FROM PHILOSOPHY TO SCIENCE (TO NATURAL PHILOSOPHY): EVOLUTIONARY DEVELOPMENTAL PERSPECTIVES

ALAN C. LOVE
Department of Philosophy, University of Minnesota
Minneapolis, Minnesota 55455 USA
E-MAIL: ACLOVE@UMN.EDU

KEYWORDS
abstraction, ectoderm, epistemology, evo-devo, generalization, innovation, methodology, multidisciplinary, novelty, problems, sea urchins, skeletogenesis

ABSTRACT
This paper focuses on abstraction as a mode of reasoning that facilitates a productive relationship between philosophy and science. Using examples from evolutionary developmental biology, I argue that there are two areas where abstraction can be relevant to science: reasoning explication and problem clarification. The value of abstraction is characterized in terms of methodology (modeling or data gathering) and epistemology (explanatory evaluation or data interpretation).

PHILOSOPHY AND SCIENCE: CONTESTED RELATIONS

THE RELEVANCE OF PHILOSOPHY to the sciences is a controversial issue. Practicing biologists often see little utility in concepts from philosophy of science, perceiving a degree of abstraction that is too far removed from investigative contexts. In a scathing review of Elliott Sober and David Sloan Wilson's *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Robert Trivers went so far as to claim that "philosophy is much better at obscuring reality than it is at explicating it, at confusing rather than clarifying, however much philosophers may justify their activity on the opposite assumption" (1998:82). While this is extreme (and unfair) in many ways, the perception of philosophy as less than helpful is common in recent history: "If the scientists were consulted, the majority of them would regard 'philosophy' as one of the least important departments" (Frank 1957:xii). Because philosophy of science has its own set of questions to address (e.g., How does conceptual change occur in the historical development of science? Is there an appropriate abstract characterization of how scientific theories or hypotheses are confirmed by evidence? Is the aim of scientific inquiry truth, empirical adequacy, or something else?), its value is not ultimately decided by its relevance to science. Nevertheless, biologists seem justified in holding that the relevance of philosophy *to* science requires explicit empirical warrant, and,

The Quarterly Review of Biology, March 2008, Vol. 83, No. 1

0033-5770/2008/8301-0008$15.00

thus, the burden of proof rests with philosophers to demonstrate their usefulness.

From a more positive if not uncommon perspective, Stephen Jay Gould claimed in his final book that philosophy had been quite valuable to recent biological theorizing.

> Future historians might judge the numerous seminal (and published) collaborations between evolutionary biologists and professional philosophers of science as the most unusual and informative operational aspect of the reconstruction of evolutionary theory in the late 20th century. . . . Most of us would scoff at the prospect of working with a professional philosopher, regarding such an enterprise as, at best, a pleasant waste of time and, at worst, an admission that our own clarity of thought had become addled (or at least as a fear that our colleagues would so regard our interdisciplinary collaboration). . . . Professional training in philosophy does provide a set of tools, modes and approaches, not to mention a feeling for common dangers and fallacies (2002:28).

The conflicting views of Gould and Trivers about the value of philosophy might be attributed to the tangled nature of issues surrounding the units and levels of selection in evolutionary theory, which is the shared context for their differing perspectives. But philosophical issues are palpable in many areas of science. Consider these recent *philosophical* claims by biologists on the topic of reductionism and emergent properties in molecular and cell biology.

> Our results suggest that the cellular responses induced by multiplex protein kinase inhibitors may be an emergent property that cannot be understood fully considering only the sum of individual inhibitor-kinase interactions (Kung et al. 2005:3587).

> Our results therefore point to the need to consider each complex biological network as a whole, instead of focusing on local properties (Guimerà and Nunes Amaral 2005:899).

> Robustness . . . is one of the fundamental and ubiquitously observed systems-level phenomena that cannot be understood by looking at individual components (Kitano 2004:826).

Thus, biologists are willing to talk philosophy even if they are not convinced of the relevance of philosophy to science. The question then is whether these forays into philosophical territory are mere divertissement from hard-nosed research. Their recurrence throughout the history of biology suggests otherwise (Grene and Depew 2004), and adds substance to the possibility that philosophy may be apposite to biological research.

