Point of View

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Naming Species in Phylogenetic Nomenclature

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Phylogenetic nomenclature (PN) is a rank-free system of biological nomenclature, designed to name species and clades (de Queiroz and Gauthier, 1990, 1992, 1994; Cantino and de Queiroz, 2006). In this system, the categories *species* and *clade* are not taxonomic ranks but different kinds of biological entities. A species is an individuated segment of a metapopulation-level lineage. A clade is a complete system of ancestry and descent, consisting of an ancestor (such as a species, population, or organism) and all its descendants (de Queiroz, 1998, 1999, 2005a, 2005b, 2005c; Cantino and de Queiroz, 2006). Both are historical entities that compose the Tree of Life, viewed as concrete individuals rather than abstract classes in the ontological sense (but see, e.g., Lee and Wolsan [2002] for a notion of the ontological distinction between synchronic individuals and diachronic historical entities). As existing independently of human perception rather than being human constructs, species and clades are discovered or inferred rather than constructed by taxonomists (de Queiroz and Gauthier, 1990, 1992, 1994; Frost and Etheridge, 1993; Cantino et al., 1999a; Brochu and Sumrall, 2001; de Queiroz and Cantino, 2001a; Bryant and Cantino, 2002; Wolsan, 2003; Cantino and de Queiroz, 2006). Conceptualized as such, species and clades are, from a theoretical perspective, among the most significant biological entities above the organism level of organization (de Queiroz, 1997; Cantino and de Queiroz, 2006).

Problems related to species names have plagued PN since its beginnings, causing the naming of species to have become probably the most controversial aspect of the new system. The controversy around species names has arisen not only because of practical problems concerned with the adequate format for species names, but also because some practitioners of PN have questioned the existence of species or denied any role of species in this system (Pleijel, 1998, 1999, 2001; Mishler, 1999, 2003; Pleijel and Rouse, 2000a, 2000b, 2003; Mishler and Fisher, 2004; Fisher, 2006). Despite doubts about the objective reality of the species category, also repeatedly raised outside of PN (e.g., Burma, 1954; Buck and Hull, 1966; Loevtrup, 1987; Ereshefsky, 2002; Rapini, 2004), there is widespread consensus among biologists that species are important for organizing knowledge of biodiversity (Gaston, 2000; Bertrand et al., 2006). This is also reflected by the use of species as basic referents in ecology as well as evolutionary and conservation biology.

Under codes of traditional rank-based nomenclature (TN), the zoological code (ICZN; International Commission on Zoological Nomenclature, 1999), the botanical code (ICBN; Greuter et al., 2000), and the bacteriological code (ICNB; Lapage et al., 1992), but not the viral code (Mayo and Horzinek, 1998), all species names are composed of a combination of two names, the first being a generic name and the second being a specific name (specific epithet). The application of this combination to species names dates back to Carl Linnaeus's *Philosophia Botanica* (1751) and the combination itself is termed a binomen or binomial. To avoid terminological ambiguity, in this paper I will refer to this combination as the *Linnaean binomen*, using a *binomen* to refer to any species name that is composed of two separate words.

Although alternative methods for naming species had been proposed already before the advent of PN (e.g., Berio, 1953; Cain, 1959a; Michener, 1963, 1964; Lanham, 1965; Amadon, 1966; Griffiths, 1976), none have gained acceptance. Although the dead weight of tradition and familiarity is undoubtedly important and likely decisive, it is not the only reason why Linnaean binominal (binary) nomenclature (LBN) continues to be kept in use. Certainly, LBN offers a number of advantages. Probably the most important of these is that the inclusion of a genus name within a species name helps avoiding homonymy. This is particularly relevant when taking into account the large number of species in nature and the fact that many species have been named using identical specific epithets. Another practical benefit of LBN is that the binominal form distinguishes the names of species from the names of other taxa, which usually consist of either one word (supraspecific taxa) or three words (infraspecific taxa). Furthermore, LBN enhances the retrieval of information on genus-level taxa because the name of a genus is part of the names of all species assigned to that genus.

It is, however, also true that LBN has introduced a number of problems into biological nomenclature

(Bailey, 1929; Cain, 1959a, 1959b; Michener, 1963; Ereshefsky, 1994, 1999, 2001a, 2001b; Cantino et al., 1999b; Lee, 2002; Pleijel and Rouse, 2003; and others). The fact that the Linnaean binomen conveys information about supposed supraspecific (genus-level) relationships may be considered an advantage (and indeed often is taken as such), but this property of LBN also causes the inherent instability of species names and is a significant destabilizing factor in biological nomenclature. As a genus name is part of a species name, every change in generic assignment of a species necessitates changes in the name of that species. At least the generic part of the species name must be replaced, but the specific epithet sometimes must be altered as well, either due to secondary homonymy under the new generic combination or because its ending no longer agrees in gender with the new generic name in the instance of adjectival or participial epithets. Furthermore, users of LBN who disagree on the generic placement of a species have to employ different Linnaean binomina to refer to that species, so that effectively there are species with multiple names in use. And that is not all. The Linnaean binomen is also unable to accommodate lack of knowledge about the genus-level relationships of a species. As a result, a user of LBN has to assign a species to a genus even if adequate evidence is lacking to accomplish that assignment nonarbitrarily.

