

# Chapter 21

## Evo-devo as a Trading Zone

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### 21.1 Introduction

Evolutionary developmental biology (Evo-devo) is philosophically fascinating because of its plurality of scientific “cultures” of practice and theory that continue making progress towards a better understanding of complex biological reality. Through an examination of a variety of the scientific cultures pertinent to Evo-devo, I show here that Evo-devo can be usefully understood as a *trading zone* (Galison 1997). That is, it is constituted by a variety of disciplines, styles, and paradigms negotiating heavily with one another. I am concerned with the differences, interactions, and relative openness and flexibility of these cultures. When are the cultures acting—individually or collectively—in ways that further research empirically, theoretically, and ethically? When do they become imperialistic, in the sense of excluding and subordinating other cultures? I wish to explore some of the key assumptions standing behind, under, and within each. Such pre-suppositions ground the concepts, methods, and models of each culture. They are also an integral aspect of the broader norms, forms of communication, and shared meanings and behaviors of each culture. The goal of this chapter is to identify six

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cultures of Evo-devo (three styles and three paradigms) and provide an initial *assumption archaeology*<sup>1</sup> of their internal structure, and mutual relations, through the concept of a trading zone. My main excavation site is Bonner (1982), a founding text of Evo-devo and product of the 1981 Dahlem conference on evolution and development. Possible future work and limitations of my analysis are sketched in the conclusion.

What exactly is a trading zone? Peter Galison developed the concept in *Image and Logic* (1997) to describe the interactions between two traditions of instrument-building and experimentation in microphysics: those using bubble chambers to form images of sub-atomic interactions, and those employing detectors arrayed around the particle collision event itself, arranged according to logical electrical circuit diagrams, to produce statistical patterns of the spatiotemporal appearance of diverse kinds of particles. Theorists also met these instrument-makers and experimentalists in this trading zone. What is the relation among researchers and among traditions?

Two groups can agree on rules of exchange even if they ascribe utterly different significance to the objects being exchanged; they may even disagree on the meaning of the exchange process itself. Nonetheless, the trading partners can hammer out a *local* coordination despite vast *global* differences. In an even more sophisticated way, cultures in interaction frequently establish contact languages, systems of discourse that can vary from the most function-specific jargons, through semispecific pidgins, to full-fledged creoles rich enough to support activities as complex as poetry and metalinguistic reflection. (Galison 1997, 783)

A pidgin is a first-generation “hybrid” language. A creole is a pidgin that has been learned by a new generation of speakers and thereby nativized; it is a full-fledged language. Interactions of various degrees of richness and texture can thus be established in trading zones. Following Galison, the coordination among cultures need only be spatiotemporally local and hardly implies agreement: “. . . in any exchange, the two subcultures may altogether disagree about the implications of the equivalencies established, the nature of the information exchanged, or the epistemic status of the coordination” (Galison 1997, 806). The often incomplete—yet powerful—trading zone dynamics identified by Galison are at work in Evo-devo. For instance, the trading zone of Evo-devo is approaching the articulation of a creole through concepts such as “gene regulatory networks” and “cell signaling” that are readily understood by workers across different cultures. Moreover, there is an exchange of molecular tools and methodologies among mechanism and mathematical modeling styles. The trading zone concept provides insight into the structure, function, and historical dynamics of Evo-devo.

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<sup>1</sup> In a forthcoming book, I develop a critical *assumption archaeology* (my term, following Michel Foucault 1966, 1969; Ian Hacking 2002; Michael Friedman 1999), which explores methods for identifying different types of assumptions (e.g., ontological, theoretical). One aim of this philosophical methodology is to investigate opportunities for collaboration of theories that make different (perhaps even conflicting) assumptions. The dialogue and self-reflexivity through which such collaboration can happen—and in which the philosopher can play a significant role—occurs in what is called an *integration platform* (Winther [under contract](#)).

In addition to the features characterized by Galison, a trading zone can be further described as a *richly overlapping domain* in which scientific cultures at different levels of abstraction interact. Disciplines, styles, and paradigms (i.e., three types of culture, each at a particular level of abstraction) interact across and within distinct levels of abstraction. Possible types of inter-cultural relations within a level can be understood in terms of different dimensions, including: (1) collaboration and competition; (2) mutual understanding and reliable translation, on the one hand, and misunderstanding, miscommunication, and incommensurability, on the other hand; and, (3) integration and fragmentation. Across levels there are complex relations of guidance (e.g., styles *guide* paradigms) and instantiation (e.g., a paradigm *instantiates* one or more styles). Understanding trading zones as richly overlapping domains provides a fine-grained tool for dissecting these manifold relations and their consequences, both within Evo-devo and elsewhere. Moreover, Evo-Devo is an important example of how science can progress through a radical plurality of perspectives and cultures.

This chapter is organized as follows. First, I explore three styles: mathematical modeling, mechanism, and history. After providing a general analysis of the concept of styles, I detail the basic components and properties of each style and locate their signature in the 1982 Dahlem volume (paying more attention to an assumption archaeology of the mathematical modeling style). Next, I analyze the concept of paradigm and initiate an archaeology of three paradigms relevant to Evo-devo: adaptationism, structuralism, and cladism. This analysis characterizes three specific paradigm cultures that often (and ideally) collaborate, understand one another, or are integrated. Finally, I explore the complex anatomy and physiology of Evo-devo as a trading zone, inviting a final reflection on the concept itself.

## 21.2 Styles in Evo-devo: Mathematical Modeling, Mechanism, and History

Styles of scientific research are very general ways of doing science, of “finding things out” (Hacking 2009). The concept was introduced by historian A.C. Crombie.

The scientific movement brought together in its common restriction to answerable questions a variety of styles of scientific argument, of scientific methods of inquiry, demonstration and explanation, diversified by their subject-matters, by general conceptions of nature, by presuppositions about scientific validity and cogency, and by scientific experience of the interaction of programmes with realizations. (Crombie 1994, vol 1, 83)

Hacking, who has articulated the concept over the last three decades, notes:

Every style of reasoning introduces a great many novelties including new types of: objects; evidence; sentences, new ways of being a candidate for truth or falsehood; laws, or at any rate modalities; possibilities. One will also notice, on occasion, new types of classification and new types of explanations. (Hacking 2002, 189)

Following these descriptions, styles provide overarching theoretical and experimental ways of doing science, and of viewing objects and processes in nature. The *standard view* of styles identifies six types: (1) deductive (postulation or axiomatic), (2) experimental, (3) analytical-hypothetical (hypothetical modeling), (4) taxonomic, (5) probabilistic, and (6) evolutionary (historical derivation or genealogy)<sup>2</sup> (Crombie 1994; Hacking 2002, 2009; Kwa 2011; cf. Pickstone 2001).

There are many other ways to identify and classify styles, such as: (1) “causal-mechanical” theorizing of German embryologists and fact-finding of American embryologists in the early twentieth century (Maienschein 1991), (2) “analysis: synthesis” and “palaetiology” in the nineteenth century (Elwick 2007), and (3) “formal” and “compositional” biology (Winther 2006a). These distinctions of style were developed for particular purposes, unrelated to the central aim of the standard view of understanding science in general. There are also classifications of styles in disciplines outside of the biological sciences (e.g., Davidson 2001; Forrester 1996). Although ongoing research explores how these styles relate to each other and to the standard view, I will not adjudicate among these classifications. Instead, I argue that biological styles are both more specific (i.e., smaller domain of application) and more concrete (i.e., more, substantive assumptions) than the standard view implies, though connections with the six generalized styles remain salient. Three biological styles are identified and discussed in this section.

