



Why we shouldn't let sleeping dogmas lie: a partial reply to Craig*

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Now, when I have spoken on these matters in the past, it has sounded to some as if I had taken upon myself the task of denigrating paleontology and individual paleontologists. That is not so. I am concerned with what I find is a real problem.—Nelson, 1969 in Williams and Ebach, 2004: 711

We were reticent to respond to Craig (2011), for worry that this might lead to an ongoing, futile exchange on who does and who does not understand homology and the workings of systematics. No reply, too, would be a reply of a sort. However, Craig's missive provides an opportunity to explore additional aspects of the issues/crises at hand. Before we do so, we would point out that in Mooi & Gill (2010a) we did not say that molecules cannot provide homology (as Craig implied), but instead argued that current popular methods are phenetic and do not discover this homology. Numerical methods do not differentiate homology from homoplasy in morphology consistently, either, and thus are a disservice to the molecular and morphological evidence; the phenograms produced do not necessarily appropriately or accurately reflect the relationships the data can provide.

Craig (2011) begins with an acknowledgment that it is a good idea to challenge dogmatic thinking – just so long as it is not his dogma (“long-settled debates”). This is reminiscent of a comment by an anonymous *Molecular Phylogenetics and Evolution* reviewer of a rejected manuscript discussing similar issues where the main criticism was that we (with others) had the audacity to write a paper where “Its purpose is to question the foundation of molecular phylogenetics, a well-established field.” Craig and that reviewer would prefer we let sleeping dogmas lie. It is ironic that in other exchanges (Mooi & Gill 2010b, contra Smith 2010; Gill & Mooi 2011 contra Wiley *et al.* 2011) we are labeled as dogmatic, whereas Craig chastised us for attacking dogmatism.

The single paragraph history of the term homology in Craig (2011) finished with what amounted to a case closed (perhaps one of the “long-settled debates” p. 38). The issues of homologue and homology have been examined for over 150 years in comparative biology and systematics and, using other terminology, some would argue for several hundred years before that (Williams & Ebach, 2008). Contrary to Craig's claims, we are well aware of the efforts to apply notions of molecular homology within the numerical cladistic paradigm, and it is that embrace of numerical cladistics that we had commented on. We note that there has been considerable discussion regarding homology since Craig's favoured source on the matter, Patterson (1988). In Patterson (1988: 621) there are some statements that deserve reflection: “In molecular phylogenetics, there is no exact equation between homology and synapomorphy...”. And Craig (2011: 39) misread Patterson in suggesting “Homology in sequence data may be detected in *ways* that are not possible with morphological data (Patterson 1988)” (our italics). Patterson (1988: 610, our italics) actually stated: “Molecular sequence homology is ‘detectable’ in *a way* that morphological homology is not, primarily because molecular sequences are one-dimensional.” We read his comments on the one-dimensionality of gene sequences (“...an Adenine is an Adenine...and so forth” of Craig 2011: 39) as a disadvantage of these data, not an advantage. At least some molecular workers agree: “There is an oft-repeated claim that sequences are easier to deal with than phenotypic characters because DNA sequences consist of only 4 types of nucleotides. However, it is straightforward to see that this fact makes homology assessment harder, not easier” (Morrison 2009:

155). Regardless, Patterson's views on homology and on the relative worth of molecular and morphological data hardly remained static (Patterson 1983; Lewin 1998; Patterson 2011). Nelson (1994), who has considered notions of homology longer and in more depth than most, continues to find much of interest in exploration of the topic (Nelson 2011). We encourage exploration of even the fundamentals, the 'givens', of numerical/statistical systematics and systematics in general. It behooves us to remain open to the possibility that some methods might not be applying cladistic principles. If, for example, Felsenstein (2004: 145) is correct in removing the distinction between 'cladistic' and 'phenetic' methods in numerical systematics, then perhaps none is cladistic.

