

Phylogenetic definitions in the pre-PhyloCode era; implications for naming clades under the PhyloCode

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The last twenty years of work on phylogenetic nomenclature have given rise to many names and definitions that are now considered suboptimal. In formulating permanent definitions under the PhyloCode when it is implemented, it will be necessary to evaluate the corpus of existing names and make judgements about which to establish and which to discard. This is not straightforward, because early definitions are often inexplicit and ambiguous, generally do not meet the requirements of the PhyloCode, and in some cases may not be easily recognizable as phylogenetic definitions at all. Recognition of synonyms is also complicated by the use of different kinds of specifiers (species, specimens, clades, genera, suprageneric rank-based names, and vernacular names) and by definitions whose content changes under different phylogenetic hypotheses. In light of these difficulties, five principles are suggested to guide the interpretation of pre-PhyloCode clade-names and to inform the process of naming clades under the PhyloCode: (1) do not recognize “accidental” definitions; (2) malformed definitions should be interpreted according to the intention of the author when and where this is obvious; (3) apomorphy-based and other definitions must be recognized as well as node-based and stem-based definitions; (4) definitions using any kind of specifier taxon should be recognized; and (5) priority of synonyms and homonyms should guide but not prescribe. Strict priority should not be observed in the pre-PhyloCode era, and should not determine which existing names are permanently established; precedence should begin only with the formal establishment of the PhyloCode.

INTRODUCTION

Senter’s (2005) discussion of the phylogenetic nomenclature of the major archosaurian clades helpfully exemplifies an approach to phylogenetic nomenclature that has not previously been widely deployed: a strict application of priority applied both to homonyms (identical names with different definitions) and synonyms (different names with equivalent definitions). Senter’s application of these principles to Archosauria Cope 1869 and related clades results in several undesirable pairings of name and definition, most obviously Gauthier’s (1986:42) definitions of *Pseudosuchia* Zittel 1890 as (*Crocodylia* Gmelin 1789 not *Aves* Linnaeus 1758), which includes true crocodiles among the “false crocodiles,” and of *Ornithosuchia* Bonaparte 1971 as (*Aves* not *Crocodylia*), which excludes the family *Ornithosuchidae* Huene 1914 for which the clade was originally named. While Senter’s application of the principle of priority is flawless, it has yet to be demonstrated that it is desirable to apply this principle before the forthcoming implementation of the PhyloCode (Cantino and de Queiroz 2006), the formal code that will govern the definition of clade names. Instead, it may be better to allow future systematists working under the PhyloCode to apply its principles with a clean slate, guided but not constrained by pre-PhyloCode precedent. In this way, definitions that are undesirable (such as that of *Pseudosuchia*) or even illegal under the PhyloCode (that of *Ornithosuchia*, see Article 11.7) need not be imposed on the coming body of formally governed clade names.

Senter’s examples also raise two further important issues that must be faced when applying precedence: first, what

counts as a phylogenetic definition in literature published prior to the availability of a formal code? And second, when are two phylogenetic definitions considered equivalent for the purpose of synonymy? I faced these issues in a recent review of the phylogenetic nomenclature of diplodocoid sauropods (Taylor and Naish 2005), but the basal archosaur definitions summarized in Senter (2005) provide many helpful examples and it is primarily these that will be discussed here.

The approach to phylogenetic nomenclature advocated in this paper is appropriate only in the current, pre-PhyloCode, era—the PhyloCode itself already provides rigorous prescriptions that will resolve most issues once it has been implemented. However, this discussion is relevant to the PhyloCode-governed era in that the principles articulated herein may guide the thoughts of workers who seek to reflect previous work as they establish definitions under the PhyloCode.

Institutional abbreviations: **NMNH**, National Museum of Natural History (Smithsonian), Washington DC, USA; **RCSM**, Royal College of Surgeons Museum, London, United Kingdom.

WHAT COUNTS AS A PHYLOGENETIC DEFINITION?

