Essay: Homology [1]

By: Brigandt, Ingo Keywords: Homology [2] Morphology [3]

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 [6], 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 [7] 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 [6] 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 [6] (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 [8] (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 they are fallible criteria for establishing homologies understood as structures with a common ancestry (Section 4). The advent of molecular phylogeny [9] and molecular evolution [5] made prominent the idea that molecular structures such as genes [10] 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 homologues exist on different levels of organismal organization [11]. 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 [10]. 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 [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 organization [11] 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 [12]'). 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 undergoing evolutionary change in its internal features. Developmental biology is essential to understand how homologues can function as units of morphological evolution [5], an issue which is central to contemporary evolutionary developmental biology [13].

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 [6].

2. Homology [4] 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 [14], or even mammals and fish [15]) 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 [16] (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 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 [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 [14], mammals), Geoffroy found homologies across these classes. His 'philosophical anatomy' posited the unity of organic composition. More precisely, his *theorie d'analogue* (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 [20] (vertebrates, mollusks, articulates, 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 furcula, the wishbone assumed to exist only in birds [14], 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 the way 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. Homologues 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 Etiennne Renaud Augustin Serres (1786–1868), among others. It established an important point of contact between embryology [6] 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 [21] the Younger (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 1811; Lorenz Oken [16] 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 unnoticed homologies. Furthermore, Serres and Geoffroy explained development with reference to the idea of a *nisus formativus* (formative drive [23]), 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 formative drive [23]. Serres's 'theory of the arrest of development' (his name for recapitulation) was closely tied to his study of teratology [24]. Malformed organs in higher animals were viewed as structures from an organism on a lower level of 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 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 [25] so that a sort of evolutionary change resulted.)

Apart from homology's role in comparative anatomy, comparative embryology [6] 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 [27] (von Baer 1828). On this theory, while the early embryos of different vertebrates cannot be distinguished from each other, later in development successive differentiation [28] 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 adult forms of lower animals. Instead, the human and the chicken [29] 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 [11] 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 development 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 [30] 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 (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 [6] was immediately picked 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 [6] for morphological studies and theorizing about the structural relations of different species (Lenoir 1982). A variant of the embryological criterion could also be used by proponents of recapitulationism. After the later more mature 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 [32] (1804–1892). By coining the distinction between 'homology' and 'analogy', Owen established a standardized terminology, which made explicit that homology as sameness of structure is independent of a structure's function and shape. While defining an analogue as a "part or organ in one animal which has the same function as another part or organ in a different animal", a homologue is the "same organ in different animals under every variety of form and function" (Owen 1843, pp. 374, 379). In his earlier (though hardly in his mature) work Owen made some use of von Baer's embryological method of establishing homologies. In addition to a clear account of the criteria and morphological nature of homology, Owen developed a systematic description of the skeleton across different kinds of vertebrates, which became standard by offering a simpler and more unified terminology of the vertebrate bones than the names used by earlier anatomists (Owen 1848, Rupke 1994).

Overall, already during the pre-Darwinian period the homology concept proved to be a vital tool for morphological practice and theorizingHomology [4] breaks down an organism into its natural bodily units—some of which were not obvious even to trained observers. For instance, an adult skeletal feature may actually consist of separate morphological units, with embryology [6] showing that this adult feature results from the fusing of separate bones during development. Homology [4] 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 contexts, it became clear that homologies but not analogies are good guides to natural relations among different species. The establishment of many homologies in taxonomically unrelated species (e.g., fish [15] and mammals) became later an important line of evidence for the idea of 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 [4] after the advent of evolutionary theory

With the advent of evolutionary theory, previous morphological and taxonomic notions became reinterpreted in the light ofphylogeny [9]. 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 [33] (1809–1882) in Chapter 13 of the *Origin of Species* (1859), but it received its most complete implementation by the discipline of *evolutionary morphology [34]*, as promoted by Carl Gegenbaur [35] (1826–1903) and Ernst Haeckel [36] (1834–1919) in Germany and Edwin Ray Lankester [37] (1847–1929) 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 [34] was less concerned with the study of the mechanisms of evolutionary change (such asnatural selection [38]), but consisted in a thoroughly phylogenetic approach in morphology [39] and taxonomy, including the establishment of phylogenetic trees and patterns of morphologicalevolution [5].

