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Explanation in Evo-devo

Marie I. Kaiser
Bielefeld University, Germany
kaiser.m@uni-bielefeld.de

Abstract
Evo-devo is a multidisciplinary field that investigates the interplay between evolutionary and developmental processes and brings together different kinds of explanatory strategies. This chapter examines the structure of paradigmatic explanations in evo-devo (e.g., the explanation of the origin of an evolutionary novelty) and raises philosophical questions about explanation in evo-devo. Much research in evo-devo is concerned with studying the developmental mechanisms that constrain and facilitate phenotypic evolution, which suggests that a distinctive feature of evo-devo is that it constructs mechanistic explanations. In this chapter, I discuss three major challenges for thinking about evo-devo as providing mechanistic explanations. First, an explanation of an evolutionary novelty consists of several mechanistic explanations, rather than being a single one. Second, developmental mechanisms are ontogenetically and phylogenetically dynamic and thus difficult to individuate. Third, an explanation of an evolutionary novelty also has a non-mechanistic, historical part. Finally, I discuss whether evo-devo's emphasis on mechanistic explanation promotes explanatory integration or results in a reductionist view of evolution.

Keywords
mechanistic explanation; historical explanation; explanatory integration; reductive explanation

1. Philosophical Debate about Scientific Explanation

Developing explanations that demonstrate how and why natural phenomena occur is a major goal of science, including the field of evolutionary developmental biology (evo-devo). Traditionally, philosophers of science have focused on explicating the nature of scientific explanation by proposing different philosophical accounts of explanation. These accounts seek to specify a feature (or a set of features) that all scientific explanations have in common and that distinguishes them from both mere descriptions or predictions and non-scientific explanations (e.g., explanations given in everyday contexts).

An influential philosophical account of explanation is Hempel and Oppenheim's (1948) *deductive-nomological model* of explanation, according to which a scientific explanation is a sound deductive argument. A sentence describing the phenomenon to be explained (the *explanandum*) is logically deduced from at least one general law statement and certain statements of antecedent conditions (the *explanans*). The basic idea behind this account is that a phenomenon is explained by showing that, given the particular circumstances and the laws in question, the phenomenon was to be expected. For instance, assuming that the generalization that all genes are composed of nucleic acids is a biological law, it follows from this law and from the circumstance that x_1 is a gene that x_1 is composed of nucleic acids.

Other philosophers have challenged the deductive-nomological model and its assumptions that explanations are characterized by their logical structure and must refer to laws. Proponents of the *causal-mechanical model* of explanation hold that scientific explanations show how and why natural phenomena occur by tracing the causes, causal processes, or causal mechanisms that lead to or compose the phenomenon. What distinguishes scientific explanations from mere descriptions is that explanations situate phenomena within the causal structure of the world. Different philosophers diverge in their views about what it means to trace the causes of a phenomenon. Woodward's (2003) *interventionist account* of causal explanation is among the accounts most relevant to the biological sciences. It emphasizes that explanations must provide answers to what-if-things-had-been-different questions that can be used to manipulate and control the phenomenon to be explained. According to this account, causal explanations must exhibit patterns of counterfactual dependency—they must describe factors that, if they were changed by interventions, would regularly lead to changes in the phenomenon to be explained. For example, there is a counterfactual dependency between the stimulation of a muscle fiber and the contraction of this muscle fiber such that if a muscle fiber were stimulated by an incoming action potential the muscle fiber would contract. Waters (2007) takes up the basic idea of interventionism and argues further that causal explanations in the biological sciences must describe actual difference makers. A second major causal-mechanical account of explanation that is relevant to biology is the *mechanistic account*. The new mechanists (e.g., Machamer et al. 2000; Craver 2007; Craver and Darden 2013; Glennan 2017) stress that many explanations in the life sciences explain a phenomenon by describing the causal mechanism that underlies or produces it.

