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A Response to Mooi, Williams and Gill*

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We thank the editor of this special series in allowing us a short response to Mooi, Williams and Gill (2011). The space allocated for this rebuttal is small, so we address only the basic points, organized by their major headings.

Algorithms and Character Selection as Authority

Mooi et al. again suggest that finding trees under various universally-used optimality criteria is “authority.” We reject this argument. Their alternative of picking “good” characters that happen to evolve at a certain rate is equally authoritarian (indeed, it is easy to characterize just about any method as “authoritarian” because, well, it’s a method; the only thing fully immune from the charge of “authoritarianism” is doing nothing). To explain: the usual manner in which characters are selected for morphological analysis follows three basic steps. (1) Characters that display random variation or as much variation within taxa as between taxa in an analysis are typically discarded. (2) Characters that show no variation between taxa in the study are discarded. (3) Characters that do not meet the above criteria but which are shared between two to N-1 taxa in the study are analyzed. This amounts to a rate model of evolution. We don’t see any particular problem with adopting such models, but investigators should recognize them as models with their own optimality criteria. We might term it the “screen data for usefulness model.” Mooi et al. argue in favor of a particular brand of this model, Three-Taxon Analysis (3ta), in which characters that change only once (i.e., without reversals) are chosen. We explain below why taking this course would be restrictive and misguided.

Outgroup Comparisons

Mooi et al., in their reply, assert—but do not demonstrate—that outgroups are used ineffectively. Their assertion that “Choice of outgroup is made moot by optimization methods in any event, as all variation (apomorphic, symplesiomorphic and homoplastic) is employed to construct trees” is made without reference to any supporting data. In fact, examination of the data and algorithms clearly shows that only synapomorphies are employed to construct trees in parsimony. Of course, some of these synapomorphies may come in the form of “reversals” and some will

be “unique and unreversed” characters. We recognize that it is true that branch lengths influence how characters are treated using likelihood methods, but again, this is a matter of whether or not one entertains reversals as evidence, not a matter of whether outgroups are used effectively.

Methodology and Phenetics

Mooi et al. assert that the four methods outlined in Wiley et al. group by both plesiomorphy as well as apomorphy. We fail to see this assertion demonstrated. Mooi et al. offer only the false assertion that, because “0” must mean something, we would group taxa with the code “0” together. Naturally, we would do no such thing if the “0” was a plesiomorphy. Only if the “0” was an apomorphic homology as shown by the weight of all other characters in the analysis (i.e., 0 is a reversal) would we use such a character, following Hennig’s lead. In any case, we always strive to recover clades by synapomorphy, never by symplesiomorphy or some combination of plesiomorphy and apomorphy; after all, we are neither pheneticists nor “gradists.”

Optimization and Argumentation: Are they the same?

Mooi et al. fail to demonstrate that optimizing is different from traditional character argumentation. Instead they argue that, in the face of ambiguous data, parsimony results in ambiguous answers, leading them to conclude that 3ta is a superior alternative. In their example, classical Hennigian argumentation would produce similarly ambiguous results, and likelihood-based methods would report ambiguous probabilities. Ambiguity providing poor resolution in this case is an accurate result, not a bad one: we get out of our data only what the data themselves have to say. That 3ta produces an unambiguous answer in the face of ambiguous data simply demonstrates that 3ta is not a phylogenetic method. Their example from Goloboff et al. (2003) only shows their aversion to considering reversals of initially coded characters; the evidence for the monophyly of the clade EFGH is the synapomorphy 1(0), that is, the character stated coded “0” for EFGH in data column “1.” Now one might question if the 1(0) is really the same as the 1(0) found in A, a philosophical argument for some kinds of characters that depends on your evolutionary assumptions and concepts of identity (see Wiley, 2008). If you analyze allozymes and entertain the infinite alleles model, then the 1(0) is not a reversal to the original 1(0), but a new allozyme with a similar mobility. If you are a morphologist you might do well to carefully inspect the 1(0) of E, F, and G to see if it is really the same character in samples of these taxa. If you are a molecular systematist where 1(0) = A and 1(1) = G, then it is a “true” reversal since A, T, C and G comprise classes of molecules, like the classes H₂O and O₂. But the point is that, if we accept the tree hypothesis, something during evolutionary descent has happened: 1(1) has transformed to 1(0). The only way around this is to adopt a particular evolutionary model, the Dollo model of irreversibility, and conclude that 1(0) coding is coding different characters with different identities that you, the investigator, have conflated with your initial coding. Naturally, Dollo assumptions amount to adopting a particular model of process. For Hennig’s view, see Hennig (1966: 116).

