Teaching Evolutionary Developmental Biology: Concepts, Problems, and Controversy

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1 Images of Science: Problems as Organizers of Inquiry

One of the most enduring images of science is due to Karl Popper: *falsification*. Instead of hypotheses receiving incremental confirmation by induction (e.g., via individual observations), Popper famously argued that hypotheses cannot be confirmed, only falsified (Popper 2002 [1963]). A reason for the endurance of this image is a natural resonance with scientific practice. Many biologists see themselves engaged in a form of reasoning that seemingly corresponds to Popperian falsification, and subsequent developments of these ideas for statistical hypothesis testing have sharpened this comparison (Mayo 1996). But Popper also recognized other dimensions of scientific practice, and one of these is germane for students of biology who are contemplating whether to pursue a career in the life sciences, as well as for a scientifically literate citizenry that will seek diverse career options.

> Try to learn what people are discussing *nowadays* in science. Find out where the difficulties arise, and *take an interest in disagreements*. These are the questions that you should take up. In other words, *you should study the problem situation of the day* (Popper 2002 [1963], p. 129, emphasis mine).

The stress on "nowadays" and "of the day" is enshrined explicitly in the *National Science Education Standards*: "Science content increases and changes, and a teacher's understanding […] must keep pace" (NRC 1996, p. 57). Although it is difficult to disagree with the recommendation to incorporate recent scientific developments into the curriculum, it is a daunting task for educators. The life sciences contain

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K. Kampourakis (ed.), *The Philosophy of Biology: A Companion for Educators*, History, Philosophy and Theory of the Life Sciences 1, DOI 10.1007/978-94-007-6537-5_16,

diverse and heterogeneous disciplines, and the time available to fit the spectrum of new findings into a school day has not increased.

Popper's emphasis on disagreements and problem situations may be even more daunting. The call to "teach the controversy" is laced with intelligent design machinations (Scott and Branch 2003; Sarkar 2007; see also Brigandt this volume), and understanding the problem situations in contemporary biology is a task that goes beyond conveying recent discoveries. And yet focusing on problem situations also exhibits a natural resonance with biological practice, as Popper was aware: "we are not students of some subject matter but students of problems" (Popper 2002 [1963], p. 88). Although the significance of problems as *initiators* of scientific inquiry is woven into the fabric of science education, there is little discussion of problems as *ongoing guides to* or *organizers of* inquiry.[1] The trajectory of research rides on *erotetic*[2] rails: "from problems to problems—to problems of ever increasing depth" (Popper 2002 [1963], p. 301). For problems to have depth, they must have structure, and it is this erotetic structure that plays an organizing role in biological practice. Because of the organizing role of problems, it is critical to incorporate this image of science into multiple levels of life science instruction (Love 2013a), especially when addressing the issue of scientific disagreement. To do so, we need to turn our attention to "what people are discussing nowadays in science."

2 Some Evo-Devo Concepts, Problems, and "Controversies"

Evolutionary developmental biology (Evo-devo) is a vibrant area of contemporary life science and is finding its way into teaching curricula at a variety of different instructional levels. From *Hox* genes to the origin of turtle shells, teaching how development evolves and how development structures the evolution of organismal traits is central to biology education and is encouraged by abundant and accessible presentations (Arthur 2004, 2011; Bateson and Gluckman 2011; Carroll 2005; Kirschner and Gerhart 2005; Minelli 2009; Shubin 2008; Stern 2011). This two-fold elucidation—how development evolves and how development structures evolution—is a helpful starting point for thinking about Evo-devo's loose conglomeration of research programs (Raff 2000; Müller 2007).

1. The *evolution of development* (how development evolves): inquiry into the patterns and processes of how ontogeny varies and changes over time.
2. The *developmental basis of evolution* (how development structures the evolution of organismal traits): inquiry into the causal impact of ontogenetic processes on evolutionary trajectories.

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[1] Theories or hypotheses are assumed to guide inquiry: "Hypotheses are widely used in science for choosing what data to pay attention to and what additional data to seek" (AAAS 2009, ch. 1).

[2] "Pertaining to questioning": derived from the Greek noun *erotisis*, which means "a question."

Although much of what gets emphasized in popular (and professional) presentations pertains to the comparative developmental genetics of metazoans (Carroll 2005; De Robertis 2008), where the focus is on conserved genetic regulatory networks and signaling pathways underlying developmental processes (commonly collected under the label 'genetic toolkit'), the two-fold characterization of Evo-devo encompasses a wider range of disciplinary approaches. For example, because the developmental genetics is *comparative*, phylogenetic systematics plays a critical role in drawing evolutionary inferences (Telford and Budd 2003). Historically, disciplines such as morphology and paleontology were the loci of concerns about both the evolution of development and the developmental basis of evolution (Love 2003, 2007).[3] In contemporary research, paleontology, comparative embryology and morphology, experimental investigations of epigenetic dynamics at different levels of organization, and computational or simulation oriented inquiry are all pertinent (Müller 2007; Raff 2007).

