

# Homology and the Origin of Correspondence

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**Abstract.** Homology is a natural kind term and a precise account of what homology is has to come out of theories about the role of homologues in evolution and development. Definitions of homology are discussed with respect to the question as to whether they are able to give a non-circular account of the correspondence or sameness referred to by homology. It is argued that standard accounts tie homology to operational criteria or specific research projects, but are not yet able to offer a concept of homology that does not presuppose a version of homology or a comparable notion of sameness. This is the case for phylogenetic definitions that trace structures back to the common ancestor as well as for developmental approaches such as Wagner's biological homology concept. In contrast, molecular homology is able to offer a definition of homology in genes and proteins that explicates homology by reference to more basic notions. Molecular correspondence originates by means of specific features of causal processes. It is speculated that further understanding of morphogenesis might enable biologists to give a theoretically deeper definition of homology along similar lines: an account which makes reference to the concrete mechanisms that operate in organisms.

**Keywords:** homology, evolution, development, molecular biology

## Introduction

Homology is one of the most important concepts in biology (Donoghue, 1992; Wake, 1994; Abouheif et al., 1997). Unfortunately, philosophical discussion has not really fo-

cused on this topic. This is astonishing because during the last decades there has been a radiation of aspects and concepts of homology. For example, pheneticists have argued for an operational approach to homology. With the rise of cladistics transformational approaches have been complemented by taxic ones, that often equate homology and synapomorphy.<sup>1</sup> In addition, homology has been expanded to molecular and ultra-structural features. There is discussion about whether homology applies to behavior or developmental processes. Several authors maintain that there cannot be such a thing as serial homology or partial homology. Finally, there are several developmental approaches to homology, which sometimes do not make reference to common ancestry at all.

Homology is a natural kind term. Homologues are characters of organisms that are grouped together because of a perceived unity of form, and it is assumed that this specific similarity is due to some non-trivial underlying mechanism.<sup>2</sup> Homology is a concept that is supposed to play a special role for theorizing in comparative, evolutionary, and developmental biology. For this reason, accounts of homology try to get a clear picture about the nature and biological basis of homology and the role of homology for certain research areas and approaches to biology. A homologue is a part of an individual that behaves somewhat like a unit in ontogeny and phylogeny. It can be kept apart from other parts of the organisms, and it gains its identity and relative individuality by processes that generate and retain this structure. In addition, a homologue reappears in subsequent generations, where it may be transformed in the course of evolution. This makes clear why homology is approached from evolutionary and developmental perspectives. This paper offers a review and discussion of various homology concepts, designed to make clear that there are different approaches to homology that often re-

flect different research interests. There is a loose analogy between homology and the species concept. Both are natural kind terms, and whereas the species concept groups organisms, homology groups parts of organisms. In the case of species, it is well-known from biological and philosophical discussion that there are different species concepts that focus on different aspects and serve sometimes different theoretical interests. Definitions of species may focus on explaining speciation, the distribution of phenotypes, lineages and phylogeny, or the ecological role of species. But there is an interesting difference between species and homology concepts. The main aim of this paper is to show that definitions of homology—as long as they do not make reference to operational criteria—employ a notion of sameness that is left unexplicated or bound to a comparable notion of sameness. The situation that species concepts usually offer a non-circular definition reflects in my view the fact that while it is clear what it means to say that one organism or population is descended from another one, it is difficult to give a precise account of the idea that a certain part of an organism reappears in subsequent generations. Definitions of homology rely on a good deal of biological understanding; they presuppose a version of homology or make reference to criteria of homology. A more precise and theoretically deeper account of homology could explicate homology with reference to better understood biological phenomena or more basic concepts (e.g., concepts that refer to processes at the molecular level). I argue finally that in the case of molecular homology a precise definition of homology is available and that accounts of homology concepts valid for other types of features might emerge along similar lines. Such an account has to make reference to the specific biological mechanisms that generate characters.

When philosophers talk about homology, it is usually in the context of systematics.

So it might be useful to keep apart the concept of homology (as it used in standard cases) from the concept of synapomorphy. The term ‘character’ may mean a property of an organism (i.e., a trait) or a part of an organism (e.g., a concrete morphological structure) (Fristrup, 1992). The definition of a synapomorphy of a taxon as a shared derived character of that taxon makes clear that a synapomorphy is a property of organisms (because several organisms have this property in common). Homologues, on the other hand, are usually regarded as characters in the sense of parts of organisms. For instance, traditionally concrete morphological structures are homologized. The definition of Richard Owen reflects this understanding of homology:

“HOMOLOGUE . . . The same organ in different animals under every variety of form and function.” (1843, p. 374)

In what follows I employ the notion of homologues as parts of individuals. Even though they are related, the concepts of synapomorphy and homology have to be distinguished analytically, because they operate on a conceptually different level.<sup>3</sup> Nevertheless, besides homologizing tokens (i.e., concrete parts of individuals) one could also say that homology is a relation between types of structures. An example of the latter would be to homologize the (type) ‘amphibian quadrate’ and the (type) ‘mammalian incus’. In my discussion homology is considered a relation between tokens because this approach makes clear that an account of why corresponding structures *within the same species* (which have virtually always the same name) are regarded as homologous. In addition, the perspective of homologues as concrete parts of individuals is crucial for approaches that want to include serial homology (= iterative or repetitive homology). This type of homology concerns structures that appear repeatedly in an organism. For instance, the different vertebrae of a vertebrate can be considered as serial homologues. In the

case of serial homology the question is exactly whether two different parts of the *same individual* are homologous. Homology as a relation between tokens makes the issue of intra-specific and intra-organismic homology more perspicuous.

