

Points of View

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Phylogenetic Nomenclature, Hierarchical Information, and Testability

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In a continuing debate about the usefulness of phylogenetic nomenclature, Platnick (2012) has apparently conceded the two main points of our previous paper (de Queiroz and Donoghue 2011) by providing no counter-arguments. First, contrary to Platnick's previous assertions, when appropriate comparisons are made (i.e., between taxonomies consisting of the same-named groups), there are no differences in information content, as measured by implied three-taxon statements, between hierarchical taxonomies whose names are governed by rank-based versus phylogenetic nomenclature. The reason is that three-taxon informativeness is a property of the clades that are recognized (the taxonomy) rather than of the rules governing their names (the nomenclatural system). Second, phylogenetic nomenclature outperforms its rank-based counterpart when the approaches are compared using a nomenclaturally relevant criterion. Specifically, phylogenetically defined names result in fewer unnecessary name changes in the context of new phylogenetic hypotheses.

Having abandoned his criticism of phylogenetic nomenclature based on three-taxon informativeness, Platnick (2012) focused his rebuttal more or less entirely on the mutual exclusivity of taxa whose names bear the same rank-signifying endings. He contended that information about mutual exclusivity gives rank-based names more predictive power and testability than their phylogenetically defined counterparts. Consequently, rather than favoring the replacement of rank-based definitions by phylogenetic ones, as advocated by ourselves and others, Platnick advocated extending the use of standard, rank-signifying endings and, by implication, rank-based definitions to the names of clades at all hierarchical levels (currently they extend only up to the rank of superfamily in zoology, and are used inconsistently above the rank of family in botany).

Contrary to the impression given by Platnick, we argue here that the information in rank-signifying endings is limited, so that any loss of such information necessitated by the current version of the *International Code of*

Phylogenetic Nomenclature (hereafter, the *PhyloCode*) would not be a great hindrance to science. In addition, incorporating that information comes at a cost in the form of unnecessary and inappropriate name changes. We also argue that the application of phylogenetic definitions leads to very explicit hypotheses about taxon composition that are no less testable than those associated with traditional taxa, the testability of which has nothing to do with rank-signifying endings or rank-based definitions. Moreover, phylogenetic definitions can be formulated so that names designate particular phylogenetic hypotheses and are therefore rejected when the hypotheses that they represent are considered falsified, a possibility that does not exist with rank-based definitions. Finally, we argue that the use of categorical ranks is not logically necessary to convey the hierarchical information associated with what are commonly thought of as rank-signifying endings. Such endings can be interpreted as signifying only relative rather than absolute (categorical) ranks, in which case they are compatible with phylogenetic nomenclature. This observation highlights the generality of the phylogenetic approach to nomenclature as well as a distinction between that general approach and the specific rules and recommendations adopted in the *PhyloCode*.

INFORMATION CONTENT

Because Platnick emphasized the information content of names with rank-signifying endings, it is useful to consider the information contained in such names. That information comes in three main forms. First, names that have the same rank-signifying ending (e.g., *-idae*), implying assignment to the same rank (e.g., family), refer to mutually exclusive taxa (e.g., *Agamidae*, *Chamaeleonidae*). Second, names that are based on the name of the same included taxon (e.g., *Agama*) but have different rank-signifying endings (e.g., *-idae*, *-inae*), implying assignment to different ranks (e.g.,

family, subfamily), refer to nested taxa (e.g., *Agamidae*, *Agaminae*). And third, names (e.g., *Agamidae*) that are based on the names of genera (e.g., *Agama*) refer to taxa that contain those genera (and by extension, their type species). Platnick emphasized the first of these three forms of information, but we will consider all three for the sake of completeness.

The information about mutual exclusivity implied by names with identical rank-signifying endings is not particularly reliable with regard to phylogenetic relationships. Platnick presupposes a taxonomic convention in which all recognized taxa are hypothesized to be monophyletic, but that presupposition is in no way guaranteed by the use of rank-based nomenclature. Because the rank-based codes allow names to be applied to paraphyletic taxa, two taxa designated by rank-based names with identical endings may be mutually exclusive only in the purely circumscriptional sense that no species is considered to belong to both. However, if one taxon is paraphyletic relative to the other, then they are not mutually exclusive in a phylogenetic sense. Although phylogenetic definitions can, in principle, also be used to define the names of paraphyletic taxa (de Queiroz and Gauthier 1990), the *PhyloCode* does not include mechanisms for implementing such definitions (Laurin et al. 2005; de Queiroz 2006).

