

Species Names in Phylogenetic Nomenclature

PHILIP D. CANTINO,^{1*} HAROLD N. BRYANT,² KEVIN DE QUEIROZ,³ MICHAEL J. DONOGHUE,⁴
TORSTEN ERIKSSON,⁵ DAVID M. HILLIS,⁶ AND MICHAEL S. Y. LEE⁷

¹Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, USA;
E-mail: cantino@ohio.edu

²Royal Saskatchewan Museum, 2340 Albert Street, Regina, Saskatchewan S4P 3V7, Canada;
E-mail: hbryant@gov.sk.ca

³Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution,
Washington, DC 20560, USA; E-mail: dequeiroz.kevin@nmnh.si.edu

⁴Harvard University Herbaria, 22 Divinity Ave., Cambridge, Massachusetts 02138, USA;
E-mail: mdonoghue@oeb.harvard.edu

⁵Bergius Foundation, Royal Swedish Academy of Sciences, Box 50017, 104 05 Stockholm, Sweden;
E-mail: Torsten@bergianska.se

⁶Section of Integrative Biology, School of Biological Sciences, University of Texas,
Austin, Texas 78712, USA; E-mail: hillis@phylo.zo.utexas.edu

⁷Department of Zoology, University of Queensland, Brisbane, Queensland 4072, Australia;
E-mail: mlee@zoology.uq.edu.au

Abstract.—Linnaean binomial nomenclature is logically incompatible with the phylogenetic nomenclature of de Queiroz and Gauthier (1992, *Annu. Rev. Ecol. Syst.* 23:449–480): The former is based on the concept of genus, thus making this rank mandatory, while the latter is based on phylogenetic definitions and requires the abandonment of mandatory ranks. Thus, if species are to receive names under phylogenetic nomenclature, a different method must be devised to name them. Here, 13 methods for naming species in the context of phylogenetic nomenclature are contrasted with each other and with Linnaean binomials. A fundamental dichotomy among the proposed methods distinguishes those that retain the entire binomial of a preexisting species name from those that retain only the specific epithet. Other relevant issues include the stability, uniqueness, and ease of pronunciation of species names; their capacity to convey phylogenetic information; and the distinguishability of species names that are governed by a code of phylogenetic nomenclature both from clade names and from species names governed by the current codes. No method is ideal. Each has advantages and drawbacks, and preference for one option over another will be influenced by one's evaluation of the relative importance of the pros and cons for each. Moreover, sometimes the same feature is viewed as an advantage by some and a drawback by others. Nevertheless, all of the proposed methods for naming species in the context of phylogenetic nomenclature provide names that are more stable than Linnaean binomials. [Phylogenetic nomenclature; species names; binomial nomenclature.]

Phylogenetic nomenclature (de Queiroz and Gauthier, 1992, 1994) is a system of biological nomenclature in which taxon names are explicitly applied to evolutionary entities by means of phylogenetic definitions. In this system, the categories “species” and “clade” are not ranks but different kinds of entities. We consider a clade to be a monophyletic group of species (de Queiroz and Donoghue, 1990; de Queiroz, 1999). A species, in its broadest conception, is a segment of a population-level lineage, but views vary as to which criteria (e.g., potential interbreeding, diagnosability, exclusivity) should be used to determine whether a particular lineage is to be formally recog-

nized as a species (de Queiroz, 1998, 1999). Although biologists disagree about which lineages to recognize as species, we suspect that most would agree that species are “fundamental units for organizing knowledge of biodiversity” (Baum, 1998) and, as such, require names. It is not our intent to add to the vast literature on species concepts (e.g., Ereshefsky, 1992; Claridge et al., 1997; Howard and Berlocher, 1998; Wilson, 1999). Rather, we address here the form that species names should take in a system of phylogenetic nomenclature and consider implications regarding their stability, degree of ambiguity, ease of pronunciation, and potential to convey information (or misinformation) about relationships.

The literature on phylogenetic nomenclature includes extensive discussion of the is-

*All authors except the first are listed alphabetically. Address correspondence to this author.

sues surrounding the naming of clades (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; Minelli, 1991, 1995; Rowe and Gauthier, 1992; Sundberg and Pleijel, 1994; Bryant, 1994, 1996, 1997; Schander and Thollessen, 1995; Lee, 1996a,b, 1998, 1999; Wyss and Meng, 1996; Cantino et al., 1997; Crane and Kenrick, 1997; de Queiroz, 1997; Kron, 1997; Baum et al., 1998; Härlin, 1998; Hibbett and Donoghue, 1998; Moore, 1998; Schander, 1998a; Sereno, 1999), but relatively little has been written about the naming of species in this system (de Queiroz and Gauthier, 1992; Graybeal, 1995; Schander and Thollessen, 1995; Cantino, 1998; Schander, 1998b). This may in part be due to a tacit assumption that there would be no fundamental difference between phylogenetic and traditional nomenclature in the application of species names (i.e., based on nomenclatural types and lacking explicit phylogenetic definitions), whereas the rules governing the application of supraspecific taxon names in the two systems are very different. There is no reason why species names could not have phylogenetic definitions in phylogenetic nomenclature, as clade names do, but the theory underlying the application of such definitions to species names has not yet been developed.

Although the manner in which species names would be applied in phylogenetic nomenclature does not necessarily differ from that in the traditional system, the form that they take in the traditional system—Linnaean binomials—is incompatible with phylogenetic nomenclature. The use of Linnaean binomials makes the genus a mandatory rank, whereas a basic tenet of phylogenetic nomenclature is abandonment of mandatory ranks (de Queiroz and Gauthier, 1992). Linnaean binomials not only are logically incompatible with phylogenetic nomenclature (Griffiths, 1976; de Queiroz and Gauthier, 1992), they also have several practical drawbacks (Cain, 1959; Michener, 1964; Cantino, 1998). The most serious of these is instability of species names. Every change in generic limits, whether based on phenetic criteria or new phylogenetic evidence, necessitates changes in species names. At the least, the genus portion of the binomial must be altered, but

the specific epithet sometimes must change as well, either because it duplicates a specific epithet under the new genus (homonymy) or because it no longer matches the gender of the new genus in the case of adjectival epithets. Another drawback of Linnaean binomial nomenclature is that it encourages the creation of monotypic and paraphyletic genera in situations in which relationships among the species in a complex of genera are poorly resolved (discussed below).

A formal code of phylogenetic nomenclature (the "PhyloCode") is in preparation. It is being designed so that it can be used concurrently with the traditional system embodied in the existing codes (i.e., International Code of Botanical Nomenclature [ICBN], International Code of Zoological Nomenclature [ICZN], and the Bacteriological Code [BC]) or similar codes that might be adopted in the future (e.g., the draft BioCode: Greuter et al., 1998). In conjunction with the phylogenetic code, plans are being developed for an Internet-accessible database in which all names governed by the new code would be registered. This would provide an easy means of cross-referencing names under different codes, facilitate access to the relevant nomenclatural literature, and prevent accidental creation of homonyms under the phylogenetic code.

The development of the PhyloCode was initiated in preparation for, and discussed and elaborated at, a workshop that took place at the Harvard University Herbaria in August 1998 and was attended by 27 people from five countries (see Acknowledgments). Of the 20 issues on the agenda at the Harvard workshop, the one that proved most contentious was the form that species names should take. No decision was reached at the workshop, and the participants debated the issue intensively during the next five months in an Internet discussion group. When it became clear that no consensus would be reached, it was decided to restrict the initial version of the PhyloCode to the naming of clades. We remain committed to the development of a parallel set of rules for species names, but we think this should be delayed until there has been an opportunity for the systematics

community to discuss the issues involved. This article is intended to initiate that discussion.

In this article, we describe and contrast the methods that have been proposed for naming species in the context of phylogenetic nomenclature. Many of these methods arose in the Internet discussion among the workshop participants and have not previously been published. Although Linnaean binomial nomenclature is incompatible with other aspects of phylogenetic nomenclature and is not under consideration for adoption in the PhyloCode, it is included here for comparative purposes.