In recent decades, philosophical attention has shifted largely from the general nature of scientific explanation towards explanatory practices in specific scientific fields. Rather than debating universal features that all scientific explanations have (or should have) in common, philosophers now focus more on actual cases of explanations and analyze the explanatory strategies that occur in scientific practice. They identify, for instance, different *types of explanations* that can be found in different scientific contexts (e.g., topological, mechanistic, reductive, functional, etiological, or mathematical explanations). They also examine the "functional roles" (Woody 2015) that explanations play in scientific practice. These philosophical analyses are often characterized by pluralist and pragmatist perspectives. Scientific pluralists emphasize the diversity of scientific approaches such as the various types of explanations that can be found in the biological sciences (Kellert et al. 2006). Pragmatists draw our attention to the fact that explanations are answers to questions (or solutions of problems) where the adequacy of an explanation depends on both the specific question that it addresses and the purpose or goal that is supposed to be achieved in a particular scientific context (van Fraassen 1980, Chapter 5). Philosophers who adopt pluralist and pragmatist stances do not deny that describing laws, revealing counterfactual dependencies (e.g., by identifying difference makers), or describing causal mechanisms are essential to scientific explanations. They rather emphasize that scientific explanations do not consist in only one of these things but differ from context to context, depending on the scientific question that they seek to answer and the functional roles they are supposed to play. In particular, not all biological explanations seem to explain a phenomenon by describing its underlying causal mechanism. For example, it is argued that biological phenomena, such as a species' optimal number of offspring or the long-term stability of human-microbe associations, are explained structurally in virtue of the mathematical properties of the system rather than in terms of the mechanisms that underlie the phenomena (Huneman 2018). Furthermore, only a few (if any) biological explanations seem to appeal to generalizations that are natural laws in a strict sense (i.e., that do not have exceptions and that are not historically contingent; see the chapter "Generalization in Evo-Devo"). Mendel's law of independent assortment, for example, explains why the two pea traits "yellow seeds" and "round seeds" are inherited and combined independently from each other. Despite its name, Mendel's law is not a natural law but a generalization with major exceptions because it does not hold for genes that are close together on a chromosome.

With this general background in view, the remainder of the chapter focuses on biological explanations that are developed in the field of evo-devo. My approach aligns broadly with pluralist and pragmatist perspectives. Evo-devo is a multidisciplinary field that brings together explanatory strategies of different kinds. The types of explanation given can vary depending on the phenomenon under study, the research question that is being asked, and the purpose of research. Despite this diversity, however, the explanatory strategies in evo-devo also share some general features that raise interesting philosophical questions about mechanisms, integration, and reduction. The starting point of my analysis is the observation that, since evo-devo investigates the interplay between evolutionary and developmental processes (e.g., how development constrains and facilitates phenotypic evolution), it provides explanations that differ from population-level explanations in standard evolutionary biology. Explanations in evo-devo often seem to be *mechanistic explanations* because they explain phenotypic evolution by describing the molecular or cellular mechanisms that figure in the development of a phenotypic trait (see the chapter "Mechanisms in Evo-Devo"). On the other hand, "[e]vo-devo is partly built around denying the correctness of one-sided explanatory strategies" (Hamilton 2009, 213). Accordingly, explanations in evo-devo not only refer to developmental mechanisms but also describe historical processes, such as the process of how a phenotypic trait or a developmental system changes over time (Calcott 2009). The integrative character of these explanations seems to pose a challenge for thinking about evo-devo as providing mechanistic explanations alone because the historical part of the explanation does not seem to be mechanistic. Other authors, however, argue that it is the mechanistic framework in particular that provides a "true integration of developmental and evolutionary processes" (Laubichler 2009, 38).

This chapter proceeds as follows. In Section 2, I clarify which kinds of phenomena evo-devo seeks to explain. Section 3 introduces the philosophical concept of a mechanistic explanation. In Section 4, I apply this concept to the explanations developed in evo-devo and highlight some challenges for thinking about evo-devo as providing mechanistic explanations. In Section 5, I discuss how far mechanistic explanations furnish explanatory integration and whether or not they result in a reductionist view of evolution.

2. What Evo-devo Seeks to Explain

Evo-devo studies the interrelations between development and evolution on multiple levels. It not only brings together developmental biology and evolutionary biology but also integrates a variety of biological disciplines, from paleontology to quantitative genetics and from morphology to ecology (Moczek et al. 2015; Brigandt 2015; see also the chapter "Interdisciplinarity in Evo-Devo"). This integration is necessary because evo-devo investigates and seeks to explain a wide range of phenomena. Two main axes of research can be distinguished (see also Müller 2007, Love 2015). First, evo-devo studies how development evolves, such as how developmental systems originated and how developmental processes are modified through time. Second, evo-devo also investigates how development constrains and facilitates evolution, such as how features of development influence the rate and direction of phenotypic variation and how development contributes to phenotypic novelty. Sometimes a third set of research questions is mentioned, which concerns the role that the environment plays in evolutionary developmental interactions. This third set of research questions considers the two main research axes in particular ways, such as by focusing on how phenotypic plasticity evolves or how ecologically responsive features of development share evolutionary trajectories (see the chapters "Eco-Evo-Devo" and "Developmental Plasticity and Evolution").

