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Letter to the Editor

More on errors

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> "We can't stop here, this is bat country!"(Hunter S. Thompson, Fear and Loathing in Las Vegas)

If only it were otherwise, but overall the paper by Brower and de Pinna (2012) is just more of the same that came before: the conflation of homology and synapomorphy. But besides that, there are numerous "oversimplifications, omissions and distortions" (their words in reference to Nixon and Carpenter, 2012) that constitute nothing less than a blatant attempt to rewrite history. They find our tone to be "magisterial"; we prefer to characterize it as efficient, and our writing to the point. This cannot be said of Brower and de Pinna's paper, and although we have attempted to avoid "prolixity" in showing the logical inconsistencies of their critique, some detail is required. The comments below follow the order in which the issues were addressed by Brower and de Pinna, and because of their rather convoluted prose, we suggest you read their paper at the same time as ours.

More on Darwin

Brower and de Pinna find our statement "Darwin's definition of homology is clearly not connected to evolution" to be "appalling", giving as reason "because the recognition of homologues is widely cited (even in popular lore) as one of Darwin's major arguments in favor of evolution." They deprecate our citation of the glossary definition, which is from the sixth edition of the *Origin* (they failed to note our citation of "6th edn" with our quotation), because the author of the glossary, "Darwin's editorial factotum William Sweetland Dallas" was not "representative of Darwin's view on homology" in that "its Owenian flavor contradicts so much of what is in the book." We, however, would observe that someone else read the *Origin* very carefully and came to the same conclusion that we did, that Darwin's concept of homology was indeed Owensian—and moreover that this was someone connected to the author (his "editorial factotum").

It is unfortunate that Brower and de Pinna resort to distortion of our quotation, which we restricted to Darwin's *definition* of homology. "Darwin's definition of homology is clearly not connected to evolution" seems a clear and concise statement, but apparently not so to Brower and de Pinna. We encourage Brower and de Pinna, and the reader, to read Darwin's *Origin*, and they will find that Darwin did indeed have an Owensian (non-evolutionary) concept of homology (as "homologies" or "homologous"). For example, "All physiologists admit that the swimbladder is homologous, or 'ideally similar,' in position and structure with the lungs of the higher vertebrate animals" (Darwin, 1859, p. 191). After distorting our meaning to suggest that we believe that Darwin did not connect homology to evolution, Brower and de Pinna surprisingly revert to the truth: "Darwin (1859) used the word 'homologies' (rather than 'homologues') to refer to similar parts in separate organisms or body regions." So, they are agreeing that Darwin did not include evolution in his concept of homology. But, they then return to distortion, this time of Darwin, claiming that Darwin really meant evolutionary "homology" when he used the term "affinity"—as if this (if true) would negate our point that Darwin worked with an Owensian definition of the concept of homology (although he later adopted Lankester's homogeny). Brower and de Pinna should also carefully read Lankester (1870), who was inspired by Darwin's work, and felt the need to invent new terms, in addition to homology, that combined evolutionary descent and similarity into a single term: homogeny. The characterization of Darwin's use of "affinity" as equivalent to evolutionary homology is double-speak—Darwin used the term as a substitute for evolutionary relationship, although never giving it precise meaning. He did not use it for "the concept of homology"—he used words such as "homologous" for that. Darwin's separation of homology (as organ similarity) is even apparent in this quotation presented by Brower and de Pinna: "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." Darwin is saying here that a particular case of homology ("homological construction") is intelligible (i.e. interpretable) if common descent is invoked —clearly indicating that common descent was not already implied in "homological construction". How anyone could promote this as meaning Darwin's definition of homology *included* descent is only possible if they did not read the quotation carefully—because surely if they had, they would realize that the audience would easily detect the fallacy of their interpretation.

