Transactions of the Royal Society of Edinburgh: Earth Sciences, **95**, 543–546, 2005 (for 2004)

Controversies on the evolutionary history of pycnodont fishes – reply to Kriwet 2004

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ABSTRACT: Criticisms by Kriwet regarding recent work on pycnodont phylogeny are based on the use of additive characters. Therefore, applying transformation series in phylogenetic reconstruction is justified in theory and in practice, and an example of additional ontogenetic evidence supporting character ordering in pycnodonts is provided. Moreover, comments on some pycnodont genera are included, and the accurate taxonomic use of the genera *Coelodus* and *Ocloedus* is emphasised.

KEY WORDS: Actinopterygii, additivity, cladistics, *Coelodus*, *Ocloedus*, ontogeny, phylogeny, Pycnodontiformes, transformation series.

In his revision of the dentition of the pycnodont fish genus *Stemmatodus*, Kriwet (2004) criticised the phylogenetic hypothesis of Poyato-Ariza & Wenz (2002). He used the data matrix from Poyato-Ariza & Wenz (2002), but in a different way, therefore obtaining different results. These results consisted of a much less resolved consensus tree, actually a multiple indetermination formed by a 12-branched polytomy (Kriwet 2004, fig. 7B). His arguments and procedures are commented on, involving both the theoretical and practical aspects of phylogenetic systematics. In addition, comments upon Kriwet's use of the generic name *Coelodus* are also included. But first of all, some typing errors in the original data matrix mentioned above are corrected herein.

1. Errata

It is necessary to point out that the data matrix of Pycnodontiformes as published by Poyato-Ariza & Wenz (2002, Appendix 3) contains at least three typing errors (L. P. Machado pers. comm. 2003), that may be detected when the data matrix itself is carefully compared with the discussion of the corresponding characters throughout the main text. These errors are: character 29 in *Gibbodon* reads 0, but should read 1; character 82 in *Coelodus* reads 3, but should read 0; and character 96 in *Trewavasia* reads 3&4, but should read 1. Consequently, the cladistic analysis has been performed again for the present paper in order to check the effect of these errors:

(A) with ordered characters, the number of most parsimonious trees (MPTs) is the same (36), although they are two steps shorter (632). Phylogenetic relationships remained exactly the same in all the various types of consensus trees. The only differences were minor ones in the distribution of these particular characters. Some indices (HI, HI excluding uninformative characters, RI, and RC) varied in 1 centesimal figure; the consistency indices (CI and CI excluding uninformative characters) maintained the same value.

(B) with unordered characters, the number of MPTs was the same (72), but two steps shorter (582). Phylogenetic relationships in the strict consensus tree have changed, because there is a new, large monophyletic group including *Anomoeodus*, (*Coelodus*+*Iemanja*), (*Proscinetes*+*Neoproscinetes*), *Tepexichthys*, *Ocloedus*, *Stemmatodus*, *Stenamara*, and *Macromesodon*. The resolution of other consensus trees is much better, but is the same as is commented upon in section 3 below.

It is worth noticing that the typing mistakes affect the phylogenetic hypothesis itself only when the characters are processed unordered, whereas the preferred hypothesis of pycnodont phylogenetic relationships (with ordered characters) remains unaltered.

2. Novelty

The phylogenetic hypothesis favoured by Kriwet (2004), obtained by processing the original data matrix by Poyato-Ariza & Wenz (2002) with all characters unordered (instead of some characters processed ordered, as was done in the original analysis), is actually not new. This same alternative, but much less resolved, hypothesis of phylogenetic relationships of the Pycnodontiformes was described in detail, but not figured, by Poyato-Ariza & Wenz in the discussion of their results (2002; p. 204–6). This was undertaken because it is clear that in any analysis it is advisable to offer a comparison between the trees run with unordered and with ordered characters (Hauser & Presch 1991), independently of which of them is the preferred hypothesis.

