THE ROLE A CONCEPT PLAYS IN SCIENCE — THE CASE OF HOMOLOGY

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Abstract

The present paper gives a philosophical analysis of the conceptual variation in the homology concept. It is argued that different homology concepts are used in evolutionary and comparative biology, in evolutionary developmental biology, and in molecular biology. The study uses conceptual role semantics, focusing on the inferences and explanations supported by concepts, as a heuristic tool to explain conceptual change. The differences between homology concepts are due to the fact that these concepts play different theoretical roles for different biological fields. The specific theoretical needs and explanatory interests of different research approaches lead to different homology concepts.

1. Introduction.

Homology is a crucial biological concept; in fact, some consider it one of the most important concepts in all of biology (Donoghue 1992; Wake 1994; Raff 1996; Abouheif et al. 1997; Laubichler 2000). Homology refers to structures and characters in different species that correspond to each other. Despite its importance for biology, the homology concept has not been extensively discussed by philosophers of science. The homology concept has a long and rich history, dating back more than 200 years. While this term was originally used mainly in comparative and later in evolutionary biology, it has recently become important for developmental and molecular biology. In the last decades several aspects and several levels of homology emerged and became relevant for some fields (e.g., serial homology, molecular homology). Nowadays the term 'homology' exhibits noticeable variation within the biological community. Different biological fields have a different perspective on homology. In fact, several so-called 'concepts' or 'definitions' of homology are proposed, criticized and defended. The term 'homology', as it seems, is used with a different content in different parts of the biological community. The aim of the present paper is to analyze this conceptual variation and to offer a philosophical account of it.

As will be argued, there are three different homology concepts used in contemporary biology. These different concepts correspond to three fields within biology — comparative and evolutionary biology, evolutionary developmental biology, and molecular biology. Using conceptual role semantics as a heuristic tool for the study of differences among scientific concepts, my claim is that these conceptual differences are due to the fact that *homology plays a different theoretical role for different fields*, i.e., homology concepts are used for different concrete epistemic goals. The following discussion will make clear that the homology concepts that are characteristic of the three communities are embedded in three different approaches and are employed in characteristically different inferences and explanations.

2. A conceptual role approach to conceptual change in science. For the study of conceptual change, it is important to recognize that concepts stand in historical relationships. Concepts form lineages so that a recent concept may stem from a former concept. The different current homology concepts are derived from an original homology concept. This concept migrated into new disciplines and underwent adaptive radiation — leading to different specialized homology concepts. It is beyond the scope of this paper to give an account of the rich history of homology and the actual origin and emergence of the three current homology concepts. In particular, I will not discuss whether there actually existed one or more homology concepts in the past (such as a pre-Darwinian and a distinct post-Darwinian concept as forerunners of the current concepts); and I will not asses whether one of the current concepts is in fact the same concept (i.e., has the same content) as one of the historical concepts. Instead, the focus of my analysis will be on the recent situation and the burden of the argument is that currently there coexist three distinct homology concepts. Thus the present discussion is about the current conceptual variation rather than a detailed study of conceptual change.[1]

Given that a discussion of the history of the current homology concepts is beyond the scope of the present discussion, the following remarks will suffice to introduce the very idea of homology and point to the basic root of the current concepts. Homology is what I call an *investigative kind concept.* An investigative kind is a group of entities that are presumed to belong together due to some underlying mechanism or a structural property. The idea that these entities belong to a kind might be due to some interesting similarities: scientists perceive a certain pattern in nature. However, these similarities are not deemed to be what characterizes this kind. Instead, an investigative kind is specified by some theoretically important, but yet unknown underlying feature or process that is presumed to account for the observed similarities. Thus an investigative kind concept is associated with a search for the basis of the kind. An example is the species concept. We are able to recognize species, but it is not immediately clear what accounts for the origin and coherence of these units — leading to different species definitions. A full theoretical account of an investigative kind can only be given after appropriate empirical study and might reveal a variety of complications. An investigative kind concept may even change its reference throughout scientific investigation. In any case, an investigative kind concept goes together with a scientific search which may be open-ended.[2]

The homology concept is an investigative kind concept for the following reasons: Biologists perceived and perceive a unity of form among different taxa. Structures in organisms from different species seem to correspond to each other. Phyla are taxa which encompass those animals that have a common body plan. This allows scientists to place the morphological structures of different species in correspondence (e.g., according to their relative position in the body plan). For instance, the human arm and the bat wing are homologous because the individual bones of the human arm correspond to the bones of the bat wing. Homology refers to this correspondence: corresponding structures in different organisms are called ‘homologues’ or said to be ‘homologous to each other’. Homologues often have the same name, even across distantly related species. The definition of Richard Owen, which is still favored by some contemporary biologists, expresses this fact:

> HOMOLOGUE … The same organ in different animals under every variety of form and function. (Owen 1843, p. 379)

Biologist are able to *recognize* homologous structures, and there are accepted *criteria* of homology. However, the perceived structural similarity is not to be confused with the nature of the correspondence called homology. (Owen's definition distinguishes between "sameness" and superficial shape or "form", that varies between species.) Considering homology an investigative kind concept means that there is a search for the biological basis of homology. An account is needed of what characterizes the structures that are (considered) homologous, i.e., an explanation of the perceived phenomenon picked out by examples and by the accepted criteria of homology. Different theoretical perspectives lead to *different historical and contemporary accounts of homology.* A few 19th century idealistic morphologists explained the unity of form with reference to Platonic ideas. Structures were viewed as homologous in case they were (empirical and imperfect) instantiations of the same abstract and perfect pattern. With the advent of Darwinism, a common evolutionary origin became the standard explanation of homologous correspondence of structures. In fact, homologues are often defined as structures that are derived from a common ancestor. For contemporary developmental approaches to homology, however, reference to inheritance from a common ancestor cannot be a complete explanation because it does not give a causal-mechanistic explanation of how the same structures develop repeatedly in different generations.

