Beyond Reduction and Pluralism: Toward an Epistemology of Explanatory Integration in Biology

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Abstract

The paper works towards an account of explanatory integration in biology, using as a case study explanations of the evolutionary origin of novelties—a problem requiring the integration of several biological fields and approaches. In contrast to the idea that fields studying lower level phenomena are always more fundamental in explanations, I argue that the particular combination of disciplines and theoretical approaches needed to address a complex biological problem and which among them is explanatorily more fundamental varies with the problem pursued. Solving a complex problem need not require theoretical unification or the stable synthesis of different biological fields, as items of knowledge from traditional disciplines can be related solely for the purposes of a specific problem. Apart from the development of genuine interfield theories, successful integration can be effected by smaller epistemic units (concepts, methods, explanations) being linked. Unification or integration is not an aim in itself, but needed for the aim of solving a particular scientific problem, where the problem's nature determines the kind of intellectual integration required.

1 Introduction

Explanatory integration as a philosophical issue can be motivated by looking back at recent debates about reductionism in biology—often taking place in a dialectic between reductionism and pluralism. The traditional model about the relation of different scientific disciplines or domains of knowledge was ‘theory reduction’, which construed reduction as a deductive relation between theories conceived of as axiomatic systems including laws. Originally developed by Ernest Nagel (1962) for science in general, theory reduction was prominently defended by Ken Schaffner (1969, 1993) in the context of biology. However, many philosophers of biology were quick to challenge the idea that theory reduction characterizes the relation between classical and molecular genetics (Hull, 1974; Wimsatt, 1979; Kitcher, 1984a). While reductionists—acknowledging that theory reduction neither has been achieved yet nor is an aim of scientists—emphasized that theory reduction is *in principle* possible, the critics wondered why this should be relevant for philosophically understanding biological research *in practice,* including reductionistic methods and explanations. Furthermore, the monolithic notion of theory reduction—assuming that all of biology can be reduced to one fundamental theory—fails to capture the diversity of methods, explanations, and modes of theoretical reasoning found within biology, being present even within a single biological field.

As a result, a largely anti-reductionist consensus coalesced, which sometimes was phrased in terms of the disunity of biology (Dupré, 1993; Rosenberg, 1994). More commonly, philosophers of biology came to embrace the label ‘pluralism’ (Mitchell, 2003), arguing that biology is and ought to be characterized by a plurality of methods, theoretical approaches, and modes of explanation. For instance, pluralism about species concepts is the widely held position that there is not a single species concept, but that many species concepts are needed, some of which put different individuals into a species (Kitcher, 1984b). More generally, John Dupré (1993) argued that there is a plethora of legitimate ways to represent nature and to form kinds, controversially maintaining that conceptual and classificatory schemes used in scientific and non-scientific contexts are equally valid (e.g., classifying plants / animals in terms of common ancestry and in terms of culinary preferences). Pluralism has been defended not only on the basis of scientists having different legitimate research interests and methods, but also with reference to the complexity of biological phenomena, rooting epistemic pluralism in objective features of nature.

The specialization and division of labor among different biological subdisciplines is one of the main factors driving the progress of the life sciences. At the same time, the current proliferation of disciplines creates potential difficulties, as different fields may use language differently, make use of different methods and ways of interpreting data, and prefer different kinds of explanations. While *arguments against* the notion of theory reduction have been successful in philosophy of biology, "*positive accounts* of the relationship [among different fields] are not a part of the antireductionist consensus", as Alex Rosenberg points out (1997, p. 447, my emphasis). Accounts of theory reduction—no matter how flawed—were at least part of a philosophical attempt to articulate the epistemic relations that exist between different fields and bodies of knowledge. Thus, discussions merely arguing for pluralism have left a philosophical vacuum, to the extent that they have not pursued the question of how different fields, methods, and concepts are related in biological practice, or how they can be integrated.

The task of this paper is to work towards an epistemology of explanatory integration, offering an account that amounts neither to reduction nor mere pluralism. 'Explanatory integration' refers to the integration of ideas and explanations from different disciplines so as to yield an overall explanation of a complex phenomenon (later discussion will make clear why I prefer the term 'explanatory integration' over 'theoretical integration'). I specifically take a look at explanations of the evolutionary origin of novelties—an ongoing problem requiring the integration of several biological fields and approaches. In contrast to the traditional assumption that disciplines studying lower level phenomena are always more fundamental in explanations (Oppenheim and Putnam, 1958), the case study shows that which combination of disciplines is needed to address a complex biological problem is determined by the problem pursued, and which theoretical approach is explanatorily more fundamental *varies with the specific problem* at hand. I argue that integration/unification is not a regulative ideal or an aim in itself, but is usually needed to solve a particular scientific problem. Furthermore, I suggest that solving such a complex problem need not require the stable synthesis of different biological fields or the development of genuine interfield theories (sensu Darden and Maull 1977), as smaller epistemic units (concepts, explanations, methods) from traditional disciplines can be related *solely for the purposes of a specific problem*.

