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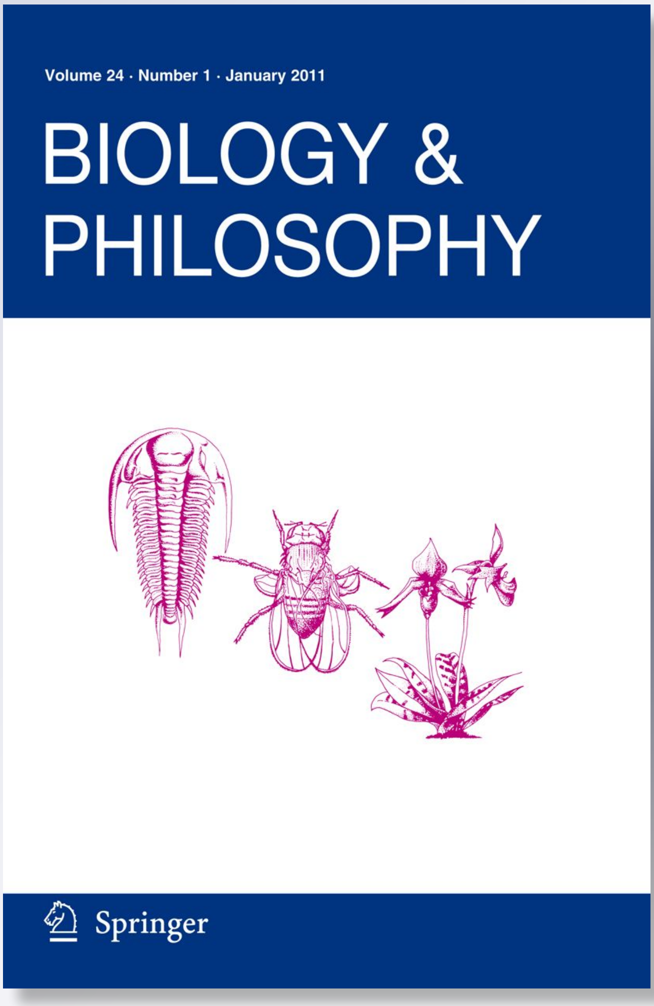

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Abstract This paper explores an important type of biological explanation called 'homology thinking.' Homology thinking explains the properties of a homologue by citing the history of a homologue. Homology thinking is significant in several ways. First, it offers more detailed explanations of biological phenomena than corresponding analogy explanations. Second, it provides an important explanation of character similarity and difference. Third, homology thinking offers a promising account of multiple realizability in biology.

Keywords Historical explanation · Historicity · Homology · Homology thinking · Multiple realizability · Reductionism

Introduction

'Homology' is a familiar term in biology, but given what prominent biologists say about it perhaps we underestimate its importance. Darwin (1887: 233) writes that "homology clears away the mist from such terms as the scheme of nature, ideal types, archetypal patterns or ideas, &c." Gould (1986: 60) talks about "evolution and the triumph of homology." Wake (1994: 284) tells us that "homology is the central concept for all of biology." What is so significant about homology that would justify such claims?

Perhaps its importance is due to the fact that "all useful comparisons in biology depend on the relation of homology" (Patterson 1987: 18). Whenever we ask if two characters are the same character, whether they are genetic, morphological, or behavioral, we are asking if they are homologous. That speaks to the centrality of

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homology in biology. Still, there is something else important about homology. Gould (1986: 60) suggests that "[Darwin's] theory taught us the importance of history, expressed… as the triumph of homology over other causes of order." Gould's point is twofold. Darwin's use of homology ushered in a significant way of understanding biological phenomena. Furthermore, that way of understanding biological phenomena turns on the historicity of homologues. Let us call this way of understanding biological phenomena 'homology thinking' to echo Mayr's (1959) phrase 'population thinking.'[1] Population thinking cites the structure of a population to explain the properties of a population. Homology thinking cites a character's history to explain its properties.

This paper covers much ground, so here is a section-by-section preview of what is to come. "What is homology?" wades into the controversy over the proper definition of 'homology.' The section does not promote a particular definition of 'homology' but highlights some features of homology that are important for homology thinking. "What is a historical explanation?" briefly discusses the nature of historical explanations. One claim of this paper is that the significance of homology thinking is due to the historicity of its explanations. Thus, a digression on the nature of historical explanation is needed. "What are homology explanations?" offers an account of homology explanations and contrasts them with analogy explanations. "The significance of homology thinking" discusses several reasons why homology thinking is significant. First, homology thinking offers more detailed explanations of biological phenomena than corresponding analogy explanations. Second, it provides an important explanation of character similarity and difference. Third, homology thinking offers a promising account of multiple realizability in biology—one that helps us understand why multiple realizability occurs and why such reductionisms as Rosenberg's (2006) fail to capture that phenomenon.[2]

What is homology?

Biologists offer numerous definitions of 'homology' and there is no consensus concerning which is the correct one. Prominent definitions of the last fifty years include the Transformational Homology Concept (Mayr 1969), the Operational Homology Concept (Sneath and Sokal 1973), the Informational Homology Concept (Van Valen 1982), the Developmental Homology Concept (Wagner 1989; Roth 1994), the Taxic Homology Concept (Patterson 1982; Rieppel 1994), and the Organizational Homology Concept (Müller 2003). Given the number of homology concepts on the market and the lack of consensus, some biologists and philosophers are pessimistic about finding a unified theoretical account of homology (Wake 2003; Griffiths 2007). Other biologists and philosophers are more optimistic (Abouheif

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[1] The phrase 'homology thinking' was introduced in Ereshefsky (2007) and Matthen (2007).

[2] This paper focuses on an important use of the concept of homology in biology, one that relies on the historicity of homologues. However, no claim is made that a historical approach to homology is the only valuable approach to homology. Nor is it claimed that every type of explanation a biologist offers concerning a homologue is historical. The aim of this paper is more modest, namely to explore one way, a significant way, that biologists use the concept of homology to understand biological phenomena.

1997; Laubichler 2000; Müller 2003; Wagner 2007; Brigandt 2007; Ereshefsky 2009). They suggest that aspects of the developmental, transformational, and taxic definitions can be wedded to provide an approach that best explains the phenomena of homology. My interest here, however, is not to pursue a unified account of homology, but to highlight the features of homology that are important for homology thinking. That requires taking a closer look at the developmental, transformational, and taxic accounts.

According to the developmental approach, two traits are homologous if they are caused by the same developmental module (Wagner 1996). Such modules cause the stable production of a homologue, yet they are sufficiently independent from one another so that a change in one module does not affect another module's efficacy. Some biologists have suggested that one type of developmental module is a gene regulatory network consisting of genes and the interactions that cause the occurrence of a homologue (Abouheif 1999; Wagner 2007). We will return to the nature of developmental modules shortly.