The industry of placing words into Darwin's mouth (or more accurately, imbuing his words with special meaning beyond his obvious intent) is not new. What is new is that avowed pattern cladists are attempting to make Darwin more evolutionary. Perhaps this is a setup for later derision. Be that as it may, that Darwin used Owensian homology as evidence of, and support for, common descent is undeniable, and of course we never denied this. As also inadvertently pointed out by Brower and de Pinna, we only stated the obvious, that his definition of homology was not evolutionary. The fact that he later adopted Lankester's concept of homogeny only makes our point; in so doing, he did not change his concept of homology, which remained the broader Owensian concept. Lankester developed new definitions and indeed, new words—because they were needed, and in particular, his colleague Darwin was not using a clear and precise terminology.

More on Hennig

Brower and de Pinna next take issue with our discussion of Hennig's concept of homology, and urge that "rigor and accuracy are necessary" when quoting from "historical texts". We find Brower and de Pinna's characterization of Hennig's concept of homology to be the opposite of rigour and accuracy. Based even on the quotations that Brower and de Pinna present, it is clear that Hennig's homology, although phrased differently in the context of character transformations and common descent, was the evolutionary concept that can be more simply stated as "similarity due to common descent". For example, on page 94 (cited more selectively by Brower and Pinna), in reference to Remane's criteria Hennig (1966) states: "But with respect to defining the concept of 'homology,' all three of his principal criteria—the belonging of the characters to a phylogenetic transformation series—cannot be directly determined."

But it gets worse. Apparently, Brower and de Pinna forgot to check each of the entries for "homology" in the index to Hennig (1966) or they would have found on page 117: "True homologies, as is well known, are character correspondences that were actually taken over from the common ancestors as such, even though with partial alteration that still permits recognition of the common ground plan." Need we quote more?

More on is symplesiomorphy homology?

Brower and de Pinna aver that "The cladistic equation of homology with synapomorphy brought precise and simple clarity to a fundamental yet formerly nebulous idea", and then proceed to cite a number of authors to whom "The insight was so appealing that several thinkers came to it independently." The earliest author cited by them is Wiley (1975), but when turning to that paper, we read, for example, "The terms apomorphous and plesiomorphous (and their derivatives) convey precise concepts which are logical derivations of a phylogenetic definition of homology. As such, they should be substituted for the word homology in systematic studies." Brower and de Pinna apparently did not read this paper very carefully, similar to their superficial reading of our paper, Darwin's *Origin*, and Hennig (1966). And so it goes.

Brower and de Pinna also cite Nelson and Platnick (1981), and this time they may have actually read the text, or at least not cherry-picked sentences to make their point. Nelson and Platnick (1981, p. 138) were among the earliest, if not the first (part of their book was based on a manuscript circulated by Nelson in the mid-1970s), to invoke the "different levels" argument to promote the idea that symplesiomorphic features (shared due to common ancestry) were not actually homologous: "but rather of shared primitive characters ('symplesiomorphies'), which are really synapomorphies associated with the wrong level of relationship." We interpret the "wrong level" here to mean the "higher level" of the authors, and "more inclusive" "level of generality" of Brower and de Pinna. Because none of the authors promoting this idea provided a graphic illustration of trees to explain it, we present an example in Fig. 1. In this example, *taxon3* and *taxon4* share a symplesiomorphy (green character state) in Fig. 1a, which of course under our and Wiley's definition (contra Brower and de Pinna) is homology, given that their common ancestor also shared that state in the most parsimonious optimization. In Fig. 1b, we have added more taxa so we can see what the tree looks like when the "synapomorphy at a higher level" (the "wrong level" of Nelson and Platnick) is shown—which we interpret to mean the presumed point of derivation of the symplesiomorphy from an even more ancient "homologue". Although Brower and de Pinna would not accept the green state as a homology uniting *taxon3* and *taxon4* in Fig. 1a, apparently it is now a synapomorphy at a higher level in Fig. 1b, and thus when comparing *taxon3* and *taxon4* it is a homology, even though it is still a symplesiomorphy for the taxa that share it. Thus, by only asking the question: is the green character state a homology of *taxon3* and *taxon4*, we are somehow transported from the conclusion that it is NOT homologous because we are looking at a smaller

