



A Comparison of Traditional and Phylogenetic Nomenclature

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A comparison of traditional and phylogenetic nomenclature

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Summary

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The traditional method of biological nomenclature and the phylogenetic nomenclature method are reviewed. Under a phylogenetic nomenclature, ranks would not be required, and names of taxa would be given definitions based on descent. The phylogenetic nomenclature method, as currently proposed, would be in conflict, not only with the Linnaean hierarchy, but also with the notion of nomenclatural types. While the phylogenetic method would increase explicitness and universality regarding the application of names, it may do so at the expense of taxonomic flexibility and circumscriptional stability of a taxon represented by a given name. Suggestions are provided on how a code of nomenclature could be designed so as to accommodate both systems.

Introduction

The current methods of biological nomenclature (Ride & al., 1985; Lapage & al., 1992; Greuter & al., 1994; see also Greuter & al., 1998) are type-based and employ ranks. Recently, an alternative to these methods has been proposed (De Queiroz & Gauthier, 1990, 1992, 1994; see also Griffiths, 1973, 1974, 1976) that would provide names of taxa with precise verbal definitions based on descent. De Queiroz (1996) argued that such a change is needed because the current nomenclatural method is “anachronistic in the context of modern biology”.

The De Queiroz and Gauthier method has been gaining support in zoology and botany. In zoology, Schwenk (1994) endorsed this alternative approach, noting that the current nomenclatural method has led to false generalisations and incorrect conclusions regarding the evolution of squamate reptiles. In botany, Donoghue (Pennisi, 1996) supported the De Queiroz and Gauthier method as a “clever alternative” to the current system, which can “goof you up if you are trying study the process of evolution”; Welzen (1997) supported De Queiroz and Gauthier’s method because “it is produced using only one criterion, common descent”. In a study of the *Labiatae*, Cantino & al. (1997) concluded that the phylogenetic approach appeared to have “fewer problems” than the traditional approach.

Definition of taxon names

In traditional nomenclature names are not defined intensionally (descriptions) or extensionally (circumscriptions). Rather, names are merely supplied with a rank and a type. Despite this, many have still maintained that names of taxa are defined by character-based descriptions (De Queiroz & Gauthier, 1990, 1992, but not 1994; Sundberg & Pleijel, 1994; Lee 1996, 1998).

However, even though names are not formally defined intensionally or extensionally, taxonomists frequently use names of taxa as a “tag” for a concept of the taxon represented by the name. Hence names frequently have intensional and extensional

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connotations even if they are not formally defined as such (see Berendsohn's, 1995, "potential taxon" concept). For example, a recent paper by Soltis & al. (1996) is titled "*matK* and *rbcL* gene sequence data indicate *Saxifraga* L. (*Saxifragaceae*) is polyphyletic". Such a title assumes an extensional connotation for the name *Saxifraga* since the only definition that can be assumed under the current system for this name is "the taxon at the rank of genus inclusive of the type, *Saxifraga granulata* L."

Even the *Codes* of nomenclature occasionally treat names of taxa with intensional or extensional connotations. In the bacteriological, botanical, and zoological *Codes*, a name whose taxon has not been provided with a description is referred to as a *nomen nudum*, thus implying that a description should be attached to the name. In the botanical *Code*, Art. 18.5 states: "When the *Papilionaceae* (*Fabaceae*; type, *Faba* Mill.) are regarded as a family distinct from the remainder of the *Leguminosae*, the name *Papilionaceae* is conserved against *Leguminosae*." However, these two family names are homotypic and thus there can only be a "remainder of the *Leguminosae*" distinct from *Papilionaceae* when the names are applied intensionally or extensionally.

In phylogenetic nomenclature (De Queiroz & Gauthier, 1990, 1992, 1994) there are three different classes of phylogenetic definitions: (1) node-based, (2) stem-based, and (3) apomorphy-based. In the node-based definition, a name is defined as referring to a clade stemming from the most recent common ancestor of two or more specified organisms, species, or clades. The stem-based definition defines the name of a clade of all species sharing a more recent common ancestor with one (or more) specified organism, species, or clade than with another. The apomorphy-based definition defines the name of a clade stemming from the first ancestor to evolve a specified character. Phylogenetic definitions can be reworded to avoid reference to hypothetical ancestors; for example, a node-based definition can take the form of "the least inclusive clade that includes B and C" (Cantino & al., 1997; Lee, 1998).

De Queiroz (1992, 1995) has also shown how species names could be defined verbally by using the type specimens as a reference point for the population lineage being defined (assuming one limits species to only lineages of populations). For example, *Uvularia perfoliata* L. could be defined as "the most inclusive population level lineage of which its holotype (*Clayton 258* (BM)) is a part".

Ranks

Under traditional nomenclature an individual organism is treated as belonging to a number of taxa of subordinate ranks of which the species rank is basic. The botanical *Code* permits an indefinite number of ranks to be recognised, and names in a given rank above the genus are provided with standardised terminations. Under the bacteriological *Code* there are five primary ranks (class, order, family, genus, species) with standardised terminations above the genus level. In zoological nomenclature there are three primary ranks (family-group, genus-group, species-group) and, unlike bacteriological and botanical nomenclature, priority is co-ordinate within each group; standardised terminations are also provided for names in a given rank above genus. Thus, under all *Codes* when a taxon's rank is changed a change in its name or termination may be required.

