Discussion

Acta Palaeontologica Polonica 52 (3): 651–655, 2007

The Phylocode: Beating a dead horse?

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The concept of the Phylocode has been evolving for some twenty years, and is supported by Lee and Skinner (2007): I argue against it here. The first issue is stability, and biologists must decide whether they seek rigidity (Phylocode) or flexibility and conservativeness of clade contents (Linnaean codes). Phylocode names for taxa are by definition stable because they are established as labels for clades that are rigidly defined as geometric constructs. But this is not real stability because the species contained within those clades can change dramatically: an example is given where Phylocode practice forces a decision about the name Deinonychosauria, which can contain 20 or 10,000 species depending on which current tree is correct. Linnaean systems offer real stability (= conservativeness + flexibility) where the taxon name can be moved subtly up and down nodes in a tree to keep its association with a particular character or group of species. Proponents of the Phylocode argue that category/rank terms should be dispensed with, and yet they have no need to do this. Everyone accepts that Linnaean ranks are subjective, and yet there is no benefit in abandoning ranks because they have proved to be of such value to users of classifications, and genera and families, for example, act as valuable surrogates for species in large-scale evolutionary and ecological studies. Finally, the Phylocode extends regulation beyond names and their proper use into determining the validity of phylogenetic hypotheses, and this will act as a limit on normal scientific debate.

Introduction

The Phylocode was proposed in 1998, and it has been enthusiastically promoted by a small group (de Queiroz and Gauthier 1992; Lee 2001; Cantino 2004; Cantino and de Queiroz 2004; de Queiroz 2006; Härlin 2005; Sereno 2005; Laurin and Cantino 2007). I have expressed my views against the Phylocode before (Benton 2000), as have others (Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Nixon and Carpenter 2000; Dyke 2002; Forey 2002; Carpenter 2003; Keller et al. 2003; Nixon et al. 2003; Monsch 2006; Rieppel 2006). The main arguments against phylogenetic nomenclature (PN) and the Phylocode have been:

– It is not needed—the suggestion that Linnaean systems cannot work with cladistic phylogenies has been demonstrated to be incorrect over the past thirty years; classifications have been brought into line with cladistic trees in many groups (Hennig 1966; Patterson and Rosen 1977; Wiley 1979; Smith 1994; Benton 2000).
– It produces rigidity of clade definition at the expense of losing the flexibility and conservativeness of classification schemes (Benton 2000).
– It is philosophically unsound, generating a clash between the essentialist claim that species (and higher taxa) are individuals and the practical problem that this means their names are proper names and cannot be defined (Rieppel 2006).
– Clades defined according to specifiers are geometric constructs that work only with reference to a particular phylogeny—change the phylogeny and the contents of the clades may change substantially (Benton 2000).
– It is next to impossible to reconcile the familiar Linnaean binomials (genus and species names) with PN and the Phylocode (Cantino et al. 1999).
– The drive to use pure principles of PN has led to a number of controversial proposals—the abandonment of the Linnaean binomen, the abandonment of ranks, and the migration of established names to crown clades; all have led to confusion for no gain (Benton 2000). Indeed, none of these issues is essential to PN or the Phylocode (Pickett 2005; Sereno 2005).
– The new regulation of clade definitions will lead to much confusion.
– The task of generating Phylocode definitions and of reading and legislating cases of dispute will divert good systematists from their core work.
– Perhaps PN will operate better without the Phylocode and the rigours of hard regulation (Sereno 2005).

Lee and Skinner (2007) were led to write their paper to *Acta Palaeontologia Polonica* as a response to an earlier short comment by Monsch (2006), in which he reviews the problems in applying PN and the Phylocode to palaeontological systematics. Lee and Skinner (2007) concentrate on two core issues of PN, stability and Linnaean ranks, and I discuss those, and add a third, compulsion. The terms PN and Phylocode are matched by the term rank-based nomenclature (RBN) and rank-based codes, for the existing codes of zoological, botanical, and microorganism nomenclature. References to PN and the Phylocode refer to the core aims of the proponents of those viewpoints, and reference to RBN encompasses the current non-PN practice and the existing codes, which happen to be rank-based. Both camps include supporters of alternative viewpoints of course, but it is simpler to focus on the mainstream views.

