Essay: Homology

By: Brigandt, Ingo

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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.

2. Homology in pre-evolutionary biology

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 (2). Thus, the position of homology and analogy in different species was controversial. (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 (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, 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 assumes that similar roles for similar structures in different species retain their relative positional 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 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 comparing embryology 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 (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 cladistics, homologies came to be consistently assessed by means of the distribution of character 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 and molecular evolution made prominent the idea that molecular structures such as genes 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 are evolutionary units of organisational (5).

Furthermore, homologies on different hierarchical levels need not align: there are many cases where a morphological structure homologous in two species develops by different developmental processes and/or by the involvement of non-homologous genes (6). 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 where homologies occur. Furthermore, apart from taxic and transformational approaches to homology (discussed in Section 4), particular importance are developmental approaches to homology (sometimes called a biological homology concept (7)). 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 (8), an issue which is central to contemporary evolutionary developmental biology (9).

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).

2. Homology in pre-evolutionary biology

The long term 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 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 homology originated with the recognition that the same structures exist in less closely related species (mammals and birds, or even mammals and fish) and that the sameness of morphological units is independent of their function. 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 (Apel 1887).

In the German context, the relevance of Johann Wolfgang von Goethe (1749–1838) and other morphologists such as Lorenz Oken (1779–1815) is well known. For the tradition of Naturphilosophie, von Baer’s laws of embryology, with the claim that the embryo has the very same development in the beginning, but then their developmental trajectories diverge. Thus, the so-called ‘formative drive’ (11) must be the right point of reference. Instead, one has to compare the adult form of lower animals with the embryonic stage of higher organisms, thereby recovering otherwise unnoticed homologies.

In France, pivotal importance was the work of Etienne Geoffroy (1763–1825). While previous anatomists, including Georges Cuvier (1769–1832), had assumed that many vertebrate structures were present in only one of the seven vertebrate classes (fishes, reptiles, birds, mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ posited the unity of functional organization. More precisely, his theory of analagoge (using the term analogue for what we now call homologue) claimed that all vertebrates consist of the same number of basic building elements (Geoffroy Saint-Hilaire 1818). Later he even attempted to homologize structures from different Cuvierian embranchements (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 the positional criterion and the concept of homology, due to the influential idea of développement. Geoffroy’s principe de connexions stated that what matters is the relative position of structures and the way in which they are topologically related to and connected with each other in an organism. For instance, the same muscles are innervated by the same nerves in different species. Homologies in different species may vary in size and shape, but the different homologies composing a body maintain their relative position (Le Guyader 2004, 30–32). This yields a way of recognizing homologies (even across unrelated species where a structure differs substantially in its form and function), nowadays called the positional criterion.

The French tradition of ‘philosophical anatomy’ was continued and developed by Geoffroy’s disciple Etienne René Augustin Serres (1786–1868), among others. It established an important point of contact between embryology and the concept of homology, due to the influential idea of recapitulation, i.e., the view that the development of higher animals recapitulates the adult forms of animals lower on the scale. Recapitulationism in the pre-Darwinian context was dubbed the Mekel-Serres law by (Russell 1916), as already the German anatomist Johann Friedrich Meckel (1769–1833) had developed the idea in his 1811 essay Sketch of a Portrayal of the Parallel that Obtains Between the Embryonic Condition of Higher Animals and the Permanent Condition of Lower Animals (12). Meckel’s (1769–1831) expressed similar views at the same time). Serres used the idea to defend the general validity of Geoffroy’s unity of organic composition tenet, by arguing that comparing adult forms only might be the wrong point of reference. Instead, one has to compare the adult form of lower animals with the embryonic stage of higher organisms, thereby recovering otherwise unnoticed homologies.

Furthermore, the development of the embryo with reference to the idea of a natus formativus (formative drive) (13), which is a force guiding the development to the final adult stage. The fact that the development of a lower animal is only an initial segment of the developmental sequence of a higher animal was explained by the claim that lower animals have less of this formative drive (14). Serres’s ‘theory of the arrest of development’ (his name for recapitulation) was closely tied to his study of teratology (15). Malformed organs in higher animals were viewed as structures from an organism on a lower level of the same order, and thus an embryological theory that explained homologies across species and included an account of morphological relations between normally and abnormally developed organisms. (Geoffroy used these ideas on teratological development for a proto-evolutionary theory, by viewing malformations as being due to external influences on the embryo and assuming that the environment was capable of directly acting on the developing embryo so that a sort of evolutionary change resulted.)

Apart from homology’s role in comparative anatomy, comparative embryology led to a major theoretical enrichment of the concept of homology and the practice in which it figured. In particular, what is now called the embryological criteria of homology found its first clear expression in the work of the Estonian comparative embryologist Karel Ernst von Baer (1792–1876). Von Baer’s embryological theory was in fact part of his broader organismic theory. In fact, as a matter of account, he conceived of the organism (the ‘same organ’) in different species. (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 (14)). 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.

