

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

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March 8, 2003

(7500 words including notes)

Abstract

The present paper gives a description and philosophical analysis of the conceptual variation in the homology concept. It is argued that different homology are concepts used in evolutionary and comparative biology, in developmental biology, and in molecular biology. The argument is based on a conceptual role semantics—the identity of concepts supervenes on conceptual roles. The differences between homology concepts are due to the fact that these concepts play different theoretical roles for different biological fields or research approaches. The specific theoretical needs and explanatory interests of different parts of biology 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). Despite its importance for biology homology 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 tokened 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 biology. These different concepts correspond to three fields within biology — comparative and evolutionary biology, 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 and research approaches*. That is, homology concepts are used for different concrete epistemic goals. A particular homology concept is used to bring about specific kinds of scientific knowledge, it is employed to yield characteristic theoretical inferences and explanations. The following discussion will make clear that the homology concepts that are characteristic for the discussed

communities are embedded in these different approaches and are used to account for things that are of specific importance for each field.

2. A conceptual role approach to conceptual differences in science. Following cognitive scientists and several philosophers of mind, I take concepts to be mental entities. Several philosophical authors deal with the concepts a particular individual possesses and thus assume that concepts are mental *particulars* (Fodor 1998). My approach focuses on the group-level instead. As I will discuss a case where a concept is used in a certain biological field in a specific way, I am interested in concepts as entities that are shared by different individuals. For this reason, I consider concepts as *population-level abstractions* of mental representations. The example I discuss is a case of conceptual differences of a term that emerged in the course of scientific history. This conceptual variation is due to changing and newly emerging theoretical perspectives.

Concepts are historical entities that form lineages. The different current homology concepts are derived from one original homology concept—the one still used in comparative and evolutionary biology. The original concept migrated into new disciplines and underwent adaptive radiation—leading to different specialized homology concepts. Homology is what I call an *investigative kind concept*. An investigative kind is a group of things 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 this kind. An example

is the species concept. We are able to recognize species, but it is not perfectly clear what accounts for the origin and coherence of these units — leading to different species definitions. A full theoretical account of the 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 might be open-ended.

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, for instance, are taxa which encompass those animals that have a common body plan. This allows setting morphological structures of different species in correspondence (e.g., according to their relative position in the body plan). 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. Biologists 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. The following definition by Richard Owen refers to this superficial similarity, which is irrelevant for homology, by “variety of form”. (Owen’s definition 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)

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 criteria is to be given. This leads—based on different theoretical perspectives—to *different historical and contemporary accounts of homology*. For instance idealistic morphology explained the unity of form with reference to metaphysical notions such as Owen’s archetype. Structures were claimed to be homologous in case they were (empirical and imperfect) instantiations of the same abstract and geometrically perfect archetype (Owen 1848). Later, a common evolutionary origin became the standard explanation of homologous correspondence of structures. In fact, reference to common ancestry was even included in definitions of homology (see Lankester 1870). For some contemporary developmental approaches to homology, reference to inheritance from a common ancestor cannot be a complete explanation, because it does not give a mechanistic explanation of how the same structures reappear again and again in different ontogenies.

This 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, this paper is about the conceptual variation in the term ‘homology’. Based on a conceptual role semantics approach, I will argue that there are different homology concepts used in biology. Conceptual role semantics is not a particular theory, rather it is a broad framework that encompasses various (sometimes very different) semantic approaches in philosophy (compare Field 1977; Harman 1987; Peacocke 1992; Brandom 1994; Wedgwood 2001) and cognitive

science (Miller and Johnson-Laird 1976; Woods 1981). 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 a language community. Particular concepts, for instance, have a specific role in theoretical thought, perception, and decision making.

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 account for conceptual differences. What I assume is that *the content of terms supervenes on conceptual roles*. This does not imply that I identify conceptual content with conceptual roles, or that I assume a one-one relationship between concepts and conceptual roles (which would lead to holism about concept individuation). Instead, the assumption is that concepts can be different only insofar they have different conceptual roles. The heuristic impact of this approach is that one has to search for possible conceptual differences by looking at the conceptual or theoretical roles of concepts.

Conceptual (in particular inferential) roles are often associated with narrow (as opposed to wide) content, for they are usually viewed as supervening on the mind, but excluding the relationship between the mind and the world. But a theory of content needs to account for the representational aspects of content — and thus for the possibility of misrepresentation and falsehood. 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 (see, e.g., Perlmann 1997). 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 be supplied by an account of reference (Field 1977; Loar 1981; Schiffer 1981; McGinn 1982; Block 1986; Lycan 1988). As I do not put forward a theory of content I am not concerned with these problems. My above assumption about the identity of concepts abstracts from possible differences in wide content, because this is not of concern for my discussion. My goal is to detect and study differences in certain scientific concepts; so for my purposes the assumption that the content of concepts supervenes on conceptual roles needs no further qualification or modification.

