Developmental Homology

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Abstract

Homology is the fundamental determinant of the sameness of biological characters or traits. When two characters stand in a relation of homology, they belong to the same character kind. For example, the eyes of humans and birds are homologous as vertebrate eyes – that is, they are the same kind of character: vertebrate eyes. Although the concept of homology originated in pre-Darwinian comparative anatomy, it was subsequently revealed to be an evolutionary phenomenon caused by common descent. Contemporary investigators work roughly within the following generic evolutionary conception of homology:

Homology: Two characters in distinct organisms or taxa are homologous if they are genealogically connected by continuous descent from a common ancestor that had the same character.

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Introduction

Homology is the fundamental determinant of the sameness of biological characters or traits. When two characters stand in a relation of homology, they belong to the same character kind. For example, the eyes of humans and birds are homologous as vertebrate eyes – that is, they are the same kind of character: vertebrate eyes. Although the concept of homology originated in pre-Darwinian comparative anatomy, it was subsequently revealed to be an evolutionary phenomenon caused by common descent. Contemporary investigators work roughly within the following generic evolutionary conception of homology:

Homology: Two characters in distinct organisms or taxa are homologous if they are genealogically connected by continuous descent from a common ancestor that had the same character.

So, human and bird eyes are homologous because every one of their evolutionary ancestors had eyes, up to and including their most recent common ancestors (the first amniotes). By contrast, human eyes are *not* homologous with insect eyes because their most recent common ancestor (urbilaterians) did not have eyes. Instead, the relation between human eyes and insect eyes is thought to be as a *homoplasy* – a similarity that is due to convergent evolution rather than inheritance from an ancestor.

The concept of homology plays many key roles in biological research, but the following are among the most important.

- R1. Homology provides a system of descriptive classification for biological characters.
- R2. Homology determines the extent of what is conserved in evolution and thus serves to identify, contrastively, what constitutes evolutionary change or novelty.
- R3. Judgments of homology enable phylogenetic inferences that place characters and taxa on phylogenetic trees.
- R4. Judgments of homology enable inferences about potential similarities in the genetic and developmental production of homologous characters as well as the propensities of those characters to vary in certain directions.

To fulfill these roles, investigators need more than just the generic evolutionary conception of homology. The latter functions as a reference point so that biologists refer to roughly the same biological phenomenon with the term “homology.” But it

does not specify how to determine genealogical continuity in the absence of direct observation. Moreover, most characters of developing organisms are typically only present for part of their life cycle, and thus their continuity has to be reconstituted across generations. Over time and across species, characters gain and lose features while still remaining homologous, thus we need ways of separating the features of homologues that can change from those that cannot.

To meet these challenges, we need robust *criteria* for individuating homologues. Among the most important criteria for homology that have been proposed are the following (partially corresponding to the above roles R1–R4):

- C1. Similarity in descriptive properties of the character, especially complex properties that are unlikely to be independently evolved homoplasies (Riedl 1978; Remane 1956).
- C2. Similarity or sameness in the topological position of the character relative to other characters on the body and in the relative positions of internal components of the character (Owen 1843; Jardine 1969);
- C3. “Congruence” or agreement with the most probable placement of other characters on a phylogenetic tree, such that homologies are *synapomorphies* or characters that define a monophyletic group (Remane 1956; Bock 1974; Patterson 1982)
- C4. Similarity or sameness in the genetic and/or mechanistic generation of the character during development (Van Valen 1982; Roth 1984, 1988; Wagner 1989a, b, 2014).

Roles and criteria (1) and (2) are generally accepted aspects of homology. From the other roles and criteria we can trace the outline of the two main different approaches to homology in the life sciences: a phylogenetic, cladistic, systematic, or “historical approach” (3) versus a developmental or “biological” approach (4).