The PhyloCode provides rigorous rules for establishing a phylogenetic definition, involving explicit designation of all specifiers either as species (including the author and year of their erection, as specified by Article 11.3) or as specimens (which must be the types of their species, which in turn must also be specified). So far, very few published phylogenetic

definitions meet all the PhyloCode's requirements. (Those that do include the definitions of Panaves, Avefilopluma, Avialae, etc. in Gauthier and de Queiroz [2001:18ff]; Titanosauria, Lithostrotia, Saltasauridae, Saltosaurinae and Opisthocoelicaudiinae in Wilson and Upchurch [2003:156]; Ichthyornithes, *Ichthyornis*, etc. in Clarke [2004:20ff]; and Testudines, Pantestudines and Testudinata in Joyce et al. [2004:996]). And because the PhyloCode is "not retroactive" (Cantino and de Queiroz 2006:22), even these few definitions will not be considered as established under the PhyloCode.

Until the yet-to-be-determined date of the PhyloCode's implementation, users of phylogenetic nomenclature must find a way to recognize and interpret previously published phylogenetic definitions. This is not always as straightforward as, for example, Gauthier and Padian's (1985:187) definition of Archosauria as including "crocodiles, birds, and all fossil taxa that share their most recent common ancestor," which is clearly intended to be read as a node-based phylogenetic definition with two specifiers. As an example of a less-explicit definition, Senter accepts Thulborn's "definition" of Neornithes Gadow 1893, an in-passing mention of "the crown-group (Neornithes)" (Thulborn 1984:124) despite observing that "it is obvious that Thulborn did not intend to establish a phylogenetic definition for Neornithes in that sentence. This is made obvious by the subject matter and wording of the sentence, the context of the sentence, and the fact that phylogenetic taxonomy had not yet come into existence when the paper was published" (Senter 2005:4). Other dubious definitions are not difficult to find in the literature. For example, Hunt et al. (1994:264) proposed that "diplodocids and dicraeosauroids share similar cranial features and probably together constitute a monophyletic superfamily Diplodocidae [*sic*]," which could be read as a phylogenetic definition of Diplodocidae with as much justification as Thulborn's definition of Neornithes.

It seems useful, then, to establish a protocol for recognizing available phylogenetic definitions from the existing literature, not only to guide nomenclatural usage in the current pre-PhyloCode era, but also to inform future definitions to be established under the PhyloCode after it has been implemented. I suggest that the key principle for this purpose is that of intent: an author who did not deliberately intend associating a name with a phylogenetic definition should not be interpreted as having done so accidentally, whereas an author who did intend to associate a name with a definition, and whose text unambiguously specified the associated clade, should be interpreted as having done so. While this approach calls for careful judgement in some situations, most cases seem clear-cut. If this guideline is followed, then Thulborn's (1984) definition of Neornithes is not available; so the clade that this name was inadvertently associated with (the crown-group of birds) would become available for subsequent definition. Under strict priority, this would mean that the widely disliked definition of Aves as

"all the descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae" (Gauthier 1986:8) would stand, thereby excluding *Archaeopteryx* Meyer 1861 from Aves. But, as discussed below, it is not a given that priority must be applied.

Another problem is raised by definitions that are simply malformed. For example, Parrish (1993:292) defined Crocodylotarsi Benton and Clark 1988 as "the last common ancestor of crocodiles and Parasuchia [Huxley 1875]," omitting mention of that ancestor's descendants. Read literally, this definition attaches the name Crocodylotarsi to the highly paraphyletic group consisting of a single individual—surely not what was intended. Should we then read this definition as specifying the clade descended from the nominated common ancestor? In a spirit of generosity, and in line with the previous guideline, I would cautiously say yes: in the absence of a formal code governing phylogenetic definitions, it is probably better to interpret malformed definitions, where the intention is clear, as meaning what the author intended rather than to discard them entirely. This latitude may be allowed because pre-PhyloCode phylogenetic definitions are best understood as the output of an ongoing learning process as the biological community gradually becomes accustomed to using phylogenetic nomenclature. Such license should certainly not be extended to future malformed definitions published under the governance of the PhyloCode, but until then it is better not to exclude such definitions from the corpus.

