



# Phylogeny and evo-devo: Characters, homology, and the historical analysis of the evolution of development

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## Abstract

The concept of homology continues to attract more and more commentary. In systematic and evolutionary biology the meaning of homology as synapomorphic similarity inherited from a common ancestor has gained wide acceptance over the last three or four decades. In recent years, however, developmental biologists, in particular, have argued for a new approach to, and new definition for, homology that revolves around the desire to make it more process-oriented and more mechanistic. These efforts raise questions about the relationship between developmental and evolutionary biology as well as how the evolution of development is to be studied. It is argued in this paper that this new approach to homology seemingly decouples developmental biology from the study of the evolution of development rather than to facilitate that study. In contrast, applying the notion of historical, phylogenetic homology to developmental data is inherently comparative and therefore evolutionary.

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## Introduction

The concepts of homology and species have much in common. Biologists widely agree that the “problem” of homology, or of species, has not been solved even after more than a century of discussion, and because of that the literature on both is large and keeps growing. Biologists also agree that both concepts are important for comparative and evolutionary biology, but many admit that the continuing debates have become boring and arcane. This leads many to conclude that we should go down the road of pluralism and accept that multiple conceptions (definitions) have their place and we should just live with it. Finally, it is interesting to note, from a

sociological perspective at least, that both are primarily systematic concepts, yet nonsystematists have been among the most active commentators about their definitions, applications, and purposes in comparative and evolutionary biology.

The homology concept arose within comparative morphological and paleontological systematics and has resided comfortably there for about 150 years. Recently, however, the fields of molecular genetics and developmental biology have been transformed into comparative genomics and evolutionary developmental biology, or evo-devo, and as soon as a field becomes comparative, it must reckon with the idea of homology. Homology has therefore become a frequent topic of discussion within both disciplines, where the discussions often mirror the different perspectives in systematics. Unfortunately,

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many of the same controversies that have characterized systematics (e.g., pattern versus process), and which have largely been unproductive in advancing the science, also exist in evo-devo. Somewhat simplistically, perhaps, these controversies persist because of precladistic notions about comparison (such as transformationism) and the lack of tree-thinking. With the rise of cladistics in the 1970s and 1980s, homology became linked to concepts of “characters”, “synapomorphy”, and to nodes on a tree (relative relationship). This form of thinking does exist in comparative genomics, but it has penetrated evo-devo only to a limited extent, where its relevancy should not be questioned.

This paper will explore recent uses of homology in evo-devo. I will first review some precladistic and postcladistic ideas about homology and then discuss their relevance to ongoing applications of homology within the burgeoning evo-devo literature. The literature on homology itself is also huge and in preparing this essay I could not hope to review all previous discussions. I therefore apologize in advance for not acknowledging predecessors who may have articulated ideas similar to those expressed here. If there is originality in this essay it is the claim that by abandoning a cladistic view of homology, one is unwittingly rejecting not only the best analytical tools for reconstructing the history of developmental patterns but also short-changing the real contribution that the exciting new data of evo-devo can make to reconstructing the Tree of Life. Nevertheless, I acknowledge Wake’s Dictum (1999, p. 24), first noted, I think, by Hall (2003, p. 410): “I will grant that someone might be able to generate an original thought concerning homology, but I doubt it.”

## Views of homology

It is not my intention to review the history of homology as that has been undertaken admirably by others, particularly Patterson (1982), Wagner (1989), Donoghue (1992), Hall (1994a, b, 2003), Gould (2002). Complex concepts such as homology are filled with nuance from one author to another, and historical analyses will generally be undertaken through the lens of one’s own discipline and current research approach. Accordingly, while not necessarily agreeing with the historical ontology of homology described by these summaries, at the same time I fully admit my own historical viewpoint is constructed from the standpoint of a systematist. In order to lay the groundwork for the argument of this paper, I recognize three historical ways of thinking about homology – historical (precladistic evolutionary), phylogenetic (cladistic character, or taxic), and biological/process. By adopting this tripartite ontology I do not imply that these are mutually

exclusive (indeed, I will argue that is not the case) or that a particular investigator is wedded only to one way of thinking. My purpose here is to discuss views about homology that have developed more or less sequentially.

## Historical homology

With the recognition of evolution (descent with modification), the word homology became associated with features said to be descended from the same structure in a common ancestor. This view of homology – often called the “historical” concept of homology – was widely accepted among advocates of the evolutionary synthesis and evolutionary systematics:

Homology is resemblance due to inheritance from a common ancestry. (Simpson, 1961, p. 78; italics in original)

*Homologous* features (or states of a feature) in two or more organisms are those that can be traced back to the same feature (or state) in the common ancestor of these organisms. (Mayr, 1969, p. 85; italics in original)

A feature...is homologous...to a feature...if the two features (or conditions) stem phylogenetically from the same feature or condition in the immediate common ancestor of these organisms. (Bock, 1969, p. 414).

