

Part-whole science

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Abstract A scientific explanatory project, *part-whole explanation*, and a kind of science, *part-whole science* are premised on identifying, investigating, and using parts and wholes. In the biological sciences, mechanistic, structuralist, and historical explanations are part-whole explanations. Each expresses different norms, explananda, and aims. Each is associated with a distinct *partitioning frame* for abstracting kinds of parts. These three explanatory projects can be complemented in order to provide an integrative vision of the whole system, as is shown for a detailed case study: the tetrapod limb. My diagnosis of part-whole explanation in the biological sciences as well as in other domains exploring evolved, complex, and integrated systems (e.g., psychology and cognitive science) cross-cuts standard philosophical categories of explanation: causal explanation and explanation as unification. Part-whole explanation is itself one essential aspect of part-whole science.

Keywords Mechanisms · History · Explanation · Natural kinds · Systems · Complexity · Styles · Evolution

1 Introduction

This paper recognizes an important kind or style of scientific theory and practice: *part-whole science*. I defend four inter-related theses:

- (1) There are multiple cross-cutting manners of abstracting a system into kinds of parts—i.e., there are multiple *partitioning frames*.

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- (2) Each of these partitioning frames provides the parts and part relations for a real, albeit incomplete, part-whole explanation of the system (e.g., mechanistic, structuralist, and historical part-whole explanations in the biological sciences).
- (3) Mechanistic, structuralist, and historical part-whole explanations can be usefully integrated into a more complete *explanatory field* and systems vision.
- (4) Part-whole explanation and, more generally, part-whole science are pervasive across the sciences.

Thesis (4) will be discussed in Sect. 1. Thesis (1) will be addressed in Sect. 2. Theses (2) and (3) will be considered with reference to the philosophical literature in Sect. 3. The way the three types of part-whole explanations of theses (2) and (3) actually operate will be elucidated in Sect. 4 by focusing on a single system: the *tetrapod limb*. Integrative relationships among the three explanatory projects are discussed in Sect. 5. I turn to three general questions in the conclusion.

In the interest of detailed analysis, I focus on the biological sciences. However, part-whole explanation and part-whole science are present in many sciences [Thesis (4)]. Let us see how. Two philosophers, Cummins and Cartwright, have argued for the importance of part-whole explanation and part-whole science in, respectively, psychology and physics:

- (1) A major contention of this study is that psychological phenomena are typically not explained by subsuming them under causal laws, but by treating them as manifestations of capacities that are explained by analysis¹ (1983, p. 1; see also Cummins 1975, pp. 758–761).
- (2) [T]he *analytic method* ... in physics: to understand what happens in the world, we take things apart into their fundamental pieces; to control a situation we reassemble the pieces, we reorder them so they will work together to make things happen as we will. You carry the pieces from place to place, assembling them together in new ways and new contexts. But you always assume that they will try to behave in new arrangements as they have tried to behave in others. They will, in each case, act in accordance with their nature (1999, p. 83).

Although their positions on explanation differ—with Cummins interpreting functional explanation as analysis, and Cartwright tying the analytical method closely to Galilean idealization and causal capacities—their pictures share an important feature: a system can be explained and understood scientifically by disarticulating it into parts and subsequently investigating the properties and relations of those parts (i.e., “analysis”).

Indeed, part-whole explanation is a core practice especially in fields exploring evolved, complex, and integrated systems. Such disciplines include psychology, cognitive science, and the biological sciences. Here are three brief examples from the first two general fields:

- (1) The first sentence of Barrett and Kurzban (2006) is “A central question in psychology concerns the parts or processes of which the mind is composed.” This

¹ Roughly, “analysis” sensu Cummins involves disarticulating a system into parts (“componential analysis”), and disarticulating system capacities into part capacities (“functional analysis”) (Cummins 1983, p. 28 ff.).

- is so even though “beyond this modest agreement that the brain has *some* parts, there is little consensus on this important issue [i.e., modularity]” (p. 628).
- (2) In defending his thesis that “the mind is said to embrace subsystems dedicated to particular kinds of reasoning or goals,” [Pinker \(2005\)](#) argues that “the intended analogy is to the body, which is composed of systems divided into organs assembled from tissues built out of cells. Our ‘organs of computation’, therefore, are not like discrete chips laid out on a board with a few solder tracks connecting them. Just as some kinds of tissue, like the epithelium, are used (with modifications) in many organs, and some organs, like the blood and the skin, interact with the rest of the body across an extensive interface, some kinds of specialized thoughts and emotions may serve as constituents that are combined into different assemblies” (p. 4).
 - (3) [Haugeland \(1997\)](#) argues that “Mind design is the endeavor to understand *mind* (thinking, intellect) in terms of its *design* (how it is built, how it works).” In fact, “it is oriented more toward structure and mechanism than toward correlation or law” (p. 1). Moreover, “[c]onnectionist systems are networks of lots of simple active units that have lots of connections among them” (p. 21); and “embodied and embedded AI” has “the intelligent system *be* the larger interactive *whole*, including the body and environment as essential components²” (p. 25).

A broad range of self-aware descriptions of explanatory practice and fragestellung in psychology and cognitive science thus appeal to the fundamental importance of parts, wholes, and their informational properties and relations. The part-whole relation is epistemically and methodologically basic rather than derivative (from causal relations, for instance). Understanding evolved cognitive and biological systems requires part-whole science.

Now, explanatory practice in science is often considered in the context of causal explanation or explanation as unification, or both (e.g., [Friedman 1974, 1983](#); [Kitcher 1981](#); [Salmon 1990](#); [Woodward 2003](#); [Strevens 2004](#); [Craver 2007](#); but see [van Fraassen 1980](#) and [Halonen and Hintikka 2005](#) for different ways of dissenting from the two standard positions on explanation). Unfortunately, these philosophical analyses have not delved into part-whole explanation and part-whole science. Two caveats. First, I focus on explanatory practice as an indicator of kind of science while fully realizing that the latter is not exhausted by the former—a kind of science also involves norms and practices of (i) understanding, (ii) intervention, and (iii) modeling. Second, just as different partitioning frames and explanatory projects can produce cross-cutting kinds of parts, so distinct philosophical analytical categories (e.g., causal explanation, explanation as unification, and part-whole explanation) can usefully cross-cut in their distinct understandings of scientific and everyday explanatory practice. Yet, the important and multiple relations among these three analytical categories will not be addressed here. This paper is thus itself a partial contribution to a full, integrated understanding of explanatory practice and kinds of science.

² This point is developed in [Noë \(2009\)](#): “My central claim in this book is that to understand consciousness—the fact that we think and feel and that a world shows up for us—we need to look at a larger system of which the brain is only one element” (p. 10).

2 Abstracted parts and partitioning frames

Parts do not pre-exist theoretical and experimental investigation. This is both too strong and too weak a statement of the thesis I defend. It is too strong because reality as such of course pre-exists. It is too weak because very little, if anything, of scientific import and relevance—not just parts—pre-exists theory and experiment. Given the importance of both reality and investigation, where do parts come from? How are they individuated? My basic claim is that parts are *abstracted through partitioning frames closely linked to explanatory projects*.

It may be helpful to start by noting the view that I do not accept. Much of the philosophy of science literature discussing parts takes these to exist independently of theoretical and experimental investigation, as well as of the wholes of which they are components (i.e., *part-of*). That is, pre-existing parts are understood as:

- (1) The primitive components of mechanisms and mechanistic systems (e.g., Glennan 1996, 2002; Machamer et al. 2000; Craver 2007).
- (2) The central subjects or central events of historical narratives (e.g., Hull 1989, 1992; Richards 1992).
- (3) The objects that combine either linearly and predictably, or in emergent patterns (e.g., Bechtel and Richardson 1993; Boogerd et al. 2005).

In each of these discussions, the dominant view is that parts pre-exist both investigation and wholes. Lewontin and Levins explicate this position thus:

Wholes are thought of as made out of parts. Systems theory likes to take as its elements unitary variables that are the “atoms” of the system, prior to it, and qualitatively unchanging as they ebb and flow. Their relations are then “interactions,” as a result of which the variables increase or decrease, emit “outputs” and thus produce the properties of the wholes. But the wholes are not allowed to transform the parts, except quantitatively. (2007, p. 109)

Although I take issue with their characterization of Systems Theory (Winther 2008), their general rendition of the *pre-existent part* position is useful and accurate. Like them, I also resist this view.

The *abstracted parts* alternative grows out of research in theoretical biology, especially that of Kauffman (1971), Wimsatt (1974), Wimsatt (2007), Levins and Lewontin (1985), and Lewontin and Levins (2007).³ In what follows, I clarify and defend this view by first turning to the process of abstraction as selection, and, subsequently, to partitioning frames.

³ There is another important tradition that discusses the abstraction of parts: *formal mereology*. Simons (1987), Smith and Varzi (1999), and Stjernfelt (2007) are useful sources that also directly address some of the biological issues of concern here. Moreover, literature in cognitive science and semantics identifies various types of part-whole relations, and makes explicit reference to formal mereology (e.g., Winston et al. 1987; Gerstl and Pribbenow 1995). Descriptions of part-whole relations include: (i) “heterogeneously structured complex[es]” that “compris[e] different sorts of components” (Gerstl and Pribbenow 1995, p. 879, their emphasis) as well as (ii) three types of inclusion relations: (a) spatial (“x is a topological part of y”), (b) class (“x is a type of y”), and (c) truly mereonymic (“x is a part-of y”) (Winston et al. 1987, pp. 420 ff.). Indeed, the pregnant relation between formal mereology and the theoretical biology framework developed in this paper requires further investigation. There are many potential fruits to be reaped.

2.1 Abstraction as selection

Abstraction is the epistemic and cognitive activity of *focusing on, and selecting, certain (i) properties, and (ii) relations, of objects and processes while omitting most others*. Through abstraction, we commit to particular categories or kinds. We can also commit to other abstractions, including laws of nature, but these will not be investigated here. Each kind (e.g., “organ,” “biochemical cycle,” “chemical element”) is a way of picking out as relevant and useful only a small subset of the large sum total of real properties and relations of objects and processes. This subset allows us to state which objects and processes are similar to which other ones in which respects. There is some flexibility and non-rigidity in the subset associated with any particular kind—i.e., it is not comprised of necessary and sufficient properties and relations, but rather is something closer to a homeostatic property cluster kind (Boyd 1999a,b). The subset we choose out of the actual multiplicity available will depend on our interests and needs (see Goodman 1978; Dupré 1993, 2002; Cartwright 1999; Radder 2006; Hacking 2007).

We also create a coherent and consistent set of commensurate kinds—i.e., a classification—by focusing on certain super-sets of related properties and relations (e.g., morphological or genetical ones; see Kauffman 1971; Wimsatt 1974, 2007; Winther 2006). The classification need not be hierarchical. Cross-cutting classifications of the same objects are also possible (e.g., ecological and genealogical classifications of species; Dupré 1993; Khalidi 1998). In short, abstraction gives us (i) kinds of objects and processes, and (ii) classifications.

This general position of abstraction as selection is both realist and pragmatic. The main goal of abstracting as selection is to make functional classifications.