3. Consensus trees

Kriwet (2004) presented a strict consensus tree to support his favoured phylogenetic hypothesis. However, strict consensus is not the only way to obtain a consensus tree, although it really is the one where all of the nodes are strictly supported. There are, however, at least six other standard, less conservative procedures to obtain a consensus tree (Kitching *et al.* 1998), and, in the case of Pycnodontiformes, they all present a much higher resolution than strict consensus, considerably reducing the multiple polytomy. For instance, in the semistrict, majority-rule and Adams consensus trees the relationships of the basal forms and their separation from the Pycnodontoidei are resolved, and the relationships within the Pycnodontoidei taxa also present more resolution. In any case, the strict consensus tree is the less resolved one, whereas other consensus procedures offer better resolved consensus trees for Pycnodontiformes, even when processing all characters as unordered.

4. Additive characters

The key point in the argument regarding the phylogenetic hypothesis favoured by Kriwet (2004) is the issue of ordered versus unordered characters. As a general introduction to this matter, let us remember that whenever a character has two or more derived states (multistate character), it can be processed during cladistic analysis as:

(A) unordered (non-additive), implying that any derived state can change to another derived state with equal probability (one evolutionary step is always counted between two any given derived states); or

(B) ordered (additive, or transformation series), implying that there is greater probability of changing from one derived state to the adjacent one than to any other (one evolutionary step is counted between each two adjacent derived states).

Kriwet's (2004) only claim was that "ordering of characters is arguable because it introduces *a priori* hypotheses that have to be explained independently", but the issue of whether characters should or should not be ordered has been, and still is, debatable. The option of favouring additivity for certain multistate characters of the Pycnodontiformes data matrix was briefly justified by Poyato-Ariza & Wenz (2002, p. 142), but, since this is the basis of the criticisms, it is worthwhile providing herein further justification for the transformation series from both the theoretical and practical points of view.

4.1. Additivity

From a theoretical point of view, a good number of authors consider that all cladistic characters should be treated as multistates and coded as additive. The reasons for using additivity are manifold. It is true to say, as claimed by Kriwet (2004), that it requires assumptions about evolutionary processes. However, so does character polarity (Mabee 1989), and polarisation is not discarded for this reason. It seems more reasonable to regard transformation series as "hypotheses about the events that have given rise to the character state distributions observed in the taxa" (Mickevich & Lipscomb 1991, p. 133), that is, statements of homology (Lipscomb 1992), hence increasing significantly the information provided by any given data set. Moreover, additivity allows the *a priori* distinction between linear and branched character state trees (Pimentel & Riggins 1987). When the hypothesised transformations are consistent with the cladogram characters, it increases the fit (the matching of the hypothesis with the observed data), and therefore, in this sense, it increases the parsimony (Mickevich & Lipscomb 1991). On the other hand, non-additive analysis ignores observed information about similarity among characters (Lipscomb 1992), since it discards "observed similarity among the states in favour of character state trees that maximize consistency" (Lipscomb 1992, p. 62). Finally, it is worth mentioning that even those authors who discourage the ordering of characters do so with nuances, within restricted conditions, and without ruling out the ordered option *per se* (e.g. Hauser & Presch 1991).

Therefore, additive characters do provide additional information, whereas non-additive characters disregard relevant evolutionary information, and one must be aware of this when choosing one or the other. As a consequence, "both the order and the polarity could be included as extra information in a cladistic analysis" (Kitching *et al.* 1998, p. 31). Briefly, "additivity is a form of information and there are many reasons to be sympathetic to this viewpoint" (Kitching *et al.* 1998, p. 36).

4.2. Apriorism

During the actual process of research, ordering characters is not made *a priori*. It is actually quite the opposite. Ordering is effectively established before the cladistic analysis itself is performed by the computer, but it is decided after, and only after, the empirical observations have been carried out. That is, from this procedural point of view, it is made *a posteriori*. Furthermore, the *non-apriorism* of additivity also arises from the fact that the ordering of the characters must pass both the similarity criterion and the congruence criterion (Lipscomb 1992). This was, of course, implicitly the case of the ordered characters in the original pycnodont data set. In addition, and before passing the similarity and congruence criteria, the pycnodont characters were considered ordered only when presenting the primitive state as one of the two ends of a series of transformations, and all intermediate states were actually observed in fossil specimens.