In addition, the implicit definitions of the rank-based codes provide no information about whether particular names are applied to monophyletic or paraphyletic taxa. A definition such as "*Agamidae* := the taxon that is ranked as a family and contains the genus *Agama*" gives no indication as to whether the designated taxon is monophyletic, paraphyletic, or polyphyletic. (Here and afterwards, we will use the symbol ":= " to mean "is defined as.") This situation contrasts sharply with the explicit definitions of phylogenetic nomenclature. For example, the definition "*Agamidae* := the least inclusive clade containing both *Agama* and *Leiolepis*" unambiguously specifies that the defined name refers to a monophyletic taxon (a clade). Similarly, if a name were defined as applying to a paraphyletic taxon, paraphyly would be evident from the definition itself (see de Queiroz and Gauthier 1990 for examples).

Finally, the mutual exclusivity of taxa whose names have the same standard endings holds only within a given taxonomy. For example, the name *Caprifoliaceae* is currently used by some authors for a paraphyletic group, by others for a clade comprising approximately 900 species (including those assigned to *Morinaceae*, *Valerianaceae*, and *Dipsacaceae* by other authors), and by still others for a smaller clade comprising approximately 200 species (which does not include *Morinaceae*, *Valerianaceae*, or *Dipsacaceae*). Thus, if one were to encounter the name *Caprifoliaceae* outside of the context of a particular taxonomy—and Platnick himself emphasized that that is the way in which taxon names are most commonly used—one could not safely conclude that the named taxon does not include *Morinaceae*, *Valerianaceae*, and *Dipsacaceae* as used in other sources.

Thus, mutual exclusivity cannot always be safely inferred for taxa whose names have the same ending.

Analogous issues exist for names whose endings imply reference to nested taxa (e.g., *Agamidae* and *Agaminae*). In this case, the taxa designated by such names may be nested only in the purely circumscriptional sense that the species assigned to one are a subset of those assigned to the other. However, if the taxon associated with the lower rank is paraphyletic relative to other taxa at the same rank, then it may originate in the same hypothetical ancestor as the taxon associated with the higher rank, in which case the taxa are not nested in a phylogenetic sense. For example, the lizard family *Scincidae* and its subfamily *Scincinae* appear to have originated in the same ancestor (see Brandley et al. 2005). And once again, the implicit rank-based definitions of such names provide no information about the monophyletic, paraphyletic, or polyphyletic status of the named taxa, nor can nesting always be safely inferred outside of the context of a particular taxonomy.

In addition, the implied nesting relationships only hold for names based on the name of the same type genus (e.g., *Agamidae*, *Agaminae*). They provide no information about whether *Leiolepidinae*, for example, is or is not nested within *Agamidae*. This kind of information is even more limited under rank-based botanical nomenclature because precedence is, at least in some cases, determined separately within each rank (as opposed to within a set of ranks, as in rank-based zoological nomenclature). Consequently, a subfamily whose name is based on the name of a particular type genus need not contain a tribe whose name is based on the name of the same type genus. For example, the subfamily *Rhododendroideae* does not contain a tribe *Rhododendreae* (International Botanical Congress 2006: Art. 19.4, Ex. 4).

Names formed by combining a standard ending with the stem of the name of an included taxon (the type genus) also contain information about the inclusion of that taxon (e.g., *Agamidae* contains *Agama*) but not about the inclusion of any other taxon of the same rank (e.g., no information is provided about whether *Draco* is included in *Agamidae*). Moreover, there are numerous exceptions to this rule that result when an established name of this kind is based on the name of an included taxon that is later rejected because of synonymy. For example, the taxon *Caprifoliaceae* does not include a currently recognized taxon (genus) *Caprifolium*. Most importantly, this third form of information does not differ between rank-based nomenclature and phylogenetic nomenclature as manifested in the *PhyloCode*, which contains a rule (Art. 11.7) to ensure that a clade whose name is based on the name of a type genus under rank-based nomenclature includes that taxon (type genus); for example, *Salticidae* must include *Salticus*.

