

## Homology and errors

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### Abstract

A recent review of the homology concept in cladistics is critiqued in light of the historical literature. Homology as a notion relevant to the recognition of clades remains equivalent to synapomorphy. Some symplesiomorphies are “homologies” inasmuch as they represent synapomorphies of more inclusive taxa; others are complementary character states that do not imply any shared evolutionary history among the taxa that exhibit the state. Undirected character-state change (as characters optimized on an unrooted tree) is a necessary but not sufficient test of homology, because the addition of a root may alter parsimonious reconstructions. Primary and secondary homology are defended as realistic representations of discovery procedures in comparative biology, recognizable even in Direct Optimization. The epistemological relationship between homology as evidence and common ancestry as explanation is again emphasized. An alternative definition of homology is proposed.

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“To the extent that discussion centers on what are conveniently taken to be the views of the ancients, substantive issues are obscured.” (Farris, 1985, p. 195)

“Claims that traditional homology embraces symplesiomorphy (and paraphyly), and that the traditional notion is more general and more meaningful than synapomorphy, are overstated at best and false at worst.” (Nelson, 1994, p. 115)

The concept of homology, of fundamental importance to systematics and evolutionary biology, has been reviewed hundreds of times, most recently in *Cladistics* by Nixon and Carpenter (2011, hereafter NC<sup>1</sup>). The particular aims of that paper were to dispute the equivalence of homology with synapomorphy (championed, but not introduced, by Patterson, 1982), and to propose a “global definition of homology.” Here, we critically examine NC’s arguments and conclusions in light of other cladists’

discussion of the homology problem over the past 30 years.

As noted by Williams and Ebach (2012), biologists never seem to tire of revisiting the “homology concept,” and although they offered some incisive comments on NC’s terminology, we feel the waters have been sufficiently roiled that further discussion is warranted. We do not presume to tell readers what or how to think about these matters, but merely encourage them to read the relevant literature and draw conclusions for themselves. Before we dissect NC, we briefly reiterate our own perspective on the nature of homology (cf. de Pinna, 1991; Brower and Schawaroch, 1996).

Few modern systematists would disagree that the identification of homologous features involves multiple steps or stages. Initially, features that evidently share similarity of form and/or position among taxa are conjectured to be manifestations of the same character. These observations are then recorded as character states in a data matrix, which formalizes the hypotheses of correspondence and state identity. Whether these initial state identity hypotheses are corroborated as synapomorphies (character state transformations

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<sup>1</sup>“NC” refers not to the authors, whose other work we greatly admire, but to the article itself.

that support clades<sup>2</sup>) is tested by assessing their distribution on a most-parsimonious tree. If a character fits that tree perfectly (i.e. without homoplasy), its hypotheses of character state identity are corroborated, and, once the tree is rooted, its states are interpreted as synapomorphy or symplesiomorphy with respect to one another. If the character does not fit the tree perfectly, then one or more of the initial hypotheses of character state identity are falsified and some states in some taxa are considered to represent independent gains or reversals (homoplasy).

Thus, the term “homology” may be employed to describe either the relation that unites all the states of a character, or the relation that separates states of a character from one another, and also to describe either the initial hypotheses or only those that pass the congruence test and are interpreted as evidence of evolutionary events. To distinguish among these, we have called them, respectively, “primary homology” and “secondary homology” (de Pinna, 1991), or “topographical correspondence/character state identity” and “homology” (Brower and Schawaroch, 1996). Others have sensibly emphasized the recognition of homologues (corresponding parts) as distinct from the inference of homology (the relationship among taxa implied by those correspondences) (Williams and Ebach, 2012).

In keeping with the magisterial tone of their “On” series (e.g. Nixon and Carpenter, 1993, 1996, 2000), NC lays down the law regarding how cladists ought to be thinking about homology and strongly criticizes what might be considered the orthodox cladistic perspective outlined above. Unfortunately, NC is rife with oversimplifications, omissions and distortions. As we disagree with so much of its essence, we feel obliged to explain why.

## The views of the ancients

### *Darwin’s concept of homology*

NC (p. 161) claims that “Darwin’s definition of homology is clearly not connected to evolution.” This is an appalling statement, because the recognition of homologues is widely cited (even in popular lore) as one of Darwin’s major arguments in favour of evolution. NC quotes “Darwin’s definition” of homology from the “glossary” of Darwin (1859). As noted by Williams and

Ebach (2008, 2012), there is no glossary in Darwin (1859), and the quote comes from the substantially revised 6th edition (1872; not listed in NC references), the glossary of which was written by Darwin’s editorial factotum William Sweetland Dallas (as indicated in the glossary itself). Clearly, Dallas’ definition is not representative of Darwin’s views on homology, especially as its Owenian flavour contradicts so much of what is in the book.