1. *mathematical modeling*: the analytical-hypothetical “Galilean style” that Edmund Husserl, Noam Chomsky, and Steven Weinberg also wrote about, together with probability and statistics. It can be seen as the first and fifth, and probably the third, styles combined around the notion of a mathematical model (see Winther 2012)
2. *mechanism*: a style essential to biology, thanks to Descartes, Claude Bernard, and others. More generally, it is associated with ubiquitous, if at times problematic, forms of reductionism. This style is also a particular sort of modeling: the non-mathematical part of the analytical-hypothetical style.
3. *history*: a *bona fide* standard view style.

### 21.2.1 *Mathematical Modeling Style*

The mathematical modeling style, as expressed in the biological sciences, is not primarily about proving conjectures through deduction from axioms (the first style of the standard view). Rather, it aims at abstracting, idealizing, and generalizing a *mathematical model* for a particular set of objects and processes that express regularities and obey causal rules. The process of generating, evaluating, and using the model can be articulated in terms of five sequential activities: (1) *setting up*,

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<sup>2</sup>The first terms are Kwa’s. When present, second terms are Crombie’s and third terms are Hacking’s.

(2) *manipulating*, (3) *explaining*, (4) *objectifying*, and (5) *pluralizing* (the *SMEO-P* account, narrated in Winther 2006b, c, [under contract](#)).

1. A model is set up by measuring and observing empirical phenomena, and in the context of a theoretical background. We set up initial equations in a language (e.g., differential equations, geometrical patterns, probability equations) with a syntax (derivation rules) and semantics (parameters, variables, and functions with real-world meanings and mappings) appropriate to the problem (i.e., the language's pragmatics is respected).
2. Manipulating the initial equations with the derivation rules, which include idealizations, heuristics, and approximations permitted by the internal demands of the model, can lead to surprising results (e.g., unexpected equilibrium conditions).
3. Models can explain real-world phenomena when they identify causes, processes, and mechanisms, increase our understanding, or provide greater integration and unification of our scientific knowledge.
4. Objectifying is a concern about how models export and impose their assumptions about the world, and about the modeling process. This fourth step has been completed when researchers consider model assumptions as independent of the model and present in nature itself.<sup>3</sup> One function of an assumption archaeology is to track the epistemic and social processes associated with objectifying.
5. Since objectifying can result in pernicious reification (as well as generative explanation), a powerful additional, fifth step is often taken—pluralize. Here assumptions, data, methods, and representations are compared across mathematical models in order to assess the strengths and weaknesses of each model, and to search for robust assumptions and results (on “robustness analysis” see Weisberg 2006; Wimsatt 2007).

My *SMEO-P* account helps analyze and troubleshoot the mathematical modeling process. Many mathematical languages and methods are used when modeling in the biological sciences. Moreover, statistical theory (together with experimentation) is invariably used to compare model and data. In short, the mathematical modeling style is ubiquitous to the life sciences, including Evo-devo. It is immediately evident in the 1982 Dahlem volume. Three levels of biological hierarchy will be considered: genetic, morphogenetic, and life history.

First, Stuart Kauffman's Boolean logic genetic networks have been important in inspiring, if not directing, a significant amount of research on complexity and self-organization. One of his first papers set the formal tone in the late 1960s, which were watershed years for theoretical biology (Kauffman 1969). In the 1982 Dahlem volume, he added a short section to the group report by Dawid on “Genomic Change and Morphological Evolution.” In his section (“General Properties of Interacting Systems of Large Numbers of Genes”), Kauffman noted how “Given certain assumptions about the rules of regulatory interactions, these model genetic

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<sup>3</sup>For a discussion of Richard Levins and Richard Lewontin's analyses of objectifying model assumptions, see Winther 2006c.

regulatory systems spontaneously crystallize ordered patterns of gene expression” (Bonner 1982, 34). These assumptions include a connectivity  $K$  of exactly two—i.e., any gene is connected to two other genes. Moreover, any gene was either on or off (1 or 0), so for 10,000 genes there were  $2^{10,000}$  possible states. For that number of genes, Kauffman’s simulations indicated approximately 100 sets of gene expression patterns (with some slight variation within each set). Each of these coordinated patterns was then argued to “correspond to a single cell type” (Bonner 1982, 34). While the assumption of  $K = 2$  may be questioned, as may the very notion of “cell type,”<sup>4</sup> of interest here is the fact that Kauffman employed abstract mathematics to articulate a predictive and explanatory research project (see also Lewin 1996).

Let us turn to the morphogenetic level. The role of morphogens in development was studied and modeled by various scientists at the 1981 Dahlem conference, including Lewis Wolpert, David Raup, and Hans Meinhardt. In an earlier paper by Meinhardt (Meinhardt and Gierer 1980), cited in the “Adaptive Aspects of Development” group report, he had outlined a plethora of ways in which local and global concentrations of morphogens of various sorts (e.g., inductive, inhibitory, fast- or slow-diffusing) could give rise to different morphological phenomena (e.g., compartments, cell differentiation, and stripes). A useful table (“Reactions which lead to pattern formation”) is in the 1982 Dahlem volume (reproduced here as Table 21.1). In the text, the group report on “Adaptive Aspects of Development” (authors include J.T. Bonner, H. Meinhardt, R.A. Raff, and S.C. Stearns) states:

Table 1 shows the kinds of patterns that are generated by mathematical models of the behavior of substances that are postulated to affect differentiation. This table teaches two important and general lessons. Many patterns typically seen in development can be generated by a few simple and realistic models. Furthermore, different patterns can be produced by changes in the parameters of one model. (Bonner 1982, 218)

Mathematical models have explanatory and predictive power. The complexity of developmental patterns can be reduced to a “few simple and realistic models.” This is a strong statement, and may be too strong in two senses. First, there may be a *reification fallacy* occurring here, an abstract-concrete conflation (i.e., step 4 of the *SMEO-P* account). This is a common bias and error in mathematical modeling practices—the abstract model is confused with, and imposed on, the concrete world (Winther 2006b, c, 2008, 2011, 2014a, b, under contract). Here is the problem: mathematical models cannot *themselves* “generate” physical patterns. Yet, mathematical modeling and model objectifying is useful and productive, as long as we are careful to avoid pernicious reification and not insist on the absolute truth of the model. Second, the claim that a toolkit of a few simple models explains most developmental patterns, and that any one of those models can satisfy the explanatory burden of a broad gamut of developmental patterns places an extraordinary amount of explanatory leverage on just a few models. An *explanatory stress*

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<sup>4</sup> Kauffman (1993) argues that there are 256 cell types, or  $2^8$ . But consider B cells of the mammalian immune system. Each human being literally makes millions of new sorts of B cells every day, each with a distinct external protein chain signature. Should these be considered different cell types?

**Table 21.1** Some of the different ways morphogens can act in morphogenesis (Bonner 1982, 219)

TABLE 1 - Reactions which lead to pattern formation (15-17).

Type of reaction	Pattern which can be generated
<p>1. Local autocatalysis and long-range inhibition (15).</p>	<p>Graded concentration profiles      Bristle-like pattern</p>
<p>2. Long-range activation of states which locally exclude each other (17).</p>	<p>Stripe-like arrangement of two or more states.</p>
<p>3. Cooperation of compartments. Cell type A produces, e.g., a precursor, cell type B the final product (16).</p>	<p>A pattern centered over the common boundary is formed. Used to organize subfields such as limbs</p>
<p>4. Local elongation (15), see type 1, and: local maximum causes cell differentiation, differentiated structure repels the maximum.</p>	<p>Long elongated structures such as veins, tracheae or nerves</p>

(overextending explanatory resources; trying to explain too much with too little) may be at play here. “Simple and realistic models” may explain some aspects of certain phenomena and regularities, but care must be taken in assessing exactly how and what is being explained. In explaining stripes with these models, do we explain the causal processes underlying relative location and size? Do we explain the physiology of the cell types and the chemical composition of the morphogens in which stripes are instantiated? Are we still explaining or providing grounds for

predicting changes in stripe patterns if we vary animal species or individual genotype? Mathematical modeling in the complex, multi-causal, and empirical life sciences is a powerful tool, but the possibilities of reification fallacies and explanatory stresses means that we must be critically aware of the nature and locations of its limits (Winther 2008, 2011, 2014a, b, [under contract](#)).

