Discussion

Acta Palaeontologica Polonica 52 (3): 643–650, 2007

Stability, ranks, and the PhyloCode

MICHAEL S.Y. LEE and ADAM SKINNER

Current codes of biological nomenclature define taxon names using types and ranks: the type determines the minimal membership of a named taxon, and the rank is supposed to determine its limits. *Homo* is "the taxon including the type species *Homo sapiens* that is assigned to the rank of genus". However, there is no "genus concept" (analogous to a species concept), and thus no way of empirically determining the limits of a particular genus, even in the context of a single agreed phylogeny. The same problems also apply to higher taxa at all other ranks under current codes, leading to great taxonomic instability. All proposed objective criteria for determining membership of taxa at a particular rank (e.g., geological age, genetic divergence) are shown to be problematic. In contrast, the clades named by phylogenetic definitions are objective and stable. Node-based and branch-based definitions are most precise; however, apomorphy-based definitions can be ambiguous due to difficulty in defining alternative character states, and optimisation uncertainty. A major benefit of ranks (information about relative nesting of taxa) can be achieved even more efficiently using standardised but rankless suffixes already widely used in phylogenetic taxonomy. Finally, in situations where the phylogeny is poorly known, phylogenetic nomenclature appears to be superior to the Linnean system. Phylogenetic nomenclature does not force one to officially name poorly corroborated groupings, whereas Linnean codes compel users to erect and name genera even when relevant supraspecific relationships are poorly known.

Introduction

The traditional, Linnean system of biological nomenclature was conceived long before the concepts of evolution and phylogeny were generally accepted (Linnaeus 1753, 1758) and, despite subsequent modifications, reconciling this system with contemporary biological theory and practice remains problematic (e.g., de Queiroz 1997; Ereshefsky 2001). As a result, many authors have suggested that an entirely new and explicitly phylogenetic nomenclatural system, regulated by the PhyloCode (Cantino and de Queiroz 2006), would better serve the needs of systematists and the general scientific community. This proposal has understandably prompted lively discussion; however, some of the debate has failed to properly characterise key issues and thus generated more heat than light. We here hope to facilitate more rational discussion by outlining the most significant differences between the PhyloCode and the traditional codes of nomenclature (Lapage et al. 1992; Greuter et al. 2000; International Commission on Zoological Nomenclature 1999). Our focus will be on the zoological code, although the points made are also relevant to the botanical and bacteriological codes. Moreover, discussion will be limited to the naming of supraspecific taxa (i.e., clades of species), since the PhyloCode does not presently incorporate rules for naming species (Laurin and Cantino 2007). Much of the debate over phylogenetic nomenclature and the PhyloCode concerns two issues, the stability of taxon names and content, and the abolition of mandatory Linnean ranks, and these topics are therefore our main concern. Some authors criticising the PhyloCode have described cases where phylogenetic nomenclature is supposedly problematic (e.g., unstable), but have failed to consider how the Linnean codes would perform in the same situations; we explicitly compare the two approaches.

Although many of the points made here have been raised previously (e.g., de Queiroz and Gauthier 1990, 1992, 1994; Sundberg and Pleijel 1994; Cantino et al. 1997; de Queiroz 1997; de Queiroz and Cantino 2001; Ereshefsky 2002; Pleijel and Rouse 2003), they have often been embedded in technical and/or lengthy papers that are not very accessible to non-taxonomists. This paper is intended as a succinct introduction to current debate. A similar, but more detailed paper by Laurin (2005) should also prove useful for general readers interested in evaluating the relative merits of the PhyloCode and the traditional codes. While this paper covers similar ground, some additional observations are made: DNA barcoding does not solve the problem of objectively assigning Linnean ranks, and the only proposed benefit of retaining Linnean ranks (conveying information on taxon nesting) can be gained using standardised but rankless suffixes, already commonly employed in phylogenetic nomenclature.

Defining taxon names

The principal difference between phylogenetic and Linnean nomenclature concerns the way in which taxon names are defined (de Queiroz 1997; de Queiroz and Cantino 2001). In Linnean nomenclature, names are defined by referring to a type and a rank. The zoological code requires taxon names up to the family level to be formally defined, the botanical code is similar but also requires suprafamilial names to be defined if derived from genus names, while the bacteriological code requires taxon names at all ranks to be defined. For all codes, the types of taxa

Acta Palaeontol. Pol. 52 (3): 643–650, 2007

http://app.pan.pl/acta52/app52-643.pdf

at the family rank are genera, the types of genera are species, and the types of species are specimens. Thus, a definition of the genus name *Homo* would be "the taxon including the type species *Homo sapiens* that is assigned to the rank of genus", or some equivalent statement. The type determines the focal point (i.e., the minimal membership) of a taxon while the rank determines its boundary (i.e., the taxon's inclusiveness), with higher ranks indicating greater inclusiveness (although see following comments on redundant ranks).

Phylogenetic nomenclature, by contrast, does not refer to types or ranks in defining taxon names, but employs two or more taxa, or a taxon and a diagnostic apomorphy (all termed specifiers) to precisely delimit named clades (see de Queiroz and Gauthier 1990; Cantino and de Queiroz 2006). There are three commonly used forms of phylogenetic definitions (Fig. 1; species abbreviations are based on an example discussed under "Stability"):

(1) Node-based definition: the least-inclusive clade containing species S and R (i.e., the most recent common ancestor of species S and R, and all of its descendants).