2 Evolutionary developmental biology as a philosophically relevant case

To be sure, there have been recent philosophical discussions going beyond reduction and mere pluralism (Darden and Maull, 1977; Maull, 1977). Sandra Mitchell (2002, 2003) has challenged the common appeal to different 'levels of analysis', where different explanations are taken to be independent as they pertain to different questions or levels of explanation. She points out that since in many cases such explanations focus on different causal factors involved in a complex phenomenon, these explanations are not independent, and ought to be integrated in some form. An important body of literature is accounts of explanations in terms of *mechanisms* in experimental biology, in particular cell biology (Bechtel, 1986, 2006; Bechtel and Richardson, 1993; Craver, 2005; Darden, 2006). Such studies have tied discovery and biological practice more closely to theoretical issues such as explanation, and provided insights into disciplinary changes within experimental biology and the relevance of institutional factors for integration. Most importantly for the context of explanatory integration, accounts of mechanistic explanation have shown how explanations in experimental biology often *combine several levels* of organization, rather than explaining only in terms of the molecular level. I will comment below on some of the existing accounts bearing on integration. At this point, I motivate why my discussion focuses on a different biological domain—evolutionary developmental biology—and why this case promises philosophical insights beyond previous studies of mechanisms in experimental biology.

Despite their close 19th century relations, evolutionary biology and developmental biology used to be independent fields throughout most of the 20th century. Evolutionary developmental biology (usually dubbed ‘evo-devo’) is a recent attempt to integrate both again (Gilbert et al., 1996; Wagner and Laubichler, 2004). (I will discuss below in which sense this is a theoretical synthesis.) Developmental biology was not a part of traditional neo-Darwinian evolutionary theory (having population genetics as its theoretical core), and some neo-Darwinists even argued that developmental biology is completely irrelevant to evolutionary explanations (Wallace, 1986). In contrast, evo-devo’s fundamental tenet is that knowledge of development is essential to solve evolutionary problems (Hall, 1998; Hall and Olson, 2003; Newman and Müller, 2000; Wagner, 2000). The move is to point out that apart from explaining adaptation and speciation—on which neo-Darwinism focused—there are other questions about evolution that require investigation, such as accounting for *phenotypic evolvability* or explaining the *evolutionary origin of body plans and novel structures*. Tackling these problems requires the involvement of developmental biology.

The recent hype in evo-devo is largely due to advances in developmental genetics. It turned out that genes involved in important early developmental events (e.g. the patterning of the embryonic axes and body plan) are shared across large groups of animals, found e.g. in both mammals and insects. Phenotypic evolution is not just due to changes in genes; of higher impact may be evolutionary changes in how the activation of genes is regulated. As a result, many scientists conceive of evo-devo as a synthesis of evolutionary and developmental biology, with developmental genetics providing the link (Love, 2003). However, several other evo-devo practitioners are aware of the fact that some of the items on the agenda of evolutionary developmental biology address longstanding macroevolutionary question—such as accounting for the origin of novel structures—and that solving such problems requires integrating knowledge from many different fields, including population genetics, developmental genetics, phylogeny, palaeontology, morphology, theoretical biology, and ecology (Hall, 2007; Müller, 2007; Wagner, 2007b; Wagner and Larsson, 2003).

In what follows I take a look at what kind of integration is needed to successfully explain the origin of novelties. Beyond previous philosophical studies on mechanistic explanations in cell biology and related disciplines, explanations of novelty in evo-devo involve several additional complexities. Such explanations include more and higher levels of organismal organization than cell biology (from changes in genes and gene regulatory elements up to the evolution of gross morphological structures), and they are essentially temporal by involving substantial change. Development is the origination of novel tissues and structures and their transformation across time. The evolution of novelties furthermore involves evolutionary change, making it necessary for such explanations to represent the spatial and functional relations of various organismal parts on different levels of organization, as these parts change across both developmental and evolutionary time (including the generation of novel parts), and to point to the respective causes of these changes. Evolutionary developmental biology faces the significant challenge of integrating quite different methods and explanations, such as experimental and theoretical approaches, microevolutionary and macroevolutionary models, developmental and population genetic explanations.

