

Parts and theories in compositional biology

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Abstract. I analyze the importance of parts in the style of biological theorizing that I call compositional biology. I do this by investigating various aspects, including partitioning frames and explanatory accounts, of the theoretical perspectives that fall under and are guided by compositional biology. I ground this general examination in a comparative analysis of three different disciplines with their associated compositional theoretical perspectives: comparative morphology, functional morphology, and developmental biology. I glean data for this analysis from canonical textbooks and defend the use of such texts for the philosophy of science. I end with a discussion of the importance of recognizing formal and compositional biology as two genuinely different ways of doing biology – the differences arising more from their distinct methodologies than from scientific discipline included or natural domain studied. Ultimately, developing a translation manual between the two styles would be desirable as they currently are, at times, in conflict.

Goals

This article examines two important ideas in biology: *parts* and *theories*. I contend that the very notion of *parts* stands in need of significantly more philosophical attention than it has received (though see, for example, Nagel 1961; Kauffman 1971; Wimsatt 1974, 1994; and recent conceptual and biological work on modularity, including: Raff 1996; Wagner and Altenberg 1996; Wagner 1996, 2001; Bolker 2000; McShea 2000; McShea and Venit 2001; Rieppel 2005; Winther 2001a, 2005). In fact, I believe that there is a style of biological theorizing – *compositional* biology – that is based on the notion of parts and wholes, as well as their respective functions and capacities. I contrast this style with *formal* biology, which focuses on mathematical laws and models that represent quantitative relations among terms (parameters and variables) (Winther 2003). The disciplines of comparative morphology, functional morphology, developmental biology, cellular biology, and molecular biology tend to employ the compositional style, while the disciplines of theoretical population genetics and theoretical ecology tend to adopt the formal style. The first three disciplines are investigated in this article.

The important differences between compositional and formal styles are neither the scientific disciplines that they tend to guide, nor the natural domains to which the styles tend to be applied. Rather, the fundamental differences lie in their respective *methodologies* of theorizing. Often, each style can, and does, examine a similar set of phenomena in the same biological system (e.g., development in organisms) in distinct ways, sometimes even reaching conflicting conclusions about the system's processes and entities.¹ Theoretical conflicts arise especially since each style *yearns for completeness* – that is, each style employs its own methods to develop a coherent and general theory, which it then takes to be necessary and sufficient to explain *all* the data in question.²

I argue that my *style of theorizing* is close to Crombie's and Hacking's respective notions of general styles, to be further discussed below (Crombie 1994; Hacking 1994, 2002), while a *theoretical perspective* – a concept that I adopt from Griesemer, Kauffman, and Wimsatt, and develop further – is a more concrete and middle-range theoretical unit, perhaps closer to Kuhn's paradigms. As we shall see, the compositional style in biology commits to general explanatory, modeling, and part-identification strategies, while theoretical perspectives in this style, for example, those perspectives strongly associated with comparative morphology and developmental biology, endorse very specific forms of explanation, modeling, and part-identification.

In what follows, I will first examine the idea of a style of theorizing (Section 2) and will subsequently investigate the notion of a theoretical perspective (Section 3). After discussing styles and perspectives, I turn to a detailed exploration of three theoretical perspectives of the compositional style using canonical textbooks as the key source of data for the theoretical structure – including the partitioning frame – of the respective perspectives (Section 4). In order to do this, I provide a justification for the use of textbooks for the philosophy of science, thereby taking issue with some of Kuhn's claims regarding “textbook science.”

Two styles of biological theorizing: formal and compositional

Formal and compositional biology have their own distinct and internally consistent ways of explaining, modeling, and partitioning (Winther 2003). Whereas formal biology relies on mathematical laws and models, compositional biology investigates the concrete structures, mechanisms, and functions, through developmental and evolutionary time, of material parts and wholes. I

¹ That is, although certain natural domains (e.g., cellular or developmental phenomena), tend to lend themselves to one style rather than the other (e.g., compositional biology), most, if not all, natural domains can be explored using either style (e.g., think of either Kauffman's or Goodwin's formal analysis of developmental processes and entities, or recent work on multi-level selection exploring the evolutionary dynamics of development – see Winther 2003, 2005).

² Since this article focuses on compositional biology, I will not discuss conflicts between styles, but see Winther (2003, 2005).

take Hacking's notion of *styles of scientific reasoning* (see also Crombie's 1994 *styles of scientific thinking*) to be useful for elaborating the two styles that I identify. Hacking writes that every style

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)

Thus, styles are much more general and encompassing than the theoretical perspectives that I will address in Section 3.

Focusing on explanation will be particularly instructive for a preliminary sketch of one of the salient methodological differences between the styles. Two philosophers, Cummins (1983) and Haugeland (1998 (1978)), have made an important distinction between what I will call *law-based* and *part-based* explanations. In the former *formal* explanatory strategy, a set of phenomena or a fairly concrete law or model is explained by relating it to, and fitting it under, a more general law or model. These laws or models are practically always mathematically expressed formalisms. For example, Cummins argues that “[m]any scientific theories are designed to explain change” and that “[s]ubsumption under causal law is the natural strategy” for this. (Cummins 1983: 1–2) Such “subsumption” is done by 1. choosing a set of state variables that will represent the state of the system and then 2. employing causal laws that adequately transform the representations of the state of the system given the initial state and disturbing forces (Cummins 1983: 2ff). Thus, a causal law explains when it accounts for measurable changes in a system. Cummins notes that standard dominant accounts of explanation, including the deductive-nomological model, have “focused attention on causal laws and their associated explanatory roles, i.e., on transition theories, to the exclusion of more important alternatives.” (Cummins 1983: 7) One central alternative, as we shall see, is part-based explanation.

Likewise, Haugeland refers to the explanatory strategy of “mathematical derivation” – i.e., explaining a formalism using another formalism – as “*derivational-nomological*” (1998 (1978): 11). “Besides mechanics,” Haugeland argues, “fields as diverse as optics, thermodynamics, and macro-economics commonly involve derivational-nomological explanations.” (1998 (1978): 11). While I believe that Cummins’ and Haugeland’s descriptions of the formal explanatory strategy, pertinent to formal biology, are probably too coarse, it will be useful to contrast this account of law-based explanation with a *compositional* explanatory strategy articulated variously by Cummins, Haugeland, Kauffman (1971), and Wimsatt (1974).

A part-based explanation is presented when 1. *parts*, 2. *the respective part-properties* (e.g., *part functions and capacities*), and 3. *the relevant organization of parts and part-properties, which also describes interactions and relations* (i.e.,

organization can be non-aggregative³), are all used to account for systemic (whole) properties. The explanatory desideratum here is to explain the properties of the system (e.g., system functions and capacities).

Cummins and Haugeland have emphasized the relevance of this explanatory strategy to psychology. First Cummins:

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 analysis.⁴ (Cummins 1983: 1)

Haugeland makes a similar argument when he writes:

Only the derivational-nomological style puts an explicit emphasis on equations of the sort that we usually associate with scientific laws. But I shall claim that only the systematic style⁵ is directly relevant to cognitive psychology. (Haugeland 1998 (1978): 14)

I extend their argument to biology. Often, part-based explanation, rather than law-based explanation, is the appropriate and common explanatory strategy for many biological sciences.⁶ Certainly it is the one pertinent to the compositional style.

Modeling strategies differ radically between these two styles as well. The formal style tends to focus on mathematical models, whereas the compositional style tends to emphasize material, diagrammatic, and narrative models (on the latter sorts of models see, e.g., Hull 1975, 1981, 1992; Richards 1981, 1992; Danto 1985; Griesemer 1990, 1991a, b, 1996; Bechtel and Richardson 1993; O'Hara 1996; Machamer et al. 2000; Plutynski 2001). I will show how diagrammatic forms of modeling are central to compositional biology (Figures 2–6).

There is also a significant difference between the two styles both in the amount of importance placed on the concept of *parts* as such in the theoretical structure of each style, and in the way that parts are conceived. The very ontology of compositional biology is based on concrete parts and wholes, even if different theoretical perspectives carve up and determine the compositional

³ See Wimsatt (1986).