The aim of this paper is take up the burden of proof and illustrate the relevance of philosophy to science. I begin with a reminder that the current boundaries between philosophy and science within the structure of modern research have not always been present; in times past, natural philosophy exhibited a more flexible intellectual climate, which is now hinted at by the demand for multidisciplinary investigation. I then turn to abstraction—a mode of reasoning that is a key method of philosophical research. I use several case studies from evolutionary developmental biology (Evo-Devo) to elucidate two ways philosophy can be relevant to science via abstraction: "reasoning explication," which includes reconstructing kinds of reasoning used in scientific investigation to identify their characteristic strengths and latent biases, and "problem clarification," which involves clarifying the structure of problems and their interrelations across biological disciplines. The value of abstraction is characterized in terms of methodology and epistemology. Methodologically, problem clarification and reasoning explication indicate more or less fruitful lines of inquiry, modeling strategies, and data gathering. Epistemologically, they bear on theory construction, data interpretation, and whether explanations are competing or complementary. I conclude that the relationship between philosophy and science can be beneficial but is inherently precarious because it requires maintaining a tension between conceptual proximity to scientific practice and interpretive distance needed for philosophical reflection.

Natural Philosophy, Multidisciplinarity, and Abstraction

The deep division between philosophy and science is of relatively recent origin; despite what appear to be fixed boundaries in the modern university, the two once intermingled more freely. The contemporary disciplinary structure of the sciences is the product of a variety of epistemic, social, and cultural forces operating throughout the 19th century (Cahan 2003). One of the places where philosophy and science previously mixed was in the domain of natural philosophy, which was especially fecund when it fused with mathematical sciences in the 17th century (Grant 2007). But natural philosophy is usually characterized as a feature of the past that has been eliminated by our current disciplinary organization (the *American Heritage Dictionary* defines it as "the study of nature and the physical universe before the advent of modern science"). It is indisputable that natural philosophy has been closely connected with many sciences throughout history by way of a shared commitment to understanding natural phenomena (Grant 2007), but its contemporary relevance is another matter.

A strategy for reintroducing natural philosophy in the present can be formulated out of the ubiquitous appeal for "multidisciplinary research." For example, evolutionary and ecological functional genomics has been described as, "[a] unique combination of disciplines . . . which focuses on the genes that affect ecological success and evolutionary fitness in natural environments and populations. Already this approach has provided insights that were not available from its disciplinary components in isolation" (Feder and Mitchell-Olds 2003:649). Disciplines in isolation are somehow handicapped in their ability to comprehend natural phenomena, and these limitations are overcome by synthesizing different approaches. Multidisciplinary investigation is a response to complex problem domains that elude scientific explanations arising from specific disciplinary matrices. Although this emphasizes different *sciences* coming together, it can also be extended to include disciplines outside of the sciences that inform these problem domains. For instance, discussions of environmental degradation or human reproductive biology require contributions from ethics, an area of philosophy, in order to adequately formulate research methodology (and public policy). The inclusion of nonscientific as well as scientific fields in multidisciplinary research makes "natural philosophy" an appropriate label for such investigation because disciplinary boundaries are porous in reply to the demands of empirical adequacy for these complex problems.

Although natural philosophy can reenter via specific topical issues that necessitate multidisciplinary interaction, there are also relevant philosophical resources pertaining to research methodology ("a set of tools, modes, and approaches," to use Gould's phrase [2002:28]). One philosophical method worth exploring in relation to science is abstraction. "Abstraction," as I apply it in this paper, is a mode of reasoning or style of argument that operates by excluding concrete particulars and seeks understanding or comprehension for claims over different degrees of exclusion. It is closely related to but distinct from "generalization," which seeks to extend claims over a wider scope or range of application and is related to scientific laws (Mitchell 2000). Sometimes a generalization is achieved by abstraction because the exclusion of concrete details facilitates extending the scope of application for a claim. But abstraction and generalization are logically distinct; abstraction can be accomplished without generalization and vice versa.

The distinction between abstraction and generalization is important because the split between philosophy and science has been characterized in terms of generalization rather than abstraction. Philosopher of science Philipp Frank (1957) attempted to describe the link between philosophy and science, as well as its relatively recent severing, by way of a metaphor regarding generalization. He argued that statements or claims about the natural world can be ordered on a continuum (or chain) in terms of differing generality between direct observations (less general) and intelligible principles (more general), such as the principle of sufficient reason ("nothing can happen without a cause"). Philosophy sits near the more general end of the chain, whereas science occupies the less general end, with the middle being populated by principles and concepts of intermediate generality, such as Newton's law of gravitation. The chain ruptured when the derivation of intermediately general statements from intelligible principles was abandoned because it did not produce practical consequences in the realm of observable facts and technological application. Claims of intermediate generality were only subjected to criteria of empirical adequacy at the direct observation end of the continuum. As a result, scientists could effectively ignore philosophy: "The rest of the chain does not interest [the scientist] at all, [they] shouldn't speak of it nor think of it" (Frank 1957:36).

