

## Are the Linnean and Phylogenetic Nomenclatural Systems Combinable? Recommendations for Biological Nomenclature

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**Abstract.**—A combination approach between the rules and recommendations from the Linnean (rank-based) and phylogenetic nomenclature is proposed, with a review of the debate. Advantages and drawbacks of both systems are discussed. Too often the debates are biased and unconstructive, and there is a need for dialogue and compromise. Our recommendations for the future of biological classification, to be considered by new editions of all codes of nomenclature, would enable the Linnean and the phylogenetic nomenclatural systems to coexist, or be combined. (1) We see it as essential that species binomen, including the formal rank of genus, are retained, and (2) species should continue to be linked to type specimens. (3) The use of other formal ranks should be minimized; however, we suggest retaining the classical supergeneric ranks (family, class, order, phylum, kingdom) for purely practical reasons. (4) For these ranks and any formally defined clades, type taxa (species, genera) should be replaced by phylogenetic definitions that explicitly hypothesize monophyly. (5) In contrast, species monophyly should not be required, because theory predicts that many species are not monophyletic. (6) It should be stressed that equal ranks do not imply comparable evolutionary histories. [Clades; classification; monophyly; PhyloCode; phylogenetics; ranks; species binomials; taxonomy.]

“The differences between phylogenetic and rank-based nomenclature are just too fundamental for them to be combined.”

Pennisi (2001) quoting Cantino

“If the community does not become actively involved in fighting the PhyloCode, they will succeed, and in so doing, demolish much of the hard work that our predecessors have built into the current codes.”

Nixon, Carpenter, and Stevenson (2003)

“Down with the type-cult.”

Strand (1929)

Binomial biological nomenclature has been in use ever since the publications *Aranei Svecici* (Clerck, 1757) and the 10th edition of the *Systema Naturae* (Linnaeus, 1758). The current standard in biological nomenclature is the binominal Linnaean (also *Linnean* as used here) system—nomenclature based on ranks (species, genera, families, etc.) and types (type specimens for species and type species for genera)—as regulated by the botanical (Greuter et al., 2000), zoological (ICZN, 1999), and bacteriological codes (ICNB, 1992) of nomenclature. Recently, however, this system has been characterized as poorly suited to the naming of clades and species. Critics of the Linnean system have proposed an alternative, rankless system, the PhyloCode (Cantino and de Queiroz, 2004). The theoretical foundation of the PhyloCode (hereafter PC) was developed in a series of papers by de Queiroz and Gauthier (1990, 1992, 1994) on “phylogenetic taxonomy” (also “phylogenetic nomenclature”; for definitions see below), which built on the premise that a taxon name should be defined by reference to a phylogenetic hypothesis. For clear communication and dissemination of biological information, taxa (clades and species) require names that explicitly and unambiguously refer to those entities and prefer-

ably rarely change (Cantino and de Queiroz, 2004). According to advocates of phylogenetic nomenclature, the rules of the currently implemented rank- and type-based codes (hereafter existing codes) result in frequent taxon name changes and hence hamper effective communication. The PC intends to overcome the instability of taxon names. While currently proposing rules and recommendations only for clade nomenclature, the PC will eventually aim to also govern species nomenclature (Laurin et al., 2005). Although “phylogenetic nomenclature” and “phylogenetic taxonomy” are often regarded as synonymous, a distinction should be made because taxonomy is concerned with taxa, and nomenclature with names (de Queiroz, 2006). Sereno (2005) claims that *phylogenetic nomenclature* entails endorsement of a formalized code governing taxonomic definitions (like PC), whereas *phylogenetic taxonomy* “refers to the logic and procedures underpinning the construction of taxonomic definitions on the basis of phylogeny” (Sereno, 2005:595, italics added). These definitions seem to narrow (de Queiroz, in litt.). Most broadly, *phylogenetic nomenclature* is concerned with naming (defining) taxa with a reference to a phylogeny. Whereas students of *phylogenetic systematics*—the discipline concerned with determining phylogenetic relationships—will often consult a phylogeny when naming taxa, regardless of their preference for a nomenclatural system, we take the specific term *phylogenetic nomenclature* to imply endorsement of the PC. *Phylogenetic taxonomy* is concerned with classification—representing phylogenetic relationships—and may use phylogenetic nomenclature.

The PC drafts and the papers leading to it have spawned lively debates (see, e.g., Artois, 2001; Lee, 1999, 2001; Pennisi, 2001; Withgott, 2000) and criticisms on both the traditional and phylogenetic nomenclature. The

phylogenetic nomenclature proponents (e.g., Baum et al., 1998; Bryant, 1994, 1996; Cantino, 1998, 2000; Cantino et al., 1997; de Queiroz, 1995a, 1997a, 1997b, 2000; de Queiroz and Cantino, 2001a, 2001b; de Queiroz and Donoghue, 2001; Joyce et al., 2004; Laurin et al., 2005, 2006) have criticized the Linnean system, stressing that superspecific and specific names often change under the existing codes, precisely because they are defined by *ranks* and *types*, the pillars of the Linnean system (for a discussion on types, ranks, and categories, see Dubois, 2005). For example, a clade name will change with a reconsideration of its rank, although its composition and apomorphies—the hypothesis—may remain unchanged. Also, in the Linnean system, name changes are required by advances in phylogenetic knowledge, e.g., novel placement of family A inside family B, or arbitrary splitting or lumping of supraspecific taxa, resulting in what seems needless nomenclatural instability. Names established under the PC are more stable as they are defined in terms of phylogenetic relationships rather than taxonomic rank and types, and will therefore not change with rank adjustments. Further drawbacks of the Linnean system were pointed out: (i) names do not (necessarily) link to clades; naming of non-natural (paraphyletic, polyphyletic) taxa poorly reflects phylogenetic hypotheses (de Queiroz and Gauthier, 1990, 1992, 1994; Joyce et al., 2004; Pleijel and Rouse, 2003); (ii) the lack of justification of ranks, which invite unwarranted comparisons across same-ranked taxa (Sundberg and Pleijel, 1994; Pleijel and Rouse, 2003); and (iii) the questionable typification practice (Sundberg and Pleijel, 1994), although, as pointed out by de Queiroz and Gauthier (1992), types could be decoupled from ranks and thus be compatible with both systems.

