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 [39], 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 [32].) 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 [9], 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 [32] 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 [4] 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 phylogenetic systematics [5], (cladistics), homologies came to be consistently assessed by means of the distribution of, or homology 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 [41] and molecular evolution [39] made prominent the idea that molecular structures such as genes [11] and proteins can be homologous across species. In general, many kinds of biological entities are nowadays homologised: 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 [31]. Furthermore, homologies on different hierarchical levels need not align: there are many cases where developmental morphology structures in two species develop 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 [31] 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 organization [8] 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 [2]). The latter attempt to explain why 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 morphological evolution [3], an issue which is central to contemporary evolutionary developmental biology [12].

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 [9].


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 idiostyractic 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 [3], or even mammals and lizards [20], 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 [7], 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 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 Saint-Hilaire (1772–1844). While previous anatomists, including Georges Cuvier [16] (1769–1832), had assumed that many vertebrate structures were present in only one of the four vertebrate classes (fishes, reptiles, birds [4], mammals), Geoffroy found homologies across these classes. His ‘philosophical anatomy’ postulated the unity of organic composition. In so doing, he based his entire theory of analogie (the term analogie, rather than homologue) on the idea 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 embranchments [4] (vertebrates, molluscs, 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 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 furcula, the wishbone assumed to exist only in birds [22], 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 states that what matters is the relative position of structures and how the parts 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. Homologies 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 law by (Russell 1916), as already the German anatomist Johann Friedrich Meckel [23] (1781–1833) 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’ [22]. Meckel [18]; Lorenz Oken [14] (1779–1851) expressed similar views at the same time.

Serres used the idea to defend 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 a nusis formavitc (formative drive [25]), 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 may be counteracted by the claim that lower animals have less of this formative drive [25]. Serres’ theory of the arrest of development [his name for recapitulation] was closely linked to his study of teratology [36]. Malformed organs in higher animals were viewed as structures from an organism on a lower level of the scale of being. This yield 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 [38] so that a sort of evolutionary change resulted.)

Apart from homology’s role in comparative anatomy, comparative embryology [4] 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 [26] (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 [26] (von Baer 1828). On this theory, the while the early embryos of different vertebrates cannot be distinguished from each other, later in development successive differentiation [23] takes place in that an embryo acquires the structures 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 fish [15] are homologous to any part of the spinal cord of vertebrates. For the spinal cord develops from the neural tube [31] that only the vertebrate type possesses. Similarly, though the tracheae of insects [30] 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 (n.e.r., air, respiratory) are homologous in the phylogenetic sense [9], they are immediately 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 [40] for morphological studies and theorizing about the structural relations of different species (Lenor 1982). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more natural formation 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 [38] (1804–1882). By coining the distinction between ‘anatomical’ and ‘embryological’ homology, Owen provided an important means of understanding the homology concept at the molecular, 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 same developmental mechanisms (in line with the embryological criterion of homology) and the involvement of homologous modules are often viewed as homologous across species. As a result, nowadays different kinds of characters—including characters on different levels of organismal organization [41]—can be considered homologous at different phylogenetic levels.

3. Homology [4] after the advent of evolutionary theory

With the advent of evolutionary theory, previous morphological and taxonomic notions were integrated in the field of phylogeny [4]. 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 [32] (1809–1882) in Chapter 13 of the Origin of Species (1859), but it received its most complete implementation by the discipline of evolutionary morphology [43], as promoted by Carl Gegenbaur [34] (1825–1903) and Ernst Haeckel [35] (1834–1919) in Germany and Edwin Ray Lankester [36] (1847–1929) in Great Britain (Lankester 1870). As one of the most convincing disciplines within all of biology in the second half of the nineteenth century, evolutionary morphology [34] was less concerned with the study of the mechanisms of evolutionary change (such as natural selection [42]), but consisted in a thoroughly phylogenetic approach in morphology [40] and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution [47]. It is often (c-facily) 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 similarity. However, this interpretation ignores the continuity that existed in the practice of nineteenth century morphology [38], including the actual use of the homology concept, and is based on the flawed essentialism story about pre-Darwinian biology (Amundson 2005). Even though homology came to be defined in terms of common ancestry, embryologists did not read off homologies from phylogenetic comparison (and the classification of species), but instead established homologies using the positional and embryological criterion, just like morphologists. This criterion was used by Haeckel’s biogenetic law hypothesis (1866) in his effort to establish that major body plans are genetically transmitted homologous traits (which is the occurrence of similar character states in two species not due to common ancestry (but parallel evolution)).