⁴ “Analysis”, roughly, involves decomposing a system into parts (“componential analysis”), and decomposing system capacities into part capacities (“functional analysis”), Cummins (1983: 28ff).

⁵ The “systematic style” is one form of part-based explanation in which the parts of a system interact non-additively and there is therefore *failure of aggregativity*, to use Wimsatt’s (1986) language.

⁶ A brief caveat is important here. These two forms of explanation can intertwine, especially when formal methods are used to explore compositional systems, interpreted as such. Consider, for example, Kauffman’s work on gene networks (Kauffman 1993). This work employs both law-based and part-based explanation. What I am describing with the distinction are the *ideal-types* of each explanatory strategy.

ontology in distinct manners. Formal biology, on the other hand, has a much more abstract ontology, in which the fundamental units (parts?) are the variables and parameters (terms) of its theoretical mathematical edifice. The *relation* between these terms (and the term-relations, expressed in equations) and a concrete material ontology is a difficult philosophical problem – the “applicability of mathematics” problem (e.g., Sober 1993; Maddy 1997; Steiner 1998; Colyvan 2001). In this article, I use the concept of the *partitioning frame* to indicate the importance of concrete parts in different perspectives of the compositional style.

Theoretical perspectives, disciplines, and textbooks

In philosophy of science, there is a long tradition of describing and emphasizing the importance of the theoretical units involved in scientific activity. Consider Kuhn’s paradigms, Lakatos’ research programs, Laudan’s research traditions, and Quine’s webs of belief. I will not here evaluate these useful accounts. Instead, I draw heavily on Griesemer’s, Kauffman’s, and Wimsatt’s views on *theoretical perspectives*⁷ because they focus on biology and take seriously the *compositional* nature of that sort of investigation (Kauffman 1971; Wimsatt 1974, 1986, 1994, 1997; Griesemer 2000). In what follows, I will first discuss some general properties of theoretical perspectives. I will then turn to the relationship between perspectives and disciplines. I will end the section by addressing the role of textbooks as legitimate sources of information regarding the perspectives.

I will focus on two important aspects of theoretical perspectives in compositional biology: *partitioning frames* and *explanatory accounts*. What I present in this section is abstract. When, in the next section, I discuss the compositional theoretical perspectives associated with the disciplines of comparative morphology, functional morphology, and developmental biology, I will present each of these aspects in detail for each perspective. These two aspects of theoretical perspectives are *guided* by the biases (sensu Wimsatt 1980), commitments (sensu Gerson 1998), and norms of the theoretical perspective.

Theoretical perspectives of compositional biology contain partitioning frames. I believe that *parts* should be considered the focal concept in the analysis of compositional biology. A pre-established definition of parts cannot be given. Parts can be many things. Depending on the perspective, they can be different kinds of 1. structure, 2. process, 3. mechanism, or 4. function. The partitioning frame of the perspective determines the relevant kinds of parts, and whether some aspect, such as a particular mechanism, should be considered a part or a relation between parts, i.e., an interaction.

⁷ Kauffman uses the term “adequate descriptions” instead of “theoretical perspectives.” But his arguments are very similar to those of Griesemer and Wimsatt.

It can be argued that *mechanisms* should be the defining concept of (compositional) biology (e.g., Bechtel and Richardson 1993; Glennan 1996, 2002; Machamer et al. 2000; Craver 2001). However, for compositional biology, the individuation and identification of mechanism is derived from both the particular theoretical perspective used and the kinds of parts the perspective's partitioning frame determines. Focusing on mechanisms emphasizes process over structure, but this is problematic since there are many kinds of processes – kinds of parts – in compositional biology (e.g., the physiological theoretical perspective will emphasize synchronic processes identified by feedback loops, whereas the developmental theoretical perspective will focus on diachronic irreversible processes) and, furthermore, there are important structural perspectives (e.g., work in comparative morphology rarely appeals to mechanisms). What *all* these perspectives share, however, is a commitment to understanding the part-whole organization (in some form or other) of biological systems. The partitioning frame is exactly what provides the interpretation of a perspective's kinds of parts, which, before specification, are left completely open, in a manner analogous to a logical variable.

My view regarding partitioning frames shares much with Griesemer's, Kauffman's, Wimsatt's, and Levins and Lewontin's stances. Griesemer, Kauffman, and Wimsatt adopt the position that there is a theoretical unit that guides the investigation of a biological system. This theoretical unit decomposes the system into its parts and processes, and provides an account (an *articulation of parts explanation*, in Kauffman's terminology) of the way these parts and processes articulate together to produce the system behavior of interest. Different theoretical units, as indicated in Wimsatt's diagram (Figure 1) decompose the system differently. In their book, Levins and Lewontin present four dialectical principles pertinent to parts and wholes; the first two are: "... [1] a whole is a relation of heterogeneous parts that have no prior independent existence *as parts*. ... [2] in general, the properties of parts have no prior alienated existence but are acquired by being parts of a particular whole." (Levins and Lewontin 1985: 273; see also their 1988). Their view is a relational dialectical one, in which the properties of parts depend on the properties of the whole, and vice-versa. Although it is not a prerequisite for part-based explanations, I am sympathetic to this view. For me, partitioning frames are what give existence to 1. the kinds of parts a perspective identifies, and 2. the *levels* (i.e., the levels of the so-called biological hierarchy, from molecules to biosphere, which may actually vary from perspective to perspective) at which these kinds of parts are taken, by the perspective, to be found.

Once a perspective has identified the parts pertinent to it, specific *explanatory accounts* can be adopted. In the previous section, we saw that compositional biology adopts a part-based explanatory pattern; all compositional perspectives *inherit* this explanatory pattern. Now, once the parts have been specified through the partitioning frame, questions of interest stated (e.g., "how does adult part X come about?"), and explanatory resources given (e.g., model-types, inference patterns, and accepted premises used in explanations), the

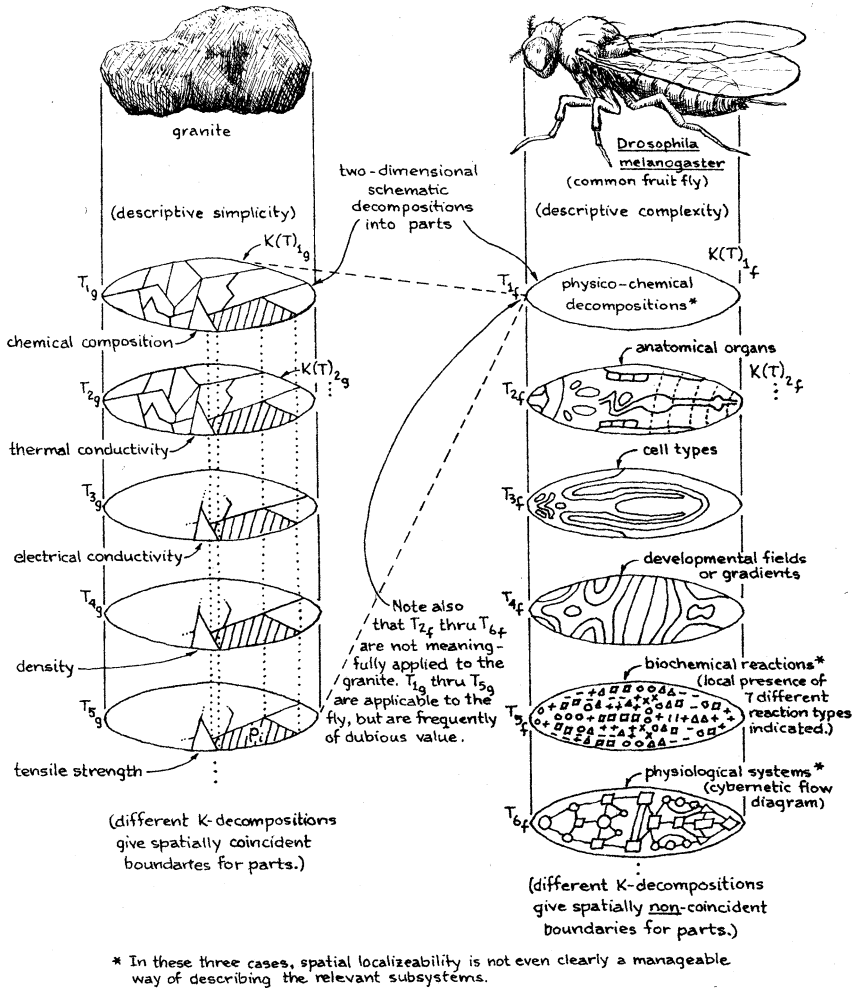


Figure 1. Wimsatt (1974: 71). Different theoretical units, in this case perspectives such as the anatomical or developmental perspective, decompose the system in different manners. For Wimsatt, the decomposition of a granite rock is *simple*, whereas the decomposition of a fruit fly is *complex*. In his figure caption, Wimsatt writes "Fig. 1. Descriptive simplicity and complexity." Reprinted by kind permission of Springer Science and Business Media from PSA 1972, edited by Kenneth F. Schaffner and Robert S. Cohen, p. 71, Dordrecht, Holland: D. Reidel Publishing Company, Copyright © 1974.