These definitions have also been considered to be “phylogenetic” (e.g., Bock, 1969 and others), but this usage should not be taken to mean it is equivalent to that of “phylogenetic systematists” (cladists; below). Simpson’s definition emphasizes that homology is inherited similarity, whereas Mayr and Bock emphasize inherited features but not similarity.

Bock’s discussion (1969, p. 415), in fact, raises some methodological problems (aside from comments by critics who might want to see a more “operational” definition) that are mirrored in discussions of homology from an evo-devo perspective, namely how might prospective homology be recognized in the first place, how might one evaluate that hypothesis, and finally, what role, if any, does homology play in understanding relationships. Thus, Bock comments (1969, p. 415):

No mention of resemblance or of similarity in ontogenetic development appears in the definition of homology. Contrary to common opinion, the concepts of homology and nonhomology [to Bock, what many call analogy] have nothing to do with the similarities of features; they are associated only with common origin versus noncommon origin.... Any methods for recognizing homologies that depend on earlier conclusions about the phylogeny of organisms should be discarded....

Bock notes that similarity is the generally accepted criterion for recognizing homology, yet at the same time he states homologous features should not be used to infer relationships, rather homology itself can only be inferred once relationships are determined on other evidence. This way of seeing homology follows from, or is related to, the lack of an objective methodology for discovering phylogenetic relationships within the context of evolutionary systematics (e.g., Mayr, 1969; Mayr and Ashlock, 1991). At base, it suggests that structures, deemed to be similar, are “optimized” (mapped) on a phylogenetic tree, and if they optimize at a single node an inference of homology can be made. As we shall see below, common approaches to homology within developmental biology are not all that different. Quite simply, the approach does not engender a research program for understanding phenotypic change (*sensu lato*, including genes, developmental pathways, morphology) or the history of life.

### Phylogenetic or cladistic-character (taxic) homology

The introduction of phylogenetic systematics (cladistics) as a method to reconstruct relationships among taxa (Hennig, 1966) had an immediate effect on refining and extending the meaning of homology. Hennig clearly saw homology in terms of phylogenetic continuity but he also recognized that the precladistic conception discussed in the previous section was devoid of empirical connotations:

Different characters that are to be regarded as transformation stages of the same original character are generally called homologous ... Since we can never directly observe the phylogenetic transformation of a character, the question arises as to what accessory criteria are available to convince us that particular characters are homologous in different species.

Apparently, it is often forgotten that the impossibility of determining directly the essential criterion of homologous characters – their phylogenetic derivation from one and the same condition – is meaningless for defining the concept ‘homology’. (Hennig, 1966, pp. 93–94).

By making the connection between homology and the idea of a transformation series (primitive to derived conditions), and then interpreting character change on a phylogenetic tree, Hennig established an objective, empirical foundation for the analysis of homology. In Hennig’s conception homologues can be taken to be synapomorphic similarity, but he was reluctant to equate the two terms because to him (Hennig, 1966, pp. 94–95) homologues were observed features of

organisms, whereas a character-state within a transformation series might be absent (i.e., lost). Nevertheless, to him a transformation sequence was unequivocal: its character-states were homologous.

As cladistics developed through the 1970s and 1980s, a “taxic” view of homology became widely endorsed, in which homology and synapomorphy were effectively equated and then “tested” or interpreted by reference to nodes on a tree (Wiley, 1975, 1981; Bonde, 1977; Cracraft, 1978; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Patterson, 1982; DePinna, 1991; Nelson, 1994). Some representative views include:

... characters are said to be homologous if they are transformation stages of the same original character present in the ancestor of the taxa which display the characters (modified from Hennig, 1966).... Homologies can be tested only at the level of universality at which they are hypothesized to exist as synapomorphies because the best test of homology is common ancestry. (Wiley, 1975, p. 235)

Homologous similarities are inferred inherited similarities that define [= diagnose] subsets of organisms [= taxa] at some hierarchical level within a universal set of organisms. Viewed in this way, homology can be conceptualized simply as synapomorphy ...” (Eldredge and Cracraft, 1980, p. 36, italics in original)

Hennig ... concluded that only shared, advanced, or derived, characters, which he called ‘synapomorphies’, constitute evidence.... The concept of synapomorphy was unambiguous, and more restrictive, relative to the traditional concept of homology, which it replaced in Hennig’s system; for all homologous resemblances may be considered synapomorphies at one or another level of phyletic relationship. (Nelson and Platnick, 1981, p. 137), from which follows:

A homology statement merely invokes the notion of a character in common.... A statement of evolutionary homology adds the possibility, but not the necessity, that a character previously thought to be of type A, or of type B, is in reality, a character of type C. In an evolutionary sense, therefore, a homology statement may be understood generally to imply the possibility of a particular character transformation: that, of two characters, one is primitive relative to the other, which is advanced. (Nelson and Platnick, 1981, p. 209)

Every hypothesis of homology is a hypothesis of monophyletic grouping and, in any particular

context, a symplesiomorphy is a hypothesis of a set, and a synapomorphy is a hypothesis of a subset of that set. Symplesiomorphy and synapomorphy are thus terms for homologies which stand in hierarchic relation to one another. (Patterson, 1982, p. 33)

The phylogenetic information of any character rests with its capacity to contribute to the diagnosis of a monophyletic group of organisms (the existence of which is explained by common ancestry). Viewed from this perspective, any conjecture of homology is informative only in the sense of synapomorphy (Patterson, 1982), i.e. in relation to *recency* of common ancestry. (Rieppel, 1992, pp. 704–705; italics in original).

The cladistic-character, taxic view of homology is a natural extension of the precladistic evolutionary view of homology in that they both link observed similarities in two or more taxa (living or extinct) to the “same” structure in the common ancestor of the group. Few would entertain the notion that we can actually “trace” character change back to an ancestor, and there are many methodological reasons why even specifying an ancestor is problematic. As cladistics developed as a science, the notion of identifying ancestors and placing them at nodes was abandoned; cladograms were substituted for trees, and tracing character change through optimization became standard. Cladistics advanced evolutionary biology because it rejected the transformational narratives of evolutionary systematics that accompanied homology and character change and replaced them with an objective method for testing proposed homologues by examining the hierarchical pattern of similarity (characters) within the context of congruence and parsimony.

Phylogenetics has largely subscribed to this approach to homology, and indeed, the widely used computer programs that analyze morphological and molecular data are designed to optimize characters and character change in both model and nonmodel contexts. Despite the ubiquity of a character-taxic concept of homology, there is not a monolithic method in force and the “problem of homology” persists in cladistics in the form of what a character is and how they should be coded (i.e., how levels of homology are conceived). Thus, from the early days of cladistics to the present, a large literature has developed on this subject (e.g., see Scotland and Pennington, 2000; Wagner, 2001), much of which is relevant for understanding evolutionary change in developmental systems.

### Biological homology

Developmental biologists, like morphologists and systematists, have used homology in different ways.

Some have adopted a traditional approach – similar structures traceable to common ancestral structures – whereas others have noted the importance of cladistics and the notion of synapomorphy as homology (e.g., Hall, 2003). Often, these researchers have tended to map (= optimize) developmental characters (such as HOX genes) on a given phylogenetic tree rather than delve into the characters of developmental data per se. What interests us here, however, is the growing numbers of developmental biologists who want to redefine homology and effectively disregard the more traditional, historical approach.

There is a perceived need on the part of some to have homology be more than similarity due to common ancestry, or to be more than synapomorphy. Instead, they argue, it should be “process-oriented”, which, they contend, is more explanatory (Brigandt, 2003). The beginning of this dialogue included Roth (1984, 1988) and Wagner’s (1989) important papers introducing and reviewing the biological homology concept. Wagner suggested that the traditional, historical (phylogenetic) conception of homology has limitations, such as ignoring serial (iterative) homology (more about this later), and that the findings of developmental biology “contradict certain implications of the current homology concept ...” (1989, p. 51) and that “a number of authors have argued for redefining homology on a mechanistic rather than a genealogical basis” (1989, p. 54). The substitute is a “biological” or “process” homology concept, some examples of which include:

Homology is resemblance caused by a continuity of information. (Van Valen, 1982, p. 305)

“A *necessary* component of homology is *the sharing of a common developmental pathway*...in which homologous structures (for example) share *common pathways of differentiation* – [which] is satisfying because it embraces not only homology between species...or between sexes...but also serial and antimeric homology (Roth, 1984, p. 17; italics in original)...and “recognition of homology entails the derivation of inferences about developmental relationships and processes from the comparison of characters.” (Roth, 1984, p. 18)

Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotypes. (Wagner, 1989, p. 62)

Whereas classical homology has been one of structures – be it of skeletons or genes – the homology of

process goes into the very mechanisms of development...the homology of process concerns the similarities of dynamic interactions. The result is that although organs (such as vertebrate and arthropod eye, the vertebrate and arthropod leg, etc.) can be structurally analogous, they may be formed by processes that are homologous!" (Gilbert et al., 1996, p. 364)

We formally define the term syngeny, or generative homology, as the relationship of a given character in different taxa that is produced by a shared generative pathway." (Butler and Sidel, 2000, p. 849; italics in original)

There are several signal transduction pathways that integrate embryonic development. We find that both within species and between species, these pathways constitute homologous modules. The processes, themselves, can be considered homologous, just as structures can be considered homologous. Just like vertebrate limbs, these pathways are composed of homologous parts (in this case, the proteins of the pathway) that are organized in homologous ways. (Gilbert and Bolker, 2001, p. 1).

