Reframing the Homology Problem

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Abstract

Recent philosophical work on biological homology has generally treated its conceptual fragmentation as a problem to be solved by new accounts that either unify disparate approaches to homology or specify sharp constraints on its meaning. I show that several proposed solutions either misunderstand or ignore central features of comparative biological research, despite attempts to capture scientific practice. I conclude that the problem is incorrectly framed and that disagreements about homology may be epistemically fruitful. Empirically tractable debates are more likely to occur among biologists who share theoretical perspectives on homology. Philosophers should consider homology not merely as a generator of inductive generalizations but also as a scaffold for meaningful empirical comparisons.

1. Introduction

"I will grant that someone might be able to generate an original thought concerning homology, but I doubt it." So complained the herpetologist David Wake nearly twenty years ago, during a revival of biological interest in the topic. Wake certainly did not doubt the importance of homology—a slippery notion perhaps most neutrally defined as correspondence between the parts of different organisms (Brigandt 2012). On the contrary, Wake elsewhere proclaimed it to be "the central concept for all of biology" (1994, 268). Having established this bedrock position for homology, however, Wake thought that continued discussion of its meaning was a distraction from more interesting biological research questions. "Isn't it time to move on?" he asked (1999, 24).

Wake's caution notwithstanding, speculation about the meaning of homology has continued apace in both biological and philosophical circles. Philosophical attention to the topic has been influenced by the rising tide of interest in scientific practice. In the first few sections of this paper, I will briefly review and critique several philosophical analyses of homology that appeal to some aspect of scientists' aims or methods. They exhibit two general approaches — some offer restrictive accounts of homology that deliberately exclude certain biological positions, while others offer compatibilist accounts that reconcile these positions. While the latter are more successful, both kinds of approach ultimately fail to capture important aspects of biological practice.

Given the diversity of biological practice, the pervasiveness of homology, and the broad theoretical level at which different accounts are traditionally characterized, this failure is not surprising. In response, I suggest that philosophers need to reconsider whether conflict between theoretical accounts of homology is really such a problem after all. Such conflict can coexist with broad agreement on the underlying methodological principles that support the reconstruction of evolutionary history. In contrast, biologists working within the same theoretical perspectives often pursue extended conflict about empirically tractable questions for which the data is still too limited, or interpretations still too underdetermined, to settle the matter. Homology is therefore just as much a tool for generating provocative comparisons as it is for supporting inductive generalizations based on natural kinds.

2. Homologizing as Kinding

Catherine Kendig (2016) offers a restrictive account of homology that is particularly emphatic about attending to practice. Her goal is to shift the focus of the debate away from "defining *homology*" to "the practices of *homologizing*" (106). She takes homology to be a natural kind concept, and *homologizing* to be a set of rule-following practices, or "kinding activities that have shaped, and continue to shape, the meaning and use of *homology*" (106–7). The first part of her paper analyzes the long history of comparative practices, from the comparative anatomical investigations of Vesalius and Belon, through Richard Owen's attempts to reconcile Cuvier's emphasis on functional unity with Geoffroy's universal body plan, to Darwin's reinterpretation of abstract archetypes as causally efficacious ancestors. The message of this history is that "[t]he concepts used within comparative biology and the activities of natural kinding have a history of being revised and retuned in response to comparative research practices" (118).

Thus far, Kendig seems poised to champion a pluralist account of homology concepts. In her account of the twentieth century, however, she switches gears to champion a particular notion of homology. She opposes the cladistic practice of mapping homology onto monophyletic groups without acknowledging its particular aim, namely to provide reliable classifications and historical hypotheses (113). "Homologizing as monophyleticizing" is an "all-or-nothing" approach that ignores all traits which are not inherited through a continuous ancestral lineage and "vociferously" objects to partial homology as a "threat to the Modern Synthesis" (115).[1] Against this foil, Kendig claims that "practices of kinding in comparative biology are reshaping the conception(s) of homology" (117). These practices, drawn from developmental and organismal biology, reveal phenotypic traits to be "mosaic" composites of modular units that can be rearranged in a combinatorial fashion during evolution. Kendig also takes symbiosis to be a source of variation that transcends individual genetic inheritance. She concludes by arguing that "multidimensional homology thinking" has replaced standard evolutionary accounts, presumably in much the same way that "[t]he historical notion of Darwin's 'ancient progenitor' replaces Owen's idealist 'archetype'" (113).