From the perspective of phylogenetic taxonomy, there are also other problems with the requirement that species be assigned to a genus in order to be named. An ancestor, whether or not it can be identified as such, is not itself part of any monophyletic taxon less inclusive than that originating with that ancestor, so that the ancestral species of a monophyletic taxon that contains more than one genus taxon cannot be referred to any descendant genus, or assigned to its own (monotypic) genus, without creating a nonmonophyletic genus (de Queiroz and Gauthier, 1992). The referral of a species to a paraphyletic or polyphyletic genus is also likely to happen in situations in which phylogenetic relationships among species are uncertain (Cantino, 1998; Cantino et al., 1999a). Creating monotypic genera to accommodate species of uncertain relationships is an alternative in such situations (Cantino et al., 1997, 1999a, 1999b). This alternative, however, is also problematic because monotypic genera introduce redundancy into classification in that the name of a monotypic genus refers to the same group of organisms as does the name of the single included species (de Queiroz and Gauthier, 1992; Cantino et al., 1997; Lee and Caldwell, 1998; Pleijel and Rouse, 2003; Laurin, 2005a).

Even though there are compelling reasons for decoupling species names from genus names, such a change in species nomenclature might require conversion of existing binomina to a different format and would also involve potential problems in communication and information retrieval on species taxa. The abandonment of the binominal form for species names is additionally discouraged by the increasing realization that an extended period of coexistence between PN and TN is unavoidable. It is therefore not surprising that proposals or suggestions have been made by some proponents of PN (Lee, 2002; Fisher and Mishler, 2004; Laurin, 2005a) to restrict the application of the code of PN (PhyloCode) to clade names and retain LBN for species names. But what precludes LBN from being integrated with clade names into a coherent system of PN is not the binominal form of species names itself, but rather the fact that LBN effectively makes the ranked category of genus mandatory, whereas PN requires the abandonment of mandatory categorical ranks (de Queiroz and Gauthier, 1992), albeit not categorical ranks as such (de Queiroz, 1997, 2005d, 2006; de Queiroz and Cantino, 2001b; Laurin, 2005a; Cantino and de Queiroz, 2006).

Altogether, 19 methods (Appendix 1: methods A to S) have been proposed to name species or least-inclusive taxonomic units sensu Pleijel and Rouse (2000a, 2000b; i.e., smallest hypothesized clades, which are by others viewed as species) in the context of PN. All these methods solve the problem stemming from the convention of mandatory categorical ranks and therefore each would enable integration of species names with clade names into a coherent system. One of these methods, method S, has most recently attracted the greatest support among proponents of PN and has been reported to be in the process of being implemented into the forthcoming version of the PhyloCode (Laurin and Cantino, 2007). This method has two practical advantages over the previously proposed methods A to R. First, it would not require conversion of existing species names. Second, it would enable the use of the same name in the contexts of PN and TN for each species at any time. Method S offers these benefits, however, at the cost of introducing most problems associated with LBN into PN. Probably the most disfavoring of these is the fact that method S would retain the inherent instability of species names. The usefulness of this method is therefore debatable. Here, I propose a similar method (Appendix 1: method T), which would preserve most advantages of method S while stabilizing species names.

The utility of each of methods A to S has been discussed or commented upon, either directly or indirectly and either favorably or critically, in one or more publications (Michener, 1963, 1964; Amadon, 1966; de Queiroz and Gauthier, 1992; Schander and Thollesson, 1995; Lidén et al., 1997; McKenna and Bell, 1997; Cantino, 1998; Moore, 1998, 2003; Schander, 1998; Cantino et al., 1999b; Ereshefsky, 1999, 2001a, 2001b; Härlin, 1999, 2001; Pleijel, 1999; Benton, 2000; Artois, 2001; Dyke, 2002; Lumbsch, 2002; Janovec et al., 2003; Nixon and Carpenter, 2003; Schuh, 2003; Dayrat, 2004, 2005; Dayrat et al., 2004; Laurin and Cantino, 2004, 2007; Stevenson, 2004; Dayrat and Gosliner, 2005; Laurin, 2005a, 2005b; Pfeil and Crisp, 2005; Stevens, 2006; Wolsan, 2007). Clearly, each naming method has advantages and disadvantages. What is seen as an advantage by some, however, can be (and indeed sometimes is) viewed as a disadvantage by others. In addition, one's preference for one method over another is usually influenced by subjective evaluation of the relative importance of the pros and cons for each. All this precludes objective evaluation of the merits of

the competing methods and is probably a major reason for the long-standing lack of agreement as to which of the methods is most appropriate for naming species in PN.

Desirable Features of Species Names

A comparative evaluation of methods A to T in this paper is based on eight equally weighted features considered desirable for species names. These are (1) uniqueness, (2) stability, (3) distinguishability from clade names, (4) consistency of form among species names, (5) consistency of form with the Linnaean binomen, (6) consistency of species names between PN and TN, (7) ease of pronunciation, brevity, and simplicity of form, and (8) no need for conversion. This approach is not free of subjectivity, as probably none could be. Not all features discussed by other authors are included and not all of the included features have unanimously been considered advantageous. The selected features, however, are among those most frequently regarded as both desirable and important. Other desirable features discussed by others are either satisfactorily shared by all compared methods or their merit is contained or emphasized in a selected feature, or they have largely been considered less important.