3 Explanations of the evolutionary origin of novelties

An evolutionary novelty (also called an evolutionary innovation) is a qualitatively new morphological structure or function feature in a group of organisms that did not exist in an ancestral species. Examples of novelties are the vertebrate jaw (the transition from primitive jawless vertebrates to jawed vertebrates), and the evolution of feathers and flight in birds. The advent of the turtle carapace involved a major reorganization of the skeleton, as in turtles the shoulder blades are located inside the rib cage, whereas in the ancestor (as represented by amphibians) the shoulder blades were outside the rib cage. It is unlikely that this could have arisen by a gradual transformation of the *adult* skeleton, raising challenges for explaining the evolution of the turtle carapace. One of the major cases on which evo-devo researchers have focused is the origin of paired fins in fish and their transformation into limbs in amphibians (Hall, 2006; Müller and Wagner, 2003). These issues have been discussed since the 19th century, and in some case biologists have acquired adequate ideas about the historical sequence of structural transformations leading to the novelty. However, the essential feature is to understand the mechanisms and causal features that offer the explanation of how a novelty arose. Despite ongoing empirical and conceptual advances, there are currently no satisfactory accounts for any of these examples by which genetic, developmental, functional morphological, and environmental causes the novel feature originated in evolution—making the explanation of novelty an important but yet unsolved problem.

As Alan Love (2005, 2008) has previously pointed out, the explanation of novelty is a ‘problem agenda’, i.e., a complex scientific problem consisting of a set of related questions (I like to call it a ‘complex explanandum’ or ‘epistemic goal’ pursued by scientists). He argues that it is important for philosophers to recognize the existence of such problem agendas, as each problem is associated with *criteria of adequacy*, which—given current empirical and conceptual background knowledge—set standards for what counts as an adequate solution. Relative to these criteria of adequacy, an epistemological evaluation is possible as to whether a certain biological approach is methodologically or theoretically equipped to solve the problem. Here I use this idea to show why any explanation of the origin of novelty requires explanatory integration, where non-molecular approaches have essential explanatory force.

The field of *phylogeny* is relevant for explanations of novelty, as well-confirmed phylogenetic trees are needed to determine the particular phylogenetic junctures at which characters were transformed and novelties arose in evolution. Phylogenetic trees are established based on the analysis of classical characters (e.g. morphological structures) and nowadays also inferred from molecular data (e.g. gene sequences). While many researchers prefer one kind of data over the other, there are several cases where classical and molecular data each supports a different phylogeny. Despite attempts of combining both kinds of data (by so-called total evidence approaches), there are currently no generally agreed upon methods of determining how to weigh the contribution of classical and molecular information. The field of *paleontology* adds a historical-temporal scale to phylogenies, and its stratigraphic data (the presence of fossils within certain time spans) provides additional information that can suggest revising hypotheses of species relations. However, given disagreement as to how to prioritize or weigh classical character data, molecular character data, and stratigraphic data, these different lines of evidence have yet to be integrated in accepted methods of establishing phylogenies (Grantham, 2004b). For understanding the evolution of novelties, paleontology and its fossil data is highly relevant, as it lays out the ancestral states of characters and structural intermediates (if any) up to the state in the descendant, suggesting the particular morphological changes that constitutes the origination of the novel feature (Wagner and Larsson, 2003).

Ecology and *biogeography* are two further disciplines, and ecological and biogeographical approaches used in the context of paleontology are germane to understanding how transitional character states in the emergence of a novelty could have been compatible with or positively favored by natural selection, and how the evolution of this character relates to changes in geographical and ecological conditions that the species underwent (including migration and relations to / changes in other species, e.g. prey species). While quantitative-explanatory models in population genetics have focused on microevolution (change in gene frequencies within a species), the theoretical models of paleontology address large-scale trends involving many species, such as extinction rates and patterns, the formation of higher taxa, and the mode and tempo of morphological evolution in several related lineages. The microevolutionary models of neo-Darwinism and the macroevolutionary models of paleontology could have co-existed largely independently as they seem to concern different levels of analysis (population geneticists, though, have been skeptical about the explanatory relevance of paleontological models, based on the idea that macroevolution is nothing but a sequence of many microevolutionary events). But for a full explanation of the origin of novelties some integration of micro- and macroevolutionary models and modes of explanation is probably necessary. For while the advent of major novelties (such as the evolution of limbs) or whole body plans involves macroevolutionary events, at the same time it has to be made plausible how the advent of a phenotypic novelty can be consistent with modes of genetic change within populations.