One way to specify the phenomena evo-devo seeks to explain is by contrast with the phenomena explained by standard evolutionary biology. Both fields study phenotypic change over time, but standard evolutionary biology typically regards it as a quantitative phenomenon that takes place on the level of populations. This focuses investigation on how variation in phenotypic traits is correlated with allele frequencies in populations and the processes that drive change in populations over time (such as natural selection, drift, and mutation). Evo-devo, in contrast, often treats phenotypic change at the level of individuals or lineages and directs our attention to how changes in developmental mechanisms give rise to both quantitative and qualitative changes in phenotypic traits and how this shapes (and is shaped) by evolutionary processes.

A major type of phenomenon that evo-devo seeks to explain is the origin of evolutionary novelties, such as how fish fins evolved into tetrapod limbs (see the chapters "Developmental Innovation and Phenotypic Novelty" and "Evolutionary Cell Biology on the Fin-to-Limb Transition"). Here the question is not which selective factors played a role in the modification and propagation of limbs in a population. Rather, many evo-devo researchers ask how a developmental mechanism that produces fins could have changed through time to become a developmental mechanism that produces limbs. One approach to explaining the origin of an evolutionary novelty involves describing a continuous trajectory of phenotypic change in a lineage of organisms in connection with how the developmental mechanisms that produce specific phenotypic traits likely changed at each stage (Calcott 2009). This evo-devo approach explains phenotypic evolution on the level of individual organisms by integrative descriptions of evolutionary processes and developmental mechanisms. Another approach to explaining the origin of evolutionary novelty involves specifying the details and governing principles of the genotype-phenotype map to understand how new possibilities arise (see the chapter "Genotype-Phenotype Map"). This distinct approach (sometimes labeled devo-evo) explains phenotypic evolution by tracing how the possible trajectories from genotype to phenotype can be modified and in what ways, as well as how easy or difficult it is to make particular modifications (see chapter the "Devo-Evo of Cell Types"). Both approaches differ from explanations in standard evolutionary theory that invoke population-level processes, such as natural selection, to account for evolutionary changes in the distribution of phenotypes.

3. The Concept of a Mechanistic Explanation

Proponents of the new mechanistic philosophy emphasize that much research in the life sciences is devoted to discovering mechanisms and developing mechanistic explanations (see chapter "Mechanisms in Evo-Devo"). To mechanistically explain a phenomenon is to describe the mechanism that underlies or produces the phenomenon (Machamer et al. 2000; Craver 2007; Craver and Darden 2013; Glennan 2017). Despite different interpretations among the new mechanists, there is a broad consensus on a minimal characterization of mechanisms that is applicable to biology and other scientific fields:

> A mechanism for a phenomenon consists of entities and activities organized in such a way that they are responsible for the phenomenon. (Illari and Williamson 2012, 120)

This characterization highlights four features: (1) a mechanism is decomposable into components of two kinds, *entities and activities*, (2) how the components are *organized* is crucial to the working of a mechanism, (3) a mechanism is individuated with respect to a specific *phenomenon*, and (4) a mechanism bears a characteristic relation to its phenomenon, namely, according to the above characterization, a mechanism is *responsible for* a phenomenon.

Explaining a phenomenon by describing the mechanism that underlies or produces it means describing how the entities and activities that compose a mechanism work together to bring about the phenomenon in question. Consider the mechanism for anterior/posterior patterning in vertebrate limb development. It consists of material objects ("entities"), such as the Zone Polarizing Activity (ZPA), which is a gradient of the protein Sonic hedgehog (Shh), the Apical Ectodermal Ridge (AER), and the proteins FGF4 and FGF8. These entities engage in activities, such as inducing, expressing, producing, and maintaining, which bring about particular kinds of effects. For example, the AER induces cell outgrowth in the nascent limb bud that leads to its enlargement.