Phylogenetic Versus Developmental Approaches to Homology

The two main different approaches to homology emphasize different criteria because they have different investigative goals. The main objective of phylogenetic approaches is to discover distributions of characters and patterns of taxa on the evolutionary tree of life. To meet this objective, candidate homologues are identified using C1 and C2 and tested as to how well they fit into known patterns of phylogeny (C3), which are in turn based on relatively more well-confirmed homologies. In the cladistic approach specifically, all homologies are synapomorphies, or characters that are present exclusively in a monophyletic group (an ancestral species together with its evolutionary descendants) (Patterson 1982). Criterion 4 is generally not taken to be a defining feature of homology in this approach, though it may provide supporting evidence for cladistic hypotheses about homology since genes and mechanisms are themselves characters that can be homologized.

The more recent developmental approach to homology – sometimes also called the “biological basis of homology” (Roth 1988; Wagner 1989b) – is oriented toward explaining patterns of conservatism of phenotypic characters and identifying which kinds of phenotypic features tend to get conserved in evolution. Proponents of this approach hold that phylogenetic methods need to be supplemented by a developmental criterion of homology, according to which characters are homologous only if they share the same developmental causes. The nature of these developmental causes is a source of ongoing discussion. They have been identified with (genetic) information (Van Valen 1982), embryological origin or developmental pathways (Roth 1984), developmental constraints (Wagner 1989a), and recently, classes of gene regulatory networks called “Character Identity Networks” (Wagner 2014). Whatever the proposed nature of the developmental basis of homology, the primary rationale is the same. The presence of developmental constraints or dedicated regulatory controls for a given phenotypic character can often explain why that character remains stable over evolutionary time and in different species or why it changes in the way it does. In view of this explanatory goal, phylogenetic approaches are limited to describing and recording character stasis and change without being able to explain them mechanistically. The developmental conception of homology is nonetheless not proposed as a total replacement to the older phylogenetic one, but as a supplemental resource. To have “the same” developmental cause (genes, pathways, constraints, etc.) is to have homologous causes, and the latter notion of homology must be cashed out in phylogenetic terms.

Developmental views of homology have been advanced as a central part of the emerging theoretical structure of evo-devo (see Amundson 2005, Wagner 2014). Although they are not consensus views in the field, they are the most recent innovation in the longstanding discussion on homology and will be the main focus of this chapter. In neo-Darwinian evolutionary theory, by contrast, homology had a less important role. There it was largely viewed as a concept of pre-evolutionary biology that had been successfully explained by Darwinian evolution (Mayr 1982; see Amundson 2005).

One of the main reasons for this disparity is that the neo-Darwinian picture of evolution attributed explanatory primacy to the sorting of variation through selection rather than to the generation and structuring of variation through development. Since evo-devo focuses more on the latter, it affords a more important role for homologues as structural units of variation and variability. Another reason is that the neo-Darwinian perspective on evolution had little to say about organismal or phenotypic evolution, drawing as it did largely from the theoretical resources of evolutionary genetics. Since evo-devo aims to describe, explain, and predict phenotypic evolution, it has more use for homologues as “organizers of the phenotype” (Müller 2003; see Müller 2007). Finally, evo-devo has opened up new possibilities for comparative generalizations across phylogenetic boundaries, and homology is the central concept of comparative biology (Wake 1994). In the neo-Darwinian picture, by contrast, evolution does not occur above the level of populations because selection does not act across reproductively isolated groups. The potential for comparative work to generate insights about *current* evolution is accordingly highly

limited, unless the comparisons are about convergence, which is based on selection. Because it never recognized the important role of development in evolution, traditional evolutionary theorizing failed to predict that a widely shared set of developmental resources, including core regulatory genes and pathways, gets repeatedly re-deployed in developmental evolution. The existence of this well-conserved repertoire, highlighted most dramatically with the discovery of the Hox genes, makes the prospects for comparative work much brighter – and with it a more important role for homology opens up in evolutionary theorizing. Developmental approaches to homology have originated as part of this broader shift in evolutionary theory.

In the remainder of this chapter, I will examine more specific aspects of the homology problem with an emphasis on current approaches and open problems.