Von Baer’s theory of comparative development—assuming a parallel early development of two species followed by divergence—entails a criterion of homology. (He did not use a specific term for homology, but simply spoke about the ‘same organ’ in different species.) On his account, the identity of a structure is determined by its mode of development, and one determines whether two adult structures in two
species are homologous by tracing the developmental processes of these structures back to its embryonic precursors, up to the point where the embryos of the two species are so similar that it is obvious whether the two species are actually the same ones. In short, homologous structures have the same development in that they develop out of the same embryonic precursor. On these grounds, von Baer denied that the ganglia on the ventral side of insects are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the neural tube [50] that only the vertebrate type possesses. Similarly, though the tracheae of insects are organs to conduct air, they are not the same organ as the windpipe in vertebrates, due to their distinct modes of development. As in both cases structures with the same function (conducting air) originate via different developmental mechanisms, nyhart [11] was immediately picked up by prominent anatomists and physiologists. The positional criterion could be applied not only to adult structures but also to different life history stages; but only the embryological criterion involved the tracing of individual ontogenies. The embryological criterion provided a widely used tool to establish homologies across species and augmented the use of phylogeny [41] for morphological studies and theories about the structural relationships of different species (Lorenz 1982). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more natural formulation of the germ layer theory, the embryological criterion came to imply that homologous structures always develop from the same germ layer.

Before the advent of Darwinian evolutionary theory, the pinnacle of the biological practice based on the homology concept was the work of the British anatomist Richard Owen (1804—1892). By coining the distinction between ‘homology’ and ‘analogy’, Owen established a terminological framework, which made explicit that homology as samseness of structure is independent of a structure’s function and shape. While defining an analogy as the same organ or organism in different taxa, Owen stated that ‘the same organ in different animals under every variety of form and use shows a result of analogous development in common’ (Owen 1843, pp. 374, 378). In his early attempts at the use of the phrase analogy, Owen employed the phrase development to indicate a relationship of homology. In addition to a clear account of the criteria and morphological nature of homology, Owen developed a systematic description of the skeleton across different kinds of vertebrates, which became standard by offering a simpler and more unified terminology of the vertebrate bones than the names used by earlier anatomists (Owen 1846, Rupke 1994).

### 3. Homology after the advent of evolutionary theory

With the advent of evolutionary theory, previous morphological and taxonomic notions became reinterpreted in the light of phylogeny [4]. 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 the Swedish professor of anatomy Carl Gegenbaur (1820—1903) and Ernst Haeckel (1834—1919) in Germany and Edwin Ray Lankester (1847—1909) in Great Britain, respectively. As one of the most inspiring disciplines across all of biology in the second half of the nineteenth century, evolutionary morphology [5] was less concerned with the study of the mechanisms of evolutionary change (such as natural selection), but consisted in a thoroughly phylogenetic approach in morpholog [45] and anatomy, including the establishment of phylogenetic trees and patterns of morphological evolution [46].

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 ‘idealistic’ homology concept defined in terms of embryonic differentiation. However, homologous structures in different species—in life with the embryological criterion—were still common (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of ontogeny [44] and phylogeny [43] as 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 the early version of the concept of homologous structures, the homology of characters was evaluated based on the distribution of features in several (not just two) extant species. This can lead to the situation where homologous structures in two species are the starting point, and the homology of characters is evaluated based on the distribution of features in several (not just two) extant species.

### 4. Development and hierarchy. Approaches to homology

Around the turn of the century, however, evolutionary morphology [41] lost in significance, largely ceding to experimental embryology [43] (developmental mechanics) as an approach concerned with the study of the experimental model organisms. The experimental embryology did not have a significant impact on the interpretation of homology and the development of phylogenetic trees. The embryological criterion was applied to establish homologies across species and augmented the use of phylogeny for morphological studies and theories about the structural relationships of different species.

### 5. Molecular and developmental homology

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 evolutionary theory did not really 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 morphologyists made existing practice more sophisticated by interpreting traditional notions in the light of common ancestry (Coley 1996).

An important element of theoretical continuity across pre- and post-Darwinian comparison was established by development. In the first half of the nineteenth century, embryological ideas had been used to account for the nature of homology, and morphological and taxonomic notions were explained in terms of embryology. The idea that homologous structures in different species—in life with the embryological criterion—were still common (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of ontogeny and phylogeny as 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 the early version of the concept of homologous structures, the homology of characters was evaluated based on the distribution of features in several (not just two) extant species.