The mathematical modeling style is also employed in life history theory, which addresses an even higher level of the biological hierarchy. The temporal sequencing and duration of the major milestones in the growth and development of individual organisms is here investigated (e.g., sexual maturity, age at first reproductive event, age of death, and number of offspring). Stephen Stearns' solo essay in the 1982 Dahlem volume, "The Role of Development in the Evolution of Life Histories" (237–258) highlighted three important points about life history theory. First, it "emerged in the 1960s out of the dual traditions of comparative demography and population regulation." Indeed, it was the "second attempt" at formulating a "predictive quantitative theory of evolution—population genetics was the first." Second, Stearns correctly argues that all disciplines and theories contain simplifying assumptions: "whereas population genetics underrates the organism, life history theory underrates the gene. The simplifications of one field are the complexities of the other." Third, the way forward in 1981 (and in 2010; see Stearns, Chap. 6, this volume) was for each field to stop ignoring the other, and to pay attention to development. After all, "developmental mechanisms could connect population genetics with life history theory to form a predictive theory of evolution more powerful than either" (Bonner 1982, 238–239). In essence, Stearns was advocating that Evo-devo become a trading zone, in which various disciplines and other scientific cultures would interact and negotiate theories, instruments, and concepts.

Let us continue the assumption archaeology by examining how the mathematical modeling style remains operative today, influencing ongoing work in Evo-devo at each of the three levels of biological hierarchy described above. With respect to gene regulatory networks, Kauffman and Eric Davidson's research programs are ongoing (e.g., see Huang et al. 2009 for gene regulatory networks and the Evo-devo of cancer; see also Winther 2008, 2009a, 2011). Other biologists interested in Evo-devo (and more broadly in Systems Theory) have incorporated mathematical gene networks (e.g., Alon 2003; Álvarez-Buylla et al. 2007; Junker and Schreiber 2008). At the morphogenetic level, Stuart Newman and Karl Niklas display the mathematical modeling style in their work on the evolution and development of tetrapod limb and plant body plans, respectively (see Newman, Chap. 19, this volume; Niklas, Chap. 2, this volume). Newman and his co-authors build on Alan Turing's (1952) powerful insights of a "reaction-diffusion" system. Morphogenesis is modeled using differential equations with parameters estimating morphogen concentrations as well as cell movement, number, differentiation, aggregation, and adhesion (Newman and Müller 2005; Forgacs and Newman 2005; see Winther 2011). Niklas' investigations concern both morphogenesis as well as life history and the "adaptive aspects of development" (e.g., Niklas 1994, 2000).



Regardless of this phytocentric bias, my thesis is that the participants of the 1981 Dahlem conference knew that neither biomechanics nor allometry *sensu stricto* could provide mechanistic explanations for the phenomena that occupied their attention because these disciplines lacked mathematical formulations that could make their observational consequences explicit. (Niklas, Chap. 2, this volume)

Niklas attempts to harness the resources of “biomechanics, allometry and network theory” in order “to answer some of the important questions raised during the 1981 Dahlem conference.” Note also that he, like most careful mathematical modelers, is well aware of “the intrinsic limitations imposed when using these tools” (Niklas, Chap. 2, this volume). Finally, it is worth noting that mathematical work on life history theory and “adaptive aspects of development” has further broadened, and helped give rise to a new field, Eco-evo-devo (ecological and evolutionary developmental biology; e.g., Gilbert and Epel 2008).

### 21.2.2 Mechanism Style

The mechanism style takes a functional system and breaks it down in order to understand how it works. The functional system may itself be part of a larger system—i.e., it may be a module (Winther 2001, 2005). Of which (types of) parts does the system consist? How do these parts behave, and what do they cause each other to do? What are the basic theoretical principles governing the parts, as well as the system as a whole?<sup>5</sup> The mechanism style searches for and constitutes mechanisms using four overarching strategies: (1) *analysis*, (2) *physicochemical (PC) reduction*, (3) *causal surgery*, and (4) *mechanism transplantation*.

1. To analyze is to break down or decompose. Analysis is the identification and abstraction of both the parts of a system and the behaviors of those parts. Once analyzed, the parts (and part-behaviors) of a system can be suitably articulated into a mechanism. For Robert Cummins, analysis is both the disarticulation of a system into parts (“componential analysis”) and the disarticulation of system capacities into part capacities (“functional analysis”) (Cummins 1983, 28ff). For Nancy Cartwright, “the analytical method” in physics is: “to understand what happens in the world, we take things apart into their fundamental pieces” (Cartwright 1999, 83). To analyze is to disarticulate, disarm, disassociate, cut, and divide.
2. Physicochemical (PC) reduction amounts to explaining and understanding biological phenomena, regularities, and principles using physicochemical phenomena, regularities, and principles. In particular, it is a reduction of the (hierarchical and complex) biological level to the principles of physics and chemistry, as well as of biophysics and biochemistry.<sup>6</sup> This strategy concerns *explanations*.

<sup>5</sup> See Valadez Blanco (2011) and Winther (2011) for recent discussions.

<sup>6</sup> For recent work on reduction in the biological sciences, see Wimsatt (2007), Brigandt and Love (2008), and Winther (2009a).

Marcel Weber calls this form of reduction “explanatory heteronomy” (Weber 2005, Chap. 2). Under a broad interpretation, PC-reduction is also very close to the “explanatory reduction” of classical genetics to molecular genetics (and its principles) defended by Sarkar (1998). Molecular genetics is here interpreted as part of biochemistry. PC-reduction is concerned with the reduction of abstract principles and explanations, not of parts and components.

3. To engage in causal surgery is to intervene in a system by removing or controlling the effects of certain parts, and thereby studying how other parts react to that intervention. Such active, experimental intervention is the foundation of how we learn about the behaviors of parts. This strategy concerns *actions carried out for understanding*. For Judea Pearl “intervention as surgery” is causal analysis discussed in terms of a generalized path analysis, with its regression equations and diagrams (Pearl 2000, 346ff, Winther 2014b). Carl Craver (2007) prefers to call this “ideal intervention”: “an *ideal* intervention I on X with respect to Y is a change in the value of X that changes Y, if at all, *only via* the change in X” (96). Causal surgery provides us with insight into the workings of the system.
4. Mechanism transplantation is the ultimate test of our understanding and causal surgery capacities. When we can move a part, or a collection of parts, into a new context and have them behave in (close to) the way we predicted, we have verified that our comprehension is accurate. This strategy is about *actions carried out for material construction*: “to control a situation we reassemble the pieces, we reorder them so they will work together to make things happen as we will” (Cartwright 1999, 398). For a purpose different but not unrelated to mine, Ian Hacking writes: “We are completely convinced of the reality of electrons when we regularly set out to build—and often enough succeed in building—new kinds of device that use various well-understood causal properties of electrons to interfere in other more hypothetical parts of nature” (Hacking 1983, 265). In other words, we transplant a part (an electron) into new causal contexts (e.g., machines) and validate that it behaves in the same way.

Each of these strategies is important to the mechanism style. Arguably, only the first three are necessary to identify and understand a mechanism, but the fourth is required to control and construct a mechanism. These strategies are also part and parcel of how we *characterize* a mechanism—that is, a “mechanism” is something that can be, and has been, analyzed, PC-reduced, and so forth.