Much of twentieth century evolutionary biology concentrated on adult phenotypes, whether morphological or behavioral.[4] The structural features and adaptive significance of different developmental pathways, such as larval stages or the environmental induction of different traits from one genotype (*polyphenisms*), were relegated to the background of evolutionary theorizing. As a consequence, a bias emerged in model organisms upon which evolutionary biology forged its theoretical commitments. Animals exhibiting complex life histories (e.g., marine invertebrates) were neglected for vertebrates and arthropods without complicated metamorphic events (e.g., a change in basic body plan symmetry), which displayed adult phenotypes that could be measured quantitatively (Love 2009). Life history theory redressed some of this neglect from a population biology standpoint (Stearns 1992), but its abstract population-based explanatory framework of resource investment strategies and parent-offspring conflict is in sharp contrast to one involving the concrete, mechanistic details of development. Many Evo-devo researchers conceptualize evolutionary change in terms of changes in gene regulation during ontogeny, with a special emphasis on *cis*-regulatory elements (Davidson 2006). Revisiting substantive questions, such as the evolutionary origin of larvae (Raff 2008), requires model systems that exhibit the relevant kind of variation in life history for gathering molecular and embryological data to test evolutionary hypotheses in the framework of explicit phylogenies (Raff et al. 2003).

Even though Evo-devo biologists are engaged in hypothesis testing, generating a theory is not central to most investigations of the evolutionary significance of

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[3] Claims of a recent, developmental genetic genesis for Evo-devo should be treated suspiciously. For example, "Evo-devo began in the pre-genomic era when genetic studies in *Drosophila* and gene cloning in *Xenopus* revealed that the *Hox* genes that control the anterior-posterior (A-P) axis were unexpectedly conserved" (De Robertis 2008, p. 186).

[4] These adult phenotypes were primarily exemplified in multicellular animals (metazoans), as well as some plants. Microbial phenotypes, whether morphological or behavioral, were largely neglected (see Duncan et al. this volume).

developmental mechanisms. This is at odds with the image of science articulated for teaching students.[5] There is no *Evo-devo theory* to complement *life history theory*; the research is not organized by an overarching theoretical structure. The evolution of development and the significance of development for evolution are routinely explored within the framework of a family of recurring concepts that includes constraints, modularity, evolvability, and novelty, among others (Arthur 2002). Instead of simply serving to categorize phenomena, these concepts play roles in marking out core research problems that represent properties relevant to understanding the evolution of development and the developmental basis of evolution (Brigandt and Love 2010, 2012b). One classic discussion centers on *constraints* or biases on the production of phenotypic variation due to characteristic features of developmental processes (Maynard Smith et al. 1985).[6] The main point of contention at first seemed to be whether these somehow retarded the operation of natural selection (e.g., leading to sustained stasis in the fossil record) or facilitated some evolutionary trajectories over others, thereby diminishing the power of adaptive explanations of phenotypes. For example, the order of formation in amphibian digit development can explain the evolutionary pattern of digital reduction in these lineages (Alberch and Gale 1985): frogs experiencing hind limb digital reduction lost pre-axial digits ('big toes') because they form last during ontogeny; salamanders experiencing hind limb digital reduction lost post-axial digits ('pinky toes') because they form last during ontogeny (Fig. 1).

This disagreement appeared to revolve around the relative explanatory power of natural selection (from evolutionary genetics) versus developmental constraints (from Evo-devo). But the disagreement actually turned on a terminological ambiguity (Amundson 1994). Many evolutionary biologists interpreted constraints through the lens of the problem of adaptation (non-optimal phenotypes are constrained), whereas Evo-devo researchers looked at constraints as an aspect of the problem of variation and how development underlies its distribution (independent of adaptive value). This was not a situation of rival explanations—a hypothesis testing perspective on scientific controversy—but rather a case of distinct explanatory endeavors. The problems representing these differences (adaptation and variation) are oriented around different features of evolution: explaining the process of evolutionary change from one adult phenotype to another via population processes such as natural selection, which sorts phenotypes, alters allele frequencies, and yields adaptive outcomes; versus, explaining the process of evolutionary change from one ontogeny to another via developmental processes such as morphogenesis, which can be altered

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[5] "Theories compete for acceptance;" science is construed as "the testing, revising, and occasional discarding of theories" (AAAS 2009, ch. 1).

[6] The terminology of constraints connotes negativity or prevention but developmental constraints sometimes provide positive evolutionary opportunities (Gould 2002). As a result, some authors prefer "bias" as a more general designator, with "constraints" being one species of the genus (Arthur 2004). Here I do not distinguish between these different connotations and use constraint and bias interchangeably.