(2) Branch-based definition (previously termed "stem-based", see Cantino and de Queiroz 2006): the most inclusive clade containing species S but not species P (i.e., the earliest ancestor of S but not P, and all of its descendants).

(3) Apomorphy-based definition: the clade diagnosed by character state X homologous (synapomorphic) with that in species S (i.e., the first species possessing character state X homologous with that in species S, and all of its descendants).

Thus, a node-based definition of the name *Homo* might be "the least-inclusive clade including the species *Homo sapiens* and the species *Homo habilis*".

The alternative approaches to defining taxon names under phylogenetic and Linnean nomenclature are the basis of all significant differences between the PhyloCode and the traditional codes that are being debated, including those relating to the stability of taxon names and content, and the use of mandatory ranks.

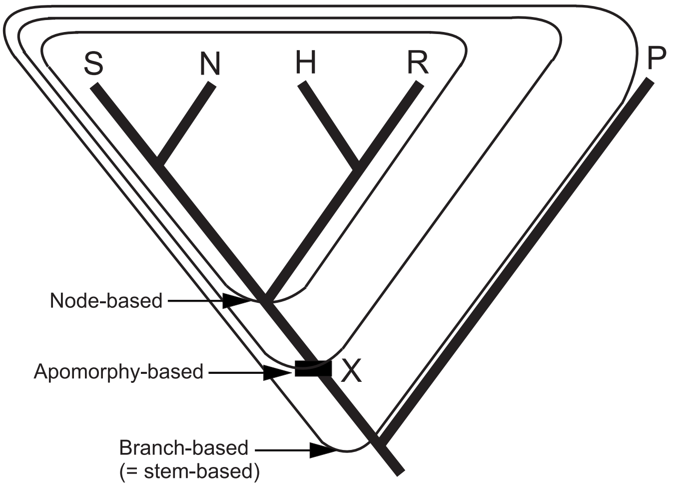

Fig. 1. The three main types of phylogenetic definitions (after de Queiroz and Gauthier 1992). Taxon abbreviations are as follows: H, (*Homo*) *habilis*; N, (*Homo*) *neanderthalis*; P, (*Kenyanthrophus*/*Homo*) *platyops*; R, (*Homo*) *rudolfensis*; S, (*Homo*) *sapiens*. X is the apomorphy used in the apomorphy-based definition.

Stability

Debate on the relative stability of phylogenetic and Linnean nomenclature has addressed two related but distinct issues. The first issue concerns the stability of taxon content: the potential for a particular name to refer to different sets of species as a consequence of taxonomic alterations (e.g., refinement of phylogenetic hypotheses, rank changes). The second issue concerns the stability of taxon names: changes to the set of names recognised by systematists (e.g., due to synonymy when different names refer to the same set of species). Typically, critics of the PhyloCode have focussed on stability in the former sense, arguing that names established according to the precepts of phylogenetic nomenclature may refer to very different sets of species depending on the phylogenetic hypothesis accepted (e.g., Dominguez and Wheeler 1997; Benton 2000; Nixon and Carpenter 2000; Monsch 2006; Rieppel 2006). Nonetheless, if one advocates the monophyly of higher taxa, the content of higher taxa named under the traditional codes will also change as phylogenetic hypotheses are altered. Furthermore, additional instability in taxon content will occur due to differing opinions about the set of species that should be included in a taxon of a particular rank. Arbitrary splitting and lumping decisions due to differing opinions over ranks will result in subjective synonymies that also increase instability in the set of valid taxon names. As a consequence, taxon content and taxon names may be considerably more unstable under traditional codes, compared with the Phylocode; these points are elaborated below.

Stability of taxon content.—Consider a definition of the species name *Homo sapiens* that might be proposed under the zoological code: "the taxon including Carolus Linnaeus (who was nominated posthumously as the type specimen) that is assigned to the rank of species". In order to delimit the set of organisms included in this taxon, one needs to apply some definition of the term "species" in order to determine whether or not an organism is part of the same species as Carolus Linnaeus. Although a plethora of species definitions have been proposed (see Mayden 1997), most are similar in equating species with lineages of populations that exhibit some degree of reproductive connectivity (e.g., de Queiroz 1998, 1999). Adopting this general concept of species, if two taxonomists disagreed on the limits of *Homo sapiens*, they could attempt to settle their dispute by presenting empirical evidence that an organism (or set of organisms) is part of the same population lineage as Carolus Linnaeus. This is possible because the term species is widely (though not universally) accepted as denoting an objective entity, namely, a population lineage.