## Sameness and similarity

According to Owen, a homologue is “the same organ in different animals”. Here sameness clearly does not mean numerical identity (or token-identity). Rather, two structures are homologous if they are of the same type. In different terms, homology is correspondence of structures. But what is the account of sameness of organs, what characterizes whether a certain type of structures is a class or a kind of homologues? Homologous characters often have the *same name*, but this cannot serve as the basis of a definition. The characterization of homology as a relation of parts of individuals reminds us that a definition of homology must tell us why we attribute this relation to two homologous structures of conspecifics, which virtually always have the same name.

A somewhat obsolete view is to define homology in the manner of idealistic morphology by reference to an ‘archetype’. Two characters are homologous if they resemble a common archetype or can be structurally derived from an archetype. But it is not clear what an archetype could be; and defining the archetype as something that can be abstracted from homologous structures would be circular. A further possibility is to characterize homology as similarity on the basis of certain criteria such as the ‘principe des connexions’ of Geoffroy Saint-Hilaire (1818) or the criteria made explicit by Adolf Remane (1952). This could include similarity in structural detail and histology, topological and positional similarity, criteria of connectivity, or similarity with respect to

the developmental origin. For the proponents of the standard view that ties homology to common ancestry it is usually clear that these criteria provide evidence for homology, but are not to be equated with the definition of homology (see, e.g., Mayr, 1982, p. 232). The usage of criteria of homology by biologists and geologists in the last century shows that homology had an operational basis and was rooted in the practice of comparative biology. Notions of ideal morphology such as Owen's archetype were attempts to explain the perceived unity of forms referred to by standard examples and operational descriptions. It became clear that ideal morphology was not able to provide an account or a definition of homology, but its proponents could meaningfully talk about correspondence by criteria that are not that different from modern morphological ones.

A definition of homology should not be conflated with criteria for homology. Nonetheless, this does not mean that it is impossible to include items which are usually considered mere criteria into a definition of homology. Such a path was taken by pheneticists who defined their concept of 'operational homology' by means of a certain kind of similarity (Sneath and Sokal, 1973, p. 79). This approach was based on an explicit operationalist agenda that wants to employ only operationally defined concepts so that taxonomic concepts are free from theoretical commitments such as evolutionary theory. Even though the importance of operational criteria is widely acknowledged, operationalism is not any longer seriously endorsed within biology. Biologists usually do not share the nominalist inclinations of the early pheneticists. Instead, homology is considered as a distinct phenomenon that has to be accounted for and that has connections to various theoretical aspects from comparative, evolutionary, and developmental biology. In addition, similarity is always similarity with respect to certain aspects and standards. Whereas phenetic approaches have to tell us why homology is about these

criteria of similarity but not about others the standard view of homology does not have *this* difficulty, because it ties homology to the common ancestor. Operational homology also faced problems of giving a stable and unique classification, i.e., an account that does not lead to a different grouping if different characters are included. Approaches that use notions such as synapomorphy provide a more reliable way of giving a stable classification of homologues.

## Homology and common ancestry

Charles Darwin largely retained the traditional idealistic characterization of homology, but thought of a new type of explanation for structural similarity across species. The reference to common ancestry was soon incorporated into the definition of homology (see Lankester, 1870, who uses the term homogeny to avoid idealistic or essentialist connotations). This is nowadays the standard definition of homology, independent of the question of whether a transformational or a taxic approach is taken. “Features are homologous if they share a common evolutionary origin” (Abouheif et al., 1997). This statement is relatively vague, if considered to be an exact definition of homology. Nevertheless, it points to the fact that the usual definition of homology involves a common cause. Homology is correspondence caused by common ancestry or similarity to be explained with reference to the same condition in the common ancestor (see, e.g., Simpson, 1967, p. 78; Wagner, 1986, p. 150). An analogous transition from a concept that describes a certain pattern to one that involves a certain cause of that situation also took place in the view of species (Donoghue, 1992). Such a definition of homology has been criticized by some pattern cladists, who hold that certain biological concepts should be only about pattern description but not about causal mechanisms (Brady,

1985).

There are classical definitions of homology that do not make explicit reference to causality, but rather to a genealogical pattern. “Different characters that are to be regarded as transformation stages of the same original character are generally called homologous” (Hennig, 1966, p. 93). “A feature in two or more taxa is homologous when it is derived from the same (or a corresponding) feature of their common ancestor” (Mayr, 1982, p. 45). Taken literally, the character of an ancestor (or an ancestral population) and a descendant (or a descendant population) are homologous, if that character appears in every individual (or intermediate population) of this lineage— independent of the causes of this genealogical pattern. Assume, for example in the case of a lineage of individuals, that major mutations occurred in the germ line of an individual such that one would expect that a completely new morphological structure would be formed in the progeny. If, however, reverse mutations occurred before reproduction, the ancestral and descendant features would be similar characters, though the structure of the parent is not causally relevant to the corresponding structure of the offspring. In this case, the feature of the descendant is somewhat due to chance and cannot be explained by the fact that the ancestor had the same trait. Nevertheless, I suppose that such a situation would not be considered a case of homology. The above statements simply reflect the fact that it is assumed that the similar pattern of parent and offspring (or ancestral and descendant population) is usually due to ancestry and that an extremely unlikely situation as in my example cannot be detected anyway. That is to say that the formulations of Hennig and Mayr are actually connected to a deeper definition of homology by empirical assumptions.

