The ‘Role’ a Concept Plays in Science — The Case of Homology

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Abstract. This article tries to clarify the idea that a concept plays a certain role for a scientific field or a research program. The discussion is based on a case study of the homology concept in biology. In particular, I examine how homology plays a different role for comparative, developmental, and molecular biology. The aspects that may constitute the role of a concept emerge from this discussion.

Introduction

This paper deals with concepts and conceptual change in science by trying to shed some light on the idea that a concept plays a certain ‘role’ for a scientific field or a research approach. My original motivation to address this topic stems from semantic considerations. I disagree with standard causal theories of reference because they do not take conceptual change in science and its reasons seriously. Causal theories often have a somewhat static (in fact preformationist) understanding of concepts (our belief about the referent is usually considered to change), and they often look to the wrong place if they have to account for apparent changes in meaning. Instead, my idea is to focus on the role a concept plays — when the role of a scientific concept changes, then we have a change in meaning of this term. This is an approach that is neither a causal nor a descriptive theory of reference, and it is able to keep change of meaning and change of theory apart — not every change of theory amounts to a new role for a concept. I will not deal with this semantic approach in this article. It is simply my motivation to clarify the locution 'the role a concept plays in science'.

Independent of this motivation, it is central for the philosophy of science to study and develop accounts of scientific concepts and conceptual change. Since concepts are a part of scientific theorizing play, there is some plausibility that concepts play something like a role for a scientific field. Concepts are introduced to address certain things, they are used to account for scientific phenomena. Specific theoretical needs or scientific interests influence how a concept is utilized and when this changes. The aim of the present paper is to examine what this means. My strategy is to develop the discussion based on a case study. The example chosen is the concept of homology. Homology is not only one of the most important concepts in biology. The main reason for discussing homology is the fact that it plays different roles in different parts of biology. Nowadays there are several aspects and several levels of homology. Different fields focus on different aspects and have a different perspective on homology. In fact, in biology there are several concepts or definitions of homology proposed, criticized and defended. For this reason, the focus of my case study is to show why and in what sense homology plays a different role in comparative, developmental, and molecular biology. Moreover, even though I mainly deal with the recent usages of and current debates on homology, the idea of homology is more than 200 years old. The concept of homology has a rich and important history. Several aspects that are important for our current understanding of homology are found in the historical usage of homology. These aspects make homology a good object of study for discussing what roles a concept can play in science.

The concept of homology

Homology is a relational notion used in comparing organisms or species. The entities that can be homologized are parts or characters of organisms, i.e., features below the organismic level. These may be morphological structures and organs, but also behavioral patterns, tissues, cell types, ultrastructural traits, genes, and proteins. Homology is often considered a qualitative relation, it is present or absent (rather than present to a certain degree). In fact, it can be characterized as an equivalence relation. For this reason, homology not only sets objects in comparison (as a similarity relation does), but it also can group characters together, which form a class of homologues. There is an analogy between biological taxa and homologues. Taxa group species and organisms together, whereas homology groups characters and parts of organisms together.[1]

Homology groups certain biological entities according to what they are, not of what they do. (In contrast, many concepts of molecular biology and physiology describe entities and activities as parts of mechanisms, or the role of entities involved in molecular and physiological processes.) Homologues form a natural kind, not a functional kind. Standard accounts of homology are clear that homology is about form as opposed to function. For this reason, homology is often contrasted with analogy (or similar notions such as homoplasy). Homology is correspondence due to common ancestry, not similarity due to parallel or convergent evolution. The origin of the idea of homology is due to the fact that among large groups of organisms biologists perceive a unity of form that goes beyond superficial similarity. Phyla are taxa which encompass those animals that have a common Bauplan or body plan. This admits to set morphological structures in correspondence. Homology is not about apparent resemblance and shape, but concerns

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[1]This analogy is most apparent in the context of cladistics and taxic approaches to homology (see below).

similarity in relative position and structural detail. This idea of the correspondence of characters across species is the basis for the general function of homology: *meaningful comparison*. It is vital for biology to compare different organisms and species, but a useful comparative approach presupposes a standard of comparison that is not arbitrary. Homology provides the basis for comparison. It makes clear that not all parts of organisms can be set into correspondence, but only homologous structures are truly the same ones. This understanding is clearly expressed in the definition of Richard Owen, which is still favored by some contemporary biologists.

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

Homology exists at every level of biological organization (Raff 1996, p. 8), and it enables meaningful comparison. When biologists talk about the same gene, cell type, or feature in another species, they usually make an implicit claim about homology. For this reason, homology is considered not only the central concept in comparative biology, but one of the most important concepts in all of biology (Donoghue 1992; Wake 1994; Raff 1996, p. 37; Abouheif et al. 1997).

Homology is a natural kind term, in the sense that homologues form a natural kind.[2] A natural kind is a class of objects that belong together in virtue of some underlying (non-obvious) mechanism. For this reason, there is a search for the biological basis of homology, with different contemporary accounts of homology. The theoretical question is not how homologues interact with other entities or how they influence biological processes (which may be the case for entities denoted by other biological concepts). An account is needed of what characterizes the structures that are perceived as homologous. For instance idealistic morphology explained the unity of form with reference to a

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[2]This does not mean that biologists speak of homology as a natural kind term. Wagner (1996) is a biologists who explicitly considers homology a natural kind term.

metaphysical notion of archetype. Later, a common evolutionary origin became the standard explanation of homologous correspondence of structures. In fact, reference to common ancestry was included in the definition of homology (see Lankester 1870). For some developmental approaches to homology, reference to inheritance from a common ancestor cannot be a complete explanation, because it does not give an account of how the same structures reappear again and again in different ontogenies.