In sum, although names with rank-signifying endings contain some information about nesting and mutual exclusivity, that information is unreliable with respect to monophyly, and it is limited to the context of a particular taxonomy. In the case of nesting, it is

also limited in scope (applies only to names based on the same type genus) and inconsistent (there are various exceptions). In addition, as we emphasized in our previous paper (de Queiroz and Donoghue, 2011), names governed by rank-based nomenclature have significant disadvantages in terms of unnecessary name changes and inappropriate applications of names. Thus, the information that Platnick considers such an important benefit of rank-signifying endings is, on closer inspection, not particularly extensive or reliable, and it comes with a significant cost.

TESTABILITY

Platnick (2012, p. 360) suggested that because of the mutual exclusivity implied by endings that signify assignment to the same rank, rank-based names are “vastly stronger, more testable hypotheses” than phylogenetically defined names. What he meant by this assertion really has little to do with testing hypotheses, as phylogenetically defined names are no less testable than their rank-based counterparts and offer some significant advantages according to that criterion.

Information about mutual exclusivity in rank-based names involves the hypothesized composition of taxa: specifically, that a taxon assigned to a given rank “exclude[s] all species belonging to any other group of coordinate rank” (Platnick 2012, p. 360). Platnick argued that formal classifications with lists of included taxa are not the primary way in which taxon names are most commonly used; however, to test hypotheses about composition, very explicit statements about included and excluded taxa are essential. Hypotheses about the composition of taxa designated by rank-based names can be tested by comparing lists of included and excluded species with phylogenetic trees. If the set of species included in the taxon in question corresponds to a monophyletic group (or, under a less strict criterion, to a paraphyletic one) on the tree, then the hypothesis can be considered corroborated, and if it does not, then the hypothesis can be considered falsified. Phylogenetically defined names are no less testable in this regard. Such names are also associated with hypotheses about taxon composition (included and excluded species), which can be tested similarly using phylogenetic trees. This similarity between rank-based and phylogenetically defined names should not be surprising, as it has nothing to do with the names of taxa (including their endings) but rather with hypotheses about taxon composition.

Hypotheses about mutual exclusivity are no different. Such hypotheses can only be tested in terms of the hypothesized compositions of the individual taxa; there is no separate test for mutual exclusivity that does not involve composition. Moreover, if two names necessarily refer to mutually exclusive taxa, as do those with the same rank-signifying endings under rank-based nomenclature, then those names certainly do not represent testable hypotheses. Because the compositions of taxa designated by such names are adjusted in

light of new phylogenetic hypotheses so as to ensure continued mutual exclusivity, propositions about their mutual exclusivity are decidedly unfalsifiable. The same is true for some but not all phylogenetic definitions (see below).

Here it is worth noting that the implementation of rank-based definitions requires information about the subjective assignment of taxonomic ranks (e.g., which of the many nested clades to which a particular type species belongs is assigned to the rank of family). Consequently, determining the composition of a taxon designated by a rank-based name requires not only the definition and a phylogenetic tree but also information about a subjective ranking scheme. By contrast, determining the composition of a clade designated by a phylogenetically defined name requires only the definition and a tree. In this respect, phylogenetically defined names are more parsimonious, less subjective, and therefore more amenable to automated implementation (e.g., Pagel and Meade 2006; Keesey 2007; Lemmon 2008).

It is also worth noting that taxonomic conventions rather than rank-based definitions are what ensure that names with the same rank-signifying endings refer to mutually exclusive taxa (and that our debate with Platnick is properly about the relative merits of rank-based versus phylogenetic definitions). There is nothing in the definitions “*Agamidae* := the taxon ranked as a family containing *Agama*” and “*Chamaeleonidae* := the taxon ranked as a family containing *Chamaeleo*” that necessitates that those names refer to mutually exclusive taxa. Regarding composition, the definitions themselves necessitate only that *Agamidae* contains *Agama* and *Chamaeleonidae* contains *Chamaeleo*. Those constraints alone do not prohibit the taxa from being nested. However, the definitions also stipulate association with a particular categorical rank (in this case family). Mutual exclusivity is then dictated by the taxonomic convention that taxa assigned to the same categorical rank must be mutually exclusive.

