors that affected this impact were more explicit attention to methodological issues in functional morphology, such as the building and testing of models (Homberger 1988), and the study of the role of ecology in the actual performance of morphological trait complexes (Wainwright and Reilly 1994). This latter area, dubbed 'ecomorphology', unites notions such as phenotypic plasticity, heterochrony, and constructional constraints (Goldschmid and Kotrschal 1989; Reilly 1994). This conjunction maps nicely onto themes observed earlier in the work of Schmalhausen and signals that an interest in the intersection of evolutionary and developmental approaches is likely to be common among ecomorphological researchers.

The interface between morphological studies and the emerging synthesis of evolution and development was explored in a variety of papers at the 2nd International Symposium on Vertebrate Morphology in 1986 (Splechtna and Hilgers 1989). Tissue interactions in morphogenesis, the development and evolution of the vertebrate limb and skeleton, heterochrony, mechanical interactions during ontogeny, and developmental constraints in the evolution of feeding systems were some of the topics discussed, as well as specific morphological novelties such as the turtle carapace or the intermaxillary joint of bolyeriid snakes arising from ontogenetic mechanisms. Not one of the thirty contributions mentioned findings from developmental genetics.[20] Rupert Riedl's opening address forcefully argued for the centrality of morphology in evolutionary theory, emphasizing the unique position of comparative anatomy in explaining complex biological characters (Riedl 1989; cf. Riedl 1983). These sentiments were echoed in the closing sessions with respect to morphology's unique position from which to understand complex evolved systems via a fundamentally comparative methodology (Duncker 1989; Gans 1989). Although aspects of Riedl's reasoning are debatable, especially the attempt to bring anatomical structures, cognition, and culture under a single theoretical umbrella, his presence is a reminder of the significance of morphology for EDB because his students (e.g. Günter Wagner and Gerd Müller) are currently key participants.

5. Innovation and novelty

> There are fashionable problems and there are neglected problems in any field of research. The problem of the emergence of evolutionary novelties has undoubtedly been greatly neglected during the past two or three decades, in spite of its importance in the theory of evolution. (Mayr 1960)

The origin of novel structures and functions is an old problem in evolutionary biology, going back to Darwin himself.[21] Standard examples include the turtle carapace (Burke 1989; Gilbert et al. 2001), avian flight (Cracraft 1990) and feathers (Prum 1999), and vertebrate feeding systems (Roth and Wake 1989), as well as more recent examples such as centipede segment number (Arthur 2000b). Ernst Mayr brought the topic back under consideration in the post-Synthesis context, trying to show how evolutionary novelties could be handled within the context of the synthetic theory of evolution without recourse to saltationism or macromutationism, which were both deeply interlinked with typological thinking (Mayr 1960). Although his discussion broadly addresses the emergence of qualitatively new 'characters' ("... any newly arisen character, structural or otherwise, that differs more than quantitatively from the character that gave rise to it"), he adopts a working definition of novelty that is functional in orientation in contrast to a structural definition more natural to the domain of traditional comparative anatomy: "Tentatively, one might restrict the designation 'evolutionary novelty' to any newly acquired structure or property which permits the assumption of a new function" (p. 351). Importantly, Mayr recognizes that the primary loci for discussions of innovation and novelty were the disciplines of comparative anatomy and paleontology but he ultimately reduces the project of explaining the emergence of evolutionary novelties to population genetics in sync with the Modern Synthesis theoretical framework.[22]

Walter Bock's functional morphology of avian jaw articulation is a good example of the connection between the origin of novelty and morphological investigation in the post-Synthesis context (Bock 1959). His study of the functional morphology of double jaw articulation in birds illustrated Mayr's point that the transfer of function for the origin of novelty can take place in the presence of a structural duplicate (Mayr 1960: 362). In particular, Bock attempted to account for the secondary basitemporal articulation in the avian mandible (the medial brace) that prevents the jaw from disarticulating under strong forces during feeding activity (such as skimming for fish). The concept of *preadaptation* plays a central role in Bock's argument, paralleling Mayr's functional approach to evolutionary innovation.[23] Bony knobs on the basitemporal plate, which served as attachment points for cervical muscles, were preadapted for the secondary articulation of the medial brace due to their position and projection with respect to the entire basitemporal plate. Bock's research also demonstrates that the study of evolutionary novelty is a natural point of intersection for morphological and developmental research perspectives, which is highlighted by his appeal to Schmalhausen's theory of stabilizing selection to account for how the jaw articulation could have arisen non-genetically and later been brought under genetic control during ontogeny.

Proponents of EDB see their nascent synthesis as a prime venue for exploring unanswered questions about the origin of evolutionary novelties.[24] Rudolf Raff holds that, "questions on the nature of homology, . . . the origin of novelties and ultimately a complete understanding of evolution lie before this young discipline [EDB]" (Raff 2000: 79; cf. Raff 1996: Ch. 12). The focus on innovation and novelty was made even more explicit in a presentation at the inauguration of the EDB professional subdivision during the annual meeting of the Society for Integrative and Comparative Biology in 2000.