Homology is a theoretical notion insofar as it plays a crucial role in theoretical accounts of comparative biology and the evolution of organisms. But operational criteria are also vital for applying the homology concept. Indeed, even though idealistic morphology and contemporary comparative biology have completely different accounts of homology, the criteria of homology used are not that different. (Compare the 'principe des connexions' of Geoffroy Saint-Hilaire (1818) with the criteria of Adolf Remane (1952).) With operational criteria, homology could be usefully applied by idealistic morphology independent of metaphysical accounts of homology.

Homology and comparative biology

In comparative morphology homology is a crucial concept enabling description and systematization of knowledge. The above mentioned idea of homology as something that refers to the same or corresponding structures is here most clearly employed. Meaningful comparison of different species presupposes that the appropriate parts and features of animals are compared. In particular bones, organs, muscles, and tissues are homologized. The criteria of homology used are the relative position with respect to other structures (topological similarity), the connectivity to adjacent structures (e.g., blood vessels and nerves), similarity in structural detail and histology, and correspondence of the developmental origin. These criteria are sometimes called a priori, because they do 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, a priori criteria play an important role in comparative morphology and are sometimes considered primary. That is, a good deal of the criteria used for practical work in this field resembles pre-Darwinian comparative anatomy to some extent.

Identifying homologues is an important aim of comparative morphology. In the case of some structures, or of more distantly related organisms, it is by no means obvious how to homologize structures. Homology establishes correspondence of structures between different species. Establishing homology is not only a goal, but homology is also a means of comparison. Structures identified as homologues can be compared in detail, the differences between them are meaningful and relevant differences because corresponding characters are compared. Homology provides a unification of description and a systematization of knowledge. Characters in different species are identified as the same ones and often given an identical name. Despite large differences between species, homology refers to common patterns.

In evolutionary biology the focus is on the change of characters in the course of phylogeny. Homology is a concept that links entities over time. In accounts of morphological evolution homologues become historical units that date back to an ancestral character. Evolutionary approaches to homology are usually *transformational accounts of homology* (Hennig 1966; Mayr 1982; Bock 1989; Donoghue 1992). Here homologues are defined as characters that are derived by transformation from an original trait. The focus is on the fact that structures change in the course of evolution, homologues are entities that transform gradually over generations. Evolutionary biology is interested in giving an account of the adaptive modification of traits. The concept of homology is necessary to conceptualize a lineage of characters. As the process of adaptation operates over many generations, the corresponding features that are subject to change have to be identified, which is a basis for talking about the same type of selection pressure over time. The transformation of these traits can now be addressed and divergence in splitting lineages can be studied and explained. Due to different adaptive histories homologues may be dissimilar in shape and function. Despite the existence of modification in the course of evolution, homology refers to a common basis of different characters (explained or characterized by inheritance from a common ancestor, evolutionary inertia, and gradual change). In addition, the existence of homology (in the sense of unity of form and the taxonomic distribution of characters) has traditionally been an argument for the fact of evolution, i.e., the common ancestral origin of species. Homology thus is an ingredient of evolutionary biology used for a specific argument.

In phylogenetic systematics or cladistics — the nowadays predominant theory of taxonomy — homology has a somewhat different role. Systematics has the task to group species to taxa. In phylogenetic systematics, the only groupings that may be admitted as taxa are monophyletic groups, where a monophyletic group consists of a species and all its descendants. (In cladistics monophyletic groups are considered the only natural kinds above the species level.) Thus systematics becomes largely identical with phylogeny. Focusing on monophyletic groups, an important idea is the fact that if we consider a character in the ancestral species, then this character is transmitted to all descendant species. Thus the species belonging to a monophyletic group have a class of homologues in common. All descendants of the ancestral species have a copy of this ancestral character. The central concepts used in the establishment of phylogenetic trees are the notions of synapomorphy and symplesiomorphy. A plesiomorphy is a phylogenetically old character, whereas an apomorphy is a new trait. A synapomorphy (symplesiomorphy) is an apomorphy (plesiomorphy) shared by a monophyletic group.[3] Phylogenetic systematics wants to classify species into monophyletic groups. The basic idea is that a synapomorphy characterizes a taxon (a monophyletic group), whereas a plesiomorphy provides no evidence for a group of species being monophyletic. (For a symplesiomorphy characterizes a higher, more encompassing taxon. The idea is that a malleus characterizes mammals, but an articular is not characteristic of mammals, because the encompassing monophyletic group of tetrapods has this feature.) Synapomorphy thus becomes the fundamental concept of cladistics.

In phylogenetic systematics homology is always assessed on the basis of a phylogenetic tree. The character distribution on the tree is considered, and when the apomorphic condition is present in all terminal (extant) species and in the common ancestor, this yields strong evidence for the fact that the considered trait was derived from the common ancestor, i.e., we are considering homologues. (Otherwise the condition is called a homoplasy. In phylogenetic systematics homology is terminologically contrasted with the homoplasy rather than with analogy.) In cladistics homology is often equated with synapomorphy, which is called a *taxic approach to homology* or a taxic concept of homology. It is argued that taxic accounts have precedence over transformational approaches (Nelson 1994; Sluys 1996). Taxic homology is a concept of homology tied to cladistic analysis. Homology has to be assessed using the cladistic method of constructing phylogenetic trees. It is often even equated with the core notion of cladistic methodology — synapomorphy. Homology is not so much a concept that is a means of comparing structures in different species (or that traces gradual change in

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[3] The distinction between plesiomorphy and apomorphy is always relative to a considered level of the systematic hierarchy. In the context of mammals as a subtaxon of tetrapods, the ear ossicle malleus is a synapomorphy derived from the symplesiomorphic character in tetrapods — the amphibian articular, which is a part of the lower jaw.

morphological evolution), rather, homology is a feature that characterizes a taxon. A monophyletic group is characterized by a trait that originated in the common ancestor and was inherited by the descendants. Whereas a taxon groups organisms, homology groups parts of the organisms of this taxon (Nelson 1994). Homology thus mirrors the aim of systematics to group species. Homology becomes a diagnostic feature of a taxon, taxa are described by their synapomorphies.