While Kendig highlights some underappreciated features of phenotype change over time, her privileging of multidimensional homology thinking over cladistic

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[1] The quote that supports this point—Donoghue's claim that "partial homology is incompatible with standard evolutionary views" (1992, 172)—seems to be taken out of context. He is referring to standard views of homology, not evolutionary theory in general.

approaches is not sufficiently motivated, and she fails to consider alternative traditions that may be more congenial to her view. For example, Wake (1999) readily admits the existence of partial homology, and Brian Hall (2003) proposes a continuum between homology and homoplasy defined by the differential conservation of developmental resources and phenotypic traits (see section 4 below for more on his view).

3. Must Homology and Homoplasy Be Kept Apart?

Adrian Currie (2014) also uses scientific practice to motivate a restriction on homology concepts, but with opposite results to Kendig. Whereas she rejects the cladists' sharp separation of homology from homoplasy (roughly, biological similarity without whatever kind of correspondence is considered necessary for homology), Currie embraces this distinction as necessary to make sense of practice. His methodology also appears more promising. While Kendig is selective in her assessment of contemporary homologizing, Currie claims to have identified four epistemic roles that are ubiquitous in biology and for which a sharp distinction between homology and homoplasy is essential.

Across these diverse situations, argues Currie, biologists use the distinction between homology and homoplasy when distinguishing signal from noise, or "splitting evidential wheat from chaff" (704). Which one is which may depend on the situation, but the need for a strict distinction remains. For Currie, the distinction must have a genealogical foundation[2]; "two similar traits [in different lineages] are homologous just

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[2] Currie uses the term "taxic" interchangeably with "genealogical" and "phylogenetic." See section 6 for an argument that this is misleading.

in case they are present in the most recent common ancestor; homoplastic just in case they are *not* present in the common ancestor.” By contrast, a developmental approach to homology would identify traits as homologous “just in case they are the products of the same developmental process” (702).[3] Currie allows that there may be some traits which are neither homologous nor homoplastic, but there must not be any overlap—no trait can be both homologous and homoplastic.

In this section, I will briefly review these roles and the particular biological case that illustrates them. I accept that Currie has identified an epistemically important distinction, but dispute that it concerns homology and homoplasy. To reinforce the point, the following section looks more closely at how the relationship between development and genealogy is construed by Brian Hall, the main foil for Currie’s account, and Günter Wagner, champion of the most worked-out developmental theory of homology.

First, Currie claims that the distinction is essential for determining phylogenetic relations in the first place. Similarity of morphological or molecular features is essential to infer these relationships but biologists have long recognized that not all similarities are equally informative. For example, distinct but related lineages may retain enough common developmental and genetic heritage that they respond to selection in similar ways. Systematists disagree as to whether these misleading characters (identified as homoplastic) can sometimes be recognized in advance of cladistic analysis (and thus excluded from consideration) or whether they can only be revealed by the topology of a

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[3] Proponents of such accounts might object to this definition, which overstates the developmental similarity required for homology.

completed tree. Currie mentions both possibilities without clearly distinguishing them. He first identifies “diagnoses of homology and homoplasy” as the *result* of “statistical analysis of patterns of similarity” (710) and later describes them as different kinds of *input* — “homologies count as data-points for common ancestry, while homoplasy is noise” (711). Both are obviously phylogenetic applications of the distinction between homology and homoplasy, and in either case Currie could argue that allowing overlap between these categories would confound their epistemic roles.