Is the phylogenetic approach, which makes reference to the common ancestry of



characters, able to give a better definition of homology than ideal morphology with its notion of the archetype? A characterization of homology as resemblance or similarity to be explained by common ancestry might use a comparable notion of similarity as phenetic approaches. Homology now becomes a subset of similarity — that similarity with a specific phylogenetic background. But this does not give an account of how the relevant kind of resemblance is to be understood. Instead of giving a definition of homology such accounts are better viewed as expressing the tenet that homology, which somehow relates to a specific type of perceived similarity, is rooted in common ancestry. Thus homology becomes a part of evolutionary theorizing. Alternatively, if homologous characters are defined by features that are derived from the same or corresponding feature or that are transformation stages of the same original character, this reduces the question of homology to the problem of defining what homologous structures in ancestor and descendant are. Phylogenetic concepts of homology, however, simply use this terminology undefined (Jardine, 1967; Wagner, 1994). When saying that one character is derived from the other, it is implied that both are homologous. As homology is a relation between parts of individuals, we ultimately need an account of homology that defines when a morphological structure of an individual and a part of its progeny are derived from one another. The fact that everybody perceives these characters as perfectly similar and in fact homologous does not yield an account of what constitutes homology.

Phylogenetic approaches to homology, which do not give an explication of this situation, do not offer a definition of homology that is clearer or more explicit than that of idealistic approaches. But standard definitions of homology are clear enough for practical purposes, because they are tied to operational criteria and the practice of

comparative biology. For instance, Michael T. Ghiselin offers a phylogenetic definition from a pragmatic point of view:

“Entities are homologous when they are elements of members of a group of precursors and derivatives having a common source, and when these entities can, in principle, be traced back through the derivational series to the same element of a precursor from which the members derive, the sense in which they are homologous being stipulated so as to avoid ambiguity.” (1976, p. 138)

As in the case of idealistic approaches, phylogenetic and evolutionary approaches have a concept of homology whose practice is rooted in an operational basis. The account of what is behind this operational level or what explains a certain pattern is substantially different. Phylogenetic approaches embed homology in theoretical accounts of the descent of species, and in the case of transformational approaches tie homology to views about evolution and the gradual transformation of characters. Accounts of homology thus become a part of the theoretical focus of these approaches.

Why is common ancestry regarded as an explanation of structural similarity in the descendant? Because it is assumed that the independent evolution of new characters in two lineages is less likely than a unique evolution. Such an argument involves probabilistic causes. The fact that two descendant species have the apomorphic character is more probable given that the ancestral species has that character than given that the common ancestor has a plesiomorphic character. This in turn assumes that it is more likely that a condition (e.g., the apomorphic one) is retained than that a character is transformed (e.g., transition from plesiomorphy to apomorphy). This is based on substantial, empirical assumptions, but which are widely accepted (see Sober, 1988 for a detailed account). The above explanatory sketch assumes that characters of a species

are causally relevant for the characters of the descendant species. Considering individuals makes clear that such a lawlike statement is not a causal law, it provides at least not a complete causal explanation. For a morphological structure of an organisms does not cause a similar part in the offspring in the desired sense. The mammary glands of a female mammal are causally relevant to the characters of the offspring, but only in so far they are fitness relevant. A change in the features of mammary glands (due to environmental factors) might affect the traits of the progeny, including its mammary glands. But a structural change in the parent does not cause the same change in the offspring. Homologues are not replicators (Wagner, 1989b). Therefore, descendant characters cannot simply be explained by means of ancestral characters. Rather, a feature of an individual is evidence for factors of its former zygotic state which are common causes of traits in the adult and in the offspring.

Such factors are sometimes integrated by the term biological information. “Homology is correspondence caused by a continuity of information” is a definition of homology by Leigh M. van Valen (1982). This informational view is favored by several authors (Roth, 1988; Minelli and Peruffo, 1991; Haszprunar, 1992). Many philosophers of biology are skeptical of the explanatory value of the notion of biological information (Sarkar, 1996; Godfrey-Smith, 1999; Griffiths, In Press; see also Wagner, 1989a) and besides, as I discuss in the next section, it is widely recognized that homologous structures can originate from different genes and/or different developmental pathways. Independent of the reliance on the notion of information, a drawback of van Valen’s definition is the use of the concept of correspondence. As structures may be transformed in the course of evolution, he avoids the term similarity and instead defines homology as correspondence caused by the continuity of information. However, correspondence is exactly the

concept that an account of homology has to clarify. Rather than providing a concrete definition of homology that does not involve a similarly unexplicated term van Valen's concept of homology is an attempt to encompass the various aspects of homology in one term. Homology exists on different levels (e.g., molecular and morphological features). In particular, reference to the continuity of information intends to include serial as well as latent homology into the account. Van Valen's definition is a statement about the wide scope of homology. The fact that it tries to include all major aspects of homology is the reason why this concept is favored by some biologists—the account has simply to be fleshed out in a case by case basis.<sup>4</sup>

