Essay: Homology

By: Brigandt, Ingo
Keywords: Homology, Morphology

1. Overview

Homology (1) 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). However, in recent times it is realized that homologies exist 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 is currently 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 criteria referred to similarities in the development of structures in different species; the homologous structures 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 criteria 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 (7) 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 (8) (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 (9) (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 are fallible criteria for establishing homologies understood as structures with a common ancestry (Section 4). The advent of molecular phylogeny (10) and molecular evolution (11) made prominent the idea that molecular structures such as genes (12) 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 not just material parts of organisms (organization (13)). 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 (14). 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 (15) cannot be reduced to homology on another (e.g. lower) level, supporting a non-reductive and hierarchically 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 (16) where homologies occur. Furthermore, apart from taxic and transformational approaches to homology (discussed in Section 4), particular importance are developmental approaches to homology (17) (sometimes called a biological homology concept (18)). The latter attempt to explain why a homologous 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 organization (19), an issue which is central to contemporary evolutionary developmental biology (20).

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 (21).

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 (22), or even mammals and fish (23)) 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 (1779–1851) is well known. For the tradition of Naturphilosophie (24), homology was central to the idea of the unity of nature that it emphasized. Of particular concern was what is nowadays called natural teleology, 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 Etienne Geoffroy (25) (Saint-Hilaire (1712–1844). While previous anatomists, including Georges Cuvier (26) (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds (27), 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 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 classes (e.g. embranchements (28) (vertebrate, molluscs, articulates, radishes), which unlike contemporary phylogeny were defined by Cuvier in terms of functional organ systems. This triggered the famous public debate between Cuvier and Geoffroy in 1830, but the disagreement was rooted in Cuvier’s emphasis on functional considerations in anatomy, whereas for Geoffroy functional variation in an organism was a key factor in understanding homologies as structures with a common ancestry. Furthermore, while Cuvier maintained development with reference to the idea of a naius formativus (formative drive (29)), 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 naius formativus (natus formativus (30)). Thus, homologous organs in higher animals were viewed as structures from an organism on a lower level, the presence of similar traits in different 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 (31) so that a sort of evolutionary change resulted.)

Apart from homology's role in comparative anatomy, comparative embryology led to a major theoretical enrichment of the concept of homology and the practice in it which 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 a more general theory of transformation, in which fact part of his theory is a theory of metamorphosis, a theory of separate development, which he summarized in four ‘laws’, later referred to as von Baer’s laws (32) (von Baer 1828). On this theory, while the early embryos of different vertebrates cannot be distinguished from each other, later in development successively different development (33) takes place in that an embryo acquires the features that characterize its order, family, and finally its species. The view is that not that the human embryo's development recapitulates the adult forms of lower animals. Instead, the human and the chicken (34) and embryo have the very same development in the beginning, but then their developmental trajectories diverge. Thus, rather than focusing on a linear arrangement of different animal 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 developmental 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 [9] are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the neural tube [10] that only the vertebrate type possesses. Similarly, though the tracheae of insects [11] 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 (nerve function and conducting air, respectively) are non-homologous, von Baer underscored that identity of structure is independent of function. This comparative approach to embryology —-are routinely studied using molecular data and trace the evolution of gene and protein lineages. Moreover, developmental features such as gene functions and expression patterns, developmental processes, and developmental modules are exchangeable and can be transferred between organisms [12]. As a result, homologous characters on the one hand, and analogous characters on the other, are routinely homologized.

It is an important insight that homology on one level of organization [13] 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 [14], 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 [15]. But this is not so, as characters on different hierarchical levels (e.g., the molecular, the organismal, the phylogenetic) may be homologous, analogous, or homoplastic. It is a matter of fact that various embryonic structures in two extant species develop out of non-homologous developmental precursors, by means of different developmental processes based on non-homologous genes [16] (Hall 1995, 2003, Raff 1996, Wagner and Ida 1999). The result is that development—-are routinely studied using molecular data and trace the evolution of gene and protein lineages. Moreover, developmental features such as gene functions and expression patterns, developmental processes, and developmental modules are exchangeable and can be transferred between organisms [12]. As a result, homologous characters on the one hand, and analogous characters on the other, are routinely homologized.

It is an important insight that homology on one level of organization [13] 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 [14], 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 [15]. But this is not so, as characters on different hierarchical levels (e.g., the molecular, the organismal, the phylogenetic) may be homologous, analogous, or homoplastic. It is a matter of fact that various embryonic structures in two extant species develop out of non-homologous developmental precursors, by means of different developmental processes based on non-homologous genes [16] (Hall 1995, 2003, Raff 1996, Wagner and Ida 1999). The result is that development—
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 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 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 evolution, 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 character state. A related question is to understand how the different characters (homologues) making up an organism can evolve independently of each other as quasi-independent units of morphological evolution. Given that characters on different levels of organismal organisation 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 causally-functional relations among characters on different levels, there are apparently partial developmental dissociations among these characters and, therefore, the traditional problematic of homology are to the explanation of evolvability as well as modularity in evolution. Since homologues have to evolve in the first place, to explanations of evolutionary novelties exists. Traditional morphology, including pre-evolutionary morphology and comparative embryology, was fundamentally concerned with understanding morphological organisation. Modern evolutionary developmental biology continues this quest, making explicit that morphological organisation is about the evolutionary potential of characters to evolve. Using the tools of molecular, cellular, and developmental biology, it promises to offer a mechanistic explanation of the developmental basis of morphological evolution.

Acknowledgements

I thank Brian Hall for comments on an earlier version of this essay and Lindsey O’Connell for catching some mistakes in a later version. The work on this paper was supported by the Social Sciences and Humanities Research Council of Canada (Standard Research Grant 410-2008-0400).

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 contrasting notion is homoplasies, 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.

Subject

Homology (Biological)

Topic

Processes

Publisher

Arizona State University. School of Life Sciences. Center for Biology and Society. Embryo Project Encyclopedia.

Rights

© Arizona Board of Regents Licensed as Creative Commons Attribution-NonCommercial-Share Alike 3.0 Unported (CC BY-NC-SA 3.0) http://creativecommons.org/licenses/by-nc-sa/3.0/