PHYLOGENETIC NOMENCLATURE

Towards a phylogenetic nomenclature of *Tracheophyta*

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Phylogenetic definitions are provided for the names of 53 clades of vascular plants. 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 *PhyloCode* (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 (Lidén & Oxelman, 1996; Dominguez & Wheeler, 1997; Lidén & al., 1997; Moore, 1998, 2003; Benton, 2000; Nixon & Carpenter, 2000; Forey, 2001, 2002; Lobl, 2001; Berry, 2002; Blackwell, 2002; Jørgensen, 2002, 2004; Carpenter, 2003; Janovec & al., 2003; Keller & al., 2003; Kojima, 2003; Nixon & al., 2003; Schuh, 2003; Barkley & al., 2004; Wenzel & al., 2004; Pickett, 2005; Polaszek & Wilson, 2005) and defenses (Lee, 1996a, 1999a, 2001; de Queiroz, 1997a; Cantino, 2000, 2004; Brochu & Sumrall, 2001; de Queiroz & Cantino, 2001; Laurin, 2001, 2005; Bryant & Cantino, 2002; Bertrand & Pleijel, 2003; Pleijel & Rouse, 2003; Donoghue & Gauthier, 2004; Pleijel & Härlin, 2004; Laurin & al., 2005, 2006). 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 widely known 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.

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 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, angiosperm clades that are currently ranked at or below the ordinal level (see APG II, 2003), even if very large and important, are not covered here because of length considerations. Rather, we focus within *Angiospermae* on large and well-supported clades that are often discussed using informal names (e.g., "core eudicots").

Fundamentals of the *PhyloCode*. — Clades are named here using phylogenetic nomenclature (de Queiroz & Gauthier, 1994). We have followed the draft *PhyloCode* (Cantino & de Queiroz, 2006) in all respects, including the use of a preexisting name if one exists, with one exception (our proposal of the new name *Lignophyta* rather than adopting the little-used preexisting name *Lignophytia*). Taxon names are given phylogenetic definitions (de Queiroz & Gauthier, 1990, 1992), which identify a particular clade by reference to a node, branch, or apomorphy. Such definitions can only be applied in the context of a hypothesized phylogeny, but it need not be the same hypothesis that provided the context for the definition.

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. Specifiers function somewhat like types in providing reference points that determine the application of a name. However, a type cannot, by itself, specify a particular taxon; it must be used in conjunction with a rank to do so. In this sense, the types and ranks of the *ICBN* are together equivalent to the specifiers of phylogenetic nomenclature (de Queiroz & Cantino, 2001). Specifiers that are not apomorphies may be species, type specimens, or (rarely) other specimens. If a type specimen is used as a specifier, the species name that it typifies must be cited. The *PhyloCode* strongly discourages the use of specimens that are not types, but it is permitted if the specimen that one would like to use as a specifier cannot be referred to a named species, so there is no type specimen that could be used instead.

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, and both codes use date of publication (priority) as the primary criterion for selecting the correct name when synonyms or homonyms exist. However, the fundamental difference in the way names are defined under the two codes leads to operational differences in determining priority. 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

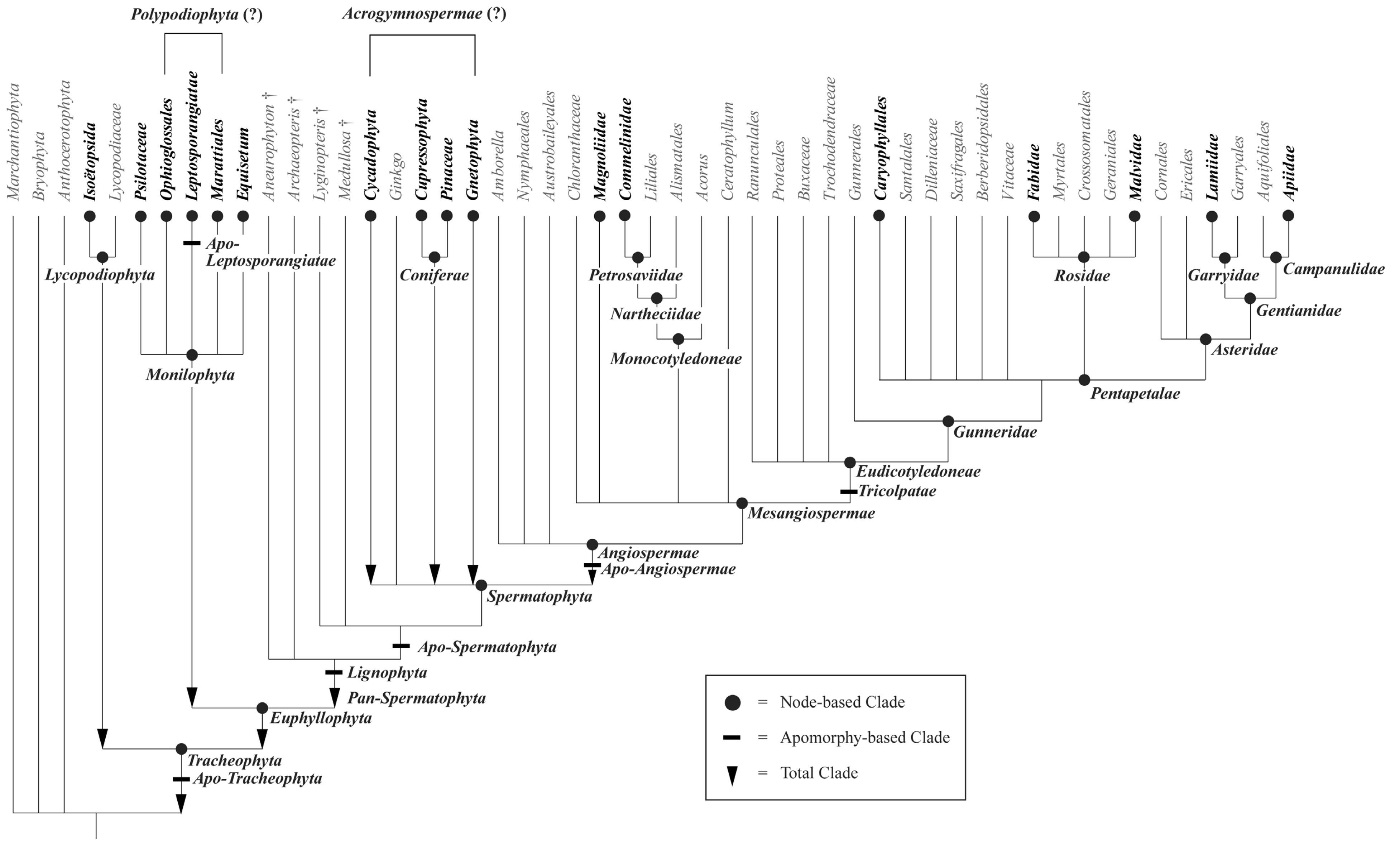

Fig. 1. Embryophyte (land plant) phylogenetic hypothesis showing the 53 tracheophyte (vascular plant) clades names that are defined phylogenetically in this paper. This is a composite tree depicting current understanding of relationships derived from numerous published phylogenetic analyses (see text for references). Each defined name is represented by a bold symbol, as follows: node-based and branch-modified node-based names are represented by a dot and accompanied by the name; apomorphy-based names are represented by a line and the name; and total clades are represented by an arrowhead alone (i.e., the name is not shown), except in the case of *Pan-Spermatophyta*, which is included here to illustrate the relationship of crown, apomorphy-based, and total clades to one another (see text). Names in gray are not defined here, but are included to represent some additional branches that are useful in understanding the circumscription of the clades that are defined. When there are phylogenetically redundant names for these branches under the *ICBN*, the lowest ranked name that is commonly applied to the set of species concerned is used here; these choices are arbitrary and not meant to imply acceptance of these names for future nomenclatural purposes. Not every relevant branch has been included; for example, the figure does not show *Petrosaviaceae*, *Dioscoreales*, or *Asparagales* within *Monocotyledoneae*, or *Sabiaceae* within *Eudicotyledoneae*. The dagger symbol (†) is used for extinct groups, and the question mark (?) for questionable monophyly.

