Evolutionary Novelty and the Evo-Devo Synthesis: Field Notes

Ingo Brigandt*

Department of Philosophy, University of Alberta

2-40 Assiniboia Hall, Edmonton, AB T6G 2E7, Canada

email: brigandt@ualberta.ca, phone: 780-492-0623, fax: 780-492-9160

*Author for correspondence

Alan C. Love

Department of Philosophy, Minnesota Center for Philosophy of Science, University of Minnesota

831 Heller Hall, 271 19th Ave. S, Minneapolis, MN 55455-0310, USA

email: aclove@umn.edu, phone: 612-625-4510, fax: 612-626-8380

Abstract:

Accounting for the evolutionary origins of morphological novelty is one of the core challenges of contemporary evolutionary biology. A successful explanatory framework requires the integration of different biological disciplines, but the relationships between developmental biology and standard evolutionary biology remain contested. There is also disagreement about how to define the concept of evolutionary novelty. These issues were the subjects of a workshop held in November 2009 at the University of Alberta. We report on the discussion and results of this workshop, addressing questions about (i) how to define evolutionary novelty and understand its significance, (ii) how to interpret evolutionary developmental biology as a synthesis and its relation to neo-Darwinian evolutionary theory, and (iii) how to integrate disparate biological approaches in general.

Keywords: evolutionary developmental biology, interdisciplinarity, evolutionary novelty, evolutionary innovation, concepts

Introduction

Explaining the evolutionary origins of morphological novelty is one of the central challenges in contemporary evolutionary biology (Müller and Newman 2005), and is intertwined with the vigorous conversation about how to relate developmental biology to standard perspectives from evolutionary theory (Hoekstra and Coyne 2007; Laubichler 2010; Minelli 2010). Extensive empirical and theoretical efforts are being devoted to novelties that have exercised biologists for more than one hundred years, such as the origin of fins in fish, the fin-to-limb transition, the origin of the turtle carapace, and the evolution of feathers (to name only a few). Developmental biology promises to make a major contribution to these explanations, in part because genotype and phenotype relations that underlie patterns of variation are studied with tools from embryology, developmental genetics, and other allied approaches (Hallgrímsson and Hall 2005; Kirschner and Gerhart 2005). "Like most scientific theories, evolutionary theory is incomplete in several respects, most conspicuously in that … it lacks a sufficient body of principles for translating between genes and phenotypes" (Futuyma 1998, 649). The renaissance of investigations into problems that demand an input from developmental researchers has catapulted the concept of novelty to the center of attention in evolutionary research. At the same time, novelty is often surrounded by controversies that include debates about its definition (Moczek 2008) and disagreement over whether it is explained adequately by different forms of gene regulation (Oakley 2007).

A novelty can be characterized as a "phenotypic trait that is new in composition or context of expression relative to established ancestral traits" (West-Eberhard 2008, 198) or more boldly as "a qualitatively new structure with a discontinuous origin" (Müller 1990, 101). While this usefully highlights the explanatory burden associated with the origin of a qualitatively new trait, it is unclear how to draw an absolute line between a quantitative variant and a qualitative difference (Moczek 2008). As a consequence, it is difficult to ascertain which phenotypic changes count as novelties in the first place. Another strategy is to define a novelty as “a new feature in a group of organisms that is not homologous to a feature in an ancestral taxon” (Hall 2005, 549). Identifying novelty with non-homology provides a precise means of identification but the clarity may be illusory given that the meaning of homology is also controversial (Donoghue 1992; Moczek 2008; Wake 2003). For example, advocates of ‘partial homology’ argue that homology is a matter of degree (Minelli 2003; West-Eberhard 2003), which seemingly returns us to a continuum between non-novelty and novelty. Other complications arise because some accounts focus on ‘key innovations’ and thus tie novelty to new adaptive capacities (Mayr 1960; Galis 2001), whereas excluding adaptive considerations is central to many discussions of the origin of novel structures (Müller and Newman 2005).

In the midst of a resurgent interest in the problem of explaining the origin of novelty, why is there so much disagreement about how to define it? Does the concept of novelty differ in this respect from other biological notions—is this a novel situation (so to speak) in evolutionary biology? Do the controversies surrounding different conceptions of novelty point towards a semantic debate, and maybe undermine the centrality assigned to this idea?

