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The Fine Structure of 'Homology'

Abstract

There is long-standing conflict between genealogical and developmental accounts of homology. This paper provides a general framework that shows that these accounts are compatible and clarifies precisely how they are related. According to this framework, understanding homology requires both (a) an abstract genealogical account that unifies the application of the term to all types of characters used in phylogenetic systematics and (b) locally enriched accounts that apply only to specific types of characters. The genealogical account serves this unifying role by relying on abstract notions of 'descent' and 'character'. As a result, it takes for granted the existence of such characters. This requires theoretical justification that is provided by enriched accounts, which incorporate the details by which characters are inherited. These enriched accounts apply to limited domains (e.g. genes and proteins, or body parts), providing the needed theoretical justification for recognizing characters within that domain. Though connected to the genealogical account of homology in this way, enriched accounts include phenomena (e.g. serial homology, paralogy, and xenology) that fall outside the scope of the genealogical account. They therefore overlap, but are not nested within, the genealogical account. Developmental accounts of homology are to be understood as enriched accounts of body part homology. Once they are seen in this light, the conflict with the genealogical account vanishes. It is only by understanding the fine conceptual structure undergirding the many uses of the term 'homology' that we can understand how these uses hang together.

Introduction

The pectoral fin of a dugong, the forelimb of a mole, and the wing of a bat, though they do not appear especially similar and though they serve distinct functions (swimming, digging, and flying, respectively), are nonetheless the "same" part: they are all variations on the vertebrate limb (Owen 2007). They are all, as biologists put it, homologous.

Homology is among the most important and most controversial phenomena in biology: important because it is the "basis of comparative biology" (Hall 1994), controversial because biologists rely on multiple, possibly incompatible accounts of homology. In particular, there is a longstanding conflict between accounts of homology based on Darwinian evolutionary theory (e.g. Lankester 1870; Hennig 1966) and accounts of homology based on morphology and development (e.g. Owen 2007; Wagner 1989).

The relationship between these two types of account remains contentious. Genealogical accounts, which today are generally framed in terms of phylogenetic systematics (Wiley and Lieberman 2011), are dominant. The status of developmental accounts of homology is less clear. Some take the two types of account to stand in an antagonistic relationship (Amundson 2005, pp. 238–44; Ramsey and Peterson 2012; Currie 2014), while others see them as merely different, useful for different purposes (Brigandt 2002; Jamniczky 2005; Griffiths 2007). If we accept the latter suggestion, then we need some picture of how the accounts relate. Not much has been written on this score (but see Brigandt 2007; Laublichler 2014).

This paper presents a general framework showing how genealogical and developmental accounts of homology fit together. In this framework, both types of account capture aspects of homology that the other type cannot. Both types of account therefore work together to contribute to a full understanding of homology.

In rough outline, I argue that the two types of account relate as follows (Figure 1). Genealogical accounts rely on notions of 'character' and 'descent' that abstract away from the particular mechanisms by which characters are inherited. Thanks to this abstraction, phylogenetic systematics can incorporate data drawn from all kinds of biological characters (genes, body parts, behaviors, etc.). However, the genealogical account presupposes the existence of inherited units. These units are inherited in different ways. Considering these differences leads to the development of enriched accounts of homology that, though tied to the genealogical account, apply to more limited domains (e.g. just to genes, or just to body parts). Even as their domain is restricted, however, these accounts expand the reference of 'homology', for they include phenomena (e.g. paralogy, serial homology) that are excluded by a strict genealogical account. Developmental accounts of homology are best understood as enriched accounts that apply specifically to body part homology.

[INSERT FIGURE 1 AROUND HERE]

There is thus a complex conceptual structure underlying the various uses of the term 'homology'. This structure consists of (1) an abstract, genealogical account that applies to all kinds of biological characters and (2) a set of locally enriched accounts that complete the genealogical account within a limited domain (e.g. body parts) while also including additional phenomena (e.g. serial homology) not covered by the genealogical account. I aim to show that, once this fine structure is appreciated, the longstanding tensions between the two types of account vanish.

Homology: the problem

Any adequate account of homology must explain how the parts of organisms can be the same part, despite potentially great dissimilarity. This problem is capture by Owen's (1843, p. 379)

classic definition of a homolog as "the same organ under every variety of form and function." This definition does not say in what sense homologs are "the same." The problem of homology might thus be put as follows: Owen's definition is correct, but what does it mean?

Here the disputes begin. Accounts of homology can be grouped into two main classes—genealogical and developmental—that provide different types of answers to this question. There are four key sources of tension between these two accounts.

Tension 1: what is the nature of homological sameness? Genealogical accounts explicate sameness in terms of shared descent: two parts are homologous if they derive from the same part in a common ancestor. Developmental accounts, by contrast, explicate sameness in terms of shared features of development. Günter Wagner's (1989, p. 1163) account of homology, for instance, treats two parts as homologous if they share "historically acquired and genetically regulated developmental constraints." This basic difference over the nature of homological sameness gives rise to three further sources of tension.

Tension 2: how much dissimilarity is permitted? Genealogical and developmental accounts of homology differ over the extent to which homologs can be dissimilar. Genealogical accounts explain homological sameness in terms of a shared origin. Because the origin is a fixed historical event, no amount of subsequent divergence can destroy the homology between two parts. Genealogical accounts thus allow for indefinite divergence. Developmental accounts do not. They explain sameness in terms of extant, causally active factors operative in development, and the requirement that these factors be conserved constrains the degree to which homologous parts can diverge.

Tension 3: how many types of homology? Genealogical and developmental accounts of homology disagree about whether serial homology (the same part repeated within a single

individual) is genuine homology. Strictly speaking, genealogical accounts exclusively concern special homology (the same part in different species). Phylogenetic systematics ties homology to the topology of phylogenetic trees (see below, "A genealogical account of homology" section), and no account of serial homology emerges from this (Cracraft 2005; cf. Lankester 1870; De Beer 1971). Developmental accounts, by contrast, explicitly include serial homology (Wagner 2014, p. 418).

Tension 4: what is the proper target of homology assessments? Genealogical and developmental accounts of homology appear to disagree over what is properly homologized. Whereas developmental accounts homologize *characters* (e.g. the vertebrate forelimb, whatever form it takes), genealogical accounts homologize *character-states* (e.g. having a forelimb shaped like a fin) (Wagner 1989; Brigandt 2007). In this way, they disagree concerning the proper targets of homology assessment.

On account of these four sources of tension, a number of philosophers have taken genealogical and developmental accounts of homology to be in competition (Amundson 2005, pp. 238–44; Ramsey and Peterson 2012; Currie 2014). Others, however, have defended the compatibility of the two accounts, on the grounds that they are useful for different purposes (Brigandt 2002; Jamniczky 2005; Griffiths 2007). Roughly, the genealogical account is useful for reconstructing phylogenies, while developmental accounts are important for understanding the evolution of novel structures. Once the different purposes of these accounts are recognized, they can be seen as no longer fighting over the same ground. Among biologists, advocates of both compatibility (Panchen 1999, discussion; Wagner 2014) and conflict (Cracraft 2005) can be found.

This paper sides with the compatibilist camp. It is not enough, however, to show that genealogical and developmental accounts serve different purposes, for that does not explain in

what sense they are both accounts *of homology*. A viable compatibilist analysis of homology must both (a) make clear how the two types of account are related and (b) do so in a way that shows how to resolve the four sources of tension described above. In what follows, I defend a framework for understanding homology that satisfies both desiderata.