What did Darwin himself say about homology? First, one needs to note that Darwin (1859) used the word “homologies” (rather than “homologues”) to refer to similar parts in separate organisms or body regions. For the concept of homology, Darwin preferred the somewhat ambiguous 19th century term “affinity” (used to describe both the relationship among taxa and the features that signify the relationship, as in Westwood, 1840, p. 143: “It is in consequence of the more complete resemblance *in the numerical majority of the essential characters* of the two beings or groups of beings contrasted together, that the relationship becomes one of affinity; while from a resemblance in the *numerical minority* of such essential characters, the relationship is deemed an analogy”<sup>3</sup> [emphasis in original]; and Strickland, 1846: “It will thus be seen that every instance of asserted affinity between two organic beings is merely a corollary deduced from an observed affinity between the corresponding organs in each; ...”).

Once terminological differences are sorted out, it is amply evident that Darwin considered homology and evolution to be related intimately: “... the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent...” (1859, p. 420); or “The homological construction of the whole frame in the members of the same class is intelligible, if we admit their descent from a common progenitor, ...” (1871, p. I:31). In the 1872 revision of the *Origin*, Darwin (p. 454) made specific reference to the “remarkable paper” by Lankester (1870), and used his terms homogenous and homoplastic with approbation. Darwin also referred to homology as “unity of type”: “By unity of type, is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is

<sup>2</sup>It is surprising to see cladists still arguing about methodology in terms of whether one ought to be “grouping by synapomorphy” or by “all states” (cf. Farris, 2012; Nixon and Carpenter, 2012). Such terminology no doubt inspires (albeit misplaced) accusations of pheneticism (cf. Brower, 2012). The quantity that is minimized by parsimony is implied transformations among states.

<sup>3</sup>An astute reviewer commented that discussion of “the congruence test” in the work of Hennig and pre-Hennigian systematists is anachronistic, and so it is. However, while the “test” may be a product of the quantitative cladistic era, Westwood’s observation (and arguments by even earlier authors, such as MacLeay, 1822) plainly indicate that for nearly two centuries systematists have determined whether the distribution of a particular character implies affinity or convergence on the basis of the weight of evidence of other characters. The observation of nested patterns of congruent characters seems to us to provide the fundamental idea of a Natural System, which is, of course, historically prior to evolutionary explanations involving descent with modification and ancestors.

quite independent of their habits of life. On my theory, unity of type is explained by descent.” (1859, p. 206). In due time, Darwinian evolutionary appropriation of the notion was so complete that homology not only became evidence of evolution, but came to be defined as a function of ancestry (Rupke, 2009).

### *Hennig’s concept of homology*

NC repeatedly refers to Hennig’s concept/definition of homology, stating, for example, that it is identical to Haas and Simpson’s (1946) homology and equivalent to Lankester’s (1870) homogeny. Of course, invoking the authority of historical texts in contemporary scientific debates hardly constitutes an irrefutable argument. Still, if such a path is taken, rigor and accuracy are necessary. Despite these historical references, NC neglects to provide clear statements of what any of these concepts are, or to quote adequately Hennig’s own views on the matter. Let us compare these definitions and see how identical they are: “Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*.” (Lankester, 1870, p. 36). Homology is “defined as a similarity between parts, organs, or structures of different organisms, attributable to common ancestry.” (Haas and Simpson, 1946, p. 323). Incidentally, Haas and Simpson considered homogeny to be synonymous with their homology definition. Both definitions exclude homoplasy, based on assessment of character congruence.

Hennig (1966) cited neither Lankester nor Haas and Simpson, and NC’s (p. 161) statement that he “clearly adopted an identical concept of homology” is unsupported by evidence. To explore this claim, let us first quote Hennig: “Different characters that are to be regarded as transformation stages of the same original character are generally called homologous. ‘Transformation’ naturally refers to the real historical process of evolution, and not to the possibility of formally deriving characters from one another in the sense of idealistic morphology.” (1966, p. 93).