Table 1. Clade names defined in this paper.

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

included within a single taxon at that rank, regardless of the clade (or non-monophyletic group) associated with the name. Under the *PhyloCode*, homonyms are identically spelled names that refer to different clades; in contrast, under the *ICBN*, homonyms are identically spelled names with different types but the same rank. In the interest of nomenclatural stability, both codes include mechanisms to overturn strict priority through a conservation process involving a governing committee.

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" (Sereno, 2005)—e.g., external specifiers in a standard node-based definition (which normally has only internal specifiers) or additional internal specifiers (beyond the one mandatory internal specifier) in a branch-based or branch-modified node-based definition. Taxon qualifiers are used in some definitions here (see Table 1).

The three basic types of phylogenetic definitions (de Queiroz & Gauthier, 1990)—node, apomorphy, and branch-based (formerly called stem-based)—are now widely known. However, there is a common misconception that these are alternative means of specifying the same clade. On the contrary, these definition types potentially specify three nested clades. These three clades may be identical in composition if one considers only extant organisms and yet differ in their extinct members.

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 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. For example, Hermsen & al. (2006) used the same name, *Cycadales*, to designate both the crown clade in the left column of their Table 1 and the total clade in the right column. Although the explanation in the caption helped clarify their intent, the use of the same name for two different clades may still be confusing to the casual reader. Use of a panclade name (see below) such as *Pan-Cycadales* for the total clade would eliminate this kind of problem.

Crown clades may be specified through three kinds of node-based definitions (*PhyloCode* Note 9.4.1): 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. Branch-modified node-based definitions take the form "the most inclusive crown clade containing A but not Z" (or Y or X, etc., as needed) or "the clade stemming from the most recent common ancestor of A and all extant organisms or species that share a more recent common ancestor with A than with Z" (or Y or X, etc., as needed). Apomorphy-modified node-based definitions take the form "the most inclusive crown clade exhibiting character M synapomorphic with that in A" (where A is a species or specimen) or "the clade stemming from the most recent common ancestor of A and all extant organisms or species that possess apomorphy M as inherited by A." In both of these definition types, "extant" refers to the date when the definition was published unless the author states otherwise, so subsequent extinction of a specifier does not affect the composition of the clade. Both of these definition types have potentially many internal specifiers, only one of which needs to be explicitly stated. The unstated internal specifiers are all extant species (or organisms) that share either a particular apomorphy or a particular relationship (closer to A than to Z) with the one stated specifier A. Thus, contrary to Sereno (2005), these are variants of the node-based, not the branch-based (stem-based), definition type.

For total clades, we have used a special kind of branch-based definition (*PhyloCode* Art. 10.5): "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. In this definition, the specifiers are only indirectly identified; the internal specifier(s) are those of crown clade *X*, and the external specifiers are the internal specifiers of all other crown clades that lie outside of *X* (though in practice, one would only be concerned about the sister crown clade to *X* in the accepted phylogeny).

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. In the case of crown clades, the node-based definition may be standard (with all internal specifiers being extant), branch-modified or apomorphy-modified. Which of these three definition types is most appropriate for a particular crown clade will depend on the degree of resolution of the ingroup and outgroup topology and whether the clade has a "good" synapomorphy (see Discussion: Choice of definition type for crown clades).

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 (Lee, 1999b; "nested referencing," Sereno, 1999) or for a pair of sister clades ("node-stem triplets"; Sereno, 1999, 2005) contributes to the simplicity and immediate informativeness of a set of definitions. 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 a phylogenetic definition is formulated 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*. It may be either a name governed by one of the rank-based codes or a scientific name that is in use but not governed by any code (e.g., zoological names ranked above the superfamily level). 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, which is designed in part to promote continuity with the current nomenclature and in part to promote the development of an integrated system of names for nested sets of crown, apomorphy-based, and total clades. 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). This approach only works for competing names that are used consistently for the same clade (e.g., *Monocotyledoneae* versus *Liliopsida*). In the case of names that are applied to more than one clade by different workers (e.g., *Filicales*; see treatment of *Leptosporangiatae* below), one can estimate frequency of use by checking how the name is applied in a random subset of the references. One must be cautious when using *Biosis* and *KBD* because the number of references is heavily biased in favor of the naming system used by these databases. For example, every article about ferns in *Biosis* comes up under the name *Filices*, regardless of whether this name was used in the paper. We also regularly consulted the names adopted by *GenBank* (http://www.ncbi.nlm.nih.gov/Taxonomy/taxonomyhome.html/).

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, euphyllophytes). 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, 1996b; 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 *Lycopsida* 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, 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*.

NOMENCLATURAL TREATMENT

The following nomenclatural treatment provides phylogenetic definitions for the names of 53 vascular plant clades (Table 1) together with information regarding composition, synonymy, and (in many cases) synapomorphies. Four kinds of definitions are used: 24 node-based, 14 branch-modified node-based, 6 apomorphy-based, and 9 total clade definitions (see below) (Table 1). 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.

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 (this is an abbreviated wording of a special kind of branch-based definition; 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. 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*.

Synapomorphies are listed for many clades as potentially useful supplementary information, but the apomorphies determine the application of the name only when they are part of the definition (e.g., see *Lignophyta* or *Apo-Spermatophyta*). The character states listed are mostly taken from the literature, and in many cases we cannot be sure that they are synapomorphic at the precise level at which they are cited here—as opposed to a somewhat more or less inclusive clade. Synapomorphies listed for crown clades are apomorphic relative to other crown clades, but many of these character states are probably synapomorphies of more inclusive clades than the crown. Some of them may also have originated or been lost one or more times within the crown clade, and some may have been lost in all but the earliest members of the crown. No synapomorphies are listed for some total clades owing to the lack of information about the character states of extinct and mostly unknown species situated along the stem. Most states that we think of as characterizing a total clade are presumably synapomorphic at a less inclusive level, somewhere between the basal node of the crown and the base of the total clade, because the splitting of lineages generally occurs before the evolution of trait differences. Some exceptions to this generalization would be traits that are causally related to the splitting of lineages, such as a polyploidy event.

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*.

Synapomorphies. — walls of water-conducting cells with a thick, lignified, decay-resistant layer. Free-living sporophyte and multiple sporangia per sporophyte are synapomorphies relative to other crown clades; however, when fossils are considered, these traits are synapomorphies at a more inclusive level (see */Pan-Tracheophyta*). Sterome (a well-developed peripheral zone of the stem consisting of thick-walled, decay-resistant cells) and pitlets in the tracheid wall are listed by Kenrick & Crane (1997: Table 7.2, pp. 114, 120) as synapomorphies of "eutracheophytes" (= */Tracheophyta*), but the extent of missing data for fossils combined with the apparent loss of these traits in extant tracheophytes reduces confidence in their inferred originations.

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.

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

Definition (apomorphy-based). — The most inclusive clade exhibiting tracheids (i.e., differentially thickened water conducting cells) synapomorphic with those in *Pinus sylvestris* L. 1753.

Reference phylogeny. — Kenrick & Crane (1997: Fig. 4.31 [as *Tracheophyta*]), Crane & al. (2004: Fig. 1 [as "Tracheophytes"]).

Composition. — Assuming that tracheids with S-type and G-type cell walls (see Kenrick & Crane, 1997: Fig. 4.26) are homologous, the clade */Apo-Tracheophyta* includes */Tracheophyta* and *Rhyniopsida* sensu Kenrick & Crane (1997). Under the alternative hypothesis that these tracheid types evolved independently, *Rhyniopsida* would not be part of */Apo-Tracheophyta* as defined here, and the currently known membership of */Apo-Tracheophyta* and */Tracheophyta* would be the same.