The transformational account of homology has its home in evolutionary taxonomy and holds that two characters are homologous if they have a common origin (Donoghue 1992). Promoters of the transformational account are interested in how the same homologue evolves and changes character states. This raises the distinction between characters and character states (Brigandt 2007; Wagner 2007). When faced with two traits, we might ask if they are homologous. Alternatively, we might agree that two traits are homologous but recognize that they come in different character states. For example, human arms, bat wings, and whale fins are homologous, they are the same character—the mammalian forelimb. Yet, that forelimb comes in different character states. Returning to the transformational account of homology, evolutionary taxonomists are interested in tracking the evolution of a homologue through its character states.

The taxic account has its home in cladistics (Donoghue 1992). Early promoters viewed homologues primarily as characters that are evidence for monophyletic taxa. Though there are differences between the transformational and taxic accounts of homology, some writers on homology treat them under one category, typically called the 'phylogenetic' or 'historical' account of homology (Wagner 1994; Hall 1994; Brigandt 2002).[3] That account merely assumes that instances of a homologue have a common evolutionary origin. As Brigandt (2002: 392) writes, "[t]his is nowadays the standard definition of homology, independent of the question of whether a transformational or a taxic approach is taken." Following the lead of others, I will subsume the taxic and transformational accounts of homology under a generic historical approach to homology.

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[3] The significant differences between the taxic and transformational approaches are twofold. For cladists homologues only mark the boundaries of monophyletic taxa, whereas for evolutionary taxonomists they mark the boundaries of monophyletic and paraphyletic taxa. Furthermore, for cladists new homologues arise only when character lineages branch, whereas for evolutionary taxonomists new homologues can arise within character lineages. The idea that a homologue can occur in different states does not distinguish the taxic and transformational accounts: cladists recognize that homologues can occur in multiple states (Donoghue 1992).

Stepping back from these details, it is not hard to see that a more general understanding of homology relies on understanding both the phylogenetic and developmental aspects of homology. On the one hand, developmental mechanisms are the *proximate causes* of homologues. A homologue's developmental module causes the construction of a homologue. Furthermore, a module's developmental constraints affect how a homologue can evolve (Kirschner and Gerhart 1998; West-Eberhard 2003). On the other hand, a homologue's phylogeny and the factors that affect its evolution are its *distal causes*. A homologue's developmental module has an evolutionary history shaped by selection, random mating, mutation, recombination, gene duplication, and developmental constraints. Changes in a homologue's developmental module, as well as the stable properties of that module, are phylogenetically transmitted to latter instances of that module. In brief, a homologue is the result of a developmental module, and that module is the result of a phylogenetically continuous history.

In this characterization of homology, phylogeny is the lynchpin of homologue identity. Instances of a homologue form a unique continuum starting at the origin of an evolutionary novelty. That raises the vexing question: What is an evolutionary novelty? A common view in developmental biology is that the origin of a new homologue occurs when a developmental module of a preexisting homologue is sufficiently altered or duplicated (Wagner 2000; Müller 2003; West-Eberhard 2003). However, the mere duplication or alteration of a developmental module is insufficient for causing a new homologue. Further events in the evolutionary path of a character are needed, such as its becoming integrated into an organism's "constructional body plan" (Müller 2003: 62). The occurrence of a new homologue turns on an origination event *and* what happens to that novelty later.[4] Turning to developmental modules, just as the identity of a homologue turns on its phylogeny so does the identity of a homologue's developmental module. Instances of a homologue's developmental module form a historical lineage starting at the occurrence of that homologue as an evolutionary novelty.

Some may worry about the historical leaning of this approach. As many note (e.g., Griffiths 2006), the developmental account was in part developed to explain what the phylogenetic approach cannot explain, such as the construction of a homologue in each generation and the occurrence of serial homologues. (Serial homologies are homologous characters that occur within a single organism, such as the different bristles on a fly.) So, the concern goes, it is wrong to make phylogeny the lynchpin of homologue identity. I agree that developmental explanations are crucial for understanding the nature of homologues. We will see the importance of development in explaining features of homologues throughout this paper. Nevertheless, the developmental and historical approaches are not that far apart. Even the most prominent proponent of the developmental definition of homology, Günter Wagner, now recognizes that developmental explanations of a homologue are not explanations of the same homology unless there is historical continuity among the instances of that character.

> Sameness, then, by definition of homology, does not refer to similarity of structure or function as such, but to historical continuity through inheritance

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[4] Compare with speciation. Not all isolated populations become new species. It depends on what happens to those populations later (Ereshefsky 2001).

> with modification. In other words, the homology concept can be applied to anything that forms a lineage. (Wagner 2007: 473)

Still, there are *prima facie* reasons for thinking that the developmental and phylogenetic accounts conflict. One such conflict concerns the *phenomenon of hierarchical disconnect*. This occurs when a homologue at one level of biological organization is caused by non-homologous developmental factors at lower levels of organization (Bolker and Raff 1996; Abouheif 1997). Let us explore this phenomenon in more detail because it is one source of homology thinking's significance. There are many well-known cases of hierarchical disconnect (de Beer 1971; Wagner and Misof 1993; Hall 2003). Consider Hall's (2003) description of the case of tetrapod digits. In tetrapods other than urodele amphibians, digit separation during ontogeny is due to genetically programmed cell death (apoptosis) that removes cells between digit primorida and leaves interdigital spaces. In urodeles, the differential growth of digits rather than apoptosis separates digital primorida. Hall (2003: 417) writes that "[w]hile the mechanisms that separate digits during ontogeny differ, the digits are homologous features." He suggests that the loss of interdigital apoptosis and the use of differential growth is the derived condition. For Hall tetrapod digits are homologous. A developmentalist that aligns homologue identity with having the same developmental factors would disagree.

Wagner (1989) did adopt such an alignment. More recently, Wagner advocates a looser connection between homologue identity and developmental factors. Wagner and Misof (1993) suggest that the identity of a homologue and its developmental module go hand in hand, but the factors within that module can vary. They cite the ontogeny of pectoral fin hooks in *Salaria pavo* as an example where developmental factors early in ontogeny vary though factors later in ontogeny remain the same. According to Wagner and Misof, the same developmental module causes pectoral fin hooks though the constituents of that module vary. Such an approach to variation among developmental factors is a welcome suggestion to an approach to homology that cites both the development and phylogenetic aspects of homology. If a developmental module remains the same despite changes in its constituent factors, and that module tracks the phylogeny of a homologue, then there is no conflict between the developmental and phylogenetic approaches to homology when it comes to the phenomenon of hierarchical disconnect.[5]

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[5] Another tension between the developmental and phylogenetic accounts concerns serial homology. Supporters of the developmental approach argue that the phylogenetic account is inadequate because it does not treat serial homologues (such as the bristles of a fly) as homologous (Wagner 1989; Roth 1994). In fact, some supporters of the phylogenetic approach deny that serial homologues are homologous (Wake 1999; Ghiselin 2005). This seems to be an impasse. However, some developmental biologists believe that serial homologues owe their origins to the duplication of developmental mechanisms deep in the phylogeny of a character (Shubin et al. 1997; Müller and Newman 1999; Striedter 1999). If instances of a serial homologue trace back to a common ancestor, then what we call 'serial homology' is historical homology. For example, Striedter (1999: 40) suggests that the evolutionary mechanism producing fly bristles has a single origin. That mechanism was subsequently duplicated and expressed in different places on the body of an organism. Whether each serial homologue has a single phylogenetic ancestry has not been conclusively shown. Nevertheless, the evidence to date indicates that the phylogenetic and developmental approaches are not necessarily at odds concerning serial homology.

