Promoting Resolution of the Percomorph Bush: A Reply to Mooi and Gill

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''If I'd asked . . . what they wanted, they'd have said a faster horse.''—Henry Ford, discussing innovation and the building of his first automobiles

IN their commentary, abstract, and presentation, Mooi and Gill (2008, 2010) sounded an alarm regarding what they perceive as an impending crisis in systematic ichthyology. This crisis is not impending; we are in the midst of it. At higher levels, systematic ichthyology has been in a stalemate for 35 years for percomorphs and for nearly a century for the ''percoids'' or moronoids. The alarm has been going off for decades, and we are now just beginning to move beyond the crisis through the explicit analysis of datasets aimed at resolving long-standing questions in percomorph systematics (Springer and Orrell, 2004; Smith and Craig, 2007; Thacker, 2009). The phylogenetic hypotheses and resulting changes to the classification recommended by these studies are intriguing and have molecular and/or morphological support, but like all hypotheses, they demand further study. In the future, I hope that Mooi, Gill, and other researchers will examine the evidence for these phylogenetic proposals or propose new evidence-based relationships for other groups. As it stands, Mooi and Gill's (2010) critique is thoughtful, but it does not provide any counter-evidence for a single clade, recommendation, or relationship proposed in the criticized studies; it just protests their existence. The percomorph bush will not resolve itself, and ichthyology will only make progress by incorporating new data and by performing explicit analyses. The days of defending a 100-year-old taxonomic *status quo* that lacks evidence for its decisions are, thankfully, numbered.

Mooi and Gill's (2010) claim that the cause for the impending crisis is ''that the movement from synapomorphy-based topologies to those based on statistical measures has removed the opportunity for rational discussion based on homology.'' I agree with Mooi and Gill that homology and synapomorphies are critical to phylogenetics, which is why every phylogeny that I have ever published is based implicitly on synapomorphies; they are present for every recovered node. Further, I have always provided diagnostic features for every named clade (note that Moronoidei's stated usage was as a temporary grade, not a clade). Despite our agreement on the value of synapomorphy, Mooi and Gill's (2010) assertion that ''systematics is in danger of making itself irrelevant to the remainder of biology because meaningful dialogue or assessment of synapomorphies has become impossible'' is hyperbole. The rise of comparative methods (e.g., models of character evolution, diversification analyses, biogeography) that have been developed via the statistical framework of model-based analyses has only strengthened the influence of phylogenetics in biology. While I do agree with Mooi and Gill (2010) that researchers should take homology assessment seriously and make use of every test available to them at the primary homology stage, I disagree with Mooi and Gill's ever-present critique of character optimization. This stance gives the impression that they disregard or reject character congruence as the final and decisive test of homology. Contrary to Mooi and Gill (2010), we cannot ''understand character homology'' or justify special pleading for the uniqueness of characters; we can only hypothesize that two entities are homologous using all available evidence and let the totality of the data in the analysis corroborate or refute the hypothesis of synapomorphy. To do anything else introduces unnecessary bias and assumptions. The difference between my view and the view expressed by Mooi and Gill (2010) regarding the importance of an explicit optimality criterion and character optimization is the core difference between the ''transformed'' and ''numerical'' phylogenetic schools (*sensu* Ebach et al., 2008). This conflict, I believe, exacerbates the molecular vs. morphological data ''rift'' in systematic ichthyology that Chakrabarty (2010) and Mooi and Gill (2010) discuss. Data chauvinism exists for both morphological and molecular systematists, so it would be most productive to focus the debate on the few fundamental differences in the treatment, presentation, and analysis of data between the two phylogenetic schools rather than the class of data being studied.