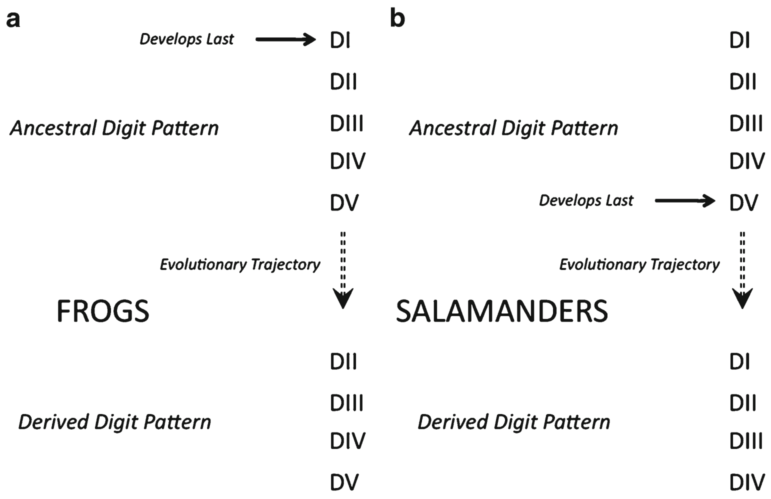

Fig. 1 Digital reduction trends in frogs and salamanders. A simplified, schematic representation of how the order of formation in amphibian digit development explains the evolutionary pattern of digital reduction in these two lineages (Alberch and Gale 1985). (**a**) Frogs experiencing hind limb digital reduction lost pre-axial digits ('big toes') because they form last during ontogeny. (**b**) Salamanders experiencing hind limb digital reduction lost post-axial digits ('pinky toes') because they form last during ontogeny

in different ways to generate novel morphologies (Amundson 2005; see also Potochnik, this volume). Recent treatments of constraint recognize these differences (Arthur 2011).

Another key concept in Evo-devo is *modularity* (Bolker 2000), which represents questions related to our two-fold elucidation of Evo-devo: (a) how do modules originate or dissolve during evolution (the evolution of development)? and, (b) how does modularity affect evolution (the developmental basis of evolution)? Modularity, in the sense of discrete sets of pleiotropic interactions during development, is pervasive (Wagner and Zhang 2011), and this architecture may channel evolutionary change in lineages. Modules, in the sense of quasi-autonomous parts, are ubiquitous in biological systems at different hierarchical levels (Kuratani 2009), whether genes, cells, tissues, organs, or anatomy, and this type of organization has evolved repeatedly. The question of how modularity affects evolution leads us to a third concept: *evolvability* (i.e., the capacity to generate heritable, selectable phenotypic variation). Modularity appears to be a key property that underlies evolvability because modules can exhibit variation and be independently modified without disrupting other features that are critical for an organism's survival and reproduction (Kirschner and Gerhart 1998).[7]

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[7] Others properties underlying evolvability include the versatility of cell components, weak regulatory linkages, and exploratory behavior (see Kirschner and Gerhart 2005).

One controversy surrounding evolvability is whether the conserved cellular machinery that produce properties like modularity during development facilitates links between random genetic mutation and phenotypic variation so that viable character assemblages are more likely to emerge (Gerhart and Kirschner 2007). This seems to contradict the standard conception that mutations are random with respect to their effects on viability. But this may not be a conflict between two different theoretical claims—a theory testing perspective on scientific controversy. As with constraint, a more fruitful interpretation is in terms of different problems. The claim about random genetic mutation is meant to apply in the context of the problem of adaptation; adaptations do not arise because genetic mutation is biased toward viability. The claim about facilitated phenotypic variation is meant to apply in the context of the problem of variation; the capacity to generate phenotypic variation is biased due to aspects of organismal development, such as developmental plasticity, which make possible coordinated changes among different traits (e.g., the innervation and vascularization of an appendage). Random genetic variation and facilitated phenotypic variation are consistent claims that emerge from work on different problems (adaptation and variation). Again, this is not a situation of rivalry, and attending to how problems organize (and not just initiate) research around different evolutionary questions can diffuse the controversy.

3 A Genuine Controversy

The diffusion of controversy in the cases of constraint and evolvability by appeal to the biological practice of working on different problems (see above, Sect. 2) might leave the impression that Evo-devo doesn’t harbor genuine controversies. Not true. One source of controversy[8] is nestled within the perspective of separate problems requiring distinct approaches in evolutionary biology. Both traditional population biologists and Evo-devo proponents have claimed that their approaches, and hence their problems, are more fundamental than the other. On the side of the former, the claim has been made forcefully:

> The litmus test for any evolutionary hypothesis must be its consistency with fundamental population genetic principles […] population genetics provides an essential framework for understanding how evolution occurs (Lynch 2007, p. 8598).

On the side of the latter, the claim has been made specifically with respect to the teaching of evolution: Evo-devo approaches better illustrate how evolutionary change can occur (Gilbert 2003), or emphasize the most central features of the evolutionary process.

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[8] Other controversies that might have been explored include disagreements about whether most molecular change during evolution occurs in *cis*-regulatory regions of the genome that control gene expression or within protein coding regions of the genome (see Hoekstra and Coyne 2007).

