Essay: Homology [1]

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1. Overview

Homology [2] 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 [3] 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 [4], 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 [5].) 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 [6], 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 [7] 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 [8] 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 [9] (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 [10], cladistics, homologies came to be consistently assessed by means of the distribution of traits, thereby 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 evolution [11] and molecular systematics [12] made prominent the idea that molecular structures such as genes [13] 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 organizational organization [14]. Furthermore, homologies on different hierarchical levels need not align: there are many cases where developmental processes in one homologous genes [15]. 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 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 organization [16] where homologies occur. Furthermore, apart from taxic and transformational approaches to homology (discussed in Section 4), of particular importance are developmental approaches to homology or the study of development itself; these latter approaches emphasize the role of development in creating the differences among species that are homologous. The development of a homologous structure in one species depends on the developmental processes in the homologous structures in the other species.

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 [10].


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 or similar anatomical structures by giving the same name to them. However, these early naming practices were idiosyncratic 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). The idea of homologized structures led to the recognition that the same structures exist in less closely related species (birds [17], or, even mammals and birds [18]) 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 [19], 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 in one and the same individual. For instance, the famous vertebral theory of Goethe maintained that the different skull bones are in fact transformed vertebrae (Nyhart 1995, Rupke 1994, Russell 1916).

In France, of pivotal importance was the work of Etienne Geoffroy Saint-Hilaire (1772–1844). While previous anatomists, including Georges Cuvier [20] (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds [21], mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ postulated the unity of organic composition. In particular, he proposed what is now the modern definition of homology: that all vertebrae consist of the same number of basic building elements (Geoffroy Saint-Hilaire 1818). Later he even attempted to homologize structures from different Cuvierian branchial arches [22] (vertebrates, mollusks, articulates, radiates; which unlike contemporary phyla were defined by Cuvier in terms of functional organ systems). This triggered the famous public dispute between Geoffroy and Cuvier in 1830, but the disagreement was rooted in Cuvier’s emphasis on functional considerations in anatomy, whereas for Geoffroy function was subordinated to structure/homology as the same structure could serve different functions (Appel 1887). For instance, Geoffroy showed that the scute, the wishbone supposed to exist only in birds [23], 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 to this discussion because he introduced a major criterion of homology and the practice in which it figured. In particular, what is now called the embryological criterion of homology found its first clear expression in the work of the Estonian comparative embryologist Karl Ernst von Baer (1792–1876). Von Baer’s embryological theory was in fact part of a critique of recapitulationism, as endorsed by Meckel and Serres. Apart from counterexamples to recapitulation, von Baer defended an alternative account of comparative development, which he summarized in four laws, later referred to as von Baer’s laws [24] (von Baer 1828). On this theory, the early embryos of different vertebrates cannot be distinguished from each other. Later in development successive differentiation [25] takes place in such an embryo acquires the features that characterize its order, family, and finally its species. The view is not that the human embryo’s development recapitulates
The adult forms of lower animals. Instead, the human and the fish species occupying different environments and having different life-styles (Owen 1849). (e.g., fish and mammals) became later an important line of evidence for the common ancestry, whereas the approach of Natural Theology could not explain why the same structures occurred in species occupying different environments and having different life-styles (Owen 1849).

3. Homology (ii) after the advent of evolutionary theory

With the advent of evolutionary theory, previous morphological and taxonomic notions became reintegrated in the light of phylogeny (46). Homologies came to be viewed as being due to common ancestry, morphological types were interpreted as shared body plans inherited from an ancestral type, and taxa came to be conceived as branches of the tree of life. This interpretation of previous ideas was already advocated by Charles Darwin (1809–1882) in Chapter 13 of the Origin of Species (1859), but it received its most complete implementation by the discipline of evolutionary morphology (49), as promoted by Carl Gegenbaur (1825–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1817–1901) in Great Britain (Lankester 1870). As one of the most defining disciplines within all of biology in the second half of the nineteenth century, evolutionary morphology (46) was less concerned with the study of the mechanisms of evolutionary change (such as natural selection (46)), but consisted in a thoroughly phylogenetic approach in morphology (46) and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution (46).

It is often (c)asually assumed that evolutionary theory introduced a novel homology concept: an ‘evolutionary’ homology concept defined in terms of common ancestry, but this interpretation ignores the continuity that existed in the practice of nineteenth century morphology (49), including the actual use of the homology concept, and is based on the flawed essentialism story about pre-Darwinian biology (Amundson 2005). Even though homology came to be defined in terms of common ancestry, evolutionary morphologists did not read off homologies from phylogenetic comparison (and the classification system), but instead established homologies using the positional and embryological criterion, just like morphologists in the first half of the nineteenth century (Russell 1916). Known homologies formed the basis for detailed morphological comparison, and only in the last step were phylogenetic trees set up. In addition to not introducing any novel concept of homology, the advent of evolutionary theory did not change what researchers attempted to achieve by the use of the homology concept. Throughout the nineteenth century, this concept was used for the purpose of morphological comparison and the classification of species. Overall, rather than overturning previous practice, evolutionary morphologists made existing practice more sophisticated by prescribing traditional notions in the light of common ancestry (Coelem 1976).