This paper focuses on *developmental biology*, because my claim is that primarily this approach carries the *explanatory force* in accounts of novelty. This becomes clear when considering why traditional neo-Darwinian evolutionary theory—using population genetics but not developmental biology—is not in a position to account for the origin of novelties (Müller, 2007; Müller and Wagner, 2003; Newman and Müller, 2000; Wagner, 2000). First, neo-Darwinism explains phenotypic change based on natural selection acting on existing heritable phenotypic variation (thereby also accounting for why phenotypic change was adaptive). However, this does not explain why the phenotypic variation could have been produced in the first place. It has been known for some while what mechanisms produce genotypic variation, but the crucial question is how genotypic variation translates into *phenotypic* variation—which is the domain of developmental biology. 'Evolvability' is the evo-devo term for the ability of developmental systems to generate heritable phenotypic variation (on which selection subsequently acts); and the task is to account for how development makes this variation possible (Kirschner and Gerhart, 2005). Furthermore, while genetic variation is produced in a largely random and unbiased fashion, this does not apply to the thereby generated phenotypic variation. Some phenotypic variants are developmentally impossible. Among the possible variants some are more likely to occur than others, resulting in a *developmentally* grounded bias in the direction and/or amount of heritable phenotypic variation generated (Hendrikse et al., 2007). Organisms are organized into characters, where a character as a complex set of features can vary across individuals and evolve. Developmental biology is necessary to explain why a character can change as a functional and integrated unit involving several coordinated phenotypic changes, sometimes based on a few simple genetic modifications. Some evo-devo biologists have emphasized the relevance of the (as yet largely unstudied) within species variation in development, and the role of phenotypic plasticity and environmental influences on development, calling for a combined ecological-developmental approach (dubbed 'eco-devo'; Gilbert, 2001).

Second, when neo-Darwinists used the term 'novelty', they actually addressed a different problem than current evo-devo. For neo-Darwinists, a ‘novelty’ is a substantial change of function in an existing structure, and the problem here is to explain how this shift to a new function could have occurred in the face of natural selection favoring features performing the currently demanded function only. “The emergence of new structures is normally due to the acquisition of a new function by an existing structure” (Mayr, 1960, p. 377). However, for evo-devo a novelty is not a change of an existing structure, but the very evolutionary advent of the structure, which can be made precise by defining that “A morphological novelty is a structure that is neither homologous to any structure in the ancestral species nor homonomous [i.e., serially homologous] to any other structures of the same organism” (Müller and Wagner, 1991, p. 243). Thus, accounting for novelties in evo-devo is a basic kind of *explanandum*, different from any explanandum or problem addressed by neo-Darwinism. The *explanans* has to involve development—features within organisms (while in neo-Darwinian explanations environmental demands external to organisms, i.e. natural selection, carry the explanatory force). For the task is to explain how an ancestral developmental system could have been re-organized such that a new mode of development possessing the novelty results. Among other things, a developmental system is governed by *developmental constraints*—features of an organism’s integrated functional and structural organization that constrain the production of novel variation. Müller and Wagner (2003) argue that many novelties “involve a breaking up of developmental or functional constraints that prevailed in the ancestral lineage” (p. 220). A case in point is the shift from reptilian scales to avian feathers. Both structures may have some common developmental roots, however, in contrast to previous assumptions feathers did not evolve in a smooth transition from scales. Since feathers are not within the *normal* mutational range of scales, scales were governed by certain developmental constraints. Thus, developmental biology is essential to account for the origin of novelties, as it has to be explained (a) how ancestral developmental constraints could have been and were broken leading to the emergence of the novelty, and (b) how the new structure was developmentally integrated with other structures (Müller and Newman, 1999).

Gerd Müller (1990) suggests that many novelties emerged as a developmental by-product of adaptive evolution. Assume that in the ancestor two tissues or developmental modules are spatially distant and do not exert a developmental influence on each other. On Müller's model, standard modification of the ancestor (e.g. its adult features) due to mutation and selection may have the side-effect that these embryonic tissues get closer to each other. This is a mere by-product of selection as—in Elliot Sober's (1984) terminology—there is no selection *for* these tissues being close to each other. If these tissues are close enough a threshold may be passed and one tissue exert a developmental influence on the other, inducing a change in the development and adult morphology of the organism so as to bring about a novelty. Natural selection was causally involved, but it does not carry the *explanatory force* in accounts of novelty, as there was neither selection for these tissues getting closer, nor selection for the novelty. Instead, development is crucial to explain how changes in one structure (due to selection) can due to particular developmental connections bring about another structure. Apart from selection, neo-Darwinian theory (population genetics) can appeal to genetic changes. Mutations were causally involved in this shift from the original mode of development to another, but appeal to mutation is non-explanatory—as long as it is not specified why a certain sequence of mutations results in particular changes in *development* resulting in the origin of the novelty.