What do I mean by conceptual roles? 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*. A particular concept licenses certain inferences. 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 distinct inferential role.¹ 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*. And it is not obvious how explanation relates to standard models of inference making. Salmon (1984) argues that explanation are not arguments (neither inductive nor deductive), so the inferential role of concepts need not encompass their *explanatory role*. Concepts are employed or intended to account for particular

phenomena. 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. My case study will argue that a crucial difference between the homology concept used in developmental biology and the homology concept of evolutionary and comparative biology is their difference in explanatory potential. In fact, developmental biology uses its particular homology concept because other homology concepts cannot yield the type of explanations that are important for developmental biology.

As I use a conceptual role approach, my focus is on the inferences and explanations licensed by concepts. This has the following advantage. My approach links concepts to the *epistemic products* and *theoretical goals* of a scientific field or research approach. Obtaining certain kinds of knowledge — the results of specific types of inferences and explanations — may be characteristic for a specific scientific theory or research approach. The idea that the meaning of concepts supervenes on conceptual role implies that conceptual differences between different research fields are to be pinned down by taking a look at their specific epistemic products. My conceptual role semantics approach thus fulfills a heuristic function by suggesting how to detect possible conceptual differences. In addition, it sets the stage for explaining these conceptual differences. The idea that a concept plays a particular role for a research approach focuses on the fact that there is a scientific need for having this particular (rather than another) concept. Particular scientific fields have specific theoretical goals. Concepts are employed to pursue these goals; in fact, concepts are shaped and designed to bring about the intended epistemic product.² Thus the existence of conceptual differences can be explained by reference to differences in theoretical goals.

Now that I have motivated my central assumption — that the identity of concepts supervenes on conceptual roles — I need to lay out the individuation criteria that I will use for the following case study. It is notoriously difficult to put forward principled individuation criteria for concepts (Thagard 1992). Authors such as Devitt (1996) endorse the notion of analyticity by arguing that there are inferences that are constitutive of the content of concepts. I do not commit myself to a clear-cut analytic-synthetic distinction. There might be no immutable distinction between matters of meaning and matters of fact. Changes in belief may bring about changes in the content of concepts. In fact, the history of science shows that changing a concept or a conceptual system may be rational in the face of new empirical evidence. For instance, the concepts of mass and energy changed in the transition from classical to relativistic mechanics; and the gene concept improved from the Mendelian to the molecular gene concept. This makes it hard to make a case for inferences that are licensed by the content of concepts alone as opposed to inferences that are justified by empirical background beliefs.

I will follow Harman (1973) and Block (1986) in assuming that not identity, but similarity 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. People 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. In what

follows, I will present a case study in which I argue that the term ‘homology’ corresponds 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 use homology differently and have a different understanding of homology. The purpose of my paper is to give a philosophical analysis of the variation in the term ‘homology’ (which is so large that we can distinguish different homology concepts). 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 account of the variation of the concept under consideration.

3. Homology in comparative and evolutionary biology. The homology concept originated in the context of comparative biology, in particular comparative morphology. Among current homology concepts the following understanding of homology in comparative and evolutionary biology is the most traditional one. In what follows, I will refer to this homology concept by the term *phylogenetic homology*. In comparative morphology 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 (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. 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 comparative anatomy to some extent.³ There is a great deal of historical continuity between the historical homology concept and homology as it is used in current comparative morphology.

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 ontogeny and phylogeny. 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). In this manner, 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. The corresponding characters in different species are identified as the corresponding (or the 'same' ones) and often given an identical name. 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.

By establishing correspondence of structures between different species homology allows for generalized descriptive knowledge across species. Properties that hold for some structures in a species are likely to hold for the homologous structure in another species. This is due to the fact that homologues are derived from a common ancestral structure. Morphological, histological, or developmental descriptions are likely to apply to a larger class of organisms and their corresponding parts. This is why neuroanatomical descriptions and theories may for instance just talk about ‘the’ cerebrum, referring to a class of homologues. 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*. Thus, *identifying homologues and basing comparative descriptions on classes of homologues yields systematic and unified morphological knowledge*. 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. Once, later on, ‘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.

