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Introduction

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When philosopher of biology Michael Ruse moved from Guelph, Ontario, to Florida State University, a very good thing happened for our understanding of the conceptual, historical, and philosophical foundations of biology. Ruse became the William H. and Lucyle T. Werkmeister Professor, which brought with it an endowment that allowed him to organize conferences on a regular basis. As usual, Michael Ruse lost no time, and the resulting series of conferences has brought together biologists, historians, and philosophers in lively discussion of a number of important topics. A favorite image of those events is that of Ernst Mayr, sitting in the boat during a swamp tour on a drowsy Florida afternoon. The aging but ever-intense Mayr seemed to be dozing, when suddenly he pointed and declared a noteworthy bird, then another, and another. That led to a discussion of whether biodiversity is declining; then to philosophical questions about how we count diversity; and finally to ethical and policy questions of why we care. Other conferences have led to debates about science and religion. And so on.

In 2005, a group of leading biologists joined philosophers and historians for four days of thinking about form and function. For this meeting, Ruse followed his usual approach. He provided the general theme, brought together a mix of enthusiastic scholars, and waited to see what happened. In this case, it was something very interesting.

While some of the papers looked at more traditional questions related to form or function, or even the two together, most asked questions about form and function in light of the (still) new emphasis on developmental evolution. They tied together what would typically have been a broad range of quite different approaches by people who would not ordinarily have been talking to each other. The (unintended) unifying theme of this conference was how form and function relate to larger issues of Evo Devo – that is, by thinking about how development informs considerations of evolution, traditional form and function questions are transformed in ways that bring them together as reflections on this new organizing theme. What we offer here are not conference proceedings, but papers that grew out of subsequent discussions inspired by that conference.

We thank Michael Ruse for stimulating the discussion, the William H. and Lucyle T. Werkmeister Endowment Fund for making such an intellectual synthesis possible, and Hilary Gaskin at Cambridge University Press for her patience as we have worked out the logistics. Our work on this volume was supported by NSF SES 0645729 to MDL and NSF SES 0623176 to MDL and JM. We offer this set of papers as an invitation to others from diverse disciplines to join the discussion. Far from addressing all possible questions or providing a summary for a mature field, this volume serves as an invitation that provides a rich collection of papers that point toward new questions and new directions for research in problems of form and function.

The papers collected here each represent a major research emphasis connected to the problem of the relationship of form and function within the diversity of approaches that make up twenty-first-century Evo Devo. Manfred Laubichler first provides a historical and conceptual analysis of the treatments of form and function within the framework of Evo Devo. He shows that many of the traditional issues connected to the relationship of form and function predate genuine Evo Devo questions, and that several of the late twentieth-century origins of Evo Devo have been focused explicitly on the relationship of form and function (Laubichler and Maienschein 2007a; Laubichler and Maienschein 2007b). Based on his analysis of the research programs, central questions, and unifying concepts of present-day Evo Devo, and current work on the developmental evolution of social behavior, Laubichler then argues that a mechanistic account of developmental evolution offers a solution to the age-old problem of integrating form and function (Laubichler 2005; Laubichler 2007a; Laubichler 2007b; Laubichler and Gadau in press; Laubichler and Müller 2007). Such a mechanistic framework of developmental evolution is based on an understanding of the general principles and molecular details of developmental systems governing phenotypic characters, and the identification of the causal connections between variation in those developmental systems and the observed patterns of phenotypic variation. It also suggests concrete evolutionary

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scenarios of how underlying developmental changes govern evolutionary transformations of phenotypes and experimental tests to uncover the selective forces driving these evolutionary transformations. This way, Laubichler proposes, the mechanistic framework of developmental evolution unites the perspectives of form and function that have so often been associated with separate explanatory frameworks and subdisciplines.

Karl J. Niklas's research program has led to remarkable insights into the general principles of plant morphology and their evolutionary origins, and it also suggests how the lessons from theoretical morphology, biomechanics, and functional analysis can be combined to arrive at a detailed understanding of plant evolution (Niklas 1994; Niklas 1997). Furthermore, his approach incorporates the developmental principles of morphogenesis and, wherever the data are available, plant developmental genetics to connect his phenotypic analysis of form and function to the larger explanatory framework of Evo Devo. Niklas's approach further demonstrates that the notion of constraint, a main focus of the first wave of Evo Devo proposals, does not just impose limits on variation, but rather is a constitutive element of any morphogenetic process that both enables and limits phenotypic possibilities.