By contrast, phylogenetic definitions can be formulated without relying on categorical ranks so that the defined names necessarily refer to mutually exclusive taxa. Reciprocal phylogenetic definitions (Serenó 1998, 1999) are branch-based definitions that use the same specifiers but reverse their roles as internal versus external reference points. Consequently, the taxa designated by the defined names are necessarily mutually exclusive. We gave examples of definitions of this kind in our previous paper (de Queiroz and Donoghue 2011): “*Agamidae* := the largest clade containing *Agama* but not *Chamaeleo*” and “*Chamaeleonidae* := the largest clade containing *Chamaeleo* but not *Agama*.” Reciprocal phylogenetic definitions are used to name sister groups and thus relate phylogenetic definitions to categorical ranks through Hennig’s (1966) proposition that “sister groups must be coordinate and be given the same rank” (p. 191 see also pp. 156–7). Similar kinds of definitions will become important later in the text when we consider the possibility of using names with standard endings

to convey hierarchical information under phylogenetic nomenclature (i.e., independent of categorical ranks). Before doing so, however, let us consider one additional issue about testability.

Unlike rank-based nomenclature, phylogenetic nomenclature allows the possibility of using names to represent truly testable hypotheses. Phylogenetic definitions can be worded so that they stand for particular phylogenetic hypotheses in the sense that the defined name will apply to a clade only in the context of phylogenies that exhibit specified relationships (Bryant 1997; Lee 1998; Cantino and de Queiroz 2010: Art. 11.9). Under such a definition, rejection of the specified hypothesis of relationships leads to rejection of the name—that is, as opposed to continuing to use the name but modifying the hypothesis of composition. For example, consider the definition “*Halecostomi* := the smallest clade containing both *Amia calva* (representing bowfins) and *Perca fluviatilis* (representing teleosts) but not *Lepisosteus osseus* (representing gars),” which embodies the hypothesis that bowfins and teleosts are more closely related to one another than either is to gars. If the evidence were considered to support the alternative hypothesis (*Holostei*) that bowfins and gars are more closely related to one another than either is to teleosts, then there would be no clade that contains both bowfins and teleosts that does not also include gars, and the name *Halecostomi* would not apply to any clade.

A similar approach could be adopted informally under traditional nomenclature, but only because the name *Halecostomi* is traditionally associated with a rank above that of superfamily and therefore does not have a rank-based definition. It cannot be adopted under rank-based nomenclature. For example, consider the rank-based definition “*Halecostomi* := the taxon ranked as an infraclass that contains *Perca*.” Under that definition, the name *Halecostomi* would be applied to whatever taxon fits the definition under either of the alternative phylogenetic hypotheses. The name would only be rejected if a different name were to have precedence (normally established by priority) at the rank in question or if no taxon were to be ranked as an infraclass.

In sum, rank-based names do not represent more testable hypotheses than do phylogenetically defined names. On the one hand, both types of names are associated with hypotheses about taxon composition, which can be tested using trees derived from explicit phylogenetic analyses. On the other hand, names defined using rank-based definitions as well as those defined using standard phylogenetic definitions are unfalsifiable in the sense that there is no phylogenetic hypothesis that rules out continued use of the names (which can always be applied to some clade by modifying the hypothesis of composition). However, phylogenetic definitions can be formulated so that the defined names are truly testable in the sense that the names themselves are rejected when the hypotheses that they represent are considered falsified. That possibility does not exist for

rank-based definitions. Thus, when Platnick asserts that rank-based names are more testable hypotheses than their phylogenetically defined counterparts, what he really seems to mean is that names with rank-signifying endings contain hierarchical information.