Synonymy. — *Tracheophyta* sensu Kenrick & Crane (1997: Tables 7.1, 7.2, p. 236). Although Kenrick & Crane (op. cit., 236) listed *Tracheidatae* Bremer (1985) as a synonym of their "Eutracheophytes," implying that that *Tracheidatae* referred to the crown group, it is clear from Bremer's comments (p. 382) that he considered rhyniopsids to be part of *Tracheidatae*; thus, based on composition, *Tracheidatae* is an approximate synonym of */Apo-Tracheophyta*. *Pteridophyta* of some earlier authors (e.g., Haupt, 1953) is a partial synonym; the pteridophytes originated from the same ancestor as */Apo-Tracheophyta* but are paraphyletic with respect to */Apo-Spermatophyta*.

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., *Aglaophyton*, *Horneophyton*) that share more recent ancestry with */Tracheophyta* than with extant mosses, liverworts, and hornworts.

Synapomorphies. — None known. An independent sporophyte and multiple sporangia are listed by Kenrick & Crane (1997: Table 7.2) as synapomorphies of *Polysporangiomorpha* (a slightly less inclusive clade than */Pan-Tracheophyta*; see Synonymy) but only the latter would be a synapomorphy of *Polysporangiomorpha* if it were given an apomorphy-based definition based on the etymology of the name. The order in which the two features evolved is not known. Sunken archegonia are also cited as a possible synapomorphy of *Polysporangiomorpha* by Kenrick & Crane (1997: Table 7.2), but it is unknown whether sunken archegonia evolved before or after multiple sporangia. Moreover, sunken archegonia also occur in *Anthocerophyta* (op. cit., Fig. 3.33, pp. 63–64) and thus may be a synapomorphy of a more inclusive clade if hornworts are the closest extant relatives of tracheophytes (e.g., Qiu & al., 2006b).

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*.

Lycopodiophyta Cronquist, Takhtajan & Zimmermann 1966: 133 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — The names *Lycophyta* and *Lycopodiophyta* have been widely applied to the same set of clades (referring variably to the crown, total clade or something intermediate). Since the former is apparently based on the name *Lycopodium*, it should be corrected to *Lycopodiophyta* under the *ICBN* (Arts. 16.1 and 18.1). The names *Lycopsida* and *Lycopodiopsida* are also widely applied to this set of clades. Our preference for the *-phyta* ending and its application to the crown are explained under Methods. Under the *ICBN*, the name *Lycopodiophyta* is attributed to Scott (1909), who spelled it *Lycopsida* (Hoogland & Reveal, 2005; Kiger & Reveal, 2006; see Methods: Attribution of authorship).

Definition (node-based). — The least inclusive clade containing *Lycopodium clavatum* L. 1753, *Huperzia selago* (L.) Schrank & Mart. 1829, *Isoëtes lacustris* L. 1753, and *Selaginella apoda* (L.) Spring 1840.

Comments on definition. — Two species of *Lycopodiaceae* are included as specifiers because the evidence for monophyly of *Lycopodiaceae* is based solely on *rbcL* (Wikström & Kenrick, 1997; Korall & al., 1999). We are aware of no morphological synapomorphy for *Lycopodiaceae*.

Reference phylogeny. — Korall & al. (1999: Fig. 2). See also Pryer & al. (2001 [as *Lycophytina*], 2004b [as "lycophytes"]), Rydin & Wikström (2002), and Qiu & al. (2006b).

Composition. — *Lycopodiaceae*, *Isoëtes*, and *Selaginella*.

Synapomorphies. — Kenrick & Crane (1997: Table 6.3, Fig. 6.19 [node 35]), Doyle (1998), and Gensel (1992) listed the following synapomorphies for the crown clade: association of a single axillary or adaxial sporangium with a sporophyll; absence of vasculature in the sporangium; metaxylem tracheids pitted; root stele bilaterally symmetrical, with phloem located on only one side of the stele (but there are a lot of missing data for fossils outside the crown, so this trait may be synapomorphic of a more inclusive clade); crescent-shaped root xylem (but there are a lot of missing data for fossils outside the crown). The following characters are synapomorphies of this crown clade relative to other crowns but are apomorphic at a more inclusive level when fossils are considered (Kenrick & Crane, 1997: Fig. 6.18, Table 7.2): microphylls ("lycophylls"; Schneider & al., 2002; Pryer & al., 2004a); exarch xylem differentiation in stem (Kenrick & Crane, 1997; Doyle, 1998; Schneider & al., 2002); stellate xylem strand in stem; reniform sporangia with transverse dehiscence (Doyle, 1998). This list is not exhaustive; see Kenrick & Crane (1997: Table 7.2) and DiMichele & Bateman (1996) for other synapomorphies listed under *Lycophytina* and *Lycopsida*.

Synonymy. — See Comments on name. The clade *Lycopsida* sensu Kenrick & Crane (1997) is somewhat larger than the crown clade */Lycopodiophyta* in that it includes fossils such as *Asteroxylon* and *Baragwanathia* that are shown (p. 216; also Pryer & al., 2004a: Fig. 10.3) as being outside the lycophyte crown clade. The same is true of *Microphyllophyta* sensu Bold (1957) and Bold & al. (1980), *Lepidophyta* sensu Smith (1955), and *Lycopodiopsida* sensu Bierhorst (1971).

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

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

Composition. — */Lycopodiophyta* and all extinct plants (e.g., *Zosterophyllum*) that share more recent ancestry with */Lycopodiophyta* than with */Euphyllophyta* (see below). Figure 1 of Crane & al. (2004) shows many of the known fossil members of */Pan-Lycopodiophyta*.

Synapomorphies. — Possibly sporangium dehiscence by a transverse, apical slit. Doyle (1998) showed this character as arising at or near the base of the (unnamed) lycophyte total clade. Kenrick & Crane (1997: Table 4.6) cited it as a possible synapomorphy of node 52, which is near the base of the total clade.

Synonymy. — Based on its composition, the name *Lycopodiobiotina* Doweld (2001) seems to be an approximate synonym of */Pan-Lycopodiophyta*. The name *Lycophytina* sensu Kenrick & Crane (1997: Fig. 4.31, Table 7.2) has an apomorphy-based definition and is somewhat less inclusive than */Pan-Lycopodiophyta*. The clade *Lyco-*

phytina sensu DiMichele & Bateman (1996) and Bateman & al. (1998) appears, based on its synapomorphies and composition, to be circumscribed similarly to *Lycophytina* sensu Kenrick & Crane (1997) and is thus presumably less inclusive than /*Pan-Lycopodiophyta*.

Isoëtopsida Cronquist & al. 1972: 177 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — Following *ICBN* Art. 16.3, Kiger & Reveal (2006) attributed *Isoëtopsida* to Rolle (1885 in *Encyklopaedie der Naturwissenschaften*; full reference unknown); see "Attribution of authorship" above. The name *Isoëtopsida* was applied to this clade by Cronquist & al. (op. cit.), Federov (1999) and GenBank (2006). We are aware of only one other preexisting name for this crown clade, *Glossopsida* Bold (1957), which is much less widely used. *Isoëtophyta* Doweld (2001) includes *Leclercqia* and therefore applies to a more inclusive clade than the crown under consideration here (see Kenrick & Crane, 1997: Fig. 7.9). Based on its synapomorphies, the name *Isoëtales* sensu DiMichele & Bateman (1996) refers to a less inclusive clade that excludes *Selaginella*.

Definition (node based). — The least inclusive clade containing *Isoëtes lacustris* L. 1753 and *Selaginella apoda* (L.) Spring 1840.

Reference phylogeny. — Rydin & Wikström, 2002. See also Kenrick & Crane (1997: Fig. 6.19), Korall & al. (1999), Pryer & al. (2001).

Composition. — *Isoëtes* and *Selaginella*. According to current understanding of phylogeny (Doyle, 1998; Judd & al., 2002; Pryer & al., 2004a), the rhizomorphic lycophytes (e.g., *Lepidodendron*) are also part of this clade.

Synapomorphies (relative to other crown clades). — Heterospory; ligules (synapomorphic at a more inclusive level when fossils are considered) (Kenrick & Crane, 1997: Fig. 6.1).