> Millions of biology students have been taught the view (from population genetics) that ‘evolution is change in gene frequencies.’ […] This view forces the explanation toward mathematics and abstract descriptions of genes, and away from butterflies and zebras […] The evolution of form is the main drama of life’s story, both as found in the fossil record and in the diversity of living species. So, let’s teach that story. Instead of ‘change in gene frequencies,’ let’s try ‘evolution of form is change in development’ (Carroll 2005, p. 294).

Simply detailing how variation and adaptation are distinct problems (see above, Sect. 2) will not diffuse this controversy. It raises thorny issues about how knowledge is structured, and whether some form of reductionism is warranted (Brigandt and Love 2012a). Should one set of approaches or discipline be considered the “main drama” or more fundamental than the others (e.g., population genetics)? Must all of the problems and the approaches necessary to address them be unified under a single explanatory framework? Should we think of some concepts as *most* central to Evo-devo, such as gene regulatory networks (Laubichler 2009) or evolvability (Hendrikse et al. 2007), or should Evo-devo and evolutionary biology be conceptualized as differentially organized depending on the problems in view (Love 2008a, 2013b; Brigandt 2010)? Does Evo-devo challenge the dominant explanatory perspective of the Modern Synthesis (Laubichler 2010), or is it simply complementary (Minelli 2010)? These issues cannot be settled quickly and are indicators of genuine controversy in Evo-devo, a big controversy about how knowledge is organized. Appeals to science as an activity of theory confirmation or hypothesis testing will be inadequate to resolve it since problems are involved in organizing inquiry, not just initiating it. Erotetic units guide biological practice, but we have yet to see how, and this is essential to finding resources for comprehending this genuine controversy over knowledge organization and whether population genetics is more fundamental than Evo-devo (or *vice versa*). One tactic for approaching this more manageably is to zero in on an issue that has been intimately related to the controversy: the origin of evolutionary novelty.

4 Controversy over Explaining the Origin of Novelty

The concept of evolutionary novelty, which represents another Evo-devo research problem (Love 2008a), provides an opportunity to see a controversy of a different kind. Instead of being defined on an axis of different problems (e.g., adaptation and variation), this Evo-devo controversy arises within the context of one problem: explaining the origin of evolutionary novelties. Novelties have been defined as morphological traits that are not homologous to features in an ancestral lineage and designate developmental variation that is not experimentally accessible in extant species meant to represent ancestral lineages (Müller and Newman 2005; see also Minelli and Fusco, this volume). How does qualitatively new phenotypic variation originate at particular phylogenetic junctures? One notable example is the origin of feathers (Prum and Brush 2002); we do not observe and cannot experimentally induce feather-like structures in existing “reptile” species with scales. The study of novelty is a defining aspect of Evo-devo because it concerns the developmental generation of phenotypic variation, not its adaptive spread through a population.

> Evolutionary innovations are outside the scope of any current research program. Through its contribution to the solution of that question, [Evo-devo] genuinely expands the explanatory range of evolutionary theory (Wagner et al. 2000, p. 822).

> It is essential to include developmental mechanisms in the explanation of evolutionary innovations. […] This is also the reason why developmental evolution makes an indispensable contribution to evolutionary biology (Wagner 2000, p. 97).

As expected given the stress on genetic regulatory evolution in Evo-devo, most explanations of novelty emphasize developmental genetics.

> The evolution of new morphological features is due predominantly to modifications of spatial patterns of gene expression (Gompel et al. 2005, p. 481).

> Ancient regulatory circuits provide a substrate from which novel structures can develop […] new structures need not arise from scratch, genetically speaking, but can evolve by deploying regulatory circuits that were first established in early animals (Shubin et al. 2009, pp. 818, 822).

But this developmental genetic explanation of the origin of novelty has a rival: the generic physical explanation. Some argue that early in evolution generic properties of cells and tissues (e.g., self-organization and geometry) and physical mechanisms of soft condensed materials (e.g., diffusion and viscoelasticity) interacted with environmental forces to yield basic metazoan morphologies with minimal developmental genetic machinery (Newman 1994; Newman et al. 2006; Newman and Bhat 2009). This 'pre-Mendelian' world was replaced through an evolutionary process in which morphologies became stabilized by developmental genetic mechanisms through genetic assimilation, yielding the 'Mendelian' world that we now observe.[9] The disagreement between the two explanations is stark:

> (i) Developmental genetic explanation: "novelty requires the evolution a new gene regulatory network" (Wagner and Lynch 2010, R50); "evolutionary change in animal form cannot be explained except in terms of change in gene regulatory network architecture" (Davidson 2006, p. 29).

> (ii) Generic physical explanation: "epigenetic mechanisms, rather than genetic changes, are the major sources of morphological novelty in evolution" (Newman et al. 2006, p. 290).

We appear to be on traditional ground; two competing hypotheses is the archetype of scientific controversy. But this may not be the only interpretation. Recall that in Sect. 3 we identified the controversy as epistemological (how knowledge is organized or structured), not empirical. Following Popper's advice—"you should study the problem situation of the day"—we need to scrutinize the anatomy of the problem of evolutionary novelty to determine whether this controversy is solely empirical, or whether it might also contain epistemological elements.