PROPOSED METHODS FOR NAMING SPECIES

In comparing the methods that might be used to name species in a system of phylogenetic nomenclature, one must keep in mind the relationship between the PhyloCode and the current codes (i.e., the ICBN, ICZN, and BC), referred to henceforth as the *preexisting codes*. Because the PhyloCode is still in preparation, the information in this paragraph must be viewed as provisional. The PhyloCode is being designed so that it can be used concurrently with the preexisting codes. Minimizing the disruption of the preexisting nomenclature is a priority. When a previously recognized species is named under the PhyloCode, its name will be based on the preexisting name that is considered to be correct (ICBN, BC) or valid (ICZN). This process is called *conversion*, and the name under the PhyloCode is the *converted name*. Conversion is the act of establishing a name as governed by the rules of the PhyloCode, and thus formalizing its independence from the concept of genus. If, at the time of conversion, there is disagreement in the current literature as to which name is correct under the preexisting code that governs it, the one that is most widely used should be chosen. The process of conversion is analogous to publishing a new combination. Thus, a clear reference to the author and place of publication of the preexisting name will be required, but a description or diagnosis will not. The converted name will retain the same type as the preexisting name on which it is based. Publication of names for

newly recognized species will require a description or diagnosis as well as a type designation.

Thirteen proposed methods for naming species in the context of phylogenetic nomenclature are briefly characterized in the form of a key in Table 1 and are described in detail in Table 2. Other variants that differ in minor ways from the options covered here were considered in the Internet discussion that led to this article but had little support. The key in Table 1 could have been organized in various ways. Our choice of properties to include in the early couplets emphasizes what we consider the most fundamental distinctions among the methods: whether converted names are based on an entire preexisting binomial or on the specific epithet alone; and whether species names are fixed or may be changed in response to new information about phylogeny. Other distinctions among the methods include (1) whether species names are unique; (2) whether species names are distinguishable from clade names; (3) whether converted names (or the converted name preceded by the name of a clade that includes the species) are identical in form to Linnaean binomials; (4) whether converted species names are identical in form to the names of newly recognized species; (5) whether species names begin with a capital letter or a lower-case letter; (6) whether species names contain numbers; and (7) whether species names contain nonalphanumeric symbols (e.g., hyphens or dots).

The proposed methods can be divided into three groups, based on the primary distinctions described above. In groups I and II (methods A–J), converted species names are derived from binomials (i.e., retain both parts of the preexisting name). In contrast, converted species names in group III (methods K–M) are derived from preexisting specific epithets (i.e., do not retain the genus portion of the preexisting name). The binomial-based methods differ in their degree of stability. In group I (methods A–H), species names will not change as a result of new information about phylogeny. Thus, although these names are derived from binomials, they function like uninomials. In group II (methods I and J), a name must be

TABLE 1. Outline of the proposed methods for naming species in phylogenetic nomenclature, organized as a dichotomous key. A converted name is a name established under the PhyloCode and derived from a preexisting Linnaean binomial. A new name is a name established under the PhyloCode for a species that has no preexisting Linnaean binomial (i.e., a newly recognized species).

1. Converted names are based on the full preexisting binomial; new names may be binomial or uninomial in form, depending on the method.	
2. Names do not change with new knowledge of phylogeny.	
3. All names consist of two parts, although not necessarily two words (a word being a string of letters that means something by itself), separated by a space, hyphen, or dot.	
4. Names are capitalized and their two parts are separated by a blank space, thus they are identical in form to Linnaean binomials.	Method A
4'. Names are distinguishable from Linnaean binomials, either by beginning with a lower-case letter or by separation of their two parts by a hyphen or dot.	
5. Genus names may not be established as clade names.	Method C
5'. Genus names may be established as clade names.	
6. New names must consist of two words.	Method B
6'. New names may consist of either two words connected by a dot or one word with a dot somewhere within it.	Method F
3'. At least some names consist of a single unbroken string of letters.	
7. Converted names are binomial in form; new names are uninomial.	Method D
8. Names are capitalized.	Method D
8'. Names are not capitalized.	Method E
7'. All names are uninomial in form; converted names are formed by the fusion of the two parts of the Linnaean binomial on which they are based.	
9. Names are capitalized.	Method G
9'. Names are not capitalized.	Method H
2'. Names sometimes change with new knowledge of phylogeny.	
10. Names are capitalized and their two parts are separated by a blank space, thus they are identical in form to Linnaean binomials.	Method I
10'. Names are distinguishable from Linnaean binomials, either by beginning with a lower-case letter or by separation of their two parts by a hyphen or dot.	Method J
1'. Converted names are based on the epithet of the preexisting binomial; all names are uninomial in form.	
11. Names are unique and sometimes contain numbers.	
12. Names end in a sequential number (shorter than the registration number) if they are not unique without it.	Method K
12'. All names end in a registration number.	Method L
11'. Names do not contain numbers and are not necessarily unique (but the combination of name and registration number is unique).	Method M

changed if its first part is the name of a clade to which the species does not belong. Within group I (stable, binomial-based names), method A differs from the others in providing names that are indistinguishable in form from Linnaean binomials. Method C differs from the others in prohibiting the use of preexisting genus names for clades, thereby eliminating the possibility that the first part of a converted species name could be the name of a clade to which it does not

belong. Methods B and D–H differ in relatively minor ways concerning form, e.g., whether the two words of a preexisting binomial are fused or connected by a hyphen or dot, and whether the names of new species must be identical in form to converted names. Within group II (binomial-based names with limited stability), the two methods differ in whether or not a converted name is distinguishable in form from a Linnaean binomial. Within group III

TABLE 2. Descriptions and examples of the proposed methods for naming species in the context of phylogenetic nomenclature. The person who proposed each method is indicated for the record, but it should not be assumed that the proposer prefers that option.

Group I. Stable, binomial-based names (methods A–H): Converted species names are derived from preexisting binomials and are stable; that is, they do not change as a result of new information about phylogeny.

Methods A–C (Griffiths, 1976; de Queiroz and Gauthier, 1992): All species names consist of two parts, separated by a space, hyphen, or dot. Converted species names are based on the accepted binomial under the preexisting code. In names of new species, the first part may be the name of a clade (except in method C), descriptive of the organism, or chosen in some other way.

Method A: All species names are identical in form to Linnaean binomials and thus indistinguishable from species names governed by the preexisting codes.

Example: The preexisting name of the Common Starling, *Sturnus vulgaris*, remains *Sturnus vulgaris* under the PhyloCode, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name must take the same form (e.g., *Sturnus phalacrocephalus*).

Method B (Cain 1959; Michener 1963, 1964; Cantino 1998): All species names are nearly identical to Linnaean binomials, differing only in a convention that makes them distinguishable from names governed by the preexisting codes (e.g., noncapitalization or separation of the first and second parts by a hyphen or dot).

Example: The preexisting name *Sturnus vulgaris* becomes *sturnus vulgaris* or *Sturnus-vulgaris* or *Sturnus.vulgaris*, depending on which convention is adopted, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name must take the same form (e.g., *sturnus phalacrocephalus* or *Sturnus-phalacrocephalus* or *Sturnus.phalacrocephalus*).

Method C (proposed by H. Bryant): Method C is identical to method B except that genus names cannot be used as clade names, and new species names must not incorporate a clade name as their first part. (Note: These restrictions could equally well be combined with the features of method A.)

Example: The preexisting name *Sturnus vulgaris* becomes *sturnus vulgaris* or *Sturnus-vulgaris* or *Sturnus.vulgaris*, depending on which convention is adopted, but no clade may be named *Sturnus*. A new species name must take the same form (e.g., *sturnus phalacrocephalus* or *Sturnus-phalacrocephalus* or *Sturnus.phalacrocephalus*).

Methods D and E (proposed by P. Cantino): Converted species names consist of the two parts of the preexisting binomial, separated by a hyphen or dot, but new species names may be any unique, Latinized word containing only letters (i.e., no hyphen or dot).

Method D: Species names are capitalized, thus new species names are indistinguishable from clade names.