However, does the proposed PC overcome these problems? Opponents of PC have defended the Linnean system. These critiques (e.g., Forey, 2001, 2002) question both whether the PC is “better” than the system it seeks to replace and raise practical issues, such as if a new system is likely to be generally endorsed. As pointed out by Nixon et al. (2003), the PC does not in all hypothetical cases result in greater nomenclatural stability than the current code. Further, PC names, precisely for not being rank-based, convey no hierarchy, i.e., no information without “an annotated reference tree for even the simplest exchanges of information” (Nixon et al., 2003). Benton (2002) argued that phylogenies are real but classifications are utilitarian. Similarly, Stuessy (2000, 2001) suggested that the PC concept is flawed because it is not taxon names but taxa that are defined (but see de Queiroz, 2000; Jørgensen, 2000; Dubois, 2005). Kraus (2004) defends the (Linnean) “system that functions almost perfectly” and suggests that “there is no chance at all that this kind of code [PC] could be generally accepted.” Similarly, Janovec et al. (2003) and Berry (2002) hold that although there is room for improving the Linnean system, the biological community is simply not ready for the PC (see also Abbey, 2001). Although most opposition to PC has been voiced among zoologists and botanists, some microbial taxonomists

(e.g., Gest and Favinger, 2001) fear that PC could lead to rampant renaming of bacterial taxa given unstable bacterial phylogenetics (where horizontal transfer, or reticulation, is arguably much more common than in most other systems) and difficulty of defining bacterial species.

Very few theoretical papers attempt a compromise between the two systems (but see Moore, 1998; Stevens, 2002; Hillis and Wilcox, 2005) and most empirical studies adopt one approach, either traditional Linnean nomenclature of ranked taxa (APG II, 2003; Kress et al., 2002) or alternative phylogenetic nomenclature reflecting rankless clades (Baum et al., 1998; Bryant, 1996; Cantino et al., 1997; Joyce et al., 2004; Kron, 1997; Laurin, 2002; Modesto and Anderson, 2004; Olmstead et al., 2001; Pleijel, 1999; Pleijel and Rouse, 2003; Rowe and Gauthier, 1992; Wyss and Meng, 1996). A combination of both systems has been attempted in botany. In a classification of Apocynaceae s.l., Sennblad and Bremer (2002) combined the rules from a traditional (botanical) code with PC, Stefanović et al. (2003) named and phylogenetically defined some rankless clades and some with assigned ranks, and, most recently, Pfeil and Crisp (2005) proposed a hybrid classification system for *Hibiscus*.

In recent systematic studies of nephilid spiders, Kuntner (2005, 2006) chose to retain Linnean hierarchy for naming taxa up to the family level, but followed the PC rules and recommendations for naming clades at all levels. Thus, species and clade names were consistent with the existing code (ICZN, 1999) but were precisely phylogenetically circumscribed using node based definitions (PC Article 9, Note 9.4.1). Here we further develop ideas for a compromise classification scheme. We discuss the advantages and weaknesses of both classical and rank-free systems and explore whether or not the Linnean and phylogenetic nomenclatural systems can profitably coexist. We conclude that the role of the Linnean system is essential only for species names, but practical reasons argue for the additional retention of the classical ranks (family, order, class, kingdom, phylum). However, many of the PC recommendations should govern clade naming at all levels (see also Lee, 2002). Based on this, we provide recommendations for the future of biological nomenclature, which needs constructive debate and compromise in order to serve its purpose: provide stable, informative, and precisely defined names of taxa (species, clades).

#### NEED FOR COMPROMISE

Some systematic biologists continue to downplay the importance of the biological nomenclature debate, suggesting it does not really matter. However, our view is that the biological community needs an efficient, and practical, nomenclatural approach that respects both tradition and advancements in phylogenetic theory in order to continue and accelerate biodiversity discovery, documentation, and research.

Although online services such as GenBank (<http://www.ncbi.nlm.nih.gov>) effectively use a compromise

system listing ranked and unranked taxa, currently only rank-based codes govern species nomenclature (Polaszek and Wilson, 2005). PC has not been formally inaugurated and contains only rules governing the names of clades, and not those of species (Laurin et al., 2005, 2006). Taxonomy has been historically slower in adopting novelties than other fields of biology (Christoffersen, 1995), an opposition that seems due to tradition rather than sound scientific reasoning. For example, Niklas (2001) commented on the PC: "This premature usurpation of well-established and time-tested scientific protocols is probably doomed to failure, but not before it may cause irreparable harm and confusion." Similarly, Abbey (2001), with no arguments but tradition, urges caution before accepting a novel approach, because it may cause confusion (see also Berry, 2002; Janovec et al., 2003; Kraus, 2004). Although the opposition to the PC from many traditional (nonphylogenetic) taxonomists (e.g., Pavlinov, 2004) is understandable, the opposition is also substantial among many practicing phylogeneticists (e.g., Carpenter, 2003; Nixon and Carpenter, 2000; Nixon et al., 2003; Pickett, 2005a, 2005b; Schuh, 2003). This is somewhat surprising as phylogenetic nomenclature seeks to name taxa with reference to a phylogeny (hence naming clades in preference to grades or polyphyletic constructs). Most would probably also agree that Linnean ranks, albeit useful in conveying hierarchical information, are arbitrary and lack biological meaning (e.g., Hennig, 1969).