Synonymy. — See Comments on name.

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

Comments on name. — There is no preexisting scientific name for this crown clade. The name *Euphyllophyta* has apparently never been published with a description or diagnosis and therefore does not qualify as a preexisting name. *Euphyllophytina* Kenrick & Crane (1997: Table 7.1, Fig. 7.10) refers to a more inclusive clade than the crown. We choose the name *Euphyllophyta* because it corresponds closely to the informal name "euphyllophytes," which is commonly applied to this clade (e.g., Judd & al., 2002; Simpson, 2006).

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

Comments on definition. — A branch-modified node-based definition normally has only one internal specifier. Two other species are included here as internal qualifiers (Sereno, 2005). In the context of a phylogeny in which ferns, horsetails or seed plants share more recent ancestry with lycophytes than they do with each other (e.g., Rothwell & Nixon, 2006: Fig. 6), the name /*Euphyllophyta* would not apply to any clade.

Reference phylogeny. — Pryer & al. (2001: Fig. 1 [as *Euphyllophytina*]). See also Pryer & al. (2004b: Fig. 3), Kenrick and Crane (1997: Fig. 7.10).

Composition. — /*Pan-Spermatophyta* and /*Pan-Monilophyta*.

Synapomorphies (relative to other crown clades). — Roots with monopodial branching and endogenous lateral roots (Schneider & al., 2002); sporangia terminating lateral branches (Pryer & al., 2004a) and dehiscing longitudinally (Doyle, 1998) (these features characterize the earliest members of /*Pan-Euphyllophyta* and were modified in most extant representatives); lobed, mesarch primary xylem strand (Stein, 1993; Kenrick & Crane, 1997: Fig. 7.10 and p. 241; Doyle, 1998), which has been modified in the stems of most extant members; multiflagellate spermatozoids (apparently convergent in *Isoëtes*) (Garbary & al., 1993; Kenrick & Crane, 1997: 240, 275); a 30-kb inversion in the chloroplast genome (Raubeson & Jansen, 1992a). Megaphylls (euphylls) are sometimes cited as a synapomorphy of /*Euphyllophyta* (Schneider & al., 2002), but analyses that include fossils suggest that the compound, fernlike megaphylls of monilophytes and seed plants evolved independently (Stewart & Rothwell, 1993; Kenrick & Crane, 1997; Doyle, 1998; Boyce & Knoll, 2002; Friedman & al., 2004). Even within /*Lignophyta*, the small, wedge-shaped leaves of *Archaeopteris* may not be homologous with the whole fernlike fronds of seed ferns but rather with individual leaflets of such fronds (Doyle & Donoghue, 1986a; Doyle, 1998).

Synonymy. — None, but see Comments on name.

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

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

Reference phylogeny. — Kenrick and Crane (1997: Figs. 4.31, 7.10 [as *Euphyllophytina*]).

Composition. — /*Euphyllophyta* and all extinct plants (e.g., *Psilophyton*) that share more recent ancestry with /*Euphyllophyta* than with /*Lycopodiophyta*.

Synapomorphies. — Several synapomorphies were listed by Kenrick & Crane (1997: 240, Table 7.2, and pages listed below), most of which have been lost or modified in some or all extant members of the clade: pseudomonopodial or monopodial branching (pp. 109, 359) (although if the fernlike leaves of early seed plants were derived from pseudomonopodial branch systems of more basal lignophytes (Doyle, 1998), the axillary monopodial branching of seed plants and the pseudomonopodial branching of more basal lignophytes may not be homologous); helical arrangement of branches (pp. 110, 360); dichotomous appendages (pp. 113, 361); recurvation of branch apexes (pp. 112–113, 360); paired sporangia grouped into terminal trusses (pp. 121–122, 364); sporangium dehiscence along one side through a single longitudinal slit (pp. 125, 366). Kenrick & Crane also cited scalariform bordered pitting of metaxylem cells as a synapomorphy, but it does not occur in *Eophyllophyton* and therefore is synapomorphic for a slightly less inclusive group than the total clade (op. cit., pp. 120, 363, Fig. 7.10).

Synonymy. — The currently known composition of *Euphyllophytina* sensu Kenrick & Crane (1997: Table 7.1) is similar to that of */Pan-Euphyllophyta*, but it is unclear whether *Euphyllophytina* refers to an apomorphy-based or total clade (see Discussion: Precision and clarity). The "trimerophytes" (which have been named at various ranks—e.g., *Trimerophytophyta* sensu Bold & al., 1980, *Trimerophytina* Banks 1968, *Trimerophytopsida* Foster & Gifford 1974) are stem euphyllophytes and therefore partial synonyms of */Pan-Euphyllophyta*.

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*.

Synapomorphies (relative to other crown clades). — A possible synapomorphy is the exclusively centrifugal development of the spore exine (Schneider & al., 2002).

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* below). 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 below under */Polypodiophyta*).

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

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

Composition. — */Monilophyta* and all extinct plants that share more recent ancestry with */Monilophyta* than with extant seed plants or lycophytes.

Synonymy. — *Pteridophytanae* Doweld (2001) does not have a phylogenetic definition, but its composition is similar to that of */Pan-Monilophyta*.

Equisetum Linnaeus 1753: 1061 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — In rank-based nomenclature, the names *Equisetum*, *Equisetophyta*, *Equisetopsida*, *Equisetales*, *Equisetaceae*, *Sphenophyta*, and *Sphenopsida* have all been applied to the same crown clade, which is widely understood to include only species of the genus *Equisetum*. (Most of these names have also been applied to larger clades that extend beyond the crown.) In the interest of compatibility with species names under the *ICBN*, the genus name should be selected for the crown clade when the alternative higher ranked names are monogeneric (see Discussion: Choosing among redundant names).

Definition (branch-modified node-based). — The most inclusive crown clade containing *Equisetum fluviatile* L. 1753 but not *Marattia attenuata* Labill. 1824 (*/Marattiales*) or *Pteridium aquilinum* (L.) Kuhn 1879 (*/Leptosporangiatae*) or *Ophioglossum reticulatum* L. 1753 (*/Ophioglossales*) or *Psilotum nudum* (L.) P. Beauv. 1805 (*/Psilotaceae*) or *Ginkgo biloba* L. 1771 (*/Spermatophyta*).

Comments on definition. — Although parsimony and maximum likelihood analysis of *rps4* sequence data (Guillon, 2004) and parsimony analysis of combined *rbcL* and *trnL-F* sequence data (Des Marais & al., 2003) suggest that *Equisetum bogotense* is sister to the rest of */Equisetum*, maximum likelihood analysis of combined *rbcL* and *trnL-F* sequence data (Des Marais & al., 2003) supports a different topology. Because low bootstrap values in the latter analysis leave some doubt about the basal phylogeny of */Equisetum*, we would have to include seven internal specifiers in a standard node-based definition to be confident that both branches of the basal dichotomy are represented. Instead, we use a branch-modified node-based definition because it is simpler (six specifiers), and the reference phylogenies leave no doubt that all plausible candidates for extant sister group of */Equisetum* are represented by external specifiers.

Reference phylogeny. — Pryer & al. (2004b: Fig. 3). See also Rothwell (1999), Pryer & al. (2001), Des Marais & al. (2003), Guillon (2004), and Schuettpelz & al. (2006).

Composition. — All extant species of the genus *Equisetum* (see lists in Des Marais & al., 2003 and Guillon, 2004) and any extinct species that fall within the crown clade.

Synapomorphies (relative to other crown clades). — Whorled leaves and branches, lateral fusion of leaf bases to form a nodal sheath, spores with elaters, peltate sporangiophores bearing eight or more sporangia, carinal and vallecular canals; Bierhorst (1971), Kenrick & Crane (1997).

Synonymy. — See Comments on name.