A Workshop Project on Novelty and Integration

In an effort to begin answering some of these questions, a workshop was held in November 2009 at the University of Alberta. This was the first event of an ongoing collaborative project involving biological and philosophical researchers from Canada and the US. As indicated by the workshop title ‘Integrating Different Biological Approaches,’ evolutionary novelty was used as a specific case to discuss the more general issue of synthesizing the diverse subdisciplines that compose evolutionary biology. Although often invoked as a mantra, the nature and dynamics of interdisciplinarity are central to answering biological problems: a successful explanation of the origin of a morphological novelty involves knowledge from many biological disciplines—evolutionary genetics, developmental biology, morphology, paleontology, phylogeny, and ecology (Love 2008; Brigandt in press). How are relevant data, methods, concepts, and models from these fields integrated? What is the structure of this interdisciplinary coordination?

The problem of explaining novelty is associated typically with evolutionary developmental biology (evo-devo) (Müller and Newman 2005). Although evo-devo is often described as an ongoing synthesis of different biological approaches, there are controversies about its aims and composition. Some view developmental genetics as the heart of evo-devo, the bridge to forge a synthesis between evolutionary and developmental biology (Carroll 2005; Wilkins 2002). Others conceive of evo-devo as an integration of many biological fields, where developmental genetics is only one among several intersecting approaches (Müller 2007), or as a constellation of research problems that were neglected in evolutionary theorizing after the Modern Synthesis (Love 2010; Love and Raff 2003). The relation between evo-devo and neo-Darwinian evolutionary theory is particularly contested (Hoekstra and Coyne 2007; Laubichler 2010; Minelli 2010). The aim of the workshop held at the University of Alberta was to discuss the diverse attempts to explain evolutionary novelty in the context of evo-devo, understood as an ongoing (and contested) synthesis, with a special focus on how different disciplinary approaches contribute to theoretically valid and empirically robust inferences (Wagner and Larsson 2003).

The workshop was initiated and organized by philosophers of science because the process of how different areas of science combine or integrate their divergent methods and conceptual resources is not well understood. While interdisciplinary research is a hallmark of contemporary science, philosophers have devoted most of their attention to 'theory reduction,' which revolves around the question of whether knowledge from one area of research, such as classical genetics, can be logically deduced from a more fundamental theory, such as molecular biology or biochemistry (see Brigandt and Love 2008 for discussion). Many philosophers have abandoned this model in favor of 'pluralism,' the idea that biology needs a diversity of methods, models, and approaches that coexist but may only operate in parallel. But most forms of pluralism have ignored a very real feature of scientific practice: how biological fields interact successfully. Given that many philosophical accounts fail to capture interdisciplinary explanation in biology, further study of how integration is facilitated and what limits integration is necessary. Recent progress on the problem of explaining evolutionary novelty provides an ideal locus for philosophers to study integration in action. For this reason, the workshop included biologists from various fields that contribute to explanations of novelty.

Instead of structuring the workshop around research presentations, a more profitable dialogue emerged by devoting more than half of the time to open discussion. This encouraged extensive intellectual exchange among the twenty-two participants and was made possible by advance circulation of literature pertaining to the four topical sessions of the day and a half workshop. Each session opened with brief overviews that focused attention on concrete examples or issues, such as novelties in the vertebrate skeleton (e.g., neural crest cells) or the complementarity of population genetic explanations and developmental explanations. All participants found the discussion stimulating and fruitful, and the intellectual momentum will not be lost. The November 2009 workshop was only the first step in an ongoing collaboration, funded by the Social Sciences and Humanities Research Council of Canada. Future workshops are planned (the next one in November 2010 at McGill University), and conference symposia and joint publications are in preparation.

No consensus on how to construe novelty?

One of the recurring themes of the workshop was the difficulty associated with giving a single, unambiguous definition of evolutionary novelty. Is it a backward-looking concept that defines a novelty as a trait that is not homologous to ancestral structures? Or is it necessary to include how novel structures open up future evolutionary opportunities (Wagner and Larsson 2006)? Highlighting the potential of new variation is important, but then a trait is only a (non-)novelty retrospectively, after further evolution has (or has not) resulted in a wide array of new structural variants. Does natural selection explain the origin of new variants or only their perpetuation and spread? Should there be only one sense of evolutionary novelty or can it take on different conceptualizations in different disciplinary contexts? Workshop discussion gravitated toward themes that reappear across different conceptions and specific conflicts that arise in empirical cases.