As pointed out by Darwin (1859), assignment of rank is an arbitrary process. Despite the arbitrary nature of rank assignment Stevens (1997) has shown how "many botanists, zoologists, ethnobiologists, and other scientists use ranks and groups of 'natural' classifications, whatever their vintage, for comparative purposes, as if dif-

ferent genera (for example) were equivalent entities whose comparison might mean something in biological terms”.

In a phylogenetic nomenclature ranks would not be required and a name would not change with a change in the taxon's hierarchical placement. Thus, a name's ending expresses nothing relative to hierarchy. This can be seen in Cantino & al.'s (1997) phylogenetic arrangement of the *Labiatae*: the six principal taxa (*Teucroideae*, *Premnina*, *Lamiina*, *Viticina*, *Nepetoideae*, *Symphorematina*) do not have a standardised termination; the *-ina* termination is used at five different hierarchical levels; and *Clerodendrina* is a subordinate taxon to *Teucroideae* yet *Scutellarioideae* is subordinate to *Lamiina*. While the hierarchical positions of such names may be easily shown in the context of a phylogeny or indented classification they are lost when used outside of these contexts.

Under the phylogenetic approach, the “principle of exhaustive subsidiary taxa” (Cantino & al., 1997; see also Buck & Hall's, 1966, discussion of “Gregg's Paradox”) would be abandoned. This would require a monotypic taxon (e.g., *Leitneria floridana* Chapm.) to be given only one name. Names normally required to represent the monotype at another rank (e.g., *Leitneriaceae*) would be superfluous since their content would be the same. Again termination uniformity at a given hierarchical level would be lost. Cantino & al. (1997) endorsed this approach on the grounds that the current approach is “redundant”. However, like Lidén & Oxelman (1996), I fail to see why such redundancy – a necessity when taxa of different ranks have the same content – is disturbing.

Under a phylogenetic system of nomenclature the binomial would no longer be based on the Linnaean hierarchy and the first name would not represent the name of a genus or clade (De Queiroz & Gauthier, 1992). Thus, the binomial would effectively function as a uninomial and combinations could not be effected. Therefore, a species with the same forename (genus name) could be more closely related to species with different forenames than with other species having the same forename.

Such a change would have substantial advantages with regards to stability by effectively “freezing” the names of binomials. Such a change in what binomials represent would also solve the most fundamental difference between the three *Codes* of nomenclature, namely the assignment of priority directly to specific epithets in zoology (which thus permits secondary homonymy) versus assignment of priority to binomials by bacteriologists and botanists.

The idea of using uninomials to denote species is nothing new. Bailey (1929) made a case for such an approach at the fifth International Congress of Plant Sciences, noting: “It is a misfortune that a person cannot exercise his talents freely in the shifting of genera without interfering with the names of plants. We should have gained much in simplicity of literature, in clarity and in popular usage, if we had a mononymy or other arrangement instead of a taxonomic dionymy.” Others (e.g., Cain, 1959; Michener, 1964) have also argued for treating binomials as uninomials.

In light of the practical advantages of such an approach one is left to wonder why it has never been adopted. Besides tradition, the answer probably lies in the fact that forename uniformity within a taxon has the same advantage that termination uniformity has at a given hierarchical level – it conveys some information regarding relationship, especially when the forename represents a clade. For example the forename uniformity in *Rhynchospora amazonica* var. *guyanensis* Kük., *R. careyana* Fernald, *R. corniculata* (Lam.) A. Gray, and *R. corymbosa* (L.) Britton conveys

some indication of a close relationship. However, their basionyms or replaced synonyms (*Ephippiorhynchum longirostre* Nees, *Ceratoschoenus macrostachyus* var. *patulus* Chapm., *Schoenus corniculatus* Lam., and *Scirpus corymbosus* L.) – the only names that would be available for these taxa had Linnaeus (and all subsequent authors) treated binomials as uninomials – convey no such information. Thus, when binomials are used outside of the context of a given phylogeny or taxonomy, forename uniformity assists in determining whether one is dealing with apples and oranges or apples and apples.

De Queiroz (1997) has stated that ranks could be maintained in a phylogenetic system (without the requirement of termination or forename uniformity at a given rank) and that other devices, such as indentation or numerical prefixes, could also be used. However, most scientists use taxon names outside the context of a phylogeny or indented classification, and in none of these approaches does the name itself provide information on categorical assignment or hierarchical position. Taxonomists must therefore decide whether ranks and the information conveyed by forename and termination uniformity outweigh the cost of name changes associated with changes in rank.

Types

Early biologists adopted typological methods to aid them in simplifying the variability in nature, to establish relationships, and to assist in identification (see Stevens 1984, 1994, for reviews of typological methods in botany). Darwin (1859) endorsed the idea of using types in classification stating, “This [using types] is what we should be driven to, if we were ever to succeed in collecting all the forms in any one class which have lived throughout all time and space.”

These early “types” were frequently conceptual and when tied to the name of a taxon, in the form of a description or circumscription, they frequently created nomenclatural instability as changes in the concept of the taxon led to changes in its name. The early debate in botany on conceptual nomenclature is captured in the following exchange between Edward L. Greene, a critic of conceptual nomenclature, and Asa Gray, a supporter of it: “Nuttall ... discovered ... the genus *Nemacaulis*, deeming the species two, ... *N. denudata* and *N. foliosa*. When ... it fell in Mr. Bentham’s way to take up the genus, he seemed to find that the species was but one, [and] he displaced both the names of Nuttall and made himself the author of the species by writing *N. Nuttallii*; and this, which a fearless critic might call a bit of scientific iniquity, has been adopted and made his own by each American author who has, since Bentham’s time, handled the *Eriogoneae* ...” (Greene, 1887). “[I]t may be well to consider ... what this iniquitous proceeding is... Bentham regarded the two species as one, ... and to the combined species he gave the name of *N. Nuttallii*, obviously because neither of Nuttall’s names was properly applicable to the species as he regarded it. This mode of proceeding ... seems to be quite justified, if not actually demanded, by the rule that false names are inadmissible.” (Gray, 1887).