Rudy and Elizabeth Raff's research program focuses on the relationship between developmental and evolutionary processes and, in particular, on several foundational questions of ontogeny and phylogeny, such as the origin of different modes of development (Raff 1996; Raff and Raff 2000; Raff and Raff 2007; Raff *et al.* 2003). To this end, they have adapted a unique model system: a pair of sister taxa of sea urchins with different modes of development – one direct developer and one with larval development. Taking advantage of all the tools of molecular biology, together with some more traditional approaches such as species hybridization techniques, they are now able to uncover the molecular basis of different developmental systems. This work has led to a re-evaluation of some of the most entrenched assumptions about the relationship between ontogeny and phylogeny. Even though Haeckel's phylogenetic law has in its narrow sense been disproven for a long time, the fundamental idea that earlier stages in development are more conserved than later ones continues to be widely held (Churchill 2007). The data that Rudy and Elizabeth Raff have collected over the years show that fundamental larval and developmental features can change relatively fast during evolution. Their work thus connects micro- with macroevolutionary perspectives, as well as comparative embryology (with its emphasis on form) with the ecological (functional) conditions that drive the evolution of different larval and developmental modes.

Peter Wainwright's main concern is the problem of innovation and how it relates to morphological diversity (Ferry-Graham *et al.* 2001; Hulsey and Wainwright 2002; Wainwright 2002). Several models of evolution relate rapid speciation events and their corresponding degrees of phenotypic variation to the emergence of key innovations that enable a group of species to conquer new territories or exploit new resources (Schluter 2000). These adaptive radiations are a prime example of how functional advantages drive evolutionary change; but as many of these functional benefits are a consequence of specific structures (form), it is difficult to disentangle form and function in these cases. The basic premise of evolutionary functional morphology is that form enables function and that function, measured by fitness, feeds back on the further refinement of forms or structures. In these cases, form and function are thus seen as complementary. But what exactly is a key innovation and how do we detect it in relevant datasets? This is not a trivial question. Simply assuming that whenever a group with a high number of species shares a common character (synapomorphy) this character has to be a key innovation is a clear case of tautological reasoning. Similarly, assuming that a specific character that is sufficiently different from others dramatically changes the evolutionary dynamics of the morphospace for all the species that share it also needs to be tested against objective measurements. Wainwright presents such a test in the form of a newly developed algorithm that compares and estimates rates of morphological evolution. Such measures of the rate of trait evolution control for confounding effects, such as time or shared evolutionary history, and therefore allow distinguishing adaptive radiations from normal or baseline rates of morphological evolution.

Paul Brakefield also focuses on the integration of form and function – in his case, the specific patterns of variation of butterfly eyespots (Beldade and Brakefield 2002; Beldade and Brakefield 2003; Beldade *et al.* 2005; Beldade *et al.* 2008; Brakefield 2001; Brakefield 2006; Brakefield 2007; Brakefield and French 2005; Brakefield and Roskam 2006; Brakefield *et al.* 1996; Brakefield *et al.* 2007). The butterfly eyespots are particularly interesting characters for addressing the relationship of form and function; not only do they have clear adaptive functions, but we also know quite a lot about the developmental mechanisms causing these phenotypes. Eyespots are thus prime examples of an integrative perspective on Evo Devo, one that combines form and function, or the internal developmental and external ecological processes of phenotypic evolution. Brakefield's particular combination of approaches – artificial selection experiments in the wild and laboratory analysis of developmental systems – allows him to address the degree to which the mechanisms of development facilitate and constrain phenotypic variation, and also to identify potential targets of selection among the regulatory elements of the developmental system. Discovering the allometric relationships underlying phenotypic transformations of the eyespot reveals the mechanistic underpinnings of how developmental processes are producing variation as the raw material for natural selection to act on. Brakefield's model system is thus a perfect example of how a combination of different approaches can lead to a mechanistic model of phenotypic evolution that combines the perspectives of both form and function and of evolutionary and developmental biology.

Günter Wagner presents a case study that focuses on a conflict of evidence between different research traditions and types of evidence, paleontology and developmental biology, in explanations of avian digit identity (Galis *et al.* 2002; Galis *et al.* 2005; Stopper and Wagner 2005; Vargas and Fallon 2005a; Vargas and Fallon 2005b; Wagner and Gauthier 1999; Wagner and Müller 2002). This case is instructive in many ways. It highlights the different explanatory frameworks of comparative anatomy and paleontology and experimental developmental biology. But it also points to the fact that in many cases the resolution of such conflicts does not lie in asking which of the conflicting interpretations has the stronger support – which would be akin to the old question whether form or function is the prime cause in explanations of biological phenomena – but rather in a conceptual innovation, in this case the frame-shift hypothesis, that enables us to integrate different types of evidence within one inclusive mechanistic model. Wagner's case study is therefore a perfect example of how Evo Devo can provide conceptual resolution and synthesis to some of the traditional antagonisms and conflicts within biological theories.