Therefore, from the point of view of proper practice, additivity does not introduce *a priori* hypotheses that have to be explained independently, and should be regarded instead as a hypothesis of character transformation which emanates from both homology and the justified interpretation of exhaustive empirical observations, and which is explained in congruence with the preferred phylogenetic hypothesis.

4.3. Additional evidence

An example of additional empirical support for ordering characters in pycnodonts is provided from ontogenetic observations based on data that were not available to Poyato-Ariza & Wenz (2002). It involves the distribution and ossification of the scales. The squamation in pycnodonts ranges from complete squamation over the whole body, to total absence of scales, and the scales, if present, can be completely ossified or reduced to scale bars. The combination of both processes of reduction results in several scale patterns that vary enormously within this group (Nursall 1996; Poyato-Ariza & Wenz (2002). Juvenile and subadult specimens of *Macromesodon* (*sensu* Poyato-Ariza & Wenz 2004), namely the holotypes of *M. gibbosus* (Bayerischen Staatssammlung für Paläontologie und historische Geologie (BSP), München, Germany, AS VII 346) and of *M. macropterus* (BSP AS VII 345), exhibit a scale pattern that is more reduced than in the adult (peltate instead of the adult loricate), thus indicating that the reduction of squamation is an orderly heterochronic process of paedomorphosis (maybe progenesis, earlier offset time during ontogeny). This forthright example of interconnection between pattern and process represents a particular additional confirmation that the ordering of the characters involving reduction of squamation in pycnodonts passes the test of similarity, and that ordering these characters does provide relevant evolutionary information.

5. Taxonomic implications

Kriwet (2004, p. 152) indicates that "the analysis performed in this paper leads to the possibility of excluding †*Stemmatodus* and related taxa from †Pycnodontidae and introducing a new family". Kriwet (2004) does not propose a revised formal taxonomic rearrangement of this group, because the basis for this would be rather weakly supported. It is better to avoid any change in previous taxonomic arrangements when the preferred, alternative phylogenetic hypothesis is much less resolved, let alone if it is, as in this case, a multiple polytomy. Furthermore, and by strictly following the principles of subordination and sequenciation, point C′ in the cladogram (Kriwet 2004, fig. 7B) does not necessarily define a distinct family, as suggested by the author. Taxonomically, that clade could, and would actually be better regarded as, either a subfamily, or even a tribe within the Pycnodontidae. The same applies to node B′ (Kriwet 2004, fig. 7B).

Although this is not explicitly mentioned by Kriwet (2004), the bottom line of this discussion lies obviously in the choice between the family Pycnodontidae in a restricted sense (before Nursall 1996) or in ample sense (*sensu* Nursall 1996). The Pycnodontidae *sensu* Nursall appears consistently in all phylogenies as a well-defined and solid clade, therefore a distinctly diagnosable taxon, whereas the family in its former sense has a much weaker support in all cases (Nursall 1996, Poyato-Ariza & Wenz 2002, 2004; Kriwet 2004; this paper).

6. Comments on certain pycnodont genera

6.1. *Paramesturus*

Kriwet (2004) claims that the attribution of *Paramesturus* to the Pycnodontiformes is arguable; this is not a new point of view. It is worth remarking that this was already clearly indicated by Poyato-Ariza & Wenz (2002, p. 206): after the necessary revision of this genus, "the phylogenetic position of *Paramesturus* would need to be reconsidered out of the Pycnodontiformes".

6.2. *Eomesodon* and *Nursallia*

The results concerning ?*Eomesodon barnesi* and *Nursallia* ? *goedeli* in Kriwet (2004) do not appear as 'conversely to' those in Poyato-Ariza & Wenz (2002) because in this paper their phylogenetic positions were not fully resolved, and alternative hypotheses were considered and discussed (Poyato-Ariza & Wenz 2002, pp. 212, 216–18). In any case, ?*Eomesodon barnesi* cannot belong to *Apomesodon* Poyato-Ariza & Wenz 2002 because its characters are incompatible with the diagnosis of this genus (Poyato-Ariza & Wenz 2002, p. 219; *Macromesodon* in Poyato-Ariza & Wenz 2004, p. 367). In turn, *Nursallia* ? *goedeli* may effectively belong to the genus *Nursallia*, but this was also envisaged by Poyato-Ariza & Wenz (2002, p. 217).