Uniqueness

Even though the critical property of a taxon name is that the name can be unambiguously referred to the taxon rather than that the name is unique, uniqueness is the simplest and surest way to make taxon names unambiguous. Nonunique species names could be made unambiguous by citing supplementary information with the name, such as a reference to the authorship of the name (author address) or the original publication of the name (bibliographic address), a reference to a taxon or group of taxa containing or being hypothesized to contain the species (taxonomic address), or a registration number, so that the combination of the name and supplementary information would be unique. This approach, however, does not guarantee that a convention to cite nonunique names in association with supplementary information would be followed by all users of those names, nor does it ensure the lack of ambiguity in instances where a nonunique name alone would be cited. Indeed, the only certain way to convey the information necessary to make a name unambiguous is to include that information in the name itself (Cantino et al., 1999b). Unique names are therefore more desirable than nonunique names, even if the latter would become unique when combined with supplementary information.

Stability

The principal objective of biological nomenclature is enabling effective communication among users of taxon names. Species names that remain stable over time increase the effectiveness of communication and therefore are more desirable than those susceptible to subsequent changes.

Distinguishability from Clade Names

As species and clades are different kinds of biological entities (e.g., Cantino and de Queiroz, 2006), different formats for species names as opposed to clade names are justified. The different formats have the advantage over a single common format for all taxa in that they convey ontological information about species versus clade taxa. A further practical benefit of the different formats is that they prevent the occurrence of homonymy between a species name and a clade name, thereby increasing the number of available names for both species and clades. The different formats would also help preserving continuity of converted species and clade names with the name from which they have been converted when a specific epithet and a genus or subgenus name are spelled the same (e.g., the epithet *martes* and the genus name *Martes*).

Consistency of Form among Species Names

A single common format for all species names has the advantage of consistency and simplicity over different formats among species names (Cantino et al., 1999b; Artois, 2001).

Consistency of Form with the Linnaean Binomen

In developing the PhyloCode, much thought has been given to minimizing disruption of the existing nomenclature (Cantino and de Queiroz, 2006) and this goal has often been considered a priority when discussing issues concerning the naming of species in PN (e.g., Cantino et al., 1999b; Lumbsch, 2002). Species names consistent in form with the Linnaean binomen would have the greatest potential to achieve this goal. In view of the nearly universal and long-standing tradition of using LBN by biologists, and a deep entrenchment of Linnaean binomina in society (through their use in legislation, museum labels and catalogues, schoolbooks, popular books, field guides, and others), species names indistinguishable in appearance from Linnaean binomina would likely have the greatest potential to be universally accepted and adopted, both by biologists and throughout society. Only by using this format could a species name accepted under the PhyloCode be also considered valid under the ICZN or correct under the ICBN or ICNB, thereby reducing redundancy and ambiguity introduced into species nomenclature by the coexistence of different names for a single species. And last but not least, a name composed of two words is less likely to cause homonymy than one consisting of a single word. It is difficult to underestimate the importance of this practical benefit of a binomen when one realizes that millions of species (living and extinct) need a name that is also different from any clade name.

Despite the sound advantages, the consistency of form with the Linnaean binomen emerges as the most controversial out of the eight features regarded in this paper as desirable for species names. This is because three drawbacks have been ascribed to this feature: (1) that a species

might have two different names that are indistinguishable in form, one of them accepted under the PhyloCode and the other one considered valid or correct under the applicable code of TN (Cantino et al., 1999b); (2) that the name of a genus-level taxon would be required to name a species, making the ranked category of genus as mandatory as it is in TN (Dayrat et al., 2004; Dayrat and Gosliner, 2005); and (3) that the initial word of a binomen might be misinterpreted as implying a phylogenetic relationship (Michener, 1963, 1964; de Queiroz and Gauthier, 1992; Schander and Thollesson, 1995; Lidén et al., 1997; Schander, 1998; Cantino et al., 1999b; Artois, 2001; Pennisi, 2001; Janovec et al., 2003; Dayrat et al., 2004; Laurin and Cantino, 2004; Dayrat and Gosliner, 2005).

Even though the perceived drawbacks have potential to add to confusion in TN, none of them need pose a problem to PN. First, referring to drawback 1, species names could be registered in an Internet-accessible database (like clade names; see, e.g., Cantino and de Queiroz, 2006), which would provide an easy means of identifying all names accepted under this code. Second, referring to drawback 2, the initial part of a binomen, even if spelled the same as the name of an existing genus or subgenus, would not need to be regarded as a genus or subgenus name in PN. The PhyloCode is explicit in stating that PN is independent of categorical ranks and that any associations of a name with categorical ranks in TN have no bearing on the application of that name in PN (Cantino and de Queiroz, 2006). Third, referring to drawback 3, the PhyloCode could state explicitly that the initial word in all binomina accepted under this code does not indicate any relationship but is only a part of the species names, thus clearing up any ambiguity on this matter, at least within PN.

