The PhyloCode, or alternative nomenclature: Why it is not beneficial to palaeontology, either

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Methodological stability in biological nomenclature is being upset recently, with potential consequences for palaeontology. Some systematists, inspired mainly by de Queiroz and Gauthier (1990, 1992, 1994), reject traditional nomenclature in favour of an alternative "Phylogenetic Nomenclature" (PN). Following de Queiroz (2006) I consistently call this Phylogenetic Nomenclature, rather than Phylogenetic taxonomy, as it is often done. Important tenets of PN are the abandonment of hierarchic ranks and binomial names, and establishing name definitions based on cladogram shape (node-, stem-, and stem-modified node-based definitions), apomorphies (apomorphy-based definitions), or a combination of apomorphies and tree topology (apomorphy-modified node-based definition). For an explanation of such definitions, see Cantino and de Queiroz (2003) and Sereno (2005). The practice of Phylogenetic Nomenclature is laid out in an Internet document, the PhyloCode (Cantino and de Queiroz 2003). PN is seen as the natural next step in the evolution of taxonomy: from Linnaeus' (1753, 1758) "creationist taxonomy" to Hennig's (1966) cladistic taxonomy. Hence, Linnaeus' ideas should be removed from nomenclature, which will then reflect phylogeny. Despite the dominance of cladistics as a framework for taxonomy, the validity of its philosophies and methodologies are still questioned (e.g., Szalay 2000). I encourage everyone, independently of school of taxonomy adhered to, to take interest in PN, because: (1) we are all creators or users of taxonomies and classifications, (2) PN is radically different from the current standard, (3) the Preface to the PhyloCode suggests it should ultimately replace the current Codes of Nomenclature (of bacteria, LaPage et al. 1992; of Zoology, ICZN 1999; of Botany, Greuter et al. 2000). I argue herein, why palaeontologists should not follow PN.

Palaeontologists have long recognised problems with ranked classifications (de Queiroz and Gauthier 1990, 1992, 1994) that they tried to solve. For example, the concept of plesion (a rankless unit for fossil taxa, to be inserted in ranked classifications of Recent groups), proposed by Patterson and Rosen (1977) is still in use (despite criticism, see Ereshefsky 1997) and supposedly alleviate rank-based problems (Forey et al. 2004). Palaeontologists (e.g., Benton 2000; Forey 2002; Sereno 2005) are an influential force in the debate on naming, even though it does not concern solely palaeontological nomenclature. This paper focuses on implications of PN for palaeontology. Brochu and Sumrall (2001) attempted to summarise all "palaeo-benefits" of PN. Dyke (2002) argued against these, but his paper does not seem to be a reaction to Brochu and Sumrall (2001) per se. I also argue that it is preferable for palaeontologists to keep traditional nomenclature, through a point-by-point rebuttal of Brochu and Sumrall (2001).

Roughly speaking, Brochu and Sumrall (2001) provide two main arguments to favour PN for palaeontology: (1) explicitness of taxon names allows for efficient communication on taxa that contain fossils, (2) through stability of taxon names, boundaries of groups with poorly known fossils are fixed and universally known. Brochu and Sumrall also address the problem of ranks, but do not clarify how this concerns palaeontology strictly. An obvious Phylogenetic Nomenclatorial argument would sound like this: (3) fragmentarily known fossil taxa in ranked classifications create more taxonomic chaos than completely known groups, hence it is better to adopt rankless nomenclature. Below, I elaborate on, and refute, each of these arguments. In doing so, I discuss points (1) and (2) together, because both concern the extension (simply put, the meaning) of names, and arguments and counter-arguments for both points are similar.

Explicitness and stability of taxon names, pro

If the meaning of taxonomic names is based on characters, taxon boundaries are ambiguous and subjective. This is especially problematic if the taxon includes fossil groups. Palaeontologists and neontologists apply different characters (often only osteology for vertebrate palaeontologists, and many other kinds of data for neontologists). Moreover, researchers of fossils work in different time frames than biologists concerned with extant groups. Palaeontologists may consider that differing forms from a (long) fossil record belong to the same clade, while neontologists, appreciating only present forms, find the taxon is less varied. An example of this is the debate on the evolution and fossil record of genus *Crocodylus* (Brochu and Sumrall 2001). While neontologists include only species of a crown group of living forms, palaeobiologists also include extinct, fossil stem group species in this genus. This discussion was full of misunderstanding, apparently not because data conflicted, but because the use of the name *Crocodylus* was ambiguous (Brochu 2000). Thus, it is better for palaeontology to define names whose meanings are unchangeably established and unambiguously reflect phylogeny, because of being based on tree topology.

PhyloCode names never change, amongst others because there is no need to create new ranks or move a taxon to a different rank. Also, definitions of such names are immutably fixed at first usage. Our understanding of taxa will change, but the boundaries of what their names include stay the same. Thus, study of organisms themselves will receive more attention, and questions of how to rename them will be irrelevant.