## Homology and development

During the last years the concept of homology has also been approached from a developmental point of view. For instance, Roth formerly proposed that “a *necessary* component of homology is *the sharing of a common developmental pathway*” (1984, p. 17). She has abandoned this strict requirement, since there are several cases of homologous structures arising by means of different developmental processes (see Wagner and Misof, 1993 for a list of examples). It is nowadays well known (though not always respected) that homologies at different hierarchical levels cannot be identified and do not translate straightforwardly into each other (Striedter and Northcutt, 1991; Bolker and Raff, 1996; Abouheif et al., 1997). Two homologous structures can involve non-homologous genes or patterns of genes expression. As single genes might acquire a new main function in the course of evolution, two homologous genes might have roles in non-homologous developmental processes. Non-homologous structures can be a part of the basis for homologous behavior patterns. The fact that lenses in the eye of congeneric

species of amphibians can develop either with or without induction from the optic cup led Brian K. Hall to the conclusion that “homology is a statement about pattern, and should not be conflated with a concept about processes and mechanisms” (1992, p. 194), basically because non-homologous processes generate obviously homologous structures (pp. 183, 186, 192). However, we need not be forced to such a conclusion. Hall calls these developmental processes non-homologous simply because they are different. This merely shows that structures in different species which are called the same ones may arise by developmental processes that are not described as the same ones. In 1971, Gavin de Beer already made explicit that homologues can owe their origin to different processes and need not be controlled by identical genes (de Beer, 1971). Nevertheless, this does not exclude the possibility of taking a transformational view which admits that the cited developmental processes are homologous, provided that one of them has been transformed into the other. That is to say that the developmental processes *as wholes* which produce homologous structures might generally be homologous. But not every gene relevant for a developmental process must be homologous to a gene involved in a homologous developmental process.<sup>5</sup>

Günter P. Wagner proposed a developmental definition of homology that does not require common developmental mechanisms. He contrasts historical (phylogenetic) and biological (developmental) approaches. His own ‘biological homology concept’ does not make reference to common ancestry:

“Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype.” (1989a, p. 62)

An important aspect for Wagner is the fact that homologous structures must have a certain ontogenetic individuality, given by self-regulatory mechanisms. In his view, “lack of genetic and developmental individuality may be the main reason for dubious homologies” (1989b, p. 1162). As his definition focuses on developmentally constrained structures, homologues also have a certain phylogenetic ‘individuality’. Because of the constraint the same structure appears over several generation and is thus evolutionary conserved. This is a developmental source of continuity. By means of conceptually distinguishing between morphogenetic and morphostatic processes Wagner and Misof (1993) offer an explanation of why adult characters may be developmentally constrained despite variation in developmental pathways. As usual for developmental approaches to homology, the biological homology concept wants to include serial homology.

Any analysis of Wagner’s approach has to address the question of what it means to share developmental constraints. When are developmental constraints in several individuals the same ones? In what follows I argue that an account of this situation has to make reference to homology among structures. The biological homology concept can only be applied if we already have homologized certain characters. Let us take a look at the notion of a developmental constraint. “A developmental constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system” (Maynard Smith et al., 1985, p. 266). Among other things it is a possible cause of evolutionary stasis due to internal factors of organisms, but not to external factors such as stabilizing selection. For instance, certain changes within the left hindlimb of tetrapods are impossible (or highly improbable) without similar changes in the right hindlimb. By means of random mutations (for example) any part of the genome is

affected with more or less the same probability. But this does not mean that any change of the phenotype is equally probable. In a tetrapod with five digits, not any loss of a digit is equally likely; the loss of digits during the evolution of several amniotes is in accordance with a certain pattern (Morse's rule). One parameter might often be affected by gene mutations and other changes of developmental factors but another one might usually not. A change of a phenotypic parameter in one direction might be more probable than in the other direction.

As any feature of an organisms is constrained to some extent (e.g., the weight of a structure has an upper limit), a developmental constraint is characterized with reference to other parameters. Some properties might have a higher variation than others, some characters might be highly correlated with different ones. A developmental constraint is not simply a mere number or probability distribution. Instead, the character must be made explicit whose distribution is considered. A claim about the bias on the production of phenotypic change must make reference to specific parts and features of an organism. Take the forelimb of two conspecific tetrapods. If the loss of a certain digit has a similar probability in both animals and the same is valid for other relevant characters, we are entitled to say that both structures share the same developmental constraint. This, however, presupposes that we have homologized the corresponding characters (e.g., digits). It does not make sense to say that two developmental constraints are the same ones if in one animal a loss of digits is much more probable than an additional digit and if in the other individual a loss of phalanges is much more probable than hyperphalangy. Therefore, Wagner's terminology of shared developmental constraints can only be meaningfully applied if structures (or other characters) are already homologized. That is to say that the biological homology concept already presupposes

some prior notion of homology.

