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Homology in Comparative, Molecular, and Evolutionary Developmental Biology: The Radiation of a Concept

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ABSTRACT The present paper analyzes the use and understanding of the homology concept across different biological disciplines. It is argued that in its history, the homology concept underwent a sort of adaptive radiation. Once it migrated from comparative anatomy into new biological fields, the homology concept changed in accordance with the theoretical aims and interests of these disciplines. The paper gives a case study of the theoretical role that homology plays in comparative and evolutionary biology, in molecular biology, and in evolutionary developmental biology. It is shown that the concept or variant of homology preferred by a particular biological field is used to bring about items of biological knowledge that are characteristic for this field. A particular branch of biology uses its homology concept to pursue its specific theoretical goals. *J. Exp. Zool. (Mol. Dev. Evol.) 299B:9–17, 2003.* © 2003 Wiley-Liss, Inc.

The homology concept is of fundamental importance for biology (Wake, ’94; Raff, ’96; Abouheif et al., ’97; Laubichler, 2000). It is used in several branches of biology—not just in comparative biology, systematics, and evolutionary biology, but also in developmental and molecular biology. In fact, different biologists have a different perspective on or approach to homology. New definitions and concepts of homology are proposed by some authors (Donoghue, ’92; Brigandt, 2002). The present paper offers a theoretical analysis of the variation in the homology concept across biology. The idea underlying the discussion is that in the course of its history the homology concept underwent a sort of *adaptive radiation*. The homology concept became increasingly employed in new disciplines; and this migration into new disciplines brought about a change of the concept. Different branches of biology have different theoretical interests and goals and thus employ the homology concept in a different manner. The consequence is that different approaches to and variants of homology that are specific for particular biological fields emerged. This paper discusses the understanding and use of homology in different parts of comparative and evolutionary biology, in molecular biology, and in evolutionary developmental biology.

Biologists might take a different stance on the fact that homology is differently understood in different scientific communities. Some defend the concept of their discipline and criticize other views on homology (Ax, ’89; Bock, ’89; Schmitt, ’89). Others suggest a more pluralist approach to homology that acknowledges that different perspectives might be useful (Wagner, ’94; Wagner, 2000). My usage of the ‘radiation’ metaphor should make clear that the point of the present discussion is not to assess whether one understanding or concept of homology is better than others. Instead, the project is to try to understand the way in which a particular variant of the homology concept is adapted to the biological field in which it is used. Different fields do not just have different theoretical goals, but they use their homology concept to pursue these goals. The homology concept characteristic for a particular part of biology is used to obtain specific items of biological knowledge and to give specific types of explanations.

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HOMOLOGY AS AN INVESTIGATIVE KIND CONCEPT

Homology is what I call an *investigative kind concept*. An investigative kind is a group of things that are assumed to belong together because they share a structural feature or mechanism that generates the characteristic features of the kind. The idea that these objects belong to the same kind is due to some interesting similarities that are perceived by scientists. However, these similarities are not the features that defines the kind. Instead, an investigative kind is defined by some biologically important, but yet unknown underlying feature or process that is presumed to explain the observed similarities. Take the species concept as an example. We are able to recognize various species taxa, but it is a non-obvious theoretical question what explains the origin and cohesion of the perceived biological units. Different possible answers to this questions lead to different species concepts. For this reason, an investigative kind concept always goes along with a scientific search for the underlying basis that characterizes the kind. A full theoretical account of the investigative kind can only be given after appropriate empirical investigation and may reveal surprises and complications.

