Sameness in Biology*

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Homology is a biological sameness relation that is purported to hold in the face of changes in form, composition, and function. In spite of the centrality and importance of homology, there is no consensus on how we should understand this concept. The two leading views of homology, the genealogical and developmental accounts, have significant shortcomings. We propose a new account, the hierarchical-dependency account of homology, which avoids these shortcomings. Furthermore, our account provides for continuity between special, general, and serial homology.

1. Introduction. It is indisputable that many distinct biological entities bear the relation of "sameness" to one another but less clear what facts determine this sameness. One reason for this is that sameness is not a homogeneous category: there is sameness of function, of form, or of composition. Two proteins, for example, may consist of identical strings of amino acids, making them compositionally the same (possessing the same "primary structure" in the parlance of the biologist), but they may be folded differently, making them different in form (different in their secondary or higher structure). And this difference in form may bring about a functional difference, changing the role that the protein plays in the physiology of the organism. These three kinds of sameness are interesting and in want of philosophical scrutiny, but the focus of this article will be a fourth kind of sameness, one much more mysterious. This kind

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of sameness, known as "homology" by biologists, is mysterious because according to it the sameness relation is purported to hold in the face of changes in composition, form, and function. The great anatomist Richard Owen, who coined the term, defined a homologue as "the same organ in different animals under every variety of form and function" (1843, 379).

Before Darwin, we had at least one clear answer to the question of what facts fixed sameness in the homological sense: a fundamental divine blueprint or "archetype" that, like a Platonic form, is eternal and unchanging. Owen astutely determined that it is not just that similar species—kudus and zebus, say—exhibit the same parts (tails, legs, ribs, etc.) but that almost every individual trait (each bone, say) in each of these species has a corresponding part in a wide range of taxa. For Owen, what made these organs instances of the same thing was not their similarity (since many homologues are quite dissimilar) but their correspondence to the same features of the vertebrate archetype.[1]

With Darwin came the downfall of the eternal, fixed archetype in biology. Instead of viewing species as having fixed essences, Darwin understood them as collections of individuals that vary from one another and that evolve over time, adapting to local circumstances. One might suppose that homology would also have met its end at the hands of Darwin, that the concept would have been discarded along with Owen's archetypes. But not only did Darwinism not annihilate homologies, it turns out that homologies are at its very basis. In order to make a claim that a trait has evolved (e.g., that jaw structure has changed), the same trait must be picked out in different individuals (the jaw in organisms A, B, C, etc.). Darwinism thus undermined the traditional basis for homology only by making key use of the notion of homology. In the wake of Darwin, then, biologists and philosophers had to ask whether there is a new foundation for homology.

The idea that homology is at the core of biology has persisted to this day. In the words of contemporary biologist David Wake, "Homology is the central concept for *all* of biology. Whenever we say that a mammalian hormone is the 'same' hormone as a fish hormone, that a human gene sequence is the 'same' as a sequence in a chimp or a mouse, that a HOX gene is the 'same' in a mouse, a fruit fly, a frog, and a human . . . we have made a bold and direct statement about homology" (1994, 268). If Wake is right, then having a clear sense of the nature of homology is of

1. Owen understood the archetype both as an ideal form and as an immanent dynamic law. The archetype thus answered two questions: what facts make a trait in one organism the same as that in another? and, what explains the pattern of form across diverse taxa? We are here focused on the answer to the first question. See Sloan (2003) for a discussion of this dual nature of the archetype.

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central importance for understanding the conceptual foundations of biology.

Although some are skeptical that a single, unifying concept of homology is achievable (Griffiths 2007), we disagree. In what follows, we argue that past attempts to provide an archetype-free foundation for homology have failed. But we do not take this as a call for the abandonment of homology or the reintroduction of the archetype. Instead, we propose and defend a novel way of understanding homology. Our proposal retains the original sense of homology as biological sameness while doing away with archetypes. To motivate our account of homology, we will first show why the concept of sameness must be at the core of homology and then why the other leading attempts to ground the concept of homology have failed.

2. Sameness, Not Similarity. The problem of homology determination is the problem of taking traits that vary and classifying them as the same. This classification task would not be necessary if homology were based on similarity instead of sameness. For this reason, it is tempting to consider homologies to be based merely on similarity. Some authors have done just this, for example, "homology is resemblance caused by a continuity of information" (Van Valen 1982, 305), while others move back and forth between sameness and similarity without sharply distinguishing between them or asserting that only one should be linked to homology. For example, Neander and Rosenberg (2009) say of homologues that "their *sameness or similarity* can be explained by their common descent" (309, emphasis added). Similarly, Hall (2003) defines homology as "*similarity* because of common descent and ancestry" (409, emphasis added) in one place and as "the *same* character continuously present in two taxa and in their most recent common ancestor" (419, emphasis added) in another place within the same article.

Unlike these authors, we feel that one should sharply distinguish sameness from similarity because homology needs to be based on sameness, not similarity.[2] There are three reasons for basing homology on sameness. First, although many traits identified as homologies are in fact similar, this is not always the case: my femur and the femur of a chicken are similar, but the malleus bone in the mammalian inner ear is not similar (in form, position, or function) to the articular bone in a reptile since the latter is part of the jaw and the former is a small hammer-shaped bone

2. Others have emphasized homology as sameness; e.g., Ghiselin suggested that "much of the confusion about homology has resulted from treating correspondence as if it were similarity" (2005, 92).

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attached to the eardrum.[3] A second reason for basing homologies on sameness instead of similarity is that sameness, but not similarity, is transitive. If trait $T1$ is similar to $T2$ and $T2$ is similar to $T3$, it does not follow that $T1$ is similar to $T3$. It is for this reason that one who defines homology merely in terms of similarity cannot classify cryptic homologies (like the malleus and articular bones) as homologies.