kinds of explanations a perspective provides can be understood. For example, developmental biology, as we shall see below, individuates parts processually, has clear questions of interest, uses diagrammatic and material models, and accepts the cause vs. outcome distinction in its explanations. With these ingredients specified, the explanatory accounts are determined; we now know what is considered a *legitimate* and *relevant* explanation for a given perspective.

I will now turn to the relation between theoretical perspectives and disciplines. I consider generally compositional disciplines, such as developmental biology, to be associated with a fairly strong compositional theoretical perspective.⁸ But we are then faced with the difficult problem of determining the exact relationship between theoretical perspectives and disciplines. I suggest both that we can identify disciplines robustly through a variety of independent means, and that general disciplinary biases, commitments, and norms are the guiding elements of the theoretical perspective (and aspects, such as partitioning frames, thereof) associated with each discipline. Let me explore discipline identification. First, there are sociological facts about how university departments and programs are structured, and this organization is common to many universities. This structure is further solidified by the organization perceived by other kinds of institutions, such as funding agencies and the press, when they interact with universities. Second, particular canonical upper-level undergraduate and introductory graduate textbooks, in their attention to detail and in the conceptual framework they provide, serve to individuate, and further entrench, disciplines. Third, our shared intuitions as science studies scholars often provide us with disciplinary identifications that match the first two identification methods. Thus, university structure, textbooks, and our intuitions all provide ways for individuating both disciplines and, given their biases, commitments, and norms, their concomitant theoretical perspectives.

Certainly more fine-grained theoretical perspectives, sometimes at odds, can exist within a discipline (e.g., Fisherian and Wrightian genetics within evolutionary genetics – key examples of formal biology; see, e.g., Coyne et al. 1997, 2000; Wade and Goodnight 1998; Goodnight and Wade 2000; Winther in press), but these *also* inherit the biases, commitments, and norms of the disciplinary theoretical perspective. This is why important practitioners of a discipline may appear to disagree on almost everything, even though they actually agree on many of the fundamental aspects of their perspective. Energetic disagreement requires a shared language and theory. So here I take a stronger position than Wimsatt when he writes, “[p]erspectives may sometimes correspond loosely to disciplines, but need not.” (Wimsatt 1994: 264). Although perspectives exist at a variety of levels, one level at which they do exist is the disciplinary one.

Let me turn to textbooks. The canonical advanced textbooks of a discipline show the relative unity and commonality of methods, theories, and data of that discipline – they index its uniqueness. I certainly accept that textbooks are *simplifications* of disciplinary activity and that they engage heavily in rhetoric and self-proclaimed authority.⁹ But even if textbooks are the ladders that

⁸ Although there are also, albeit significantly weaker, general formal theoretical perspectives in this case (see footnote 1).

⁹ See, e.g., Kuhn’s discussion of the role of textbooks in science in Kuhn (1970, pp. 136–138). He claims that they are loci of authority and ignore the richness of the history of the discipline.

researchers subsequently kick away, their importance¹⁰ as 1. a summarized collection of the theory, as well as of the biases, commitments, and norms, of a discipline, and 2. a key resource with which the next generation of practitioners learns the tools of the trade, can neither be underestimated nor should it be forgotten. It is precisely because textbooks indicate 1. *the generally accepted* and 2. *that which is learned early* that I use them.¹¹ They are excellent loci for understanding the basic assumptions of a discipline.

The three disciplines in compositional biology, together with their (compositional) theoretical perspectives, that I will focus on are: 1. comparative morphology, 2. functional morphology, and 3. developmental biology. I choose these three disciplines both because each relates to evolutionary developmental biology, an important and relatively new field (even if it has strong historical roots), and because each provides a very different analysis of the same system, the organism.

Three actual theoretical perspectives operating in compositional biology

As motivated above, I will now turn to an analysis of three generally compositional biological sciences. My analysis is empirical in the sense that I am gleaning data regarding the theoretical structure of biology from its textbooks. For each discipline, and theoretical perspective, I describe the overall structure of the canonical textbook(s) and, from both this and a closer analysis of the text, I indicate the partitioning frame and explanatory accounts of each discipline and perspective. I will first start with a structural perspective, comparative morphology, and will then elaborate on two processual perspectives with radically distinct partitioning frames and explanatory accounts, functional morphology and developmental biology.

It is worth noting that, despite their differences, some common themes emerge from both of the processual perspectives. First, since processes happen in time, both partition *time into periods* (see Griesemer 1996). Second, the parts of the processes can be thought of as having *causal role functions*,¹² even if the functions are of distinct kinds: functional morphological and developmental

¹⁰ Michael Wade informed me that when a potential candidate for tenure is up for review in a biology department, a criterion often used is whether that candidate's work has made it into the advanced textbooks of her field. Thus, since textbooks provide credibility, this suggests that they are considered important.

¹¹ A very useful text regarding these two points, which also provides an antidote to both Kuhn's critique and the subsequent mythology that accreted around it, is Lundgren and Bensaude-Vincent (2000). This anthology defends the utility of textbooks (and related kinds of texts, such as lecture notes) as sources of data for the historian of science. I trust that through *use* rather than through *argument*, I will be able to further convince the reader that textbooks are useful as sources of data for the philosopher of biology trying to reconstruct the theoretical structure of a discipline.

¹² Roughly, causal role functions are the causal contributions a part has to the overall working and capacity of a whole (or system of a whole) that contains it (e.g., Cummins 1975, 1983; Godfrey-Smith 1993; Griffiths 1993; Amundson and Lauder 1994).

functions. On the one hand, the parts of functional morphology have the causal role functions of contributing to behavior in an ecological context. The distinction I make here is between 1. kinds of activity-parts and 2. processually identified structural parts. On the other hand, the parts of developmental biology have the causal role function of contributing to the end products of development. The distinction I formulate here is between 1. cause-parts and 2. outcome-parts. These two pairs of kinds of parts cannot yet be clearly and neatly mapped onto one another.

Comparative morphology

A standard textbook in comparative anatomy for a number of years was Libbie Hyman's *Comparative Vertebrate Anatomy* (Hyman 1942). In her preface to the 2nd edition, Hyman expresses her "intention that the book shall now serve as a text as well as a laboratory manual" (Hyman 1942: ix). This book had such an influential impact that, as we will see towards the end of this section, it was eventually revised and updated by key contemporary morphologists. Important differences between Hyman's (1942) 2nd edition and M. Wake's (1979) anthology are indicative of the distinct partitioning frames and explanatory accounts of comparative morphology and a *functionally oriented* comparative morphology. I will first turn to Hyman's text.

The general structure of her text is expressed in the table of contents. The book starts with five introductory chapters which set the stage for the subsequent structural analysis of vertebrates. Her first chapter discusses "animal form" in a variety of respects. Subsequently, she discusses: (Chapter 2) the general properties and classification of chordates (replete with Linnean classifications, *not* phylogenetic trees), (Chapter 3) the "essential features of lower [chordate] types," (Chapter 4) the "external anatomy and adaptive radiation in gnathostomes [jawed vertebrates]," and (Chapter 5) "general features of chordate development." Chapters 3 and 4, thus, provide further detail regarding structure, and the comparison of structure in terms of adaptive function, whereas the fifth chapter sets the stage for an analysis of structure (particularly homology) in terms of development.

