

## Preface

*Copeia* has maintained a manuscript category entitled “Comments” for some time, but with little usage. In order to spur interest in the journal via exchange of ideas on timely topics of particular interest to the readership, I have solicited the following commentaries on the topic of evidence in phylogenetic systematics. The opening comment was written in early 2009 in response to Mooi and Gill’s abstract and oral presentation at the 2008 ASIH meetings in Montreal. In the future, I expect to publish such comments and debates on a semi-regular basis and invite any and all readers with suggestions and contributions for potential consideration to contact me in advance of manuscript submission.—Scott Schaefer, *Editor*.

## The Transitioning State of Systematic Ichthyology

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THE publication of Smith and Craig’s (2007) percomorph phylogeny has sparked a controversy within the systematic ichthyology community (Mooi and Gill, 2008). This controversy reveals a substantial rift between some classically trained ichthyologists that only trust morphology and those ichthyologists comfortable with using morphology and modern molecular systematics. Although no rebuttal or criticism has been published to Smith and Craig (2007), the fish systematics sessions at the 2008 Joint Meeting of Ichthyologists and Herpetologists implied that an open debate about the direction of our field is in order. The 2008 meeting included lively (sometimes contemptuous) debate, and revealed that some think that systematic ichthyology is moving too quickly from its rigorous organismal roots into a messy era of molecular taxonomy. The real point of contention is over what kinds of data are acceptable as evidence for changing higher-level fish taxonomy. Mooi and Gill (2008) state, “Altering taxonomy based on such fluid constructs [molecular characters] is problematic, particularly as there has been no attempt to provide character definitions for identified groups based on testable synapomorphies.” I argue that contrary to this statement, Smith and Craig’s (2007) contribution is more transparent in showing tested evidence derived from phylogenetic analysis than other well known higher-level systematic studies in ichthyology.

What is controversial about Smith and Craig’s (2007) publication was not necessarily the phylogenetic relationships they recovered but their revision of long-standing percomorph taxonomy using a phylogeny derived from molecular characters. Although the relationships presented in Smith and Craig (2007) were in some cases surprising, they are generally comparable to what others have recently recovered (Dettai and Lecointre, 2004; Miya et al., 2005; Smith and Wheeler, 2006).

Mooi and Gill (2008) argued against Smith and Craig (2007), and similar molecular work, insisting that synapo-

morphies were not presented and that support indices (bootstrap, Bremer, etc.) are mistakenly used to measure phylogenetic robustness—in lieu of homology. Mooi and Gill state, “Without evidence (characters) for nodes, there is no way to choose among these competing topologies.” Mooi and Gill’s (2008) call to present phylogenies with molecular characters mapped onto them is shortsighted, and their notion that statistical support is the sole metric for comparison of molecular phylogenies is wrong. Although molecular and morphological characters are utilized equally in support of hypotheses of relationships, molecular characters cannot be presented in the same way on a phylogeny because of the enormous number of transitions associated with these data. Molecular characters are typically represented as 5 character states, (e.g., A, C, T, G, insertion/deletion) and are characteristically highly homoplasious over large-scale phylogenies (i.e., consistency indices of  $\leq 0.3$  are typical). Little can be learned from displaying all transitions and transversions onto a molecular phylogeny, except that there are many of them on each node. What Mooi and Gill are perhaps arguing for is better transparency in these molecular phylogenies so that the evidence can be more easily examined. To this, I would argue that phylogenies such as Smith and Craig (2007) are far more transparent, repeatable, and scientific than our previous standard. Our previous standard for what justified rearranging and naming higher-level fish taxonomy included phylogenies derived from subjective evolutionary taxonomy. These early attempts do not represent the products of phylogenetic analyses as they lacked optimality criteria for choosing among alternative hypotheses of relationships.

The higher-level percomorph relationships that have been most cited in ichthyology (Greenwood et al., 1966; Rosen, 1973; Lauder and Liem, 1983) are important summaries of how morphological features are distributed among a scattering of taxa, but not from any formal analysis of features (i.e., the relationships are not derived from

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phylogenetic analyses but solely from the mapping of characters). A review below of these venerable papers shows them to employ the kind of Mayrian evolutionary taxonomy that dominated biology before the cladistic revolution (Hull, 1990). Evolutionary taxonomy emphasized the expertise of established authority in revealing relationships among taxa (Hull, 1990). This kind of systematic work has been allowed to prevail in ichthyology too long.