Other comments. — It would be useful to have a name (e.g., *Equisetophyta* or *Sphenophyta*) for at least one apomorphy-based clade that includes */Equisetum* and some members of its stem group. However, we do not think that the phylogeny of this group is well enough understood to define such a name at this time. The only publication that has attempted a broad phylogenetic analysis of this group included only extinct representatives and discussed various hypotheses but did not provide a consensus tree (Stein & al., 1984).

Polypodiophyta Cronquist, Takhtajan & Zimmermann 1966: 133 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — The five most frequently used names for the crown clade containing all plants traditionally considered to be ferns are *Filicophyta*, *Filicopsida*, *Polypodiophyta*, *Pterophyta*, and *Pteropsida*. Three of these have our preferred *-phyta* ending (see Methods: Choice of names). Of these, we have selected *Polypodiophyta* because it is the most frequently used in references indexed by *Biosis* and the *Kew Bibliographic Databases*.

Definition (node-based). — The least inclusive clade containing *Polypodium vulgare* L. 1753 (*/Leptosporangiatae*), *Marattia attenuata* Labill. 1824 (*/Marattiales*), and *Ophioglossum reticulatum* L. 1753 (*/Ophioglossales*).

Comments on definition. — The internal specifiers for this name are all traditionally classified as "ferns." Recent molecular analyses (Nickrent & al., 2000; Pryer & al., 2001, 2004b; Wikström & Pryer, 2005; Schuettpelz & al., 2006) suggested that a group that contains all extant "ferns" is paraphyletic unless it also includes horsetails (*/Equisetum*). In contrast, some morphological analyses (Rothwell, 1999; Renzaglia & al., 2000) and summary phylogenies (Doyle, 1998) suggested that extant ferns form a clade. Because ferns (excluding horsetails) were formally recognized in virtually all botany textbooks until very recently, we feel that it is useful to provide a phylogenetically defined name for this group even though there is conflicting evidence on its monophyly. */Equisetum* is not represented among the internal specifiers in our definition and may therefore fall either inside or outside the clade */Polypodiophyta* as defined here. In the context of most recent phylogenies, */Equisetum* falls within the clade, and */Monilophyta* and */Polypodiophyta* are synonyms. It is our intent that */Monilophyta* have precedence over */Polypodiophyta* whenever they are synonyms. However, under other phylogenetic hypotheses (e.g., Doyle, 1998: Fig. 1), they are not synonyms, and */Polypodiophyta* is nested within */Monilophyta*.

Reference phylogeny. — Rothwell (1999: Fig. 2). See also Doyle (1998), Renzaglia & al. (2000), and Rothwell & Nixon (2006).

Composition. — The total clades of */Ophioglossales*, */Marattiales*, */Leptosporangiatae*, and, under some hypotheses, */Psilotaceae*.

Synapomorphies (relative to other crown clades). — Kenrick & Crane (1997) listed circinate vernation (though this feature is weakly manifested in */Ophioglossales* and absent in */Psilotaceae*) and septate rhizoids on the gametophyte as synapomorphies. They also listed "fern megaphylls," but this character is poorly defined. Moreover, there appear to have been several independent origins of megaphylls among euphyllophytes (Boyce & Knoll, 2002), and it would not be surprising if megaphylls originated more than once within */Polypodiophyta*. Rothwell (1999) listed the following as synapomorphies of their "fern clade 3" (which corresponds to */Polypodiophyta*):

stele with leaf gaps in xylem and phloem, absence of radial rachis/axis trace, adaxially convex "C" shaped trace, and adaxial protoxylem in rachis.

Synonymy. — Approximate synonyms include *Filicophyta* (e.g., GenBank, 2006), *Filicopsida* (e.g., Scagel & al., 1984), *Pterophyta* (e.g., Bold, 1957), and *Pteropsida* (e.g., Benson, 1957). */Monilophyta* may also be a synonym; see Comments on definition.

Psilotaceae Eichler 1886: 22 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — There are several preexisting names for this clade that differ only in their rank-based ending: *Psilotophyta*, *Psilotopsida*, *Psilotales*, *Psilotineae*, and *Psilotaceae*. In addition, the abbreviated names *Psilophyta* and *Psilopsida* are often used but are incorrectly formed from the base name *Psilotum* (or, in some cases [e.g., Eames, 1936] possibly from two base names—*Psilotum* and *Psilophyton*). Of all of these names, *Psilotaceae* is by far the most frequently used. Eichler was the first to publish *Psilotaceae* with the correct orthography, but the name is attributed to Griffith & Henfrey (1855; as "*Psiloteae*") under the *ICBN* (Hoogland & Reveal, 2005).

Definition (branch-modified node-based). — The most inclusive crown clade containing *Psilotum nudum* (L.) P. Beauv. 1805 but not *Ophioglossum reticulatum* L. 1753 (*/Ophioglossales*) or *Marattia attenuata* Labill. 1824 (*/Marattiales*) or *Pteridium aquilinum* (L.) Kuhn 1879 (*/Leptosporangiatae*) or *Equisetum telmateia* Ehrh. 1783.

Comments on definition. — We know of no published phylogeny of */Psilotaceae* and therefore have no basis to hypothesize the monophyly of either *Psilotum* or *Tmesipteris*. Bierhorst (1971: 155) stated that "in most details they intergrade." Because we cannot rule out the possibility that *Psilotum* or *Tmesipteris* might be paraphyletic, a node-based definition with one specifier representing each of these genera would be risky. Content stability is best served by a branch-modified node-based definition with every plausible candidate for extant sister group represented among the external specifiers.

Reference phylogeny. — Pryer & al. (2004b).

Composition. — *Psilotum* and *Tmesipteris*.

Synapomorphies (relative to other crown clades). — Sporangia fused to form synangia. Other features that may be synapomorphies if the clade */Psilotaceae* falls within */Monilophyta* (as in the phylogeny of Pryer & al. [2001, 2004b]) are the absence of roots and isotomous branching, but these features may be plesiomorphic if */Psilotaceae* are the extant sister group of the rest of */Euphyllophyta* (as in the phylogenies of Stevenson & Loconte [1996] and Rothwell [1999]).

Synonymy. — In addition to those mentioned under Comments on name, *Psilotophytina* sensu Doweld (2001) is a synonym.

Ophioglossales Link 1833 (vol. 2): 151 (as "*Ophioglosseae*") [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — There are several preexisting names for this clade that differ only in their rank-based ending: *Ophioglossophyta*, *Ophioglossophytina*, *Ophioglossopsida*, *Ophioglossales*, and *Ophioglossaceae*. The last two names are much more frequently used than the others. We prefer *Ophioglossales* because this name apparently always refers to the entire group, while the name *Ophioglossaceae* is applied by some authors to a smaller clade (e.g., Stevenson & Loconte [1996] recognized two families and Doweld [2001] three within *Ophioglossales*).

Definition (branch-modified node-based). — The most inclusive crown clade containing *Ophioglossum vulgatum* L. 1753 but not *Psilotum nudum* (L.) P. Beauv. 1805 (*/Psilotaceae*) or *Marattia attenuata* Labill. 1824 (*/Marattiales*) or *Equisetum telmateia* Ehrh. 1783 or *Pteridium aquilinum* (L.) Kuhn 1879 (*/Leptosporangiatae*) or *Ginkgo biloba* L. 1771 (*/Spermatophyta*).

Comments on definition. — Although a phylogenetic analysis of this clade based on morphology and chloroplast DNA data has been published (Hauk & al., 2003), the authors were unable to include a distinctive, recently discovered species (*Mankyua chejuense* B.-Y. Sun., M.J. Kim & C.H. Kim), which may have diverged early. Rather than include this poorly known species as an internal specifier in a node-based definition on the chance that it is sister to the rest of the clade, we are opting for a branch-modified node-based definition with every plausible candidate for extant sister group represented among the external specifiers.

Reference phylogeny. — Pryer & al. (2001: Fig. 1; 2004b: Fig. 3). See also Stevenson & Loconte (1996), Rothwell (1999), Wikström & Pryer (2005), Rothwell & Nixon (2006), and Schuettpelz & al. (2006).