There are two take-home messages concerning the ongoing debate over 'homology' when it comes to homology thinking. First, the debate is often characterized as the developmental account versus the historical account (or some other account), where the proper resolution is winner takes all –we either adopt the phylogenetic account or the developmental account but not a mixture of the two. The above discussion suggests that a fuller understanding of homology requires understanding both the developmental and phylogenetic aspects of homology. Moreover, those aspects are not as conflicting as many argue. Second, for a substantial number of biologists that work on homology, a core feature of homology is that homology is a historical relation. I take it that Gould is citing this feature of homology in his 1986 article "Evolution and the Triumph of Homology, or Why History Matters."

What is a historical explanation?

The significance of homology thinking depends on the historicity of its explanations. So before discussing the nature of homology explanations we should discuss what makes an explanation a *historical* explanation. A good place to start is Crombie's *Styles of Scientific Thinking in the European Tradition* (1994). According to Crombie, Darwinian biology falls under the scientific style "Historical Derivation and the Genetic Method." Crombie (1994: xxx) describes this style as follows:

> [T]he two main principles of the method of historical derivation [are] the diagnosis of common characteristics from a common source, and the postulation of causes to account for the diversification from that source.

A historical derivation, in other words, cites the common source of a set of effects ("common characteristics"). It also cites those factors that cause the diversification of those effects. Not surprisingly, Crombie's description of historical derivation is similar to Darwin's description of the naturalist's understanding of homologues:

> The naturalist thus guided sees that all homologous parts or organs, however much they may be diversified, are modifications of one and the same ancestral organ; tracing existing gradations he gains a clue in tracing, as far as possible, the probable course of modification through which beings have passed during a long line of generations. (1877: 233)

Again, there is the idea of a common source (an "ancestral organ") and the causal factors in the historical path ("the probable course of modification") that modify descendents of that ancestral organ ("homologous parts").

As a first pass, let us contrast historical explanation from inference explanation. Hempel's (1965) account of explanation is the paradigmatic account of inference explanation. Typically, an inference explanation cites an initial condition and a generalization that describes a regularity between classes of events. Why, for instance, did a particular piece of copper dissolve in sulfuric acid? According to the Hempelian account, we explain that phenomenon by citing the initial condition that a piece of copper was placed in sulfuric acid and the chemical law that all (or most) pieces of copper dissolve in that acid. Causal models of explanation, such as Salmon's (1984), are similar to Hempel's but require that the law cited is causal. What is salient in inference models of explanation is that an initial condition and an inference maker (a law or generalization) are cited. Furthermore, the events explained are independent of each other: pieces of copper need not be spatiotemporally or causally connected for such explanations to work.

Historical explanations in Crombie's sense are different. A historical explanation explains the features of an entity (or set of entities) by placing that entity in a historical path (a spatiotemporal sequence) and citing multiple factors in that path. Why, for example, are the hind wings of mosquitoes club-shaped sensory organs rather than the wing blades found in many insects? To answer this we trace how some insect hind wings have evolved such that they became sensory organs. The explanation is not merely an appeal to an initial condition and a generalization, but a narrative citing a series of events that have affected mosquitoes' hind wings and their predecessors. The historical path leading to contemporary mosquitoes' hind wings bears much explanatory weight. Still, one might wonder, what is the difference between citing a historical path and citing an initial condition? The answer is found in the notions of historical contingency and path dependency.

According to Beatty (2006), Gould (1989) offers two different but complementary accounts of historical contingency. The first is unpredictability: knowing the initial conditions of a system is insufficient to predict the outcome of a system. The other is causal dependence: the outcome of a system "depends strongly on which particular states preceded it" (Beatty 2006: 339). Causal dependence occurs when various factors between the initial condition and the end state of a system are necessary to bring about that end state. We can see how these two versions of historical contingency complement one another. Citing the initial conditions in a historical sequence is insufficient for predicting an end state; one must cite relevant intermediary factors as well. Another way to describe this twofold account of historical contingency is path dependency (Szathmary 2006; Desjardins 2010). As Desjardins (2010) writes, the key to understanding path dependency is to see that an "outcome is not merely a result of initial or recent conditions, but a matter of the path taken." Citing the initial state is insufficient to predict a system's outcome; causal factors along the path taken are also necessary for bringing about that outcome.

One might respond that though path dependent explanations are different from explanations that cite initial conditions and generalizations, both types of explanation are historical because they cite a diachronic sequence of events. If 'historical explanation' merely means citing a diachronic sequence of events, then that is right. Still, that weak notion of historical explanation should be distinguished from a stronger notion of historical explanation. Furthermore, both of these types of historical explanation should be distinguished from non-historical explanations. According to van Fraassen (1980), some inference explanations do not have a temporal component but explain the value of a variable by citing the cotemporaneous values of other variables and a model. Van Fraassen cites the explanation of why the pressure within a balloon has a certain value at a time by citing Boyle's gas law and the temperature, volume, and the number of moles in the balloon at that time. Stepping back, then, a more careful explication of historical explanation should make a threefold distinction. Weak historical explanations cite an initial condition to explain the occurrence of a later event. Strong historical explanations (path dependent explanations) cite multiple factors along the historical path leading up to the event explained.[6] Non-historical explanations contain no temporal element but explain one aspect of a system by citing other cotemporaneous aspects of that system.

The strong notion of historical explanation, the one that requires path dependency, captures Gould's notion of historical contingency. It also captures Crombie's account of historical derivation and Darwin's description of the naturalist's understanding of homologues.

What are homology explanations?

The homology explanations discussed in this paper are historical explanations. They are distinct from analogy explanations because they cite the historical sources of a character rather than a character being an adaptation. Before exploring the nature of homology explanations, it would useful to contrast them with analogy explanations. A paradigmatic analogy explanation explains a property of an analogue by citing the contribution that property makes to a function that analogue performs. Such explanations do not cite the history of a trait, but explain the presence of its features through reverse engineering. Analogues are aggregates of homologues. The analogue organic wing, for example, consists of over twenty distinct homologues, including bat, insect, and bird wings. Suppose we want to explain a common feature of wings, say their being rigid. We explain that property by its contribution to a wing's function of flight. Wings need to be rigid to have the relatively flat surface required for lift and thus flight. Such an explanation is a version of design analysis. It does not cite the individual history of any homologue that is a member of the analogue wing, nor does it cite the aggregate history of all wings. It explains a property of wings by how it contributes to a function of wings.