The first modern attempt at summarizing higher levels fish systematics was in the Greenwood et al. (1966) effort at a classification of teleosts. Prior to this monograph, teleost classification was written as a list of orders from the primitive to the advanced (Berg, 1940; Gosline, 1966; citations within Patterson, 1994). Greenwood et al. (1966) was written by the most prominent ichthyologists of the day in the same year that Hennig (1966) was translated into English and introduced many biologists to phylogenetic systematics. The authors were the first to use a tree diagram to divide teleosts into three divisions and eight suborders based on morphological features. These morphological features were listed and discussed for each group but were never part of a phylogenetic analysis. Therefore, the features used in support of groups are not synapomorphies, but hypotheses of synapomorphies: the difference being that synapomorphies are the byproduct of a phylogenetic analysis. Prior to analysis these characters are simply features observed in the taxa of interest; they can only be called synapomorphies after analysis shows them to support relationships on the recovered topology and after they are distinguished from symplesiomorphy.

Lauder and Liem (1983) made an attempt at looking at the interrelationships of actinopterygian fishes that summarized the progress made from the time of Greenwood et al. (1966) and framed it in the language of cladistics by emphasizing monophyletic groups on a cladogram; however, what is actually presented (in their words) are “nested sets of structural features which can serve as a basis for interpretations of evolutionary trends and processes.” No phylogenetic analysis is associated with the hypotheses of relationships, so again there are no tests of their characters and therefore no synapomorphies.

One of the best-known stumbling blocks in systematic ichthyology is what is known as the “percomorph problem.” This problem stems from the fact that Percomorpha (representing 200 families and nearly 15,000 species) was originally proposed without supporting features (Rosen, 1973), and it constitutes the largest polytomy in vertebrates. This polytomy represents nearly all the “derived fishes” (Nelson, 1989) atop the teleost tree. To remedy the “percomorph problem,” Johnson and Patterson (1993) presented some of the best-known and most cited hypotheses of the relationships among fishes. Their work, perhaps the most instructive and important work in systematic ichthyology to that point, does not include a phylogenetic analysis: the relationships they presented are therefore untested.

The only test of homology is phylogenetic analysis (whether the optimality criterion is parsimony, likelihood, or other). Only those relationships that are supported by evidence acquired through phylogenetic analyses have been tested. Greenwood et al. (1966), Lauder and Liem (1983), and Johnson and Patterson (1993) are important works that provide morphological characters as evidence of relationships; however, those features are untested statements of

homology and therefore the trees based on them are untested hypotheses of relationships.

Prior to Smith and Craig (2007), no taxonomic changes of higher percomorph groups applied “tested” synapomorphies. This is the case despite the fact that an abundance of researchers have been using phylogenetic systematics to test relationships in fishes for many years (Wiley, 1976; Fink, 1985; Stiassny, 1991). Phylogenies based on morphological features like those used in Greenwood et al. (1966) and Lauder and Liem (1983) continue to be published to this day (Chakrabarty, 2007; Parenti, 2008; Sparks, 2008) and constitute valid systematic works just as much as they would have 40 years ago. Although some may disagree with the relationships recovered by Smith and Craig (2007), the only basis for refutation can be other phylogenetic analyses with additional data and taxa. Mooi and Gill (2008) claimed that molecular phylogenies could not be objectively compared because synapomorphies are not explicitly presented. Molecular phylogenies should be judged as all phylogenies are, on the basis of the quality and quantity of the data and analysis. This does not require publication of the synapomorphies on the phylogeny as Mooi and Gill suggest, but access to this data is important. All published molecular phylogenies are required to make their data available online; therefore, molecular data are perhaps much more accessible than other forms of evidence that typically require repeating the observations of the original investigator. These molecular data are certainly far more accessible than those of the earlier taxonomic studies cited here that often provided few references to examined specimens or even images of most characters.