The homology concept is an investigative kind concepts because its historical origin stems from the fact that biologists perceived and perceive a unity of form among different groups of organisms (Riedl, '78; Wagner, '86; Young, '93; Müller, 2003). Structures in different species seem to correspond to each other, and homology refers to this correspondence of structures and characters. We are able to *recognize* homologous structures in many cases, and there are homology *criteria* that are largely shared and accepted. However, the perceptual similarity is not to be confused with the nature of homology (Bock, '73; Mayr, '82; Müller, 2003). Homologues may be dissimilar due to their adaptive history, and non-homologous structures may be similar due to convergence. Thus, an account is needed of what makes the structures that are perceived to be homologous in fact homologous. We need an explanation of the perceived phenomenon that is picked out by our criteria and examples of homology. This leads—based on different theoretical perspectives—to *different historical and contemporary accounts of homology*. For instance idealistic morphology explained the unity of form with reference to notions such as Owen's archetype. Structures were claimed to be homologous in case they were (empirical and imperfect) instantiations of the same abstract and geometrically perfect archetype (Owen, 1848). Later, a common evolutionary origin became the standard explanation of homologous correspondence of structures. In fact, reference to common ancestry was even included in definitions of homology (Lankester, 1870).[1] For some contemporary developmental approaches to homology, reference to inheritance from a common ancestor cannot be a complete explanation, because it does not give a mechanistic explanation of how the same structures reappear again and again in different ontogenies.[2]

On the one hand, the investigative kind account points to the historical root of the homology concept. On the other hand, it shows why it is possible that there are different approaches to and definitions of homology used by different biologists, even though different biologists largely agree on the criteria and standard examples of homologous characters. In what follows, I will analyze the way homology is understood in comparative and evolutionary biology, in molecular biology, and in evolutionary developmental biology. The goal is to show that the homology concept characteristic for a particular biological field is effectively used to bring about the type of knowledge that is important for that field, so that homology helps to pursue the theoretical goal of that field.

HOMOLOGY IN COMPARATIVE AND EVOLUTIONARY BIOLOGY

The historical root of the homology concepts is comparative biology, in particular *comparative anatomy*. In this field, the criteria of homology used are the relative position with respect to other structures (topological similarity), the connectivity to adjacent structures, similarity in structural detail and histology, and correspondence of the developmental origin. These criteria by itself do

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[1] Lankester actually used the term 'homogeny' instead of 'homology' to contrast his phylogenetic definition with the idealistic understanding of homology. But his 'homogeny' is an early phylogenetic homology concept that makes reference to the common origin of structures.

[2] My notion of conceptual radition would make a more thorough historical analysis of the homology concept necessary. However, an adequate discussion of the origin of the current homology concepts (and the history of the fields in which they are used) is beyond the scope of this paper. The focus of the following case study is on current homology concepts—how they are used and understood, why they are different, and how they relate to the field which they are currently used. Discussion on the history of homology can be found in Rieppel ('88), Rupke ('93), Panchen ('94), and Laubichler (2000).

not presuppose knowledge of the phylogeny of the compared organisms. While it is nowadays widely recognized that the distribution of characters on a phylogenetic tree is an important criterion for assessing hypotheses of homology (Lauder, '86), the above criteria play an important role in contemporary comparative morphology. In fact, many of the criteria used for practical work in this field resembles pre-Darwinian comparative anatomy to some extent. (Compare the homology criteria of Geoffroy Saint-Hilaire, 1818 and Owen, 1848 with Remane, '52 and Ruppert, '82.)

Homology refers to the same structure in different species (Owen, 1843). But why are characters in different species identified by homology (rather than by analogy or in another manner)? One scientific aim of comparative anatomy is to give unified descriptions of organisms from different taxa. The homology concept is important for this field because it allows for effective morphological descriptions. A structural property that holds for a character in one species is likely to hold for the homologous structure in other species. This is due to the fact that homologous structures are derived from a common ancestor. For this reason, morphological, histological, and developmental descriptions are likely to hold for a larger group of species. Neuroanatomical descriptions and theories may just talk about 'the' epithalamus, referring to a structure and its properties in a larger taxon such as vertebrates. Despite large differences between species, homology refers to common patterns across larger groups of organisms.

Choosing homologues as the corresponding characters between (and of course within) species allows for *effective descriptions and unified morphological knowledge*. In addition, the comparison of characters is an important step in giving taxonomic classifications of organisms. Structures identified as homologues can be compared in detail; the similarities and differences obtaining between homologues of different species provide the data for classification. Meaningful comparisons and stable classifications can only be obtained by comparing homologous structures (Rohde, '96). In this manner, *homology serves the end of comparative biology, producing and justifying systematic and general descriptions across species and providing comparisons that are effective for classifications*.