For the third reason for basing homology on sameness, consider the definition of homology by Hall (2003) quoted above, "similarity because of common descent and ancestry," which is typical of how homology as similarity is defined. How are we to read "because of" in this quote? We could read it definitionally or causally. If we read it definitionally, then it means that we are defining something as "similar" just in case it is shared through descent and ancestry. There are two problems with this reading. First, this is a violation of what we mean by "similarity"—we do not take common ancestry to be a necessary or sufficient condition for similarity. Second, it smuggles sameness into the definition, for what are claims of common descent and ancestry if not claims about common ancestors possessing the same trait? In other words, although this account of homology is prima facie based on similarity, it presupposes an appeal to sameness.

If we instead read the "because" in "similarity because of common descent and ancestry" causally, then the statement is too strong. Under this reading, the claim that trait T is homologous in taxa X and Y implies the truth of this counterfactual: had the ancestor of X and Y not had T, then X and Y would not have T. Thus, the claim that velvet worm eyes and arthropod eyes are homologous would be true only if it is the case that had the ancestor of the *Onychophora* and the *Arthropoda* not had eyes, the *Onychophora* and the *Arthropoda* would not have eyes. But this is too strong, since it is conceivable that the *Onychophora* and the *Arthropoda* could have separately evolved eyes had their common ancestor lacked eyes.

Weaker ways of understanding causation in this context could be formulated—for example, causation might be understood probabilistically. The fact that the ancestor of X and Y possessed T might merely raise the probability of X and Y possessing T. Thus, the claim that velvet worm eyes and arthropod eyes are homologous would be true only if it is the case that their independent evolution would have had a low probability. But such a reading of this causal claim would not help the situation. For the probabilities of evolving eyes in these lineages are independent of

3. There are some similarities in this case, of course, like similarity of composition (both are made of bone), but there is nothing preventing composition or other features from changing over time while homologousness is retained.

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whether *Onychophora* and *Arthropoda* eyes are homologous: even if the probability of evolving eyes independently were 0.99, this would not change the fact that they are homologous. (Analogously, the fact that someone was killed by a bullet is not undermined if it turns out that they had a 0.99 probability of dying of a heart attack had the bullet not done them in.) Moreover, employing the probabilistic understanding of causation in reading this claim would, if anything, only make it more difficult to test claims of homologousness.

In addition to these conceptual difficulties with this causal reading of "because of," it also goes against actual biological practice and would be overly burdensome for biologists were it imposed. Not only would biologists need to prove common ancestry of a potential homologue, but they would have to show that had the ancestor lacked the trait, it would not have appeared—or would probably not have appeared—in the descendants. If this burden of proof were levied on biologists, claims of homologies would all but cease.

We are led, therefore, to conclude that homologies must, in the spirit of Owen, rest on a foundation of sameness. The challenge, then, is to accomplish this without invoking eternal, static archetypes. There have been two main attempts to accomplish this, and each, we will see in the following section, falls short of the goal.

3. In Need of a Theory. Founding homologies on sameness instead of similarity gets us out of the difficulties just elaborated. But there is a cost. Similarity is, in some sense, more basic, more prior to, and independent of theory. Sameness, on the other hand, requires theory to be able to digitize the continuous variation in the world into "same" and "not same." How is this digitization to be accomplished? Before proffering our answer, we will consider how others have answered.

The two most prominent accounts of homology are the *genealogical account* and the *developmental account*.[4] According to the former, generally put, traits in different organisms count as homologous if and only if the organisms in which each is found share a common ancestor with the same trait. It is this account that we employed in section 2 in our discussion of the meaning of "because of" in accounts of homology that consider traits to be homologous "because of" their existence in shared ancestors. The central difficulty with the genealogical account, as we have just seen, is that it seems to beg the question. It purports to give us criteria for the

4. The genealogical account, also called the *evolutionary account* or *taxic account* of homologies, is the view of homology advanced by Darwin (1859) and elaborated and modified by others, e.g., Patterson (1982) and de Pinna (1991). The developmental account is classically explicated by Wagner (1989).

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homologousness (i.e., sameness) of traits in different organisms but helps itself to the notion of what it would be for a trait in a common ancestor of these organisms to be the same as the traits in each of the organisms. As Wagner (1989) points out, since traits pass on their structure only indirectly, through the reproduction of the organisms in which they are found, the *ancestral trait/descendent trait* relation is not manifest and unproblematic in the way that the *ancestral organism/descendent organism* relation is. Hence, it cannot be taken for granted. But if we had an answer to the question of what makes the trait the same in the ancestor and the descendants, this would also serve as an answer to the question of what it would be for the traits of the two original organisms to be homologous. The genealogical account thus analyzes homology between two traits only by taking for granted homology between each of these traits and a trait in an ancestral organism (Brigandt 2002).

Furthermore, if shared ancestors with the same trait are required for homologies, then traits cannot be homologous between ancestor-descendent pairs. But this would be too exclusive. Given two organisms, X and Y, there are three ancestor-descendent relationships that they can bear: X can be an ancestor of Y, Y can be an ancestor of X, or X and Y can share a common ancestor without one of them being the ancestor of the other. In the scenario where X is the ancestor of Y, it could be that the trait in question, T, arose in X for the first time. Thus, X and Y share no common ancestor with T, yet it would be a mistake to conclude that T is therefore not homologous in X and Y. These and other difficulties with the genealogical account have compelled some to seek an account of homology based on development instead of genealogy.[5]

In contrast to the genealogical account, the strategy of the developmental account is to count two traits as homologous if and only if they are products of the same developmental phenomenon. More specifically, Wagner writes, "Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation" (1989, 62). This account is not circular, but it faces difficulties just as grave as those faced by the genealogical account. First, on the practical side, its adoption would severely undermine the practice of paleontology (not to mention other areas, like comparative anatomy). The paleontologist does not require additional evidence about the development of a particular bone over geological time in order to support a claim of ho-

5. For those wishing to bite the bullet and maintain that homologies require common ancestory, we would point out that a notion of sameness is needed to identify the trait in question in the ancestor as the same as those in the descendents. And if one needs this notion of sameness, why not include it under the rubric of homology?