HIERARCHICAL INFORMATION WITHOUT CATEGORICAL RANKS

Interestingly, the property that Platnick finds most beneficial about names with standard endings is only historically associated with categorical ranks, as opposed to being logically dependent on them. Although standard endings are most commonly used to signify categorical ranks, Platnick emphasized their use in indicating mutual exclusivity. Categorical ranks are traditionally associated with mutual exclusivity in that taxa assigned to the same rank are traditionally considered mutually exclusive; however, taxonomic categories are not necessary for conveying information about mutual exclusivity. That is to say, there is no logical reason why standard endings cannot be used to indicate mutual exclusivity independent of categorical ranks.

Stevens (2002, 2006) has used the term “flagged hierarchy” to refer to a set of names whose endings indicate only relative position in a hierarchy (higher or lower) rather than assignment to absolute (categorical) ranks (class, order, family, etc.). Although Stevens used the concept of a flagged hierarchy to argue against phylogenetic nomenclature, the concept is, in fact, compatible with that approach and can be used to address both his and Platnick’s criticisms. Because the standard endings in a flagged hierarchy have no necessary connection to categorical ranks, there is no conflict between such endings and phylogenetic nomenclature—that is, the application of taxon names independent of categorical ranks using phylogenetic definitions. As shown in the previous section, names with endings traditionally associated with ranks can be given phylogenetic definitions: for example, “*Agamidae* := the most inclusive clade containing *Agama* but not *Chamaeleo*.” Once provided with such a definition, the name can be applied to a taxon (in the context of a phylogenetic tree) independent of categorical ranks.

The key to implementing a flagged hierarchy in the context of phylogenetic nomenclature, then, is devising methods for defining names with particular endings so that they refer to clades with particular hierarchical relationships. For the case under consideration, methods would be needed for defining names with the same standard (but no longer rank-signifying) endings so that they refer to mutually exclusive taxa. This could be accomplished by modifying an approach proposed by Bremer (2000) for the names of angiosperm taxa traditionally associated with the rank of order and thus ending in *-ales*. Bremer proposed defining those names as in the following example: “the order *Asterales* is

the most inclusive clade comprising its type but none of the types of the 39 other orders listed in Table 1" (p. 131). Although Bremer explicitly ranked the taxa in question as orders, ranking was unnecessary. His definition can be modified so that reference to ranks is eliminated as follows: "*Asterales* := the most inclusive clade containing *Aster amellus* but none of the types of the 39 other names ending in *-ales* in Table 1 of Bremer (2000)." Definitions of this kind are conceptually similar to the reciprocal definitions discussed in the previous section in guaranteeing that the defined names will always refer to mutually exclusive taxa; however, they differ in using multiple external specifiers (except in special cases) and thus in not necessarily applying to sister groups. In any case, the critical issue is that the application of such definitions depends only on a relevant phylogenetic hypothesis; it does not require categorical ranks. Incorporating this convention into a codified system would simply require a rule stipulating that for any name with a particular standard ending, the types of all other names with the same ending are to be considered external (explicitly excluded) specifiers.

It should be noted that although Stevens (2006) advocated the combination of flagged hierarchies with rank-based nomenclature, that combination is incompatible. Because rank-based nomenclature requires the use of categorical ranks, it cannot be used to apply names with terminations that indicate only relative position in a hierarchy and not assignment to absolute (categorical) ranks. Consider a definition that takes the same general form as a rank-based definition but makes no reference to categorical ranks, for example, "*Agamidae* := the taxon containing *Agama*" (the phrase "ranked as a family" has been removed). Such a definition is too ambiguous to permit unequivocal application of the defined name because there are hundreds, if not thousands, of clades (and even more paraphyletic groups) that contain *Agama*. To put it another way, once a name is defined as being associated with a categorical rank, as it must be under rank-based nomenclature (e.g., "*Agamidae* := the taxon ranked as a family that includes *Agama*"), it can no longer be considered part of a flagged (uncategorized) hierarchy.