The investigative kind concept account of homology points to the historical root of the homology concept. In addition, it explains why there can be different accounts of homology, even though different fields of biology use the same criteria of homology and consider largely the same structures as homologous. Often, biologists just speak about *the* homology concept. This is due to the common historical root, accepted criteria and instances of homology, and the general idea that homology refers to the corresponding structures in different organisms. Nevertheless, there is conceptual variation in the current term ‘homology’, which is actually so large that we can identify several homology concepts. In order to be able to argue for this, we need an account of the content and the individuation of concepts. The idea that concepts form historical lineages presumes that we have an account of what defines a split of a lineage, creating novel concepts. To be able to track conceptual change, we need a theory of what a change in the content of a concept is and whether it amounts to a new concept. In addition, an account of the content of concepts is the basis for explaining why an instance of conceptual change occurred and for assessing whether it was progressive.

Most discussions in the philosophy of science about conceptual change have focused on the reference of terms (Newton-Smith 1981; Hacking 1983; Psillos 1999). The focus on reference often stems from the attempt to show that theoretical change does not lead to semantic incommensurability. Philosophers point out that substantial theoretical change need not lead to reference change among the fundamental terms of the theory, so that both theories address the same entities and thus can be compared (Scheffler 1967; Devitt 1979; Sankey 1994). However, such a framework is of limited use for the study of conceptual change because a conceptual lineage may split into distinct concepts with referential continuity (as it is the case with some contemporary species concepts) and conceptual change and progress within a lineage may occur without change of reference. For example, take the term ‘gene’. The molecular gene concept refers to the same entities as its predecessor, the Mendelian gene concept. However, the molecular gene concept is a much more powerful concept in that it supports explanations in molecular and developmental biology which the Mendelian gene concept did not support.

Kitcher (1978, 1993) offers a framework that does not just study reference. His core notion is that of the 'reference potential' of a term, which is the set of the different ways scientists refer to a category. For Kitcher, conceptual change is change of reference potential, and conceptual progress occurs if we acquire new ways of referring to a category. However, we need a better account of why the molecular gene concept is more powerful than pointing out that we nowadays have more ways to refer to this entity. A theory of concepts has to capture the way in which concepts facilitate explanations and discovery, so that we can view the transition from Mendelian to molecular genetics as an instance of explanatory progress *because of the change of the gene concept*. Kitcher (1993), however, does not connect the issue of conceptual progress to his discussion of explanatory progress. In addition, Kitcher does not intend to explain why conceptual change occurred, which I view as an important task for a theory of conceptual change. It may be possible to develop Kitcher's framework to include these issues. But this would mean to first have an account of reference, then develop a notion of reference potential, and in a third stage try to address the issues that are at the core of understanding conceptual change. My strategy instead is to focus from the very beginning on those aspects of concepts that allow for a more direct explanation and evaluation of conceptual change.

Concepts are knowledge producers, and scientists use concepts to justify claims and give explanations of phenomena. By supporting inferences and explanations concepts help to create specific kinds of scientific knowledge. This knowledge is an *epistemic product* of scientific reasoning, and obtaining certain kinds of knowledge may be characteristic for a particular branch of science. Different scientific fields and research approaches have different *theoretical goals*, and thus demand different epistemic products. Concepts are employed to pursue these goals; in fact, concepts are shaped and designed to bring about the intended epistemic product. Thus, my approach is to link concepts to the epistemic products and the theoretical goals of a scientific field. My focus is on the *inferences and explanations that are supported by a particular concept*, which yield the kinds of knowledge that a specific field needs. Conceptual change and possible conceptual differences have to be detected by examining the inferential and explanatory potential of concepts. I will argue that the different homology concepts actually support different types of inferences and explanations. And these inferences and explanations are specific and important for the field in which a particular homology concept is used. Thus, my framework attempts to explain conceptual change by reference to the goals of a field; and conceptual progress can be evaluated based on whether a particular concept is actually able to provide kinds of knowledge and explanations that are scientifically significant. The molecular gene concept, for instance, is an advance because it supports molecular explanations that could not have been given using the Mendelian gene concept.

My focus on the inferences and explanations supported by a scientific concept fits with a general approach to conceptual content — *conceptual role semantics*, which I will use as an account of concepts and concept individuation. Conceptual role semantics is not a particular theory, rather it is a broad framework that encompasses various (sometimes very different) semantic approaches (compare Field 1977; Block 1986; Harman 1987; Brandom 1994; Wedgwood 2001). The idea of conceptual role semantics — also called functional role or inferential role semantics — is that the content of syntactic entities and mental representations is at least partially constituted by the cognitive or inferential role they have for a thinker or community. Concepts have a specific role in thought, perception, decision making, and action. Conceptual role semantics has been advanced as an account of mental and semantic content. However, I am not concerned with general issues from the philosophy of mind and language, but only with concepts and conceptual change in science. I use conceptual role semantics as a *heuristic tool* to detect and explain conceptual differences.