By contrast, homology explanations are weak or strong historical explanations. Consider an example of a homology explanation that is a weak historical explanation. Why do insect wings come in two pairs rather than one pair? The explanation cites the historical source of insect wings. According to Carroll (2005), insect wings are descended from the gills of ancient aquatic crustaceans. Those gills had multiple appendage segments. In the evolutionary path from crustacean gill to insect wing, the number of segments was reduced to two pairs. That is why insects

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[6] Though I distinguish types of historical explanations by calling some 'strong historical explanations' and others 'weak historical explanations,' I do not mean to imply that strong historical explanations are in any way more significant. Strong historical explanations are more historical in that they cite multiple factors that occur at different times in the history preceding an event. Not only are those factors spread over time, even the temporal order of those factors may be significant. Weak historical explanations merely cite the initial conditions of a later event. The distinction between weak and strong historical explanations is nicely captured by Desjardins (2011) distinction between initial condition dependent and path dependent explanations.

have two pairs of wings rather than one pair. This explanation is a homology explanation rather than an analogy explanation because it explains the number of wings in insects by citing the historical source of insect wings, not whether having two pairs of wings is more adaptive than having one pair. Consider a different homology explanation. Why do bats have one pair of wings versus two pairs? Bat wings evolved from mammalian forelimbs. Those limbs came in single pairs. That is why bats have a single pair of wings. Not because having one pair of wings confers a higher adaptive advantage than having two pairs of wings. Bat wings come in single pairs because of their historical source. Insects have multiple pairs because they evolved from organisms with multiple pairs of appendages. Different starting points, different evolutionary results.

The above examples are of homology explanations that are weak historical explanations. Some homology explanations are historical in the stronger sense. They are path dependent explanations. A fuller explanation of why insects have two pairs of wings rather than a greater number not only traces back to the occurrence of multiple crustacean appendages, but also to gene duplication events that introduced Hox genes that suppress appendage development. Insects have two pairs rather than more pairs because Hox genes that suppress the formation of appendage segments were duplicated multiple times in the evolutionary path leading to insect wings (Carroll 2005). Thus, in providing a fuller explanation concerning why insects have two pairs rather than a greater number of pairs, we cite multiple events in the evolutionary path leading to insect wings. This is a strong historical explanation.[7]

Thus far, the homology explanations discussed explain a particular feature of a character. Another prevalent type of homology explanation aims to explain the range of variation found among a homologue's character states. Consider Prum and Brush's (2002) seminal work on the origin and diversification of feathers. Feathers are homologous—they have a common origin in non-avian dinosaur theropods. Feathers come in five prominent character states, which Prum and Brush call "Stages I–V." Stage I, the most primitive form of feathers, is an undifferentiated follicle. Stage II, the next most primitive feather state, is a follicle that branches into a tuft of barbs. Stage III consists of numerous barbs that interlock to form a smooth and rigid surface. Stages IV and V feathers have nicks and grooves allowing for stronger surfaces. Prum and Brush explain feather variation by showing that feathers began as single undifferentiated follicles, and then sequential changes in their developmental mechanisms introduced more and more complexity in feather morphology.

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[7] A referee for this journal asked about the relation between proximate and distal explanations and weak and strong historical explanations. The type of homology explanation highlighted in this paper concerns the use of homology in the distal sense. Such explanations refer to the evolutionary history of a homologue and, as we have seen, come in both historically strong and weak forms. Proximate explanations concerning homology cite the developmental factors that cause the ontogeny of a homologue. Such proximate explanations of homology are historical as well: the ontogeny of a homologue occurs over time, through a sequence of developmental events. For example, the imaginal disks of insect larvae develop into legs and wings through a sequence of gene and cellular interactions (Winther 2006: 493). Though the time scale of ontogenetic explanations is much shorter than the time scale of evolutionary explanations, they are historical explanations. Winther (*ibid.*) calls those ontogenetic explanations "temporal narratives." Such ontogenetic explanations come in both historically strong and weak forms.

Consequently, if we want to know why feathers have the range of diversity they have, we cite the introduction of evolutionary changes in the developmental mechanisms that cause feathers. Such explanations may be weak or strong historical explanations, depending on the information sought. To explain why Stage II and Stage III feathers differ, Prum and Brush cite the change introduced to the developmental mechanism of Stage II feathers—a weak historical explanation. To explain the difference between Stage II and Stage V feathers, Prum and Brush cite the changes in developmental mechanisms at Stage III, Stage IV, and Stage V. This is a strong historical explanation. Alternatively, to explain why the differences between Stage II, III, and IV feathers are constrained to a certain range of variation, Prum and Brush cite feathers' common developmental module and the fact that all instances of that module share common developmental constraints. Moreover, they point out that instances of that module share common developmental constraints because they trace back to a common ancestral module. Prum and Brush's explanatory schema for understanding feather similarity and difference clearly relies on feathers' shared history.

We have seen the contrast between homology and analogy explanations. Sometimes biologists offer strictly historical explanations, sometimes they offer strictly analogical explanations. But biologists often offer explanations that are a mixture of the two. Carroll's (2005: 175–179) more inclusive explanation of the current properties of insect wings cites the historical source of insect wings and the selective forces that have helped shape those properties. According to Carroll, insect wings evolved from the gills of aquatic crustaceans through a number of evolutionary steps. First, such appendages occurred as gills in primitive aquatic nymphs. Later those appendages evolved such that they occurred as gills in the larval stage of insects and wings in their adult stage. More recently, those appendages evolved to occur only as wings. Each evolutionary step is accompanied by an ecological transition and a different set of selective pressures: from aquatic environments, to mixed environments, to aerial ones. Along with these morphological and environmental changes came a parallel change in the number of Hox proteins that suppress the formation of appendage segments.

Teasing out Carroll's overall explanation of insect wings we see both homology and analogy explanations at work. Why do insects come in two pairs versus a greater number of pairs? We rely on homology explanations that cite the sources of insect wings—ancient crustacean gills and the occurrence of Hox gene duplications. Alternatively, we might ask why insects have limbs that are aerodynamic and good for flight. Here we rely on analogy explanations. Ancestral forms of insect wing came in different character states such that there was selection for the more aerodynamic states. Such explanations rely on design analysis: some limb designs are more aerodynamic than others. Putting both strands of this explanation together, we get an example, Carroll's example, of an explanation that is a mixture of homology and analogy explanations.[8]

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[8] In some cases we can tease apart homology and analogy explanations. However, there are many cases where it is not clear whether a character is a homologue and whether a homology explanation is appropriate. For example, it is not clear whether atavisms and vestiges are homologues. This paper does not weight in on such cases. In a series of papers, Hall (2003, 2007a, b) discusses them. He suggests that the distinction between homologues and analogues should be viewed as a continuum. Nevertheless, Hall (2003, 409; 2007a, 442) concludes that the only clear case of analogy is convergence.