I have argued that our field's lack of progress on higher-level relationships, generally, and within percomorphs, specifically, is due to (1) our reliance on inexplicit analyses, (2) dogmatic thinking about characters and relationships, and (3) analyzing insufficient data (as discussed in Smith and Craig, 2007). In that study, we proposed novel relationships and a revised classification for the Percoidei, Epinephelidae, and Serranidae. These revisions were based on a synapomorphy-rich parsimony hypothesis, which required a substantive break from the traditional percoid classification handed down nearly 100 years ago from the likes of Regan (1913) and Jordan (1923). Mooi and Gill (2010) criticized our results (in non-specific terms) and the conclusions of this and several other recent analyses that have changed acanthomorph classification. Instead of discussing the three arguments put forward by Smith and Craig (2007), Mooi and Gill (2010) focused their critique on (1) ''the clear trend in systematics towards a completely statistical and tree-based cladistics away from an evidence and character-based approach,'' (2) ''the apparent confusion between homology, homoplasy, and the meaning of evidence,'' and (3) ''the impact of methods of analysis that are, for all intents and purposes, phenetic.'' Concerns 1 and 3 are effectively redundant because a study that is phenetic would definitionally not be discretely character based, and if a study were phenetic, it would not make the distinction between homology and homoplasy (concern 2). In a sense, these concerns are a single criticism against numerical phylogenetics and character optimization: Mooi and Gill

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believe these methods are phenetic. The criticized studies use techniques that are not phenetic for several reasons. First, phenetics relies on the analysis of a table of pairwise distances (a distance matrix) rather than the raw character matrix. Because of the reduction of the discrete character matrix to pairwise distances, individual character changes (e.g., synapomorphies) cannot be optimized on the resulting phenogram. In contrast, maximum likelihood, Bayesian, and parsimony analyses are based on the analysis of the raw molecular sequence (character and character-state) data; this use of the discrete character data allows for the optimization/mapping/tracing of hypothesized transformations through ancestral states reconstruction (i.e., the identification of synapomorphies). Second, likelihood, Bayesian, and parsimony analyses use an explicit root to polarize all hypothesized transformations; this outgroup rooting results in phylogenies that are informed solely by synapomorphy, not similarity. These methods are simply not phenetic. Beyond this criticism, Mooi and Gill make additional claims that demand address. Several of these issues will be discussed below with the goal of promoting this discussion further, so that ichthyologists can once again focus on resolving the phylogeny and taxonomy of fishes.

Character congruence and molecular homology.—Mooi and Gill (2010) implore systematists to ''return to homology,'' and they suggest that ''molecular data are really not substantively different from morphological data and should be treated in much the same manner.'' While I agree with this statement from the analytical, evidential, or secondary-homology perspective, these two classes of data cannot be treated identically from the perspective of Mooi and Gill's core concerns of primary homology and synapomorphy presentation (also see Evidence below). In their raw form, DNA sequence data have exactly four states. Further, every adenine, for example, is physically and chemically identical to every other adenine. The end product of these facts is that molecular systematists never need to question the identity of their character states; it is known *a priori*. The difficult homology question in molecular systematics is whether a particular adenine is homologous to a particular adenine, guanine, indel, etc. in another species (i.e., whether the characters [columns in a matrix] are homologous). If we focus on Patterson's (1982) three tests of homology, molecular systematists cannot use the test of conjunction, so they can only assess homology through tests of similarity and congruence (Rieppel and Kearney, 2007). Compared to most morphological features, DNA sequence data have fewer tests of similarity because of the limited number of character states, the linear nature of DNA that only provides for a maximum of two adjacent nucleotides (for connectivity), and a limited number of situations where functional implications may be relevant. Therefore, character congruence dominates homology assessment for the computer-aided molecular and total evidence analyses that Mooi and Gill (2010) eschew. For morphological data, the more difficult homology questions are often related to discretizing the homologous character states, not the characters (columns) themselves. For example, we rarely question whether a suborbital stay is composed of a connection between the third circumorbital and the preopercle, but we must make use of all evidence (ontogeny, topographic correspondence, connectivity [Rieppel and Kearney, 2002]) to assess whether the presence of a suborbital stay in a cottoid, a scorpaenoid, or a gasterosteioid is an analogous or homologous character state across all these groups in the primary homology assessment stage. Even with this additional testing, it is irresponsible for any systematist to assume that they can fully ''understand'' a character system and bypass the test of character congruence.