The remaining nine chapters concern the comparative morphology of distinct structurally described systems with their constituent parts (e.g., skeletal system in four chapters, followed by five chapters on, respectively, the muscular, coelom and digestive/respiratory, circulatory, urogenital, and nervous systems). That is, Hyman presents each of these systems across different chordate groups [e.g., sharks, bony fish, mudpuppy (an amphibian), turtle, pigeon, cat, and rabbit]. Each of the nine chapters focuses on the relevant system's comparative morphology, and only briefly describes its physiology, development, and evolution.

The partitioning frame of this text is thoroughly structural and identifies primarily tissue-level and organ-level structures. *Anatomical structures, not*

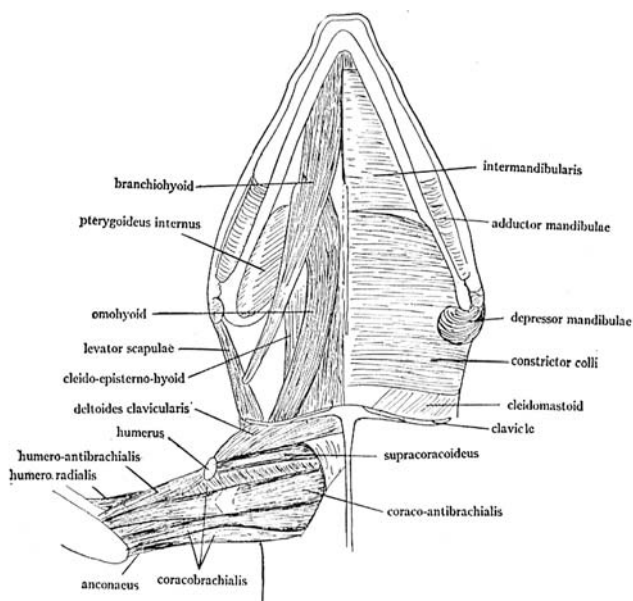


FIG. 79.—Branchial, hypobranchial, and upper-arm musculature of *Sphenodon* (combined from figures by Fürbringer, 1900). Superficial throat layer on left has been removed on the right; the pectoral muscle has been removed also.

Figure 2. Hyman (1942: 220). The muscular anatomy of *Sphenodon*, a reptile.

dynamic processes, are the order of the day. Let us examine two examples. With respect to the skull, Hyman notes that:

The skull is a hard, bony case composed of separate bones, immovably jointed together in dovetail fashion along the sutures. The *facial* region supporting the nose and eyes is distinguishable from the expanded posterior *cranial* region inclosing the brain and including the middle and internal ears. (Hyman 1942: 182)

Note that the parts are structures – objects that include both the separate bones of the skull and higher-level structures, such as the facial and cranial region. This structural partitioning is seen throughout the text, as in the case of muscles (see also Figure 2):

In studying the muscles it is necessary to separate each muscle from its neighbors. This is done by searching carefully for the white lines of connective tissue which mark the boundaries of muscles and slitting along these lines with the point of the scalpel. ... After freeing the margins of a muscle the fingers should be worked under the muscle until it is separated from its fellows. (Hyman 1942: 222)

This passage indicates that partitioning occurs not just in theory, but also in the laboratory. Furthermore, Hyman's understanding of morphological parts is rather individualistic and does not include the functional interactions or relations among the parts; *homologous* relations of the same parts in different species are, however, important.

Now that I have characterized the partitioning frame of comparative morphology, I will turn to the question of what an explanatory account looks like here. Although Hyman's book is extremely *descriptive*, explanatory accounts in this context include answers to questions like, "which structures are homologous?" and "how did a particular structure originate?" Regarding the first question, she does provide multiple explicit comparisons of the structures of different groups (e.g., reptiles and mammals) to specify similarities (homologies) and novelties. In Hyman's time, before the rise of cladistics, homology postulation and assessment was considered an explanatory activity in its own right, and was within the purview of comparative morphology. However, with the rise of cladistics, most now consider this sort of intuitive and a priori homology assessment incomplete and even unjustified. Today, cladistics is interpreted as necessary to *test* hypotheses of homology relations; it therefore explains such relations. Thus, whether and, if so, how, comparative morphology, independently of cladistics, can still be understood as being concerned with explaining homologies is an open question.

In asking how a structure originated, functional and developmental answers need to be given. One crucial kind of morphological (functional) explanatory account places the pertinent parts in an ecological selective scenario, thereby explaining them as adaptations, that is, as having etiological or selective functions.¹³ A developmental explanatory account is concerned with the ontogenetic history of the parts. In Hyman's text, the developmental explanatory account is found at a gross scale of theoretical resolution – she mentions it for each system, but often with scant detail. The functional account, however, is completely missing.

Today, comparative morphology has become more functionally oriented, even though it can still be clearly differentiated from *functional* morphology, which I will describe in the next section. In her introduction to the 3rd edition of Hyman's work – which retains the same chapter structure as Hyman's own

¹³ The literature on functions is rich and complex (e.g., Allen et al. 1997; Ariew et al. 2002). Unless stated otherwise, here and in the following section on functional morphology, I focus on causal role functions. I do *not* deny that there often are important selective reasons for the existence of these processes, or the structures involved in these processes, (i.e., functions sensu the etiological view; see Wimsatt 1972; Wright 1973; Millikan 1984; Godfrey-Smith 1993; Sterelny and Griffiths 1999), and I do explicitly refer to selection at a few points in my discussion. Causal role function and selective/etiological function are thus the two distinct uses of the term "function." Furthermore, causal role functions can be directly *homologized*, whereas selective functions are independent of homology claims. For a biological view regarding the necessity of determining both causal role and selective kinds of function for a "complete explanation... for the enormous diversity of form and function of organisms," see Liem and Wake (1985: 366).

book, but with each chapter now written by a contemporary expert – Marvalee Wake notes that the discipline of comparative morphology has indeed changed:

Until the early 1950s, comparative morphology emphasized the evolution of structure alone. Since that time evolutionary morphologists have emphasized the history of change of function (i.e., evolution) as well as of structure, for the concept of adaptation stresses that structures change to provide functional advantage. This book [3rd edition], then, presents, system by system, the evolution of structure and function of vertebrates. (M. Wake (ed.) 1979: 1)

Change in function has now become both an explanandum and, when related to selection, an explanans for change in structure. In so far as contemporary comparative morphology has taken function – in both causal role and etiological senses of the term – more seriously, while still committing to structural parts identified by clear structural criteria in a comparative context, it has developed explanatory accounts of function. As we will see, such an expanded comparative morphology still differs significantly from the deeply functional nature, especially in the causal role sense, of functional morphology.

Two examples of the use of causal role function in comparative morphology will suffice to indicate the change. In the chapter on the cardiovascular system, Ronald Lawson writes,

The prime function of the cardiovascular system is to ensure that all tissues are adequately supplied with blood. However, there are occasions when, because of changing demands, it is necessary that the established pattern of blood flow be changed. (M. Wake (ed.) 1979: 500)

I have not been able to find any passage in the chapter on the circulatory system in Hyman's (1942) text that resembles this short and punchy functional explanatory account. Furthermore, in contrast to Hyman's individualist intra-systemic structuralist partitioning commitment, Leonard Radinsky – like Hyman, also from the University of Chicago – presents, in a chapter on the muscular system, a thoroughly relational and inter-systemic partitioning commitment used for functionally oriented explanatory accounts of a kind absent in Hyman's text:

To understand the functional significance of the muscular system, it must be studied in conjunction with the skeletal and articular systems. The bones individually or collectively serve as rigid bars or *levers* even though some may have peculiar shapes. A joint (or articulation) is a *fulcrum* around which movements occur. The *power* or force is exerted by muscles. The result is the overcoming of a *resistance*, weight, or load. (M. Wake (ed.) 1979: 329)

Note the emphasis on the structural, processual, and conceptual intertwining of the muscular and skeletal systems. An emphasis on interactions among systems is more natural when structure is examined together with the structure's causal role function.