The significance of homology thinking

With an account of homology explanations in hand, let us turn to the significance of homology thinking. As we shall see in this section, homology thinking is significant in several ways. First, it offers more detailed explanations of biological phenomena than corresponding analogy explanations. Second, it provides an important explanation of character similarity and difference. Third, homology thinking offers a promising account of multiple realizability in biology.

Detailed explanations

Both homology explanations and analogy explanations are explanatory. Yet homology explanations are more detailed than corresponding analogy ones. Others (Griffiths 1994, 1997; Matthen 1998; Ereshefsky 2007) have made this point, so I will be brief. An analogy explanation for the properties of insect wings explains the features needed for performing the function of flight. It explains through design analysis such general features as being aerodynamic, being rigid, and being made of a certain range of materials. By contrast, a homology explanation of insect wings explains more specific features of wings by citing their morphological, genetic, and ontogenetic sources. For instance, a homology explanation tells us why insect wings are membranous and supported by rigid veins, rather than being made of feathers supported by bones. An analogy explanation will tell us why a general class of materials rather than another class of materials will allow an organism to fly, but it does not tell us which specific materials are used by a particular taxon of organisms. Consider a different insect wing example. The hind wings of mosquitoes are club-shaped sensory organs rather than wing blades. They operate as vibrating gyroscopes that maintain stability in flight. An analogy explanation for a mosquito's balance system will not explain why that system consists of external body organs that flap up and down. A homology explanation explains those details by citing the morphological and genetic sources for mosquito balance systems. In these examples, we see the work history is performing in homology explanations. Characters have the properties they do in no small part because of the historical sources of those characters. Information about those historical sources allows homology explanations to be more specific than comparable analogy explanations.

When suggesting that homology explanations are more detailed than corresponding analogy ones, I have encountered the following response from philosophers: Analogy explanations can be as detailed as homology explanations. Just take a character, say organic wing, study many of its features, and perform a number of reverse engineering calculations on those features. This response, however, ignores the relationship between a homology class and its corresponding analogy class. An analogy class consists of multiple homology classes. The analogue organic wing, for instance, consists of a diverse group of homologues, including eagle, bat, and mosquito wings. The variation among the members of the analogue organic wing is more extensive than the variation among the members of a particular homologue within that analogue. As a result, detailed inferences about the homologue bird wing (such as being made of hollow bones) are more likely to be correct than comparable detailed inferences about the analogue wing. This point is generalizable. The variation among the members of the homologue mammalian eye or the homologue insect eye is smaller than the variation among the members of the analogue eye (Griffiths 1994: 220). Consequently, we can make more successful detailed inferences about the homologue insect eye (such as the specifics of its anatomy) than comparable detailed inferences about the analogue eye. Notice what is being asserted here. The claim is not that any homology class will contain less variation than any analogy class. The claim is that an analogy class will contain more variation than any homology class that is a member of that analogy class. Therefore, homology explanations are more detailed than *corresponding* analogy explanations, because inferences about the specific properties of a homologue are more likely to be correct than similar inferences about the analogue that contains that homologue.

Besides providing more detailed explanations, homology explanations explain features of characters that are not explained by analogy explanations. Consider another wing example. Wings evolved three separate times in vertebrates: in Pterosaurs, in birds, and in mammals. These wings are not homologous, though the structure they employ—the tetrapod forelimb—is homologous. Each type of vertebrate wing uses a different set of anatomical parts of the tetrapod forelimb: bird wings develop along the entire limb; Pterosaur wings are a membrane attached to a single elongated digit on the limb; and bat wings are attached to multiple digits of the forelimb and extend to the hind limb (Carroll 2005: 108ff.). These differences are not due to general principles concerning the design of a wing needed for flight, but due to the different anatomical resources each group of organisms drew on. Knowing that bat wings have an evolutionary origin in mammalian forelimbs explains why they come in single pairs and why bat wing surfaces are attached to multiple digits (fingers). An analogy explanation cannot explain those features. Again, we see the historicity of homology explanations: characters have the features they do in no small part because of the historical sources of those characters.

Similarity and difference

Another significant feature of homology thinking is its role in explaining character similarity and difference. At a proximate level, such similarities and differences are explained by citing the developmental mechanisms of a homologue (Abouheif 1999; Wagner 2007). The homologous hind wings of butterflies and mosquitoes are similar in that they are appendages that occur on the same part of the body. Yet, the shapes and functions of those wings are different: in butterflies they develop as wing blades; in mosquitoes they develop as club-shaped sensory organs. The gene Ubx is crucial for the development of the hind wings in both butterflies and mosquitoes. The differences between butterfly and mosquito wings are in part caused by differences in their underlying genes (Wagner 2007). At the proximate level, then, similarity and difference in phenotypes is explained by similarity and difference in development. Here is where history and homology thinking come in. These proximate developmental explanations are explained by more distal historical explanations. The gene Ubx crucial for hind wings in butterflies and mosquitoes is part of the developmental module underlying that homologue. Were it not for the common historical source of that module in butterflies and mosquitoes, those organisms would not have that similar appendage. Phenotypic similarity due to similarity in a developmental module is, in turn, due to instances of that module having a common history.

Homology thinking provides a distal explanation for the differences among a character as well. Some differences among the states of a character are due to corresponding differences among their developmental modules. To understand those developmental differences, we highlight the genealogical tree of that character's developmental module and focus on evolutionary changes in that module that correspond to the different states of a character. This sort of explanation is offered in Prum and Brush's (2002) account of the diversification of feathers. Prum and Brush maintain that differences in the five primary character states of feathers are due to differences in the common developmental module for feathers. Why, for instance, is a Stage I feather an undifferentiated follicle, while a Stage II feather is a follicle that branches into a tuft of barbs? First, Prum and Brush (2002) offer a developmental explanation. The epidermal collars of Stage I feathers develop as single undifferentiated rings, and that causes Stage I feathers to be undifferentiated follicles. The epidermal collars of Stage II feathers develop as rings of differentiated barb ridges, and that causes Stage II feathers to be branching follicles. Prum and Brush (2002) then offer a phylogenetic hypothesis to explain why these developmental differences exist. Stage I and II feathers vary because the developmental module for Stage I feathers was modified, and that gave rise to two genealogical branches of developmental modules—one for Stage I feathers and one for Stage II feathers. According to Prum and Brush, paleontological evidence and evidence from extant species confirm this hypothesis.[9]