Mooi and Gill (2010) never discuss character congruence as a test of homology except when they dismissively state, ''optimization procedures are being relied upon to 'solve' issues of homology rather than relying on biology.'' As noted above, character congruence has always had an important role in homology assessment (Patterson, 1982; Rieppel and Kearney, 2007), and it is, after all, the final arbiter of what character states are synapomorphies in a given study. To suggest that relying on character congruence, or what is effectively the preponderance of the data or the weight of the evidence, is equivalent to ignoring homology goes against logic and the scientific method. Mooi and Gill (2010) suggest, ''a change in topology with the addition of taxa is an indication that there is no understanding of character homology.'' This suggests that a systematist can know the Truth regarding all questions of homology, homoplasy, convergence, and relationships prior to an analysis. Minimally, these types of assumptions about homology and monophyly (see Outgroup analysis below) will introduce bias into the analysis for all but the simplest of datasets. It is not possible to assess synapomorphy vs. convergence without explicit analyses, and all ichthyologists agree that homoplasy is rampant within Percomorpha. As Johnson and Patterson (1993:555) noted, ''very few of the characters found among percomorphs and their relatives are uniquely derived, and progress will not be made without some special pleading.'' This special pleading is the same as Mooi and Gill's (2010:516) ''understanding . . . character homology.'' This is an assumption-laden approach that inexplicitly weights characters (from an undisclosed cost of zero to infinity), identifies synapomorphies *a priori* and often without benefit of a specific sister group, casts a narrow taxonomic net for ingroup monophyly and relationships (e.g., see Outgroup analysis below), and does not use a repeatable optimality criterion. Despite these issues, there has been progress on the percomorph bush with this reduced-character approach (Johnson and Patterson, 1993), but the current impasse requires that we delve into the morass of more variable characters as was done successfully with groups such as the Stomiiformes (Fink, 1985). The full resolution of Percomorpha will require us all to relinquish our biases and collect as many well discretized characters as we can, regardless of whether those characters are morphological or molecular.

Outgroup analysis.—One example of the differences between the transform cladist research program of Mooi and Gill and a numerical phylogeneticist program involves the testing of ingroup monophyly. Mooi (1993) analyzed the relationships within Plesiopidae using an all-zero root (based on set theory presence/absence coding [Ebach et al., 2008]) as the only non-plesiopid terminal. His non-plesiopid material examined included *Notograptus* and representatives from ten other percomorph families, but he did not explicitly code any of the examined ''outgroup'' species despite the suggestion from Smith-Vaniz and Johnson (1990) that *Notograptus* likely belonged within Plesiopidae. Gill and Mooi (1993:348) also examined possible alignments for Notograptidae in a descriptive (inexplicit) study, but despite

the preponderance of the evidence suggesting a placement of *Notograptus* within Plesiopidae, they chose to exclude it ''pending discovery of more conclusive corroborative evidence.'' Apparently, the corroborative evidence they were looking for was the lack of a gas bladder in *Notograptus* and all plesiopids except *Trachinops* and *Assessor*. When Mooi and Gill (2004) eventually placed *Notograptus* in Plesiopidae, the lack of the gas bladder was the sole character they added beyond the characters derived from Smith-Vaniz and Johnson (1990) and Mooi (1993). All of these other characters were available to Mooi (1993) and Gill and Mooi (1993). So, why did it take so long to place *Notograptus* in the Plesiopidae when sufficient evidence had been published in the early 1990s? Mooi and Gill and other researchers believed that they ''understood'' the characters that diagnosed Plesiopidae, so rather then testing plesiopid monophyly, they assumed it. From a different perspective, one might also ask how Mooi's (1993) all-zero (or presence/absence coded) root terminal was created when *Notograptus* (one of only 11 non-plesiopid families examined) was later coded (Mooi and Gill, 2004) with non-zero entries for 13 of the 26 characters analyzed in Mooi (1993). This inexplicit study of ''outgroup(s)'' poses a lot more questions then it answers. In the end, I do give credit to Mooi and Gill (2004) for continuing to refine their studies by collecting additional data and getting more comprehensive results; that is, after all, how science progresses.