Second, according to Currie, biologists need the distinction when they use analogical reasoning to infer the traits of inaccessible organisms from those that are better characterized. Extinction is one cause of inaccessibility; others include extreme habitats, practical constraints, and ethical concerns. In all these cases, some features can still be known but others remain beyond reach. Unobserved traits are often attributed to the (inaccessible) *target lineage* by appealing to a (better known) *model lineage* that exhibits the trait of interest alongside other some other characteristic(s) known to be shared by both lineages. What justifies the projection from the coupling of traits in one lineage to their coupling in another lineage? According to Currie, homologous and homoplastic relationships answer this question differently and thus must be kept apart.

If the trait were present and coupled in the common ancestor of the model and target, then the inference is justified by an appeal to the stability of inheritance. If the trait was not present in the common ancestor, we have to appeal to a different kind of regularity, one grounded in the similarity of selective regimes. In both cases, there are additional factors to consider. We may be cautious about inferring the continuous inheritance of traits that are especially labile or between lineages that are especially distant. Likewise, strong selection in related lineages may increase the probability of parallel evolution. Not all cases of homology and homoplasy can ground the inference, but both provide important evidence for such an inference. The evidence, however, is of fundamentally different types, and so we should keep these two concepts distinct.

A third reason to maintain the distinction is that it aids in testing adaptive hypotheses. The independent appearance of some trait in two lineages — an example of parallel evolution, which Currie classifies as homoplasy — can furnish evidence of adaptive function, particular when the environments are similar. But if the trait was not independently acquired, any adaptive hypothesis must first consider the ancestral environment and the original function of the trait.

Finally, Currie argues that evolutionary developmental biology, with its interest in evolutionary novelties, needs at least a derivative form of the delineated genealogical account. Under one definition, a novel trait is just one that has no homologue in any ancestral taxon. This is certainly a phylogenetic definition, but it does not require any particular contrast with homoplasy. The concept of novelty is itself rather vexed (Brigandt 2012) so this example provides perhaps the weakest support for Currie’s claim.

Currie illustrates the example by referring to the dispute over a remarkable hypothesis that the birdlike dinosaur *Sinornithosaurus* was venomous. Gong et al. (2010, 2011) advance this hypothesis on the basis of particular morphological traits and analogies with extant venomous taxa. Gianechini et al. (2011) dispute their interpretation of both the anatomical and the phylogenetic evidence. According to Currie, understanding this exchange requires “requires contrasting homoplasy and homology along taxic lines—to make sense of the dispute we need the distinction” (707). Without going into details of the dispute, I will present four questions that exemplify Currie’s four epistemic roles for the distinction between homology and homoplasy.

1) What is the relationship between the theropod clade to which *Sinornithosaurus* belongs and other major dinosaur clades? 2) Was *Sinornithosaurus* venomous? 3) Are *Sinornithosaurus* fangs an adaptation to deliver venom to feathered prey or were they selected for some other function (or not directly selected at all)? 4) At what point did venom first evolve in the lineage leading to *Sinornithosaurus* — in other words, when and how did the evolutionary novelty arise?

In order to answer all four questions, biologists must know something about how venom and its anatomical correlates are distributed on the phylogenetic tree leading to *Sinornithosaurus.* 1) In reconstructing *Sinornithosaurus* ancestry, some morphological traits will be better indicators than others. Likewise, a solid tree will constrain our hypotheses about the evolution of traits like venom. 2) The analogy between the coupling of morphological traits in venomous lizards and snakes and their alleged coupling in *Sinornithosaurus* will be justified differently depending on whether or not the traits were present in a common ancestor. 3) If venom was present in the common ancestor of *Sinornithosaurus* and extant venomous taxa, we need to consider its adaptation to the ancestral environment. If it is a parallel evolution, we can more confidently analogize the ecological functions of venom. 4) Identifying the evolutionary novelty depends on which precursor traits the ancestor possessed.