Hennig indeed seems to be advocating a Haas and Simpson-like definition of homology, and yet, his concept differs from “similarity due to common ancestry” in that the statement about what elements are homologous (characters of a transformation series, equivalent to character states of a character in modern parlance) is more precise. NC (p. 162) argues: “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.” This statement is partly true, yet does not faithfully characterize what Hennig said: “(T)he concepts of symplesiomorphy and synapomorphy go somewhat beyond the range of what are ordinarily called ‘homologous characters’” (1966, p. 94). Going beyond

something is not the same as being part of something. On p. 120, Hennig draws a sharp distinction between the initial question of whether characters are homologous, and the subsidiary question of whether characters conjectured to be homologous are “synapomorphies, convergences, homoiologies, or parallelisms” (see also pp. 128, 146). The clear implication of this statement is that Hennig considered that, as parts of transformation series, both the first two categories *as well as the latter three* represent hypotheses of homology. Thus, Hennig’s homology definition/concept appears to be equivalent to de Pinna’s (1991) primary homology, or Brower and Schawaroch’s (1996) topographical identity (with Hennig’s individual characters exhibiting Brower and Schawaroch’s “character state identity”), and not to Haas and Simpson’s or Lankester’s definitions, because convergences, homoiologies and parallelisms have not yet been inferred to represent homoplasy.

### **Overstated at best and false at worst: is symplesiomorphy homology?**

The cladistic equation of homology with synapomorphy brought precise and simple clarity to a fundamental yet formerly nebulous idea. The insight was so appealing that several thinkers came to it independently (e.g. Wiley, 1975, 1976; Bonde, 1977; Platnick and Cameron, 1977; Cracraft, 1978; Nelson, 1978; Patterson, 1978; Gaffney, 1979; Platnick, 1979; Nelson and Platnick, 1981), prior to the widely cited paper by Patterson (1982). Although these publications have been cited many times in the mainstream literature, we have little doubt that they will be ignored many times more and that Patterson will continue to be credited/scapegoated as creator of the idea.

Rejecting the cladistic equivalence of homology and synapomorphy, NC (p. 162) asserts that homology ought to encompass both synapomorphy and symplesiomorphy: “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.” Similar ideas were proposed by Eldredge (1979) and Ax (1984), but rejected by Rieppel (1988). Indeed, the NC concept closely echoes that of evolutionary taxonomists, as well as a motley assortment of more recent articles: Roth (1984, 1994), De Queiroz (1985), Szalay and Bock (1991), Haszprunar (1992), McKittrick (1994), and Reif (2004). If, as NC (p. 161) states, Haas and Simpson’s (1946) definition “fixed modern usage,” then one might question the need for further discussion.

Platnick (1979) suggested that the differences among instances of symplesiomorphy, synapomorphy and homoplasy were based upon their level of generality: if a synapomorphy implies a character state transformation

pertaining to the clade of interest, then a symplesiomorphy represents a transformation supporting a more inclusive clade, and homoplasy represents separate transformations of less inclusive clades. This framework offers a unifying explanation why, in NC's figures, the synapomorphies and symplesiomorphies appear to have a common ancestor, while the homoplastic character(s) do not. Such a perspective has been endorsed by Engelmann and Wiley (1977), Eldredge and Cracraft (1980), Patterson (1980, 1982), Farris (1983), Rieppel (1988, 2004), de Pinna (1991), Brower and Schawaroch (1996) and many others. In rejecting this idea, it seems to us that NC misconstrues synapomorphy and symplesiomorphy as antagonistic concepts, when, in fact, the latter is a subset of the former. Cladists characterize similarities as symplesiomorphic only when synapomorphies have been determined. Thus, from an epistemological perspective, symplesiomorphy is a logical derivative of synapomorphy and the difference is one of level of generality only.<sup>4</sup>

However, while “symplesiomorphies can be homologies” (Farris, 2012) as synapomorphies of more inclusive clades, not every symplesiomorphy “is homology” under the NC definition. Complementary absences (atypophaenous homologues of Källin, 1945; neomorphic characters of Sereno, 2007) are not shared as the product of any evolutionary event: what “common ancestry” unites taxa exhibiting a symplesiomorphic absence? For example, “presence of feathers” unites birds, but what is the “homology” that unites other archosaurs, invertebrates, bacteria, rocks, etc.? (cf. Farris, 1979; Wiley, 1981, pp. 128–129; Patterson, 1982). This example—non-feathers—could be rescored as some other epidermal derivative that would be present in a more inclusive but still circumscribed group of taxa (cf. Fitzhugh, 2006). As stated by Nelson (1994, p. 129) “(a)lthough it is true in a conventional sense that feathers are absent from nonbirds, the absence need not be construed to mean that there really is no homologue of feathers in these organisms. In a strict sense the ‘0’ means only that no homologue is specified.”

