**Essay: Homology [1]**

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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], 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., 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 [7], 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 [8] 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 [9] 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 homologous structures across 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 [11] and molecular evolution [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 organismal organization [11]. Furthermore, homologies on different hierarchical levels need not align: there are many cases where developmental processes in two different species are not homologous at any level of comparison [11]. 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 [11] 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 [11] where homologies occur. Furthermore, apart from taxonomic and transformational approaches to homology (discussed in Section 4), of particular importance is the homology concept (sometimes called a biological homology concept [12]). The latter attempts 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 [13], an issue which is central to contemporary evolutionary developmental biology [12].

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 [2] 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 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 [14], or even mammals and lizards [15]) 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 [16], homology was one of the manifestations of the unity of nature that it emphasized. Of particular concern was what is nowadays called serial homology, i.e., the repeated occurrence of same morphological unit across one and the same individual. For instance, the famous vertebral theory of the skull 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 Étienne Geoffroy Saint-Hilaire (1772–1844). While previous anatomists, including Georges Cuvier [17] (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds [18], mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ posited the unity of organic composition, and more precisely, his theory of analogue (using the term analogue from the Greek homologuein), which stated 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 [19] (vertebrates, mollusks, arthropods, 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 subdivided into 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 princip de connexions stated that what matters is the relative position of structures and 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 shape and function, but the different homologues composing a body maintain their relative position (Le Guyader 2004, 30–32). This yields a way of recognizing 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 Meckel-Serres concept (by Russell 1916), as already the German anatomist Johann Friedrich Meckel [20] (1781–1833) had defended 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’ [21]. Meckel and Oken [22] expressed similar views at the same time). Serres used his theory to defend the general validity of Geoffroy’s unity of organic composition tenet, by arguing that comparing adult forms only may be the starting point of reference. Instead, one has to compare the adult form of lower animals with the embryonic stage of higher organisms, thereby recovering otherwise unrecognised homologies.

Furthermore, Serres and Geoffroy explained development with reference to the idea of a nusus formative (formative drive [23]), 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 implied by the claim that lower animals have less of this formative drive [23]. Serres’s theory of the arrest of development [24] (his notion 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 scale of being. This yielded 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 the cause of the ‘formative drive’ [23].) 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.

2. **Homology [3] after the advent of evolutionary theory**

The embryological theory of the development of the embryo project encyclopedia (https://embryo.asu.edu)
the adult forms of lower animals. Instead, the human and the
chicken's embryonic development and tissues to develop into homologous structures. In short, homologous structures have the same development in different species. One has little hope of understanding the evolutionary history of a species unless one knows how the species descended from common ancestors.

2. Evolutionary biology and phylogeny.

While defining an analog as a "part of an organism in which the same function is performed in another part or in a different animal," a homolog is the "same organ in different animals under every variety of form and function" (Owen 1843, pp. 374, 379). In his earlier (though hardly in his mature) work Owen made some use of von Baer's embryological method of establishing homologies. 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 1849, Rupke 1994).

Overall, already during the pre-Darwinian period the homology concept proved to be a vital tool for morphological practice and theorizing. Homology breaks down an organism into its natural bodily units—one of which are not obvious even to trained embryologists. For instance, an adult skeleton is made up of bone, cartilage, and connective tissue, and the shape of each bone results from the fusing of separate bones during development. Homology also links those natural bodily units across species as the same structures. Individuating biological characters in terms of homology (as opposed to another scheme such as analog) permitted general morphological descriptions applying to larger groups of animals (e.g., vertebrates and their skeleton). It triggered theoretical reflections on the 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 taxonomic context, it became clear that homologies but not analogues are good guides to natural relations among different species. The establishment of many homologies in taxonomically unrelated species (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 lifestyles (Owen 1849).