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mology—indeed, such evidence is for the most part absent. If the developmental account were adopted, paleontologists would, for every putative case of homology, have to discern whether the developmental basis for two traits had persisted over time. Furthermore, it has long been recognized that the developmental basis for a trait can change over time. Owen (1848) asserted this when he argued that "there exists doubtless a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated" (6). While paleontologists have departed from archetypes, they have not, for good reason, moved to developmental constraints as the basis of homology.

In addition to this practical difficulty, though, the developmental account suffers from an even more fundamental problem: it gives us an account of homology for traits that are the product of development only by presupposing a distinct account of homology for developmental constraints. This would not be unsatisfying were the account to appeal to homology at the genic level instead, for, as Brigandt (2002) argues, homology at the genic level is relatively unproblematic (genes reproduce from ancestral gene templates and thus sameness of genes is based in whether the genes are made from the same template). But the same is not the case for the level of developmental constraints. And pretty clearly, the homology of developmental constraints cannot simply be taken to supervene on the homology found at the genic level, for it could be the case that homologous developmental phenomena are underlain by different gene sequences (e.g., this might happen over time within a single lineage). So, the developmental account presupposes a further substantive account of the homology of developmental constraints. But for all we know, the question of what makes these developmental constraints homologous is just as difficult to answer as the question of what makes the products of development homologous, and if so, the developmental account only pushes the brunt of the problem back a step.

We will now argue that there is an account of homology that avoids these difficulties. Ours is a hybrid account, drawing on the strengths of both the developmental and genealogical positions while avoiding their shortcomings.[6]

4. The Hierarchical-Dependency Account of Homologies. We have shown that both the genealogical and developmental accounts suffer from deep

6. Other hybrid accounts have been suggested (e.g., Abouheif 1997; Laubichler 2000; Wagner 2007; Ereshefsky 2009), although none of these accounts has suggested combining development and genealogy in the way that we propose to do so in sec. 4.

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problems. We will now introduce a novel account of homology that attempts to evade these problems as well as to capture the right set of phenomena and thus accord with and ground scientific practice.

Our account is based on hierarchical levels, and thus before we introduce our account, we must say a few words about these levels. Although the account requires that there be distinct, independently individuatable levels in organisms, it has no stake in the nature and quantity of the levels. Keeping this flexibility in mind, in what follows we will assume for the sake of exposition that there are just three levels. These levels, from bottom to top, are *L*1 (the genes employed by the developmental module), *L*2 (the developmental module(s) responsible for the product), and *L*3 (the product of development such as a morphological or behavioral trait). We will use "*L*" generically to refer to one of the levels, "*L*-1" to refer to the next level below *L*, and "*L*-2" to refer to the level below *L*-1. We acknowledge that an argument could be made, for example, that there is a "gene network" level between the gene and developmental module levels or that there is a behavioral level above the morphological level. This more complex layering would not challenge our account of homology—our account merely requires the existence of levels.

We can now introduce our account, which we will label the *hierarchical-dependency account of homology:*

> *Homology*.—Traits *T* and *T** at level *L* belonging to organisms *O* and *O**, respectively, are homologous just in case:
>
> 1. There is complete *continuity:* Each organism in the shortest path (on a phylogenetic tree) traveling from *O* to *O** possesses *T*, and each from *O** to *O* possesses *T**. In the absence of complete continuity of *T*/*T** at *L*, the gap can be bridged if the features of the organism (from which *T*/*T** is derived) at *L*-1 are continuously present over the gap.
> 2. There is *correspondence*: In each organism along the path, *T* and *T** must be numerically identical. (If there is complete continuity from *O* to *O** without *T* and *T** being numerically identical in every organism along this path, then if *T* and *T** are derived from a single feature at the next level down either in *O* and *O** themselves or in an organism ancestral to both *O* and *O**, *T* and *T** are homologous at a higher level of generality—they are what we label g-homologous.)

In order to best understand this conception of homology, consider figure 1. This figure has phylogenetic trees with ancestor Z and descendants X and Y. The three lines represent continuity in the presence of a morphological or behavioral trait (*top line*) and in the underlying developmental

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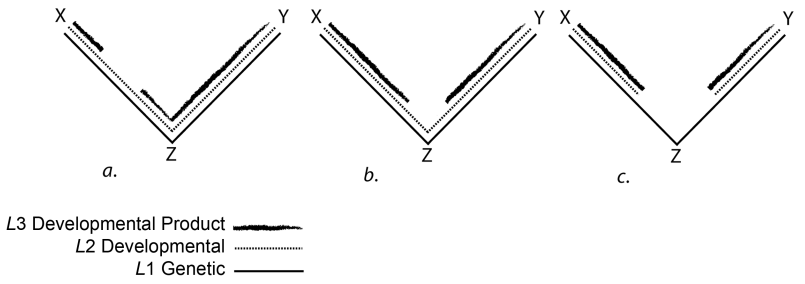


Figure 1.

(*middle line*) and genetic (*bottom line*) material responsible for bringing about this trait. In figures 1*a* and 1*b*, the trait at *L*3 is homologous between X and Y, since there is continuity at *L*2. However, in figure 1*c*, the trait at *L*3 is not homologous between X and Y because of a lack of continuity at *L*2.

This is not to say that the hierarchical-dependency account of homologies (HDAH) has solved all of the problems of homology. One big question lurking in the background is the following: What is the proper way to individuate traits? Our account assumes that (1) the traits at each level can be individuated, (2) the individuation of one level is separable from the individuation of another (e.g., the developmental level is not merely individuated based on products of development), and (3) traits bear quantifiable similarity relations to one another (see sec. 4.3 for why this is the case). Although the full implementation of the HDAH requires items 1–3, this is true of the other accounts of homology as well. Our proposed account of homology needs further explication, clarification, and justification, the task to which we now turn.

