Essay: Homology [1]

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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 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.

Despite the phylogenetic nature of homology, the homology concept was introduced in early nineteenth century comparative anatomy and embryology, and became an influential aspect of comparative practice well before the advent of Darwinian evolutionary theory. In this period and until the first half of the twentieth century, two main criteria were used to establish homologies across species. The positional criterion 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 of different species are more similar than the respective adult forms. While the positional criterion primarily relies on comparing the adult morphologies of different species, the embryological criterion involves comparing embryology as an additional source of evidence. However, there are cases where both criteria disagree, which historically led to a conflict between approaches favoring the comparative anatomy of adults and those relying on comparative embryology (Section 3 below).

In addition to its central role for biology and its longstanding history, developments in the second half of the twentieth century strongly enriched and diversified the homology concept. With the advent of phylogenetic systematics, homologies were to be constantly assessed by means of the distribution of homologous structures or homologous gene products. 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 evolution and molecular homology made prominent the idea that molecular structures such as gene products 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 homologs exist at different levels of organismal organization. Furthermore, homologies on different hierarchical levels do not align: there are many cases where different developmental processes and/or stages are involved in the homologization of different species. 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 criteria for homologization. Furthermore, apart from taxic and transformational approaches to homology (discussed in Section 4), homologous structures are a source of evidence. This is particularly true for homologies across species. The positional criterion, for instance, is based on the similarity of adult morphologies across species, and is therefore used to infer homologies across species. The embryological criterion, on the other hand, is based on the similarity of developmental processes across species, and is therefore used to infer homologous structures across species.

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

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 lizards) 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, the 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 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 Etienne 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’ postulated the unity of organic composition. More precisely, his theory of ‘analogie (using the term analogie which had been previously used to refer to the idea of a nasus formatus (formative drive) 20 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

Embryology is the study of the embryo, or the development of the embryo, from conception to birth. It is a branch of developmental biology that examines the processes by which an organism develops from a single cell to a complex adult structure. Embryologists study the growth, development, and differentiation of organisms, focusing on the earliest stages of life, including the development of organs and tissues.

Homology, on the other hand, is the study of similarities in structures or functions that are believed to be due to common ancestry. Homologous structures are structures that are derived from a common ancestor, while analogous structures are structures that have a similar function but are not derived from a common ancestor. Homology is a key concept in comparative anatomy and evolutionary biology, helping scientists understand the relationships between different species.

The history of homology spans centuries, with contributions from many scientists and philosophers. The concept has evolved over time, with different criteria and approaches being used to identify homologous structures and functions. This evolution has been shaped by advances in science and technology, as well as by philosophical and cultural influences.

In the early days of comparative anatomy, homology was often based on the idea of parallel evolution, where similar structures were believed to have evolved independently in different species. However, this theory was later overturned by the work of Charles Darwin and others, who proposed the theory of evolution by natural selection, emphasizing the importance of descent with modification.

In the 19th century, the concept of homology was further refined with the development of the theory of evolution. Scientists began to recognize that homologous structures were not just similar in function but also derived from a common ancestral structure. This led to the development of the concept of homology as a key tool for understanding evolutionary relationships and the history of life on Earth.

In the 20th century, advances in genetics and molecular biology provided new insights into homology. The discovery of genes and the genetic basis of evolution led to the development of molecular homology, where homologous structures are defined by genetic sequences and gene products. Molecular homology has become a crucial tool for understanding the history of life and the evolution of species.

Today, homology remains a central concept in comparative anatomy and evolutionary biology, with ongoing debates and controversies about its definition and application. The concept continues to evolve as new technologies and approaches are developed, reflecting the dynamic and ever-changing nature of our understanding of life and the natural world.
the adult forms of lower animals. Instead, the human and the insects are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the embryological criterion comes to imply that homologous structures always develop from the same germ layer.

In addition to not introducing any novel criterion of homology, the advent of evolutionary theory did not really change what researchers attempted to achieve by the use of the homology concept. Throughout the nineteenth century, this concept was used for the purpose of morphological comparison and the classification of species. Overall, rather than overturning previous practice, evolutionary morphologists made existing practice more sophisticated by interpreting traditional notions in the light of common ancestry (Coleman 1976).