It is clear from the literature that evolutionary developmental biologists are finding homology to be an intriguing concept, yet at the same time many are uncomfortable with the historical view ("tracing features back to common ancestors") and especially with the idea of homology being equated to synapomorphy (there are exceptions, of course, notably Hall, 2003). Developmental biologists are accustomed to thinking about developmental pathways or "processes", so in the interest of being evolutionary (and comparative) they have sought to use the implications of homology in organizing their comparative observations. In doing so, they have created new terminology and given new meaning to the word homology, and some are not shy in thinking that historical or phylogenetic homology is limited in making sense of the observations of their discipline (e.g., Roth, 1984; Wagner, 1989; Brigandt, 2003). Their criticisms and concerns, however, raise interesting issues. If evo-devo is also about evolution, how is the evolution of development among taxa to be studied? What are the developmental characters (entities) being compared? Does it mean that the observations ("characters") of evo-devo are merely to be mapped on a tree of choice? Or do the comparative observations themselves have a contribution to make about relationships, alternative hypotheses of which affect interpretations of change? In short, can evo-devo advance as an evolutionary discipline using biological homology, process homology, or other similar concepts?

The remainder of the paper explores some of these questions. For simplicity, I will use the term *historical-phylogenetic (or H-P) homology* to refer to the joint concept that encompasses both historical and phylogenetic (taxic) homology. Thus, historical homology can be interpreted as referring to the ultimate cause for shared synapomorphy, that is, shared ancestry and descent (Rieppel, 1992).

## Pattern versus process

A line of argumentation is being developed within evo-devo that parallels the same argument that exists in other contexts within population biology/genetics. The implication is that systematics is concerned with pattern; developmental biology, however, is focused on process. It is then argued that "biological homology" is about process, whereas H-P homology is about pattern:

Systematists and phylogeneticists, particularly cladists, are concerned primarily with ancestry and taxa. They view the homology of any character as strictly dependent on the test of homology prescribed by cladistic methodology....This conceptual school of homology is...concerned with pattern. Morphologists are concerned with similarity and the developmental individuality of structures. They seek to understand the preservation of structural identity over evolution.... This conceptual school is referred to as biological or transformational homology. It is concerned with process. (Butler and Sidel, 2000, p. 847; citing papers by Roth, Wagner, and others noted earlier).

While it is certainly the case that many phylogeneticists have also made this type of distinction – cladistics is about the discovery of phylogenetic pattern, we will leave the process to others – I suggest this is a false dichotomy that can only diminish the potential contributions of each of these fields to understanding the history of life. There are a number of roots to the dichotomy, but the propensity on the part of scientists to believe that fine-scale, reductionist approaches are more about process (= "causation") whereas those at "higher" levels are not is largely to blame. It has arisen, time and time again: biology versus chemistry and physics, morphology versus genetics, molecular versus nonmolecular biology, population biology/ecology versus systematics, and now developmental biology versus systematics or comparative morphology.

In another contribution (Cracraft, in press) I have argued that this distinction between pattern and process is problematic and that the idea of "process" is a conceptual framework linking together different observations (call them patterns) over time. Thus, process

might be considered to be pattern differentiated with respect to time. My example (Cracraft, *in press*) was taken from speciation analysis, where it is often claimed that cladists provide a historical pattern of gene or species trees whereas population biologists and geneticists study the process of speciation. I suggested, however, that geneticists and population biologists also make observations of pattern (e.g., gene frequency measurements, population size, variation in bill size) at one point in time, then at another point, and so on, and then string these observations together temporally and term it process. Cladists effectively do the same thing when hypothesizing character change or transformation. By optimizing change on a cladogram, an inherent temporal dimension is placed on change.

I would similarly argue that the claim of developmental biologists that they are studying process is heavily theory- and assumption-laden. Same thing for molecular developmental biology. The observations (patterns) are at a finer spatial and temporal scale, perhaps, than a systematist might deal with, but it would be rare for developmental sequences or developmental pathways to be observed directly in continuous, as opposed to discontinuous, time-slices.

