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On homology

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Abstract

Homology in cladistics is reviewed. The definition of important terms is explicated in historical context. Homology is not synonymous with synapomorphy: it includes symplesiomorphy, and Hennig clearly included both plesiomorphy and synapomorphy as types of homology. Homoplasy is error, in coding, and is analogous to residual error in simple regression. If parallelism and convergence are to be distinguished, homoplasy would be evidence of the former and analogy evidence of the latter. We discuss whether there is a difference between molecular homology and morphological homology, character state homology, nested homology (additive characters), and serial homology. We conclude by proposing a global definition of homology.

> "As I've tried to teach you, undisciplined thinking can make even the simplest task impossible."

(Ultra Magnus in *Transformers*, "Five Faces of Darkness", 1986)

Homology has been a topic of great interest to systematists for the past 150 years. Most modern morphological systematists view homology as the overriding paradigm of all comparative work, while at the same time the concept is largely ignored by molecular systematists. Although various definitions have been proposed, and the philosophical and methodological basis of homology has been discussed in numerous papers, the concept of homology remains controversial. In part this is because the meaning of homology has changed over the years, from early usages that were largely operational without reference to causality, to modern evolutionary usage that is tied directly to phylogeny.

We review the concept of homology in cladistics, beginning with a clarification of the deeper history and definition of important terms. Consequently, we discuss how plesiomorphy is homology, how homoplasy is error, whether there is a difference between molecular homology and morphological homology, character state homology, nested homology, and touch on how homology is dealt with in the case of serial homology. Finally, we propose an explicit global definition of homology that provides a logically consistent framework for parsimony analysis.

On history and definition

Original, pre-evolutionary concepts of homology were positional or topographical similarity, for example, "the same organ" (Owen, 1843), and later came to be based largely on consideration of development. Even after embracing evolution as the causal factor of similarities among different taxa (e.g., the limbs of vertebrates), Darwin (1859) explicitly referenced Owen in the definition of homology in the glossary from *Origin of Species*:

> "That relation between parts which results from their development from corresponding embryonic parts, either in different animals, as in the case of the arm of man, the fore-leg of a quadruped, and the wing of a bird; or in the same individual, as in the case of the fore and hind legs in quadrupeds, and the segments or rings and their appendages of which the body of a worm, a centipede, etc., is composed. The latter is called serial homology. The parts which stand in such a relation to each

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> other are said to be homologous, and one such part or organ is called the homologue of the other. In different plants the parts of the flower are homologous, and in general these parts are regarded as homologous with leaves.'' [6th edn]

Although Darwin's definition of homology is clearly not connected to evolution, the ontogenetic and positional or topographical concept of homology is the operational context in which all modern homology assessment is undertaken. It is difficult to imagine how homology might be assessed without such a framework (although consider the notion of ''percent homology'' in molecular systematics).

Lankester (1870a,b) explicitly referenced Darwin and incorporated evolution directly into his definitions of homology. Lankester's concept of homology is not identical to modern concepts, rather it is a broader concept that distinguishes similarity due to ancestry (homogeny: ''depending simply on the inheritance of a common part'') from similarity due to common function and causality (homoplasy: ''depending on a common action of evoking causes or moulding environment on such homogeneous parts, or on parts which for other reasons offer a likeness of material to begin with'').

Lankester (and others) also differentiated homology as similarity in both form and function from analogy, which is similarity only in function:

> ''It may be said that the term 'analogy,' already in use, is sufficient to indicate what is here termed 'homoplasy;' but analogy has had a wider signification given to it, in which it is found very useful to employ it, and it could not be used with any accuracy in place of homoplasy. *Any* two organs having the same function are analogous, whether closely resembling each other in their structure and relation to other parts or not; and it is well to retain the word in that wide sense. Homoplasy includes all cases of close resemblance of form which are not traceable to homogeny, all *details* of agreement not homogenous, in structures which are broadly homogenous, as well as in structures having no genetic affinity.'' (Lankester, 1870a, pp. 40–41).

Shortly after Lankester's (1870a) original definitions, matters were obscured by Mivart's (1870) proliferation of terms, and Lankester's terms subsequently were largely ignored. But Lankester's distinctions between homogeny and homoplasy were eventually transformed, respectively, into the modern phylogenetic concepts of homology, in which common ancestry is a necessary condition for two things to be homologous; and homoplasy, that is, non-homology.

Hennigian homology

Haas and Simpson (1946) clarified the terms homology and homoplasy, and fixed modern usage. Although Hennig (1966) clearly adopted an identical concept of homology, the word homoplasy does not occur in *Phylogenetic Systematics*. It is important to re-emphasize that under Lankester's definitions, homoplasy is a kind of homology (functional similarity), while under a modern definition, homoplasy is similarity that is not homology—that is, not due to common ancestry. Lankester's ''homogeny'' (a term no longer used) is equivalent to Hennig's concept of homology. Although to some extent Lankester's original definitions provide a clearer way to view homology, homoplasy = non-homology has become the standard definition used in systematics. In either case, as discussed below, ontogenetic/positional similarity (Owen's homology) is the basis of developing character definitions, which are then tested by character corroboration. What passes this test is Hennig's (1966) homology; what fails is homoplasy.

