Essay: Homology [1]

By: Brigandt, Ingo

Keywords: Homology, Morphology

1. Overview

Homology [1] is a central concept of comparative and evolutionary biology, referring to the presence of the same bodily parts (e.g., morphological structures) in different species. The existence of homologies is explained by common ancestry, and according to modern definitions of homology, two structures in different species are homologous if they are derived from the same structure in the common ancestor. Homology [1] has traditionally been contrasted with analogy, the presence of similar traits in different species not necessarily due to common ancestry but due to a similar function or convergent evolution [2], resulting from similar selective pressure in different species. (A more recent contrasting notion is homoplasy, the presence of similar traits in different species without common ancestry, i.e., as an instance of parallel evolution [3].) This sounds straightforward, but in fact the homology concept has a rich history and currently is the subject of extensive theoretical reflection, resulting in different contemporary approaches to homology.

Despite the phylogenetic nature of homology, the homology concept was introduced in early nineteenth century comparative anatomy and embryology [4], and became an influential aspect of comparative practice well before the advent of Darwinian evolutionary theory. In this period and until the first half of the twentieth century, two main criteria were used to establish homologies across species. The positional criterion maintains that homologous structures in different species retain their relative topological positions. For instance, the shape of a certain bone may vary across different species (e.g. if it serves a different function in different species), but this bone will usually be adjacent to or articulate with the same set of other bones across these species. The embryological criterion assumes that homologous structures in different species develop out of the same developmental precursors. This made many cases of homology discovery possible, as the early developmental stages [5] of different species are more similar than the respective adult forms. While the positional criterion primarily relies on comparing the adult morphologies of different species, the embryological criterion involves comparative embryology [6] as an additional source of evidence. However, there are cases where both criteria disagree, which historically led to a conflict between approaches favoring the comparative anatomy of adults and those relying on comparative embryology [6] (Section 3 below).

In addition to its central role for biology and its longstanding history, developments in the second half of the twentieth century strongly enriched and diversified the homology concept. With the advent of phylogenetic systematics [7], cladistics, homologies came to be consistently assessed by means of the distribution of derived states on phylogenetic trees. The positional and embryological criteria could be and were used independently of any phylogenetic tree, but they are fallible criteria for establishing homologies understood as structures with a common ancestry (Section 4). The advent of molecular phylogeny [8] and molecular evolution [9] made prominent the idea that molecular structures such as genes [10] and proteins can be homologous across species. In general, many kinds of biological entities are nowadays homologized: molecules, cellular structures, cell types, tissues, developmental modules and processes, gross morphological structures, and behavioral patterns. It is widely recognized that homologies exist on different levels of organismal organization [11]. Furthermore, homologies on different hierarchical levels need not align: there are many cases where developmental processes and/or the involvement of non-homologous genes [12]. Conversely, the same, homologous gene can be involved in the development of non-homologous structures in different species. As a result, it is nowadays often assumed that homology on one level of organization [13] cannot be reduced to homology on another (e.g. lower) level, supporting a non-reductive and hierarchical view of organisms.

Since homologous structures can develop by different developmental mechanisms, and may develop out of non-homologous developmental precursors, the embryological criterion of homology ultimately fails. However, this does not diminish the role of developmental biology for homology. On the contrary, embryonic structures and developmental processes are an additional and independent level of consideration in anatomy, whereas for Geoffroy function was subordinated to structure/homology as the same structure could fulfill different functions (Appel 1987). For instance, Geoffroy showed that the furcula, the wishbone assumed to exist only in birds [14], is present in fishes as well, and he homologized structures of normally developed animals with malformed structures and teratologies, which have an altered or no function. Geoffroy is so important for this discussion because he introduced a major criterion of homology. His principe de connexions (sometimes called a biological homology concept [15]) was the latter attempt to explain why a homologue reappears in different generations and is often present as the same morphological unit across many species, despite undergoing evolutionary change in its internal features. Developmental biology is essential to understand how homologies can function as units of morphological evolution [16], an issue which is central to contemporary evolutionary developmental biology [17].

A detailed survey of the history of the homology concept follows, which pays particular attention to the relation of this concept to development and embryology [8].

2. Homology [1] in pre-evolutionary biology

Long before the term 'homology' was introduced and the idea of homology clearly spelled out, seventeenth and eighteenth century comparative anatomists and naturalists studied biological characters of known and newly discovered species, recognizing that different species can have the same anatomical structures by giving the same name to them. However, these early naming practices were idiographic and not based on explicit criteria. Usually the same name was applied to characters with a similar shape, internal structure, and function, and only to taxonomically closely related species (e.g. different mammals). This idea of homology originated with the recognition that the same structures exist in less closely related species (mammals and birds [18], or even mammals and lizards [19]) and that the sameness of morphological units is independent of their function and form. This idea developed in comparative anatomy independently in Germany and France, though from 1820 onwards both traditions influenced each other as well as British zoology (Appel 1987).