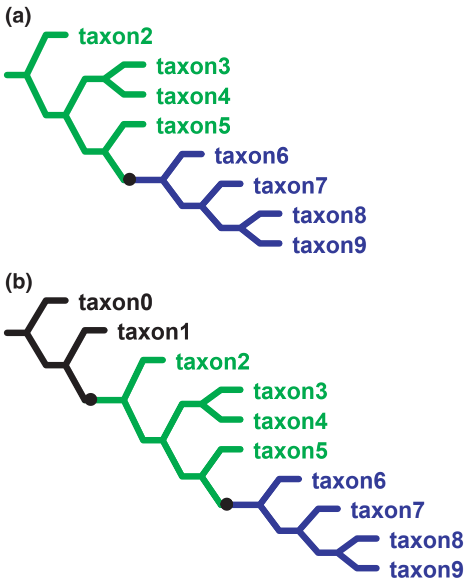

Fig. 1. (a) Example of "wrong level" in interpretation of homology. Green represents optimization of a symplesiomorphy and blue represents optimization of a synapomorphy. In this case, the green state shared by taxon3 and taxon4 is not homologous, according to Brower and de Pinna, even though it is shared due to common ancestry. (b) Example in (a) with additional taxa added. Green represents optimization of a symplesiomorphy, blue represents optimization of a synapomorphy, and black is the character state of the additional taxa. The green character state is now a "synapomoprhy at a higher level" and thus we presume that Brower and de Pinna would now call its presence in taxon3 and taxon4 homologous, because it is at a "higher level"—even though nothing has changed in the comparison.

tree, to it IS homologous in the same tree with taxa added to the base that do not share the character in question. This, of course, assumes that we are correctly interpreting the meaning of "higher level" or "more inclusive" from the vague, imprecise and confused explanations of the several independent thinkers Nelson and Platnick, and Brower and de Pinna. We feel compelled to repeat here the simple observation that homology is a matter of comparison of two character states among two or more taxa, and taxa outside the realm of comparison have no logical bearing on the decision unless they are part of the most recent descendancy (i.e. from the most recent common ancestor). Thus it is with both consternation and concern about the logical framework of these authors that we observe that they embrace shifting definitions in which shared features due to common ancestry (symplesiomorphies) are not homologous in one tree, but become homologous by adding taxa outside the immediate minimal lineage of the taxa being compared. We are taken on a(n) (il)logical rollercoaster that changes the definition of homology depending on irrelevant and possibly unknowable comparisons. We go from (1) symplesiomorphy is not homology and (2) symplesiomorphy is not equal to synapomorphy and (3) homology is only synapomorphy and (4) symplesiomorphy is not homology to (5) simultaneously (depending on which part of the tree we squint at) symplesiomorphy is really synapomorphy and (6) therefore symplesiomorphy is homology. Assertions 5 and 6 negate assertions 1, 2, 3 and 4. During this illogical and self-negating path, we are also forced to ignore the simple, clear definition of homology as a shared condition due to common ancestry. Theirs is merely a flawed and unnecessary redefinition of homology, not a discovery of its fundamental nature. If Brower and de Pinna wish to cast their redefinition of homology as a "fundamental idea" then they should make it consistent and reject the commonly used and accepted definition of homology, as the redefinition is indeed new, different, and inconsistent. They cannot have it both ways—to redefine homology by restricting it to equivalence with synapomorphy, and then claim that it is the same old homology as before. If they continue to embrace these concepts, then they need to explicitly reject the modern definition of homology that is based on common ancestry, because in their view common ancestry is insufficient for homology, and rephrase it this way: "homologous features are only shared *derived* features due to common ancestry and exclude shared plesiomorphic features due to common ancestry." Of course, such a definition has no value, because it merely eliminates a useful concept and makes it equivalent to an existing narrower concept for no particular reason other than the authors' obvious confusion about the way we construct trees in a post-Hennigian world. They continue to insist that they are not redefining homology, but are instead discovering a (*faux*) fundamental principle—a principle which is neither fundamental nor consistent with the way we do parsimony with Farrisian cladistics.