Thus far, the discussion concerns variation at the level of a homologue. Contrast this sort of variation with variation among the developmental factors that cause a homologue. This is the phenomenon of hierarchical disconnect discussed earlier. Recall that a homologue at one level of biological organization may be caused by different, non-homologous developmental factors at lower levels of biological

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[9] A referee for this journal asked what role phylogenetic inference plays in the historical explanations of homology thinking. Prum and Brush's work on feathers can help answer this. In their explanation of character diversity, Prum and Brush pursue two lines of research. One line develops and tests hypotheses concerning the ontogenetic mechanisms that cause feather character states (e.g., undifferentiated epidermal rings cause Stage I feathers, differentiated epidermal rings cause Stage II feathers, and so on). The second line of research develops and tests a phylogenetic tree tracing the character states of feathers. The culmination of Prum and Brush's research is establishing congruence between the developmental model and the phylogenetic hypothesis. Prum and Brush use this congruence to offer historical explanations of feather diversity. For example, to explain the differences between Stage II and Stage V feathers, they cite the phylogeny of those character states and the sequence of changes in their developmental mechanisms. Those changes, in that order, and their stable transmission explains the differences between Stage II and V feathers. Phylogenetic inference itself is not a part of this explanation. Nevertheless, phylogenetic inference makes an important contribution: it provides the phylogenetic hypothesis that allows us to trace the relevant changes in the developmental module of feathers. Stepping back from this example, Prum and Brush's two avenues of research—one involving the developmental module of a homologue, the other investigating a character's phylogeny, and whether those two lines of research are congruent—is just the pattern of research Wagner suggests in his (1999) paper "A research programme for testing the biological homology concept."

organization. There are many well-known cases of hierarchical disconnect (Abouheif 1999; de Beer 1971; Minelli 1998; Hall 2003; and Müller 2003). As we saw earlier, homologous tetrapod digits are in part caused by non-homologous developmental mechanisms. Another form of hierarchical disconnect occurs when non-homologous genes contribute to the same morphological homologue (Abouheif 1999). A third form of hierarchical disconnect occurs when different morphological elements underlie the same behavioral homologue (Wenzel 1992).

What causes a homologue at one level of biological organization to be the result of non-homologous elements at a lower level of organization? During the history of a homologue, earlier developmental factors for a homologue are replaced by other developmental factors (Wagner and Misof 1993). This is the explanation that Hall (2003) offers when explaining why tetrapod digits are caused by two different developmental mechanisms. Interdigital apoptosis is the ancestral developmental mechanism for tetrapod digits. Differential growth is the derived mechanism. Here we have an intriguing explanation of similarity in character states due to dissimilar causes. Moreover, this explanation turns on the historical nature of homologues. Tetrapod digits and their corresponding developmental module trace back to a common evolutionary novelty –the start of tetrapod digits as a distinct homologue. During that history, changes in one branch of that module caused variation at the developmental level: some tetrapod developmental modules employ interdigital apoptosis; others use the newer mechanism of differential growth. This sort of explanation is not foreign to philosophers. A similar type of reasoning is at work for those that think that the Ship of Theseus is the same ship despite a change in its parts. The Ship of Theseus remains the same ship despite a change in all of its parts because that change occurs in a continuous manner. In the case of tetrapod digits, differential growth replaced interdigital apoptosis in one lineage of tetrapods. The result is two branches of tetrapod digit developmental modules causing instances of the same homologue.

Multiple realizability

A less recognized feature of homology thinking is its role in explaining multiple realizability in biology. Multiple realizability exists when a kind at one level of organization cannot be reduced to a kind at a lower level of organization (Bickle 2006). The phenomenon of hierarchical disconnect is an instance of multiple realizability. As Laubichler and Wagner (2001: 65) write, "developmental processes often vary more profoundly than the characters that develop from them." As mentioned earlier, some morphological homologues are caused by different non-homologous genes. Laubichler and Wagner highlight the case of non-homologous genes causing the development of the anterior–posterior body axis. Then there are behavioral homologues, such as homologous grasshopper mating sounds, caused by non-homologous morphological parts (Striedter and Northcutt 1991). When hierarchical disconnect occurs, instances of a homologue cannot be reduced to a single type of physical substructure. That homologue, in other words, is multiply realized.

What sort of explanation does homology thinking offer of multiple realizability? It provides a well-founded empirical account of why multiple realizability occurs in biology: as the phylogenetic history of a homologue unfolds, the underlying factors that cause that homologue are substituted. Genes underlying a homologue are replaced (Abouheif 1999). Morphological elements that cause a behavioral homology are substituted (Wenzel 1992). Even significant portions of a character's ontogenetic mechanisms can be replaced (Hall 2003). As we have seen, the formation of tetrapod digits is due to different ontogenetic processes –interdigital apoptosis and differential growth. The former is the ancestral state and the latter the derived condition. Through a historically continuous sequence of events, differential growth replaced interdigital apoptosis in one lineage of tetrapods. The result is two lineages of a homologue caused by different developmental mechanisms.

Multiple realizability can be the bane of reductionists. One aim of reductionism is to reduce kinds at one level of organization to kinds at a lower level. However, if a kind at one level cannot be reduced to a single kind at a lower level, then reductionism is thwarted. Rosenberg takes up this challenge to reductionism in his *Darwinian Reductionism* (2006). Let us look at Rosenberg's reductionism. In doing so we will see that multiple realizability in the form of hierarchical disconnect poses a threat to reductionism. Along the way, we will see that homology thinking offers a better account of multiple realizability.

According to Rosenberg, biological kinds are functionally defined analogy classes. He argues that because such kinds are functionally defined, their members lack a common physical basis. As an example, he reminds us that the kind organic wing corresponds to different physical kinds. Rosenberg concludes that because no single physical kind corresponds to a biological kind, biological kinds are multiply realized. Rosenberg sees multiple realizability as threat to biological reductionism. He responds to that threat by focusing on what he takes to be the only law in biology, the principle of natural selection (2006: Chapters 4–6). He suggests that this principle is true of both biological phenomena and chemical macromolecules. He then offers the following reductionist strategy: "whenever selection does operate, it must eventually be explained by selection at some "level" in the succession of reductive explanations that eventually terminate at the behavior of macromolecules" (2006: 199). Rosenberg's suggested reductionism does not reduce an analogy class to a particular physical selection process. Such a strategy would fail because, for example, the analogy class organic wing has evolved over twenty times. Instead, Rosenberg (personal communication) suggests that each homologue within an analogy class is reducible to a complex set of macromolecular selection processes.