4.1. No Further Account of Homology Presupposed. The developmental account of homology at *L*3 falters because it presupposes a prior account of the homology at *L*2, without giving an account of homology at this level. Our account makes no such presupposition, for *T* and *T** can refer to an entity at any of the three levels; hence, our account does not presuppose, but instead explains, lower-level homologies. If *T* and *T** refer to something at the product of development level, then any gap in the shortest phylogenetic pathway between them can be bridged if there is continuity at the level of the developmental module responsible for the trait's production (as depicted in the path from X to Y in figs. 1*a* and 1*b*). If *T* and *T** refer to something at the level of the developmental module, any gap in the shortest phylogenetic pathway between them can

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be bridged if there is continuity at the level of the genes employed by the developmental module. However, once we reach the genic level, complete continuity on the shortest phylogenetic pathway from *O* to *O** is a necessary condition for the homology of *T* and *T** since there is no lower level of continuity that can be appealed to as a principle for bridging a gap in this pathway. But this result is not counterintuitive; if there is no continuity at any level, there is no reason to consider the traits on either side of the gap to be homologous. Therefore, our account applies to homologues at every level; at no level does the account presuppose some further (unexplained) account of homology in the way that the developmental account does (as pointed out in sec. 3).

4.2. Epistemological Worries. Our account of homology implies an algorithm for determining whether two traits are homologous: first, investigate the continuity and correspondence of the trait. If it meets both of these conditions at *L*, it is homologous. If it fails to be continuous at *L*, investigate whether there is continuity and correspondence at *L*-1 over the gap in *L*. One may be tempted to object to our account because this algorithm will not be executable in practice for any interesting cases of homology. Even if there were fossils of all the individuals from *O* to *O**, information about the basis of *T*/*T** at *L*-1 would be all but impossible to access, since it is not likely to fossilize. If our account did indeed require such information to tell whether two traits were homologues, it would be a failure in this respect. But fortunately such a process is not necessary for determinations of homology. The algorithm shows what information would be needed to make diagnoses of homologousness in all situations and with complete certainty. In practice, one will often use indirect information to investigate possible homologies. For example, features of morphological traits (especially nonadaptive features unlikely to be present in convergences) may support the idea that these traits were produced by the same developmental module(s) without the presence of direct evidence for continuity at the developmental level. Indeed, a similar method is employed for many other concepts in science. For example, the temperature of gas is understood as the mean kinetic energy of the molecules composing the gas. The algorithm implied by this definition for determining the temperature of a volume of gas would be to record the momenta of all of the molecules in the volume, sum these values, and then divide by the number of molecules. The fact that such an algorithm could never be executed in no way undermines the account of temperature or makes it impossible to tell what something's temperature is. Instead, there are many indirect ways of determining the mean kinetic energy, such as by observing the expansion of mercury in a tube or the deflection of a bimetallic strip. Moreover, on our account such indirect ways of deter-

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mining whether there is continuity at the developmental level would only be needed in cases in which there is a gap in continuity at the level of the trait. On the other hand, as previously pointed out, given the developmental account of homology, such indirect tests would have to be performed in every case.

4.3. Sameness from Similarity. Continuity requires sameness, but whence does sameness derive in the absence of a typological account of homologies? If organisms were built by template matching—that is, if each organism were formed directly from an adult organism's phenotype—then sameness would merely consist in template-copy correspondences: T^* in an offspring would be the same as T in the parent just in case T^* was formed from the T part of the parental template. As it turns out, however, things are much more complex. Organisms are rebuilt in each generation, making correspondences more difficult to discern and requiring sameness to be inferred from similarity. We have argued in section 2 that homologies consist in sameness, not similarity. Although this is true, similarity is needed for sameness in the following way: when moving between O and O^*, the sameness of the traits from one generation to the next is derived from their similarity (in form, but also in the "relative position and connection of the parts"; Owen 1848, 6). Although the malleus bone in the mammalian inner ear is not similar to the articular bone in a reptile, the bone in each parent-offspring pair (in all likelihood) exhibited similarity. It is this similarity in parent-offspring pairs that allows us to conclude, at each step of the way, that we are still referring to the same trait. If there were not similarity at the level of the bones, then there would be similarity at the developmental level. And if there were no similarity at any level, the trait in question should be considered an evolutionary novelty, and T/T^* should not be considered a homologous pair.

Because we build our account on the foundation of similarity, it might seem tempting to infer that there is no reason to bring sameness into the account. But a key reason, as mentioned above, is that transitivity is required for homologies that span more than one generation (as all interesting ones do), and sameness, not similarity, exhibits transitivity.

4.4. The Nature of the Hierarchy and the Reason for Dependency. Hall (2003) incisively noted that homology can occur at multiple levels and that there is a degree of independence between these levels—homology at one level does not imply homology at other levels. A morphological trait, say, could be homologous without the underlying genes or developmental module(s) exhibiting homology. We agree. But, as our account makes clear, we are arguing for a certain kind of dependency between the levels. The reason for this dependency is that, without it, many traits that

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seem clearly homologous (and are identified by biologists as such) would not be classified as homologous. Consider the unique dominance displays performed by alpha males in a number of species. If we were to take two alpha males in one of these species and ask whether their dominance displays are homologous, operating under a strict rule of continuity, we would likely infer that the behaviors were not homologous. The reason is that there is a good chance that some of the ancestors (including the most recent common ancestor) were not alpha males (since although the alpha males often do the bulk of the breeding, they do not do all of it). We thus need the appeal to interlevel dependency in our account in order to identify the behavior of the alpha males as homologous.