For this reason, Wagner's biological homology concept does not provide a definition of homology that characterizes homology without prior understanding of this phenomenon. Conceptually, homology among morphological characters or among developmental features are presupposed by Wagner's approach. Furthermore, Wagner's definition, which does not make reference to common ancestry, does not offer a distinction between homology and analogy as it is usually done.<sup>6</sup> Wagner's work can be viewed as an important contribution to the biological basis of homology. He is concerned with a theory which tries to account for the developmental individualization of structures and for evolutionary change and conservation of characters (that are considered homologous). As structures arise and are retained by means of developmental processes, an approach which tries to account for the structural identity of homologous characters in the course of phylogeny is indispensable for a theory of homology. His definition sets the stage for a specific research program that focuses on the developmental aspects of homology and proposes developmental constraints as a key for the understanding of homology. Homologous structures may in fact share developmental constraints. Nonetheless, it is interesting to notice that even though Wagner does not take a phylogenetic approach with its unexplicated notion of correspondence among ancestral and descendant structures, his developmental account as it stands is not able to reduce homology to something that does not make direct reference to homology. Instead, homology of morphological structures or developmental processes is (implicitly) presupposed.

While the definition of Wagner's biological homology concept does not make explicit reference to phylogeny (1989a), common ancestry is for him an important factor for



the phenomenon of homology (1986,1989b). An approach which holds that homology is independent of phylogeny is process structuralism. On this account, homology is about the relations of natural forms, and common ancestry is irrelevant to their theoretical explanation (Webster, 1984). The aim is to recover a pre-Darwinian concept of homology by grouping structures according to morphogenetic laws. Individuals, as well, should be classified with respect to generative principles. This yields a classification which is independent of the actual historical appearance of taxa, similar to the periodic table of chemical elements (Goodwin, 1982). For instance, a class of homologous structures such as the tetrapod limb can probably be characterized by means of fields equations which model the generative process of limb formation and ossification. Different limb structures in several genera can be described by changes of parameters of the same set of equations (Goodwin, 1984). This approach to homology clearly reflects the structuralist theoretical framework and research agenda.

There are some fundamental unsolved problems for a structuralist approach (besides the fact that this way of thinking about organismic life is nowadays hardly seriously entertained by biologists). Taxa and homologues are to be characterized by common generative explanations. A common explanation as such has nothing to do with homology, because analogues are explained by common selection mechanisms. Why do common *developmental* explanations simply characterize homology? Moreover, what could an exact definition of generative process look like? For instance, would serial homologues belong to the same process? Gerry Webster refers to these mechanisms as laws. As he admits that they have exceptions (1984), it seems to be inadmissible to call these principles laws. In addition, why does a certain law encompass mutually homologous structures, but not different ones? This would mean that the alleged law

is not universal. Therefore, a *one homology–one law* approach is impossible, assuming that a law is something which is universal, fundamental and does not change over time. In my view, instead of making reference to laws process structuralism is forced to rely on the situation that we simply model the development of a class of homologous structures by one set of field equations. The fact that two homologous structures share the *same model* is due to the fact that their developmental precursors are sufficiently similar, so that by means of the laws of physics and chemistry similar processes take place, which can be described by one model. This means, however, that the basis of homology is a similar developmental starting point. The sameness of models would now be tied to similarity or resemblance of certain features. While a phylogenetic definition of homology has to tell us when structures of parent and offspring are homologous or the same ones, it has no difficulty in specifying the sameness or similarity of starting points, because it makes reference to only one—the common ancestor. In my view, process structuralism is likely to end up with a kind of developmental phenetics.

Another approach that tries to take developmental aspects seriously is that of Georg F. Striedter (1998), who offers his own account of homology called ‘epigenetic homology’. The motivation for him is to combine phylogenetic and developmental aspects. Striedter’s concept of homology derives from the idea of epigenetic landscapes (see Waddington, 1957). In an epigenetic landscape the process of development is represented by a topography including a series of valleys that usually branch. Moving downwards in this landscape represents the developing phenotype, which may end up at different end points. An epigenetic landscape tries in particular to take into consideration the fact that development is canalized against small disturbances. The shape of an epigenetic landscape is determined by several developmental factors and resources.

Striedter focuses more precisely on *energy landscapes*, which are used in modeling developmental processes as (complex) dynamical systems. The study of dynamical systems in biology grew out of empirical models of development. The idea is to account for the emergence of stable patterns by processes that are very complicated and may take different routes when they are disturbed. An energy landscape depicts the stable states of the dynamical system by troughs. The bottom point of such a valley—a point of locally minimum energy—is called an attractor. Once the system is in a state close to such an attractor, e.g., if it is in a basin, it tends to converge towards it. As during ontogeny the complexity and the kind of interactions changes, an *epigenetic landscape* is considered by Striedter as a series of energy landscapes representing different successive point in time. Based on these notions epigenetic homology is defined as follows:

“Characters that represent corresponding valley bottoms (attractors) in the epigenetic landscapes of two or more organisms are homologous if they have continuously reappeared in the ontogenies of individual organisms since their origin in a single population of ancestral organisms.” (1998, p. 224)

Striedter applies his understanding of homology to an examples from his research field by discussing the homologization and evolution of certain cortical areas.