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[9] Thus, 'Mendelian' refers to standard transmission and developmental genetic processes we find in contemporary organisms. 'Pre-Mendelian' signifies that these standard processes were not yet in place even though phenotypes were being generated through environmental forces interacting with soft condensed materials according to physical principles.

5 Explaining the Origin of Novelty: Problem Structure

Although it is true that complex scientific problems are not structured logically or "well-defined" (Osbeck et al. 2011, ch. 3), this does not mean that they are unstructured and their role in guiding inquiry suggests otherwise. But what is this structure and how does it organize research? Popper argued that as scientists, "we are not students of some subject matter but students of problems" (Popper 2002 [1963], p. 88). This is the role of problems in initiating inquiry, and one often noted when teaching biology. By observing a pattern in the history of science, Popper also saw a role for problems to guide inquiry: "from problems to problems—to problems of ever increasing depth" (p. 301).

For a problem to have 'increasing depth,' it cannot be equated with a standard interrogative. Biological problems—such as how cells differentiate or how evolutionary novelties originate—are not single questions similar to interrogatives like "who broke the window?" They constitute an agenda, a list of things that need to be addressed, and concern many different but interrelated questions. To keep this in mind, we can designate them explicitly as *problem agendas* (Love 2008a). They are indicative of long-term investigative programs and require contributions from more than one disciplinary approach. The interrelations among the questions are not haphazard but constitute an anatomy or problem structure ('depth'), which provides an organizational framework for coordinating inquiry among different disciplinary approaches.

Problem agenda structure has at least three dimensions. First, problem agendas have a *history*, and the discussions and debates surrounding their historical pathways yield structural relations (Hattiangadi 1978, 1979). Second, problem agendas are epistemologically *heterogeneous* in the sense of containing different kinds of questions (Laudan 1977), among which there are specific relationships. Third, structure can be found in the *hierarchical* relationships among questions in problem agendas, such as definable arrays of questions that can be thought of as parts to the whole (Nickles 1981). These three dimensions of problem agenda structure can be observed concretely in the case of explaining evolutionary novelty:

- History: To the extent that twentieth century neo-Darwinian evolutionary theory recognized the evolution of novelty as a problem at all, it assumed that population genetic processes were explanatorily sufficient. Marginalized disciplines, including morphology and paleontology, maintained an active interest in the problem (Love 2007) and the explosion of experimental tools from developmental genetics over the past two decades has facilitated a revisiting of these questions in many disciplines simultaneously (Love and Raff 2003). This historical controversy structures the problem agenda through debate about its component questions and what disciplines are needed to address them.
- Heterogeneity: The existence of different types of questions in the problem agenda requires distinct intellectual contributions to answer them. Empirical questions ('what regulatory genes control axis specification?') are answered differently than theoretical questions ('how is pleiotropy represented in a mathematical model?'); pattern questions ('what are the phylogenetic junctures for understanding the origin of segmentation?') are answered differently from

process questions ('how can changes in *cis*-regulatory binding sites contribute to heterotopy?[10]'); questions about the cellular level of organization are answered differently from questions about anatomy.

- Hierarchy: Different question components and strands of historical debate stand in systematic relations of abstraction and generalization (Love 2008b). Questions that are more abstract ('how is variation generated?' or 'how can complex traits overcome developmental constraints?') are higher up in the hierarchy of the problem structure than others ('how is gene regulatory network variation generated?' or 'how can appendicular skeletal traits overcome developmental constraints due to pleiotropy?'). Questions that are more general ('how do novelties originate in metazoans?') are higher in the hierarchy of problem structure than others (how do novelties originate in mammals?).

We can fill out these three dimensions of structure by noting that they come with associated *criteria of explanatory adequacy*. This provides a template for how explanatory contributions are coordinated, so that reflecting on the problem agenda anatomy makes clear how an interdisciplinary explanatory framework can be generated (Brigandt 2010; Love 2008a):

1. Historical controversy highlights the need for different disciplinary contributors to answer distinct and previously neglected questions in the problem agenda of evolutionary novelty, including phylogeny and paleontology (to reconstruct character polarity, ancestral character states, and transitional stages), morphology (to determine the compositional identity of a feature), and development (to detail the genotype-phenotype mapping relations for how variation emerges during ontogeny). Additionally, the emphasis on the adaptive modification of traits in neo-Darwinian population biology (see Depew, this volume; Forber, this volume) led to a neglect of questions about the origin of structure. The stress on explaining the origin of new morphological units corresponds to an attempted correction of this functional bias and indicates that any adequate explanatory framework for the origin of new characters must address both morphology (form) and function.
2. Different disciplinary approaches and methods will be required to address the heterogeneous types of questions in the problem agenda of novelty. Adequate explanatory frameworks must exhibit sufficient complexity and balance: complexity to match the heterogeneous questions in the problem agenda with corresponding answers, and balance to handle empirical and theoretical questions, not neglect pattern questions for process questions, and deal with lower levels of

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[10] Differences ('hetero') in development that contribute to evolutionary change can be classified according to the kind of difference in view: (i) *heterochrony*: differences in the timing of developmental events; (ii) *heterotopy*: differences in the spatial location of developmental events; (iii) *heterotypy*: differences in the type of developmental event, such as cavitation versus invagination; and, (iv) *heterometry*: differences in the amount of activity in developmental events, such as the up-regulation of gene expression (Arthur 2002).

organization as well as higher levels. The focus of one discipline on some questions rather than others creates a fruitful division of labor and organizes different lines of investigation in terms of the kinds of questions they tackle.