Craig (2011: 38) suggested that, "However one treats a statement of homology, there is a need to test the statement, and if a statement is testable, it is, by definition, a hypothesis." So what *is* the hypothesis that requires testing? Presumably that a statement of homology = evidence of relationship. Here is a column from a molecular alignment:

Outgroup	A
Taxon 1	A
Taxon 2	A
Taxon 3	C
Taxon 4	C

The statement of homology should be 12(34), but analysis of the matrix can allow the relationship (12)34 or (12)(34) to prevail should the process of optimization require a 'reversal' to fit all characters to an optimal tree. So where, in optimization, is the statement? Where is the testing when the character is merely mapped onto a tree? The hypothesis of homology, as expressed in the modern matrix, is phenetic in that it doesn't specify any particular taxon relationships. The point of our review (Mooi & Gill 2010a) was that optimization is not a viable substitute for testing hypotheses of homology. When confronted by this shifting and plastic view of evidence where homologies become homoplasies and vice versa, Craig (2011: 39) responded, "Of course they do...If one adds taxa to an existing matrix, and new data derived from them help us to realize a more cogent and logical transformation series, why should we be tied to a previous hypothesis?" What are these "more cogent and logical transformation series"? We might challenge Craig to provide a comparative list of these transformation series from one study to the next and defend their relative logic; such is never presented in numerical systematics. To us, these transformations are not more logical, just different, and are not related to any initial statement of homology. To continually reinterpret characters on any given tree makes them, in essence, always 'true'; in numerical systematics, statements of 'homology' are produced to fit the tree.

Commenting on an aging morphological study by Johnson (1983—a computer with a 20kb hard drive was a wonder at that juncture!), Craig (2011: 39) lamented, "no character matrix was presented that could be used to test his hypotheses of synapomorphy, and without a complete list of materials examined, it is nearly impossible to repeat his study or know the entire distribution of character states." One might wonder where such an "entire distribution of character states" is to be found in molecular analyses, noting that sequences without alignment do not provide character states. Similarly, Craig (2011: 39; italics original) suggested that Gill and Mooi (2010), in a study of microdesmine systematics, "...provided no *test* of their hypotheses of homology. There is no phylogenetic tree, no explicit transformation series, and no identification of a sister group by which their characters were polarized." In essence, Craig is complaining that neither Johnson (1983) nor Gill and Mooi (2010) provided a matrix that he could manipulate with a statistical program. Disputes with the data need the specimens, not the matrix; homologues are to be found in specimens. The matrix and its various transformations in statistical programs are algorithmic doodlings.

Craig (2011: 39) is concerned that Gill and Mooi (2010) provided synapomorphies for microdesmines based only on "intimate knowledge" of character distributions within that group, and that by not specifying a particular sister taxon "the characters may very well be present in the sister group or have been reversed in a subclass [?] that they excluded." As for the last point, we are not aware of any methods (even numerical) that might exclude the possibility of features occurring in taxa that had not been examined. However, we would extend that claim of "intimate knowledge" beyond the boundaries of microdesmines to gobioids in general. The suborder is perhaps the most thoroughly corroborated monophyletic higher taxon among acanthomorphs (Springer 1983; Winterbottom 1993; Johnson & Brothers 1993), and although the finer points of gobioid phylogeny have yet to be ascertained, morphological (and molecular) work has consistently placed microdesmines deeply within the Gobioidae (Hoese & Gill

1993; Thacker 2003, 2009). As noted in our paper, we had examined over one half of the 300 or so genera in the suborder, including representatives of all recognized major phenetic groupings (Birdsong *et al.* 1988). Several of our listed and described synapomorphies are unique to the Microdesminae among *all* gobioids; a specified sister taxon is irrelevant to these hypotheses. Would it be preferable that we survey very distantly related acanthomorph taxa such as *Beryx* or *Polymixia* to 'root' our tree? Other synapomorphies we proposed could be interpreted as occurring in other gobioid taxa, although very rarely or in somewhat modified form, and for these we provided a thorough accounting of their distribution and anatomical differences, but, admittedly, not interpreted into a matrix. Craig's criticisms bring to mind Williams's (2007: 20) modification of Patterson's original comments on paleontology: "By about 1990 numerical systematists had achieved such a hold on phylogeny reconstruction that there was a commonplace belief that if a group had no numerical analysis its phylogeny was totally unknown and unknowable."