Characters: The Relata of Homology

So far homology has been treated as a relation between characters, but what is a character? Can any organismic part, property, or activity whatsoever be homologous with something else? In nineteenth century comparative anatomy, where the concept of homology originated, homology was treated primarily as a relation between anatomical body parts – i.e., organ systems, organs, and their observable components. Since then, the relata of homology have been steadily extended to increasingly diverse features of organisms at multiple levels of organization. Homologues can be organs, but also, tissues, cells, organelles, genes, gene networks, and properties of each. In addition to homologies of structure, theorists have recognized that developmental processes (Gilbert and Bolker 2001), organismic behaviors, and activities of parts can be homologous. With each extension of homology, the guiding rationale is typically to organize the domain of study under a comparative evolutionary framework. From the perspective of the generic evolutionary conception of homology, there is no reason to restrict the relata of homology as long as the general condition of common descent is met, though of course not every judgment of homology is guaranteed to be biologically interesting.

Approaches to homology from systematics and cladistics tend to share this permissive view of the relata of homology, but with an additional pragmatic restriction. Homologues or synapomorphies should be “good” characters for purposes of cladistic analysis: they should be readily identifiable and should be able to provide operational identifying features of monophyletic groups. In general, structural features are more likely than functional features to be good cladistic characters, due primarily to their greater stability over organism lifetimes and their potential to leave behind fossil traces.

Developmental approaches to homology are more restrictive about what can be a homologous character. In Wagner’s (1989a, b, 2014) approach, genuine characters should be “developmentally individualized”: there should be a dedicated regulatory module that controls a character’s development and constrains it against variation. Organism features that do not meet this requirement include pseudo-characters and character states. Pseudo-characters are those that arise merely as by-products of

interaction, adjacency, or overlap between individualized characters. An example is the bone protrusion of the human chin, which is a structural by-product of the differential regression of parallel growth fields of the jaw due to ancestral selection for smaller teeth (McKinney and McNamara 1991, 232; Gould and Lewontin 1979). Character states include properties of characters such as size, shape, and color (Müller 2003). Both kinds of noncharacter lack the key feature of variational independence in the process of developmental evolution (Brigandt 2007) and are expected to be much more evolutionarily labile than individualized characters. Accordingly, they are less relevant to the phenomenon of morphological stasis that developmental approaches seek to explain. The evolutionary lability of character states also makes it more difficult to determine if they are homologous or homoplastic than it is with individualized characters. On this more restricted construal, characters will generally be body parts and cells. But the requirement of developmental individualization also means that the underlying developmental causes (modules and genes) must be homologized – under a phylogenetic definition.

Systematists such as Bock (1974) and Patterson (1982) reject the idea that the distinction between characters and character states has general evolutionary or phylogenetic significance beyond the fact that character states are homologues within a narrower taxonomic group. Moreover, something that is a pseudo-character from the perspective of development (like the human chin) could nonetheless be a good character for taxonomic purposes. Another difference between approaches on the character issue is that phylogenetic relatedness of characters can diverge from developmental or mechanistic sameness, especially when we are comparing an ancestral character with a highly derived one. For example, the remarkable homology between the jaw joint of reptiles and the ear ossicles of mammals captures a relationship of phylogenetic transformation, but these characters are not homologous or the same from a developmental or mechanistic point of view (Bock and Cardew 1999, 21). Individualized characters produced by the same developmental processes may turn out to be sympleisomorphies – i.e., shared ancestral characters not definitive of monophyletic groups – more often than synapomorphies (Roth 1991, 173).

Serial Homology

In classical approaches such as that of Richard Owen (1843), homology was not just a relationship between characters in different organisms but could also be a relationship between characters in the same organism. The former is traditionally referred to as “special” homology, whereas the latter is “serial” or “iterative” homology. Examples of serial homology include vertebrae in the vertebral column, insect body segments, tree leaves, moth and butterfly wing spots (see Fig. 1), cells belonging to the same cell type, and right-left symmetric organs such as kidneys, hands, or eyes (sometimes called “antimeric” homologies).