Entities and activities are spatially, temporally, and hierarchically organized in a specific way, which is why mechanisms differ from mere aggregates, mere spatial arrangements, and mere temporal sequences. For instance, the Shh proteins are spatially distributed in the limb bud in a characteristic way. The activities of entities are temporally ordered in a specific way; for example, Shh induces the AER, which produces FGF4 and FGF8, which in turn maintain the expression of Shh. Hierarchical ordering is found in the ZPA, which consists of a gradient of Shh proteins. Mechanistic explanations describe which entities and which activities are organized in which ways to bring about the phenomenon to be explained.

Mechanisms consist of all and of only those entities and activities that are relevant to a specific phenomenon. In other words, the components and boundaries of mechanisms are individuated with regard to a specific phenomenon. This is why mechanisms are said to be mechanisms *for* phenomena. The mechanism for anterior/posterior patterning in vertebrate limb development typically excludes ATPases producing ATP because they are not specifically relevant to the formation of the anterior/posterior axis in limbs. Spelling out the relevance condition is controversial (Kaiser 2018). One idea, "constitutive relevance" (Craver 2007, 139), is that an entity engaged in an activity is a component of a mechanism for a phenomenon only if the components and the phenomenon are mutually manipulable: changing a component (e.g., knocking out the Shh gene) changes the phenomenon (e.g., syndactyly or loss of digits) and changing the phenomenon requires changes to one or more of the components.

A mechanism can be 'responsible for' a phenomenon in many ways, such as regulating, maintaining states, or exhibiting behaviors (Illari and Williamson 2012, 123-125), with different degrees of regularity (Machamer et al. 2000). Because mechanisms can be related to phenomena in different ways, it is important to distinguish etiological mechanisms from constitutive mechanisms (Kaiser and Krickel 2017). The former cause or produce a phenomenon and therefore etiological mechanistic explanations describe the antecedent causes that lead up to the phenomenon in question. By contrast, constitutive mechanisms constitute or compose a phenomenon and therefore constitutive mechanistic explanations describe the entities and activities that constitute the phenomenon to be explained, similar to explanations of the behavior of a whole in terms of its parts (Kaiser 2015, Chapter 6).

4. Evo-devo and Mechanistic Explanation

Evo-devo not only studies evolutionary processes but also takes into account the developmental mechanisms that produce phenotypes of individual organisms. It is called a "mechanistic science" (Wagner et al. 2000, 819) because it "represents a causal mechanistic approach towards the understanding of phenotypic change in evolution" (Müller 2007, 945). However, the relationship between mechanistic explanations, as described in Section 3, and this "causal mechanistic approach" is not so clear. Evo-devo does not simply explain evolutionary phenomena in terms of developmental mechanisms, but it also integrates explanatory strategies from different fields in more complex ways (Love 2008). The resulting "mechanistic" explanations refer to developmental mechanisms *and* evolutionary processes and it is unclear whether and how these correspond to mechanistic explanations as discussed by proponents of the new mechanistic philosophy.

Importantly, the central question is not whether evo-devo provides *only* mechanistic explanations. The phenomena that evo-devo investigates and seeks to explain are diverse and suggest multiple explanatory strategies (recall Section 2). However, exploring the question of whether paradigmatic examples of evo-devo explanations can be characterized as mechanistic explanations (*sensu* Section 3) reveals three major challenges (Sections 4.1-4.3). One such paradigmatic example of explanation is the origin of evolutionary novelties such as the origin of tetrapod limbs (see the chapter "Developmental Innovation and Phenotypic Novelty"). These explanations constitute a central explanatory focus of evo-devo, in part because they lie outside the explanatory capacities of standard evolutionary biology (Wagner et al. 2000, 822). They require understanding how developmental mechanisms generate trait variability on the trajectory from genotype to phenotype in individual organisms.

Reconsidering the example from above, how does evo-devo attempt to explain the origin of tetrapod limbs from fish fins? Calcott characterizes one approach as "lineage explanations" (2009, 52), which have two dimensions. First, they describe a continuous trajectory of phenotypic change in a lineage of organisms (continuity dimension). Second, they demonstrate how developmental mechanisms bring about each of the phenotypic traits in the continuous trajectory (production dimension). On this approach, the origin of tetrapod limbs is explained by describing a continuous sequence of phenotypic traits that starts from fish fins and ends with tetrapod limbs with there being only small changes between the successive traits and their underlying mechanisms at any one juncture. Furthermore, each phenotypic trait in the continuous sequence is given a mechanistic explanation that shows how a developmental mechanism brings about this trait in an individual organism. So, an evo-devo explanation of the origin of tetrapod limbs demonstrates how organisms that develop fins could have continuously changed and transformed into organisms that develop limbs: "how something that works like *this* could have turned into something that works like *that*" (Calcott 2009, 56; emphasis in the original). They provide an understanding of how a phenotypic trait is produced and how it could have changed.