Even outside of PN, the potential for the envisioned confusion is rather not as strong as it may seem at first glance. First, referring to drawback 1, a plethora of different names for a single species, though certainly disadvantageous, is nothing unusual in TN. Perhaps most species names have their synonyms and many species continue to be referred to by different names (generic combinations) in different publications. Users of TN have learned to cope with this problem (e.g., by employing synonymy lists). Second, referring to drawback 2, probably the only negative consequence of significance for the genus-level nomenclature of TN, resulting from the use of a binominal form to name species in PN, would be that the initial word of a binomen established under the PhyloCode could be interpreted in TN as the name of a new monotypic and thus redundant genus if that initial word were different from the name of any existing genus-level taxon. Monotypic genera, however, are quite common and their redundancy, though evident, is not perceived as a problem by many users of TN (see, e.g., Lidén and Oxelman, 1996; Moore, 1998). Third, referring to drawback 3, many practitioners of TN are well aware of the fact that the initial word of a Linnaean binomen does not necessarily yield a reliable indication of the affinities of the species referred to by that binomen. Whereas phylogenetic interrelationships among living species have great potential to be ultimately elucidated, this is rather not the case for many extinct species that are known only from fragmentary and fossilized remains. The persisting uncertainty and multiplicity of views on the phylogenetic placement of many species, not only extinct but also living, is well illustrated by the use (both in the past and at present) of different generic combinations to refer to such a species, which urges caution in inferring phylogenetic information from the initial word of a binomen. Moreover, there are Linnaean binomina in use in which the initial word usually does not even pretend to convey any phylogenetic information. A classic example is Linnaean binomina for ichnotaxa based on the fossilized work of organisms, such as fossilized trails, tracks, or burrows (e.g., Pickerill, 1994; Bromley, 1996; Pickerill and Keighley, 1997), which are governed by the ICZN (International Commission on Zoological Nomenclature, 1999: Article 1.2.1). Other prominent examples include Linnaean binomina for ootaxa based on fossil eggshells (e.g., Mikhailov et al., 1996; Hirsch et al., 1997; Bibi et al., 2006), as well as Linnaean binomina for morphotaxa based on plant fossils and form taxa based on asexual forms of certain pleomorphic fungi, the last two categories of taxa governed by the ICBN (Greuter et al., 2000: Articles 1.2 and 59). There are even identically spelled genus names that are referred to different taxa under different codes of TN. For example, the name *Prunella* refers to a genus of birds under the ICZN but is applied to a genus of flowering plants under the ICBN.

I agree with Lumbsch (2002) and others that the advantages of species names that are congruent in form with the Linnaean binomen outweigh the disadvantages, especially that the disadvantages would not need to affect PN and even in the context of TN, their potential for confusion has been rather overemphasized.

Consistency of Species Names between PN and TN

Using the same name in reference to the same species under the PhyloCode and the applicable code of TN would maximize continuity in species names between the codes and also would minimize the disadvantage to the scientific community and other users of species names resulting from the parallel operation of PN and TN.

Ease of Pronunciation, Brevity, and Simplicity of Form

The ease of pronunciation, brevity, and simplicity of form are useful and convenient properties of a name that aid in its memorization and improve communication among users of the name. Names that are difficult to remember or excessively long or complex in form are not only awkward but easily suffer undetected transpositions, additions, or omissions of the component parts. To be practicable in both verbal and written communication, a species name requires being both pronounceable and of reasonable length and complexity.

No Need for Conversion

Given the large number of existing species names and the fact that the conversion of a name under the

PhyloCode would require publication and registration (Cantino and de Queiroz, 2006), species names that do not need to be converted are more practical and thus more desirable than those that would necessitate conversion (Lee, 2002; Laurin and Cantino, 2007).

Evaluation of Naming Methods

As the features of stability and consistency of species names between PN and TN are mutually exclusive, no naming method can have all eight desirable features. Instead, there are two methods that have cumulative scores of seven. These are the currently favored method S and method T proposed in this paper (Table 1). Method A, recently recommended by Lumbsch (2002), combines six desirable features. Other methods combine two to five. Method O, which has until recently received the greatest support (Laurin and Cantino, 2004; D. A. Baum in Pfeil and Crisp, 2005; Dayrat, 2005; Laurin, 2005b; Cantino and de Queiroz, 2006), combines only two and so is one of two methods that scored the least number of the desirable features. These results suggest that methods S and T are most advantageous and equally desirable and also provide support for the recent decision of dropping the initial plan to adopt method O for naming species under the PhyloCode (Laurin and Cantino, 2007).

Methods S versus T

Methods S and T are quite similar. Both would retain Linnaean binomina, which would continue to be formed and regulated in accordance with the relevant provisions of the applicable code of TN. Both would treat the generic name of the Linnaean binomen as only the initial part of the species name (calling it a prenomen) rather than accepting the ranked category of genus as mandatory. The difference between the methods is that method S would allow the use of any potentially valid (ICZN) or legitimate (ICBN, ICNB) generic combination to refer to a species in PN, whereas method T would stabilize the species name by adopting only the original combination (i.e., the oldest potentially valid or legitimate name applied to the species). This difference leads to advantages and disadvantages for both methods.

Method S is the only one of the 20 competing methods that has the advantage of offering possibility to use the same generic combination in the contexts of PN and TN for each species at any time. This does not mean, however, that each species would be referred to by the same combination, nor does it mean that the same combination would be consistently used in PN, because species names would remain inherently unstable (as they are in TN) and depend entirely on the generic assignment of the species under the applicable code of TN. Even though users of PN would probably tend to employ the combination considered prevailing in usage under the applicable code of TN, one may doubt if all will employ the same combination to refer to the species when alternative combinations are available. It may be argued that generic names in Linnaean binomina improve over time based on new data such that more of them represent supported hypotheses of monophyly, and that one of the competing generic combinations ultimately wins out and becomes universally adopted. True enough, but nonmonophyletic genera are nevertheless inevitable (de Queiroz and Gauthier, 1992) and one's decision on which generic combination to prefer depends not only on views on phylogenetic relationships of the species, but also on one's subjective recognition of generic limits, which encourages arbitrary taxonomic decisions like splitting or lumping.

The advantage of method T over method S is that species names would remain stable regardless of changes in generic assignment of the species under the applicable code of TN. Although there would still be some instability in species names under the PhyloCode, either due to differing opinions among users of PN on the circumscription of the species or for purely nomenclatural reasons (like a newly detected senior homonym) under the applicable code of TN, the magnitude of the overall instability would under method T be far less than that under method S.