One feature of this framework is that the scope of different accounts of homology varies not only in terms of the range of characters covered, but in terms of the range of taxa covered. Accordingly, the sections of this paper vary in scope. The discussion of the genealogical account of homology ("A genealogical account of homology" section) covers all taxa, reflecting the unifying role of the genealogical account. The discussion of gene homology ("The enriched account of gene homology" section) likewise applies to all taxa. By contrast, the discussion of body part homology ("Wagner's enriched account of body part homology" section) covers only animal taxa, since that is the scope of the enriched account under discussion. The scope of the paper as a whole, however, is general: it provides a framework for making sense of applications of 'homology' to all taxa and for all characters.

The easiest way to introduce this framework is by presenting a genealogical account of homology ("A genealogical account of homology" section), as the limitations of such an account reveal the need for enriched accounts of homology. After explaining the general features of enriched accounts ("Enriched accounts of homology" section), I provide examples of two such enriched accounts: one for gene homology ("The enriched account of gene homology" section) and one for body part homology ("Wagner's enriched account of body part homology" section). I then return to a more abstract discussion of the nature of enriched accounts of homology ("Enriched accounts of homology are local" section). With the framework in place, I show how it resolves the four sources of tension just described ("Resolving the problem of homology" section),

then compare my account to two other recent proposals ("Other accounts of homology" section).

A genealogical account of homology

In this section, I present a genealogical account of homology, based on the methods and conceptual framework of phylogenetic systematics. This account unifies applications of 'homology' to all kinds of biological entities. It does so by relying on abstract notions of 'descent' and 'character'. Subsequent sections will show how making these abstract notions concrete by incorporating mechanistic details give rise to locally enriched accounts of homology.

According to the genealogical account of homology, homologs are characters or character states (the distinction is explained below) that descend from the same character (state) in a common ancestor. Character state homology is tied to the topology of phylogenetic trees, while homology of characters ("transformational homology") is importantly presupposed in the methodology of phylogenetic systematics. I take up these two types of genealogical homology in turn.

Homology of character states

Phylogenetic systematics aims at reconstructing the phylogenetic relationships between taxa. Phylogenetic relationships are distinct from tokogenetic relationships (Figure 2; see Hennig 1966, pp. 29–32). Tokogenetic relationships hold between parents and offspring within an interbreeding population. When a single interbreeding population splits into two, this yields phylogenetic relationships between the ancestral and descendant populations. Phylogenetic relationships produce a strict hierarchy representable in a phylogenetic tree; tokogenetic relationships do not.[1]

[1] I do not here consider phylogenetic networks (Huson, Rupp, and Scornavacca 2010) that take into account tokogenetic relationships (produced by e.g. hybridization and lateral gene transfer). This issue is discussed briefly below ("The enriched account of gene homology" section).

[INSERT FIGURE 2 AROUND HERE]

To reconstruct phylogenetic relationships systematists record the similarities and differences between a given set of taxa (Wiley and Lieberman 2011). Figure 3 shows a data matrix recording the similarities and differences of nine characters among four taxa. In the figure, the columns are taxa, while the rows are characters. Each character can occur in at least two character states. For example, "number of digits" might be a character, while "one" and "five" are possible states of that character. For simplicity, the characters in Figure 3 come in only two character states, coded as '0' or '1'.

[INSERT FIGURE 3 AROUND HERE]

Next, the systematist searches for the phylogenetic tree that is best supported by the data (Figure 4). Inferring a phylogenetic tree from the data requires adopting a model of evolution, capturing the possible and probable transitions between states of a given character. For instance, for molecular data, the Jukes-Cantor model of DNA evolution assumes that all four bases of DNA occur with equal frequencies, and that the rate of transition is the same for all pairs of bases (Huson, Rupp, and Scornavacca 2010, pp. 29–31). For morphological data, a model might assume that loss of a complex character is more likely than gain. In generating Figure 4, I assumed that 0 is the ancestral state for each character, that $0 \rightarrow 1$ is the only possible transformation for each character, and that otherwise all transitions are equally likely.

[INSERT FIGURE 4 AROUND HERE]

For understanding character state homology, however, what matters is not the model used to infer the phylogenetic tree from the data, but rather the topology of the tree produced. Once a tree is inferred, homology relationships can be read off the tree directly. There are two ways in which

character states can be homologous. Symplesiomorphies are shared ancestral character states, while synapomorphies are shared derived character states. As both are shared due to common descent, both fall under a genealogical account of homology.

Transformational homology

Character state homology does not exhaust the genealogical account of homology. To construct a data matrix, one must recognize a second kind of homology: transformational homology. Even to ask whether two shared character states are homologous or independently derived, they must be treated as states of a single character. Characters must be able to transform from one state to another (e.g. reduction in digit number during the evolution of horses). In this sense, characters form "transformation series" (Hennig 1966). Just as a data matrix encodes hypotheses of character state homology by giving two taxa the same value for some character, so it encodes hypotheses of transformational homology by placing the features of distinct taxa in the same row.

This point is independent of the sort of data one considers in phylogenetic analysis. In the morphological case, for instance, it would be incorrect to compare the coloration of bird wings to the coloration of butterfly wings, since the two groups evolved wings independently. Wing coloration thus does not form a transformation series in the two groups. In the molecular case, it is essential to compare base identity at homologous loci. This is the purpose of sequence alignment, a necessary stage in the phylogenetic analysis of molecular data (Huson, Rupp, and Scornavacca 2010, chap. 2).

Though the process of inferring a phylogenetic tree from the data evaluates the hypothesis that shared character states are shared due to common ancestry, it presupposes hypotheses of transformational homology. Hypotheses of transformational homology are thus "logically prior"

to hypotheses of character state homology (Brower and Schawaroch 1996, p. 269).

Both transformational homology and character state homology are intelligible within and indeed necessary to a phylogenetic framework (Assis and Brigandt 2009, p. 251). The genealogical account of homology thus includes both.

'Descent' and 'character'

The genealogical account of homology just described unifies applications of the term 'homology' to biological entities of all kinds. It is able to serve this unifying role because it relies on a purely formal understanding of both 'descent' and 'character'. Anything can be a "character" (i.e. used in phylogenetic systematics), provided that it yields transformation series. Likewise, a phylogenetic descent relationship is simply any relationship that gives rise to phylogenetic patterns recoverable by phylogenetic analysis. Such patterns hold among biological taxa, but can also be found outside of biology, as in the relationships between languages: Darwin quite properly spoke of linguistic homologies (Darwin 1981, p. 59).

By relying on formal notions of 'descent' and 'character', the genealogical account achieves broad applicability. Any character that is informative of phylogenetic relationships between taxa can be homologized. This is so even though the processes by which different kinds of parts are inherited can be quite different. DNA is replicated by copying from a template. Body parts are not. Nonetheless, both can form transformation series. Later, we will see how these differences give rise to locally enriched accounts of homology. For now, however, what matters is that the genealogical account of homology is able to apply to all kinds of characters, despite these differences.