Example: The preexisting name *Sturnus vulgaris* becomes *Sturhus-vulgaris* or *Sturnus.vulgaris*, depending on which convention is adopted, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name might take the form *Phalacrocephalus* or *Sturnusphalacrocephalus*.

Method E: Species names begin with a lower-case letter; thus all species names are distinguishable from clade names.

Example: The preexisting name *Sturnus vulgaris* becomes *sturnus-vulgaris* or *sturnus.vulgaris*, depending on which convention is adopted, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name might take the form *phalacrocephalus* or *sturnusphalacrocephalus*.

Method F (proposed by M. Donoghue): Converted species names consist of the two parts of the preexisting binomial separated by a dot. New species names may be any unique, Latinized, nonhyphenated 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.

Example: The preexisting name *Sturnus vulgaris* becomes *Sturnus.vulgaris*, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name might take the form *Phalacro.cephalus* (providing that this name, or one differing only in the presence or position of the dot, has not previously been established) or *Sturnus.phalacrocephalus*.

Method G and H (Michener, 1963): Converted species names consist of one word, formed by the fusion of the two parts of the preexisting binomial. New species names may be any unique, Latinized word containing only letters.

Method G: Species names are capitalized and thus are indistinguishable from clade names.

Example: The preexisting name *Sturnus vulgaris* becomes *Sturnusvulgaris*, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name might take the form *Phalacrocephalus* or *Sturnusphalacrocephalus*.

Method H: Species names begin with a lower-case letter and thus are distinguishable from clade names.

Example: The preexisting name *Sturnus vulgaris* becomes *sturnusvulgaris*, but *Sturnus* may or may not be the name of a clade to which the species belongs. A new species name might take the form *phalacrocephalus* or *sturnusphalacrocephalus*.

(Continued on next page)

TABLE 2. Continued.

Group II. Binomial-based names with limited stability (methods I and J; proposed by P. Cantino): Converted species names are derived from preexisting binomials. The first part of a species name must be changed if it is the established (under the PhyloCode) name of a clade to which the species does not belong.

Method I: Method I is identical to method A except that the first part of the species name must be changed if it is the name of a clade to which the species does not belong.

Example: The preexisting name of the Common Starling, *Sturnus vulgaris*, remains *Sturnus vulgaris* under the PhyloCode. A new species name must take the same form (e.g., *Sturnus phalacrocephalus*). If *Sturnus* is the established name of a clade to which this species does not belong, the word *Sturnus* within the species name must be formally changed to the name of a clade to which this species belongs or to some other Latinized word that is not the name of a clade.

Method J: Method J is identical to method B except that the first part of the species name must be changed if it is the name of a clade to which the species does not belong.

Example: The preexisting name *Sturnus vulgaris* becomes *sturnus vulgaris* or *Sturnus-vulgaris* or *Sturnus.vulgaris*, depending on which convention is adopted. A new species name must take the same form (e.g., *sturnus phalacrocephalus* or *Sturnus-phalacrocephalus* or *Sturnus.phalacrocephalus*). If *Sturnus* is the established name of a clade to which this species does not belong, the word *Sturnus* within the species name must be formally changed to the name of a clade to which this species belongs or to some other Latinized word that is not the name of a clade.

Group III. Epithet-based names (methods K–M) (Graybeal 1995; Schander and Tholleson 1995; Schander 1998b): Converted species names are derived from the epithets of preexisting binomials and are stable; that is, they do not change as a result of new information about phylogeny. To provide a reference to the preexisting binomial, the name of the genus to which the species belongs under the preexisting code may (but need not) be cited as a taxonomic address; it is recommended that this be done if the species name alone might be confusing (proposed by M. Lee and T. Eriksson).

Method K (proposed by K. de Queiroz): Species names are terminated by a number (which is part of the name) if the rest of the name has previously been established for a different species under the PhyloCode. The number must be the lowest integer >1 that has not previously been used as part of a name that is otherwise spelled the same. The number may be dropped after the first use of the name in a particular publication. When a species name is converted, the nonnumerical portion of the name is the epithet of the accepted binomial under the preexisting code. When a species name is new, the nonnumerical portion of the name may be any Latinized word. If a taxonomic address is cited, the combination of address and species name may or may not be distinguishable from a Linnaean binomial, depending on whether the two names are separated by a delimiter of some sort (e.g., a slash or parentheses). If a delimiter is not used, the combination of taxonomic address and species name will be identical in form to a binomial if the name does not contain any numbers (i.e., if it is the first name established under the PhyloCode based on this epithet) or if the number is omitted subsequent to its first use in a publication.

Example: The preexisting name *Sturnus vulgaris* becomes *vulgaris*. If *vulgaris* has already been established for another species, the name *vulgaris2* is used (or *vulgaris.2* or *vulgaris [2]*, depending on which convention is adopted). If *vulgaris2* has already been established for another species, *vulgaris3* is used, and so forth. If the name *vulgaris2* by itself might be confusing to readers, it is recommended that *Sturnus* be cited as a taxonomic address; this would take the form *Sturnus vulgaris2* or *Sturnus/vulgaris2* or (*Sturnus*) *vulgaris2* or *vulgaris2* (*Sturnus*) or *Sturnus:vulgaris2*, depending on which convention is adopted.

Method L (proposed by T. Eriksson): Species names are terminated by a unique registration number (which is part of the name). The number may be dropped after the first use of the name in a particular publication. When a species name is converted, the nonnumerical portion of the name is the epithet of the accepted binomial under the preexisting code. When a species name is new, the nonnumerical portion of the name may be any Latinized word. If a taxonomic address is cited, the combination of address and species name may or may not be distinguishable from a Linnaean binomial, depending on whether the two names are separated by a delimiter of some sort (e.g., a slash or parentheses). If a delimiter is not used, the combination of taxonomic address and species name will be identical in form to a binomial if the number is omitted subsequent to its first use in a publication.

Example: The preexisting name *Sturnus vulgaris* becomes *vulgaris###* (or *vulgaris.###* or *vulgaris [###]*, depending on which convention is adopted). If the name *vulgaris###* by itself might be confusing to readers, it is recommended that *Sturnus* be cited as a taxonomic address. The taxonomic address plus species name would take the form *Sturnus vulgaris###* or *Sturnus/vulgaris###* or (*Sturnus*) *vulgaris###* or *vulgaris###* (*Sturnus*) or *Sturnus:vulgaris###*, depending on which convention is adopted.

(Continued on next page)

TABLE 2. Continued.

Method M (proposed by D. Hillis and K. de Queiroz): Species names do not contain numbers, but it is recommended that the unique registration number be cited at least once within any publication in which the name is used. When a species name is converted, the name is the epithet of the accepted binomial under the preexisting code. When a species name is new, the name may be any Latinized word. If a taxonomic address is cited, the combination of address and species name may or may not be distinguishable from a Linnaean binomial, depending on whether the two names are separated by a delimiter of some sort (e.g., a slash or parentheses). If a delimiter is not used, the combination of taxonomic address and species name will be identical in form to a binomial.

Example: The preexisting name *Sturnus vulgaris* becomes *vulgaris*. If the name *vulgaris* by itself might be confusing to readers, it is recommended that *Sturnus* be cited as a taxonomic address. The species name with its taxonomic address could take the form *Sturnus vulgaris*. Other options for combining the species name and the taxonomic address (see previous examples) could also be used with this method.

(epithet-based names), methods K and L provide unique names by including numbers as part of the name. In contrast, names provided by method M do not contain numbers and are not necessarily unique but are complemented by a unique registration number. A unique registration number exists under all methods, but only methods L and M take advantage of it to clear up potential ambiguities when names are not unique. Method L requires that the registration number be part of every name to ensure that names are unique (in contrast, the number is not part of the name in method M). In method K, only those names that have been previously established for a different species require addition of a number, and the number used is not the registration number (it is generally much shorter than the registration number).