2.2 Partitioning frames

A partitioning frame is *a set of theoretical and experimental commitments to a particular way of abstracting kinds of parts*. For instance, in biology a morphological partitioning frame is distinct from a physiological frame (Winther 2001, 2006). The former focuses on static, adult structures; the latter identifies processes throughout development, many of which are cyclical or homeostatic, or both. A consequence of distinct partitioning frames existing is that abstracted parts of different frames (e.g., skeleton and muscle structures versus immunological and digestive activities) often fail to map neatly onto one another. Part classifications cross-cut, even if various sorts of overlap are also possible (e.g., cells as trans-frame reference parts). Moreover, a partitioning frame identifies types of part relations: (i) interaction relations, (ii) level relations, (iii) organization relations, and (iv) precursor–product relations. Strong relations produce emergent (i.e., non-aggregative) higher-level properties (e.g., Simons 1987; Emmeche et al. 1997; Gilbert and Sarkar 2000; Boogerd et al. 2005; Wimsatt 2007). In short, the frame determines not only the types of parts, but also the types of relations among parts.

This view of abstraction of kinds of parts through partitioning frames is very close to Kauffman’s (1971) philosophical investigation of analysis—“articulation of parts

explanation.” Kauffman argues that a system is decomposed into parts in various ways depending on which system activity (among many) needs to be explained. The parts identified by the “adequate description” of system activity (p. 258 ff.) are subsequently articulated in a mechanistic explanation. One caveat. Kauffman connects the acceptability of decompositions too tightly to explanation. I argue that additional scientific norms of acceptability for system analysis are operative: (i) understanding, (ii) intervention, and (iii) inferential reliability. My argument is here closer to [Wimsatt \(1974, 2007\)](#), where plurality of system decomposition (done through a “theoretical perspective”) is also tied to *complexity* (see [Winther 2006](#)).

The necessity of employing a partitioning frame for abstracting kinds of parts (and part relations) out of a systemic whole is expressed in four questions by Lewontin and Levins:

Because parts do not come together to make wholes but come into being in them only as the whole comes into being, the real questions about parts and wholes are:

1. What is the relation between the units described as “parts” in one whole to the units described as “parts” in some other whole?
2. What are the properties of units within their respective wholes, that is, in their respective contexts?
3. What are the similarities of contextual properties of units identified as the “same” units in different contexts?
4. What is the causal relation between properties of contextually defined “parts” and the contextual “whole” of which they are parts? [“Aspects of Wholes and Parts in Population Biology”, Ch. 18 of 2007, p. 132]

Lewontin and Levins deny the existence of parts prior to investigation. By writing “units” rather than “parts,” they leave the referent open. I suggest that the partitioning frame provides the *interpretation* of “unit”; it answers Lewontin and Levins’ central questions.

Moreover, [Levins and Lewontin \(1985\)](#) defend a “dialectical view” against “Cartesian reductionism.” Two of the four principles of the dialectical view (pp. 273–275) are general meta-principles for any partitioning frame: “a whole is a relation of heterogeneous parts that have no prior existence *as parts*” and “the properties of parts have no prior alienated existence but are acquired by being parts of a particular whole” (p. 273). The second two principles are: the interpenetration of parts and wholes, and the ubiquity of change. It is unclear whether the partitioning frames of contemporary part-whole science realize these two deep principles. However, I suspect that any part-whole science seeking completion will have to face their truth. Levins and Lewontin provide useful, general questions and principles regarding parts and wholes.

In short, the essential role of abstracting kinds of parts of a system for scientific inquiry is endorsed by a variety of authors, including Kauffman, Levins and Lewontin, and Wimsatt (see also footnote 3 above).⁴ Neither parts nor their relations

⁴ There is a further pre-history of the “systems tradition” of explanation. For instance, [Simon \(1962\)](#) explored complexity in terms of “nearly decomposable systems.” Moreover, [Cummins \(1975, 1983, 1999\)](#) and [Haugeland \(1998\)](#) contrast subsumptive and deductive-derivational mathematical explanatory strategies

(including interactions and level relations) are pre-given. A partitioning frame is requisite.⁵

3 Varieties of part-whole explanation: mechanistic, structuralist and historical explanation

This section focuses on part-whole explanations in the biological sciences. The plurality of robust, biological part-whole explanatory projects includes, but is not exhausted by, (i) *mechanistic*, (ii) *structuralist*, and (iii) *historical* explanations. No single explanatory project can reduce the other two. None is fundamental. Each has its own legitimate norms, explananda, and aims. Each abstracts parts in its own manner. I defend a pluralism, rather than a monism, of explanatory perspectives (cf. Craver 2007). Despite their important differences, one important shared feature is that each is a type of part-whole explanation.

3.1 Mechanistic explanation

The recent philosophical literature on mechanistic explanations is vast (e.g., Bechtel and Richardson 1993; Glennan 1996, 2002; Machamer et al. 2000; Craver 2007; Tabery 2004). I focus on Glennan's and Craver's accounts. The main lesson is that both proposals are effectively part-whole explanations.

Glennan defines mechanism thus:

A mechanism for a behavior is a complex system that produces that behavior by the interaction of a number of parts, where the interactions between parts can be characterized by direct, invariant, change-relating generalizations. (2002, p. S344)

He explicitly refers to parts. Moreover, “these parts must be objects, in the most general sense” and they “can be spatially localized.” Glennan's example of the gear of the clock shows that he considers these parts to be static and spatially individuated objects. Furthermore, “‘interaction’ is a causal notion that must be understood in terms of the truth of certain counterfactuals” (all quotes from p. S344). Rather than ground the notion of interaction in laws (see Glennan 1996), Glennan is here inspired by the manipulationist account of causation (Woodward 2003). In short, parts together with their causal interactions explain system behavior.

Footnote 4 continued

with, respectively, “functional analysis” and “systemic style” explanations. Cummins' analytical and Hugelund's systemic explanations are explicitly part-whole explanations. This crucial literature, however, does not discuss the abstraction of parts. Systems Theory is also pertinent pre-history. This includes work by Nicholas Rashevsky, Robert Rosen, Ludwig von Bertalanffy, and Mihajlo Mesarovic (see Winther 2008, 2009b).

⁵ Partitioning frames are also operative in cognitive science. For instance, in his critique of “representationalism,” the robotics pioneer, Rodney Brooks, critiques “decomposition by function” while advocating “decomposition by activity” (1997, pp. 402–404). These are two strikingly different partitioning frames on an “intelligent system.”

Craver and co-authors provide a different characterization of “mechanism”:

Mechanisms are entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions. (Machamer et al. 2000, p. 3)

They explicitly oppose what they call the “interactionist” account of Wimsatt, Bechtel and Richardson, and Glennan. This view apparently fails to do justice to the importance of activities in mechanisms. Indeed, under the “dualist” perspective of Machamer, Darden, and Craver, the importance of both objects *and* processes is emphasized (pp. 4, 5).

Craver (2007) further develops the dualist analysis:

A mechanism ...is a set of entities and activities organized such that they exhibit the phenomena to be explained. ...Entities are the components or parts in mechanisms.... They typically have locations, sizes, structures, and orientations. ...Activities are the causal components in mechanisms. I use the term “activity” here and throughout the book merely as a filler term for productive behaviors (such as opening), causal interactions (such as attracting), omissions (as occurs in cases of inhibition), preventions (such as blocking), and so on. ...mechanisms are entities and activities organized such that they exhibit the *explanandum phenomenon*. (Craver 2007, pp. 5–6)

...one needs to add that mechanistic explanations are constitutive. They explain the behavior of the mechanism as a whole in terms of the activities of its component parts. (Craver 2007, p. 161)

Craver distinguishes mechanisms from mechanistic explanations. The former are entities and activities. Both are parts: (i) entities are structural “components or parts” with location and size, and (ii) activities are “causal components.” A partitioning frame is required to identify them. Craver also develops the notion of mechanistic explanation in detail. A mechanistic explanation is sufficient when (i) mechanistic models and sketches adequately represent the explanandum phenomena (i.e., part or system behavior), and (ii) certain norms of explanation are satisfied (including norms of causal explanation, pp. 26, 63). This is an all too brief sketch of Craver’s analysis and of the differences between Glennan and Craver.⁶ The critical point is that both accounts appeal to parts of some kind or other.

Precisely which partitioning frame is relevant to mechanistic part-whole explanation? According to Glennan, parts are low-level objects that interact. Craver concurs that parts are structures, but insists that activities are also bona fide mechanism components. (These can be called either *activity-parts* or *process-parts*). The mechanistic partitioning frame abstracts *low-level structure-parts that themselves do things or that are associated with causal activity-parts*.

⁶ For a closer examination of the similarities, differences, and complementarities between these two accounts, see Tabery (2004).

3.2 Structuralist explanation

A structuralist explanation *shows how kinds (i.e., equivalence classes) of structure-parts develop, and are organized, according to mathematical laws of form embodied in emergent physico-chemical morphogenetic processes*. There is a long tradition of biological structuralist explanation 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 Pere Alberch, Brian Goodwin, Gerd Müller, Stuart Newman, and Gerry Webster, among others, at the end of the twentieth century and beginning of the twenty first. This tradition itself 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 *Kritik der Urteilkraft*.⁷

One way of understanding structuralist explanation and structuralism more generally is to contrast it with mechanistic explanation and a mechanistic world-view. Here are three differences:

- (1) The tradition of structuralism focuses on the *whole* and the *system* as the focal unit of investigation (e.g., the organism in biology) rather than solely on low-level parts (e.g., molecules). Strong part relations and emergent higher-level properties are emphasized, rather than atomistic and monistic part properties.
- (2) The central explanandum is *system form and development* rather than the nature of mechanistic causes.⁸
- (3) Explanatory force stems from *abstract mathematical-logical formalisms* rather than solely from causal bits and pieces of matter.

In short, structuralism rescues the integrity of the whole system, studies form in its own right, and explains systemic form in terms of mathematical formalisms. One point of contact between mechanistic and structuralist explanation is that both appeal to present, rather than past, phenomena.

In what follows, I explore the structuralist explanatory project in terms of form and process.

First, form. Kinds of structure-parts or kinds of species are identified using notions such as *equivalence class* (Simons 1987, Ch. 9; Goodwin 1994; Goodwin and Dawkins 1995; Webster and Goodwin 1996) and *isomorphic transformation* (Woodger 1945). Structural properties of parts or species are captured by kinds. A kind is invariant under certain (i) intra-generational and (ii) inter-taxa transformations. For instance, in defining the tetrapod limb as a general equivalence class of homologous kinds, we idealize away from important differences and claim that this is the *same* kind (i) over developmental time and process of a single organism and (ii) over the evolutionary time of different tetrapod taxa (e.g., see Woodger 1945, pp. 101–103; Goodwin 1994, pp. 154–158). A hierarchy of nested kinds is thus forthcoming. Indeed, amphibian or

⁷ The mechanistic tradition has very different modern origins, especially Descartes and central figures of the seventeenth century scientific revolution such as Boyle (e.g., Shapin 1996).

⁸ The explanandum in mechanistic explanations is strictly speaking systems behavior. However, in actual practice, and even in the background principles and norms of significant parts of psychology and the biological sciences, the explananda of mechanistic explanations are just the mechanisms themselves.

mammalian limb kinds are more specific, nested invariant equivalence classes of the tetrapod limb kind.

