

PHYLOGENETIC NOMENCLATURE

Towards a phylogenetic nomenclature of *Tracheophyta*

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This is an abbreviated version of a paper that appears in full in the Electronic supplement to *Taxon*. Phylogenetic definitions are provided for the names of 20 clades of vascular plants (plus 33 others in the electronic supplement). Emphasis has been placed on well-supported clades that are widely known to non-specialists and/or have a deep origin within *Tracheophyta* or *Angiospermae*. These treatments follow the draft *PhyloCode* and illustrate the application of phylogenetic nomenclature in a variety of nomenclatural and phylogenetic contexts. Phylogenetic nomenclature promotes precision in distinguishing crown, apomorphy-based, and total clades, thereby improving communication about character evolution and divergence times. To make these distinctions more transparent without increasing the number of entirely different names that must be learned, the following naming conventions (which have been adopted in the most recent draft of the *PhyloCode*) are employed here: widely known names are applied to crown clades, and the corresponding total clade (i.e., crown plus stem) is named “*Pan-X*”, where “*X*” is the name of the crown (e.g., *Pan-Spermatophyta* for the total clade of plants that share more recent ancestry with extant seed plants than with any other crown clade). If a name “*X*” that is based etymologically on an apomorphy is applied to the crown, the name “*Apo-X*” is applied to the clade for which this trait is synapomorphic (e.g., *Apo-Spermatophyta* for the clade originating from the first plant with seeds). Crown clade names can be defined by three kinds of definitions, two of which are used here: standard node-based and branch-modified node-based. The latter is particularly useful when outgroup relationships of a crown clade are better known than basal relationships within the clade. Criteria and approaches used here to choose among competing preexisting names for a clade, to select a definition type, to choose appropriate specifiers, and (in some cases) to restrict the use of a name to certain phylogenetic contexts may be widely applicable when naming other clades. The phylogenetic definitions proposed here should help focus future discussions of the *PhyloCode* on real definitions rather than simplified hypothetical ones.

KEYWORDS: crown clade, total clade, *Tracheophyta*, vascular plants

INTRODUCTION

Phylogenetic nomenclature (de Queiroz & Gauthier, 1990, 1992, 1994), as embodied in the *PhyloCode* (Cantino & de Queiroz, 2006), is designed to name clades by explicit reference to phylogeny. We anticipate that the *PhyloCode* and its online registration database will be implemented within a few years. Its starting date for the purposes of precedence will be a “companion volume” of phylogenetically defined names that will be published simultaneously with the first paper version of the *Phylo-*

Code (the electronic version currently available at www.phylocode.org is a draft). The companion volume will contain names and phylogenetic definitions of many major clades and will demonstrate the application of the *PhyloCode*. Some groups of organisms will be better represented in this book than others because of the availability of well-supported phylogenies and knowledgeable systematists who are interested in contributing to the phylogenetic nomenclature of their specialty groups. We expect that vertebrates and vascular plants will be among the best represented.

Because the names and definitions in the companion volume will have precedence under the *PhyloCode* and will include major clades that are of broad interest, it is desirable that they be well vetted by the systematics community. It will also be useful, now that the *PhyloCode* is in a well-developed form, to provide some examples of its application that are both real and complex. Towards both of these ends, we present here a set of vascular plant clade names that we have defined phylogenetically following the rules of the draft *PhyloCode*. Discussion and constructive criticism of these examples would be timely, as there is still the opportunity both to revise the rules and to change clade names and definitions before the *PhyloCode* and companion volume are published. Some of the names and definitions published here will subsequently be included in the companion volume, but their publication here does not constitute establishment under the *PhyloCode* (see below) because this paper will come out before the official starting date of the code.

Vascular plants are an ideal clade with which to explore the use of the *PhyloCode*. Tracheophyte phylogeny is relatively well known compared to many other groups of organisms, but there are still many parts of it that remain incompletely resolved, reflecting poorly supported or conflicting relationships. Poor resolution presents a challenge for phylogenetic nomenclature but does not prevent its use. In the process of defining names for plant clades with incompletely known basal phylogeny or outgroup relationships, we will demonstrate strategies that are broadly applicable to similar situations in other groups.

Phylogenetic nomenclature has several advantages over the rank-based system that is embodied in the *ICBN* (McNeill & al., 2006). It eliminates a major source of instability of clade names under the rank-based codes—name changes due to shifts in rank. By divorcing naming from ranking, the *PhyloCode* makes it easier to name clades one at a time (just as one can currently name species as they are discovered) without developing or changing a classification (Hibbett & Donoghue, 1998). Under the rank-based codes, naming a clade often requires either using an unconventional intermediate rank (e.g., supersubtribe) or changing the ranks (and therefore the names) of less or more inclusive clades (Cantino & al., 1997; Kron, 1997; Hibbett & Donoghue, 1998). This problem discourages systematists from naming clades until an entire classification is developed (Hibbett & Donoghue, 1998). Meanwhile, well-supported clades are left unnamed, and taxonomy lags behind knowledge of phylogeny. This is a serious drawback at a time when advances in molecular biology and computer technology have led to a burst of new information about phylogeny. For many researchers, naming clades is just as important as naming species. In this respect, the *PhyloCode* reflects a philosophical shift from naming and subsequently classifying species

to naming both species and clades (Cantino, 2004). This does not mean that all clades must be named. The decision to name a clade will be based on criteria such as level of support, diagnosability, whether it has been named traditionally, and estimated need to communicate about the clade.

Another benefit of phylogenetic nomenclature is that it permits (though it does not require) the abandonment of categorical ranks, which would eliminate the most subjective aspect of traditional taxonomy. Because ranking decisions are arbitrary, they often rely on an appeal to authority (Donoghue, 2001). One of the supposed benefits of ranking is that biodiversity is often assessed through counts of families, genera, etc. (Forey, 2001), but this use of ranks is inappropriate because it assumes incorrectly that taxa of the same rank are comparable in a biologically meaningful way (Robeck & al., 2000; de Queiroz & Cantino, 2001; Bertrand & al., 2006). Use of informal unranked plant names above the ordinal level has become widespread in phylogenetic works (Soltis & al., 2005), but in some cases, the same name has been applied to more than one clade (e.g., “eurosids II” has been applied to three different, nested clades; see treatment of *Malvidae* below). By providing phylogenetic definitions, we hope to standardize the application of names for these clades. Moreover, phylogenetic definitions, unlike name determinations based on a rank and a type, can be translated algorithmically in a phylogenetic context (Hibbett & al., 2005) and may therefore play a key role in the emerging field of phyloinformatics. Development of an effective phyloinformatic database will make it far easier to determine how names are applied in the context of different phylogenetic hypotheses (Donoghue, 2004) and to answer questions such as the geographic distribution of a particular clade (Edwards & al., 2007).

In spite of its strengths, phylogenetic nomenclature is controversial and has been the subject of a series of critiques (e.g., Benton, 2000; Nixon & Carpenter, 2000; Forey, 2001; Moore, 2003; Pickett, 2005) and defenses (e.g., Cantino, 2000, 2004; de Queiroz & Cantino, 2001; Bryant & Cantino, 2002; Donoghue & Gauthier, 2004; Pleijel & Hårlin, 2004; Laurin & al., 2005). The phylogenetic definitions used by critics are mostly hypothetical and often simplistic. Discussion of the *PhyloCode* should focus on definitions that follow it. Of the phylogenetic definitions that have been published for plant clade names (Judd & al., 1993, 1994; Cantino & al., 1997; Baum & al., 1998; Bremer, 2000; Donoghue & al., 2001; Olmstead & al., 2001; Smedmark & Eriksson, 2002; Wolfe & al., 2002; Stefanovic & al., 2003), only those published in and after 2001 were formulated with access to the *PhyloCode*, the first draft of which became available in 2000. Although a few of the clades in these recent papers are widely known (e.g., *Caprifoliaceae*, *Convolvulaceae*), most are

familiar only to specialists. We hope that the availability of carefully crafted definitions for the names of widely discussed clades that illustrate a range of topologies and problems will improve the quality of the discussion about phylogenetic nomenclature and provide models that can be adopted for other clades.

The objectives of this paper are to: (1) provide preliminary phylogenetic definitions for the names of some frequently discussed vascular-plant clades, thereby facilitating communication about phylogeny; (2) provide botanical examples of phylogenetic definitions that follow the current draft of the *PhyloCode*, involving clades that most plant taxonomists will be familiar with, so that future discussion of the *PhyloCode* can focus on real definitions rather than hypothetical ones; and (3) illustrate a variety of phylogenetic and nomenclatural situations that may commonly be encountered in preparing phylogenetic definitions, and some widely applicable strategies for dealing with them.

What appears here is an abbreviated version of a paper that appears in full in the Electronic supplement to Taxon.

METHODS

Phylogeny of *Tracheophyta*. — Current knowledge of tracheophyte phylogeny is summarized in Fig. 1. This representation is based on both molecular and morphological analyses, and both extant and fossil plants (references are cited in the Nomenclatural treatment). The summary phylogeny incorporates our judgments about strength of support (i.e., some topological resolutions that can be found in the literature are shown as unresolved here) and is quite similar to summary trees presented by Doyle (1998), Judd & al. (2002), Friedman & al. (2004), Pryer & al. (2004a), Soltis & al. (2004, 2005), and Donoghue (2004, 2005). This paper is not a review of vascular-plant phylogeny (for which, see Bateman & al. [1998] and the references cited above). Rather, we start with a consensus phylogeny and focus on naming selected clades. Most of the clades that we have elected to name in this paper have strong molecular support, and many of them also have morphological synapomorphies.

Deciding which clades to name is bound to be somewhat subjective. We focus here, and in the Electronic supplement, on clades that have some combination of the following features: strong support, ideally from more than one dataset; an origin deep in the phylogeny of the vascular plants or of one of its two most species-rich subgroups (ferns and angiosperms); large size; frequent inclusion in introductory textbooks; and frequent designation with either an informal or a scientific name in papers, indicating a need to communicate about it. With one exception

(*Caryophyllales*; see Electronic supplement), we have not included angiosperm clades that are currently ranked at or below the ordinal level (see APG II, 2003). Rather, we focus within *Angiospermae* on large and well-supported clades that are often discussed using informal names.

Fundamentals of the *PhyloCode*. — Clades are named here using phylogenetic nomenclature (de Queiroz & Gauthier, 1994), following the draft *PhyloCode* (Cantino & de Queiroz, 2006). Taxon names are given phylogenetic definitions (de Queiroz & Gauthier, 1990, 1992), which identify a particular clade by reference to a node, branch, or apomorphy. Species, specimens, and apomorphies cited in phylogenetic definitions are called specifiers because they specify the clade to which the name applies. Internal and external specifiers are members and non-members, respectively, of the clade that is being named. What follows is an abbreviated summary of our methods, much (but not all) of which was dictated by the *PhyloCode*. For further details, see the Electronic supplement.

The *PhyloCode*, like the *ICBN*, stipulates that each taxon can have only one correct name and each name can be correct for only one taxon. Both codes use date of publication (priority) as the primary criterion for selecting the correct name when synonyms exist. However, under the *PhyloCode*, synonyms are names whose phylogenetic definitions specify the same clade, regardless of the rank (if any) associated with the name. In contrast, under the *ICBN*, synonyms are names of the same rank whose types are included within a single taxon at that rank, regardless of the clade (or non-monophyletic group) associated with the name. Both codes include mechanisms to overturn strict priority through a conservation process.