Although this is a within-species example, homology comparisons are typically cross-taxa comparisons. One could simply extend this example to such a case. Let us say that a new species of chimpanzee is formed from *Pan troglodytes*. If we investigate the alpha male dominance display and note that the new clade was formed by a non–alpha male (thus lacking such behaviors), it would be wrong to therefore conclude that the behavior is not homologous in the two species. The social *Hymenoptera* provide another example. It makes sense to ask whether the fungiculture behaviors shared by attine worker ants are homologous even though all such ants are infertile (and thus have neither progeny nor ancestors with the trait). A strict genealogical account—such as Hall's "the same character *continuously present* in two taxa and in their most recent common ancestor" (2003, 419, emphasis added)—would incorrectly rule out such cases as potential homologues if one interprets "continuously present" to operate at the level of individuals (as parent-offspring continuity). If one instead interprets "continuously present" at a higher level (present in the population or present in the species), then the above cases do not serve as counterexamples, but homology so defined would be too permissive: consider a trait that exists in one part of the species, separately evolves in another part, and then goes extinct in the first part. The trait is thus continuously present, but the past and present versions are not homologous.

One advantage of our account is that traits can be homologous even if there is a gap at the level of the trait, L, as long as there is no gap at L-1, and this gap can occur anywhere along the path from O to O^*, even in the most recent common ancestors (as in fig. 1*b*). This is an advantage, since in cases like the social *Hymenoptera* or alpha males, it is clear that the continuous presence of a trait is too strong a criterion for homology. It is also true that homologies are not equivalent to shared, derived traits, that is, synapomorphies (*pace* Patterson 1982; de Pinna 1991). A trait can be homologous between members of a clade without being shared—without, that is, all of the members of the clade possessing the trait. And a trait can be homologous without being derived (i.e., absent in ancestors).

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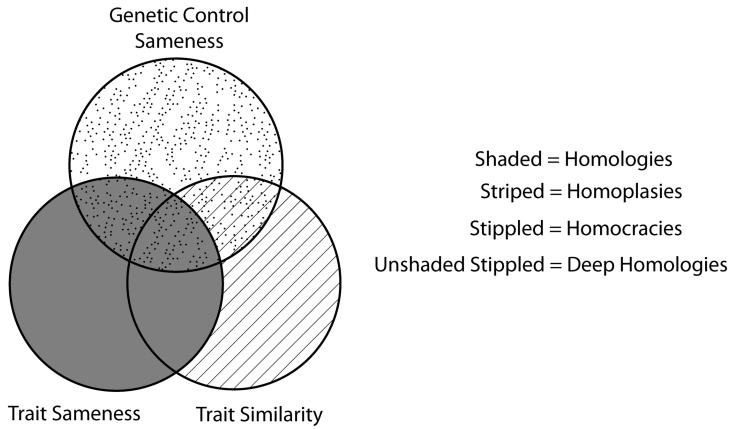


Figure 2.

Thus, neither being derived nor being shared is a necessary condition for homologies.

5. Distinguishing Homologies, Homoplasies, Homocracies, and Deep Homologies. Homoplasy is contrasted with homology, and the two are often thought to be opposites. For example, Hall writes, "Homology is similarity because of common descent and ancestry, homoplasy is similarity arrived at via independent evolution" (2003, 1). But because our account does not define homologies in terms of similarities, we have broken the symmetry of this relationship. Under our account, homologies include both similar and dissimilar traits, while homoplasies include only similar traits (fig. 2). How does our framework categorize convergences, parallelisms, reversals, rudiments, vestiges, and atavisms?

Like the account of Hall (2003), our framework classifies convergence as the only class of traits that is clearly homoplastic—convergences are similarities that are not homologous and thus fall in the striped portion of figure 2. Rudiments and vestiges are clearly homologous under our account, since these are traits exhibited by ancestors and still present, although in a diminished/modified form, in extant individuals. Reversals/atavisms are traits not present in recent ancestors, but they are present in both distant ancestors and current forms.[7] The HDAH framework categorizes such cases as homologies just in case the trait(s) at the next

7. The distinction between atavisms and reversals is usually made in terms of frequency of occurrence—atavisms occur in few of the current forms, while reversals occur in most or all of the current forms. See table 1 in Hall (2003).

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level down (on which it depends) exhibits continuity and correspondence over the span in which the trait is absent.

The implications of the HDAH for parallelisms will be more controversial than for these other categories, since parallelisms are often categorized as homoplasies, not homologies. Recall that under our account, a trait at level L is homologous if there is continuity and correspondence at L or, if there is not complete correspondence at L, if there is continuity and correspondence at L-1. Because the HDAH makes no restrictions regarding whether this gap occurs during a branching event or in the absence of branching, level L parallelisms are properly considered to be homologous as long as there is continuity and correspondence at L-1. A case of homologous parallelism is represented by figure 1*b*.

Although our view accords in some ways with Hall (2003), there are some important differences. Hall sees a continuum "extending from homology → reversals → rudiments → vestiges → atavisms → parallelism" (412). Our view does not take this to be a continuum. Instead, the HDAH distinguishes cases of gapless evolution (rudiments and vestiges) from gappy evolution (reversals, atavisms, and parallelism). There may be continua within each of these categories (e.g., gap size can vary continuously), but each of these categories does not occupy a spot in a larger continuum.

While convergences, as just shown, are categorized by the HDAH as homoplasies, in many cases of convergent evolution the traits have been built in part from the same genes. Take the well-known case of PAX6, for example. Not only does the PAX6 gene have something to do with eyes in such disparate taxa as insects and vertebrates, but some mutations in the gene will produce similar effects across these taxa, like *aniridia* in humans, *Small eye* in mice, and *ey* in *Drosophila* (Quiring 1994). This is surprising, since the most recent common ancestor of these taxa lacked eyes, or at least anything resembling the eyes in these extant taxa. The similar way in which the same genes are being employed in eyes and other features of distantly related taxa has compelled some to refer to these traits as exhibiting "deep homology" (Shubin, Tabin, and Carroll 1997). The HDAH framework correctly places deep homologies outside of the category of homology proper—deep homologies are not a kind of homology but fall under a related concept. A deep homology is a trait that is in part built from homologous genes (or gene networks). In deep homologies, there is not continuity at either $L3$ or $L2$ but only at $L1$ (see fig. 1*c*), and continuity at $L1$ does not suffice for homology at $L3$. Nielsen and Martinez (2003) recognized this and introduced the term *homocracy* for "organs/structures which are organised through the expression of identical patterning genes" (149) to help stem the homocracy-homology conflation. Because homocracies can (and often will) underlie homologies,

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homocracy is a broader category than deep homology: deep homologies can be understood as nonhomologous homocracies (see fig. 2).