It should also be noted that although the *PhyloCode* does not currently use standard endings to convey information about mutual exclusivity, phylogenetic nomenclature has used standard endings to convey information about nesting. Moreover, those endings have been associated with classes of clades based not on arbitrary rank assignments but on theoretically and operationally significant properties. Thus, following Hennig's (1965) discussion of three different conceptualizations of the time of origin of a clade, practitioners of phylogenetic nomenclature have applied the most widely used name from a set of alternatives to a crown clade and then formed the names of more inclusive intermediate (often one associated with a characteristic apomorphy) and total clades by adding the endings *-formes* and *-morpha*, respectively, to the

name of the crown (e.g., Gauthier et al. 1988a, 1988b; Schwartz 2012). Other authors have used names with the same endings to imply the same relative hierarchical relationships but without applying the name ending in *-morpha* to a total clade (e.g., Rowe 1988; Wyss and Flynn 1993; Berta and Wyss 1994). Analogous proposals for crown, apomorphy, and total clades have been developed using standard prefixes rather than suffixes (e.g., Meier and Richter 1992; Gauthier and de Queiroz 2001; de Queiroz 2007) and have been incorporated into the *PhyloCode* (see esp. Articles 10.3–10.5, 10.7).

PHYLOGENETIC NOMENCLATURE AND THE *PHYLOCODE*

The possibility of using standard endings in conjunction with phylogenetic definitions to indicate mutual exclusivity highlights an important distinction between the general approach of phylogenetic nomenclature, the application of taxon names using phylogenetic definitions, and one particular codification of that approach, the specific set of principles, rules, and recommendations adopted in the *PhyloCode*. This distinction is analogous to that between the general approach of rank-based nomenclature and its particular codifications in the Bacteriological, Botanical, and Zoological Codes, and it explains why those codes differ in various ways (e.g., Sprague et al. 1944) despite adopting the same general rank-based approach. In any case, if Platnick (2012, p. 360) is talking specifically about the *PhyloCode*, he is correct in stating that "the mutual exclusivity of names with standardized endings is no longer certain." The *PhyloCode* does not contain rules to ensure that names with the same standardized endings always refer to mutually exclusive taxa, and it is therefore possible for such names to end up referring to taxa that are nested rather than mutually exclusive. Although this is an accurate characterization of the *PhyloCode*, it is not a legitimate criticism of phylogenetic nomenclature.

We have demonstrated previously in the text that phylogenetic nomenclature can accommodate the use of standardized endings to indicate mutual exclusivity. That is to say, the mutual exclusivity of taxa whose names have the same standardized endings can be made certain using definitions stated in terms of clades and common ancestry that can be implemented independent of categorical ranks. That the *PhyloCode* does not currently contain rules to enforce the use of such methods is a consequence of the fact that the *PhyloCode* is only one of several possible ways in which phylogenetic nomenclature could be codified.

The situation could be different in the future, and it could have been different in the present had history played out differently. At the Second International Workshop on Phylogenetic Nomenclature, which took place at Yale University on 28–30 July 2002, one of us (KdQ) raised the issue of incorporating rules into the *PhyloCode* to preserve the hierarchical relationships

(both nesting and mutual exclusivity) implied by particular endings. That idea was not supported by the other Workshop participants, so the rules were not incorporated (although the *PhyloCode* does include rules to ensure that names based on the names of subordinate taxa [type genera in rank-based nomenclature] are applied to clades that include those subordinate taxa; see INFORMATION CONTENT).

There are likely two primary reasons why participants in the Workshop rejected the idea that the *PhyloCode* should include rules for incorporating (preserving) certain types of taxonomic information in names. First, such rules could lead to greater instability in the hypothesized composition of taxa designated by particular names, particularly with regard to excluding subtaxa that were previously included (e.g., the exclusion of *Leiolepis* and its relatives from *Agamidae* in some of our previous examples; de Queiroz and Donoghue 2011). Second, some (but not all) proponents of phylogenetic nomenclature are also advocates of rank-free taxonomy (for the distinction see de Queiroz 2006), and they may have wanted to dissociate the endings in question from categorical ranks.

