Essay: Homology [1]

By: Brigandi, Ingo Keywords: Homology, Morphology

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 [2] 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 [3], 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 [4]). 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 [5], 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 [6] 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 [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 phyletistic systematics [10], 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 [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 [14]. 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 [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 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 (sometimes called a biological homology concept [17]). The latter attempt to explain why and how homologues reappear 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 developmental evolution [18], an issue which is central to contemporary evolutionary developmental biology [19].

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].


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 [20], or even mammals and fish [21]) 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 [22] (1779–1851) is well known. For the tradition of Naturphilosophie [23], 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 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 [24] Saint-Hilaire (1772–1844). While previous anatomists, including Georges Cuvier [25] (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds [26], mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ posited the unity of organic composition. The idea, according to his theory of homologue (the term analogus was another name for homologue) was 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 [27] (vertebrates, mollusks, articulate, 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 fulfill different functions (Appel 1987). For instance, Geoffroy showed that the forelimbs of birds were used only in flight in [28] this (i.e., present in fishes as well, and he homologized structures of normally developed animals with malformed structures and taxonologies, which have an altered or no function. Geoffroy is so important to 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 in the way they are topologically related to and connected with each other in an organism. For instance, the same musciles 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 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 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 [29] (1771–1852) 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” (Meckel 1811). Serres [30] (1779–1851) expressed similar views at the same time. The developmental sequence was used to define 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 unrecognised homologies.

Furthermore, Serres and Geoffroy explained development with reference to the idea of nius formativus (formative drive) [31], 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 [32]. Serres’ theory of the arrest of development (his name for recapitulation) was closely tied to his study of metamorphosis [33]. 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 capable of directly acting on the developing fetus [34] so that a sort of evolutionary change resulted.)

Apart from homology’s role in comparative anatomy, comparative embryology [35] 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 [36] (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 [37] (von Baer 1828). On this theory, while the early embryos of different vertebrates cannot be distinguished from each other, later in development successive differentiation [38] 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 placental mammals, with different life-styles and the mammalian form of the placenta, together with a highly specialized endometrium, constitute the higher evolutionary grade (placental mammals). This view had some attraction in the first half of the nineteenth century, especially for those who opposed the recapitulationist pattern postulated by the Charles Darwin (1809–1882) in Chapter 13 of the Origin of Species (1859), but it received its most complete implementation by the discipline of experimental embryology (1859), as promoted by Carl Gegenbaur (1826–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1827–1901) in Great Britain (Lankester 1870). As one of the most thriving disciplines within all of biology in the second half of the nineteenth century, evolutionary morphology criticized the idea of special creation by introducing the evolutionary concept and the biogenetic law and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution.

The advent of evolutionary theory, which was not only to revolutionize the study of comparative anatomy but also to give rise to the discipline of comparative embryology (see above), was due to many factors, in particular to the establishment of a phylogenetic classification of the existing species. This classification was based on the idea that living organisms change over time and that these changes can be studied by comparing the anatomical structures of different species. This led to the development of a new field of science called comparative anatomy, which was initially called comparative morphological anatomy and later comparative embryology. The development of comparative anatomy was also influenced by the biogenetic law, which states that the development of an organism is guided by the genetic information that is present in the organism's DNA. This led to the idea that the development of an organism is a process that is determined by the genes and that this process is the same in all organisms that have the same genetic information.

While defining an analogue as "a part or organ in one animal which has the same function as another part or organ in a different animal", a homologue 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 nature) work Owen made some use of von Baer's embryological method of establishing homologies. In addition to a clear advantage 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 1848, Rupke 1994).

Overall, 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—some of which were not obvious even to trained observers. For instance, an adult skeleton may actually consist of separate morphological units that result 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 analogy) 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 homologues 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 life-styles (Owen 1849).

3. Homology after the advent of evolutionary theory

The advent of evolutionary theory, previous morphological and taxonomic notions became reintegrated in the light of phylogeny. 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 (1859), as promoted by Carl Gegenbaur (1826–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1827–1901) in Great Britain (Lankester 1870). As one of the most thriving disciplines within all of 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), but consisted in a thoroughly phylogenetic approach in morphology and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution.

It is often (tolerably) 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 characters. However, this interpretation ignores the continuity that existed in the practice of nineteenth century morphology, including the actual use of the homology concept, and is based on the flawed essentialism 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) but instead homologized homologies using the positional and embryological criterion, just like morphologists who opposed the homology concept. The impact of evolutionary theory was not felt until the second half of the nineteenth century, when the concept of homology started to be used in a more general sense, and when the idea of common descent was becoming more widely accepted.

An important element of theological continuity across pre- and post-Darwinian biology was given by development. In the first half of the nineteenth century, embryological ideas had been used in the service of the natural classification and phylogenetic theory. In particular, the embryological concept of homology was used to explain the similarity of adult structures in different species—in line with the embryological concept of homology. This idea was not only a result of the idea of common descent but also of the idea of recapitulation. The idea of recapitulation states that the development of an organism is a process that is guided by the genetic information that is present in the organism's DNA. This led to the idea that the development of an organism is a process that is determined by the genes and that this process is the same in all organisms that have the same genetic information. This led to the idea that the development of an organism is a process that is determined by the genes and that this process is the same in all organisms that have the same genetic information.

Around the turn of the century, however, evolutionary morphology married (in significance, largely due to experimental embryology) developmental mechanics as an approach concerned with the experimental study of model organisms but not with comparative or phylogenetic questions. One factor fueling this development was a clash between comparative anatomy (e.g., the use of the positional criterion) and comparative embryology (e.g., the use of the embryological criterion) and comparative embryology. A new approach to developmental mechanics was required to resolve this contradiction, and this led to the establishment of a new field of science called developmental biology. This field was characterized by the use of experimental techniques to study the development of model organisms, and it was primarily concerned with the study of the genetic and environmental factors that influence the development of an organism. This led to the development of a new field of science called developmental biology, which was characterized by the use of experimental techniques to study the development of model organisms, and it was primarily concerned with the study of the genetic and environmental factors that influence the development of an organism.
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Acknowledgements


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