Currie thus clearly illustrates that different phylogenetic patterns allow different kinds of inference, but it is not necessary to cash out these distinctions in terms of the contrast between homology and homoplasy. To reinforce this point, I turn to proponents of a developmental account.

4. Developmental Perspectives on Phylogeny

Brian Hall, one of the founding figures of evolutionary developmental biology, has insisted that homology and homoplasy should be understood as elements of a continuum. Does this view stand in tension with Currie's emphasis on phylogenetic clarification of ancestral relations? I argue that it does not. While Hall does indeed give developmental mechanisms a role in assessing homology, he remains adamant that they are insufficient for this purpose. In fact, questions about their significance for homology "are best posed—perhaps can only be posed—within the context of a sound phylogenetic analysis. Questions of mechanisms are second to phylogeny when assessing homology or homoplasy" (2007b, 476). The secondary place of development mechanisms reflects their complicated relationship with phenotypic evolution. Development can diverge even as a phenotypic trait is continuously inherited, and the phenotypic output of a conserved developmental mechanism can change over time.

"The history of life has been descent with modification" (Hall 2003, 427). For Hall, this unitary process underwrites a continuum between homology and a collection of relationships traditionally grouped under the heading of homoplasy.

> Whether we are examining homoplasy (convergence), parallelism, reversals,

> rudiments, vestiges, atavisms or homology, we are dealing with common descent with varying degrees of modification of features as a result of natural selection tinkering with the genetic and developmental bases responsible for producing those features (ibid).

This passage reflects Hall's argument that only convergence—the evolution of similar traits in independent lineages—should be understood as truly homoplastic. However, he recognizes that independence cannot be precisely defined since *all* taxa share an evolutionary history that in many cases leads to conservation of genetic and developmental processes across great phylogenetic distances (2007a, 437–8).

The main difference between Hall and Currie, then, is simply that Hall recognizes parallel evolution as a type of homology because it depends on shared developmental resources. He still distinguishes this category from traditional homology, in which the trait itself is conserved along the ancestral lineage. Why does the distinction matter, in his view? Without emphasizing the affinity between homology and the other phenomena, he worries, we will be inclined to "search for different developmental and genetical mechanisms" and thus neglect the implications of shared evolutionary history. (2007b, 442). Rather than neglecting the importance of common ancestry, Hall places it at the base of his developmental account.

Hall's respect for genealogical approaches to homology led the systematist Joel Cracraft (2005) to count him as a "phylogenist" in his critique of evo-devo approaches to homology. The case of Günter Wagner, the originator and current champion of a developmental approach, therefore provides an instructive contrast. Wagner's original articulation of the “biological homology concept” (BHC) made no mention of phylogeny and emphasized only shared developmental constraints (MacLeod 2011). But Wagner (1999) explicitly recognizes the importance of phylogeny in constraining mechanistic investigation. The initial steps in his early proposal for testing the BHC depend on phylogenetic analysis — putative homologues should be identified within two different but related taxonomic groups, and their distribution mapped onto a phylogenetic tree, ideally one constructed independently with molecular data. His recent (2014) book-length development of this approach is replete with phylogenetic trees and full of references to phylogenetic distributions that constraint the set of mechanistic hypothesis for the individuation and evolution of characters.

This sketch of Hall and Wagner gives us no reason to doubt that they would accept each of Currie’s epistemic functions. They could maintain their differing views of homology by arguing that these examples, while sometimes framed in terms of homology, do not exhaust the meaning of the term.

5. Compatibilist Solutions

Given the failure of these two attempts to mount a practice-based restriction on homology, we might consider other approaches that emphasize the compatibility of different concepts.