Unfortunately, debate about the codes (e.g., Berry, 2002; Brochu and Sumrall, 2001; Janovec et al., 2003; Keller et al., 2003; Kojima, 2003; Sereno, 2005) is often more deconstructive than constructive (but see, e.g., de Queiroz, 1995, versus Ghiselin, 1995; de Queiroz, 1997, versus Lidén and Oxelman, 1996). In some cases arguments from both sides are personal, nonscientific, or ommissive, and thus counterproductive. For example, Nixon et al. (2003) label PC as "poorly reasoned, logically inconsistent, and fatally flawed new code that will only bring chaos" and accuse PC proponents of "subscientific spin and sloganeering" with the reference to the claims of PC being the "greatest thing since sliced bread." The PC "spinmeisters" have been accused that "they are going to erect a shadow government and [set up] a coup" (Pennisi, 2001, quoting Nixon), referring to the PC tendency to meet in workshops separated from more traditional venues, e.g., international congresses: "The differences between phylogenetic and rank-based nomenclature are just too fundamental for them to be combined" (Pennisi, 2001, quoting Cantino). Strangely, among phylogeneticists, the division between *pro*- and *contra*-PC seems to roughly mirror the divide between *pro* and *contra* model-based phylogenetics. These two divisions, in our view, are unrelated, because *phylogenetic taxonomy* is concerned with "the representation—rather than the reconstruction or estimation—of phylogenetic relationships" (de Queiroz and Gauthier, 1990; see also de Queiroz, 2006). Thus, phylogenetic nomenclature should be compatible with diverse philosophical perspectives in systematic biology (Pleijel and Härlin, 2004).

No code of nomenclature, existing (Greuter et al., 2000; ICNB, 1992; ICZN, 1999) or proposed (PC and BioCode; Greuter et al., 1998), is flawless, as the numerous criticisms have repeatedly pointed out. Further, to take effect and for subsequent refinement, any new code needs congressional endorsement (Blackwell, 2002). For the PC, such endorsement seems impossible at this point without some compromise (see also Moore, 1998; Stevens, 2002). As Langer (2001) concluded, now is the time to discuss what practices (if any) the PC should govern in taxonomy.

#### SPECIES AND THE FUTURE OF TAXONOMY

Codes based on phylogenetic nomenclature should not govern species nomenclature, because, as reflected by many species concepts (for reviews see Davis, 1997; Wheeler and Meier, 2000; Lee, 2003), species need not be monophyletic. Hence, naming species requires different rules than naming clades (PC proponents intend to regulate species naming with a separate code, a so called Species Code; see Laurin et al., 2005). Lee (2002) contends that the PC should be adopted immediately but to govern only clade, not species, nomenclature. Although some PC architects only wish to convert species epithets into code names (see Cantino et al., 1999; Pfeil and Crisp, 2005), thereby ridding the species of the genus name (for criticism, see Nixon et al., 2003), the view of some of the PC proponents is more extreme. For example, Pleijel and colleagues' (Pleijel, 1999; Pleijel and Rouse, 1999, 2000, 2003) extreme view (one that will certainly not be advocated by the PC or the species code; de Queiroz, personal communication) is that species should simply be abandoned. Pleijel (1999) revised so-called parts and Pleijel and Rouse (1999, 2000, 2003) introduced LITUs (least inclusive taxonomic units), which are themselves clades identified by apomorphies. We see the abandonment of species as entirely mistaken and cannot see how they can be replaced by LITUs—the study of reproductively cohesive groups (that need not be monophyletic) such as species and the study of tiny clades are simply different things. Furthermore, their system would require revision of all existing species names and thus maximally deviate from one of the major objectives of PC—taxonomic stability.

The literature on species concepts is vast (e.g., see Cracraft, 1987; Eldredge, 1993; Mayden, 1997; de Queiroz, 1998, 1999; Wheeler and Meier, 2000). Recently, 5 out of 22 species concepts compatible with modern evolutionary biology were debated in the context of phylogenetic theory (Wheeler and Meier, 2000). Of the five, only the Phylogenetic Species Concept *sensu* Mishler and Thériot (2000) required a phylogeny for recognizing species (for competing species concepts, see Mayr, 2000; Meier and Willmann, 2000; Wheeler and Platnick, 2000; Wiley and Mayden, 2000; for critique and rebuttals, see other chapters in Wheeler and Meier, 2000). Theoretical considerations aside, one should remember that the majority of known species have been described in the absence of a phylogenetic hypothesis, although it could be argued

that by placing a species in a genus, at least implicit hypothesis of relationships exist in the Linnean system. If naming species were to require a phylogenetic analysis (note that such an approach need not be advocated in a PC-based Species Code), the taxonomist's fight to describe global biodiversity before it goes extinct is lost. If all existing (binomial) species names are to be converted into new code names (Cantino et al., 1999), the cost for taxonomical stability is enormous, and if species are no longer (Pleijel, 1999), conservation biology resets itself to the starting point. Sacrificing species is detrimental for biology and we strongly oppose it.