Another overlooked consequence of the Nelson–Patterson redefinition of homology to exclude symplesiomorphy is the unintended affect it has on the concept of homoplasy. Under a standard (logical) definition, homoplasy refers to features that are shared but are not homologous. If (given a particular tree) symplesiomorphy is not homology, then we would logically need to redefine the term homoplasy as well, because the occurrence of shared features that are uncontradicted symplesiomorphies does not constitute homoplasy (at least in a logically applied framework). Thus, the conflation of homology and synapomorphy renders the term homoplasy ambiguous as well.

More on transformations

Hennig considered the transformation series as an assumption when designating a synapomorphy. Hennig's

(1966, p. 89) definition of symplesiomorphy and synapomorphy is clear: ‘‘We call the presence of plesiomorphous characters in different species *symplesiomorphy*, the presence of apomorphous characters *synapomorphy*, always with the assumption that the compared characters belong to one and the same transformation series.’’ In contrast, Brower and de Pinna define synapomorphies as ‘‘character state transformations that support clades’’. This shifts the definition from comparison of states (homologues) in two or more taxa, to the implied transformation. In so doing, they divorce synapomorphy from observation and comparison among taxa and change it to hypothesizing about character transformation—of course, an evolutionary process. Both traditionally and in our world, homology, symplesiomorphy, and synapomorphy are all based on observation and comparison, with the simplest explanation (ancestry), not conjecture of transformation, which follows from (explains), not determines, synapomorphy.

More on absences

Brower and de Pinna also seem confused about the nature of absences in cladistic analysis. A statement of homology is simply that: that the state (as scored) in two or more terminal taxa is shared due to common ancestry. Only cladistic analysis (e.g. parsimony) can determine where optimized character changes occur and whether the absence may be symplesiomorphic, synapomorphic, or have multiple origins on a given tree. In all cases, by defining a state as ‘‘absence of x’’ and scoring it as the same (absent) in two or more terminals, we are hypothesizing that it was absent in the common ancestor and intervening descendants that link the two terminals. An analysis may support this (the state is mapped as homologous) or it may negate this in part or rarely even entirely (if the retention index is 0). Brower and de Pinna and other authors, most notably Nelson (1978), have conflated the uncertain nature of absence with something more fundamental. Simply said, presence without absence is uninformative (but, given the matrix transformations of 3TA, it is not surprising that Nelson misses this point). All working cladists understand that some kinds of presence–absence data are difficult to score with certainty—and indeed, Nelson and Platnick (1981) placed much import on this. All characters are constructs, defined by the architect of the matrix, and as such (more often in the case of morphology), we know little or nothing about the underlying genetic codes that determine presence or absence. In the more straightforward case of indels in DNA sequence data, the condition of absence or presence of a piece of DNA is resolved by parsimony such that the absence may be apomorphic or plesiomorphic. In either case, the condition of not having the segment of DNA, when any two taxa are compared, can be determined to be homologous—their ancestor did not have it either—or independently derived. There is nothing mysterious about this. There is no alternative to coding this way. There is no need here to discuss coding of indels and the various available options, none of which is completely satisfactory, and none of which negates the basic way in which parsimony evaluates hypotheses of homology—sameness due to common descent, whether it is presence and absence or two or more alternative states.

More on roots

Brower and de Pinna claim that our discussion of rooting is ‘‘an incomplete representation’’. As an ‘‘argument’’ they offer the astonishing statement, ‘‘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.’’ They then proceed through a long passage with allusions to roots as variously ‘‘immaterial entities’’, ‘‘uniquely special’’, ‘‘real’’, ‘‘joker’’, ‘‘puppet’’, and ‘‘phylogenetic zombie’’, accompanied by non-parsimonious optimizations of our hypothetical examples, that all are supposed to support the assertion that ‘‘Rooting is not a neutral procedure.’’ This passage could only have been written by someone unfamiliar with how character optimization actually operates. All we can really say is: what? Adding a new root is adding new data, changing both the matrix and the tree, and in our discussions we were not talking about imagined additional data, nor trees generated by such data. Although we concede the obvious, that adding a root or any additional taxa may change optimizations on a tree, this is not relevant to anything discussed in our paper, and it is puzzling that Brower and de Pinna would devote such confusing hyperbole to the topic. The effect of either a hypothetical root or adding another taxon as a real root is non-existent in the context of whether symplesiomorphies, as optimized on a particular tree, meet the criterion of evolutionary homology.