In a nutshell, my view is that phylogenetic nomenclature and the abandonment of ranks are unnecessary and that the Phylocode is a burdensome regulatory framework looking for a problem that does not exist.

Stability

There are two meanings of the word "stability", and proponents of the Linnaean codes mean one thing, while PN supporters mean another. Both agree, of course, that classifications must not be constantly changing, and that names applied to clades should remain as close to their traditional meanings as possible. But, PN stability involves two additional measures of rigidity not seen in rank-based classifications, the geometric property by which a clade name is tied to two or more specifiers, and the principle of priority, which means that a disputed definition has to be formally rejected and replaced through the Phylocode rules. So, RBN clade names remain stable in that they can move subtly every time a new fossil is discovered, or a new phylogeny is published, whereas PN clade names remain stable because they have been fixed. The difference in the end is the choice between fluidity and evolution, as with languages, or the firmness of a one-off decision that is protected by rules and is hard to modify.

Lee and Skinner (2007) refer to examples in support of the greater stability of PN. In Benton (2000), I presented a case study from the phylogeny of theropod dinosaurs including birds that shows the rather wild behaviour of PN names when the phylogeny changes. There are three or four competing cladograms for the tree of basal birds and their nearest theropod relatives, each tree based on thorough analysis of numerous characters and specimens by reputable palaeontologists. I showed how RBN rules did not force any hard decisions to be made about what to call each clade, and that the debate can roll out over the next decades until a consensus is reached. Key clades such as Aves, Maniraptora, and Deinonychosauria can be modified subtly as new taxa are discovered and as the currently most parsimonious tree changes. The key point is that the meanings of the RBN clade names remain stable in a conservative sense. At the end of the process, the larger clades will still contain essentially the same species and will still include those taxa that possess certain characters. Under PN on the other hand, a decision about the naming of the higher-clade names would be forced—proponents of different competing theropod trees are known PN supporters. I showed how the PN names changed when switched from one tree to the other. The scale and hierarchical order of names flipped as they were applied from one tree to the other: for example, the clade Deinonychosauria, including some twenty dinosaurian species according to one tree, changes to include those twenty plus another fifty species of theropod dinosaur, plus all 10,000 species of birds according to the other tree. The meaning of the PN names remains stable as a geometric construct, but not the meaning in terms of contents, key characters, or hierarchical position: a shift in the content of a named clade from twenty species to ten thousand is not trivial, and is certainly not stable!

Such shifts in meaning can happen in RBN, but they are rarer: an example has been the Family Iguanidae, that includes over 800 species according to traditional classifications, and about 40 according to the revision by Frost and Etheridge (1989). But the key point is that the debate over iguanid classification has not been constrained by a predetermined definition: herpetologists have been free to make their decisions about whether Iguanidae is a huge clade, or whether its subclades should be re-ranked as families.

It is this infinitely elastic property of PN names that most people would find disturbing—what was once a "genus" becomes a "phylum" or *vice versa*. A further example could be if Lipotyphla had been fixed as a PN clade name on tenrec and hedgehog as specifiers. Now that tenrec is moved out of Lipotyphla and into Afrotheria, PN Lipotyphla would then have to encompass most placental mammals, and would be virtually identical to Eutheria. Under the RBN codes, nobody has lost any sleep over the extraction of Tenrecidae (tenrecs) and Chrysochloridae (golden moles) from Lipotyphla and Insectivora, and their transfer to Afrotheria and new clades within that clade. Under PN, either the major change in meaning of Lipotyphla would have to be stomached, or a special case made to change the original accepted PN definition by nominating a new specifier for Lipotyphla other than the tenrec.