Greene would ultimately win this argument as conceptual approaches to nomenclature were abandoned in favour of nomenclatural types, first spelled out in detail in the Stricklandian *Code* of zoological nomenclature (Strickland & al., 1843), developed by a committee (including Darwin) of the British Association for the Advancement of Science (see Melville, 1995). In botany, nomenclatural types were first adopted in the Brittonian *Code* (Arthur & al., 1907) and its precursors

(Fairchild, 1892; Britton, 1893; Swingle, 1893; Arthur & al., 1904; see also Nicolson, 1991).

Nomenclatural types are fundamental elements in the current bacteriological (Lapage & al., 1992), botanical (Greuter & al., 1994), and zoological (Ride & al., 1985) *Codes* of nomenclature. These name-bearing types simply serve as the element to which the name of a taxon is permanently attached and, unlike conceptual types, need not represent the most typical or representative element of a taxon (see Cook, 1898, 1900; Hitchcock, 1905; Farber, 1976, for discussions of the nomenclatural type method).

It is this device of nomenclatural types that allows nomenclature to remain distinct from taxonomy (Ride, 1988, 1991). This was best summarised by Dr Luella Weresub (in Nicolson, 1977) who stated in effect: “Taxa have circumscriptions but no types while names have types but no circumscriptions.”

That is not to say that there are not elements of taxonomy in the current method of nomenclature. One example is the presence of three *Codes*, requiring one to make the taxonomic judgement: animal, plant, or bacterium? Another example is the presence of rules in the botanical *Code* specific to certain groups of organisms (e.g., fungi, algae).

Under the botanical and zoological *Codes*, names above the level of family (family group in the zoological *Code*) need not be typified, although most modern botanical classifications (e.g., Dahlgren, 1980; Cronquist, 1988; Thorne, 1992; Takhtajan, 1997) use typified names at such ranks. However, names above the family group are not covered by the zoological *Code* and are frequently not typified. (e.g., *Mammalia*, *Rodentia*). In bacteriological nomenclature, typification is required at all ranks.

In traditional nomenclature, nomenclatural types refer to two distinct entities: classification types and collection types (Farber, 1976). A classification type is the type of a name of a subordinate taxon, which serves to typify the name of a higher taxon; above the level of genus the generic name corresponding to that type will frequently serve as the basis for the name of the higher taxon (e.g., *Magnoliaceae* based on and typified by [the type of] *Magnolia* L.). A collection type is a specimen that is permanently attached to a name. In botany, an illustration may sometimes serve in lieu of a specimen.

While De Queiroz & Gauthier (1992) have suggested that typification is not incompatible with the naming of clades, others have suggested that adoption of a phylogenetic nomenclature should be accompanied with the abandonment of the type concept. Sundberg & Pleijel (1994) noted that a phylogenetic definition “embraces the whole clade, and the need for designing any subgroup as ‘typical’ has ceased to exist”. Rasnitsyn (1996) also noted that De Queiroz & Gauthier “failed to draw the self-evident conclusion from their proposal that [it] should abandon the type concept”.

De Queiroz & Gauthier (1992) provided a stem-based definition for *Lepidosauromorpha* (“*Lepidosauria* and all saurians sharing a more recent common ancestor with *Lepidosauria* than with *Archosauria*”) as an example of their approach being compatible with types, since only *Lepidosauria* is identified for inclusion in the clade defined. However, *Archosauria* is specifically excluded from the clade defined and the designation of such “antitypes” is inconsistent with the current method of typification. Node-based definitions conflict with current typification practice, since two (or more) names of subordinate taxa must be included in the definition. The

apomorphy definition also conflicts with the type system since it does not require the designation of a type.

In order for a name to be properly typified a nomenclatural “cascade” must be present that “flows” in one direction to a specimen (an ultimate type). Thus, the name *Magnoliaceae* “flows” to *Magnolia* L., thence to its type *M. virginiana* L., and finally to the type specimen of *M. virginiana* L. In De Queiroz & Gauthier’s (1992) example, *Lepidosauromorpha* is “typified” by the name *Lepidosauria* but the name *Lepidosauria* (representing a taxon between the ranks of order and class) is not typified; thus I do not regard the name *Lepidosauromorpha* to be fully typified since it has a classification type (*Lepidosauria*) but no collection (ultimate) type. A nomenclatural “cascade” that “flows” to the name upon which it is based but does not capture all the elements that must be included under it or excluded from it (*Lepidosauromorpha* “flowing” to *Lepidosauria* but not *Archosauria*) represents a definition that places additional circumscriptional limitations beyond inclusion of the type. Thus, one who uses such a defined name has less flexibility in how the taxon designated by the name can be circumscribed.