An important element of theoretical continuity across pre- and post-Darwinian biology was given by development. In the first half of the nineteenth century, embryological ideas had been used to see the nature of homology and the shared morphological organization (46) of different species. After the advent of evolutionary theory, definitions of homology as the common development of structures in different species—on line with the embryological scheme—were already common (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of nature of homology and the shared morphological patterns as two parts of one coin, by viewing phylogenetic patterns in analogy to patterns of development and sometimes using assumptions about developmental processes to theorize about the mechanisms of evolutionary change, in particular in the models of recapitulationism, the biogenetic law (46) and the ontogenetic recapitulationist pattern postulated by the biogenetic law (46) (i.e., features of early embryonic development that originated late in ontogeny (46), such as larval adaptations to particular aquatic lifestyle-patterns and the mammalian placenta (46)). These exceptions were acknowledged by proponents of the biogenetic law (46) and led many other evolutionary morphologists to adopt more sophisticated views about the relation of evolution (46) and development (Hall 2000). In particular, comparative embryological studies provided an additional source of data to assess homologies and establish hypothesis about phylogenies and patterns of morphological evolution (46), keeping development germane to evolution (46) even without an adherence to the alleged biogenetic law (46).

Around the turn of the century, however, evolutionary morphology (46) lost its importance, largely ceding to experimental embryology (46) (developmental mechanics) as an approach concerned with the experimental study of the processes that led to the formation of the organism (46) and comparative anatomy (46) and comparative embryology (46) (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 (46). 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 thus which ontogeny evoked from which ancestral features. The symphomatic debate concerned the origin of paired fins in fish (46), a question central to the evolution (46) of vertebrate appendages (and still a core issue for contemporary studies). The gall-arch theory claimed fins to be derived from the 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 (continuous) longwise along the fish side, and that later evolved rays were woven into pectoral and pelvic fins. This theory was favored by embryological methods, viewing other taxa as representing the primitive condition in a given arch. The conflict between anatomical and embryological methods was never resolved. The historical consequence was that many young researchers who could have entered evolutionary morphology (46) preferred to work in experimental embryology (46) instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). From this period there is the conceptual question of what to do with the analysis 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 (46) and sometimes using additional criteria (e.g., features of early embryonic development that originated late in ontogeny (46), such as larval adaptations to particular aquatic lifestyle-patterns and the mammalian placenta (46)), it is important to note that these particular features originated in an ancestral species and has been inherited to all its descendants, a situation called homoplasy. (The phylogenetic tree is obtained by the study of many different characters, where the most likely phylogeny is that 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 (46)).

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, Briggs and Giffiths 2007). In addition to traditional anatomical structures, anatomy (46) introduced the idea that behavioral patterns in different species can be homologous. With the rise of molecular biology, genes (46), proteins, and other molecular structures have become homologous, making possible the fields of molecular phylogeny (46) and evolution (46) which establish phylogenetic trees based on molecular data (46). The function of homologous structures, developmental processes, and developmental modules are often viewed as homologous (46).

It is an important insight that homology on one level of organization (46) must not be confused with and cannot be reduced to homology on another (e.g. lower) level (Rennane 1961). Adult anatomical features are built by certain developmental processes based on the action of particular genes (46), so that it originally seemed reasonable to assume that homologous anatomical structures develop by means of the same developmental mechanisms (in line with the action of particular genes (46), and the involvement of homologous genes (46)). But this is not so, as characters on different hierarchical levels (e.g., the molecular, the developmental, the morphological, the ecological) can be related to the same ancestral character (aka homology (46)). This can lead to the situation where homologies in structures in two
extrant species develop out of non-homologous developmental precursors, by means of different developmental processes or based on non-homologous genes (Hall 1995, 2003, Raff 1996, Wagner and Misof 1993). For instance, a homologue such as the alimentary canal (in different vertebrates can be formed from the roof of the embryonic gut cavity (as in sharks), the floor (lampreys), the roof and floor (amphibians) (or from the embryonic disc (reptiles). Homologous structures can even develop out of different germ layers (in different species (De Beer 1971). Conversely, in different extrant species the same gene can be crucially involved in the development of the non-homologous anatomical structures. For instance, an ancient gene such as pair-rule is important for the development of both the compound eyes of insects and the outer eyes of vertebrates, which did not involve from a common ancestral eye. In general, a gene is not homologous as any structure develops based on the influence of many developmental and genetic resources, so that some developmental components can in the course of evolution gradually change and in a stepwise fashion be replaced by others (while the resulting anatomical structure remains) unless some of the developmental-genetic components do not homologues any longer. Or a gene can acquire (be co-opted) for an additional function and finally lose its original developmental function.

These findings resolve the two puzzles surrounding the embryological criterion of homology (maintaining that homologous structures develop out of the same embryonic precursors), which in particular led to the clash (mentioned in Section 3) between approaches within nineteenth century evolutionary morphology (preferring either adult morphological data or embryological data in phylogenetic reconstructions). The criterion turns out, nevertheless, that homology on every level of organizational organization (i.e., to be assessed based on phylogenetic trees, and such phylogenies demonstrate that homology of developmental and anatomical structures can be dissociated, and more generally that characters on different levels can develop independently of each other. The failure of the traditional embryological criterion does not mean that developmental data is irrelevant for phylogenetic reconstruction and evolutionary theory. On the contrary, development enters as a new hierarchical level of organization, on which evolution takes place and that yields independent characters relevant for the establishment of phylogenies.

In the last few decades, novel and different theoretical approaches to homology have been proposed (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 general description of a property of a taxon, such as the presence or absence of a certain structure, or a certain behavior. A character state is the expression of this property in an individual. The concept of a character state is important for the study of evolution, as it allows for the assessment of evolutionary trends and patterns.

The advent of evolutionary developmental biology, recently developed approaches to homology have been introduced (Roth 1988, Wagner 1989b, 1996), sometimes advocated as a so-called biological homology concept (Wagner 1993a, Laubichler 2000). Evolutionary developmental biology is generally concerned with the development of the theme of the evolution of the evolutionary morphological theme (i.e., the developmental theme of evolution). But 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 general description of a property of a taxon, such as the presence or absence of a certain structure, or a certain behavior. A character state is the expression of this property in an individual. The concept of a character state is important for the study of evolution, as it allows for the assessment of evolutionary trends and patterns.

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