However, including function as an important aspect of the contemporary discipline of comparative morphology is not universal. For example, regarding etiological functions, both Brian Goodwin and Clifford Baron,¹⁴ a comparative morphologist, argue against the causal efficacy of selection in explaining the appearance and developmental dynamics of variant morphologies of organisms (Goodwin 1989, 1994; Baron 1991). While theoretical debate over the precise relation between selection and morphology is ongoing, a significant amount of work in comparative morphology today is still practiced as represented in Hyman's (1942) text. Much work, for example, still concerns explanatory accounts regarding homology, as described above. This is especially true at museums closely associated with a university context, such as Berkeley's Museum of Vertebrate Zoology, the Field Museum in Chicago, Harvard's Museum of Comparative Zoology, and the California Academy of Sciences in San Francisco. While including function to an extent, comparative morphology can still be differentiated from functional morphology to which I will now turn.

Functional morphology

An important text in functional morphology, *Functional Vertebrate Morphology* (1985), was edited by, among others, Milton Hildebrand and David Wake, morphologists at UC Davis and Berkeley, respectively. Even a cursory glance at the table of contents reveals a completely different organization as compared to Hyman's book. The book chapters, each written by a different expert, are primarily *activities*: "Walking and Running," "Jumping and Leaping," "Swimming," "Ventilation," and "Feeding Mechanisms of Lower Tetrapods," among others.¹⁵ Activities are essential to the theoretical content of functional morphology.

The partitioning frame of functional morphology is fundamentally a processually based one. *Organismic functional activities, rather than structures, are the order of the day*. The activities are primarily pertinent to tissue-level and organ-level structures; functional morphology thus operates at the same compositional levels as comparative morphology. In functional morphology, however, the partitioning frame includes two main sorts of part-individuation strategies: 1. individuating the parts of activities, and 2. individuating structures as parts using the reference activities as individuation criteria. I will explore each in turn.

¹⁴ See also M. Wake (1992) who is sympathetic to Baron's concerns while not endorsing them fully.

¹⁵ Hildebrand et al. (1985), Chapters 3, 4, 7, 11, and 13, respectively.

In the first part-individuation strategy, activities themselves are subdivided into distinct activity-parts. For example, Bramble and David Wake, in their chapter “Feeding Mechanisms of Lower Tetrapods,” partition the process of “the final approach [to] and contact [with]” the prey by the predator into whole body projection, craniocervical (roughly: head and neck) projection, and hyolingual (roughly: tongue) projection (Bramble and Wake 1985: 252). These can be either *activity-parts*, in “generalized predators [that] frequently combine all three tactics in a single predatory act” (Bramble and Wake 1985: 252) or *activity-kinds*, in cases where specialized predators rely, for example, primarily on hyolingual projection (e.g., “salamanders, most anurans, and chameleons”). In the former case, the type of behavior is simply divided into parts. In the latter case, a concrete dominant activity-part can become a stand-in, a *name* (e.g., “HLP” – hyolingual projection; Bramble and Wake 1985: 253), for a *type* of behavior when that activity-part constitutes a significant portion of the entire behavior. Even in this case of *nominalization*, however, the process is still divided into parts and the prevalent part of the process simply provides the name to the whole process. In many of the other chapters of the Hildebrand et al. (1985) book, activities are also divided into their activity-parts and nominalization also occurs. It is important to note that in the context of identifying activity-parts, *time is also partitioned* – there is a periodization of time based on functional morphological activities. The temporal periods provide a frame in which the relative order of activity-parts can be organized.

Furthermore, many of the chapters provide *classifications* of the different types of activities under their purview – each particular activity-kind, pertinent to a set of taxa, is then subdivided into its activity-parts. For example, in Webb and Blake’s chapter on swimming, the authors differentiate between axial undulatory propulsors (e.g., animals, including many fish, that use their “body and, where relevant, caudal fin” to move through the water, Webb and Blake 1985: 111–112), and appendage propulsors (animals that use appendages or fins, besides the caudal fin, to move through the water, Webb and Blake 1985: 110–111). These are activity-kinds. This last category is further subdivided into two, more specific, activity-kinds: undulatory (such as mantarays, which undulate their huge fins in a direction orthogonal to the direction of motion), and oscillatory (such as amphibians, reptiles, birds, and mammals, which jerk their appendages through the water) (Webb and Blake 1985: 111). Division into activity-parts then occurs; for example, in the case of oscillatory drag-based-propulsors (*also* a further kind), such as seals and manatees, the activity-parts of the rowing include the “power stroke and recovery stroke” (Webb and Blake 1985: 122). Classification of activity-kinds,¹⁶ and subsequent dis-articulation of

¹⁶ Note that this classification is different from classification in the sense of cladistics and comparative morphology, which is based strictly on homology and similarity by descent. Classification in functional morphology categorizes primarily by similarity of activity. It is also important to note that, though this is not common practice in functional morphology, some of these activities (with causal role functions) can themselves be homologized – i.e., their phylogenetic distribution is explained by common descent (e.g., Lauder 1990; Griffiths 1993).

particular activity-kinds into activity-parts, are guided by the biases, commitments, and norms of the partitioning frame.

The second strategy available in the partitioning frame of functional morphology is to individuate structural parts by both structural criteria (as in comparative morphology) *and* behavioral processual activity criteria. Structural criteria provide conditions for identifying some structures as *possible* or *putative* parts or components of parts. But there is now a further aspect to the individuation. Relevant parts are identified according to what they *do*. For example, Hildebrand (1985) depicts the leg as an integrated unit that undergoes movement, and Bramble and Wake (1985) unite a variety of head muscles and bones into particular groups in their representation of feeding behaviors.¹⁷ As we saw above, muscles and bones are *not* grouped together in Hyman's structurally oriented text. In functional morphology, however, process is employed as a criterion for the determination of (structural) part individuation and identification.

I will now turn to explanatory accounts in functional morphology. Functional morphology contains a variety of explanatory questions of interest, including, "how are the different parts (and different systems), with their respective causal role functions, integrated to form a systemic behavior such as feeding?";¹⁸ and "does the process have a selective history that accounts for its origin (and, perhaps, maintenance)?". Answering these questions employs explanatory resources found within functional morphology.

Investigating an example of modeling in functional morphology provides a way to analyze its explanatory accounts. Bramble and Wake provide a model of "'chewing' or intraoral transport cycles." (1985: 235–242) They partition the feeding cycle into a series of stages, "identified on the basis of characteristic changes in the gape profile": slow open I, slow open II, fast open, fast close, and slow close – power stroke. (Bramble and Wake 1985: 236 ff.) They represent this model – with its associated temporal periodization and appeal to integration of muscle, skeletal, and nervous systems – in a variety of diagrammatic ways: 1. a "composite kinematic profile," which represents the movements of different parts of the head at each stage of the process (thus integrating muscle and skeletal system) (Figure 3), 2. the "electromyographic activity patterns" for each muscle group at each stage (thus integrating muscle and nervous system) (Figure 4), and 3. an anatomical sketch showing the movement of different parts of the head at each stage of the process (thus integrating muscle and skeletal system) (Figure 5) (Bramble and Wake 1985: Figures 13–3, 13–4, and 13–5 on pp. 236, 237, and 238, respectively). Note that

¹⁷ This activity-based grouping of structural subparts to make a unit, which is then part of some larger unit, can be seen especially in Hildebrand's cartoons of animals in motion and an idealized diagram of a leg in motion (Hildebrand 1985: e.g., 39, 46); it can also be seen in a diagram with the title "the mechanism of intraoral transport in the model generalized tetrapod" in Bramble and Wake's chapter (1985: 238), Figure 5.

¹⁸ This is related to Wimsatt's idea of *overlapping functional loops*, where there are functional dependencies among parts both within a system and *across* different systems (Wimsatt 1997).