Although there is certainly something correct about the metaphor offered by Frank (and more to it than I have reconstructed here), it leaves out a large part of the difference between philosophy and science that is better characterized in terms of abstraction. Much of the generality for intelligible principles came from *abstract* concepts such as "cause" or "substance." Also, because abstraction is distinct from generalization, concentrating on abstraction emphasizes a different dimension of interaction between philosophy and science. Another continuum can be conceptualized in terms of the degree of abstraction with philosophy occupying the more abstract end of the continuum and science spread out toward the less abstract. The relationship between philosophy and science is then understood as the movement back and forth along this abstraction continuum. Philosophers of science "abstract from . . . the actual practice of science to reconstruct the significant patterns of scientific activity . . . analyzing or criticizing an activity in terms of how well it serve[s] the ends of the scientist . . . the activity itself and the analysis of it furthers these ends" (Wimsatt 1976:673). I take these ends to include methodological and epistemological aspects of scientific research because the way in which research proceeds and the evaluation of explanations offered by such research are ends for all scientists.

The next two sections are attempts to manifest abstraction in reasoning explication and problem clarification for specific biological contexts. Special attention is given to the methodological and epistemological value of this philosophical reasoning mode for ongoing scientific research. A positive relationship is observable when tracing the movement back and forth between more abstract philosophical considerations and less abstract scientific contexts.

Reasoning Explication

One key task of philosophy of science is reasoning explication—reconstructing and evaluating the kinds of reasoning used in scientific investigation. These can be very general, such as the use of induction and deduction, or very specific, such as the use of parsimony in phylogenetic reconstruction (Sober 1988). Different reasoning strategies have characteristic strengths and latent biases. For example, reductionist research heuristics tend to overlook the causal role of entities external to a system of study, in comparison with the interactions of internal parts, when determining the behavior of that system (Wimsatt 1980). One general mode of reasoning used in science is representation: natural phenomena must be symbolized, embodied, pictured, or designated through media such as equations, scale miniatures, or abstract diagrams. This reasoning strategy is natural to explore via philosophical abstraction because scientific representation involves ignoring or simplifying details of the phenomena to be explained (e.g., cellular interiors are depicted as relatively empty to emphasize causal processes even though intracellular space is known to be highly crowded). Idealized objects and approximations that abstract away from particular, known details are pervasive features of scientific reasoning (for example, the "frictionless planes" and "ideal gases" of physical science [cf. Harré 1970, chapter 2]).

One aspect of representation is the partitioning of a complex system into components ("decomposition") in order to comprehend its properties or behavior (Bechtel and Richardson 1993). In developmental biology, researchers must choose both spatial and temporal decompositions, dividing tissues into cellular components or setting boundaries for the initiation and conclusion of processes such as gastrulation. Both require ignoring known details such as temporal variation in developmental events. How these choices are made make a difference in both data gathering (methodology) and explanation (epistemology). For example, decompositions sometimes become standardized ("preferred decompositions") and are then presumed in explanations. Discussions of different kinds of modularity in Evo-Devo connect with reasoning strategies of decomposition (Callebaut and Rasskin-Gutman 2005; Schlosser and Wagner 2004) and can be observed in the less abstract context of two examples: the decomposition of developmental processes associated with ectoderm differentiation and larval arm morphogenesis in sea urchins.

Indirect developing sea urchins have two basic ectoderm territories, oral and aboral, which are established by the early gastrula stage and demarcated by a ciliary band (Okazaki 1975). Each has distinctive cell shapes and is distinguished by which end of the gut terminates into the territory. Morphological landmarks and molecular markers define these ectoderm territories as modules (Raff and Sly 2000). The ectoderm of the developing sea urchin can be decomposed into three parts: oral ectoderm, aboral ectoderm, and ciliary band. Two closely related sea urchin species from Australia differ radically in their developmental mode, yet are phenotypically similar as adults: *Heliocidaris tuberculata* (*Ht*) is an indirect developing echinoid with a pluteus larval stage (the ancestral state in this group), whereas *H. erythrogramma* (*He*) has evolved direct development in the form of a nonfeeding larval morphology (no oral opening or functional gut) with shortened time to metamorphosis (Raff 1992). Ectoderm differentiation in *He* has been substantially reorganized. Its larval epithelium ("extravestibular" ectoderm) is composed of cells with a distinct shape and exhibits no regionalization, and the ciliary band (a belt across the lower ventral side of an individual, curving into nonconnecting tips dorsally) demarcates no boundary (Raff and Sly 2000). The only other candidate territory is the left-side "vestibular ectoderm" where the adult rudiment forms, which emerges shortly after gastrulation and signifies a precocious transition to metamorphosis. Foregrounding the reasoning strategy of decomposition, the ec toderm of *He* appears to have two ectoderm territories, extravestibular and vestibular, with the status of the ciliary band remaining unclear.