More on primary and secondary homology: bat country

Brower and de Pinna do not like (of course) our suggestion that the terminology ‘‘primary homology’’ and ‘‘secondary homology’’ is unfortunate. We suggested this because it is based on an inconsistent (restricted) definition of homology, as = synapomorphy. The inconsistency is readily seen. If characters in matrices are ‘‘primary homologies’’ and then some become ‘‘secondary’’ homologies after the analysis (those that have ‘‘passed the test’’), then unless parsimony somehow treats apomorphies and plesiomorphies differently (which it does not), how can symplesiomorphies not be homologies (they passed the test, after all, and do not have any extra steps)? If "secondary homologies" are only synapomorphies, then are primary homologies equivalent to all shared identical character states? Perhaps most importantly, if these primary homologies are tested and only some pass, how are they not hypotheses of homology? In the world of most scientists, something that is proposed and then tested is an hypothesis, not a "primary something". If parsimony actually operates the same whether a character is scored as a 0 or 1, and A, C, G or T, then how can it be that only synapomorphies pass the test to become homologous on the tree? If only synapomorphies are homologous and symplesiomorphies are not, then why do symplesiomorphies fit the definition of homology? If symplesiomorphies are not homologies at one level because they exclude some derived states then why are they suddenly homologies at a "higher level" when they exclude precisely the same states? If symplesiomorphies are synapomorphies at a higher level and synapomorphies = homology then why are symplesiomorphies not homologies? Look out! The bats are getting closer!

More on 3TA

Although Brower and de Pinna would appear to distance themselves from three-taxon analysis (3TA) in their present paper, that was not always the case: "Another point in favor of three-item analysis is that it goes a step further toward eliminating symplesiomorphy as basis for grouping. On any data matrix analyzed by traditional methods, a group may appear as monophyletic by the common possession of primitive states only. This happens when other synapomorphies force those plesiomorphies to behave as reversals." (de Pinna, 1996, p. 11). Perhaps this is the real source of the "misplaced" accusations of pheneticism mentioned by Brower and de Pinna. Be that as it may, pattern cladistics in recent years has been tied directly to 3TA. Nelson and Platnick (1981), favourably cited by Brower and de Pinna for the equivalence of homology and synapomorphy, could be considered the first manifesto of 3TA, as is more than evident on pp. 254–255: "The minimum mode, then, is a suite of 3-taxon problems that, once solved, result in the informative components of the cladogram that, with respect to a certain sample of information, is the true and final resolution. Thus a cladogram is definable in two different, but related, senses: (i) as a suite of components; (ii) as a suite of 3-taxon problems for which the solutions are the suite of components." The same ideas that resulted in the unfortunate development and promotion of 3TA are also evident in Brower and de Pinna's argumentation. And, like Brower and de Pinna, Nelson and Platnick (1981, p. 246) also experimented with falsehoods about preceding icons: "That cladograms for large groups have been achieved without the aid of a computer (e.g., Hennig 1969) suggests that the 3-taxon approach was either the method of choice or the method intuitively applied." Allow us to retort: it suggests nothing of the kind.

More on pattern cladists

It is clear that the critique by Brower and de Pinna (2012) is an effort to defend the failed approach of pattern cladistics from any and all efforts to introduce even the simplest hypothesis of evolution into the gathering of data for phylogenetic analysis. There is a final, ordinary inconsistency to point out here. As they state: "Common ancestry is the a posteriori explanation of the congruent pattern of features shared among taxa discovered by systematic analysis." Indeed—and common ancestry is usually also part of the concept of homology that motivates the data gathering in the first place. If one does not have a question or hypothesis, this is not science, it is simple description, and it is uncertain what is being described. Pattern cladists give evolutionary interpretation to the *results* of phylogenetic analysis—in this sense, they are not creationists [which was not our charge anyway, it was Farris's (2011)], merely inconsistent. But, we realize that pattern cladists are not really what they say they are, and actually do select characters that have some reasonable chance of being evolutionary homologies, or in other words, are hypotheses of such.

Acknowledgements

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