3. Homology after the advent of evolutionary theory

With the advent of evolutionary theory, previous morphological and taxonomic notions became reintegrated in the field 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 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 (5), as promoted by Carl Gegenbaur (1825–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1847–1892) in Great Britain (Lankester 1870). As one of the most thriving disciplines within all biology in the second half of the nineteenth century, evolutionary morphology was less concerned with the study of the mechanisms of evolutionary change (such as natural selection) (6), but consisted in a thoroughly phylogenetic approach in morphology (7) and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution (8).

It is often (cursedly) 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 morphological similarity. However, this interpretation ignores a common denominator that existed in the practice of nineteenth century morphology (9), including the actual use of the homology concept, and is based on the flawed essentialism about pre-Darwinian biology (Amundsen 2005). Even though homology came to be defined in terms of common ancestry, evolutionary morphologists did not read off homologies from phylogenetic comparison (and so called classification), 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 criterion 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 interpreting traditional notions in the light of common ancestry (Coleman 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 make sense of the nature of homology and the shared morphological organization (10) of different species. After the advent of evolutionary theory, definitions of homology as the common development of structures in different species—e.g. with embryological homologs—were still common (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of homology as the identity of body plans of different species on the basis of their embryological similarity, considering that the adult features of different species (either in life or from the study of adults) were 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 recapitulationism (11). This originally very influential theory maintained first that 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 homology (12). It triggered theoretical reflections on the mechanisms of evolutionary change (such as natural selection) (13), but consisted in a thoroughly phylogenetic approach in morphology (14) and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution (15).

Around the turn of the century, however, evolutionary morphology (16) was still insufficient, largely ceding to experimental embryology (17) (developmental mechanics) as an approach concerned with the experimental description of the development of the body plan (18) (comparative embryology) and the use of the embryological criterion to assess homology (19) and comparative embryology (20), 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 (21). 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 evolutionary history was correct. The conflict between namely embryological and anatomical methods was never resolved. The historical consequence was that many young researchers who could have entered evolutionary morphology (22) preferred to work in experimental embryology (23) instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). From this period until the end of the nineteenth century the (use of animal 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 (24) (cladistics) in the second half of the twentieth century made a thorough phylogenetic assessment of homologies the only reliable method. Here a tree depicting the phylogeny of several species was used to formulate the evolutionary history of the homologs. 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 phylogeny (25). The (phylogenetic tree is obtained by the study of many different characters, where the most likely phylogeny 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) (26).

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, Bridgant and Griffiths 2007). In addition to traditional anatomical structures, ethology (27) introduced the idea that behavioral patterns in different species can be homologous. With the rise of molecular biology, genes (28), proteins, and other molecular structures as well as evolutionary processes and developmental stages have been shown to evolve independently of each other (Abouheif 1997). This can lead to the situation where homologous structures in two
Sources

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characters and levels (yet to be understood), which permit the independent organisms makes it possible that a character is inherited across generations and often keeps its identity as the same (homologous) character across species, while at the same time undergoing change in its taxon of which B is the most recent common ancestor. This 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 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 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 evolutionary developmental biology, recently developmental approaches to homology have been introduced (Dunnoughue 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Bigrand 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 (Bigrand 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 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 modification in its state from ancestor to descendant. The phylogenetic approach as the dominant perspective on homology in phylogenetic systematics (Brigandt 2003) 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 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.

Given that characters on different levels of organismal classification (organism, species, etc.) can evolve independently of each other, even though an anatomical structure develops based on developmental processes and the action of genes (so that in development there are close causal-functional relations among characters on different levels), there are apparently partial developmental dissociations among these characters and levels (yet to be understood), which permit the independent evolution of characters. Thus phylogenetic approaches to homology are germane to the explanation of evolvability as well as modularity in evolution and development. Since homology has to evolve in the first place, a connection to explanations of evolutionary novelties exists. Traditional morphology, including pre-evolutionary developmental biology, comparative embryology and the understanding of morphological variation (Brigandt 2003) is fundamentally a comparative (ontogenetic) discipline focused on understanding morphological variation (Brigandt 2003) and 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 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.

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Sources

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.

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