In addition to developmental biology, *functional morphology* is essential in complete explanations of novelty. For the evolutionary origin of novel structures includes also function features (function in the sense of activity or causal role rather than selected effect). For instance, accounting for the origin of feathers in birds (a structure) involves understanding how they made thermoregulatory and biomechanical functions (e.g. those involved in gliding and flight) possible. Likewise, the origin of the jaw in vertebrates involved the functional articulation of different jaw bones, muscles, and nerves, having various implications for feeding modes. Thus, in accounts of novelty the explanans includes reference to functional relations among structures (internal to an organism) and how they support behaviors (relation between organism and features external to it)—the domain of functional morphology. In this paper, I do not discuss functional morphology in more detail, as Love (2003, 2006, 2005) has emphasized this issue. Love argues that despite the explanatory significance of functional morphology, it tends to be overlooked in current evo-devo accounts focusing on structure, simply because structures are easier to study than function features, which involve the relation of many structures and the temporal change thereof.

I have argued that the nature of the biological problem considered here requires the integration of different approaches, involving biological fields such as developmental biology and morphology that traditionally study entities above the cellular level (Love, 2006). Despite many evo-devo biologists taking a multidisciplinary approach and acknowledging the study of organismal organization on several levels, some may still wonder whether a reduction to molecular biology or developmental genetics is not possible after all. One reason why reduction is not promising is that during development certain tissues and precursor structures may exist and exert a stable causal influence, while their molecular constitution changes. A developmental process includes molecular and genetic causes, but may also contain higher level developmental modules that are more robust developmental causes in case they are less influenced by disturbances than molecular causes. More important for the explanation of novelty—an evolutionary context—is the fact that structures on different levels can sometimes evolve independently of each other. It is well known that an adult morphological structure can remain the same character during evolution, while its genetic and molecular basis changes substantially, leading to morphological structures that are homologous in two extant species, though they develop based on non-homologous genes and different developmental processes. Vice versa, the same gene can be involved in different developmental pathways or in the production of non-homologous structures in different species (Brigandt, 2007; Brigandt and Griffiths, 2007). As a result, biologists have to find the various natural kinds or units relevant for a particular developmental or evolutionary explanation, some of which occupy higher levels of organization. For instance, in the case of butterfly wing eyespots as a novelty, Wagner (2000) argues that the eyespot organizer, a developmental module consisting of cells exerting a developmental influence on surrounding cells, is likely to be of particular significance for explaining the evolutionary origin of eyespots.

The fact that characters on different levels often evolve independently entails that evo-devo biologist have to study structures on *several levels at the same time*. For the task is to understand how developmental systems are organized such that different entities can evolve relatively independently of each other and be rearranged, so as to permit the evolution of novelties. While there are developmental-functional relations between characters on different levels—an adult structure develops based on developmental processes under the influence of genes—there are apparently partial dissociations (dubbed ‘modularity’) that permit a structure on one level to evolve without disrupting other levels, making it necessary to understand the *relations and partial dissociations* of characters on several levels.

4 An approach’s explanatory significance varies with the problem pursued

The foregoing case study supports the following philosophical conclusions, which move toward an epistemology of explanatory integration by going beyond traditional reductionism and mere pluralism. Against a pluralism that simply asserts that biology needs a diversity of disciplines and theoretical approaches, solving some complex biological problems (meeting some explanatory or epistemic goals) requires at least the partial integration of concepts and explanations from different fields. In the case of the explanation of novelty, I discussed how items of knowledge from phylogeny, paleontology, ecology, biogeography, developmental biology, and functional morphology have to be brought together. It is not just the case that methods from several disciplines have to be used and data generated by different approaches have to be aggregated, but accounting for the evolutionary origin of novelties also makes it necessary to integrate different theoretical models and modes of explanations. For instance, the microevolutionary theories of population genetics (focusing on gene frequency changes in populations) and the macroevolutionary models of paleontology (focusing on the origin and evolution of higher taxa) have to be combined. Likewise, explanations of developmental biology and functional morphology (addressing the causes that change the internal properties of an individual) have to be integrated with neo-Darwinian modes of explanation (focusing on how variation across individuals causes evolutionary change).