Striedter does not give a more concrete account than the one outlined above, but his discussion clearly displays the basic idea of epigenetic homology. An advantage of his approach is that he tries to focus on how ontogeny brings about structure over phylogenetic time. In addition, an account is given of how different developmental pathways can create homologous structures. Even though Striedter’s main motivation is similar to my own approach (to be discussed below), I am not sure whether his

concept of epigenetic homology will prove to be successful. In virtue of his reliance on energy landscapes he intends to represent development in one currency. The sameness of characters in this approach is the sameness of attractors in a sequence of dynamical systems. For this reason, the important task is to give a representation of ontogeny by means of energy flow and distribution—a complete representation that takes all relevant structural and causal features and dimensions into account. It is not clear whether it is feasible to achieve an adequate representation of development in this abstract framework. Instead of trying to find a unique energy space that describe all developmental processes, Striedter is probably to be interpreted as claiming that the variables of dynamical systems have to come out of empirical research in a case by case basis. Nonetheless, he does not provide a way of how this could proceed. Moreover, if the homologization of characters simply consist in identifying an identical (or similar) pattern in a quantitative representation of energy landscapes, the ontogeny of an individual has to be modeled in a manner that includes not only some possible representation of characters but a meaningful representation of them that implies directly what features of one individual correspond to the characters of another organism. That is to say that on Striedter's approach, what homology is on the different levels of biological organization has to be contained in the (right) way of modeling development by epigenetic landscapes. This task resembles the problem of the process structuralist approach. Even though Striedter does not consider the ontogenies of organisms temporally isolated but as a historical sequence, the question in both cases is basically to offer an (ultimately quantitative) model of the development of organisms and to set the descriptions of the ontogeny of different organisms in comparison so that homology can be read off. For this reason, Striedter's account — as it stands — offers a new idea

about the concept of homology, but it gives neither a concrete definition of homology nor a clear way of how to carry out his proposal.

## **Lessons from molecular homology**

To sum up my discussion so far, there are several concepts of homology that reflect the different research focus of different biological approaches and fields. Phylogenetic accounts concentrate on how structures get transformed and correspondence remains in the course of evolution. Developmental approaches study how characters are generated as units during ontogeny, which includes consideration from molecular, cellular, and developmental biology. Homology concepts play a different role for different approaches. Taxic homology is about characters in different species (but does not include or admit serial homology), because it is favored by systematics who are concerned with the comparison of species. Developmental accounts usually want to include serial homology, because it is an important question how the same structure develops several times in one organism. In addition, latent homology and process homology are important for this perspective. Some concepts of homology (e.g., van Valen's and Wagner's definitions) include a statement about a research program on homology or about what such a program has to take into account. Nonetheless, all these different approaches use rather similar operational criteria to root the homology concept in biological practice.

As homology is a natural kind term, a precise account of it has to emerge out of theories about the role of homologues in development and evolution. I argued that all proposed definitions of homology either make reference to operational criteria or conceptually presuppose homology or a kind of correspondence of the same kind. Ide-

alist accounts used the metaphysical notion of the archetype. Phylogenetic approaches do not give an account of the sameness of the characters of ancestor and descendant. Wagner's biological homology concept presupposes the homologization of morphological structures (or other characters). Van Valen simply uses the unexplicated term 'correspondence' in his definition, and the accounts by process structuralists and also Striedter are likely to have to rely on a notion of similarity or sameness on the level of models of morphogenesis. In this sense, all current accounts of homology are not able to provide a precise definition of homology which ties this concept to something that is better explicated. In the case of species concepts the situation is easier. For species concepts that rely heavily on descent and lineages the idea that one group of organisms descends from another one can be quite clearly explicated. It is difficult, on the other hand, to give an account of the idea that certain parts or structures of an organism can be found in subsequent generations. A more precise account of homology has to relate homology to certain combinations of homologies at lower levels of biological organization, or to other biological concepts and phenomena that are theoretically sufficiently understood. That is not to say that there is no level of homology where an account is already available that relates homology to something more fundamental. This is the case for molecular homology.

Among molecular biologists, homology in genes is often equated with similarity of DNA sequences. In fact, sometimes it is said that two sequences are homologous with a certain percentage, which means that this percentage of nucleotides is identical in the aligned sequences (Hillis, 1994). This usage has been criticized by several molecular biologists (see, e.g., Reeck et al., 1987). The terminological position of the latter authors is due to the fact that the (more recent) concept of molecular homology is

viewed as derived from or parallel to the concept of homology in morphological structures. The latter is not considered a mere statement about similarity (as in the case of operational homology), but a claim about the phylogenetic origin of structures. For this reason, the detection of DNA sequence similarity has to be distinguished from the hypothesis that two sequences can be traced back to a common parental cell (where the possibility of mutations must be taken into account). True enough, a high degree of sequence resemblance is evidence for the common origin of genes. This explains the conflation of molecular homology with similarity, because using the standard criterion of homology as a definition of homology does not harm the practice of molecular biologists. Nonetheless, homology as a statement about the origin of structures has to be conceptually kept apart from sequence similarity.