In practice, most morphological matrices (and DNA sequence data that include “gaps”) contain numerous states encoded and treated as identical in parsimony analysis that are unobserved complements for features that are present in some of the included taxa. For example, a recent morphological and behavioural data set for vespid wasps includes “absent” as a character state for 107 of 333 characters (Pickett and Carpenter, 2010). While some of those absences may represent

apomorphies, many of them are symplesiomorphies. As noted by Nelson (1978, p. 340), “absence of a character is not a character,” but it can still be a symplesiomorphy (Sereno, 2007). We view complementary absences as primary homologues (epistemologically identical character states) but not as secondary homologues. Clearly, primitive absence is merely an operational placeholder for those taxa lacking the observable derived feature, and as such cannot be “shared due to common descent.” NC's assertion that “plesiomorphy is homology” does not apply to such symplesiomorphies under its definition of homology, which therefore is not “global.”

Finally, NC's (p. 162) argument that plesiomorphy is homology based on “occurrence of the same condition in the most recent common ancestor” is identical in its reasoning to the evolutionary taxonomists' argument that paraphyly is monophyly (*sensu* Ashlock, 1971). We suspect that Hennig would have felt the same way about plesiomorphic “homologies” that he felt about paraphyletic groups: “they have no independent history and thus possess neither reality nor individuality.” (Hennig, 1966, p. 146).

### The rooting problem

We agree with NC's description of Farris' parsimony procedure regarding character polarity, and have stated much the same ourselves: “It hardly needs to be reiterated that in standard cladistic analysis, the length of the most parsimonious cladograms is unaffected by the position of the root (Farris, 1970), that current programs build unrooted networks, and that *a priori* character polarization is therefore unnecessary (Farris et al., 1970).” (Brower, 2000a). NC's definition determines homology/non-homology after testing by congruence, but prior to establishing character polarity. This brings us to rooting, a subject central to NC's argument.

NC presents some superficially convincing cartoon trees with different placements of the root: the taxa exhibiting the plesiomorphic state do indeed share a presumptive “common ancestor,” no matter where the root is placed. While their examples are uncontroversial as far as they go, we believe that they rely on an incomplete representation of rooting. Rooting is not a neutral procedure as implied in their paper, and may exert an impact on homology assessments previously inferred on an unrooted tree. Early formalizations of rooting, such as by Farris (1970) and Lundberg (1972), were keenly aware of and realistic about the practical implications of rooting an undirected network. The length of a tree is unaffected by the *position* of the root, but it is certainly not unaffected by the *inclusion* of a root. Subsequent developments in the field, however, mostly neglected those initial considerations. Gradually,

<sup>4</sup>The absence of evidentiary contribution from symplesiomorphy to the operational calculus of quantitative cladistics is manifest in that the most parsimonious optimization of a character with  $N$  states is  $N-1$  steps long: the “-1” represents the lack of transformation in the taxa exhibiting the plesiomorphic state.

rooting came to be seen as a rather bureaucratic step to crown a phylogenetic analysis. Thus, the root is nowadays often treated as an immaterial entity detached from the rest of phylogenetic analysis, or simply as a marker that indicates where the root would go if it actually existed. In fairness, such shortcomings did not originate with NC, although the paper certainly embraces the now widespread immaterial view of rooting.

The root is a uniquely special branch that serves as a basal vector for the time arrow. But it is otherwise a normal branch that carries with it character-state information. This character information comes either in the form of an optimized state-set derived from analysis of a more inclusive set of terminals (as when an ingroup is rooted onto a more inclusive group, usually implemented by some form of outgroup method) or from a summary of character states inferred from a comparative analysis (as in Lundberg rooting). Other forms of rooting such as midpoint rooting and ontogenetic rooting (de Pinna, 1994; Weston, 1994) carry no character-state input, but only directionality, and are simply root locators, not actual rooting methods. As such, they suggest where the root should be, but do not provide a real root that will connect the analysed taxa to a more inclusive set of terminals. The reason we say these are not “real” roots is because every phylogenetic hypothesis has a root, whether or not we know where it goes: every taxon is connected to the rest of the tree of life somewhere.