How is mechanism discussed in the 1982 Dahlem volume articles? It is often used synonymously with *causal process*. For instance, “evolutionary”, “developmental”, and “genetic” mechanisms are appealed to throughout the volume (e.g., metamorphosis is a mechanism; Bonner 1982, 226). These causal processes are intended to be explanatory. Let us look at just two examples, and apply the four strategies discussed above.

First, the last group report on “The Role of Development in Macroevolutionary Change” (authors include P. Alberch, B.C. Goodwin, S.J. Gould, A. de Ricqlès, G.P. Wagner, and D.B. Wake) states: “perhaps such homeostatic mechanisms are the key to understanding why stasis is encountered in phylogeny” (Bonner 1982, 287).

The group is appealing to developmental systems as “resilient to environmental and genetic perturbations” and as a possible explanatory processes for long-term stasis of species in phylogeny, under the punctuated equilibrium model of Eldredge and Gould. The broad system of a species (i.e., a species-as-an-individual) is analyzed into one of its parts: the development of individual organisms. While analysis is employed, PC-reduction may not be. Causal surgery on, and transplantation of, homeostatic mechanisms is difficult to imagine, but it would not be impossible to set up experiments for the role of developmental homeostasis in speciation, perhaps through chemical or temperature shock that perturbs otherwise robust canalization. A second example—“diffusion-reaction mechanism”—is observable in Wolpert (Bonner 1982, 183) and the last group report (290–293). (This is the mechanism that was modeled mathematically in the above section.) Morphogenic gradients, and cell-type and tissue/organ formation can be measured biochemically. Parts are identified, complex processes are (partly) reduced to physicochemical principles, experimental causal surgery can be carried out, and transplantation into other species is possible. The four mechanism strategies are also satisfied for the “genetic mechanisms” determining “heterochronic shifts” (Bonner 1982, 2) or the “specification of body pattern” (192). Further assumption archaeology of the mechanism style in Evo-devo today (e.g., David Stern’s research program on *cis*-regulatory elements in *Drosophilids*; Stern and Orgogozo 2009) would shed light on the power of causal and experimental analysis, and on the rich relations of this style to other styles.

### 21.2.3 History Style

The history style in the biological sciences aims to present the narrative or biography of a part, placing it in its organizational and causal whole; this biography is justified by a phylogeny (see Winther 2006a, 2011). Here we consider two general sorts of parts: (1) a part of an organism, and, (2) a species as a part of a clade and an ecosystem.

Consider first a part of an organism. There is a well-known narrative about the evolution of the inner ear in mammals from the first two gill arches—the “visceral arches”—of agnathans (“jawless” fish) *via* the throat skeleton and stapes of early tetrapods (Radinsky 1987; Olivier Rieppel, personal communication). In this biography of the inner ear, the “central subject” (Hull 1989) of the narrative is placed in the context of the organism. The historically changing dynamics and topological organization of the inner ear with respect to surrounding organs and tissues are investigated, recognized, and weaved into the biography. Moreover, the central subject’s changing functions (and associated selective pressures) are also explored and incorporated into the narrative. Form and function are intertwined; comparative morphology, functional morphology, and life-history theory are integrated (Wake 1979; Winther 2006a, b). A phylogeny—the abstracted and postulated

ancestor-descendant relations—is the necessary theoretical background to this morphological and functional biography. In order to trace the changing content and context of the central subject, we must know the history of the species in which it is found.

Second, consider the narrative of an entire species. It also is articulated in a specific context—its clade and ecosystem. The species' biography includes (i) who it came from (its ancestors) and who it gave rise to (its descendants), and (ii) to whom it is related in a nested manner (its clade). Depending on the philosophy of systematics, (i) and (ii) are related (e.g., process cladism, many Bayesian schools) or utterly distinct (e.g., pattern cladism) matters (Hull 1988; De Queiroz 1988; Sober 2008). Furthermore, the biography includes an account of the selective and ecological pressures to which the species is subject. A given species' history and environment are necessary components for telling a justified and coherent narrative of a species.

In the 1982 Dahlem volume, considerations of history and systematics are sparse and phylogenetic reconstruction is dramatically undertheorized. There is no mention of cladism or cladistics (see below, Sect. 21.3). The term “classification” is rarely used, and then only for the classification of mutations (Bonner 1982, 196; e.g., “homeotic mutations”) or “styles of heterochrony” (334). The term “phylogeny” is a little more frequent, but is used in a vague and general manner. The only drawn phylogenies (97) are highly abstract (and now quaint) representations of deuterostome and protostome relationships, indicating the presence or absence of metamerism. Phylogenies are significantly more standardized and formalized today. Even the term “history” is almost absent (apart from its use in “life-history”). “Systematics” is used only once, almost ironically, in Alberch's contribution. The explicit use of, and reflection about, the history style is absent, which is curious for at least three reasons: (1) some of the biologists at the 1981 Dahlem conference (e.g., Raff, de Ricqlès, Wagner, and Wake) did phylogenetic work then and subsequently; (2) the history style became very important to Evo-devo subsequently; and, (3) the “cladistic wars” were raging in nearby professional contexts.

In light of the above observations, a range of interpretations is possible, so I informally surveyed some of those who had been present at the 1981 Dahlem conference for their recollections. All of those whom I surveyed ( $n = 5$ ) agreed that there was no explicit discussion of phylogeny, classification, systematics, or history at the workshop. But they disagreed as to why. Some felt that historical considerations were not deemed important by the participants of a workshop focused explicitly on developmental mechanisms rather than on technical issues in phylogenetic reconstruction (i.e., *phylogeny was not part of the problem* view). Others thought that history was indeed judged to be significant, and was seen as an indispensable part of the attempt to incorporate mechanism, constraint, and heterochrony/allometry into evolutionary theory, but that history either was already a “core principle” not requiring special attention or the correct general outline of a single phylogeny was already at hand, and further work would not change that outline significantly, a position also found in Dobzhansky (1937) (both of these can be summarized as *we already have the admittedly important phylogeny*).

The importance of history for Evo-devo was not fully appreciated by many of those present at the 1981 Dahlem conference and may hint that mechanism and constraint were overemphasized.<sup>7</sup>

### 21.3 Paradigms in Evo-devo: Structuralism, Adaptationism, and Cladism

A classic analysis of another type of scientific culture is Kuhn's "paradigms". Paradigms are also frameworks or ways of looking at the world. They are guided by styles, and nested within them; they are more specific than styles, or even than style hybrids. Paradigms employ particular methods and theories, are motivated by certain questions and meanings, and emphasize (as well as reify) specific sorts of objects and processes.

There is no simple definition of the concept in Kuhn's work. But Kuhn's (1970 [1962]) first use of it stated that paradigms stemmed from the "classics of science," especially the work of great theoretical innovators, including Aristotle, Ptolemy, Newton, Lavoisier, and Lyell. The term is polysemous, and Kuhn used it to mean at least:

1. A specific and standard *exemplar*, including a new mathematical procedure (e.g., "Maxwell's mathematization of the electromagnetic field") or experimental set-up (e.g., "Lavoisier's application of the balance," 23).
2. The *general framework* ("disciplinary matrix", 1969 postscript, 182) with various components, including: laws and symbolic generalizations (e.g.,  $F = ma$ ), ontological assumptions, values (e.g., theoretical/epistemic virtues, such as simplicity and scope), and exemplars.
3. The *sociological community* embedding and co-constituting the paradigm. While Kuhn distinguished theoretical and experimental practices and products from the community of origin within which they were shared, this third sense of paradigm appeals directly to the composition and practices of the social group in order to individuate a paradigm (see Masterman (1970) on "sociological paradigms.")