The criteria used to identify serial homologues are descriptive similarity (C1) and similarity or sameness in genetic and/or mechanistic generation (C4). Because serial homologues are different particular characters within the same organism, they

Fig. 1 Serial (a) and special (b) homologies between the central symmetry systems (highlighted) of lepidopteran wing patterns. In *Hypercompe permaculata* (pictured left), the central symmetry system on the right forewing is serially homologous with the same character on the left forewing, and specially homologous with the central symmetry system on the right forewing of other species such as *Sebastia argus* (pictured right). Individual spots within each central symmetry system are also serial homologues. (Photo credit: Richard Gawne. Specimens are from the collection of the Natural History Museum of Vienna)

cannot occupy the same topological position (C2) without modification of that criterion, and phylogenetic methods don't apply at all (C3). Accordingly, serial homology can play similar theoretical roles as special homology except for enabling phylogenetic inference (R3). Many of the same arguments concerning characters and relata can be applied to serial homology as well. Serial homologues can include many kinds of organism features such as genes and behaviors, but only if they can be partitioned into countable units. In the case of special homology, by contrast, noncountable features like color and shape can be homologized more easily because they inhere in countable organisms. The requirement of developmental individualization therefore has an additional motivation in the case of serial homology.

As might be expected, proponents of the phylogenetic approach do not consider serial homology to be a genuine case of homology (Patterson 1982). Since congruence (C3) is taken to be the ultimate test of homology in this approach, and is inapplicable here, serial homology is viewed as untestable, ill-defined, and potentially arbitrary. Serial homologues are not synapomorphies and have no role to play in phylogenetic inference (except to the extent that having iterated parts of a certain sort is a special homology that could be a good cladistic character).

Proponents of developmental or biological approaches have, in turn, interpreted the lack of a phylogenetic definition of serial homology as a strike against the phylogenetic view (Roth 1984; Wagner 1989b; Ramsey and Peterson 2012). Clearly, there is an important sense in which a human's vertebrae are repetitions of the same character, and so purely phylogenetic approaches to homology seem to miss an important aspect of character sameness. Since phylogenetic methods and criteria don't apply, the reasoning goes, a developmental, genetic, or organizational criterion must be constitutive of homology. Serial homology also has an important role to play in evolution. Duplication and subsequent divergence of characters is a key evolutionary mechanism for generating phenotypic complexity and functional

specialization. This is particularly true of gene duplication, where serially homologous genes (*paralogues*, as opposed to *orthologues*, which are specially homologous genes) can acquire new functions fairly rapidly.

Parties to the debate about serial homology have not provided much justification for the guiding assumption that serial homology, if it is to exist, must fall under the same definition as special homology. Developmentalists assume that a unified definition is a desideratum that phylogeneticists are unable to satisfy (Roth 1984; Wagner 1989a, b). Phylogeneticists are under pressure to reject serial homology in order to maintain their definition, but only on the assumption that the phylogenetic conception of special homology is threatened by serial homology. It is worth asking what would be lost, aside from simplicity, if we were to maintain different definitions, such as a phylogenetic definition of special homology and a developmental definition of serial homology, under the recognition that they represent different phenomena of character sameness. The resolution of this issue depends on whether special and serial homologues have similar roles to play in developmental evolution, which is an open question.

Homology, Homoplasy, Parallelism, and Deep Homology

Homology as the determinant of character sameness is standardly contrasted with homoplasy and parallelism. *Homoplasy*, we saw, is character similarity due to convergent evolution rather than common origin. *Parallelism* is similarity due to convergent or independent evolution of characters *that share the same (homologous) developmental basis* (Hall 2003). The developmental homology underlying parallel characters means their evolution is not totally independent, thus parallelism is distinguished from “true” convergence. A term that is no longer commonly used in technical discussions is *analogy*, which is functional similarity of any sort, considered without reference to phylogeny. Whereas homology and homoplasy are dichotomous, homologous characters can be analogous if they have similar functions.

