Essay: Homology

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1. Overview

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 concept of homology 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. 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 homology. 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). 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, an issue which is central to contemporary evolutionary developmental biology.

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.

2. Homology in pre-evolutionary biology

The long 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 (Aeppli 1887).

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, homology was one of the central tenets of the unified nature that it emphasized. Of particular concern was what is nowadays called natural homology, i.e., the repeated occurrence of the same morphological unit in 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 (1769–1832), had assumed that many vertebrate structures were present in only one of the four 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 extended analogism (using the term analogue for what we now call homologue) claimed that all vertebrae consist of the same number of basic building elements (Geoffroy Saint-Hilaire 1818). Later he even attempted to homologize structures from different Cuvierian embranchements (vertebrates, mollusks, articulates, radiates, which unlike contemporary phyla were defined by Cuvier in terms of functional organ systems). This triggered the famous public debate between Geoffroy and Cuvier in 1830, but the disagreement was rooted in Cuvier’s emphasis on morphological units and his argument that 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). 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, an issue which is central to contemporary evolutionary developmental biology.


Appl. 1887.

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 ganglia on the ventral side of insects [34] are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the neural tube [35] that only the vertebrate type possesses. Similarly, though the tissue of the heart, lungs, or 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 (new term, in each case) are derived from different embryological origins, it is 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 embryology [4] for morphological taxonomies and theories about the structural homologies of different species (Lenoir 1986). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more mature formulation of the germ layer theory, the embryological criterion tended to imply that homologous structures always develop from the same germ layer.

Before the advent of Darwinian evolution 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 ‘homologious’ 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 occurring in different species—some of which not related—Owen asserted that existent homologies are only valid if they ascertained to be homologous. Homologization of biological structures 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 repeat structures (and within organisms in the case of serial homology) and the variation of these corresponding morphological units. In anaxiomatic terms it was assumed that homologous structures were the result of spin homologization, and morphological units in taxonomically related species (e.g., fish [36] 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).

3. Homology after the advent of evolution theory

With the advent of evolution theory, previous morphological and taxonomic notions became reinterpreted in the light of thephylogeny. 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 the Origin of Species (Chapter 13 of the 1859 edition). Darwin (and also Owen) developed a standardized terminology, which made explicit that homology as sameness of structure is independent of a structure’s function and shape. In particular, homologization of biological structures 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 repeat structures (and within organisms in the case of serial homology) and the variation of these corresponding morphological units. In anaxiomatic terms it was assumed that homologous structures were the result of spin homologization, and morphological units in taxonomically related species (e.g., fish [35] 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 [4] lost in significance, largely ceding experimental embryology [6] (developmental mechanics) as an approach concerned with the experimental study model organisms studied by pre- and post-Darwinian Morphology usually was developed by way of homologization. In the first half of the nineteenth century, embryological ideas had been used to account for the nature of homology and the shared morphological organization of species. In this context, homology is contrasted with 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 occurring in different species—some of which not related—Owen asserted that existent homologies are only valid if they ascertained to be homologous. Homologization of biological structures 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 repeat structures (and within organisms in the case of serial homology) and the variation of these corresponding morphological units. In anaxiomatic terms it was assumed that homologous structures were the result of spin homologization, and morphological units in taxonomically related species (e.g., fish [35] 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).

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different 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[11] on which evolution[12] takes place and that yields independent characters relevant for the establishment of phylogenies.

In the last few decades, novel and different theoretical approaches to homology have been proposed (Donoghue 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Brigandt 2003). While these perspectives 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 underlying process or approach. Thus it is useful to recall the distinction between the homology concept 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[30], recent developments approaches to homology have been introduced (Roth 1988, Wagner 1989b, 1996), sometimes advocated as a so-called biological holism[31]. Early attempts to recall the distinction between the homology concept 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.


Homology is a central concept of comparative and evolutionary biology, referring to the presence of similar structures (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 contrasting 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.