The formal nature of the genealogical account also makes room for the fact that homology

"dissociates" across different kinds of biological entity. For instance, homologous body parts may develop via non-homologous developmental pathways and involve the expression of non-homologous genes (De Beer 1971; Wray and Abouheif 1998). In the other direction, homologous genes and developmental precursors may be involved in the development of non-homologous adult structures (Havstad, Assis, and Rieppel 2015). The genealogical account of homology permits (but does not require) such dissociations, because the formal notions of 'descent' and 'character' impose no *a priori* requirements on the relations between different homologs. Once the means by which different kinds of homologs are inherited are considered, constraints on dissociation will become important, but no such constraints are required by the genealogical account considered in isolation.

As represented in Figure 1, the genealogical account of homology, in addition to covering transformational and character state homology, also includes special homology and orthology. Special homologs are body parts shared due to descent from a common ancestor (e.g. the vertebrate forelimb); orthologs are the same for genes. These stand in a one-to-many relationship to transformational homologs: each special homolog/ortholog is the basis for multiple transformation series. For instance, orthologous genes contain multiple loci, each of which forms a transformation series. Likewise, the vertebrate forelimb is the basis of many transformation series, such as digit number and length. They thus stand in the background of phylogenetic analysis without featuring in it directly. To see how they enter the picture, we need to look at the reasons why enriched accounts of homology are required.

Enriched accounts of homology

The methodology of phylogenetic systematics requires the identification of characters whose

character states are informative of phylogenetic relationships among taxa. Only once such characters are recognized can phylogenies be reconstructed. How are they to be recognized? Answering this question will reveal the need for locally enriched accounts of homology. I first explain why such accounts are needed, then summarize their key features.

Why enriched accounts of homology are necessary

Phylogenetic relationships are produced by the evolutionary process of descent with modification. When an ancestral species splits into two descendant species, the descendants resemble the ancestor (and each other) in some respects, but differ in others. Thus, shared descent can explain shared similarities. A phylogenetic relationship, however, is simply one that answers to a particular formal structure (Hennig 1966, pp. 18–21). There is no principled reason that ancestors and descendants, *qua* ancestors and descendants, cannot be radically different. Phylogeny alone places no limits on the extent of possible divergence between them.

To understand why real-world phylogenetic relationships show these similarity relationships, we must therefore look beyond phylogeny itself. Because offspring resemble their parents, descendant populations resemble their ancestors. If we want to know why common ancestry can explain similarities between taxa, we therefore need to consider the processes that produce parent-offspring similarities.

This is especially important for understanding homology, because, as we saw above, applying the methods of phylogenetic systematics requires that we first recognize comparable features of distinct taxa. The data used to infer phylogenetic relationships are laden with assumptions about which characters can be and are shared by descent. The grounds for such assumptions, however, lie in our understanding of how such characters are inherited. In this sense, *the genealogical*

account of homology is internally incomplete: it assumes that certain characters are shared by descent without explaining how this is possible. It requires completion by consideration of the details of inheritance, which will furnish an explanation of what it means for parts to be shared by descent.[2]

At this point, a complication arises: what it means for two parts in different taxa to be shared by descent depends on the nature of the part in question. The reason is that different processes underlie the inheritance of different kinds of biological entities. The mechanisms of DNA replication, which involve copying from a template, are responsible for genomic parent-offspring resemblances. Body parts, by contrast, are reproduced each generation without the benefit of a template, relying instead on complex networks of regulatory interactions between genes (among other causes). Still other kinds of characters (e.g. behaviors) are inherited differently than either genes or body parts.

For this reason, the manner in which the genealogical account is to be completed will depend on the type of character in question—thence the need for local, not global enrichment. These local differences in the nature of inheritance matter for two reasons. First, from the standpoint of phylogenetic systematics, comparisons between character states that do not belong to the same transformation series introduce error into the process of phylogeny reconstruction (Fitch 1970). As accurate identification of transformational homologs is essential, it is necessary to understand how different kinds of characters are inherited.

Second, though phylogenetic systematics is the basis for the genealogical account of

[2] This argument resembles others in the literature on homology (Wagner 1989, p. 1158; Müller and Newman 1999, p. 65; Laublichler 2014, p. 73). These authors defend the need for a developmental account of homology, but do not draw the broader conclusion about the need for enriched accounts.

homology, homology matters beyond systematics (Jamniczky 2005). For instance, understanding how a particular kind of character evolves requires establishing comparability for that kind of character. For example, during the modern synthesis, the attempt to uncover the genetic basis of species differences required identifying homologous genes across species (Spencer 1963). Likewise, contemporary evolutionary-developmental biology's attempt to explain the origin of morphological novelty requires contrasting the evolution of genuine novelties from the (often extreme) modifications of pre-existing parts (Müller and Wagner 1991).[3]

We should therefore expect that consideration of the local processes of descent for different kinds of characters will inflect our understanding of homology both within and beyond systematics. Consideration of these processes leads to accounts of homology that apply to only a limited subset of biological entities. These I refer to as enriched accounts of homology.

Three features of enriched accounts of homology

Enriched accounts of homology have three key features. Here, I state them dogmatically; the examples of the next two sections will justify my claims.

First feature. Enriched accounts of homology apply to a more limited domain than the genealogical account of homology; enrichment is therefore local. For instance, the enriched accounts considered below apply, respectively to genes ("The enriched account of gene homology" section) and to (animal) body parts and cell types ("Wagner's enriched account of body part homology"). These domains must be determined empirically. It happens to be the case that Günter Wagner's account of homology applies to both body parts and cell types. It may turn out that

[3] This distinction is controversial (Minelli 2016). The issue is treated below ("Wagner's enriched account of body part homology" section).

Wagner's account is wrong, and that these actually require separate enriched accounts. Further, it is an open question whether Wagner's account can be extended to the parts of plants. He suggests it can in at least some cases, but there are reasons to worry (Wagner 2014, chap. 12; Kendig 2016). There is no way to intuit what types of characters can be subsumed under a single enriched account.

Second feature. Enriched accounts of homology are connected to the genealogical account of homology. This connection has two aspects. *First*, enriched accounts must pick out a type of homolog that is shared due to common ancestry, and that forms the basis for recognizing transformation series. Wagner's enriched account of body part homology includes special homology, while the enriched account of gene homology includes orthology (Figure 1). As mentioned above ("A genealogical account of homology" section), special homologs and orthologs stand in a one-to-many relationship to transformational homologs. Enriched accounts thus constrain but do not determine the choice of transformational homologs, and so play an important background role in the methodology of phylogenetic systematics.

Second, enriched accounts must, for the relevant type of genealogical homolog, explain what it means for such homologs to be shared by descent. That is, enriched accounts must elucidate the particular processes that enable these parts to be related by descent. As we saw above, the genealogical account, because it presupposes the ability of parts to be so related, is internally incomplete. In explaining how such relationships are possible for a particular kind of character, *enriched accounts of homology complete the genealogical account within a limited domain*.

Third feature. Enriched accounts of homology include types of homology that do not fall under the genealogical account. This is because enriched accounts of homology explain homological sameness not in terms of a purely formal notion of 'descent', but rather in terms of the particular processes that make shared descent possible. It turns out (empirically) that these

enriched accounts of homological sameness can be applied in cases where the genealogical account cannot, yielding phenomena such as serial homology, paralogy, and xenology (Figure 1). While the genealogical account recognizes no connection between, e.g., special and serial homology (Cracraft 2005), there is such a connection, and this is captured by enriched accounts.