4.1 Several Mechanistic Explanations

A lineage explanation of the origin of an evolutionary novelty is a mechanistic explanation because it describes the developmental mechanism that produces a trait and shows how the components of this mechanism could have continuously changed into a mechanism that produces a different trait. However, this approach does not yield a single mechanistic explanation but rather several different mechanistic explanations – one mechanistic explanation for each trait in the continuous sequence of changing traits. Each mechanistic explanation describes how the underlying developmental mechanism brings about a specific phenotypic trait that some organisms in the lineage exhibit. For each trait, we have an account of which entities engage in which activities and how they are spatially, temporally, and hierarchically organized so that they generate the phenotypic trait in question (Figure 1).

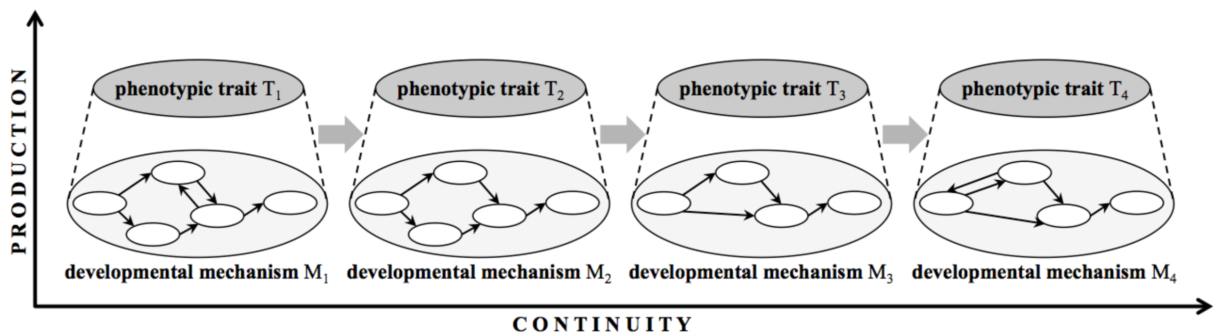

Fig. 1: A Schematic Representation of a Lineage Explanation for the Origin of Evolutionary Novelties. Redrawn from (Craver 2007, 7) and (Calcott 2009, 58, 60).

A lineage explanation for the origin of vertebrate limbs contains one mechanistic explanation for each phenotypic trait in the continuous sequence of traits. In our example, it describes the mechanism of how fish develop fins (M_1), the mechanism of how vertebrates develop limbs (M_4), and the mechanisms of how each intermediate phenotypic trait is developed, so how the extinct *Eusthenopteron* develops fins with lobes (M_2) and how the extinct *Tiktaalik roseae* develops relatively strong and robust pelvic fins (M_3). (A four-step sequence is an idealization still; obviously, there would be more intermediate steps in the sequence.) Although current scientific research might lack information about intervening steps in a sequence because not all of the developmental mechanisms are known, evo-devo biologists aim to provide a complete lineage explanation of the origin of vertebrate limbs that contains a description of all relevant mechanisms.

The entities and activities in a mechanism that are relevant to bringing about a phenotypic trait and how they are organized varies from trait to trait. This is why the white circles and arrows in Figure 1, representing the entities, activities, and their organization, vary from mechanism to mechanism. In the fin case, the developing fin bud has an elongated structure, the apical fold (AF), which is missing in the limb bud, and the limb skeleton is composed of endochondral bones (endoskeleton), whereas the fin skeleton consists almost entirely of fin rays (exoskeleton), without a robust endoskeleton. The developmental mechanisms, however, share many entities and activities (e.g., *Hox* genes that are expressed, gradients of the protein Shh that induces the expression of other genes, etc.), which gives rise to continuity in the sequence of developmental mechanisms and makes plausible that organisms with one phenotypic trait (e.g., T_3) have evolved from organisms with the preceding phenotypic trait (e.g., T_2).