### 6. Developing an approach to morphology

The past few decades have been of intense interest in the concept of homology, making possible new interpretations and increased theoretical perspectives of homology have been proposed (Donoghue 1992, Brigandt and Griffiths 2007). In addition, the increased attention on the role of molecular biology, proteins, and other molecular structures came to be homologized, making possible the fields of molecular phylogeny [4] and evolution [47] which establish phylogenetic trees based on molecular data and trace the evolution of gene and protein lineages. Moreover, developmental features such as gene functions and expression patterns, developmental processes, and developmental modules are now considered to be homologous. As a result, early characters on the ontogenetic tree are increasingly being recognized as homologous.

It is an important insight that homology on one level of organization [48] must not be confused with and cannot be reduced to homology on another (e.g., lower) level (Remane 1961). Adult anatomical features are built by certain developmental processes based on the action of particular genes [49], 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 [50]. But this is not so, as characters on different hierarchical levels (e.g., the molecular, the cellular, the anatomical, the physiological) are not necessarily homologous. In the same way, gene expression patterns in two extant species develop out of non-homologous developmental precursors, by means of different developmental processes or based on non-homologous genes [49] (Hall 1995, 2003; Raff 1996, Wagner and Mialon 1993). For instance, a homologous muscle group [51] in different vertebrates can be formed from the roof of the embryonic gut cavity (as in sharks), the floor (lampreys), and the roof (lampreys) of the pharynx (as in their respective homologs). In different species (De Beer 1971). Conversely, in different extant species the same gene can be crucially involved in the development of non-homologous anatomical structures. For instance, an ancient gene such as fox-3 is important for the development of both the fly’s eyes of insects and the camera eyes of vertebrates, which did not involve from a common ancestral eye. Whole genomes, in general terms, is possible as any structure develops based on the influence of many molecular biology, genes [48], proteins, and other molecular structures came to be homologized, making possible the fields of molecular phylogeny and evolution which establish phylogenetic trees based on molecular data and trace the evolution of gene and protein lineages. Moreover, developmental features such as gene functions and expression patterns, developmental processes, and developmental modules are now considered to be homologous. As a result, early characters on the ontogenetic tree are increasingly being recognized as homologous.
differing levels can evolve independently of each other. The failure of the traditional embryological criterion does not mean that developmental data is irrelevant for phylogenetic reconstruction and evolutionary theorizing. On the contrary, development enters as a new hierarchical level of organization in which evolution places 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 and approaches to homology. To explore and a character state. A (properly speaking) is a homolog, i.e., a morphological unit present in many individuals and which can take on a different form 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 undergoes gradual change from one state to another. The taxic approach as the dominant perspective on homology in systematics focuses on how a certain character state is shared by a taxon. Here situations are relevant where the character’s state in ancestral species is significantly different from its state in the descending species B (the character’s ‘pleiomorphic’ condition in A vs. the ‘apomorphic’ condition in B), while all extant 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 taxon of which B is the most recent common ancestor.

With the advent of developmental biology (Brigandt 2003), recent developments approach to homology have been introduced (Roth 1988, Wagner 1989b, 1996), sometimes advocated as a so-called “biological homology” (e.g., Pfenninger 2006, Empson 2007). Homology can generally be considered as a developmental basis of the evolution (of morphological organization (Brigandt 2003), and developmental approaches to homology focus on the developmental basis of the evolution (of characters (homologues). One feature to explain is how the developmental-morphological constitution of organisms makes it possible that a character is inherited across generations and often retains its identity as the same (homologous) character across species, while at the same time undergoing change in its 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 evolution (Brigandt 2003). Given that characters on different levels of organization (Brigandt 2003) can evolve independently of each other, even though an anatomical structure develops based on developmental processes and the action of genes (Roth 1988) (so that in development there are close cause-effect relations among characters on different levels), there are apparently partial developmental dissociations among these characters and functionally independent entities of morphological characters. Therefore developmental approaches to homology are germane to the explanation of evolvability as well as modularity in evolution (Brigandt 2003) and development. Since homologues have to evolve in the first place, to explanations of evolutionary novelties exists. Traditional morphology (Wagner 1988), including pre-evolutionary morphology (Wagner 1988) and comparative anatomy (Wagner 1988), was fundamentally concerned with understanding morphological organization (Wagner 1988). Modern evolutionary developmental biology (Wagner 1988) continues this quest, making explicit that morphological organization (Wagner 1988) is about the evolutionary potential of characters to evolve. Using the tools of molecular, cellular, and developmental biology, it promises to offer a mechanistic explanation of the developmental basis of morphological evolution (Wagner 1988).

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Sources

31. Homology is a central concept of comparative and evolutionary biology, referring to the presence of similar body 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 pressures 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 the fact the homology concept has a rich history and currently is the subject of extensive theoretical reflection, resulting in different contemporary approaches to homology.

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