Second, process. Structural properties are explained by generative processes. That is, higher system-level, developmental processes, referred to as “fields of force” (D’Arcy Thompson), “morphogenetic fields” (Goodwin) or “epigenetic processes” (Newman and Müller), provide a processual explanation of kinds of parts and species, kinds that are abstracted structurally. These systems-level processes instantiate or *realize* mathematical laws. The structuralist tradition is explicit about (i) subsumption and (ii) integration under mathematical law as norms of explanation:

We want to see how... the forms of living things, and of the parts of living things, can be explained by physical considerations, and to realise that in general no organic forms exist save such as are in conformity with physical and mathematical laws. (Thompson [1917] 1961, p. 10)

However, the goal of scientific explanation is to reduce accidentals to the minimum possible and to seek the principles according to which systems are organized. (Goodwin 1994, p. 87)

These processes are often referred to as *self-organizing* (e.g., Kauffman 1993; Newman and Müller 2000, 2005; Winther 2008). After all, the emergent processes exist at the level of the entire system. Moreover, ontogenetic process is the basis of evolutionary change—ontogeny dictates phylogeny. The structuralist partitioning frame thus abstracts *kinds of invariant structures (at a variety of compositional levels) that are themselves explained by emergent processes*.

3.3 Historical explanation

Historical explanation is the *placement of kinds of parts (e.g., organism-parts, or species qua parts of lineages) in their contextual (and long-term) temporal whole by means of a narrative—a biography—justified by a phylogenetic tree*. In what follows, I sketch the close conceptual relation between parts and characters in phylogenetic inference. The logic of narratives is developed in the context of the species as individuals thesis.

Characters of an organism are the data with which phylogenetic trees are constructed, tested, and corroborated. What is a character? Colless (1985) usefully distinguishes three senses of “character”: (1) character-part (e.g., wings), (2) character-variable (e.g., wing color), and (3) character-attribute (e.g., has brown wings) (p. 230). Thus, the data for phylogenetic tree reconstruction consist in: (1) *kinds of parts of an organism of a species*, (2) *their characters*, and (3) *their character-states*. This is true even when the parts are genes of the genome system, the characters are gene sequence, and the character-states are the particular gene sequences (i.e., alleles). As Rieppel points out: “The method of systematic biology requires decomposition of the organism into parts, or ‘characters,’ which can then be used in the reconstruction of phylogenetic relationships” (2001, p. 58). Moreover, in order to identify objective, non-reified kinds of parts (and their characters and character-states) of an organism, objectivity criteria must be employed; such criteria include: (1) special similarity,

(2) conjunction, and (3) causal grounding (Rieppel 1988; Kearney and Rieppel 2006; Rieppel and Kearney 2007; Winther 2009a; see also Lewontin 2001). Processes such as cellular respiration or certain metabolic cycles can also be organism-parts, with characters and character states useful for phylogenetic inference. Organism-parts can thus be structure-part or process-parts, at a variety of intra-organismic levels. Characters always make reference to organism-parts.⁹

What is a narrative? Turn to the Ghiselin-Hull thesis of species as individuals (SAI) (e.g., Ghiselin 1997; Hull 1989). According to SAI, species are continuous “space-time worms” (Hull 1989, p. 187) with a history: a beginning, a life, and an end. Moreover, an individual organism is a *part-of*, rather than an *instance-of*, a species. A species is itself a part-of a larger lineage. A species is not a natural kind, *sensu stricto*: it does not have essences, nor are there any laws about it, nor is it an instance-of a genus or of any other higher-order taxonomic rank. A narrative, then, is a *biography* of (i) a species (e.g., the spectacular keel-billed Toucan, *Ramphastos sulfuratus*) or (ii) a part of an organism (e.g., the panda’s thumb, Gould 1980; see also Ghiselin 2005). Hull (1989) calls the agent of the narrative biography the “central subject.”¹⁰ How did the subject change? How did it remain invariant? How do new subjects arise? The narrative also includes the evolutionary relevant ecological stage, and functional and developmental constraints. Inferred phylogenetic trees ground narratives in that they justify inferences about changes and invariances of parts.

Two caveats on the SAI. First, individuals must always be identified through individuation criteria. Indeed, such criteria give us explanatorily relevant information for narratives (e.g., Napoleon was a certain type of person: a military general, cf. Hull 1989, p. 188; the panda’s thumb is of type bone and not of type muscle or neuron). Second, it has been cogently argued that species are *also* kinds—this is an epistemic, methodological, and ontological point (Boyd 1999b; Griffiths 1999; Brigandt 2009; see the articles in Vergara-Silva and Winther 2009). In short, organism-parts and their characters, as well as species *qua* parts, are also kinds.

Thus, the historical partitioning frame abstracts *kinds of temporally changing organism-parts (and their characters and character-states) through objectivity criteria, and explains the organism-parts, or species qua parts, through a narrative biography justified by a phylogenetic tree*. Rather than investigate parts and part relations within a single type of whole, a historical explanation explores stability/invariance and innovation/change in parts and part relations across historically-related (i.e., evolutionarily related) types of wholes.

In summary, the three part-whole explanatory projects have distinct partitioning frames, practices, and norms. They also have different aims and explananda:

⁹ Moreover, various methodologies, with associated optimization criteria, are used on the character data in order to infer the best phylogenetic tree(s): Sober (2004) contrasts two particularly important methodologies: “*ML* [maximum likelihood] seeks to find the tree topology that confers the highest probability on the observed characteristics of tip species. *MP* [maximum parsimony] seeks to find the tree topology that requires the fewest changes in character state to produce the characteristics of those tip species” (p. 644). See also Sober (1988, 2008) and Guerrero McManus (2009).

¹⁰ Another crucial aspect of narratives is their temporality. A productive analysis can be found in Richards (1992). Richards distinguishes among various types of narrative time: “time of events”, “time of narrated events;” “time of narration,” and “time of narrative construction.”

- (1) Mechanistic explanation aims to provide an account of the whole in terms of the causal properties of basic parts. Its explananda are system behavior and development, or the mechanisms themselves.
- (2) Structuralist explanation intends to furnish an account of the system in terms of (i) structural parts found at many levels and (ii) the realization of formal mathematical laws in emergent processes. Its explananda are emergent system form and development.
- (3) The goal of historical explanation is to present a narrative, a biography, of a temporally-changing organism-part, or species qua part, by placing it in its contextual whole. Its explananda are the long-term temporal changes of organism-parts, species qua parts, and their respective wholes.

Let us now turn to the case study.

4 Part-whole explanation of the tetrapod limb

The tetrapod limb is an important study system for developmental biology, cell biology, genetics, paleontology, and theoretical biology (Figs. 1, 2). In what follows, I present the three part-whole explanatory projects discussed in Sect. 3 as they apply to the limb: *geno-mechanistic*, *self-organization structuralist*, and *historical*.

By examining a single system in light of three types of part-whole explanation, I illustrate the respective partitioning frames, norms, practices, explananda, and aims of each explanatory project. Questions about potential tensions and complementarities among the projects immediately arise. These are addressed in Sect. 5.

4.1 Geno-mechanistic explanation of the tetrapod limb

The dominant, low-level mechanistic view emphasizes three spatial axes determined by gradients of diffusing, genetically-produced morphogens. Limb patterning is a function of cellular differentiation resulting from every cell interpreting its positional information in the three-dimensional spatial grid, at particular times (Wolpert 1969; Tickle 2006). Each cell expresses genes differentially depending on *where* it is and *when* it is there.

Two tissue regions are essential to setting up the limb bud reference frame: the Apical Ectodermal Ridge (AER) and the Zone of Polarizing Activity (ZPA) (Fig. 3). First, the AER sustains growth along the proximal-distal axis (“shoulder-to-hand”). Behind the ectodermal cells of the AER, there is a Progress Zone (PZ) of undifferentiated mesodermal (in particular, mesenchymal) cells. Second, the ZPA ensures the patterning of anterior-posterior polarity (“thumb-to-pinkie”). The establishment of dorsal-ventral polarity (“back-of-the-hand-to-palm”) is still the subject of controversy, although some genetic details are known (see Capdevila and Izpisua Belmonte 2001; Tanaka and Tickle 2007).

According to the geno-mechanistic account, there is a complex genetic story to be told about the initial formation and subsequent employment of the spatial grid (Fig. 4). Distinct genes activate and inhibit each other within and across cells. For instance, the gene *Sonic hedgehog* (*Shh*) produces the protein SHH. Particularly in the distal

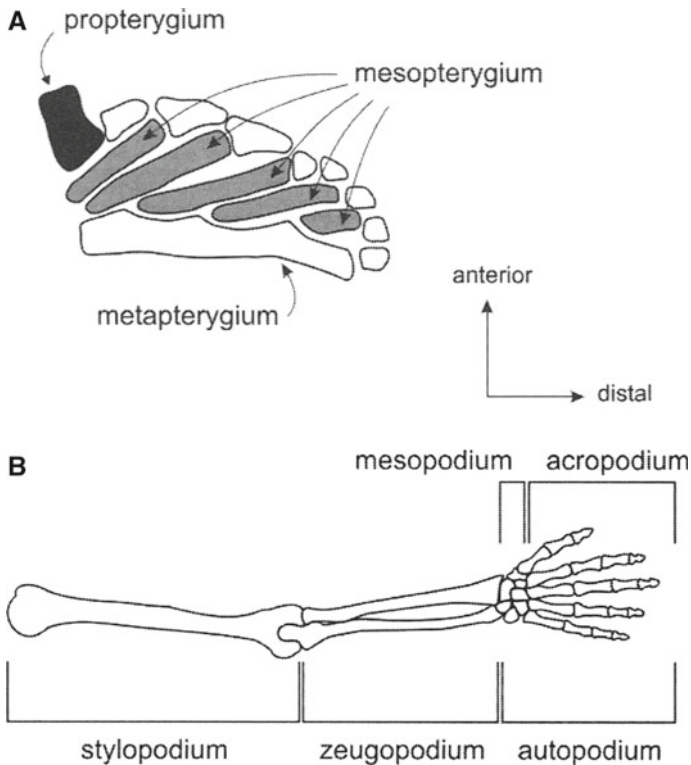


Fig. 1 Basic anatomy of fins and limbs. From [Wagner and Larsson \(2007, p. 53\)](#). [[Hall \(2007\)](#) notes: “fins minus fin rays plus digits equal limbs,” p. 1.] Reprinted with kind permission of the publisher from *Fins into Limbs. Evolution, Development, and Transformation*, edited by Hall BK, p. 53, University of Chicago Press, Copyright © 2007 by The University of Chicago

end of the limb bud, SHH is “absolutely required for the maintenance of growth and patterning” ([Capdevila and Izpisua Belmonte 2001, p. 108](#)). It is a key gene for establishing the anterior-posterior axis. Moreover, since the activation of *Shh* itself depends on genes expressed (i) distally in the AER (e.g., *Fgf*) and (ii) dorsally (e.g., *Wnt7a*), *Shh* is a genetic “relay station,” as it were. In other words, *Shh* is central to “coordinat[ing] signaling with respect to all three axes of the developing limb” ([Tanaka and Tickle 2007, p. 73](#)). The example of *Shh* provides a glimpse into the role of genes in establishing axes.

After the basic parts and part relations have been produced—i.e., (i) tissue regions, (ii) spatial axes, and (iii) initial cell types—cellular differentiation into cartilage and subsequent bone occurs. Here is a summary. As the AER grows distally, with the PZ in its wake, mesenchymal stem cells exit the PZ. Those that leave first, start differentiating first [[Tickle \(2003\)](#) reviews two models for this]. The focus in my paper is on the differentiation of mesenchymal stem cells into chondrocytes (cartilage cells).¹¹

¹¹ A separate pathway of the differentiation of mesenchymal stem cells leads to osteoblasts (bone cells) that invade the cartilage elements once the elements are set up and vascularization starts. Bone replaces cartilage.