Senter (2005) followed Rowe and Gauthier (1992), Bryant (1994), and others in deprecating the use of apomorphy-based definitions (*contra* Gauthier and de Queiroz 2001), and for that reason did not consider available the definition of Aves as "the clade that is demarcated from its antecedents by the appearance of the evolutionary novelty 'feathers'" (Charig 1985:26; see Senter 2005:4). While it may be argued that apomorphy-based definitions should usually be avoided, the PhyloCode explicitly allows them (Cantino and de Queiroz 2006:32, Note 9.4.1) as well as such exotica as branch-modified and apomorphy-modified node-based definitions; it also provides guidance for establishing such definitions (Cantino and de Queiroz 2006:36-37, Article 9.8 and Recommendations 9E and 9F). To discourage the establishment of apomorphy-based clade names is one thing; to consider those that have been established as invalid is another altogether, and not justified in the light of the provisions of the PhyloCode. Apomorphy-based definitions, even if considered ill-advised, are just as valid as node-based and stem-based definitions in determining precedence.

WHEN ARE TWO PHYLOGENETIC DEFINITIONS EQUIVALENT?

Senter (2005:1) cites among "the major principles of phylogenetic taxonomy" that "Taxonomic names are considered synonymous if they refer to the same clade. . . . Among synonymous names, priority is given to the name that is tied to the clade, by means of a phylogenetic definition, in

the earliest publication.” In order to apply this principle, however, it is necessary to determine when two names are synonymous: that is, when they refer to the same clade. But what does “same” imply here? Clades that have the same content? Clades that have the same specifiers but expressed in different ways? Clades with specifiers that are equivalent under the prevailing phylogenetic hypothesis but not under others? I consider these possibilities in turn.

1) Clades with different definitions but equal content

Senter (2005:2) discussed the case of Pseudosuchia, which Gauthier (1986:42) defined as “extant crocodiles and all extinct archosaurs that are closer to crocodiles than they are to birds,” and Crurotarsi Sereno and Arcucci 1990, which Sereno (1991:27) defined as “Parasuchia, Ornithosuchidae, Prestosuchus [Huene 1942], Suchia [Krebs 1974], and all descendants of their common ancestor.” Senter noted that while these taxa are equal in content under currently accepted phylogenies, the former stem-based taxon may contain as-yet unknown or unrecognized taxa that are not included in the latter node-based taxon. He concluded therefore that these two definitions cannot be equivalent. This interpretation concurs with that of the PhyloCode, which states that “Phylogenetic definitions are considered to be different if . . . they are of a different kind [e.g., node-based, stem-based, etc.]” (Cantino and de Queiroz 2006:51, Article 13.2). It is for this reason that Taylor and Naish (2005:2) recommended continuing to recognize both *Macronaria* Wilson and Sereno 1998 and *Camarasauromorpha* Salgado et al. 1997. While not all of the draft PhyloCode’s recommendations can be usefully applied to pre-PhyloCode phylogenetic definitions, this one can and should be. The synonymy or otherwise of pre-PhyloCode clade names must be judged not on their contents but only on their definitions.

2) Clades with the same specifiers expressed in different ways

Specifiers (other than apomorphies) can be of several different types (Cantino and de Queiroz 2006:43, Article 11.1): species or specimens (allowed and encouraged by the PhyloCode); clades (not allowed by the PhyloCode—see Note 11.1.1); genera (not allowed by the PhyloCode but widely used anyway); rank-based suprageneric taxa (not allowed by the PhyloCode but sometimes used); and vernacular names such as “birds” and “crocodiles” (not allowed by the PhyloCode but surprisingly common). Using specifiers of these kinds, we see that clades equivalent to Archosauria *sensu* Gauthier and Padian 1985:187 are indicated by each of the following candidate definitions:

Species—(*Crocodylus cataphractus* Cuvier 1825 + *Cathartes melambrotus* Wetmore 1964).

Specimens—(RCSM 710 + NMNH 483532) [type specimens of *Crocodylus cataphractus* and *Cathartes melambrotus* respectively.]