In any case, the point is that the absence of rules in the *PhyloCode* for using standard endings to convey information about mutual exclusivity is a contingent rather than a necessary property of that document. Such rules could be incorporated in the future if proponents of phylogenetic nomenclature were to decide that the benefits outweigh the costs. The general approach of phylogenetic nomenclature is fully compatible with the use of standard endings to convey certain types of hierarchical information as long as those endings are interpreted as indicating only relative and not absolute ranks—that is, as long as they are used to represent elements of a flagged rather than a categorized hierarchy. Thus, Platnick's criticism does not apply to the general approach of phylogenetic nomenclature but rather to the specific set of rules and recommendations that make up the current version of the *PhyloCode*. It cannot therefore be considered a reason for rejecting phylogenetic nomenclature—that is, for rejecting definitions of taxon names that are stated in terms of clades and common ancestry rather than in terms of categorical ranks.

CONCLUSION

Our debate with Platnick has revealed that the issue underlying our disagreements is a tradeoff between building hierarchical taxonomic information directly into names versus maintaining the associations between names and clades and thus avoiding unnecessary name changes. However, we have also demonstrated that phylogenetic nomenclature is compatible with the use of standard endings to convey hierarchical information. The conflict, therefore, is not between rank-based and phylogenetic nomenclature but simply

between two factors, minimizing unnecessary name changes and incorporating hierarchical information into names, both of which can be considered within the context of phylogenetic nomenclature. The ability of phylogenetically defined names to convey hierarchical information once again demonstrates the generality and power of the phylogenetic approach to nomenclature and leaves little basis for continued opposition.

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APPENDIX

Reasons for not Extending Rank-Based Nomenclature to Additional Ranks

In concluding his article, Platnick (2012, p. 361) advocated "... extending the system of coordinated ranks with readily identifiable suffixes to other higher taxa (such as the orders, classes, and phyla of animals)." A response to this proposal is tangential to our main points, so we present it here as a postscript. Based on our arguments earlier in the text, Platnick's proposal could be implemented within the context of phylogenetic nomenclature; however, assuming that his intent was for it to be implemented in the context of rank-based nomenclature, we are not in favor of the proposal. Extending rank-signifying endings and their associated rank-based definitions to additional hierarchical levels would have several negative consequences from the perspective of nomenclatural stability and continuity. On the other hand, adopting that proposal would highlight problems with rank-based names and thus might, ironically, help to promote phylogenetic nomenclature.

One disadvantage of extending rank-based nomenclature to additional ranks is that it would extend the problems caused by that approach to names that are currently unaffected. Taxa traditionally associated with higher ranks would then become subject to the same sorts of unnecessary name changes and inappropriate applications of names that currently affect only taxa below the rank of superfamily in zoology and the rank of family (for the most part) in botany. Currently, the names of most taxa assigned to higher ranks do not have either rank-signifying endings or rank-based definitions, and therefore those names behave similarly to phylogenetically defined names. For example, the name *Squamata* is spelled the same whether the clade that it designates is ranked as an order or a superorder (de Queiroz 2012), and the name *Osteichthyes* is applied to a clade originating in the same hypothetical ancestor as under its previous application

to a paraphyletic group (e.g., Janvier 1996). If rank-based nomenclature were to be extended to higher ranks, the name of the squamatan clade would be spelled differently (it would require a different rank-signifying ending) depending on whether it was ranked as an order or a superorder, and the name of the clade of bony vertebrates would not be *Osteichthyes* despite its long-standing association with a particular hypothetical stem species and some or all of its descendants. *Osteichthyes* is traditionally ranked as a class, but the names *Mammalia*, *Aves*, *Amphibia*, and *Pisces* of Linnaeus (1758) all have priority over *Osteichthyes* at that rank despite their long-standing associations with different clades or hypothetical ancestors (though none of those names conforms to the rules of rank-based nomenclature; see next paragraph).