There are several ideas about what a conceptual role is. As the present discussion deals with scientific concepts, I focus on the role concepts play in *theoretical reasoning.* Theoretical reasoning does not presuppose that there is an explicitly formulated theory. The molecular homology concept has a theoretical role independent of whether there is something like a 'theory of molecular biology'. One important aspect of the theoretical role of concepts is their *inferential role.* By virtue of its content, a concept has inferential connections to other concepts. If two concepts support two classes of inferences that are different, then they have a different inferential role.[3] The inferences that scientific concepts make possible are important for producing scientific knowledge and justifying scientific claims. While philosophical accounts along the line of conceptual role semantics have stressed the inferential potential of concepts, one needs to keep in mind that concepts — in particular scientific concepts — are also used for *explanations.* Propositions containing a concept can explain certain facts. A particular concept might be crucial for explaining a specific class of processes or situations, while in order to account for another class of phenomena a different concept needs to be employed. It is not obvious how explanation relates to standard models of inference making. Salmon (1970) argues that explanations are not arguments (neither inductive nor deductive), so the inferential role of concepts need not encompass their *explanatory role*. In the case of statistical explanations, concepts may pick out a class and appropriate reference classes and link them to statistical relevance relations. In causal explanations a concept picks out a set of entities that are part of similar causal processes or governed by the same causal law. My case study will argue that a crucial difference between the homology concept used in evolutionary developmental biology and the homology concept of evolutionary and comparative biology is their difference in explanatory potential. In fact, evolutionary developmental biology uses its particular homology concept because other homology concepts cannot yield the type of explanations that are important for developmental biology.[4]

Even though I use a conceptual role semantics, I do *not* identify concepts (or conceptual content) with conceptual role. For this would lead to holism about concept individuation; any difference in inferential role would amount to a new concept, so that every scientist might have a different concept. Instead, I assume that the content of terms supervenes on conceptual roles. In particular, two concepts can be different only insofar they have different conceptual roles. I follow Harman (1973) and Block (1986) in assuming that merely similarity, not necessarily identity in conceptual role is sufficient to share the same concept. The inferential roles of a term may differ slightly between persons — people have differing beliefs and endorse different inferences. Individuals may differ in their mental representations. I view a concept as a cluster of similar mental representations. Taking a concept as a group-level entity abstracts from this inter-personal variation and focuses on the more substantial difference between different concepts. I take two terms to have a different content in case they make inferences or explanations possible that are relevantly dissimilar. What counts as relevant is dependent on the scientific standards of the given situation. The concrete scientific situation determines what counts as giving a justification or an explanation that is different in kind from other justifications or explanations.[5] In what follows, I will present a case study in which I argue that the term ‘homology’ can be considered as corresponding to different concepts. These different homology concepts support different kinds of inferences and explanation, and biologists consider these differences as important — it matters for biology whether a specific type of explanation can be supported or not by a particular homology concept.

The point of my claim that there are different homology concepts used is not that biologists are confused when they just use the term ‘homology’. Instead, biologists may be aware of the fact that other fields have a different understanding of homology and use this concept differently. The purpose of my paper is to give a philosophical analysis of the variation in the term ‘homology’. I intend to show that this variation consist in differential *inferential and explanatory roles*, so that different homology concepts yield different *epistemic products.* And I make clear how this difference in epistemic products relates to the *theoretical goals* of the respective biological disciplines. The upshot of my argument is that a conceptual role approach gives a good explanation of the variation of the term under consideration.[6]

3. Homology in comparative and evolutionary biology. The homology concept originated in the context of comparative biology, in particular comparative anatomy. Among current homology concepts the understanding of homology in comparative and evolutionary biology is the most traditional one. In what follows, I will refer to this contemporary homology concept by the term *phylogenetic homology.* In comparative anatomy the above mentioned idea of homology as something that refers to the corresponding structures is in this field most clearly employed. In particular bones, organs, muscles, and tissues are the types of characters that are homologized. The criteria of homology used are the relative position with respect to other structures, the connectivity to adjacent structures (e.g., blood vessels and nerves), similarity in structural detail and histology, and correspondence of the developmental origin. Even though the character distribution on a phylogenetic tree is an additional important criterion for assessing hypotheses of homology, many of the criteria used for practical work resemble pre-Darwinian anatomy (Russell 1916). There is a great deal of historical continuity between the original homology concept and the current phylogenetic homology concept.[7]

The *aim of comparative biology* is to compare the characters of different species, yielding systematic descriptions of large groups of organisms. Homology is a relational notion used in comparing organisms or species. It identifies characters in different species that correspond to each other. A homologue behaves and changes as a unit in development and evolution. The fact that a considered part of an organism can be homologized with a part in another species is evidence for this part actually being a unit of the organism, while not sufficiently individualized parts of the body may lead to dubious or conflicting hypotheses of homology (Wagner 1989b; Wagner and Gauthier 1999). Homology helps to break organisms down into natural units and it links these units across species. *Homology individuates biological characters.* (This is clearly expressed by the above quoted definition of Owen.) For this reason, identifying homologues is an important step in comparison and classification. In the case of some structures, or of more distantly related organisms, it is by no means obvious how to homologize structures. Despite large differences between species, homology refers to common patterns across large groups of organisms.