One of the research questions pertaining to these congenerics is whether the ectoderm territories are homologous (Love and Raff 2006). Because a vestibule forms on the left side of the oral ectoderm much later in the ontogeny of indirect developers, vestibular ectoderm in *He* is likely homologous with vestibular ectoderm of *Ht* when heterochronies are taken into account. This removes the vestibular ectoderm in *He* from comparison with the oral or aboral ectoderm in *Ht*. An early hypothesis was that the extravestibular ectoderm of *He* is modified aboral ectoderm and that oral ectoderm has been lost (Raff and Sly 2000). One part or module has been evolutionarily transformed and another is no longer present in ontogeny. Another hypothesis, based on a variety of molecular, morphological, and developmental considerations, is that the extravestibular ectoderm is a new part or module not directly comparable to the oral or aboral ectoderm of *Ht*, i.e., an evolutionary novelty (Love and Raff 2006). The decomposition utilized for indirect developers is no longer applicable to the direct developing embryo because of evolutionary transformation.

The second example of decomposition reasoning relates to larval arm morphogenesis. The pluteus larvae of indirect developing echinoids have multiple appendages that function in the capture of planktonic food. These larval arms arise sequentially during ontogeny and are traversed by an unbroken ciliary band—the same structure dividing the oral and aboral ectoderm. Most work relevant to larval arm morphogenesis has focused on larval skeletogenesis. Skeletal structures originate from primary mesenchyme cells, which undergo epithelial-mesenchymal transition and ingress into the blastocoel before gastrulation. These cells form a stereotypical ring at the vegetal end of the embryo with two foci of concentration, fuse into syncytial cables, and biomineralization initiates. A similar pattern can be found within the larval arms later in development, largely after skeletogenesis in the main body cavity has occurred (Okazaki 1975). Recently, we have argued that larval arm morphogenesis should be treated separately from skeletogenesis on the basis of coordinated gene expression patterns, integral organization of the appendages, and distinctness of their ontogenetic processes (Love et al. 2007). Larval arm morphogenesis can be separated from the process of skeletogenesis and not considered simply one of its parts. Instead of construing larval arm skeletogenesis and body cavity skeletogenesis as parts of a larger whole ("skeletogenesis"), larval arm morphogenesis is treated independently as an instantiation of organogenesis with skeletal element formation being one component. A similar kind of decomposition is observable in studies of vertebrate limb development and skeletogenesis.

The methodological and epistemological value of focusing on these two empirical cases philosophically, as instantiations of decomposition reasoning strategies, can be documented at three levels of generality: (a) the system of study itself, (b) broadly similar Evo-Devo research in different systems, and (c) any biological research utilizing decomposition as a mode of representational reasoning. At each level, the effect of choosing one decomposition over another is emphasized in order to demonstrate how moving back and forth on the continuum of abstraction between science and philosophy facilitates the isolation and characterization of methodological and epistemological issues relevant to ongoing research.

(a) In the system of congeneric sea urchins, the methodological value or utility of rethinking ectoderm differentiation in *He* includes searching for shared patterns of gene expression in likely homologous ectoderm territories (the vestibule) and isolating the transformation of underlying genetic regulatory networks in the origin of direct development. New lines of inquiry are opened up with a different decomposition of larval arm morphogenesis: evolutionarily, when considering events related to the origin of the derived echinopluteus, as well as the ophiopluteus of brittle stars, which have similar appendages used for trapping food particles, and developmentally, in terms of concentrating on ectodermal rather than mesenchymal aspects of larval appendage ontogeny, in addition to species-specific aspects of larval arm skeletogenesis (e.g., fenestration patterns in skeletal rods).

Epistemologically, the ectoderm reevaluation generates a mechanistic scenario for the evolution of the ectoderm territories that can be correlated with the putative morphological transitions from indirect to direct developing larval forms (Love and Raff 2006). This generates predictions for intermediate morphologies and gene expression that can be tested in extant echinoids. It also provides part of the explanation of adult morphological similarity due to homologous vestibules. Data interpretation is also affected because shared vestibular homology emphasizes the biphasic nature of the *He* life cycle. "Direct development" is a heterogeneous category that should be treated cautiously when making generalizations across taxa in Evo-Devo research. In the case of larval arm morphogenesis, epistemological value is also gleaned for explaining the loss of larval arms in the origin of direct development with altered gene expression, as well as for the patterns of molecular correlations and dissociations involved in the repeated convergence of larval morphology occurring in echinoderms and other marine invertebrates.

(b) With respect to similar research in Evo-Devo, the methodological value includes modeling developmental evolution under different decompositions and looking for biases in data gathering incurred by preferred decompositions. The later onset of larval arm morphogenesis can encourage an asymmetry of data collection related to earlier skeletogenesis events in the body cavity. One epistemological benefit pertains to isolating the assumptions underlying a description of ontogeny as discrete stages. Gene expression patterns and other developmental data attributed to ontogenetic stages used in explanations involve implicit claims of causal connection between stages (Alberch 1985). These assumptions can then be characterized more explicitly to ascertain their effect on the kinds of explanations offered for these and related developmental phenomena.