It is interesting to point out that even before the explicit use of the homology concept, comparative biologists gave the same names to corresponding structures of different species. In this way, they followed an effective comparative practice. Once the homology concept was explicitly introduced, this comparative practice could be made theoretically explicit and discussed. The availability of the homology concept allows for reflecting on the criteria and the nature of homology. After the advent of Darwinism and an evolutionary account of homology, it could be explained why this comparative practice was so effective.

In *evolutionary biology*, the theoretical role of the homology concept is somewhat different. A crucial goal of this field is the explanation of the adaptive modification of traits. An ancestral and descendant character are defined as being homologous in case they are connected by a transformation series of intermediate homologues. For this reason, evolutionary approaches to homology are usually so-called *transformational* accounts (Hennig, '66; Simpson, '67; Ghiselin, '76; Mayr, '82; Bock, '89; Donoghue, '92). Homology becomes a concept that links structural entities over time. As the process of adaptation operates over many generations, the character that is subject to evolutionary modification needs to be identified. Once a series of characters is identified, one can examine the transformation in detail and try to explain the modification by reference to natural selection. Even though the homology concept does not yield the explanation of adaptation, this concept is necessary to refer to a lineage or series of characters, which is a precondition for starting with adaptation explanations. Thus, *transformational homology is used to pursue a theoretical goal of evolutionary biology—describing and explaining the adaptive modification of characters*.

In *phylogenetic systematics*, the goal is to detect and characterize monophyletic groups—the real and natural taxa. Taxa are classified by studying the distribution of shared characters, in particular shared derived characters—synapomorphies. Cladists often have a *taxic* approach to homology, which identifies homology with synapomorphy. It is argued that taxic approaches have precedence over transformational approaches (Patterson, '82; Brady, '85; Rieppel, '94; Sluys, '96). Homology is not so much a concept that is a means of comparing structures in two species (or that traces gradual change in morphological evolution), rather, homology refers to a feature that characterizes a taxon. Whereas a taxon groups organisms, homology groups parts of the organisms of this taxon (Nelson, '94). Homology becomes a *diagnostic feature of a taxon*, taxa are described by their synapomorphies. In this manner, taxic homology is tied to the methodology of cladistics and used to provide classifications.

HOMOLOGY IN MOLECULAR BIOLOGY

In molecular biology it is mainly genes and proteins that are homologized. Evolution-oriented molecular biologists, working for instance in molecular evolution or molecular phylogeny, view the (more recent) concept of molecular homology as derived from or parallel to the concept of homology in morphological structures (Fitch, '70; Patterson, '88; Hillis, '94). Their focus is on how genes evolve and how they are related. The question of sequence similarity due to common ancestry (homology) or due to convergence (analogy) has to be addressed. Thus, genes are homologous in case they are derived from an ancestral gene. Sequence similarity is just a criterion for homology (Reeck et al., '87; Fitch, 2000).

However, in many parts of molecular biology, homology just refers to the similarity of DNA or amino acid sequences. In fact, it is said that two sequences are 60% homologous, which means that this percentage of nucleotides is identical in the aligned sequences. Thus molecular homology is not a qualitative notion, but comes in degrees. Even more important is the fact that molecular homology is a statement about the similarity of genes and proteins, not about their evolutionary origin—inheritance from a common ancestor.[3] This is due to the research scope of most parts of molecular biology. In this field the focus is on how molecular entities operate and interact; the theoretical goal is to describe molecular processes and explain phenomena at the molecular level. For this purpose, a comparison of genes and proteins (and their parts) is important, because similar genes have similar genes products and similar proteins are likely to behave similarly in biochemical reactions or to be part of a similar pathway. A good deal of easily accessible information about the structure and function of genes and proteins is given by the mere DNA or amino acid sequence. Discovery in molecular biology depends to a large extent on the search for correspondence among sequences. Genes and proteins are grouped into families and classes in the case of high similarity of relevant parts or domains. Knowing that a protein has a certain domain that is known from other proteins yields information about how it probably behaves in molecular and cellular processes. For instance, proteins with a GPI anchor are known to be membrane bound, so when a newly studied protein reveals to have such a domain it is very likely that it is membrane bound, too. To take another well-known example, all proteins with a homeodomain bind to DNA. Molecular biology often does not deal with the classification and comparison of organisms or with phylogenetic or evolutionary aspects. Instead the focus is on molecular substances and the pathways in which they figure. A new gene or protein is compared to known ones. *Similarity allows for an inference or a hypothesis about the function or effect of a new molecular entity. This provides the possibility to examine a new protein more effectively using knowledge about established proteins and their pathways*. The knowledge about certain molecular systems can be used to transfer experimental approaches and research strategies to other yet unstudied systems, provided that both are known to be similar.