Composition. — *Botrychium*, *Helminthostachys*, *Mankyua*, *Ophioglossum*; Smith & al., 2006.

Synapomorphies (relative to other crown clades). — Rothwell (1999) listed the following synapomorphies (though only *Ophioglossum* and *Botrychium* were included in his analysis): planation of vegetative leaves in distal regions only, basal division of trophophore, exarch protoxylem in stem, and absence of sclerenchyma from cortex. Stevenson & Loconte (1996), who included three genera of */Ophioglossales* in their analysis, did not discuss synapomorphies of this clade. However, their data matrix suggests that the following additional features may be synapomorphic: dilated leaf base, fibrillar perispore ultrastructure, "coniferous pitting," and absence of root hairs. Many of these characters were also cited by Hauk & al. (2003: 143) as "collectively [distinguishing] this family from other pteridophyte lineages," but other characters in their list (e.g., homosporous spores produced in eusporangia) are almost certainly pleisomorphic. Their morphological cladistic analysis was limited to relationships within /*Ophioglossales* and thus did not provide synapomorphies for the clade as a whole.

Synonymy. — See Comments on name.

Marattiales Link 1833 (vol. 2): 148 (as "Marattiaceae") [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — There are several preexisting names for this clade that differ only in their rank-based ending: *Marattiophyta*, *Marattiopsida*, *Marattiales*, and *Marattiaceae*. The last two names are much more frequently used than the first two. We prefer *Marattiales* because this name apparently always refers to the entire group, while the name *Marattiaceae* is applied by some authors to a smaller clade (e.g., Bierhorst [1971], Stevenson & Loconte [1996], and Doweld [2001] recognized two extant families within *Marattiales*).

Definition (branch-modified node-based). — The most inclusive crown clade containing *Marattia alata* Sw. 1788 but not *Equisetum telmateia* Ehrh. 1783 or *Ophioglossum reticulatum* L. 1753 (/*Ophioglossales*) or *Psilotum nudum* (L.) P. Beauv. 1805 (/*Psilotaceae*) or *Pteridium aquilinum* (L.) Kuhn 1879 (/*Leptosporangiatae*).

Comments on definition. — Because no thorough study of the internal phylogeny has been published, content stability is best served by a branch-modified node-based definition with every plausible candidate for extant sister group represented among the external specifiers.

Reference phylogeny. — Pryer & al. (2001: Fig. 1; 2004b: Fig. 3). See also Stevenson & Loconte (1996), Rothwell (1999), Wikström & Pryer (2005), Rothwell & Nixon (2006), and Schuettpelz & al. (2006).

Composition. — *Angiopteris* (including *Archangiopteris*), *Christensenia*, *Danaea*, *Marattia*; Smith & al., 2006.

Synapomorphies (relative to other crown clades). — Rothwell (1999) listed the following synapomorphies (two extant genera and one extinct one were included in his analysis): an elongate stem that elevates the leaves above ground level, polyarch vascular cylinder in root, stipules, polycyclic dictyostele in stem, no borders on metaxylem pitting, amphiphloic stele, and sporangia fusion to form synangia. Stevenson & Loconte (1996) considered synangia to be apomorphic at a less inclusive level within /*Marattiales*. They did not list synapomorphies for /*Marattiales* as a whole, but their data matrix (which includes all four extant genera) suggests that the following additional features are apomorphic: multicellular root hairs, unbranched stem, pulvinus, and mucilage canals or cavities.

Synonymy. — See Comments on name.

Leptosporangiatae Bessey 1907: 318 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — This clade is sometimes called *Filicales* (Eames, 1936; Benson, 1957), but that name is more often applied to a paraphyletic group that excludes the heterosporous leptosporangiate ferns (Haupt, 1953; Smith, 1955; Bierhorst, 1971; Foster & Gifford, 1974; Bold & al., 1980; Taylor, 1981; Gifford & Foster, 1989; Stewart & Rothwell, 1993; Taylor & Taylor, 1993; GenBank, 2006) or sometimes to the group that includes all ferns regardless of sporangium type (Bower, 1923, 1935). The name *Filicopsida* is also sometimes applied to all leptosporangiate ferns (GenBank, 2006) but is more frequently circumscribed to include all plants that are traditionally considered to be ferns (Foster & Gifford, 1974; Scagel & al., 1984; Stewart & Rothwell, 1993; Tutin & al., 1993). The name *Pteridophyta* was applied by Doweld (2001) to this clade but has traditionally been applied to the paraphyletic group that includes all seedless vascular plants (e.g., Lawrence, 1951). In the most recent fern classification (Smith & al., 2006), *Polypodiopsida* was used for this clade, but this name has been applied by other authors (e.g., Cronquist & al., 1972; Fedorov, 1999) to a larger clade that includes other extant ferns. Because of the ambiguity of these names, we prefer to adopt the name *Leptosporangiatae*, which has been applied only to this clade (Bessey, 1907; Diels, 1936; Lawrence, 1951; Melchior & Werdermann, 1954; Smith, 1955; Stevenson & Loconte, 1996) and does not imply a particular rank. The informal equivalent, "Leptosporangiates," was used for this clade by Smith & al. (2006), even though they selected *Polypodiopsida* as the scientific name.

Definition (node-based). — The least inclusive clade containing *Osmunda cinnamomea* L. 1753, *Hymenophyllum hirsutum* (L.) Sw. 1801, *Gleichenia dicarpa* R. Br. 1810, *Schizaea dichotoma* (L.) J. Sm. 1793, and *Pteridium aquilinum* (L.) Kuhn 1879.

Reference phylogeny. — Pryer & al. (2004b: Fig. 3). See also Stevenson & Loconte (1996), Rothwell (1999), Pryer & al. (2001), Rothwell & Nixon (2006), and Schuettpelz & al. (2006).

Composition. — *Osmundaceae*, *Hymenophyllaceae*, *Gleicheniales*, *Schizaeales*, *Salviniales*, *Cyatheales*, and *Polypodiales* (Smith & al., 2006). Paleozoic leptosporangiate ferns (e.g., *Botryopteris*, *Ankyropteris*) are part of this clade according to some analyses (Rothwell, 1999) but not others (e.g., Rothwell & Nixon, 2006: Fig. 6).

Synapomorphies (relative to other crown clades). — Stevenson & Loconte listed the following synapomorphies: leptosporangia, gametophytes with exposed antheridia and archegonia, less than 100 sperm per antheridium, prone embryos with a small foot, and mesarch protoxylem (but the last character is probably a synapomorphy of the larger clade /*Euphyllophyta*; Doyle, 1998).

Rothwell (1999) listed rhizomatous stem (though there is a great deal of homoplasy in this character), first division of zygote more or less longitudinal, and several features that characterize leptosporangia: sporangial stalk broad, capsule small with thin wall, presence of annulus, ≤ 512 spores per sporangium, ontogenetic origin of sporangium from two cells.

Synonymy. — Approximate synonyms include *Filicales*, *Filicopsida*, *Pteridophyta*, and *Polypodiopsida* of some authors but not others (see Comments on name).

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

Definition (apomorphy-based). — The most inclusive clade exhibiting leptosporangia (i.e., sporangia with a thin wall [only one cell layer thick] and dehiscing by means of an annulus [a patch or band of thick-walled cells]; Gifford & Foster, 1989; Stewart & Rothwell, 1993) synapomorphic with those in *Pteridium aquilinum* (L.) Kuhn 1879.

Reference phylogeny. — Rothwell & Nixon (2006: Fig. 6); see also Rothwell (1999).

Composition. — /*Leptosporangiatae* and Paleozoic taxa including *Anachoropteris*, *Ankyropteris*, *Boytropteris*, *Psalixochlaena*, *Sermaya*, and *Skaaripteris*.

Synonymy. — The name *Filicales* of some authors (e.g., Taylor, 1981; Stewart & Rothwell, 1993) is a partial synonym referring to a paraphyletic group originating from the same ancestor as /*Apo-Leptosporangiatae* but excluding the heterosporous members of this clade.