Although the distinctions between homology, homoplasy, and parallelism are clear conceptually, they are often difficult to distinguish in practice in real biological systems (Wake 1991). One general issue concerns how to determine homology of developmental causes. The development of morphological characters typically involves interactions between networks of regulatory genes. But the conditions for homology of gene regulatory networks are not well-established (Abouheif 1999). Do homologous networks need to share all the same genes and interactions, or just some, and if it's the latter, how many? One way to handle these questions is to say that network homology can be partial rather than being an all-or-nothing affair (Abouheif 1999; Minelli 1998). Allowing this move has important consequences, however. If homology between developmental causes can be partial and is also required for homology between morphological characters – as in developmental approaches – then homology between morphological characters should also be allowed to be partial. That means characters can be partly homologous and partly

parallel, or partly parallel and partly homoplastic, depending on the degree of homology of their developmental causes. The clear-cut distinctions between homology, parallelism, and homoplasy become somewhat blurred. One way of resisting this conclusion and maintaining that homology between gross morphological characters is all-or-nothing is to hold that only a core subset of regulatory networks needs to be the same in order for the characters to be homologous (Wagner 2014).

A new reconfiguration of the distinctions between homology, homoplasy, and parallelism has arisen from the discovery from developmental genetics that the same “toolkit” of regulatory genes and circuits is widely shared across very different taxonomic groups. A famous example of this came when Gehring and colleagues discovered that homologous regulatory genes (*eyeless/Pax-6/Aniridia*) control the morphogenesis of eyes in *Drosophila*, mice, and humans, respectively (Quiring et al. 1994). Traditionally, the similarity between compound insect eyes and camera vertebrate eyes had been considered a paradigm case of convergent evolution – as expressed in our opening example above – demonstrating the power of natural selection to produce similar outcomes from independent starting points. But in fact, even though vertebrates and insects diverged over 500 million years ago, their starting points are not independent because they share much of the same regulatory circuitry. This evolutionary pattern, in which characters that have diverged deep in the evolutionary past share the same toolkit genes or networks, has been called *deep homology* (Shubin et al. 1997). Deep homology does not mean that the characters are homologous (though they could be) but that they share homologous genes and/or networks. Deep homologies have been discovered for many other characters besides eyes, such as between tetrapod limbs and fish fins, and between beetle horns and insect legs (Shubin et al. 2009), and may prove to be extraordinarily common.

These recent developments have a number of empirical and conceptual implications for our understanding of homology and evolution. The occurrence of deep homology suggests that novel phenotypic structures need not arise from de novo genetic changes but instead can result from the re-deployment of existing regulatory circuitry. In turn, this throws some light on the apparent ease and speed with which evolutionary novelties can arise and become adaptive. But it also means that the conceptual distinction between homology and novelty (R2) may become more difficult to parse whenever the new is produced by a modification of the old. Deep homology also explains the common occurrence of multiple gains and losses of characters in related taxa by pointing to the persistence of developmental potentials that are not always expressed. This raises the conceptual question of whether characters that lack genealogical continuity because they are “blinking” on and off in evolution should nonetheless count as homologous in virtue of the continuity of their developmental causes (Ramsey and Peterson 2012). The same question can be asked about atavisms and ectopically expressed characters. Finally, the occurrence of deep homology suggests that standard methods have overestimated the extent of convergent evolution, and parallelism may be much more common than has been assumed (McGhee 2011). More generally, the role of development may have to be stronger and the role of selection weaker, in explaining patterns of phenotypic evolution.