The disadvantage of method T is that this method would cause partial divergence between a set of accepted (PhyloCode) generic combinations used in PN versus a set of valid (ICZN) or correct (ICBN, ICNB) generic combinations used in TN. Although each accepted original combination would also be a potentially valid or

Table 1. Comparison of methods A to T (Appendix 1) for naming species in phylogenetic nomenclature (PN) according to eight desirable features. TN = traditional nomenclature; + = species names have the desirable feature; − = at least some species names do not have the desirable feature.

	Methods																			
Desirable feature	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
Uniqueness	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−	−	−	+	+
Stability	+	+	+	+	+	+	+	+	−	−	+	+	+	−	−	+	+	+	−	+
Distinguishability from clade names	+	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+
Consistency of form among species names	+	+	+	−	−	+	+	+	+	+	+	+	+	−	−	+	+	+	+	+
Consistency of form with the Linnaean binomen	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	+
Consistency of species names between PN and TN	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Ease of pronunciation, brevity, and simplicity of form	+	+	+	+	+	+	−	−	+	+	+	+	+	−	−	+	+	+	+	+
No need for conversion	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Number of scored desirable features	6	5	5	3	4	5	3	4	5	4	5	5	4	2	2	4	3	3	7	7

legitimate combination for the species (and as such could be used in TN), and some accepted original combinations (e.g., *Homo sapiens*) would continue to be the valid or correct combinations, many species would be referred to by differing combinations in the contexts of PN versus TN. Indeed, many original combinations have not been considered valid or correct for decades or even a century or more. As accepted original combinations would remain fixed in PN, whereas valid or correct combinations are subject to change over time in TN, the two sets of names would likely gradually diverge rather than converge with time. It should be noted, however, that method T provides means to mitigate this problem. If an accepted species name alone might be confusing, supplementary information could be cited with the name, such as the valid or correct combination or its generic part alone, the author and publication year of the species name, or one or more names for clades that contain or are hypothesized to contain the species (Appendix 1).

CONCLUSION

Methods S and T (Appendix 1) combine the same number of seven desirable features, more than any other competing method (Table 1), and are therefore considered most advantageous to PN. Preference of one of the two methods over the other is debatable and largely depends on the subjective evaluation of the relative importance of enabling the use of the same species name in PN and TN at the cost of retaining the inherent instability of species names (method S) versus having fixed species names in PN at the cost of partial divergence between species names used in PN versus TN (method T). Systematists will likely differ in their assessment of the relative importance of these two attributes. Method S better fits the needs of TN and has therefore greater potential not to discourage systematists who are attached to LBN from using the PhyloCode (Laurin and Cantino, 2007). Method T, however, is closer to the needs of PN and also yields a feasible solution to increase stability in biological nomenclature (also in TN). For these reasons, and given that the inherent instability of species names has raised considerable criticism both within and outside of PN (e.g., Cain, 1959a, 1959b; Michener, 1963, 1964; Griffiths, 1976; Ereshefsky, 1994, 1999, 2001a, 2001b; Cantino, 1998, 2000; Cantino et al., 1999a, 1999b; Bryant and Cantino, 2002; Lee, 2002; Lumbsch, 2002; Pleijel and Rouse, 2003), I am rather inclined to advocate method T. I agree with Cantino (1998), Cantino et al. (1999b), Ereshefsky (2001a, 2001b), and others that ambiguity introduced into TN by the implementation of method T in the PhyloCode would probably pass with time as users of species names grew accustomed to the new nomenclatural system and likely increasingly appreciated its stable species and clade names that are themselves not intended to convey phylogenetic information, but only to provide a means of an unambiguous reference to a taxon, thus effectively separating nomenclature from taxonomy (de Queiroz, 1997, 2006; de Queiroz and Cantino, 2001b; Lumbsch, 2002).

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APPENDIX 1

DESCRIPTIONS AND EXAMPLES OF METHODS FOR NAMING SPECIES IN PHYLOGENETIC NOMENCLATURE (PN)

The methods are referred to by a capital letter (A to T), in correspondence with designations of Cantino et al. (1999b). The scientific name of Lion originally coined by Linnaeus (1758:41) as *Felis leo* and currently usually cited as *Panthera leo*, as well as a new name for a hypothetical, thus far unrecognized, closely related species X, are used in examples illustrating the methods. All scientific taxon names used in these examples are italicized following Recommendation 6.1A in the current draft version of the PhyloCode (Cantino and de Queiroz, 2006). The *accepted name* of a species is the name adopted for that species under the PhyloCode. The *converted name* of a species is the name established under the PhyloCode on the basis of an available (ICZN) or validly published (ICBN, ICNB) name of that species. The *substitute name* of a species is an informal form of the scientific name of that species. The *taxonomic address* of a species name is a reference to a taxon or group of taxa that contain or are hypothesized to contain the species.

Method A

Description.—Converted and new species names are indistinguishable in form from the Linnaean binomen but remain stable regardless of changes in views on phylogenetic relationships of the species. Griffiths (1976) coined the term *forename* or *praenomen* for the first word of the binomen to emphasize that it is only the initial part of the species name, not a taxonomic unit recognized under this method. Converted species names are identical to the generic combination that is at the time of conversion most widely used in reference to the species under the applicable code of traditional nomenclature (TN). The first part in new species names may be the name of a clade or is chosen in some other way; the second part is a Latinized word.