Pattern cladistics is a special doctrine within cladistics that stresses the independence of systematics from evolutionary theory (in fact any theory that describes phylogenetic processes rather than mere patterns of character distribution; see Brady 1985; Nelson and Platnick 1984). Pattern cladists simply take the cladistic criteria of tree construction as the aim of systematics. (Thus the cladistic method is not evaluated as to whether these criteria reflect the true phylogeny, which depends on how evolution proceeds.) Similarly, cladistic criteria of homology are taken as the definition of homology. (E.g., apomorphy and plesiomorphy are kept apart using the ontogeny of extant organisms as criterion, see Patterson 1982.) By using criteria that deal only with extant species pattern cladistics becomes independent of hypothesis about the process of evolution. This is an example where the concept of homology is identified with criteria of homology. This is possible because taxic homology is embedded in systematic practice and has accepted criteria.[4]

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[4]Another (nowadays hardly endorsed) approach to systematics that wants to be independent from evolutionary theory is phenetics or numerical taxonomy. This is an operationist approach with nominalistic tendencies. Species are to be grouped according to phenotypic similarity independent of phylogenetic relatedness. Numerical taxonomy has its own similarity based homology concept called 'operational homology'. See Sneath and Sokal (1973).

Homology and developmental biology

Developmental biology studies molecular mechanisms and morphogenetic processes. The focus in this part of biology is on how differentiation takes place and structures are formed in the course of ontogeny by means of developmental resources such as genes, cytoplasmic factors, and extracellular signals. It is the branch of biology that addresses most completely all levels of biological organization. It takes into account molecular and biochemical mechanisms in the nucleus and cytoplasm. It analyzes cell-cell adhesion and signal transduction. Developmental biology studies different cell types, cell lineages, and differentiation. It deals with tissue types and tissue formation. It describes changing structures, transient structures, and developmental precursors. Finally, developmental biology attempts to account for adult morphology.

Due to its explanatory scope, developmental biology has to address entities and processes at all levels of biological organization. In particular, it has to study how these different levels interact. 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. Genes and proteins in different species can be homologous (when they are derived from a common ancestral gene or protein). An important method in comparing the development of distantly related organisms is to compare their gene expression patterns in different kinds of tissues. Calling types of cells and tissues the same amounts to an implicit statement of homology. And, of course, standard morphological structures are to be homologized.

It became clear that homology at different levels has to be kept apart. In fact, 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 1988; Striedter and Nothcutt 1991; Bolker and Raff 1996; Abouheif et al. 1997). 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 so finally acquire a new function. The same point applies to features at intermediate levels. V. Luise 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. 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 1971; see Wagner and Misof 1993 for a list of more examples). Due to the explanatory focus of developmental biology homology has to be studied on different levels of biological organization, and thus the concept of homology is explicitly applied to different levels or aspects.[5] In addition, it becomes clear that homology on one level cannot be equated with homology on another level.

In the context of development another aspect of homology becomes relevant. Sometimes an organism has a structure or a certain pattern that occurs repeatedly, for instance hair in mammals, leafs in plants, the vertebrae in vertebrates, or the segments in metameric animals. This multiple occurrence of basically the same structure is referred to by the term *serial homology* (or also iterative or repetitive homology). This type of homology was recognized by idealistic morphology because of their geometrical-topological approach to homology. (For instance, Owen considered the different vertebrae of an organism as derived from a common archetypal 'vertebrae'.) Within an

[5] An example of an account that wants to homologize developmental processes is Gilbert, Opitz, and Raff (1996).

evolutionary framework, this aspect of homology was largely ignored by accounts in comparative biology. Obviously the different vertebrae are not derived from an ancestor with only one vertebrae. For current developmental approaches, serial homology becomes an important aspect of homology again, because developmental biology is concerned with the origin of form. It studies morphogenesis not so much by the comparison of organisms of different species, but instead, by focusing on the various developmental processes that take place within an organism of a single species. 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. For instance, limb development is one of the best studied morphogenetic phenomena in tetrapods. Due to their common topology the front limb and the hind limb are considered as serial homologues (even though they may look for adaptive reasons quite dissimilar). Hypotheses take into consideration that this repeated pattern might be due to the duplication of genes or developmental programs (among other things).

In comparative biology the focus is on the comparison of characters in different species. In this context homology is mainly a relation between organisms, not within organisms. For this reason, ideas about serial homology are not important for comparative biology. The idea of serial homology is often ignored or sometimes attacked by representatives from that field (Mayr 1982, Ax 1989; Bock 1989). In developmental biology, on the other hand, serial homology is widely accepted and utilized (de Beer 1971; van Valen 1982; Wagner 1989a; Minelli and Peruffo 1991; Haszprunar 1992; Roth 1994; Gilbert, Opitz, and Raff 1996). This is due to the fact that developmental biology describes and compares processes going on within organisms. It is an important explanatory idea that serial homologues exist because homologous genes are possibly at work in different places of the organism and bring about homologous morphogenetic fields and similar developmental pathways. While these aspects are crucial for explanation of morphogenesis and the systematization of knowledge in developmental biology, they are of no importance for the theoretical and practical scope of comparative biology. The issue about whether there is something like serial homology gives the best illustration of the fact that homology plays a different role in comparative and developmental biology.