The crucial type of *inferences supported by the homology concept* is the following: Homologues are derived from a common ancestral structure. For this reason, properties that hold for a structure in a particular species are likely to hold for the homologous structure in another species. As phylogenetic homology makes reference to the common ancestry of homologous structures, *the homology concept allows for inferences from the properties of one type of organism to other organisms.* This is important because individuating biological characters by means of homology allows for unified descriptions that apply to a relatively large class of organisms. For instance, neuroanatomical descriptions and theories may just talk about 'the' cerebrum, referring to a class of homologues in a taxa as large as the vertebrates. This is possible because many morphological, histological, or developmental descriptions of a structure such as the cerebrum apply to a larger class of organisms. Thus, identifying homologues and basing comparative descriptions on classes of homologues yields *general and unified morphological knowledge*, which is an important epistemic product of comparative biology. Even before the explicit use of the homology concept, biologists gave the same name to corresponding structures of different species. In this manner, they followed a practice that allowed for effective descriptions. Later, once 'homology' was clearly available as a concept, this comparative practice could be made explicit, discussed, and defended. Having homology as a concept allows for reflection about the nature of homology and the criteria of homology employed. Biologists make in particular explicit use of the homology concept when they need to defend their hypothesis of homology, thereby justifying their naming of structures and comparative descriptions made in particular cases. For these reasons, the phylogenetic homology concept is vital for the types of inferences and their justification made in comparative biology. By establishing correspondence of structures between different species homology allows for generalized descriptive knowledge across species.

In addition, apart from providing comparative descriptions of organisms, the comparison of characters is necessary to obtain taxonomic classifications of species. Structures identified as homologous are compared in detail; and their similarities and differences provide the data for classification. Stable classifications can only be obtained by comparing corresponding structures in different species. Reference to homology justifies the fact that certain structures of different species are compared. Thus, phylogenetic homology serves the goal of comparative biology, producing and justifying general comparative descriptions applying to large groups of organisms and providing comparisons that are effective for classifying species.

In *evolutionary biology* the focus is on the change of characters in the course of phylogeny. Homology is a concept that temporally links entities. In accounts of morphological evolution, homologues become historical units that date back to an ancestral character. Evolutionary approaches to homology are usually so-called transformational accounts of homology (Hennig 1966; Mayr 1982; Bock 1989; Donoghue 1992), because an ancestral and descendant character are defined as being homologous in case they are connected by a transformation series of intermediate homologues (in a lineage of species leading from the ancestor to the descendant). A *main goal* of evolutionary biology is to explain 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. The homologues in a lineage are the entities underlying change. For instance, in order to talk about the same (type of) selection pressure operating in some morphological structure over time one needs to identify the lineage of characters on which this selection pressure operates. Once a lineage of characters has been identified 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 quite dissimilar in shape and function. Identifying homologous structures in ancestor and descendant is a precondition for giving an adaptation explanation of the change of these structures. Thus, phylogenetic homology is used to yield (together with other concepts) an epistemic product of evolutionary biology — describing and explaining the adaptive modification of characters. While homology in comparative biology allows for inferences, in evolutionary biology it is in addition a conceptual precondition for explanations by justifying which character transformations need to be studied and explained. In short, the theoretical role of the phylogenetic homology concept — used in comparative morphology and evolutionary biology — is to link characters across species in order to conceptualize the natural units that underlie variation across species or evolutionary change, yielding systematic comparative knowledge and making adaptation explanations possible.

4. Homology in evolutionary developmental biology. This section is about developmental approaches to homology, but the understanding of homology described in this section does actually not apply the developmental biology as a whole. For instance, the homology concept of many developmental geneticists is the molecular homology concept described in the next section. This section is about the homology concept of those developmental biologists who take evolutionary as well as theoretical issues seriously. This is in particular the case for representatives of the discipline of evolutionary developmental biology.

Developmental homology — as I will call this homology concept — is a quite recent concept and it is historically derived from phylogenetic homology. Due to the migration of the older phylogenetic homology concept into a new discipline, the concept underwent change.[8] Biologists both from comparative/evolutionary and developmental biology largely use the same criteria of homology (Roth 1994), and consider the same structures of different species as homologous. Nevertheless, the homology concept of evolutionary developmental biology has a wider extension. Two points are worth mentioning. First, developmental biologists apply homology to lower levels of biological organization than comparative or evolutionary biologists usually do. In developmental biology, the theoretical focus 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. Developmental biology studies different cell types, tissue types, transient structures, and developmental precursors. It is the branch of biology that addresses most completely all levels of organismic organization and how they interact. For this reason, when the issue of homology arises conceptually in the comparison of the development in different organisms, 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). Calling types of cells and tissues the same amounts to an implicit statement of homology. 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 became explicitly applied to different levels.

Second, there is the issue of *serial homology.* This is the most telling evidence for the existence of different homology concepts in different biological fields. 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 pre-Darwinian morphology because of their geometrical-topological approach to homology. (For instance, Owen considered the different vertebrae of an organism as derived from unique geometric scheme, the 'ideal vertebra'.) Within an 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 vertebra. In contemporary *comparative and evolutionary biology*, serial homology is usually ignored. Sometimes its possibility is denied and the idea of serial homology is attacked (Ax 1989; Bock 1989; Schmitt 1989). This is due to the theoretical and explanatory focus of this branch of biology. Comparative biology compares *different* species (and evolutionary biology deals with lineages of different species). Important goals of these disciplines are to identify homologues of distinct species and to compare different species and their characters. Serial homology, however, sets two parts of the very same organism in correspondence; and this is why it is not important for comparative and evolutionary biology. Thus, serial homologues are not part of the extension of this homology concept. In the case of *developmental approaches to homology*, 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* 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. For instance, limb development is one of the best studied morphogenetic phenomena in land-living vertebrates. 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 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.