Fig. 2 Skeletal elements of various tetrapods. From Capdevila and Izpisúa Belmonte (2001, p. 90). Reprinted, with permission, from the *Annual Review of Cell and Developmental Biology*, Volume 17 © 2001 by Annual Reviews www.annualreviews.org

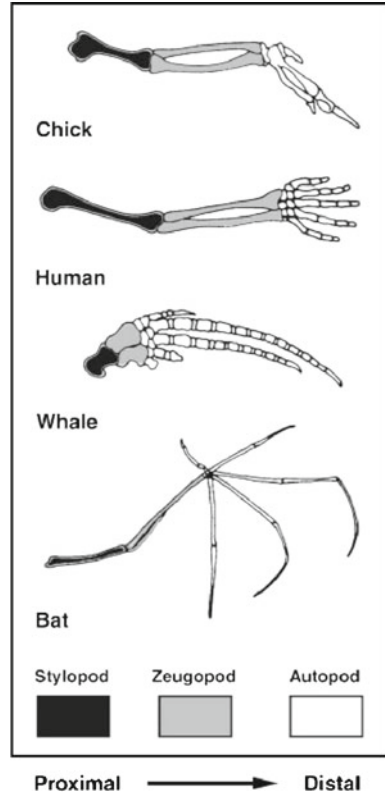


Fig. 3 Sketch of limb bud polarity, and respective locations of AER, PZ, and ZPA. From Capdevila and Izpisúa Belmonte (2001, p. 90). Reprinted, with permission, from the *Annual Review of Cell and Developmental Biology*, Volume 17 © 2001 by Annual Reviews www.annualreviews.org

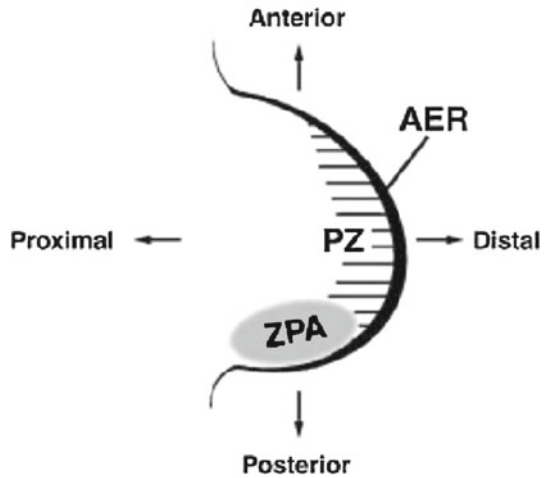


Fig. 4 Establishment of the three spatial axes of the limb through sequential gene action. From [Tanaka and Tickle \(2007, p. 71\)](#). Reprinted with kind permission of the publisher from *Fins into Limbs. Evolution, Development, and Transformation*, edited by Hall BK, p. 71, University of Chicago Press, Copyright © 2007 by The University of Chicago

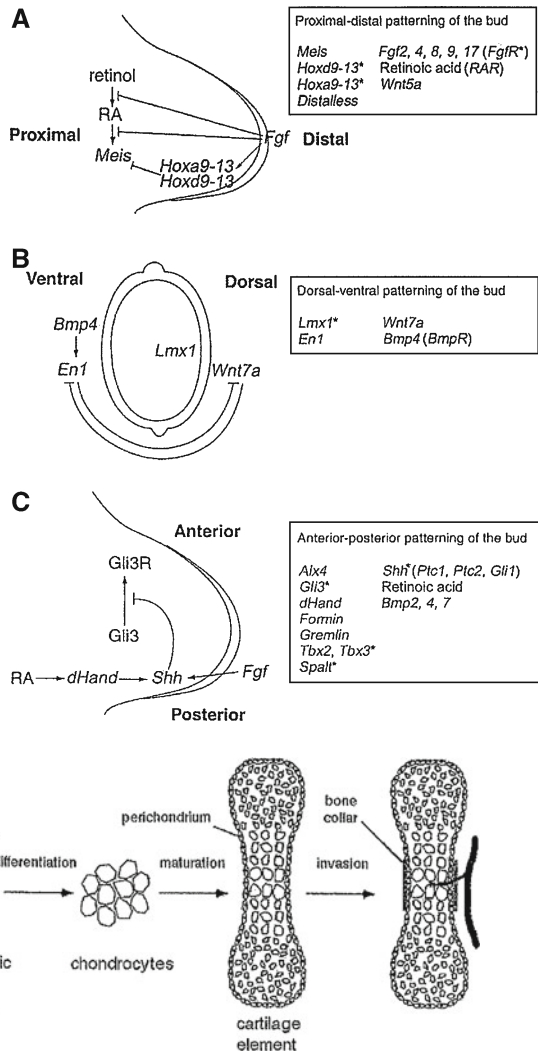


Fig. 5 Chondrocyte condensation and bone formation in limb development. From [Weatherbee and Niswander \(2007, p. 95\)](#). Reprinted with kind permission of the publisher from *Fins into Limbs. Evolution, Development, and Transformation*, edited by Hall BK, p. 95, University of Chicago Press, Copyright © 2007 by The University of Chicago

Centers of precartilaginous mesenchymal condensation appear, specified by positional information. Subsequently, the aggregating chondrocytic cells hypertrophy as further chondrocytes are added and as a surrounding layer of connective tissue, the perichondrium, is formed (Fig. 5). This process of the formation of cartilage elements is:

tightly regulated both temporally and spatially. A number of signaling pathways (FGF, BMP, PTHLH, IHH, WNT) are involved in orchestrating this multistep process leading from mesenchymal condensation to bone formation.

Mutations in genes from these pathways adversely affect skeletal development...
(Weatherbee and Niswander 2007, p. 95).

Chondrogenesis occurs last at the most distal end, where the autopodium (hand/foot) forms. Proteins important for digit identity include SHH, BMP, and various products of the *Hox* code (see Capdevila and Izpisua Belmonte 2001; Lovejoy et al. 2003; Tickle 2003, 2006; Harfe et al. 2004). Well-known adult parts eventually result: stylopodium (humerus/femur), zeugopodium (radius-ulna/tibia-fibula) and autopodium of vertebrates (Figs. 1, 2).

Under this mechanistic account, genes are the essential structure-parts and activity-parts that explain system level behavior (i.e., spatial patterning, and cartilage and bone maturation). They are also sometimes thought of as parts with informational properties.

4.2 Self-organization structuralist explanation of the tetrapod limb

The self-organization structuralist perspective focuses on higher-level systemic processes rather than on gene activation and inhibition. Moreover, it interprets cellular differentiation as primarily an outcome of cell relations, rather than of monadic low-level differential genetic expression dictated by positional information. It agrees with much of the cell-level descriptive phenomenology of Sect. 4.1. But its partitioning frame *spans parts at many levels and with many sorts of relations*. Relevant parts, part properties, and part relations include biomechanical stresses and strains on cells and tissues; cells and their diffusion, movement, division, and relative affinity; and various types of extracellular matrices (ECM). I explore a dynamical and epigenetic “bare bones” structuralist mathematical model of limb development and, more specifically, chondrogenesis.

In their “bare bones” model, Newman and co-authors build on Alan Turing’s general insights of a “reaction-diffusion” system (Turing 1952; Hentschel et al. 2004; Newman and Müller 2005; Forgacs and Newman 2005). Under Turing’s model, an activator auto-catalyzes and also induces an inhibitor, while the latter inhibits the activator and diffuses more rapidly. These activator–inhibitor systems express robust patterns. Newman and collaborators also refer to parts, part properties, and part relations at levels higher than the biochemical level: cellular movement, differentiation, aggregation, and adhesion as well as pattern-producing geometrical discontinuities and breaks imposed by the asymmetric distribution of different cell types across the proximal–distal length of the developing limb. The basic toolkit of abstracted parts in Hentschel et al. (2004) is:

- (1) Four mesenchymal cell types: R_1 , R_2 , R'_2 , and R_3 . Each type is defined by the FGF receptors it expresses: 1, 2 or 3. (Cell type 2 is further sub-divided: R_2 produces minimal levels of fibronectin, R'_2 elevated levels; n.b., R_3 is the cartilage cell type)
- (2) FGF protein produced by the AER
- (3) TGF- β protein (activator) produced by R_1 and R_2 cells
- (4) A hypothesized inhibitor protein produced by R_2 cells

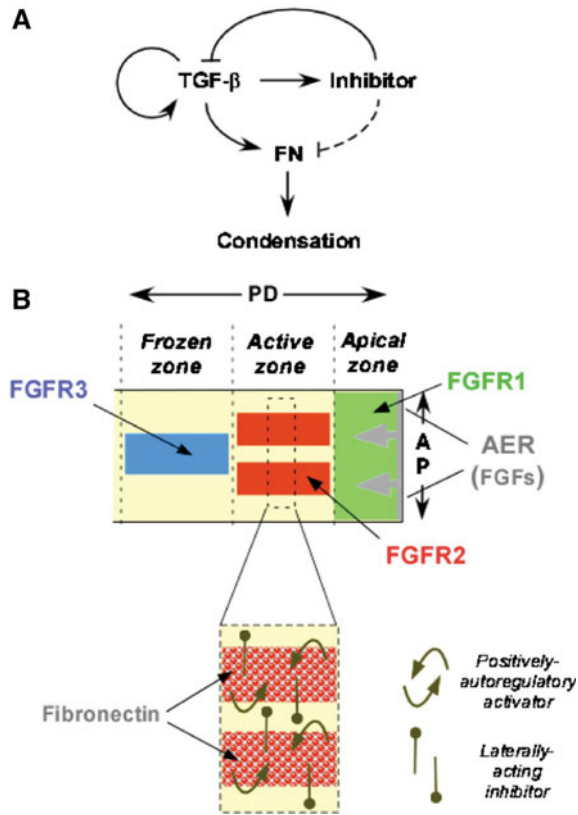


Fig. 6 “(A) Schematic representation of the biochemical–genetic circuitry underlying the self-organizing pattern forming core mechanism... (B) Interactions of the core mechanism are superimposed on a two-dimensional schematic limb bud organized into zones defined by experimentally determined expression patterns of FGF receptors 1, 2, and 3.” From Newman and Müller (2005, p. 599). Reprinted with permission of John Wiley & Sons, Inc. from “Origination and Innovation in the Vertebrate Limb Skeleton: An Epigenetic Perspective,” *Journal of Experimental Zoology (Mol Dev Evol)*, Vol. 304B, No. 6, p. 599, Copyright © 2005 by Wiley-Liss, Inc

(5) Fibronectin, a molecule that attracts R_1 , R_2 , and R'_2 cells, and that forms adhesive patches, which captures chondrocytes. Adhesion is essential for chondrocyte condensation.

A few observations. Mesenchymal cells leading to chondrocytes differentiate thus: $R_1 \leftrightarrow R_2 \rightarrow R'_2 \rightarrow R_3$ (n.b., differentiation of R_1 to R_2 occurs at a much higher rate than R_2 to R_1). Prechondrocytic cells diffuse and move up fibronectin concentration gradients. Fibronectin production is stimulated by TGF- β and is inhibited by the hypothetical inhibitor (Fig. 6).

The “reactor-diffusion” system of the bare-bones model is characterized by eight coupled differential equations modeling, respectively: (1)–(4) the density of the four cell types, (5) FGF concentration, (6) TGF- β concentration, (7) the inhibitor concentration, and (8) fibronectin concentration (Hentschel et al. 2004; Newman and Müller 2005; Forgacs and Newman 2005). The general form of each equation is:

$$\partial u / \partial t = D \nabla^2 u + F(u) \quad (1)$$

where u is the molecular concentration or cell density, D is the diffusion constant for that species of molecule or cell, ∇^2 is the Laplacian operator, and $F(u)$ describes the behaviors of the reactions and cells and may depend on all or just a subset of the total variables (Zhu et al. 2009; Forgacs and Newman 2005, p. 217).