Example.—The accepted name of Lion is *Panthera leo* and that of species X might be *Panthera nova*.

Reference.—Method A was proposed by Griffiths (1976) and introduced into PN by de Queiroz and Gauthier (1992). See also Sundberg and Pleijel (1994) and Cantino et al. (1999b).

Method B

Description.—Species names resemble the Linnaean binomen in form, differing only in the noncapitalization or the separation of the first and second parts by a hyphen or dot, and also in remaining stable regardless of changes in views on phylogenetic relationships of the species. Converted species names are based on the generic combination that is at the time of conversion most widely used in reference to the species under the applicable code of TN. The first part in new species names may be the name of a clade or is chosen in some other way; the second part is a Latinized word.

Example.—The accepted name of Lion is *panthera leo* or *Panthera-leo* or *Panthera.leo* (or *panthera-leo* or *panthera.leo*), depending on which option is adopted. The accepted name of species X might be *panthera nova* or *Panthera-nova* or *Panthera.nova* (or *panthera-nova* or *panthera.nova*).

Reference.—Method B was proposed by Cain (1959a) and introduced into PN by Cantino (1998). See also Michener (1963, 1964), Cantino et al. (1999a, 1999b), and Artois (2001).

Method C

Description.—This method is as method B except that the first word in converted species names must not be used as a clade name under the PhyloCode and new species names must not contain a clade name as their first part.

Example.—The accepted name of Lion is *panthera leo* or *Panthera-leo* or *Panthera.leo*, depending on which option is adopted. The accepted name of species X might be *panthera nova* or *Panthera-nova* or *Panthera.nova*. No clade may be named *Panthera* under the PhyloCode.

Reference.—Method C was proposed by H. N. Bryant in Cantino et al. (1999b).

Method D

Description.—Converted species names are based on the generic combination that is at the time of conversion most widely used in reference to the species under the applicable code of TN, differing from that combination only in the separation of its two parts by a hyphen or dot. New species names also begin with a capital letter but consist of a Latinized string of letters (representing one word or two) with no hyphen or dot within the name. All species names remain stable regardless of changes in views on phylogenetic relationships of the species.

Example.—The accepted name of Lion is *Panthera-leo* or *Panthera.leo*, depending on which option is adopted. The accepted name of species X might be *Nova* or *Pantheranova* in either option.

Reference.—Method D was proposed by P. D. Cantino in Cantino et al. (1999b).

Method E

Description.—This method is as method D except that species names begin with a lowercase letter.

Example.—The accepted name of Lion is *panthera-leo* or *panthera.leo*, depending on which option is adopted. The accepted name of species X might be *nova* or *pantheranova* in either option.

Reference.—Method E was proposed by P. D. Cantino in Cantino et al. (1999b).

Method F

Description.—Converted species names are based on the generic combination that is at the time of conversion most widely used in reference to the species under the applicable code of TN, differing from that combination only in the separation of its two parts by a dot. New species names also begin with a capital letter and consist of a nonhyphenated Latinized string of letters (representing one word or two) with a dot placed somewhere within the name, but not immediately following the first or second letter and not at the beginning or end of the name. All species names remain stable regardless of changes in views on phylogenetic relationships of the species.

Example.—The accepted name of Lion is *Panthera.leo* and that of species X might be *Nov.a* or *Panthera.nova*, providing that the name, or one differing only in the presence or position of the dot, has not previously been established.

Reference.—Method F was proposed by M. J. Donoghue in Cantino et al. (1999b).

Method G

Description.—Converted species names consist of one word formed by the fusion of the two parts of the generic combination that is at the time of conversion most widely used in reference to the species under the applicable code of TN. New species names also begin with a capital letter and consist of a Latinized string of letters (representing one word or two) with no hyphen or dot within the name. All species names remain stable regardless of changes in views on phylogenetic relationships of the species.

Example.—The accepted name of Lion is *Pantheraleo* and that of species X might be *Nova* or *Pantheranova*.

Reference.—Method G was proposed by Michener (1963) and introduced into PN by Cantino et al. (1999b).

Method H

Description.—This method is as method G except that species names begin with a lowercase letter.

Example.—The accepted name of Lion is *pantheraleo* and that of species X might be *nova* or *pantheranova*.

Reference.—Method H was proposed by Cantino et al. (1999b). See also Graybeal (1995).

Method I

Description.—This method is as method A except that the first word of a species name must be changed if it is the name established under the PhyloCode for a clade that is hypothesized not to contain the species.

Example.—The accepted name of Lion is *Panthera leo* and that of species X might be *Panthera nova*. If *Panthera* is the name established under the PhyloCode for a clade that is hypothesized not to contain the species, the word *Panthera* within the species name will need to be changed either to the name of a clade containing or being hypothesized to contain the species or to some other Latinized word that itself is not the name of a clade.

Reference.—Method I was proposed by P. D. Cantino in Cantino et al. (1999b).

Method J

Description.—This method is as method B except that the first part of a species name must be changed if it is the name established under the PhyloCode for a clade that is hypothesized not to contain the species.

Example.—The accepted name of Lion is *panthera leo* or *Panthera-leo* or *Panthera.leo*, depending on which option is adopted. The accepted name of species X might be *panthera nova* or *Panthera-nova* or *Panthera.nova*. If *Panthera* is the name established under the PhyloCode for a clade that is hypothesized not to contain the species, the word *Panthera* (or *panthera*) within the species name will need to be changed either to the name of a clade containing or being hypothesized to contain the species or to some other Latinized word that itself is not the name of a clade.