The *PhyloCode* permits one to restrict the application of names with respect to clade composition by making the name inapplicable under certain conditions. For example, if one wants to ensure that a name refers to a clade that either includes or excludes particular taxa, the definition may contain a “qualifying clause” that makes the name inapplicable to any clade in certain phylogenetic contexts (Lee, 1998). The same result can often be accomplished more simply with “taxon qualifiers” (Serenó, 2005)—e.g., external specifiers in a standard node-based definition (which normally has only internal specifiers). Taxon qualifiers are used in some definitions here (see Table 1).

Because biologists can potentially obtain a wider range of information about extant organisms than extinct ones, it is useful to distinguish crown clades from non-crown clades when communicating about character evolution and the ages and distributions of clades. A crown clade (de Queiroz & Gauthier, 1992; “crown group” of Jefferies, 1979) (e.g., *Spermatophyta* in Fig. 1) is a node-based clade in which both (or all) branches originating directly from the basal node have extant members. A total clade (“total group” of Jefferies, 1979) (e.g., *Pan-Spermatophyta* in

Table 1. Clade names defined here (bold type) and in the Electronic supplement (normal type).

Clade name	Definition type
Tracheophyta	BN
<i>Apo-Tracheophyta</i>	A
Pan-Tracheophyta	T
<i>Lycopodiophyta</i>	N
<i>Pan-Lycopodiophyta</i>	T
<i>Isoëtopsida</i>	N
<i>Euphyllophyta</i>	BN with IQ
<i>Pan-Euphyllophyta</i>	T
Monilophyta	BN with IQ
<i>Pan-Monilophyta</i>	T
<i>Equisetum</i>	BN
<i>Polypodiophyta</i>	N
<i>Psilotaceae</i>	BN
<i>Ophioglossales</i>	BN
<i>Marattiales</i>	BN
<i>Leptosporangiatae</i>	N
<i>Apo-Leptosporangiatae</i>	A
<i>Lignophyta</i>	A
Spermatophyta	N
Apo-Spermatophyta	A
Pan-Spermatophyta	T
Acrogymnospermae	N with EQ
<i>Cycadophyta</i>	N
<i>Pan-Cycadophyta</i>	T
Coniferae	N
<i>Pan-Coniferae</i>	T
<i>Pinaceae</i>	BN
Cupressophyta	N with EQ
<i>Gnetophyta</i>	N
<i>Pan-Gnetophyta</i>	T
Angiospermae	BN
<i>Apo-Angiospermae</i>	A
Pan-Angiospermae	T
Mesangiospermae	BN
<i>Magnoliidae</i>	N
<i>Monocotyledoneae</i>	N
<i>Nartheciidae</i>	N with EQ
Petrosaviidae	N with EQ
<i>Commelinidae</i>	N
Eudicotyledoneae	N
<i>Tricolpatae</i>	A
Gunneridae	N
Pentapetalae	N
<i>Caryophyllales</i>	N
<i>Rosidae</i>	BN
Fabidae	N
Malvidae	N
<i>Asteridae</i>	N
<i>Gentianidae</i>	N
Garryidae	BN with IQ
<i>Lamiidae</i>	N
Campanulidae	BN
<i>Apiidae</i>	BN with IQ

Definition types: A, apomorphy-based; BN, branch-modified node-based; N, node-based; T, total clade (a kind of branch-based definition); EQ, external qualifiers; IQ, internal qualifiers.

Clades are listed in the same order as in the Nomenclatural treatment.

Fig. 1) is composed of a crown clade and all organisms that share a more recent common ancestor with that crown clade than with any mutually exclusive crown clade; in other words, the total clade comprises the crown clade plus its entire, paraphyletic stem group. An apomorphy-based clade is one that originated from the earliest ancestor to possess a particular apomorphy. There may be many apomorphy-based clades nested between the crown and the total clade. There is no requirement that all (or any) of these clades be named, but for a well-known group with a good fossil record, it may facilitate communication to have different names for the crown, the total clade and one or more intermediate clades that are diagnosed by commonly fossilized apomorphies.

Crown clades may be specified through three kinds of node-based definitions: standard, branch-modified (formerly called stem-modified; de Queiroz in Wyss & Meng, 1996) and apomorphy-modified (de Queiroz, unpublished), but we have used only the former two here. See *PhyloCode* Note 9.4.1 (or the Electronic supplement) for recommended wordings of these definitions. For total clades, a special kind of branch-based definition is recommended in the *PhyloCode*: “the total clade composed of the crown clade *X* and all extinct organisms or species that share a more recent common ancestor with *X* than with any other mutually exclusive (non-nested) crown clade.” An abbreviated form of this definition, which we used in our Nomenclatural treatment, is “the total clade of *X*”, where *X* is the name of a crown clade.

Choice of definition type and specifiers. — The primary determinant of definition type is the author’s conceptualization of the clade. If one wishes to name the clade originating with the origin of a particular feature, only an apomorphy-based definition will ensure that the clade will include all fossil organisms possessing this apomorphy that are discovered in the future and will exclude all fossil organisms that lack the apomorphy (Lee, 1999a). Similarly, naming a clade that originates at, or immediately above a node, requires a node-based or branch-based definition, respectively.

If the name of the clade is converted from a preexisting genus name or is based on the name of a genus, the type of the genus under the *ICBN* must be an internal specifier (*PhyloCode* Art. 11.7; e.g., the type species of *Rosa* or its type specimen must be an internal specifier for *Rosidae*). Beyond this one rule, the *PhyloCode* provides only a little guidance in selecting specifiers (Recommendations 11A–F; see Discussion: Specifiers). It has been suggested that specifiers should be well-known species that are easily available to researchers (Lee, 1999b; Sereno, 1999, 2005), and that species that are nested deeply within the clade of interest are preferable to those that are not (Lee, 1999b; Sereno, 1999, 2005). Use of the same specifiers for a series of nested clades or for a pair of sister clades contributes

to the simplicity and immediate informativeness of a set of definitions (Lee, 1999b; Sereno, 1999, 2005). Finally, we suggest that it is desirable to choose specifiers from among the species that were used in the reference phylogeny. Doing so makes it easier for users of the definition to locate the clade on the reference phylogeny if the clade name is not labeled on the diagram, (which is often the case when one is formulating a phylogenetic definition based on a previously published phylogeny). Except for the required use of the type as an internal specifier when the clade name is based on a genus name, all of the other considerations mentioned above are optional, and in some cases they conflict. We have attempted to select specifiers that satisfy as many of these criteria as possible.

Choice of names. — Although choosing an appropriate name for a clade has received less attention than constructing a phylogenetic definition, it is often a more difficult problem. A clade name governed by the *PhyloCode* may be new or converted. A converted name is a preexisting name that has been established by publishing a phylogenetic definition for it. (Establishment under the *PhyloCode* is roughly equivalent to valid publication under the *ICBN*.) A preexisting name is a scientific name that has been in use prior to its establishment under the *PhyloCode*. In order to qualify as preexisting under the *PhyloCode*, a plant name must be legitimate under the *ICBN*, with one exception. Names that lack a Latin diagnosis or reference to a previously published Latin diagnosis (and thus are not validly published under the *ICBN* [Art. 36.1] if published in or after 1935) but include a diagnosis in some other language and otherwise qualify as legitimate names under the *ICBN* are accepted as preexisting names under the *PhyloCode* (Art. 6.2).

Choice of names is covered in *PhyloCode* Article 10. In general (but exceptions are detailed in Art. 10.2), one must use a preexisting name if possible, the coining of a new name generally being permitted only when there is no preexisting name for a particular clade. Because most preexisting names do not have phylogenetic definitions, the decision on whether a name applies to a particular clade must be inferred from the circumscription and diagnostic features of the taxon to which it has been applied. Such inferences are not always simple. It can be difficult to determine with certainty whether a name that was used before cladistic reasoning became widespread applied to a group that we today recognize as being a clade. If there is no preexisting name that has been applied to a particular clade, one may select a preexisting name of a paraphyletic group originating from the same immediate ancestor as that clade, or one may coin a new name; the choice between these two options is left to the discretion of the author.

If more than one preexisting name has been applied to a particular clade, the *PhyloCode* (Rec. 10.1A) recommends that the name that “is most widely and consistently

used” for that clade be selected, but considerable discretion is left to the author. As a general guideline, if there is less than a twofold difference in the frequency of competing names, the converting author may choose any of them. To estimate the relative frequency of competing names, we checked the number of references cited by *Biological Abstracts / BIOSIS Previews* (<http://www.biosis.org>) and the *Kew Bibliographic Databases (KBD)* (<http://www.kew.org/kbd/searchpage.do>); for some caveats on this approach, see the Electronic supplement.

In selecting names, we have also followed two conventions that are not covered by the *PhyloCode*. (1) If there is a choice between a currently used descriptive name (e.g., *Monocotyledoneae*) and a nondescriptive, rank-based name (e.g., *Liliopsida*), we have selected the descriptive name unless the rank-based name is far more widely used for that clade. We feel that descriptive names are easier for people to remember, in part because they often parallel widely used informal names (e.g., “monocots”). (2) If there is no descriptive name for a particular clade and two or more names that differ only in their rank-based ending have been applied to it, we have selected the name ending in *-phyta* unless one of the alternative endings is far more widely used. We prefer names ending in *-phyta* for three reasons: ease of memory, correspondence to informal names, and de-emphasis of rank. Because it is widely understood that “*phyta*” means plants, it will be easier for people to remember the names of deep clades that have this uniform ending than if they had a variety of endings. This is particularly true because the informal names currently used for many of these clades end in “*phytes*” (e.g., monilophytes, euphyllphytes). Finally, although *-phyta* is the ending designated by the *ICBN* for the rank of division (or phylum), the fact that it also means “plants” is likely to reduce its mental association with a particular rank. In contrast, endings such as *-opsida* and *-phytina* are exclusively associated with particular ranks and thus less appropriate in phylogenetic nomenclature, where rank assignment (if any) has no effect on the spelling of a name.

Crown, total, and apomorphy-based clades.

— De Queiroz & Gauthier (1992) recommended that widely known names be applied consistently to crown clades (for contrary views, see Lucas, 1992; Lee, 1996; Sereno, 2005). The *PhyloCode* (Rec. 10.1B) extends this recommendation to any name that is the most widely used preexisting name for a crown clade, regardless of whether it is widely used in an absolute sense. The rationale for this convention is explored in depth by de Queiroz (in revision). One advantage is that it standardizes the meanings of names so that neontologists and paleontologists apply the name to the same clade. Applying well-known names to the crown clade also discourages biologists from making poorly supported generalizations about extinct

relatives outside the crown clade (de Queiroz & Gauthier, 1992; Doyle & Donoghue, 1993; Gauthier & de Queiroz, 2001). For example, Jager & al. (2003: 843) discussed the need for data from cycads and *Ginkgo* “to infer the MADS-box gene content of the last common ancestor of *Spermatophyta*”. Since there is currently no way to study the MADS-box genes of extinct plants, such an inference would be poorly justified if the name *Spermatophyta* referred to a clade that is more inclusive than the crown. If widely used names like *Spermatophyta* are defined to refer to the crown clade, poorly justified inferences about clades that extend below the crown are less likely to be made. Conversely, the greatest number of well-supported inferences can generally be made about crown clades (de Queiroz & Gauthier, 1992). For related reasons, crown clades are generally easier to diagnose.