Some accounts of reduction in biology have assumed that there is a more fundamental, lower level theory, such as molecular biology or biochemistry, that can in principle explain all biological phenomena (Schaffner, 1993). However, my discussion showed that in the explanation of evolutionary novelties, disciplines that necessarily include higher level phenomena such as developmental biology and morphology are essential, and that these explanations cannot be effectively reduced to the molecular level as developmental and morphological structures form units that may undergo evolutionary change independently of features on the genetic and molecular level. Disciplines such as phylogeny and paleontology contribute relevant descriptions to explanations of novelty, by setting out the historical pattern of character transformation in need explanation. It is developmental biology and functional morphology that lay out the causes or mechanisms actually accounting for the origin of novelty, so these disciplines carry the *explanatory force*. However, there is nothing intrinsically about developmental biology (or morphology) that would make it explanatorily more fundamental than other approaches; rather, this situation is contingent upon the fact that a specific problem or epistemic goal is pursued—in this case the explanation of evolutionary novelty. This yields the following epistemological conclusion.

Oppenheim and Putnam’s (1958) reductionistic account endorsed a hierarchical (layer-cake) model of scientific disciplines, where disciplines are ordered according to the size and mereological inclusion of the units studied: microphysics on the lowest level, chemistry and molecular biology on higher levels, organismal biology and sociology on even higher levels. This ontological order is adequate, but Oppenheim and Putnam assumed that it also corresponds to an *epistemological* order, where a lower level theory can reduce the ones on higher levels and thus is always explanatorily more fundamental. In contrast, the present case shows that there is no linear ordering of explanatorily more or less fundamental theories or disciplines that generally holds. Instead, the epistemic relations between different approaches are quite complex and the relative contribution and *explanatory fundamentality of different such approaches depends on and varies with the particular problem* (complex explanandum or epistemic goal) pursued by scientists. There are clearly scientific problems where biochemistry or molecular genetics have explanatory force, but for another problem such as the explanation of novelty higher level disciplines (according to the ontological order) are explanatorily more fundamental.

The reason is that—as previously pointed out by Love (2006, 2008)—a complex problem (a kind of explanandum) is associated with criteria of explanatory adequacy. These criteria set the standards of what shape a satisfactory explanation has to take, determining which theoretical and empirical ideas are relevant for solving the problem (by forming the overall explanans for the explanandum). Previous philosophical accounts have acknowledged one role that problems have. Darden and Maull (1977) have argued that a motivation for integration is often the existence of a scientific problem that cannot be solved by any field in isolation. However, apart from simply motivating integration, a problem together with its associated criteria of explanatory adequacy determines the nature and structure of the integration needed. The particular problem at hand influences which biological disciplines are needed, what relative contributions each theoretical approaches makes, and which approach is explanatorily particularly fundamental. As a result, in addition to the well-known epistemological notions bearing on theory structure, reduction, and integration—such as theory, law, explanation, concept, method—the notion of a *problem* / *epistemic goal* pursued by scientists has to be taken into account by any epistemology of explanatory integration.

5 Unification, stable synthesis, or integrative relations relative to problems?

I now discuss what the epistemological shape of a theoretical or disciplinary integration is, by analyzing the difference between the philosophical notions of unification, synthesis, and integration, and assessing into which of these categories evolutionary developmental biology falls. Lindley Darden and Nancy Maull were at the forefront of developing a non-reductive account of unification (Darden and Maull, 1977; Maull, 1977). On this account, unification among different fields can result from the origination of what they call ‘interfield theories’. These are theories that establish relations between traditional fields so as to solve problems that could not be solved by these fields in isolation. E.g., the chromosome theory of inheritance is an interfield theory that came to connect Mendelian genetics (the study of phenotypic inheritance across generations) and cytology (the study of the material contents of cells). This was a *non-*

reductive unification because neither did genetics reduce cytology, nor did cytology reduce genetics. Whereas on the model of theory reduction one field is reduced to a more fundamental one once both are connected by appropriate bridge laws, an interfield theory does not effect the reduction of one discipline to the other. Thus, unification by interfield theories provides an account going clearly beyond reduction and pluralism. Bill Bechtel (1986) prefers to use the term ‘integration’ rather than ‘unification’ for such cases as described by Darden and Maull (1977), because unification—in line with the unity of science program—is often understood as a global characterization of science as a whole (unifying physics, chemistry, biology, …), while disciplinary integration in biology is more local in that it involves only a few disciplines. One could alternatively use the label ‘synthesis’ for this more local type of unification, in analogy with the idea that the Modern Synthesis (neo-Darwinian evolutionary theory) unified fields within biology: genetics, systematics of living species, paleontology, and ecology. In what follows, I construe *unification* (more global) or *synthesis* (more local) to refer to the existence of *stable* theoretical and disciplinary relations across several scientific disciplines, where each such discipline has a *unique* set of relations to others.