3. Hierarchical structure in the problem agenda marks out criteria of adequacy with respect to abstraction and generality. The demand of abstraction requires that necessary disciplinary contributions have been made, such as the generation of variation being investigated using methods from quantitative genetics, developmental genetics, epigenetics, and phenotypic plasticity at different levels of organization. Since more concrete questions involve distinct biological processes (‘how is gene regulatory network variation generated?’ versus ‘how is epigenetic variation generated?’), the ability to offer an explanatory framework at the desired level of abstraction requires multiple methodological approaches. The demand of generality requires that diverse characters in different clades are investigated using many methods, and that appropriate proxies for extinct taxa are utilized in experimental research (Metscher and Ahlberg 1999). Successful explanatory proposals for particular novelties must be evaluated with respect to their applicability to others. Since more specific questions involve clade-level differences, appropriately diverse taxa must be studied and the results judiciously compared. Because the precise phylogenetic pattern leading up to a novelty (character transformations at particular junctures) must be settled prior to assessing the developmental mechanisms that contributed to an evolutionary transition, the architecture of the problem agenda not only requires different approaches (paleontology, phylogeny, developmental biology) but also shows how contributions from different approaches articulate. Thus, the hierarchical structure of a problem agenda provides a scaffold upon which to insert the relevant disciplinary contributions.

We now have a detailed picture of how problems organize research and guide inquiry. This problem structure makes explicit why multiple disciplinary contributors are needed to address complex scientific problems like the origin of evolutionary novelty: “problems may cut right across the borders of any subject matter or discipline” (Popper 2002 [1963], p. 88). This organizing architecture of problems is not in conflict with an image of science focused on hypothesis testing or theory confirmation, but it does lay bare why so much of contemporary life science investigation is interdisciplinary. And because the anatomy of problem agendas underlies the research practices of biologists, it must be communicated to students of biology, especially in the context of scientific controversy.

Returning to the Evo-devo controversy between developmental genetic and generic physical explanations of the origin of novelty, there is no doubt that some of it is empirical (i.e., about the way the world is). But we now have resources for picking out previously invisible epistemological elements. Consider the hierarchical dimension of problem agenda structure. The controversy pertains to the mechanisms that generate variation during development. The more abstract question (‘how is variation generated?’) is higher up in the hierarchy of problem structure than its subunits (‘how is gene regulatory network variation generated?’ or ‘how is epigenetic variation due to generic physical mechanisms generated?'). This means there is disagreement about the way in which answers to more concrete component questions are fed into an answer at the more abstract level. These disagreements are not just empirical but involve disciplinary biases about what causes are significant (i.e., there is an epistemological element of the controversy). In particular, many developmental biologists interested in evolution have neglected the potential role of physical mechanisms in ontogeny.[11] There also is substantial agreement embedded within this mixture of empirical and epistemological disagreement. Both approaches concur that their explanations must be framed by an explicit phylogenetic hypothesis (a different disciplinary contributor) and that the problem itself is genuine (an element from the historical dimension).

Turning to generalization, the primary focus of the generic physical explanation is the early history of metazoans because this is the time when the 'pre-Mendelian' world exists (according to this viewpoint). There is agreement with the developmental genetic explanation that the clade of interest is metazoans (and not bacteria, for example), in part because multicellular animals exhibit complex developmental processes that can be subject to evolutionary change. But there is disagreement about whether developmental variation has always been produced in the same way, i.e., whether you can generalize from extant experimental inquiry to past evolutionary events. This is an epistemological disagreement about actualism[12] (causes now operating explain past events). The generic physical explanation is committed to the ontogeny of early metazoans operating differently than it does today: "ancient organisms undoubtedly exhibited less genetic redundancy and metabolic integration and homeostasis than modern organisms […] ancient metazoa were even more developmentally plastic than modern ones" (Newman et al. 2006, p. 290). As a result, simulation methods become more relevant for testing the generic physical explanation since contemporary developmental genetic experiments can only be executed on organisms *as they are today*. Therefore, the hierarchical structure of the problem agenda shows that the empirical disagreements are modulated by epistemological agreements and disagreements about relationships among component questions, assumptions underlying these questions, and the methods required to answer them.