For a preexisting name to be phylogenetically defined as applying to a crown clade, it must have been used in the past for that clade. However, many of the names we define in this paper have been variably and often imprecisely applied to a crown clade and one or more larger clades that include extinct organisms outside the crown (see Discussion: Precision and clarity). In the absence of a phylogenetic definition, it is often difficult to determine the precise clade, within a set of closely nested clades, to which a name was meant to refer. In some cases, the circumscription associated with a name in a particular work included extinct taxa that are known to lie outside of the crown, but in works that deal only with extant organisms (e.g., floras, molecular studies), it is often unclear whether the user of the name intended to apply it to the crown or to a more inclusive clade. In such cases, the name may be interpreted as a preexisting name for the crown clade (*PhyloCode* Note 10.1B.1).

It is often useful to name total and apomorphy-based clades as well, and these names will be easier to remember if they are based on the name of the corresponding crown. The most recent draft of the *PhyloCode* adopted a convention used by Joyce & al. (2004), the formation of a total clade name by adding the prefix *Pan-* to the name of the crown (including the hyphen and retaining the capitalization of the crown clade name). For example, *Pan-Spermatophyta* is the total clade comprising all organisms that share more recent ancestry with the crown seed plants (*Spermatophyta*) than with any other mutually exclusive crown clade (Fig. 1). Such total clade names are termed panclade names in the *PhyloCode*. If there is a preexisting name for a total clade, the choice between converting that name and establishing a panclade name is left to the discretion of the author. None of the total clades treated in this paper have unambiguous preexisting names, but some have names that, based on composition, seem to apply approximately to the total clade. In all such cases, we have opted for panclade names.

It is sometimes worthwhile to name apomorphy-based clades, particularly if a key apomorphy is commonly preserved in the fossil record. For example, because seeds fossilize well, many seed plants from outside the crown clade *Spermatophyta* have been discovered and named. These plants do not belong to *Spermatophyta* as defined here. They do belong to the total clade *Pan-Spermatophyta*, but so do some extinct plants (e.g., *Archaeopteris*) that did not have seeds but share more recent ancestry with seed plants than with the closest extant relatives of seed plants (Fig. 1). If one wants to be able to refer to the clade comprising all and only plants that bear seeds, another name is needed. In such cases, if the name of the corresponding crown clade refers etymologically to that apomorphy, the *PhyloCode* (version 3a) recommends or requires (depending on the situation) that the prefix “*Apo-*” be added to the capitalized name of the crown clade—e.g., *Apo-Spermatophyta*.

Attribution of authorship. — When attributing authorship in the context of phylogenetic nomenclature, it is useful to distinguish between the nominal and definitional authors of converted names (creators of the name and definition, respectively; Sereno, 2005). The nominal author need not have applied the name to the same clade as the definitional author, though there must be overlap in the two circumscriptions (i.e., the application of the name to the clade concerned must be derived from the nominal author’s use of the name). Under the *PhyloCode* (Art. 20), if authorship is cited and if the definitional and nominal authors differ, the definitional author is to be cited in square brackets following the nominal author. In the case of new clade names, the nominal and definitional authors are the same and are cited only once (without brackets). The definitional authors in our nomenclatural treatment are the authors of the entire protologue.

Determining nominal authorship of suprageneric plant names is sometimes difficult. The indices prepared by Reveal (2004), Hoogland & Reveal (2005), and Kiger & Reveal (2006) are very helpful but do not include descriptive names such as *Angiospermae*. In determining authorship of a name, the *PhyloCode* differs from the *ICBN* in focusing on orthography rather than rank. Under the *ICBN*, the author of an automatically typified suprafamilial name (i.e., a name based on a genus name) is the first person who published a name based on that genus at a particular rank, regardless of whether the ending of the name was appropriate for that rank. If the ending is inappropriate, it is to be changed but without changing the authorship (*ICBN* Art. 16.3). For example, the name *Lycopsidea* Scott (1909), which was published as a division, must be changed to *Lycopodiophyta* under the *ICBN*, but Scott is still credited with the name (Hoogland & Reveal, 2005). In contrast, under the *PhyloCode* (Rec. 9.6A), the author of *Lycopodiophyta* is not considered to be Scott

but Cronquist & al. (1966), who first validly published the name with this spelling. This difference from the *ICBN* makes it more difficult for *PhyloCode* users to determine the nominal authorship of converted names, because most indices to suprageneric names (Reveal, 2004; Kiger & Reveal, 2006) list only the authorship that is considered correct under *ICBN* Art. 16.3 (an exception is Hoogland & Reveal's [2005] index to family names, which also lists the earliest use of the correct orthography). In recognition of this practical problem, the *PhyloCode* (Note 9.6A.3) permits attribution of the name in a manner consistent with the *ICBN* provided that the difference in spelling is explicitly stated. In this paper (and the Electronic supplement), we usually attribute nominal authorship of converted names to the authors that are considered correct under the *ICBN* according to Kiger & Reveal (2006). In the cases where we instead attribute nominal authorship to the earliest author of the orthography that is accepted today, we also cite the authorship that is considered correct under the *ICBN*.

Another discrepancy between the two codes in the attribution of authorship derives from the *ICBN* requirement for a Latin diagnosis or description (discussed above), which is not required under the *PhyloCode*. Thus, the nominal author of a converted name under the *PhyloCode* is the first person who published the name with a description or diagnosis (provided that the name otherwise qualifies as legitimate under the *ICBN*), regardless of whether Latin was used. For example, Sinnott (1935) first published the name *Tracheophyta*, but Cavalier-Smith (1998) was the first person to provide a Latin description or diagnosis. The name is attributed to Cavalier-Smith under the *ICBN*, but nominal authorship of the converted name is attributed to Sinnott under the *PhyloCode*.

NOMENCLATRURAL TREATMENT

The following nomenclatural treatment provides phylogenetic definitions for the names of 20 vascular plant clades together with information regarding composition and synonymy (see the Electronic supplement for treatments of 33 other clades). Four kinds of definitions are used here (Table 1): 10 node-based, 6 branch-modified node-based, 1 apomorphy-based, and 3 total clade definitions (see below). Each protologue includes the information required by the *PhyloCode* for establishment of names and, in some cases, additional information explaining the choice of name and the definition. Parenthetical taxon names within phylogenetic definitions clarify the phylogenetic positions of specifiers but are not themselves specifiers. Information on synapomorphies is provided (as recommended in the *PhyloCode*) for many of the 53 clades in the Electronic supplement, but it is omitted here due to space considerations.

Our phylogenetic definitions use species names as specifiers. However, since species names are based on types, it is the type specimens represented by the species names that are the de facto specifiers. In all crown clade definitions, “crown clade” and “extant” refer to species that are extant as of the publication of this paper. Total clade names are defined as “the total clade of *X*”, where *X* is the name of a crown clade (see Methods: Fundamentals of the *PhyloCode*).

All scientific names are italicized regardless of which code governs them, and a slash (/) is used to designate names defined in this paper (including the Electronic supplement). This “clademark” (Baum & al., 1998) is not part of the name or mandated by the *PhyloCode*; it is simply a convention used here (nomenclatural treatments and discussion below) to distinguish phylogenetically defined names from names governed by the *ICBN*.

In phylogenetic nomenclature, synonyms are differently spelled names that refer to the same clade. Synonyms may be unambiguous or approximate (terms suggested by K. de Queiroz, pers. comm.). Determination of unambiguous synonymy requires either a phylogenetic definition or a clearly labeled phylogenetic tree. Even published trees are sometimes ambiguous if the labeling does not make it clear whether a particular name refers to a node-based, apomorphy-based, or branch-based clade. In the absence of a phylogenetic definition or unambiguously labeled tree, a preexisting scientific name or an informal name may be considered an approximate synonym of a clade name if the composition or characters of the two taxa are similar. Such interpretations must be made with caution because emphasis on composition versus characters can lead to different conclusions regarding synonymy (Gauthier & de Queiroz, 2001). In the following treatments, all synonyms are approximate unless otherwise noted. We have also noted some partial synonyms—names that refer to a paraphyletic group originating from the same ancestor as the clade of concern. We have listed only synonyms that are in current or relatively recent use. There are probably many old, disused names that would qualify as approximate synonyms, but delving into the old literature to determine their circumscriptions would be very time consuming and of little interest for present purposes.

Tracheophyta Sinnott 1935: 441 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — Sinnott introduced the name, but the Latin diagnosis required by the *ICBN* was first provided by Cavalier-Smith (1998: 251).

Definition (branch-modified node-based). — The most inclusive crown clade containing *Zea mays* L. 1753 (*Spermatophyta*) but not *Phaeoceros laevis* (L.) Prosk. 1951 (*Anthocerotophyta*) or *Marchantia polymorpha* L.

1753 (*Marchantiophyta*) or *Polytrichum commune* Hedw. 1801 (*Bryophyta*).

Comments on Definition. — We use a branch-modified node-based definition here to ensure a stable composition for */Tracheophyta*. There is strong molecular evidence for the monophyly of the mosses (Cox & al., 2004), liverworts (Davis, 2004; He-Nygrén & al., 2004), and hornworts (Duff & al., 2004), and the extant sister group of */Tracheophyta* is either one of these clades or a clade comprising two or more of them (Nickrent & al., 2000; Delwiche & al., 2004; Kelch & al., 2004; Wolf & al., 2005; Qiu & al., 2006b). A standard node-based definition with two internal specifiers representing */Lycopodiophyta* and */Euphyllophyta* would be simpler, but compositional stability is more certain with the definition proposed here. We estimate the likelihood that the crown group of either mosses, liverworts or hornworts is paraphyletic because it gave rise to tracheophytes to be even lower than the likelihood that the lycophyte or euphyllophyte crown group is not monophyletic.

Reference phylogeny. — Qiu & al. (2006b: Fig. 1). See also Kenrick & Crane (1997: Fig. 4.31), Duff & Nickrent (1999), Nickrent & al. (2000), Renzaglia & al. (2000), Pryer & al. (2001), Crane & al. (2004: Fig. 1), Kelch & al. (2004), and Wolf & al. (2005).

Composition. — */Pan-Lycopodiophyta* and */Pan-Euphyllophyta*.

Synonymy. — “Eutracheophytes” sensu Kenrick & Crane (1997: 236) was described as “the tracheophyte crown group” and is thus an unambiguous synonym. *Cormatae* Jeffrey (1982) is an approximate synonym; all listed subordinate taxa are extant.

Pan-Tracheophyta P.D. Cantino & M.J. Donoghue, new clade name.

Definition. — The total clade of */Tracheophyta*.

Composition. — */Tracheophyta* and all extinct plants (e.g., *Aglaphyton*, *Horneophyton*) that share more recent ancestry with */Tracheophyta* than with extant mosses, liverworts, and hornworts.

Synonymy. — The name *Polysporangiomorpha* (polysporangiophytes) sensu Kenrick & Crane (1997: Table 7.2, Fig. 4.31) has an apomorphy-based definition and thus cannot be fully synonymous with */Pan-Tracheophyta*. Its currently known composition is similar to that of */Pan-Tracheophyta*, but there may have been pantracheophytes that preceded the origin of *Polysporangiomorpha*.

Monilophyta P.D. Cantino & M.J. Donoghue, new clade name.

Comments on name. — There is no preexisting scientific name for this crown clade. We choose the name *Monilophyta* because it corresponds closely to the informal name “monilophytes”, which is often applied to this clade

(e.g., Judd & al., 2002; Simpson, 2006; Smith & al., 2006). The name *Monilophyta* has apparently never been published with a description and therefore does not qualify as a preexisting name. It has been used for this clade in a field guide (Cobb & al., 2005) but was not provided with a description. The other possible candidate name, *Moniliformopses* Kenrick & Crane (1997: Table 7.1), was apparently an apomorphy-based name (op. cit., Table 7.2) and thus was not applied to the crown. Moreover, one recent analysis (Rothwell & Nixon, 2006) suggested that the set of extinct taxa to which Kenrick & Crane applied this name may be quite distantly related to the crown group that is now referred to as “monilophytes.”