Explicitness and stability of taxon names, contra

It is a myth that names under PN are explicit. Only one definition of a certain phylogenetic name exists, but it may be ambiguous which taxa fall under that name, especially in palaeontology. For example, Benton (2000) compared cladograms of birds and their relatives, published first by Sereno (1998) and then by Padian et al. (1999). These authors applied phylogenetic name definitions, which results only in confusion (Benton 2000). I illustrate this by focusing on the name "Deinonychosauria", which is only one of the names applied by Sereno and Padian et al. whose meaning is not explicit. Sereno's node-based name Deinonychosauria is valid for terminal clades Dromeosauridae and Troodontidae, their common ancestor, and all its descendants (Fig. 1). When applying this to Padian et al.'s phylogeny, all taxa in their tree would fall under "Deinonychosauria", because of the topological differences with Sereno's tree (Fig. 1). Besides, Padian et al. apply their own definitions, disregarding earlier ones (thereby violating the PhyloCode!). Their "Deinonychosauria" (a stem-based name that applies to all species closer to Dromeosauridae than to other Eumaniraptora) covers fewer taxa than Sereno's.

In general, the most confusion about name meanings would be caused by stem-based definitions (Dyke 2002), because "stem names", in general, cover more taxa than other name types, and hinge often on poorly known fossils. Since these lack many characters, new discoveries may radically change tree shape. Besides, phylogenetic definitions "instead" of character-based definitions will not solve the problem of imprecise name meanings, since the PhyloCode allows for definitions based on apomorphies anyway.

Our understanding of what a name refers to may change over time, especially when dealing with fragmentary fossils. Hence, it is hard to ever know what a PhyloCode name means. What if a primitive sistergroup taxon in a future cladogram moves to the ingroup? Is the original stem-based definition still valid then? Should not the meaning of a name be changed in that case? Brochu and Sumrall argue, that not every node in a cladogram has to be named, so it is up to taxonomists not to name labile nodes that differ from one cladogram to another, and wait until there is enough taxonomic knowledge to name them. However,

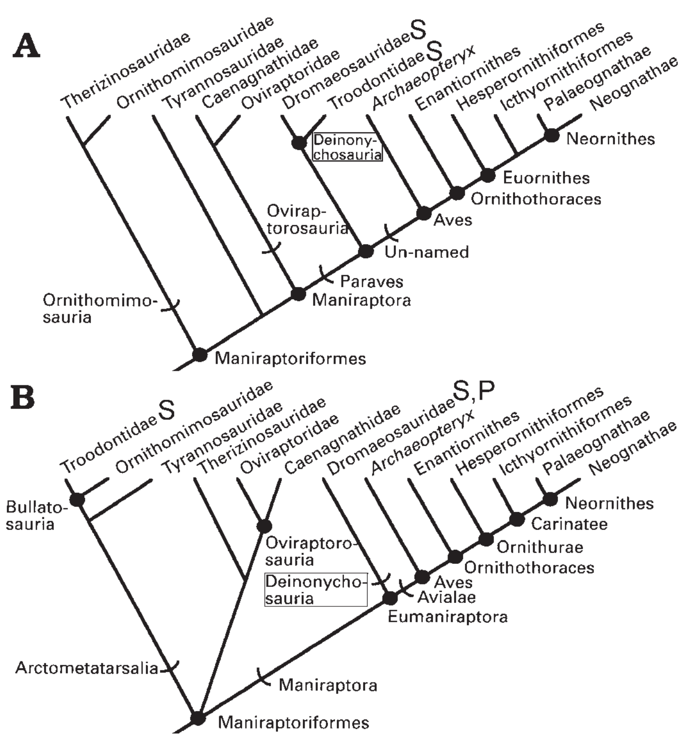

Fig. 1 Comparison of cladograms of Sereno (1998) (**A**) and Padian et al. (1999) (**B**), showing phylogenetic hypotheses of birds and theropods (modified from Benton 2000). Names in these cladograms are "phylogenetically" defined; dots denote "node-based names"; crescents denote "stem-based names"; S denotes taxa that are included in Sereno's node-based definition of Deinonychosauria (this is boxed because the text features a discussion concerning this name); P denotes a taxon to which Padian et al's stem-based definition of the same name points.

Padian et al. (1999) ignored taxonomic instability of primitive theropods and named also labile clades. Hence, that what Brochu and Sumrall called "common practice", is not upheld (Dyke 2002). In traditional nomenclature, names may change because a group has to get a different rank. What changes is only the suffix, but the stem remains recognisable (e.g., Sardini–Sardinae). What may stay the same when the name changes, is taxon content: exactly the same set of species may still be there (see also Dyke 2002). This is in no way a less stable system than PN. Bryant and Cantino (2002) and Cantino and de Queiroz (2003) state, however, that fixed names attached to changing taxon contents is a strength of PN names that answers a great variety of concerns regarding that type of nomenclature. That view of stability is based on an erratic philosophy (see Nixon and Carpenter 2000 for more details).

The nature of palaeontological species implies that implementation of PN would have a destabilising effect in nomenclature. As Smith (1994) pointed out, one should apply morphology-based species concepts to fossils rather than pattern-based concepts. If such incomplete, morphology-based species are used to define names, this causes taxonomic instability because of unclear phylogenetic positions of fossils (Nixon and Carpenter 2000).