Another example of phylogenetic nomenclature not following current typification practices is the abandonment of basing names on the type of the higher taxon. For example in Cantino & al.’s (1997) phylogenetic arrangement of the *Labiatae*, neither of the names of the two principal taxa of *Lamiina* (*Scutellarioideae* and *Achrospermina*) is based on the name *Lamium* L. Cantino & al. (1997) also seem to abandon types when they use the name *Labiatae* in their phylogenetic arrangement but *Lamiaceae* for their traditional classification on the grounds that “the former name was used first to designate this clade”. I find this conclusion troubling for it indicates that in a phylogenetic nomenclature the names *Lamiaceae* and *Labiatae* would no longer be congruent (i.e., *Labiatae* \equiv *Lamiaceae*) and that the name *Lamiaceae* could remain available for definition in a sense that would be different from *Labiatae*. This example highlights a critical distinction between the two systems – homotypic synonyms will not necessarily be objective synonyms in a phylogenetic nomenclature.

Unlike Sundberg & Pleijel (1994), I believe that the development of a phylogenetic nomenclature should seek to comply with the current system of typification. I doubt that working taxonomists will be willing to accept an apomorphic definition for the name *Magnoliaceae* that does not explicitly require the inclusion of *Magnolia* L., nor do I think that they will accept verbal definitions for taxon names that place additional restrictions on the circumscription of the taxon beyond the inclusion of its type.

The trick here is to develop an ontological statement that identifies a clade without placing limits on the content beyond inclusion of the type. A “type-modified” apomorphy definition does just that. For example, the *Liliopsida* (monocots) could be defined as the clade stemming from the first ancestor of *Lilium* L. possessing a single cotyledon.

Nomenclatural instability

Under the current system of nomenclature the only reasons for changing the name of a taxon are (1) changes in taxonomic opinion relating to circumscription, rank, and categorical assignment and (2) the need to give up a nomenclature that is contrary to the rules. The following discussion involves instability as a result of the former.

One of the most common forms of nomenclatural instability is when the taxonomic placement of a nomenclatural type is significantly altered. This results in nomenclatural and application changes. For example, many taxa currently recognised as scrophs are now believed to share a more recent common ancestry with non-scrophs than with *Scrophularia* L. (Olmstead & Reeves, 1994; Olmstead & al., 1998). Thus, in order to achieve a monophyletic classification, many taxa formerly included in the *Scrophulariaceae* will have to be recognised under different family names and the *Scrophulariaceae* will have a more restricted circumscription.

In phylogenetic nomenclature stem-based and node-based definitions would require at least two taxa to be included in the definition of a taxon's name. In both definitions more than two taxa could be used; two is simply the minimum. Such subordinate taxa do not fossilise the circumscription of the taxon but serve to identify the particular clade to which the defined name applies; beyond inclusion of the subordinate taxa, the content of the clade is subject to taxonomic judgement.

The more subordinate taxa are added to the name of the higher taxon, the clearer it is as to what its name applies to. Thus it is worth asking why, if one of the primary goals of nomenclature is stability of names, haven't detailed extensional (denotative) definitions for taxon names replaced the ostensive definitions (i.e., pointing to the type; see Ghiselin, 1997) that the current *Codes* require? The answer is that the likelihood of circumscriptional shifts of the taxon represented by the name, due to altered phylogenetic concepts, increases with the number of subordinate taxa named in the definition (assuming that all such taxa have an equal likelihood of having their taxonomic placement shifted significantly). Names that are defined by inclusion of two taxa, instead of a single type, in their definition (e.g., node- and stem-based definitions) are twice as likely to be affected by circumscriptional shifts in the taxon because as defined they are inextricably linked to the inclusion of two taxa; a name defined by three subordinate taxa is thrice as likely to be affected by circumscriptional shifts, etc.

An example of potential content instability could be noted when trying to define the monocots (*Liliopsida*) phylogenetically. The monocots' circumscription is universal among all practising botanists; the monocots are also widely regarded to be a monophyletic group (Cronquist, 1988; Chase & al., 1993). In order to maintain the current circumscription of the *Liliopsida*, a stem-based definition would have to be "all organisms sharing a more recent common ancestry with *Lilium* L. than with [the sister group of *Liliopsida*]"; a node-based definition would have to be "the clade stemming from the most recent common ancestor of *Lilium* L. and [basalmost lineage of *Liliopsida*]". However, while it is generally accepted that the *Magnoliidae* are closely related to the monocots, the specific sister lineage within the *Magnoliidae* has not been identified. Data from *rbcL* led Qiu & al. (1993) to dismiss the *Nymphaeales* and *Ranunculales* as the potential sister taxon to the monocots, but they further noted: "Any other major lineage of the *Magnoliidae* could be placed as a sister group to the monocots with only an insignificant loss of parsimony."

Following Davis's (1995) results based on chloroplast DNA restriction site variation, a node-based definition of the monocots could be "the clade stemming from the most recent common ancestor of *Lilium* L. and *Gymnostachys* R. Br. [a taxon represented in the basalmost clade]". However, Duvall & al.'s (1993a-b) phylogeny based on *rbcL* sequence data does not have *Gymnostachys* in the basal-most clade within the monocots.

The positive identification of basal-most lineages can be expected to be a stubborn problem due to the use of “exemplars” (i.e., placeholder taxa representing larger lineages) and the long-branch attraction phenomenon (Felsenstein, 1978). Sytsma & Baum (1996) noted the following when using exemplars in re-examining the Chase & al. (1993) *rbcL* data set: “Reducing the number of representatives of a clade is most likely to result in that clade appearing at the base of the tree, presumably due to the attraction between long-branches of the exemplars and the outgroups.”