Lee and Skinner (2007) complain that "for repeated adjustments to have a stabilising (rather than destabilising) effect, taxonomists would need to arbitrarily agree on the 'appropriate' content of the taxon concerned". They indicate further that where there are competing phylogenies for a group it is hard to see how names can be fixed. But that is just the point: do we want an open system, as at present, where higher ranks are not regulated and scientific discourse can proceed and the meanings of names can evolve slowly and conservatively to track new discoveries, or do we want a PN system where names are rigid and divorced from scientific discourse about phylogeny?

So, which system offers greater stability? There are two answers:

(1) The PN system offers most stability because names are rigid and refer to fixed geometric constructs. This is inevitable because PN names are by definition fixed, so the observation is trivial.

(2) The RBN system offers most stability because catastrophic changes to the content of named clades are avoided in practice; such catastrophic changes in clade contents cannot be avoided under PN. This is for two reasons: current practice and the lack of legislation. Current practice by most systematists is to assume that clades are elastic and can readily be modified subtly to include newly discovered species or to accommodate a change in the phylogenetic model. The RBN codes do not regulate the meaning and content of higher taxon names, and that permits normal scientific debate to proceed (see below). Systematists are free to modify earlier work based on new evidence, and that allows them to retain the conservative stability of taxon names.

This contrast of meanings of stability relates to the different import of taxon names under RBN and PN systems: whether the names function for circumscription or definition of a taxon

(Nixon and Carpenter 2000). As Langer (2001) noted, stability is the essence of PN names, and they can be nothing other than stable—in fact they are absolutely fixed. Rieppel (2006) terms them "rigid designators" and clarifies that, if species and higher taxa are individuals, then PN taxon names are proper names and so cannot be defined. If species and higher taxa are classes their names are "kind names" and so can be associated with lists of diagnostic characters, and those diagnoses can change as the composition (meaning) of the taxon changes with further research. Such class/ kind names readily reflect phylogeny and encompass hypotheses of origin (Rieppel 2006). The question then is whether it is preferable to have rigid geometrically determined proper names and nearly infinitely fluid contents of clades that may change unpredictably (PN codes) or adaptable names and stable content (RBN codes).

Linnaean ranks

There is no logical reason why the Linnaean codes and the Phylocode should be associated with the use of ranks and the abandonment of ranks respectively (de Queiroz 2006; Lee and Skinner 2007), but most supporters of "traditional" or "Linnaean" codes use ranks, while most supporters of PN and the Phylocode abandon ranks, even though that is not demanded in the Phylocode, and the debate continues. My key point here is to argue that ranks are of value, and this need not bear directly on the use or not of the Phylocode.

The RBN codes do not specify how to set categorical rank levels, and Lee and Skinner (2007) are correct that many unsuccessful suggestions have been made. No one can say that one family is equivalent to another on the basis of time since origin, genetic differentiation, or anything else. But, few have ever tried to set such general rules to determine rank, so this is a slight red herring in evaluating Linnaean nomenclature. PN proponents object to the need to change clade endings when ranks change (e.g., family Iguanidae becomes Superfamily Iguanoidea or Subfamily Iguaninae, according to the ICZN). Arguably, what is happening in a case like this is not that one name is moving up and down and being modified, but that new clade terms are being introduced to make a complex situation more manageable. Many would argue that common endings for clades of roughly equivalent size/ rank/ age might actually be useful.

Supraspecific taxa are real in two senses. First, they should be monophyletic and, if so, their lower bound is marked by a node in a cladogram. Second, they have an inclusive hierarchical property: taxa called genera always fit inside taxa called families, families within orders, orders within classes, and so on. So, the inclusive hierarchy of category terms (kingdom, phylum, class, order, family, genus) reflects a linear hierarchy of times of origin (family A containing genus X must have originated at the same time as, or before, genus X) and a linear hierarchy of amount of genetic differentiation or morphological disparity (family A containing genus X must have the same amount of, or greater, divergence/ disparity than genus X). Of course, the inclusive fitting of clades within clades is true whether they are ranked or not.