Most scientists want to study process (= causation in most people's minds). Addressing why and how things happen in nature is part of the scientific endeavor and reductionist approaches are one way to advance this understanding. At the same time, an inference of causation is complex – philosophically, empirically, and methodologically – when applied to real-world systems. In most, perhaps all, real-world cases there is no single “cause” but multiple layers of events, at different spatial and temporal scales, and if any one of these events disappeared the causal chain might well be broken.

### **Definitions, entities, and ontology: is devo really evo-devo?**

The above discussion of homology reveals a diversity of thought about what the term homology should mean, whether it refers to a physical thing or structure (i.e., an entity), a group of developmental observations or inferences linked together spatially and/or temporally (a process), or a relational property. Just as systematics has had a broad diversity of opinion over homology (the phenetic school of systematics, for example, was not discussed above), so too has the field of evo-devo. The question arises: can evo-devo, let alone evolutionary biology and systematics, become integrated conceptually – indeed, can developmental biology become truly evolutionary – if we are willing to tolerate a pluralistic approach to homology?

Definitions of terms or concepts in science are sometimes seen as being unimportant or of little concern

empirically. An alternative opinion, and the one adopted here, is that definitions are crucially important in helping establish the ontological context of thinking about a scientific problem and in promoting a common language for scientific discourse (Gaukroger, 1978; Laudén, 1989; Sober, 1989). This is not merely a semantic or linguistic issue. Theories (hypotheses) are largely about the relationships among, and the behavior of, entities – things that scientists conjecture exist in nature. Definitions for those entities are thus formulated within the context of some explanatory structure, and their individuation is also made within that framework. If there is a disjunction between the entities and the empirical world, then either (1) the observations may be insufficient or incorrect, (2) the theory may be wrong, and what it implies about the nature of entities may thus be incorrect, or (3) we may have individuated entities incorrectly because the definition (as implied by a theory) is inexact or inappropriate. Consequently, there is a dialogue between what theories lead us to expect about the world and what the empirical world leads us to think about the theory. Scientists make ontological commitments to the world, with the caveat that alternative theory or empirical knowledge can lead to a change in that ontology.

Definitions of entities in biology can have profound theoretical and empirical consequences as long as they are not taken to be *stipulative* (Sober, 1993, p. 6), in which case those definitions would be taken as given and without error. Arguments over what entities are – species, niche, gene, developmental modules, developmental pathways, and homologues, among countless others – are about the ways of seeing the things of the empirical world (Wilson, 1999). The many definitions for homology within evo-devo signal how different investigators are trying to come to grips with ideas like “sameness”, “similarity”, “process”, and “comparable” when they investigate developmental systems. There are powerful differences in disciplinary worldviews. Systematists, for example, might conclude that serial homology or parallelism cannot be “explained” or understood outside the framework provided by phylogenetic homology (that is, a tree-thinking, taxic worldview; see below). Conversely, many evo-devoists no doubt think that if these phenomena are not addressed within the framework of biological homology and the approaches and developmental tools it implies, then the investigator is abandoning a process, mechanistic worldview. Both are right, and at the same time, a bit wrong: they are talking past one another, in part because of their differences in thinking about ontology.

Scientific concepts, as expressed through definitions, should be as precise and empirically useful as possible. If the same word means different things to different people, then endless debate ensues because, if those definitions are central to a research program, there is a lot at stake

(the best example, perhaps, is the debate over species concepts). The concept of homology is another example, and debate about its meaning is important for biology. What is counterproductive, however, is the idea that there can be many meanings of homology in use simultaneously, that is, a pluralistic approach to the meaning of homology is considered acceptable (Brigandt, 2003). My objections to a pluralistic approach toward homology are the same I have raised for species (Cracraft, 1989a, b): it creates ontological confusion and confounds empirical research.

### Should biological (process) homology be abandoned?

If one goal of evo-devo is to understand innovation (novelty) – whether of gene product, changes in developmental pathways, or phenotypic end-product – then it *must* see these changes in terms of synapomorphy and tree thinking (Rieppel, 1992, p. 706). In order for developmental biology to be evolutionary, it must be comparative. If it is to be comparative, then interpreting developmental data through the eyes of H-P homology will be essential, a viewpoint already acknowledged by some developmental biologists (Hall, 1992, 1995). Phylogenetic homology and synapomorphy provide the theoretical and methodological tools to enable comparisons in developmental biology to be comparative and evolutionary. Under biological homology, relational statements about two developmental pathways being the “same” or being “different” are divorced from evolutionary history – that is, what is more or less meant here is a phenetic notion: the two pathways “look alike” or “don’t look alike” (see below). If, instead, two developmental pathways are taken to be H-P homologues, then that would *only* make sense once they are tested by phylogenetic analysis (see also Rieppel, 1992).