Definition (branch-modified node-based with an internal qualifier). — The most inclusive crown clade containing *Equisetum telmateia* Ehrh. 1783 and *Pteridium aquilinum* (L.) Kuhn 1879 (*/Leptosporangiatae*) but not *Ginkgo biloba* L. 1771 (*/Spermatophyta*) or *Selaginella apoda* (L.) Spring 1840 (*/Lycopodiophyta*).

Comments on definition. — A branch-modified node-based definition normally has only one internal specifier. A second internal species is included here as a qualifier. In the context of a phylogenetic hypothesis in which extant ferns share more recent ancestry with seed plants than with */Equisetum* (e.g., Bremer & al., 1987: Fig. 1), or one in which */Equisetum* shares more recent ancestry with seed plants than with extant ferns (e.g., Rothwell, 1999: Fig. 2), the name */Monilophyta* would not apply to any clade. Abandonment of the name would be appropriate in these cases because the name “monilophytes” is universally associated with the hypothesis that ferns (including “whisk ferns”) and horsetails form a clade exclusive of seed plants.

Reference phylogeny. — Pryer & al. (2001: Fig. 1; 2004b: Fig. 3). See also Nickrent & al. (2000), Wikström & Pryer (2005), Rothwell & Nixon (2006: Fig. 6), and Schuettpelz & al. (2006).

Composition. — The total clades of */Equisetum*, */Psilotaceae*, */Ophioglossales*, */Marattiales*, and */Leptosporangiatae*.

Synonymy. — The names *Filicophyta*, *Filicopsida*, *Polypodiophyta*, *Pterophyta*, and *Pteropsida* are partial synonyms, commonly applied to a paraphyletic group originating from the same ancestor as the clade */Monilophyta* (see */Polypodiophyta* in Electronic supplement). See also Methods: Choice of names.

Other comments. — In the context of phylogenetic hypotheses in which */Monilophyta* and */Polypodiophyta* are synonyms, it is our intent that precedence be given to */Monilophyta* (see comments under */Polypodiophyta* in the Electronic supplement).

Spermatophyta Britton & Brown 1896: 49 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — Britton & Brown (1896) may not have been the first to publish the name *Spermatophyta*, but this is the earliest use of the name we have found that is valid under the *ICBN*. Although the name *Spermatophyta* is probably more often applied to the apomorphy-based clade originating with the origin of the seed than it is to the crown, it is applied to the crown in many works focusing on extant taxa (e.g., floras, molecular studies). We are aware of only one other name having been applied to the crown (see Synonymy), and only one use of it.

Definition (node-based). — The least inclusive clade containing *Liquidambar styraciflua* L. 1753 (*Angiospermae*), *Pinus strobus* L. 1753 (*Coniferae*), *Ginkgo biloba* L. 1771, *Cycas revoluta* Thunb. 1782 (*Cycadophyta*), and *Gnetum gnemon* L. 1767 (*Gnetophyta*).

Comments on definition. — When molecular data, apparent morphological synapomorphies, and the fossil record are considered together, there remains great uncertainty about relationships among the five extant subgroups of *Spermatophyta*. Therefore, all five subgroups should be represented among the internal specifiers.

Reference phylogeny. — Rydin & al. (2002: Fig. 1). See also Doyle & Donoghue (1992), Doyle & al. (1994), Rothwell & Serbet (1994), Chaw & al. (2000), Bowe & al. (2000), Magallón & Sanderson (2002), Soltis & al. (2002), and Burleigh & Mathews (2004).

Composition. — *Pan-Angiospermae*, *Pan-Coniferae*, *Pan-Cycadophyta*, *Pan-Gnetophyta*, and the total clade of *Ginkgo*.

Synonymy. — The name *Spermatophytatinae* sensu Jeffrey (1982) is an approximate synonym; all listed subordinate taxa are extant. The “platyspermic clade” of Doyle & Donoghue (1986a: 354) is an approximate synonym based on composition, but the “platysperms” of Crane (1985b) excluded *Cycadophyta*.

Apo-Spermatophyta P.D. Cantino & M.J. Donoghue, new clade name.

Definition (apomorphy-based). — The most inclusive clade exhibiting seeds synapomorphic with those in *Zea mays* L. 1753 (*Angiospermae*), *Pinus sylvestris* L. 1753 (*Coniferae*), *Ginkgo biloba* L. 1771, *Cycas circinalis* L. 1753 (*Cycadophyta*), and *Gnetum gnemon* L. 1767 (*Gnetophyta*). A seed is a fertilized ovule, the ovule being an indehiscent megasporangium surrounded by one or two integuments (represented by unfused or partially fused integumentary lobes in the earliest members). Presence of integument(s) (fused or unfused) and megasporangium indehiscence are fully correlated in all known seed plants, with the exception of some parasitic angiosperms (e.g., *Loranthaceae*; Cronquist, 1981) in which the integuments have been lost. If only one of the two features is present, indehiscence rather than the presence of an integument

will determine whether it is an ovule according to the definition used here.

Comments on definition. — If the seeds in the five specifiers are not homologous because the seeds represented in extant plants evolved more than once, a view that was formerly common (Arnold, 1948; Beck, 1966) but has not been supported by any cladistic analysis, the name *Apo-Spermatophyta* will not apply to any clade. The definition of “ovule” adopted here includes what some authors (e.g., Stewart, 1983; Stewart & Rothwell, 1993) have referred to as preovules. Various features are closely associated in the reproductive biology of seed plants (Stewart & Rothwell, 1993): e.g., an indehiscent megasporangium, an integument, pollination, and one functional megaspore (with derived exceptions in *Angiospermae* and *Gnetophyta*; Gifford & Foster, 1989). However, for the purposes of a phylogenetic definition, it is best to focus on one feature to determine whether a particular structure is an ovule (and thus whether the plant that bears it is a member of *Apo-Spermatophyta*). We have chosen indehiscence of the megasporangium (as suggested by G.W. Rothwell, pers. comm.) because it is fundamental to the reproductive biology of seed plants. However, the presence of an integument is widely used as a surrogate for megasporangium indehiscence to classify a fossilized structure as an ovule (Stewart, 1983; Stewart & Rothwell, 1993).

Reference phylogeny. — Rothwell & Serbet (1994: Fig. 3; the key synapomorphy originated on branch 33 but seems to have been accidentally omitted from their Table 2; it [character 35] is included in their Table 1). See also Crane (1985a) and Doyle & Donoghue (1986a).

Composition. — *Spermatophyta* and extinct seed-bearing plants that lie outside the crown (e.g., Paleozoic seed ferns).

Synonymy. — The name *Spermatophytata* Kenrick & Crane (1997: Table 7.2) has an apomorphy-based definition. Although the authors did not mention megasporangium indehiscence, the two synapomorphies they cited (single megaspore per megasporangium and presence of an integument) are closely associated characters (see Comments on definition), and the known content of *Spermatophytata* is identical to that of *Apo-Spermatophyta*. The name *Gymnospermae* is a partial synonym; the gymnosperms originated from the same immediate ancestor as *Apo-Spermatophyta* but are paraphyletic with respect to angiosperms.

Pan-Spermatophyta P.D. Cantino & M.J. Donoghue, new clade name.

Definition. — The total clade of *Spermatophyta*.

Composition. — *Spermatophyta*, extinct *Lignophyta* and all other extinct plants (e.g., possibly *Pertica*; Kenrick & Crane, 1997: Fig. 4.31; Pryer & al., 2004a: Fig. 10.6)

that share more recent ancestry with *Spermatophyta* than with any extant plants that do not bear seeds.

Synonymy. — The name *Radiatopses* (Kenrick & Crane, 1997: Tables 7.1, 7.2) is an approximate synonym. It has a “synapomorphy-based definition,” but its currently known composition appears to be identical to that of *Pan-Spermatophyta*.

Acrogymnospermae P.D. Cantino & M.J. Donoghue, new clade name.

Comments on name. — There is no preexisting scientific name for the clade that includes all extant gymnosperms. *Gymnospermae* is not an appropriate name for this crown clade because this name is widely understood to apply to a paraphyletic group (when fossil taxa are included, as they generally are) that originated from a different ancestor—the immediate ancestor of *Apo-Spermatophyta*. “*Acro-*” means top, summit or peak (Brown, 1956).

Definition (node-based with external qualifier). — The least inclusive clade containing *Cycas circinalis* L. 1753 (*Cycadophyta*), *Pinus sylvestris* L. 1753 (*Coniferae*), *Ginkgo biloba* L. 1771, and *Gnetum gnemon* L. 1767 (*Gnetophyta*), but not *Magnolia virginiana* L. 1753 (*Angiospermae*).

Comments on definition. — *Magnolia virginiana* is a qualifier (Serenó, 2005). If crown gymnosperms do not form a clade (as in many analyses that included morphological data and/or fossils [Hill & Crane, 1982; Crane, 1985a; Doyle & Donoghue, 1986a, b, 1992; Loconte & Stevenson, 1990; Doyle & al., 1994; Nixon & al., 1994; Rothwell & Serbet, 1994; Doyle, 1996] and some analyses of exclusively molecular data [Sanderson & al., 2000; Magallón & Sanderson, 2002; Rydin & al., 2002; Soltis & al., 2002; Rai & al., 2003]), the name *Acrogymnospermae* will not apply to any clade.

Reference phylogeny. — Bowe & al. (2000: Fig. 3A). See also Chaw & al. (2000), Magallón & Sanderson (2002), Rydin & al. (2002), and Soltis & al. (2002).

Composition. — The crown clade that includes extant conifers, cycads, ginkgo, and gnetophytes but not angiosperms.

Synonymy. — None.

Coniferae Jussieu 1789: 411 [P.D. Cantino, M.J. Donoghue & J.A. Doyle], converted clade name.

Comments on name. — The names *Coniferae*, *Pino-psida*, *Coniferophyta*, *Coniferopsida*, and *Coniferales* are all widely applied to this clade. The name *Pinophyta* is ambiguous because it is often applied to the paraphyletic group that includes all gymnosperms (Cronquist & al., 1972; Jones & Luchsinger, 1986; Meyen, 1987; Fedorov, 1999; Woodland, 2000). In accordance with our preference (see Methods: Choice of names) for names that are

descriptive or end in *-phyta*, *Coniferae* and *Coniferophyta* are the best candidate names for this clade. We have chosen *Coniferae* over *Coniferophyta* because the informal name “coniferophytes” traditionally referred to a larger group that includes *Ginkgo* and *Cordaitales* as well as conifers (e.g., Coulter & Chamberlain, 1910; Chamberlain, 1935; Foster & Gifford, 1974). The name *Coniferophyta* is best reserved for this larger group in the context of phylogenies in which it is a clade (e.g., Crane, 1985a; Doyle & Donoghue, 1986a; Doyle, 1996), although we do not define *Coniferophyta* here.

Definition (node-based). — Least inclusive clade containing *Pinus strobus* L. 1753, *Cupressus sempervirens* L. 1753, *Podocarpus macrophyllus* (Thunb.) Sweet 1818, and *Taxus baccata* L. 1753.