Post-Hennigian concepts

Hennig's concept of homology, consistent with Lankester's homogeny, seems to have persisted as the mainstream view among systematists for the past 50 years. However, controversies also persist and different interpretations of the word have appeared in print at various times. Some authors have argued that homology should be restricted to the ontogenetic/positional definition of Owen (e.g., Wagner, 1994; although he apparently did not read Owen), while others have modified the definition well beyond concepts proposed by Owen, Lankester or Hennig. We see no a priori problem with extending or modifying definitions to improve accuracy of communication and provide conceptual clarity—indeed, this is exactly what Hennig accomplished when he returned to the original definition of monophyly as meaning only species derived from a common ancestor and excluding all others (Farris, 1990), after a century of obfuscation and confusion. The issue is not whether terms can be modified, but whether the proposed modifications clarify or obfuscate concepts.

The most prominent alternative definition of homology is as synapomorphy, as exemplified especially by Patterson (1982). Patterson cited numerous authors in characterizing the equation of synapomorphy and homology as ''widespread,'' but his explication was widely heralded in the cladistic community as somehow having intrinsic value (e.g., de Pinna, 1991, p. 369; ''Perhaps the most relevant contribution to the homology problem in the last few decades''). Patterson argued that plesiomorphies were not homologies, although they could be considered synapomorphies at a higher level, and therefore homologies at a higher level—that is, that symplesiomorphy should be considered a subset of synapomorphy. Patterson (1982, p. 29) cited Hennig as sharing this position, in stating ''the equivalence of homology and Hennig's concept of synapomorphy is implicit in Hennig's work (e.g., 1966, p. 95),'' but this

interpretation is at best wishful thinking, or perhaps careless reading. Hennig (1966, p. 95) stated:

> "This discrepancy between the concepts 'organ' and 'character' explains the tortured impression produced by many phylogenetic discussions that try to make do with concepts such as 'special homology,' 'limited homology,' and so on (instead of 'synapomorphy')."

But the "special similarity" referred to there was only part of homology, and reading, say, the page before (Hennig, 1966, p. 94), we find:

> "Finally, the concepts of symplesiomorphy and synapomorphy go somewhat beyond the range of what are ordinarily called 'homologous characters.'"

While reading further (Hennig, 1966, p. 120), we see:

> "In deciding whether *different* characters of several kinds are to be regarded as homologous, and therefore generally comparable with one another for the purposes of phylogenetic systematics, it is a question of determining whether they can be regarded as transformation conditions of a character that was present in a different condition in a stem species, which did not have to be the stem species of only the compared species."

Hennig considered both plesiomorphy and apomorphy to be parts of transformation series, ipso facto both plesiomorphy and synapomorphy are kinds of homology according to Hennig.

Plesiomorphy is homology

In order to appreciate fully why plesiomorphy is homology, we must explore further the relationship among homology, parsimony, and synapomorphy. Farris (1983, and many of his other papers) championed the application of parsimony (only hinted at by Hennig) as the basis for cladistic analysis. In Farris' approach, *character polarity is unimportant prior to a cladistic analysis*, and Farris showed very early that trees have the same length (number of steps) no matter where the root is placed (see review by Nixon and Carpenter, 1993). If character polarity is unnecessary during tree search, then how does parsimony accomplish Hennig's goal of grouping by synapomorphy? Clearly, there is no difference in a cladistic analysis between a hypothesis of homology ("primary homology" of de Pinna, 1991) scored as 0 or scored as 1. Either state might turn out to be a plesiomorphy or synapomorphy on a particular tree, and as implemented in all modern cladistic analysis, it is unnecessary to know which state will turn out to group taxa apomorphically and which will not (or, depending on the root, they might both be synapomorphies of collateral groups).