Linnean definitions of higher taxon (genus, family, etc.) names are more problematic. Taking the definition of the genus name *Homo* provided above—"the taxon including the type species *Homo sapiens* that is assigned to the rank of genus"—it is evident that a definition of the term genus is required if we are to determine the boundaries of this taxon. Moreover, this definition must enable us to determine empirically whether two species are members of the same genus or different genera; "a rank in the Linnean hierarchy above that of species and below that of family" will not suffice. However, no appropriate definition is provided in the any of the Linnean codes, and no generally (or even widely) accepted definition has been proposed elsewhere (e.g., Ereshefsky 2001). Possible criteria for identifying congeneric species that have been used by various authors include recency of shared ancestry, phenotypic or ecological similarity, genetic divergence, and continuity of morphological variation (e.g., Bock and Farrand 1980). The now prevalent view that higher taxa should be monophyletic has prompted many current systematists to adopt the first of these criteria (at least implicitly), however, this is not dictated by the traditional codes. And even if it is agreed that recency of shared ancestry should be used to delimit higher taxa, it is unclear *how* recent shared ancestry must be for two species to be considered members of the same genus (see later). The only prescription given in the traditional codes is that a proposed classification must be a nested hierarchy; family-level taxa must completely contain (and thus be at least as old as) included genus-level taxa, which in turn must completely contain included species-level taxa. This grants taxonomists virtually unlimited latitude in specifying the limits of a higher taxon; nothing in the zoological code would prevent one taxonomist from adopting a very narrow view of genera and restricting *Homo* to the type species, while another taxonomist, employing a much broader view, could delimit the genus to include all species possessing a vertebral column. By including ranks as an integral part of the definitions of taxon names without specifying how ranks can be used to delimit taxa, the Linnean nomenclatural system effectively places no limitation on changes in taxon content.

Notably, diagnoses are not part of Linnean definitions (which consist of only a type and a rank). The zoological code stipulates only that the definition of a name "be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon" or reference to such a statement (Article 13.1). A taxonomist who has decided that a particular clade including *Homo sapiens* should, in their subjective opinion, be considered a genus and accordingly be given the name *Homo* is therefore enjoined to provide a list of diagnostic character states. However, another taxonomist, deeming that the same clade warrants family rank (and so should be designated Hominidae), may apply the genus name *Homo* to a less-inclusive clade, proposing a new and very different diagnosis. Both interpretations are valid under the zoological code. Thus, the provision of diagnoses under the traditional codes has minimal effect on the stability of taxon content; the same name can be applied to different sets of species having different diagnoses, while different names can be applied to the same set of species (evidently) having the same diagnosis.

In contrast, in the context of a particular phylogenetic tree, taxon names defined using node- or branch-based phylogenetic definitions will always refer unambiguously to a single set of species; species either are, or are not, part of the clade identified by the definition (see Fig. 1). Apomorphy-based definitions can also be very precise; however, delimiting the set of species to which they refer depends not only on tree topology, but also on decisions regarding the delimitation of alternative character states, and ancestral character state reconstructions (e.g., Sereno 1999; Gauthier and de Queiroz 2001). An apomorphy-based definition of the taxon name Hominini such as "the clade diagnosed by bipedality homologous with that in the species *sapiens*" could, for example, incite debate about whether species closely related to *Homo sapiens* are (or were) bipedal: many extant primates are facultatively bipedal, while the gait of fossil forms may be undetermined. And even if all species of concern could be indisputably classified as bipedal or not, homoplasy may engender uncertainty in identifying the internal branch along which bipedalism originates (and thus the clade diagnosed by this apomorphy). Indeed, ancestral character state reconstructions may often be associated with a considerable degree of uncertainty (e.g., Schluter et al. 1997). However, as with phylogenetic trees, ancestral character state reconstructions and statements concerning the distribution of homologous character states are hypotheses that may be assessed on the basis empirical evidence. Although multiple competing hypotheses might be plausible at a particular time, these will typically be a subset of all possible hypotheses, thus partially restricting the set of species that could be delimited by a systematist applying an apomorphy-based phylogenetic definition. Moreover, this set of species would be delimited with increasing precision as accumulating evidence narrows the field of plausible hypotheses, so that taxon content may be expected to become more stable over time. This is not the case for taxa established under the traditional codes; no amount of data can render one subjective opinion on the inclusiveness of a genus more plausible than another.

A number of authors have construed the instability of taxon content resulting from the subjectivity of rank assignments as desirable flexibility, arguing that if an accepted phylogeny is altered, the boundaries of a taxon may be freely adjusted to minimise changes in composition (e.g., Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Lidén et al. 1997; Nixon and Carpenter 2000; Benton 2000). However, 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. Considering the potential for disagreement over taxon content given an accepted phylogeny (e.g., Rowe and Gauthier 1992), it appears overly optimistic to expect consensus where several competing phylogenetic hypotheses exist. A more likely scenario is that the alternative phylogenies will result in different authors applying the same name to taxa of varying content (e.g., Cannatella and de Queiroz 1989). Also, where a previously recognised clade is totally dismembered in the modification of a phylogenetic hypothesis, a traditional taxonomist will be unable to delimit a similar taxon; in this situation, dramatic changes in taxon composition are unavoidable.