Under a paradigm's guidance, "normal science," with its associated activity of "puzzle-solving," occurs. Most of science is normal, but anomalies do accumulate. When there are too many, or the anomalies are too significant (or both), a crisis ensues. The resolution of a crisis is often a revolution, with the adoption of a new

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<sup>7</sup> A more complete archaeology of the history style would require further investigation of the way history, and cladism in particular, became incorporated into Evo-devo. This would include looking at ways in which initially open and exploratory theory became stabilized into standardized computer platforms and molecular biotechnology that could produce phylogenies at industrial scales.

paradigm. On rare occasions, a crisis can defuse with the old paradigm declaring victory.

Thus, paradigms are frameworks constituting and periodizing the historical scientific process. They consist of (1) symbolic generalizations, (2) ontological assumptions, (3) values, (4) exemplars, (5) sociological communities, and also, I argue, (6) specific theories and experiments, (7) acceptable research questions, and (8) (partly reified) objects and processes (see Winther 2012). Analyzing these paradigm components is one burden of an assumption archaeology. I now will characterize three operative paradigms in Evo-devo by pointing to their components (ignoring exemplars since they were not pertinent to the 1981 Dahlem conference). My treatment is not balanced: the relation between adaptationism and structuralism will be explored; the cladism paradigm will only be sketched.

### 21.3.1 *Adaptationism Paradigm*

The adaptationism paradigm holds that “the fit” between organism and environment is the most important problem in evolution. Moreover, natural selection is considered the strongest explanatory principle in evolutionary theory. Adaptationism is associated with a variety of theoretical and experimental methods (e.g., game theory and optimality modeling), and objects and processes (e.g., atomized adaptations, as well as directional, disruptive, and correlated selection). Here is a formulation from Gould and Lewontin (1979):

[Adaptationism] regards natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behavior (584–585).

Gould and Lewontin’s well-known critique of the “adaptationist programme” (or “Panglossian paradigm”) focused on how this paradigm was imperialistic in its exclusion and subordination of other explanations and paradigms (e.g., structuralism and history). Moreover, they accused the paradigm of frequently committing a reification fallacy. That is, adaptationist thinking first postulates atomized traits, and subsequently believes in their true and independent existence (cf. John Dewey’s “the philosophic fallacy,” discussed in Winther 2014a). Indeed, the maintenance in natural populations of these traits is now seen as requiring explanation. The move from postulation to objectification is a reification. However, the adaptationism paradigm is also creative and generative, and remains (and was always) operative and relevant. Indeed, it highlights important aspects of the natural world, while its perceived competitor paradigm—structuralism—emphasizes others. Ultimately, these two paradigms act collaboratively in the Evo-devo trading zone.

Adaptationism is a paradigm with the theories and methods, objects and processes, and ontological assumptions mentioned above, and more. But one can also be an adaptationist with respect to distinct sorts of questions. It might be useful to explore the multidimensionality of the paradigm, rather than just its core. It is in this

multidimensionality that the collaborative aspects of the paradigm come to the fore. Godfrey-Smith (2001) distinguishes between *empirical*, *methodological*, and *explanatory* adaptationism. Empirical adaptationism focuses on the causal ubiquity of natural selection. This interpretation of adaptationism answers “natural selection” to the question: what is the most important and prevalent evolutionary causal factor? Methodological adaptationism focuses not on nature, but on research programs—“adaptation is a good ‘organizing concept’ for evolutionary research.” (337) This kind of adaptationism answers “adaptation” to the question: which phenomenon or concept is best for organizing our perspective on nature? Explanatory adaptationism also focuses on science, but this time on what is interesting—design and adaptedness “are the *big questions*, the amazing facts in biology.” (336) In short, these three interpretations of adaptationism focus, respectively, on nature, the structure of research, and the explanatory interest of research. Godfrey-Smith’s analysis provides a nuanced picture of the multidimensionality and flexibility of adaptationism. When research commits to all three interpretations, to the exclusion of other questions, adaptationism becomes *imperialist*. When research adopts one or another kind, but remains open to other different types of questions, adaptationism is *collaborative*.

The adaptationism paradigm, as it gets used in Evo-devo and elsewhere, is guided by all three styles (Sect. 21.2). Mathematical modeling is commonplace. The “calculus and algebra of frequencies” is essential to a paradigm concerned with fitness and changes in relative gene frequencies. Mechanistic analyses identify the objective (rather than reified) characters to which we ascribe adaptation; mechanistic investigations also “increase the strength of inferences regarding the evolutionary history of characters and their adaptive consequences” (Autumn et al. 2002, 383). The history style is necessary for stating which characters are derived, and might thereby be present due to (possibly strong) selective forces.

### 21.3.2 *Structuralism Paradigm*

The structuralism paradigm emphasizes the development and organization of kinds of parts of a system typically understood as self-organizing. Parts—or rather kinds or equivalence classes of parts—are connected and mutually dependent in complex and hierarchical ways. This paradigm often appeals to both mathematical laws of development and physicochemical morphogenetic mechanisms, and is guided by mathematical modeling, history, and mechanism styles. This paradigm has a long tradition in the post-Darwinian English-speaking world, starting with William Bateson, D’Arcy Thompson, and Joseph Woodger in the early twentieth century, and continuing through to many of the participants at the 1981 Dahlem conference. This tradition is the *sociological paradigm* (see above, Sect. 21.3) of structuralism. Structuralism has roots in the transcendental morphology of Goethe and St. Hilaire, and even in Kant’s view of the organism as a purposive whole, as defended in his third Critique, *Kritik der Urteilskraft*.

The structuralism paradigm has multiple components. With respect to *form*, Olivier Rieppel writes: “structuralism comprehends biological structures in terms of constituent elements and their relations to each other” (Rieppel 1990, 299). Both the parts and the relations among them are critical. D’Arcy Thompson warns against focusing exclusively on the parts: “As we analyse a thing into its parts or into its properties, we tend to magnify these, to exaggerate their apparent independence, and to hide from ourselves (at least for a time) the essential integrity and individuality of the composite whole” (1961 [1917], 262). Structuralism’s commitments to emergence, complexity, and non-linearity are in contrast with the atomism, reductionism, and additivity of adaptationism. With respect to developmental and morphogenetic *process*, Alberch’s contribution to the 1982 Dahlem volume identifies “three interacting levels”:

Level 1—the genome itself is compartmentalized and highly integrated. . . Level 2—There are second order interactions among enzymes and proteins which interact and assemble themselves according to physicochemical laws. . . . Level 3—Tissues can also interact in complex ways and according to sets of well-defined rules. (Bonner 1982, 320)

Note the appeal to “laws” and “rules” in this three-tiered nested division of form (i.e., parts and part-organization) and process (i.e., development and morphogenesis). Indeed, under the structuralism paradigm evolution itself is sometimes redefined: “evolution can be viewed as the process of phenotypic transformations resulting from the genetically mediated perturbations of these basic developmental parameters through phylogeny” (322). The meanings of key terms can change across paradigms (Amundson 2005).

Structuralism has all the hallmarks of a paradigm in the 1982 Dahlem volume. It has a variety of theoretical and experimental methods (e.g., the mathematical and biochemical/cellular identification of a few simple rules of development and morphogenesis) and objects and processes (e.g., constraints). Exemplars include limb bud development and morphogenetic gradients/positional information, which were discussed extensively (e.g., “the Cellular Basis of Morphogenetic Change” group report, authored by, among others, J.C. Gerhart, C. Nüsslein-Volhard, G.F. Oster, G.S. Stent, and L. Wolpert, and Wolpert’s solo contribution, “Pattern Formation and Change”). Values include simple and unified explanations, and an attention to the whole organism rather than to atomized parts (see Wagner, Chap. 15, this volume). Ontological assumptions include definitions of evolution and process, as well as an emphasis on what requires explanation—i.e., the integration rather than the design of organisms.

