Letter to the Editor

More on homology

Sir,

"Galileo, Galileo" (Queen, Bohemian Rhapsody)

The response by Williams and Ebach (in press [b]) to "On Homology" (Nixon and Carpenter, in press) provides a welcome opportunity to further distance mainstream parsimony analysis from methods that reject evidence on the basis of presupposed knowledge of the direction of evolution. The casual reader might conclude that whether one wishes to state that two parts are homologs, or state this as a hypothesis of homology, is a matter of semantic convention, and has no bearing on the underlying concepts of homology and parsimony. But there is a real debate here, and it is not over nuance of terminology, and should not involve the unnecessary and distracting injection of Williams and Ebach's "philosophy" into what is an argument over methodology. The use of quasi-philosophical distraction has resulted in the sidelining of many important issues in cladistics, through the bludgeoning of readers into disinterest as a result of obscuring important points with hyperbole. Williams and Ebach focused their attack on our terminology, even though it was consistent with numerous preceding papers that they failed to mention (e.g. Patterson, 1982). The focus on semantics may thus be dismissed as merely an effort to cloak their real concern—the impact of accepting potential plesiomorphies as evidence that must be explained. The basis of their resistance is clear—acceptance of *all* observed character data as evidence (the way in which mainstream cladistics operates)—is completely counter to their favorite methodology, three-taxon analysis (see Nelson and Platnick, 1991; for detailed explication, see Farris's (2011) review of Williams and Ebach, 2008).

Our premise was a simple one—and was not addressed by Williams and Ebach (in press [b])—except for their continued and deceptive attempt to equate numerical cladistics with phenetics. This misguidance is now old news—they were called out on this particular equivocation by Farris (2011), in his review of Williams and Ebach (2008), and Brower (in press). Farris also

documented numerous other examples by those authors of deception, evasion and imaginary history, in so blatant a manner as to well merit the term "double-think". Their recent response to Brower (Williams and Ebach (in press [a])) carefully avoids mention of any of this, but illustrates that the attempted deception continues. Williams and Ebach's (in press [b]) present effort is no better. To put it simply, three-taxon analysis (3-ta) is an outgrowth of pre-Farrisian cladistics, and even so misconstrues Hennig's (1966) definition, usage and understanding of homology. All of it should have stayed on the barroom napkins on which it was first drawn into existence. But alas, it refuses to die, and continues to be disseminated by philosophical "walkers" who remain a danger to unsuspecting students, who might misconstrue 3-ta as a valid method of analysis.

We can repeat our basic premise, the premise of parsimony analysis as currently implemented: yes, synapomorphy is a kind of homology (and synapomorphous parts are kinds of homologs). However, the two are not equivalent (contra Patterson and others), because symplesiomorphy is also homology (and symplesiomorphous parts are also homologs). Parsimony analysis minimizes homoplasy, whether it occurs in apomorphic or plesiomorphic states, and indeed, it is irrelevant which is which during branch-swapping and selection of most parsimonious trees. Hennig and Farris (both of whom Williams and Ebach, 2008, claimed to be reacting against) understood the nature of both synapomorphy and symplesiomorphy, and Farris implemented this premise in his development of the modern method of parsimony analysis (Kluge and Farris, 1969; Farris, 1970). This was the beginning of post-Hennigian, modern cladistics. Since that revelation, we no longer "group by synapomorphy" nor construct trees by hand; instead, we read synapomorphies from trees that minimize homoplasy over all character states, be they zeros or ones, A, C, G or T. This requires accounting for all evidence of descent, not just synapomorphy, as Farris (1983, p. 18) pointed out:

A genealogy is able to explain observed points of similarity among organisms just when it can account for them as identical by virtue of inheritance from a common ancestor.

Why this simple and logical approach to cladistic analysis, already the mainstream tree construction method for decades, is so misunderstood even by those who employ it regularly is quite incomprehensible. In parsimony analysis, observed points of similarity are scored as character states that may later become interpreted as symplesiomorphies, synapomorphies, secondary plesiomorphies (reversals), and various levels and conditions of non-homology (homoplasy). There is no distinction between symplesiomorphy and synapomorphy as evidence of relationship during an analysis—by rooting a tree (see Nixon and Carpenter, 1993), we determine which groups are monophyletic and which character states are synapomorphies for those groups. This is what we (but not Nelson, Platnick, Williams, Ebach and other proponents of 3-ta) have done for the past four decades in cladistic analysis, and our paper on homology only clarifies the obvious relationship between homology and parsimony—something that may never become apparent for Williams and Ebach.

Strangely, proponents of 3-ta believe they are avoiding unnecessary assumptions about evolution, and that method is now closely tied to "pattern cladistics" and often favorably cited by creationists and others who deny evolution. Of course, the opposite is true—believing that one must not account for evidence of similarity reflected in perceived symplesiomorphies requires the belief (charitably viewed as an assumption) that evolution occurs in a particular, rather odd way—and that only synapomorphies are due to common ancestry. If we minimize homoplasy only among synapomorphies, then we must believe that synapomophries change less than symplesiomorphies, or that an extra step in a plesiomorphic state should have less weight than one in an apomorphic state. Clearly, the belief that only synapomorphies must be accounted for requires a particular model of evolution, that derived features change less than ancestral features. Hence, as pointed out by several authors independently (e.g. Kluge, 1993; Deleporte, 1996; Farris, 1997), 3-ta favours irreversibility of characters, an evolutionary model once again.

Perhaps if Nelson, Platnick, Williams and Ebach had understood Farris (1983) they would have avoided the logical, philosophical and methodological errors embodied in 3-taxon analysis, and the community would not be saddled with such fruitless distractions. Farris' prescient paper pointed out every major flaw in 3-ta before it was published (e.g. the need to include plesiomorphies as evidence, the fallacy of pairwise counting of homoplasies, and the dead-end of character irreversibility, among others). One might even suspect that Farris had obtained a copy of the original 3-ta manuscript long before it was published and craftily countered it before it was born. But of course, that was unnecessary, because Farris (1983) only presented the (now obvious) logical basis of phylogenetic analysis—which precludes the development of methods that have no obvious (or even obscure) logical basis. But alas, the game of quasi-philosophical wack-a-mole continues.

Acknowledgements

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Kevin C. Nixon[a] and James M. Carpenter[b]
[a]*Bailey Hortorium, Cornell University, Ithaca, NY 14853, USA;* [b]*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA*
E-mail address: kcn2@cornell.edu