Reference.—Method J was proposed by P. D. Cantino in Cantino et al. (1999b).

Method K

Description.—Species names end with a number if the rest of the name has previously been established for another species under the PhyloCode. The number is the lowest integer greater than 1 that has not previously been used as part of a species name that is otherwise spelled the same. The number is either fused to the rest of the name or both are separated by a dot or the number is enclosed in brackets and preceded by a space. The numerical ending may be dropped after the first use of the name in a particular publication to form the substitute name. The nonnumerical part is either the specific epithet of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen (in converted names) or a noncapitalized Latinized word (in new names). The name of the genus to which a species is assigned under the applicable code of TN may be cited in association with the species name as a taxonomic address. When the genus name precedes the species name, both are separated by a space, slash, or colon or the genus name is enclosed in parentheses and followed by a space. When the genus name follows the species name, the genus name is enclosed in parentheses and preceded by a space.

Example.—The accepted name of Lion is *leo*. If *leo* has already been established for another species under the PhyloCode, the name *leo2* or *leo.2* or *leo [2]* (depending on which option is adopted) is used. If *leo2* has already been established for another species, *leo3* or *leo.3* or *leo [3]* is used, and so on. The accepted name of species X might be *nova* or, if already established for another species under the PhyloCode, *nova2* or *nova.2* or *nova [2]*, etc. The substitute names would consistently be *leo* and *nova*, respectively. The combination of a species name (e.g., *leo2*) with the genus name *Panthera* used as a taxonomic address takes the form *Panthera leo2* or *Panthera/ leo2* or *Panthera*:*leo2* or (*Panthera*) *leo2* or *leo2* (*Panthera*), depending on which convention is adopted.

Reference.—Method K was proposed by K. de Queiroz in Cantino et al. (1999b).

Method L

Description.—Species names end with a unique registration number. The number is either fused to the rest of the name or both are separated by a dot or the number is enclosed in brackets and preceded by a space. The numerical ending may be dropped after the first use of the name in a particular publication to form the substitute name. The nonnumerical part is either the specific epithet of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen (in converted names) or a noncapitalized Latinized word (in new names). The name of the genus to which a species is assigned under the applicable code of TN may be cited as a taxonomic address as it is done under method K.

Example.—The accepted name of Lion is *leo*# or *leo*.# or *leo [#]* (depending on which option is adopted), where "#" represents a unique registration number. The accepted name of species X might be *nova*# or *nova*.# or *nova [#]*. The substitute names would consistently be *leo* and *nova*, respectively. The combination of a species name (e.g., *leo*#) with the genus name *Panthera* used as a taxonomic address takes the form *Panthera leo*# or *Panthera/ leo*# or *Panthera*:*leo*# or (*Panthera*) *leo*# or *leo*# (*Panthera*), depending on which convention is adopted.

Reference.—Method L was proposed by T. Eriksson in Cantino et al. (1999b).

Method M

Description.—Converted species names consist of the specific epithet of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen. New species names consist of a noncapitalized Latinized word. It is recommended that the unique registration number of a species name, preceded by a space, be cited behind the name at least once within any publication in which the name is used. The name of the genus to which a species is assigned under the applicable code of TN may be cited as a taxonomic address as it is done under methods K and L.

Example.—The accepted name of Lion is *leo* and that of species X might be *nova*. The combination of a species name (e.g., *leo*) with its unique registration number (symbolized by #) takes the form *leo* #. The combination of a species name (e.g., *leo*) with the genus name *Panthera* used as a taxonomic address takes the form *Panthera leo* or *Panthera/ leo* or *Panthera:leo* or (*Panthera*) *leo* or *leo* (*Panthera*), depending on which convention is adopted.

Reference.—Method M was proposed by D. M. Hillis and K. de Queiroz in Cantino et al. (1999b).

Method N

Description.—Species names consist of multiple capitalized words (separated by spaces) and may be changed in response to new information about phylogeny. When a species name is converted, the first and second words are the specific epithet and generic name (in this order) of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen. When a species name is new, its initial part is a Latinized word. The rest of a species name, whether converted or new, is composed of a series of names for clades that contain or are hypothesized to contain the species. These are ordered from the smallest to the largest clade. Substitute names (everyday names sensu Mishler [1999]) contain only the first and second words of the species name.

Example.—The accepted name of Lion takes the form *Leo Panthera Felidae Carnivora Mammalia Chordata Animalia Eukaryota* or another form differing in the number of included clade names. The accepted name of species X might be *Nova Panthera Felidae Carnivora Mammalia Chordata Animalia Eukaryota*. The substitute names would be *Leo Panthera* and *Nova Panthera*, respectively. If *Panthera* or any other word following it within a species name is the name established under the PhyloCode for a clade that is hypothesized not to contain the species, the species name will need to be changed to a form that includes names for only those clades that contain or are hypothesized to contain the species.

Reference.—Method N was proposed by Mishler (1999) for naming least-inclusive taxonomic units.