In the case of molecular biology, it is rather obvious how (homologous) resemblance of DNA sequences can be explained by common molecular origin and how the criterion of similarity relates to the concept of homology. Homologous sequences can in principle be traced back cell by cell. The fact that a stretch of DNA corresponds to one in a parental cell is not simply due to the situation that both have a (virtually) identical sequence. Rather, the *process* of replication generates a site-by-site correspondence of DNA sequences, as it is well known. The sequence of a strand corresponds to the one of a copy not in virtue of sequence identity, but because of specific features of the (complicated) causal process that generated the copy. Basically, the sites of a coding strand correspond to certain sites of the anticoding strand, because one acted as a template for the other. Within the next replication, the anticoding strand is a template for the progeny coding strand, the sites of which thus correspond to the original coding strand. This *mechanism* gives an account of why genes may be called homologous.<sup>7</sup> Corresponden-

dence among genes is generated by the molecular processes related to replication and their specific features. This is in particular shown by the fact that knowledge about the possibility of deletions and insertions is important for assessing hypotheses of *positional homology*, the correspondence of one site with another. Substantial changes of DNA sequence in the course of evolution sometimes make it very hard to match a site in one species with a site in another species. In addition, the question of whether and how exon shuffling occurs has implications for what homology of genes is and whether partial homology in genes exist. For many questions in molecular evolution it is of paramount importance to distinguish between orthologous and paralogous genes. Orthology, paralogy, and xenology are different types of molecular homology that are distinguished by the processes that generate these kinds of homology (speciation, gene duplication, and horizontal gene transfer, respectively).

When van Valen defined homology as “correspondence caused by the continuity of information”, he clearly wanted to offer a concept of homology that includes homology of genes. As argued above, the open question of van Valen’s definition is the fact that he does not explicate the term correspondence. In the case of homology in DNA, it can be defined along the above lines. In addition, this concept of correspondence *implies* what several would call the continuity of information. My considerations suggests that causal processes such as replication bring about a correspondence of biological features that may rightly be termed homology. But it may seem to be inadmissible to propose that homology among morphological structures can eventually be defined in a similar manner with reference to features of morphogenetic processes that generate correspondence, because one gene is simply the copy of another one but morphological structures are not replicators. Nonetheless, it has first of all to be kept in mind that



calling genes replicators does not mean that genes are autonomous agents that produce copies of themselves simply on their own. Instead, it means that genes are parts of a specific mechanism that produces a DNA sequence in accordance with a given DNA strand. Various cellular processes such as proofreading are essential for the accurate replication of genes. For this reason, the replication of genes is indirect and depends on the cellular machinery, but this machinery is (almost) universal and we understand how it works. Moreover, an analogous definition of molecular homology can be put forward for proteins as well, and proteins are not replicators. Such an account based on how proteins are produced and how they are related in different organisms has to make reference not only to replication, but also to other molecular processes, in particular transcription and translation. Correspondence among proteins and cellular ultrastructural features such as the cytoskeleton or mitochondria is due to certain aspects of the various molecular processes that account for the inheritance, synthesis, and duplication of these molecular features. My (speculative) suggestion is that a homology concepts on other levels might be developed which explicate correspondence with reference to specific features of developmental mechanisms. Causal processes are possibly the key to the origin of correspondence, which is a question about how organisms generate transgenerational resemblance.

This suggestion is not that different from Wagner's general aims. His writings on homology are based on the attempt to offer an account of how certain structures that are generated by developmental processes reappear in the course of evolution (Wagner, 1989a, 1989b, 1994, 1996). I agree that the developmental individuality of structures is an aspect that is of central importance for a deeper understanding of homology. In addition, I am also sympathetic to the general motivation of Striedter (1998) that is the

background for his concept of epigenetic homology. The goal for him is to achieve a synthesis of phylogenetic and developmental approaches. The phylogenetic understanding of homology focuses on the idea that homologues are derived from a common ancestor, whereas developmental approaches concentrate on the morphogenetic origin of individualized structures. Even though in my view no unique definition of homology might accommodate different research interest and in particular the different levels of biological organization, I agree with Striedter that a precise understanding of homology has to take both aspects into account — homology is a both a historical, transgenerational phenomenon and it concerns (among others) morphological structures that originate and gain their identity during ontogeny. Striedter thinks that the dichotomy between evolutionary and developmental approaches to homology is “based on false conceptualizations of development as being based on genetic blueprints or serial computer programs” (p. 219). He considers the blueprint metaphor as a “sophisticated version of preformationism” (p. 221), and a concept of homology which is like van Valen’s definition based on the concept of information “remains quite hollow” (p. 220) as long as no biological account of the term information is given. I concur in the following sense. The term of information is a concept making reference to the fact that homology is about continuity in inheritance and development, that it appears on several hierarchical levels of organismic life, and that it can also include serial and latent homology. Using the concept of information reflects the aim to make reference to all these aspects with one word. Nonetheless, it is only a conceptual placeholder that awaits a detailed account of what constitutes homology on the different levels of biological organization. Phylogenetic approaches might either bind the homology of ancestral and descendant structures to criteria of homology or they might use terms such as genetic

information and blueprints. But besides being likely to endorse implicitly a variant of preformationism the latter option does not give us insight about the features that bring about structures of organisms, which is necessary to understand why the same characters reappear in following generations. Blueprint talk does not tell us what the individuality and identity of characters actually is (only that it resides in the genes). It is likely not to address the complex mechanisms that generate structures, which involve besides genes other crucial developmental factors. An account including developmental aspects is needed for an adequate concept of homology, because homology traces the history of morphological (and other) units, which gain their specific features and identity during ontogeny (see also Wagner, 1989b). For similar reasons, Striedter urges an epigenetic perspective that tries to take to complex nature of development into account. His ideas are based on the fact that “developmental information does not pre-exist within the zygote but is constructed as the organism develops” (p. 223). In my view, an indispensable feature of developmental approaches to homology is to shed light on the complicated mechanisms that generate biological structures during ontogeny. I would like to add that phylogenetic aspects like common ancestry, the relation to evolution, and the inheritance of genes and other biological features have to be taken into consideration. Homology is a phenomenon that usually operates over a long span of time.