Comments on definition. — Many molecular analyses (e.g., Stefanovic & al., 1998; Bowe & al., 2000; Chaw & al., 2000; Gugerli & al., 2001; Magallón & Sanderson, 2002; Rydin & al., 2002; Soltis & al., 2002; Burleigh & Mathews, 2004) and a morphological analysis (Hart, 1987) of extant conifers agreed that the clade *Pinaceae* (or a clade comprising *Pinaceae* and *Gnetophyta*; see Electronic supplement) is sister to the rest of the conifers. However, cladistic analyses that included fossils suggested that *Taxaceae* are the extant sister to the rest (Miller, 1988, 1999), that a clade comprising *Podocarpaceae* and *Pinaceae* occupies this position (Doyle, 1996; Hilton & Bateman, 2006), or that the position of *Podocarpus* is unresolved relative to *Pinaceae* and the rest of the conifers (Doyle, 2006: Fig. 6)—hence our inclusion of species of *Taxus* and *Podocarpus* as internal specifiers. Because no member of *Gnetophyta* is an internal or external specifier, this definition permits application of the name *Coniferae* in the context of the “gnepine hypothesis” (Bowe & al., 2000), in which case the clade *Gnetophyta* is nested within *Coniferae*, but it does not require the inclusion of *Gnetophyta*.

Reference phylogeny. — Rydin & al. (2002: Fig. 1). See also Hart (1987: Fig. 2), Stefanovic & al. (1998: Fig. 5), Miller (1999: Fig. 21), Bowe & al. (2000), Chaw & al. (2000), Magallón & Sanderson (2002).

Composition. — The total clades of *Pinaceae* and *Cupressophyta*. The clade *Coniferae* also includes *Gnetophyta* in many analyses of molecular data.

Synonymy. — See Comments on name.

Cupressophyta P.D. Cantino & M.J. Donoghue, new clade name.

Comments on name. — There is no preexisting scientific name for this clade, which is referred to informally as “conifer II” in several recent papers (Bowe & al., 2000; Gugerli & al., 2001; Rydin & al., 2002).

Definition (node-based). — Least inclusive clade containing *Cupressus sempervirens* L. 1753, *Podocarpus macrophyllus* (Thunb.) Sweet 1818, and *Araucaria*

araucana (Molina) K. Koch 1873 but not *Pinus strobus* L. 1753 (*/Pinaceae*).

Comments on definition. — There is strong molecular support (Stefanovic & al., 1998; Rydin & al., 2002) for the basal dichotomy, with the *Araucariaceae-Podocarpaceae* clade being sister to the rest of */Cupressophyta*. However, a morphological cladistic analysis (Hart, 1987) and some molecular analyses (Soltis & al., 2002) suggest that *Podocarpaceae* alone are sister to the rest of */Cupressophyta*. Contrary to these results, some morphological analyses found *Podocarpaceae* to be sister to */Pinaceae* (Doyle, 1996; Doyle, 2006: Fig. 7; Hilton & Bateman, 2006). *Pinus* is included as an external qualifier to render the name */Cupressophyta* inapplicable to any clade in the latter phylogenetic context.

Reference phylogeny. — Rydin & al. (2002: Fig. 1) and Stefanovic & al. (1998: Fig. 5). See also Hart (1987: Fig. 2), Gugerli & al. (2001), Magallón & Sanderson (2002), Soltis & al. (2002).

Composition. — *Araucariaceae*, *Cephalotaxaceae*, *Cupressaceae* (including “*Taxodiaceae*”), *Podocarpaceae*, *Sciadopitys*, and *Taxaceae*. If one accepts the phylogeny hypothesized by Miller (1999: Fig. 21), *Taxaceae* are not part of */Cupressophyta*.

Synonymy. — None.

Angiospermae Lindley 1830: xxxvi [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — *Angiospermae* and *Magnoliophyta* are the principal names for this clade. We adopt the name *Angiospermae* here because we prefer to avoid names with a rank-based ending if there is a reasonable alternative, and it appears to be the more widely used of the two names. The name *Magnoliopsida* is sometimes applied to this clade (e.g., Jeffrey, 1982; Scagel & al., 1984) but is more widely applied to the paraphyletic group, “dicots” (e.g., Takhtajan, 1987, 1997; Cronquist, 1981; and many texts that adopted Cronquist’s system). Although Lindley published *Angiospermae* as a tribe that contains orders, and thus it was not validly published by Lindley according to *ICBN* Art. 33.9, this does not disqualify Lindley as the earliest author of the preexisting name *Angiospermae* under the *PhyloCode* (see *PhyloCode* Rec. 9.6A). Crantz (1769) applied the name *Angiospermae* to a group of 13 genera, but it is clear that he did not intend the name to apply to all flowering plants. Lindley did not refer to *Angiospermae* Crantz, so there is no evidence that he was simply broadening the circumscription associated with Crantz’s name. Furthermore, *Angiospermae* Crantz is a nomen nudum, whereas Lindley included a very brief description (“seeds enclosed in a pericarpium”). We therefore attribute the name *Angiospermae* to Lindley.

Definition (branch-modified node-based). — Most inclusive crown clade containing *Zea mays* L. 1753 but

not *Cycas circinalis* L. 1753 (*/Cycadophyta*) or *Ginkgo biloba* L. 1771 or *Gnetum gnemon* L. 1767 (*/Gnetophyta*) or *Pinus sylvestris* L. 1753 (*/Coniferae*).

Comments on definition. — In various cladistic analyses, the extant sister group of the angiosperm crown clade has been inferred to be either */Gnetophyta* (Crane, 1985a; Doyle & Donoghue, 1986a, b, 1992; Loconte & Stevenson, 1990; Doyle & al., 1994; Rothwell & Serbet, 1994; Doyle, 1996, 2006; Stefanovic & al., 1998; Rydin & al., 2002: Fig. 3; Hilton & Bateman, 2006), a clade comprising *Gnetum* and *Welwitschia* (Nixon & al., 1994), */Acrogymnospermae* (Bowe & al., 2000; Chaw & al., 2000; Gugerli & al., 2001; Magallón & Sanderson, 2002; Soltis & al., 2002: Figs. 2, 4, 5, 6), a clade comprising conifers, cycads, and *Ginkgo* (Hamby & Zimmer, 1992; Magallón & Sanderson, 2002; Rydin & al., 2002: Figs. 1, 2; Soltis & al., 2002: Fig. 3; Rai & al., 2003), a clade comprising conifers and */Gnetophyta* (Hill & Crane, 1982; Soltis & al., 2002: Fig. 1), or */Cycadophyta* (Doyle, 2006: Fig. 7). Because of this uncertainty about outgroup relationships, four external specifiers are used here. A standard node-based definition with three specifiers (two of which would be *Amborella trichopoda* and any species of *Nymphaeales* or *Hydatellaceae*) would be simpler. However, the immensity of */Angiospermae* and the recency of the discovery that *Amborella* or a clade comprising *Amborella* and *Nymphaeales/Hydatellaceae* is (apparently) sister to the rest of the angiosperms argue against this sort of definition. Regardless of how confident one may currently feel about the position of *Amborella*, one must consider the possibility that some other angiosperm that has to date not been included in a molecular analysis may turn out to be sister to the rest. The recent discovery (Saarela & al., 2007) that *Hydatellaceae*, formerly thought to be monocots, are related to *Nymphaeales* near the base of the angiosperm tree illustrates this point. Compositional stability is better served by a branch-modified node-based definition with the relatively few candidates for extant sister group represented among the external specifiers.

Reference phylogeny. — Rydin & al. (2002: Figs. 1–3). See also Doyle & Donoghue (1992), Rothwell & Serbet (1994), Magallón & Sanderson (2002), Soltis & al. (2002), and Doyle (2006).

Composition. — *Amborella*, *Nymphaeales*, *Hydatellaceae*, *Austrobaileyales*, *Ceratophyllum*, *Chloranthaceae*, and the total clades of */Magnoliidae*, */Monocotyledoneae*, and */Eudicotyledoneae*.

Synonymy. — See Comments on name. *Anthophyta* of some authors (e.g., Bold, 1957; Bold & al., 1980) is also a synonym.

Pan-Angiospermae P.D. Cantino & M.J. Donoghue, new clade name.

Definition. — The total clade of */Angiospermae*.

Composition. — *Angiospermae* and all extinct plants that share more recent ancestry with *Angiospermae* than with any other extant seed plants. *Caytonia*, *Bennettitales*, *Pentoxylon*, and *Glossopteridales* are pan-angiosperms in the consensus tree of Hilton & Bateman (2006). Doyle's (2006) analysis also suggested that *Bennettitales* are pan-angiosperms, but *Caytonia*, *Pentoxylon*, and *Glossopteridales* were members of this clade in some trees but not others.

Synonymy. — *Magnoliophyta* sensu Doweld (2001) may be synonymous; its inclusion of extinct, non-carpel bearing seed plants such as *Caytonia* and *Leptostrobus* suggests that it is conceptualized as a total clade. Although not a scientific name, "angiophytes" (Doyle & Donoghue, 1993: 146) refers unambiguously to the angiosperm total clade.

Mesangiospermae M.J. Donoghue, J.A. Doyle & P.D. Cantino, new clade name.

Comments on name. — There is no preexisting scientific name for this large and well-supported clade, which includes the vast majority of the angiosperms. In most recent analyses of the basal angiosperm problem (e.g., Mathews & Donoghue, 1999; Doyle & Endress, 2000; Qiu & al., 2000; Zanis & al., 2002), which have focused on resolving relationships among *Amborella*, *Nymphaeales*, and *Austrobaileyales* (the so-called ANITA grade of Qiu & al., 1999, now extended to include *Hydatellaceae* [Saarela & al., 2007]), the clade comprising the remaining angiosperms has not been labeled in the accompanying trees, though it was referred to in discussion as "euangiosperms" by Qiu & al. (2000: S7). Similarly, it has not received even an informal name in phylogenetic studies of the angiosperms as a whole (e.g., Soltis & al., 2000; Hilu & al., 2003) or in summary treatments (e.g., APG II, 2003; Soltis & al., 2005) despite rather high levels of support. In one text (Judd & al., 2002: 178), it has been called the "core angiosperms." We propose the new name *Mesangiospermae* for this clade, which is a rough translation of "core angiosperms"; the prefix "mes-" means "middle" or "central."

Definition (branch-modified node-based). — The most inclusive crown clade containing *Platanus occidentalis* L. 1753 but not *Amborella trichopoda* Baill. 1869, *Nymphaea odorata* Aiton 1789 (*Nymphaeales*), or *Austrobaileya scandens* C.T. White 1933 (*Austrobaileyales*).

Comments on definition. — Because outgroup relationships are better resolved than basal relationships within *Mesangiospermae*, compositional stability can be achieved more simply with a branch-modified node-based definition than a standard node-based definition (see Discussion: Choice of definition type for crown clades). Relationships among five clades at the base of *Mesangiospermae* (*Chloranthaceae*, *Ceratophyllum*, *Magnoliidae*,

Monocotyledoneae, *Eudicotyledoneae*) remain poorly resolved. Some analyses have suggested that *Chloranthaceae* (e.g., Doyle & Endress, 2000; Qiu & al., 2005: Fig. 1) or a clade comprising *Chloranthaceae* and *Magnoliidae* (Saarela & al., 2007: Fig. 2) is the sister group of the rest of *Mesangiospermae*. Others have supported *Ceratophyllum* alone (e.g., Zanis & al., 2002, Fig. 4), *Monocotyledoneae* alone (Qiu & al., 2005: Fig. 2), or a clade consisting of *Ceratophyllum* and monocots (Qiu & al., 2005: Fig. 3C; Zanis & al., 2002: Fig. 3) as sister to the rest (see Soltis & al., 2005, for discussion). In still other analyses, *Ceratophyllum* has been linked instead with eudicots (Hilu & al., 2003; Qiu & al., 2005: Fig. 2; Graham & al., 2006; Saarela & al., 2007) or with *Chloranthaceae* (Qiu & al., 2005: Fig. 3A, B; Qiu & al., 2006a: Fig. 3). By using a branch-modified node-based definition, and citing all plausible candidates for the extant sister group among the external specifiers, we ensure that all of the major clades of *Mesangiospermae* will be included regardless of their basal topology. This definition also ensures that the name *Mesangiospermae* will still apply to a clade that includes the three major subclades *Magnoliidae*, *Monocotyledoneae*, and *Eudicotyledoneae* in the unlikely event that *Chloranthaceae*, *Ceratophyllum* or both are shown to be linked with one of the more basal angiosperm clades.