The emphasis in molecular biology is on the practical, experimental level. The aim is to discover mechanisms, which is crucial for explanations on the molecular level the possibility of technological manipulation. For this reason, an operational account of homology is important. Molecular homology as mere similarity of DNA or amino acid sequence is an understanding of homology that is tied to the experimental practice of molecular biology. It is effective to *organize knowledge about molecular mechanisms and direct experimental practice*.

HOMOLOGY IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY

The term homology is used in developmental biology as a whole—at least in the sense of homology among genes and proteins. However, since the homology concept of many developmental geneticists is just the molecular homology concept discussed in the last section, the present discussion focuses on those parts of developmental biology that have a connection to evolutionary questions, and that take theoretical issues such as

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[3] Egel (2000) points out that the concept of molecular homology is also derived from the notion of homologous chromosomes. But a comparative notion of molecular homology (genes of different species being homologous) was already used in the context of Mendelian genetics. Some authors contrasted homologous and analogous genes, but this evolutionary notion of molecular homology was strongly embedded in the Mendelian framework—genes in different species were considered homologous only insofar as they are the same allele (Kosswig, '48, '61).

the homology concept seriously. Among current approaches, this includes in particular evolutionary developmental biology.

Developmental biology is the branch of biology that addresses most completely all levels of organismal organization—from the molecular level to the level of the organisms. Due to its explanatory scope, developmental biology has to address entities and processes at all levels of biological organization. For this reason, when the issue of homology arises conceptually in the comparison of the development in different species, it becomes apparent that homology exists on different levels of the biological hierarchy. In the last decades, the homology concept became increasingly important for developmental approaches and was applied to different levels (de Beer, '71; van Valen, '82; Dickinson, '95; Trevarrow, '98). However, it is nowadays well known (though not always respected in practice) that homologies at different hierarchical levels cannot be identified and do not translate straightforwardly into each other (Roth, '88; Striedter and Northcutt, '91; Bolker and Raff, '96; Abouheif, '97; Abouheif et al., '97; Hall, '98). For instance, non-homologous genes may be involved in the production of homologous structures, and, conversely, non-homologous structures may essentially depend on the expression of the same gene. This is possible because in the course of evolution the importance of a gene for the origin of a structure may diminish and it may become relevant for another character and finally acquire a new function (co-option). The same point applies to features at intermediate levels. Roth ('84) formerly proposed that ''a necessary component of homology is the sharing of a common developmental pathway''. She abandoned this strict requirement, since there are several cases of homologous structures arising by means of different developmental processes. For instance, lenses in the eye of closely related (congeneric) species of frogs can develop either with or without an inductive signal from the optic cup (de Beer, '71).[4]

Apart from different levels of homology, the integration of homology into a developmental approach to evolution brought about additional aspect of and perspectives on homology. Some authors argue that homology is not an all-or-nothing affair, but that there are degrees of homology, just like in the case of molecular homology (Roth, '84; Minelli and Peruffo, '91; Minelli, '98; Trevarrow, '98). Others endorse the idea of process homology, i.e., homology between developmental processes (Gilbert et al., '96; Gilbert and Bolker, 2001; Minelli, 2003). Despite these different levels and aspects of homology that became apparent in the last few decades, evolutionary developmental biologists usually assume that this is still the reflection of one unified phenomenon—homology (van Valen, '82). The notion of biological or developmental information is used to encompass all different aspects of homology (van Valen, '82; Roth, '88; Minelli and Peruffo, '91; Haszprunar, '92). The term 'information' is flexible because it is a sort of placeholder. The kind of information and its material basis have simply to be specified in concrete applications.