A similar example is that of latent homology. This is apparent homology of structures that were not necessarily present in all ancestral species. For instance, some birds retain the potential to develop teeth, even though this structure has not been formed in the ancestors for at least 70 million years (van Valen 1982). In Titanotheres, an extinct species of mammals, knobs on the head were present as soon as the animals had a certain minimum size. However, this trait had not been present in the common ancestor. The hypothesis is that the descendants inherited a certain developmental resource or potential from the ancestor, and expressed the structure when reaching a certain size (de Beer 1971). Developmental approaches to homology are usually interested in taking these different aspects of homology into account. Haszprunar (1992), for instance, talks about iterative, ontogenetic, di-/polymorphic, and supraspecific homology. A prominent definition of homology is that of Leigh van Valen, who states that homology is "correspondence caused by a continuity of information" (1982, p. 305). This definition is explicitly intended to encompass aspects of homology such as molecular homology, serial, and latent homology. The idea is that a lineage of information may not only split due to speciation (standard homology between species), but information may duplicate and diverge within an organism (serial homology), or it may be transmitted, but not expressed (latent homology). Several authors favor this informational definition of homology (Roth 1988; Minelli and Peruffo 1991; Haszprunar 1992), in part because it is considered to be the most flexible one. It includes all relevant aspects of homology (for developmental biologists), the kind of information and its material basis have simply to be specified in concrete applications.

Developmental biology is interested in the ontogenetic rather than the phylogenetic origin of structures. For this reason, not only developmental features between organisms but also within organisms are described and compared. Knowledge about developmental mechanisms and explanations of the origin of structures are systematized by concepts that refer to a commonality of developmental mechanisms and pathways. Prevalent are the analysis of gene expression patterns, the study of the interaction of cell and tissues, and developmental pathways. Because of the focus on the explanation of morphogenesis, developmental accounts of homology do not necessarily make reference to common ancestry. There is a shift towards considerations about a corresponding causal origin, a common maintenance, or a comparable developmental role, behavior, or nature of structures (e.g., whether a part is a module of an organism). For example, the proposed necessary component of homology by Roth cited above focuses on shared developmental pathways. Günter Wagner's 'biological homology concept' does not make explicit reference to common ancestry. Instead the focus is on the ontogenetic individualization of organimal parts and their evolutionary behavior due to developmental constraints:

> "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)

Theoretical approaches in developmental biology try to find the biological basis of homology. Reference to inheritance from a common ancestor is considered as an incomplete explanation, because homologues are not replicators that are simply copied like genes (Wagner 1989b; Roth 1994). Instead, an account is needed that explains why the same structures reliably reappear in subsequent generations (Wagner 1996). This makes a focus on developmental processes necessary. The goal of a developmental approach is to identify the mechanistic underpinnings of the structural identity of homologous characters in the course of phylogeny. This task cannot be fulfilled by the homology concepts of comparative biology, which only make reference to common ancestry and thus can only account for the taxonomic distribution of homologous characters (Wagner 1994).

Developmental approaches to homology have another perspective on homology that brings further definitions and tentative concepts of homology. Wagner (1989a) distinguishes between the historical and biological homology concept (besides the idealistic homology concept). The former refers to traditional accounts of homology as common in comparative biology (also called phylogenetic homology), the latter to developmental approaches to homology (see Minelli and Peruffo 1991; Roth 1991; Shubin 1994; Wagner 1994). Whereas comparative approaches are interested in the phylogenetic relationship of species and in grouping organisms into taxa, developmental approaches are not concerned with this (Roth 1991; Wagner 1994; Sluys 1996). Rather than identifying homologues, developmental approaches ask how structures emerge in ontogeny, why they are how they are, and why they are conserved or transformed in the course of phylogeny. These different explanatory aims bring about different perspectives on homology. In contrast to homology in comparative biology, the role of homology in developmental biology is to account for the formation of similar structures within and between organisms and for structural identity in ontogeny and phylogeny.[6]

[6] A further developmental approach to homology is process structuralism. This position regards common ancestry as irrelevant for homology and the nature of form. See Goodwin (1982); Goodwin (1984); Webster (1984); Goodwin (1994).

Homology and molecular biology

In molecular biology it is mainly genes and proteins that are homologized. The concept of molecular homology often refers to the similarity of DNA or amino acid sequences (Reeck et al. 1987; Hillis 1994). In fact, sometimes it is said that two sequences are 65% homologous, which means that this percentage of nucleotides is identical in the aligned sequences. Thus homology is not a qualitative notion, but comes in degrees. Even more important is the fact that homology is a statement about the similarity of genes and proteins, not about their evolutionary origin — inheritance from a common ancestor. Even though a criterion for molecular homology becomes the definition of homology, this usage is rather common in molecular biology. This is due to the research scope of many parts of molecular biology. In this field the focus is on how molecular entities operate and interact, in an attempt to describe molecular processes and explain phenomena on 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 similar 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. For instance, it is of particular importance to know whether two proteins have similar functional domains. 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. 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, effect, or role 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 emphasis in molecular biology is on the practical, experimental level. For this reason, an operational account of homology is important. Thus, molecular homology as similarity of DNA or amino acid sequence is an understanding of homology that is tied to the experimental practice of molecular biology. It is adequate to organize knowledge about molecular mechanisms and direct experimental practice.