#### LINNEAN VERSUS PHYLOGENETIC NOMENCLATURE

Naming clades is useful and should be governed in phylogenetic taxonomy. According to Stevens (2002), "flagged" (= ranked) hierarchies are more useful at the lower levels (but, see Pfeil and Crisp, 2005). In our view, the main advantage of phylogenetic nomenclature as governed by PC over the traditional nomenclature governed by the existing codes is its explicitness in name definition with reference to the phylogeny; in other words, name association with a hypothesized evolutionary history of the taxon. The existing codes require no reference to evolutionary history. However, as shown below, names in ranked systems can provide information on hierarchical relationships without a phylogeny (and without an additional reference to clade association, as has been proposed in PC). Both the phylogenetic and the Linnean system, if used for monophyletic groups, are able to communicate phylogenies, but are sensitive to low phylogenetic resolutions (Dayrat and Gosliner, 2005) and to changes in phylogenetic hypotheses, which often demand widespread name changes in rank-based taxonomy (Sennblad and Bremer, 2002). No existing or proposed code (PC included) has all the desired attributes: convey hierarchical information, provide absolute name stability, simplicity, and continuity in communicating the identities of taxa (Schuh, 2003) in addition to providing explicit clade-based definitions. Furthermore, the legacy of species names and types is so immense and so deep-rooted in scientific communication that any changes to the basic ideas of species binomials may encounter insurmountable opposition, and in our opinion such changes are entirely unnecessary. Thus, instead of replacing existing codes, it may be more desirable to fix their flaws (see Nixon et al., 2003), a task that will be aided by many of the ideas stemming from the PC. We propose to combine both approaches in a classification method (see also Sennblad and Bremer, 2002) based on the premises that only monophyletic superspecific clades should be named, and equal ranks imply only exclusivity, not comparability.

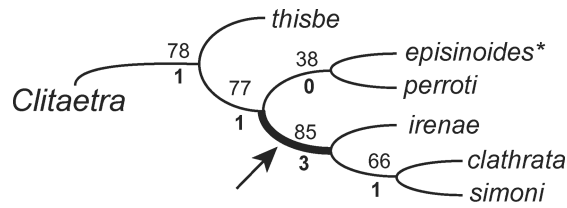
Character-based taxon diagnoses (a standard practice in Linnean taxonomy) were viewed by de Queiroz and Gauthier (1990, 1992) as epistemological (only indirectly providing the evidence for the existence of a group). On the other hand, phylogenetic definitions are ontological, referring to the entity itself (clade) and thus imple-

ment Darwin's (1859) evolutionary theory in taxonomy. Group diagnoses (as opposed to species diagnoses) are also problematic when the features defining a clade are modified further distally in the phylogeny, a very common phenomenon exemplified by the loss of appendages in snakes, which are nevertheless tetrapods (de Queiroz and Gauthier, 1990). Sereno (2005) labels the traditional differential diagnosis as a "grab bag of symplesiomorphies and synapomorphies that may, or may not, be present in most group members." Clearly, phylogenetic definitions are preferable to character-based definitions in the light of evolutionary theory, although character-based diagnosis can certainly be useful. Definitions, as regulated by the PC (Cantino and de Queiroz, 2004), are node based, stem based, or apomorphy based (de Queiroz and Gauthier, 1990, 1992), or combinations of these (Cantino and de Queiroz, 2004; Sereno, 2005).

Although in strict terms the PC does not *require* named taxa to be monophyletic (Pickett, 2005a, 2005b; but see Brummitt, 2002), it explicitly provides rules to name clades, hence taxa named under PC are necessarily hypothetically monophyletic. On the other hand, the Linnean system, as enforced by the current codes, readily allows monophyletic, paraphyletic, and polyphyletic taxa (de Queiroz and Gauthier, 1990; Schander, 1998; Pfeil and Crisp, 2005; Pickett, 2005a, 2005b), diagnosed by synapomorphic, symplesiomorphic, and homoplastic characters, respectively. However, if superspecific (ranked) taxa are circumscribed phylogenetically (e.g., Specht and Stevenson, 2006) their names convey information on their monophyly and hierarchy. Thus, a compromise system, where Linnean ranks are combined with phylogenetic definitions, is informative of descent. The combined approaches in zoology (Hillis and Wilcox, 2005; Kuntner, 2005, 2006) and botany (Sennblad and Bremer, 2002; Pfeil and Crisp, 2005) clearly circumvent the problem of non-monophyly in a ranked system, while requiring minimal alterations of the existing codes.

PC facilitates the naming of new clades as they are discovered (Cantino and de Queiroz, 2004). Under the existing codes, naming a new clade often requires an intermediate rank (e.g., superfamily), if available, or alternatively changes in ranks, and thus names, of more and less inclusive clades. This problem discourages systematists from naming clades until an entire classification is developed (Cantino and de Queiroz, 2004). However, caution in naming clades, especially in the absence of a thorough study aimed at a new classification, is advised in any system. Further, there is no need to formally name all or even most clades (Brochu and Sumrall, 2001; Jørgensen, 2002; PC article 2.1.2.), in contrast to naming species, which is important in documenting biodiversity. In a large tree it may suffice to name only well-supported clades as and when their naming facilitates discussion (de Queiroz and Cantino, 2001).