Thus, it is undoubtedly easier to circumscribe the taxon represented by the name *Liliopsida* (monocots) than it is to come up with a node-based or stem-based phylogenetic definition for the respective clade. Thus, there appears to be validity to Nicolson’s (1996) “sense that [a phylogenetic nomenclature] may limit what stability we currently enjoy”. Frost & Kluge (1994) identified this problem with phylogenetic definitions when they noted: “This [assigning phylogenetic definitions to taxon names] of course is just semantic trickery and is effectively, just the assertion that there *must* [emphasis theirs] be a prescriptive definition even though we can never know it precisely.”

De Queiroz (1996) correctly indicated that the current nomenclatural system has two sources of instability (relationships, categorical assignments), whereas the phylogenetic system has only one (relationships). However, the reduced sources of instability in a phylogenetic nomenclature should not be construed to mean that there will be an overall decrease in instability under a phylogenetic nomenclature. Rather, when there are changes in ideas about relationships, a phylogenetic nomenclature will probably have more content (circumscriptional) instability than the current system since node- and stem-based definitions must employ two or more taxon names (each name a potential “bomb” of instability), as opposed to one taxon name (type). This instability has been viewed either in terms of the content of clades (De Queiroz & Gauthier, 1990, 1992, 1994) or, when clades are equated with components, identity of clades (Bryant, 1996, 1997).

Lidén & Oxelman (1996) raised similar concerns regarding a phylogenetic definition for the angiosperms (*Angiospermae*), noting “the more than one type system will be disastrous, as it may force renaming of well-supported and familiar clades if our ideas of *intra*-taxon relationships change”. Lee (1996) rebutted Lidén & Oxelman, claiming they had failed to show how the traditional nomenclature differed in this respect. However, the difference is that the phylogenetic system has more “bombs” of instability.

Attempts to address this problem involve (1) not using the names of taxa with uncertain relationships in definitions (Schander & Tholleson, 1995); (2) “buffering” definitions by using additional taxa as reference points in a definition (e.g., Lee, 1996; Wyss & Meng, 1997); (3) restricting the use of a name through contingency clauses (De Queiroz & Donoghue in Cantino & al., 1997), adaptive definitions (Schander & Tholleson, 1995), and designated phylogenetic contexts (Bryant, 1996, 1997).

The first approach is certainly appropriate and doing so would obviously lessen the likelihood of shifting circumscriptions. However, it may also result in some taxa having to go unnamed, and a nomenclatural system has to accommodate the naming of all taxa.

The second approach achieves content stability within a clade by adding additional taxa to the definition. Thus, uncertainty regarding internal relationships is

resolved by explicitly citing them in the definition. For example, De Queiroz (1997) suggested that the name *Angiospermae* could be defined as “the clade stemming from the most recent common ancestor of *Ceratophyllaceae*, *Magnoliales*, *Laurales*, paleoherbs, monocots and eudicots”. However, such buffered definitions, solve the circumscriptional problem only in the context of a given phylogeny – in the context of a different phylogeny, they are likely to create greater circumscriptional instability than the current system, due to the greater number of subordinate taxa. Confusion over the application of the name can also persist if the names of the subordinate taxa cited in the definition are not themselves provided with phylogenetic definitions (Bryant, 1996); this possible source of ambiguity led Cantino & al. (1997) to use only species names (whose applications are fixed by collection types) in their phylogenetic definitions. Regardless of the wording, such definitions conflate the current distinction between taxonomy and nomenclature by using the definition of the name to place further circumscriptional restrictions on the taxon.

The third approach would limit the use of the name to a designated phylogenetic context through the use of a contingency clause (De Queiroz & Donoghue in Cantino & al., 1997), an n-taxon statement [e.g., ((A, B)C)] (Bryant, 1997) or an adaptive definition (Schander & Thollesson, 1995) that provides guidelines on how the definition is to be emended once the original phylogenetic context is altered. In each case the definition places limits on what the taxon can represent well beyond inclusion of the type, and thus again there is conflation of the current distinction between taxonomy and nomenclature. Also once a contingency clause is proven untrue or phylogenetic concepts change so as to be contrary to those in the n-taxon statement, the name would have to be abandoned or would be limited to usage only in the context of a generally unaccepted phylogenetic context, such as Bryant’s (1997) assertion (based on Gardiner, 1993) that use of the name *Haemothermia* is to be limited to the unorthodox phylogenetic context that *Aves* and *Mammalia* are extant sister taxa.

All of these different methods of limiting the content of a taxon through the definition of its name, besides blurring the current distinctions between nomenclature and taxonomy, may be trying to reconcile issues that are irreconcilable – the nominalism of phylogenetic nomenclature and the need for classification systems to be pragmatic (and hence essentialistic). Trying to accommodate both can get rather onerous, as seen in Cantino & al.’s (1997) “cumbersome” adaptive definition for *Paradoxa* as “either the most recent common ancestor of *Adoxa*, *Tetradoxa*, and *Sinadoxia* and all of its descendants, if *Sinadoxia* is more closely related to *Adoxa* and/or *Tetradoxa* than it is to anything else, or, if the sister group of *Sinadoxia* is not *Adoxa* and/or *Tetradoxa*, the most recent common ancestor of *Adoxa* and *Tetradoxa* and all of its descendants”.

Cantino & al. (1997) defended such a definition on the grounds that it is explicit, and De Queiroz (1997) stated that such “complicated definitions are ... simply the price that must be paid to make intended meanings of taxon names unambiguous in the context of uncertain relationships”. However, this explicitness is the result of the definition of the name placing considerable restrictions on the circumscription of the taxon beyond inclusion of its type. If such definitions become accepted the currently regarded distinction between taxonomy and nomenclature will be lost.