Another epistemological consequence relates to challenging preferred explanations for the evolution of modularity. The hypothesized phylogenetic fusion of oral and aboral ectoderm territories into the extravestibular ectoderm instantiates "integration," or the establishment of pleiotropic effects among previously independent characters. Evo-Devo research has concentrated primarily on gene duplication and divergence or the specialization of serial homologues, which explains modular origin via "parcellation," when units are subdivided through the reduction of pleiotropic effects. Presumptive explanations using parcellation to account for the origin of modules should be reevaluated to determine whether descriptions using integration might be relevant. These different types of analysis in Evo-Devo also bear on interpretations of evolution from other disciplinary approaches, such as those found in population biology, because distinct selection regimes are associated with integration and parcellation (Wagner 1996). Thus, particular explanations from one discipline will be compatible only with particular explanations from another. Considering these reasoning preferences from the philosophical standpoint of abstraction highlights that epistemological consequences can be cross-disciplinary in nature.

(c) One of the most substantial consequences concerning any biological research utilizing this mode of reasoning relates to data gathering and interpretation under different *temporal* decompositions (e.g., stages). Decompositional reasoning is often assumed to be spatial, but temporality also must be partitioned, which can significantly impact the kinds of data accumulated and their significance for explanation (e.g., Minelli et al. 2006). This suggests pursuing lines of inquiry that explicitly test the robustness of data and explanations under different temporal decompositions. In turn, the compatibility or competition between explanations within and across disciplinary approaches may be modified. A second consequence pertains to decompositions at different levels of organization. Principles used to decompose a gene into parts may diverge significantly from those used to partition a developmental process involving tissue interactions. Tacit assumptions about the transfer of these principles across levels of organization can be experimentally explored and the sensitivity of explanations ascertained. This is especially critical in biological reasoning where data gathering and explanation are inherently multi-level, simultaneously trafficking across levels of organization.

Although I have framed my discussion of the above examples in terms of isolating preferred decompositions, it is necessary to stress that a variety of decompositions are always available and are chosen as functions of explanatory interests. The treatment of larval arms as part of skeletogenesis was not uninformative; the relevant question is what biases were involved, such as attention to earlier rather than later ontogenetic events. Multiple representations using different decomposition decisions are capable of being empirically informative in a complementary fashion. Attending to representational reasoning at the abstract level of philosophy serves as a reminder of these methodological and epistemological possibilities that contribute to ongoing research.

Problem Clarification

The second philosophical endeavor dependent on abstraction that I illustrate in this paper is problem clarification—clarifying the structure of problems and their interrelations across biological disciplines, often through analyzing central concepts. I have concentrated my attention on the problem of explaining evolutionary innovations and novelties in Evo-Devo (Love 2003, 2006). Innovations and novelties are usually understood to be features, such as avian flight or the vertebrate jaw, whose origination marked a significant departure from the variation available in ancestral lineages. These structures and activities often profoundly transformed the evolutionary trajectories of lineages possessing them (Müller and Wagner 2003), and are frequently claimed to be outside the explanatory capabilities of contemporary evolutionary theory (e.g., Kirschner and Gerhart 2005).

One aspect of problem clarification is the individuation of the problem; i.e., what makes it a distinct problem in the first place. Rationale for making these determinations can be obtained from abstract discussions of problem individuation and characterization, both ancient and modern (Lennox 2001a; Nickles 1981), as well from tracing the origins of problems historically (Lennox 2001b). Problems can be considered different when the explanation of one problem constitutes a problem in and of itself requiring a different explanation. This strategy necessitates agreement about the legitimacy of problems. Agreement can be secured by appeal to consensus principles such as the three necessary conditions required for natural selection to operate: phenotypic variation, its differential contribution to fitness, and the heritability of the variation. The problem of how adaptive evolution occurs is explained in large part by natural selection when these three conditions are met. But this explanatory strategy begets three new problems corresponding to each condition: How did the phenotypic variation originate? How does it contribute to differential fitness? How is it heritable? *That* the three conditions were met does not answer *how* they were met. Explaining innovation and novelty involves the problem of how variation originates, how a particular kind of variation came into being at a definitive phylogenetic juncture in the history of life. This individuation strategy shows that the origin of innovation and novelty needs to be addressed in part by developmental investigation into variation generating processes, rather than by natural selection-focused inquiry about the problem of adaptive evolution. Natural selection is an answer to the problem of the preservation and spread of beneficial variants in populations, but not to the origin of phenotypic variation itself.