A lacuna in Rosenberg's account of multiple realizability is that it neglects the fact that homologues themselves are multiply realized. In other words, it neglects the phenomenon of hierarchical disconnect. Once the phenomenon of hierarchical disconnect is brought to the fore we see a pressing problem with Rosenberg's reductionism. Any number of examples of hierarchical disconnect can show this, whether it be non-homologous genes contributing to a morphological homologue, different developmental mechanisms causing the same morphological pattern, or different morphologies causing the same behavioral homologue. In each case, the multiplication of developmental factors is the source of multiple realizability. This is particularly salient in some cases of behavioral homology (Striedter and Northcutt 1991;Wenzel 1992; Lauder 1994; Ereshefsky 2007). Consider the homologous song produced by acridid grasshoppers (Striedter and Northcutt 1991: 185–186). In most acridids, an insect produces this song by rubbing its hind legs against the lateral edges of its forewings. However, one species of acridids, *Caplliptamus italicus*, produces the song by rubbing the apical surfaces of its mandibles. Hind legs and mandibles are different morphological structures, so this song is the result of different physical structures. Nonetheless, Streidter and Northcutt argue that instances of this song are homologous because they occur in the same contexts. As further evidence that these songs are homologous they point out that when *C. italicus* produce this song with their mandibles they also make the characteristic movement of hind legs found in other acridids, though the legs of *C. italicus* never make contact with their wings. Streidter and Northcutt suggest that during the evolution of this behavioral homology "one set of effector organs, namely the mandibles, has been substituted for another, namely the hind limb and forewings" (*ibid*., 186).

What are we to make of this case in relation to reductionism? Rosenberg's reductionism fails to capture this case because no single physical kind corresponds to the given behavioral homologue. The song is produced by different parts of a grasshopper's body: the hind limb and forewings in some cases, the mandibles in other cases. Hind limbs and mandibles are different physical kinds. They are composed of different arrangements of macromolecules. Thus, this behavior does not correspond to a single physical configuration. Simply stated: no physical unity, no reduction.

Nevertheless, let us try to reduce this behavioral homologue according to Rosenberg's suggestion that macro-level biological phenomena can be reduced to micro-level selection processes. This requires reducing the history of a homologue to the history of its physical substrata. According to Striedter and Northcutt (1991), hind leg movement is the ancestral state underlying this behavioral homologue, and mandible movement is the derived state. At some point in acridid evolution, mandible movement replaced hind leg movement in one lineage of acridids. Suppose we are able to describe the replacement of hind leg movement with mandible movement in terms of changes in the macromolecules underlying such movements. That is, suppose we can describe the replacement of the macromolecular ancestral state with the macromolecular derived state. Are we any closer to a satisfactory reductionist account of this behavioral homologue? Such a macromolecular account of the song's history would be an account of two historical branches of molecular phenomena: one corresponding to hind leg movement, another corresponding to mandible movement. Once again, there is no physical unity at the micro-level: there is one historical account of the macro-level phenomenon, the behavioral homology, yet two historical accounts of its underlying micro-level substrata. If there are two distinct macromolecular histories then there is no unified macromolecular account of the macro-level phenomenon. If there is no unified macromolecular account of the macro-level phenomenon, there is no reductionism. Rosenberg's reductionism fails to capture this case of multiple realizability.[10] Homology thinking, on the other hand, does. More generally, Rosenberg's reductionism cannot capture the phenomenon of hierarchical disconnect. Homology thinking can, and it helps us understand how such cases of multiple realizability come about.

Conclusion

What is homology thinking? It is an approach to understanding biological phenomena that focuses on the historical nature of homologues. Homology thinking explains the properties of a homologue (or the range of properties among a homologue's character states) by citing either an initial condition or a series of events in the history of a homologue. The historicity of homology thinking allows it to be significant in several respects. First, by drawing on information about the history of a homologue, homology explanations are more detailed than corresponding analogy explanations. Second, homology thinking provides an important explanation of character similarity and difference. At a proximate level, such similarities and differences are explained by citing the developmental mechanisms of a homologue. At a more distal level, the occurrence and persistence of such mechanisms is explained by citing the evolutionary history of a homologue's developmental module, namely its origin, alterations, and transmission. Finally, homology thinking offers a promising account of multiple realizability in biology. It helps us understand how multiple realizability occurs, and it shows why such reductionisms as Rosenberg's fail to capture that phenomenon.

We have seen that the range of homology thinking is broad. It applies up and down the biological hierarchy, from genes to behaviors. Homology thinking may even help us understand certain psychological categories (Ereshefsky 2007). Griffiths (1994, 1997) and Matthen (1998, 2000) suggest that such psychological categories as the emotions are homologues. If that is correct, then homology thinking can be a useful tool in psychology. More speculatively, perhaps homology thinking can apply to cultural categories. Hull (1988), for example, suggests that at least some scientific theories are homologues. If some cultural categories are homologues then homology thinking applies to them. Whether homology thinking is an appropriate way to understand a category is an empirical question: it depends on whether the category is a homology class or not. Where homology thinking does apply, it offers an important way of understanding the phenomenon at hand.

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[10] A crucial element of Rosenberg's reductionism is the reduction of selection processes at the macro-level to selection processes at the micro-level (2006, 199). However, it is not obvious that all cases of hierarchical disconnect (multiple realizability) are the result of selection. In the grasshopper song example, Striedter and Northcutt (1991) make no mention of selection for a second physical substructure for the homologous song. The change in physical substructures underlying the song could be selectively neutral. Consider a different type of case. Given what we know about gene substitution, it is plausible to suppose that some substitutions in the gene regulatory mechanisms of homologues are selectively neutral. Thus, some cases of hierarchical disconnect due to gene substitution may be the result of non-selective processes.

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References

Abouheif E (1997) Developmental genetics and homology: a hierarchical approach. TREE 12:405–408

Abouheif E (1999) Establishing homology criteria for regulatory gene networks: prospects and challenges. In: Bock G, Cardew G (eds) Homology. Wiley, New York, pp 207–221

Beatty J (2006) Replaying life's tape. J Philos 53:336–362

Bickle J (2006) Multiple realizability. In: Zalta E (ed) The Stanford encyclopedia of philosophy. http://plato.stanford.edu/entries/multiple-realizability

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

Brigandt I (2002) Homology and the origin of correspondence. Biol Philos 17:389–407

Brigandt I (2007) Typology now: homology and developmental constraints explain evolvability. Biol Philos 22:709–725

Carroll S (2005) Endless forms most beautiful: The new science of Evo Devo. Norton, New York

Crombie A (1994) Styles of scientific thinking in the European tradition. Duckworth, London

Darwin F (ed) (1877) The life and letters of Charles Darwin. Including an autobiographical chapter. John Murray, London

Darwin C (1887) The various contrivances by which orchids are fertilized by insects, 2nd edn. D Appleton, New York

De Beer G (1971) Homology: an unresolved problem. Oxford Biol. Readers No. 11. Oxford University Press, London

Desjardins E (2010) Historicity as path dependence in evolutionary biology and community ecology (unpublished)