It should be noted that in providing an additional layer of interpretation for the controversy between developmental genetic and generic physical explanations,

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[11] "The current preeminence of the molecular genetic approach to biology, in which living systems are conceptualized as networks of interacting genes and proteins, may have obscured this inevitable link between physics and biology in the mind of scientists" (Mulder 2008, p. 1643); "there has been a renewed appreciation of the fact that to understand morphogenesis in three dimensions, it is necessary to combine molecular insights (genes and morphogens) with knowledge of physical processes (transport, deformation and flow) generated by growing tissues" (Savin et al. 2011, p. 57).

[12] Uniformitarianism is a stronger principle that actualism. The former combines actualism and a commitment to extant causes operating with the same intensity throughout history.

we also have generated resources for addressing the larger controversy over fundamentality identified in Sect. 3. The anatomy of problem agendas strongly suggests that different disciplines play explanatory roles to which they are well suited but that no one approach is fundamental *per se*. The "fundamentality" of one particular perspective producing the most empirically adequate explanations is rejected, *even when one hypothesis is favored*: "paleontologists, comparative anatomists, developmental biologists, and molecular geneticists are all contributing data aimed at clarifying the *genetic* basis for novel structures like heads, tails, and limbs" (Freeman 2002, pp. 475–476, emphasis mine). The three dimensions of structure and their concomitant criteria of explanatory adequacy facilitate a more transparent picture of what intellectual contributions are needed for an adequate explanation. Different novelties at different levels of organization may require different explanatory ingredients in different combinations. Successful multidisciplinary coordination with respect to different problems is likely to involve different integrative relations across fields (Brigandt 2010), and therefore we can relinquish the aim of securing a single set of fundamental relations between population genetics and Evo-devo. Viewing science in terms of the erotetic organization that governs its reasoning practices gives us a new perspective on controversy, especially its epistemological elements.

6 Teaching the (Controversial) Elephant of Science

The main result of the preceding discussion is that we need to teach more than one image of science if we are going to adequately convey its diverse aspects. If we only conceptualize scientific reasoning in terms of theory construction and hypothesis testing, we run the risk of miscommunicating the practice of science to our students and misdiagnosing the nature of controversies. This is dangerous because it presents a biased picture of the sciences to students and potentially discourages them from participating. A prophylactic against this possibility is to teach how structured problems organize research and guide inquiry (Love 2013a), not just initiate it. I have illustrated the value of this strategy through specific concepts in Evo-devo (constraints, modularity, evolvability, and novelty). A closer look at attempts to explain the origin of novelty displayed how problem agendas demand a synthesis of methodologies from different biological disciplines to generate empirically adequate explanations. This illuminates the interdisciplinarity of biological practice in a way that is often ignored when science is taught only from the perspective of theory or hypothesis. And the *National Science Education Standards* [*NSES*] encourage the teaching of interdisciplinarity, whether in terms of scientific inquiry generating knowledge via "different types of investigation" (p. 176) or the analysis of alternative explanations and models (pp. 148, 175). The present perspective also fleshes out key claims made in the *NSES*, such as "having students reflect on the concepts that guide the inquiry" (p. 174), because there is now a detailed picture of how concepts—as representative of problem agendas—actually structure inquiry.

At the outset we observed that a challenge to keeping up with the current problem structure in biology is that the life sciences contain diverse and heterogeneous disciplines. Evo-devo is just one example where the structure of problems informs how scientific inquiry is and should be organized. A recent National Research Council study on the role of theory in twenty-first century biology acknowledged this directly in the traditional folk tale about the blind men and the elephant (NRC 2008, ch. 10). As is familiar, each man accesses some feature of the elephant and forms a judgment of the whole in terms of the particular part, subject to his idiosyncratic tactile exploration: the side (like a wall), the tusk (like a spear), the trunk (like a snake), the knee (like a tree), the ear (like a fan), and the tail (like a rope).

The moral is straightforward,[13] but can be given a novel epistemological interpretation in light of our discussion of problem structure. Problems, like the elephant, have structure due to history, heterogeneity, and hierarchy. Teaching this problem structure in the context of Evo-devo—and other areas of biology—assists students in learning about how different data, methods, and theoretical assumptions are brought to bear on complex biological phenomena. This structure is not esoteric (i.e., only comprehensible to a small group of specialists), but can be vague or implicit. Reliance on philosophical reconstruction and explication serves the teacher in this endeavor, as shown in the case of evolutionary novelty. We need to investigate phenomena in the world (like the elephant) with a combination of theories, experiments, methods, and observations, but we need to explore different but complementary images of scientific investigation as well, such as hypothesis testing, modeling, and problem structure (Fig. 2). One immediate advantage of teaching the erotetic image of science is an expanded understanding of controversy.

Eugenie Scott and Glenn Branch provided five conditions for when it is appropriate to teach scientific controversy (Scott and Branch 2003, pp. 499–500).

1. The controversy ought to be of interest to students.
2. The controversy ought to be primarily scientific, rather than primarily moral, social or religious.
3. The resources for each side of the controversy ought to be comparable in availability.
4. The resources for each side of the controversy ought to be comparable in quality.
5. The controversy ought to be understandable by the students.