The three styles guide structuralism in a different manner from how they guide adaptationism. The mathematics of structuralism is analytical geometry and the “calculus of space.” Transformations in space, grounded in physicochemical mechanisms of temporal morphogenesis, are essential. Some structuralism is anti-historical (e.g., Brian Goodwin), but much structuralism appeals to the historical (meta-)transformations of developmental transformations. Phylogenetic information is necessary to make meaningful statements about how changes in form and process happen over long-term evolution.



### 21.3.3 *Adaptationism and Structuralism: Collaborations ca. 1982*

Many controversies in the life sciences are “relative significance disputes” (Beatty 1997), in part because multiple types of causes must be taken into account to explain complex systems. I distinguish between two forms of relative significance disputes: *zero-sum* and *complementarity*. These are associated, respectively, with *imperialist* and *collaborative* interpretations of a paradigm. I contend that Lewontin and Gould critiqued only a zero-sum, imperialist version of adaptationism. We can comprehend these two related distinctions more deeply by looking at adaptationism in its various guises in the 1982 Dahlem volume. First, there is an explicit critique of imperialist adaptationism in the last group report on “the role of development in macroevolutionary change,” which was written by researchers such as Alberch, Goodwin, Gould, Wake, and Wagner. In discussing the “theories of evolutionary genetics”, which rely on natural selection, the group report states:

Yet for many of the changes that we know did occur in evolution, it is difficult to discern what must have been their relation to adaptation, and we should examine the possibility that they resulted from components of systems of developmental, architectural, and functional constraints (cite to Gould and Lewontin 1979). (Bonner 1982, 295)

Underlying this critique is a zero-sum perspective: changes and characters arise either through adaptation or through constraints. Selection and constraints are mutually exclusive and collectively exhaustive causal factors. When the adaptationist paradigm is seen as an imperialist foe, it is common for its critics to endorse a zero-sum perspective and claim that *some*—indeed *many*—evolutionary changes require explanations that appeal to internal factors, rather than to natural selection. Gould continues this form of critique in his 1982 solo chapter.

However, a different attitude focusing on the complementarity of causal factors, and on collaborative adaptationism, is also present in the volume. In his chapter, Alberch writes: “internal correlations and constraints might impose directional change and they can be a mechanism for the origin of new morphologies and for drastic structural rearrangements that open up a new adaptive realm for the organism” (Bonner 1982, 330). Here, constraints interact with adaptive demands, and the two factors (and explanations) are interpreted as complementary rather than as zero-sum. Adaptationism is understood as collaborative rather than imperialist. The group report on “Adaptive Aspects of Development” also emphasizes collaborative adaptationism. The group insists on adaptation being “inherently comparative” (215) in two senses: an adaptive developmental pattern is comparatively better than others in a given environment, and an adaptive developmental pattern has an environment in which it is best, compared to other environments. Gould and Lewontin’s critique is mentioned, as are worries about “epistemological difficulties” of the concept of adaptation, such as “circularity, teleology, or unfalsifiability” (216). However, the group argues, if the comparative notion of adaptation is taken to heart, these difficulties can be lessened. Moreover, comparative analyses of adaptation ground predictions and “provide[. . .] an observational setting that is

the logical equivalent of experiment and control” (216–7). The group’s adoption of a complementarity perspective emphasizes emergent and non-linear causal (and explanatory) interaction between selection and constraint. The structuralism paradigm collaborates with the adaptationism paradigm by making explicit the dynamics underlying “evolutionary opportunity” and “flexibility” (217) with which selection may act. Despite this potential for complementarity, the ongoing relation between structuralism and adaptationism, in Evo-devo and elsewhere, is a complex love-hate relationship.

One final analytical point regarding language in the context of relative significance disputes is worth making. Under the former zero-sum perspective and dynamics, concepts such as “constraints” and “selection” are typically used with radically different—and perhaps incommensurable—meanings by adaptationists and structuralists (e.g., see analysis in Amundson 2005). Distinct languages flourish on different discursive islands. In contrast, according to the attitude of complementarity, at least some discursive market places exist to hash out shared meanings across paradigms. Creoles can emerge in the collaborations of trading zones.

### **21.3.4 Cladism Paradigm**

The cladism paradigm holds that taxonomies must reflect the evolutionary process as captured in phylogenetic trees, and that parsimony is the best method for inferring such trees, called cladograms. In order for our classifications to be natural and objective, they must refer to the systematizations captured in cladograms, which show a nested clade structure. One central aim of cladism is thus to provide natural phylogenetic classifications. As Darwin (1859 [1964], 420) wrote: “all true classification is genealogical.” Following Mishler (2009), and the work of David Hull (e.g., Hull 1988), Elliott Sober (e.g., Sober 2008), and others, it can be argued that cladism is a paradigm that was born in the work of Willi Hennig and continues in a robust fashion with a range of methods for character analysis, phylogenetic inference, and naming (see also De Queiroz 1988; Doolittle 1999; Winther 2009b). The cladism paradigm was not evident at the 1981 Dahlem conference, but through an increasing emphasis on phylogenetic reconstruction, it has come to play an important role in Evo-devo research (e.g., Wagner 2000; Hall and Olson 2003). Therefore, even though adaptationism, structuralism, and cladism are all operative in Evo-devo today, only the first two were clearly evident in 1981, whereas the influence of cladism for conceptualizing the relationship between development and evolution was no more than immanent.

## **21.4 Evo-devo as a Trading Zone**

Evo-devo is an ambitious, integrative, and interdisciplinary domain. Its problems and questions are multi-faceted. The biological reality it explores is complex. As a consequence, Evo-devo requires the operation of many styles and paradigms,

which in turn demands bringing together a variety of cultures. Other domains are undoubtedly also trading zones in this sense (e.g., genomics and climate modeling), but Evo-devo is philosophically interesting because it brings together some of the greatest theoretical questions of biology pertinent to function, form, process, and history. It cannot be understood without knowledge of a broad diversity of the most advanced theories and experiments in the biological sciences. Evo-devo trades across cultures and, precisely because it does so, we can identify a trading zone at its intersection of multiple, complex levels of abstraction (e.g., styles and paradigms).

Adaptationism and structuralism are negotiating intensely in the trading zone of Evo-devo. In the past, there was primarily segregation. Different national and philosophical contexts tended to stress one paradigm to the detriment of the other (e.g., Germanic contexts are more structuralist, Anglo-American more adaptationist). Moreover, evolutionary questions usually have been asked within the adaptationism paradigm, and developmental questions within the structuralism paradigm. Tools also differ radically: mathematical modeling has been common to adaptationism, mechanism to structuralism. (Here the difference is smaller as each paradigm also employs the other style.) Evo-devo has provided a locus where collaboration, mutual understanding, and integration between adaptationism and structuralism can and does occur—they are no longer allowed to ignore each other. Indeed, it is a mistake to critique Evo-devo *tout court* from the (imperialist) adaptationism often found in evolutionary genetics (e.g., Hoekstra and Coyne 2007). Mathematical modeling tools (e.g., simulations, closed-form analytical equations, and statistical tests), as well as instruments and experimental protocols from molecular biology and biochemistry, are shared across paradigms within Evo-devo. For instance, genomics and developmental biology have influenced standard evolutionary theory, as seen in the research programs of Scott Gilbert and Günter Wagner. Moreover, mathematics from evolutionary genetics is used to understand development in Maynard-Smith and Szathmáry (1995) and Michod (1999). Sometimes the inter-paradigm dynamics are collaborative and integrative, and mutual understanding occurs, particularly when explanatory labor is divided. At other times, miscommunication, incommensurability, and fragmentation are rampant, especially when terms exhibit different meanings or tools and theories have explicitly different goals and content. All of this is exactly what we would expect from an active trading zone. And let us not forget competition and fighting—a shared perspective with common aims and questions is still being built. But the key point is that these paradigms will continue meeting and interacting in the Evo-devo trading zone.