All of the proposed methods differ from Linnaean binomial nomenclature in that species names do not attempt to convey information about supraspecific relationships. Even when a species name begins with a word that is a genus name under one of the preexisting codes, one cannot assume that the species belongs to a clade bearing that name. For example, the genus (under the preexisting code) may be paraphyletic, or it may correspond to a clade for which a name has not yet been established under the PhyloCode. This is further discussed below (see Information About Phylogenetic Relationships). To indicate relationship, the species name would have to be combined with the name(s) of one or more subsuming clades (i.e., clades to which the species belongs); we refer to such a name or names metaphorically as a "clade address" because it indi-

cates the "location" of the species within the nested hierarchy of subsuming clades. A similar practice is already used when one wishes to impart more phylogenetic information than is conveyed by the genus name in a Linnaean binomial; e.g., *Oxyuranus scutellatus* (Serpentes, Reptilia).

DESIRABLE FEATURES

In evaluating the merits of the proposed methods for naming species, we consider several features to be desirable. No method has all of them (Table 3); indeed, none could have all of them because some desirable features are mutually exclusive.

Stability and Continuity

The communication function of nomenclature is best served if names remain stable through time. In phylogenetic nomenclature, there are two components of stability: continuity of converted names with the names used under the preexisting codes, and stability of names once they are established under the PhyloCode.

When applied to taxa that already have names, phylogenetic nomenclature does not attempt to replace the existing names with new ones but, rather, governs the application of the existing names in a different way. Thus, existing species names ideally should not change when they are converted. The proposed methods attempt to meet this objective in different ways. Methods A–J preserve the entire binomial, with or without minor changes in form (e.g., hyphenation or fusion of the two parts). Methods K–M preserve only the epithet, but the genus name may optionally be cited as a

“taxonomic address,” which may or may not also be a clade address. If the genus is monophyletic, its name would be a clade address. If the monophyly of the genus has not been demonstrated, its name can be placed in quotation marks to avoid confusion with a clade address. (Some of us feel that only clade names that have been established under the PhyloCode should be cited as clade addresses and that all other names cited as taxonomic addresses should be placed in quotation marks or marked in some other way to indicate that they have not been established under the PhyloCode; others of us consider it acceptable to cite as a clade address any taxon for which there is evidence of monophyly, whether or not its name is established under the PhyloCode. In any case, such conventions will develop gradually through usage by the systematics community and will not be legislated by the PhyloCode.)

In all proposed methods except I and J, species names are stable once they are established under the PhyloCode. This is in marked contrast to Linnaean binomial nomenclature, in which species names change frequently as a result of several phenomena: (1) “lumping” and “splitting” at the genus level, based on new phylogenetic evidence that indicates a genus is not monophyletic; (2) lumping and splitting based on phenetic or other nonphylogenetic considerations; and (3) discovery of older names in the literature (although changes due to strict application of priority are now discouraged by the ICBN, and will be discouraged in the fourth edition of the ICZN [S. Minelli, pers. com.]). The first two phenomena will not cause name changes under any of the methods proposed here because the genus concept is not part of phylogenetic nomenclature. However, new evidence about phylogeny (i.e., phenomenon 1 uncoupled from the genus concept) may result in name change under methods I and J, as discussed below. The third phenomenon will be eliminated by the implementation of a registration system for names governed by the PhyloCode. Under methods A–H and K–M, the only reasons that a species might appear to be renamed would be the discovery of typification errors (i.e., if the type of a species name is found to belong to a different

species than that supposed by the author of the name) and lumping and splitting at the species level. However, in these cases, what is changing is not the name of the species, but rather the application of the name or the hypothesized boundaries of the species.

Under the “limited stability” methods, I and J, species names are based on binomials and must be changed if the first part of the name is the phylogenetically defined name of a clade to which the species does not belong (e.g., see the *Caryopteris* example described below under Information About Phylogenetic Relationships). However, they do not change if the first part of the name is not a phylogenetically defined clade name. Nor do they change because of the other causes, unrelated to phylogeny, that lead to name changes under the traditional system. Thus, methods I and J provide species names that are more stable than Linnaean binomials but less stable than the other options proposed here.

Uniqueness and Ambiguity

One of the principles underlying the PhyloCode is that names must be unique; that is, each taxon should have only one accepted name, and each accepted name should refer to only one taxon (de Queiroz and Gauthier, 1994). This presents a problem for epithet-based species names because many epithets are not unique. The critical feature that taxon names must have is not uniqueness per se, but lack of ambiguity; however, uniqueness is the simplest and surest way to make names unambiguous. Nonunique species names can be rendered unambiguous by citing a clade address that includes only one species with that name, but this approach presents practical problems. Users of names who are not specialists on the group may not know whether a clade that might be cited as a clade address contains more than one species with a particular epithet-based name, unless the clade address is the name of the genus to which the species belongs under the preexisting code. Alternatively, one might cite the preexisting genus name as a taxonomic address regardless of whether it is a clade name (placing it in quotation marks if the genus is not monophyletic).

Unique names are critical for bibliographic searches. Entering the name *vulgare* in a computerized search for information on the plant species currently known as *Clinopodium vulgare* will turn up a vast number of irrelevant references. This will rarely occur if one enters a Linnaean binomial (e.g., *Clinopodium vulgare*), and perhaps never with binomial-based names (e.g., *Clinopodium-vulgare*), but the much greater frequency of homonymy in the case of epithets creates a serious problem that citation of a clade address will not always solve. For example, the least inclusive taxon that contains this species and is unquestionably a clade is Nepetoideae (in Lamiaceae; Wagstaff et al., 1995), which includes well over 100 genera. Combining Nepetoideae and *vulgare* in a bibliographic search would not eliminate irrelevant output because there are other species of Nepetoideae with the same epithet (e.g., *Origanum vulgare*). A convention to cite the preexisting genus name as a taxonomic address would solve the problem if everyone followed it, but conventions (as opposed to nomenclatural rules) may be ignored. The only way to guarantee presence of the information necessary to make a name unambiguous is to include that information in the name itself.

Graybeal (1995) discussed this problem and proposed that if the genus is not a clade, and if ambiguity persists even when the least inclusive named clade is cited (because of homonymy within that clade), then the species should be renamed. She suggested that this be done by fusing the two parts of the preexisting binomial. For example, given the situation described in the previous paragraph, *vulgare* would be renamed *clinopodiumvulgare*, to distinguish it from other species named *vulgare* within the least inclusive named clade (Nepetoideae). This resembles our method H and has the same potential for pronunciation problems (discussed below under Other Desirable Features). It differs from method H in that names would take this form only if ambiguity would otherwise result, whereas in method H all converted names take this form. In groups for which the phylogeny is poorly known, and in which most genus names would therefore not be estab-

lished clade names, many species with common epithets would likely have to be named in this way under Graybeal's method. This might occur when a preexisting name is converted, or long afterwards. A species name that is unambiguous when converted may later become ambiguous when another species name based on the same epithet is converted, if both species are part of the same least inclusive named clade. Thus, Graybeal's method introduces a source of nomenclatural instability that does not exist in any of the methods proposed here.

Schander and Tholleson (1995) proposed another way of reducing the confusion caused by the nonuniqueness of epithet-based species names. They suggested that it be required that the author and year of publication be cited with the name; thus, the species currently known as *Polycera quadrilineata* (Müller, 1776) would become *Quadrilineata* Müller, 1776. However, as they pointed out, this would not completely eliminate the problem because some authors (e.g., Linnaeus) published more than one name with a particular epithet in the same year.

A different solution to the uniqueness problem is adopted in the epithet-based methods proposed here: Numbers are used to eliminate the ambiguity that might otherwise result from nonunique names. In Linnaean binomials, it is the combination of the epithet and the genus name that is usually unique (though the existence of homonyms can occasionally lead to ambiguity if the authors of the names are not cited); under the epithet-based methods described here (K–M), it is the combination of the epithet-like species name and a number that is unique. These methods thus use a number rather than a ranked category (genus) to compensate for the nonuniqueness of the specific epithet.