Measures for reducing instability in taxon content in the context of changing phylogenetic hypotheses have been discussed by several proponents of phylogenetic nomenclature (e.g., Wyss and Meng 1996; Lee 1998, 1999, 2005; Sereno 1999). These include judicious choice of specifiers, use of the appropriate type of definition (i.e., node-, branch-, or apomorphy-based) for a particular situation, and careful phrasing of definitions so that they can not be used in inappropriate phylogenetic contexts (Bryant 1998). For example, if monophyly of a group is well-supported but basal internal relationships are unstable, a node-based definition could employ all possible basal members, thereby ensuring that all intended species are included regardless of how basal relationships are resolved. Constructing robust definitions, however, requires sound knowledge of phylogenetic nomenclature and phylogenetic methods (enabling judgements about the future stability of clades). Again, as with taxa named under the traditional codes, taxon composition may need to change significantly where phylogenetic hypotheses are drastically altered.

Thus, for a specified phylogeny, taxon content will be at least as stable under the PhyloCode as under traditional nomenclature, and often considerably more so; phylogenetic definitions delimit a single clade, whereas Linnean definitions (for higher taxa) may be interpreted as delimiting any grouping that includes the type. In the less ideal (and more realistic) situation where any of several alternative phylogenies could be adopted, compositional stability under the traditional codes requires agreement among taxonomists on the "appropriate" content of taxa. Phylogenetic nomenclature, by contrast, allows stability to be built into the definitions of taxon names, negating subjective disputes about "appropriate" taxon content.

Stability of taxon names.—The subjectivity inherent in delimiting higher taxa named under the Linnean codes contributes not only to instability in the content of a particular named taxon, but also to instability in the set of names recognised by systematists. This is apparent when we consider the circumstances in which synonyms are generated (resulting in changes to the set of valid taxon names). In Linnean nomenclature, objective (or homotypic) synonyms occur where different taxon names are defined using the same type and rank; the names *Homo* and *Pithecanthropus* would be objective synonyms where both are defined as "the taxon including the type species *Homo* (or *Pithecanthropus*) *sapiens* that is assigned to the rank of genus". Almost invariably, objective synonyms will be the result of an error on the part of a taxonomist, stemming from a lack of knowledge of an existing definition. They are potentially avoidable (through the use of a name registration system, for example) and do not reflect a deficiency in the nomenclatural system itself. In most instances, however, synonyms will be subjective (heterotypic) rather than objective. Subjective synonyms are produced where the content of a taxon is altered such that it includes the type of another taxon at the same rank. As an example, suppose the names *Homo* and, later, *Kenyanthropus* are defined as the genus-level taxa including, respectively, the type species *Homo sapiens* and *Kenyanthropus platyops*. The two type species are closely-related hominids (Fig. 1). A taxonomist proposing that the genus *Homo* should be broadly delimited such that it encompasses the species "*Kenyanthropus*" *platyops*, would render *Kenyanthropus* a junior subjective synonym of *Homo* (e.g., Cela-Conde and Ayala 2003). The potential nomenclatural instability associated with subjective decisions regarding rank inclusiveness becomes evident when we consider that another taxonomist (or perhaps even the same taxonomist) might later restrict the boundaries of *Homo* such that *platyops* is excluded, resulting in the reinstatement of *Kenyanthropus* as a valid name. This alternation of opinion on the limits of *Homo* could continue indefinitely, as the zoological code permits either interpretation (and many others); the name *Kenyanthropus* would consequently be repeatedly synonymised and resurrected, even if there was total agreement on hominid phylogeny. There will always be debate over phylogeny that leads to necessary taxonomic uncertainty; however, under the Linnean codes, two workers can agree totally on phylogeny yet disagree substantially on the content named taxa. These taxonomic arguments are unnecessary and avoidable in phylogenetic nomenclature.

Objective and subjective synonyms are also possible in the phylogenetic nomenclatural system. An objective synonym results if two different names are given identical definitions (i.e., the same specifiers are employed in the same type of definition); thus, if both *Homo* and *Pithecanthropus* were established using the node-based definition "the least-inclusive clade including the species *habilis* and the species *sapiens*", the younger name would be a junior objective synonym. Objective synonyms (as well as homonyms) reflect poor implementation of the PhyloCode rather than a deficiency in the code itself, and are potentially avoidable, as new taxon names and their definitions will have to be entered into a registration database prior to being accepted (de Queiroz and Cantino 2001). As in Linnean nomenclature, subjective synonyms occur where names with different definitions refer to the same taxon. Consider, for example, a (hypothetical) situation where the names *Homo* and *Pithecanthropus* are defined respectively as "the least-inclusive clade including the species *sapiens* and the species *habilis*" and "the least-inclusive clade including the species *neanderthalis* and the species *rudolfensis*". Assuming the phylogenetic tree in Fig. 1, these definitions refer to the same clade (the smallest clade marked), and the later name *Pithecanthropus* is therefore a junior subjective synonym of *Homo*. Subjective synonyms may be generated as a consequence of adopting alternative phylogenetic hypotheses. However, this is the only source of nomenclatural instability; additional changes in the set of accepted names are not generated by subjective opinions about the inclusiveness of ranks and the boundaries of taxa in the context of a single accepted phylogeny. Accordingly, as estimates of phylogeny become more robust with the accumulation of data, the stability of taxon names will increase under the PhyloCode. This contrasts with the potential under the traditional codes for continual synonymy and resurrection of taxon names due to differing views on rank inclusiveness, regardless of the stability of phylogenetic hypotheses.