Despite the fact that comparative/evolutionary and evolutionary developmental biology have a different perspective on homology, the same criteria of homology are used (Roth, '94). Similarly, the same structures are considered as homologous. The only real difference is serial homology. Traditional comparative or evolutionary biologists do not homologize structures within the same organism (Ax, '89; Bock, '89; Schmitt, '89). In evolutionary developmental biology, on the other hand, serial homology (or iterative or repetitive homology) is widely accepted and utilized (de Beer, '71; van Valen, '82; Wagner, '89a; Minelli and Peruffo, '91; Haszprunar, '92; Roth, '94; Gilbert et al., '96). The issue of serial homology is instructive because it points to conceptual and theoretical differences between these two fields. Many traditional comparative biologists reject the idea of serial homology, because for them homology is about the comparison of different species (Ax, '89). Biologists with a developmental approach, however, are also interested in processes going on *within* individuals, trying to account for the formation of structures in the course of ontogeny. When similar structures are present several times within an organism, it is natural to ask whether this is due to similar development using similar developmental factors and processes. Hypotheses take into consideration that repeated patterns might be due to the duplication of genes or developmental programs, or the use of a the same developmental resource in different parts of the organism.

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[4] See Wagner and Misof ('93) for a list of more examples. Based on examples of lens regeneration, Spemann ('15) already criticized the idea of common ontogenetic origin as being part of the definition of homology.

The difference between traditional phylogenetic and developmental approaches to homology is recognized among biologists (Wagner, '89a; Minelli and Peruffo, '91; Shubin, '94), and sometimes attributed to differences in research interests (Roth, '91; Wagner, '94; Sluys, '96; Butler and Saidel, 2000). The important point, however, is not that these two fields have a different perspective on the same phenomenon—homology. What I want to stress is that two different *concepts* of homology are used; and these two *concept yield different types of biological knowledge*. In the case of developmental approaches, *the goal is the explanation of the origin and formation of structures*. Accounting for the origin of form essentially involves studying the development of organisms and their parts. Knowledge about developmental mechanisms and explanations of the origin of structures are systematized by concepts that refer to a commonality of developmental mechanisms. In developmental explanations the focus is on considerations about a corresponding causal origin, a common maintenance, or a comparable developmental role or behavior of structures. Developmental homology refers to similar, repeated, or corresponding structures of organisms. This homology concept is used to explain this similarity of structures within and between organisms by pointing to a (yet hardly understood) common underlying developmental basis. A developmental homology concept is intended to explain why the same structures (homologues including serial homologues) reliably reappear in different parts of the organism and in subsequent generations (Wagner, '96), *by referring to those causal factors and developmental features that account for this*. Such a homology concept is about the mechanistic underpinnings of structural identity of homologous characters in the course of ontogeny and phylogeny. In this manner, the developmental homology concept serves one fundamental aim of evolutionary developmental biology—explaining how structures emerge in ontogeny, why they are how they are, and why structures are conserved or transformed in the course of phylogeny.

Approaches in comparative and evolutionary biology just refer to inheritance from a common ancestral structure as the defining feature of homology. For a developmentally oriented biologist, reference to common ancestry (or to the inheritance of genetic information) is non-explanatory, because it does not give us a causal account of how and why the same morphological structures are formed in different organism (Wagner, '89b; Roth, '94). Instead, reference to the developmental processes generating this structures in different organisms is a necessary part of any developmental approach. As development is not yet sufficiently understood, there are different tentative developmental definitions of homology proposed (van Valen, '82; Roth, '84; Wagner, '89a; Striedter, '98). Homology is an investigative kind concept—there is a scientific search for the biological basis of homology. The notion of an investigative kind concept also explains why there can be different accounts and definitions of homology in different parts of biology despite the fact that largely the same criteria and standard examples of homology are used. In spite of these different developmental proposals, evolutionary developmental biologists agree on the fact that a developmental homology concept has to account for the above mentioned features—explaining the reappearance of similar structures within one or several individuals. For this reason, homology definitions proposed refer to developmental features such as shared pathways or shared developmental constraints, but they need not make explicit reference to common ancestry (Roth, '84; Goodwin, '84; Wagner, '89a; Rieppel, '92; Goodwin, '94; Hall, '95). Given the current state of evolutionary developmental biology and the developmental homology concept, the explanatory potential of developmental homology is still limited.