Here are two examples. The equation governing the spatio-temporal evolution of TGF- β protein is:

$$\partial c_a(\mathbf{x}, t) / \partial t = D_a \nabla^2 c_a + F_{a1} R_1 + F_{a2}(c_a) R_2 - k_a c_1 c_a \quad (2)$$

The spatial vector \mathbf{x} represents at least two dimensions: proximal-distal and anterior-posterior. The first RHS term captures, through a diffusion constant D_a and a Laplacian (in this case, the Laplacian is the second partial derivative of c_a with respect to the spatial coordinates), the diffusion rate of TGF- β out into the ECM. TGF- β is released by R_1 cells at a constant rate, F_{a1} , as represented by the second term. Moreover, R_2 cells release it at a rate positively correlated to local TGF- β concentration. That is, cell type R_2 auto-activates the production of TGF- β . Thus, F_{a2} is a function of c_a , as can be seen in the third term. The concentration of TGF- β diminishes as it forms a non-reactive complex with the inhibitor; the rate of formation of this complex depends on the rate parameter k_a , as captured by the fourth term.

The equation governing the density of the mobile cell type, R_1 is:

$$\begin{aligned} \partial R_1(\mathbf{x}, t) / \partial t = D_{\text{cell}} \nabla^2 R_1 - \chi \vec{\nabla} \cdot [R_1 \vec{\nabla} \rho] \\ + r R_1 (R_{\text{eq}} - R) + k_{21} R_2 - k_{12}(c, c_a) R_1 \end{aligned} \quad (3)$$

Here, the first RHS term indicates cell diffusion. The second term characterizes R_1 condensation as the cells move up the fibronectin gradient; χ is a constant, ρ represents fibronectin concentration, and the divergence of the gradient can be rewritten as the product of the partial derivative of fibronectin concentration with respect to the spatial coordinates and the partial derivative of R_1 density with respect to the spatial coordinates. It is negative since condensed cells are removed from the mobile cell population. The third term captures logistic growth in cell number through mitosis (r is the intrinsic rate of growth). The fourth term indicates reverse differentiation of R_2 to R_1 ; the last term captures differentiation of R_1 into R_2 . The rate of differentiation k_{12} is a function negatively correlated with c (concentration of FGF) and positively correlated with c_a (concentration of TGF- β). For realistic concentration gradients, $k_{21} \gg k_{12}$. Equations 2 and 3 are two of eight equations capturing the complex relationships among the different sorts of parts modeled in the reactor-diffusion system (see Hentschel et al. 2004; Forgacs and Newman 2005).

Finally: How does the skeletal pattern of 1, 2, N elements, proximal-distally arranged, emerge? Radically different populations of cell types are found in the three zones of the limb bud: *frozen zone* (primarily R_3 cells), *active zone* (primarily R_2 cells), and *apical zone* (primarily R_1 cells) (Fig. 6). Over time, all chondrocytes become R_3 , but while they are R_2 , there are local autoactivation-lateral inhibition dynamics (LALI) in condensation centers. Skeletal element number depends on exact values of the initial

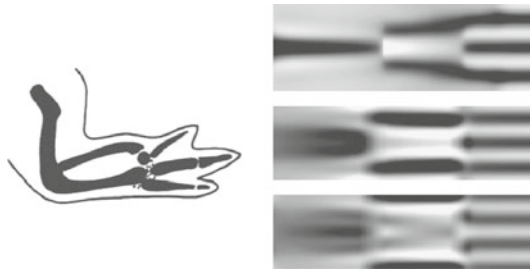


Fig. 7 Results of the Hentschel et al. (2004) reactor-diffusion simulations. From Newman and Müller (2005, p. 600). Reprinted with permission of John Wiley & Sons, Inc. from “Origination and Innovation in the Vertebrate Limb Skeleton: An Epigenetic Perspective,” *Journal of Experimental Zoology (Mol Dev Evol)*, Vol. 304B, No. 6, p. 600, Copyright © 2005 by Wiley-Liss, Inc

conditions and parameter settings in the eight coupled differential equations, especially as the values impact the behavior of R_2 cells (Hentschel et al. 2004, p. 1720; Zhu et al. 2009). These conditions and settings differ significantly in each of the three zones, also because of differing geometry (i.e., shape and form; Fig. 7).

This bare bones model is but one example of complex and epigenetic structuralist models of the tetrapod limb (see also Shubin and Alberch 1986; Oster et al. 1988; Webster and Goodwin 1996, Ch. 6, “Putting the Organism Together Again”). This perspective resists the gene-mechanistic explanatory project. Oster et al. (1988) argue that “the effect of genes on morphology is mostly indirect.” Indeed, there is a “complex feedback loop wherein regulation by genes affects the behavior of cells, and the geometric pattern of heterogeneous cell populations affects gene expression via inductive interactions” (p. 873). The self-organization perspective survived the explanatory reductionism (sensu Sarkar 1992; see also Winther 2009b) of molecular genetics, including the *Hox* revolution of the 1980s and 1990s. In a recent defense, Newman and Müller observe that:

In contrast with this mainly genetically programmed mode of development, patterns can readily arise from the reciprocal interaction of a system’s components (e.g., cells, their genes, and gene products) if the regulatory modules are employed in a reciprocal, multidirectional fashion, rather than in strict hierarchies. (Newman and Müller 2005, p. 594)

The structuralist tradition continues to emphasize models and laws of form that span multiple levels and many kinds of parts.

4.3 Historical explanation of the tetrapod limb

The first two explanatory perspectives focus on parts in contemporary tetrapod limbs. But these parts also have a history. Consider the history of digits and digit identity in birds. Birds are theropod dinosaurs (Figs. 8, 9; Fig. 9 is nested within Fig. 8). To which ancestral digits are the three digits of birds homologous? To which embryonic avian digits do adult bird digits correspond? What is the correct digit identity? Paleontological fossil data (e.g., *Archaeopteryx lithographica*) suggests that the three

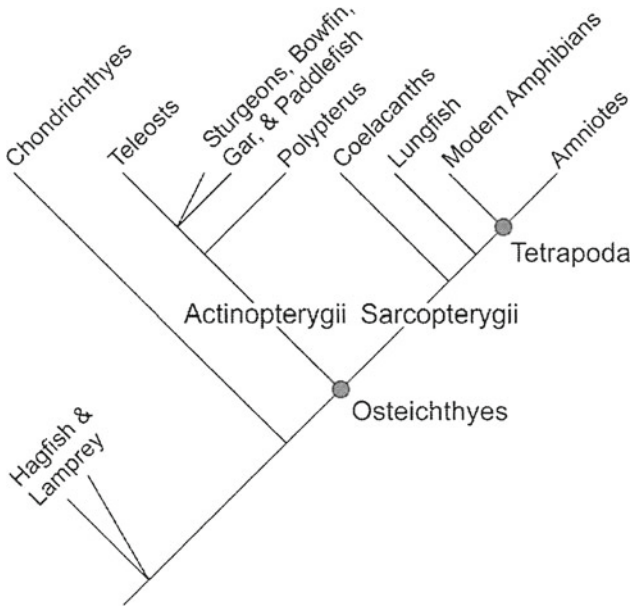


Fig. 8 Idealized phylogeny of tetrapods and their living relatives. From [Wagner and Larsson \(2007, p. 52\)](#). Reprinted with kind permission of the publisher from *Fins into Limbs. Evolution, Development, and Transformation*, edited by Hall BK, p. 52, University of Chicago Press, Copyright © 2007 by The University of Chicago

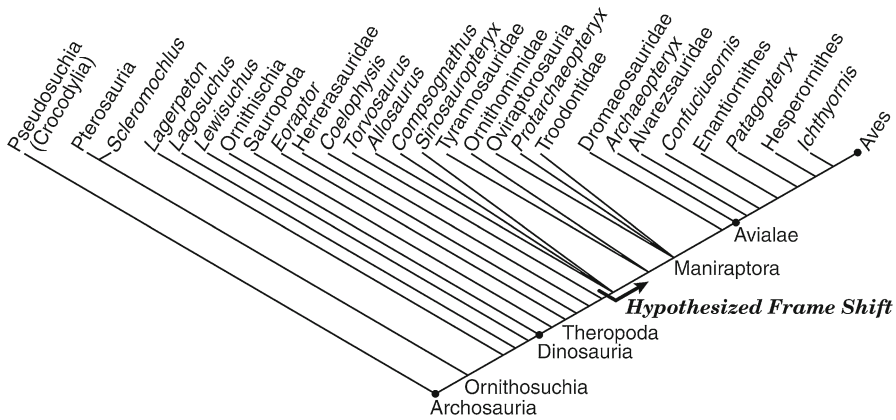


Fig. 9 “Consensus cladogram depicting phylogenetic relationships among bird-line archosaurs.” From [Wagner and Gauthier \(1999, p. 5112\)](#). Reprinted with kind permission of the publisher from Wagner and Gauthier (1999). 1, 2, 3 = 2, 3, 4: A Solution to the Problem of the Homology of the Digits in the Avian Hand. *Proceedings of the National Academy of Sciences* 96:5111–5116, Copyright © 1999, National Academy of Sciences, U.S.A.

avian digits correspond to digits I, II, and III of dinosaur ancestors.¹² However, there is excellent embryological data indicating that bird digits develop from chondrogenetic

¹² Interestingly, in amphibians, mammals, lizards, and turtles, the first adult digits lost are I and V.

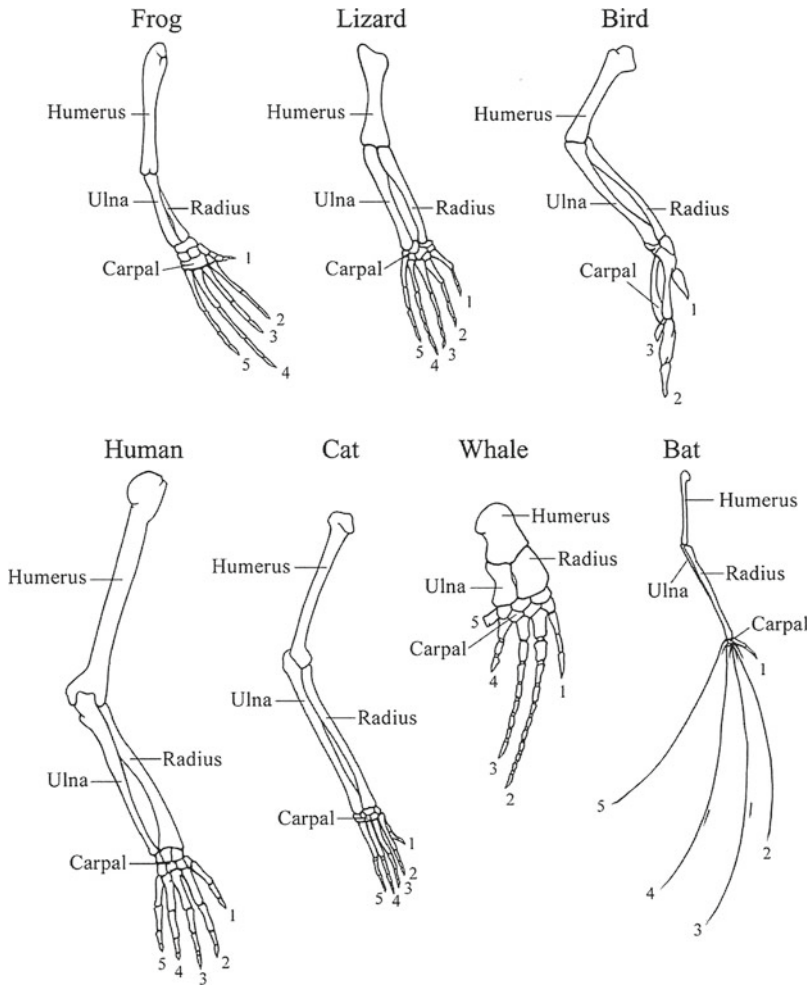


Fig. 10 “A sampling of tetrapod forelimb skeletons.” Digit identity is indicated. Weatherbee and Niswander (2007, p. 94). Reprinted with kind permission of the publisher from *Fins into Limbs. Evolution, Development, and Transformation*, edited by Hall BK, p. 94, University of Chicago Press, Copyright © 2007 by The University of Chicago