In sum, that lineage explanations consist of several different mechanistic explanations is an important aspect of their structure, though it does not present a serious obstacle for claiming that evo-devo provides mechanistic explanations.

4.2 Difficulties with Individuating Mechanisms

The entities and activities that compose a developmental mechanism and how they are organized within it changes dramatically during the time of its operation (i.e., from its starting conditions to its finishing conditions). Entities come into existence, transform, and sometimes go out of existence again. How entities are spatially located and how they are spatially related to each other can vary extremely. Likewise, in different developmental stages entities engage in different activities, and the temporal ordering of continuing activities changes. This "dynamic constitution and organization" (Love 2018, 343) of developmental mechanisms makes it challenging to individuate them or draw the boundaries of a particular mechanism by telling apart those entities and activities that belong to it from those that do not (Kaiser 2018, 124-126).

This holds especially for developmental mechanisms that are described in lineage explanations since they span evolutionary time as well. Lineage explanations describe developmental mechanisms that *evolve*. They not only describe (changing) mechanisms for how a phenotypic trait originates developmentally in an individual organism, but they also describe how those dynamic mechanisms have undergone radical evolutionary shifts in their components and how they are organized. It is even more difficult to individuate developmental mechanisms that evolve because one has to decide when the dynamic organized components of a mechanism have changed enough to be characterized as a new developmental mechanism that is distinct from its precursor (see the chapter "Mechanisms in Evo-Devo"). Identifying the ontogenetic and phylogenetic boundaries of developmental mechanisms is a serious challenge for evo-devo biologists, but it does not provide us with an argument against the claim that, at least sometimes, evo-devo biologists do succeed in individuating developmental mechanisms and providing mechanistic explanations.

4.3 The Historical Part of Lineage Explanations

Lineage explanations describe not only developmental mechanisms but also evolutionary processes that are historical in character. Explaining the origin of an evolutionary novelty requires describing how the different developmental mechanisms bring about the different phenotypic traits (production dimension), as well as how these mechanisms and their components could have gradually changed (continuity dimension). As "genuine explanations of evolutionary change" (Calcott 2009, 72) lineage explanations must also describe the historical process of how developmental mechanisms of individual organisms are continuously modified to give rise to a specific sequence of phenotypic traits. If the mechanistic explanations in the sequence of change are predicated of individual organisms, then the historical process of how a mechanism can change to become a different mechanism is not itself a mechanistic explanation. Instead, it is a historical explanation of how the components of a mechanism can change so that the mechanism transforms into a new mechanism (and so on) until the mechanism that brings about the evolutionary novelty has evolved. However, if we predicate the mechanism of the lineage rather than individual organisms, then this interpretation can be avoided (Nuño de la Rosa and Villegas 2019; see the chapter "Dispositional Properties in Evo-Devo").

Another conception of mechanism could avoid this interpretation. One might argue that even though the historical part of the lineage explanation does not describe the working of a developmental mechanism it still describes the working of the mechanism of natural selection. This would make lineage explanations in evo-devo mechanistic in a different sense. Some argue that the study of ultimate causes in evolutionary biology results in mechanistic explanations because natural selection can be characterized as a mechanism (Barros 2008). However, there are difficulties with this conception since there are good reasons to worry that natural selection is not mechanistic in the appropriate sense (Millstein and Skipper 2005). Glennan has argued that historical explanations can describe "ephemeral mechanisms" (2017, 129), which are non-stable and produce singular events (and thus are non-regular). Whether the corresponding weakening of the regularity and the stability requirement on mechanisms should be embraced remains an open question.

There is another reason for focusing on mechanistic explanations in evo-devo without appealing to natural selection as a mechanism. First, although it is plausible (in principle) to speak of natural selection as an evolutionary mechanism, this is not how the notion of mechanism is primarily used in evo-devo. Practitioners typically invoke 'causal mechanism', 'mechanistic relationships' or 'mechanistic approach' to refer to developmental mechanisms. If the aim is to characterize lineage explanations in evo-devo as "purely" mechanistic, then an alternative interpretation, such as predicating mechanisms of lineages, is preferable to avoid the misleading impression that they describe developmental mechanisms only. Second and more importantly, lineage explanations and other evo-devo approaches to the origin of evolutionary novelties simply do not refer to natural selection. They focus on how developmental mechanisms, including mapping relations between genotype and phenotype, could have changed to produce novel traits; they do not refer to populations and specify population processes that could have modified these phenotypic traits.