Figure 1 illustrates a logical problem with formally naming clades in the Linnean system, and the arbitrariness in their rank assignments (example from Kuntner, 2006). A well-supported clade within the genus *Clitaetra* was named (subgenus) *Afroetra*. However, following the

**RANKED**

- supergenus *Clitaetra*  
 genus *Indoetra*  
   *Indoetra thisbe*  
 genus *Clitaetra*  
   *Clitaetra episinoides*  
   *Clitaetra perroti*  
 genus *Afroetra*  
   *Afroetra irenae*  
   *Afroetra clathrata*  
   *Afroetra simoni*

**OR**

- genus *Clitaetra*  
 subgenus *Indoetra*  
   *Clitaetra thisbe*  
 subgenus *Clitaetra*  
   *Clitaetra episinoides*  
   *Clitaetra perroti*  
 subgenus *Afroetra*  
   *Clitaetra irenae*  
   *Clitaetra clathrata*  
   *Clitaetra simoni*

**RANKLESS**

- clade *Clitaetra*  
 thisbe  
 episinoides  
 perroti  
 clade *Afroetra*  
   irenae  
   clathrata  
   simoni

**COMBINATION**

- genus *Clitaetra*  
 clade *Indoetra*  
   *Clitaetra thisbe*  
 clade *Clitaetra*  
   *Clitaetra episinoides*  
   *Clitaetra perroti*  
 clade *Afroetra*  
   *Clitaetra irenae*  
   *Clitaetra clathrata*  
   *Clitaetra simoni*

so-called principle of exhaustive subsidiary taxa (de Queiroz and Gauthier, 1992:456–457) and to avoid the paraphyly of the remaining lineages within the genus, such action triggered the naming of two more new subgenera (despite their meager cladistic support), one of them, following the principle of coordination (ICZN, 1999), subgenus *Clitaetra* with the type species of the genus. An alternative in the ranked system (Fig. 1) would be to treat *Afroetra* at the genus level, but that would change species binominal in all species but two. The poor alternatives in a ranked system (see Nixon et al., 2003; Kuntner, 2006) are informally or not naming the clade at all, taxonomically placing species as *incertae sedis* or abandoning the strict principle of exhaustive subsidiary taxa. These appear to be inferior to a rankless system with precise phylogenetic definitions, which only affect that, and no adjacent clades. Figure 1 shows one possibility. However, such nomenclature is not in agreement with the zoological code. As one of the solutions to a similar problem, Nixon et al. (2003) proposed to use unranked taxa intercalated between Linnean ranks. For reasons discussed below, we favor a similar combination approach (Fig. 1), which retains the genus rank but names and phylogenetically defines unranked intercalated taxa.

PC eliminates a major source of instability under the existing codes: name changes due to rank shifts (Cantino and de Queiroz, 2004). For example, a new classification proposed by Kuntner (2006), following the zoological code, changes the rank of the subfamily name Nephilinae to the family Nephilidae. Because Nephilinae had been previously catalogued in the families Tetragnathidae or Araneidae (see Kuntner, 2005), but the most complete recent phylogenies (Kuntner, 2006) support neither such placement of the genera within the clade Nephilinae, the only obvious nomenclatural choice in a ranked classification is to treat the name at the family level (Nephilidae). However, in a rankless system, the name Nephilinae

FIGURE 1. An example of arbitrariness in rank assignments and the resulting nomenclatural instability under the Linnean (ranked) system, with alternatives. Part of the nephilid spider phylogeny proposed by Kuntner (2006), with the six currently known *Clitaetra* species (\* = type species). Note mostly low clade support values (Bootstrap above, Bremer below). The only relatively well-supported clade (bold, arrow) contains the three known African mainland species; naming it would facilitate biological communication. A few possibilities are outlined below: two possible naming schemes in agreement with the zoological code, one possibility in the rankless system, and one combination approach. The ranked naming above erects a new genus for the clade in question, but in order to avoid *Clitaetra* paraphyly, such action requires two more genera, one nominal (principle of coordination) and one for a single species, an unnecessary action considering few species and low clade supports. Similarly, the second ranked alternative (below) names not only one subgenus but three; Kuntner (2006) opted for this to preserve the stability of the six species binomina. The rankless alternative (though more possibilities exist), where only the clade *Afroetra* is newly named, seems to make minimal disruptions to the existing species nomenclature but is not in agreement with the zoological code. We prefer the combination approach, which is in agreement with the code because it retains the genus rank and species binomina, but also names new rankless clades.

could persist without the implication that (as a subfamily in the traditional system) it has to be included within Araneidae, Tetragnathidae, or any other family. Which is better? Certainly, nomenclatural stability (as the retention of the name) would be better preserved under PC. However, names in a combined system (Kuntner, 2005, 2006) convey information on hierarchy without reference to phylogeny (see also Pfeil and Crisp, 2005); e.g., Nephilidae is monophyletic and includes the monophyletic Nephilinae but excludes, by definition, other family-ranked groups. Thus, a combined nomenclatural approach is more informative and can be predictive.

Another example shows the difficulty of adjusting ranks when phylogenetic hypotheses change (Fig. 2). Perissodactyla, Artiodactyla, and Cetacea are three related groups of the class Mammalia, traditionally each in the rank of order. However, it is now becoming clear based on multiple data sets that Cetacea nests within Artiodactyla (for reviews, see, e.g., O'Leary et al., 2004; May-Collado and Agnarsson, 2006). Hence the new group Cetartiodactyla was suggested (Montgelard et al., 1997), containing Cetacea and a paraphyletic Artiodactyla. Cetartiodactyla is sister to the order Perissodactyla, so it seems logical that it also gets an order rank. Cetacea then could become suborder, with new subor-

ders created for the remaining clades of artiodactylans, but Cetacea already contains the suborders Mysticeti (baleen whales) and Odontoceti (toothed whales). These in turn could become superfamilies, but that would lead to even greater changes because both contain a number of superfamilies already. Perhaps they could then become infraorders, although there would still be a problem with the existing, albeit rarely used, infraorder Autoceta, and so on. Alternatively, new ranks—legions, cohorts, magnorders, mirorders, etc.—could be added so that existing ranks can remain unchanged. However, this solution magnifies the problem (Fig. 2C). Regardless, adjusting ranks in the era of rapid improvement of phylogenetic knowledge is a difficult task and one mostly devoid of biological meaning.