In addition, besides just providing comparative descriptions of organisms, the comparison of characters is an important step in giving taxonomic classifications of organisms. Structures identified as homologues can be compared in detail; and the similarities

and differences obtaining between homologous structures of different species provide the data for classification. Stable classifications can only be obtained by comparing homologous structures. Reference to homology justifies the fact that certain structures of different species are compared. In this manner, phylogenetic homology serves the end of comparative biology, producing and justifying systematic and general descriptions across species and providing comparisons that are effective for classifications.

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 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). 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. 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. Despite the existence of modification in the course of evolution, homology refers to a common basis of different character

tokens. 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. 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

4. Homology in developmental biology. Developmental homology — as I will call the homology concept used in developmental biology — is historically derived from phylogenetic homology.⁵ Due to the migration of the original homology concept into a new discipline, the concept underwent change. Despite the similarities between phylogenetic and developmental homology, there are relevant differences. 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 developmental biology has a wider extension. Two points are worth mentioning. First, developmental biologists apply homology to a larger domain of biological characters 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. 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 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 often 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.⁶

Second, there is the issue of *serial homology*. This is the most apparent evidence of the fact that there are differences among homology concepts in different biological fields. Sometimes an organism has a structure or a certain pattern that occurs repeatedly, for instance, hair in mammals, leaves 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 former 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 ‘ideal vertebrae’.) 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 vertebrae. In contemporary *comparative and evolutionary biology*, serial homology is usually ignored. Sometimes its possibility is denied and the idea of serial homology is attacked (Mayr 1982; Ax 1989; Bock 1989). This is due to the theoretical and explanatory focus of these branches of biology. Comparative biology

compares *different* species (and evolutionary biology deals with lineages of different species). Important goals of these disciplines are identifying homologues of distinct species, detailed comparisons of different species and their characters. Serial homology, however, sets two parts of the very same organism in correspondence; this is why it is not important for comparative and evolutionary biology. Thus, serial homologues are (usually) not part of the extension of this homology concept. 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* 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 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 repeated patterns might be due to the duplication of genes or developmental programs, or the use of a the same developmental resource on different parts of the organism.

In the same manner that comparative and evolutionary biologists sometimes attack the understanding of homology in developmental biology, developmental biologists are aware of this conceptual difference, too (Wagner 1989a; Minelli and Peruffo 1991; Roth 1991; Shubin 1994; Sluys 1996). The discussion already pointed to the fact that this 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 the explanation of the formation of structures*. Accounting for the origin of form essentially involves studying the development of organisms and their parts. Knowledge about developmental mechanisms and explanations of the origin of structures are systematized by concepts that refer to a commonality of developmental mechanisms. In developmental explanations the focus is on considerations about a corresponding causal origin, a common maintenance, or a comparable developmental role, behavior, or nature of structures (e.g., whether a part is a module of an organism). Developmental homology refers to similar, repeated, or corresponding structures of organisms. This homology concept is used to explain this similarity of structures within and between organisms by pointing to a (yet hardly understood) common underlying developmental basis. A developmental homology concept is intended to *explain* why the same structures (homologues including serial homologues) reliably reappear in different parts of the organism and in subsequent generations (Wagner 1996), *by referring to those causal factors and developmental features that account for this*. Such a homology concept is about the mechanistic underpinnings of structural identity of homologous characters in the course of ontogeny and phylogeny. In this manner, the developmental homology concept serves one fundamental aim of 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. As development is not yet sufficiently understood, there are different tentative developmental definitions of homology proposed ([van Valen 1982](#); [Roth 1984](#); [Wagner 1989a](#); [Striedter 1998](#)). Despite these different proposals, developmental biologists agree on the fact that a developmental homology concept has to account for the above mentioned features—explaining the reappearance of similar structures within one or several individuals. For this reason, in developmental approaches there is an emphasis on common developmental features rather than on common ancestry. For example, the homology definition proposed by [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).⁷ 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 and nothing else (Ax 1989), but not about comparing structures within organisms (serial homologues) or explaining the origin of characters.⁸ 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 mainly 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 qualitative notion, but comes in degrees. Even more important is the fact that molecular homology is a statement about the similarity of genes and proteins, not about their evolutionary origin—inheritance from a common ancestor. 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 (see below). Nevertheless, the usage of molecular homology as sequence similarity is quite 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; *the theoretical goal is to describe molecular processes and explain phenomena at the molecular level.* For this purpose, a comparison of genes and proteins (and their parts) is important, because similar genes have similar genes products and similar proteins are likely to behave similarly in biochemical reactions or to be part of a similar pathway.