To conclude, lineage explanations consist of two parts. The mechanistic part of the explanation describes the developmental mechanisms that underlie each phenotypic trait in the sequence of traits leading to the evolutionarily novel trait. The historical, non-mechanistic part of the explanation describes the continuous changes between the different developmental mechanisms and how this led to the evolution of the developmental mechanism that brings about the evolutionarily novel trait. Hence, evo-devo provides mechanistic explanations but they are not fully mechanistic.

5. Mechanistic Explanation, Integration, and Reduction

Does evo-devo's emphasis on developmental mechanisms and mechanistic explanation indicate an underlying commitment to a reductionist approach? Or do these explanatory approaches also suggest forms of integration? Consider the relation between mechanistic explanation and explanatory integration first. Evo-devo is said to provide not only an "extended, more inclusive explanatory framework" (Müller 2007, 500; see the chapter "Evo-Devo's Contributions to the Extended Evolutionary Synthesis") but also an approach that is *integrative* in at least two ways. First, it is a multidisciplinary field that brings together a variety of disciplines (Moczek et al. 2015; Brigandt 2015). Accounting for evolutionary novelty requires integrating insights from evolutionary genetics, developmental biology, paleontology, phylogeny, morphology, and other scientific fields (Love 2008). Second, evo-devo brings together different explanatory strategies in one explanation. It integrates the analysis of historical processes with that of extant developmental systems, bringing together form-related and function-related causes into a single explanatory model (Hamilton 2009, 215; see the chapter "Form and Function in Evo-Devo"). Laubichler argues for "a true integration" (2009, 38) of evolution and development through the molecular analysis of developmental mechanisms and gene regulatory networks in combination with the comparison of these mechanisms across taxa. This provides an explanatory integration in terms of a mechanistic understanding of both the development and evolution of phenotypic traits (Laubichler 2009, 36-39).

Mechanistic explanations often combine several levels of organization and thus provide some sort of explanatory integration (Brigandt 2010, see the chapters "Mechanisms in Evo-devo" and "Levels of Organization in Evo-Devo"). However, if adopting a "mechanistic framework" means that only mechanistic explanations are legitimate, then this could impede forms of explanatory integration that bring together different approaches for both development and evolution. The preceding section indicated that paradigmatic explanations in evo-devo, such as lineage explanations, involve the integration of multiple parts and these may not always be construed as mechanistic. Successful explanatory integration in evo-devo need not result in *purely* mechanistic explanations and the more salient aspect is evo-devo's efforts to integrate different explanatory strategies in a single explanation to account for the origin of evolutionary novelties and other phenomena.

One might worry that evo-devo's focus on mechanistic explanations runs contrary to promoting plurality and integration because it is based on a *reductionist* approach. By seeking to explain phenotypic evolution in terms of molecular developmental mechanisms and gene regulatory networks, mainstream evo-devo appears to privilege the molecular gene in its explanatory framework and neglect to investigate other potentially relevant causes (Hamilton 2009, 215). Explanations of phenotypic evolution that refer only to the actions of and interactions between genes are a kind of reductive explanation that can be characterized as a "fundamental-level explanation" (Kaiser 2015, 202) because it assumes that the level of genes is explanatorily fundamental and that any successful explanation must refer to genes. The criticism that evo-devo's emphasis on mechanistic explanations results in gene-centrism and misleading reductive explanations may be true for several evo-devo research programs. However, mechanistic explanations need not be gene-centric, fundamental-level explanations. Evo-devo's actual explanatory practice shows that there are also research programs that take into account epigenetic causes and the influence of environmental factors on development and evolution (Müller 2007; see the chapter "Evo-Devo's Contributions to the Extended Evolutionary Synthesis"). Whether the resulting mechanistic explanations would still be reductive explanations (e.g., because they refer to lower-level and internal factors; Kaiser 2015) is an important question, but clearly, they would not be "naively reductionist" (Hamilton 2009, 216).

In conclusion, evo-devo's emphasis on developmental mechanisms and mechanistic explanation can furnish explanatory integration because it integrates evolution and development and because mechanistic explanations often bridge several levels of organization. If this emphasis on developmental mechanisms, however, comes along with gene-centrism and the search for fundamental-level explanations, evo-devo is practiced in a reductionistic fashion.

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