With respect to empirical cases, discussion revolved around the importance of finding precursor structures in the cases of tetrapod digits (Boisvert et al. 2008) and neural crest cells (Jeffery et al. 2004), especially whether this changes our categorization of these traits as novelties. If a novelty is a “new constructional element in a body plan that neither has a homologous counterpart in the ancestral species nor in the same organism (serial homologue)” (Müller and Wagner 2003), then are these ancestral precursors homologous to the derived structure? There was general agreement that hierarchy matters for homology and novelty. A structure at a level of spatial organization and with specific cellular and histological properties can be novel (and, on this level, non-homologous to ancestral structures), even if some of the structure's parts on lower levels were present in the ancestor (Stone and Hall 2004). However, given that new structures generally consist in a mixture of conserved and novel elements (e.g., the tetrapod autopodium; Wagner and Larsson 2006), deciding whether or not they are genuinely novel may be moot.

Another question concerned how different lines of evidence are weighted in determinations of homology, especially when conflicts emerge between molecular and morphological/paleontological data (Delsuc et al. 2006; Grantham 2004). The case of avian digital homologies provided one of the most probative case studies (Wagner 2005) because recent research validates the need to synthesize diverse approaches to the problem rather than deciding in favor of one of them (Xu et al. 2009). The need for combining distinct methods when explaining novelty also connects to the importance of hierarchy because the diversity of levels of spatial organization and number of steps in a functional sequence make it implausible that a single causal factor or explanation will suffice (Love 2006). Biological mechanisms operate differently in different kinds of hierarchies (*pace* Ganfornina and Sanchez 1999).

One reality of contemporary research is the need to secure grant monies. Alongside of conceptual and empirical issues, workshop participants drew attention to the possibility that the invocation of evolutionary novelty serves more as a rhetorical device in the process of grant writing than as an important biological concept. It is true that novelty per se is often rewarded with publication in high impact journals (Michon and Tummers 2009). Researchers focused on the problem of evolutionary novelty live with a semantic curse. In recent decades the term 'novel' has increased in usage in all areas of biomedical science, appearing in the titles of 1 in every 2500 papers in 1970, but 1 in every 71 papers in 2007 (Schonberger and Rosenbaum

2009). This terminological reality does not indicate that evolutionary novelty is an unimportant concept, but it does constitute an occupational hazard for scientists working on explaining it.

The nature of the evo-devo synthesis

What's in a name? Does it matter? Evolution of development – evolutionary developmental biology – developmental evolution – comparative development – microevolution of development… Each label picks out something different but often they are run together (Hall 2000). Sticking with the label evo-devo for expository simplicity, most concur that these junctions of evolutionary and developmental themes are self-conscious combinations of biological subdisciplines, including but not limited to developmental genetics, morphology, paleontology, systematics, quantitative genetics, and ecology. Biologists recognize that the task of explaining evolutionary novelties requires integration, and evo-devo is labeled routinely as a 'synthesis' of different disciplines (Gilbert et al. 2004; Love 2003; Pigliucci 2009; Wake 1996). Yet there are very different visions of this synthesis. Is evo-devo the merging of different fields, is it a cluster of transiently overlapping approaches, or is evo-devo a genuinely autonomous discipline with its own problems and methods (Hendrikse et al. 2007; Raff 2000)? Furthermore, the integration is not a guaranteed outcome: "[it] is still in a stage where the contributing disciplines are in conceptual discontinuity" (Wagner and Larsson 2003, 3). The emphasis on integration offers an opportunity for philosophers to analyze and interpret these scientific practices to comprehend how interdisciplinarity functions, and compare these analyses with the stated views of the biologists involved, including assumptions about what constitutes desirable integration or synthesis.

In addition to these competing visions of synthesis, there are also disagreements about the importance of different developmental mechanisms for generating new variants in a population. Gene regulatory networks (GRNs) are considered by many to be the major factor that accounts for variation relevant to the origin of novelties (e.g., Davidson and Erwin 2006; Sauka-Spengler et al. 2007). Workshop participants discussed the significance of GRNs in relation to other developmental mechanisms, such as epigenetic interactions (e.g., Hallgrímsson et al. 2007), biomechanical and self-organizational processes (e.g., Newman and Müller 2005), and environmental induction via phenotypic plasticity (e.g., Palmer 2004; West-Eberhard 2003). In particular, questions were raised about whether these different mechanisms can be reduced to GRN alterations and, if so, whether this would make developmental genetics the core of a disciplinary integration or even eliminate the need for other approaches to be integrated.