In fact, evolutionary developmental biology is often called a ‘synthesis’, both by evo-devo biologists (Gilbert et al., 1996; Wagner and Laubichler, 2004; Wake, 1996) and by philosophers (Love, 2003). Evo-devo is conceived of as an ongoing synthesis or as an attempt at a synthesis of at least evolutionary and developmental biology (possibly involving more biological fields). However, in general it is unclear whether a genuine synthesis or theoretical unification of major fields is possible. Even though integration has occurred and systematic intellectual relations across fields have been established, most fields have retained their distinct identity rather merging with others into a whole. Modern biology is characterized by specialization and the generation of new (in fact, the proliferation of) subdisciplines, as pluralists have pointed out.

Bechtel (1986) argues that while the origin of cell biology as a novel field is a case of integration that created new disciplinary links, at the same time it also contributed to "disintegration (or fractionation) of science" (p. 278). Even in the case of the Modern Synthesis as the prime example of a successful theoretical synthesis (that is claimed to include paleontology), critiques of the neo-Darwinian conceptual framework have traditionally been launched by paleontologists (e.g., the debates about punctuated equilibria and developmental constraints). As far as evo-devo is concerned, it is still open whether traditional neo-Darwinian evolutionary theory and evo-devo's developmental approach to evolution can be reconciled and effectively integrated (Amundson, 2005; Wagner, 2007a).

While a synthesis or unification of major fields may not be possible, it may not be necessary for genuine integration. Above I argued that which combination of fields is needed to address a complex biological problem (and which theoretical approaches are explanatorily more significant) varies with the problem pursued. In line with this, it may be sufficient for a genuine explanatory *integration* of disciplines to relate and integrate items of knowledge from traditional disciplines *solely for the purposes of a specific problem* (epistemic goal). While a synthesis/unification is a stable connection of disciplines, on my more flexible model, a discipline can retain its traditional identity and independence but enter more *transient* relations to other fields, depending on which problem is currently addressed. In particular, a discipline can address several complex problems and does not have a unique set of relations to other fields—as in a synthesis/unification—but can set up and make use of *several* sets of relations to other fields. Relative to one epistemic goal the discipline establishes one combination of connections, for another problem relations to other disciplines are active. This offers a more dynamic model of intellectual relations across disciplines than Darden and Maull's (1977) approach. They take into account the change from two disciplines being unrelated to being integrated (after the development of an interfield theory), but even at one point in history a discipline or a scientist can—depending on the particular research *context*—change from engaging in one kind of integrative intellectual relation to another one (if the research context shifts from focusing on one epistemic goal to another one). Mitchell (2002) can be interpreted as distinguishing between ‘unification’ as the same theory applying to every biological case and ‘integration’ as different combinations of models applying to different cases. My account is consistent with this notion of integration, but it adds the idea that there are scientific problems and epistemic goals that structure integration (which models and explanations are to be integrated and how).

Acknowledging that unification cannot actually be achieved, Philip Kitcher (1999) and Todd Grantham (2004a) suggest that unification is still a regulative ideal. But from the present perspective, it is not the case that unification/integration is an a priori condition that is to be achieved in every context. Integration is not an aim in itself, but integration is likely to be needed *for the aim of* solving a complex scientific problem. In a certain context where scientists attempt to tackle a particular problem, in some respects a good deal of integration is necessary, though in other respects disciplinary and intellectual specialization may be needed at the same time (Bechtel, 1986). To which extent integration and specialization are needed is not an a priori matter but depends on the case. In contrast to Kitcher’s “ideal of finding as much unity as we [scientists] can” in a complex world (1999, p. 339), I recommend the ideal of finding as much unity as scientists need to solve a scientific problem. (This is a claim about scientific aims; in my above critique of pluralism I made plain that studying the existing integration in science and how it can be furthered is an important philosophical aim.)