In combination, these three features show that enriched accounts of homology overlap with the genealogical account but are not nested within it. Neither is complete without the other. The genealogical account unifies the application of 'homology' to many different kinds of character, but only by ignoring the details that explain how these characters can be related by descent at all. In ignoring these details, it overlooks the real connections between genealogical homology (e.g. special homology and orthology) and non-genealogical homology (e.g. serial homology, paralogy, and xenology). Enriched accounts, by focusing on these details, are able to (a) explain the connections between genealogical and non-genealogical homology (third feature) and (b) explain how characters can be related by descent (second feature). Because enriched accounts apply only within limited domains (first feature), however, the sense in which they are all accounts *of homology* is lost without the genealogical account, to which each is connected (second feature).

That is why a compatibilist picture that recognizes the need for multiple co-existing accounts is correct. As noted above ("Homology: the problem" section), any viable compatibilist view must explain in what sense developmental and genealogical accounts of homology are accounts of the same thing. The framework just described satisfies this demand. In their regions of overlap, the genealogical account and a given enriched account provide different perspectives on the same phenomenon. The next two sections justify this framework by looking in detail at two particular enriched accounts, one for gene homology and one for body part homology.

The enriched account of gene homology

Enriched accounts of homology complete the genealogical account within a limited domain. They do so by considering the processes that allow entities within that domain to be related by descent. In the case of DNA, these processes are well understood, with the result that homologizing genes is conceptually, though not always practically, a simple process. DNA consists of two anti-parallel strands with complementary nucleotide sequences. During replication, the strands are separated, with each strand serving as a template for its complement, such that two new double-stranded DNA molecules are created, each consisting of one old and one new strand. Though errors may occur in this process, it is generally quite faithful, with the result that the new molecules are nearly identical to each other and to the original.

On this basis, an enriched account of gene homology emerges: genes (in this context, any stretch of DNA of interest) are homologous just in case they descended, via this replication mechanism, from the same stretch of DNA in a common ancestor. Thus far, this is just a genealogical account of homology that makes reference to the specific mechanism by which DNA is inherited. It possesses the first two features of enriched accounts, but not the third. However, the behavior of DNA during replication forces us to complicate the account. Occasionally, the molecular machinery required for replication "slips" and copies a particular stretch of DNA twice, resulting in a new DNA molecule with two genes that both descended from a single gene in the ancestor. Other mechanisms (e.g. unequal crossing over and mobile genetic elements) can also give rise to duplicated genes, or even to a duplication of the entire genome.

Biologists thus recognize two sameness relations that can obtain between genes, both of which involve being descended from the same stretch of ancestral DNA. Two copies of the same gene that are the result of duplication and so coexist within a single organism are *paralogs*, while two

copies of the same gene that are the result of speciation are *orthologs*. Only orthologs fall under the genealogical account of homology. Character states of paralogous genes cannot be treated as part of the same transformation series: "phylogenies require orthologous, not paralogous genes" (Fitch 1970, p. 113). Paralogy thus falls under the enriched account of gene homology, but not under the genealogical account of homology, illustrating how enriched accounts expand the reference of 'homology' beyond the domain of the genealogical account.

Other features of how DNA is inherited complicate the account still further. Lateral gene transfer, in which stretches of DNA (not necessarily functional) are transferred between different species, is rampant among prokaryotes and known, though rare, in eukaryotes (Eme and Doolittle 2016). It allows for the same gene to be present in different species. Like orthologs, laterally transferred genes are the same gene in different species, and biologists perfectly readily speak of laterally transferred genes as "homologous" (e.g. Mohanraju et al, 2016). Unlike orthologs, however, laterally transferred genes produce tokogenetic rather than phylogenetic relationships between species, and so require the addition of a third category of gene homology: xenology (Gray and Fitch 1983).[4]

Thus we can see that consideration of the mechanisms by which DNA is inherited is the basis for an enriched account of gene homology that possesses all three features of a locally enriched account. It applies to a limited class of biological entities, namely stretches of DNA. It can also apply to proteins (Fitch 1970), but not, for instance, to body parts or behaviors (first feature). It is

[4] Unlike paralogy, xenology is not a problem to be avoided in systematics, but a phenomenon to included. Where xenology is prevalent, systematists cannot simply assume that relationships between taxa can be captured by a strict tree, and must instead infer from the data to a phylogenetic network (Huson, Rupp, and Scornavacca 2010). However, whether one infers a tree or a network, one must still undertake a sequence alignment step that furnishes the relevant transformation series, and this is presupposed, but not tested, by the data-to-tree/network inference.

connected to the genealogical account, explaining how it is possible for genes to stand in descent relationships, i.e. be orthologous (second feature). Lastly, the enriched account of gene homology expands the reference of 'homology' by including paralogy and xenology, even though these are excluded by the genealogical account (third feature).

Wagner's enriched account of body part homology

Understanding body part homology requires understanding development, and knowledge of developmental processes has played a role in determining body part homologies since at least the late 18th century (Goethe 2009; Owen 2007). The fertilized embryo contains a nucleus (including DNA) and surrounding cytoplasm. In the strictest sense, that is all that an offspring inherits from its parents.[5] Adult morphology must be developed epigenetically each generation. In contrast to DNA replication, a parent's limbs do not serve as templates for its offspring's limbs. Thus, when body parts are homologized, they are homologized in accordance with an enriched account distinct from the enriched account that applies when genes are homologized. The crucial consideration is the nature of the continuity between ancestral and descendant body parts.

Because homology dissociates between genes and body parts (De Beer 1971; Wray and Abouheif 1998), body part homology cannot be easily reduced to gene homology (Brigandt 2002). Furthermore, homologous body parts may develop via different developmental pathways (De Beer 1971), and different body parts may develop from the same developmental precursors (Havstad, Assis, and Rieppel 2015). An enriched account of body part homology must be compatible with

[5] The discussion of development in this section primarily applies to animal development, and it focuses exclusively on the role of gene regulation in development, ignoring the role of non-genetic resources that shape development. I exclude such considerations because they do not feature in Wagner's account of body part homology.

these phenomena. Specifically, any attempt to explain body part homology in terms of shared developmental processes must (a) identify what developmental features are conserved between homologs and (b) explain why dissociation in other features is possible.

No consensus account of body part homology currently exists. I here present Günter Wagner's (1989, 1994, 1999, 2014) account, not out of commitment to its correctness, but because it illustrates in detail what an enriched account of body part homology might look like.[6] Wagner (1989, p. 1163) sets himself the task of accounting for three core explananda. First, homologous body parts share conserved features. Despite variation in form and function, there is deep evolutionary conservation of animal body plans, and an account of body part homology should explain why body plans are conserved. Second, homologous body parts are individualized, i.e. they possess "a certain minimal degree of complexity, differentiation, and genetic/epigenetic autonomy" (Wagner 1989, p. 1160). Wagner emphasizes variational individuality: the ability for genetic mutations to affect one part but not another. Third, homologous body parts possess a single evolutionary origin and thus characterize a monophyletic taxon.

The latest incarnation of Wagner's account explains the conserved similarity, individualization, and phylogenetic uniqueness of homologs in terms of shared character identity networks, or ChINs (Wagner 2014, chap. 3). ChINs are gene regulatory network (GRN) subcircuits, usually wired in a positive feedback loop, that "form the interface between developmental signals and those genes that actually engender the morphological character during morphogenesis and differentiation" (Wagner 2014, p. 97).