The above examples are rank shifts due to a revised phylogeny. However, a further problem in the Linnean system is that ranks can be arbitrarily reassigned in the absence of a novel phylogenetic hypothesis, which can force yet other name changes (Laurin et al., 2006).

Clearly, ranks are problematic, but should we completely abandon them? According to Cantino et al. (1999), PC will eventually unlink the specific name from the genus name because the latter is rank based. Our view is that PC, at least in its present state of development,

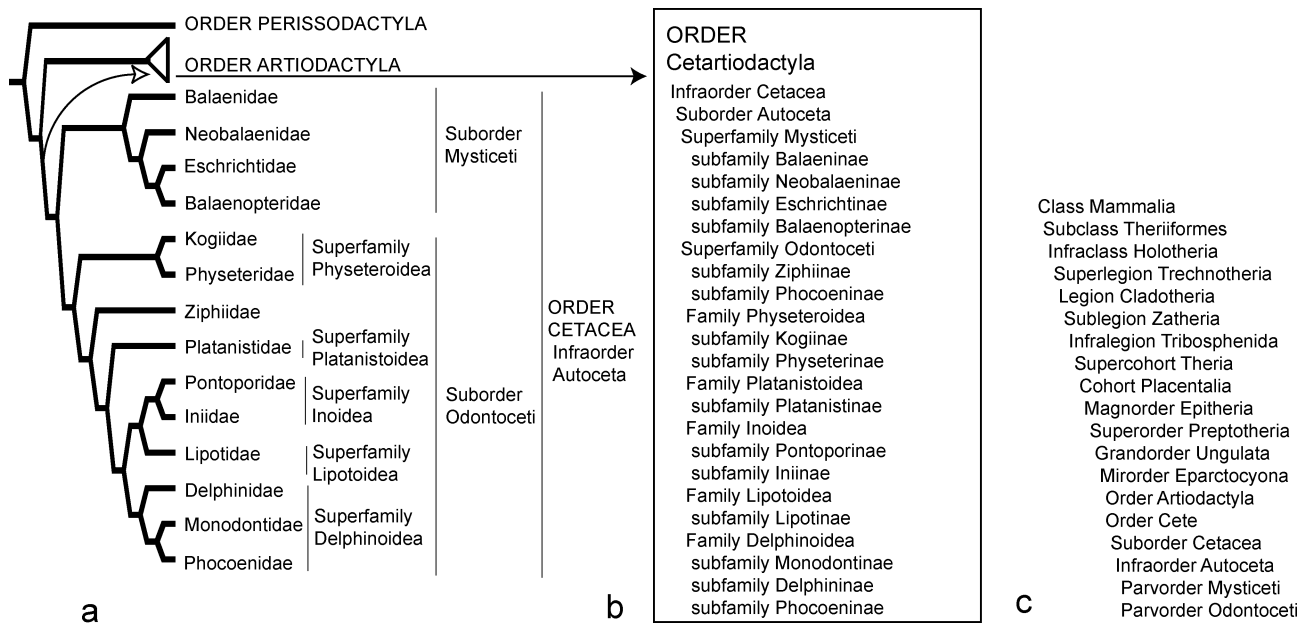


FIGURE 2. Example of changes in ranks necessitated by advance in phylogenetic knowledge. In A, the cladogram shows the traditional hypothesis of relationship of three mammalian orders using one of the most widely used but relatively simple divisions. The novel placement of whales (Cetacea) within the even-toed ungulates (Artiodactyla) (B, arrow) requires changes in numerous cetacean ranks even though relationships within Cetacea remain unchanged. One option is shown on the right, but note that other lower ranks not shown here will also need adjusting. This infers changes in what taxa are families, genera, etc., and can cause much needless instability. Note also that additional changes in endings are required for superfamilies from A that in B become families. However, this creates additional problems, e.g. Delphinoidea becomes Delphinidae, but refers to a different group than Delphinidae in A. This problem is often solved by adding divisions—new ranks such as legions, cohorts, magnorders, and mirorders so that existing ranks can remain unchanged. However, this solution makes the problem even worse. In C, a small portion of a fully ranked classification of mammals from McKenna and Bell (1997) is given, showing ranks from Mammalia to baleen (Mysticeti) and toothed (Odontoceti) whales (note that here Cetacea is a suborder of the order Cete, which includes whales and the fossil group Acroodi). This classification makes use of all the classical ranks in addition to many that are rarely used, and hence has not been generally accepted. Here, when advances in phylogenetic knowledge place order Cete inside order Artiodactyla, the adjusting of ranks would create a ripple effect up or down (or both) the ranking system, re-ranking a grand portion of the mammalian part of the tree of life, unless yet other new ranks are created. Not only is this exceedingly complicated but also effectively pointless, for no knowledge is added by this exercise and, as experience has shown, most researchers would ignore the changes.