While comparative and evolutionary biologists sometimes attack the developmental homology concept, biologists with a developmental are also aware of these two distinct understandings of homology (Wagner 1989a; Minelli and Peruffo 1991; Roth 1991; Shubin 1994; Sluys 1996). The discussion already pointed to the fact that this conceptual difference has something to do with the different theoretical interests and goals of these fields. Indeed, the conceptual difference goes beyond a difference in extension; the difference in reference is due to a difference in sense or content. My following account of the conceptual variation is that it is due to the fact that homology concepts play different theoretical roles in these two parts of biology. That is, homology concepts are used to generate different types of biological knowledge or to explain different types of phenomena. Each homology concept serves the theoretical interests of the field in which it is used by being a necessary conceptual ingredient in bringing about the epistemic product characteristic of that field.

In the case of developmental biology, *the epistemic product is explanations of the formation of structures*. Knowledge about developmental processes is generalized by concepts that refer to commonalities of different concrete developmental mechanisms. Explanations of the formation of a class of structures are based on considerations about a corresponding causal origin, a common maintenance, or a comparable developmental behavior of these structures. Developmental homology refers to repeated or corresponding structures of organisms. This homology concept is used to account for the similarity of structures within and between organisms by pointing to a (as yet barely understood) common underlying developmental basis. It focuses on the mechanistic underpinnings of the structural identity of homologous characters in the course of development and evolution. 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 1996), by picking out structures that participate in similar developmental processes and by referring to those causal factors and developmental features that account for this reappearance of structures. In this manner, the developmental homology concept serves one fundamental aim of developmental biology — explaining how structures emerge in ontogeny and why they are how they are (which has a bearing on explaining why structures are conserved or transformed in the course of phylogeny).

A consequence of the difference in content or theoretical role of the developmental and phylogenetic homology concept is a difference in reference — developmental homology applies to a larger domain of characters and to homologues within the same organism (serial homology). Even if one abstracts from this and considers nothing but homology among morphological structures in different species (i.e., the extension of the phylogenetic homology concept), the different biological branches discussed offer a different account of why these structures are homologous. Approaches in comparative and evolutionary biology just refer to inheritance from a common ancestral structure as the defining feature of homology. For a developmental 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 structure are formed in different organism (Wagner 1989b; Roth 1994). Instead, reference to the developmental processes generating this structures in different organisms is a necessary part of any developmental approach. The emphasis is on common developmental features rather than on common ancestry. For example, the homology definition proposed by Louise Roth (1984) talks about shared developmental pathways. Günter Wagner's definition of homology, his so-called 'biological homology concept', focuses on shared developmental constraints, but does not make explicit reference to common ancestry (1989a).

The *phylogenetic* homology concept has a very limited explanatory potential, its main role is to yield *inferences*. Phylogenetic homology — just making reference to common ancestry — can only account for the taxonomic distribution of characters (Wagner 1994).[9] 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. This difference in conceptual role between phylogenetic and developmental homology justifies the claim that they are actually two different concepts. *Developmental homology supports types of explanations that phylogenetic homology does not support* and these explanations are distinct (in fact, developmental) and important explanations. Phylogenetic and developmental homology serve different epistemic and explanatory goals. Biologists are aware of the fact that comparative biology is interested in the phylogenetic relationship of species and in grouping organisms into taxa, but that developmental approaches have different aims (Roth 1991; Wagner 1994; Sluys 1996). Rather than identifying and comparing homologues, the aim of developmental biology is to explain how structures emerge in ontogeny and why the same structure develops in the next generation. Since both disciplines use their homology concept for their theoretical goals, the different understanding of homology is a matter of meaning rather than of belief. The dispute of how homology is to be understood or to be defined cannot be settled by standard empirical findings. For instance, comparative biologists criticize the understanding of homology in developmental biology, because for them homology is *about* comparing different species (Ax 1989), but not about comparing structures within organisms (serial homologues) or explaining the origin of characters. In contrast to homology in comparative and evolutionary biology, the conceptual 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.

5. Homology in molecular biology. In molecular biology it is generally genes and proteins that are homologized. The concept of *molecular homology* often refers to the similarity of DNA or amino acid sequences (Hillis 1994; Reeck et al. 1987). 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 molecular homology is not a all-or-nothing affair, but comes in degrees. Even more important is the fact that molecular homology is a statement about the mere similarity of genes and proteins, but not about their evolutionary origin — inheritance from a common ancestor. For a more evolutionary understanding that views homology as a concept referring to the common evolutionary origin of structures, mere sequence similarity is just a criterion for common ancestry (i.e., homology), but not to be equated with the concept of homology. Despite some criticisms of the way in which many molecular biologists use the term ‘homology’, I will focus on the concept of molecular homology as sequence similarity, because it is the predominant use in molecular biology. This usage 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; the *theoretical goal* is to describe mechanisms and explain phenomena on the molecular level.