Reference phylogeny. — Qiu & al. (2005: Fig. 2). See also Mathews & Donoghue (1999), Doyle & Endress (2000), Qiu & al. (2000), Soltis & al. (2000), Zanis & al. (2002), Hilu & al. (2003), and Qiu & al. (2006a).

Composition. — *Chloranthaceae*, *Ceratophyllum*, and the total clades of *Magnoliidae*, *Monocotyledoneae*, and *Eudicotyledoneae*.

Synonymy. — None.

Petrosaviidae S.W. Graham & W.S. Judd, new clade name.

Comments on name. — The name *Petrosaviidae* is chosen to emphasize a deep split in monocot phylogeny that is well supported but only recently discovered, with *Petrosaviales* sister to most other monocots. The clade has not been named previously, and the name *Petrosavianae* Doweld (2001) has not been applied to this clade.

Definition (node-based with two external qualifiers). — The least inclusive clade containing *Typha latifolia* L. 1753 (*Commelinidae*), *Lilium regale* E.H. Wilson 1913 (*Liliales*), and *Petrosavia stellaris* Becc. 1871 (*Petrosaviales*), but not *Acorus calamus* L. 1753 or *Gymnostachys anceps* R. Br. 1810 (*Alismatales*).

Comments on definition. — The name applies to a clade that includes most extant monocots. External qualifiers are used to prevent the name from applying to any clade that includes *Acorus calamus* or *Gymnostachys anceps* in the event that current estimates of phylogeny turn out to be incorrect.

Reference phylogeny. — Tamura & al. (2004: Fig. 1). See also Cameron & al. (2003), Chase & al. (2006), Davis & al. (2004, 2006), and Graham & al. (2006).

Composition. — *Asparagales*, *Dioscoreales*, *Liliales*, *Pandanales*, *Petrosaviales*, and the total clade of */Comelinidae*.

Synonymy. — None.

Eudicotyledoneae M.J. Donoghue, J.A. Doyle & P.D. Cantino, new clade name.

Comments on name. — The new name *Eudicotyledoneae* is proposed here for the clade that has widely been referred to informally as either “eudicots” or “tricolpates.” There is no preexisting scientific name for this large clade, which was originally recognized, though only equivocally supported, based on morphology (Donoghue & Doyle, 1989) and subsequently strongly supported by molecular data (cited under Reference phylogeny). This clade was originally referred to as the “tricolpates” (Donoghue & Doyle, 1989). Doyle & Hotton (1991) later coined the name “eudicots” to signify that this very large group of the traditional (paraphyletic) dicotyledons formed a true (eu-) clade. Since that time, the name eudicots has been used most frequently, and it has been adopted in widely cited phylogenetic studies and classification schemes (e.g., APG, 1998; APG II, 2003; Doyle & Endress, 2000; Hilu & al., 2003; Soltis & al., 2003, 2005; Soltis & Soltis, 2004), as well as in textbooks (e.g., Judd & al., 2002; Soltis & al., 2005; Simpson, 2006). Although cogent arguments have been made in favor of reverting to use of the name tricolpates (Judd & Olmstead, 2004), we have chosen *Eudicotyledoneae* for the crown clade owing to the widespread use of the name eudicots, which now extends well beyond the plant systematics literature. We define the name *Tricolpatae* (Electronic supplement) for the apomorphy-based clade.

Definition (node-based). — The least inclusive clade containing *Ranunculus trichophyllus* Chaix ex Vill. 1786 (*Ranunculales*), *Platanus occidentalis* L. 1753 (*Proteales*), *Sabia swinhoei* Hemsl. 1886 (*Sabiaceae*), *Trochodendron aralioides* Siebold & Zucc. 1838 (*Trochodendraceae*), *Buxus sempervirens* L. 1753 (*Buxaceae*), and *Helianthus annuus* L. 1753 (*/Gunneridae*).

Comments on definition. — A simpler node-based definition with only two specifiers (e.g., species of *Ranunculus* and *Helianthus*) might have been used, reflecting the hypothesis that *Ranunculales* form a clade that is the sister group of a clade containing the remaining eudicots. Evidence for this basal split within eudicots has grown steadily as more comprehensive molecular analyses have been carried out (e.g., compare confidence measures in Soltis & al., 2000; Hilu & al., 2003; Soltis & al., 2003; Kim & al., 2004). The position of *Euptelea* as sister group to the remaining *Ranunculales* seems to have stabilized

in more recent analyses. However, because measures of confidence remain rather low for the monophyly of the clade that includes *Proteales*, *Sabiaceae*, *Trochodendraceae*, *Buxaceae*, and */Gunneridae*, as well as for the relationships among these groups, we have opted for a more conservative node-based definition that includes specifiers representing each of these groups. The definition makes no reference to *Chloranthaceae*, *Ceratophyllum*, */Magnoliidae*, or */Monocotyledonae*, whose relationships to one another, and to */Eudicotyledoneae*, have not yet been confidently resolved (see discussion of */Mesangiospermae* above). Although any of these may be closely related to */Eudicotyledoneae*, it seems highly unlikely that they will fall within the clade.

Reference phylogeny. — Soltis & al. (2003: Fig. 2). See also Doyle & Endress (2000), Soltis & al. (2000), Zanis & al. (2002), Hilu & al. (2003), Kim & al. (2004).

Composition. — *Ranunculales* (sensu APG II, 2003) and its presumed sister clade, the latter including *Proteales* (*Proteaceae*, *Platanus*, *Nelumbo*), *Sabiaceae*, *Trochodendraceae* (including *Tetracentron*), *Buxaceae* (including *Didymelea*), and */Gunneridae*.

Synonymy. — None.

Gunneridae D.E. Soltis, P.S. Soltis & W.S. Judd, new clade name.

Comments on name. — There is no preexisting scientific name for this clade. The new name *Gunneridae* is proposed for the clade that has been called the core eudicots or core tricolpates in several phylogenetic classifications (e.g., APG, 1998; APG II, 2003; Hilu & al., 2003; Soltis & al., 2003, 2005; Judd & Olmstead, 2004; Soltis & Soltis, 2004).

Definition (node-based). — The least inclusive clade containing *Gunnera perpensa* L. 1767 (*Gunnerales*) and *Helianthus annuus* L. 1753 (*/Pentapetalae*).

Reference phylogeny: Soltis & al. (2003: Fig. 2). See also Hoot & al. (1999), Savolainen & al. (2000a, b), Soltis & al. (2000), and Hilu & al. (2003).

Composition. — *Gunnerales* and the total clade of */Pentapetalae*.

Synonymy. — None currently known. If */Gunneridae* and */Pentapetalae* become synonymous in the context of a future phylogeny, we intend that */Pentapetalae* have precedence.

Pentapetalae D.E. Soltis, P.S. Soltis & W.S. Judd, new clade name.

Comments on name. — There is no preexisting scientific name for this clade. The new name *Pentapetalae* is proposed for the clade that is called the “core eudicots” by Stevens (2006) (but not other authors; see */Gunneridae*), a clade that is resolved (but not named) in several phylogenetic analyses and summary trees (e.g., Hilu & al.,

2003; Soltis & al., 2003, 2005; Judd & Olmstead, 2004; Soltis & Soltis, 2004).

Definition (node-based). — The least inclusive clade containing *Viscum album* L. 1753 (*Santalales*), *Berberidopsis corallina* Hook. f. 1862 (*Berberidopsidales*), *Stellaria media* (L.) Vill. 1788 (*Caryophyllales*), *Dillenia indica* L. 1753 (*Dilleniaceae*), *Saxifraga mertensiana* Bong. 1832 (*Saxifragales*), *Vitis aestivalis* Michx. 1803 (*Vitaceae*), *Photinia × fraseri* Dress 1961 (*Rosidae*), and *Helianthus annuus* L. 1753 (*Asteridae*).

Reference phylogeny. — Soltis & al. (2003: Fig. 2). See also Hilu & al. (2003), Hoot & al. (1999), and Savolainen & al. (2000a).

Composition. — *Berberidopsidales* (including *Aetoxiaceae*; Hilu & al., 2003; Soltis & al., 2005), *Dilleniaceae*, *Santalales*, *Saxifragales*, *Vitaceae*, and the total clades of */Asteridae*, */Caryophyllales*, and */Rosidae*.

Synonymy. — None currently known. If */Gunneridae* and */Pentapetalae* become synonymous in the context of a future phylogeny, we intend that */Pentapetalae* have precedence.

Fabidae W.S. Judd, D.E. Soltis & P.S. Soltis, new clade name.

Comments on name. — There is no preexisting scientific name for this clade. The new name *Fabidae* is proposed for the clade that has been informally named “eurosids I” in several recent phylogenetic treatments of angiosperms (Savolainen & al., 2000a, b; Soltis & al., 2000, 2005; Judd & al., 2002; APG II, 2003; Hilu & al., 2003; Soltis & Soltis, 2004) or “fabids” by Judd & Olmstead (2004).

Definition (node-based). — The least inclusive clade containing *Photinia × fraseri* Dress 1961 (*Rosales*), *Guaicum sanctum* L. 1753 (*Zygophyllales*), *Malpighia coccigera* L. 1753 (*Malpighiales*), *Oxalis dillenii* Jacq. 1794 (*Oxalidales*), *Euonymus alatus* (Thunb.) Siebold 1830 (*Celastrales*), *Vicia faba* L. 1753 (*Fabales*), *Cucurbita pepo* L. 1753 (*Cucurbitales*), *Fagus grandifolia* Ehrh. 1788 (*Fagales*), and *Afrostryax* sp. (*Cheek 5007 [K]*) (*Huaceae*).

Reference phylogeny. — Soltis & al. (2000: Figs. 7–8). See also Hilu & al. (2003), Savolainen & al. (2000a, b), and Soltis & al. (2003).

Composition. — *Celastrales*, *Cucurbitales*, *Fabales*, *Fagales*, *Huaceae*, *Oxalidales*, *Malpighiales*, *Rosales* and *Zygophyllales*.

Synonymy. — None known.

Malvidae W.S. Judd, D.E. Soltis & P.S. Soltis, new clade name.

Comments on name. — There is no preexisting scientific name for this clade. The new name *Malvidae* is proposed for the clade that has been informally named “eurosids II” in several recent phylogenetic treatments of

the angiosperms (Soltis & al., 2000, 2005; Judd & al., 2002; APG II, 2003; Hilu & al., 2003; Soltis & Soltis, 2004) or “malvids” by Judd & Olmstead (2004). The name “eurosids II” has also been applied to a larger clade that included *Myrtales* (Savolainen & al., 2000a), a metaphyletic group (i.e., uncertain whether mono- or paraphyletic) that included *Myrtales* (APG, 1998), and a smaller clade that included only *Brassicales* and *Malvales* (Savolainen & al., 2000b).

Definition (node-based). — The least inclusive clade containing *Tapiscia sinensis* Oliv. 1890 (*Tapisciaceae*), *Malva sylvestris* L. 1753 (*Malvales*), *Koelreuteria paniculata* Laxm. 1772 (*Sapindales*), and *Brassica oleracea* L. 1753 (*Brassicales*).