Thus, an actual root is not an abstract concept detached from the empirical reality of character analysis: it carries character-state information. A root, like any additional taxon (real or hypothetical), may imply changes to the results of a phylogenetic analysis. Even if no topological change is implied, it may disturb the optimization scenario.

In all NC’s examples, the root is assumed to be an extra terminal, which results in an additional node at the base of the tree. However, it is a “joker” terminal, in the sense that it meekly adopts whichever state fits the states of terminals around it. Such a puppet root takes up whichever optimization is determined by its neighbours and voices no character-state input of its own. Such conditions are unrealistic and such a “root” is neither a terminal nor a node, but is instead a phylogenetic zombie. This problem is only manifest when the root is placed exactly at the state-set partition, necessarily resulting in ambiguous state assignment. But such is allowed to appear only once in all of NC’s examples, in fig. 2 (bottom left tree), and not discussed at all. Such root-state ambiguity is in fact general, albeit hidden under the carpet in most cases. If we allow the root to take up hypothetical state assignments, ambiguity looms everywhere around the base of trees. In NC fig. 1, assignment of state 0 to the root on the bottom left tree

renders optimization ambiguous, so that we no longer know if state 1 is actually homologous in taxa 5–9. That hypothesis only holds under the optimization that renders state 0 in taxa 0–4 non-homologous to state 0 in the root. Under an alternative optimization, state 1 in taxa 6–9 is not homologous to state 1 in taxon 5. In sum, we cannot be certain that states 0 and 1 are homologous among the taxa that share them, even in the absence of homoplasy in the unrooted tree. Similar uncertainties hold true to all other situations, as in an unrooted tree we know neither the position of the root nor its associated character-states. The root *may* introduce uncertainty in the homology assessment of the scheme (although, of course, it will not necessarily do so). Surely some hypotheses of homology are refuted conclusively in the unrooted scheme. However, while an undirected network indeed represents a test of a hypothesis of homology, it is only a partial test. Rooting represents a further challenge to all hypotheses of homology.

It might be argued that the root with its state assignments, however estimated, might be included as one more terminal in the unrooted analysis, and then the unrooted result could be read as a reliable guide to homology. That is obviously true, as roots will not violate the workings of parsimony. But in that case, homology assessment is actually being conducted with an operational root, even if the analysis itself is undirected. The conclusion is the same: addition of a root may impact homology assessments. Note that the distinction here is conceptual and not merely technical. The root is not simply any additional taxon. It is an additional taxon that is expected to represent the branch which will connect the analysed taxa to the rest of the tree of life. In other words, it is the open end of an otherwise closed system. If it is not taken as such, then the root is still unspecified and eventual addition may be expected to introduce changes in our interpretation of character-state distributions.

The situation of homology in relation to rooted and unrooted trees parallels that of monophyly. An unrooted tree shows that some groupings simply cannot be monophyletic regardless of the root position. One can say that the monophyly of such groups is refuted with no further need of a root. However, rooting will bring further refutations of potential monophyly. Similarly, an unrooted tree may refute certain hypotheses of homology among character-state occurrences. But further cases of non-homology may still be revealed by a root. Thus, an unrooted tree is a necessary but not sufficient test of homology (cf. Brower, 2002).

### Ontogenetic/positional similarity

Throughout, NC refers to ontogenetic/positional similarity, sometimes viewing it as a definition of

homology, sometimes as a criterion for hypothesizing homology, and sometimes as a stage of homology assessment. This is very confusing, and it seems to have been a source of confusion to the authors as well. Let us juxtapose a few NC quotations:

1. ... 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 ... (p. 161).

2. ... ontogenetic/positional similarity ... is the basis of developing character definitions, which are then tested by character corroboration (p. 161).

3. According to pattern cladist arguments, initial scoring of characters is based solely and entirely on ontogenetic/positional criteria ... and is thus merely Owensian [sic] non-evolutionary observation ... (p. 165).

4. Owen's positional and eventually the ontogenetic definition of homology is the basis for the discovery and development of hypotheses of relationship (p. 168).

5. They [pattern cladists] embrace an Owensian [sic] 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 (p. 168).

As stated in de Pinna (1991) and Brower and Schawaroch (1996) and reiterated above, we view ontogenetic/positional similarity as a criterion for establishing hypotheses or conjectures of homology, to be subsequently tested by character congruence. As such, it corresponds to a stage of homology discovery, not a "definition of homology." NC's authors have either fundamentally misunderstood or deliberately misrepresented our perspective on this.