The resolution of this issue occurs by examining the phylogenetic definition of homology (that of Hennig; = homogeny of Lankester and "secondary homology" of de Pinna, 1991). If homology is similarity due to the occurrence of the same condition in the most recent common ancestor, then symplesiomorphic features satisfy this requirement just as do synapomorphic features. Illustration of this requires only simple examples (Figs 1 and 2) of character optimization on a tree. Given the same topology without homoplasy but rooted at different points (Fig. 1), if hypothetical ancestral states are assigned to the nodes by the method of Farris (1970) or Fitch (1971) optimization (which are the same for binary characters), it is seen that there are two groups of taxa, one group with homologous state 0 (taxon0–taxon4) and the other group with homologous state 1 (taxon5–taxon9). It can be seen in Fig. 1 that, for any selected rooting of the same topology, exactly the same groups are homologous for this character under Hennig's definition of common ancestry. Any two taxa bearing state 0, for example taxon0 and taxon4, always have an uncontroverted descent from a common ancestor bearing the same state (mapped as grey in this figure). That this is true for both the plesiomorphic and the apomorphic state is not surprising. Given that parsimony analysis results in the tree that best eliminates or reduces

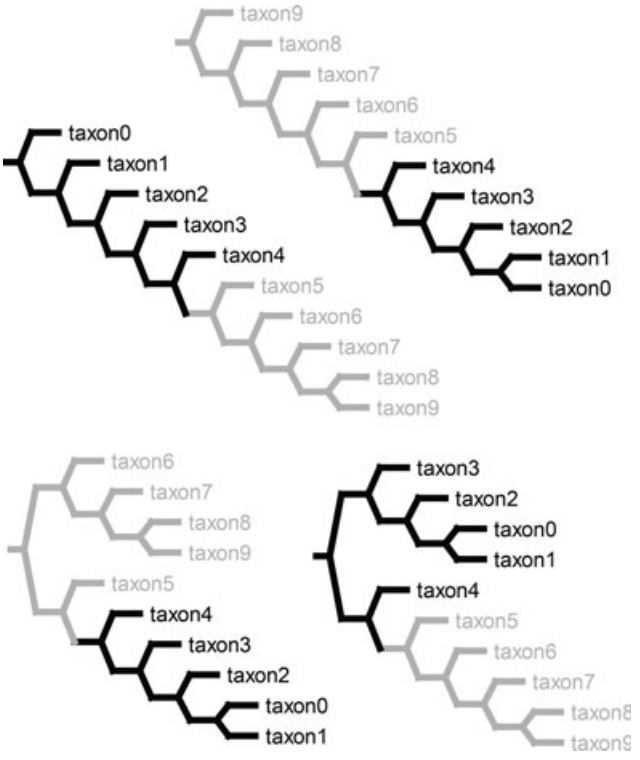

Fig. 1. Simple example of character optimization on a tree without homoplasy, independent of the placement of the root. All trees are of the same topology. Black = state 0, grey = state 1. Note that for any two taxa scored for state 0, the common ancestor of those two taxa is always also state 0, independent of the root and independent of whether the state is "plesiomorphic" or "apomorphic" for the given root.

error (ad hoc hypotheses explaining non-homology) in our original assessment (hypothesis) of homology, then both character states have passed the test of homology when there are no extra steps on the tree, and state 0 is homologous (under Hennig's definition) in all taxa that bear it, as is state 1. Which states are considered synapomorphies for a particular clade is dependent solely on the placement of the root, such that the state 0 is always homologous because there is no homoplasy, but is either a plesiomorphy or synapomorphy depending on the root. In all cases, synapomorphies must first pass the test of homology imposed by the particular selected topology under consideration.

The situation for a tree in which there is homoplasy for the character under consideration is equally enlightening, and fundamentally no different. A tree with the same character distribution but a different topology that implies two independent origins of state 1 is shown in Fig. 2. This topology implies one homologous group for state 0 (taxon0–taxon4) and two independent origins

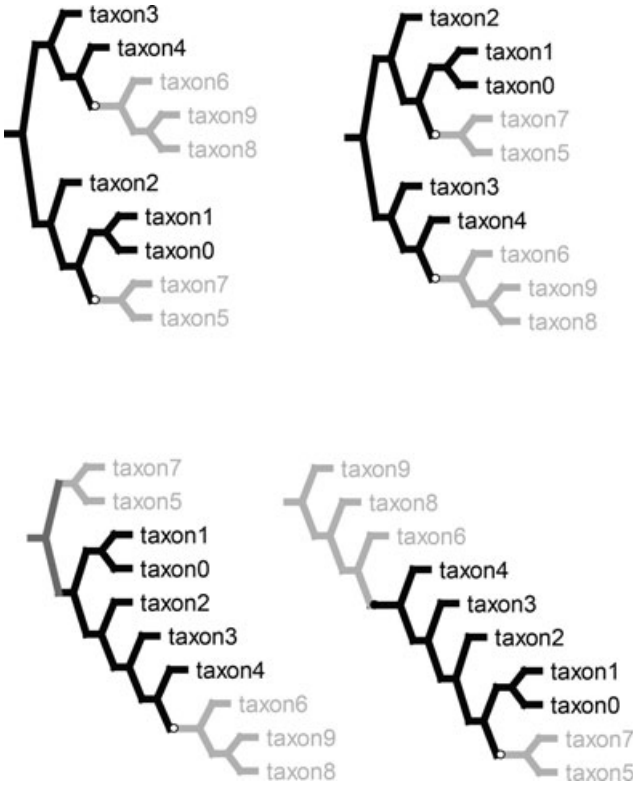

Fig. 2. Simple example of character optimization on a tree *with homoplasy*, independent of the placement of the root. All trees are of the same topology. Black = state 0, grey = state 1. Note that for any two taxa that are derived from a single origin of state 1 (grey), the common ancestor of those two taxa is always also state 1, independent of the root and independent of whether the state is "plesiomorphic" or "apomorphic" for the given root. Note that any two taxa that are not homologous for state 1 are not connected by ancestors that also share state 1.

