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The Allure of Perennial Questions in Biology: Temporary Excitement or Substantive Advance?

Alan C. Love

Manfred D. Laubichler and Jane Maienschein (eds), *Form and Function in Developmental Evolution*. New York: Cambridge University Press (Cambridge Studies in Philosophy and Biology), 2009. xviii + 234pp. A\$110; US\$95 HB.

In a provocative editorial entitled “The evo-devo comet” (2010, *EMBO Reports*, 11:489), Denis Duboule laments that evolutionary developmental biology (Evo-devo) is caught in the throes of “theoretical antagonism” due to a “conflicting *ménage*” of methodological and explanatory standards. As such, it is predisposed to diverge, “like a comet that returns closer to a planet every hundred years to fill itself with concepts and energy before leaving for yet another journey.” Duboule expresses pessimism about the possibility of achieving an “integrated theory of evolution” while recognizing that the questions involved are perennial. Evo-devo’s advertising emphasizes that substantive theoretical, empirical, and conceptual advances on longstanding questions about the origin and evolution of biological form and function are within grasp, promising a more comprehensive evolutionary theory (see, e.g., 2010, M. Pigliucci and G. Müller, eds, *Evolution—The Extended Synthesis*, MIT Press). But Duboule is worried that we are observing temporary excitement, or even false promise, and researchers will soon get off the bandwagon, give up the ideal of integration, and return to their disciplinary cubicles as the comet soars off into deep space.

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One editor of *Form and Function in Developmental Evolution* agrees that Evo-devo’s main challenge is to “integrate different perspectives on form and function...within one consistent explanatory framework” (Laubichler, 11), but begs to differ with Duboule about its prospects; a “mechanistic account of developmental evolution offers a solution to the age-old problem of integrating form and function” (2). But as the opening blurb reminds us, the volume is an “*effort* to understand very *old* questions about biological form, function, and the relationships between them” (my emphasis), and it is precisely the enduring nature of these questions that undergirds Duboule’s pessimism, even if we live in a time when the concepts and energy that overflow from Evo-devo encourage redoubled efforts at integration.

In addition to the editors’ introduction, the volume has contributions from six prominent biologists (Paul Brakefield, Karl Niklas, Elizabeth and Rudy Raff, Günter Wagner, and Peter Wainwright) working on diverse organisms from different disciplinary perspectives, three philosophers (Andrew Hamilton, Richard Richards, and Roger Sansom), and one historically trained, conceptually reflective biologist (Manfred Laubichler). Brakefield and Niklas wrestle with how constraints on form relate to adaptive function. Niklas uses computer simulation and biomass-partitioning patterns in the context of an optimality model composed of functional tasks (e.g., light interception and water conservation) to show that plant morphospace is governed by the performance requirements of these functions in combination—convergence due to selection trumps historical and developmental constraints. Brakefield mobilizes artificial selection experiments, developmental genetics, and allometry to investigate the evolution of butterfly wing morphology. Through detailed empirical work, the contours of developmental constraints on wing eyespots are identified, including differential rates of morphological change and the evolutionary limitations imposed by correlated characters.

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Wainwright’s game is functional morphology and its roots run deep in the perennial questions of form and function. He offers a general framework for how innovations that radically alter a lineage’s evolvability (e.g., the origin of flowers) lead to morphospace diversity and evolutionary radiations. These innovations increase the dimensionality of morphospace (measured by variables like trait variance), thereby facilitating the evolution of functional multiple realization (“multiple morphologies can have the same functional property”, 136). In turn, this pattern yields regions of “mechanically neutral” variation and the multi-functionality of body parts, both of which contribute to breakthroughs in the exploration of adaptive landscapes. A case study of parrotfish feeding mechanism diversity displays the fecundity of the conceptual framework.