> [EDB] may lead to a mechanistic explanation of the origin of *evolutionary innovations* and the *origin of body plans*. . . . Evolutionary innovations and the evolution of body plans are hard to understand in population genetic terms since they involve radical changes in the genetic/developmental architecture of the phenotype. . . . evolutionary innovations are outside the scope of any current research program. Through its contribution to the solution of that question, [EDB] genuinely expands the explanatory range of evolutionary theory. We think that this is the one area where [EDB] will have its most lasting impact on evolutionary theory and biology in general. . . . we see in the problem of innovation and the evolution of body plans a unique opportunity for [EDB] to develop its own independent identity as a research program." (Wagner et al. 2000: 820, 822)

Wagner and his colleagues intentionally emphasize the explanatory poverty of traditional population genetic analyses for understanding evolutionary innovation (pp. 822–823). Although both population and developmental genetic mechanisms contribute to evolutionary processes, one or the other may have more explanatory force for a particular phenomenon (Wagner 2000). Many advocates of EDB incline towards the significance of epigenetic dynamics in relevant ontogenetic processes as the source of the origin of morphological novelty (cf. Newman and Müller 2000). EDB makes an essential contribution to the problem of innovation and novelty by providing the mechanistic details of these epigenetic processes.[25]

An important variant on the concept of innovation is the notion of a *key innovation*, referring to the capacity of a morphological change to elicit a significant adaptive radiation. One of the most famous examples is the origin of the pharyngeal jaw apparatus in cichlid fish, which allowed a massive proliferation in African lake habitats by differential specialization of feeding structures (Liem 1973, 1980, 1990). The morphological reorganization within the pharyngeal jaw apparatus brought about by the presence of two new joints, a sutured connection, and a shift of insertion points for two muscles made it possible for cichlids to adopt a wide range of feeding specializations with amazing efficiency in adaptive zones with different diet opportunities. The origin of this new morphological complex is in part dissected by attending to the ontogenetic trajectories of its components, providing a possible mechanism whereby "relatively simple genetic alterations could slightly affect the scheduling or velocity of ontogenetic events, which in turn are capable of producing adult phenotypic changes of rather profound but not monstrous dimensions" (Liem 1973: 439). The adaptive complex of cichlids that conferred the competitive advantage in feeding capacity was in part identified using functional morphological experimentation, such as electromyography. Although subsequent work has qualified these conclusions (Jensen 1990), the importance of the adjective 'key' is meant to point to the adaptive significance of a morphological novelty, which may also be considered a synapomorphy for a monophyletic clade and explain the relative abundance of a species within a larger family of organisms.

Another good example of a key innovation is the hypocone in mammalian dentition, which is an additional cusp to the triangular upper molar teeth that has evolved repeatedly in mammalian lineages (Hunter and Jernvall 1995). Although the phenotypic change required to produce a hypocone is minimal, analysis of lineage diversification reveals that the mammalian species with hypocones are extremely diverse, correlated with the advantage obtained in herbivorous adaptive niches. A related analysis of seal populations reveals that discrete variation in dental cusp number (between three and five) is generated in a biased fashion through small developmental changes (Jernvall 2000). By implication, the key innovation of the hypocone can be understood as a product of the capacity of evolvability exhibited in the ontogenetic processes of mammalian tooth formation. The quantification of gene expression patterns during odontogenesis in mice and voles (using data from whole-mount *in situ* hybridization in combination with Geographic Information Systems to 'map' the dental topography) demonstrates that differences in dental morphology can be accounted for by a spatial shift in gene regulation (heterotopy) during initial cusp formation and multiple iterations of one particular topographical region (Jernvall et al. 2000). This data has recently been incorporated into a gene network model that captures the features of dental development while simultaneously revealing that small parameter changes lead to significant morphological changes analogous to paleontological observations of evolutionary transitions in mammalian dentition (Salazar-Ciudad and Jernvall 2002).

The concept of innovation is not without difficulties. It has been linked (with controversy) to the origin of higher taxa, the proliferation of diversification, and evolvability (see Hunter 1998). Some have questioned the ontological status of the characters typically taken to be innovations, pointing out that they are largely artifacts (Cracraft 1990). Part of this difficulty would be addressed by agreement on a character concept in biological research (Wagner 2001), and the importance of a delineated character concept is in part driven by an attempt to genuinely identify 'new' characters in lineages (Wagner et al. 2000). Evolutionary innovations can also be seen as the origin of particular homologies, resulting from epigenetic mechanisms overcoming developmental constraints (Müller and Newman 1999). But studies of the multiple origins of moveable abdominal lobes in male sepsid flies indicate that sexual selection may be causally responsible with developmental processes providing little to no 'barrier' (Eberhard 2001; but see Wagner and Müller 2002). Adjudicating the competition or compatibility of selection mechanisms, epigenetic processes, and development constraints is a critical question for analyzing explanations of innovation (Mitchell 1992).