Ranks and DNA barcoding

Ranks are a fundamental component of the Linnean system of nomenclature. All Linnean definitions of taxon names refer to a rank, and all taxa established under the traditional codes must be assigned to a minimal set of ranks. Nonetheless, as discussed previously, there are no generally accepted criteria for specifying the rank to which a taxon should be referred. Moreover, there are difficulties with those criteria that have been proposed. Thus, the use of a standard degree of morphological similarity (i.e., among the species composing a clade) in assigning ranks is problematic as such similarity may be exceedingly difficult to quantify, especially for phylogenetically distant species. Consequently, assessments of morphological similarity are, to a significant extent, subjective. The assignment of ranks on the basis of shifts to different "adaptive zones" (e.g., Mayr 1950; Cela-Conde and Ayala 2003) presents a similar difficulty; there are no objective means of quantifying the magnitude of such shifts. Geological age may initially appear a more usable criterion: for example, as suggested by Hennig (1966), clades originating in the Miocene could be ranked as genera, while those originating in the Upper Cretaceous could be ranked as families. However, this proposal, which has been espoused more recently by Avise and Johns (1999), suffers from at least three problems. Firstly, a series of nested clades may originate in the Miocene (continuing with the above example) – which of these should be assigned to the rank of genus? Secondly, there will be errors associated with estimates of clade age (due to incompleteness of the fossil record and uncertainties in molecular dating), encouraging taxonomic instability associated with rank changes (albeit uncertainty that may be reduced with additional data). And thirdly, fossil taxa can not readily be incorporated into such a ranking scheme; according to Hennig's (1966) system, every Miocene fossil would have to be assigned to a separate genus, while every Upper Cretaceous fossil would have to be referred to a separate family (see Laurin 2005).

The advent of DNA barcoding (e.g., Hebert et al. 2003a, b) could be considered to afford an objective, quantifiable criterion for assigning taxa to Linnean ranks. The rapidly-evolving mitochondrial gene cytochrome *c* oxidase subunit 1 (COI) is emerging as a standard marker for DNA barcoding in metazoans, and sequence divergences for this gene might provide an unambiguous, widely applicable measure for allocating ranks; clades separated by a maximum uncorrected sequence divergence of 5–10%, for example, could be assigned to different genera, while those separated by divergences of 10–15% could be assigned to different families. There is a problem of deciding which divergence metric should be used (e.g., nearest neighbour, average pairwise), however, even if some agreed but arbitrary standard was adopted, several difficulties would remain: (1) A series of nested clades will often be separated from their respective sister clades by divergences within the "genus range"—which of these should be identified as the genus? (2) Fossils cannot be accommodated in this system; (3) COI sequences will experience relatively rapid saturation, so that sister-clade pairs that diverged 400 million and 500 million years ago, for example, will exhibit very similar divergences; (4) different rates of molecular evolution across different groups means that similar levels of genetic divergences in different groups cannot be assumed to equate to similar divergence times, (5) employing sequence divergences in identifying the content and rank of taxa amounts to phenetic clustering, and is consequently problematic. Groups based on overall similarity (as measured by sequence divergence, for example) will often not correspond to clades, due to variability in evolutionary rate. One can envisage recognising a group of species as family "Xidae" because pairwise distances within the group are less than 15%, while those between this group and other groups are greater than 15%. However, a relatively rapidly-evolving species (phylogenetically) nested within "Xidae" could be placed in another family because the average divergence between it and members of "Xidae" exceeds 15%. Finally, attempting to avoid these problems by using divergences calculated in the context of a phylogeny (rather than raw sequence difference) is not practical, as different phylogenetic methods and molecular models can result in very different divergences, especially for fast-evolving genes experiencing saturation.

The absence of a widely accepted, objective criterion for allocating (supraspecific) ranks means that ranking decisions are arbitrary and may often be inconsistent among authors. Consequently, taxa assigned to a particular rank are rarely equivalent entities and, accordingly, their employment as basic units in assessing biodiversity, a common practice in ecological and palaeontological studies, is problematic (Bertrand et al. 2006). Instead of counting higher taxa, a more accurate approach would be to directly count the units of interest (species, functional groups, etc). In arguing that the elimination of mandatory ranks deprives biologists of an efficient means of measuring biodiversity, critics of phylogenetic nomenclature (e.g., Forey 2001) encourage unjustified assumptions of the equivalence of higher taxa.

The association of ranks with standard name endings (e.g., -ini for tribes, -idae for families) in Linnean nomenclature contributes to instability in the content of taxa. If, for example, a taxonomist decides that the clade currently named Hominini should be elevated from the rank of tribe to that of family, its name must be changed to Hominidae. While both names can still be recognised, each name would now refer to a less inclusive group than previously, and this could precipitate a cascade of similar changes in the other names. Mandatory ranks also complicate taxonomy by necessitating the creation of redundant taxa. A systematist placing a single species in a new phylum would have to refer this species to a class, order, family, and genus; all of these taxa would be identical in content and (potentially) diagnosis. The elimination of mandatory ranks would remove the potential for such redundancy, thereby simplifying taxonomy.

Nonetheless, several arguments for the utility of ranks have been offered (e.g., Lidén and Oxelman 1996; Lidén et al. 1997; Benton 2000; Nixon and Carpenter 2000). We briefly discuss the more prominent of these, indicating why we do not consider them compelling.