This abstract process of problem individuation indicates that the "problem" of innovation and novelty is actually an agenda composed of multiple, complex empirical problems (for example, "how did the vertebrate jaw originate?" or "how did avian flight originate?"), as well as conceptual questions regarding the relative contributions of different variation-generating mechanisms, such as the regulation of gene expression or phenotypic plasticity due to environmental variables. We can understand the "problem" as a *problem agenda* abstracted from these component questions and characterized in terms of explaining how qualitatively new phenotypic variation originates at particular phylogenetic junctures—an inquiry about development from the viewpoint of phylogeny, comparing discrepancies between past ranges of variation and those presently available.

A second aspect of problem clarification relates to what is required to solve a problem. Criteria of explanatory adequacy can be isolated for the problem agenda by asking three abstract questions about the phenomena under scrutiny (Love 2006): (i) What are evolutionary innovations and novelties? (ii) Where do we find them? (iii)

How are they related to one another? An answer to the first question includes distinguishing between innovation (the origin of *function* features) and novelty (the origin of *form* features). Any adequate explanatory framework for the origin of new features must address both form and function, ideally in terms of form-function complexes or characters. Explaining the origin of vertebrate jaws (a novelty) requires attention to how jaws function and to how form and function features combine together into characters. Too much attention to novelties rather than innovations (or vice versa) introduces a problematic bias from the perspective of this criterion.

Answering the second question demonstrates that any adequate explanatory framework must address the origination of innovations and novelties at all levels of biological organization, and articulate relations between these levels relevant to the production of variation. These relations can be understood as compositional or procedural hierarchies, in both developmental processes and evolution across generations. When combined with the first criterion, a possibility space is generated that directs us to inquire about particular relationships, such as nested parts or sequences of events, to comprehend the origination of pertinent phenotypic variation (cf. Love 2006). For example, a procedural function hierarchy in ontogeny pertinent to the origin of neural crest cell migration relates to gene expression involved in the folding of the neural tube prior to the gene expression involved in the detachment or migration of neural crest cells. All relevant possibilities must be taken into account when attempting to explain particular novelties and to assess whether a more general explanatory framework is adequate.

The third abstract question can be answered by attending to two subordinate questions: First, can investigations of particular innovations or novelties be generalized so that they can be applied to research on other innovations or novelties? Second, can investigations of model systems be generalized to the phylogenetic juncture relevant to the innovation or novelty under scrutiny? The former pertains to generalization from one case to another, and the latter assesses the relevance of generalizations from contemporary model systems used in developmental research to putative taxa at the phylogenetic juncture. These abstract questions can be related back to empirical questions within the problem agenda. Do explanatory principles invoked to explain the vertebrate jaw also apply to the origin of cephalopod appendages? Is the developmental patterning of the branchial arches in zebrafish a relevant model for comprehending jaw origins? When combined with the other criteria, the burden of explanation becomes more specific: are the compositional and procedural hierarchies related to various form and function features (e.g., cell types, muscles, bones, gene expression, neural crest cell migration, muscle firing) observed in the developing zebrafish jaw appropriate models for explaining how phenotypic variation originated at the base of the gnathostome clade?

In addition to the clarification accomplished above, we can derive further methodological and epistemological consequences from viewing innovation and novelty as an illustration of abstract problem explication. Epistemologically, the criteria of adequacy serve as a template for indicating where and how different explanatory contributions are made, such as establishing a phylogenetic context and nonhomology for the trait in question, or elucidating causes that generate phenotypic variation during ontogeny relevant to the origination of the innovation or novelty. These criteria can only be met through a synthesis of multiple disciplinary approaches, which leads to methodological consequences for research on innovations and novelties (Love 2006). Explanatory generalizations at lower levels of organization do not propagate "upwards" as a consequence of dissociation between gene expression and higher levels of organization, where many innovations and novelties occur. Principles or mechanisms from one organizational level are not necessarily applicable to others (*pace* Ganfornina and Sánchez 1999; Wilkins 2002), and their sufficiency for explaining other levels is an empirical question even whey they do apply. Additional methodological consequences include the difficulty of acquiring data about function as opposed to form (Lauder 1990), and the choice of model organisms for the developmental study of variation relevant to phylogenetic junctures of interest (Metscher and Ahlberg 1999). A philosophical perspective focused on clarifying the structure of problem agendas in scientific inquiry yields specific consequences relevant to ongoing research and scientific reasoning, as well as meshing directly with those issues already of concern to some investigators.