Method O

Description.—Species names contain either the specific epithet of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen (in converted names) or a noncapitalized Latinized word (in new names), in either instance followed by the surname(s) of the author(s) and publication year of the name. If there is another species named under the PhyloCode or a code of TN by using the first word of the name and with the author's surname (or coauthors' surnames) spelled the same and with the same year of publication, the number of a page on which the name is cited in the original publication is added at the end of the name. If this still does not guarantee the uniqueness of the name, a lowercase letter is added behind the page number ("a" for the first name, "b" for the second, and so on). As such, species names do not require changes in response to new information about phylogeny but may vary for other reasons (see Wolsan, 2007). Substitute names (common names sensu Dayrat [2004], Dayrat et al. [2004], and Dayrat and Gosliner [2005] or combinations sensu Dayrat [2005]) may be used on condition that the species name is cited at least once in a particular publication. Substitute names are composed of a taxonomic address followed by no less than the first part of the species name. The taxonomic address consists of one or more clade names ordered from the largest to the smallest clade and separated by spaces, or it is the name of the genus to which the species is assigned under the applicable code of TN, either alone or accompanied by one or more names of subsuming clades.

Example.—The accepted name of Lion is *leo Linnaeus, 1758* (with or without the comma). The accepted name of species X (as established by J. Smith on page 21 in his article published in year 2015) might be *nova Smith, 2015*. If *nova* has already been used by Smith (or another author with the same surname) to name a different species in the same year, the name *nova Smith, 2015:21* could be used. If that species was established with the same page number, the name *nova Smith, 2015:21a* (or *nova Smith, 2015:21b*, etc.) could be used. A substitute name (e.g., for the species name *leo Linnaeus, 1758*) takes the form *Panthera leo Linnaeus, 1758* or *Panthera leo Linnaeus* or *Panthera leo* or *Felidae Panthera leo* or *Carnivora Felidae Panthera leo* or another form that differs in the number of included clade names.

Reference.—Method O was originally proposed by Lanham (1965) and subsequently modified by Dayrat et al. (2004), who introduced the method into PN. See also Dayrat (2004, 2005), Dayrat and Gosliner (2005), and Wolsan (2007).

Method P

Description.—Converted species names consist of the specific epithet of the valid (ICZN) or correct (ICBN, ICNB) Linnaean binomen. New species names consist of a noncapitalized Latinized word.

Example.—The accepted name of Lion is *leo* and that of species X might be *nova*.

Reference.—Method P was proposed by Pleijel and Rouse (2000a, 2000b) for naming least-inclusive taxonomic units. Graybeal (1995) proposed a similar method to name species. See also Härlin and Härlin (2001) and Pleijel and Rouse (2003).

Method Q

Description.—This method is as method P except that species names begin with a capital letter. A taxonomic address composed of one or more taxon names listed in order of decreasing inclusiveness from left to right and separated by spaces may be added in front of the species name.

Examples.—The accepted name of Lion is *Leo* and that of species X might be *Nova*. Examples of a species name (e.g., *Leo*) combined with its taxonomic address are *Panthera Leo* or *Felidae Leo* or *Carnivora Leo* or *Carnivora Felidae Panthera Leo*.

Reference.—Method Q was proposed by Schander and Thollesson (1995). See also Schander (1998).

Method R

Description.—This method is as method Q except that the taxonomic address of a species name, if cited, is enclosed in parentheses and placed behind the name. The address itself is composed of a full or abbreviated taxon name or two taxon names separated by a comma.

Examples.—The accepted name of Lion is *Leo* and that of species X might be *Nova*. Examples of a species name (e.g., *Leo*) combined with its taxonomic address are *Leo* (*Panthera*, *Felidae*) or *Leo* (*Panthera*) or *Leo* (*P*.).

Reference.—Method R was proposed by Pleijel (1999) for naming least-inclusive taxonomic units.

Method S

Description.—The governance of species names is left to the applicable codes of TN, but the generic part of the Linnaean binomen is under the PhyloCode referred to as the *prenomen* (after Griffiths's [1976] "praenomen") to emphasize that it is only the initial part of the species name, not a taxonomic unit recognized under this code. Accepted species names are inherently unstable and depend on the generic assignment of the species under the applicable code of TN.

Example.—The accepted name of Lion is *Panthera leo* or *Felis leo* or *Leo leo* or another generic combination, depending on the hypothesized phylogenetic position of the species (and the user's subjective genus concept). The accepted name of species X might be *Panthera nova* or *Felis novus* or *Leo novus* or another generic combination.

Reference.—Method S was proposed by J. A. Clarke, B. Dayrat, P. D. Cantino, and K. de Queiroz in Laurin and Cantino (2007).

Method T

Description.—Species names are formed and regulated in conformity with the relevant provisions of the applicable code of TN except that the oldest potentially valid (ICZN) or legitimate (ICBN, ICNB) name (original generic combination) applied to a species is the accepted name of that species under the PhyloCode, and the initial word of the species name is not recognized under the PhyloCode as a genus name, but instead conceptualized in the sense of Griffiths's (1976) "praenomen" and referred to as the prenomen (as under method S). Accepted species names remain stable regardless of changes in generic assignment of the species under the applicable code of TN. To provide a reference to the generic combination favored in TN, that combination or only its generic part, enclosed in parentheses, may be cited following the accepted species name. The author and publication year of the species name (author address or bibliographic address), as well as one or more names for clades that contain or are hypothesized to contain the species (clade address), may also be combined.

Example.—The accepted name of Lion is *Felis leo* and that of species X might be *Panthera nova*. The combination of a species name (e.g., *Felis leo*) and a reference to the generic combination currently favored in TN takes the form *Felis leo* (*Panthera leo*) or *Felis leo* (*Panthera*). Other information, such as the author, bibliographic, or clade address of the accepted species name, may also be combined as, e.g., *Felis leo* Linnaeus, 1758 (*Panthera*, *Felidae*).

Reference.—Method T is proposed in this paper.