Stability could of course be maintained by simply changing the definition as needed. A new definition that would maintain the current application could be pro-

posed for conservation over the old phylogenetic definition, just like the current botanical *Code* (Art. 14.9) allows names to be conserved with a different type than that designated by the original author. However, such an approach would work only when there was a change in the identity of the basal-most or sister clades; it is less useful when there is simply ambiguity regarding the identity of these groups. Also, determining what would constitute a “significant change” in content would be difficult to define and codify.

All of these concerns regarding content stability apply to the node- and stem-based definitions. The apomorphy-based definition does not have these problems since it need not identify two or more subordinate taxon names in its definition. However, the apomorphy-based definition so far has proven to be the least popular of the three phylogenetic definitions. It has been viewed as the “weakest option” (Schander & Tholleson, 1995), which is best “avoided” (Bryant, 1994; Schander & Tholleson, 1995; Cantino & al., 1997) due to potential homoplasy of the cited apomorphy resulting in the definition being ambiguous.

The potential problems of content stability and blurring of the current distinctions between nomenclature and taxonomy associated with the other two phylogenetic definitions justify a re-evaluation of the apomorphy-based definition. The concerns of homoplasy could be addressed through the citation of a subordinate taxon (type). Such a definition is explicit, citing a type and an apomorphy, without placing any circumscriptional limits on the taxon beyond inclusion of the type. Potential ambiguity associated with the use of apomorphy definitions can also be lessened by citing an apomorphy that is particularly complex such as that used by Cantino & al. (1997) in their apomorphy definition of *Symphorematina*.

The need for a Code of phylogenetic nomenclature

Despite the employment of phylogenetic nomenclature by many workers, no *Code* of phylogenetic nomenclature exists. Thus, many nitty-gritty nomenclatural issues remain unresolved. For example, how is one to handle names that were established under the existing system but now in use in the phylogenetic system? Cantino & al. (1997) employed the name *Paradoxa* for a clade of vascular plants. However, the name *Paradoxa* Mattir. is also in current use for a genus of fungi (Greuter & al., 1993). Under the existing nomenclatural system *Paradoxa* Mattir. has priority over “*Paradoxa* Cantino & al.” But under the phylogenetic system “*Paradoxa* Cantino & al.” would seem to have priority since it was first provided with a phylogenetic definition, even though its authors applied the name to a taxon not including *Paradoxa monospora* Mattir., the type of *Paradoxa* Mattir. It was obviously not the intent of Cantino & al. (1997) to displace the current application of *Paradoxa*, but in nomenclature it matters not what one intends to do but rather what one actually does.

Kron (1997) suggested that the currently used Latin endings be replaced by the suffix “-ina” when designating any clade name, irrespective of its hierarchical position. Such a universal termination would signal a new system of nomenclature and would prevent problems caused by adopting under a phylogenetic nomenclature names established under the existing system of nomenclature. However, it limits the number of names that can be derived from a generic stem to one. Thus, in the *Labiales*, only one name could be based on the genus *Lamium*, *Lamiina*. Kron (1997) failed to remove all of the Latin ending (-ales) of *Ericales* in forming *Ericalina*, which explains her simultaneous use of *Ericalina* and *Ericina*.

Also unclear is how to assign priority to species names. If names are provided with verbal definitions as outlined by De Queiroz (1992, 1995), then presumably priority would rest on the date of publication of the definition. This would require the extraordinary effort of developing new indices (equivalent to *Index kewensis*) listing first definitions.

If species are not provided with a verbal definition then assignment of priority is uncertain. Current usage would obviously have to play a role, but how would one choose between multiple names that may be in use due to current disagreement regarding a taxon's taxonomic position? For example, under the phylogenetic system, would the correct name for the tomato be *Solanum lycopersicum* L. or *Lycopersicon esculentum* Mill.? *L. esculentum* is preferred in agricultural literature but the use of *S. lycopersicum* has been advocated by those (Spooner & al., 1993; Bohs & Olmstead, 1997; Olmstead & Palmer, 1997) who seek to make the genus *Solanum* L. monophyletic by sinking *Lycopersicon* into it. However, under a phylogenetic nomenclature there is no splitting or lumping, and the names *Solanum* and *Lycopersicon* could both be used, presumably *Solanum* for the more inclusive clade corresponding to the current circumscription of the genus *Solanum* s. l. and *Lycopersicon* for the clade of tomato species nested within *Solanum*. Should *S. lycopersicum* be used in order to establish forename uniformity in *Solanum* or should *L. esculentum* be used so as to indicate the taxon's inclusion in the smaller clade of tomatoes? Reasonable arguments can be made for either approach, and without a *Code* of phylogenetic nomenclature the choice remains arbitrary.

Guidelines will also be needed for author citation of taxon names. Would those who validly published names under the existing system still be cited as the authors of the name or would they be replaced by the authors who first provided a phylogenetic definition? Citing the authorship of *Labiatae* as *Labiatae* Cantino & al. instead of *Labiatae* Juss. could be viewed as historically inaccurate, but is no more so than citing Linnaeus as the author of *Limosella* when the name was first published by Lindern in 1728 (see Pennell, 1935). Shifting authorships are a logical consequence when there is a change in the starting date of valid publication, but guidelines on author citation are needed so that the process is uniform.

These examples express the need for the development of a *Code* of phylogenetic nomenclature. Before any further attempts are made at adopting a phylogenetic nomenclature, it is suggested that such a *Code* be drafted.