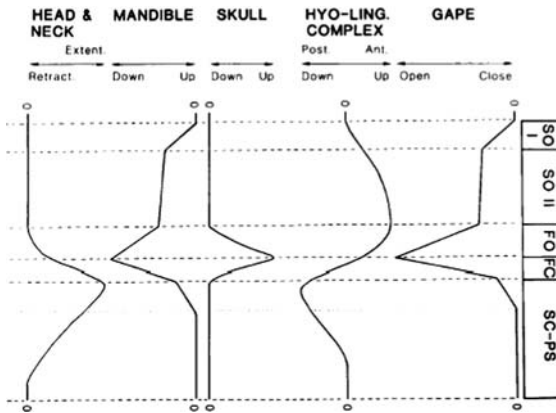


Figure 13-3 Composite kinematic profile of a theoretical model feeding cycle as would be expected in a primitive, generalized tetrapod. Major kinematic stages of the cycle are slow open I (SO-I), slow open II (SO-II), fast open (FO), fast close (FC), and slow close-power stroke (SC-PS). The dotted line indicates the boundary between the SC and PS intervals of the final stage. For each profile the zero point is the baseline or resting position.

Figure 3. Bramble and Wake (1985: 236). Composite kinematic profile of the model feeding cycle. Reprinted by kind permission of the publisher from *Functional Vertebrate Morphology*, edited by Milton Hildebrand, Dennis M. Bramble, Karel F. Liem, and David W. Wake, p. 236, Cambridge, Mass.: The Belknap Press of Harvard University Press, Copyright © 1985 by the President and Fellows of Harvard College.

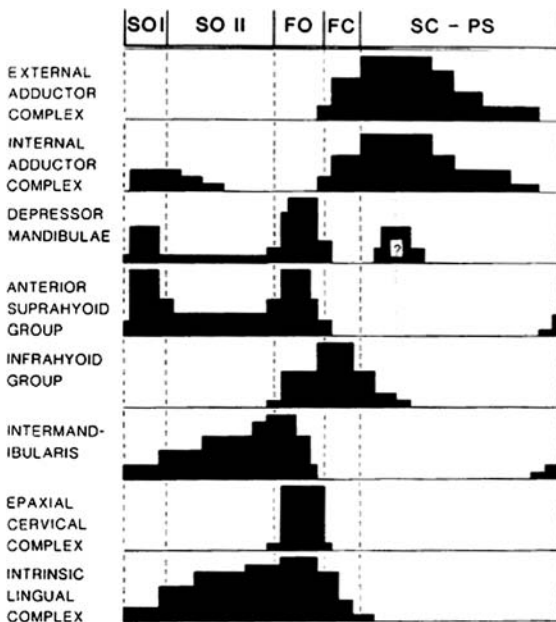


Figure 13-4 The expected electromyographic activity patterns of eight selected muscle units during the model feeding cycle. Width between dotted lines indicates timing of stages. External adductor complex = chiefly M. adductor mandibulae; internal adductor complex = chiefly M. pterygoideus; anterior suprahyoid group = Mm. geniohyoideus and genioglossus; infrahyoid group = chiefly M. rectus cervicis; epaxial cervical complex = muscles linking neck with occiput.

Figure 4. Bramble and Wake (1985: 237). Expected electromyographic activity patterns of the model feeding cycle. Reprinted by kind permission of the publisher from *Functional Vertebrate Morphology*, edited by Milton Hildebrand, Dennis M. Bramble, Karel F. Liem, and David W. Wake, p. 237, Cambridge, Mass.: The Belknap Press of Harvard University Press, Copyright © 1985 by the President and Fellows of Harvard College.

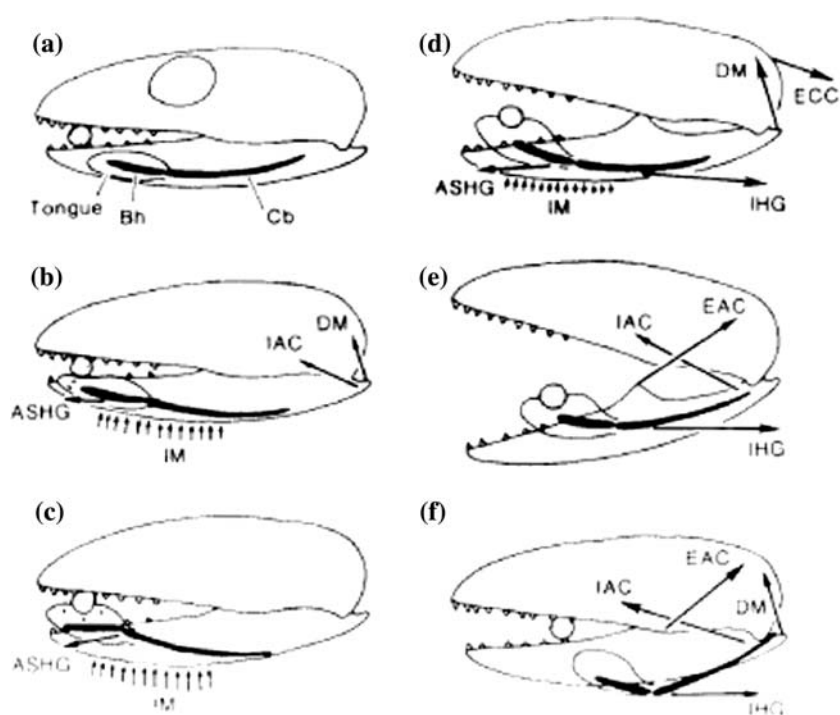


Figure 13-5 The mechanism of intraoral transport in the model generalized tetrapod. A: System at rest with food object (*stippled*) in jaws. B: Slow open I, hyolingual unit advancing beneath food. C: Slow open II, tongue being fitted to food. D: Middle of fast open with tongue cradling food and cranium and mandible accelerating in opposite directions. E: Early in fast close with cranium descending, mandible elevating, and tongue and hyoid rapidly accelerating rearward. F: Slow close stage of slow close-power stroke, showing food fixed by teeth and tongue and hyoid at maximally retracted position. ASHG = anterior suprahyoid group; Bh = basihyal; Cb = ceratobranchial; DM = depressor mandibulae; EAC = external adductor complex; ECC = epaxial cervical complex; IAC = internal adductor complex; IHG = infrahyoid group; IM = intermandibularis; arrows indicate direction of muscle force.

←

Figure 5. Bramble and Wake (1985: 238). Anatomical sketches summarizing movement as predicted by the model feeding cycle. Note that the direction of action of most of the muscle groups indicated in Figure 4 are here represented by arrows and capital letters. Reprinted by kind permission of the publisher from *Functional Vertebrate Morphology*, edited by Milton Hildebrand, Dennis M. Bramble, Karel F. Liem, and David W. Wake, p. 238, Cambridge, Mass.: The Belknap Press of Harvard University Press, Copyright © 1985 by the President and Fellows of Harvard College.

they employ both strategies of the partitioning frame: 1. an activity-kind (e.g., intraoral transport cycle) is partitioned into activity-parts and 2. (structural) parts are identified using structural *and* processual criteria. They also specify a temporal periodization. Bramble and Wake's model thus includes three particular models, represented in Figures 3–5 (perhaps model-*descriptions*), as well as a *general* feeding cycle model. It would be interesting to explore further philosophical questions regarding model structure and relations among models, at various levels of abstraction, using this non-orthodox case. What I wish to do here, instead, is to investigate how their model is employed in explanatory accounts.

Bramble and Wake's feeding cycle model is explanatory in at least two ways. First, it provides an account of how the parts, including activity-parts and processually individuated structural parts, of different systems are integrated to give rise, in a suitable manner, to the appropriate higher-level behavior – feeding. Note that in the different diagrammatic models (Figures 3–5) pertinent to this model, different stages of the process are clearly indicated, and the transitions from one stage to the next can be neatly followed. A clear articulation of parts explanation is presented. Second, this model plays an important role in explaining specialized adaptations for feeding behavior. In an informative passage, they state:

The most basic implication of the model feeding cycle is that the trophic mechanisms of all modern tetrapods, no matter how unusual or specialized, *represent departures from the generalized ancestral mechanism*. This concept challenges morphologists *to explain* how such highly derived feeding behaviors as ballistic tongue projection... might have originated, and how transitional stages can be characterized as regards morphological organization, mechanics, and motor programming. (Bramble and Wake 1985: 242, emphasis mine)

The model is an explanatory resource in that it indicates the *default* – i.e., generalized and ancestral – properties of the feeding cycle and, when the default is not met, demands an explanatory account in terms of specialized adaptations to distinct environments and niches (e.g., capturing distant prey). Succinctly put, the model sets the stage for demanding explanatory accounts in terms of adaptations.