It is curious that the progression of Mooi and Gill's ideas about the phylogenetic placement of *Notograptus* is acceptable to them; whereas, a similar progression proposed by Smith and Craig (2007) about the relationships of Percidae, Serranidae, and Epinephelidae, relative to Smith and Wheeler (2004) warranted criticism. These two progressions differ in scale, type of data, and in that Smith and Wheeler (2004) explicitly analyzed all of their examined taxa and tested ingroup monophyly, but the logical progression and taxonomic changes instigated by the addition of more characters and taxa between these two studies is similar. Despite this similarity, Mooi and Gill (2010) confront this approach:

> But why choose Smith and Craig (2007) over Smith and Wheeler (2004)? Each examined similar sets of acanthomorph taxa . . . The studies used essentially the same molecules or portions of them and both used the same methods and statistical measures. But the results differed. Do we choose based on numbers of taxa and characters included in an analysis?

From my perspective, the choice between the hypotheses is obvious, and it depends on the taxonomic question you are asking. If you are interested in cottoids, then Smith and Wheeler (2004) is superior, if you are interested in any other group, then Smith and Craig (2007) is superior because of the increased taxon sampling (i.e., more data). The same is obviously true for Plesiopidae, where the increased taxon sampling in Mooi and Gill (2004) makes it superior to Mooi (1993). However, it is must be pointed out that Mooi and Gill's (2010) claim that ''similar sets of acanthomorph[s]'' were examined in my two studies is simply not true. The taxonomic focus (cottoids, gasterosteioids, percoids, scorpaenoids, and zoarcoids), which they do not really discuss, are similar, but the outgroup sampling differs dramatically. Overall, Smith and Wheeler (2004) included 105 terminals and Smith and Craig (2007) included 180 terminals. Further, when the species from those two studies are combined, there are 221 unique taxa, leaving only 64 shared species (or overlap in 29% of species examined). By whose concept is 29% similar?

The explicit analyses of outgroups presented by Smith and Wheeler (2004) and Smith and Craig (2007) opened those studies up to criticism that cannot be explored in the studies of Mooi (1993) and Mooi and Gill (2004) because they did not disclose explicit ''outgroup'' character states. Mooi and Gill (2010) do not discuss any specifics in their critique, but Mooi and Gill's (2008) ASIH presentation highlighted the movement of the pseudochromoid, blennioid, and atheriniform assemblage (adhesive-egg clade) between these two supposedly ''similar'' studies to exemplify the supposed confusion caused by numerical phylogenetics. The movement of this clade (or *Salarias* and *Gramma* since they were the only two taxa from this clade in both studies) relative to *Hoplichthys* was the topic of my 2006 presentation at the Annual Meeting of ASIH (Smith, 2006). In that presentation, I highlighted that 16S sequence data for the 116 new species that were included in Smith and Craig (2007) beyond the taxa in Smith and Wheeler (2004) had clarified the homology of nucleotides in several large loops in this fragment. This new outgroup information suggested that the insertion-deletion events that had originally been considered homologous in the ''adhesive-egg clade'' and the ''stonefishes'' had convergently evolved. These changes were not discussed in Smith and Craig (2007) because refining homology statements (realigning the nucleotides) with the addition of new data is how systematics progresses and because the placement of *Gramma*, *Salarias*, and *Hoplichthys*, while important, is not crucial to understanding the interrelationships of epinephelids, serranids, and percids. Further, it should be noted that variation in the relationships among outgroups should be expected in explicit analyses when the number of outgroup species triples and homology assessment improves concomitantly. This variation is just masked when an all-zero set-theory root is assumed and used in morphological studies.

Data transparency and repeatability.—In an attempt to refute a claim from my oral presentation (Smith, 2008) that molecular studies are more transparent than most morphological studies, Mooi and Gill (2010) state that, ''sequences on-line (if not erroneous) are not different from the specimens available in traditional museum collections.'' This analogy is flawed. Tissue vouchers, tissues, and DNA extracts are equivalent to the specimen vouchers (material examined) in traditional morphological studies. Online sequences are the equivalent of a photograph/digital image of every character state in every taxon being stored on a website or in a book; these are the raw data. With few exceptions, for example, Grande and Bemis (1998), morphological characters are never completely documented in photographic form in phylogenetic studies. Molecular studies are required to provide this high level of data transparency (complete raw sequence deposition on GenBank) for public scrutiny. Editors have not demanded that morphological studies have this level of openness (e.g., requiring deposition of digital images on MorphoBank). Ironically, the explicit deposition of sequence data on GenBank is precisely how one could determine whether a sequence is ''erroneous.'' Mooi and Gill's (2010) flippant parenthetical statement highlights the need for more

transparency and thorough documentation in morphological studies. Further, it drives home a major component of this commentary, which is that all systematists need to be more explicit about their data and analytical assumptions. It leaves the work as open as possible to criticism and revision. This, in turn, leads to progress.