Animal development involves the precise control of gene expression in space and time (Peter

[6] Gerd Müller (2003) offers a distinct enriched account of body part homology. Alessandro Minelli (2016) raises serious challenges to Wagner's approach to homology. I defer discussion of these challenges to the end of this section.

and Davidson 2015, chap. 1). As the embryo develops, it is progressively subdivided into more and more domains, each characterized by a distinct regulatory state. In this process, transient chemical signals furnish positional information that blocks out a domain. These signals activate a positive feedback loop that stabilizes the regulatory state of that region (Peter and Davidson 2015, chap. 6). Downstream of this positive feedback loop, "realizer" genes are expressed that are responsible for the formation of a particular body part within that domain (morphogenesis). This feedback loop (Wagner's ChIN) stabilizes the identity of the region, fating it to express a particular set of realizer genes. As lineages evolve and diverge, the realizer genes downstream of the ChIN can change, leading to variation in form and function. So long as the ChIN is conserved, however, these body parts share what Wagner calls a "character identity"—they remain homologous.

Just as the complications of DNA replication and lateral transfer forced the recognition of different types of gene homology, so the complications of development force the recognition of different types of body part homology. Wagner ties homology to character identity. Character identity can be shared across species (special homology), as in the case of the dugong's fin and the bat's wing. However, it can also be shared within an individual (serial homology). The dugong, after all, has two pectoral fins, and the bat two wings. If Wagner's account is correct, this is because the same ChIN is activated in two regions of the embryo.

Wagner's account can explain all three explananda described above. Because ChINs are recursively wired, and because they are responsible for ensuring the expression of an entire suite of genes essential for body part development, they are likely to be refractory to evolutionary change (Davidson and Erwin 2006). They thus tend to be conserved, even as the downstream genes they regulate are gradually changed. Wagner can thus explain the sense in which two body parts can retain the same identity despite substantial modifications of form and function.

Wagner can also explain the individualization of body parts. A given gene can come to be regulated by a given ChIN without necessarily being regulated by any other ChIN. Body parts whose development is controlled by distinct ChINs can therefore vary independently. At the same time, Wagner can explain why individualization is often incomplete. Serial homologs, in which the same ChIN is activated in multiple regions of the embryo, tend to vary in tandem because a downstream gene activated in one serial homolog is likely to be activated in every other.

Lastly, any individual ChIN emerges in a particular lineage at a particular time and, unless it is modified or lost, can be found in all members of that lineage. In this way, Wagner captures the phylogenetic uniqueness of homologs.

Wagner's account of body part homology has all three features of enriched accounts of homology. It applies only to a limited domain of biological entities, namely animal body parts. Wagner (2014, chap. 8) also extends his account to cell types, on the grounds that cell type identity is also determined by ChINs (first feature). Wagner's account is tied to the genealogical account, because character identities are phylogenetically unique. By tying character identity to the expression of conserved ChINs, Wagner explains how body parts can be shared due to descent from a common ancestor, even as they are modified. Wagner's special homologs are thus the proper basis for recognizing transformation series (second feature). Lastly, Wagner's account expands the reference of 'homology' to include serial homology, which is not covered by the genealogical account (third feature; Figure 1).[7]

[7] In this discussion, I have simplified things for ease of exposition. In fact, the appropriate bearer of character states is not the entire organism (or part) over the entire course of its life, but a suitably thick time-slice of the organism (part), called a *semaphoront*. In an excellent paper, Havstad, Assis, and Rieppel (2015) show that ontogenetic identity (identity of a part across the different semaphoronts of a single individual) and phylogenetic identity (identity of a part across evolutionary transformations) can come apart. For example, in *Drosophila melanogaster*, female genitalia develop from the embryonic segment A8. In males, however, A8 develops into a tergite-

While Wagner's account of homology illustrates what an enriched account of animal body part homology might look like, it is controversial. In a recent paper, Alessandro Minelli (2016) argues that Wagner is too sanguine about the manner in which body parts remain "the same" over time, even as their features change. On Wagner's account, body parts possess an underlying identity that persists even as the features of those parts change. Wagner thus has a two-layer ontology, in which characters possess both an identity (determined by their underlying ChIN) and a particular realized state (determined by the operation of downstream realizer genes). Minelli rejects this approach in favor of a single-layer ontology. On Minelli's view, traits are to be understood as "complex and ever-changing intersections of an indeterminate number of features." This disagreement has further consequences. Wagner's approach lends itself to the traditional assumption that homology is an all-or-nothing relation (cf. Fitch 2000), while Minelli favors a combinatorial approach to homology that allows for parts to be partially homologous. Relatedly, Wagner's account permits a sharp distinction between the origin of novel features and their respective diversification, while Minelli's account denies the possibility of drawing such a distinction.

The crucial question, for the purposes of this paper, concerns the basis for Minelli's objections. Here Minelli is explicit that his criticisms are founded on an understanding of how body parts are inherited, which includes their manner of development. He accepts that there exist conserved developmental modules, but argues that these modules are related to body parts in a many-to-many fashion: many such modules go into the building of any single part, and each individual module is

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like structure (Keisman, Christiansen, and Baker 2001). A8 in females is phylogenetically identical to A8 in males, and it is ontogenetically identical to the adult female genitalia. Likewise, A8 in males is ontogenetically identical to the tergite-like structure. Yet the female genitalia and the male tergite-like structure are not homologous. Over the course of development, a homologous precursor develops into non-homologous structures. One task of an enriched account is to explain why this is so. Wagner's account would analyze such cases as involving initially homologous precursors that come to express non-homologous ChINs.

used in the building of distinct parts. Body parts are thus the product of a "peculiar intersection (both spatial and temporal) of developmental modules" (Minelli 2016, p. 49). This has two implications: first, that there are no grounds for a Wagnerian two-layer ontology, since all developmental modules are on a par; and, second, that these intersections, due simply to the number of modules they involve, are unlikely to be deeply conserved.

Though Minelli's account challenges Wagner's at crucial points, it serves the same basic function: it attempts to explain how it is that body parts can be related by descent. That is, Minelli challenges Wagner not by denying the need for an enriched account of body part homology, but by offering a competing enriched account. Whichever view of body part homology should prove correct, my central contention—that some enriched account is needed—stands.

Enriched accounts of homology are local

I have shown how consideration of the processes by which characters are inherited leads to the development of enriched accounts of gene and body part homology. The genealogical account is unifying in the sense that it furnishes abstract requirements that all (genealogically) homologous characters must meet: they must be shared due to common descent. The ability of particular kinds characters to satisfy these requirements depends on concrete processes by which those kinds of characters are inherited. These processes are distinct for different kinds of characters. Genes are homologous in case they descend via replication from the same ancestral sequence. Body parts are homologous (if Wagner is right) in case they develop via the activation of shared ChINs. Enriched accounts thus show how it is possible to satisfy the requirements of the genealogical account within particular domains.

A central feature of the framework I have presented and defended is that these enriched

accounts are local, in the sense that they apply to different domains. According to this framework, biologists work with more than two accounts of homology (one genealogical and one enriched). They work with one genealogical account and multiple enriched accounts, each with its particular, limited domain. My aim in this section is to defend this claim against an objection.