Clades—(*Crocodylia sensu* Brochu 1999 + *Aves sensu*

Chiappe 1992)

Genera—(*Crocodylus* Laurenti 1768 + *Cathartes* Illiger 1811)

Suprageneric rank-based taxa—(Order *Crocodylia* Gmelin 1789 + Class *Aves* Linnaeus 1758)

Vernacular names—(crocodiles + birds)

Notwithstanding the PhyloCode’s prohibition on the use of genera, suprageneric rank-based taxa, and vernacular names as specifiers, existing definitions have used all of these types of definitions. The questions then arise of which of these kinds of specifier we should accept, and whether specifiers of different kinds should be considered equivalent. With the possible exception of vernacular names, which lack precision, all of these should be considered acceptable in pre-PhyloCode definitions, as they are all unambiguous. In practice, even vernacular names are usually sufficiently precise for the definitions in which they are used—no-one could fail to understand the scope of the definition (crocodiles + birds) above.

The PhyloCode indicates its stance on specifier equivalence in the strong wording used when it states that “a species and its type specimen are considered to be the same specifier” (Cantino and de Queiroz 2006:52, Note 13.2.2). When dealing with pre-PhyloCode definitions, this principle should be extended to all the kinds of specifier listed above, so that all six candidate definitions of Archosauria above are equivalent (and hence would be synonyms if assigned names).

Note that this recommendation absolutely does not signify any approval for definitions that use rank-based taxa or vernacular names as specifiers—it merely provides an approach for evaluating pre-PhyloCode definitions that use them. Once the PhyloCode is implemented, and ideally with immediate effect, specifiers in phylogenetic definitions should be limited to species, specimens, and possibly clades.

3) Clades with specifiers that are equivalent under the prevailing phylogenetic hypothesis

Senter (2005:2) discussed the case of Crurotarsi, which Sereno (1991:27) defined as “Parasuchia, Ornithosuchidae, *Prestosuchus*, *Suchia*, and all descendants of their [last] common ancestor,” and *Crocodylotarsi*, which Parrish (1993:292) defined as “the last common ancestor of crocodiles and Parasuchia [and all its descendants].” Both definitions share the specifier *Parasuchia*, and Parrish’s use of the specifier “crocodiles” in his definition is equivalent to Sereno’s use of *Suchia*. Under prevailing phylogenies such as that of Benton (1999), then, these two clades are identical, because Sereno’s other specifiers (*Ornithosuchidae* and *Prestosuchus*) are included within Parrish’s clade.

Should two names be considered synonymous if, as in this example, their definitions are equivalent only under certain phylogenetic hypotheses? According to the draft PhyloCode, yes: “Synonyms must be established and may be homodefinitive (based on the same definition) or heterodefinitive (based on different definitions). . . . In the case of names with different definitions, the phylogenetic context deter-

mines whether the names are heterodefinitional synonyms or not synonymous” (Cantino and de Queiroz 2006:53, Article 14.1 and Note 14.1.1). The draft PhyloCode’s clear commitment to this approach suggests that we are correct to apply it also to pre-PhyloCode definitions. Nevertheless, because synonymy status changes with the wind, it remains an unhappy bedfellow with so rigorous a concept as priority of publication, which seeks to establish a single definition as definitive in preference to all other candidates.

SHOULD WE OBSERVE PRIORITY IN THE PRE-PHYLOCODE ERA?

Senter (2005:5) asserted that “the principles of phylogenetic taxonomy do not allow their own suspension for certain taxa and do not make allowances for widespread preference or historical usage.” As with rank-based taxonomy, this is not true. Just as the existing rank-based codes include provisions for conserving junior synonyms and homonyms, so the whole of Article 15 of the PhyloCode is dedicated to procedures for conservation of names (Cantino and de Queiroz 2006:54). In addition, a proposal raised at the second meeting of the International Society for Phylogenetic Nomenclature would, if accepted, greatly relax the barriers to redefinition when the intent is to preserve content (Laurin and Cantino 2007:111–122). The PhyloCode preface describes the possibility of overriding priority as one of the important similarities between the new phylogenetic code and the existing rank-based codes: “both phylogenetic and rank-based systems have conservation mechanisms that allow a later-established name to have precedence over an earlier name for the same taxon if using the earlier name would be contrary to the fundamental goal of promoting nomenclatural stability and continuity” (Cantino and de Queiroz 2006:4). For example, this goal might be served by suppressing Gauthier’s (1986:8) definition of Aves as the avian crown clade and conserving the later definition of Chiappe (1992:348) (not Chiappe [1996], *contra* Senter [2005]) as (*Archaeopteryx* + modern birds). (I am not arguing here about the relative merits of these and other candidate definitions of the name Aves, merely observing that the definition of Chiappe (1992) better reflects historical usage.)