There is an equivalence of taxa assigned the same categorical level within broad groupings. So, for example, dogs (Canidae) are separate from cats (Felidae), and all "families" within the order Carnivora share common characteristics: a similar amount of morphological disparity, genetic divergence, and time since origin. The species in "families" of Carnivora, assessed in terms of any genetic or morphological measure, plot in hyperspace as equivalent-sized clouds of points separated from each other by equivalent distances. The decision by generations of Linnaean taxonomists to name these clusters all as families was not therefore random. The decision reflects a reality in the way taxa plot on trees, as well as evolutionary conservativeness and ecological adaptations of closely related species. It is no wonder then that generations of biologists have accepted the practical equivalence of families of carnivores, and perhaps of all mammals. It might not be unreasonable to suggest that the marsupial Family Petauridae has broad equivalence to the placental Family Canidae. But few, if any, have ever claimed that a family of fishes, bivalves or angiosperms is equivalent in any meaningful way to a family of mammals.

Everyone agrees that ranks cannot be mapped onto trees objectively, and the dispute is about whether ranks should therefore be abandoned (majority PN view) or not (RBN view). Many PN supporters have rejected ranks, and rank-free classifications dominate in some journals such as *Journal of Vertebrate Paleontology*, even though there is no reason whatsoever that they should, as Lee and Skinner (2007) note—the Phylocode claims only to regulate the geometric specification of clades, and it doesn't matter to the success or failure of the Phylocode whether people wish to add a rank designator to their clade terms (de Queiroz 2006).

Linnaean/RBN apologists (e.g., Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Benton 2000; Nixon and Carpenter 2000; Forey 2001; Monsch 2006) have asked why many or most PN advocates demand the abandonment of ranks when (1) they need not abandon rank terms to establish the Phylocode, nor (2) is anything gained. The only reason for abandoning ranks is a perceived improvement in objectivity: ranks are broadly subjective, so they should be scrapped. Reasons for retaining rank terms are classed as informativeness and utility (Lee and Skinner 2007).

Ranks give us information about relative inclusiveness of clades (subfamilies ending -inae fit inside families ending -idea, and these fit inside superfamilies ending -oidea) as well as about exclusivity (one family cannot fit inside another). Lee and Skinner (2007) present real and hypothetical examples where these kinds of informativeness become problematic: such examples do not detract from the *general* usefulness of rank terms in indicating inclusiveness and exclusivity. In their example concerning *Homo* they suggest that a PN approach would resolve the current debates about the application of the names *Homo*, species of *Homo*, Hominini, Homininae, Hominidae, and the like. Of course, a PN approach would not really resolve the debate; it would merely impose a rigid set of definitions over the debate. It's worthwhile to consider whether *Homo neanderthalensis* is a valid species or a race of *Homo sapiens*, and DNA coding of Neanderthals may resolve this. Likewise, it is important to con-

sider the content of Hominini, Homininae, Hominidae— fixing the content by fiat will not stop the debate, because the debate is not baldly about content of the taxon and its category level, but about much bigger issues such as the genetic diversity of the species of *Homo*, the meaning of races today and in the past, the "out of Africa" *versus* "candelabra" models of recent human evolution, the comparability of our species with other mammal species, and the like. Fixing the semantics will not stop the debate—competing palaeoanthropoligsts will continue to argue about the key questions about phylogeny and will be merely irritated by the imposition of a set of naming conventions.

