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# 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.


***Keywords:*** Evo-devo; Phylogeny; Systematics; Homology; Cladistics; Comparative biology

## 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….