A good deal of easily accessible information about the structure and function of genes and proteins is given by the mere DNA or amino acid sequence. Discovery in

molecular biology depends to a large extent on the search for correspondence among sequences. 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. For instance, proteins with a GPI anchor are known to be membrane bound, so when a newly studied protein reveals to have such a domain it is very likely that it is membrane bound, too. To take another well-known example, all proteins with a homeodomain bind to DNA. Molecular biology often does not deal with the classification and comparison of organisms or with phylogenetic or evolutionary aspects. Instead the focus is on molecular substances and the pathways in which they figure. A new gene or protein is compared to known ones. Similarity allows for an inference or a hypothesis about the function, 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 knowledge about certain molecular systems can be used to transfer experimental approaches and research strategies to other yet unstudied systems, provided that both are known to be similar. *Often the 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.*

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

molecular biology. It is effective to organize knowledge about molecular mechanisms and direct experimental practice. *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 developmental biology support.⁹

6. Conclusion. I 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 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 ho-

mology 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 homology in *comparative and evolutionary biology*, the goals are the comparison (and taxonomy) of species and characters and the explanation of descent with modification. The theoretical role of homology in comparative morphology and evolutionary biology is the individuation of characters across species and the conceptualization of a lineage of species characters despite variation and potentially unlimited evolutionary change. This allows for systematic and unified knowledge about the structure of organisms in the case of comparative morphology, and is a precondition for explaining adaptation in the case of evolutionary biology. In *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 study of biological processes at the molecular level and their explanation by means of mechanisms. The role of molecular homology is the inference of information about the molecular behavior of genes and proteins (and their parts), particularly in order to guide further experimental investigation and technological manipulation.

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 finer than extension — concepts with the same content may have the same extension. 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. Biologists 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 of adopting or criticizing particular homology concepts — which seem to involve more than the extension of these concepts. My discussion tried to explain how the variation in the homology concept came about by the different theoretical demands of biological fields.

I used a conceptual role semantics approach as a heuristic device for the study of homology. 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. 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 several scientific concepts.

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Notes

¹More precisely, inference is a relationship between sentences or propositions — the primary objects of semantic evaluation. 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. See [Brandom \(1994\)](#) for a detailed account along these lines. Some authors that endorse conceptual role semantics have done this based on their commitment to functionalism. The notion of inferential role I employ is general enough so that I need not endorse a particular theory of the mind.

²This does not mean that a concept is always successful in accounting for what is supposed to. Failure to do so is a reason for conceptual change.

³Compare the ‘principe des connexions’ of Geoffroy Saint-Hilaire ([1818](#)) with the criteria of Adolf Remane ([1952](#)).

⁴Phylogenetic systematics or cladistics is the nowadays predominant theory of taxonomy and emerged in the last few decades. In this field of comparative biology a new understanding of homology emerged (*taxic* as opposed to transformational homology), which is tied to the methodological approach of cladistics. This paper is not the place to discuss this other variant of the homology concept. In a nutshell, the conceptual role of taxic homology is the characterization of natural groups of species (taxa). See [Henning \(1966\)](#) and [Sober \(1988\)](#) for a discussion of the cladistic methodology, and [Nelson \(1994\)](#) and [Sluys \(1996\)](#) for a defense of taxic homology.

⁵The understanding of homology described in this section is common to those developmental biologists who take theoretical issues such as questions about homology seriously or are interested in developmental issues beyond molecular biology. The homology concept of many developmental geneticists, on the other hand, might quite well

be the molecular homology concept described in the next section.

⁶It became clear, however, that homology at different levels has to be kept apart. In fact, it is nowadays well known that homologies at different hierarchical levels cannot be identified and do not translate straightforwardly into each other (de Beer 1971; Roth 1988; Striedter and Nothcutt 1991; Wagner and Misof 1993; Bolker and Raff 1996; Abouheif et al. 1997).

⁷As 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.

⁸The purpose of this paper is not take a normative stance as regards these different views of homology, e.g., by maintaining that only one of the discussed concepts is really about homology. The philosophical project is to describe the different usages of the term ‘homology’ and to explain them with reference to the theoretical goals of different approaches.

⁹To 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—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). 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 sequence similarity due to common ancestry (homology) or due to convergence (analogy) has to be addressed (see, e.g.,

[Fitch 1970](#)). Such a homology concept as used in molecular phylogeny and evolution does not refer to mere similarity of genes and proteins, but also to the explanation of this resemblance. This homology concept is theoretically more robust and more like the application of phylogenetic homology to the molecular level.