Utilitarian functions of classifications include equating clades for purposes of learning and reference and as proxies (surrogates). It would be easy to deride the argument about utility of reference systems to non-systematists who find it manageable to cope with the 18 orders of placental mammals or the 233 families of angiosperms, but a key function of the whole taxonomic enterprise is to provide authoritative classifications for the world, whether professional, student or avocational. Lee and Skinner (2007) say that "biologists will familiarise themselves with and use names of important taxa… whether or not they are associated with Linnaean ranks". True, but they will want lists of equivalent-scale taxa, and that implies ranks. Further, taxa at particular ranks, notably genera and families, are important proxies or surrogates in macroevolution, biogeography and biodiversity studies: certain kinds of analyses (e.g., measurements of long-term evolutionary rates, extinction magnitudes, large-scale ecological analyses, global studies of biodiversity, biogeography and conservation) can only be carried out at the level of supraspecific categories such as genera or families for practical reasons (species-level data are often of poorer quality than genus-level data in palaeontology; it takes ten times as long to do a census to species level than to generic level). The use of equivalent-rank higher taxa as surrogates makes many assumptions of course (Bertrand et al. 2006), but the practice will doubtless continue because the benefits outweigh the problems in certain fields. Indeed, the fact that generic and familial diversity patterns correlate well with species-level patterns in many studies in ecology (Balmford et al. 1996; Williams et al. 1994, 1997; Báldi 2003; Doerries and Van Dover 2003; Villaseńor et al. 2005; Magierowski and Johnson 2006) and palaeontology (Raup 1979; Foote 1996; Roy et al 1996; Robeck et al. 2000; Adrain 2006) suggests there might just be something in the long-held assumption of rough equivalence of taxa by rank.

My question remains: why abandon ranks when nothing other than semantic purity is gained by doing so?

Compulsion

In most papers, whether for or against the Phylocode, relatively little attention has been given to the legislative aspects (but see Benton 2000; Nixon and Carpenter 2000). If PN is to be applied and the principles of the Phylocode established, we have to accept a new level of regulation and compulsion in systematics. Current codes present rules about naming and type specimens, and concentrate mainly on the species level, with additional rules for forming names up to superfamily level (ICZN) and division (ICBN). The Phylocode consciously extends to regulate priority for higher ranks, and the implications are far wider than just a new kind of nomenclatural control that will affect a small band of people interested in semantic issues. The net will extend through systematics and evolutionary biology and the distress could be immense if the Phylocode is ever accepted.

My first point is a minor one. Working systematists are a small, and perhaps diminishing group, and they should devote their efforts to discovering nature (i.e. describing new taxa and reconstructing phylogeny) and not to semantic issues that are liable to suck too many people dry with anger and unhappiness. Systematists expend energy at present over disputes about type specimens, priority of generic and specific names, and appeals to the boards of the codes are slow and time-consuming. To add a new formal, legislated activity in defining all existing suprageneric names in PN terms, and then dealing with disputed priorities, will add further disputes and eat up valuable time and energy.

My second point is more significant. The world would change under the Phylocode, and most systematists have not thought this through. Linnaean codes do not involve any supervision of the bulk of the work of systematists, whereas the Phylocode proposes new activities and new levels of regulation. PN names (whether new or redefined old ones) all have to published in the usual way, and then registered in the Phylocode registration database. This represents a large amount of new work, because all the millions of existing names have to be redefined at some point—for new names, the new system would not imply extra work. New work means new confusions. PN naming will doubtless attract enthusiastic contributors who will seek to sweep through large clades and provide coherent listings of clade definitions, and mistakes will be made and disputes will arise. Experience so far is limited, but early efforts to use Dinosauria as a demonstration example led to two independent systems, published at the same time (Sereno 1998; Padian et al. 1999) and offering different names for the same clades, and the same names defined to different clades. This happened before the Phylocode was in force: the registration of the name definitions would have been an extra effort, and there is an issue of who gets to the registration portal first—synonyms can be uploaded, but the Phylocode indicates the need for priority, and systematists might very well end up bickering over days and hours! There will have to be a system of appeals and formal determinations of priority through the Committee on Phylogenetic Nomenclature (CPN), and indeed rejection of inappropriate names or definitions. Imagine the volume of work that could be generated, and the lobbying and acrimony as opposing camps square up to each other! And for what?

Conclusion

My conclusion is simple. Why would anyone be interested in forcing themselves into the straightjacket of the Phylocode, which offers no advantages, and could stifle their research if their tree is rejected in favour of another study, when the Linnaean codes have proved adaptable and reasonable adjuncts to systematic work?

Acknowledgements

I thank Zofia Kielan-Jaworowska for the invitation to write this short essay, and Mike Lee, Adam Skinner and Kevin de Queiroz for helpful comments.

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