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 morphology [39], 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 often to be defined in terms of common ancestry, evolutionary morphologists did not read off homologies from phylogenetic trees (showing common ancestry), but instead established homologies using the positional and embryological criterion, just like morphologists in the first half of the nineteenth century (Russell 1916). Known homologies formed the basis for detailed morphological comparison, and only in the last step were phylogenetic trees set up. 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 theoretical 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 account for the nature of homology and the shared morphological organization [11] 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 (see e.g. Darwin 1890, p. 512). More generally, biologists in the second part of the nineteenth century conceived of *ontogeny [40] and phylogeny [9]* as two parts of one coin, by viewing phylogenetic patterns in analogy to patterns of development and sometimes using assumptions about developmental processes to theorize about the mechanisms of evolutionary change, in particular in the models of Lamarckism [41] and orthogenesis [42] (Bowler 1988). A clear-cut connection betweenevolution [5] and development was given by Haeckel's *biogenetic law [43]*. This originally very influential theory maintained first thatontogeny [40] recapitulates phylogeny [9] and second that ontogeny [40] is mechanically caused by phylogeny [9]. Many exceptions to the recapitulationist pattern postulated by the biogenetic law [43] were known, i.e., features of early embryonic development that originated late inphylogeny [9], such as larval adaptations to particular aquatic life-styles and the mammalian placenta [44]. These exceptions were acknowledged by proponents of thebiogenetic law [43] and led many other evolutionary morphologists to adopt more sophisticated views about the relation of evolution [5] 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 [5], keeping development germane to evolution [5] even without an adherence to the alleged biogenetic law [43].

Around the turn of the century, however, evolutionary morphology [34] lost in significance, largely ceding to experimental embryology [6] (developmental mechanics) as an approach concerned with the experimental study of model organisms but not with comparative or phylogenetic questions. One factor fueling this development was a clash between comparative anatomy (e.g., the use of the positional criterion to assess homology) and comparative embryology [6] (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 [45]. 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 thus which extant structures evolved from which ancestral features. The symptomatic debate concerned the origin of paired fins in fish [15], a question central to theevolution [5] 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 arches, which had migrated from the head to form the pelvic 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 had formed (originally continuous) lengthwise along the fish [15]'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 [34] preferred to work in experimental embryology [6] instead, viewing the pursuit of phylogenetic questions as riddled with subjective methods (Nyhart 1995). Examples from this period show that the positional criterion (or the 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 and embryological criterion (and some additional criteria) that do not presuppose a phylogenetic tree, the advent of phylogenetic systematics [8] (cladistics) in the second half of the twentieth century made a thoroughly phylogenetic assessment of homologies the only reliable method. Here a tree depicting the phylogeny [9] of several species is the starting point, and the homology of characters is evaluated based on the distribution of features in several (not just two) extant species. Homology [4] likely obtains if given the phylogeny [9] the overall feature distribution across species is best explained by the assumption that a particular feature originated in an ancestral species and has been inherited to all its descendants, a situation called synapomorphy. (The phylogenetic tree is obtained by the study of many different characters, where the most likely phylogeny [9] is the one that best explains the distribution of all characters across extant species.) In this context, homology is contrasted with *homoplasy*, which is the occurrence of similar character states in two species not due to common ancestry (but parallelevolution [5]).