In the German context, the relevance of Johann Wolfgang von Goethe (1749–1832) and other morphologists such as Lorenz Oken (1779–1851) is well known. For the tradition of Naturphilosophie [20], homology was one of the manifestations of the unity in nature that it emphasized. Of particular concern was what is nowadays called serial homology, i.e., the repeated occurrence of same morphological unit across unrelated species, despite undergoing evolutionary change in its internal features. Developmental biology is essential to understand how homologues can function as units of morphological evolution [16], an issue which is central to contemporary developmental biology [17].

However, this does not diminish the role of developmental biology for homology. On the contrary, embryonic structures and developmental processes are an additional and independent level of consideration in anatomy, whereas for Geoffroy function was subordinated to structure/homology as the same structure could fulfill different functions (Appel 1987). For instance, Geoffroy showed that the furcula, the wishbone assumed to exist only in birds (Appel 1987), is present in fishes as well, and he homologized structures of normally developed animals with malformed structures and teratologies, which have an altered or no function. Geoffroy is so important for this discussion because he introduced a major criterion of homology. His principe de connexions (sometimes called a biological homology concept [15]) was the latter attempt to explain why a homologue reappears in different generations and is often present as the same morphological unit across many species, despite undergoing evolutionary change in its internal features. Developmental biology is essential to understand how homologues can function as units of morphological evolution [16], an issue which is central to contemporary developmental biology [17].

A detailed survey of the history of the homology concept follows, which pays particular attention to the relation of this concept to development and embryology [8].

3. Homology [1] and the process of development

Sources
the adult forms of lower animals. Instead, the human and the fish became later an important line of evidence for the idea of common ancestry, whereas the approach of Natural Theology could not explain why the same structures occurred in radically different species. As one of the most thriving disciplines within all of biology in the second half of the nineteenth century, evolutionary morphology[43] was less concerned with the study of the mechanisms of evolutionary change (such as natural selection[38]), but consisted in a thoroughly phylogenetic approach in morphology[39] and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution[41].

It is often (tacitly) assumed that evolutionary theory introduced a novel homology concept: an 'evolutionary' homology concept defined in terms of common ancestry, to be distinguished from the pre-Darwinian concept of homology and the shared morphological developmental-morphological features generating the repetition of parts across species (and within organisms in the case of serial homology) and the variation of these corresponding morphological units. In particular, comparative embryological studies provided an additional source of data to assess homologies and establish hypothesis about phylogenies and patterns of morphological evolution[39], keeping development germane to evolution[40] even without an adherence to the alleged biogenetic law[41].

Around the turn of the century, however, evolutionary embryology[39] lost in significance, largely to experimental embryology[41] (developmental mechanics) as an approach concerned with the experimental determination of the ontogenetic pathways of the embryo. Comparative phylogenetic embryology[40], with its focus on the functional homology[39] of developmental processes, and development modules, is often viewed as homologous to comparative embryology (e. g., the use of the embryological criterion to assess homology) and comparative embryology (e.g., the use of the embryological criterion). Some evolutionary morphologists, following Gegenbaur, favored the comparison of adult morphological structures to establish homologies and relations between taxa. Others, in line with Haeckel, preferred using embryological data to determine homology and character polarity[41]. Yet morphological and embryological methods led in some cases to conflicting interpretations as to which structures were homologous, which taxa represented the more primitive character state, and which extent structures evolved from which ancestral features. The symposia debate concerned the origin of paired fins in fish[39], a question central to the evolution[39] of vertebrate appendages (and still a core issue for contemporary studies). The gill-arch theory claimed fins to be derived from the two hindmost gill arches, which had migrated from the head to form the pelvis and pectoral fin girdles, with the rays of the gill arches becoming fins. This hypothesis was supported by the comparison of adult fins and girdles. The rival lateral fin-fold hypothesis assumed that paired fins had evolved from lateral folds that had formed (originally continuous) lengthwise along the fish's side, and which later evolved rays and were broken up into pectoral and pelvic fins. This theory was favored by embryological methods, viewing other taxa as representing the primitive condition compared to the gill-arch theory. The conflict between anatomical and embryological methods was never resolved. The historical consequence was that many young evolutionary morphologists who could have entered evolutionary embryology[39] preferred to work in experimental embryology[41] instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). From this period show that the positional criterion (or use of adult anatomy more generally) and the embryological criterion of homology can clash in many cases. Section 4 explains how this issue has been resolved in contemporary biology.