Advocates of biological homology cannot entirely abandon phylogenetic homology because of its importance as synapomorphy, thus a pluralistic approach is generally deemed acceptable. It is argued (Wagner, 1994, pp. 274–275) that “sameness” means different things to different biologists who have different scientific goals (“conceptual engineering”) in making comparisons, and therefore “homology concepts can be classified according to the aspect of sameness considered most fundamental” (1994, p. 274). According to Wagner (1994, p. 275):

The goal [of biological homology] is to explain patterns in the origin (Müller and Wagner, 1991) and evolution of morphological characters. It is thus intended to be part of evolutionary biology, i.e. it should provide the conceptual framework for explaining patterns of intra- and interspecific variation. Therefore, the primary emphasis is on constraints which cause the conservation of features characteristic for homologous characters. The purpose is not

to provide criteria for recognizing phylogenetic relationships. Therefore criticisms that blame this approach as inadequate because it does not imply operational criteria for recognizing homology miss the point (Hall, 1992; Rieppel, 1992).

There is a fundamental philosophical difference being implied here between this view of biological homology and that of H-P homology. The latter does not attempt to explain anything, rather *homologues are to be explained by ancestry and descent with modification* (Wake, 1999). H-P homology is agnostic with respect to the proximate processes that might “explain” the shared similarities called homologues (synapomorphies). Even “developmental constraints,” however they may be conceptualized, might be expected to contribute to inherited shared similarity.

In contrast, advocates seemingly want biological homology *to explain* instead of *to be explained*; after all, they *define* biological homology in terms of shared developmental pathways or shared developmental constraints (see above):

... the main goal of a biological homology concept is to explain why certain parts of the body are passed on from generation to generation for millions of years as coherent units of evolutionary change (Roth, 1991). Hence, the problem is to explain why there are individualized parts of the body that behave as units which retain their structural identity despite variation in form and function (Wagner, 1994, p. 279).

Given that all manner of structures of organisms share some developmental pathways or “constraints” at some stage of development, where are the spatial, and most importantly, temporal boundaries of such biological homologues? This is an ontological problem faced by biological homology that has been more or less resolved by H-P homology (Rieppel and Kearney, 2002). As demonstrated by the successes of comparative morphologists and systematists, it is possible to perceive similarities among taxa and then test that “similarity as conjectured synapomorphy” by phylogenetic congruence. The underlying structure of developmental processes, in contrast, is typically nonhierarchical and reticulate, therefore similarities – shared genes, network connections, gene products, etc. – are found at so many spatial and temporal levels that applying biological homology objectively becomes almost an impossible task. Unless a methodology can be articulated for discerning developmentally constrained biological (= process) homologues objectively, they amount to little more than vague descriptors of an investigator’s developmental observations (inferences).

The research program of developmental biology, it can be suggested, does not need the biological homology concept as an organizing principle, at least not in the

same way that historical biology needs the H-P concept of homology. For reasons already noted, biological homology cannot form the foundation for the study of the evolution of development. The key to studying innovation and change within development is to see that change in terms of H-P homology. Moreover, by rejecting homology as character synapomorphy, biological (process) homology abandons the direct use of developmental data within comparative biology and Tree of Life research, and instead must be content with mapping developmental data on a tree.

This is certainly not an argument against understanding the mechanics of development from the gene level on up. Yet, all biologists, no matter how reductionist, noncomparative, or nonevolutionary their research may be, whether they realize it or not, are dependant on H-P homology. The names of all their genes, gene products, cell structures, and so on are based on an assumption that the names for these entities signify the *same* entities (H-P homologues) as do the same names found in other organisms. The unstated assumption is of synapomorphy – an essential foundation of all discourse in biology.

Statements of “similarity” (= topographic similarity; Rieppel, 1988) have a basis in empirical observation, even though observation and interpretation are theory-laden. A statement that a similarity is a character and a synapomorphy does not follow directly from observation but is an inference contingent on character congruence. Within the framework of biological homology, in contrast, its “homologues” are seemingly identified empirically. Yet, it is presently unclear just how these “homologues” are identified and individuated and what observations might be needed to reject an entity as a biological homologue (see also Rieppel, 2005). Wagner (1994, quoted above) speaks of “structural identity” of a set of body parts “despite variation in form and function”, others speak of “modules” (Wagner, 1996; von Dassow and Munro, 1999; Winther, 2001), “fields” (Puelles and Medina, 2002), or developmental pathways (Roth, 1984, 1988) as the homologues of biological homology.