Evidence.—Mooi and Gill (2010) suggest that the molecular studies they criticize lack ''substantive evidence'' or suffer from a ''misunderstanding of the meaning of evidence.'' These criticisms seem to indicate that Mooi and Gill (2010) either do not believe that molecular transformations are evidence of relationships or do not believe this evidence exists because the transformations are not indicated/optimized/mapped on the resulting phylogeny. First, as with all heritable character variation, molecular transformations are obviously informative (evidence) for the interpretation of evolutionary relationships. Second, a visual depiction of synapomorphies (tick marks) on a phylogeny can be informative, but its absence does not mean that synapomorphies are not present on the nodes resulting from an analysis of molecular data. Chakrabarty (2010) discussed the difficulty in depicting the tens of thousands of synapomorphies on a phylogeny in large-scale molecular studies, so I will not repeat those issues. Sparks and Smith (2004:509) and Frost et al. (2006:330–354) took a different approach and provided tables or appendices with partial listings of the diagnostic molecular synapomorphies from their studies. Given unlimited space, it certainly cannot hurt to provide this information, but it will not provide subsequent studies with Mooi and Gill's (2010) ''opportunity for rational discussion based on homology'' because base positions are necessarily taxon sampling and alignment dependent. This issue is why the raw data are made available on GenBank for people to download, align, and analyze for themselves for any particular phylogenetic question. To highlight this issue, we can compare the positional variation of a single nucleotide in one species across two of my studies compared by Mooi and Gill (2010). As an example, the 400th raw base pair in the 12S–tRNA-Val–16S amplicon (a cytosine) in *Perca flavescens* is alignment position 621 in Smith and Wheeler (2004) and position 1164 in Smith and Craig (2007). The increased taxon sampling and the evolution of an intergenic spacer within Anthiinae (Smith et al., 2009) caused the dramatic positional change. If, hypothetically, the transformation to a cytosine at this position were a synapomorphy of Percidae, it too would differ as character 621 and character 1164 between these studies. This necessary, but obscuring, change of roughly 543 positions would preclude a ''rational discussion based on homology'' across studies for any individual synapomorphy because there is no way to track individual base pairs outside of alignments. As such, I would recommend that authors make their alignments available on journal or personal websites.

Classification and concluding remarks.—Chakrabarty (2010:513) argued that ''the real point of contention is over what kinds of data are acceptable as evidence for changing higher-level fish taxonomy.'' Mooi and Gill (2010) perhaps somewhat disingenuously suggested that their presentation and commentary were not motivated by the taxonomic changes, yet all of the studies that they criticized were among the few molecular studies that dared to change taxonomy. The fact remains that substantial portions of the teleostean classification, particularly within Perciformes, lack evidence for their conclusions. The taxon and character sampling in molecular studies has now reached the point where researchers are rightfully comfortable with breaking from the taxonomic *status quo* and making evidence-based changes to the evidence-free portions of the teleostean classification. We are on the verge of a renaissance in the phylogeny and taxonomy of fishes that should parallel the first pass of the cladistic revolution (1966–1977). As Patterson (1995) noted, this period is when ''the entire higher classification was invented . . . it isn't that these groups were put somewhere else or called something different—none of them had been recognised before.'' As I see it, Mooi and Gill's (2010) impending crisis is, in reality, the impending phylogenetic and taxonomic renaissance.

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LITERATURE CITED

Chakrabarty, P. 2010. The transitioning state of systematic ichthyology. Copeia 2010:513–515.

Ebach, M. C., J. J. Morrone, and D. M. Williams. 2008. A new cladistics of cladists. Biology and Philosophy 23:153–156.

Fink, W. L. 1985. A phylogenetic analysis of the family Stomiidae (Teleostei, Stomiiformes). Miscellaneous Publications of the Museum of Zoology, University of Michigan 171:1–127.