Addressing all the issues at stake surrounding the concepts of innovation and novelty is important but beyond the present discussion (see Müller and Wagner 1991; Love, in preparation). Both concepts have been treated in a plurality of biological disciplines including genetics, developmental biology, morphology, physiology, and paleontology (Nitecki 1990). If EDB is a disciplinary synthesis, then it is a natural strategy to see what kind of conceptual synthesis might occur with respect to innovation and novelty when different disciplines are included. Links between generative processes that produce morphology and ecological factors that affect norms of reaction for various traits along with their respective fitness values move to the foreground. If the problem of innovation and novelty is central to EDB, then the explicit inclusion of morphology (functional or otherwise) appears to be a necessary component for the disciplinary synthesis. Reconsidering the role of morphology becomes more urgent given the increasing tendency to highlight the central role of developmental genetics in explaining innovation and novelty (Carroll et al. 2001; Marshall et al. 1999; Shimeld and Holland 2000), especially given the rapid emergence of new studies and striking results (e.g., Ronshaugen et al. 2002).[26]

6. Reconsidering the disciplinary synthesis of evolutionary developmental biology

> . . . the success of the synthetic theory in unification of highly diverse areas has gained for it remarkably wide acceptance. Such success and agreement, while natural, pose certain dangers – danger that matters pertinent to the area of study may be missed, obscured, or deemed unimportant if they are peripheral to the central construction; danger that actually relevant fact and inference that cannot be incorporated in the theory will be summarily dismissed as inapplicable; and danger of expenditures of vast amounts of time and energy in much too limited contexts. (Olson 1960)

Most advocates of EDB would argue that Olson put his finger on an important point with respect to the Modern Synthesis; but what about the EDB synthesis currently under construction? Where do success and agreement pose similar dangers? Of four prospective trends identified in an editorial in *Evolution and Development*, Wray identifies more conscious interdisciplinarity as an important future direction for EDB (Wray 2000).[27] Although he mentions paleontology, embryology, systematics, life histories, phylogenetics, and genetics, morphology is absent. Some presentations of EDB include paleontology rather than morphology as a component of the disciplinary synthesis (Holland 1999; Raff 2000; cf. Hall 2002), while comparative anatomy is distinguished from paleontology in other representations (Wagner et al. 2000).[28] In contrast to this emphasis on interdisciplinarity, others have urged the adoption of a common theoretical framework for EDB purely in terms of genetic pathways and networks (Wilkins 2002).[29] The future composition of EDB will in part depend on recognizing the potential for unique and desirable contributions from different disciplinary approaches to the problem of innovation and novelty, as well as a determination of where particular disciplines are unable to contribute. In the terminology introduced in Section 2, central concepts for EDB may demand that the disciplinary synthesis have a particular composition.

The importance of functional morphology in particular, and morphology more generally, for EDB often comes from practitioners in these disciplines. At a 1991 discussion of EDB, David Wake led a session on the relation between development and morphological evolution, which concentrated on questions such as, “What can evolutionary morphology and systematics offer students of development?” (Wake et al. 1991: 584). The concern of morphologists with the emergence of complex structures provides one intersection for evolution and development (Wake and Roth 1989). Morphometrics, a quantitative approach to analyzing morphology that attempts to discern statistical covariations among structural traits, is another point of contact and was displayed at a recent symposium on EDB (Roth and Mercer 2000). Although its foundations are not new (cf. Olson and Miller 1999 [1958]), morphometric research has been growing rapidly over the past fifteen years. Roth and Mercer recognize that morphometrics brings morphology into EDB discussions: "Most exciting is the conceptual link that morphometric characterizations may be able to provide between morphology and the genetic, developmental, and evolutionary processes and factors that influence it" (Roth and Mercer 2000: 809). Another intersection is the relation between morphology and systematics, the latter of which is unequivocally understood to be an essential disciplinary participant of EDB (Mabee 2000; Raff 1996). Most convincing of all may be research projects that are able to integrate different disciplinary components. A recent article on the origin of arthropod 'segmentation' exhibits an intersection of methodologies from systematics, functional morphology, paleontology, and development (Budd 2001). Budd argues for the gradual origin of a serially iterated epidermis in arthropods via a functional morphological scenario of preadaptation that is couched in a rigorous phylogenetic framework, attends to the particulars of the fossil record, and discusses shifts in the expression pattern of regulatory genes during ontogeny. This argument for the emergence of a major, distinctive arthropod novelty is inherently strengthened by its interdisciplinary nature but it is even more striking that functional morphology is the primary pivot for the entire paper.