While I am sympathetic to the general motivation and aims of Wagner and Striedter, I critically discussed their proposed definitions of homology. In my view, these concepts can serve as a guidelines for research programs into the nature of homology, but do not offer a precise account of homology that does not make reference to a similarly unexplicated notion of similarity. In addition, these definitions by themselves do not

include the following aspect, which I would like to emphasize. Rather than using a descriptions of biological processes based on an unexplicated concept of information, laws of development, an abstract notion of developmental constraint, or energy landscapes, I suggest that an adequate account of homology has to include reference to the various concrete biological mechanisms that operate in organic life. This is one lesson from my brief discussion of molecular homology. Rather than dealing with the question of whether molecular processes can be represented informatively by the distribution of energy at a certain time, mechanisms at work within the cell and between cells are successfully described by making reference to the different kind of entities that are involved (DNA, RNA, proteins, ...) and the kind of interaction of and between them (binding, activation, diffusion, transport, ...).<sup>8</sup> An account of homology in proteins based on how correspondence emerges by causal processes producing proteins in different organisms has to make reference to different (or more) mechanisms than an account of homology in genes. It is plausible that a good account of homology in general has to emerge out of an account of how organisms generate transgenerational resemblance and correspondence of characters. Derived from considerations about molecular homology, my tenet is that a more precise definition of homology — independent of to which level of biological organization this concept of homology refers — has to make reference to specific features of causal processes. In addition, these causal processes are best described by mechanisms, which includes a concrete account of the various entities and their interactions involved.

## Conclusion

Biologists employ the idea of homology for sometimes different purposes. For this reason, it is quite possible that a unique definition of homology is not able to accommodate all different research interests. Moreover, homology exists at different hierarchical level (genes, developmental processes, morphological structures, behavior, ...). Homology at one level does not translate straightforwardly into homology at another level, so that different concrete account of homology are needed for the various levels of biological organization. Definitions of homology have to emerge out of the theorizing about the biological basis of homology. This calls in particular for considerations about development. In addition, homology is a historical phenomenon and it is transformational—characters that are derived from a common ancestor may change in various details. I argued that current definitions of homology often make reference to an equivalent concept of sameness or some version of homology. This reflects the fact that homology in general is a phenomenon that is not well enough understood. In fact, homology concepts are usually bound to operational criteria or are statements about research agendas. My considerations suggested that homology is about specific features of causal processes that account for the generation of characters. In particular, a more precise definition of homology has to make reference to the different concrete mechanisms that are at work within cells and organisms. I have tried to make this proposal plausible by showing that this agenda is able to give an adequate account of molecular homology.

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## Notes

<sup>1</sup>Transformational approaches usually define homologues as characters that are obtained by a transformation series from a feature of the common ancestor, i.e., the change of structures in the course of evolution is taken explicitly into account. Taxic approaches determine homology by means of the character distribution on a phylogenetic tree. Two (apomorphic) characters are homologous if the least common ancestor had the same character (i.e., if the structure is a synapomorphy). If—on the other hand—two apomorphic characters are derived from a plesiomorphic character (in the least common ancestor), we are dealing with a homoplasy (due to convergent evolution).

<sup>2</sup>Wagner (1996) is a biologist who explicitly considers homology a natural kind term.

<sup>3</sup>See Wagner, 1989b for similar remarks. By saying that homologues are parts (rather than properties) I do not mean that homology applies only to morphological structures; behavioral patterns and developmental processes might be homologized as well.

<sup>4</sup>Roth ties van Valen's definition to operational criteria by stating that the term correspondence in this approach involves "similarity of position, shape, material, structure, chemical composition, color, connection with other parts, etc. — Remane's criteria of position and special quality" (1994, p. 305).

<sup>5</sup>An example of an account that wants to homologize developmental processes is Gilbert et al., 1996.

<sup>6</sup>The fact that structural features are conserved in the course of evolution is a starting point for the biological homology concept (Wagner, 1989b). However, Wagner does not include stabilizing selection and universal developmental constraints as factors of continuity in his definition, simply because they are not internal or historically acquired properties of the developmental system. For phylogenetic accounts which want to trace structures back to the common ancestor selection and constraints do not matter—characters are the same or correspond to each other independent of the question whether they have been transformed or not. If similarity is to be explained by common ancestry, selection and

constraints are relevant factors, as outlined above. It is not clear to me why Wagner rules out selection and universal, but not local developmental constraints.

<sup>7</sup>Obviously, a DNA sequence and its direct replica are usually not called homologous, but rather simply identical. This is due to the fact that an interesting hypothesis about homology emerges only after some mutations have taken place, i.e., after several generations. Nonetheless, it is in accordance with the concept of homology to consider immediate copies of genes as homologues. Indeed, the (contingent) fact that replication is highly accurate is the basis of molecular homology.

<sup>8</sup>See Machamer et al. (2000) for a recent philosophical account of mechanisms in molecular biology and neuroscience.

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