If suspension of priority is to be allowed even when the PhyloCode is formally established, then we should certainly also allow it to be overridden in the current, relatively informal, era. As argued above, the last two decades of phylogenetic definitions are best understood as the output of a learning process, during which experience has yielded increasing understanding of what constitutes a good phylogenetic definition—precision, stability of content, appropriateness of name, etc. This is not at all to denigrate the contributions of early definitions: they have been instrumental not only in demonstrating the use of phylogenetic nomenclature, but also in exploring the qualities that make one definition better than another—exploration by real examples and real use. Therefore, when formal and permanent definitions are

established under the PhyloCode, although they should most certainly be informed by the existing corpus of definitions, they should not be ruled by them—and especially not by the order in which they were published. Priority of pre-PhyloCode definitions should be used as a guideline that informs new definitions, not as a rule that prescribes them.

For example, when the archosaur specialist who defines the clades described in Senter (2005) comes to deal with the node-stem triplet based on the most recent common ancestor of birds and crocodiles, he may conclude that comprehensibility of nomenclature is not best served by the three names that Senter recommends as “correct” at that node: Archosauria, Pseudosuchia and Ornithosuchia. Such a specialist may believe it would be better to use junior synonyms for some or all of these names in order to produce a coherent triplet, perhaps even introducing one or more entirely new names. For example, while Archosauria would probably be preferred for the crown-clade, it might be complemented by the Panaves of Gauthier and de Queiroz (2001:24) and a new name such as “Pancrocodylia” for the reflexive stems. Such decisions should be made by informed specialists in the groups in question, and not blindly dictated by publication order.

For this very reason, and in order to make space for informed judgement in the light of two decades’ experimentation, the PhyloCode is explicitly “not retroactive” (Cantino and de Queiroz 2006:22). Senter (2005:4) is mistaken in asserting that “if the PhyloCode is published . . . the valid phylogenetic definition of Aves will be the apomorphy-based definition of Charig (1985), which ties the name Aves to the origin of feathers”—the PhyloCode’s non-retroactivity provides protection from just such consequences of early definitions.

I have alluded to an “experimental period” during which priority should be treated as a guideline rather than a rule. This experimental era will end with the implementation of the PhyloCode, as its strict and explicit requirements will make it impossible to repeat many of the flaws that beset some early definitions. Therefore, definitions proposed now, in the last days of the pre-PhyloCode era, should be treated in the same way as those of ten and fifteen years ago—with respect, but not with deference.

CONCLUSIONS

Two decades of phylogenetic nomenclature have provided many examples of phylogenetic definitions, some more rigorous than others and many of them conflicting in providing either alternative names for the same clade or alternative clades with the same name. I recommend the following principles in evaluating pre-PhyloCode phylogenetic definitions—both when using these terms in new pre-PhyloCode literature and when formulating definitions for establishment under the code when it is implemented.

1) Do not recognize “accidental” definitions (such as that of Neornithes by Thulborn (1984:124).

2) Be generous in recognizing deliberate but malformed definitions (such as that of *Crocodylotarsi* by Parrish [1993:292])

3) Recognize apomorphy-based and other more exotic phylogenetic definitions as well as the more widely used node-based and stem-based definitions.

4) Recognize definitions using any kind of specifiers (species, specimens, clades, genera, rank-based names, and informal names) so long as the intent is clear.

5) Use priority of synonyms and homonyms as a guideline, not as a rule.

Adherence to these principles in formulating PhyloCode-compliant definitions will facilitate the establishment of a coherent body of names providing the optimal blend of consistency and continuity with prior usage.

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