6. Homology at Higher Levels of Generality. Our account of homology has the benefit of accounting for both homology in the strictest sense and homology at a higher level of generality (hereafter g-homology).[8] Furthermore, as we will see below, on our account g-homologies are the basis for another type of homology, serial homology, which is often taken to be quite distinct. (Serial homology is the relationship of homology for traits within an organism—e.g., multiple vertebrae in the spinal column.) Our account is thus unifying, bringing serial and general homology under the same rubric. Let us now draw out the implications of g-homology and show how it is related to serial homology.

6.1. Levels of Generality. Just as the first condition in our account of homology (the continuity condition) asserts that there are distinct hierarchical levels at which homology can be exhibited, the second condition notes that there are multiple levels of generality at which homology can be exhibited. Support for such a notion of homology at higher levels of generality can be found in, for example, Shubin et al. (1997): "Determination of whether two structures are homologous depends on the hierarchical level at which they are compared. For example, bird wings and bat wings are analogous as wings, having evolved independently for flight in each lineage. However, at a deeper hierarchical level that includes all tetrapods, they are homologous as forelimbs, being derived from a corresponding appendage of a common ancestor" (647). Some authors who have noted that homology can occur at multiple levels of the hierarchy have not sharply distinguished hierarchy from generality. Hall, for example, asserts that "both homology and homoplasy can be defined at different levels without making judgments about homology or homoplasy, or lack of homology/homoplasy at other levels. Indeed, to identify the hierarchical level of homology or homoplasy being specified, we should always speak of 'homologous as limbs, homologous as digits, homologous as a developmental process, homologous as a gene network, etc.,' and ditto for 'homoplastic as . . . '" (2003, 425). He is thus using "hierarchical level" to refer to both levels of hierarchical organization as well as levels of generality within these hierarchical levels. By distinguishing between

8. For homology in the strictest sense, we will simply use the term "homology" or, after Owen (1843), "special homology." Our "g-homology" should not be confused with Owen's (1843) "general homology," the latter being the homological relationship between organisms and the archetype.

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these two concepts, we are, as we will now argue, able to derive both general and serial homology from our account.

To better understand g-homology, consider the following example. The third cervical vertebra (C3) in one macaque is clearly homologous to C3 in another macaque. This is what our account tells us, and this accords with scientific practice. But suppose we ask the question whether the second cervical vertebra (C2) in one macaque, *O*, is homologous to C3 in another macaque, *O**. The answer that our account gives is that these vertebrae are not homologous, although they are g-homologous. For there is complete continuity of these traits on the phylogenetic pathway between the two macaques but not complete correspondence—when moving from parent to offspring along the phylogenetic pathway from *O* to *O**, picking out the homologous trait each step of the way (as our account instructs), one will pick out C2 each step of the way. On the other hand, when moving in the direction from *O** to *O*, one will pick out C3 each step of the way. Thus, *T* and *T** will not be numerically identical each step of the way, so there is not correspondence at the level of the traits in question. However, supposing that C2 and C3 are derived from a single feature at the next level down (the level of the developmental basis for the traits) either in *O* and *O** themselves or in an organism ancestral to both *O* and *O**, then our account counts C2 in the first macaque and C3 in the second macaque as g-homologous. Whereas C3 in *O* and C3 in *O** are homologous qua third cervical vertebrae, C2 in *O* and C3 in *O** are homologous qua vertebrae.[9]

Although in this case C2 and C3 share the same developmental basis in all organisms from *O* to *O**, this need not be the case. As the HDAH implies, all that is needed is that C2 and C3 share a developmental basis either in *O* and *O** themselves or in an organism ancestral to *O* and *O**. The developmental basis could therefore be quite distinct in *O* and *O**. Thus, the semi-independence of homology at one level from homology at other levels is mirrored by the semi-independence of the levels in g-

9. It is important to note that the parenthetical part of condition 2, which accounts for g-homology, is not merely an ad hoc addition to the HDAH. The way in which it modifies condition 2 to account for g-homology is precisely the way in which condition 1 accounts for homology at distinct hierarchical levels: by appealing to the condition's being met at *L*-1, although it is not met at *L* (the level of the traits in question). To see this, notice that just as condition 1 holds that *T* and *T** can be homologous even if there is not complete continuity at *L* (as long as there is continuity at *L*-1), so the parenthetical addition to condition 2 holds that *T* and *T** can be g-homologous as long as there is correspondence at *L*-1 (either in *O* and *O** themselves or in an organism ancestral to both *O* and *O**), even if there is not complete correspondence at *L*. So this parenthetical part of condition 2 allows for g-homology in just the way in which condition 1 allows for homology at distinct hierarchical levels. We thus account for homology and g-homology in a way that is as continuous as can be expected, given that g-homology is more general than homology.

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homology. As we will now see, this has important implications for the nature of serial homology.

6.2. Serial Homology. As we have just seen, C2 in organism *O* and C3 in organism *O** are not homologous but only g-homologous; it is C2 in *O* and C2 in *O** that are homologous, as are C3 in *O* and C3 in *O**. But now consider the question of what the relationship is between C2 and C3 within the same organism—traits that our account likewise labels as g-homologous. As scientific practice has it, the relationship that they bear is one of serial homology. On our account, the serial homology of two traits, *T* and *T**, is to be understood as a special case of their g-homology—the special case in which *O* and *O** are numerically identical. In other words, in addition to *T* and *T** being g-homologous between *O* and a numerically distinct conspecific, *O**, *T* and *T** can bear the relationship of g-homology within a single organism—and it is this case of g-homology that we label "serial homology."