NC (p. 165) further states that "Brower and Schawaroch (1996) explicitly denied that characters and character states are hypotheses of homology ..." However, at the top of the same page, 52 words earlier than the passage quoted in NC, Brower and Schawaroch said, "... all shared, identical character states represent conjectures of *potential* homology ..." Hypotheses. Conjectures. Where is the "explicit denial"? Brower and Schawaroch said the same thing in nine other places. We encourage the reader to judge which of these papers is more self-contradictory.

### Characters vs. states, and sequence alignment

We have little disagreement with NC's discussion of these topics, primarily because we have already expressed similar views ourselves, which NC fails to acknowledge. For example, NC (p. 166) says, "The

conclusion is that homology among and between character states in the same character is an assertion that is not tested by cladistic analysis ...." Brower (2000b, p. 15) said: "Character state identity, but not topographical identity, is tested by character congruence in cladistic analysis." Regarding sequence alignment, NC (p. 166) says, "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." Brower (2000b, p. 15) said, "DNA characters are treated the same as morphological characters in this stepwise scheme. Topographical identity of nucleotide sites is provided by alignment of the sequences, ... the individual character state identities are tested by cladistic analysis, but not the alignment, which is an *a priori* statement of topographic identity among the sequences being compared." Regarding dynamic homology assessment, NC (p. 167) says: "In essence, the act of sequencing provides the initial homology assessment by linear ordering of the bases." Schuh and Brower (2009: p. 79) said: "... the sequences that are analyzed are assumed to be 'homologous,' and the nucleotides are maintained in their 'sequential' front-to-back linear order with respect to one another. These constraints obviously represent some sort of assumptions or hypotheses of primary homology." To be sure, great minds think alike, but one would expect that a thoughtful "review" of "homology in cladistics" would take into account other such efforts.

We agree with NC's brief discussion and conclusions about the procedure called "dynamic homology" (DO). However, there is a related issue worth mentioning. It has been said that in DO there is no distinction between primary and secondary homology (Wheeler et al., 2006, p. 10; Agolin and D'Haese, 2009, p. 367). The reasoning behind this assertion is that direct optimization, in making simultaneous optimal estimates of both alignment (i.e. base-pair equivalence and transformation series) and topology, obliterates the distinction between the stages of generation and legitimization of homology propositions. We disagree with that interpretation. First, the fact that alignment and tree-building are simultaneous does not imply that observed similarity is automatically translated into homology. The optimal tree may or may not reflect specific character similarities. The simple fact that there can be homoplasy under DO is evidence that there is a distinction between observed similarity (primary) and actual homology (secondary). Subsequent to the inference of the tree, some similarities in base distribution are likely to be the result of homoplastic change. Such cases represent instances where hypothetically homologous identical

bases (i.e. primary homology) are not corroborated by character analysis (i.e. secondary homology). No matter how the sequences were converted into a hypothesis of relationships, there is inevitably an element of expectation and an element of corroboration or refutation of that expectation. That expectation is primary homology and its corroboration is secondary homology (or lack thereof, in case of homoplasy). Although the threefold interconnections among homoplasy, alignment, and DO are only now being untangled (Wheeler, 2011), an alignment can be obtained from a DO analysis, based on the optimal tree found, and from which the relationship among specific bases can be traced, including possibly identical yet non-homologous states.

Thus, we consider that the primary/secondary homology duality persists under DO, albeit in fuzzy form. In fact, it is difficult to conceive of a method that would entirely obliterate the distinction between generation and legitimization of hypotheses. As noted above, the sequences or other data included in a POY data set are assumed to be “homologous” (topographically corresponding) before the analysis is begun. Such duality underlies all of comparative biology, both pre- and post-evolutionary, and is in fact central to most of the discovery procedure in the natural sciences—echoes of “conjectures and refutations” (cf. Popper, 1965; Farris, 1995). Similarities are taken to be a manifestation of hierarchical pattern at face value, and non-homology is only revealed by incongruence. Non-homology is the actual discovery of phylogenetic analysis. Homology, the “null hypothesis,” is assumed until proven non-parsimonious.