Taxonomic freedom and the codification of monophyly

De Queiroz & Gauthier (1992) noted: "If the use of phylogenetic definitions becomes predominant ... paraphyly and polyphyly will become superfluous except in a historical context." Welzen (1997) noted that under the phylogenetic method "paraphyletic [groups] will be made to include the once separated monophyletic taxa". Are we inching towards the codification of monophyly?

While the cladistic approach (i.e., recognition of only monophyletic taxa) "[t]o a large degree, has now become widely accepted within the systematic community" (Hoch & Raven, 1995) there are those who continue to recognise paraphyletic taxa (Brummitt, 1996a-b, 1997; Mayr, 1997; Sosef, 1997; Wilbur, 1997). Knox (1998) termed paraphyletic taxa as "inescapable in a phylogenetic classification" and Ghiselin (1997) regarded systems with paraphyletic taxa "as simpler, better in accord with vernacular language, and more conveniently expressive of features deemed

important (such as major changes in organization)". The De Queiroz and Gauthier approach has the advantage that non-monophyletic groups can be recognised, but not as a result of mistakes about phylogeny, since their recognition would have to be explicit in the definition of the name.

For example, based on Chase & al. (1993), the paraphyletic *Magnoliopsida* (dicots) could be defined as "the most recent common ancestor of *Ceratophyllum* L., *Magnolia* L., and *Aster* L. and all of its descendants except *Liliopsida* (monocots)". Since the name has been applied this way for so long, perhaps it is best to define it as such. This would not mean that a paraphyletic taxon would have to be recognised – those who choose only to recognise monophyletic taxa simply would not use the name, except in a historical context. However, it would be much more difficult, as well as pointless, to craft phylogenetic definitions for highly artificial groups currently maintained for convenience' sake, such as *Deuteromycota* (a group inevitably due to become obsolescent anyway due to the increasing use of phylogenetic classification and the linking of anamorphs to their respective teleomorphs through molecular markers; see Bruns & al., 1991, and Vilgalys & Hibbett, 1993).

It is not the goal of this paper to defend the recognition of non-monophyletic taxa. However, regarding the question of "Must one recognise only monophyletic taxa?" the answer from anyone who respects taxonomic freedom has to be: no.

The current botanical Code: too complex?

Welzen (1997) would welcome a new nomenclature because he believes the present botanical *Code* is too complex. Any complexity in the botanical *Code* can be explained by the fact that it has been around a long time, and not "because it took shape much too late, when all sorts of problems had already been caused" (Welzen, 1997). Candolle's (1867) *Laws* of botanical nomenclature were only 19 pages long; the *Rochester Code* of botanical nomenclature (Fairchild, 1892) was a mere 3 pages long! Thus, early botanical *Codes* were not complex at all. But with age comes experience with situations not previously addressed (see Castroviejo & Brummitt, 1996, for an example involving the current botanical *Code*). Such situations may result in two logical conclusions from which only one must be chosen.

For example in botany, should combinations based on illegitimate later homonyms also be regarded as illegitimate or should they be viewed as legitimate *nomina nova*? Reasonable arguments can be made for both approaches. The current botanical *Code* directs that such names may be regarded as legitimate *nomina nova* (Art. 68.3).

Thus, the current botanical *Code* is more complex than its predecessors because it addresses numerous situations not addressed in the earlier botanical codes; therefore, users of the current botanical *Code* are much less likely to encounter situations that are not covered – a big advantage. Were a phylogenetic *Code* of nomenclature developed, I would also expect it to become increasingly complex with age.

Biological theory and biological nomenclature

Perhaps the most controversial aspect of phylogenetic nomenclature is that it links nomenclature with biological theory, by defining the name by means of a verbal statement. While De Queiroz & Gauthier (1994) claim that the current system is "non-evolutionary", I would argue that, except for its requirement of using the Linnaean hierarchy, it is simply silent on matters of biological theory (see also Lidén &

al., 1997). The current system of nomenclature has been able to survive revolutions in biological theory because theory-laden statements have not been attached to taxon names. Thus, the current system has supported artificial, natural, evolutionary, phenetic, and cladistic classifications. Would these shifts have been easier had detailed definitions laden with theory been attached to the names of organisms? Certainly not. Nor should it be assumed that there will not be another theoretical shift some time in the future.

Furthermore, it must be recognised that there is no complete agreement in the taxonomic community on the rule that the taxonomy of organisms should be based solely on common descent. Accepting the theory of evolution and accepting that the taxonomy of organisms be based solely on common descent are two very different issues, and not everyone accepts the latter. There are those who prefer to classify organisms based on descent and degree of similarity; such approaches have been referred to as “phyletics” (Stuessy, 1990, 1997), “evolutionary” or “Darwinian classification” (Mayr, 1997), and “phylistics” (Rasnitsyn, 1996). Knox (1998) advocated such a dualistic (descent, modification) approach to classification, terming cladistic classification an “oxymoron”. De Queiroz & Gauthier (1990) criticised traditional nomenclature on the grounds that “existing taxonomic practices are taken for granted and the evolutionary world view is overlaid upon them as a superficial interpretation”. Yet under a phylogenetic nomenclature those attempting to do phyletic or phenetic classification would be faced with a similar problem.

Conclusion

In closing, I will state that, despite the concerns raised, I like the idea of developing precise verbal definitions for taxon names. As I am going to argue, such definitions are a logical step in the separation of epistemological statements (e.g., descriptions) from the names of organisms. In pre-Linnaean times, through the use of polynomials, plant names and taxon definitions were the same thing; thus, the name itself was an epistemological statement. The first fracture occurred with Linnaean binomials, but conceptual nomenclature still allowed names to be defined either intensionally (character-based descriptions) or extensionally (circumscriptions). This was later broken with the nomenclatural type method which assigned descriptions and circumscriptions to taxa and types to names. However, confusion between a taxon and its name has persisted because no precise verbal statement is provided for the name while verbal descriptions are currently provided for the taxon. Attaching ontological statements to the names of taxa solves this problem.