Reference phylogeny. — Soltis & al. (2000: Fig. 9). See also Savolainen & al. (2000a, b), Hilu & al. (2003), Soltis & al. (2003), and Alford (2006).

Composition. — *Brassicales*, *Dipentodontaceae*, *Gerrardinaceae*, *Malvales*, *Sapindales*, and *Tapisciaceae* (Alford, 2006).

Synonymy. — None.

Garryidae R.G. Olmstead, W.S. Judd & P.D. Cantino, new clade name.

Comments on name. — There is no preexisting scientific name for this clade, which has been referred to informally as “asterid I” (Chase & al., 1993), “euasterids I” (Olmstead & al., 2000; Soltis & al., 2000; Savolainen & al., 2000a; Albach & al., 2001b; Hilu & al., 2003; APG II, 2003) and “lamiids” (Bremer & al., 2002; Judd & Olmstead, 2004). The name *Lamiidae* is applied here to the slightly less inclusive clade to which it was applied by Olmstead & al. (1992, 1993; see */Lamiidae* in Electronic supplement).

Definition (branch-modified node-based with an internal qualifier). — The most inclusive crown clade containing *Garrya elliptica* Douglas ex Lindl. 1834 (*Garryales*) and *Lamium purpureum* L. 1753 (*/Lamiidae*) but not *Campanula elatines* L. 1759 (*/Campanulidae*) or *Cornus mas* L. 1753 (*Cornales*) or *Erica carnea* L. 1753 (*Ericales*).

Comments on definition. — A branch-modified node-based definition normally has only one internal specifier. A second internal species is included here as a qualifier (Serenó, 2005). In the unlikely event that *Garryales* turn out in the future to have quite a different phylogenetic position than is currently believed (for example, if they are found to be related to *Cornaceae*, as proposed by Cronquist [1981]), the name */Garryidae* will not apply to any clade.

Reference phylogeny. — Bremer & al. (2002: Fig. 1). See also Soltis & al. (2000), Olmstead & al. (2000), and Kårehed (2001: Figs. 1, 2).

Composition. — *Garryales*, *Icacinaceae*, *Oncothecaceae*, and the total clade of */Lamiidae*.

Synonymy. — None.

Campanulidae M.J. Donoghue & P.D. Cantino, new clade name.

Comments on name. — There is no preexisting scientific name for this clade, but it has been referred to informally as “asterid II” (Chase & al., 1993), “euasterid(s) II” (APG, 1998; Olmstead & al., 2000; Savolainen & al., 2000a; Soltis & al., 2000; Albach & al., 2001a, b; Lundberg, 2001; APG II, 2003), and “campanulids” (Bremer & al., 2002; Judd & Olmstead, 2004). The name *Campanulidae* is chosen here to formalize the use of “campanulids” for this clade.

Definition (branch-modified node-based). — The most inclusive crown clade containing *Campanula latifolia* L. 1753 (*/Apiidae*) but not *Garrya elliptica* Douglas ex Lindl. 1834 (*Garryales*) or *Lamium purpureum* L. 1753 (*/Lamiidae*) or *Cornus mas* L. 1753 (*Cornales*) or *Erica carnea* L. 1753 (*Ericales*).

Comments on definition. — There is some possibility that *Ilex* (*Aquifoliaceae*) is a member of */Garryidae* rather than being closely related to */Apiidae* as in the reference phylogeny. *Ilex* was linked with */Garryidae* in an analysis of *RPB2* duplications (Oxelman & al., 2004). Oxelman & al. did not include any members of *Helwingia*, *Phyllonoma*, *Cardiopteridaceae* or *Stemonuraceae*, but these taxa have been linked quite strongly with *Ilex* in several studies (see Reference phylogeny) and thus presumably could also be related to */Garryidae*. Our definition of */Campanulidae* is designed to include *Ilex* and its relatives if they are more closely related to */Apiidae* than to */Garryidae* and to exclude them if this is not the case. If all of these taxa are more closely related to */Garryidae*, then */Campanulidae* and */Apiidae* would become phylogenetic synonyms. Since both names are first defined in this paper, we hereby state our intent that */Campanulidae* have precedence over */Apiidae* in the unlikely event that they refer to the same clade.

Reference phylogeny. — Kårehed (2001: Fig. 1), Bremer & al. (2002: Fig. 1). See also Olmstead & al. (2000), Soltis & al. (2000), Albach & al. (2001b), Lundberg (2001), Hilu & al. (2003).

Composition. — *Aquifoliales* sensu APG II (2003) and the total clade of */Apiidae*. There is a slight possibility that some or all of *Aquifoliales* do not belong here (see Comments on definition).

Synonymy. — None.

DISCUSSION

Precision and clarity. — Biological nomenclature is plagued by inconsistency and ambiguity in the application of names, which can lead to confusion and unjustified inferences (de Queiroz & Gauthier, 1992; Gauthier & de Queiroz, 2001). The same name may be applied to differ-

ent clades (or non-monophyletic groups) in different classifications (Griffiths, 1976; de Queiroz & Gauthier, 1994; de Queiroz, 1997; Hibbett & Donoghue, 1998). Under the *ICBN*, this can result from the application of priority within rank and from *ICBN* Arts. 19.4 and 22.1, which mandate the names that must be used for subdivisions of a family or genus that include the type (Cantino & al., 1997; Cantino, 2004). Inconsistency in the application of names may also result simply from an author’s desire to apply the name to a different clade than other authors (Bryant & Cantino, 2002). This last problem currently occurs in phylogenetic nomenclature as well as rank-based nomenclature, but the *PhyloCode* (once implemented) will provide a mechanism to establish precedence among competing definitions of a name. Moreover, the registration database for phylogenetically defined names, which will be implemented with the *PhyloCode*, will help ensure that competing phylogenetic definitions are not accidentally published for the same name. Registration will be required for all names established under the *PhyloCode*.

Even when there is universal agreement about the set of closely nested clades to which a particular name applies, it is often difficult to determine whether a name applies (within this set) to the crown, the total clade or one of the apomorphy-based clades nested between them. This can lead to miscommunication. For example, Bowe & al. (2000: abstract) referred to “all gymnosperms as a monophyletic sister group to angiosperms.” Elsewhere in that paper, including in the title, it was clear that they were referring to extant gymnosperms, but the assertion that “gymnosperms are monophyletic” (based on molecular evidence) is frequently heard in casual conversation and easily misunderstood by students and others who may not be familiar with the long fossil record of extinct gymnosperms that could not be included in these molecular analyses (see Axsmith & al. [1998] for some related points). To avoid this confusion, we have proposed here that the name */Acrogymnospermae* apply to the crown clade of extant gymnosperms, thereby leaving the term “gymnosperms” available for informal use in its traditional, paraphyletic sense.

Even studies that include fossils and have an explicitly cladistic approach do not necessarily make clear the precise clade to which a name applies. For example, Kenrick & Crane (1997: Table 7.2) provided “synapomorphy-based definitions” for many names, but more than one apomorphy was listed for most of them, and each apomorphy potentially delimits a different clade. Furthermore, the discussion of some of the names implies a total clade, rather than an apomorphy-based clade, concept. For example, *Euphylllophytina* was given a “synapomorphy-based definition” in Table 7.2 but was described (p. 240) as the sister group of *Lycophytina*, suggesting that both of these clades were conceptualized as stemming from their point

of divergence rather than originating with the evolution of a particular apomorphy some indeterminate time after their divergence.

We do not intend to single out Kenrick & Crane's excellent book for criticism; failure to identify precisely the clade to which a name applies is widespread in the plant systematic literature, even by authors with a cladistic orientation. One of the most important contributions offered by phylogenetic nomenclature is much greater precision in the application of names. Linking names explicitly to a particular node, branch, or apomorphy will facilitate clear communication about phylogeny, character evolution, and the ages of clades.

In groups with a poor fossil record, it may seem unimportant whether a name applies to a crown, apomorphy-based, or total clade, but there can be huge differences in the composition of these clades in paleontologically well-known groups (e.g., crown seed plants, versus the clade originating with the first seed, versus the sister group of the monilophyte total clade; see Fig. 1). An advantage of the *Pan-* and *Apo-* naming conventions adopted by the *PhyloCode* is that hierarchical information is communicated in the name. The crown-total clade relationship of the names *X* and *Pan-X* will be apparent from the names, and anyone seeing the name *Apo-X* will know that it refers to the most inclusive clade that possesses the apomorphy referred to etymologically in the name *X*. This is analogous to the conveying of hierarchical relationship in the rank-based terminations of names governed by the *ICBN* (de Queiroz, in revision), but the information communicated by the *Pan-* and *Apo-* prefixes concerns hypothesized evolutionary-historical entities (clades) rather than artificial constructs (ranks). Naming total clades by adding a standard prefix to the corresponding crown clade name also improves the cognitive efficiency of the system, reducing the number of names to be memorized; if one knows the name of a crown clade, one automatically knows the name of the corresponding total clade, and vice versa (Joyce & al. 2004; de Queiroz, in revision).

Choosing among redundant names. — One problem not covered under “Methods” is the selection of a name for a crown clade such as *Equisetum* that includes only one extant genus. There are typically several phylogenetically redundant rank-based names for such a clade (e.g., *Equisetophyta*, *Equisetopsida*, etc., as well as *Equisetum*), only one of which is established for the crown clade under the *PhyloCode*. In our treatment of this clade (see Electronic supplement), we adopted Bryant's (1994) suggestion to give the crown the lowest ranked of these names (in this case, *Equisetum*), leaving the other names available for application to more inclusive clades. If, instead, a name associated with a more inclusive grouping (e.g., *Equisetophyta*) were applied to the crown, and if fossils traditionally assigned to *Equisetum* were found

to lie outside the crown, *Equisetophyta* would become a subgroup of *Equisetum*—an undesirable reversal of the hierarchical relationships associated with these names under the *ICBN*. One negative consequence of applying the genus name to the crown clade is that fossils that are currently assigned to the genus *Equisetum* would not be members of the clade *Equisetum* if they lie outside the crown. Use of a symbol (e.g., /) to distinguish phylogenetically defined clade names from genus names would help prevent confusion in such cases.

Choice of definition type for crown clades.

— The *PhyloCode* (Note 9.4.1) provides three kinds of definitions that always specify a crown clade: (1) standard node-based with all internal specifiers extant, (2) branch-modified node-based, and (3) apomorphy-modified node-based. In choosing among these definition types, our primary concerns were compositional stability and definitional simplicity, with priority given to the former. To maximize stability of the clade composition associated with a standard node-based definition, we included as internal specifiers members of every subclade that could plausibly be sister to the rest of the clade (Cantino & al., 1997; *PhyloCode* Rec. 11D). Had we not done this, the name would end up applying to a less inclusive clade than we intend if it turned out that one subclade arising from the basal split was not represented by an internal specifier. If the basal dichotomy is very well supported, the simplest kind of node-based definition—one with only two internal specifiers—will provide high compositional stability in the context of a range of plausible phylogenies. In contrast, if the basal topology of a clade is unresolved (e.g., the five-way basal polytomy within the crown clade */Spermatophyta*) or poorly supported (e.g., the basal topology of */Pentapetalae*), a standard node-based definition would have to include more than two (and in some cases many) internal specifiers to ensure that both subclades arising from the basal dichotomy are represented (Lee, 1998). This is why */Pentapetalae* and */Fabidae* have eight and nine specifiers, respectively.