Another connection between EDB and functional morphology is found in the concept of *phenotypic plasticity*, which can be seen historically through the neglect of Schmalhausen's work in the post-Synthesis context. The concept of a *norm of reaction* (adaptively interpreted), critical for understanding phenotypic plasticity, played a significant role in Schmalhausen's thinking (Sarkar 1999). Novel morphology or behavior can emerge across a norm of reaction through exposure to new environmental influences and later be canalized through natural selection into a stable ontogenetic outcome through processes such as 'genetic assimilation' (Hall 1999: Ch. 19; Newman and Müller 2000; Sarkar and Fuller 2003; Schlichting and Pigliucci 1998; West-Eberhard 1989). Heterochronic events can be induced by diet or population density differences during development leading to distinct morphologies and life histories, thereby allowing for different evolutionary possibilities (Collins et al. 1994; Meyer 1987; Reilly 1994). Environmental perturbations during ontogeny can affect embryonic motility, which initiates and modulates mechanosensitive interactions that determine the presence and extent of cartilage and bone, thereby providing a potential route to novel cartilaginous or skeletal elements (Müller 2003).[30] Because ecological factors such as fluctuating or extreme environments during ontogeny can be determinative of novel phenotypes, understanding adaptive radiations within lineages and the role of key innovations requires attending to the juxtaposition of ecological morphology and developmental evolution (Hoffman and Parsons 1997; Møller and Swaddle 1997; Schluter 1996). Besides these connections,[31] it is worthwhile to briefly consider a philosophical motif that might alter how EDB is conceptualized when the inclusion of morphology is reevaluated – typology.

The distinction between population and typological thinking was introduced by Ernst Mayr to identify the unique perspective Darwin introduced to biological investigation (Mayr 1959: 2–5). He traced 'typology' back to the ancient Greeks, connecting it with idealism and essentialism, and held that these two mutually exclusive viewpoints were the source of almost every controversy in evolutionary theory.[32] Contemporaneous researchers inclined to think 'typologically' were bothered that their research was being effectively confined to the pre-Darwinian rubbish heap by Mayr's distinction. "The statement is made, in effect, that those who do *not* agree with the synthetic theory do *not* understand evolution and are incapable of so doing, in most cases because they think typologically" (Olson 1960: 526). Olson's comments are not an exaggeration, as Mayr's writings amply demonstrate: "[M]odern evolutionary theory can only be understood in the light of population thinking" (Mayr 1959: 4). Mayr attributes the bulk of difficulties in the construction of the Modern Synthesis to typology/essentialism (Mayr 1980: 13, 17, 18, 29). Mayr's worry about misunderstanding evolution because of 'typological thinking' extends directly to the introduction of ontogenetic considerations into theorizing about evolution.

> Any author who uses findings from the ontogeny of an individual to prove one or another evolutionary theory proves thereby that he completely misunderstands the working of evolution. To extrapolate from the individual to the evolutionary 'type' and its fate is, of course, still another manifestation of typological thinking. (Mayr 1959: 8)[33]

Those seeking similarity in the pattern of evolution have not grasped their own typological predilections or the fact that contemporary evolutionary theory is primarily concerned with variation and diversity.[34]

Mayr both implicitly and explicitly tied typology to an underlying philosophical essentialism and idealism. While it is true that varieties of essentialism and idealism were barriers to evolutionary thinking, it is not clear that typological thinking logically implies either. Amundson has identified one ironic historical consequence of associating typological thinking with idealism; transcendental anatomists like Geoffroy become idealists and materialists simultaneously! (Amundson 1998: 159).[35] Recent philosophical treatments of ‘natural kinds’ suggest a viable application for biology without any appeal to microstructural essences (Boyd 1999; Griffiths 1999; cf. Wagner 1996). Natural kinds or types can be understood as homeostatic property clusters that evolve over time or historical essences (relationally defined) with detectable counterfactual force in explanations. Once any necessary link between typology and essentialism is severed, the importance of typological thinking arising within morphological investigation becomes a live issue. Typological and population thinking can be compatible but distinct viewpoints on the form-function complexes that make up organisms.

This compatibility was recognized by a number of evolutionary morphologists and paleontologists who were marginalized in the wake of the Modern Synthesis. In the midst of Olson’s complaint of exclusion we also see a nuanced approach to articulating the value of both population and typological thinking.

> [T]he attention of the morphologist tends to be centered upon form and involves to some extent a typological aspect – typological in that there is some rather concrete, visual image involved. Students with this point of view are not quite the unreconstructed villains of the field of evolution as those described by Mayr (1959). But there is the strong tendency to think in terms of morphology as characteristic of an animal, that there is a *form* representative of a species and *metric characters* characteristic of a genus. What often may appear to be a purely typological view is not, in fact, based on a disregard or ignorance of population concepts and variability but upon initial concern with stages in evolution *represented* by some genus or species, or even a representative of some higher category. (Olson 1960: 535)

In contrast to the mantra that typological thinking ignores variation because of its underlying philosophical essentialism, Olson is arguing that typological representation can be useful in elucidating broad scale patterns in the history of life. Variation is critical for understanding the dynamics of populations but the morphologist and paleontologist are often concerned with identifying patterns of *similarity*, which can then shed light on evolution at the level of complex characters across geological time.