Developmental biology

With respect to developmental biology, there is little doubt that the standard contemporary textbook at universities in the United States is Scott Gilbert's *Developmental Biology*. The table of contents indicates a concern with both ontogenetic time and hierarchy of biological organization. With respect to ontogenetic time, Gilbert writes, "Developmental biology is a science of becoming, a science of process" (Gilbert 5th edition: 1). Concerning hierarchy, Gilbert notes:

Developmental biology is a great science for people who want to integrate different levels of biology. We can take a problem and study it on the molecular and chemical levels ... on the cellular and tissue levels ... on the organ and organ system levels ... and even at the ecological and evolutionary levels (1997: 1–2)

Although there is a clear developmental temporal component to the textbook's organization, there is also a clear switching among different levels (e.g., molecules, cells, and organs).

The book is divided into five sections. After an introductory section addressing basic concepts, techniques, and levels, there are sections on "Patterns of [early] Development," "Mechanisms of Cellular Differentiation," "Specification of Cell Fate and the Embryonic Axes," and "Cellular Interactions During Organ Formation." Note that these sections trace a clear ontogenetic temporal dimension – from the early stages of development (with chapters on cleavage, gastrulation, and early axonal specificity¹⁹), through the middle stages (with chapters on cell fate specification through cell–cell interactions, and the establishment of body axes in mammals and birds²⁰), and to the final embryonic stages of organ formation, which are key parts of adult morphology (with chapters on secondary induction, the tetrapod limb, and hormones as long-distance mediators of development²¹). Within each section, some of the conceptual structure revolves around biological hierarchical organization. For example, in the section discussing mechanisms of cellular differentiation, the first two chapters of the section (Chapters 10, 11) concern transcriptional regulation of gene expression, whereas the third chapter (Chapter 12) concerns RNA processing. The presence of this structure in this and other sections also indicates a *temporal–hierarchical* bias – developmental processes at lower levels are typically understood as occurring *before* processes at higher levels.

The partitioning frame of developmental biology is also a processually based one, but here *the* formational *processes, rather than processes involving the use*

¹⁹ Chapters 5, 6, and 8, respectively.

²⁰ Chapters 15 and 16, respectively.

²¹ Chapters 17, 18, and 19, respectively.

of already-existing parts, are the order of the day. The parts exist at various compositional levels.

Due to its focus on the genesis of individual form and function, at the heart of developmental biology there are ancient philosophical questions regarding cause and effect, agent and patient. What is the nature of the causation and formation of parts? What is the causal articulation of changing and developing interactive parts? It would be sheer hubris for me to attempt to provide an answer to these classic questions, but here I will suggest a way to at least frame a variety of distinct responses to them. On the one hand, a significant part of developmental biology practice is committed to a fairly strong distinction between what I will call *cause*-parts and *outcome*-parts. Note that the causal role functions of the former involve the formation of the latter. On the other hand, there are a variety of critiques of this distinction. First, there are subtle and important philosophical critiques of this general commitment to a strong causal divide and, specifically, to genes as *prime mover* and *homunculi* cause-parts. These critiques endorse an interactionist distributed-cause thesis (e.g., Levins and Lewontin 1985; Oyama 2000a, b; Oyama et al., 2001). Second, there are also critiques which focus on the self-organization and self-determination of parts and wholes (e.g., Maturana and Varela 1980; Goodwin 1989, 1994). I will follow *contemporary practice* in my subsequent description of the partitioning frame of developmental biology; I take the distinction between cause-parts and outcome-parts to be fundamental to its partitioning frame. I thus endorse biological practice without depreciating the importance of the distributed-cause or self-organization critiques, and with full awareness that developmental biology may yet shift the content of its partitioning frame in response to such criticisms.

The partitioning frame thus individuates two kinds of parts: 1. cause-parts and 2. outcome-parts. Cause-parts are causally potent in that they form parts at subsequent ontogenetic stages. Genes are, quintessentially, considered to be cause-parts. Dynamic signaling processes, such as cell signaling activities and morphogenetic gradients can also be considered cause-parts. Outcome-parts constitute the organism's structure, process, and organization, at a particular time, and are the *effects*, the patients, of the cause-parts, the processual agents. This distinction is not always a neat one. Higher-level parts, which, to an extent, can be explained by gene action, may themselves become cause-parts later in development. For example, consider germ-layers such as endoderm and mesoderm. Thus, the same part can be identified as either one of the two kinds of parts, depending on the developmental stage and its causal role during that stage.

Figure 6 presents a common periodization of the temporal narrative of developmental biology, which includes stages of cleavage, gastrulation, and organogenesis. This is a form of partitioning – *temporal periodization* – also discussed in the section on functional morphology. Note that parts such as ectoderm and mesoderm, as well as the causally and conceptually important

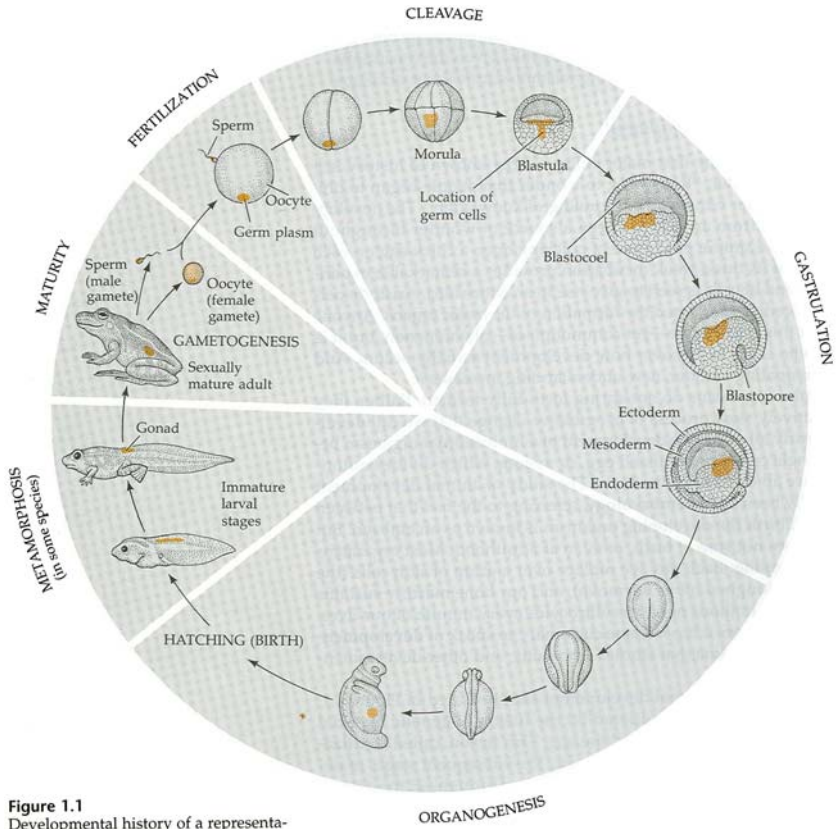


Figure 1.1
 Developmental history of a representative animal, a frog. The stages from fertilization through hatching (birth) are known collectively as embryogenesis. The region set aside for producing germ cells is shown in color. Gametogenesis, which is complete in the sexually mature adult, begins at different times during development, depending on the species.

Figure 6. Gilbert (1997: 4). The cyclical and partitioned process of development. Reprinted by kind permission of Sinauer Associates Inc. from *Developmental Biology*, 5th edition, Scott Gilbert, p. 4, Sunderland, Mass.: Sinauer Associates Inc., Copyright © 1997.

germ-soma divide,²² are also portrayed. Despite the fact that this figure does not depict genes, it provides an informative model of the part-organization, in time, structure, and process, of the cyclical, but irreversible, process of development.