To be sure, in branches of molecular biology that are not so much life science oriented but deal with molecular evolution or molecular phylogeny things are different. Here it is important to know whether two genes actually have the same evolutionary origin. For this reason, the understanding of molecular homology as sequence similarity has been criticized by several molecular biologists (see, e.g., Reeck et al. 1987). These authors view the (more recent) concept of molecular homology as derived from or parallel to the concept of homology in morphological structures. In molecular evolution and phylogeny the focus is on how genes evolve and how they are related. The question of similarity due to homology or analogy has to be addressed (see, e.g., Fitch 1970). The study of molecular lineages makes it necessary to keep apart different ways of how lineages split (and subsequently diverge). Genetic lineages may split due to speciation (this is called orthology), gene duplication within an organism (paralogy), or horizontal gene transfer (xenology). When a gene exists in two paralogous forms (e.g., α- and β-hemoglobin in humans), in the case of comparison with the genes of another species it is important to know which of the similar genes correspond to each other (as orthologues). Due to the possibility of gene duplication a gene lineage may split within an organism. For this reason, the relationship between a tree depicting molecular lineages and the corresponding phylogenetic tree of the species involved has to be clarified. For the purposes of molecular evolution and phylogeny, different types of molecular homology have to kept apart, due to the process that brought about a split in a genetic lineage. Such a concept of homology does not refer to mere similarity of genes and proteins, but also to the explanation of this resemblance.

The role a concept plays

Concepts allow scientists to refer to objects and phenomena. They provide the basis of communication and intersubjective access to knowledge and its formation. A concept helps a scientist to address a phenomenon, investigate it, and develop an account of it by relating it to other concepts and building theories about the referent. How this is done in concrete situations may differ from concept to concept. The different aspects that can constitute the role a concept plays for a scientific community may be more or less important in different concrete cases. This is due to specific reasons, depending on the purpose for which the concept is used. Concepts may have fuzzy boundaries, i.e., the may be used in slightly different variants within a community. This need not simply be due to the fact that language is vague, or that its speakers are imperfect and do not interact thoroughly enough. When one concept has a greater variation of meaning than another concept this might be due to the epistemic interests that are associated with the use of this concept and how they can be pursued given knowledge about the referent. That is to say that the variation within a concept might be something that has specific reasons and has to be explained. In the case of the homology concept there is variation, which is of course continuous, i.e., between two distinct ways of characterizing homology there are many intermediate variants. Nonetheless, as my discussion showed homology is grouped around distinct poles that correspond to different research fields. In other words, considering a space of possible homology concepts (i.e., concepts that can be considered homology concepts but need not be actually employed), the actualized homology concepts (or the predominantly used concepts) are non-equally distributed in the space of possible concepts in accordance with the existence and structure of different biological fields. Despite continuous variation the concrete structure of that variation has specific reasons.

Biologist know that there are different homology concepts. The fact that these different ways of approaching and understanding homology are perceived as substantially different concepts is shown by the fact that some biologist attack the homology concept of another community. This is in particular the case for the core concept of homology in comparative biology (not admitting serial homology) versus homology in developmental biology (considering serial homology as an important type of homology). On the other hand, some biologists state that a 'pluralist' approach to homology is appropriate and that different aspects of homology are justified according to scientific goals that are important in some cases but not necessarily in others (see Rieppel 1987; Wagner 1994). In this sense, the homology concept is similar to the species concept, where different concepts exist depending on whether the focus is on explaining speciation, the distribution of phenotypes, lineages and phylogeny, or the ecological role of species.

In contrast, concepts like the molecular gene concept show a conceptual unity. Even though there is no unique definition of the gene and the term 'gene' may refer in different situations to different concrete objects, no biologist would talk about different molecular gene concepts. Due to the idiosyncrasies of the details of molecular genetics the term gene varies in its concrete application depending on the context. But the gene is perceived as one concept, it has a unique role for molecular biology, namely it refers to a stretch of DNA with a particular structure (and function) in order to account for the production of molecular substances important for the cellular machinery such as RNA and polypeptides.[7] Despite the fact that there are different homology concepts these concepts are all concepts of *homology* because they conform to a common broad and general role of homology or are historically and conceptually derived from it. The origin of homology is structural similarity that goes beyond superficial resemblance but instead has to be explained by an underlying root (e.g., common ancestry). Due to this fact homology is supposed to refer to the corresponding parts of organisms. It links characters in different species and thus allows for meaningful comparison of organisms by designating the same structures. All homology concepts endorse this role to some extent or are derived from it for instance by sticking to operational definitions of such homology concepts (e.g., in the case of molecular homology as sequence similarity).