Nomenclatorial stability is an important issue in this discussion. Nixon and Carpenter (2000) found, after performing tests, that "traditional" names are more stable than PN ones. However, as Lee (2001) pointed out, Nixon and Carpenter mistook PN's apomorphy-based name definitions for traditional nomenclatorial acts (despite this, I sympathise with Nixon and Carpenter's 2000 counterarguments against PN). Nevertheless, I do not accept that stability of apomorphy-based name definitions is an argument for PN. Instead, I suggest applying apomorphy-based definitions, to taxa rather than names, within the current framework (see Monsch 2003 for more details). This will result in relatively stable nomenclature, without a need for completely new Nomenclature Codes.

Based on the above, I advise to keep ranked names following traditional Codes, but explain what they cover before arguing over their meaning. In addition, considering the confusion surrounding *Crocodylus*, I think it is wrong to exclude stem taxa from a name, and reserve popular names such as *Crocodylus* only for crown clades of Recent species.

Abolition of ranks creates order, pro

In systematic palaeontology monotypic taxa often appear (e.g., a monotypic order containing eventually one monotypic genus). Thus, many redundant ranks are being created (de Queiroz and Gauthier 1992, 1994). When dealing with poorly known genera, especially fossils, ranks pose another problem. Establishing new species is here likely to create paraphyletic, polyphyletic or many monotypic genera. Would it be likely, according to the real phylogeny, that a group contains numerous monotypic genera? Additions of new material of incomplete fossils analyses may radically change cladogram shape, and thus hierarchical order in a classification: sometimes, most taxa require a different rank than before (excessive name change). Besides, the tree of life would have more divisions than ranks can handle (Hibbett and Donoghue 1998), especially when considering monotypic fossil clades.

Abolition of ranks creates order, contra

There are ways to deal with problems posed by ranks (Benton 2000), for example not applying all ranks. The fossil with species eptithet *sarissa* (Sytchevskaya and Prokofiev 2002) is now classified as follows: family Hemingwayidae (monotypic), genus *Hemingwaya* (monotypic), species *H. sarissa*. However, this species does not need to be placed in a family, which reduces the degree of redundancy. Ranks have a utility that PN would do away with: they indicate mutual inclusivity and exclusivity for monophyletic taxa (see Forey 2002; Schander and Tholleson 1995 for detailed discussion). Because fossils are incomplete, new specimens may change previous hypotheses. Dyke (2002) gave a hypothetical example of such a revision (proving the superiority of ranked names), which I will somewhat expand. If one discovers that material previously identified as *Archaeopteryx rubblei* belongs to *Coelophysis*, the name of the species, according to the ICZN, is to be revised into *Coelophysis rubblei*. The genus and species rank here convey that species *rubblei* has the same common ancestor as all others classified in *Coelophysis*. This would not be obvious from a PhyloCode name, which is not binomial, and unchangeable, even if new information appears. The problems that incomplete fossils pose for taxonomy and nomenclature are not the fault of nomenclature, but caused by the fragmentary nature of data. Hence, rather than applying PN to tackle those problems, I advise using methodologies such Safe Taxonomic Reduction (Wilkinson 1995) to maximise information retrieval from incomplete fossils in phylogenetic analyses (e.g., Fierstine and Monsch 2000). Besides, in more than 200 years of adding new taxonomic information to existing classifications, the argument that ranks cannot handle the divisions of the tree of life, has not proved to be practically relevant. I do not recall reports of taxa that have too many subdivisions to classify them, besides hypothetical examples of Hibbett and Donoghue (1998). These authors did not consider classifying without redundant ranks, which I think would solve this problem. It needs to be mentioned that the PhyloCode (Cantino and de Queiroz 2003) permits, but does not *require* rankless names, which I think is in contrast with the aims of PN.

Discussion

The reasons for creating the PhyloCode are understandable. The current system has drawbacks such as excessive name changes and multiple name meanings. The PhyloCode supposedly solves taxonomic problems that especially consider palaeontology. These are caused by incompleteness of material and the fact that fossils are often in stem groups that neontologists may ignore. The PhyloCode, however, is criticised from the viewpoint of taxonomy in general (e.g., Forey 2002), and the net result of this discussion seems to be negative for PN. From a strictly palaeontological point of view, the PhyloCode is not a beneficial nomenclatural code either. For example, it is not flexible enough to cope with changing insights of phylogenies that include fossils, which are very likely to change because of the nature of fossil data. It is preferable to have changeable names for stable taxon contents, which is possible now. Traditional nomenclature is more beneficial to palaeontological taxonomy. This does not mean we should ignore its drawbacks. We can combat these, for example, by proposing changes in the nomenclatural codes (e.g., my proposal on the use of apomorphies in definitions, Monsch 2003). Ranks and binomials exist for over 200 years. Names like *Tyrannosaurus rex* and *Homo erectus* are well known, widely understood, so it would not make sense to abolish the system that created them.

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