Lignophyta M.J. Donoghue & J.A. Doyle, new clade name.

Comments on name. — The only preexisting name is *Lignophytia* Kenrick & Crane (1997). The unusual -*phytia* ending was apparently used because the taxon was ranked as a supercohort rather than a phylum or division. In the present context of a set of unranked names, most of which end in -*phyta*, inclusion of a single name ending in -*phytia* would be confusing to users, difficult to teach, and subject to frequent misspelling. The name *Lignophytia* has rarely if ever been used subsequent to its publication (no references in *Biological Abstracts* or the *Kew Bibliographic Databases*). In contrast, the informal name "lignophytes" (first used by Doyle & Donoghue, 1986a: 334), which corresponds most directly to the latinized name *Lignophyta*, has been unambiguously applied to this clade in two recent plant systematics textbooks (Judd & al., 2002; Simpson, 2006) and in research publications (e.g., Rothwell & Serbet, 1994). Although the *PhyloCode* calls for the adoption of a preexisting name if one exists, we feel strongly that the unpublished name *Lignophyta* is preferable to the preexisting name *Lignophytia* for the reasons explained above. In this one case, we are taking advantage of the fact that the *PhyloCode* has not yet been implemented to publish a new name for this clade in spite of the existence of a little-used preexisting name. The *PhyloCode* (Art. 15), like the *ICBN*, provides a mechanism for conserving names. After the code is implemented, we plan to appeal to the Committee on Phylogenetic Nomenclature to conserve *Lignophyta* over *Lignophytia*.

Definition (apomorphy-based). — The most inclusive clade exhibiting a bifacial vascular cambium synapomorphic with that in *Pinus sylvestris* L. 1753. A bifacial vascular cambium is a meristematic layer producing secondary xylem (wood) toward the inside and secondary phloem toward the outside.

Comments on definition. — Although a bifacial vascular cambium has been documented in *Sphenophyllum* (Eggert & Gaunt, 1973), it is not homologous under current estimates of phylogeny. Thus, the phrase "synapomorphic with that in *Pinus sylvestris*" excludes *Sphenophyllum* from /*Lignophyta* unless new evidence were to indicate (for example) that *Sphenophyllum* is sister to the clade comprising seed plants and progymnosperms, in which case its vascular cambium could be considered homologous with that in *Pinus*.

Reference phylogeny. — Rothwell & Serbet (1994: Fig. 1). See also Doyle & Donoghue (1986a), Doyle (1998), and Judd & al. (2002: 164).

Composition. — /*Apo-Spermatophyta* and the "progymnosperms" (e.g., *Aneurophytales*, *Archaeopteridales*, *Protopityales*).

Synapomorphies. — Bifacial vascular cambium (Kenrick & Crane, 1997: Table 7.2). Other correlated apomorphies that first appear in the early lignophytes include a cork cambium, producing periderm, and cortical fiber strands (retained by many seed ferns and cordaites but apparently lost in more advanced lignophytes) (Doyle & Donoghue, 1986a). Heterospory is synapomorphic for the large subclade that includes all of /*Lignophyta* except *Aneurophytales* (Doyle & Donoghue, 1986a; Rothwell & Serbet, 1994).

Synonymy. — *Lignophytia* Kenrick & Crane (1997); see Comments on name. Based on composition, the name *Cycadophytanae* sensu Doweld (2001) is an approximate synonym of /*Lignophyta*. *Progymnospermopsida* (Beck, 1960) and *Progymnospermophyta* (e.g., Taylor, 1981; Gifford & Foster, 1989) are partial synonyms; the progymnosperms originated from the same ancestor as /*Lignophyta* but are paraphyletic with respect to seed plants (/*Apo-Spermatophyta*).

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*.

Synapomorphies. — Possible synapomorphies of the crown clade are endarch primary xylem in the stem (with a possible subsequent reversal in *Callistophyton*, depending on the position of this taxon; Doyle, 2006), meiospores and microgametophytes with distal aperture (with subsequent reversal in *Cordaitales* and *Emporia*; Rothwell & Serbet, 1994; Doyle, 2006), a linear tetrad of megaspores (Doyle & Donoghue, 1986a; Doyle, 2006), and platyspermic ovules (Doyle, 2006). Because most cycads have radiospermic ovules, the level at which platyspermy is synapomorphic is uncertain if the clade */Cycadophyta* is sister to the rest of */Spermatophyta* (e.g., Doyle, 2006: Fig. 6). Furthermore, Rothwell & Serbet (1994) divided ovule symmetry into four states, rather than just two (radiospermic and platyspermic). Other possible synapomorphies of the crown that were found to be synapomorphic at a more inclusive level by Rothwell & Serbet (1994) in a topologically different tree include a sealed micropyle (Pryer & al., 2004a; Doyle, 2006) and honeycomb alveolar pollen infratectal structure (Doyle, 2006). The following are synapomorphies of this crown clade relative to other crowns but are apomorphic at a more inclusive level when fossils are considered (not an exhaustive list): heterospory (which evolved independently in some monilophytes and lycophytes), ovule (i.e., an integumented, indehiscent megasporangium that develops after fertilization into a seed; Stewart, 1983), embryo dormancy, axillary branching, eustele, and cataphylls; Doyle & Donoghue (1986a), Rothwell & Serbet (1994), Doyle (1998), Schneider & al. (2002).

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).

Synapomorphies. — Ovules and seeds; some associated apomorphies are cited under "Comments on definition."

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.

Synapomorphies. — None known. However, Kenrick & Crane (1997: Table 7.2) listed two synapomorphies for *Radiatopses*, a clade that closely approximates /*Pan-Spermatophyta*: tetrastichous branching (though this occurs only in the earliest members of the clade) and "a distinctive form of protoxylem ontogeny with multiple strands occurring along the midplanes of the primary xylem ribs."

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 (Sereno, 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.

Synapomorphies (relative to other crown clades). — There are no unambiguous non-DNA synapomorphies. Abaxial microsporangia are a possible synapomorphy (Doyle, 2006), but polarity is equivocal because of missing data in the basal taxa of the sister group.

Synonymy. — None.

Cycadophyta Bessey 1907: 321 [P.D. Cantino & M.J. Donoghue], converted clade name.

Comments on name. — The names *Cycadophyta*, *Cycadopsida*, and *Cycadales* are widely applied to the same set of clades (referring variably and often ambiguously to the crown, total clade or something intermediate). Our preference for the -*phyta* ending and its application to the crown are explained under Methods.

Definition (node-based). — The least inclusive clade containing *Cycas circinalis* L. 1753 and *Zamia floridana* A.DC. 1868.

Comments on definition. — Two internal specifiers are sufficient to ensure compositional stability because the basal dichotomy has strong morphological and molecular support.

Reference phylogeny. — Hill & al. (2003: Figs. 9, 10). See also Crane (1988: Fig. 5.7), Stevenson (1990: 49–51), Treutlein & Wink (2002), Rai & al. (2003: Fig. 2), Bogler & Francisco-Ortega (2004), Chaw & al. (2005), and Hermsen & al. (2006).

Composition. — *Cycadineae* and *Zamiineae* sensu Stevenson (1992).

Synapomorphies. — Cone domes (Hermsen & al., 2006: Fig. 18). Additional likely synapomorphies relative to other crown clades (but possibly synapomorphic at a more inclusive level than the crown) include: girdling leaf traces, cycasin, coralloid roots, primary thickening meristem that produces most of its derivatives centrifugally, curculionid pollination, buffer cells surrounding archegonium, omega-shaped pattern of petiole vascular bundles, pith cell packets, double vasculature of the integument, three unique biflavones, and BMAA (a neurotoxic amino acid; Brenner & al., 2003) (Crane, 1985a, 1988; Stevenson, 1990; Hermson & al., 2006).

Synonymy. — See Comments on name.

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

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

Composition. — /*Cycadophyta* and all extinct plants (e.g., *Antarcticycas*, *Michelilloa*; Hermsen & al., 2006) that share more recent ancestry with /*Cycadophyta* than with any other extant seed plants.