Another major disadvantage of extending rank-based nomenclature to the highest ranks is that this practice would lead to the replacement of an enormous number of well-known names. To cite only a very few examples, all of the following names would likely have to be replaced: *Archaea*, *Eucarya*, *Foraminifera*, *Angiospermae*, *Monocotyledonae*, *Fungi*, *Arachnida*, *Insecta*, *Teleostei*, and *Mammalia*. At the very least, the same word stems would have to be combined with new rank-signifying endings. For example, the name *Mammalia* would have to be replaced by *Mammalopsida* if the clade in question were to continue to be ranked as a class and *-opsida* were to be adopted as the standard ending for that rank. However, the full application of rank-based nomenclature would require much more radical changes. Under rank-based nomenclature, higher taxon names (except those associated with the rank of genus) not only have standard rank-signifying endings, they are also formed from the stems of the names of included genera. Therefore, the name *Mammalia*, for example, would have to be replaced by a name such as *Hominopsida* or *Elephantopsida* (whatever was the first-published name based on the name of a genus of mammals and associated with the rank of class).

A third disadvantage of extending rank-based nomenclature to the highest ranks is that it would require so many standard endings that their effectiveness in conveying taxonomic information would be seriously compromised. Currently, there are only 5 mandatory rank-signifying endings in zoology (International Commission on Zoological Nomenclature 1999: Art. 29.2) and 4 in botany (International Botanical Congress 2006: Arts. 18, 19), one of which has exceptions (Art. 18.5), although 6 others are used inconsistently (International Botanical Congress 2006: Arts. 16, 17). By contrast, over 30 years ago, systematic biologists were already finding that the 21 categories commonly used by mid-20th century workers (Simpson 1945) were insufficient to rank all of the clades that were being discovered. This situation led them to propose 1) new primary and secondary categories (e.g., McKenna 1975; Gaffney and Meylan 1988); 2) systematic ways of generating additional categories, including tertiary categories (e.g.,

supersuborder) and additional rank-modifying prefixes (e.g., giga-, micro-, pico-) (Farris 1976); 3) ways to avoid the proliferation of categories, including conventions such as phyletic sequencing (Nelson 1972) and the rankless plesion category (Patterson and Rosen 1977); and 4) the replacement of named categories with numerical labels as used in hierarchical outlines (e.g., Hennig 1969, 1981, 1983; Griffiths 1974, 1976; Løvtrup 1977).

Although commonly ignored because of taxonomic provincialism (i.e., restricting considerations to a relatively small part of the tree of life), the problem of insufficient ranks is substantial when attempting to develop comprehensive taxonomies under the principle of monophyly. For example, systematic biologists have already named at least 50 nested clades between (but not including) crown *Chordata*, traditionally ranked as a phylum, and crown *Aves*, traditionally ranked as a class (see Haaramo 2010). Even restricting considerations to extant species and thus counting only crown clades, 12 have been named. Clearly, the standard ranks, of which there are currently only 3 between phylum and class, are insufficient to rank all of the clades that systematic biologists have already named. Moreover, this example involves only a small part of phylogeny bounded traditionally by the adjacent primary ranks of phylum and class. Many more categories would be needed to cover the intervals from the origin of life to the basal split within the chordate crown clade and from the basal split within the avian crown clade to the origins of extant species. And the problem is only getting worse. Twenty-first century systematic biologists are discovering, with increasing confidence, ever more clades in all parts of phylogeny. If the names of all of those clades are to have rank-signifying endings, then an increase in the number of ranks is inevitable.

Considering the tally of at least 50 named clades between the ranks of phylum and class in the *Chordata*-to-*Aves* example, 100 ranks would seem to be a conservative estimate of the number needed to handle the phylogenetic information that will be available in the near future, if not already. Given that only 5 ranks currently have standard rank-signifying endings in zoology, some 95 additional endings would be needed to extend that convention throughout the hierarchy. Simply generating 95 new rank-specific endings that are easily distinguished and pronounceable (i.e., not just arbitrary combinations of letters) would be a challenge by itself. Even if that challenge could be met, it would remain to be seen whether users would remember the associations between all of the standard endings and their categorical ranks as well as the positions of the new ranks in the hierarchy. If not, the rank-specific endings would effectively become meaningless. Ironically, that would be yet another reason for abandoning the rank-based approach in favor of phylogenetic nomenclature. It would be far easier simply to state the rank directly (e.g., "infraphylum *Gnathostomata*"), and keep it independent of the definition and spelling of the name, rather

than using a redundant ending whose signification of a particular rank would have to be memorized and which might change repeatedly with revisions to the phylogeny.

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