(1) Ranks convey information about the relative inclusiveness of clades; specifically, taxa of different rank having the same name stem (e.g., *Homo*, Hominidae, Hominoidea) may be inferred to be nested. This inference is not possible where the names of ranked taxa have different stems (e.g., *Australopithecus*, Hominidae) unless one already possesses knowledge of phylogenetic relationships (de Queiroz and Gauthier 1992). Thus, *Australopithecus* could be a member of any family, and there is no reason to assume it is nested within the family Hominidae. Information about taxon nesting is therefore im-

parted only in very limited circumstances. Furthermore, this information can be conveyed without employing a scheme of absolute ranks by adopting standardised suffixes. In phylogenetic nomenclature, a common practice when naming nested clades is to add the suffixes -iformes and -omorpha to a particular stem to indicate clades of increasing inclusiveness (e.g., Archosauria is included in Archosauriformes, which in turn is included in Archosauromorpha). Aside from eliminating the need for subjective decisions about the inclusiveness of ranks, this system can be used to represent relative nesting at multiple levels of taxon inclusiveness. For example, Archosauromorpha may be a subclade of the nested taxa Tetrapoda, Tetrapodiformes, and Tetrapodomorpha. This is not possible in Linnean nomenclature, where particular suffixes (e.g., -idae, -oidea, etc.) may be used only once when naming a series of nested taxa. Thus, although ranks may convey information about taxon nesting, the same information can be communicated more effectively using a system of standardised suffixes.

(2) Ranks convey information about taxon exclusivity; in particular, taxa of the same rank can not be overlapping. Although this information can not be imparted using the system of standardised suffixes described above, it is difficult to envisage many contexts where knowledge that taxa are non-overlapping would alone be useful.

(3) Ranks enable biologists to more easily organise their knowledge of biodiversity, facilitating communication. We propose that biologists will familiarise themselves with and use the names of important taxa (e.g., those diagnosed by "key innovations", or having economic significance) whether or not they are associated with Linnean ranks. Evidence for this view is provided by recently discovered clades such as Lophotrochozoa and Ecdysozoa within Metazoa (Eernisse and Peterson 2004), and Cetartiodactyla and Afrotheria within Mammalia (e.g., Murphy et al. 2002). These are too inclusive to be governed by the zoological code (comprising clades above the rank of family) and are usually not assigned to a Linnean rank; however, they are now well known and the subject of considerable discussion and investigation. Additionally, it may be noted that many non-scientists comprehend what is meant by the terms bird, insect, and mammal, but have no knowledge of the ranks of these clades. It might be argued that the perceived equivalence of taxa of the same rank aids in the construction of taxon lists (e.g., the three subclasses of mammals: monotremes, marsupials and placentals); but such lists can be constructed in the absence of ranks. Furthermore, the Linnean lists can be unstable due to arbitrary splitting and lumping, even in the context of an agreed phylogeny. Having to recall not only clade names, but also subjective and potentially labile rank assignments, actually impedes efficient organisation of our knowledge of biodiversity.

Extending argument (3) above, it might be presumed that ranks are important in environmental and conservation legislation, and the management of biological collections and databases. For example, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) refers to higher taxa (e.g., Felidae) as well as species in prescribing its regulations, while museum collections are typically ordered taxonomically. However, in neither case do the ranks of higher taxa provide useful information. Felidae is referred to in CITES appendices because it is a stable, well-diagnosed group, not because it is a taxon assigned to the rank of family. If the name Felidae was defined under the PhyloCode such that it referred to the same group (clade), it could be employed by legislators in exactly the same manner as it is presently. Indeed, the increased stability of taxon names and content attained by adopting phylogenetic nomenclature (see above) would benefit legislation. Significantly, databases such as GenBank and the Tree of Life are increasingly organised according to a nested hierarchy of clade names.

In concluding this section, we note that the elimination of Linnean ranks is not a necessary consequence of adopting phylogenetic nomenclature, despite statements to the contrary (e.g., Lidén and Oxelman 1996). Although ranks are not employed in defining taxon names under the PhyloCode, taxa may still be allocated to ranks according to an independent set of rules (e.g., the "age rule" described by Hennig 1966). Thus, ranks may be used regardless of the nomenclatural system adopted. The distinction between Linnean and phylogenetic nomenclature concerns the significance afforded to ranks in naming taxa; ranks are an integral part of the definitions of taxon names in Linnean nomenclature, but have no such role in phylogenetic nomenclature.

Applying Linnean and phylogenetic nomenclature when phylogenetic information is lacking

Phylogenetic definitions refer explicitly to clades and, accordingly, their implementation is dependent on our knowledge of phylogeny. As a consequence, the applicability of phylogenetic nomenclature might be severely limited by inadequate phylogenetic information; several colleagues have suggested informally that we lack sufficient knowledge to construct phylogenetic definitions for perhaps the majority of invertebrates. Linnean definitions, by contrast, have no necessary relationship to phylogeny and may be applied in the absence of phylogenetic information. Thus, even where we have no knowledge of phylogenetic relationships within the family Ptiliidae (a clade of beetles), for example, it would be possible to name and delimit genera (on the basis of morphological similarity) under the zoological code. Indeed, taxonomists are compelled to designate such genera, as all species when described must be assigned to a genus. Nonetheless, the value in this situation of naming genera, many of which may be non-monophyletic assemblages, is surely questionable. As phylogenetic information eventually became available, numerous taxonomic changes would undoubtedly be required to render para- or even polyphyletic taxa monophyletic, resulting in substantial instability in taxon names and content. Few taxonomists would wish to name taxa given insufficient information; yet the need to assign every species to a genus (in Linnean nomenclature) often compels systematists to name genera without adequate knowledge of phylogeny. Such genera will probably be very unstable.