In methods K and L, a number is included as part of the name to make it unique, whereas in method M a unique registration number (which is not part of the name itself) provides an unambiguous reference to the species even when the nonunique name does not. In method L, the registration number is added to all names. In method K, a shorter number is added—

and only to those names that are not unique without it. In both options, one may abbreviate a name by dropping the number, as long as the number has been included with the name at least once within a particular publication or paragraph (depending on editorial practice). This is analogous to the current practice, in many journals, of dropping the author citation or abbreviating the genus name after the first use of the name.

Method M differs from L in that the registration number is not part of the name; thus, some names will not be unique. The resulting potential for confusion is mitigated by a convention that a unique registration number be cited the first time a name is used in a particular publication. In method M, the registration number functions in a manner analogous to a U.S. social security number, which can be used to distinguish between people whose names are identical. In practice, methods L and M would probably work similarly, even though the number is part of the name in L but not in M. However, a nomenclatural code can determine only the form that a name takes when it is first published, not the subsequent use of that name. Thus, the PhyloCode will have no power to enforce inclusion of the registration number when citing a previously published name under either method L or M (or inclusion of the shorter numbers used in method K). This will be determined by editors, authors, and the community of biologists. If method L or M is adopted, we anticipate that most authors will include the registration number for a name at least once within any publication in which the name is cited, out of common sense and self-interest; the registration number is the only thing that eliminates the potential for ambiguity in options L and M, and authors will presumably want their publications to be found by other biologists who are searching for literature on the cited species. However, some of us believe it is important to emphasize the importance of the registration number by making it an integral part of the name (method L), whereas others think this is unnecessary and object to the inclusion of numbers within names.

The problem of avoiding ambiguity is not limited to phylogenetic nomenclature. Under the current codes, species names are

not necessarily unique; homonyms exist both within the jurisdiction of a given code and between codes. The resulting ambiguity is largely eliminated by citing the authorities of names and by contextual information. Citation of authorities will be unnecessary under the PhyloCode if a registration system is implemented, as planned. Use of a registration database will prevent the accidental creation of homonyms as well as provide an easy way to access publication data for all names.

Information About Phylogenetic Relationships

Linnaean binomials contain information about genus membership. When genera are monophyletic, such species names convey phylogenetic information. This information is provided at the expense of stability (discussed above), because species names must change when generic boundaries are redrawn. A related drawback of Linnaean binomials is their inability to accommodate lack of knowledge about the genus-level relationships of a species. New species are sometimes discovered that cannot be referred with confidence to a genus because of incompleteness of preservation or the absence of a diagnostic structure or ontogenetic stage. This problem occurs most frequently when species are described on the basis of fossilized remains but may also occur with extant species (e.g., when a new plant species is described on the basis of flowering material but fruits are needed to diagnose the genus). However, Linnaean nomenclature requires the systematist to place the species in a genus to be able to describe it as new. Furthermore, this requirement creates taxonomic dilemmas when the phylogenetic relationships among species in a complex of genera are poorly resolved (Cantino, 1998; Cantino et al., 1999). If only some of the species in the complex can be referred to clades, then one must choose between two alternatives, both of which are unacceptable to many phylogenetic systematists: creating a genus that is likely to be paraphyletic or polyphyletic to accommodate the species of uncertain relationships, or classifying each of these species as a monotypic genus, thereby increasing the redundancy of the classification. This prob-

lem is not inherent to Linnaean binomial nomenclature but arises when systematists try to combine the Linnaean method with the requirement that all supraspecific taxa be monophyletic.

None of the naming methods proposed here attempts to convey phylogenetic information within the species name (although methods C, I, and J are designed to avoid the appearance of conveying incorrect information, as discussed below), so ignorance of phylogeny is not an impediment to naming species. It may seem paradoxical that phylogenetic nomenclature requires less knowledge of relationships to name species than the traditional system does, but this occurs because the naming of species is separated from their referral to clades. A benefit of this separation is greatly improved stability of species names.

Although species names are not intended to convey phylogenetic information in any of the methods proposed here, names that consist of two parts may be misunderstood to imply relationship, when encountered by people who assume that they function like Linnaean binomials. In some cases, the relationships inferred will be correct, but in some cases they will not. For example, the first part of a converted species name may be a preexisting genus name that has not been established as a clade name under the PhyloCode, perhaps because that name traditionally refers to a paraphyletic group. Even if the name of a paraphyletic genus has been established as a clade name (with its membership expanded so that it is monophyletic), the paraphyly of the genus can cause confusion. Two species whose converted names begin with the same word (the name of a paraphyletic genus) are not necessarily more closely related to each other than to a third species whose name begins with a different word. For example (Eriksson et al., 1998), *Potentilla* is a large, paraphyletic plant genus that includes the sister groups of several smaller, segregate genera. If the current names for the species in this complex were converted to binomial-based names (e.g., method B), and if *Potentilla* were established as the name of the clade comprising the paraphyletic group to which it is traditionally applied plus all of the segregate genera (as discussed by Eriksson et al.), then *Potentilla-*

bifurca would be more closely related to *Alchemilla-alpina* than to *Potentilla-norvegica*.

Moreover, the first part of the species name may be the established name of a clade to which the species does not belong. For example, the genus *Caryopteris* (Lamiaceae) has both a wide and a narrow circumscription (Cantino et al., 1999). *Caryopteris* s. str. is a clade, but *Caryopteris* s. l. is not. The species widely known as *Caryopteris divaricata* is not a member of *Caryopteris* s. str. For the sake of argument, suppose that the implementation of the PhyloCode had preceded our current understanding of the phylogeny of this group. If the name *Caryopteris divaricata* had been converted to *Caryopteris-divaricata* under the PhyloCode, and subsequent phylogenetic study led to the establishment of the name *Caryopteris* for the clade corresponding to *Caryopteris* s. str., then *Caryopteris-divaricata* would not belong to the clade *Caryopteris*. This would be misleading for users who had not yet adjusted to a system in which species names more or less resemble Linnaean binomials but are not intended to convey information about relationship.

It is possible to avoid the most severe manifestation of this problem, the inference of relationships that are known to be incorrect, in two ways. The PhyloCode could prohibit using genus names for clades (method C). Alternatively, a "limited stability" method could be used (methods I and J), in which species names must be changed if the first part of the name seems to imply membership in a clade to which it does not belong. Each of these solutions introduces its own problems. Methods I and J reduce the stability of species names (although not as seriously as the Linnaean binomial method does). Prohibiting the use of genus names for clades (method C) would require abandoning many familiar names, even though many of them currently apply (at least implicitly) to monophyletic groups. The problems discussed in this section apply only to binomial-based names. Inference of incorrect relationships cannot occur with epithet-based names (methods K–M).

Distinguishability

Some people feel that species names should differ in form from clade names to

make it immediately evident to which kind of entity a name refers. All of the proposed methods satisfy this requirement except methods D and G, in which the names of new species (method D) or all species (method G) are capitalized uninomials and thus indistinguishable from clade names. Capitalization of species names under these options is based on the argument that all scientific names should be capitalized because they are proper nouns. For uninomial species names, there is a conflict between this consideration and distinguishability from clade names. One solution might be to use italics for species names but not clade names, permitting both to be capitalized but still distinguishable. However, unless some other font (e.g., boldface) were used for clade names, they could be confused with vernacular (common) names. Many genus names, some of which would eventually be converted to clade names, are identical to vernacular names, which may not even apply to the same organisms. For example, the plant genus *Lotus* and the plant with the vernacular name Lotus are very distantly related. To avoid confusion with vernacular names, the draft PhyloCode recommends that all names established under it be italicized.