A concept allows one not only to address a phenomenon, but it also determines the way in which things are conceptualized and understood. By means of concepts certain things or aspects are implicitly considered as relevant. Concepts provide a focus for certain phenomena or types of phenomena, and they may emphasize certain

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[7] This role differs from the role of the Mendelian gene concept which is not only a precursor of the molecular gene, but is also still used in population genetics. The role of the Mendelian gene consist in accounting (by means of a genotypic entity) for the inheritance of phenotypic characters; more exactly, it accounts for specific patterns of inheritance by explaining differences in phenotype by genetic differences. The crucial function of the molecular gene, on the other hand, is not to explain patterns of Mendelian inheritance. The molecular gene designates a specific heritable substance that plays a crucial role in the synthesis of cellular components studied by biochemistry and cell biology. Thus, this gene concept is 'designed' for the theoretical focus of molecular biology. The Mendelian gene concept as such cannot fulfill this theoretical role (even though the entity referred to by this concept is the material substance that explains the phenomena that molecular biology tries to account for).

perspectives on a phenomenon. Transformational homology, for instance, focuses on the gradual change of homologous structures due to adaptation. Taxic homology, on the other hand, focuses on discrete character states and characters as diagnostic features uniting a monophyletic group. Molecular homology addresses the structure of genes and proteins, while developmental homology focuses on the developmental commonality of structures that are apparently the same ones. A concept shows not only that something is perceived as a phenomenon, but it also reflects the way this phenomenon is perceived. In addition, a concept determines what is considered as the same phenomenon and with what other things this phenomenon has to be contrasted. Sometimes a concept is simply kept apart from other terms, sometimes it is contrasted with another opposing or contrary term (as a dichotomy or using a continuum). Homology is contrasted with analogy (in the context of transformational homology) or homoplasy (in the context of taxic homology).

In the case of homology it is very apparent (and very important for some usages of homology) that this concept claims certain phenomena to be essentially the same phenomenon. There are several possible aspects of homology, homology between species, serial homology, and latent homology. Developmental homology concepts regard all these aspects as types of homology, which is not uncontested in other parts of biology. Van Valen states from a developmental point of view that

> "Homology is resemblance caused by a continuity of information. In biology it is a unified developmental phenomenon. ... the apparently disparate relations called homology really can be considered as one." (van Valen 1982, p. 305)

Homology exist also on different levels. Molecular substances can be homologized, but also cell types, tissues, morphological structures and behavioral patterns. These are very different types of biological entities. For this reason, homology on different levels may need a different concrete account and different operational criteria. Despite the fact that homology on one level cannot be identified with homology on another level, having one concept for these different issues reflects the fact that they are considered as belonging to the same phenomenon. Roth expresses this very clearly (endorsing Van Valen's informational definition):

> "There is no neat congruence between that information as it is described in genetic, developmental, and gross morphological or evolutionary contexts, even though the fields of genetics, development, and comparative morphology represent only different points of view of the *same* phenomenon." (Roth 1988, p. 21)

Using the term homology in the case of behavioral patterns amounts to the claim that behavioral homology is in fact a kind of homology. This includes implicitly the idea that a theoretical account of behavioral homology can be giving along lines similar to accounts of homology in morphological structures (independent of whether this idea is substantiated).

Besides these general aspects of the function of concepts in science, the role a specific concept plays for a research program is in particular the reason why this concept is introduced, the need of having this concept, and the reasons why the concept changes. Concepts often do something for a scientific field; e.g., having one concept rather than another might provide a benefit for scientific investigation. This relates to the theoretical and practical needs and interests of a scientific community with respect to a certain topic. Comparative, developmental, and molecular biology not only address different phenomena and have different scientific goals, but the foregoing case study also made clear that the concepts of homology that are characteristic for these communities are embedded in these different approaches and are used to account for things that are of specific importance for each field. A certain concept might be specific and even crucial for a specific research program, or a certain theoretical approach might have a specific focus that makes new concepts or a different perspective on existing concepts necessary.

The role of a concept is exhibited by the objective of a scientific field in contexts where this concept is used. Scientific investigation associated with a particular concept has a certain kind of intended product. In the case of homology in comparative biology, the objective is the taxonomy of species and characters. In the case of biological homology, the aim is to figure out how and why certain structures emerge in ontogeny and reappear in other parts of the organism or in other organisms. The product in comparative biology is statements of homology, taxonomically organized and interpreted character distributions, and the classification of species. In developmental biology the product of investigation is a systematic account of similarities and differences in the development of characters. Homology concepts are deliberately employed to bring about and organize these products of investigation. The fact that different branches of biology have different homology concepts is not so much due to the fact that they have different theories or scientific results. More important is the fact that the homology concept is used for different concrete epistemic and explanatory goals, this is what the role of a concept is about. For example, the role of taxic homology is the characterization of natural groups (of species), in the case of transformational homology it is the conceptualization of a lineage of species characters despite potentially unlimited evolutionary change (in order to account for adaptation). The role of developmental homology is to account for the formation of similar structures within and between organisms and for structural identity in ontogeny and phylogeny. In the case of molecular homology as sequence similarity, its role is the inference of information about the molecular behavior of genes and proteins (and their parts).

The role a concept plays in science can involve different aspects. It is the way it is used or in which theoretical contexts it occurs. The role a concept plays is what it is supposed to describe or systematize. In comparative biology homology provides a certain unification of description and knowledge by conceptually linking the parts of organisms of different species. Molecular homology (in particular as sequence similarity) allows for an inference of hypothesis and research strategies from a known molecular system to a new system. The role a concept plays is what it is intended to explain, for what phenomenon it accounts. Homologues qua homologues are not causal agents, but homology makes reference to explanation and causation. Either it is considered as a pattern to be explained, or an explanatory factor (such as common ancestry) that is included in the definition of homology. In comparative biology homology is thought to explain the distribution of characters in a taxonomic hierarchy (and in the case of transformational homology it accounts for correspondence despite adaptive change). In developmental biology homology is rather used to account for the ontogenetic emergence of the same patterns and the evolutionary stasis of characters (e.g., the biological homology concept focuses on developmental constraints). Important for the role of a concept may be also how it relates to other concepts and why it is of more importance for a field than other concepts. In addition, it has to be considered how a concept is embedded into theories and how it related to experimental practice (and why this obtains this way). Homology is involved in evolutionary theory and cladistic methodology, on the one hand, and in systematized knowledge in molecular biology, on the other hand. Discussions about the criteria and application of homology is important for comparative morphology, and the focus on the experimental level of molecular biology brings about a stress on the operational aspects of molecular homology.