for state 1 (one group with taxon5 and taxon7, and another group with taxon6, taxon8 and taxon9). Although state 1 is homologous (according to Hennig's definition) in taxon5 and taxon7, it is not homologous when one considers taxon5 and any member of the other group (e.g., taxon8). Note that once again the position of the root, and the designation of state 0 or 1 of a binary character as plesiomorphic or apomorphic, is irrelevant to the simple observation that homology—shared state due to common ancestry—is the same for any two taxa for the same topology, no matter where the root is placed. Thus, for example, in Fig. 2, state 1 (grey) is always homologous (i.e. shares a common ancestor with the same state) in taxon6 and taxon8 under any rooting, whether the root is placed such that state 1 is plesiomorphic or apomorphic. Under the criterion of parsimony, the total number of steps is always the same given the same topology, independent of the root; the number of extra steps is the same; and all homology statements are the same. In certain situations, alternative optimizations may differ in which taxa will have homologous states, but these situations still follow the same rules—for a given optimization on the same unrooted topology, the same homology statements are implied no matter where the root is placed.

This holistic view of parsimony and homology also resolves misunderstandings about parsimony. Parsimony does not involve favouring synapomorphy over plesiomorphy per se; the criterion seeks to *minimize error in homology assessment*, and reduce the necessity for ad hoc hypotheses explaining this error. Which homologies on a tree are considered to be synapomorphies is entirely dependent on the location of the root, but which shared character states of any two terminals are considered homologous on a given tree/optimization is the same *no matter where the root is placed* (and different trees imply different homologies). This recalls Farris's (1983) insightful comparison of cladistic parsimony and statistical regression: both methods seek to reduce residual error (homoplasy in the case of cladistics). One method produces the line that best explains the data, and represents an estimate of the measurements that would have been made if there had been no error (or residual variation); the other represents the best estimate of the tree that would have been found if there were no homoplasy and all characters mapped perfectly, that is, all identically scored states are homologous. We are left with the absolute necessity of rejecting the proposal that homology and synapomorphy are equivalent terms, as such equivalence would be inconsistent with both our definition of phylogenetic homology and our understanding of parsimony. A synapomorphy, instead, is one kind of homology: homology that is diagnostic of a particular clade and is found in the common ancestor of that clade (and thus requires designation of a root). We might note here that

the term synapomorphy is somewhat ambiguous when character states are considered that originate in the common ancestor of a clade but are controverted somewhere within the clade (i.e. there is subsequent modification of the character). As this is not the focus of this discussion, and is merely terminological, we will not consider it further here.

More on homoplasy as error

As discussed above, an important distinction in Lankester (1870a,b) is the difference between homoplasy and analogy, which were not considered by him to be synonyms. Analogy is similarity in function, without necessarily similarity of form (development). In a cladistic context, homoplasies are *only* those similarities that were first hypothesized to be homologous, but failed to pass the test of character congruence (i.e. parsimony analysis).

