Homology is a central concept of comparative and evolutionary biology, referring to the presence of the same bodily parts (e.g., anatomical 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 to a similar function or convergent evolution. 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 criteria of homology—structures in different species retain their relative positional 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 the 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 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 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, cladistics, homology came to be consistently assessed by means of the distribution of character states on phylogenetic trees. The positional and embryological criteria could and were used independently of any phylogenetic tree, but they are fallible for estimating homologies understood as structures with a common ancestry (Section 4). The advent of molecular phylogeny and molecular evolution made prominent the idea that molecular structures such as genes 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 a manifestation of organismal organization. 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 mechanisms and/or by the involvement of non-homologous genes. 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 an additional and independent level of organization where homologies occur. Furthermore, apart from taxonomic and transformational approaches to homology (discussed in Section 4), particular importance 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 underlying evolutionary change in its internal structures. Developmental biology is constant 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

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 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 (Apeil 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 is a central concept 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 (Niharti 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 and 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 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 (vertebrates, mollusks, arthropodes, radices, 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 Geoffroy thought the homologous structures needed to be subordinated to structure/homology as the same structure could fulfill different functions (Apeil 1887). For instance, Geoffroy showed that the furcula, the wishbone assumed to exist only in birds, is present in fishes as well, and he homologized structures of normally developed animals with malformed structures and teratologies, which he assumed to be equally functional. Geoffroy’s theory is so important to this discussion because he introduced a major criterion of homology. His concept of homology failed. 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 where homologies occur. Furthermore, apart from taxonomic and transformational approaches to homology (discussed in Section 4), particular importance developmental approaches to homology (sometimes called the 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 underlying evolutionary change in its internal structures. Developmental biology is constant to understand how homologues can function as units of morphological evolution, an issue which is central to contemporary evolutionary developmental biology.

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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  
is actually one of the main points of evidence for the idea of homology as sameness of structure. After the advent of evolutionary theory, this idea was used for the purpose of morphological comparison and the classification of species. As a result, homology became a standard tool in comparative anatomy and led many other evolutionary morphologists to adopt more sophisticated views about the nature of homology and the shared morphological and molecular patterns of different species.
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 on which evolution takes place and that yields independent characters relevant for the establishment of phylongies.

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 (Briggsand 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 and may also provide complementary approaches. To explore and a character state. A character (properly speaking) is a homologue, i.e., a morphological unit present in many individuals and which can take on a 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 genealogical change from one generation to the next. The taxon approach as the dominant perspective on homology in phylogenetic systems focuses on how a particular character state is shared by a taxonomic group. Here, situations are relevant where the character state in species is significantly different from its state in the species it descends from and the species that state is shared 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 (EDB), recent approaches to homology have been introduced (Roth 1989, Wagner 1989b, 1996), sometimes advocated as a so-called biological homology (Wagner 1996b, 1996c, 2000). For any developmental basis of the evolutionary development of characters (homologues), one feature to explain is how the developmental-morphological constitution of organisms makes it possible that a character is inherited across generations and often remains identical as the (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 organization (homologues) 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 causal-functional relations among character on different levels), there are apparently partial developmental dissociations among these characters and it 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.

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Sources