Another consideration is distinguishability of names governed by different codes. This issue has been a major source of disagreement among the authors of this paper. Some of us maintain that species names governed by the PhyloCode should be immediately distinguishable from the Linnaean binomials governed by the preexisting codes, whereas others of us argue that they need not, or even should not, be distinguishable from Linnaean binomials because the context will usually clarify which code governs the name. Methods A and I are the only ones in which species names are identical in form to Linnaean binomials. In the other binomial-based options, converted names (and in some methods, all names) are similar in form to Linnaean binomials but differ in minor ways, such as hyphenation or fusion of the two parts of the name. In the epithet-based methods (K–M), the combination of species name and a taxonomic address may be indistinguishable from a Linnaean binomial under

certain circumstances. If more than one clade is cited or if the species name and clade name are separated by a symbol such as a slash, colon, or parentheses, the names together are distinguishable from a Linnaean binomial. However, if only one clade is cited, and if its name precedes the species name and is separated from it by a blank space, the two names together are indistinguishable from a Linnaean binomial if the species name does not contain numbers. Names produced by method M never contain numbers, which makes this method attractive to those who would like the combination of a PhyloCode name and a taxonomic address to look exactly like a Linnaean binomial. Numbers may also be absent from names produced by methods K and L if the numerical portion of the name is omitted after its first use in a particular publication or (in method K) if the name is the first one established under the PhyloCode based on a particular epithet.

Those who favor indistinguishability of PhyloCode species names from Linnaean binomials argue that, to minimize disruption of the preexisting nomenclature, binomials should not be changed in any way when converted under the PhyloCode. In addition to this philosophical argument, some of us have a practical concern that people will refuse to use names that differ in appearance, even in minor ways, from the ones with which they are familiar. Others of us believe this is unlikely to be a problem; i.e., users of names will be flexible enough to accept minor changes in format such as a hyphen or a dot connecting the two words of a binomial. Those who favor distinguishability of species names governed by the PhyloCode are concerned about potential confusion if a single species has two different names that are indistinguishable in form, one of them correct under the PhyloCode and the other one correct under the preexisting code governing it. This will occur whenever a species name changes under the preexisting code (e.g., because of generic realignment) after it has been converted and thereby stabilized under the PhyloCode. In most cases, only the genus portion of the binomial will change under the preexisting code, but homonymy under the new genus will sometimes cause

the epithet to change as well. The longer the two codes coexist, the greater will be the divergence of species names under the two systems. This is a serious problem, particularly if names governed by the two systems are not distinguishable. However, the draft PhyloCode suggests a convention for distinguishing between PhyloCode names and names governed by the preexisting codes when confusion might otherwise result.

Other Desirable Features

Because scientific names are spoken as well as written, they must be pronounceable. Most of the naming methods proposed for the PhyloCode are no worse than the current one in this regard, but the fusion of the two parts of a binomial to form a single word in methods G and H may lead to pronunciation problems. When faced with long names like *Amsoniatabernaemontana* and *Agastachescrophulariaefolia*, or even relatively short ones based on binomials in which the genus name ends in an unusual vowel, people who are unfamiliar with the binomials on which these names are based are likely to have trouble figuring out how to split them into syllables. For example, someone who is unfamiliar with the genus *Muscari*, might assume that *Muscaribotryoides* is based on *Musca ribotryoides* or *Muscaribotryoides* and pronounce it accordingly. It is likely that such names will also be more difficult to memorize because pronunciation plays an important role in memorization for many people. One could argue that the inclusion of numbers in species names (methods K and L) would make verbal communication more awkward by lengthening the names, but the more likely result would be omission of the numbers (particularly the registration numbers in method L) when the name is spoken. The citation of a clade address or the context of the conversation would generally make it clear to which species the name refers, making it unnecessary to say the number.

In most of the proposed naming methods, all species names have the same form, whether they are new or converted. This has the advantage of consistency, but one might argue to the contrary that it is useful to be able to tell at a glance whether a species name is converted or applies to a

species that was first recognized after the implementation of the PhyloCode. In methods D and E, new species names take a different form from that of converted names. Converted names are based on binomials, whereas new species names must have a uninomial form, the name consisting of either one word or two fused words. These methods were proposed in response to a criticism of methods such as A and B, in which names with a binomial form would have to be found for new species in perpetuity, even though the genus category, and thus the need for a binomial name, does not exist under the PhyloCode. Methods D and E attempt to combine the advantages that a binomial-based method has for converted names (i.e., continuity through retention of the entire preexisting binomial; uniqueness without addition of numbers) with the advantages that an epithet-based method has for new names (i.e., simplicity of form; species names cannot be misunderstood to imply relationships). However, this is done at the expense of consistency of form.

Method F also attempts to combine the advantages of binomial-based and epithet-based methods, while avoiding the pronunciation problems of methods G and H and providing greater flexibility and consistency of form than methods D and E. In method F, converted species names are based on preexisting binomials, with a dot (or period) inserted between the two words as a pronunciation aid. New species names may be binomial-like with a dot between the parts (as for converted names), or they may be epithet-like with a dot inserted somewhere within the name to maintain consistency of form with converted names. The stipulation that the dot may not be placed after the first or second letter is necessary to avoid confusion with abbreviated species names governed by the preexisting codes, in which the genus name is commonly abbreviated as a single capital letter or occasionally by the first two letters (e.g., *Ph. arundinacea* for *Phalaris arundinacea*).

COMPARISON OF PROPOSED NAMING METHODS

The distinctions among the proposed methods for naming species are summarized in Table 3. No method combines all of

TABLE 3. Comparison of proposed methods for naming species.

Method ^a	Continuity between codes ^b	Stability after conversion ^c	Uniqueness ^d	Information about relationship ^e	Phylogenetic knowledge requirement ^f	Limits choice of clade names ^g	Distinguishable from clade names ^h	Distinguishable from Linnaean binomials ⁱ	Ease of pronunciation ^j	Consistency of form ^k
LB	na ^l	u	n	g	y	n	d	na	na	s
A	b	s	u	m	n	n	d	i	p	s
B	b	s	u	m	n	n	d	d	p	s
C	b	s	u	n	n	y	d	d	p	s
D	b	s	u	m	n	n	d/i	d	p	d
E	b	s	u	m	n	n	d	d	p	d
F	b	s	u	m	n	n	d	d	p	s
G	b	s	u	m	n	n	i	d	d	s
H	b	s	u	m	n	n	d	d	d	s
I	b	ls	u	n	n	n	d	i	p	s
J	b	ls	u	n	n	n	d	d	p	s
K	e	s	u/#	n	n	n	d	c/#	p	s
L	e	s	#	n	n	n	d	c/#	p	s
M	e	s	n	n	n	n	d	c	p	s

^aA–M are described in the text. "LB" designates the Linnaean binomial method.

^bb, the converted name preserves the full binomial; e, the converted name preserves only the specific epithet.

^cs, completely stable; ls, limited stability (the name must change if its first part is the established name of a clade to which the species does not belong); u, unstable (the name may change for reasons unrelated to phylogeny).

^du, species names are unique and do not contain numbers; #, species names may not be unique without numbers and therefore contain numbers to make them unique; n, species names are not necessarily unique and do not contain numbers.

^eg, species names provide information about genus membership; n, species names provide no information about relationships but also no misinformation (i.e., a species name will never seem to imply that the species belongs to a clade to which it is known not to belong); m, the name is not intended to imply relationship but in some cases may be misunderstood to imply that a species belongs to a clade to which it is known not to belong.

^fn, knowledge about the phylogenetic relationships of a species is not required to name it; y, if supraspecific taxa must be monophyletic, then phylogenetic knowledge is required to refer a species to a genus and thus to name it.

^gy, the method for naming species limits the choice of names for clades; n, the method for naming species does not limit the choice of names for clades.

^hd, species names and clade names differ in form and thus are distinguishable; i, species names are indistinguishable from clade names.

ⁱi, species names governed by the PhyloCode are indistinguishable from Linnaean binomials; d, species names, with or without a taxonomic address, are distinguishable from Linnaean binomials; c, species names are distinguishable from Linnaean binomials, but the combination of a species name and taxonomic address can be made identical to a Linnaean binomial (or may differ only in the inclusion of a number, c/#).

^jp, converted names are no more difficult to pronounce than the preexisting names on which they are based; d, converted names are sometimes more difficult to pronounce than the preexisting names.

^ks, all species names have the same form; d, new species names differ in form from converted names.