These examples illustrate how maximizing compositional stability sometimes reduces definitional simplicity if a standard node-based definition is used. However, the other two kinds of crown clade definitions may provide both stability and simplicity in spite of poor ingroup resolution. If outgroup relationships are better supported than basal ingroup relationships (Fig. 2), a branch-modified node-based definition (“the most inclusive crown clade containing *A* but not *Z*”) is useful. Lee (1998) made similar observations about the advantages of branch-based versus node-based definitions, but a branch-based definition cannot specify a crown clade while a branch-modified node-based definition can. If one adopts the convention of assigning widely known names to crown clades, the branch-modified node-based definition becomes an impor-

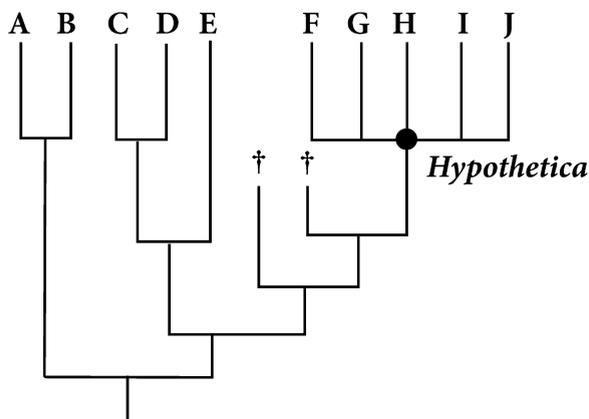


Fig. 2. A reference phylogeny (adapted from Lee, 1998) for the crown clade “*Hypothetica*” with a poorly resolved basal topology but well-resolved outgroup relationships. All resolved crown clades have high support values. Capital letters A–J designate extant clades, and lower case a–j (in definitions, below) are particular species representing these clades. Extinct taxa are indicated with a dagger symbol (†). A standard node-based definition for *Hypothetica* (“the least inclusive clade containing species f, g, h, i, and j”) would require five internal specifiers to ensure that clades F, G, H, I, and J are included within *Hypothetica* regardless of the true topology. However, the same compositional stability could be achieved more simply with a branch-modified node-based definition: “the most inclusive crown clade containing j but not c”. A branch-based definition (e.g., the most inclusive clade containing j but not c”) would achieve the same degree of stability but specifies a different clade—a larger one that includes some extinct taxa outside the crown.

tant tool. Although none of the instances in which we used a branch-modified node-based definition is as extreme as that shown in Fig. 2, we opted for this definition type in several cases in which we had more confidence in the outgroup relationships than in the basal ingroup topology (e.g., see comments above under */Tracheophyta*, */Angiospermae*, and */Mesangiospermae*). When using a branch-modified node-based definition, care must be taken to select a representative of the extant sister group of the crown clade being named as an external specifier. If this is not done, the name may end up applying to a more inclusive clade than intended. Thus, branch-modified node-based definitions are not necessarily simple if outgroup relationships are poorly supported. For example, we used seven external specifiers in our definition of */Rosidae* (see Electronic supplement), but a standard node-based definition would have been even more complex. In this case, neither the outgroup nor ingroup relationships are well supported, and no non-DNA synapomorphy is known.

An apomorphy-modified node-based definition (“the most inclusive crown clade exhibiting character M synapomorphic with that in A”) is simple and is worth considering when both the internal topology and outgroup

relationships of the clade to be named are poorly known. However, apomorphies are subject to ambiguity in character coding and optimization (Bryant, 1994; Schander & Thollessen, 1995; Sereno, 1999, 2005; Donoghue, 2005), and we have therefore avoided using them in definitions when possible. Their use is necessary for clades that originate with the evolution of an apomorphy (Lee, 1999a), but the inclusion of an apomorphy in a crown clade definition may rarely be the best option. We did not encounter any crown clade for which we felt that an apomorphy-modified definition was preferable, but such a definition may be the best choice for a clade that has: (1) many plausible candidates for sister group, (2) a basal polytomy giving rise to many subclades, and (3) a morphological synapomorphy that can be unambiguously described.

Specifiers. — We have selected specifiers in a way that (1) captures the spirit of historical usage to the degree that this is consistent with monophyly (*PhyloCode* Rec. 11A), and (2) minimizes the likelihood of large changes in clade composition in the context of a range of plausible phylogenies (*PhyloCode* Recs. 11B–E; Schander & Thollessen, 1995; Cantino & al., 1997; Lee, 2005). The latter point is discussed in the previous section. Recommendation 11A states that definitions should not necessitate (though they may allow) the inclusion of subtaxa that were historically excluded from the taxon. Consequently, species that were not traditionally considered to be part of a taxon should not be chosen as internal specifiers. The application of Rec. 11A is illustrated by the definition of */Coniferae*. Gnetophytes are not traditionally considered to be conifers, but some recent molecular evidence (e.g., Bowe & al., 2000) suggests that the clade */Gnetophyta* is sister to */Pinaceae* (both defined in the Electronic supplement). Following Rec. 11A, we have not included any gnetophyte species as an internal specifier for */Coniferae*. */Gnetophyta* may or may not be part of */Coniferae*, depending on the phylogeny, but the definition does not necessitate their inclusion (or exclusion).

Although phylogenetic definitions are often designed to maintain the same composition in the context of a variety of phylogenetic hypotheses, some names are better restricted to a limited set of hypotheses. For example, we have coined the name */Acrogymnospermae* for the clade containing all extant seed plants except */Angiospermae*. The hypothesis that such a clade exists has considerable molecular support but conflicts with the findings of a few molecular studies and with many studies that included morphological data and/or fossils (see references above under */Acrogymnospermae*). Although some of us have doubts that extant gymnosperms form a clade, we feel that it is useful to have a unique, phylogenetically defined name for this putative clade that has generated so much recent interest. This way, biologists can communicate about it while avoiding the incorrect inferences that can

result when it is referred to as *Gymnospermae* or “gymnosperms”. However, because the hypothesis is controversial and the name */Acrogymnospermae* is new (and thus has no previous mental associations for users), we feel that it will be best for the name to be abandoned if the hypothesis turns out to be incorrect, rather than undergoing a change in composition. The inclusion of an angiosperm as an external specifier (a “taxon qualifier”; Sereno, 2005) in the node-based definition of */Acrogymnospermae* effectively restricts the name to the hypothesis that all extant gymnosperms form a clade. If gnetophytes turn out to be the extant sister group to the angiosperms (as in most morphological analyses), the name */Acrogymnospermae* will not apply to any clade.

Similarly, the inclusion of three internal specifiers in the branch-modified node-based definition of */Euphyllophyta* (Electronic supplement) will cause the name to become inapplicable if ferns, horsetails or seed plants are determined to share closer ancestry with lycophytes than with each other. Non-applicability of the name would be appropriate in this situation because euphyllophytes are widely understood to comprise seed plants plus monilophytes.

Alternative phylogenies and nomenclatural outcomes. — We have tried to present some guidelines and strategies for the choice of definitions and specifiers, but constructing good phylogenetic definitions is not a “cut and dried” procedure. The choice of an appropriate definition requires knowledge of the alternative phylogenetic hypotheses for the group, a thoughtful analysis of the nomenclatural outcomes of various possible definitions in the context of all plausible phylogenies, and consideration of how these outcomes will affect the users of the name. Ultimately, the best definition will be the one that brings about the outcome that the author intends, provided that the author’s intent is consistent with the needs of the systematics community.

An example may be instructive here. Defining the name */Campanulidae* (for the clade that is informally known as “campanulids” or “euasterids II”) was complicated by uncertainty about the position of *Ilex* and its relatives. Although most molecular analyses have placed *Aquifoliales* (sensu APG II, 2003) within the campanulid clade, as sister to */Apiidae* (i.e., the rest of the campanulid clade; see Electronic supplement), one recent analysis found *Ilex* to lie outside of the campanulid clade (see */Campanulidae* treatment above for references and other details). Because *Ilex* was the only member of *Aquifoliales* included in that study, it is possible that some or all of *Aquifoliales* actually lie outside */Campanulidae*. Given this uncertainty, how do we construct a definition for */Campanulidae*?

To answer this question, we first considered three possible phylogenies: (1) *Aquifoliales* sensu APG are sister

to */Apiidae* (as indicated by most analyses); (2) *Ilex* and perhaps its closest relatives, *Helwingia* and *Phyllonoma*, lie outside of */Campanulidae* but the rest of *Aquifoliales* sensu APG (i.e., *Cardiopteridaceae* and *Stemonuraceae*) occupy a basal position within */Campanulidae*; and (3) *Aquifoliales* as a whole lie outside of */Campanulidae*. We then determined our preferred outcomes under each scenario. Under phylogeny (1), we prefer that */Campanulidae* include *Aquifoliales*, consistent with APG II (2003) and most recent phylogenetic studies. Under phylogeny (2), we prefer that */Campanulidae* include *Cardiopteridaceae* and *Stemonuraceae*. Under phylogeny (3), only */Apiidae* would be left in */Campanulidae*, thus the two names would refer to the same clade and be synonyms under the *PhyloCode*. If this were to occur, we have a slight preference that the name */Campanulidae* be used (though arguments can be made either way). We then considered several possible definitions—including both standard and branch-modified node-based definitions, with and without taxon qualifiers—and concluded that the simplest way to bring about our intended outcome under all three scenarios was a branch-modified node-based definition (the most inclusive crown clade containing *Campanula* but not *Garrya*, *Lamium*, *Cornus*, and *Erica*), combined with a statement that if */Campanulidae* and */Apiidae* become synonyms, we intend that */Campanulidae* have precedence.

This mechanism is possible in this case because */Campanulidae* and */Apiidae* will be published simultaneously here (including the Electronic supplement), so neither would automatically have priority over the other (if the *PhyloCode* were already in effect). If a phylogenetic definition for */Apiidae* had been published earlier (again, assuming for the sake of argument that the *PhyloCode* were already in effect), this name would automatically have precedence. In this case, the only way we could bring about our preferred outcome under scenario (3) would be to propose that the Committee on Phylogenetic Nomenclature conserve */Campanulidae* over */Apiidae* (which we would not do, and the CPN would probably not approve, because the argument in favor of conservation in this case is not compelling). Although, as illustrated by this example, it is not always possible to ensure the author’s preferred outcomes under every plausible phylogenetic scenario, this kind of analysis of scenarios and outcomes is critical to the framing of robust phylogenetic definitions that minimize the likelihood of undesirable changes in membership associated with a name.

CONCLUSIONS

In the course of defining the names of 53 clades (including those in the Electronic supplement), we have encountered a variety of tree topologies, degrees of sup-

port, and nomenclatural histories, but no insurmountable problems. In all cases, we were able to construct phylogenetic definitions that we anticipate will be applicable as our knowledge of phylogeny continues to improve. This is not to say that we expect these definitions to be the final word. On the contrary, we hope that they will be examined critically and, if problems are found, that suggestions will be made on how to improve the definitions and/or the *PhyloCode* before it is implemented. Such constructive dialogue is critical at this juncture.

Not only has it been possible to frame phylogenetic definitions for these many clade names, but we argue that phylogenetically defined names are more useful than informal names or rank-based scientific names. By linking names explicitly to particular crown, apomorphy-based, and total clades, and by using a standard set of prefixes to designate clade type, this naming system will help biologists communicate more precisely about evolution and avoid miscommunication and incorrect inferences. This is essential from the standpoint of phyloinformatics. Phylogenetic definitions provide a means to associate a name precisely with a part of a tree—something that the rank-based system cannot do—and this capacity will be critical in the future for the storage and retrieval of all sorts of biological data within a phylogenetic framework.

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