The objection I have in mind claims that enriched accounts are more unified than I have let on. Granting that, at the level of details, enriched accounts are clearly distinct, the objection claims that the resulting pictures, conceived more abstractly, share certain structural similarities. In this regard, only a single enriched account is required. Such a view might be motivated by considering an apparent structural similarity between the two enriched accounts provided above. For both gene and body part homology, we can distinguish the same part/gene in different species (special homology, orthology) from the same part/gene in a single organism (serial homology, paralogy). It is true that the enriched account of gene homology recognizes xenology, whereas Wagner's enriched account of body part homology involves nothing of the sort. However, there is no conceptual difficulty in imagining a laterally transferred ChIN, merely a host of practical difficulties.

On this basis, one might suggest that there is a basic template for constructing enriched accounts. No matter what processes are responsible for the inheritance of a particular type of character, there are three ways in which two tokens of that character type might be related. They might be related in different species due to shared descent (special homology, orthology), or in different species due to lateral transfer (xenology), or in a single individual due to duplication (serial homology, paralogy). In some cases, one or more of these conceptual possibilities may be unrealized (as there is no analog of xenology for animal body parts), but these three conceptual possibilities are exhaustive, no matter the type of character.

I do not deny that enriched accounts will involve some subset of these three possibilities. However, I contend that, despite these similarities, the differences between distinct enriched accounts are more important. In the remainder of this section, I consider special homology and orthology, in order to illustrate the nature of these differences and the reasons they matter.[8]

On Wagner's (2014, pp. 58–65) account of body part homology, two types of special homologs are recognized: strict special homologs and variational modalities. Variational modalities capture cases where special homologs come in two or more distinct forms. The tetrapod limb and teleost fin are special homologs, even though they are structurally quite distinct. The array of actual fin forms occupies a distinct region of morphospace than the array of actual limb forms. They are thus two variational modalities of the same special homolog. Note that this is a structural distinction. In the case of gene homology, however, no similar structural distinction can be drawn.

Among genetic phenomena, the closest corresponding distinction is between orthologs that share a molecular function and orthologs that serve distinct molecular functions (Wagner 2014, p. 80). The defining difference is in terms of molecular function, in contrast to the case of body parts, where the difference is in terms of variational properties. It is true that orthologs with different molecular functions are likely to occupy discrete regions of sequence space, and so generate a pattern similar to variational modalities. But it is shared function that creates this pattern. By contrast, a tetrapod limb is a tetrapod limb even if it serves, as in the case of a whale's flipper, the same function as a fish fin.

In short, it is possible to draw a structural division between types of special homolog, but not between types of ortholog. This matters for understanding how special homologs and orthologs

[8] For reasons of space, I do not discuss serial homology and paralogy, but similar considerations apply.

evolve. Special homologs are subject to both developmental and functional constraints, whereas orthologs are subject only to functional constraints. As Amundson (1994) has argued, developmental and functional constraints have distinct evolutionary implications and should not be conflated. The reason for this difference lies in the nature of the homological sameness relation. Body parts are homologous if they share the same character identity. This requires sharing an underlying ChIN, which in turn constrains their patterns of variability. The mechanisms of DNA replication do not furnish any comparable constraints on variability.

These differences between special homology and orthology point to a deeper difference in how these two enriched accounts explain sameness "under every modification of form and function." The genealogical account explains this in terms of shared descent (with modification). Because the genealogical account refers homology to historical origin, it permits potentially unlimited divergence after that origin. No amount of subsequent divergence can change the fact that two parts share a common origin. The genealogical account *by itself* thus places no constraints on subsequent divergence.

But, as we saw above ("Enriched accounts of homology" section), the genealogical account is incomplete. It furnishes abstract requirements that homologous characters must satisfy, but does not consider the specific processes of inheritance that make the satisfaction of these requirements possible. Once the details are considered, limits to divergence may be discovered. In Wagner's theory of body part homology, what is homologized are character identities, as fixed by ChINs. Preserving body part homology thus requires the evolutionary conservation of ChINs. Homology-preserving divergence is limited to divergence that occurs via the modification of the genes downstream of the relevant ChIN. Wagner's account thus makes the conservation of particular similarities essential to the conservation of homological sameness.

By contrast, the mechanisms of DNA replication set no limits on divergence. Two stretches of DNA in different species may be homologous (descended via replication from the same stretch in a common ancestor) even if, over evolutionary time, every single nucleotide has diverged between the two sequences. Unlike the case of body part homology, no particular similarities are essential to the preservation of homology. It is true that the recognition of orthologous DNA sequences requires the preservation of sufficient similarity to distinguish similarity due to common descent from similarity due to chance (Strimmer, von Haeseler, and Salemi 2009, pp. 137–40). However, the difficulty of recognizing that two highly dissimilar sequences are related by descent does not change the fact that they are so related. Even leaving that point aside, recognizing orthology requires only a sufficient degree of overall similarity, not similarity in any particular subset of bases. Wagner's account of body part homology, by contrast, sets no limits on overall dissimilarity, so long as the essential similarity (the ChIN) is preserved.

The enriched accounts of body part homology and gene homology thus lead to importantly divergent pictures of how these different kinds of characters evolve. These differences matter both within systematics (recall that inferring phylogenies from morphological or molecular data requires adopting a model of how the characters used evolve) and in the study of evolutionary change more generally. Thus, the surface similarities between orthology and special homology are just that: superficial. Enrichment truly is local, ineliminably dependent on the particular processes involved in the inheritance of particular kinds of characters.

Resolving the problem of homology

According to the framework I am defending, developmental accounts of homology should be understood as enriched accounts of body part homology. Other enriched accounts arise when other

kinds of characters (genes, behaviors, etc.) are homologized. These enriched accounts are not in competition with the genealogical account of homology. Rather, they complete (and extend) that account within particular domains.

This compatibilist view of the relationship between enriched accounts and the genealogical account is tenable only if the four sources of tension between genealogical and developmental accounts ("Homology: the problem" section) can be resolved. My aim in this section is to show that the framework I have offered eliminates these tensions.

The first tension concerns the nature of homological sameness. Genealogical accounts say that homologous parts are the same in virtue of their shared descent. 'Descent' here is understood purely formally, in the context of the methodology of phylogenetic systematics. There are multiple mechanisms that can produce such descent relationships between parts: replication in the case of genes, development controlled by a ChIN in the case of body parts. In saying that body parts are homologous because they share the same character identity, Wagner is not denying the genealogical account. He is explaining how it is possible that body parts can answer to that account's formal requirements. This point is not limited to Wagner's account. Other enriched accounts are compatible with the genealogical account for the same reason: one of their key features is that they explain how characters can be shared due to descent. Thus the first tension disappears.

The second tension concerns the amount of dissimilarity between homologs that each account permits. Developmental accounts limit the amount of allowable dissimilarity between homologs. Genealogical accounts do not. This generates no inconsistency, however. The key consideration here is that the genealogical account imposes purely formal requirements on homology, in terms of the topology of phylogenetic trees. Because the genealogical account says nothing about what

it is to be the same character, it is silent about the degree to which homologs can diverge. For this, we must look to enriched accounts. Wagner's developmental account says that body part homology requires the conservation of the underlying ChIN. By contrast, in the case of genes, the appropriate enriched account does not require the conservation of any essential similarity. The genealogical account is consistent with both. It permits but does not require the possibility of complete dissimilarity. Similar considerations apply to the issue of dissociation. The genealogical account is consistent with all kinds of dissociation, while developmental accounts reveal limits to the dissociation that is actually possible. The second tension disappears along with the first.