Another aspect of the nature and significance of evo-devo is its bearing on neo-Darwinian evolutionary theory. Some proponents see these as strictly complementary (Minelli 2010; Sterelny 2000), whereas others see them in conflict over basic assumptions (Laubichler 2010; Robert 2002). A major component of this debate revolves around how to relate the plurality of biological explanations to one another (population genetic, quantitative genetic, paleontological, developmental genetic, embryological, ecological, etc). For example, quantitative genetic approaches to the evolution of development start with a phenotypic trait and either ask how selection can modify its underlying ontogeny or how patterns of variation constrain phenotypic evolution (Rice 2004, ch. 8). The origination of a new phenotypic trait is less clear from this methodological perspective, and is a reminder of the different conceptions of evo-devo. Does evo-devo extend standard evolutionary theory by offering a more complex genotype-phenotype map (Pigliucci 2009; Wagner 2007), or does evo-devo require a radical reconceptualization that transforms evolutionary biology from a mathematical to a mechanistic science (Laubichler

2010)? Another manifestation of this issue is observable in questions about the relationships between micro- and macro-evolutionary models: are macroevolutionary processes emergent from or not governed by microevolutionary processes (Erwin 2010; Grantham 2007)? That these debates seem intractable may be dismaying for some researchers, but workshop participants (both biological and philosophical) devoted a large chunk of time to these issues because they reflect the core dilemma: how do you integrate different approaches in evolutionary biology?

Novelty as a concept that sets a problem agenda

One assumption pervading prior philosophical studies of integration was that theories were the appropriate unit of analysis. Regardless of the preferred account of how two different areas of science relate to one another, most philosophers saw scientists as engaged in the construction of empirically adequate theories that involved laws and other generalizations. The biological discourse on explaining evolutionary novelty suggests a different (though complementary) strategy. Most researchers emphasize the origin of novelty as a distinct problem agenda and do not articulate their efforts in theory-centered terms. Therefore, a philosophical account of how different disciplines blend their conceptual and methodological resources can fruitfully focus on this problem-centered language. Elements of the problem can be characterized and articulated, revealing assumptions about what it means to generate an adequate explanatory framework. The problem of evolutionary novelty has an implicit structure consisting of different component questions and their hierarchically organized relations. Some of these questions pertain to the determination of non-homology, which requires input from fields like systematics and paleontology. Other questions involve developmental investigations of how novel variants are produced during ontogeny (e.g., gene regulation changes or epigenetic interactions). These questions will take on different shapes depending on the empirical example under scrutiny and also require that we articulate how the questions asked in particular empirical cases relate to one another. Not only does the problem of novelty call for some integration, but apprehending this problem agenda in terms of interrelated questions exposes possible locations for different disciplinary contributions and foreshadows how methodological and conceptual resources can and must be coordinated (Love 2006, 2008; Brigandt in press). A problem-focused perspective foregrounds these specific explanatory aims that stretch across scientific approaches and account for the dynamics of interdisciplinary coordination, and thereby substantially augments a conception of science that focuses only on the content and structure of theories.

A problem-centered approach aligns with general research on interdisciplinarity (e.g., Repko 2008; Szostak 2002, 2009). Explicitly adopting tactics such as redefining concepts to find consensus terminology or probing the precise location of disciplinary conflicts complement the strategy of problem clarification and characterization described above. But these efforts skirt around the edges of larger questions: how much integration is enough? Is a more unified explanatory account preferable? How much local disciplinary context is required? Does this prevent a broad explanatory synthesis? A problem-centered approach encouraged fruitful debate about evolutionary novelty at the workshop, but a fully unified perspective may not be forthcoming and even inhibit ongoing explanatory integration. Pluralism in biological research may be a necessary condition for simply moving forward. There is some solace in the fact that problems like evolutionary novelty have created a demand for systematic, interdisciplinarity connections. The associated wrangling over the nature and significance of evo-devo can be interpreted as a sign that important conceptual and explanatory work is underway.