Students are fickle about their interests, and whether they find Evo-devo topics intriguing is difficult to ascertain *a priori*. The controversies discussed herein are clearly scientific, and the resources in the controversy are comparable in quality and availability, even though the number of advocates on each side is not equal in all cases (e.g., there are fewer advocates of the generic physical explanation of novelty

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[13] This conception, minus the metaphorical pachyderm, is present in the *NSES*: "The natural […] world is complex; it is too large and complicated to investigate and comprehend all at once. Students and scientists learn to define small portions for the convenience of investigation" (p. 116).

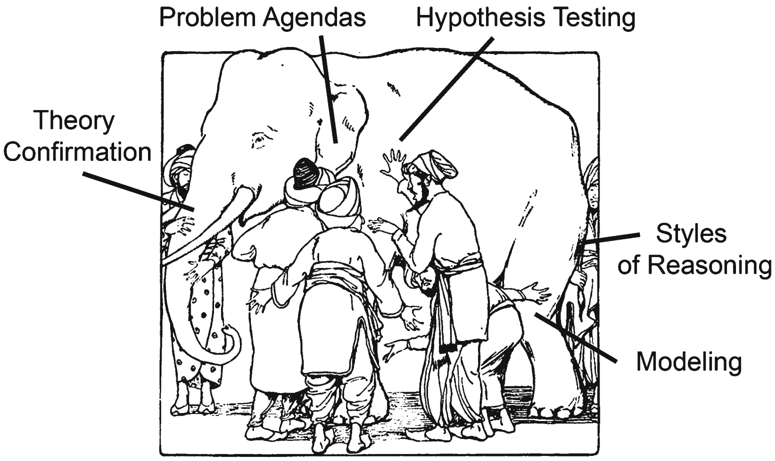

Fig. 2 A multi-faceted image of scientific reasoning. Just as the blind men studying the elephant mistake the part for the whole, so also our image of science can be subject to similar biases. Thus, we can think of teaching epistemological aspects of science as another version of the elephant and recognize that the emphasis on particular features, such as problem structure, illuminate specific and distinctive aspects of scientific reasoning, such as interdisciplinarity. Focusing on problem structure also sheds light on genuine scientific controversies, revealing differences between their empirical and epistemological elements (Source: Holton and Curry 1914, illustrator unknown; public domain, http://commons.wikimedia.org/wiki/File:Blind_men_and_elephant.png)

than the developmental genetic explanation). The controversies are not simple but also are not beyond the reach of high school and college age students. Therefore, there is a *prima facie* case for teaching these controversies.

If we scrutinize these conditions in light of our discussion of problem structure and Evo-devo controversy, then it becomes clear that we must distinguish between teaching empirical and epistemological aspects of scientific controversies. To do so reveals how controversies are often complex mixtures of epistemological agreements and disagreements, and even sometimes stem from terminological ambiguity, rather than a competition between mutually exclusive hypotheses. Teaching empirical controversy is not the same as teaching epistemological controversy; students need to know the difference and be able to distinguish them in exemplars from scientific reasoning, such as the controversy between developmental genetic and generic physical explanations of evolutionary novelty.

When this pedagogical strategy is executed in the context of biological problem agendas that demand interdisciplinary explanations, it fulfills training goals for instructors ("to make conceptual connections within and across science disciplines"; *NSES*, p. 59), and students: "No matter how the curriculum is organized, it should provide students with opportunities to become aware of the great range of scientific disciplines that exist" (AAAS 2009, ch. 1). It also foregrounds the Nature of Science considerations that are at the heart of teaching biology, including alternative explanations and methods across disciplinary approaches, the roles of consilience and collaboration, variability in experimental practices, and different standards for what counts as evidence in interdisciplinary situations (Allchin 2003, 2011). This meshes well with the *NSES* emphasis on distinct evidential standards in different disciplinary contexts, which implies that the evaluation of explanations involves more than empirical confirmation. The *Benchmarks for Scientific Literacy* paint a congruent picture:

> Scientific investigations may take many different forms [and]…are conducted for different reasons […] There are different traditions in science about what is investigated and how […] disciplines differ from one another in what is studied, techniques used, and outcomes sought […] many problems are studied by scientists using information and skills from many disciplines (AAAS 2009, ch. 1).

To construe scientific reasoning solely in terms of one image (e.g., hypothetico-deductive methodology; Lawson 2003) is to mistake one part of the elephant for the whole. An image of science that highlights how problem structure organizes research—depicted here in a snapshot from Evo-devo—can increase our appreciation of the complex nature of scientific inquiry. We need a multi-faceted image of scientific reasoning; it's time to grasp the different parts of the elephant simultaneously.

Acknowledgments I am grateful to Kostas Kampourakis for the invitation to contribute this chapter. Many of the ideas set forth here emerged in collaboration with my colleague Ingo Brigandt and I acknowledge my debt to him in working out details related to a problem-oriented conception of scientific inquiry. Wallace Arthur and Kostas Kampourakis provided helpful comments and critical feedback on an earlier version of the manuscript.

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