While in the nineteenth century homologies were established using the positional and embryological criterion (and some additional criteria) that do not presuppose a phylogenetic tree, the advent of phylogenetic systematics[39] (cladistics) in the second half of the twentieth century made a thoroughly phylogenetic assessment of homologies the only reliable method. Here a tree depicting the phylogeny[39] of several species is shown and the homology[39] of the left and right lateral line[41] in the fish is compared to the homologies in the amphibia[40], reptilia[41], and mammals[42]. However, the overall feature distribution across species is best explained by the assumption that a particular feature originated in an ancestral species and has been inherited to all its descendants, a situation called synapomorphy. The phylogenetic tree is obtained by the use of many different characters, where the most likely phylogeny[39] is the one that best explains the distribution of all characters across extant species. In this context, homology is contrasted with homoplasy, which is the occurrence of similar character states in two species not due to common ancestry (but parallel evolution[39]).

4. Development and hierarchy. Approaches to homology

Over the past few decades there has been an intensification of interest in the concept of homology. Its scope of application has increased and new theoretical interpretations of homology have been proposed (Donoghue 1992, Brignati and Griffoths 2007). In addition to traditional anatomical categories, anatomy[41] introduced the idea that behavioral patterns in different species can be homologous. With the rise of molecular biology, genes[43], proteins, and other molecular structures came to be homologized, making possible the fields of molecular phylogeny[41] and evolution[41] which establish phylogenetic trees based on molecular data. These new phylogenies have been used to infer the direction of evolution[41], and to test hypotheses about evolution[41], homologous structures, and developmental processes, and development modules are now viewed as homologous to molecular systematics[39], which is the occurrence of similar character states in two species not due to common ancestry (but parallel evolution[39]).

It is an important insight that homology on one level of organization[41] (such as homology of blood vessels) must not be confused with and cannot be reduced to homology on another (e.g., lower) level (Remane 1961). Adult anatomical features are built on different developmental processes based on the action of particular genes[43], so that it originally seemed reasonable to assume that homologous anatomical structures develop by means of the same developmental mechanisms (in line with the embryological criterion of homology) and the involvement of homologous genes[43]. But this is not so, as characters on different hierarchical levels (e.g., the molecular, the developmental, the functional, the structural, the behavioral) can be the result of different causative processes (Jacob 1967). This leads to the situation where homologous structures in two
Acknowledgements

characters and levels (yet to be understood), which permit the independent character state. A related question is to understand how the different characters (homologues) making up an organism can evolve independently of each other as quasi-independent units of morphological biological homology concept

With the advent of evolutionary developmental biology, recently development approaches to homology have been introduced (Donoghue 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Brigandt 2003). While these are sometimes viewed as different interpretations that are hard to reconcile, they may very well be compatible accounts that focus on different aspects of an overall phenomenon (Brigandt 2007). To explain the main approaches, it is useful to recall the distinction between a character and a character state. A character (properly speaking) is a homologous character unit present in many individuals and which can take on a different role and function in different individuals or species. A character state is the particular condition (e.g. form) a character has in an individual. The transformational approach to homology, as the traditional perspective in evolutionary biology, focuses on how a character is inherited in a single evolutionary lineage and undergos gradual modification in its state from ancestor to descendant. The spec approach as the dominant perspective on homology in phylogenetic systematics, focuses on how a certain character state is shared by a whole taxon. Here situations are relevant where the character’s state in ancestral species A is significantly different from its state in the descending species B (the character’s ‘plesiomorphic’ condition in A vs. the ‘apomorphic’ condition in B), while all species descending from B still possess the state found in B, so that this state is a novel condition that originated in B and characterizes the taxonomy of which B is the most recent common ancestor.

With the advent of evolutionary developmental biology, recently development approaches to homology have been introduced (Donoghue 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Brigandt 2003). While these are sometimes viewed as different interpretations that are hard to reconcile, they may very well be compatible accounts that focus on different aspects of an overall phenomenon (Brigandt 2007). To explain the main approaches, it is useful to recall the distinction between a character and a character state. A character (properly speaking) is a...
Homology is a central concept of comparative and evolutionary biology, referring to the presence of the same bodily parts (e.g., morphological structures) in different species. The existence of homologies is explained by common ancestry, and according to modern definitions of homology, two structures in different species are homologous if they are derived from the same structure in the common ancestor. Homology has traditionally been contrasted with analogy, the presence of similar traits in different species not necessarily due to common ancestry but due to a similar function or convergent evolution resulting from similar selective pressure in different species. (A more recent contrastive notion is homoplasy, the presence of similar traits in different species without common ancestry, i.e., as an instance of parallel evolution.) This sounds straightforward, but in fact the homology concept has a rich history and currently is the subject of extensive theoretical reflection, resulting in different contemporary approaches to homology.