So how would Craig approach the examination of microdesmine monophyly with molecular/numerical methods? How would he identify a sister group? Would his survey include half of all gobioid genera? Would he report the synapomorphies that define microdesmines? Assuming prevailing numerical systematics practice was followed and synapomorphies remained unidentified, what would the statements of homology be and how could they be tested?

The implication that we are responsible for the decline of student interest in systematics cannot be taken seriously (Craig 2011: 40). What is science but a contest of ideas? One might just as easily (and perhaps more fruitfully) correlate the decline in number of systematists with the rise of numerical systematics. Regardless, we did not enter this discussion as anti-molecular nor as anti-numerical systematist; we question the methods in use to understand DNA's contribution to systematics. We opened here with an epigraph quoting Nelson's 1969 remarks on reaction to his critique of paleontology because we feel it reflects a similar reaction to our remarks concerning optimization and numerical cladistics. We are not directing our comments at individuals but at methods. If individuals wish to identify themselves with the methods, that is their prerogative. However, the 'real problem' remains: optimization is phenetic because it does not differentiate homology from homoplasy. We deal with this aspect of the replies of Wiley *et al.* (2011) and Craig (2011) elsewhere (Mooi *et al.* 2011). We look forward to a revolution in numerical systematics that is as stimulating as that initiated by Nelson concerning paleontology. Nelson's paleontological revolution removed ancestors from cladograms; the new revolution, in part, will entail removing ancestral states from character trees: "Seeing characters and their states as trees with only terminals may appear objectionable. Nevertheless, at one time phylogenetic trees with only terminals were also considered objectionable. Fortunately, that time has passed (Patterson, 1987; Nelson, 1994: 128). Ancestral characters (or states) seem much like ancestral taxa: empirically hollow" (Williams 1996: 277).

Nelson and Platnick (1981: 304–5) ably and simply summarized what cladistic systematics should be about: "It would appear, then, that systematics in general consists of the search for defining characters of groups. Admittedly, the search seems to have been abandoned, on occasion, by persons who would search instead for overall phenetic similarity, or overall gradistic similarity. But what justification is there for abandoning the search for defining characters? Certainly we can make mistakes; we may fail to recognize that one character is a modified form of another, and thereby underestimate the generality of the latter one (plesiomorphy), or we may mistakenly consider attributes (such as absences, or physical properties like total length and color) defining characters when they're not. But we do not need to fear such mistakes: should we make them, future research will reveal them quickly enough, through incongruences with other characters. Indeed, one might contend that the utility of the cladograms is precisely that: to point up incongruences and allow us to predict that mistakes have been made, and that more intensive study will reveal them."

We do not see numerical methods meeting these rather straightforward requirements of cladistic systematics. In numerical systematics, defining characters are neither sought nor reported, and incongruence is ignored or, worse, 'reinterpreted' as reversal, as if distorting original homology statements to remove conflict can provide evidence. Is this not crisis enough?