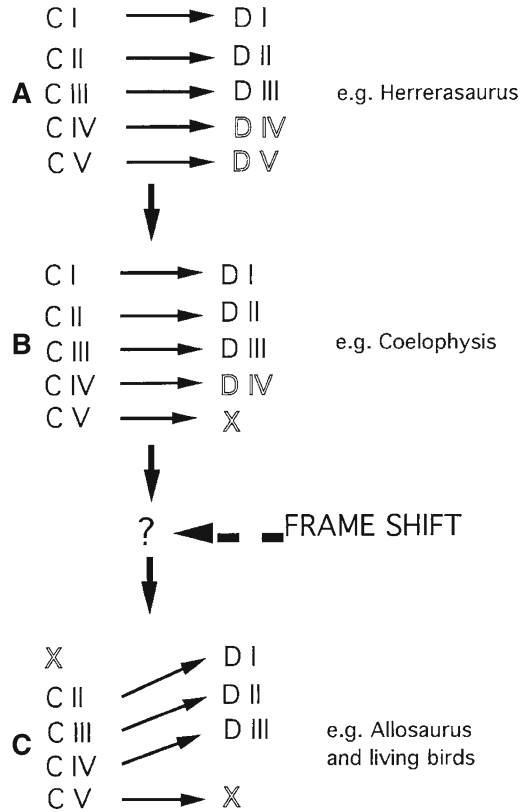
digit anlagen II, III, and IV. Thus, the paleontological and embryological data conflict (Wagner and Gauthier 1999; Wagner 2005; see also Burke and Feduccia 1997; Fig. 10 illustrates the Roman numeral notation).

The Frame Shift Hypothesis (FSH) is intended to account for this tension in the empirical data (Wagner and Gauthier 1999). It postulates that the developing digit, CN assumes the morphology and identity of the adult $D(N-I)$ digit, as defined in ancestors (where $II < N < IV$). For instance, embryological chondrocyte condensation CII is forced to become adult digit DI (see Fig. 11). The FSH is a historical explanation: there are (i) clear organism-parts (in this case, structure-parts at the skeletal level), (ii) a generally accepted tree, and (iii) a narrative biography with an ecological and

Fig. 11 “Hypothesis about the phylogenetic transformation of digit development leading from an ancestral five-digit theropod hand (e.g., *Herrerasaurus*) to the three-digit hand of *Allosaurus* and the maniraptorans including living birds.” Wagner and Gauthier (1999, p. 5115).

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1, 2, 3 = 2, 3, 4: A Solution to the Problem of the Homology of the Digits in the Avian Hand. *Proceedings of the National Academy of Sciences* 96: 5111–5116, Copyright © 1999, National Academy of Sciences, U.S.A.



developmental scenario. Moreover, the constraints are strong. Wagner and Gauthier (1999) observe: “early theropod dinosaurs faced a conflict between the functional constraints favoring the retention of digits I, II, and III and the developmental constraints that favored the loss of the condensation that normally develops into the first finger” (p. 5111). An independently moving thumb, DI, is necessary for the functioning of the crucial alula (the “bastard wing”), ubiquitous in birds. In addition, for a variety of genetic and embryological reasons, the most anterior and last formed condensation CI is easily lost, and a reduction in CV constrains a reduction of CI. Thus, the part CII was forced to give rise to DI (and CIII to DII, and CIV to DIII). The FSH provides a biography of the digits that is justified by a phylogenetic tree.

The FSH has been criticized and opposing hypotheses have been suggested, including the “axis shift hypothesis” (Shubin 1994; cf. Wagner 2005). Moreover, the paleontological data has been interpreted differently or simply ignored. Some deny that birds are theropods and also claim that the three avian digits are homologous to digits II, III, and IV of amniotic ancestors, and descendants (e.g., Burke and Feduccia 1997; Feduccia and Nowicki 2002; Galis et al. 2005). However, the ultimate outcome of this controversy does not alter the fact that FSH is an example of a robust historical explanation of structure-parts (digits) of the tetrapod limb (Vargas and Wagner 2009).

Table 1 Summary of the mechanistic, structuralist, and historical explanatory projects

	Mechanistic explanation	Structuralist explanation	Historical explanation
Which kinds of parts are abstracted by the partitioning frame?	General: low-level structure-parts and process-parts Limb: genes, spatial reference frame	General: hierarchical structure-parts, and emergent processes Limb: epigenetic and cellular processes	General: kinds of (long-term) temporally changing organism-parts, and species qua parts Limb: digits and digit identity
Basic commitments, norms, and practices	Atomistic Bottom-up Focus on causal processes, and interactions of genes Explain system in terms of parts Explain parts	Holistic Top-down Focus on mathematical “laws of form” Explain system in terms of organization of parts	Temporal Phylogenetic inference Focus on long-term temporal changes of parts and wholes Explain organism-part, or species qua part, through a narrative biography (justify the narrative with a phylogenetic tree)

Not only are there many good reasons to favor the FSH, but it has already made an important contribution to our understanding of the evolution of the tetrapod limb. It need not *also* provide a new mechanistic or structuralist explanation (Wagner 2005, p. 179).¹³

Again, historical explanation aims to explore *stability* and *innovations* in form and development across historically-related (i.e., evolutionarily related) parts, and wholes. It intends to tell the long-term temporal narrative biography of parts.

In short, each one of these explanatory projects provides a different type of part-whole explanation for the structure and development of the tetrapod limb.

Table 1 summarizes Sects. 3 and 4.

5 Relationships among the explanatory projects

Questions regarding the compatibility of these explanatory projects arise. The projects have been individuated based on their importance as constitutive perspectives for biological research. In what follows, I argue that although conceptual and sociological tension may exist (Lewontin 1969; Longino 2001), relations of integrative *explanatory complementarity* are clear, present, and desirable. We should seek complementarity.

It is commonly suggested that the structuralist explanatory project and world-view inherently conflicts with mechanistic and historical explanatory projects and world-views. Structuralist explanation is holistic, top-down, and appeals to higher-level processes; mechanistic explanation is atomistic, bottom-up, and refers to genes. This

¹³ Moreover, it is also becoming clear that digit identity itself must be assessed by gene expression dynamics rather than by position assignments (Wagner, pers. comm.).

interpretation of inherent conflict among part-whole explanatory projects *also* exists in the cognitive science literature, where genetically programmed nativism is sometimes contrasted with emergent “developmental process... as change within a complex dynamical system” (Smith and Thelen 2003, p. 343).¹⁴ Moreover, structuralist explanation appeals to essentialist natural kinds without a history, and general laws of form accounting for necessary and repeatable processes; in contrast, historical explanation refers to concrete individuals with contingent and unique narratives (Table 1).

Rather than endorsing this interpretation of *explanatory competition* in which explanatory force of one project seems to remove explanatory force from another project in a zero-sum fashion, I defend explanatory complementarity. Indeed, the projects are not irreducibly in tension, either conceptually or empirically. The tension can be overcome. The projects should be integrated and would thereby gain strength. How so?

First, top-down structuralist and bottom-up mechanistic accounts are often partial explanations of the same system. They simply focus on distinct (i) levels, (ii) causal influences, and (iii) temporal stages of systems behavior. Second, sometimes both are needed to explain even the same aspect of the system (e.g., Newman and Müller 2005, pp. 602–604). After all, a complete, robust explanation must account for part (e.g., structure-part) behavior (i) at and across multiple levels and (ii) at different temporal stages. Of course, the projects may also ground alternative explanatory hypotheses for particular cases, but then these can be tested and one hypothesis chosen.

Second, structuralist and historical explanations are also compatible and complementary. Kinds of parts have histories (Griffiths 1999; Brigandt 2009; Love 2009). Moreover, a narrative can always be told about the historical (i) emergence, (ii) stability and innovation, and (iii) distribution, of higher-order processes instantiating general laws of form. A robust structuralist explanation should include an understanding of shifts in system form and development across generations of potentially different system types. For instance, a deep concern with the epigenetic processes of autopodium formation also involves a historical explanation of changes in such processes.

One of the motivations behind my defense of explanatory complementarity is to recognize and avoid the *reification* of explanatory projects. Each project *yearns for completeness* and wishes to make an entire ontologically-independent world out of its conceptual, theoretical, and experimental resources. When you have a hammer every problem *becomes* a nail. We construct a picture of the actual world out of our limited perspective, step inside and start inhabiting that image, and then believe *that* to be the world.

I resist such reification. I advocate the simultaneous use of various explanatory projects in confronting a shared empirical system (e.g., the tetrapod limb). Simultaneity can mean (i) that distinct projects are endorsed by various, interacting units of inquiry (e.g., different laboratory groups) or (ii) the adoption of multiple projects by a single, broadly, and deeply trained unit of inquiry (e.g., an insightful researcher, or laboratory group), or both. Put differently, the projects are heuristics that should not be ontologically solidified; rather they should (i) enter into dialogue with each other and the data (thereby gaining robustness sensu Martínez 1992; Wimsatt 2007) and,

¹⁴ Mechanistic, structuralist, and historical explanation are found in psychology and cognitive science. However, these fields also have their own part-whole explanatory projects.

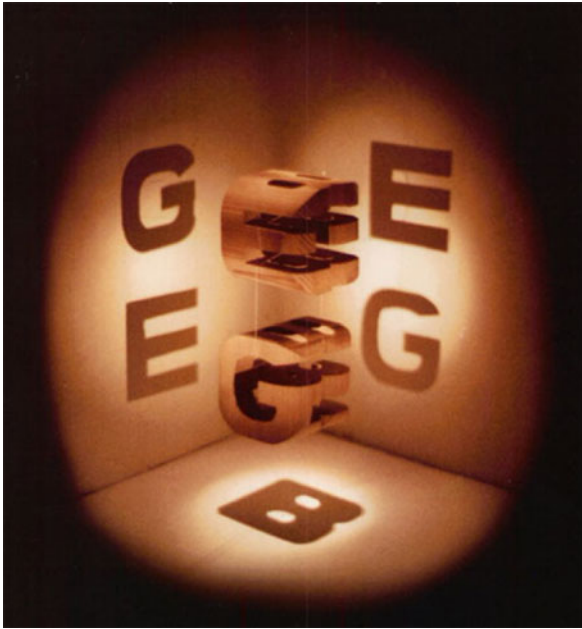


Fig. 12 Cover image of Douglas Hofstadter’s *Gödel, Escher, Bach: An Eternal Golden Braid*. A system is projected from various perspectives. Each projection is essential for understanding the entire system. Ideally, the “spotlight” projections should be replaced by a global “floodlight” illumination. (See text.) Reprinted with kind permission of Basic Books, a member of Perseus Books Group, Copyright © 1979 by Basic Books, Inc., Copyright © 1999 by Douglas R. Hofstadter

ultimately, (ii) themselves be seen as distinct and complementary aspects of a higher-level, integrated, and robust *explanatory field*. Explanatory projects merely provide partial “spotlight” projections of complex reality (Fig. 12). In contrast, an explanatory field (e.g., part-whole science as a synthetic explanatory project) grants a complete “floodlight,” felt-sense vision of the entire system, its integration, and the different kinds of abstracted parts and part relations of which it is composed.¹⁵

6 Conclusion

Parts and wholes are essential to a family of scientific explanatory projects, and to a unique kind of science. Part-whole science involves the abstraction of kinds of parts by means of partitioning frames. In order to describe the three explanatory projects—mechanistic, structuralist, and historical—on their own terms, I addressed neither

¹⁵ There is productive overlap here with Simons (1987). Simons develops the notion of an “integral whole.” Moreover, in articulating the concept of “Gestalt,” he provides the general context for a formal framework for how to understand that “a complex [roughly: an integral whole] is something other than the sum of its parts” (p. 357). Indeed, the explanatory field provides an integrative vision of how the whole is more than the sum of its (different kinds of) parts. See also Smith (1987) and, for a different understanding of integral whole, Wimsatt (2007). I am grateful to Jeremy Klein for discussion of these themes.

function nor natural selection. However, each project can be rendered consistent with them, and a full account of complex and evolved systems requires their inclusion.