In dealing with the “percomorph problem” we must recognize its potential intractability: too many terminals and too few characters. In the past this has led us to a reliance on authority, but the challenge is not so great that we can’t apply modern phylogenetic tools to the problem. We will never know the “true” relationships of all fishes, but progress can only be made through systematic study. For this reason, Smith and Craig (2007) must be used as part of the new starting block for resolving higher-level fish taxonomy. A satisfying phylogeny of acanthomorphs, teleosts, or all “fishes” will likely need to include multiple forms of evidence (see the collaborative work currently being done via the “Euteleost Tree of Life” project, <http://www.fishtree.org/>). The building blocks for a thorough analysis of higher fish relationships should include the recent work of both molecular and morphological phylogenetic researchers, but it must exclude a return to evolutionary taxonomy and our past reliance on authority.

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#### LITERATURE CITED

- Berg, L. S.** 1940. Classification of fishes, both Recent and fossil. *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR* 5:87–517.
- Chakrabarty, P.** 2007. A morphological phylogenetic analysis of Middle American cichlids with special emphasis on the section “*Nandopsis*” sensu Regan. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 198:1–31.

- Dettai, A., and G. Lecointre.** 2005. Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *Comptes Rendus Biologies* 328: 674–689.
- Fink, W. L.** 1985. A phylogenetic analysis of the family Stomiidae (Teleostei, Stomiiformes). *Miscellaneous Publications, Museum of Zoology, University of Michigan* 171:1–127.
- Gosline, W. A.** 1966. *Functional Morphology and Classification of Teleostean Fishes*. The University Press of Hawaii, Honolulu.
- Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers.** 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* 131:341–455.
- Hennig, W.** 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois.
- Hull, D. L.** 1990. *Science as a Process, An Evolutionary Account of the Social and Conceptual Development of Science*. The University of Chicago Press, Chicago.
- Johnson, G. D., and C. Patterson.** 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science* 52:554–626.
- Lauder, G. V., and K. F. Liem.** 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin Museum of Comparative Zoology* 150:95–197.
- Miya, M., T. P. Satoh, and M. Nishida.** 2005. The phylogenetic position of toadfishes (order Batrachodiformes) in the higher ray-finned fishes as inferred from partitioned Bayesian analyses of 102 whole mitochondrial sequences. *Biological Journal of the Linnaean Society* 85:289–306.
- Mooi, R. D., and A. C. Gill.** 2008. Phylogenies without synapomorphies—a crisis in systematics or what we don't node—the imperative of character evidence for phylogeny reconstruction. *In: Abstracts of the 88<sup>th</sup> Meeting of the American Society of Ichthyologists and Herpetologists*.
- Nelson, G. J.** 1989. Phylogeny of major fish groups, p. 325–336. *In: The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis*. B. Fernholm, K. Bremer, and H. Jörnvall (eds.). Excerpta Medica, Amsterdam, Netherlands.
- Parenti, L. R.** 2008. A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Belontiiformes, Adrianichthyidae). *Zoological Journal of the Linnean Society* 154:494–610.
- Patterson, C.** 1994. Bony fishes, p. 57–84. *In: Major Features of Vertebrate Evolution*. D. R. Prothero and R. M. Schoch (eds.). *Short Courses in Paleontology, Vol. 7*, Paleontological Society, University of Tennessee, Knoxville.
- Rosen, D. E.** 1973. Interrelationships of higher teleostean fishes, p. 397–513. *In: Interrelationships of Fishes*. P. H. Greenwood, R. S. Miles, and C. Patterson (eds.). Academic Press, London.
- 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 percoid fishes. *Copeia* 2007:35–55.
- Smith, W. L., and W. C. Wheeler.** 2006. Venom evolution widespread in fishes: a roadmap for the bioprospecting of piscine venoms. *Journal of Heredity* 97:206–217.
- Sparks, J. S.** 2008. Phylogeny of the cichlid subfamily Etroplinae and taxonomic revision of the Malagasy cichlid genus *Paretroplus* (Teleostei: Cichlidae). *Bulletin of the American Museum of Natural History* 314:1–151.
- Stiassny, M. L. J.** 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview, p. 1–35. *In: Cichlid Fishes: Behaviour, Ecology and Evolution*. M. H. A. Keenleyside (ed.). Chapman Hall, London.
- Wiley, E. O.** 1976. *The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae)*. University of Kansas Miscellaneous Publication 64:1–111.