Frost, D. R., T. Grant, J. Faivovich, R. H. Bain, A. Haas, C. Haddad, R. O. de Sá, A. Channing, M. Wilkinson, S. C. Donnellan, C. J. Raxworthy, J. A. Campbell, B. Blotto, P. Moler, R. C. Drewes, R. A. Nussbaum, J. D. Lynch, D. M. Green, and W. C. Wheeler. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297:1–370.

Gill, A. C., and R. D. Mooi. 1993. Monophyly of the Grammatidae and of the Notograptidae, with evidence for their phylogenetic positions among perciforms. Bulletin of Marine Science 52:327–350.

Grande, L., and W. E. Bemis. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Paleontology Supplement 1, Memoir 4 18:1–690.

Johnson, G. D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52:554–626.

Jordan, D. S. 1923. A classification of fishes including families and genera as far as known. Stanford University Publications, University Series, Biological Sciences 3:77–243.

Mooi, R. D. 1993. Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. Bulletin of Marine Science 52:284–326.

Mooi, R. D., and A. C. Gill. 2004. Notograptidae, sister to *Acanthoplesiops* Regan (Teleostei: Plesiopidae: Acanthoclininae), with comments on biogeography, diet and morphological convergence with Congrogadinae (Teleostei: Pseudochromidae). Zoological Journal of the Linnean Society 141:179–205.

Mooi, R. D., and A. C. Gill. 2008. Phylogenies without synapomorphies—a crisis is systematics or what we don't node—the imperative of character evidence for phylogeny reconstruction. *In*: Abstracts of the 88th Meeting of the American Society of Ichthyologists and Herpetologists.

Mooi, R. D., and A. C. Gill. 2010. A transitioning state or harmful mutation in systematic ichthyology? A reply to Chakrabarty. Copeia 2010:516–519.

Patterson, C. 1982. Morphological characters and homology, p. 21–74. *In*: Problems of Phylogenetic Reconstruction. K. A. Joysey and A. E. Friday (eds.). Systematic Association Special Volume Number 25. Academic Press, London.

Patterson, C. 1995. Adventures in the fish trade. Unpublished manuscript from the Annual Address to the Systematics Association.

Regan, C. T. 1913. The classification of the percoid fishes. Annual Magazine of Natural History, series 8 12:111–145.

Rieppel, O., and M. Kearney. 2002. Similarity. Biological Journal of the Linnean Society 75:59–82.

Rieppel, O., and M. Kearney. 2007. The poverty of taxonomic characters. Biology and Philosophy 22:95–113.

Smith, W. L. 2006. The advantages of combining morphological characters with DNA sequences: an example from the Percomorpha. *In*: Abstracts of the 86th Meeting of the American Society of Ichthyologists and Herpetologists.

Smith, W. L. 2008. Relationships of the stonefishes, scorpionfishes, and allies. *In*: Abstracts of the 88th Meeting of the American Society of Ichthyologists and Herpetologists.

Smith, W. L., and M. T. Craig. 2007. Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. Copeia 2007:35–55.

Smith, W. L., K. R. Smith, and W. C. Wheeler. 2009. Mitochondrial intergenic spacer in fairy basslets (Serranidae: Anthiinae) and the simultaneous analysis of nucleotide and rearrangement data. American Museum Novitates 3652:1–10.

Smith, W. L., and W. C. Wheeler. 2004. Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. Molecular Phylogenetics and Evolution 32:627–646.

Smith-Vaniz, W. F., and G. D. Johnson. 1990. Two new species of Acanthoclininae (Pisces: Plesiopidae) with a synopsis and phylogeny of the subfamily. Proceedings of the Academy of Natural Sciences of Philadelphia 142: 211–260.

Sparks, J. S., and W. L. Smith. 2004. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). Cladistics 20:501–517.

Springer, V. G., and T. M. Orrell. 2004. Appendix: phylogenetic analysis of 147 families of acanthomorph fishes based primarily on dorsal gill-arch muscles and skeleton. Bulletin of the Biological Society of Washington 11:236–260.

Thacker, C. E. 2009. Phylogeny of Gobioidei and placement within Acanthomorpha with a new classification and investigation of diversification and character evolution. Copeia 2009:93–104.