Griffiths (2007) rejects the assumption “that principles of classification that can unify diverse particulars into broad categories…must be derived from our best explanatory theories of the domain to be classified” (655). Roughly, competing “definitions” of homology are best understood as complementary explanations for a broad set of homology *phenomena* that are recognizable apart from those definitions. Operational criteria for recognizing homology, particularly the relative position of the parts and the existence of intermediates between them, have remained relatively constant since the nineteenth century. Both the genealogical and developmental approaches offer causal explanations of the phenomena of homology, the former in terms of common descent and the latter in terms of shared mechanisms.

Brigandt (2009) also emphasizes the compatibility of the two approaches, which “simply address different aspects and temporal stages of one complex phenomenon” (89). The unity of this complex phenomenon is provided by the HPC (homeostatic property cluster) view of natural kinds. Assertion of a homology relation between body parts in different lineages picks them out as members of a kind united by the homeostatic mechanisms that determine their individuality as units of phenotypic evolution. These mechanisms are in turn genealogically related in patterns that are traced by the methods of phylogenetic reconstruction. The developmental approach to homology emphasizes the individuating mechanisms, and the genealogical approach emphasizes their evolutionary relationships.

This view depends on a particular theoretical concept of biological characters as modular, quasi-independent units individuated by developmental genetic control mechanisms. There is good evidence (Wagner 2014) that such mechanisms exist for many body parts, and that they can change their component parts while maintaining their individuating potential. In such cases the two accounts may indeed be related by the natural kind view. But what happens when the morphological characters proposed as homologous are not individuated in this way? Or when the lineages are extinct and the mechanisms are inaccessible? In these situations the unity seems likely to break down.

I am convinced by the argument of MacLeod (2011, 2013) that the natural kind picture glosses over importance methodological differences between the two approaches. Those characters which are most informative for reconstructing phylogenies will not be the most informative for understanding the developmental individuation of parts. A systematist, for example, will seek synapomorphic characters that uniquely diagnose all the descendants of a common ancestor. A developmental biologist, on the other hand, may be more interested in underlying mechanisms that are shared across groups, and thus homoplastic by cladistic reckoning. The account of Griffiths (2007) fares better on this analysis since it allows biologists to have different explanatory aims, but it does not account for the fact that proponents of different theoretical accounts see themselves as *identifying* homology, not merely explaining it. The two phases cannot be separated as neatly as Griffiths supposes.

6. Which Conflicts Should We Capture?

So far I have argued that a set of philosophical responses to conflicts over the meaning of homology—differing in their approaches but united in their concern to represent practice—fail to capture practice in important ways. The more restrictive accounts either simply ignore important epistemic functions (Kendig) or incorrectly assume that other important functions constrain empirical and theoretical research more than is actually the case (Currie). The more compatibilist accounts do a better job of accounting for the range of approaches to homology, but they still gloss over important methodological differences both within and between the two main branches.

Given the immense diversity of scientific practices, philosophical accounts must face the challenge of determining how to individuate those practices. With sufficiently careful scrutiny, we might find nearly as many approaches to homology as there are individual scientists. Which ones should we try to capture? Recent philosophical work uniformly identifies a broad dichotomy between approaches focused on history and approaches focused on development. Is this the best way to frame the problem? Like earlier dichotomies—reviewed by Roth (1994, 303)—this one maps roughly onto the disciplinary divisions between systematists and biologists of other disciplinary persuasions. But a closer examination of those earlier dichotomies shows some uncertainty in how to count the categories. The original version of taxic homology, for example, deliberately broke with the requirement that homologous parts be traceable through "transformation series" to parts in common ancestors (Patterson 1982, Donoghue 1992).

I suggest we avoid such difficulties entirely by focusing our attention elsewhere, on the research practices that undergird the different theoretical accounts of homology (however we count them). My analysis of Currie (2014) shows that biologists with radically different theoretical accounts of homology might nevertheless agree that phylogenetic patterns constrain inferences about ancestral traits and adaptations in particular ways. They could likewise agree that not all traits are equally informative for constructing evolutionary trees in the first place. Insofar as they disagree about what makes those traits novel, those disagreements do not turn their differing views about homology.

