Essay: Homology [1]

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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 [4] 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 [5], 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 [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 [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 [5] 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 [5] 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 [5] (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 [6] (cladistics), homologies came to be consistently assessed by means of the distribution of clades 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 [6] and molecular evolution [5] 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: molecular, 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 organisational organization [11]. Furthermore, homologies on different hierarchical levels do not align: there are many cases where developmental processes and structures are not homologous [4]. 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 organisation [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 evidence 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 [5] 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 [5] 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 [5] (Section 3 below).


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 [16], even more comprehensively) and that the same morphological structures are 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 [14] (1779–1851) is well known. For the tradition of Naturphilosophie [17], 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 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 France, of pivotal importance was the work of Étienne Geoffroy [18] Saint-Hilaire (1772–1844). While previous anatomists, including Georges Cuvier [19] (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds [16], mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ postulated the unity of organic composition. More precisely, his theory of analogue (using the term analogue for what is nowadays called homologue) established 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 [20] (vertebrates, molluscs, arachnids, 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 scutula, the wishbone assumed to exist only in birds [16], 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 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 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. As a result, it is nowadays often assumed that homology on one level of organisation [11] cannot be reduced to homology on another (e.g., lower) level, supporting a non-reductive and hierarchical view of organisms.

The French tradition of ‘philosophical anatomy’ was continued and developed by Geoffroy’s disciple Étienne Reneau 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 on 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 his theories on teratological development for a proto-evolutionary concept, 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 [20] so that a sort of evolutionary change resulted.

Apart from homology’s role in comparative anatomy, comparative embryology [20] 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 [21] (1792–1876). Von Baer’s embryological theory was in fact part of a critique of recapitulationism, as endorsed be 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 [21] (von Baer 1828). On this theory, while the early embryos of different vertebrates cannot be distinguished from each other, later in development successive differentiation [21] 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 arrest of development [R] as maintained by da Vinci’s. This view is rather that homologous features are acquired, at the same time that other features are shed, and that these features are those which are characteristic of the species to which the individual belongs.
the adult forms of lower animals. Instead, the human and the fish, for instance, are built by certain developmental processes based on the action of particular 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 some of which were not obvious even to trained observers. For instance, an adult skeletal feature may actually consist of separate morphological units, with the adult form resulting 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 homologies but not analogies or homoplasy were good guides to natural relations among different species. The establishment of many 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)

With the advent of evolutionary theory, previous morphological and taxonomic notions became reinterpreted 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 were to become 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, as promoted by Carl Gegenbaur (1825–1903) and Ernst Haeckel (1834–1919) in Germany and Edwin Ray Lankester (1817–1897) in Great Britain (Lankester 1870). As one of the most intriguing 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 tacitly 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 types. However, this interpretation ignores the continuity that existed in the practice of nineteenth century phylogeny, 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 characters (and classifying the common ancestry, instead homologized homologies using the positional criteria, and only in the case of homologous structures in different species. After the advent of evolutionary theory, definitions of homology as the common development of structures in different species—i.e., homologous structures back to its embryonic precursors, up to the point where the entire body of the two species are so similar that it is obvious whether the two species are actually the same ones. In short, homologous structures have the same developmental origin in that they develop out of the same embryonic precursor. On these grounds, von Baer denied that the embryology 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 for morphological studies and theorizing about the structural relations of different species (Lenoir 1882). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more formal formulation of the germ layer theory, the embryological criterion came to imply that homologous structures always develop from the same germ layer.

Before the advent of Darwinian evolutionary 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 embryology and development, Owen distinguished the developmental mechanics (in line with the embryological criterion of homology) and the involvement of homologous genes that 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, 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. But this is not so, as characters on different hierarchical levels (e.g., the molecular, the developmental, the morphological, the organological, and the character levels of Haeckel 1867) can lead to the situation where homologous structures in two

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Sources


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