The third tension concerns the role of serial homology: the genealogical account excludes it, while developmental accounts include it. Here it is important to see that the term 'homology' covers multiple distinct (though related and overlapping) phenomena. Genealogical sameness (shared descent) and developmental sameness (shared ChIN) are distinct types of sameness. There is no special homology of body parts without the overlap of both of them. It is in virtue of sharing a ChIN that body parts are able to stand in descent relationships. Thus, in this region of overlap, developmental sameness is part of the account of what genealogical sameness is.

But neither sameness relation is limited to this region of overlap. Genealogical sameness is shared by other kinds of characters that lack developmental sameness altogether (e.g. genes) or that lack the specific kind of developmental sameness (conserved ChINs) shared by body parts (e.g. behaviors). Equally, character identity is shared not just among special homologs, but also among serial homologs. The third tension, too, has vanished.

The fourth tension concerns the proper target of homology assessments: characters or character states. We are now in position to see that this is misleading. "Character" is ambiguous here: it can refer both to transformation series (e.g. number of digits) and to the parts that underlie these

transformation series (e.g. the vertebrate forelimb). Since we already have the term 'transformation series' for the former, I will use 'character' for the latter. Then we can distinguish three targets of homology assessment: (1) characters (special homologs, orthologs, etc.), (2) transformation series, and (3) character states. As we have seen, the genealogical account covers all three (Figure 1). Genealogical and developmental accounts overlap in the first category and, insofar as developmental accounts constrain (without determining) the identification of transformation series, also the second. Homologizing character states is indeed peculiar to the genealogical account, but there is no incompatibility here. Both accounts agree that characters and transformation series can be homologized. About homologizing character states, developmental accounts are simply silent. And so the fourth tension disappears along with the rest.

In the end, we can see that there is truth in both of the traditional views about the relationship between genealogical and developmental accounts of homology. Those who have treated them as antagonistic have correctly recognized that they cover, at least in part, the same phenomena. The genealogical sameness of body part homologs is not a wholly distinct phenomenon from their developmental sameness. Rather, their developmental sameness is precisely what allows them to be genealogically the same. Thus, the two accounts had better be consistent in what they say about special homology. Nonetheless, the compatibilists are correct that they cannot be unified into a single account. The developmental sameness relationship (and enriched sameness relationships more generally) can be instantiated in cases where genealogical sameness is not (e.g. serial homology), and vice versa (e.g. orthology). Genealogical and enriched accounts overlap but are not identical. Where they overlap, they are compatible. Where they do not overlap, the issue fails to arise.

Other accounts of homology

I am not the first to attempt to bridge the gap between genealogical and developmental accounts of homology. Recently, Brigandt (2007) and Ramsey and Peterson (2012) have defended accounts with similar aims. Ramsey and Peterson defend a genealogical account of homology that incorporates input from developmental biology, while Brigandt defends a developmental account of homology that fits with systematic practice. I contend that the framework I have defended marks an improvement over both. It is compatible with Brigandt's account but has greater generality, and it preserves the advantages of Ramsey and Peterson's account without sharing that account's central flaw (discussed below). I discuss them in turn.

Brigandt is concerned, as I am, to make sense of the relations between genealogical and developmental accounts of homology. But whereas I begin from genealogical accounts and expand outward to enriched accounts (including developmental accounts), Brigandt starts with development. He characterizes homologs as units of heritable phenotypic variability—i.e. as characters that can take different character states. Understanding the developmental sameness of body part homologs offers an explanation for why it is possible to perform phylogenetic analyses that take for granted the existence of characters that come in different character states.

According to the framework I have defended, Brigandt can be understood as showing how a developmental account of homology fulfills the function of an enriched account. Brigandt does not, however, draw the conclusion that such accounts are required for every kind of character used in phylogenetic analysis. Philosophical work on homology has focused on understanding the legitimate roles (if any) of a developmental account of body part homology, largely ignoring the fact that there has long existed an enriched account of gene homology. In fact, however, the situation is exactly comparable in the two cases. My aim has been to draw attention to this more

general state of affairs, while Brigandt's aim, expressed in my terminology, was to look at the proper role of a particular enriched account. Our views are compatible, and complementary.

I turn now to Ramsey and Peterson's genealogical account of homology. They argue that a single definition of 'homology' can be offered that (a) incorporates the role of information about the mechanisms of descent and (b) subsumes all legitimate uses of the term (including serial homology and paralogy). They present an abstract schema for how to include information about descent mechanisms. As this schema applies in all cases, they can be seen as offering a fully general template for constructing enriched accounts. I aim to show that this template imposes arbitrary restrictions on the nature of the relations between different types of character.

Ramsey and Peterson begin with a straightforward genealogical account of homology. Traits T and T* belonging, respectively, to organisms O and O* are homologous if they are present in every organism along the shortest path (on a phylogenetic tree) connecting O and O*. But there is a problem: there can be failures of continuity that do not undermine homology. For instance, sexually dimorphic traits need not be continuously present. The posterior lobe is a male-specific genital structure found in certain *Drosophila* species. Suppose a male has a female offspring, who in turn has a male offspring. In this case, the female lacks the structure (violating continuity), and yet clearly the lobes in the males are homologous.

What is required here is some account of how such characters are inherited, an account that explains how a part can remain the same through descent despite such violations of continuity—an enriched account, in other words. Moreover, though the example I chose involved a morphological structure, such violations of continuity can affect other kinds of character as well, for instance behaviors. Ramsey and Peterson provide a general-purpose solution to this problem.

Ramsey and Peterson's solution rests on the assertion that there exist distinct biological levels

that stand in a strict ordering, such that for a given level L_{N-1} (e.g., development), one can distinguish a higher level L_N (morphology) and a lower level L_{N-2} (genes). They then allow for violations of continuity at L_N provided that there is continuity at L_{N-1}, but not if continuity is only preserved at L_{N-2}. For instance, a violation of continuity at the morphological level might be bridged by continuity at the developmental level, but not by continuity at the genetic level. Though they make the point using the morphology, development, and genes as example levels, their claim is general. Whatever levels biologists identity, violations of continuity can be bridged by continuity at the next level down, but no lower.

This account assumes the existence of an objective (i.e. research agenda-independent) hierarchy of levels in biology, with a clear ordering, such that it is unambiguous, given a particular L_N, what is L_{N-1} and what is L_{N-2}. At a minimum, this assumption requires further elaboration.[9] Levels are not simply size scales, given that developmental processes involve entities at both genetic and morphological size scales. Moreover, whereas genes and morphological parts are entities, development is a process involving those entities. Thus, it is unclear what it means to say that development is a level intermediate between the genetic and the morphological levels.

Even granting the assumption, however, their account runs into serious trouble. In trying to solve the problem of failures of continuity, Ramsey and Peterson recognize the need for understanding how characters are inherited—the need, that is, for an enriched account. The role of this account is to show how a character can be continuously inherited even if the character itself, for whatever reason, fails to appear in particular individuals. What Ramsey and Peterson's account does is to impose a restriction on what enriched accounts can include: they can involve continuity at L_{N-1}, but not at L_{N-2}. I contend, however, that this restriction is arbitrary, and that it runs the risk

[9] For additional critique of this assumption, see Currie (2014).

of ruling out successful enriched accounts of homology on illegitimate grounds.