4. 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, Brigandt and Griffiths 2007). In addition to traditional anatomical structures, ethology [46] introduced the idea that behavioral patterns in different species can be homologous. With the rise of molecular biology, genes [10], proteins, and other molecular structures came to be homologized, making possible the fields of molecularphylogeny [9] and evolution [5] which establish phylogenetic trees based on molecular data and trace the evolution [5] of gene and protein lineages. Moreover, developmental features such as gene functions and expressions patterns, developmental processes, and developmental modules are often viewed as homologous across species. As a result, nowadays different kinds of characters—including characters on different *levels of organismal organization [11]*—are routinely homologized.

It is an important insight that homology on one level oforganization [11] 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 [10], 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 [10]. But this is not so, as characters on different hierarchical levels (e.g., 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 extant species develop out of non-homologous developmental precursors, by means of different developmental processes or based on non-homologous genes [10] (Hall 1995, 2003, Raff 1996, Wagner and Misof 1993). For instance, a homologue such as the alimentary canal [47] in different vertebrates can be formed from the roof of the embryonic gut cavity (as in sharks), the floor (lampreys), the roof and floor (amphibians [48]), or from the embryonic disc (reptiles). Homologous structures can even develop out of different germ layers [49] in different species (De Beer 1971). Conversely, in different extant species the same gene can be crucially involved in the development of non-homologous anatomical structures. For instance, an ancient gene such as *pax-6 [50]* is important for the development of both the compound eyes of insects [30] 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 [5] gradually change and in a stepwise fashion be replaced by others (while the resulting anatomical structure remains homologous) until some of the underlying developmental-genetic components are not homologous any longer. Or a gene can acquire (be co-opted for) an additional function and finally lose its original developmental function.

These findings resolve the traditional puzzles surrounding the embryological criterion of homology (maintaining that homologous structures develop out of the same embryonic precursors), which in particular led to the clash (mentioned in Section 3) between approaches within nineteenth century evolutionary morphology [34] preferring either adult morphological data or embryological data in phylogenetic reconstructions. The embryological criterion turns out to merely be a defeasible criterion of homology, and can be wrong in many cases. Instead, homology on every level of organismal organization [11] is to be assessed based on phylogenetic trees, and such phylogenies demonstrate that homology of developmental features and anatomical structures can be dissociated, and more generally that characters on 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 [11] on which evolution [5] takes place and that yields independent characters relevant for the establishment of phylogenies.

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 (Brigandt 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 (Brigandt 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 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 gradual modification in its state from ancestor to descendant. The *taxic approach* as the dominant perspective on homology in phylogenetic systematics [8] focuses on how a certain character state is shared by a whole taxon. Here situations are relevant where the character's state in ancestral species A is significantly different from its state in the descending species B (the character's 'plesiomorphic' condition in A vs. the 'apomorphic' condition in B), while all extant species descending from B still possess the state found 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 [13], recently *developmental approaches* to homology have been introduced (Roth 1988, Wagner 1989b, 1996), sometimes advocated as a so-called biological homology concept [12] (Wagner 1989a, Laubichler 2000). *Evolutionary developmental biology* is generally concerned with the developmental basis of the evolution [5] of morphological organization [11]; and developmental approaches to homology focus on the developmental basis of the evolution [5] 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 keeps it 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 [5]. Given that characters on different levels of organismal organization [11] can evolve independently of each other, even though an anatomical structure develops based on developmental processes and the action of genes [10] (so that in development there are close causal-functional relations among characters on different levels), there are apparently partial developmental dissociations among these characters and levels (yet to be understood), which permit the independent evolution [5] of characters. Thereby developmental approaches to homology are germane to the explanation of evolvability as well as modularity in evolution [5] and development. Since homologues have to evolve in the first place, a connection to explanations of evolutionary novelties exists. Traditional morphology [39], including pre-evolutionary morphology [34] and comparative embryology [6], was fundamentally concerned with understanding morphological organization [11]. Modern evolutionary developmental biology [13] continues this quest, making explicit that morphological organization [11] 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 [5].

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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.

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