Challenges and Outlook

An ongoing challenge for work on homology is to understand how phylogenetic and developmental approaches ultimately relate to each other. One perspective on their relationship is that the approaches are incommensurable and retain different definitions because they have different scientific goals. There is some truth to this idea, but it is only part of the story. As we saw earlier, developmental approaches are parasitic on phylogenetic approaches when it comes to determining the homology of developmental causes for a morphological character. But phylogenetic views also stand to be enriched by developmental considerations. Congruence tests (C3) typically operate with a differential weighting of characters according to their probabilities of independent loss or gain, or modification. Clearly, these probabilities will be influenced by the causal structure of development. Ontogeny also plays a major role in determining the “polarity” of character transformation series – i.e., deciding which homologies are primitive and which are derived – often on the basis of recapulationist principles (Patterson 1982). In general, if evolution is the evolution of development, then the biological study of development will tell us something about the historical course that evolution has actually taken. The relationship between approaches to homology is therefore more of a mutualism than parasitism or independence (Roth 1991). What exactly is required for a productive integration of approaches is less clear. For example, does the coordination of their descriptive and explanatory resources require a unified definition of homology, or some weaker kind of linkage?

A major challenge specific to the newer developmental approaches concerns the idea of a one-one mapping between developmental causes and phenotypic characters. Among other things, this mapping is supposed to provide the element of continuity for characters that must be rebuilt across generations, i.e., most characters (Van Valen 1982; Roth 1984). But is this one-one mapping requirement actually satisfied in evolution? Embryologists have long been aware that homologous morphological characters can have nonhomologous developmental origins, and similar dissociations have been recorded at all levels of organization since then (Wray and Abouheif 1998). Proponents of the developmental approach have kept pace with these conflicting data by specifying increasingly narrow types of developmental causes that carry the thread of character identity, with Wagner’s (2014) “character identity networks” being the most recent model. However, a challenge for all genetic models of developmental homology comes from cases of “developmental system drift” (DSD) (see the chapter on ► “Developmental System Drift”). DSD occurs when homologous characters accumulate differences in the genes or networks that control them. It can be caused by neutral drift, selection on characters controlled by pleiotropic genes, or a combination of selection and drift. DSD presents a picture of evolution in which the thread of character identity doesn’t always lie at the level of specific genes or even gene networks. This picture of character identity fits more readily with developmental theories that stress the autonomy of morphological homology from homology at lower levels of organization (Müller 2003; Newman and Müller 1999; Scholtz 2005). DSD as well as genetic models of homology are

nonetheless active and ongoing topics of research, and their relationship constitutes an important unresolved problem of homology. Different responses in evo-devo to the dissociation of homologues across levels of organization are discussed in more detail in Nuño de la Rosa and Etxeberria (2009).

Finally, homology is a problem-area where philosophical resources can be – and have been – productively deployed. The topics raised by reflection on homology include definitions of scientific concepts, character individuation and decomposition of biological systems, typological versus population thinking, biological classification and natural kinds, conceptual change in science, explanatory pluralism and integration of perspectives, and more. To take the first of these, it is important to ask what sort of definition and criteria of individuation should be sought. With homology, biologists are attempting to ascertain character sameness in spite of the many variations in form, growth pattern, function, and mode of life that are found in divergent taxonomic groups. If no constitutive feature of homology (e.g., sameness of topological position) is immune to the contingencies of evolutionary change, then we should not expect to find a definition of homology that provides universally valid necessary and sufficient conditions for homology and that is at the same time theoretically adequate and practically useful. A natural response to this situation is to shift towards pluralism about definitions or a context-sensitive framework in which homology may be determined by different combinations of factors in different cases (Minelli 1998). A challenge for such alternatives is to offer directives that are not too vague to be concretely implemented and that can successfully deliver judgments of homology in practical contexts. For this task, it will be essential to keep the major biological roles for homology (R1-R4) in focus, while mapping out the classes of contexts where criteria of homology (C1-C4) tend to break down. Then workers can identify how to use the criteria of homology in specific biological contexts in a way that accesses the considerable utility of the concept.

Cross-References

- ▶ [Convergence](#)
- ▶ [Developmental System Drift](#)
- ▶ [Form and Function](#)
- ▶ [Inherency](#)
- ▶ [Typology and Natural Kinds in Evo-Devo](#)

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