The idea that homoplasy is a process in nature, combining convergence and parallelism into a single term, persists in the literature over the past 40 years (e.g., Donoghue and Sanderson, 1994). We consider the interpretation of *homoplasy as process* to be flawed and logically inconsistent both in terms of definition (''similarity that is not due to homology''), and in the context of a generalized scientific method of hypothesis testing. Whether or not a feature in a particular taxon or clade is considered to be homoplasy is determined by its inclusion in an analysis—in other words, whether it is first hypothesized to be a homology (''homologized'' following Darwin's terminology). The simplest and best known examples of convergence (i.e. functional, but not genetic, similarity) will suffice to illustrate this point, such as the oft-invoked wing character of insects and vertebrates. In this case, if we (naively) hypothesize insect wings and bird wings to be homologous, any reasonable cladogram based on additional characters will indicate that they are not, and are therefore homoplastic. However, if we (more intelligently) do not hypothesize bird and insect wings to be homologous in the first place, they are never considered to be homoplastic, and instead are analogous (this recalls the definition of analogy promoted by Lankester). Another very simple and obvious example can be seen in the comparison of the bill of the (mammalian) platypus and the bill of birds. If we score the platypus bill and bird bill as the same state of a single character, then the occurrence of a bill in the platypus is interpreted as homoplasy, and will have two origins on any reasonable phylogeny. If (for whatever reason) we do not score these as the same character (perhaps two different characters, presence and absence of mammalian bill and presence and absence of bird bill), then they are not homoplasy, but analogous features, and will not (cannot) add any extra (homoplastic) steps to the tree. In both these cases, *homoplasy is merely a conclusion that we were in error when we hypothesized two conditions to be homologous*. Homoplasy can be viewed only in the context of a particular cladogram, and is interpreted as error in our original hypotheses of homology (''primary homology'' of de Pinna, 1991). Without a particular cladogram, homoplasy does not exist, only hypotheses of homology that may fit one topology and not another. As such, homoplasy is not, and cannot be, a process in nature, any more than homology is a process (which seems to be generally agreed). This is not to deny the fact that some taxonomic groups, character complexes, or particular genes have ''higher levels of homoplasy'' than others. In such groups, we are more apt to score terminals as having the same state (hypothesize homology) not because homoplasy is higher—the reverse is true, homoplasy is higher because of our inability to recognize similar conditions as non- homologous. An explanation of why we might make such an error of homology determination that results in homoplasy is found in the concepts of parallelism or convergence—which, by definition, *are* process interpretations of phylogenetic history. Homoplasy, as an error, can be ''corrected'' by rescoring the matrix such that the homoplastic states are considered to be states of separate characters, at which point they are analogies, not homoplasy. Such corrections, obviously, should have a basis in primary homology assessment, and not be based just on the results of the analysis, or one risks circularity. Parallelism or convergence may be an explanation for homoplasy or analogy, but in both cases we must first assert similarity (homology or merely functional similarity). It is easy to see that insect wings are only functionally similar to bird wings (they allow flight), and thus we never make the *mistake* of scoring them as homologous, since they do not pass any of the standard criteria for hypothesizing homology. If we do make such a mistake, avoidable or not, homoplasy is the result.

Thus, *homoplasy is error in our preliminary assignment of homology* while scoring the character matrix. The source of this error might be character definition (we are including analogous features) or error in assignment of terminals to particular states. Analogous features are those that may share similarity of function (e.g., insect and bird wings), but which have not been hypothesized to be homologous in an analysis. It is apparent that, although many situations are clear-cut, the line between homoplasy and analogy may be subjective in some instances, and depends entirely on our willingness to put forth a hypothesis that the two conditions are the same because of common ancestry—the only reason that we would score them as such in a matrix.

Understanding that homoplasy represents error in homology assessment that is minimized by parsimony

on a particular tree also provides insight into the recurrent controversy between so-called ''pattern cladists'' and the rest of the phylogenetics community. In reality, there are almost no cladists who can be categorized as pattern cladists, and as Farris (2011) has observed, the true pattern cladists may be those few remaining (e.g., Williams and Ebach, 2008) who adhere to the method termed ''three taxon analysis'' of Nelson and Platnick (1991), mixed with Patterson's (1988) ''pattern analysis.'' According to pattern cladist arguments, initial scoring of characters is based solely and entirely on ontogenetic/positional criteria (character definition, or ''topgraphical identity'' followed by ''character state identity'' of Brower and Schawaroch, 1996), and thus it is merely Owensian non-evolutionary observation [our words]. Given that parsimony minimizes homoplasy, and homoplasy is thus non-homology, it is very easily seen that there is a problem with this explanation for tree building. Brower and Schawaroch (1996, p. 268) explicitly denied that characters and character states are hypotheses of homology, stating that the ''parsimony criterion is employed to choose the network that maximizes the character state agreement among all the characters in the data matrix.'' What is one minimizing if there is no initial hypothesis of phylogenetic homology (common ancestry) when two terminals are scored the same for a particular character state? Brower and Schawaroch (1996, p. 268) subsequently contradicted themselves: ''Although these character states were *hypothetical homologies* at Step 2, the hypotheses are rejected due to lack of continuity on the most parsimonious network as established by the *weight of evidence* and are therefore deemed homoplastic'' [italics ours]. Here, they admitted that the character states are hypothetical homologies to be tested. However, they have not defined how the ''weight of evidence'' can be used to reject hypotheses of homology if the evidence (similarity) is not actually related to homology. Later, they stated that ''homology cannot be identified prior to cladistic analysis'' (with which we agree; this does not mean we cannot *hypothesize* homology based on similarity). Because Brower and Schawaroch conflated synapomorphy and homology (following Patterson, 1982 and de Pinna, 1991), they also asserted that homology can then be identified only by ''rooting the cladogram'' that was determined by the ''weight of evidence'' of features that are ''hypotheses of grouping'' (not homology). This confusing explanation of the cladistic method, divorcing hypotheses of homology from evidence, viewing characters/states as vacuous ''hypotheses of grouping'' without reference to homology, then using such grouping information to infer homology, is beyond comprehension for most evolutionary biologists, and has led to the view in some quarters that the few remaining pattern cladists are in league with creationists (Farris, 2011).