In this paper, I have side-stepped a number of important questions. I conclude by mentioning three.

- (1) What is a kind of science? This paper only focuses on abstraction and explanation. Other practices and norms associated with a kind, or style of science (e.g., [Hacking 2002, 2009](#); [Winther 2006, 2007](#), forthcoming b), include (i) understanding, (ii) intervention, and (iii) modeling. A full understanding of kinds of science (e.g., axiomatic and statistical, [Crombie 1994](#)) requires investigating unique, systemic patterns of co-adapted norms and practices. Kinds of science are general, constitutive units of scientific inquiry. They move beyond disciplinary boundaries and the same discipline can adopt more than one kind. Moreover, styles can hybridize and change historically.
- (2) What is the relationship among part-based explanation, causal explanation, and explanation as unification? They cross-cut. First, part-based explanations involve causal explanation. Mechanistic explanations appealing to genes, and structuralist explanations employing emergent processes, have distinct pictures of causation. For instance, the latter involves mathematical laws of form and even multi-level causation not employed in the former. Second, explanation as unification and unification as a central norm of scientific activity is not equally important across part-based explanations. Mechanistic explanation can be seen as not subject to this norm (e.g., [Craver 2007](#), pp. 48–49); in contrast, structuralist explanation strongly advocates this norm (e.g., [Goodwin 1994](#), p. 87). Introducing a new philosophical category of explanation—part-based explanation—invites new insights into the nature of scientific explanation.
- (3) Can a plurality of cross-cutting classification of parts be equally real? Some readers may be nervous regarding the source of objectivity and truth of the part classifications given by partitioning frames. Following [Goodman \(1978\)](#), [Dupré \(1993\)](#), [Khalidi \(1998\)](#), and [Hacking \(2007\)](#), among others, I argue that the interest relativity of abstraction need not result in socially constructed and relativistic classifications. Dupré observes:

One final question must be addressed: Is the kind of pluralism I have been advocating consistent with a realistic attitude to the various kinds, and even individuals, that I have discussed? There are a number of pluralistic possibilities that I have defended, but none, as far as I can see, forces one to abandon realism. ... Provided realism is separated from certain essentialist theses, I see little more reason why the possibility of distinct and perhaps overlapping kinds should threaten the reality of those kinds. (1993, p. 57)

Khalidi notes:

The idea that there are crosscutting taxonomies is closely related to the view that scientific classification is *interest relative*. If classification is always relative to certain interests, we would expect some

taxonomies to reorganize some of the same entities in different ways without displacing existing ones. (1998, p. 42)

I concur with their analyses, which can be thought of as types of interest-sensitive, pragmatic realism.

With respect to (3), I would also add the notion of *inferential reliability* as a criterion of the reality of the parts and part relations individuated by a partitioning frame. The partitioning frame—which is itself embedded in a discipline—must furnish resources for grounding reliable ampliative inferences (Winther 2001, 2006). That is, it must produce classifications of kinds of parts that (i) allow for the discovery of new sorts of phenomena, (ii) justify surprising, dangerous, and correct predictions,¹⁶ (iii) employ projectable predicates, and (iv) support counterfactual claims. When robust ampliative inferences are no longer forthcoming from a partitioning frame, it ceases to be inferentially reliable. In short, the objectivity of a partitioning frame is constituted by (i) complex reality as well as (ii) the disciplines, theories, and practices in which it is embedded and which focus on particular aspects of reality. Better explanations and predictions are produced in the history of science when inferentially reliable, objective partitioning frames are articulated and employed. Moreover, the integration of distinct partitioning frames, and explanatory projects, is necessary for developing an informed, accurate picture of the whole system.

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References

- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review*, 113, 628–647.
- Bechtel, W., & Richardson, R. C. (1993). *Discovering complexity. Decomposition and localization as strategies in scientific research*. Princeton: Princeton University Press.
- Boogerd, F. C., Bruggeman, F. J., Richardson, R. C., Stephan, A., & Westerhoff, H. V. (2005). Emergence and its place in nature: A case study of biochemical networks. *Synthese*, 145, 131–164.
- Boyd, R. (1999a). Kinds as the “workmanship of men”: Realism, constructivism, and natural kinds. In J. Nida-Rümelin (Ed.), *Rationalität, realismus, revision: Proceedings of the third international congress, Gesellschaft für Analytische Philosophie* (pp. 52–89). Berlin: de Gruyter.
- Boyd, R. (1999b). Homeostasis, species, and higher taxa. In R. A. Wilson (Ed.), *Species. New interdisciplinary essays* (pp. 141–185). Cambridge: MIT Press.
- Brigandt, I. (2009). Natural kinds in evolution and systematics: Metaphysical and epistemological considerations. (Vergara-Silva, F., & Winther, R. G., Eds.) *Acta Biotheoretica*, 57, 77–97.

¹⁶ See Winther (forthcoming a) for a brief philosophical and scientific analysis of “surprising, dangerous, and correct” predictions.

- Brooks, R. A. (1997). Intelligence without representation. In J. Haugeland (Ed.), *Mind design II. Philosophy, psychology, artificial intelligence* (pp. 395–420). Cambridge: MIT Press.
- Burke, A. C., & Feduccia, A. (1997). Developmental patterns and the identification of homologies in the avian hand. *Science*, 278, 666–668.
- Capdevila, J., & Izpisua Belmonte, J. C. (2001). Patterning mechanisms controlling vertebrate limb development. *Annual Review of Cell and Developmental Biology*, 17, 87–132.
- Cartwright, N. (1999). *The dappled world. A study of the boundaries of science*. Cambridge, UK: Cambridge University Press.
- Colless, D. H. (1985). On “character” and related terms. *Systematic Zoology*, 34, 229–233.
- 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* (3 Vols.). London: Duckworth.
- Cummins, R. (1975). Functional analysis. *Journal of Philosophy*, 72, 741–765.
- Cummins, R. (1983). *The nature of psychological explanation*. Cambridge, MA: MIT Press.
- Cummins, R. (1999). “How does it work?” vs. “what are the laws?”: Two conceptions of psychological explanation. In F. C. Keil & R. A. Wilson (Eds.), *Explanation and cognition* (pp. 117–144). Cambridge, MA: MIT Press.
- Dupré, J. (1993). *The disorder of things. Metaphysical foundations of the disunity of science*. Cambridge: Harvard University Press.
- Dupré, J. (2002). Is ‘natural kind’ a natural kind term? *The Monist*, 85, 29–49.
- Emmeche, C., Køppe, S., & Stjernfelt, F. (1997). Explaining emergence: Towards an ontology of levels. *Journal for General Philosophy of Science*, 28, 83–119.
- Feduccia, A., & Nowicki, J. (2002). The hand of birds revealed by early ostrich embryos. *Naturwissenschaften*, 89, 391–393.
- Forgacs, G., & Newman, S. A. (2005). *Biological physics of the developing embryo*. Cambridge: Cambridge University Press.
- Friedman, M. (1974). Explanation and scientific understanding. *Journal of Philosophy*, 71, 5–19.
- Friedman, M. (1983). *Foundations of space-time theories. Relativistic physics and philosophy of science*. Princeton: Princeton University Press.
- Galis, F., Kundrát, M., & Metz, J. A. J. (2005). Hox genes, digit identities, and the theropod/bird transition. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution*, 304B, 198–205.
- Gerstl, P., & Pribbenow, S. (1995). Midwinters, end games, and body-parts: A classification of part-whole relations. *International Journal of Human-Computer Studies*, 43, 865–889.
- Gilbert, S. F., & Sarkar, S. (2000). Embracing complexity: Organicism for the 21st century. *Developmental Dynamics*, 219, 1–9.
- Ghiselin, M. (1997). *Metaphysics and the origin of species*. Albany, NY: State University of New York Press.
- Ghiselin, M. (2005). Homology as a relation of correspondence between parts of individuals. *Theory in Biosciences*, 124, 91–103.
- Glennan, S. (1996). Mechanisms and the nature of causation. *Erkenntnis*, 44, 49–71.
- Glennan, S. (2002). Rethinking mechanistic explanation. *Philosophy of Science*, 69, S342–S353.
- Goodman, N. (1978). *Ways of worldmaking*. Indianapolis: Hackett Publishing Co.
- Goodwin, B. (1994). *How the leopard changed its spots. The evolution of complexity*. New York: Simon & Shuster.
- Goodwin, B., & Dawkins, R. (1995). What is an organism?: A discussion. In N. S. Thompson (Ed.), *Perspectives in ethology. Volume 11: Behavioral design* (pp. 47–60). New York: Plenum Press.
- Gould, S. J. (1980). The panda’s thumb. In S. J. Gould (Ed.), *The panda’s thumb. Reflections in natural history* (pp. 19–26). New York: W.W. Norton & Co.
- Griffiths, P. E. (1999). Squaring the circle: Natural kinds with historical essences. In R. A. Wilson (Ed.), *Species. New interdisciplinary essays* (pp. 209–228). Cambridge: MIT Press.
- Guerrero McManus, F. (2009). Rational disagreements in phylogenetics. (Vergara-Silva, F. & Winther, R. G., Eds.). *Acta Biotheoretica*, 57, 99–127.
- Hacking, I. (2002). *Historical ontology*. Cambridge, MA: Cambridge University Press.
- Hacking, I. (2007). Natural kinds: Rosy dawn, scholastic twilight. *Royal Institute of Philosophy Supplements*, 61, 203–240.
- Hacking, I. (2009). *Scientific reason*. Taipei: National Taiwan University Press.