On Zeroes: Transformational Homology, Symplesiomorphy and Reversals;

And Homologue vs. Homology

Gary Nelson (1994) might assert that homologies are parts of organisms, but this does not mean that he is correct. Mooi et al. discuss Nelson as if he were the final arbiter of the nature of homology. Most of us conceive of homology as a hypothesis that describes the relationships between parts of different individual organisms and Wiley (2008) described them as properties of monophyletic groups at some level of the hierarchy. Of course, both Michael Ghiselin (1984) and Willi Hennig (1966: 120) said this long before Wiley. And, if we are to think about the deeper biological properties of characters, we may come to the conclusion that the “real” homologies we are seeking reside in the information that specifies the characters we study since it is that information, and not the characters themselves, that are passed, modified and unmodified, from generation to generation (e. g. Van Valen, 1982; Brooks and Wiley, 1986; Haszprunar, 1992; Roth, 1994). We leave it to the reader to decide which metaphysics is more suitable for an evolutionary research program such as Phylogenetic Systematics.

Transformational Homology versus Hierarchical Relationship

With regard to 0: yes, “0” in this regard means having pectoral fins and the hypothesis is that the ancestral species of all gnathostomes had pectoral fins, meaning that the ancestor of all chordates did not have pectoral fins. At the level of Chordata, having pectoral fins and having legs are both synapomorphies, one at one level and the other at a less inclusive level in the hierarchy. The possession of pectoral fins does not imply a relationship at the hierarchical level at which pectoral fins are plesiomorphic. It is the hypothesis that the information that specifies pectoral fins is transformed into the information that specifies legs that leads us to conclude that Gnathostomata and Tetrapoda are at the same time nested clades in terms of their appendages. Lungfish pectoral fins do have a single articulation with the shoulder girdle that is somewhat like tetrapods; this is taken by some as evidence that lungfishes are sarcopterygians. The ancestral gnathostome is not hypothesized to have both pectoral fins and front legs. Pectoral fins are still homologous among gobies and basses even if the level of universality of the problem to be solved does not reach that where pectoral fins are apomorphic and this does not imply that gobies and basses form a clade apart from sharks and tetrapods based on possession of pectoral fins. We fail to see why this presents a problem. The fact that the coding at the level of teleostomes (gnathostomes in a less inclusive clade of gnathostomes) is coded 0: for purposes of an analysis is simply an expedient since we are not raising the level of inquiry (Wiley, 1975) to the level where we would code unmodified body wall = 0, pectoral fins = 1, loss of pectoral fins = 2, legs = 3, and loss of legs = 4; or whatever coding scheme captures the variation. We assume that the hypothesis of pectoral fin homology has already been tested; because pectoral fins meet various initial criteria (such as those outlined by Remane, 1956, and discussed by Wiley, 1981, Patterson, 1982, and others) and the phylogenetic criterion, pectoral fins are hypothesized properties of Gnathostomata. Having performed that test, we can assume pectoral fin homology at lower levels of the hierarchy as a background assumption (see Wiley, 1975, 2008). Certainly, Hennig (1966:120) had the same concept, though we do not call him out as an authority but simply someone who shared our views of characters and biological hierarchies.