With a phylogenetic definition of homology, we are clearly minimizing error in stating that terminals share features due to common ancestry, and thus our interpretation of both homoplasy and the meaning of the resulting shortest tree as our best estimate of phylogeny is *abundantly* clear. The pattern cladist, however, has not explained what is being minimized if each character state is simply an observation of similarity (or ''hypotheses of grouping''). Surely, error in similarity itself is being minimized only if similarity has a phylogenetic component, that is, we are speaking of phylogenetic homology. We thus find the pattern cladist position to be untenable. Whether or not proponents are willing to admit it, the pattern cladist approach is identical to the phylogenetic approach, both operationally and in terms of results, and it is hard to escape the conclusion that even the pattern cladist would reject coding character states that are ontogenetically similar but clearly not inherited—such as plastic expression of indument or form due to environmental conditions—which may fulfil criteria of ontogeny but not phylogenetic relevance.

Molecular homoplasy as error

This discussion can easily be extended to molecular sequence data. An initial (or dynamic) alignment of a DNA sequence provides a series of characters that can then be scored for character states—in this case, A, C, G or T. By scoring two taxa as both having an A at a certain aligned position, we are hypothesizing that the two A's are homologous—the same because of common ancestry. If we are wrong, then this will be reflected as homoplasy on the most optimal tree. If we consider two A's occurring at different positions, we are *not* hypothesizing them as homologous; we are treating them as different characters because we have decided (through alignment, whether static or dynamic) that the A's are merely analogous—the same functionally (i.e. combining in the same genetic code) but not homologues. Thus two A's at different aligned positions are not homoplasy, and do not reflect error in homology. However, two A's at the same position, but not with a single origin in a common ancestor, reflect error in our assessment of homology. Some may protest that this is not error, because we had no possible way to differentiate homologous from non-homologous A's prior to an analysis. Such a position is unscientific—the existence of unavoidable error is a part of virtually all scientific endeavour. In the case of the molecular sequence, the error in a priori homology assessment—our inability to differentiate non-homologous from homologous bases—is equivalent to residual error in a standard multivariate statistical analysis. It would be equivalent to denying the existence of a true answer because we cannot attain it:

"As though it mattered for the definition of the concept 'truth' that we cannot recognize truth itself, and everywhere in science are limited to erecting hypotheses concerning truth." (Hennig, 1966, p. 94)

The importance of treating homoplasy as error, and not something that occurs as a process in nature, is apparent in modern justifications of parsimony as a method. Minimization of homoplasy in a parsimony analysis, and the selection of the shortest tree (the tree with least homoplasy), is consistent with the general scientific attempt to reduce error in estimation. This principle is used when calculating a regression line through a set of points as described above (Farris, 1983, p. 14). Note that, as in parsimony, error in statistics does not necessarily denote human/measurement error—if all samples are measured accurately, there is still residual "error" around a mean or regression for the sample. In parsimony, the analogy is a simple one: the method minimizes error in homology. If there were no error in homology, then all characters would map perfectly on the tree, and each would have a consistency index of 1.0. By reducing the error (homoplasy), parsimony "calculates" the tree that best explains the data. As Farris (1983) pointed out, the greater this error (homoplasy), the less confidence there is that the tree is optimal.

Character versus state homology

As already shown, the process of sorting specimens by character state using ontogenetic/positional similarity, or scoring a molecular sequence for the states A, C, G or T, is clearly the act of hypothesizing phylogenetic homology. Shared plesiomorphies are consistent with this phylogenetic definition because, in a character without homoplasy, the most recent common ancestor of any two taxa that share the same state (whether plesiomorphic or apomorphic) also shares that state. How do we apply the same concept and logic to an entire character that describes transformations of more than a single state? We have already pointed out that by not coding two states as belonging to the same transformation series (character) we are designating any similarity between those states to be analogy, not homology. Are we also hypothesizing homology among all three states when we score red, blue, and yellow flowers as alternative states of a character called flower colour? The conclusion is that homology among and between character states in the same character is an assertion that is not tested by cladistic analysis (or the acceptance of any phylogenetic tree, whether or not by cladistic means). In the example of flower colour, any tree topology we consider will require at least the minimum number of character transformations, implying that one of the states must be plesiomorphic to others in the transformation if we select an unambiguous optimization. Restating this in the context of ancestry, transformational homology requires only that all hypothesized ancestral states connecting any two terminals in a phylogeny will be among the original hypothesized states of the character transformations implied by the asserted definition of the character (whether or not the basal node is ambiguously optimized). This must be true with any traditional two-step cladistic analysis (ontogenetic/positional homology or alignment followed by cladistic analysis).