A good deal of easily accessible information about the structure as well as the 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 sequence correspondence among genes and proteins (and their parts). This is due to the fact that similar genes have similar genes products and similar proteins are likely to be part of a similar pathway or to behave similarly in biochemical reactions. 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 functional 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 comparison of different species or with questions about the classification and evolution of organisms. Instead, the focus is on the structure of molecular substances and the mechanisms in which they figure. If the sequence of a new gene or protein is available, it is compared to known genes and gene products. Molecular homology refers to the degree of sequence similarity. Similarity allows for an inference or a hypothesis about the effect or function of a new molecular entity. This provides the opportunity to examine a new protein more effectively using knowledge about established proteins and their pathways. The knowledge about certain molecular systems can be employed to transfer experimental approaches and research strategies to other yet unstudied systems, provided that both are known to be similar. Often the similarity-based inference from one system to a new one yields *effective ways of discovery rather than a direct confirmation of the properties of the new system.*

In molecular biology, the research focus is on the experimental level. The goal of this discipline is to discover mechanisms, which is crucial for explanations on the molecular level and basis for 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 approach of molecular biology. It is effective to organize knowledge about the structure and function of molecular substances and to direct experimental practice. The conceptual role of molecular homology is to infer theoretical hypothesis and experimental strategies about molecular entities and mechanisms. Molecular homology is an operational concept that is theoretically not as robust as phylogenetic or developmental homology. The fact that two gene sequences are similar is not to be equated with the fact that they are derived from a common ancestral gene. A collection of similar genes is not a lineage of characters to which phylogenetic homology refers. Structural similarity refers to a pattern, but does not include the ontogenetic or phylogenetic processes that brought about the similarity. For this reason, the molecular homology concept is not able to support the phylogenetic inferences and developmental explanations that the homology concepts of evolutionary and evolutionary developmental biology support.[10]

6. Conclusion. I have argued that the term 'homology' actually corresponds to different concepts. My account of homology as an investigative kind concept pointed to the common root of these homology concepts. These different concepts are referred to by the same term because they are historically descended from one concept and they are similar in certain respects. Across biological fields homology is assumed to designate corresponding characters in different organisms, and the same criteria of homology are used. The idea of an investigative kind concept also allows for an explanation of why there are different accounts of largely the same objects that are grouped together as homologues.

The focus of the present discussion was on the current conceptual variation in the term 'homology'. My conceptual role approach suggests searching for conceptual differences by studying the different theoretical roles of concepts. The variation in the case of homology is actually grouped around distinct poles that correspond to different biological fields. I explained this variation with reference to the different epistemic interests and theoretical goals of particular biological fields. Homology concepts are used to obtain characteristic types of inferences and explanations. In the case of *comparative and evolutionary biology*, the goals are the comparison and taxonomy of species 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 lineage of species characters despite variation and potentially unlimited evolutionary change. This allows for unified knowledge about the structure of large groups of organisms in the case of comparative biology, and is a precondition for explaining adaptation in the case of evolutionary biology. In *evolutionary developmental biology* the goal is to figure out how and why certain structures emerge in ontogeny. The conceptual 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. Finally, in *molecular biology* the epistemic aim is the description of molecular mechanisms and the explanation of molecular phenomena. 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.

Conceptual differences of a term have been subject to philosophical investigation. While many former accounts of conceptual change focused on the reference of concepts, studying differences in extension alone may in some cases be of limited value. Conceptual roles cut sometimes finer than extension — concepts with the same extension may have a different content. We saw that the conceptual variation in the homology concept goes beyond mere difference of reference. The phylogenetic and developmental homology concepts differ in their explanatory potential. Conceptual roles not only offer a more fine-grained analysis than the study of extension, they also explain why there is a difference in content and possibly in extension. Biologist sometimes criticize the homology concept of another field because the rival concept does not do the (in their view) right theoretical job. A philosophical account should not just determine possible differences of extension among homology concepts, but it should have a grasp on the reasons for adopting or criticizing particular homology concepts. The discussion tried to explain how the variation in the homology concept came about by the different theoretical demands of biological fields. Former approaches to conceptual change usually attempted to rebut the incommensurability threat and thus focused on reference. My approach, instead, is primarily concerned with explaining conceptual change, using an account of concepts that captures the way in which concepts figure in reasoning and are used to pursue explanatory goals.

My philosophical frameworks allows for evaluating whether an instance of conceptual change is an advance by studying the types of knowledge that are produced by concepts. The inferences supported by the phylogenetic homology concept are the basis of an effective comparative practice in biology, which is of fundamental importance because it individuates characters across large groups of organisms. Molecular homology is an effective conceptual tool given the focus on discovery in this field. Biologists with a developmental approach to evolution are trying to develop a developmental homology concept that has an explanatory potential that goes fundamentally beyond the phylogenetic homology concept. Currently developmental homology has still a limited explanatory potential and it remains to be seen whether empirical and theoretical progress will bring about a substantial improvement on phylogenetic homology.