The cladism paradigm has been integrated into Evo-devo. This was not evident in 1982. History was understood to be a core principle by many at the Dahlem meeting, but the relevance or possibilities for success of the nascent cladistic revolution in the 1970s and early 1980s were not evident. Today, phylogenetic reconstruction is commonplace in Evo-devo and elsewhere. The large-scale phylogenetic branching patterns of metazoans had to be tested and redrawn (Raff, personal communication). If adaptation is “inherently comparative” (Bonner 1982, 215), then a correct phylogeny with which to formulate comparisons of potentially

adaptive characters across taxa is necessary. And if, as Gould claims, “development has a special ‘relevance’ to macroevolution insofar as it imposes styles of evolution departing from the extreme Darwinian notion that virtually all change is a result of natural selection working on a spectrum of small, random variation” (Bonner 1982, 337), then a correct phylogeny is necessary to determine the overall macroevolutionary pattern and thereby show where developmental “styles of evolution” may be operating. Every hypothesis, or set of hypotheses, concerning adaptation or developmental pattern requires a referent phylogeny in order to be testable. Due to the internal logic of Evo-devo, the cladism paradigm became intertwined with adaptationism and structuralism. The meeting and rich negotiation of these three paradigms occurred for the first time in Evo-devo. It may even be definitional of Evo-devo to say that it is the trading zone where these three paradigms negotiate, sometimes without success, but often with high pay-off.

Styles are self-vindicating in that they produce and stabilize their own culture (Hacking 2009). There is a vicious side to this: the methods can become an end in themselves and lose their relevance and empirical adequacy, such as when the ongoing articulation of mathematical modeling becomes the ultimate goal rather than its application to biological phenomena. But there is also a useful side. Styles can mature, develop tools and theories, and grow stronger when they meet and interact. This is especially true given the questions and goals of Evo-devo. Consider the collaborative relationship between the mathematical modeling and mechanism styles. The first is “theoretical”, the second “experimental.” In many studies, the former makes predictions and tells us where to look. Mathematics can only hint at underlying causal mechanism. Causal surgery is necessary to identify these. History (built with molecular *and* morphological data, e.g., Winther 2009b) can predict the taxa in which we might expect to find a mechanism acting. But again, only actual searching will reveal the mechanism. Thus, theoretical predictions are produced by math and history, but verification through actual mechanism identification and characterization is ultimately required.

Finally, there are the relationships between styles and paradigms in a trading zone. Each paradigm is guided by each style. In other words, there are many-to-many relations between styles and paradigms. More specifically, styles are *multiply realized* in distinct paradigms. The latter instantiate the former—paradigms express all the assumptions of styles, and also are more specific. We saw in Sect. 21.3.3 how structuralism and adaptationism each coordinated the three styles in unique ways. The complex trading zone is such that the different styles are negotiated in distinct manners for each paradigm.

To summarize, in this chapter I have argued that Evo-devo is a trading zone. The method of assumption archaeology can help us understand how three paradigms and three styles interact intensely. They overlap richly within and across levels of abstraction. A specific trading interaction may be between just two cultures, but a trading zone is a domain of interaction among multiple cultures, at several related levels of abstraction. Competition exists. Many deep rifts, misunderstandings, and miscommunications remain. The cultures are still sometimes fragmented. But collaboration, mutual understanding, and integration are in

progress and desirable. I have descriptively identified Evo-devo as a trading zone and undertaken assumption archaeologies of some of its foundational assumptions.

Many outstanding matters, and possible limitations, remain. What are the institutions and instruments, goals and costs/benefits, associated with each culture (see Gerson, Chap. 20, this volume)? How might the cultures here excavated ca. 1982 transform over time? A complete assumption archaeology requires analytical angles from sociology, history, political science, economics, and ethics. Moreover, possible limitations of my analysis must be considered. Might these cultures evaporate or disappear—or crosscut too richly to individuate—if and when we perform micro-sociological and detailed historical studies of the different individuals, labs, and “cultural” contexts involved? If so, does this disprove my paper’s thesis that Evo-devo *is* a trading zone? What else might Evo-devo, broadly construed, then be—a “domain” à la Shapere (1977), a “scene of inquiry” with “questions” à la Jardine (2000), etc.? Finally, pivotal normative questions remain. Which institutional, political, experimental, theoretical, and ethical constellations should and must be in place to achieve mutual understanding and integration? Is synthesis worthwhile? Where do we want the busy and blooming trading zone of Evo-devo to go, today and tomorrow?

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## References

- Alon, U. 2003. Biological networks: The tinkerer as an engineer. *Science* 301: 1866–1867.
- Álvarez-Buylla, E.R., M. Benítez, E. Balleza Dávila, Á. Chaos, C. Espinosa-Soto, and P. Padilla-Longoria. 2007. Gene regulatory network models for plant development. *Current Opinion in Plant Biology* 10: 83–91.
- Amundson, R. 2005. *The changing role of the embryo in evolutionary thought. Roots of Evo-devo.* Cambridge: Cambridge University Press.
- Autumn, K., M.J. Ryan, and D.B. Wake. 2002. Integrating historical and mechanistic biology enhances the study of adaptation. *Quarterly Review of Biology* 77: 383–408.
- Beatty, J. 1997. Why do biologists argue like they do? *Philosophy of Science* 64: S432–S443.
- Bonner, J.T. (ed.). 1982. *Evolution and development. Report of the Dahlem workshop on evolution and development Berlin 1981, May 10–15.* Berlin: Springer.
- Brigandt, I., and A. Love. 2008. Reductionism in biology, In *The Stanford encyclopedia of philosophy*, ed. E.N. Zalta, Fall 2008 edition, <http://plato.stanford.edu/archives/fall2008/entries/reduction-biology/>
- Cartwright, N. 1999. *The dappled world. A study of the boundaries of science.* Cambridge: Cambridge University Press.
- Craver, C. 2007. *Explaining the brain. Mechanisms and the mosaic unity of neuroscience.* Oxford: Oxford University Press.
- Crombie, A.C. 1994. *Styles of scientific thinking in the European tradition*, vol. 3. London: Duckworth.
- Cummins, R. 1983. *The nature of psychological explanation.* Cambridge, MA: MIT Press.
- Darwin C.R. 1859 (1964). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* With an introduction by Ernst Mayr. Cambridge, MA: Harvard University Press.