A concept often has the general role of linking the theoretical and practical level. Concepts are of importance for both contexts. They operate on the theoretical level as parts of theories, descriptions, explanations, and systematic accounts. They embody a certain theoretical understanding of a phenomenon. By means of criteria and operational definitions concepts are involved on the experimental and practical level. They make reference to methods and organize experimental research. Criteria and operational accounts enable the application of a concept and the practical reference to a phenomenon. Theoretical accounts, on the other hand, provide an understanding of the phenomenon and guide the assessment of operational criteria. Homology is the core theoretical concept for comparative biology, while comparative practice rests largely on criteria of homology. Despite the different accounts of the nature of homology, idealistic and historical concepts of homology referred to the same objects and admitted a sufficiently meaningful comparative practice by means of similar criteria of homology. Concepts specify and organize the relationship between the theoretical and practical level. The case of pattern cladistics and numerical taxonomy shows that there are approaches to homology that use only operational accounts of homology because an independence from evolutionary theory is intended.

Finally, a concept may guide research, or it may initiate or characterize a research program. Certain new concepts may be central for the attempt to understand a class of new phenomena or to answer new scientific questions and problems. For example, this was the case for the genotype/phenotype distinction in classical genetics or the concept of behavioral homology in ethology. A different understanding of an existing term can be specific for a new theory or a new scientific approach to an existing issue. Concepts that are relevant for a scientific community guide discovery and theory formation by pointing to phenomena and methods considered as important and by endorsing a specific point of view of the objects under study. Van Valen's definition of homology, for instance, is to be considered an explicit statement about the wide scope of homology. It expresses a characteristic feature of developmental approaches to homology. A developmental account has to consider all the various aspects of homology and to include them. Moreover, in the context of developmental approaches it becomes apparent that homology is a natural kind term. For these approaches search explicitly for the biological basis of homology (see the titles of Roth 1988 and Wagner 1989b). Homology in development points to the fact that an account is needed that characterizes what sameness of structures is by explaining how similar morphological patterns are formed in different organisms and in different parts of the same organism.

On the other hand, even though some concepts might express the need for investigation and the formation of a specific account, in general a concept allows for reference to a phenomenon independent of whether a theoretical account of this phenomenon is available. Concepts enable scientists to address something perceived as a phenomenon or an entity and may suggest a certain understanding of the referent. They give the possibility to investigate the existence and the features of this thing and organize scientific discovery. This is independent of whether an account of the referent is available or whether the understanding of the referent is adequate. The concept of homology admits application in particular in comparative and evolutionary biology independent of whether the biological basis of homology is understood at all.[8]

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[8]Rheinberger (2000) uses the history of the gene concept to show that fuzzy and imprecise concepts are vital for investigation at the boundary of scientific knowledge.

References

Abouheif, E., M. Akam, W. J. Dickinson, P. W. H. Holland, A. Meyer, N. H. Patel, R. A. Raff, V. L. Roth, and G. A. Wray (1997). Homology and developmental genes. *Trends Gen. 13*, 432–433.

Ax, P. (1989). Homologie in der Biologie – ein Relationsbegriff im Vergleich von Arten. *Zool. Beitr. N. F. 32*, 487–496.

Bock, W. J. (1989). The homology concept: Its philosophical foundation and practical methodology. *Zool. Beitr. N. F. 32*, 327–353.

Bolker, J. A. and R. A. Raff (1996). Developmental genetics and traditional homology. *BioEssays 18*, 489–494.

Brady, R. H. (1985). On the independence of systematics. *Cladistics 1*, 113–126.

de Beer, G. (1971). *Homology, An Unsolved Problem.* Oxford Biology Readers. Glasgow: Oxford Univ. Press.

Donoghue, M. J. (1992). Homology. In E. Fox Keller and E. A. Lloyd (Eds.), *Keywords in Evolutionary Biology*, pp. 170–179. Cambridge, MA: Harvard Univ. Press.

Fitch, W. M. (1970). Distinguishing homologous from analogous proteins. *Syst. Zool. 19*, 99–113.

Geoffroy Saint-Hilaire, E. (1818). *Philosophie Anatomique, vol. 1, Des Organes Respiratoires sous le Rapport de la Détermination et de l'Identité de leurs Piecès Osseuses.* Paris: J. B. Baillière.

Gilbert, S. F., J. M. Opitz, and R. A. Raff (1996). Resynthesizing evolutionary and developmental biology. *Dev. Biol. 173*, 357–372.

Goodwin, B. C. (1982). Development and evolution. *J. Theor. Biol. 97*, 43–55.

Goodwin, B. C. (1984). Changing from an evolutionary to a generative paradigm in biology. In J. W. Pollard (Ed.), *Evolutionary Theory: Paths into the Future*, pp. 99–120. Chicester: John Wiley & Sons.

Goodwin, B. C. (1994). Homology, development, and heredity. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 229–247. San Diego: Academic Press.

Haszprunar, G. (1992). The types of homology and their significance for evolutionary biology and systematics. *J. Evol. Biol. 5*, 13–24.

Hennig, W. (1966). *Phylogenetic Systematics*. Urbana: Univ. of Illinois Press.

Hillis, D. M. (1994). Homology in molecular biology. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 339–368. San Diego: Academic Press.