There are two interesting and important implications of defining serial homology in terms of g-homology. The first is that because g-homology requires only that *T* and *T** have the same basis at *L*-1 (either in *O* and *O** themselves or in an organism ancestral to both *O* and *O**), precisely how ancestral the organism in which *T* and *T** share a common basis at *L*-1 is can vary greatly: if *T* and *T** are derived from the same features at *L*-1 in *O* (since in the case of serial homology, *O* and *O** are identical, we refer here simply to *O* rather than to *O* and *O**) or a recent common ancestor of *O*, then *T* and *T** are serial homologues because of very proximate causes. If, on the other hand, *T* and *T** are derived from the same features at *L*-1 but only in a very distant ancestor of *O*, *T* and *T** are serial homologues because of very distant causes. It might be thought that if the homology is based on a very distant ancestor, this is what is meant by "deep homology." But as we have articulated our position in section 5, deep homologies are a distinct phenomenon. We know of no term for making this distinction and would suggest *proximal* serial homologues for cases in which *T* and *T** are derived from *L*-1 in *O* or a recent ancestor of *O* and *distal* serial homologues for cases in which *T* and *T** are derived from *L*-1 only in a distant ancestor of *O*. A parallel distinction will hold among the g-homologues that are not serial homologues: if the ancestor in which the traits are derived from the same features at *L-1* is a recent common ancestor of *O* and *O** (in the case where *O** is an ancestor of *O*, this recent common ancestor could just be *O**), the traits will be proximal g-homologues, while if this ancestor is more distant they will be distal g-homologues. Additionally, the HDAH correctly categorizes serial homologues that have no evolutionary history: the origin of a novel trait *T* in *O* from a basis at *L*-1 shared by *T** in *O*, *T* and *T** will be

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considered serial homologues because they are g-homologues found within a single organism.

The second important implication of defining serial homology as a special case of g-homology is that, given the connection between special homology and g-homology in our account, we successfully sidestep one of the major criticisms of the genealogical account—that under that account there is no continuity between serial and special homology. We will now suggest that, while the HDAH provides for continuity between serial and special homology, both the genealogical and developmental account fail to do so.

6.3. Serial Homology and the Shortcomings of Traditional Views. Wagner (1989) faults a strictly genealogical account of homology for implying that the concept of serial homology is at bottom a misnomer, since it is not concerned with the relation between traits in ancestors and descendants: "This seems to imply that the similarity of two hairs on the same animal has a different cause than the similarity of two hairs from two mammalian species. . . . This is hard to believe" (54). As an example of this lack of continuity between serial and special homology, consider the account of serial homology proposed by Lauder (1994): "In my view, iterative (i.e., serial) homology simply refers to homology of one or more developmental processes (or patterns of genetic covariation) at a greater level of phylogenetic generality than the individual organism. To say that cervical vertebra 4 is serially homologous to cervical vertebra 5 in an individual mammal is simply to say that species in the *Mammalia* share an homologous developmental pathway (or set of pathways) that produces serially arranged phenotypic structures similar in size and shape" (174).

First, there is no continuity between Lauder's account of serial homology and the genealogical account of homology. Whereas, on the genealogical account, homology is based on the presence of the trait in a common ancestor, Lauder's view would have it that the ground of the homology of cervical vertebrae 4 and 5 within a single organism is entirely different: it is grounded in a fact of homology at the level of features within species, not within individuals. More specifically, reference to serial homology is nothing more than a shorthand for reference to the mere similarity of size and shape between two traits within an organism, traits which are the product of a developmental process which is homologous within some higher-level taxon under which that organism falls. So we have no continuity whatsoever between homology and serial homology of traits on this view. Second, what account of homology at the level of species is being employed here? It is difficult to see, on the face of it, how the genealogical account of homology could be transferred seamlessly from the case of organisms to the case of species. After all, whereas it is

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clear whether two individual organisms share the relationship of ancestor and descendent, ancestor-descendent relationships become far less clear when we move to higher taxa, such as species. The genealogical account, in sum, is unable to provide for any continuity between special and serial homology. What about the developmental account? Wagner (1989) argues that his developmental account, unlike the genealogical account, is able to apply to serial homology and nonserial homology continuously. For according to his account, "Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype" (62). On the face of it, it appears that the developmental account achieves the desired continunity. But is it truly unifying? Recall that the developmental account presupposes a prior account of the homology of developmental constraints. Given this, the developmental account can only be continuous between serial and nonserial homology if the account of the homology of developmental constraints which it employs (but does not explicate) is continuous between serial and nonserial homology. Prior to an account of homology at the developmental level, then, we must be agnostic about whether the developmental account is truly unifying. The HDAH, as opposed to the developmental or genealogical accounts, does provide for continuity between special, serial, and general homology, without presupposing such continuity at lower levels.

7. The Marriage of the Genealogical and Developmental Accounts. For the biologist reading this essay, two concerns are likely to emerge. First, what would adopting the HDAH account do to past homology determinations based on the genealogical or developmental accounts? (In other words, would the HDAH framework sufficiently remap the homology relation so that traits previously taken to be homologues should no longer be considered as such?) And second, how is it possible to provide an account of the homology relation without first providing an account of traits?