Around the turn of the century, however, evolutionary morphology [8] lost significance, largely ceding to experimental embryology [9] (developmental mechanics) as a field of study. This was in part because the Darwinian morphologists had failed to develop a comparative anatomy of the type that was needed to establish the homology [33] among structures across species. This was first recognized by the major works of Haeckel, which were later followed by those of Edwin Ray Lankester (1847–1929) in Great Britain, who was the first to define morphological homology as the occurrence of similar character states in two species not due to common ancestry. For example, 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 had formed from the fusing of separate bones during development. Homology [40] also links those natural body units across species as the same structures. Individualizing biological characters in terms of homology (as opposed to another scheme such as analogy) permitted general morphological descriptions applying to larger groups of species (e.g., vertebrates and their skeleton). It triggered theoretical reflections on the development-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. Within a thoroughgoing phylogenetic approach in morphology [40] and taxonomy, including the establishment of phylogenetic trees and patterns of morphological evolution [47].

Overall, already during the pre-Darwinian period the homology concept proved to be a vital tool for morphological practice and theorizing. Homology [40] breaks down an organism into its natural body units—some of which may be homologous (in line with the embryological criterion of homology) and the involvement of homologous modules are often viewed as homologous across species. As a result, nowadays different kinds of characters—including characters on different levels of organismal organization [41]—can be considered homologous at different phylogenetic levels.
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Acknowledgements

3. Appel, Toby A. and the Camera eyes of vertebrates, which did not involve from a common ancestral eye. In general terms, this is possible as any structure develops based on the influence of many developmental and genetic resources, so that some developmental components can in the course of evolution gradually change and in a stepwise fashion be replaced by others (while the resulting anatomical remodelling remains) until some of the developmental-genetic components no longer homologous or any gene can acquire (be co-opted) for an additional function and finally lose its original developmental function.

With the advent of evolutionary developmental biology, recent developmental approaches to homology have been introduced (Domingue 1992). Typically, different biological disciplines dealing with evolutionary issues have a different perspective on homology (Bridgland 2003). While these 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 overall phenomenon (Bridgland 2007). To explain the main approaches, it is useful to recall the distinction between a character and a character state. A character (properly speaking) is a homologous structure present in many individuals and which can take on different form and function in different individuals or species. A character state is the particular condition (e.g. form) a character has in an individual. The transformational approach to homology, as the traditional perspective in evolutionary biology, focuses on how a character is inherited in a single evolutionary lineage and undergoes gradual modification in its state from ancestor to descendant. The speciose approach as the dominant perspective on homology in phylogenetic systematics focuses on how characters evolve in a shared lineage and the evolutionary potential of characters.

Evolutionary developmental biology and evolutionary morphology is generally concerned with the developmental basis of the evolution of morphological organization. Evolutionary developmental biology is a way of asking about homology and organization: does a structure develop based on developmental processes and the action of genes on the germ layers or is it an organ that is the result of a change in developmental processes or based on different developmental genes. This definition is possible as any structure develops based on the influence of many developmental and genetic resources, so that some developmental components can in the course of evolution gradually change and in a stepwise fashion be replaced by others (while the resulting anatomical remodelling remains) until some of the developmental-genetic components no longer homologous or any gene can acquire (be co-opted) for an additional function and finally lose its original developmental function.

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