Lankester, E. R. (1870). On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. *Ann. Mag. Nat. Hist. 4th Ser., Vol. 6*, 34–43.

Mayr, E. (1982). *The Growth of Biological Thought*. Cambridge, MA: Belknap Press.

Minelli, A. and B. Peruffo (1991). Developmental pathways, homology, and homonomy in metameric animals. *J. Evol. Biol. 4*, 429–445.

Nelson, G. (1994). Homology and systematics. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 101–149. San Diego: Academic Press.

Nelson, G. and N. Platnick (1984). Systematics and evolution. In M.-W. Ho and P. T. Saunders (Eds.), *Beyond Neo-Darwinism: An Introduction to the New Evolutionary Paradigm*, pp. 143–158. London: Academic Press.

Owen, R. (1843). *Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, Delivered at the Royal College of Surgeons, in 1843.* London: Longman, Brown, Green, and Longmans.

Patterson, C. (1982). Morphological characters and homology. In K. A. Joysey and A. E. Friday (Eds.), *Problems of Phylogenetic Reconstruction*, London, pp. 21–74. The Systematics Association: Academic Press.

Raff, R. A. (1996). *The Shape of Life: Genes, Development, and the Evolution of Animal Form*. Chicago: Univ. of Chicago Press.

Reeck, G. R., C. de Haën, D. C. Teller, R. F. Doolittle, W. M. Fitch, R. E. Dickerson, P. Chambon, A. D. McLachlan, E. Margoliash, T. H. Jukes, and E. Zuckerkandl (1987). "Homology" in proteins and nucleic acids: A terminological muddle and a way out of it. *Cell 50*, 667.

Remane, A. (1952). *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Königsstein: Otto Koeltz. Reprinted in 1971.

Rheinberger, H.-J. (2000). Gene concepts: Fragments from the perspective of molecular biology. In P. J. Beurton, R. Falk, and H. Rheinberger (Eds.), *The Concept of the Gene in Development and Evolution: Historical and Epistemological Perspectives*, pp. 219–239. Cambridge University Press.

Rieppel, O. (1987). Pattern and process: The early classification of snakes. *Biol. J. Linn. Soc. 31*, 405–420.

Roth, V. L. (1984). On homology. *Biol. J. Linn. Soc. 22*, 13–29.

Roth, V. L. (1988). The biological basis of homology. In C. J. Humphries (Ed.), *Ontogeny and Systematics*, New York, pp. 1–26. Third International Congress of Systematics and Evolutionary Biology: Columbia Univ. Press.

Roth, V. L. (1991). Homologie and hierarchies: Problems solved and unsolved. *J. Evol. Biol. 4*, 167–194.

Roth, V. L. (1994). Within and between organisms: Replicators, lineages, and homologues. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 301–337. San Diego: Academic Press.

Shubin, N. H. (1994). History, ontogeny, and evolution of the archetype. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 249–271. San Diego: Academic Press.

Sluys, R. (1996). The notion of homology in current comparative biology. *J. Zool. Syst. Evol. Res. 34*, 145–152.

Sneath, P. H. A. and R. R. Sokal (1973). *Numerical Taxonomy: The Principles and Practice of Numerical Classification*. San Francisco: W. H. Freeman and Co.

Striedter, G. F. and R. G. Nothcutt (1991). Biological hierarchies and the concept of homology. *Brain Behav. Evol. 38*, 177–189.

van Valen, L. M. (1982). Homology and causes. *J. Morphol. 173*, 305–312.

Wagner, G. P. (1989a). The biological homology concept. *Ann. Rev. Ecol. Syst. 20*, 51–69.

Wagner, G. P. (1989b). The origin of morphological characters and the biological basis of homology. *Evolution 43*, 1157–1171.

Wagner, G. P. (1994). Homology and the mechanisms of development. In B. K. Hall (Ed.), *Homology: The Hierarchical Basis of Comparative Biology*, pp. 273–299. San Diego: Academic Press.

Wagner, G. P. (1996). Homologues, natural kinds and the evolution of modularity. *Amer. Zool. 36*, 36–43.

Wagner, G. P. and B. Y. Misof (1993). How can a character be developmentally constrained despite variation in developmental pathways? *J. Evol. Biol. 6*, 449–455.

Wake, D. B. (1994). Comparative terminology. *Science 265*, 268–269.

Webster, G. (1984). The relation of natural forms. In M.-W. Ho and P. T. Saunders (Eds.), *Beyond Neo-Darwinism: An Introduction to the New Evolutionary Paradigm*, pp. 193–217. London: Academic Press.

Selected background reading

A short summary of all important aspects of and approaches to homology; including reference to the main articles:

Donoghue, M. J. (1992). Homology. In E. Fox Keller and E. A. Lloyd (Eds.), *Keywords in Evolutionary Biology*, pp. 170–179. Cambridge, MA: Harvard Univ. Press.

Collection containing contributions by several main figures involved in discussions on theories and concepts of homology; it covers all main aspects of and approaches to homology; many useful references (the collection is an overview of the state of art 150 years after Richard Owen's seminal lectures):

Hall, B. K. (Ed.) (1994). *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press.

Useful overview of several aspects of homology (including serial and latent homology as well as homology and development); due to its examples and illustrations nice introduction for someone who is not familiar with homology (this 13 page booklet is in fact a seminal article, which anticipates many issues on homology that have been important for developmental approaches to homology in the last two decades):

de Beer, G. (1971). *Homology, An Unsolved Problem.* Oxford Biology Readers. Glasgow: Oxford Univ. Press.