Essay: Homology [1]

By: Brigandt, Ingo

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1. Overview


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Acknowledgements

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1. Overview

Homology [4] 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 [5] 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 [6]. These similarities result from certain mechanisms and it is not a fact that structures 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 [7]). 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 phylegetic nature of homology, the homology concept was introduced in early nineteenth century comparative anatomy and embryology [8], 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 criteria stipulated that homologous structures in different species retain their relative positional forspings. 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 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 cases of homology discovery possible, as the early developmental stages [9] 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 [10] (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 phylegetic systematics [11], 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 [12] and molecular evolution [13] made prominent the idea that molecular structures such as genes [14] 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 defined by the organization of the organism [15]. 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 [16]. 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 [17] 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 [18] 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 [19]). 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 phylogeny [20], as an issue which is central to contemporary evolutionary developmental biology [21].

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.


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 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 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 1887).

In the German context, the relevance of Johann Wolfgang von Goethe (1749–1832) and other morphologists such as Lorenz Oken (1779–1815) is well known. For the tradition of Naturphilosophie [22], homology would be the name of the only category of nature that it emphasized. Of particular concern was what is nowadays called ontogeny, i.e., the repeated occurrence of the same morphological unit in one and the same individual. For instance, the famous vertebra theory of the skull maintained that the different skull bones are in fact transformed vertebrae (Nyholt 1995, Rupke 1994, Russell 1916).

In France, of pivotal importance was the work of Etienne Geoffroy (1772–1844). While previous anatomists, including Georges Cuvier (1769–1832), had assumed that many vertebrate structures were present in only one of the two vertebrate classes (fishes, reptiles, birds, mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ posited the unity of organic composition. More precisely, his theory of analogy (using the term analogie 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 Cuvier’s embranchements (vertebrates, mollusks, articulates, radiales), which unlike contemporary phylogeny were defined by Cuvier in terms of functional organ systems. This triggered the famous public dispute between Cuvier and Geoffroy in 1830, but the disagreement was rooted in Cuvier’s emphasis on functional considerations in anatomy, whereas for Geoffroy was homology function was subordinated to structure/homology as the same structure could fulfill different functions (Appel 1887). For instance, Geoffroy showed that the furcula, the wishbone assumed to exist only in birds, is present in fishes as well, and he homologized structures of normally developed animals with malformed structures and teratologies which had an altered or no function. Geoffroy is so important in this discussion because he introduced a major criterion of homology. His 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. Homologues in different species may vary in shape and function, but the different homologues composing a body maintain their relative position (Le Guaudier 2004, 30–32). This yields a recognition of homologues (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 Renaud 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 organic scale. Recapitulationism in the pre-Darwinian context was dubbed the Méckel-Serres law (by Russell 1916), as already the German anatomist Johann Friedrich Meckel (1781–1833) had defended the idea in his 1811 essay, ‘Ein Schick of a Portrayal of the Parallel that Occurs Between the Embryonic Condition of Higher Animals and the Permanent Condition of Lower Animals’ (Meckel 1811; Lorenz Oken [22] 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 may 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, he maintained that development with reference to the idea of a nuaux formatives (formative drive [23]), which is a force guiding the development to the final adult stage. The fact that 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 [24]. Serres’s theory of the ‘arrest of development’ (his name for recapitulation) was closely tied to his study of teratology [25]. Malformed organs in higher animals were viewed as structures from an organism on a lower level of the same type and 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 fetus [26], so that a sort of evolutionary change resulted.)

Apart from homology’s role in comparative anatomy, comparative embryology [27] 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 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 his von Baer’s laws of comparison, an attempt to account for the similarity of adult organisms, which he summarized in four ‘laws’, later referred to as von Baer’s laws [28] (von Baer 1828). On this theory, the early embryos of different vertebrates cannot be distinguished from each other, later in development successive differentiation [29] takes place in that 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 chicken [30] embryos have the very same development in the beginning, but then their developmental trajectories diverge. Thus, rather than forming on a linear arrangement of different animals groups on a complexity scale (as recapitulationism does), von Baer endorsed a parallel between development and the hierarchical organization of the taxonomical system. Each individual has generic features that characterize it as belonging to an order, but also more specific features that put it in a particular family. Von Baer’s claim was that the generic features develop first, while the more specific features develop subsequently.

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 development 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 precursors 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 ganoid on the ventral side of insects are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the general tube [8] 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 (e.g., to conduct air) develop in separate lineages, it was concluded that they are not homologous. This evidence 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 [9] for morphological studies and theories about the structural homologies of different species (Lenoir 1982). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more formal 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 terminology, which made explicit that homology as sameness of structure is independent of a structure’s function and shape. While defining an analogy as a structure or organ ‘bearing no relation to any other part of the body’, homology “has the same function as another part or organ in a different animal”, a homologous is “the same organ in different animals under every variety of form” (Owen 1843, pp. 374, 378). In his early days Owen used the term homology to mean the physical resemblance of embryonic morphological and embryological systems of different species, 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).

Over all, already during the pre-Darwinian period the homology concept proved to be a vital tool for morphological practice and theorizing [8]. It breaks down an organism into its natural bodily units—some of which are homologous in different species, while others are not. Homologous structures are formed (originally continuous) lengthwise along the same line(s), that is to say in homologous tissues or embryonic modules. As a result, homology was often seen as an 'idealistic' homology concept defined in terms of morphological types. However, this interpretation ignores the continuity that existed in the practice of nineteenth century embryology. Evolutionary morphologists who based their work on the use of adult anatomical system as the basis of their arguments, were known, i.e., features of early embryonic development that originated late in ontogeny [9].