Another advantage of viewing the concept of evolutionary novelty as setting a problem agenda is that it decreases the significance of disagreements about defining novelty or difficulties in distinguishing between novel and non-novel characters. Instead of a worry about circularity ('don't we need a definition of novelty before we can even state the problem of novelty?'), the problem-centered perspective permits prosecuting research on novelties without having to decide in advance which evolutionary steps count as 'genuine' novelties. Something similar holds in other areas of research. There are debates about whether the definition of adaptation should include current fitness effects only (Reeve and Sherman 1993). Whether something counts as a genuine adaptation (on one or more definition) does not preclude investigation and attempts to address the problem of adaptation. Homology provides another case because homologues could be established reliably before the advent of evolutionary theory and the existence of different definitions has not diminished its practical applicability or its theoretical importance (Griffiths 2007). Scientific concepts can point to natural phenomena in need of explanation even if different definitions are debated and rival accounts of a phenomenon are proposed. The definitional worry about novelty focuses on identification, not explanation, but identifying a structure as novel (or non-novel) falls short of explaining its evolution. The concept of evolutionary novelty can set a problem agenda that is stable across changes in particular scientific conceptions and explanations. Agreement that novelty is an important scientific problem coexists with disagreements about which characters are novelties, which explanatory accounts are appropriate, and which standards should be used to assess specific explanations.

The common criticism that definitions of novelty fail to make a precise distinction between merely quantitative and genuinely qualitative morphological changes is as an indicator of expectations about our scientific concepts. Some concepts are used primarily to categorize and classify, but a key role of the concept of evolutionary novelty is to highlight a research agenda—

the need to offer a mechanistic explanation of the origin of structures. The evolution of a derived character such as digits in the tetrapod limb may be deemed a genuine novelty. Subsequent investigation might reveal that this morphological transition is the result of a rather minor rearrangement of ancestral developmental pathways and tissue interactions. For some, this suggests that digits are not really a novelty; in fact, “we may be surprised by how much new is possible through modifications of the familiar” (Moczek 2008, 443). But an explanation of the origin of tetrapod digits is an important achievement regardless of whether a particular definition categorizes it as a novelty. The same holds for other domains; an explanation of a putative adaptation is important even if it concludes that the trait is a by-product of adaptive evolution (i.e., an ‘exaptation’). This accounts for why agenda-setting concepts such as adaptation or novelty are unlikely to disappear or be eliminated as increasingly robust explanations emerge from biological research. Thus, we must ask whether the scientific purpose of the concept of evolutionary novelty is to set a problem agenda, or rather to ensure a precise categorization that sharply distinguishes novelties from non-novelties.

The diverse roles that concepts play in scientific reasoning are further support for an ongoing dialogue between biologists and philosophers about explanatory integration in evolutionary biology. We take this to be an auspicious beginning that sets high expectations for the future. We also hope that it inspires other collaborations of a similar nature on the diverse cognitive landscape commonly referred to as ‘biology.’

Acknowledgements

Ingo Brigandt's work is supported by the Social Sciences and Humanities Research Council of Canada (Standard Research Grant 410-2008-0400). Alan Love's work is supported by the McKnight Land-Grant Professorship at the University of Minnesota.

References

Boisvert CA, Mark-Kurik E, and Ahlberg PE. 2008. The pectoral fin of Panderichthys and the origin of digits. Nature 456:636-638.

Brigandt I. in press. Beyond reduction and pluralism: toward an epistemology of explanatory integration in biology. Erkenntnis.

Brigandt I, Love AC. 2008. Reductionism in biology. In: Zalta EN, editor. The Stanford Encyclopedia of Philosophy. Fall 2008 Edition. http://plato.stanford.edu/archives/fall2008/entries/reduction-biology.

Carroll, SB. 2005. Endless Forms Most Beautiful: The New Science of Evo-Devo. New York: WW Norton.

Delsuc, F, Brinkmann H, Chourrout D, and Philippe H. 2006. Tunicates and not cephalochordates are the closest living relatives of vertebrates. Nature 439:965-968.

Davidson EH, Erwin DH. 2006. Gene regulatory networks and the evolution of animal body plans. Science 311:796-800.

Donoghue MJ. 1992. Homology. In: Keller EF, Lloyd EA, editors. Keywords in Evolutionary Biology. Cambridge, MA: Harvard University Press. p 170-179.

Erwin DH. 2010. Microevolution and macroevolution are not governed by the same processes. In: Ayala F, Arp R, editors. Contemporary Debates in the Philosophy of Biology. Malden: Wiley-Blackwell. p 180-193.