Conclusion

The claims put forward in this paper are broad in scope, but the interpretation of empirical details is open to revision. The structure of my argument for a beneficial relation between philosophy and science has two main elements. First, the divide between the two must be recognized as an historical contingency that is reified in our current academic structure. Difficulties in seeing the relationship between philosophy and science are temporally provincial; within natural philosophy, the boundaries were not there to be traversed in the first place, and multidisciplinary investigation pulls us back toward these less familiar epistemic practices. Second, abstraction is primarily a philosophical research method. Abstraction takes researchers away from their specialized topic by excluding types and amount of detail, but it has the potential to yield methodological and epistemological benefits similar to those detailed in reasoning explication for sea urchin ectoderm territories and larval arm morphogenesis, and also to those detailed in problem clarification for explaining evolutionary innovation and novelty.

It would be wrong to infer from my discussion that there is no substantial and significant traffic from science to philosophy worthy of analysis—it simply has not been the focus herein. It also would be wrong to criticize my argument for not being philosophy or sufficiently philosophical, perhaps better described by a label like "theoretical biology." This objection arises out of a conceptualization of philosophy's disciplinary structure that sharply demarcates it from other disciplines, especially the sciences. Reintroducing natural philosophy intentionally challenges these boundaries, whether invoked for protective resistance by philosophers or scientists. By implication, the back and forth movement on the abstraction continuum that I described can be executed by philosophers, scientists, and others, but the tools, modes, and approaches relevant to this activity often accompany professional training in philosophy. This serves as a reminder that there are many advantages (both methodological and epistemological) to specialized disciplinary research that I have omitted here, although without the intent of disparagement. My perspective has focused on why that specialization is not an unalloyed good. I am under no illusion that our existing disciplinary structure, including the divide between philosophy and science, is headed for extinction (but see Collins 2002). Thus, the most productive front for a beneficial relation between philosophy and science is arguably the complex problem domains that demand multidisciplinary investigation (Love 2006), which includes comprehending the nature of science itself (Kellert 2006).

A century ago in the journal *Nature*, an anonymous reviewer opined that

> The relation of science to philosophy is, in theory, filial. It is, perhaps, no contradiction of the filial relationship that in practice it has an unfortunate tendency to run to mutual recrimination. The [scientist] too often ignores the philosopher, or despises him as an obscurantist who habitually confounds abstraction with generalization. To the metaphysical philosopher, on the other hand, the typical specialist in science is a variety of day labourer, dulled by the drudgery of occupational routine. Amidst such conjugal plain-speaking on both sides, it is no wonder that we hear

> much of what is called the divorce of philosophy and science; and yet there are many problems which for their adequate treatment surely require the combined resources of both science and philosophy (1905:505).

As long as the commitment to empirical adequacy remains a central motivation to understanding natural phenomena, especially as they appear in complex problems, then a combination of resources will be sought across the divide between philosophy and science, thus exemplifying their filial relationship. But establishing a bridge between the two requires maintaining a tension between conceptual proximity to scientific practice and interpretive distance needed for philosophical reflection. In the movement back and forth between philosophy and science, whether on the continuum of abstraction or generality, a path must be navigated between the twin dangers of losing touch with actual scientific research and becoming a partisan in ongoing explanatory controversy. Therefore, the relationship between philosophy and science is inherently precarious and requires eternal vigilance. The only alternative is to settle for never-ending mutual recrimination.

ACKNOWLEDGMENTS

I am grateful to Ingo Brigandt, Jim Lennox, Ric Otte, and Massimo Pigliucci for helpful comments on an earlier version of this paper, as well as to participants of the Sci-Phi 2007 Symposium in Manhattan for insightful feedback.

REFERENCES

Alberch P. 1985. Problems with the interpretation of developmental sequences. *Systematic Zoology* 34:46–58.

Anonymous. 1905. The classification of the sciences. Review of *Philosophy as Scientia Scientiarum: and, a History of Classifications of the Sciences,* by Robert Flint. *Nature* 71:505–506.

Bechtel W, Richardson R. 1993. *Discovering Complexity: Decomposition and Localization as Strategies in Scientific Research.* Princeton (NJ): Princeton University Press.

Cahan D, editor. 2003. *From Natural Philosophy to the Sciences: Writing the History of Nineteenth-Century Science.* Chicago (IL): University of Chicago Press.

Callebaut W, Rasskin-Gutman D. 2005. *Modularity: Understanding the Development and Evolution of Natural Complex Systems.* Cambridge and London (UK): MIT Press.

Collins J P. 2002. May you live in interesting times: using multidisciplinary and interdisciplinary programs to cope with change in the life sciences. *BioScience* 52:75–83.

Feder M E, Mitchell-Olds T. 2003. Evolutionary and ecological functional genomics. *Nature Reviews Genetics* 4(8):649–655.

Frank P. 1957. *Philosophy of Science: The Link Between Science and Philosophy.* Englewood Cliffs (NJ): Prentice Hall.