I will now address explanatory accounts in developmental biology. The questions demanding explanation include, “What are the causes, structures, mechanisms, and processes – the cause-parts – involved in forming

²² On the history and philosophy of the germ-soma divide, see, for example, Buss (1987), Griesemer and Wimsatt (1989), Winther (2001b, 2005).

outcome-parts?”, and the very general question, “how does difference arise from sameness?”.

Investigating the example of imaginal disks in insects will provide a way to describe explanatory accounts in developmental biology. The imaginal disks are the source tissues – cause-parts – for what will become the parts of the adult, such as legs, wings, and eyes. The full developmental narrative is extremely complex. As described in Gilbert’s text (1997: 746–753), the disks are first outcome-parts when they are constructed and gain identity and polarity both by the interaction of a number of different genes (e.g., homeobox and downstream signaling genes), and by processes happening at the cell (e.g., signaling) and tissue (e.g., formation of axes) level. The disks subsequently become cause-parts when they serve as the source of adult body parts such as legs and wings during the metamorphosis of holometabolous insects (e.g., flies, beetles, and hymenopteran social insects). I will not here attempt to summarize the complex events involved in this process. Instead, I will use a simple example of a stage of imaginal disk ontogeny to flesh out the explanatory accounts pertinent to developmental biology.

A temporal narrative involving cause-parts such as homeotic genes, together with their protein products, as well as non-homeodomain signaling proteins, is articulated to explain the *sources* and *dynamics* of the development of outcome-parts. Such an explanatory account also addresses how difference arises from sameness. Here is a representative paragraph from Gilbert’s text:

In the wing disc, posterior cells express Hedgehog protein which acts as a short-range signal to induce the expression of Dpp in adjacent anterior cells, while the expression of *engrailed* in the posterior cells render them non-responsive to the Hedgehog they secrete. The Dpp protein acts as a long-range signal to establish the anterior–posterior axis of the wing (1997: 751)

Production of proteins (i.e., gene expression) is localized (posterior cells or anterior cells). *Previous* gene action (the segment polarity gene *engrailed*) renders some tissues responsive and others unresponsive to the effects of the signaling protein (Hedgehog). Differential tissue response (production of the Dpp protein) leads to a higher-level developmental property: axis specification. Note a few aspects of this explanation, which are fairly common to developmental explanatory accounts: 1. there is a *temporal* and *hierarchical* sequence to gene (cause-part) action (e.g., early and general effects of the homeobox genes), 2. there is *localized* gene expression, as well as localized *sensitivity* (e.g., anterior vs. posterior cells) to these gene products, 3. outcome-parts (e.g., cells and the organ axis) are *hierarchically organized*, and 4. outcome-parts *can become* cause-parts (e.g., posterior cells which were first made unresponsive by *engrailed* and, subsequently, secrete Hedgehog protein to affect anterior cells). Explanatory accounts of developmental biology rely on temporal periodization as well as on cause-parts and outcome-parts.

Three theoretical perspectives: a summary

In this section, I have thus described the partitioning frames and explanatory accounts of three theoretical perspectives. I will now summarize my analysis.

With respect to partitioning frames, comparative morphology has a fundamentally structural one, whereas the latter two employ a generally processual one. Both processual perspectives partition time into periods (through the use of different criteria). Functional morphology is concerned primarily with the functional morphological causal role functions of gross-level parts of adults, whereas developmental biology is interested mainly in the developmental causal role functions of hierarchically organized parts. They each individuate distinct kinds of parts within their respective partitioning frames. Functional morphology divides activities themselves into parts and also individuates structures using structural as well as processual criteria. Developmental biology appeals to two kinds of parts pertinent to its explanations: cause-parts and outcome-parts. Since functional morphology is not concerned with the actual formation of its parts, this distinction is of no importance to it. It would be useful to find a set of mappings between the two pairs of kinds of parts pertinent to these perspectives. As I hope to have shown, partitioning frames within compositional biology can take a variety of forms, specifying a variety of kinds of parts.

Explanatory accounts, because of the variety of partitioning frames and the difference in questions of interest and explanatory resources available, also differ radically among perspectives. I have shown this by presenting examples from each theoretical perspective, including the cases of the muscular system for comparative morphology, Bramble and Wake's (1985) feeding model for functional morphology, and Gilbert's (1997) account of imaginal disks for developmental biology.

Conclusions

I have attempted to detail the importance of parts in biological theory. Parts are pertinent especially to compositional biology. Within this style, there are a variety of theoretical perspectives operating. I have explored styles and perspectives in biology by investigating two different aspects of compositional theoretical perspectives: partitioning frames and explanatory accounts. The partitioning frame is what provides the criteria – the biases, commitments, and norms – for identifying and individuating kinds of parts. Different perspectives (e.g., comparative morphology, functional morphology, and developmental biology) have different partitioning frames. Partitioning frames, together with the questions of interest and the explanatory resources made available by the perspective, determine the operative explanatory accounts – i.e., what counts as a legitimate explanation for that perspective.

There are a variety of philosophical views regarding the organization of the biological mechanical–functional systems studied by compositional biology. In the units of selection context, Griesemer compares his processual view of *reproducers* to both the functional interpretation of Dawkins and Hull and the structural interpretation of Lewontin, and notes that “In order to detect pseudo-robustness – false consilience – a third anchor-point is needed, a perspective from which to ‘triangulate’ results rather than reinforce potentially misplaced trust in dichotomies” (Griesemer 2004: 354). This sort of *triangulation model* (see also van der Weele 1995) can be used to identify and compare four philosophical frameworks within which mechanical–functional systems have been represented and analyzed: 1. my investigation into parts, styles of theorizing, and compositional theoretical perspectives, 2. the mechanism account, 3. a functional analysis (closer, I would suggest, to McLaughlin’s (1997) analysis of self-reproducing compositional systems than to either a causal role or selective function analysis), and 4. a distributed cause, in time and space, examination à la Developmental Systems Theory. While all four frameworks can be useful, in this article I have provided arguments for the strength of my part-based approach to understanding the investigation of mechanical-functional systems. A further examination of the relations among these four frameworks remains to be done.

Compositional and formal styles of doing biology differ radically from each other. They each endorse, for example, distinct explanatory strategies. Compositional biology relies on part-based explanation, which has been explored by Kauffman, Wimsatt, Cummins, and Haugeland, and which I have further elaborated in the context of explanatory accounts. In addition, different kinds of modeling (e.g., diagrammatic and narrative) tend to be present in compositional biology. In order to provide a full-blooded comparison of formal and compositional styles, a detailed examination of the aspects of formal theoretical perspectives must also be presented (e.g., *frames of mathematical and symbolic abstraction*, in which a variety of mathematical term-types and model-types are specified in distinct formal theoretical perspectives in a manner loosely analogous to specification of a variety of kinds of parts in different partitioning frames of distinct compositional theoretical perspectives).

It is often supposed that formal biology is *the* theoretical biology. Theoretical population genetics, which employs the formal style and is concerned with the dynamics of evolutionary change in populations, is often considered the paradigmatic theoretical biology. Significant philosophical analysis has been devoted to it. Compositional biology, on the other hand, is accused of being mere stamp-collecting or of being obsessed with mechanistic detail. This is mistaken because the compositional style is also highly theoretical – for example, it involves sophisticated theoretical commitments to part-identification and part-based explanation. Furthermore, it is unfortunate and even ironic that the compositional style, which is fundamental to research in many biological domains, including diverse practical areas of biotechnology, has received relatively little

philosophical attention. For both theoretical and practical reasons, a detailed philosophical analysis of compositional biology is thus necessary.

The differences between formal and compositional styles, as I have noted, have less to do with natural domain studied or scientific discipline guided, and more to do with deep methodological differences between the two styles. These differences guide distinct ways of theory-construction, which, together with the yearning for completeness that each style expresses, results in mutual ignoring and even theoretical conflicts (Winther 2003, 2005). Both scientific styles are operative in contemporary biology. Members of each tradition would benefit more from exploring ways of relating to the other culture than from forcing theory and experiment into their own world view. Articulating a translation manual between the two biological styles would also be useful.

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