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 phylogenetics. 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 a number of prominent anatomists, which is the origin of the modern concept of homology [4] and including the establishment of phylogenetic trees and patterns of morphological evolution [5].

It is often (tautologically) 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 ‘idealist’ homology concept defined in terms of the uniformity of embryological pattern. But this is not the case. [6] In fact, homology was always defined in terms of common ancestry, and this is also true of the modern concept of homology. [7] The distinction is not between homology and analogy, but between the embryological and developmental criterion. For example, all fish, amphibians, and insects share the same basic body plan, which is the occurrence of similar character states in two species not due to common ancestry (but parallel evolution). The gill-arch theory claimed fins to be derived from the two hindmost gill arches, which had migrated from the head to form the pelvic and pectoral fin girdles, with the rays of the fins formed by the fusing of separate bones during development. Homology also links those natural bodily units across species as the same structures. Individualizing biological characters in terms of homology (as opposed to another scheme such as analogy) permitted general morphological descriptions applying to larger groups of animals (e.g., vertebrates and their skeleton). [8] It triggered theoretical reflections on the developmental-morphological features generating the repetition of patterns across species (and within organisms in the case of serial homology) and the variation of these corresponding morphological units. In taxonomic practice, homology was defined as the similarity of structures that have been derived from a common ancestor. This implies that homologous structures in taxonomically unrelated species (e.g., fish and mammals) 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 species occupying different environments and having different life-styles (Owen 1849).

Around the turn of the century, however, evolutionary morphology [9] lost in significance, largely ceeding to experimental embryology (developmental mechanics) as an approach concerned with the study of experimental model organisms. Homology and embryology did not come into conflict or have a deconstructive impact on each other. Embryology and morphological 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 evolutionary theory of evolution really made which researchers attempt to achieve by using the homology concept. Throughout the nineteenth century, this concept was used for the purpose of morphological classification and the comparison of species. Overall, rather than overturning previous practice, evolutionary morphologists made existing practice more sophisticated by interpreting traditional notions in the light of common ancestry (Coleman 1976).

An important element of theoretical continuity across pre- and post-Darwinian Morphology was established using development. In the first half of the nineteenth century, embryological ideas had been used to account for the nature of homology. Both morphological and embryological methods were used to establish homologies in Chapter 13 of the Origin of Species (1859). Even though evolution theory came to be defined in terms of common ancestry, evolutionary morphologists did not refer homologies from off homologies from phylogenetic trees (showing common ancestry), but instead established homologies using the positional and embryological criterion, Just like morphologists, who used the positional criterion for homologies, 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 criterion of homology, the advent of embryological theory did not really mean that researchers attempted to achieve by using the homology concept. Throughout the nineteenth century, this concept was used for the purpose of morphological classification and the comparison of species. Overall, rather than overturning previous practice, evolutionary morphologists made existing practice more sophisticated by interpreting traditional notions in the light of common ancestry (Coleman 1976).

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 homoplasy. The phylogenetic tree is obtained by the study of many different characters, where the most likely phylogenies 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 paralell evolution).

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 (J. Hall 1995, 2003, Raff 1996, Wagner and Alberch 1996, Alberch and Wagner 2004, Alberch 2005). An important reason for this intensification of interest was the realization that homologous structures are a complex of gene and protein lineages. Moreover, developmental processes such as gene functions and expression patterns, developmental processes, and developmental organizers are known to be conserved across species. As a result, homologous characters on different hierarchical levels (e.g., the use of the embryological criterion). Some evolutionary morphologists, following Gegenbaur, favored the comparison of adult organization, which is the occurrence of similar character states in two species not due to common ancestry (but parallel evolution).

Homology 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).

It is an important insight that homology on one level of organization 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, 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. But this is not so, as characters on different hierarchical levels (e.g., the molecular level) share no homologous genetic ates. For example, an adult skeletal feature may actually consist of several different tissues, with the most likely phylogenies 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).
differently levels can evince 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 (1) on which evolution (2) 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 (Douglas 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Gribandi 2003). While these perspectives are seen as different interpretations that are hard to reconcile, they may very well be compatible accounts that focus on different aspects of an overall homology concept. To explore a character state, it is useful to recall the distinction between a character and a character state. A character (properly speaking) is a homologue, 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 gradient changes at different points in the species tree. The taxon approach as the dominant perspective on homology in phylogenetic 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 A is significantly different from its state in the species A and B, where the character is shared by A and B.

With the advent of developmentally oriented approaches to homology, a new homology concept has been introduced (Roth 1988, Wagner 1989b). The developmentally oriented homology (Roth 1988) focuses on how a certain character state of an organism is acquired during development. In contrast, the traditional approach to homology (Wagner 1989b) focuses on how a certain character state is shared by different organisms. The failure of the traditional homology concept (Wagner 1989b) does not mean that developmental data is irrelevant for phylogenetic reconstruction and evolutionary theorizing.

**Sources**


Homology is a concept intended for evolutionary biology, referring to the present as well as presumed past (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 homoplasmy, 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.

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Processes

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