- Hall B. K. (Ed.). (2007). *Fins into limbs. Evolution, development, and transformation*. Chicago: University of Chicago Press.
- Hall, B. K. (2007). Introduction. In B. K. Hall (Ed.), *Fins into limbs. Evolution, development, and transformation* (pp. 1–3). Chicago: University of Chicago Press.
- Halonen, I., & Hintikka, J. (2005). Toward a theory of the process of explanation. *Synthese*, 143, 5–61.
- Harfe, B. D., Scherz, P. J., Nissim, S., Tian, H., McMahon, A. P., & Tabin, C. J. (2004). Evidence for an expansion-based temporal Shh gradient in specifying vertebrate digit identities. *Cell*, 118, 517–528.
- Haugeland, J. (1997). What is mind design? In J. Haugeland (Ed.), *Mind design II. Philosophy, psychology, artificial intelligence* (pp. 1–28). Cambridge: MIT Press.
- Haugeland, J. (1998). The nature and plausibility of cognitivism (1978). In J. Haugeland (Ed.), *Having thought. Essays in the metaphysics of mind* (pp. 9–45). Cambridge, MA: Harvard University Press.
- Hentschel, H. G. E., Glimm, T., Glazier, J. A., & Newman, S. A. (2004). Dynamical mechanisms for skeletal pattern formation in the vertebrate limb. *Proceedings of the Royal Society of London. Series B*, 271, 1713–1722.
- Hull, D. (1989). *The metaphysics of evolution*. Albany: State University of New York Press.
- Hull, D. (1992). The particular-circumstance model of scientific explanation. In M. H. Nitecki & D. V. Nitecki (Eds.), *History and evolution* (pp. 69–80). Albany, NY: SUNY Press.
- Kauffman, S. A. (1971). Articulation of parts explanation in biology and the rational search for them. In R. C. Buck & R. S. Cohen (Eds.), *PSA 1970. (and Boston studies in the philosophy of science, Vol. 8)* (pp. 257–272). Dordrecht: Reidel
- Kauffman, S. A. (1993). *The origins of order. Self-organization and selection in evolution*. Oxford: Oxford University Press.
- Kearney, M., & Rieppel, O. (2006). Rejecting “the given” in systematics. *Cladistics*, 22, 369–377.
- Khalidi, M. A. (1998). Natural kinds and crosscutting categories. *Journal of Philosophy*, 95, 33–50.
- Kitcher, P. (1981). Explanatory unification. *Philosophy of Science*, 48, 251–281.
- Levins, R., & Lewontin, R. C. (1985). *The dialectical biologist*. Cambridge: Harvard University Press.
- Lewontin, R. C. (1969). The bases of conflict in biological explanation. *Journal of the History of Biology*, 2, 35–45.
- Lewontin, R. C. (2001). Foreword. In G. P. Wagner (Ed.), *The character concept in evolutionary biology* (pp. xvii–xxiii). San Diego: Academic Press.
- Lewontin, R. C., & Levins, R. (2007). *Biology under the influence. Dialectical essays on ecology, agriculture, and health*. New York: Monthly Review Press.
- Longino, H. (2001). *The fate of knowledge*. Princeton: Princeton University Press.
- Love, A. (2009). Typology reconfigured: From the metaphysics of essentialism to the epistemology of representation. (Vergara-Silva, F., & Winther, R. G., Eds.). *Acta Biotheoretica*, 57, 51–75.
- Lovejoy, C. O., McCollum, M. A., Reno, P. L., & Rosenman, B. A. (2003). Developmental biology and human evolution. *Annual Review of Anthropology*, 32, 85–109.
- Machamer, P., Darden, L., & Craver, C. (2000). Thinking about mechanisms. *Philosophy of Science*, 67, 1–25.
- Martínez, S. F. (1992). Objetividad contextual y robustez. *Diánoia*, 38, 143–152.
- Newman, S. A., & Müller, G. B. (2000). Epigenetic mechanisms of character origination. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution*, 288, 304–317.
- Newman, S. A., & Müller, G. B. (2005). Origination and innovation in the vertebrate limb skeleton: An epigenetic perspective. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution*, 304B, 593–609.
- Noë, A. (2009). *Out of our heads*. New York: Hill and Wang.
- Oster, G. F., Shubin, N., Murray, J. D., & Alberch, P. (1988). Evolution and morphogenetic rules: The shape of the vertebrate limb in ontogeny and phylogeny. *Evolution*, 42, 862–884.
- Pinker, S. (2005). So how does the mind work?. *Mind and Language*, 20, 1–24.
- Radder, H. (2006). *The world observed/the world conceived*. Pittsburgh: University of Pittsburgh Press.
- Richards, R. J. (1992). The structure of narrative explanation in history and biology. In M. H. Nitecki & D. V. Nitecki (Eds.), *History and evolution* (pp. 19–53). Albany, NY: SUNY Press.
- Rieppel, O. (1988). *Fundamentals of comparative biology*. Basel, Switzerland: Birkhauser Verlag AG.
- Rieppel, O. (2001). Preformationist and epigenetic biases in the history of the morphological character concept. In G. P. Wagner (Ed.), *The character concept in evolutionary biology* (pp. 57–75). San Diego: Academic Press.

- Rieppel, O., & Kearney, M. (2007). The poverty of taxonomic characters. *Biology and Philosophy*, 22, 95–113.
- Salmon, W. C. (1990). *Four decades of scientific explanation*. Minneapolis: University of Minnesota Press.
- Sarkar, S. (1992). Models of reduction and categories of reductionism. *Synthese*, 91, 167–194.
- Shapin, S. (1996). *The scientific revolution*. Chicago: University of Chicago Press.
- Shubin, N. H. (1994). History, ontogeny, and evolution of the archetype. In B. K. Hall (Ed.), *Homology: The hierarchical basis of comparative biology* (pp. 249–271). San Diego: Academic Press.
- Shubin, N. H., & Alberch, P. (1986). A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology*, 20, 319–387.
- Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society*, 106, 467–482.
- Simons, P. (1987). *Parts. A study in ontology*. Oxford: Oxford University Press.
- Smith, B. (Ed.). (1987). *Foundations of gestalt theory*. Munich: Philosophia.
- Smith, B., & Varzi, A. C. (1999). The niche. *Noûs*, 33, 198–222.
- Smith, L. B., & Thelen, E. (2003). Development as a dynamic system. *Trends in Cognitive Sciences*, 7, 343–348.
- Sober, E. (1988). *Reconstructing the past. Parsimony, evolution, and inference*. Cambridge: MIT Press.
- Sober, E. (2004). The contest between parsimony and likelihood. *Systematic Biology*, 53, 644–653.
- Sober, E. (2008). *Evidence and evolution. The logic behind the science*. Cambridge: Cambridge University Press.
- Stjernfelt, F. (2007). *Diagrammatology. An investigation on the borderlines of phenomenology, ontology, and semiotics*. Synthese Library Vol. 336. Dordrecht, Netherlands: Springer.
- Strevens, M. (2004). The causal and unification accounts of explanation unified—causally. *Noûs*, 38, 154–176.
- Tabery, J. G. (2004). Synthesizing activities and interactions in the concept of a mechanism. *Philosophy of Science*, 71, 1–15.
- Tanaka, M., & Tickle, C. (2007). The development of fins and limbs. In B. K. Hall (Ed.), *Fins into limbs. Evolution, development, and transformation* (pp. 65–78). Chicago: University of Chicago Press.
- Thompson, D. ([1917] 1961). *On growth and form*. Abridged from 1917 edition by J. T. Bonner. Cambridge: Cambridge University Press.
- Tickle, C. (2003). Patterning systems—from one end of the limb to the other. *Developmental Cell*, 4, 449–458.
- Tickle, C. (2006). Making digit patterns in the vertebrate limb. *Nature Reviews. Molecular Cell Biology*, 7, 45–53.
- Turing, A. M. (1952). The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London. Series B*, 237, 37–72.
- van Fraassen, B. (1980). *The scientific image*. Oxford: Oxford University Press.
- Vargas, A. O., & Wagner, G. P. (2009). Frame-shifts of digit identity in bird evolution and cyclopamine-treated wings. *Evolution and Development*, 11, 162–168.
- Vergara-Silva, F., & Winther, R. G. (Eds.). (2009). Symposium issue. Systematics, Darwinism, and the philosophy of science. *Acta Biotheoretica* 57(1–2), 1–307.
- Wagner, G. P. (2005). The developmental evolution of avian digit homology: An update. *Theory in Biosciences*, 124, 165–183.
- Wagner, G. P., & Gauthier, J. A. (1999). 1, 2, 3 = 2, 3, 4: A solution to the problem of the homology of the digits in the avian hand. *Proceedings of the National Academy of Sciences*, 96, 5111–5116.
- Wagner, G. P., & Larsson, H. C. E. (2007). Fins and limbs in the study of evolutionary novelties. In B. K. Hall (Ed.), *Fins into limbs. Evolution, development, and transformation* (pp. 49–61). Chicago: University of Chicago Press.
- Weatherbee, S. D., & Niswander, L. A. (2007). Mechanisms of chondrogenesis and osteogenesis in limbs. In B. K. Hall (Ed.), *Fins into limbs. Evolution, development, and transformation* (pp. 93–102). Chicago: University of Chicago Press.
- Webster, G., & Goodwin, B. (1996). *Form and transformation. Generative and relational principles in biology*. Cambridge: Cambridge University Press.
- Winston, M. E., Chaffin, R., & Herrmann, D. (1987). A taxonomy of part-whole relations. *Cognitive Science*, 11, 417–444.

- Wimsatt, W. C. (1974). Complexity and organization. In K. Schaffner & R. S. Cohen (Eds.), *PSA 1972*. (and *Boston studies in the philosophy of science*, Vol. 20) (pp. 67–86). Dordrecht: Reidel.
- Wimsatt, W. C. (2007). *Re-engineering philosophy for limited beings. Piecewise approximations to reality*. Cambridge: Harvard University Press.
- Winther, R. G. (2001). Varieties of modules: Kinds, levels, origins and behaviors. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution*, 291, 116–129.
- Winther, R. G. (2006). Parts and theories in compositional biology. *Biology and Philosophy*, 21, 471–499.
- Winther, R. G. (2007). Estilos de investigación científica, modelos e insectos sociales. In E. Suárez (Ed.), *Variación Infinita. Ciencia y representación. Un enfoque histórico y filosófico* (pp. 55–89). Mexico City: UNAM and Editorial Limusa.
- Winther, R. G. (2008). Systemic Darwinism. *Proceedings of the National Academy of Sciences*, 105, 11833–11838.
- Winther, R. G. (2009a). Character analysis in cladistics: Abstraction, reification, and the search for objectivity. (Vergara-Silva, F. & Winther, R. G., Eds.). *Acta Biotheoretica*, 57, 129–162.
- Winther, R. G. (2009b). Schaffner's model of theory reduction: Critique and reconstruction. *Philosophy of Science*, 76.
- Winther, R. G. (forthcoming a). Prediction in selectionist evolutionary theory. *Philosophy of Science*, 76.
- Winther, R. G. (forthcoming b). Teorías, prácticas y estilos de investigación científica. In S. Martínez, X. Huang, & G. Guillaumin (Eds.), *Filosofía de las prácticas científicas. Hacia una filosofía de la ciencia no centrada en teorías*. Universidad Autónoma Metropolitana.
- Wolpert, L. (1969). Positional information and the spatial pattern of cellular differentiation. *Journal of Theoretical Biology*, 25, 1–47.
- Woodger, J. H. (1945). On biological transformations. In W. E. Le Gros Clark & P. B. Medawar (Eds.), *Growth and form. Essays presented to D'Arcy Thompson* (pp. 95–120). Oxford: Clarendon Press.
- Woodward, J. (2003). *Making things happen. A theory of causal explanation*. Oxford: Oxford University Press.
- Zhu, J., Zhang, Y. T., Newman, S. A., & Alber, M. (2009). Application of discontinuous Galerkin methods for reaction-diffusion systems in developmental biology. *Journal of Scientific Computing*, 40, 391–418.