I believe that my framework could be applied to other instances of conceptual change such as the transition from the Mendelian to the molecular gene concept or the emergence of various species concepts. Several authors have argued for or against pluralism about the species concept. My discussion of homology suggests a pluralist approach insofar as I view the emergence of different homology concept as rational and progressive given the demands of particular fields. An implication for biological practice is that the debate between different fields about the right understanding of ‘the’ homology concept is of limited use. The different homology concepts can coexist because each is an effective tool for certain purposes. A biologist can simply stick to the homology concept used by her field — as long as it is explicitly recognized that there are other homology concepts that satisfy different theoretical needs. This upshot is not to be construed as the idea that the current situation has to persist. I do not claim that biology must necessarily have three or more homology concepts or that none of the current homology concepts might disappear in the future. Some might want to argue that a successful future developmental homology concept could encompass a phylogenetic homology concept, or that we should not use the term ‘homology’ for an operational concept such as the molecular homology concept. In contrast to past discussions about species pluralism, my focus was more on the rational explanation of conceptual diversity rather than its ultimate justification. My approach is also different from some former discussions of pluralism in that former accounts often simply assumed that different species definitions amount to different concepts. My discussion explicitly used a theory of conceptual content so that I have a better basis for justifying the claim that we actually deal with different concepts.

I used a conceptual role semantics approach as a heuristic device for the study of conceptual variation. My approach suggested pinning down potential differences in the content of the term ‘homology’ by looking at the theoretical role of this concept — the types of inferences and explanations that a particular homology concept makes possible. This account has the advantage that it links the individuation of concepts with the epistemic product and theoretical goals of particular scientific fields or research approaches, which in turn makes intelligible why a particular concept is used in a specific field. The approach also allows to evaluate whether conceptual change is progressive by studying the change in the inferential and explanatory potential of concepts and their significance. My discussion of the homology concept suggests that a conceptual role semantics approach might be a fruitful approach for the study of conceptual change and variation of other scientific concepts.

References

Abouheif, Ehab, 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 in Genetics* 13: 432–433.

Ax, Peter (1989), "Homologie in der Biologie – Ein Relationsbegriff im Vergleich von Arten", *Zoologische Beiträge Neue Folge* 32: 487–496.

Block, Ned (1986), "Advertisement for a Semantics for Psychology", in Peter A. French, Theodore E. Uehling, Jr., and Howard K. Wettstein (eds.), *Studies in the Philosophy of Mind, Midwest Studies in Philosophy, Vol. 10.* Minneapolis: University of Minnesota Press, 615–678.

Bock, Walter J. (1989), "The Homology Concept: Its Philosophical Foundation and Practical Methodology", *Zoologische Beiträge Neue Folge* 32: 327–353.

Boyd, Richard (1999), "Homeostasis, Species, and Higher Taxa", in Robert A. Wilson (ed.), *Species: New Interdisciplinary Essays.* Cambridge, MA: MIT Press, 141–185.

Brandom, Robert B. (1994), *Making It Explicit: Reasoning, Representing, and Discursive Commitment.* Cambridge, MA: Harvard University Press.

de Beer, Gavin (1971), *Homology, An Unsolved Problem.* Glasgow: Oxford University Press.

Devitt, Michael (1979), "Against Incommensurability", *Australasian Journal of Philosophy* 57: 29–50.

Donoghue, Micheal J. (1992), "Homology", in Evelyn Fox Keller and Elisabeth A. Lloyd (eds.), *Keywords in Evolutionary Biology.* Cambridge, MA: Harvard University Press, 170–179.

Field, Hartry (1977), "Logic, Meaning, and Conceptual Role", *Journal of Philosophy* 69: 379–408.

Gilbert, Scott F., John M. Opitz, and Rudolf A. Raff (1996), "Resynthesizing Evolutionary and Developmental Biology", *Developmental Biology* 173: 357–372.

Hacking, Ian (1983), *Representing and Intervening.* Cambridge: Cambridge University Press.

Harman, Gilbert (1973), *Thought.* Princeton: Princeton University Press.

——— (1987), "(Non-Solipsistic) Conceptual Role Semantics", in Ernest LePore (ed.), *New Directions in Semantics.* London: Academic Press, 55–81.

Haszprunar, Gerhard (1992), "The Types of Homology and their Significance for Evolutionary Biology and Systematics", *Journal of Evolutionary Biology* 5: 13–24.

Hennig, Willi (1966), *Phylogenetic Systematics.* Urbana: University of Illinois Press.

Hillis, David M. (1994), "Homology in Molecular Biology", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press, 339–368.

Kitcher, Philip (1978), "Theories, Theorists, and Theoretical Change", *The Philosophical Review* 87: 519–547.

——— (1993), *The Advancement of Science: Science without Legend, Objectivity without Illusions.* Oxford: Oxford University Press.

Laubichler, Manfred (2000), "Homology in Development and the Development of the Homology Concept", *American Zoologist* 40: 777–788.

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

McGinn, Colin (1982), "The Structure of Content", in Andrew Woodfield (ed.), *Thought and Object: Essays on Intentionality.* Oxford: Oxford University Press, 207–258.

Minelli, Alessandro, and Beatrice Peruffo (1991), "Developmental Pathways, Homology, and Homonomy in Metameric Animals", *Journal of Evolutionary Biology* 4: 429–445.

Newton-Smith, William Herbert (1981), *The Rationality of Science.* Boston: Routledge & Kegan Paul.

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

Panchen, Alec L. (1994), "Richard Owen and the Concept of Homology", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press, 21–62.

Psillos, Stathis (1999), *Scientific Realism: How Science Tracks Truth.* London: Routledge.

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

Reeck, Gerald 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.

Roth, V. Louise (1984), "On Homology", *Biological Journal of the Linnean Society* 22: 13–29.

——— (1991), "Homology and Hierarchies: Problems Solved and Unsolved", *Journal of Evolutionary Biology* 4: 167–194.