But DO does offer an interesting perspective on the homology problem as applied to sequences. The optimality procedure in sequences done by DO is equivalent to the often informal procedure of determining canalization of possible character-state transformations in morphological characters (i.e. the reason why, say, state 0 of character 1 is not allowed to transform into state 2 of character 15 in a data matrix). We believe that the recognition of primary homologues in phenotypic characters (more precisely, the topographical identity phase of Brower and Schawaroch, 1996) is done by optimizing multiple parameters of equivalence (mostly, but not exclusively, ontogenetic and topographic) according to basic principles of comparative anatomy. This is implemented non-quantitatively, “by eye” (cf. Hennig, 1966; fig. 37), in much the same way as alignment is still sometimes done today. Direct optimization offers a way to quantify that procedure. The idea to formalize propositions of primary homologues has historical forerunners in morphological characters (e.g. Jardine and Jardine, 1967; Jardine, 1969), never fully developed or widely employed. Several recent papers also apply DO on non-molecular data (Robillard et al., 2006; Ramírez, 2007; Agolin and D’Haese, 2009; Japyassú

and Machado, 2010). Recent criticism of DO has correctly focused on its apparent dissolution of the basic separation between observations and hypotheses (Morgan and Kelchner, 2010). The procedure blurs the traditional boundaries between phenomenological and interpretational realms in systematics. The breadth of such criticism, however, depends on the interpretation given to results of a DO analysis. Seen as phylogenetic hypotheses, where actual (historical) homologies are inferred, DO trees indeed incur major assumptions, as yet unwarranted and in need of further study. On the other hand, as a discovery procedure targeting subtle primary homologies not detectable by independent criteria, DO is promising.

### Primary and secondary homology

Over the past 20 years, the terms primary and secondary homology have been used in hundreds of theoretical and applied papers, as well as textbooks. The terms have also found parallel in biogeography (e.g. Morrone, 2001). While they are obviously considered useful by the systematic community, we re-emphasize that the division proposed by de Pinna (1991) was intended not as a normative rule, but rather as a description of a *de facto* situation in the real world of phylogenetic inference. Phylogenetic analyses are done in a such a way that data are expected to be homologous (as per Hennig’s auxiliary principle) and then corroborated or refuted by their distribution on a most-parsimonious tree. This is a simple operational duality which has been perceived by numerous authors, both pre- and post-evolutionary, as noted by de Pinna (1991). The terms primary and secondary were intended to reflect that duality plus the fact that both levels are interdependent, sequential, and, as noted earlier, have been treated as “homology” in one form or another in the course of history. The central issue that the terminology was supposed to underline was that hypotheses of homology cannot be corroborated or refuted outside of a scheme of relationships, i.e. that homology is a pattern-dependent concept.

So, we find it rather curious that NC calls the widespread use of the terms primary and secondary homology “undesirable” (Nixon and Carpenter, 2011; p. 9), especially because it offers no explanation for the reproach. If those terms reflect an actual situation in the real world of comparative biology, the only alternative would be to use different terms for the same concepts. Indeed, a number of such alternatives were proposed before 1991: “paralogy and homology” (Hunter, 1964), “observational and theoretical components of homology” (Jardine, 1969), “putative synapomorphy and synapomorphy” (Farris and Kluge, 1979), “topographical homology and phylogenetic homology” (Rieppel,

1980), “preliminary and final testing of homology” (Kluge and Strauss, 1985), and “topographical correspondence and homology” (Rieppel, 1988) (all cited in de Pinna, 1991), but for various reasons primary and secondary homology have come to predominate. NC has its own contribution to this list: “hypothesis of homology” and “homology,” but we contend that such terminology is misleading because “homology” (i.e. secondary homology) is also hypothetical, inasmuch as it depends on a specific hypothesis of relationships as implied by the evidence from all characters analysed.

In sum, the concepts are the same and the choice of words to describe them is entirely semantic. Therefore, we see little of substance to discuss further. We only note that NC carefully avoids using de Pinna’s terms (except in quotes) and this has resulted in some rather cumbersome phraseology (e.g. “the kind of homology statements we have after reviewing ontogenetic data and scoring taxa for character states in a morphological matrix,” cf. p. 166; i.e. primary homologues). Such strenuous prolixity to circumvent the familiar terms, primary and secondary homology, seems obfuscatorily recalcitrant. The allure of these terms must be insidious, however, because at least one standard usage of primary homology sneaked into the text (cf. p. 164).