Hennig’s Auxiliary Principle

Yes, Hennig (1966:121) said exactly what Mooi et al. state, but they do not seem to recognize that a particular alignment is, in fact, a hypothesis that each column of data comprises bases hypothesized to be homologous, that each column of data then forms a transformation series, and that outgroup analysis sorts out the apomorphies from the plesiomorphies. We demonstrated how ancestral states reconstruction can be used to show the presence of *particular* derived nucleotides at *specific* nodes and the probabilities of transformation *at those nodes*. Mooi et al. do not counter this demonstration by citing specific shortcomings; instead, they simply assert that the method is flawed. So precisely what is the problem—the First Principles problem, that is—not the shortcomings of individual investigators, as those shortcomings are envisioned by Mooi et al.?

Dealing with Conflict

We concur that characters should be carefully evaluated before an analysis, but apriori polarization is not necessary to perform a perfectly acceptable phylogenetic analysis (i.e., an analysis that groups terminal taxa into hypothesized monophyletic clades by synapomorphy). We certainly agree with Morrison (2009) and suggest that this is exactly what molecular systematists have been doing, or at least attempting to do. The claim that “no distinction is made between apomorphic and plesiomorphic characters” is inaccurate; no distinction is made apriori, but distinction is certainly made aposteriori by rooting the tree with one or more outgroups. Mooi et al. do not seem to understand modern algorithms and how they work. We do not have to trick programs into using only apomorphies by pretending that there are no plesiomorphies, as if fishes had no pectoral fins when analyzed with tetrapods. Zero (“0”) can, and does, mean something other than “not having 1.”

The Usefulness of Support Measures

Character 1 (i.e., the first column of data) is not acting in an odd way—unless, of course, reversal of initial homology statements is considered “odd.” There simply is a reversal during evolution to an initially investigator-coded symbol; see remarks above.

Increased Objectivity : “Alignment differences aside, one may also question whether it is appropriate to simply map characters on to solutions (trees) and claim that this procedure somehow identifies evidence (synapomorphies).”

Mapping is absolutely appropriate if the mapping is a mapping of synapomorphies. Optimization is simply the action of placing synapomorphies at nodes where they corroborate monophyletic groups. One can optimize characters on any given tree topology, but only that topology that maximizes synapomorphy and minimizes homoplasy is considered the optimal tree topology under the parsimony criterion (Farris, 1983), and only the tree that maximizes the likelihood of observing the data (given the model and tree topology) is considered the optimal tree topology under the likelihood criterion. Naturally, you have to specify a root that is the polarizing outgroup. Mooi et al.’s preferred alternative, 3ta, uses only apriori-polarized transformation series, discards data, treats plesiomorphic homologues as if they did not exist in organisms where we can observe them, adopts a Dollo model of evolution, and does not recognize the possibility that reversals of initially coded characters might obtain, or if it does so (as in Carine and Scotland’s, 1999, version), allows plesiomorphies to be treated as synapomorphies (see a sample of critiques that address these points by Farris and Kluge, 1998; Kluge and Farris, 1999, Farris, 2010). Three-taxon analysis is based on “Assumption 2,” which was originally applied to area cladogram analysis. Assumption 2 in biogeography allows groups corroborated by synapomorphies to be treated in an area cladogram analysis as if they were either paraphyletic or polyphyletic. We leave it to the reader to judge whether or not such treatment of data is warranted. To our minds, it is not.

Discussion

One may wonder why Mooi et al. reject the very foundations of evolutionary biology by calling up Gary Nelson’s assertions that character transformation and ancestry are myths to be discarded. One answer is that at least one of them (Williams) does not even consider himself to be “Hennigian,” but rather a “pattern Cladist” who does not use “Concepts such as character rooting and synapomorphies” and who counts likelihood and Bayesians advocates as among the “gradists” along with Mayr and Simpson and includes the gradists among those within Phylogenetic Systematics community (Ebach et al., 2009: 154). This is, to our mind, sweepingly Orwellian. Their attitude apparently is due to the fact that we do not “see” transformation or “see” ancestral species. Of course, no one has actually “seen” a chemical reaction or the true relationships among organisms. What we actually see is the effect of a chemical reaction, and what we see as the effects of ancestry and character transformation is simple: we see a tree of life that is largely hierarchical and ever divergent. What we “see” are the effects of the evolution of life on Earth.

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