——— (1994), "Within and Between Organisms: Replicators, Lineages, and Homologues", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press, 301–337.

Russell, E. S. (1916), *Form and Function: A Contribution to the History of Animal Morphology.* London: J. Murray.

Salmon, Wesley (1970), "Statistical Explanation", in Robert G. Colodny (ed.), *The Nature and Function of Scientific Theories.* Pittsburgh: University of Pittsburgh Press, 173–231.

Sankey, Howard (1994), *The Incommensurability Thesis.* Brookfield: Avebury.

Scheffler, Israel (1967), *Science and Subjectivity.* Indianapolis: Bobbs-Merrill.

Schmitt, Michael (1989), "Das Homologie-Konzept in Morphologie und Phylogenetik", *Zoologische Beiträge Neue Folge* 32: 505–512.

Shubin, Neil H. (1994), "History, Ontogeny, and Evolution of the Archetype", in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press, 249–271.

Sluys, Ronald (1996), "The Notion of Homology in Current Comparative Biology", *Journal of Zoological Systematics and Evolutionary Research* 34: 145–152.

van Valen, Leigh M. (1982), “Homology and Causes”, *Journal of Morphology* 173: 305–312.

Wagner, Günter P. (1989a), “The Biological Homology Concept”, *Annual Review of Ecology and Systematics* 20: 51–69.

——— (1989b), “The Origin of Morphological Characters and the Biological Basis of Homology”, *Evolution* 43: 1157–1171.

——— (1994), “Homology and the Mechanisms of Development”, in Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology.* San Diego: Academic Press, 273–299.

——— (1996), “Homologues, Natural Kinds and the Evolution of Modularity”, *American Zoologist* 36: 36–43.

Wagner, Günter P., and Jacques A. Gauthier (1999), “1,2,3 = 2,3,4 : A Solution to the Problem of the Homology of the Digits in the Avian Hand”, *Proceedings of the National Academy of Sciences of the United States of America* 96: 5111–5116.

Wake, David B. (1994), “Comparative Terminology”, *Science* 265: 268–269.

Wedgwood, Ralph (2001), “Conceptual Role Semantics for Moral Terms”, *Philosophical Review* 110: 1–30.

Notes

[1] For discussions of the history of homology see Russell (1916), Panchen (1994), and Laubichler (2000).

[2] This idea of an investigative kind is similar to Boyd's (1999) concept of a natural kind. My notion of a investigative kind *concept* stresses the research attitude taken by scientists and the fact that a scientific search may have an unexpected outcome such as the emergence of new homology concepts.

[3] More precisely, inference is a relationship between sentences or propositions. The inferential role of a concept is the class of inferences between propositions that this concept makes possible by virtue of being part of some of these propositions (Block 1986; Brandom 1994). Some authors that endorse conceptual role semantics have done this based on their commitment to functionalism. The notion of interferential role I employ is general enough so that I need not endorse a particular theory of the mind.

[4] Conceptual roles are often associated with narrow (as opposed to wide) content, i.e., the relationship between the mind and the world is not part of the conceptual role. It has been argued that versions of conceptual role semantics focusing on inferential role or narrow content alone cannot give a satisfactory account of content, because they cannot account for the representational aspects of content, and thus for the possibility of misrepresentation and falsehood. Proponents of conceptual role semantics have reacted to this problem by including the mind-world relationship in the conceptual role (Harman 1987), or by saying that inferential role/narrow content is only one aspect of content to by supplied by an account of reference (Field 1977; McGinn 1982; Block 1986). I favor this second option, but since my goal is to study differences in certain scientific concepts rather than putting forward a general theory of content I am not

concerned with this issue in the present paper.

[5] What counts as a relevant difference may also be dependent on the explanatory interests of the person ascribing concepts — in this context the philosopher of science studying conceptual change. The present analysis of the homology concept is primarily concerned with *explaining* conceptual change. My way of picking out certain clusters of similar conceptual roles as different concepts is fruitful because I can explain the emergence of these different concepts by reference to the theoretical goals of different fields.

[6] Some parts of the case study stem from a biological manuscript on the homology concept.

[7] The continuity is so large that I am inclined to assume that the advent of Darwinism did not create a new and distinct homology *concept*. The current phylogenetic homology concept is still used for largely the same purposes and in the same way. But assessing this difficult issue is not subject of the present discussion.

[8] Homology was approached from the point of view of development from the very beginning of its pre-Darwinian origin (e.g., in the form of the embryological criterion). But in my view these developmental considerations probably did not amount to a distinct concept. The recent concept of developmental homology is a distinct concept because it is used for different explanatory purposes.

[9] As we saw in the case of evolutionary biology, phylogenetic homology is a conceptual *precondition* that makes adaptation explanations possible. Homology refers to the entities that undergo evolutionary change, but by itself it *does not explain* the change.

[10] To be sure, in branches of molecular biology that are not so much oriented towards biomedical applications 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 — whether they are actually the same ones. For this reason, the understanding of molecular homology as mere sequence similarity has been criticized by several molecular biologists (see, e.g., Reeck et al. 1987). In molecular evolution the 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. Such a homology concept does not refer to mere similarity of genes and proteins, but also to the explanation of this resemblance. This homology concept as used in molecular phylogeny and evolution is theoretically more robust and more like the application of phylogenetic homology to the molecular level.