### Hypotheses concerning truth, and another definition of homology

But if we imagine ourselves in the position of gods surveying the whole evolutionary process, then of course the taxonomic groupings would appear as the outcome of the branchings of the phylogenetic stream in the course of time, and in that sense the former would be based upon the latter. But no such vision is vouchsafed to mortal morphologists. They must content themselves with the results obtainable by attempting to connect generalizations reached by observation with the help of explanatory hypotheses. (Woodger, 1945, p. 113)

The question still remains, however, why pattern cladists in particular are so often selected to serve as negative examples, when surely pheneticists or a host of others would be far more suitable for the purpose. Nominally, the reason is that pattern cladists wish to divorce cladism from evolution, but this charge, too, fails under inspection. (Farris, 1985, p. 198)

We will not stoop to defend pattern cladistics against accusations of creationism, which attempt to impute metaphysically incorrect beliefs to systematists whose philosophical approaches to the cladistic method are de facto less burdened by ad hoc hypotheses than those who consider “descent with modification” and “common ancestry” as necessary for “the justification of parsimony.” Not *assuming* evolution *a priori* is not the same thing as “not believing in evolution.” We also reject the claims that pattern cladists are pheneticists or necessarily advocates of three-taxon analysis, contumelies we have rebutted elsewhere (Brower, 2000a, 2012).

Perhaps 3tans are pattern cladists (Nixon and Carpenter, 2012), but not all pattern cladists are 3tans.

The NC argument (p. 165, again echoing an earlier observation by Brower, 2000a) that “the pattern cladist approach is identical to the phylogenetic approach, both operationally and in terms of results” seems to us not to support the idea that the *a priori* assumption of evolution is necessary in systematics, but rather that it is *unnecessary*. If assuming something or not assuming something has no impact on the outcome of a scientific endeavour, then is it not more “parsimonious” to not make that assumption?

Let us be clear. Common ancestry is the a posteriori explanation of the congruent pattern of features shared among taxa discovered by systematic analysis. Sentiments to this effect have been stated many times: “This analogy of forms [...] strengthens the supposition that they have an actual blood-relationship, due to derivation from a common parent; a supposition which is arrived at by observation of the graduated approximation of one class of animals to another, [...]” (Kant, 1790, p. 79); “unity of type is explained by unity of descent.” (Darwin, 1859, p. 206); “... descent from a common ancestor is something assumed, not observed. It belongs to theory, whereas morphological correspondence is observed.” (Woodger, 1945, p. 109); “The explanation is then provided by assuming common descent, by inferring that community of similarity = community of descent.” (Hennig, 1966, p. 15); “The fact is that the ancestor of one or two individuals (the prehistoric ancestor, of course) can be guessed at exclusively on taxonomic evidence, on the basis of similarities of attributes.” (Blackwelder, 1967, p. 142); “Homologies ... are structural similarities which force us to suppose that any differences are explicable by divergence from an identical origin.” (Riedl, 1979, p. 33); “... synapomorphies constitute the only available evidence on genealogy.” (Farris, 1983; p. 7); “the observations comprise shared characters—points of similarity—among organisms, and hypotheses of genealogical relationship are potentially able to explain such similarities as the result of inheritance.” (Farris and Kluge, 1985, p. 133); “Evolution is not a first cause which must be ‘trusted;’ instead, it is a theory explaining the observed pattern of order in nature.” (Rieppel, 1988; p. 169); “The development of cladograms independently of process theories makes tests of such theories possible.” (Carpenter, 1989, p. 137). See also Brady (1985), Brower (2000a,b), and Tschulok (1910, 1922); cf. Rieppel, 2010).

In light of these quotations and the arguments above, we view NC’s “global definition of homology” to be neither global, nor novel, nor adequate. “Phylogenetic homology ... is similarity due to common ancestry” restates the standard, non-operational, metaphysically burdened, evolutionary taxonomists’ definition found in



most freshman biology textbooks (cf. Schuh and Brower, 2009, p. 53).

Although it is possible to fruitfully build upon a concept in the absence of a precise definition (or even if it is indefinable; cf. Wittgenstein, 1953), we feel obliged to offer an alternative: *Homology is the relationship among parts of organisms that provides evidence for common ancestry*. This definition expresses the real-world praxis of phylogenetic inference and applies to both layers of homology assessment, primary and secondary. Also, it places evidence where it belongs: before models. It does not specify that a hypothesized relationship is corroborated through parsimonious accounting of character state transformations, although that is the method that we advocate. Nor does it assume *a priori* an evolutionary causal mechanism, although it implies that evolution is the best explanation for the observed pattern. Those familiar with phylogenetics are welcome to abbreviate our definition by replacing “synapomorphy” for all that follows the verb “is”.

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