Desjardins E (2011) History and experimental evolution. Biol Philos 26:339–364

Donoghue M (1992) Homology. In: Keller H, Lloyd E (eds) Keywords in evolutionary biology. Harvard University Press, Cambridge, pp 171–179

Ereshefsky M (2001) The poverty of the Linnaean hierarchy: A philosophical study of biological taxonomy. Cambridge University Press, Cambridge

Ereshefsky M (2007) Psychological categories as homologies: lessons from ethology. Biol Philos 22:659–674

Ereshefsky M (2009) Homology: integrating phylogeny and development. Biol Theory 3:225–229

Ghiselin M (2005) Homology as a relation of correspondence between parts of individuals. Theory Biosci 124:91–103

Gould S (1986) Evolution and the triumph of homology, or why history matters. Am Sci 74:60–69

Gould S (1989) Wonderful life: the burgess shale and the nature of history. W Norton, New York

Griffiths P (1994) Cladistic explanation and functional explanation. Philos Sci 61:206–227

Griffiths P (1997) What emotions really are: the problem of psychological categories. University of Chicago Press, Chicago

Griffiths P (2006) Function, homology and character individuation. Philos Sci 73:1–25

Griffiths P (2007) The phenomena of homology. Biol Philos 22:643–658

Hall B (ed) (1994) Homology: the hierarchical basis of comparative biology. Academic Press, San Diego

Hall B (2003) Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biol Rev 78:409–433

Hall B (2007a) Homology and homoplasy. In: Matthen M, Stephens C (eds) Philosophy of biology. Elsevier, Amsterdam, pp 429–454

Hall B (2007b) Homoplasy and homology: dichotomy or continuum? J Hum Evol 52:473–479

Hempel C (1965) Aspects of scientific explanation. Free Press, New York

Hull D (1988) Science as a process. Chicago University Press, Chicago

Kirschner M, Gerhart J (1998) Evolvability. Proc Nat Acad Sci 95:8420–8427

Laubichler M (2000) Homology in development and the development of the homology concept. Am Zool 40:777–788

Laubichler M, Wagner G (2001) How molecular is molecular developmental biology? Biol Philos 16:53–68

Lauder G (1994) Homology, form, and function. In: Hall B (ed) Homology: the hierarchical basis of comparative biology. Academic Press, San Diego, pp 151–196

Matthen M (1998) Biological universals and the nature of fear. J Philos XVC 3:105–132

Matthen M (2000) What is a hand? What is a mind? Revue Internationale de Philosophie 214:653–672

Matthen M (2007) Defining vision: what homology thinking contributes. Biol Philos 22:675–689

Mayr E (1959) Typological versus Population Thinking. In: Evolution and Anthropology: a Centennial Appraisal. The Anthropological Society of Washington, Washington D.C., pp 409-412.

Mayr E (1969) Principles of systematic zoology. McGraw Hill, New York

Minelli A (1998) Molecules, developmental modules, and phenotypes: a combinatorial approach to homology. Mol Phylogenet Evol 9:340–347

Müller G (2003) Homology: the evolution of morphological organization. In: Müller G, Newman S (eds) Origination of organismal form: beyond the gene in developmental and evolutionary biology. MIT Press, Cambridge, pp 51–69

Müller G, Newman S (1999) Generation, integration, autonomy: three steps in the evolution of biology. In: Bock G, Cardew G (eds) Homology. Wiley, New York, pp 65–72

Patterson C (1982) Morphological characters and homology. In: Joysey K, Friday A (eds) Problems of phylogenetic reconstruction. Academic Press, London, pp 21–74

Patterson C (1987) Introduction. In: Patterson C (ed) Molecules and morphology in evolution: conflict or compromise?. Cambridge University Press, Cambridge, pp 1–22

Prum R, Brush A (2002) The evolutionary origin and diversification of feathers. Q Rev Biol 77:261–291

Rieppel O (1994) Homology, topology, and typology: the history of modern debates. In: Hall B (ed) Homology: the hierarchical basis of comparative biology. Academic Press, San Diego, pp 64–101

Rosenberg A (2006) Darwinian reductionism. Or, how to stop worrying and love molecular biology. Chicago University Press, Chicago

Roth L (1994) Within and between organisms: replicators, lineages, and homologues. In: Hall B (ed) Homology: the hierarchical basis of comparative biology. Academic Press, San Diego, pp 302–338

Salmon W (1984) Scientific explanation and the causal structure of the world. Princeton University Press, Princeton

Shubin N, Tabin C, Carroll S (1997) Fossils, genes and the evolution of animal limbs. Nature 388:639–648

Sneath P, Sokal R (1973) Numerical taxonomy. W H Freeman, San Francisco

Striedter G (1999) Homology in the nervous system; of characters, embryology and levels of analysis. In: Bock G, Cardew G (eds) Homology. Wiley, New York, pp 158–170

Striedter G, Northcutt G (1991) Biological hierarchies and the concept of homology. Brain Behav Evol 38:177–189

Szathmary E (2006) Path dependence and historical contingency in biology. In: Wimmer A, Kössler R (eds) Understanding change: models, methodologies, and metaphors. Palgrave Macmillan, New York, pp 140–157

Van Fraassen B (1980) The scientific image. Oxford University Press, New York

Van Valen L (1982) Homology and causes. J Morphol 173:305–312

Wagner G (1989) The biological homology concept. Annu Rev Ecol Syst 20:51–69

Wagner G (1994) Homology and the mechanisms of development. In: Hall B (ed) Homology: the hierarchical basis of comparative biology. Academic Press, San Diego, pp 273–299

Wagner G (1996) Homologues, natural kinds and the evolution of modularity. Am Zool 36:36–43

Wagner G (1999) A research programme for testing the biological homology concept. In: Bock G, Cardew G (eds) Homology. Wiley, New York, pp 125–134

Wagner G (2000) What is the promise of developmental evolution? Part I: Why is developmental biology necessary to explain evolutionary innovations? J Exp Zool (Mol Dev Evol) 288:95–98

Wagner G (2007) The developmental genetics of homology. Nat Rev Genet 8:473–479

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

Wake D (1994) Comparative terminology. Science 265:268–269

Wake D (1999) Homoplasy, homology and the problem of 'sameness' in biology. In: Bock G, Cardew G (eds) Homology. Wiley, New York, pp 24–33

Wake D (2003) Homology and homoplasy. In: Hall B, Olson W (eds) Keywords and concepts in evolutionary developmental biology. Harvard University Press, Cambridge, pp 191–200

Wenzel J (1992) Behavioral homology and phylogeny. Annu Rev Ecol Syst 23:361–381
West-Eberhard M (2003) Developmental plasticity and evolution. Oxford University Press, New York
Winther R (2006) Parts and theories in compositional biology. Biol Philos 21:471–499