Phylogenetic nomenclature, in contrast, does not force systematists to name taxa where a relevant phylogenetic hypothesis is lacking. A taxonomist could define the name Ptiliidae under the PhyloCode, but defer naming groups within this clade until sufficient information on internal relationships was acquired to permit the construction of robust phylogenetic definitions. Prior to such information becoming available, informal names could be used for morphologically distinctive (but possibly non-monophyletic) groups for the purpose of communication, however, these names would not be defined and could be replaced (by formal clade names) or discarded without compromising nomenclatural stability.

Conclusion

Linnean nomenclature appears to be considerably less stable than phylogenetic nomenclature with respect to the names and content of taxa. This relative instability results from the incorporation of ranks as an integral part of Linnean definitions of taxon names; changes to the composition of taxa and the set of names recognised by systematists are produced not only by alterations to phylogenetic hypotheses, but also differing opinions about rank inclusiveness. Linnean ranks have no consistent biological meaning and do not assist the comprehension and study of biodiversity. Moreover, a major proposed benefit of employing ranks—conveying information regarding taxon nesting—is delivered more effectively by a system of standardised suffixes, already commonly adopted in phylogenetic nomenclature. Although phylogenetic nomenclature can not be implemented in the absence of knowledge of phylogenetic relationships, the value of applying Linnean nomenclature in this situation is questionable. Thus, we conclude that there is little reason to persist with the traditional codes of nomenclature, and encourage all taxonomists to consider the potential advantages of adopting the PhyloCode.

Acknowledgements.—We thank the Australian Research Council for support, and the editors for the invitation to write this paper.

References

Avise, J.C. and Johns, G.C. 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proceedings of the National Academy of Sciences of the United States of America* 96: 7358–7363.

Benton, M.J. 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews* 75: 633–648.

Bertrand, Y., Pleijel, F., and Rouse, G.W. 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Systematics and Biodiversity* 4: 149–159.

Bock, W.J. and Farrand, J. Jr. 1980. The number of species and genera of Recent birds: a contribution to comparative systematics. *American Museum Novitates* 2703: 1–29.

Bryant, H.N. 1998. Cladistic information in phylogenetic definitions and designated phylogenetic contexts for the use of taxon names. *Biological Journal of the Linnean Society* 62: 495–503.

Cannatella, D.C. and de Queiroz, K. 1989. Phylogenetic systematics of the anoles: is a new taxonomy warranted? *Systematic Zoology* 38: 57–69.

Cantino, P.D. and de Queiroz, K. 2006. *PhyloCode: A Phylogenetic Code of Biological Nomenclature*. Revised June 16, 2006. Available at http://www.ohio.edu/phylocode/.

Cantino, P.D., Olmstead, R.G., and Wagstaff, S.J. 1997. A comparison of phylogenetic nomenclature with the current system: a botanical case study. *Systematic Biology* 46: 313–331.

Cela-Conde, C.J. and Ayala, F.J. 2003. Genera of the human lineage. *Proceedings of the National Academy of Sciences of the United States of America* 100: 7684–7689.

de Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* 15: 125–144.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. *In*: D.J. Howard and S.H. Berlocher (eds.), *Endless Forms: Species and Speciation*, 57–75. Oxford University Press, Oxford.

de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. *In*: R.A. Wilson (ed.), *Species: New Interdisciplinary Essays*, 49–89. The MIT Press, Cambridge, MA.

de Queiroz, K. and Cantino, P.D. 2001. Phylogenetic nomenclature and the PhyloCode. *Bulletin of Zoological Nomenclature* 58: 254–271.

de Queiroz, K. and Gauthier, J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology* 39: 307–322.

de Queiroz, K. and Gauthier, J. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23: 449–480.

de Queiroz, K. and Gauthier, J. 1994. Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 9: 27–31.

Dominguez, E. and Wheeler, Q.D. 1997. Taxonomic stability is ignorance. *Cladistics* 13: 367–372.

Eernisse, D.J. and Peterson, K.J. 2004. The history of animals. *In*: J. Cracraft and M.J. Donoghue (eds.), *Assembling the Tree of Life*, 197–208. Oxford University Press, Oxford.

Ereshefsky, M. 2001. *The Poverty of the Linnaean Hierarchy: A Philosophical Study of Biological Taxonomy*. 328 pp. Cambridge University Press, Cambridge.

Ereshefsky, M. 2002. Linnaean ranks: vestiges of a bygone era. *Philosophy of Science* 69: S305–S315.

Forey, P.L. 2001. The PhyloCode: description and commentary. *Bulletin of Zoological Nomenclature* 58: 81–96.