The papers by Roger Sansom and Richard Richards represent some of the recent philosophical work in response to the new Evo Devo orientation within biology (Amundson 2005; Sansom and Brandon 2007; Wimsatt 2007). In general, from its early inception in the 1970s, Evo Devo as a field has sought the contact of both historians and philosophers of biology. This has arguably been a most productive relationship. One of the reasons why scientists have found this contact profitable lies precisely in the integrative and interdisciplinary nature of

Evo Devo, which benefits from the kind of conceptual analyses that we see in both papers. The difficulty of establishing character transformation series (Richards) and the question of constraints (Sansom) are both central problems of Evo Devo that are connected to the problem of the relationship of form and function. Both are also in many ways foundational to the empirical studies represented in this volume.

Richards analyzes one of the central issues connected to the relationship of phylogeny and morphological evolution/character transformation. He argues that the question of whether functional considerations are a legitimate part of phylogenetic inference is ultimately an empirical one, but by delineating the various theoretical assumptions behind the two competing approaches – one privileging form, the other function – he has contributed in significant ways to the eventual resolution of this debate.

Similarly, Roger Sansom's paper presents a conceptual analysis of the notion of constraint and its roles in explanations of phenotypic evolution. As in Richard's case, Sansom does not "solve" the problem, but he provides a useful road map for future discussions, both within the philosophy of biology and within Evo Devo itself.

In a final paper, Andrew Hamilton picks up the theme of mechanistic explanation from the volume's first chapter, asking how such explanations work, what challenges arise from this approach, and how mechanistic thinking might integrate form and function on the one hand and evolutionary biology and developmental biology on the other. The paper has two central themes. The first is a discussion of the ways in which a mechanistic Evo Devo that focuses heavily on gene regulatory networks is and is not reductionistic. After arguing that mechanistic thinking leads Evo Devo toward a responsible variety of reductionism, Hamilton moves on to discuss a specific new challenge for mechanistic Evo Devo: how to understand and explain what he calls "levels of development." Hamilton's concern with levels of development grows out of asking what happens when an epistemic commitment to mechanistic thinking is combined with the ontological commitment that colonies of social insects are "superorganisms" in something more than a metaphorical sense. The challenge of the paper is for researchers to find ways to ask and answer what it means to give a mechanistic explanation of development at the colony level that is informed by what we know about development at the organismal level, as well as how the two levels inform each other's evolution.

This collection contains an embarrassment of riches. The biological studies included here should serve as a starting point for further and deeper conversations about form and function and what they mean against the backdrop of Evo Devo as a biological project. Evo Devo, of course, is as much a conceptual project as an experimental one, and we hope that the context provided here by the historical and philosophical chapters stimulates more discussion about the scope, goals, methods, assumptions, and aims of Evo Devo. These pieces taken as a whole show something of the exciting intellectual pursuit that lies ahead as Evo Devo serves as a framework for addressing long-standing issues like the relationship between form and function. Evo Devo is still new, but it is also maturing. The structure that is coming into view holds promise, and there is much work to be done in understanding how form, function, evolution, and development go together to form a nuanced picture of the biological world.

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2

Form and function in Evo Devo: historical and conceptual reflections

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The success of grand historical narratives and conceptual reflections rests, in no small part, on the selection of their central characters and features. If, as in our case here, the focus is on the development and integration of those ideas that have shaped our understanding of the living world, it is hardly possible to think of one pair of concepts more appropriate to structure a *longue durée* narrative than form and function. These linked concepts are uniquely suited to organizing the rich diversity and idiosyncratic developments within the history and philosophy of the life sciences in general, and within evolutionary developmental biology in particular.

The concepts of form and function, and everything connected to them, have been used as an organizing principle in several influential analyses of the development of the biological sciences. Their symbiotic and often dialectic relationship forms the backbone of such treatises as Ernst Mayr's *The Growth of Biological Thought*, William Coleman's *Biology in the Nineteenth Century*, Ernst Cassirer's *Theory of Knowledge* (specifically the section on the biological sciences), Edmund Beecher Wilson's *The Cell in Development and Heredity*, and, of course, Edward Stuart Russell's *Form and Function: A Contribution to the History of Animal Morphology* (Cassirer 1950; Coleman 1971; Mayr 1982; Russell 1916; Wilson 1925).

Focusing on the concepts of form and function rather than the numerous historical and empirical details of biological research allowed these scholars to capture what Russell called "typical attitudes" and their connected theoretical positions, supporting empirical evidence and the historical dynamics of scientific change. Such an approach is also useful for us, as we seek to localize the main theoretical positions of present-day evolutionary developmental biology, represented in this volume in