I suggest that we are more likely to find philosophically interesting disagreements among biologists who *share* broad theoretical approaches to homology. The paleontologists arguing over *Sinornithosaurus* venom do not reveal their hand on this topic (in fact they never explicitly discuss either homology or homoplasy) but given their subject matter, it seems a safe assumption that they will not consider developmental genetic individuation of body parts to be necessary for identifying homology. On the other hand, they disagree mightily about the interpretation of many empirical details. Are the teeth of *Sinornithosaurus* really as elongated as they appear, or just displaced from their sockets? Is one particular cavity in its skull, allegedly specialized to hold a venom gland, really anatomically separate from a neighboring cavity? Does the recent discovery of venom in new lizard and mammal taxa raise the plausibility of finding venom in ancestral dinosaurs?

To take another example from across the disciplinary aisle, evolutionary developmental biologists are currently engaged in a lively debate as to how the five digits of ancestral tetrapods gave rise to the three digits found in bird wings. The idea that developmental mechanisms delineate evolutionary units is implicit in this debate, so its participants are united in taking a broadly developmental approach to homology. The experimental evidence has ruled out certain simple scenarios in which the pattern of developmental control remained constant even as some digits were lost. However, it has so far been insufficient to determine which of several plausible complex transformations have actually occurred (Young et al. 2011, Larsson and Wagner 2012). Some have therefore doubted whether digits are really developmentally individuated in the first place (Wagner 2014).

For Wagner, this kind of empirical ferment is a sign of the success of his view of homology. "The developmental account makes stronger assumptions about biological reality" than other approaches which do not postulate specific mechanisms for the maintenance of part individuality "and, thus, leads to testable predictions" (2014, 75). In general, he takes a pragmatic notion of homology concepts that prioritizes empirical fruitfulness over precise definitions. "*Any concept is only as good as the research program it inspires*" (245).

This sentiment is reflected by biologists from other perspectives. Though Donoghue (1992) worried that early versions of Wagner's program were overly narrow, he pointed out that "[a]chieving consistency with every version of homology may yield a definition that is of little use to anyone (179). De Pinna (1991, 368) argues that "an evaluation of definitions of homology acquires sense only against a specific frame of reference" defined by "a more encompassing method or theory," so that definitional disputes only have meaning against the backdrop of certain common assumptions. David Wake puts the point most strongly, in a paper arguing that the homology debate is a "distraction" from real research questions.

> I want to get on with it and to leave behind debates that started when biologists really did not have sufficient biological knowledge to appreciate the causes of biological similarity and when they did not yet understand that Darwin was right

in his view that there is one genealogy for all of life (1999, 45).

7. Conclusions

What would it mean for philosophers to follow Wake's lead and get on with it—to move past attempts to adjudicate or supersede debates about the meaning of homology? Various compatibilist approaches have taken a step towards this aim by characterizing the ways in which different theoretical accounts of homology are useful for different purposes (e.g. Brigandt 2003, 2012). We still need much more careful attention to the types of arguments that homology concepts, in their various forms, make possible, and we need to move away from the assumption that conflict between approaches is something to be explained away. This conflict is a natural consequence of the complexity of the phenomena under study and mirrors the disciplinary specialization necessary for propagating empirically successful techniques.

I am not saying, however, that we should simply defer to scientists when giving account of homology. Though metaphysical or definitional unification has brought only limited success, philosophical work has only scratched the possibilities for identifying some kind of epistemic commonality among the various homology practices. Several authors (Griffiths 2007; MacLeod 2011, 2013) have emphasized the role that homology plays in creating meaningful categories that can be subsequently used for inductive generalizations (for example from mouse to human physiology). This is one important function, but we should also consider the ways in which homology facilitates contrastive reasoning—the identification of meaningful differences between comparable individuals (organisms, body parts, gene networks, etc.)—and the underlying causes of those differences. This would be a worthy application of the growing enthusiasm for practice-centered philosophy of science.

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