Futuyma DJ. 1998. Evolutionary Biology. 3rd ed. Sunderland: Sinauer Associates.

Galis F. 2001. Key innovations and radiations. In: Wagner GP, editor. The Character Concept in Evolutionary Biology. San Diego: Academic Press. p 581-605.

Gilbert SF, Opitz JM, Raff RA. 1996. Resynthesizing evolutionary and developmental biology. Developmental Biology 173:357-372.

Grantham TA. 2004. The role of fossils in phylogeny reconstruction: why is it so difficult to integrate paleontological and neontological evolutionary biology? Biology and Philosophy 19:687-720.

Grantham TA. 2007. Is macroevolution more than successive rounds of microevolution? Palaeontology 50:75-85.

Griffiths PE. 2007. The phenomena of homology. Biology and Philosophy 22:643-658.

Hall BK. 2000. Evo-devo or devo-evo: does it matter? Evolution & Development 2:177-178.

Hall BK. 2005. Consideration of the neural crest and its skeletal derivatives in the context of novelty/innovation. Journal of Experimental Zoology (Molecular and Developmental Evolution) 304B:548-557.

Hallgrímmson B, Hall BK, editors. 2005. Variation: A Central Concept in Biology. San Diego: Elsevier, Academic Press.

Hallgrímsson B, Lieberman DE, Liu W, Ford-Hutchinson AF, Jirik FR. 2007. Epigenetic interactions and the structure of phenotypic variation in the cranium. Evolution & Development 9:76-91.

Hendrikse JL, Parsons TE, Hallgrímsson B. 2007. Evolvability as the proper focus of evolutionary developmental biology. Evolution & Development 9:393-401.

Hoekstra HE, Coyne JA. 2007. The locus of evolution: evo-devo and the genetics of adaptation. Evolution 61:995-1016.

Jeffery WR, Strickler AG, and Yamamoto Y. 2004. Migratory neural crest-like cells form body pigmentation in a urochordate embryo. Nature 431:696-699.

Kirschner MW, Gerhart JC. 2005. The Plausibility of Life: Resolving Darwin's Dilemma. New Haven: Yale University Press.

Laubichler M. 2010. Evolutionary developmental biology offers a significant challenge to the neo-Darwinian paradigm. In: Ayala F, Arp R, editors. Contemporary Debates in the Philosophy of Biology. Malden: Wiley-Blackwell. p 199-212.

Love AC. 2003. Evolutionary morphology, innovation, and the synthesis of evolutionary and developmental biology. Biology and Philosophy 18:309-345.

Love AC. 2006. Evolutionary morphology and evo-devo: hierarchy and novelty. Theory in Biosciences 124:317-333.

Love AC. 2008. Explaining evolutionary innovation and novelty: criteria of explanatory adequacy and epistemological prerequisites. Philosophy of Science 75:874-886.

Love AC. 2010. Rethinking the structure of evolutionary theory for an extended synthesis. In Müller G, Pigliucci M, editors. Evolution: The Extended Synthesis. Cambridge, MA: MIT Press. p. 403-441.

Love AC, Raff RA. 2003. Knowing your ancestors: themes in the history of evo-devo. Evolution & Development 5:327-330.

Mayr E. 1960. The emergence of evolutionary novelties. In: Tax S, editor. Evolution after Darwin, Vol. 1, The Evolution of Life: Its Origin, History, and Future. Chicago: University of Chicago Press. p 349-380.

Michon F, and Tummers M. 2009. The dynamic interest in topics within the biomedical scientific community. PLoS ONE 4:e6544.

Minelli A. 2003. The Development of Animal Form: Ontogeny, Morphology, and Evolution. Cambridge: Cambridge University Press.

Minelli A. 2010. Evolutionary developmental biology does not offer a significant challenge to the neo-Darwinian paradigm. In: Ayala F, Arp R, editors. Contemporary Debates in the Philosophy of Biology. Malden: Wiley-Blackwell. p 213-226.

Moczek AP. 2008. On the origins of novelty in development and evolution. BioEssays 30:432-447.

Müller GB. 1990. Developmental mechanisms at the origin of morphological novelty: a side-effect hypothesis. In: Nitecki MH, editor. Evolutionary Innovations. Chicago: University of Chicago Press. p 99-130.