The issue of typology is directly relevant for understanding evolutionary innovations because some believe ‘innovations’ are artifacts of typological thinking (Cracraft 1990). Mayr’s original discussion attributed all saltational explanations of novelty to the residue of typological thinking (Mayr 1960). Typological research strategies have also been a part of recent criticisms of evolutionary developmental studies of the putative phylotypic stage in vertebrates (Richardson et al. 1997). In a commentary on the status of developmental archetypes, it is acknowledged that there are some advantages to the typological approach but caution is necessary to avoid pitfalls supposedly associated with understanding types as more than artifactually selected clusters of conserved features (Richardson et al. 1999). Although Richardson and his colleagues argue for 'alternatives' to typologism, their main suggestion is that typological models reflect the reality of variation and diversity – a compatibility thesis for population and typological thinking aims for exactly this result.[36]

One way for typology to reenter is through a strict distinction between pattern and process in the history of life (Dullemeijer 1981; Rieppel 1988). Once we restrict our attention to pattern, "[t]he basic goal of comparative anatomy is to determine regularities of structural organization that enable a classification and understanding of the ordered diversity of form" (Shubin and Alberch 1986: 377). Notions such as '*the* tetrapod limb' can be understood as scientific idealizations or abstractions, defined by patterns of relations that obtain among the relevant components and processes, which are explanatorily deployed rather than metaphysically motivated (Amundson 2001).[37] In other words, the tetrapod limb is typologically characterized by historical essences relationally defined without an implicit 'natural state'. The study of the morphogenesis of the tetrapod limb by Shubin and Alberch reveals that the intersection of evolution and development is precisely where one would expect typological thinking to be necessary for explanation.

> . . . this typological and static approach is not opposed to evolution or even to natural selection. . . . it does not draw from evolutionary mechanisms based on environmentally defined selection and random mutation. The quest for a general set of principles of form is legitimate if we exchange the metaphysical concept of the *Bauplan* for a mechanistic one based on principles of morphogenesis and internal integration. (Shubin and Alberch 1986: 377)

Mechanistic components in the ontogenetic trajectory of the tetrapod limb type include *de novo* condensation of a single proximal element and the bifurcation of this element into two distal elements establishing the preaxial and postaxial series (pp. 360–362). The tetrapod limb is not an artificial construct but a significant suite of conserved characters in evolution that is generated by morphological processes and results in discrete forms due to developmental constraints (cf. Hall 1996). It must be understood in terms of its stable internal relations across all tetrapods and not just with respect to the diversity of relations manifested in the populations of particular species (Shubin 1991).[38] Sub-types of the tetrapod limb can be informatively compared across distant phylogenetic spans of time, generating both explanations of form and suggesting evolutionary mechanisms. Analyses of intrapopulational variation within these sub-types (or 'standard patterns') can

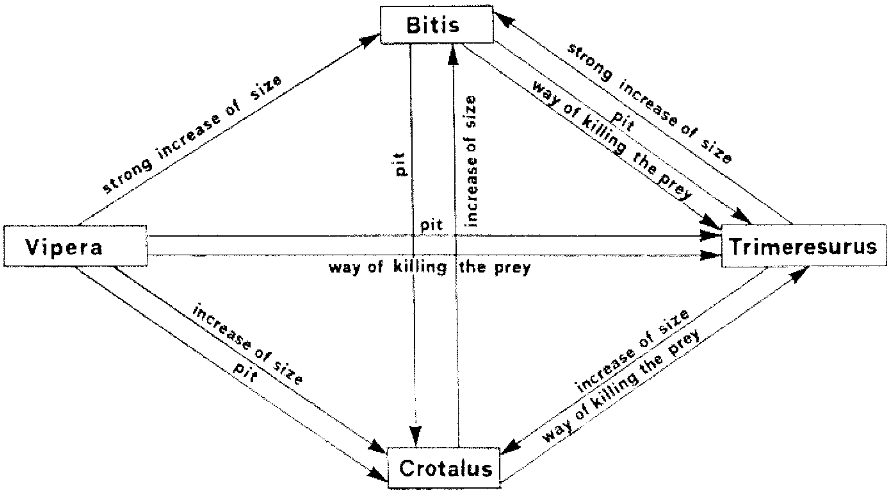

Figure 1. Idealized transformations of viperid snake heads (Dullemeijer 1974: 206. Reprinted with the permission of P. Dullemeijer).

reveal idealized transformation possibilities that can then be dissected with respect to polarity and homoplasy for a particular lineage, such as major transformations of salamander limb structure, directing attention to underlying generative mechanisms of variability in the origin of novelty (Shubin and Wake 1996; Shubin et al. 1995).