Where I break with the phylogenetic nomenclators is in their willingness to allow names to be defined by the inclusion of multiple subordinate taxa in the named taxon. Such definitions effectively remove one source of entanglement between taxonomy and nomenclature (lack of verbal statements for names) but produce another (the name’s definition placing circumscriptional restrictions on the taxon beyond inclusion of the type). For example, Cantino & al. (1997) define the name *Labiatae* using 15 subordinate taxa. All subsequent circumscriptions of the taxon *Labiatae* would have to include all 15 subordinate taxa – any circumscription not inclusive of the 15 listed taxa would result in a change of name.

The traditional and phylogenetic methods of nomenclature represent a real choice that taxonomists must make between flexibility (as provided by the current method’s attaching only a single entity – the nomenclatural type – to the name) and explicit-

ness (as provided by node- and stem-based definitions' anchoring the name on multiple entities). This is not the first time taxonomists have had to address the issue of flexibility versus explicitness. In the 1700s and 1800s, the debate over the nomenclatural type and circumscriptional methods of nomenclature was largely one of flexibility (nomenclatural type method) versus explicitness (circumscription method). Taxonomists ended up choosing flexibility over explicitness with the acceptance of nomenclatural types.

Flexibility can be maintained in a phylogenetic nomenclature if definitions remain open to emendation (i.e., are not permanently attached to the name of the taxon). This would allow intensional and extensional connotations frequently associated with a name to be taken into consideration in the application of the name. Bryant (1997), who regarded the emendation of definitions as "neither appropriate nor practical", conceded that it may be necessary in some cases to "preserve historical usage". De Queiroz & Gauthier (1990) advised that "due consideration should be given to diverse criteria, including implicit associations with ancestors, current and historical usage, alternative names, priority, ... and utility to the greatest number of biologists". The best way to accommodate such practical considerations is to allow "the practical systematist [to be] victorious over the scholastic theoretician" (Stafleu, 1971) and permit definitions (particularly those involving the names of more than one subordinate taxon) to remain open for emendation. Doing this alleviates the system from having to accommodate both the nominalistic aspects of phylogenetic nomenclature and the need for practicality in a classification system.

For example, had verbal definitions been required during the time of Engler (1887-1889) he might have chosen to include *Acorus* as a subordinate taxon in the definition of the name *Araceae*. Molecular evidence now indicates *Acorus* to be basal to the rest of the extant monocots (Duvall & al., 1993a-b; Davis, 1995), and any definition of the name *Araceae* using *Arum* and *Acorus* as subordinate taxa would force application of the name *Araceae* to the monocots as a whole; hence the name would be a synonym of *Liliopsida*. Emending the definition so as to exclude *Acorus* from *Araceae* would prevent the radical shift in circumscription.

Using the various modified definitions discussed earlier would oftentimes prevent the need to emend definitions, but would not eliminate it. Only through the option of emendation can it be guaranteed that a name's long-standing historical usage can be preserved.

Apomorphy-based definitions do not have to use multiple subordinate taxa; therefore they allow more flexibility regarding the circumscription of the taxon represented by the defined name. Citing a nomenclatural type, as well as an apomorphy, brings this definition into conformity with the type concept and protects against possible homoplasy and its associated effects on the application of the name.

I view the issues associated with rank as less problematic. Allowing taxonomists to use names without association to rank will require changes in the current *Codes* of nomenclature, but I believe the need of the phylogenetic nomenclators could be accommodated on this point without precluding the recognition of ranks by those who still choose to construct traditional classification systems. Such changes would effectively allow names to be used outside the context of a formal rank. The "family *Magnoliaceae*" could be changed to the "clade *Magnoliaceae*". These changes would have to be accompanied by the development of a special *Code* of phylogenetic nomenclature that would govern the use of such names.

Such a change would address concerns raised by some that the Linnaean hierarchy is incompatible with a strictly phylogenetic (i.e., monophyletic) approach to taxonomy (Meacham & Duncan, 1987; Minelli, 1995; Brummitt, 1996a-b, 1997; Sosef, 1997; Knox, 1998; see Lidén, 1997; Freudenstein, 1998 for a contrary viewpoint). Fensome & Skog (1997) noted: “It has generally been recognized that the *Code* should deal only with nomenclature, not with taxonomy, except perhaps in that it assumes a hierarchical system of names (family, genus, etc.).” Removing the requirement of rank designation eliminates this assumption.

In the ongoing debate on this issue it must be remembered that any code of nomenclature is a product of compromise (Fernald, 1929). However, in such situations it is worth remembering Nicolson’s (1991) observations on past compromises perhaps resulting in the “the worst of both worlds: a complex and constantly changing Code (trying to maintain past usage) and constant conservations (to set aside the rules that, despite complexity, are not maintaining the past)”. I believe the best of both worlds between traditional nomenclature and phylogenetic nomenclature is a system where names are provided with verbal definitions (an aspect of phylogenetic nomenclature) but without mandatory restrictions on circumscription beyond inclusion of the type (an aspect of traditional nomenclature). Flexibility needs to be maintained regarding the current differences in various conventions (e.g., recognition of formal ranks, termination uniformity, forename uniformity).

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