Müller GB. 2007. Six memos for evo-devo. In: Laubichler MD, Maienschein J, editors. From Embryology to Evo-Devo: A History of Developmental Evolution. Cambridge, MA: MIT Press. p 499-524.

Müller GB, Newman SA. 2005. The innovation triad: an EvoDevo agenda. Journal of Experimental Zoology (Molecular and Developmental Evolution) 304B:487-503.

Müller GB, Wagner GP. 2003. Innovation. In: Hall BK, Olson WM, editors. Keywords and Concepts in Evolutionary Developmental Biology. Cambridge, MA: Harvard University Press. p 218-227.

Newman SA, Müller GB 2005. Origination and innovation in the vertebrate limb skeleton: an epigenetic perspective. Journal of Experimental Zoology (Molecular and Developmental Evolution) 304B:593-609.

Oakley TH. 2007. Today's multiple choice exam: (a) gene duplication; (b) structural mutation; (c) co-option; (d) regulatory mutation; (e) all of the above. Evolution & Development 9:523-524.

Pigliucci M. 2009. An extended synthesis for evolutionary biology. Annals of the New York Academy of Sciences 1168:218-228.

Palmer AR. 2004. Symmetry breaking and the evolution of development. Science 306:828-833.

Raff RA. 2000. Evo-devo: the evolution of a new discipline. Nature Reviews Genetics 1:74-79.

Reeve HK, Sherman PW. 1993. Adaptation and the goals of evolutionary research. Quarterly Review of Biology 68:1-32.

Repko AF. 2008. Interdisciplinary Research: Process and Theory. Thousand Oaks: Sage Publications.

Rice SH. 2004. Evolutionary Theory: Mathematical and Conceptual Foundations. Sunderland: Sinauer Associates.

Robert J. 2002. How developmental is evolutionary developmental biology? Biology and Philosophy 17:591-611.

Sauka-Spengler T, Meulemans D, Jones M, Bronner-Fraser M. 2007. Ancient evolutionary origin of the neural crest gene regulatory network. Developmental Cell 13:405-420.

Schonberger RB, Rosenbaum SH. 2009. Not much novel under the sun. Science 326:1480-1481.

Sterelny K. 2000. Development, evolution, and adaptation. Philosophy of Science 67:S369-S387.

Stone JR, Hall BK. 2004. Latent homologues for the neural crest as an evolutionary novelty. Evolution & Development 6:123-129.

Szostak R. 2002. How to do interdisciplinarity: integrating the debate. Issues in Integrative Studies 20:103-122.

Szostak R. 2009. The Causes of Economic Growth: Interdisciplinary Perspectives. Berlin: Springer.

Wagner GP. 2005. The developmental evolution of avian digit homology: an update. Theory in Biosciences 124:165-183.

Wagner GP. 2007. How wide and how deep is the divide between population genetics and developmental evolution? Biology and Philosophy 22:145-153.

Wagner GP, Larsson HCE. 2003. What is the promise of developmental evolution? Part III: the crucible of developmental evolution. Journal of Experimental Zoology (Molecular and Developmental Evolution) 300B:1-4.

Wagner GP, Larsson HCE. 2006. Fins and limbs in the study of evolutionary novelties. In: Hall BK, editor. Fins into Limbs: Evolution, Development, and Transformation. Chicago: University of Chicago Press. p 49-61.

Wake DB. 1996. Evolutionary developmental biology: prospects for an evolutionary synthesis at the developmental level. Memoirs of the California Academy of Sciences 20:97-107.

Wake DB. 2003. Homology and homoplasy. In: Hall BK, Olson WM, editors. Keywords and Concepts in Evolutionary Developmental Biology. Cambridge, MA: Harvard University Press. p 191-201.

West-Eberhard MJ. 2003. Developmental Plasticity and Evolution. Oxford: Oxford University Press.

West-Eberhard MJ. 2008. Toward a modern revival of Darwin's theory of evolutionary novelty. Philosophy of Science 75:899-908.

Wilkins AS. 2002. The Evolution of Developmental Pathways. Sunderland: Sinauer Associates.

Xu X, Clark JM, Mo J, Choiniere J, Forster CA, Erickson GM, Hone DWE, Sullivan C, Eberth DA, Nesbitt S, Zhao Q, Hernandez R, Jia C-K, Han F-L, Guo Y. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459:940-944.