These idealized transformations also suggest particular adaptive scenarios based on functional morphology. Dullemeijer studied the head morphology of the common viper and was able to detail all the relevant cartilaginous, myological, and osteological elements from which a distinct number of functions could be discerned – such as swallowing, vision, and smelling (Dullemeijer 1974: 206ff; 1981: 226–228; cf. Schwenk 2001: 172–173). Explicit consideration of these functions and their underlying components allowed Dullemeijer to dissect where key interactions among elements existed, revealing dependencies among the functions. Once these elements and their interconnections were understood, an idealized possibility space for the evolution of head morphology among four genera of viperid snakes could be diagrammed according to these functional interdependencies (Figure 1). These transformation possibilities can be historically ordered through phylogenetic considerations, which now not only yield character polarity but also an idea of the mechanistic transitions between characters that constitutes the evolutionary history of this group of organisms.

Ultimately, the most basic rationale for an inclusion of morphology in EDB when trying to understand the composition, construction, and interactions of organisms is the desire for integrated explanations (Wray 2000: 126). The identification of both stability and variability at different levels of abstraction as seen in some of the examples above appears to be critical for accurate evolutionary explanations and, therefore, for EDB. A difficulty lies in deciding what exactly is in need of explanation. A gene-centered (or even cell-centered [Hall 2001; Hall, this volume]) EDB will undoubtedly marginalize organism-centered research programs like functional morphology in the long run. Many functional morphologists do not work on the prevalent model organisms where the genetic architecture and ontogeny have been finely dissected. The presence or absence of research on non-model organisms at higher levels of organization may significantly alter how EDB will evolve in the future, including any attempts to explain evolutionary novelties. Recognizing these issues is critical to the continuing project of synthesizing evolutionary and developmental biology and motivates a reevaluation of the role of typological thinking.

7. Concluding remarks

> No phenomenon has ever been found in organic nature that cannot be interpreted within the framework of the modern, synthetic theory of evolution. (Mayr 1959)

Many proponents of EDB find Mayr’s one time confidence unsustainable in the present, believing that the framework of the modern, synthetic theory of evolution is problematic precisely because development is excluded. This recognized problem in the conceptual foundations of contemporary biology (‘rejoining’ evolution and development) is traceable to historical factors such as the exclusion of embryology from the Modern Synthesis. But since morphology was also excluded, there is more to the foundational problem. Because evolutionary biology is often conceived of in predominantly ‘genetic’ terms, the genetics and embryology exclusion historiography tends to overemphasize developmental genetics as the route to an EDB synthesis. If we concentrate on the concept of innovation (or novelty), the inclusion of morphology as a discipline in EDB appears critical and suggests a reevaluation of how the notion of innovation from functional morphology and comparative anatomy bears on the one desired in the EDB synthesis. The historical connection between morphological studies and novelty encourages the explicit consideration of morphology as a participating discipline within the emerging synthesis precisely because evolutionary innovation is so central to EDB. Additionally, the exclusion of morphology from neo-Darwinism directs our attention to the nature of the evolutionary biology that is to be synthesized with developmental biology. If we share the concern that "evolutionary developmental biology should not be reduced to the functioning of genes" (Wake et al. 1991: 588), then considering the historical absence of disciplinary morphology can mitigate the tendency to conceptualize the synthesis of evolution and development solely in terms of developmental genetics.[39] As noted, research on evolutionary novelties is not immune from this tendency, as the co-option of regulatory genes often occupies center stage.

My research also casts further doubt on the thesis that developmental genetics is what stirred recent interest in a synthesis of evolution and development. As one prescient researcher noted, "much work needs to be done in the use of data supplied by relations between embryonic development and evolution in order to obtain a better knowledge of genetic mechanisms. It seems to us that the phenomena we have described could, one day, be very useful to geneticists" (Delsol 1977: 134–135). More attention needs to be given to disciplines such as morphology and paleontology, especially since the Modern Synthesis, to understand historical trajectories relevant to contemporary EDB (Love 2003). And since EDB is a synthesis in the process of construction rather than a completed product, how the history is understood is even more critical – nothing less than the future shape of EDB is at stake.

This paper has been exploratory in nature, pointing in the direction of further philosophical analysis based on historical investigation,[40] while simultaneously providing a provisional conclusion. The suggestion to openly utilize typological thinking within EDB is more controversial than merely explicitly including morphology, both in its nature and relationship to population thinking for evolutionary explanations. Exploring the role of typological thinking in biological explanation also suggests dissecting the natural links between disciplines, such as functional morphology and paleontology (Thomason 1995; cf. note 17). A philosophical analysis of the emerging synthesis of EDB requires an understanding of the historical development of its disciplines, theories, explanations, and concepts to determine both the present state of the synthesis, as well as the desired state, regardless of their current fit. Any foundational problem in biology can be more adequately disentangled through attention to the phylogenetic pathway by which it arose, providing clues to articulating normative philosophical aims for contemporary science.

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Notes

[1] I will use evolutionary developmental biology [EDB] in the body of the paper and do not distinguish 'evo-devo' from 'devo-evo', though important issues lurk here (Hall 2000; Wagner et al. 2000). The NSF recently established an explicit funding program for 'evo-devo' research called the "Evolution of Developmental Mechanisms", an element within the Division of Integrative Biology and Neuroscience (Plesset et al. 2000).