Although much of this essay has been spent pointing out the weaknesses of the developmental and genealogical accounts and pushing our alternative, this alternative should not be seen so much as a replacement for these accounts but more as a marriage of them: it is not that the genealogical and developmental accounts are wrong, in that they label the wrong set of traits as homologues. Rather, it is that they are incomplete—while they do a good job picking out homologues within a limited domain, they cannot pick them out in all domains. And this becomes especially clear when we consider homologies at multiple levels of generality, as we have done in section 6.2. Our account combines important theoretical

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insights from the genealogical and developmental accounts in a systematic way, so as to capture homologues across the restricted domains reached by each of these mainstream accounts. Moreover, our account can be of practical use to biologists already accustomed to using either of these mainstream accounts because, in thus systematizing their insights, it makes clear under what conditions each of them goes astray and under what conditions each succeeds.

For the biologist, then, adopting the HDAH would not be a revolutionary act and would not undermine past work in fields like comparative anatomy or evolutionary biology. The biological consensus that traits like fungiculture in attine ants is homologous across the *Attini*, or that the second and third cervical vertebrae in an individual macaque are serial homologues, will not be undermined. Instead our account is simply pointing out that the traditional accounts of homology, taken individually, do not have the theoretical resources to justify all such homology determinations. But the HDAH, by marrying the two accounts, is equipped with a set of resources for justifying these diverse homology determinations.

The advantages of the HDAH over the traditional accounts do not, however, extend to the question of how traits should be individuated. As was discussed in section 4, the HDAH account requires that traits at the different levels be individuated independently of one another but does not provide a framework for how this individuation should take place. This fact does not undermine the HDAH, since although homology determinations in practice require one to first individuate traits, theoretical accounts of homology show what kind of relation to one another traits must bear in order to be homologues, while leaving open the question of what it is for something to be a trait. The questions what is a trait? and what is a homologue? can thus be addressed independently of one another, despite the fact that the biologist needs answers to both.

8. Conclusion. As one of the foundational concepts in the biological sciences, it is imperative that we work toward a clear and precise concept of homology that is readily contrasted with related concepts such as those of homoplasy and deep homology. We are hopeful that the HDAH will help in this clarification. We have shown that the two main ways of understanding homology—the genealogical and developmental accounts—fall short of being able to fully ground the concept of homology and its relations to serial homology and what we call g-homology. The alternative that we have provided draws on some of the concepts and strategies of both of these accounts while avoiding the counterexamples that they generate. The HDAH draws on the strategy of the genealogical account by requiring continuity along a phylogenetic pathway between two organisms as a necessary condition for the homologousness of traits

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had by those organisms, and on the strategy of the developmental account by relaxing the constraint on what we mean by continuity—allowing a lack of strict continuity at one level to be compensated for by continuity at the next level down. Through this hybrid account, biological sameness in the homological sense is given a new foundation, one that can ground biological theory and practice and that is free of abstract archetypes.

REFERENCES

Abouheif, Ehab. 1997. "Developmental Genetics and Homology: A Hierarchical Approach." *Trends in Ecology and Evolution* 12 (10): 405–8.

Brigandt, Ingo. 2002. "Homology and the Origin of Correspondence." *Biology and Philosophy* 17 (3): 389–407.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. London: Murray.

De Pinna, Mario G. G. 1991. "Concepts and Tests of Homology in the Cladistic Paradigm." *Cladistics* 7 (4): 367–94.

Ereshefsky, M. 2009. "Homology: Integrating Phylogeny and Development." *Biological Theory* 4 (3): 225–29.

Ghiselin, Michael T. 2005. "Homology as a Relation of Correspondence between Parts of Individuals." *Theory in Biosciences* 124 (2): 91–103.

Griffiths, Paul E. 2007. "The Phenomena of Homology." *Biology and Philosophy* 22 (5): 643–58.

Hall, Brian K. 2003. "Descent with Modification: The Unity Underlying Homology and Homoplasy as Seen through an Analysis of Development and Evolution." *Biological Reviews* 78 (3): 409–33.

Laubichler, Manfred D. 2000. "Homology in Development and the Development of the Homology Concept." *American Zoologist* 40 (5): 777–88.

Lauder, George V. 1994. "Homology, Form, and Function." In *Homology: The Hierarchical Basis of Comparative Biology*, ed. B. K. Hall and D. Cannatella, 151–196. New York: Academic Press.

Nielsen, C., and P. Martinez. 2003. "Patterns of Gene Expression: Homology or Homocracy?" *Development Genes and Evolution* 213 (3): 149–54.

Owen, R. 1843. *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals: Delivered at the Royal College of Surgeons, in 1843*. London: Longman.

———. 1848. *On the Archetype and Homologies of the Vertebrate Skeleton*. London: van Voorst.

Patterson, C. 1982. "Morphological Characters and Homology." In *Problems of Phylogenetic Reconstruction*, ed. K. A. Joysey and A. E. Friday, 21–74. New York: Academic Press.

Quiring, R., U. Walldorf, U. Kloter, and W. J. Gehring. 1994. "Homology of the Eyeless Gene of *Drosophila* to the Small Eye Gene in Mice and *Aniridia* in Humans." *Science* 265 (5173): 785–89.

Rosenberg, Alex, and Karen Neander. 2009. "Are Homologies (Selected Effect or Causal Role) Function Free?" *Philosophy of Science* 76 (3): 307–34.

Shubin, Neil, Cliff Tabin, and Sean Carroll. 1997. "Fossils, Genes and the Evolution of Animal Limbs." *Nature* 388 (6643): 639–48.

Sloan, P. R. 2003. "Whewell's Philosophy of Discovery and the Archetype of the Vertebrate Skeleton: The Role of German Philosophy of Science in Richard Owen's Biology." *Annals of Science* 60 (1): 39–61.

Van Valen, L. M. 1982. "Homology and Causes." *Journal of Morphology* 173 (3): 305–12.

Wagner, G. P. 1989. "The Biological Homology Concept." *Annual Review of Ecology and Systematics* 20 (1): 51–69.

———. 2007. "The Developmental Genetics of Homology." *Nature Reviews Genetics* 8 (6): 473–79.

Wake, David B. 1994. "Comparative Terminology." *Science* 265 (5169): 268–69.

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