For reasons already noted, the issue of individuation of biological homologues is made more problematic as soon as one moves away from similarity in structure to criteria based on processes (developmental pathways, networks, constraints). A fuzzy ontology cannot be expected to bring clarity to theoretical and empirical research.

### Characters, H-P homology, and comparative evo-devo

Adopting H-P homology provides the framework for developmental biology to be a comparative and evolutionary science (in other words, evo-devo), and thinking

about characters and trees emphasizes the importance of developmental data as evidence for evolutionary relationships. Characters and trees, moreover, are the basis for the historical study of developmental novelties. By delineating developmental characters and interpreting their change on trees, our understanding of the boundaries of developmental pathways (networks) and how they change and become modified over time should be enhanced (see also Bang et al., 2002).

### H-P homology and tree-thinking: individuals versus taxa

One of the reasons the concept of biological homology appeals to some developmental biologists is the proposition that it facilitates comparisons *within* individuals: structures or sets of structures sharing a common developmental pathway would be homologues. It hardly seems necessary to create confusion by using homology in this case, when another term, homodynamy (Baltzer, 1950; Rieppel, 1992), has already been suggested.

One of the most often-cited applications of biological homology to developmental pattern within individuals is to serial homology. Serially “homologous” features, seen as a whole, are generally not H-P homologues (Hall, 1995 and others). Different segments, for example, may be added, subtracted, or modified at different times in the history of a group. Those individual changes could be expected to be optimized at different nodes on a tree. Moreover, the fact this is the case implies that the various segments do not completely share a common developmental pathway, nor, dare we say, do they possess the same “constraint”. Naturally, they share some developmental circuitry at earlier or later stages of development, yet it is also true that any of those segments might share some developmental background with other nonsegmental structures of the organism. I would argue “serial homology” should be seen as another example, or subset, of H-P homology.

H-P homology does not apply to the description of developmental commonality within individuals but to comparisons among taxa. As such, it can bring clarity to the study of serial homology. Thus, if there is a “problem” presented by serial homology, it is that the relevant characters and the nodes they might specify have not been identified (I am fully aware that there are important developmental questions to be asked of the serially expressed features within and among individuals and taxa). If we consider potential characters such as “serially homologous” genes (duplications) or “serially homologous” morphological structures like vertebrae or arthropod limbs, and make comparisons across taxa, there are multiple levels at which the characters might be individuated: (1) Taxa may or may not have the serially



represented structure. (2) Within the presumed serial homologue one taxon may have a leg on a given segment, another a mouth part. (3) The character may also reside at the genetic or at the developmental level: one taxon may have a particular genetic state or developmental change that adds or subtracts segments, whereas another taxon may not have that change. In other words, so-called serially homologous structures can be analyzed for character change at multiple levels. If there is taxonomic variation among these structures, whether at genetic, developmental, or phenotypic levels, the history of those character changes can be analyzed using H-P homology and cladistic methods.

### Characters of evo-devo and their phylogenetic analysis

There is a substantial literature that interprets the phylogenetic history of developmental genes by mapping them on a predetermined phylogeny. In contrast, insufficient attention has been paid to applying developmental data directly to phylogenetic analysis by coding developmental data as cladistic characters. Some investigators have incorporated the presence or absence of developmental genes in their analyses (e.g., Eernisse and Peterson, 2004; Rowe, 2004). Likewise, there has been moderate discussion of coding developmental sequences or events, such as the relative timing of the first appearance of features in ontogeny (Smith, 1997, 2001; Velhagen, 1997; Jeffrey et al., 2002; Bininda-Emonds et al., 2002; Schulmeister and Wheeler, 2004). The future of this approach is unclear, however, due to analytical complexities dealing with nonindependent data such as developmental events, as noted by Schulmeister and Wheeler (2004). These latter authors propose an alternative method of coding and analysis based on search-based optimization, but it remains to be seen whether these types of data will contribute significantly to phylogenetics. Still, understanding evolutionary shifts in developmental events is important for many questions in development and evolution. The issue is whether these shifts can be inferred accurately, even when mapped onto predetermined trees, if the “characters” themselves are questionable.

Advocates of biological homology in general want to go beyond the “developmental sequences” just discussed and seek to interpret the history of developmental pathways or networks. This becomes a much more difficult, and little explored, problem. One of the more explicit statements about developmental “characters” of this kind is that of Janies and DeSalle (1999), who directed their discussion to gene expression data, given that gene expression analysis is one of the most commonly used tools to investigate developmental pathways. Their critical perspective suggests that gene

expression data will frequently be difficult to interpret as characters (see also Wray and Abouheif, 1998) – genes become co-opted for multiple developmental roles, multiple expression patterns for individual genes can be present in diverse tissues – but they do point out that expression data are likely to be more phylogenetically informative at low taxonomic levels (e.g., Raff, 1996). Despite the difficulty in coding such data, Janies and DeSalle conclude that the best way to understand their phylogenetic importance is to subject these characters to independent phylogenetic analysis and not simply map their distribution on a tree. What is apparent, however, is that using expression data to conclude two embryonic or adult structures (or regions) are H-P homologues will often be problematic, unless those structures are individuated clearly and there is sufficient taxonomic coverage to establish the hierarchical level of the expression character.