For example, consider Wagner's account of body part homology, taking body parts as L_N. If we take ChINs as L_{N-1}, his account fits their schema. But ChINs are almost certainly not L_{N-1}. Suppose we accept Ramsey and Peterson's distinction of three levels: morphological, developmental, and genetic. On this division of levels, ChINs arguably fit best at the genetic level. Gene regulatory networks are based on regulatory information encoded in *cis*-regulatory DNA sequences. True, ChIN activation depends on processes of gene regulation that can reasonably be treated as developmental. In the case of our lobeless female *Drosophila*, however, the (hypothetical) ChIN is never activated, so the violation of continuity extends to these processes. All the female inherits is the underlying genetic information—L_{N-2}.

Nonetheless, we may wish to treat gene networks, which involve a great deal of genetic information distributed throughout the genome, as a level distinct from that of single genes. Salazar-Ciudad and Jernvall (2013) have made a recent proposal along these lines. They, however, distinguish three levels below morphology: genes, gene networks, and epigenetic networks. ChINs, once again, are L_{N-2}. Finally, even if we set aside these issues and allow that gene networks are one level below morphology, it is questionable whether all morphological characters belong to a single level. Morphology includes quite distinct kinds of characters besides morphological parts, such as tissues, cell types, and organelles. Many analyses treat them separately, including, pertinently, those based on GRN theory (Wagner 1989, 2014; Peter and Davidson 2015).

No matter how Ramsey and Peterson choose to flesh out 'level', then, we will almost certainly be forced to recognize at least one level intervening between ChINs and body parts. Thus, Wagner's account is illegitimate, according to Ramsey and Peterson's schema. This is exactly the wrong result. Wagner's account, if correct, solves the very problem that motivated their schema.

It explains how body parts can be continuously inherited despite violations of continuity at the morphological level. In insisting that continuity be preserved at L_{N-1}, Ramsey and Peterson arbitrarily limit the search space for solutions to the problem they identify. There is no reason to expect that the world will respect these limitations, as Wagner's theory shows.

Nonetheless, Ramsey and Peterson do have a reason for imposing this limitation: without it, they worry, cases of spurious continuity will be admitted. Here they are concerned about cases of deep homology, in which independently evolved structures make use of homologous genetic resources. For example, homologous transcription factors (Eyeless in *Drosophila*, PAX6 in mice) play important roles in eye development in their respective taxa (Shubin, Tabin, and Carroll 2009). Our best evidence, however, suggests that eyes evolved independently in these lineages. In this sense, deeply "homologous" structures are not really homologous at all. Ramsey and Peterson's account can account for this: deep homology involves genetic continuity (L_{N-2}), but developmental discontinuity (L_{N-1}).

But, while they get the right result, they get it for the wrong reason. The trouble with deep homology isn't that it involves violations of continuity at both L_N and L_{N-1}. The reason why deep homology is not genuine homology is that it does not solve the problem posed by such violations. Eyeless and PAX6 are implicated in a conserved pathway involved in opsin production. But opsin production is not eye production, and the eyes that rely on this conserved pathway evolved independently. That is why the continuous presence (the homology) of the underlying pathway does not ensure the homology of the structure. It has nothing to do with the level at which the continuity occurs. If Wagner (2014, pp. 102–5) is right, there is a conserved ChIN underlying insect eyes, and this is at the same level as the opsin pathway (indeed, it includes the gene that codes for Eyeless). Unlike the opsin pathway, however, this ChIN is crucial for establishing eye

identity. It is this difference that explains why one, but not the other, can account for the preservation of homology across violations of continuity.

The difficulty with Ramsey and Peterson's account stems from their attempt to impose an arbitrary restriction on what an enriched account of homology can look like. Beyond setting out a problem that such accounts must solve (the problem of failures of continuity), they claim that any adequate solution must involve only a very particular sort of lower-level continuity, regardless of the sort of character under discussion. But it is a matter for empirical determination, not stipulation, what sort of continuity can and cannot solve the problem.

I conclude that, instead of trying to find a single schema that can simultaneously perform the unifying work of the genealogical account and the detailed work of locally enriched accounts, we should accept that 'homology' has a fine structure of the sort illustrated in Figure 1.

Concluding remarks

In this paper, I have presented a general framework for understanding how distinct accounts of homology are related. The core claim I have defended is that there is a fine structure underlying uses of 'homology', consisting of a single genealogical account and multiple locally enriched accounts (Figure 1). I have argued that recognizing the existence of this fine structure dissolves the several alleged sources of tension between genealogical and developmental accounts of homology.

The genealogical account unifies the application of 'homology' to all kinds of biological characters by showing they can all play the same formal role in phylogenetic systematics. It does so by relying on notions of 'descent' and 'character' that abstract away from the processes by which characters are inherited. All that is required is that characters stand in phylogenetic

relationships.

Because of this, however, the genealogical account takes for granted the existence of transformational homologs: stable characters that can come in multiple distinct states. Recognizing transformational homologs requires consideration of the manner in which characters are inherited. Accounts of homology that consider such information are enriched accounts of homology.

Enriched accounts of homology have three key features. First, they apply to a limited domain, i.e. they are locally, not globally enriched. Second, they are connected to the genealogical account. This connection has two aspects: (a) enriched accounts overlap with the genealogical account concerning certain phenomena (e.g. special homology and orthology), and (b) within the region of overlap, enriched accounts complete the genealogical account by explaining how it is possible for a particular kind of character to stand in descent relationships. Third, enriched accounts expand the reference of 'homology' beyond what is covered by the genealogical account, including such phenomena as serial homology, paralogy, and xenology.

According to this framework, genealogical and developmental accounts of homology are compatible and inextricably intertwined. Specifically, developmental accounts of homology are to be understood as one type of enriched account of homology, applying within a particular domain. Once this is recognized, developmental accounts are seen to be consistent with and indeed complementary to the genealogical account in the regions where they overlap.

I have defended a compatibilist view of the relationship between different accounts of homology. I have tried, not merely to register that distinct accounts serve distinct functions, but to make clear in what sense the accounts, despite their differences, concern the same thing. The key lies in recognizing the fine structure that binds together the many different uses of the term.

Figure captions

All figures were created using Adobe Illustrator

Fig 1 A partial representation of the fine structure of the 'homology' concept. Large boxes with thick borders represent accounts of homology, including the genealogical account and the enriched accounts for gene and body part homology. Small boxes with thin borders represent particular phenomena covered by different accounts of homology. Further explanation in text

Fig 2 Phylogenetic relationships between taxa (left) and tokogenetic relationships within a species (right). For the right side of the figure, black circles represent males and white circles represent females. Arrows point from parents to offspring. Further explanation in text

Fig 3 Hypothetical data matrix. Rows are characters, columns are taxa. It is assumed for each character that character state '0' is the ancestral state, while character state '1' is a derived modification. Further explanation in text

Fig 4 Phylogenetic tree produced from the data matrix in Figure 3. Horizontal lines indicate the transition from the ancestral character state ('0') to the derived character state ('1') for the character listed. Further explanation in text

Conflict of interest. The author declares he has no conflict of interest.

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