[2] The 'phylogenetic approach' does not engage debates within evolutionary epistemology, which are more directly concerned with causal mechanisms (Cf. Hull 2001; Hussey 1999).

[3] A number of proposals for reconciling evolution and development have been made. (Atkinson 1992; Gilbert et al. 1996; Horder 1989; Smith 1992) My argument differs in emphasizing the possible role of morphology based on an exploration of the history of science and the contemporary stress on the concept of evolutionary innovation.

[4] That is, accomplishing conceptual synthesis does not mandate disciplinary synthesis or integration and the latter may be undesirable, impractical, or impossible. These issues have been discussed extensively elsewhere with respect to many different scientific disciplines (e.g., Bechtel 1986a).

[5] Another parallel theme, which will not be a part of my analysis, is *unification*. It has recently been carefully treated (Smocovitis 1996) and is clearly related to synthesis and integration, as discussed above.

[6] Bechtel's notion of disciplinary integration brings this out by pointing to conceptual integration and synthesis that emerges from interdisciplinarity (Bechtel 1986b: 38–47).

[7] The arguments in this section are developed and expanded with further documentation and illustration in a forthcoming paper (Love 2003).

[8] Exclusion historiography is only one way of approaching a rationale for a new synthetic approach. One could also characterize the synthesis in terms of later developments in biology (e.g., cladistics) that need to be included but were not part of the Modern Synthesis in the 1940s.

[9] If the national scope of the Modern Synthesis is construed broadly to include research that was not widely known or incorporated, then evaluating the 'exclusion' of research emphases becomes more difficult (Reif et al. 2000).

[10] Gilbert's textbook remarks both summarize a widely held viewpoint and represent aspects of his own nuanced account. E.g, "Classical evolutionary theory considered evolution a subset of population genetics and explained natural selection in terms of changes in gene frequencies. . . . The present synthesis of evolutionary biology and developmental genetics provides

a different, and complementary, view of the roles of genes in evolution" (Gilbert and Bolker 2001: 452).

[11] Another prominent example of this viewpoint is found in the work of Wallace Arthur (1997: 32, 43; cf. Arthur 2002). Population genetics is considered the core of evolutionary theory and developmental genetics is the critical missing component. This perspective is enhanced by an accompanying diagrammatic representation of evolutionary theory (Arthur 1997: 287), which I discuss at length elsewhere (Love 2003).

[12] I am *not* claiming that the results of developmental genetics are insignificant. My concern is whether the recent empirical success of developmental genetics is thought to be the core of EDB because of a particular historiography and if developmental genetics is the primary component in an understanding of innovation for EDB. For a critical discussion of developmental genetics in the context of EDB, see Robert (2001). Understanding developmental genetics as the 'bridge' between evolution and development for the formation of EDB does not imply that ecological issues such as selection and population dynamics have been duly incorporated by practitioners of EDB (Greg Davis, pers. comm.; cf. Wilkins 2002: 13).

[13] Carl Gegenbaur (1826–1903) was a German morphologist who developed a research program in evolutionary morphology in the wake of Darwin's publication of *On the Origin of Species* (1859). The main goal of Gegenbaur's comparisons of animal structure was an elucidation of phylogenetic relationships in order to discern the evolutionary laws of form. Gegenbaur's evolutionary morphology attracted a number of younger researchers but was foundering by the beginning of the 20th century. (For more details, see Nyhart 1995.)

[14] "In morphology, the norm is the morphotype which is an abstraction of the actual form variety within a group of organisms of the same structural plan. It is arrived at by abstraction . . . disregarding all the numerous peculiarities of form in the individual representatives of the group, and including only those features that are unspecialized and mutually present in all . . ." (Zangerl 1948: 357).

[15] The contribution of Bernard Rensch can be understood similarly (Rensch 1959). Although a zoologist trained in comparative morphology, his comprehensive study comports with the synthetic theory of evolution, highlighting the importance of allometry. His use of the notion of 'type' and its idealist connotations came under the suspicious eye of architects of the Modern Synthesis (Simpson 1949: 184).

[16] Functional morphology is not equivalent to evolutionary morphology, although many practitioners now see the two as intricately intertwined through the necessity of a phylogenetic perspective (Dullemeijer 1981; M. Wake 1992).

[17] Gould's comments are a reminder that an important connection exists between morphology and paleontology, already indicated by Olson. A full exploration is beyond the scope of the present paper but relevant sources include Raup (1972) and Seilacher (1973).

[18] Notably, E.S. Russell's *Form and Function: A Contribution to Animal Morphology*, was brought back into print (Russell 1982 [1916]). George Lauder commented in the introduction that, "[t]he discipline of morphology is currently undergoing a renaissance in evolutionary biology. . . . comparative morphology has emerged at the center of many active areas of research and controversy and promises to contribute new and significant theoretical concepts to our understanding of evolutionary patterns and processes" (Lauder 1982b: xi).