Gauthier, J. and de Queiroz, K. 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name "Aves". *In*: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*, 7–46. Peabobdy Museum of Natural History, Yale University, New Haven.

Greuter, W., McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Filgueiras, T.S., Nicolson, D.H., Silva, P.C., Skog, J.E., Trehane, P., Turland, N.J., and Hawksworth D.L. 2000. *International Code of Botanical Nomenclature (St. Loius Code)*. 474 pp. Koeltz Scientific Books, Königstein.

Hebert, P.D.N., Cywinska, A., Ball, S.L., and deWaard, J.R. 2003a. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270: 313–321.

Hebert, P.D.N., Ratnasingham, S., and deWaard J.R. 2003b. Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London. Series B: Biological Sciences (Supplement)* 270: S96–S99.

Hennig, W. 1966. *Phylogenetic Systematics*. 286 pp. University of Illinois Press, Urbana. [1999 reprint]

International Commission on Zoological Nomenclature 1999. *International Code of Zoological Nomenclature, 4th Edition*. 306 pp. The International Trust for Zoological Nomenclature, London.

Lapage, S.P., Sneath, P.H.A., Lessel, E.F., Skerman, V.B.D., Seeliger, H.P.R., and Clark, W.A. 1992. *International Code of Nomenclature of*

Bacteria, 1990 Revision. 232 pp. American Society for Microbiology, Washington D.C.

Laurin, M. 2005. The advantages of Phylogenetic Nomenclature over Linnean Nomenclature. *In*: A. Minelli, G. Ortalli, and G. Sanga (eds.), *Animal Names*, 67–97. Istituto Veneto di Scienze, Lettere ed Arti, Venice.

Laurin, M. and Cantino, P. 2007. Second meeting of the International Society for Phylogenetic Nomenclature: a report. *Zoologica Scripta* 36: 109–117.

Lee, M.S.Y. 1998. Phylogenetic uncertainty, molecular sequences, and the definition of taxon names. *Systematic Biology* 47: 719–726.

Lee, M.S.Y. 1999. Stability of higher taxa in phylogenetic nomenclature – some comments on Moore (1998). *Zoologica Scripta* 28: 361–366.

Lee, M.S.Y. 2005. Choosing stable reference taxa in phylogenetic nomenclature. *Zoologica Scripta* 34: 313–318.

Lidén, M. and Oxelman, B. 1996. Do we need “phylogenetic taxonomy”? *Zoologica Scripta* 25: 183–185.

Lidén, M., Oxelman, B., Backlund, A., Andersson, L., Bremer, B., Eriksson, R., Moberg, R., Nordal, I., Persson, K., Thulin, M., and Zimmer, B. 1997. Charlie is our darling. *Taxon* 46: 735–738.

Linnaeus, C. 1753. *Species Plantarum*. 2 volumes: 1–560 and 561–1200 + index (unpaginated). Salvius, Stockholm.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Laurentius Salvius, Stockholm.

Mayr, E. 1950. Taxonomic categories in fossil hominids. *Cold Spring Harbor Symposia on Quantitative Biology* 15: 109–118.

Mayden, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. *In*: M.F. Claridge, H.A. Dawah, and M.R. Wilson (eds.), *Species: The Units of Biodiversity*, 381–424. Chapman & Hall, London.

Monsch, K.A. 2006. The PhyloCode, or alternative nomenclature: why it is not beneficial to palaeontology, either. *Acta Palaeontologica Polonica* 51: 521–524.

Murphy, W.J., Eizirik, E., O’Brien, S. J., Maden, O., Scalley, M., Douady, C.J., Teeling, E., Ryder, O. A., Stanhope, M.J., de Jong, W. W., and Springer, M.S. 2002. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294: 2348–2351.

Nixon, K.C. and Carpenter, J.M. 2000. On the other “phylogenetic systematics”. *Cladistics* 16: 298–318.

Pleijel, F. and Rouse, G.W. 2003. Ceci n’est pas une pipe: names, clades and phylogenetic nomenclature. *Journal of Zoological Systematics and Evolutionary Research* 41: 162–174.

Rieppel, O. 2006. The Phylocode: a critical discussion of its theoretical foundation. *Cladistics* 22: 186–197.

Rowe, T. and Gauthier, J. 1992. Ancestry, paleontology, and the definition of the name Mammalia. *Systematic Biology* 41: 372–378.

Schluter, D., Price, T., Mooers, A.Ø., and Ludwig, D. 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* 51: 1699–1711.

Sereno, P.C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. *Systematic Biology* 48: 329–351.

Sundberg, P. and Pleijel, F. 1994. Phylogenetic classification and the definition of taxon names. *Zoologica Scripta* 23: 19–25.

Wyss, A.R. and Meng, J. 1996. Application of phylogenetic taxonomy to poorly resolved crown clades: a stem-modified node-based definition of Rodentia. *Systematic Biology* 45: 559–568.

Michael S.Y. Lee [Michael.S.Lee@adelaide.edu.au] and Adam Skinner [adam.skinner@adelaide.edu.au], School of Earth and Environmental Sciences, Darling Building, University of Adelaide, SA 5005, Australia.