^lna, not applicable.

the desirable features discussed above; each has advantages and disadvantages. The authors of this paper have not been able to reach a consensus about the best approach because we disagree about the relative importance of the advantages and drawbacks of the various options, and because some features are viewed as advantages by some of us and as drawbacks by others (e.g., see Distinguishability). Currently, the epithet-based methods have the greatest support among the participants in the PhyloCode project, but there is also substantial support for method B among the binomial-based methods.

A fundamental dichotomy among the proposed methods distinguishes those in which converted species names are based on binomials (A–J) from those in which they are based on epithets (K–M). Epithet-based names are preferred by those who are attracted to their logical simplicity and by those who object to the fact that binomial-based names may be misinterpreted as implying relationships. Binomial-based names are preferred by those who place a premium on continuity and view the binomial as the full preexisting name and by those who object to nonunique names (method M) or to changing the name by adding numbers to it (methods K and L).

Continuity with the preexisting nomenclature is a complex issue. In Linnaean nomenclature, the binomial is traditionally viewed as the name of the species, and this is reflected in how the preexisting codes deal with homonymy. Names are treated as homonyms only if the entire binomial is identical. However, there is a way in which the epithet functions more like the true name of the species: It is the only part of the name that remains constant when new combinations are published.

Even if the binomial is considered the true name of a species, it is possible to preserve continuity with preexisting names when using an epithet-based method. This can be accomplished by citing the genus portion of the preexisting name as a taxonomic address preceding the converted species name (epithet). For example, under method K, if *Rhus radicans* were converted to *radicans*¹², and if *Rhus* is a clade, it would be possible to cite the species as *Rhus radi-*

*cans*¹² the first time it is used in a particular publication, and *Rhus radicans* or *R. radicans* subsequently. If *Rhus* is not a clade, the species could be cited as "*Rhus*" *radicans*¹² (and subsequently abbreviated as "*Rhus*" *radicans* or "*R.*" *radicans*). However, the inclusion of a taxonomic address is optional, and if one is used, it does not have to be the name of the genus of the preexisting name. For example, an author could cite this species as *Anacardiaceae radicans*¹² (assuming *Anacardiaceae* is a clade), thereby greatly reducing the continuity with the preexisting species name. In contrast, under the binomial-based options, continuity with the preexisting name at the time of conversion is ensured.

However, the epithet-based methods offer continuity of a different kind. As species names change under the preexisting codes because of generic realignments, while PhyloCode names remain stable, the two sets of names will gradually diverge. The epithet-based methods allow one to track some of the name changes that occur under the preexisting codes if one wishes, as long as the epithet doesn't change. For example, if the name *Toxicodendron radicans* were to become more widely accepted for poisonivy than *Rhus radicans* under the traditional system, one could choose to combine the species name *radicans*¹² with the clade address *Toxicodendron* instead of *Rhus*. This would not be possible with a binomial-based method. If *Rhus radicans* were converted to *Rhus-radicans* (method B), this name would have to be retained, even if users of the traditional system were to abandon *Rhus radicans* in favor of *Toxicodendron radicans*. Even under the limited stability methods (I and J), one could not change *Rhus-radicans* to *Toxicodendron-radicans* unless *Rhus* was the established name of a clade that did not include *Rhus-radicans*. If generic realignments under the preexisting codes result in an increasing proportion of monophyletic genera, the use of epithet-based names and citation of the appropriate genus name as a clade address may to a large extent avoid divergence of the names governed by the two systems.

Some of the differences among the ten options that involve binomial-based names concern distinguishability of PhyloCode

species names from Linnaean binomials (A vs B, I vs J), or from clade names (D vs E, G vs H). Some methods (C, G, H, I, and J) were introduced to circumvent or mitigate a major problem with the binomial-based options—the potential for confusion when users incorrectly assume that the first part of the name implies relationship—or to reduce the frequency of this problem by permitting new names to have a uninomial form (D and E) or a uninomial-like origin (F). All of these methods except F have the disadvantage of decreasing the stability (I and J), consistency of form (D and E), or ease of pronunciation (G and H) of species names or limiting the choice of clade names (C). Those of us who prefer binomial-based methods tend to feel that the confusion will pass with time, as users of names grow accustomed to the idea that relationships cannot be reliably inferred from the first part of a species name governed by the PhyloCode. Some of us believe this is likely to occur more quickly if PhyloCode names are readily recognizable as such (B–H, J) rather than being identical in form to a Linnaean binomial (A and I), because distinguishability of names governed by the two nomenclatural systems will hasten popular recognition that two systems are in operation and will stimulate people to ask how they differ.

Methods D–F are superficially similar but differ in some important ways. In methods D and E, new species names must consist of only one part. Because binomial form is not permitted for new names, it would not be possible to start the species name with the name of a clade whose members the new species resembles (unless the clade name is fused with the rest of the species name, as in methods G and H, which would often yield names that are difficult to pronounce, as discussed above). Methods D and E were proposed so that the binomial form would not be required for new species names, but the corresponding drawback is that the binomial form is not permitted even when it would be useful. Method F is more flexible. A new species name may derive from one word or two; the only requirement is that there be a dot somewhere within the name. The presence of the dot distinguishes species names from clade

names despite the fact that both kinds of names are capitalized (which is consistent with the fact that they are proper names). In method E, species names begin with a lower-case letter and thus are also distinguishable from clade names. In method D, species names are capitalized, and new species names are indistinguishable from clade names.

A fundamental dichotomy among the three epithet-based methods is whether names are required to be unique (K and L) or are permitted to be nonunique (M). The practical consequences will depend on the degree to which everyone follows two conventions that would eliminate the potential ambiguity caused by nonunique names: citing the unique registration number associated with a species name when the name is first used in a publication, and citing an appropriate genus name as a taxonomic address. A particular concern is the impact that rampant homonymy would have on bibliographic searches if these conventions were not followed. Some of us are confident that they would be followed, thus the nonuniqueness of names in method M would not lead to confusion; others of us strongly doubt this. An underlying disagreement is whether the registration number is more likely to be cited if (a) it is officially part of the name but may be dropped as an abbreviation (method L) than if (b) it is not an official part of the name but there is a recommendation that it be cited at least once in any publication in which the name is used (method M).

Methods K and L differ in whether the registration number is attached to every name (L) or a shorter number is added to a name only when needed to make it unique (K). In method K, no number is added if the name is based on a unique epithet or is the first instance of a particular epithet being converted to a PhyloCode name. Thus *Zea mays* would probably not require a number under method K, because the epithet *mays* is probably unique. Under method L, however, the name would end in a registration number. The advantages of method K are that many names would not require numbers, and when a number is used it would be shorter than the registration number and thus easier to remember. On the other hand,

every name will have a registration number regardless of which naming method is adopted, but method L is the only one that incorporates the number within the name to make it unique. In this sense, the shorter numbers used in method K might be viewed as redundant.

CONCLUSIONS

Although the authors of this paper do not agree which of the proposed methods for naming species is best, these methods all have advantages over Linnaean binomials. Linnaean binomials are logically inconsistent with phylogenetic nomenclature because they make the genus category mandatory. Furthermore, even if ranks are used, the requirement that species be assigned to a genus to be named encourages systematists to create paraphyletic and monotypic genera when phylogenetic resolution is too poor to refer species with confidence to genus-level clades. Even users of names who have no interest in either phylogeny or nomenclature are likely to appreciate the greater stability that these naming methods offer. And for users who are interested in phylogeny, the information about genus membership that is lost if Linnaean binomials are abandoned is easily replaced by citing a clade address. Furthermore, the citation of a clade address is more useful than inclusion of the genus as part of a Linnaean binomial because many genera are not clades. We hope that this article will stimulate discussion and ultimately lead to the acceptance of a better method for naming species than Linnaean binomials.