should not be extended to govern species-level nomenclature. Removing binomials (i.e., ridding nomenclature of genera) would seem to improve nomenclatural stability at the cost of informativeness (acknowledged by Cantino and de Queiroz, 2004), not to mention the catastrophic effects of instantly outdating existing scientific names and references to them. Legacy apart, names in a rankless system fail to convey relatedness in the absence of a phylogeny, particularly useful information at the species/genus level. Of course, a rankless system using mononyms could achieve a similar result by use of some reference conventions (see Cantino et al., 1999). For example, the species *trogloodytes* and *paniscus* could in a given study, be presented as “*trogloodytes* in Pan” and “*paniscus* in Pan,” where “Pan” was not a genus, but a rankless clade. Or more simply, species could be followed by a reference to more inclusive clades as in *trogloodytes* (Pan, Pongidae) or Pongidae/Pan/*trogloodytes*. Such conventions could also show exclusion as well as inclusion; e.g., *trogloodytes* (Pan (-Homo), Pongidae). However, it remains to be seen if such conventions could approach the information content of a ranked system while retaining simplicity and avoiding the burdens ranks carry. For example, without ranks, each author’s reference clades of choice could differ (e.g., what do we know about the relationships of Hominini/*trogloodytes* versus Panina/*paniscus*), potentially hindering communication.

Phylogenetic definitions of taxon names make the use of type concepts above the species level, as regulated by the existing codes, superfluous (de Queiroz and Gauthier, 1992; Sundberg and Pleijel, 1994). (Note that the specifiers used in phylogenetic definitions function analogously to types in serving as reference points.) We agree that phylogenetic definitions should replace type taxa (type species, type genus). However, type specimens (these are retained in drafts of the PC and species codes, de Queiroz, personal communication), which fix the species names, should continue to be used (*contra* Strand, 1929; Pleijel, 1999), as they eliminate arbitrariness in species definitions and preserve voucher specimens for future generations.

In PC, the name can be unambiguously defined (name stability), but its content may depend on phylogenetic hypotheses, and thus be unstable. In the PC introduction, Cantino and de Queiroz (2004) stress the nomenclatural stability over informativeness:

There will, of course, be a consequent absence of hierarchical information in species names governed by the PhyloCode; one will not be able to infer phylogenetic relationships from these names in the way that one can infer genus assignment from species names governed by the rank-based codes. However, under both the PhyloCode and the rank-based codes, the primary purpose of a taxon name is to provide a means of referring unambiguously to a taxon, not to indicate its relationships. From this perspective, the loss of nomenclatural stability of species names under the rank-based codes is too high a price to pay for incorporating taxonomic information (genus assignment) into the names. Moreover, although such information will not be built into species names under the PhyloCode, phylogenetic relationships can easily be indicated by associating the species name with the names of one or more clades to which it belongs.

In summary, the PC promotes group monophyly and name stability, whereas the Linnean (superspecific) names, if used phylogenetically, provide hierarchical information and a legacy of species binomials whose abandonment would be over costly. Apparently, name stability is more important to PC proponents and hierarchical informativeness to PC critics. Our proposed combination approach promotes what we view as two salient elements of an evolutionary nomenclatural system: group monophyly and hierarchical informativeness.

#### COMBINATION/COMPROMISE APPROACHES

Sennblad and Bremer (2002) proposed a compromise approach to classification in a case study on Apocynaceae s.l., combining the rules from the botanical code with those from PC. According to Sennblad and Bremer (2002), the advantage of the Linnean system is a standard set of used names, whereas the PC system provides more exact definitions, which reduce instability due to subjectivity (splitting versus lumping). Pfeil and Crisp (2005) explored a hybrid classification of the subfamily Malvoideae; although these authors concluded that there is no objective and discoverable rank for any taxon, they used ranks above the generic level but used unranked taxon names within the genus *Hibiscus*. Kuntner (2005, 2006) presented a combined classification method using the rules from the International Code of Zoological Nomenclature (ICZN, 1999) but with phylogenetic definitions (PC Article 9, Note 9.4.1). Kuntner (2005, 2006) presented character support as evidence for monophyly, but, due to ambiguous optimizations, used no apomorphy-based definitions (for further problems with apomorphy-based definitions, see Bryant, 1994; Sereno, 1999, 2005; Kojima, 2003; but, see Gauthier and de Queiroz, 2001). Because PC has not taken effect yet and registration database not implemented, the names proposed by Kuntner (2005, 2006) have not been registered (PC Article 8).

Our proposed combined approach goes further than the above: (1) We maintain that species binomials based on type specimens must be preserved. First, type specimens are a necessary link between the name and a species concept. Second, genera, if used in conjunction with phylogenetic definitions, are implicitly informative of species relationships and species exclusivity, whereas the PC would require external reference to convey the same information (see above). Third, the legacy of species names as binomials is simply too great to sacrifice and such an act seems needless. Finally, most concerns with the Linnean system that we agree with refer to taxa above the species level. (2) In general, ranks, especially excessive intermediate ranks, should be avoided because they are problematic and offer little that a sensible rankless reference system could not capture (see above). However, we see two main reasons, both purely practical, for retaining and regulating the classical, and most widely used ranks: genus, family, class, order, phylum, kingdom. One is tradition—these are the ranks most deeply ingrained in biological nomenclature; hence, their

abandonment is most likely to hinder communication and least likely to be accepted by the scientific community. The other is structure—retaining a few ranks provides basic structure that facilitates communication and organization. For example, it is standard practice for authors discussing a given taxon to help the reader by indicating its location in the tree of life with reference to classical ranks; e.g., *Steatoda* (Theridiidae, Araneae). Without any ranks, each author might make a different, though accurate, choice, e.g., *Steatoda* (Latrodectinae, Arachnida), with confusing results. Similarly, natural history museums are organized based on these classical ranks, and much would be lost if each museum based their organization on different, arbitrarily chosen clades. (3) Following the PC, explicit phylogenetic name definitions should be required, where type taxa (species, genera) should not play a role, but specifiers should (see Cantino and de Queiroz, 2004; Sereno, 2005). (4) Clades and monophyly are synonymous and only clades should be named. However, monophyly and species are concepts that should not be mixed because nearly all species concepts allow for species paraphyly (see below)—as they should because paraphyly is an expectation of many speciation processes.