- Davidson, A. 2001. *The emergence of sexuality: Historical epistemology and the formation of concepts*. Cambridge, MA: Harvard University Press.
- De Queiroz, K. 1988. Systematics and the Darwinian revolution. *Philosophy of Science* 55: 238–259.
- Doolittle, W.F. 1999. Phylogenetic classification and the universal tree. *Science* 284: 2124–2128.
- Elwick, James. 2007. *Styles of reasoning in the British life sciences: Shared assumptions, 1820–1858*. London: Pickering & Chatto.
- Forgacs, G., and S.A. Newman. 2005. *Biological physics of the developing embryo*. Cambridge: Cambridge University Press.
- Forrester, J. 1996. If *p*, then what? Thinking in cases. *History of the Human Sciences* 9: 1–25.
- Foucault, M. 1966. *Let mots et les choses*. Paris: Gallimard. (*The Order of Things*. 1973. New York: Vintage).
- Foucault, M. 1969. *L'archéologie du savoir*. Paris: Gallimard. (*The Archaeology of Knowledge*. 1972, translated by A. Sheridan Smith. New York: Harper Row).
- Friedman, M. 1999. *Dynamics of reason*. Stanford: CSLI Publications.
- Galison, P. 1997. *Image and logic. A material culture of microphysics*. Chicago: University of Chicago Press.
- Gilbert, S.F., and D. Epel. 2008. *Ecological developmental biology: Integrating epigenetics, medicine, and evolution*. Sunderland: Sinauer Press.
- Godfrey-Smith, P. 2001. Three kinds of adaptationism. In *Adaptationism and optimality*, ed. S.H. Orzack and E. Sober, 335–357. Cambridge: Cambridge University Press.
- Gould, S.J., and R.C. Lewontin. 1979. The spandrels of San Marco and the Panglossian Paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society B: Biological Sciences* 205: 581–598.
- Hacking, I. 1983. *Representing and intervening*. Cambridge: Cambridge University Press.
- Hacking, I. 2002. *Historical ontology*. Cambridge, MA: Cambridge University Press.
- Hacking, I. 2009. *Scientific reason*. Taipei: National Taiwan University Press.
- Hall, B.K., and W.M. Olson. 2003. *Keywords and concepts in evolutionary developmental biology*. Cambridge, MA: Harvard University Press.
- Hoekstra, H.E., and J.A. Coyne. 2007. The locus of evolution: Evo-devo and the genetics of adaptation. *Evolution* 61: 995–1016.
- Huang, S., I. Ernberg, and S. Kauffman. 2009. Cancer attractors: A systems view of tumors from a gene network dynamics and developmental perspective. *Seminars in Cell and Developmental Biology* 20: 869–876.
- Hull, D. 1988. *Science as a process*. Chicago: University of Chicago Press.
- Hull, D. 1989. *The metaphysics of evolution*. Albany: State University of New York Press.
- Jardine, N. 2000. *The scenes of inquiry. On the reality of questions in the sciences*. New York: Oxford University Press.
- Junker, B.H., and F. Schreiber. 2008. *Analysis of biological networks*. New York: Wiley.
- Kauffman, S.A. 1969. Metabolic stability and epigenesis in randomly constructed genetic nets. *Journal of Theoretical Biology* 22: 437–467.
- Kauffman, S.A. 1993. *The origins of order. Self-organization and selection in evolution*. New York: Oxford University Press.
- Kuhn, T.S. 1970 [1962]. *The structure of scientific revolutions*, 2nd ed. Chicago: University of Chicago Press.
- Kwa, C. 2011. *Styles of knowing. A new history of science from ancient times to the present*. Pittsburgh: University of Pittsburgh Press.
- Lewin, R. 1996. *Complexity. Life at the edge of chaos*. New York: Macmillan.
- Maienschein, J. 1991. Epistemic styles in German and American embryology. *Science in Context* 4: 407–427.
- Masterman, M. 1970. The nature of a paradigm. In *Criticism and the growth of knowledge*, ed. I. Lakatos and A. Musgrave, 59–89. Cambridge: Cambridge University Press.
- Maynard-Smith, J., and E. Szathmáry. 1995. *The major transitions in evolution*. Oxford: W.H. Freeman.

- Meinhardt, H., and A. Gierer. 1980. Generation and regeneration of sequence of structures during morphogenesis. *Journal of Theoretical Biology* 85: 429–450.
- Michod, R. 1999. *Darwinian dynamics. Evolutionary transitions in fitness and individuality*. Princeton: Princeton University Press.
- Mishler, B.D. 2009. Three centuries of paradigm changes in biological classification: Is the end in sight? *Taxon* 58: 61–67.
- Newman, S.A., and G.B. Müller. 2005. Origination and innovation in the vertebrate limb skeleton: An epigenetic perspective. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 304B: 593–609.
- Niklas, K.J. 1994. *Plant allometry: The scaling of form and process*. Chicago: University of Chicago Press.
- Niklas, K.J. 2000. The evolution of plant body plans—a biomechanical perspective. *Annals of Botany* 85: 411–438.
- Pearl, J. 2000. Epilogue: The art and science of cause and effect. In *Causality: Models, reasoning, and inference*, 346–358. Cambridge: Cambridge University Press.
- Pickstone, J.V. 2001. *Ways of knowing. A new history of science, technology and medicine*. Chicago: University of Chicago Press.
- Radinsky, L.B. 1987. *The evolution of vertebrate design*. Chicago: University of Chicago Press.
- Rieppel, O. 1990. Structuralism, functionalism, and the four causes. *Journal of the History of Biology* 23: 291–320.
- Sarkar, S. 1998. *Genetics and reductionism*. Cambridge: Cambridge University Press.
- Shapere, D. 1977. Scientific theories and their domains. In *The structure of scientific theories*, ed. F. Suppe, 518–565. Urbana: University of Illinois Press.
- Sober, E. 2008. *Evidence and evolution. The logic behind the science*. Cambridge: Cambridge University Press.
- Stern, D.L., and V. Orgogozo. 2009. Is genetic evolution predictable? *Science* 323: 746–751.
- Thompson, D. 1961 [1917]. *On growth and form*. Abridged from 1917 edition by J.T. Bonner. Cambridge: Cambridge University Press.
- Turing, A.M. 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 237: 37–72.
- Valadez Blanco, E.O. 2011. La parte y el todo en la explicación científica del cáncer. *Masters Thesis, Graduate School in Humanities, Universidad Autónoma Metropolitana, Iztapalapa, Mexico City*.
- Wagner, G.P. 2000. *The character concept in evolutionary biology*. New York: Academic.
- Wake, M. (ed.). 1979. *Hyman's comparative vertebrate anatomy*, 3rd ed. Chicago: University of Chicago Press.
- Weber, M. 2005. *Philosophy of experimental biology*. Cambridge: Cambridge University Press.
- Weisberg, M. 2006. Robustness analysis. *Philosophy of Science* 73: 730–742.
- Wimsatt, W.C. 2007. *Re-engineering philosophy for limited beings: Piecewise approximations to reality*. Cambridge, MA: Harvard University Press.
- Winther, R.G. 2001. Varieties of modules: Kinds, levels, origins, and behaviors. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 291: 116–129.
- Winther, R.G. 2005. Evolutionary developmental biology meets levels of selection: Modular integration or competition, or both? In *Modularity: Understanding the development and evolution of complex natural systems*, ed. W. Callebaut and D. Rasskin-Gutman, 61–97. Cambridge, MA: MIT Press.
- Winther, R.G. 2006a. Parts and theories in compositional biology. *Biology & Philosophy* 21: 471–499.
- Winther, R.G. 2006b. Fisherian and Wrightian perspectives in evolutionary genetics and model-mediated imposition of theoretical assumptions. *Journal of Theoretical Biology* 240: 218–232.
- Winther, R.G. 2006c. On the dangers of making scientific models ontologically independent: Taking Richard Levins' warnings seriously. *Biology & Philosophy* 21: 703–724.

- Winther, R.G. 2008. Systemic Darwinism. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11833–11838.
- Winther, R.G. 2009a. Schaffner's model of theory reduction: Critique and reconstruction. *Philosophy of Science* 76: 119–142.
- Winther, R.G. 2009b. Character analysis in cladistics: Abstraction, reification, and the search for objectivity. *Acta Biotheoretica* 57: 129–162.
- Winther, R.G. 2011. Part–whole science. *Synthese* 178: 397–427.
- Winther, R.G. 2012. Interweaving categories: Styles, paradigms, and models. *Studies in History and Philosophy of Science (Part A)* 43: 628–639.
- Winther, R.G. 2014a. James and Dewey on abstraction. *The Pluralist* 9: 1–28.
- Winther, R.G. 2014b. Determinism and total explanation in the biological and behavioral sciences. *Encyclopedia of Life Sciences*. Online.
- Winther, R.G. Under contract. *When maps become the world. Abstraction and analogy in philosophy of science*. Chicago: University of Chicago Press. <http://ihr.ucsc.edu/when-maps-become-the-world/>