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References

- Birdsong, R.S., Murdy, E.O. & Pezold, F.L. (1988) A study of the vertebral column and median fin osteology in gobioid relationships. *Bulletin of Marine Science*, 42, 174–214.
- Craig, M.T. (2011) The ghost of crises past: a reply to Mooi and Gill. *Zootaxa*, 2946, 38–40.
- Felsenstein, J. (2004) *Inferring Phylogenies*. Sinauer Associates, Sunderland, pp. 664.
- Gill, A.C. & Mooi, R.D. (2010) Character evidence for the monophyly of the Microdesminae, with comments on relationships to *Schindleria* (Teleostei: Gobioidae: Gobiidae). *Zootaxa*, 2442, 51–59.
- Gill, A.C. & Mooi, R.D. (2011) A show of character: a partial response to Wiley et al. *Zootaxa*, 2946, 29–32.
- Hoese, D.F. & Gill, A.C. (1993) Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidae). *Bulletin of Marine Science*, 52, 415–440.
- Johnson, G.D. (1983) *Nippon spinosus*: a primitive epinepheline serranid with comments on the monophyly and intrarelationships of the Serranidae. *Copeia*, 1983, 777–787.
- Johnson, G.D. & Brothers, E.B. (1993) *Schindleria*, a pedomorphic goby (Teleostei: Gobioidae). *Bulletin of Marine Science*, 52, 441–471.
- Lewin, R. (1998) Family feuds. *New Scientist*, 2118 (January 24), 36–40.
- Mooi, R.D. & Gill, A.C. (2010a) Phylogenies without synapomorphies—a crisis in fish systematics: time to show some character. *Zootaxa*, 2450, 26–40.
- Mooi, R.D. & Gill, A.C. (2010b) A transitioning state or harmful mutation in systematic ichthyology? A reply to Chakrabarty. *Copeia*, 2010, 516–519.
- Mooi, R.D., Williams, D.M. & Gill, A.C. (2011) Numerical cladistics, an unintentional refuge for phenetics—a reply to Wiley et al. *Zootaxa*, 2946, 17–28.
- Morrison, D.A. (2009) Why would phylogeneticists ignore computerized sequence alignment? *Systematic Biology*, 58, 150–158.
- Nelson, G.J. (1994) Homology and systematics. In: Hall, B.K. (Ed.). *Homology: The Hierarchical Basis of Comparative Biology*. Academic Press, San Diego, pp. 101–149.
- Nelson, G. (2011) Resemblance as evidence of ancestry. *Zootaxa*, 2946, 137–141.
- Nelson, G.J. & Platnick, N.I. (1981) *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York, pp. 567.
- Patterson, C. (1983) How does ontogeny differ from phylogeny? In: Goodwin, B.C., Holder, N. & Wylie, C.C. (Eds), *Development and Evolution*. Cambridge University Press, Cambridge, pp. 1–31.
- Patterson, C. (1988) Homology in classical and molecular biology. *Molecular Biology and Evolution*, 5, 503–625.
- Patterson, C. (2011) Adventures in the fish trade. *Zootaxa*, 2946, 116–134.
- Smith, W.L. (2010) Promoting resolution of the percomorph bush: a reply to Mooi and Gill. *Copeia*, 2010, 520–524.
- Springer, V.G. (1983) *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussion of gobioid osteology and classification. *Smithsonian Contributions to Zoology*, 390, 1–40.
- Thacker, C.E. (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidae). *Molecular Phylogenetics and Evolution*, 26, 354–368.
- Thacker, C.E. (2009) Phylogeny of Gobioidae and placement within Acanthomorpha, with a new classification and investigation of diversification and character evolution. *Copeia*, 2009, 93–104.
- Wiley, E.O., Chakrabarty, P., Craig, M.T., Davis, M.P., Holcroft, N.I., Mayden, R.L. & Smith, W.L. (2011) Will the real phylogeneticists please stand up? *Zootaxa*, 2946, 7–16.
- Williams, D.M. (1996) Characters and cladograms. *Taxon*, 45, 275–283.
- Williams, D.M. (2007) Whatever happened to cladistics? *The Systematist*, 28, 19–21.
- Williams, D.M. & Ebach, M. (2004) The reform of paleontology and the rise of biogeography: 25 years after ‘Ontogeny, Phylogeny, Paleontology and the Biogenetic law’ (Nelson, 1978). *Journal of Biogeography*, 31, 1–27.
- Williams, D.M. & Ebach, M. (2008) *Foundations of Systematics and Biogeography*. Science and Business Media, New York, 310 pp.
- Winterbottom, R. (1993) Search for the gobioid sister group (Actinopterygii: Percomorpha). *Bulletin of Marine Science*, 52, 395–414.