From this outsider’s perspective, there will be several challenges to applying H-P homology statements to data derived from the study of developmental mechanisms. First is the sheer complexity of the developmental process itself. The idea of a “developmental pathway” is an oversimplification (but perhaps a necessary one; see below) of developmental history. The term “pathway” invokes a linear series of events ( $a \rightarrow b \rightarrow c$ ), whereas developmental processes are arranged in highly complex systems involving gene regulatory networks, structural gene products, tissue interactions, and numerous other events at different temporal and spatial scales (Hall, 1992; Dickinson, 1995; Davidson et al., 2003; Levine and Davidson, 2005). There are empirical reasons to believe that developmental processes are organized into “modules” but complex interconnections among them are the norm, and it is unlikely these modules will be “stable” (constrained) even over short periods of time, thus complicating partitioning them into characters (von Dassow and Munro, 1999). “Pathways” could be construed as tiny portions of developmental networks, and it may be that this is the level at which developmental observations could be translated to H-P statements. Second, in order to individuate characters one should have information about intra- and interspecific variation. Even though the study of developmental networks is a scientific growth industry, knowledge of these networks, especially across species, is in its infancy (Arnone and Davidson, 1997). Thus, the lack of comparative data currently impedes the search for developmental characters. Finally, granting that data are available for cross species comparisons (e.g., sea urchin, mouse, *Drosophila*), characters are likely to be individuated only by partitioning networks into small discrete and comparable (putatively H-P homologous) “pathways” that have character differences (Laubichler, 2000). These pathways could be chunks of the developmental system, from the gene regulatory end of the

network down to the “tissue-event” end. The characters, I suspect, will be novel connections, losses of connections, or novel outputs in an individual taxon as compared to others. In an interesting paper [Abouheif \(1999\)](#) confronted the obvious problem of determining homology when “choosing or defining boundaries around a nonlinear and continuous network” (1999, p. 212). The proposed solution was to require the elements of bounded networks (genes and their interactions) to be identical across species if that network were to be called homologous; if a difference existed in one or more of the elements of a species, then the networks would be “partially” homologous. This approach places emphasis on demarcating boundaries of networks rather than on potential character differences, and leads to an unnecessary distinction between “full” homologues and “partial” homologues. The “boundaries” of a network for the purpose of comparative analysis could simply be a description of a circumscribed set of genes, gene products, or interactions. The characters (homologues) would then describe discrete variation within that set found across taxa. This avoids imprecise and confusing references to concepts like partial homology.

### Coda: taxon sampling and the origin of novelties

The large literature on evolutionary innovations, primarily within systematics, paleontology, and now evo-devo, is largely focused on the origins of highly complex structural features manifested in comparisons at higher taxonomic levels: the origin of feathers, limbs, eyes, and so on. The origins of such structures, moreover, have generally been entangled with complex theoretical and methodological problems such as macroevolutionary change (in this sense, the rapid origin of major phenotypic differences), key innovations, the origin of higher taxa, among others.

These studies have unquestionably provided a wealth of exciting information about the evolution of character systems and various taxonomic groups. Yet, higher taxonomic levels are not where structural change, along with its underlying developmental causal mechanisms, arises and gets fixed, to be passed on to descendent taxa. The origin of novelty is tied to the origin of basal taxa (species), which means that a mechanistic understanding of the origin of genetic, developmental, and structural diversity is most properly studied using comparisons among closely related species ([Cracraft, 1990](#)). It is widely appreciated, of course, that “large-scale” features (eyes, feathers, etc.) do not usually arise *de novo*, but certainly that viewpoint is often set aside when trying to “explain” the origin of such features by developmental comparisons of a few taxa having very distant relationships. This is understandable for the reasons noted above, and it often leads to very attractive, high profile

conclusions. Yet much more attention is needed at the species level where change is generated and incorporated into evolutionary history, and the studies of [Raff and colleagues \(Raff, 1996\)](#) on closely related sea urchins are exemplars of this approach. Comparative studies of developmental networks, undertaken at the species-level or within closely related groups (e.g., [Hinman et al., 2003](#)), can be expected to provide powerful insights into those genetic and developmental novelties that underlie evolutionary change at all levels.

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