[19] "To understand ontogenetic trajectories one must understand epigenetics and developmental dynamics. One of the most intriguing aspects involves the complex nonlinear interactions during development. Small changes in development control parameters can be amplified during ontogeny to give dramatically different morphological results. *It is this final point that has led to the recent excitement in analyzing ontogeny in relation to evolutionary morphology and phylogeny*" (Liem and Wake 1985: 376; my emphasis).

[20] This should not be misunderstood as implying that the authors were uninterested in developmental genetics. Rather, the significance lies in the existence of a large "Development and Evolution" symposium that does not mention developmental genetics at this point in time.

[21] Evolutionary *innovations* are not equivalent to major evolutionary *transitions* (*sensu* Maynard Smith and Szathmáry 1995), the latter being a species of the former. Distinguishing innovation from novelty is important but I have not observed the distinction here and it is not essential to my argument in this paper. I am currently working on these issues in a paper entitled, 'The Problem of Innovation and Novelty'.

[22] "The problem of the emergence of evolutionary novelties then consists in having to explain how a sufficient number of small gene mutations can be accumulated until the new structure has become sufficiently large to have selective value" (Mayr 1960: 357).

[23] "A structure is said to be preadapted for a new function if its present form which enables it to discharge its original function also enables it to assume the new function whenever need for this function arises" (Bock 1959: 201). Bock took the discussions of preadaptation in Simpson (1953) and Davis (1949) as points of departure. Davis's lifelong morphological study of innovation in giant pandas was published shortly thereafter. (Davis 1964; cf. Love 2003).

[24] Recent textbooks on evolution and development devote entire chapters to novelty (Carroll et al. 2001: Ch. 6; Gerhart and Kirschner 1997: Ch. 5; Hall 1999: Ch. 13).

[25] Newman and Müller argue that external physico-chemical factors shaped morphology, generating innovations prior to the existence of a genetic architecture that later allows for a fixed inheritance of the morphology and its construction rules (Newman and Müller 2000). Their position is strikingly similar to Schmalhausen's.

[26] Wagner's discussion of the innovation of the 'eyespot organizer', emphasizing the inability of traditional explanatory accounts and the essential need to understand developmental mechanisms, trades on a primary distinction between population genetics and developmental genetics (Wagner 2000).

[27] The other three are denser phylogenetic sampling, shorter timescales, and an emphasis on gene interactions.

[28] Brian Hall's EDB textbook also explicitly recognizes the role of functional morphology (Hall 1999: 396).

[29] "The implicit claim is that this concept [of genetic pathways and networks] provides a useful framework not merely for the best-understood developmental processes in key model organisms and their nearest relatives, but, in principle, for *all* evolutionary developmental changes" (Wilkins 2002: 504).

[30] Müller recognizes that these kinds of studies would constitute a *functional embryology*, or functional morphology of embryos, which seems highly appropriate for the EDB synthesis (Müller 2003: 59).

[31] There are further connections that I have not explored here. For example, morphometric methods are also utilized in functional morphological studies of ecology and ontogeny (Collins et al. 1994).

[32] "The ultimate conclusions of the population thinkers and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different" (Mayr 1959: 2).

[33] Mayr's distinction between ultimate and proximate causation affords him a different rationale for why ontogenetic studies cannot contribute to evolutionary theory (Mayr 1994).

[34] Very few biologists have located sources of difficulty for biological theorizing in population thinking (but see Baron 1991).

[35] When Riedl brought the decline of morphology to the attention of Ernst Mayr, Mayr responded, “Morphology is nothing but German idealistic philosophy” (Riedl 1983: 206).

[36] Very few EDB proponents have been willing to positively discuss typology or challenge the typological/populationist thinking dichotomy (but see Hall 1996, 1999: 398).

[37] Amundson further articulates this distinction in a forthcoming essay review entitled ‘Phylogenic Reconstruction Then and Now’.

[38] “. . . talk of *the urodele limb* is not just a way of referring to the limbs of urodeles. Like the bauplan, the urodele limb is an abstract theoretical construct that expresses shared patterns of development” (Amundson 2001: 321).

[39] A recent conference entitled ‘The Developmental Basis of Evolutionary Change’ (University of Chicago, October 25–28th, 2001) focused primarily on developmental genetics. Although I have emphasized the exclusion of morphology, the trope of disciplinary exclusion points towards other potential absences. The same conference had only one poster on plants, which play a muted role in EDB discussions of innovation (but see Graham et al. 2000).

[40] For example, how does the concept of allometry fit within the morphological tradition and evolutionary theory (Gayon 2000; Gould 1966), and what are its relations to contemporary morphometrics, functional morphology, and EDB? (Bookstein 1991; Klingenberg et al. 2001; Roth and Mercer 2000). Other potential ramifications lie in conceptual connections between *innovation* and adaptive radiation, evolvability, homology, macroevolution, model organisms, modularity, preadaptation, and syn/apomorphy.

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