Developmental approaches view homologues as building blocks of organisms; homology is a principle of organismal organization (Wagner, '95; Müller and Wagner, '96; Müller and Newman, '99; Laubichler, 2000; Müller, 2003). Part of the theoretical job of the homology concept is to account for the formation of homologues and the organization of form. In addition, the notion of homology becomes linked to the concept of novelty, insofar as a novelty is construed as a structure for which no ancestral homologues exists (Müller and Wagner, '91; Wagner et al., 2000; Minelli, 2003). In contrast to homology in comparative and evolutionary biology, *the theoretical role of homology in evolutionary developmental biology is to account for the origin of similar structures within and between organisms and for structural identity in ontogeny and phylogeny*. As we saw above, the homology concept used in comparative and evolutionary biology is used to yield unified *descriptions*. However, it is not used for giving *explanations*.[5] By just making reference to common ancestry the traditional phylogenetic homology concept can only account for the taxonomic distribution of characters (Wagner, '94). But it cannot fulfill the explanatory tasks of developmental biology; it cannot explain why the same structure emerges in different places of an organisms or in different generations. A developmental homology concept—making reference to developmental processes—is needed to yield these types of explanations. Thus, phylogenetic and developmental homology are used to yield different types of knowledge and in this manner serve different theoretical and explanatory goals. Laubichler (2000) points out that developmental homology is a conceptual tool that brings together genetic, embryological, and comparative data. My discussion made clear that this does not only hold for developmental homology, but that several branches of biology make effective use of their homology concepts. The fact that I stress in particular is that homology concepts do not just summarize and link existing data, but they can be and are used to *generate new knowledge*—unified descriptions in the case of comparative biology, and explanations of form in the case of developmental approaches.

CONCLUSION

I argued that the homology concept underwent a conceptual radiation. Different branches of biology have a different concept of or perspective on homology, because they use homology to bring about types of knowledge and explanations that are important for the particular field. Different homology concepts are shaped to pursue the theoretical aims of specific branches of biology. In the case of homology in *comparative and evolutionary biology*, the goals are the comparison (and taxonomy) of species and characters and the explanation of descent with modification. The theoretical role of homology in comparative morphology and evolutionary biology is the individuation of characters across species and the conceptualization of a series of characters despite variation and potentially unlimited evolutionary change. This allows for systematic and unified knowledge about the structure of organisms in the case of comparative morphology, and is a precondition for explaining adaptation in the case of evolutionary biology. In phylogenetic systematics, homology is a diagnostic feature for monophyletic groups, which helps to detect and characterize taxa. In *molecular biology* the scientific aim is the study of biological processes at the molecular level and their explanation by means of mechanisms. The role of molecular homology is the inference of information about the molecular behavior of genes and proteins (and their parts), particularly in order to guide further experimental investigation and technological manipulation. Finally, in *evolutionary developmental biology* the goal is to figure out how and why certain structures emerge in different ontogenies. The theoretical role of developmental homology is to explain the formation of similar structures within and between organisms and to account for structural identity in ontogeny and phylogeny. My notion of homology as an investigative kind concept explained why there can be different accounts and definitions of homology, even though largely the same criteria and standard examples of homology are used.

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[5] In the case of evolutionary biology homology is a conceptual *precondition* that makes adaptation explanations possible. Homology refers to the characters that undergo evolutionary change, i.e., the pattern that needs to be explained, but by itself it *does not explain* the change. As far as morphology is concerned, this branch of comparative biology does not just offer descriptions, but also explanations (e.g., in the context of functional morphology). The question is whether whether the homology concept has a bearing on explanations in morphology; and morphology hardly offers the type of causal and mechanistic explanations on which developmental approaches focus. In any case, the homology concepts in comparative and in evolutionary developmental biology support different inferences and explanations and yields different types of knowlegde.

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