ACKNOWLEDGMENTS

This paper is an outgrowth of a workshop on phylogenetic nomenclature that took place on 7–9 August 1998 at the Harvard University Herbaria, Cambridge, Massachusetts, USA. The workshop was organized by Michael Donoghue, Philip Cantino, and Kevin de Queiroz and was supported in part by Harvard University funds provided to M. Donoghue. We are grateful to the staff of the Harvard Herbaria and especially to Bill Knox and Heidi Robeck for logistical support. The following people, in addition to the authors of this paper, attended the workshop and participated in relevant discussions: William Alverson, David Cannatella, Julia Clarke, Peter Crane, Noel Cross, Jacques Gauthier, Kancheepuram Gandhi, Ken Halanich, David Hibbett, Kathleen Kron, Alessandro Minelli, Richard Olmstead, Fredrik Pleijel, J. Mark Porter, Heidi

Robeck, Timothy Rowe, Christoffer Schander, Per Sundberg, Mikael Thollesson, and André Wyss. David Baum was not able to attend the workshop but participated in the subsequent Internet discussion of species nomenclature, during which many of the ideas presented in this article were developed.

REFERENCES

- BAUM, D. A. 1998. Individuality and the existence of species through time. *Syst. Biol.* 47:641–653.
- BAUM, D. A., W. S. ALVERSON, AND R. NYFFELER. 1998. A durian by any other name: Taxonomy and nomenclature of the core Malvales. *Harv. Pap. Bot.* 3:315–330.
- BRYANT, H. N. 1994. Comments on the phylogenetic definition of taxon names and conventions regarding the naming of crown clades. *Syst. Biol.* 43:124–130.
- BRYANT, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: A case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Syst. Biol.* 45:174–189.
- BRYANT, H. N. 1997. Cladistic information in phylogenetic definitions and designated phylogenetic contexts for the use of taxon names. *Biol. J. Linn. Soc.* 62:495–503.
- CAIN, A. J. 1959. The post-Linnaean development of taxonomy. *Proc. Linn. Soc. Lond.* 170:234–244.
- CANTINO, P. D. 1998. Binomials, hyphenated uninomials, and phylogenetic nomenclature. *Taxon* 47:425–429.
- CANTINO, P. D., R. G. OLMSTEAD, AND S. J. WAGSTAFF. 1997. A comparison of phylogenetic nomenclature with the current system: A botanical case study. *Syst. Biol.* 46:313–331.
- CANTINO, P. D., S. J. WAGSTAFF, AND R. G. OLMSTEAD. 1999. *Caryopteris* (Lamiaceae) and the conflict between phylogenetic and pragmatic considerations in botanical nomenclature. *Syst. Bot.* 23:369–386.
- CLARIDGE, M. F., H. A. DAWAH, AND M. R. WILSON (EDS.). 1997. *Species: The units of biodiversity*. Chapman & Hall, New York.
- CRANE, P. R., AND P. KENRICK. 1997. Problems in cladistic classification: Higher-level relationships in land plants. *Aliso* 15:87–104.
- DE QUEIROZ, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* 15:125–144.
- DE QUEIROZ, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pages 57–75 in *Endless forms: Species and speciation* (D. J. Howard and S. H. Berlocher, eds.). Oxford University Press, Oxford.
- DE QUEIROZ, K. 1999. The general lineage concept of species and the defining properties of the species category: Pages 49–89 in *Species: New interdisciplinary essays* (R. A. Wilson, ed.). MIT Press, Cambridge, Massachusetts. In press.
- DE QUEIROZ, K., AND M. J. DONOGHUE. 1990. Phylogenetic systematics and species revisited. *Cladistics* 6:83–90.
- DE QUEIROZ, K., AND J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Syst. Zool.* 39:307–322.

- DE QUEIROZ, K., AND J. GAUTHIER. 1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23:449–480.
- DE QUEIROZ, K., AND J. GAUTHIER. 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9:27–31.
- ERESHEFSKY, M. (ED.). 1992. The units of evolution: Essays on the nature of species. MIT Press, Cambridge, Massachusetts.
- ERIKSSON, T., M. J. DONOGHUE, AND M. S. HIBBS. 1998. Phylogenetic analysis of *Potentilla* using DNA sequences of nuclear ribosomal internal transcribed spacers (ITS), and implications for the classification of *Rosoidae* (*Rosaceae*). *Plant Syst. Evol.* 211:155–179.
- GRAYBEAL, A. 1995. Naming species. *Syst. Biol.* 44:237–250.
- GREUTER, W., D. L. HAWKSWORTH, J. MCNEILL, M. A. MAYO, A. MINELLI, P. H. A. SNEATH, B. J. TINDALL, P. TREHANE, AND P. TUBBS. 1998. Draft BioCode (1997): The prospective international rules for the scientific names of organisms. *Taxon* 47: 127–150.
- GRIFFITHS, G. C. D. 1976. The future of Linnaean nomenclature. *Syst. Zool.* 25:168–173.
- HÄRLIN, M. 1998. Taxonomic names and phylogenetic trees. *Zool. Scr.* 27:381–390.
- HIBBETT, D. S., AND M. J. DONOGHUE. 1998. Integrating phylogenetic analysis and classification in fungi. *Mycologia* 90:347–356.
- HOWARD, D. J., AND S. H. BERLOCHER (EDS.). 1998. Endless forms: Species and speciation. Oxford University Press, Oxford.
- KRON, K. A. 1997. Exploring alternative systems of classification. *Aliso* 15:105–112.
- LEE, M. S. Y. 1996a. The phylogenetic approach to biological taxonomy: Practical aspects. *Zool. Scr.* 25:187–190.
- LEE, M. S. Y. 1996b. Stability in meaning and content of taxon names: An evaluation of crown-clade definitions. *Proc. R. Soc. Lond. B Biol. Sci.* 263:1103–1109.
- LEE, M. S. Y. 1998. Phylogenetic uncertainty, molecular sequences, and the definition of taxon names. *Syst. Biol.* 47:719–726.
- LEE, M. S. Y. 1999. Reference taxa and phylogenetic nomenclature. *Taxon* 48:31–34.
- MICHENER, C. D. 1963. Some future developments in taxonomy. *Syst. Zool.* 12:151–172.
- MICHENER, C. D. 1964. The possible use of uninominal nomenclature to increase the stability of names in biology. *Syst. Zool.* 13:182–190.
- MINELLI, A. 1991. Names for the system and names for the classification. Pages 183–189 in *Improving the stability of names: Needs and options* (D. L. Hawksworth, ed.). Koeltz Scientific Books, Königstein, Germany.
- MINELLI, A. 1995. The changing paradigms of biological systematics: New challenges to the principles and practice of biological nomenclature. *Bull. Zool. Nomencl.* 52: 303–309.
- MOORE, G. 1998. A comparison of traditional and phylogenetic nomenclature. *Taxon* 47:561–579.
- ROWE, T., AND J. GAUTHIER. 1992. Ancestry, paleontology and definition of the name Mammalia. *Syst. Biol.* 41:372–378.
- SCHANDER, C. 1998a. Types, emendations and names—a reply to Lidén et al. *Taxon* 47:401–406.
- SCHANDER, C. 1998b. Mandatory categories and impossible hierarchies—a reply to Sosef. *Taxon* 47:407–410.
- SCHANDER, C., AND M. THOLLESSON. 1995. Phylogenetic taxonomy—some comments. *Zool. Scr.* 24:263–268.
- SERENO, P. C. 1999. Definitions in phylogenetic taxonomy: Critique and rationale. *Syst. Biol.* 48: 329–351.
- SUNDBERG, P., AND F. PLEIJEL. 1994. Phylogenetic classification and the definition of taxon names. *Zool. Scr.* 23:19–25.
- WAGSTAFF, S. J., R. G. OLMSTEAD, AND P. D. CANTINO. 1995. Parsimony analysis of cpDNA restriction site variation in subfamily Nepetoideae (Labiatae). *Am. J. Bot.* 82:886–892.
- WILSON, R. A. (ED.). 1999. *Species: New interdisciplinary essays*. MIT Press, Cambridge, Massachusetts.
- WYSS, A. R., AND J. MENG. 1996. Application of phylogenetic taxonomy to poorly resolved crown clades: A stem-modified node-based definition of Rodentia. *Syst. Biol.* 45:559–568.

Received 28 March 1999; accepted 30 April 1999.

Associate Editor: R. Olmstead