An important element of theoreti?cal 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 explain the nature of homology and the shared morphological organization (4) of different species. After the advent of evolutionary theory, definitions of homology as the common development of structures in different species—in line with the embryological criterion—were still common (e.g., Darwin 1890, p. 512). More generally, biologist?s in the second part of the nineteenth century conceived of the adult forms of lower animals as 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 (4), as promoted by Carl Gegenbaur (1826–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1854–1892) 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 (4) was less concerned with the study of the mechanisms of evolutionary change (such as natural selection (4)), but consisted in a thoroughly phylogenetic approach in morphology and anatomy, including the establishment of homologized and homologized, the developmental, the anatomical, the behavioral level) can sometimes evolve independently of each other (Abouheif 1997). This can lead to the situation where homologous structures in two species—in line with the embryological criterion—were still common (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of features to assess homologies and establish hypothesis about phylogenies and patterns of morphological evolution (4), keeping development germane to evolution (4) even without an adherence to the alleged biogenetic law (4).

Around the turn of the century, however, evolutionary morphology (4) was in significant, largely coincident to experimental embryology (4) (developmental mechanics) as an approach concerned with the experimental determination of the steps in the processes of development of the embryo (developmental comparative anatomy [4]). This life history stage) and which later evolved rays and were broken up into pectoral and pelvic fins. This theory was favored by embryological methods, viewing other taxa as representing the primitive condition compared to the gill-arch theory. The conflict between anatomical and embryological methods was never resolved. The historical consequence was that many young researchers who could have entered evolutionary morphology (4) preferred to work in experimental embryology (4) instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). From this period the position (or use of adult 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 embryological criterion to assess homology) and comparative embryology (4) (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 (4). 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 which thus extinct structures evolved from which ancestral features. The sym?matic debate concerned the origin of paired fins in fish (4), a question central to the development of vertebrate appendages (and still a core issue for contemporary studies). The gill-arch theory claimed fins to be derived from the two hindmost gill archs, which had migrated from the head to form the pelvis and pectoral fin girdles, with the rays of the gill arches becoming fins. This hypothesis was supported by the comparison of adult fins and girdles. The rival lateral fin-fold hypothesis assumed that paired fins had evolved from lateral folds that formed (originally continuous) lengthwise along the fish’s side, and which later evolved rays and were broken up into pectoral and pelvic fins. This theory was favored by embryological methods, viewing other taxa as representing the primitive condition compared to the gill-arch theory. The conflict between anatomical and embryological methods was never resolved. The historical consequence was that many young researchers who could have entered evolutionary morphology (4) preferred to work in experimental embryology (4) instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). From this period the position (or use of adult 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.

2. 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, Briggs and Grif?ths 2007). In addition to traditional anatomical structures, ethology (4) introduced the idea that behavioral patterns in different species can be homologous. With the rise of molecular biology, genes (4), proteins, and other molecular structures came to be homologized, making possible the fields of molecular phylogenetics (4) and evolution (4) which establish phylogenetic trees based on molecular data (4). This reflects a general trend in the function of the embryological criterion in biology, and a particular function in the specification of homologous structures, and developmental modules, which are often viewed as homologous across species. The embryological criterion 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).

It is an important insight that homology on one level of organization (4) 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 (4), so that it originally seemed reasonable to assume that homologous anatomical structures develop by means of the same developmental mechanisms, such as larval adaptations to particular aquatic larval development that originated late in phylogenetic analysis (4), such as larval adaptations to particular aquatic larval life-styles and the mammalian placenta (4). These exceptions were acknowledged by proponents of the biogenetic law (4) and led many other evolutionary morphologists to adopt more sophisticated views about the relation of evolution (4) and development (Hall 2000). In particular, comparative embryological studies provided an additional source of data to assess homologies and establish hypothesis about phylogenies and patterns of morphological evolution (4), keeping development germane to evolution (4) even without an adherence to the alleged biogenetic law (4).
Acknowledgements

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Sources


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