Ganfornina M D, Sánchez D. 1999. Generation of evolutionary novelty by functional shift. *Bioessays* 21:432–439.

Gould S J. 2002. *The Structure of Evolutionary Theory.* Cambridge (MA): Harvard University Press.

Grant E. 2007. *A History of Natural Philosophy: From the Ancient World to the Nineteenth Century.* New York: Cambridge University Press.

Grene M, Depew D. 2004. *The Philosophy of Biology: An Episodic History.* New York: Cambridge University Press.

Guimerà R, Nunes Amaral L. 2005. Functional cartography of complex metabolic networks. *Nature* 433:895–900.

Harré R. 1970. *The Principles of Scientific Thinking.* London (UK): Macmillan.

Kellert S H. 2006. Disciplinary pluralism for science studies. Pages 215–230 in *Scientific Pluralism*, edited by S H Kellert et al. Minneapolis (MN): University of Minnesota Press.

Kirschner M W, Gerhart J C. 2005. *The Plausibility of Life: Resolving Darwin's Dilemma.* New Haven (CT): Yale University Press.

Kitano H. 2004. Biological robustness. *Nature Reviews Genetics* 5(11):826–837.

Kung C, Kenski D M, Dickerson S H, Howson R W, Kuyper L F, Madhani H D, Shokat K M. 2005. Chemical genomic profiling to identify intracellular targets of a multiplex kinase inhibitor. *Proceedings of the National Academy of Sciences USA* 102(10): 3587–3592.

Lauder G V. 1990. Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecology and Systematics* 21:317–40.

Lennox J G. 2001a. Aristotelian problems. Pages 72–97 in *Aristotle's Philosophy of Biology: Studies in the*

Origin of Life Science. New York: Cambridge University Press.

Lennox J G. 2001b. History and philosophy of science: the phylogenetic approach. *História, Ciências, Saúde—Manguinhos* 8(3):655–669.

Love A C. 2003. Evolutionary morphology, innovation, and the synthesis of evolutionary and developmental biology. *Biology and Philosophy* 18(2):309–345.

Love A C. 2006. Evolutionary morphology and evo-devo: hierarchy and novelty. *Theory in Biosciences* 124:317–333.

Love A C, Andrews M E, Raff R A. 2007. Gene expression patterns in a novel animal appendage: the sea urchin pluteus arm. *Evolution & Development* 9:51–68.

Love A C, Raff R A. 2006. Larval ectoderm, organizational homology, and the origins of evolutionary novelty. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 306B:18–34.

Metscher B D, Ahlberg P E. 1999. Zebrafish in context: uses of a laboratory model in comparative studies. *Developmental Biology* 210(1):1–14.

Minelli A, Brena C, Deflorian G, Maruzzo D, Fusco G. 2006. From embryo to adult—beyond the conventional periodization of arthropod development. *Development Genes and Evolution* 216:373–383.

Mitchell S D. 2000. Dimensions of scientific law. *Philosophy of Science* 67(2):242–265.

Müller G B, Wagner G P. 2003. Innovation. Pages 218–227 in *Keywords and Concepts in Evolutionary Developmental Biology*, edited by B K Hall and W M Olsson. Cambridge (MA): Harvard University Press.

Nickles T. 1981. What is a problem that we may solve it? *Synthese* 47:85–118.

Okazaki K. 1975. Normal development to metamorphosis. Pages 177–232 in *The Sea Urchin Embryo: Biochemistry and Morphogenesis*, edited by G Czihak. Berlin (Germany) and New York: Springer-Verlag.

Raff R A. 1992. Direct-developing sea urchins and the evolutionary reorganization of early development. *BioEssays* 14(4):211–218.

Raff R A, Sly B J. 2000. Modularity and dissociation in the evolution of gene expression territories in development. *Evolution & Development* 2(2):102–113.

Schlosser G, Wagner G P. 2004. *Modularity in Development and Evolution*. Chicago (IL): University of Chicago Press.

Sober E. 1988. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge (MA): MIT Press.

Trivers R L. 1998. As they would do to you. Review of *Unto Others: The Evolution and Psychology of Unselfish Behavior*, by David Sloan Wilson and Elliot Sober. *Skeptic* 6:81–83.

Wagner G P. 1996. Homologues, natural kinds, and the evolution of modularity. *American Zoologist* 36:36–43.

Wilkins A S. 2002. *The Evolution of Developmental Pathways*. Sunderland (MA): Sinauer Associates.

Wimsatt W C. 1976. Reductive explanation: a functional account. *PSA Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1974:671–710.

Wimsatt W C. 1980. Reductionistic research strategies and their biases in the units of selection controversy. Pages 213–259 in *Scientific Discovery: Case Studies*, edited by T Nickles. Boston (MA): D. Reidel Publishing Company.