Alignment and homology

Commonly used methods for alignment of DNA sequence data use various approaches to calculating or heuristically searching for optimal alignments based on cost functions for various kinds of changes to sequences. Most commonly, "gaps" or indels are allowed at a greater cost than (implied) point mutation changes. If one considers the most optimal alignment without allowing indels, such an alignment could be considered an initial hypothesis of homology. By assigning cost and inserting gaps at a cost to improve the alignment and seeking the minimal cost alignment, these costs imply the cost of error in the initial alignment, just as we assign weights (cost) to characters in a cladistic analysis (most typically equal) that minimize the amount of error in our homology assessment. Thus the operation of defining characters/states by alignment (including shifts and gap insertion) with costs for mutation and gaps is analogous to minimizing homoplasy in a phylogenetic tree, by minimizing deviations from our original hypothesis of alignment (the best alignment without gaps). The alignment obtained is not tested phylogenetic homology, but instead is equivalent to the kind of homology statements we have after reviewing ontogenetic data and scoring taxa for character states in a morphological matrix—it is a set of character definitions (base positions) that provide homology statements about A's, C's, G's and T's in each column. These hypotheses must still be tested through cladistic analysis, and the resulting homologies indicate which bases should in fact still be interpreted as homologous. Although this is a straightforward interpretation of static alignment, issues arise as to whether the gap cost (and mutation cost) invoked in pairwise alignment is in fact sufficient, or whether this can be improved by evaluating alignment simultaneously with phylogenetic homology.

Methods that actually test phylogenetic homology of bases simultaneously with sequence alignment belong to a family of approaches called "dynamic homology" (Wheeler, 2001, 2005). These methods were developed for use with molecular sequence data, although recently efforts have been made to align morphological or

behavioural states dynamically as well (Robillard et al., 2006; Ramírez, 2007; Agolin and D'Haese, 2009; Japyassú and de A. Machado, 2010). Although with molecular sequences dynamic homology is a straightforward concept, it becomes unpredictable with data that cannot easily be conceived of as being constricted in sequence. An absurd example might be as follows. Given two separate characters of flower colour and leaf margin, should we realign these to reduce "homoplasy" such that we create two new characters as follows: character 1: flowers red, leaves entire vs. character 2: leaves serrate, flowers yellow? This would imply two separate transformations, each between a leaf character and a flower colour, with no basis in ontogenetic criteria of homology. In molecular sequences, there is an obvious phylogenetic constraint in the order of states within the sequence (note that there are no actual states defined until a particular tree and implied alignment is obtained). This order provides an initial constraint on homology assessment that is analogous to ontogenetic homology in morphological characters. In essence, the act of sequencing provides the initial homology assessment by linear ordering of the bases. Morphological characters, on the other hand, are constrained only by ontogenetic/positional criteria, so dynamic alignment is not an obvious choice for evaluating homology.

Additivity and homology (nested homology)

The above discussions focus on simple binary and nonadditive characters. Additive multistate characters are merely a special case of nonadditive characters when considering homology. While nonadditive multistate characters do not have hierarchical relations among the states, additive characters can be viewed as hierarchically nested homologies. Fortunately, homology assessment of nested states is identical to nonadditive states. The best way to decompose the problem of nested additive states is to decompose the additive character into a series of binary characters. Long ago, Farris et al. (1970) showed that such binary decomposition produces trees of identical length, with the same state distributions, as the multistate additive characters (even when tree-like and branched) that are represented. By such decomposition, individual homology statements are clarified. Each 0 and 1 in the binary additive coding represents a separate homology statement. Thus, if each binary homology statement is justifiable as a hypothesis of homology, scoring a character as additive is also justifiable, and the simple hypotheses that compose the compound additive homology assessment are revealed. It follows that the attitude sometimes expressed (e.g., by Hauser and Presch, 1991) that all multistate characters should be treated as nonadditive often discards information that could be useful in an analysis. Additive characters are just more explicit, compound hypotheses of homology. The fact that nonadditive codings tend to produce shorter trees does not a priori make them better. Throwing away characters, or lying, can also produce shorter trees. Nonadditive codings are better only when they are better justified (or more defensible) in terms of homology assessment. In fact, a nonadditive multistate character implies ambiguity in our understanding of the homology among the states, because it is not generally possible that all allowed transformations are simultaneously true. It is this increased ambiguity that explains why nonadditive characters produce shorter trees, just as removing data (increasing ambiguity) will produce shorter trees.