6.3. *Coelodus* and *Ocloedus*

Kriwet (2004) creates confusion with the species names '*Coelodus subdiscus*' and '*Coelodus costae*'. These two specific names were explicitly removed by Poyato-Ariza & Wenz (2002) to the new genus *Ocloedus*, the former being the type species of this genus. Poyato-Ariza & Wenz (2002) provided the corresponding detailed historic record, character discussions and full formal systematic palaeontology, including diagnoses of the two genera and their type species. The valid species names, then, according to the International Zoological Code of Nomenclature (IZCN), are now *Ocloedus subdiscus* and *Ocloedus costae*. In addition, a set of characters was provided with the purpose of testing if any previous specific name assessed to *Coelodus* should actually be assigned to *Ocloedus* (Poyato-Ariza & Wenz 2002, p. 214).

Kriwet (2004) briefly mentions this issue in his discussion, but then, without justification, uses '*Coelodus*' and *Coelodus*, without explaining the meaning of the former, thus creating additional confusion, while incorrectly writing *'Coelodus' subdiscus* instead of the correct *Ocloedus subdiscus*. However, this problem has been thoroughly elucidated by Poyato-Ariza & Wenz (2002) following the rules of the IZCN. The genus *Coelodus* is now explicitly restricted to its type species, *C. saturnus*. In turn, *Ocloedus* is a valid genus according to the IZCN, clearly diagnosed, described, discussed, and figured in a published scientific paper (Poyato-Ariza & Wenz 2002), with a type species that is precisely *Ocloedus subdiscus*. Kriwet (2004) only confused this matter.

An additional problem arises from Kriwet assigning the specific name *costae* back to *Coelodus* on the basis of 'very similar' dentitions, but the precise 'similar' characteristics are not explained. As discussed in detail by Poyato-Ariza & Wenz (2002, p. 214), *costae* clearly does not present the dental autapomorphic character of the genus *Coelodus* (extremely elongated teeth on the prearticular) or any other diagnostic character of this genus. Pending revision, all available evidence indicates that the specimens with the specific name *costae* must bear the species name *Ocloedus costae*, because they present the diagnostic characters of this genus, not those of the genus *Coelodus*.

7. Final comments

"Neither considerations of interest, nor visions of ambition, but only honesty moved me to publish them! . . . Therefore show yourself more human than critical, and then your pleasure will increase . . . Live happily" (D. Scarlatti, Introduction to *Essercizi* 1738, *in* De Pinna 1994). Any given cladogram is nothing but an expression of our understanding of the phylogenetic relationships of certain taxa with the maximum information that is available at the time it is produced. As such, it is not, and should not be, considered as final, fixed, or unchangeable. It is always just one more step towards a better understanding of those relationships with additional information and revised data. That is, it is a hypothesis in the most epistemological sense of this word. Improving a phylogenetic hypothesis can only be achieved through positive, constructive criticism, continuous revision and scientific collaboration. In this sense, controversies on phylogenetic hypotheses are healthy and desirable, but only if they positively contribute to improve previous ones. The same goes for the proper use of scientific names. After all, the dynamic of statement, disagreement, and agreement (=new statement) is what makes science progress forward.

8. Acknowlegements

The author thanks B. Reichenbacher (BSP), for kind assistance while studying material under her care; L. P. Machado (Rio de Janeiro) for straightforward communication of data matrix typing errors to the author; R. Diogo (Université de Liège) for assistance with cladistic bibliography; A. Buscalioni, J. L. Sanz (both Universidad Autónoma de Madrid) and S. Wenz (Paris) for critical reading of the manuscript; V. Ingpen for efficiency and for constructive and fluent communication; and the Editors of the journal, for allowing publication of this reply.

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MS received 1 August 2003. Accepted for publication 6 January 2005.