Raff and Raff demonstrate how a non-standard model system of congeneric sea urchins with different developmental modes acts as a fulcrum to gain leverage on questions about larval origins and the structure of rapid developmental evolution. The vexing question of whether feeding larval forms came first or were secondary intercalations is reviewed in favour of the latter (in part because the ‘larvae first’ hypothesis involves a gratuitous number of convergences in gene expression patterns). New tools from developmental genetics allow the Ruffs to lift up the hood on recent larval evolution and demonstrate specific changes involved in the origin of direct developing echinoids, including the surprising result that the loss of larval features (e.g., arms for feeding) is correlated with the emergence of novel embryonic complexity, and that it occurs by similar regulatory mechanisms in other lineages. Wagner’s (previously published) piece succinctly encapsulates the conflicting methodological and explanatory standards between embryology and paleontology/systematics in the controversy over avian digit homology: “the acid test for interdisciplinary integration is the ability of researchers from different fields to agree

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on the relevant evidence and the inferences made from it” (154). Disciplinary disagreements over the interpretation and weighting of evidence need reconciliation, not adjudication, and recent research validates a synthetic approach to the problem (Xu et al., 2009, *Nature* 459:940–944). One lesson is that productive evidential integration occurs more readily in the local context of a specific question (avian digit homology), rather than at a global or theoretical level.

The philosophical contributions cover a narrower territory than that tackled by the biologists, and this is an unfortunate drawback to the volume. Sansom’s paper on constraints links well with the chapters by Brakefield and Niklas, although the discussion is somewhat abbreviated. He introduces the valuable idea of a modal hierarchy organized on the principle of specificity “to capture the complexities of the relationship between constraints that rely on the same developmental mechanisms” (209). Hamilton sketches a picture of mechanistic explanation for Evo-devo that embodies a “responsible form of reductionism” (i.e., not gene regulatory networks alone) with two concepts: ‘cohesion-generating relationships’ and ‘levels of development.’ This picture is germane to platforms of integration for different disciplinary standards, and is especially salient in the case of social insects, but Hamilton’s discussion also ends abruptly. We are given just enough of a taste to want more. The thematic links are more tenuous for the chapter by Richards, which is focused on systematics and rehearses a dated methodological debate over functional analysis and its role in comprehending character transformations. How this touches on the canvas of Evo-devo is opaque, and the unblinking treatment of a nonstandard approach using morphological hydrostatics adds to the confusion.

Laubichler’s contribution is the most bracing and directly confronts the conflicting ménage of methodological and explanatory standards in Evo-devo. Adopting gene regulatory networks as the locus of integration for a “mechanistic framework of developmental evolution”

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in conjunction with four unifying themes (regulation, modularity, plasticity, and innovation),

Laubichler traces historical connections between perennial form and function questions and their modified manifestation in Evo-devo’s diverse research programs. He sees the pendulum swings between function-dominated and form-dominated evolutionary investigations resolving into a stable equilibrium in this mechanistic framework that promises to “accomplish integration across these different explanatory frameworks and intellectual traditions” (19) by uncovering the origins and patterns of phenotypic variation that underwrite evolvability in different lineages.

There is no doubt that this volume stimulates reflection on questions of interdisciplinary integration. How much is supplied beyond stimulation is another matter. Many issues remain unaddressed, especially on the philosophical side: how do methodological and explanatory standards from the different disciplinary strands come together around form and function? How does one combine functional morphology and molecular developmental genetics? What about the tension between “organism-based developmental biology and population-based evolutionary biology (27)? How is it that “generality leads necessarily to a typological orientation” (37)? Tantalizing exemplars appear in the combinations of investigative techniques displayed by the scientific contributors, but mostly it is puzzle pieces without a box to know how they fit together. Laubichler recognizes that the volume largely represents fruitful steps forward in a difficult task: “synthesis talk is cheap; really accomplishing integration between different research traditions...is not easy” (19). I concur, but I’m not quite sure it will allay Duboule’s fears of disintegration. As Hamilton notes: “it is not clear at all what it means to have a complex mechanistic explanation that captures more than the organization of very local phenomena, particularly in ways that integrate causes at different scales” (222). A more direct antidote would be a challenge to the very idea of an integrated theory of evolution. Local and pragmatic models

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of integration that are dynamic and transient across conceptual domains may be more appropriate, and Laubichler’s discussion of model system choice is in this vein. Instead of waiting every hundred years for the comet’s return, the energizing mix of new concepts and interdisciplinarity can be synthesized from the perspective of these local, pragmatic models on the temporal scale of an NSF grant. But these piecemeal models harbor the possibility that a pluralist stance on evolutionary theory is not a temporary state of affairs (i.e., there is no single, integrated account). This is just one of the intriguing questions that the present volume prompts and it should be taken up in that spirit—as a spur to thinking differently, to “point toward new [philosophical and scientific] questions and new [philosophical and scientific] directions for research in problems of form and function” (2).

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