Serial homology

Serial homology was of great interest early in the development of evolutionary theory (cf. Owen, 1843; Darwin, 1859). Serial homology differs from homology in general in that differing "states" of the homologous features co-occur in the same individual organism. Darwin noted examples such as the vertebrae, and floral organs of angiosperms; another prominent example of serial homology is appendages of Arthropoda. Floral organs are analogous to segments of arthropods if each whorl or zone of organs is viewed as equivalent to a segment, and the organs (appendages) on those segments (e.g., sepals, petals, stamens, carpels) are viewed as equivalent to arthropod appendages. In each case, there is a relationship in expression among organs in the different series. As is the case with arthropod appendages, the floral organs in adjacent segments may share morphological features even though they are differentiated in function or other features (e.g., in some cases, the sepal whorl is petaloid and virtually indistinguishable from the petal whorl). Serial homology in essence is no different than non-serial homology, which may be viewed as binary. The "domain" of effect of a particular homologous feature may be restricted to one "segment" or several. The issue of hypothesizing, coding, and analysing serial homology is one of determining a unit or domain of effect. This is not to say it is a simple task, and the very occurrence of multiple structures with varying levels of similarity in the same individual creates a complexity that is difficult to parse easily. This complexity may result in overweighting of a particular homologous feature that is expressed in multiple series (e.g., different segments of an insect, or different whorls of a flower). Complexity, however, does not negate the fact that serial homology is identical to "plain" homology in every important aspect—it is similarity due to an ancestral condition, and it is homologous whether plesiomorphic or apomorphic. Because each taxonomic group (e.g., angiosperms or centipedes) presents its own

issues in deciphering the underlying homologous domains of serial homologues, it really cannot be the focus of the discussion here. We can refer the reader to examples of underlying domains of homologous gene expression in studies of the MADS box genes in floral development (e.g., Jack et al., 1992) and *Hox* genes in arthropods (Averof and Akam, 1995) as examples of advances in understanding serial homology from a genetic standpoint.

Conclusions

Clearly, two types of definition of homology coexist currently in systematics. One is devoid of phylogenetic content and is operational; the other is a concept that explicitly invokes an evolutionary context for similarity. The former can be traced to Owen (1843); the latter concept (but not terminology) to Lankester (1870a). It was Lankester's (1870a) concept of homogeny, shared similarity due to common ancestry, which eventually became Hennig's (1966) concept of homology. In application, these two concepts are equivalent to "primary homology" and "secondary homology" (de Pinna, 1991). Lankester (1870a) also first presented the concept of homoplasy, which is more or less equivalent to Hennig's concept of "homoiology."

Owen's positional and eventually the ontogenetic definition of homology is the basis for the discovery and development of hypotheses of relationship. By comparing individuals in developmentally equivalent phases and observing similarity of features, we can then hypothesize which features are likely to be similar due to common ancestry. Such features become the "primary homologies" auctt., scored as character states which are hypotheses of phylogenetic homology sensu Hennig. The use of the terminology "primary homology" and "secondary homology" is unfortunate, and we instead use "hypothesis of homology" and "homology" in their places. We also prefer the use of the term phylogenetic homology to distinguish homology based on common ancestry from homology based solely on ontogenetic similarity.

A concept of homology that seeks to eliminate common descent and shared ancestry as the basis for formulating character states and scoring taxa has been promoted by those self-identifying as pattern cladists (e.g., Williams and Ebach, 2008). They embrace an Owensian ontogenetic definition of homology as sufficient, without reference to common ancestry. If such a position is dissected, identifying homology solely with similarity/ontogeny, then it would appear that the test of congruence imparted by a parsimony analysis must consequently be interpreted as a test of similarity/ontogeny, not of similarity due to relationship. This would imply that our observations of ontogeny and similarity are negated by homoplasy. Following parsimony analysis, the test of congruence somehow is shifted to be interpreted as indicating relationship, even though hypotheses of similarity due to relationship are denied in the selection of scoring of characters. We take the position that phylogenetic analysis tests neither the ontogeny nor the similarity of characters, but instead tests the hypotheses of similarity due to common ancestry. A phylogenetic tree does not negate our observations, or the possibility of identical states in unrelated taxa. It negates only our original interpretation that the similarity observed in these taxa was due to common ancestry, and instead provides the alternative explanation that the similarity is due to independent (sometimes genetically indistinguishable) evolutionary changes.

Phylogenetic homology therefore is similarity due to common ancestry, following Hennig (1966). Homoplasy is an erroneous interpretation of phylogenetic homology, shown to be such on a particular cladogram or phylogenetic tree. These definitions are necessary parts in justification of parsimony, which minimizes homoplasy, if we are to interpret our results as cladograms. Following these observations, both plesiomorphy and apomorphy are homologies, and whether a homology is a synapomorphy is dependent on placement of the root of the particular tree on which the character is mapped. Homoplasy is not a process in nature: difficult or rapidly evolving characters are not "prone to homoplasy"—they may be prone to high rates of mutation or to high levels of convergence, but it is we who are prone to homoplasy, since we are the source of the character codings that imply homologies that are not supported in the results of our analyses.

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