This nomenclatural approach can easily be used in all biological systems. For species nomenclature it follows the rules from the existing codes; e.g., International Code of Zoological Nomenclature (ICZN, 1999). However, for all clade nomenclature precise phylogenetic definitions, following the PC articles 7, 9 to 11 (Cantino and de Queiroz, 2004), are to be used; thus, all superspecific names explicitly refer to (hypothetically) monophyletic taxa, and nomenclatural definitions imply group composition. Phylogenetic definitions (PC Article 9, Note 9.4.1) are node based, where “clade (A and B)” means the least inclusive clade containing A and B; stem-based, where “clade (A not Z)” means the most inclusive clade containing A but not Z; apomorphy-based, where “clade (M in A)” means the most inclusive clade exhibiting character (state) M synapomorphic with that in A; or a combination of these, with specifiers and qualifying clauses, if applicable (Article 11.9). This approach also explicitly recommends that any intermediate ranks (such as sub-, superfamily, etc.) be officially abandoned, while for any retained ranks it should be stressed that equal ranks do not imply comparability.

Our requirement that superspecific names represent monophyletic groups is likely to be seen as trivial for the simple fact that such an approach is already practiced by most phylogeneticists in the context of the rank-based system. However, it is important to note that the existing codes only require taxon diagnosibility, not monophyly. In fact, the words “monophyly” and “synapomorphy” are absent from the zoological and botanical codes (ICZN, 1999; Greuter et al., 2000) and monophyly is not a requirement even for names under the PC (de Queiroz, 2006). In contrast, we propose that superspecific names be required to explicitly refer to (hypothetically) monophyletic taxa. We propose the explicit retention of species binomials (see also Lee, 2002) and the

introduction of phylogenetic definitions to the Linnean system such that the name explicitly makes reference, via specifiers, to either (1) the evidence for monophyly (apomorphic definition), or (2) the taxa that a monophyletic group includes/excludes (node-/stem-based definition). We advocate abandoning all intermediate ranks and all rank-based definitions, while explicitly retaining the six classical ranks (phylogenetically defined). Finally, it should be stressed that equal ranks do not represent comparable evolutionary entities (unless the equal ranked clades happen to be sisters). The last point may seem needless to many evolutionary biologists. However, many biological studies continue to compare rank (e.g., genus, family) traits, as opposed to sister clades. In fact, a brief glance at virtually any lower level phylogenetic study will reveal a rank-comparison statement in the introduction; e.g., “the family x is one of the largest families . . .” etc.; our own studies are no exception (e.g., Agnarsson, 2004; Agnarsson and Kuntner, 2005). As simple statements these are merely rather meaningless, but as the ranks themselves, they imply comparability and invite error; i.e., the use of species number within ranks as comparative data points in evolutionary analyses.

#### CONCLUSIONS AND RECOMMENDATIONS

In our view the PhyloCode, when formally proposed, should not aim to govern species nomenclature (see also Lee, 2002). Such PC, also known as the Clade Code (Laurin et al., 2005) would govern naming clades (not species) at all levels, with name stability outweighing name information. Existing codes, in turn, would continue to govern nomenclature of species and genera, with informativeness and tradition outweighing stability. We maintain that any code of biological nomenclature should retain and regulate the classic ranks for the sake of hierarchic informativeness, legacy of data, and compatibility with the current codes, but intercalated ranks should be abandoned. Phylogenetic definitions should replace rank-based definitions linked to type species and genera, and all codes should adopt the rule that superspecific names imply taxon monophyly.

Some PC proponents contended that rejection of ranks has never been a fundamental principle of phylogenetic nomenclature (Laurin et al., 2005). Although criticized for inconsistency with their original principles (Pickett, 2005a, 2005b), this position of the PC proponents seems to facilitate a combined approach. If the traditional (existing) codes fail to adapt to the advances in evolutionary biology, the developing PC will have a theoretical advantage over the classical codes. Likewise, if the PC goes too far and ultimately sacrifices the species binomen, then general acceptance of PC seems unlikely.

Although we thus see room for coexistence of the Linnean system and the PC, in practice, it may be simpler to adjust the existing codes by implementing in them the best elements of the PC. The following are our recommendations for new editions of all codes of biological nomenclature:



- (1) Species binomials, including the genus rank, should be retained.
- (2) Type specimens should continue to fix species names.
- (3) For practical reasons, the classical supergeneric ranks (family, class, order, phylum, kingdom) should also be retained, but intermediate ranks should not, thus striking a balance between stability, tradition, and information content.
- (4) Type taxa (species, genera) should be abandoned. Instead, phylogenetic definitions (PC articles 7, 9 to 11) should be required at all superspecific levels; names should refer to hypotheses of monophyly (clades).
- (5) Species monophyly should not be required because theory predicts that many species are not monophyletic.
- (6) It should be stressed that equal ranks, per se, do not imply comparability or comparable evolutionary histories.

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