In addition to the assumption that integration consists in a stable, unique, and context-independent set of relations across fields—an idealization that turns out to be problematic—Darden and Maull’s (1977) account relied on the notion of a ‘theory’ as the main epistemic unit describing science. Conceptualizing biology in terms of theories alone has been proven to be too rigid in general. In the context of my more specific case, even though evo-devo is viewed as a beginning synthesis of evolutionary and developmental biology, I contend that it cannot ever be described as an 'interfield theory' linking these two fields (and possibly others). Apart from various institutional factors, evo-devo's identity as an independent discipline derives from the pursuit of specific problems—accounting for evolvability, and explaining the evolutionary origin of novelties and body plans. Even if solving such problems does not require the theoretical unification or stable synthesis of major fields—as I argued above—the continued pursuit of these problems will be necessary to solve them. Evo-devo's integrative potential derives from addressing the problems of evolvability and novelty, and its future success and survival as a discipline depends on rigorously pursuing them. Evo-devo has already developed several concepts: heterochrony, canalization, modularity, developmental reprogramming, … However, in addition to the fact that most of these concepts derive a good deal of their explanatory content from connections to concepts and knowledge from *other* fields (evolutionary biology, and in particular developmental biology), the fact that evo-devo possesses various concepts to describe and potentially explain the evolution of developmental systems does not entail that there is a genuine theory. It is of course hardly controversial that as of now evo-devo does not possess a theory of its own (given how new this discipline is), but I doubt that even if a satisfactory explanation of novelty (or evolvability) will have arrived, it can be characterized as a real theory.

Instead—judging from the current state of evo-devo and other branches of biology—the future intellectual framework of evo-devo is likely to consist of various concepts, data items, experimental methods, ways of interpreting data, explanations, conceptual and quantitative models that are related (including relations to items of knowledge from other biological fields). For example, an explanation of the origin of limbs in land-living vertebrates will point to possible evolutionary changes in gene-regulatory networks resulting in developmental changes including cell condensation and cartilage / bone formation patterns as an important step in limb formation, related to muscle formation and innervation. Such an explanation will also pay attention to how these newly generated structures functionally interact and articulate together resulting in limb movement, making possible a selective advantage in the respective environment. This yields the following general picture. The identity of a scientific discipline is constituted by many different factors—institutional aspects, the pursuit of problems / epistemic goals, the possession of methods, concepts, explanations, laws, theories—which can (and should) be subject to change, while the discipline can still be regarded as the same discipline. Integration need not consist in two or more theories being bridged by an interfield theory, but successful integration may result from various smaller epistemic units—individual methods, concepts, models, explanations—being linked in an appropriate fashion. (Grantham, 2004a discusses a case exhibiting some degree of integration that does not involve any integration of explanatory theories, but consists in reconciling and combining different methods and ways of interpreting data.) In sum, my suggestion—to be philosophically explored in more detail by taking a look at further cases of integration—is that solving a complex problem need not require the stable synthesis of different biological fields or the development of genuine interfield theories, as smaller epistemic units from traditional disciplines can be related solely for the purposes of a specific problem.

6 Conclusion

This essay discussed evolutionary developmental biology as an ongoing attempt to integrate different biological disciplines. The focus was on one item on evo-devo’s agenda, the complex problem (epistemic goal) of explaining the evolutionary origin of novel structures. I argued that solving this problem requires integrating items of knowledge from population genetics, developmental genetics, phylogeny, paleontology, and ecology, with the non-molecular disciplines of developmental biology and functional morphology carrying the explanatory force in accounts of novelty. This supports my tenet that the particular combination of disciplines and theoretical approaches needed to address a complex biological problem and which among them are explanatorily more fundamental *varies with the problem pursued*. Such an epistemology of explanatory integration is at variance with the Oppenheim-Putnam (1958) model of reductive unification according to which disciplines studying lower level phenomena are always explanatory more fundamental. Moreover, I argued that genuine explanatory integration does not require a unification or stable synthesis of different fields. Instead, it is sufficient to relate items from different traditional disciplines *solely for the purposes of a specific problem*. Having particular intellectual relations to other fields need not be a stable or characteristic property of a discipline, rather the discipline can set up and engage in different integrative relations with other fields in different research contexts (relative to different problems the discipline may address). In addition to different theories being linked by genuine interfield theories, integration in biology may require no more than relating various smaller epistemic units—such as methods, concepts, models, and explanations—from different disciplines. Integration/unification is not a regulative ideal or an aim in itself, but is usually needed to solve a particular scientific problem. The nature of such a problem (complex explanandum or epistemic goal) *determines the amount and in particular the kind of integration required*. These philosophical considerations—especially the notion of a problem or epistemic goal pursued by scientists—are a central part of an epistemology of explanatory integration that amounts to neither reduction nor mere pluralism.

Acknowledgements

I thank Alan Love for helpful comments on earlier versions of this paper. The work on this essay was funded with a Standard Research Grant by the Social Sciences and Humanities Research Council of Canada.

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