Synapomorphies. — It is not known where on the stem the synapomorphies listed under /*Cycadophyta* arose, but the earliest fossils that can confidently be referred to /*Pan-Cycadophyta* have girdling leaf traces (Crane, 1988: 240).

Synonymy. — See Comments on name under /*Cycadophyta*.

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

Comments on name. — The names *Coniferae*, *Pinopsida*, *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 below) is sister to the rest of the conifers. However, cladistic analyses that included fossils suggested that *Taxaceae* are the extant sister group of 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.

Synapomorphies (relative to other crown clades). — Needlelike leaves, tiered proembryos (Doyle & Donoghue, 1986a), siphonogamy (not homologous with siphonogamy in angiosperms and gnetophytes if the phylogenies of Crane [1985a], Doyle [1996] and others are correct), and loss or extreme reduction of one copy of the inverted repeat in the chloroplast genome (Raubeson & Jansen, 1992b; Wakasugi & al., 1994).

Synonymy. — See Comments on name.

Pan-Coniferae P.D. Cantino, M.J. Donoghue & J.A. Doyle, new clade name

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

Composition. — /*Coniferae* and all extinct plants that share more recent ancestry with /*Coniferae* than with any other extant seed plants. Depending on the position of *Ginkgo*, /*Pan-Coniferae* may include *Cordaitales*, Paleozoic conifers such as *Emporia* and *Lebachia*, both, or neither (Crane, 1985a; Rothwell & Serbet, 1994; Doyle, 1996, 2006; Hilton & Bateman, 2006).

Synonymy. — None known.

Pinaceae Spreng. ex F. Rudolphi 1830: 35 [P.D. Cantino & M.J. Donoghue], converted clade name.

Definition (branch-modified node-based). — Most inclusive crown clade containing *Pinus sylvestris* L. 1753 but not *Araucaria araucana* (Molina) K. Koch 1873 (/*Cupressophyta*) or *Cupressus sempervirens* L. 1753

(/*Cupressophyta*) or *Podocarpus macrophyllus* (Thunb.) Sweet 1818 (/*Cupressophyta*) or *Gnetum gnemon* L. 1767 (/*Gnetophyta*).

Comments on definition. — In all published phylogenies, the extant sister group of this crown clade is either the rest of the conifers (e.g., Hart, 1987; Stefanovic & al., 1998; Rydin & al., 2002), the rest of the conifers except *Taxaceae* (Miller, 1999), *Araucariaceae* (Nixon & al., 1994), *Podocarpaceae* (Doyle, 1996; Doyle, 2006: Fig. 7; Hilton & Bateman, 2006) or the gnetophytes (e.g., Bowe & al., 2000; Gugerli & al., 2001). A standard node-based definition with species of *Pinus*, *Cedrus*, and *Tsuga* as internal specifiers would be simpler but perhaps prone to greater compositional instability if no additional internal specifiers are used, because the internal phylogeny of /*Pinaceae* has received only one comprehensive molecular phylogenetic study (Wang & al., 2000), in contrast to the many such studies of its outgroup relationships. Our inclusion of three external specifiers representing /*Cupressophyta* may not be necessary, but we prefer a conservative approach here because only two molecular studies to date are reasonably comprehensive in their taxonomic coverage of conifers (Stefanovic & al., 1998; Rydin & al., 2002).

Reference phylogeny. — Rydin & al. (2002: Fig. 1). See also Hart (1987: Fig. 2), Stefanovic & al. (1998: Fig. 5), Bowe & al. (2000: Fig. 3), Chaw & al. (2000), Magallón & Sanderson (2002), Soltis & al. (2002).

Composition. — *Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga*, and *Tsuga* (Wang & al., 2000).

Synapomorphies (relative to other crown clades). — Proembryo four-tiered (Sporne, 1965: 136–137), two vascular bundles per leaf (Hart, 1987) (reduced to one bundle in one subgroup of *Pinus*), sieve element plastids accumulate protein (Behnke, 1974, Hart, 1987). See Hart (1987) for other possible synapomorphies.

Synonymy. — None in recent literature.

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*.

Synapomorphies. — Phloem fibers forming regular, uniseriate tangential bands (modified to irregular masses or bands in *Araucariaceae*) are a possible synapomorphy (Doyle, 2006). Hart's (1987: Fig. 2) cladogram showed three apomorphies for this node, but none of them appear to be synapomorphies of /*Cupressophyta* when Hart's data are mapped onto the DNA-based reference phylogeny.

Synonymy. — None.

Gnetophyta Bessey 1907: 323 (as "*Gnetales*"; Hoogland & Reveal, 2005) [M.J. Donoghue, J.A. Doyle & P.D. Cantino], converted clade name.

Comments on name. — The names *Gnetophyta*, *Gnetopsida*, and *Gnetales* are widely applied to this clade. Our preference for the -*phyta* ending is explained under Methods: Choice of names.

Definition (node-based). — Least inclusive clade containing *Gnetum gnemon* L. 1767, *Ephedra distachya* L. 1753, and *Welwitschia mirabilis* Hook. f. 1862.

Reference phylogeny. — Rydin & al. (2002: Fig. 1). See also Doyle & Donoghue (1992), Doyle & al. (1994), Rothwell & Serbet (1994), Doyle (1996), Soltis & al. (2002), and Burleigh & Mathews (2004).

Composition. — *Ephedra*, *Gnetum*, and *Welwitschia*.

Synapomorphies (relative to other crown clades). — Multiple axillary buds, opposite phyllotaxy, terminal ovules, basally fused microsporophylls with terminal microsporangia, vessels in xylem (assuming non-homology with angiosperm vessels), compound microsporangiate strobili, striate pollen (modified to echinate in *Gnetum*; Yao & al., 2004), micropylar tube, apical meristem with one tunica layer (Doyle & Donoghue, 1986a,b, 1992; Crane, 1988; Rothwell & Serbet, 1994; Doyle, 2006).

Synonymy. — See Comments on name.

Pan-Gnetophyta J.A. Doyle, M.J. Donoghue & P.D. Cantino, new clade name.

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

Composition. — /*Gnetophyta* and all extinct plants that share more recent ancestry with /*Gnetophyta* than with any other extant seed plants.

Synapomorphies. — It is not known where on the gnetophyte stem the synapomorphies listed above for /*Gnetophyta* (relative to other crown clades) evolved. Striate pollen similar to that of *Ephedra* and *Welwitschia* occurs in the earliest fossils that are thought to be gnetophytes (Crane, 1988), so this character is a good candidate for a synapomorphy of the total clade. *Dechellyia* (Late Triassic), one of the earliest macrofossils that is associated with striate pollen, has opposite phyllotaxy and possibly terminal ovules (Ash, 1972; Crane, 1996), suggesting that these apomorphies may also have arisen near the base of /*Pan-Gnetophyta*.

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*.

Synapomorphies. — The following are synapomorphies relative to other crown clades, some of which also occur in fossil plants that may be stem relatives of /*Angiospermae* (these are noted parenthetically; Crane, 1985a; Doyle & Donoghue, 1986a, 1992; Doyle, 1996, 2006): closed carpel, which develops into a fruit; ovule with two integuments; cuticle of megasporangium thick (also in *Caytonia*, *Bennettitales*, *Pentoxylon*, and *Glossopteridales*); lack of a cutinized megaspore membrane (also in *Caytonia*, *Bennettitales*, and *Pentoxylon*); highly reduced female gametophyte, usually with no more than eight nuclei; endosperm resulting from double fertilization (but see Friedman & Floyd, 2001); microgametophyte with three nuclei; scalariform pitting or perforations in secondary xylem (also in *Bennettitales*); two or more orders of leaf venation; poles of stomatal guard cells level with aperture (also in *Caytonia*); axially aligned companion cells derived from the same mother cells as the sieve elements; pollen with unlaminated endexine; stamen with two pairs of pollen sacs (Crane, 1985a; Doyle & Donoghue, 1986a, 1992; Rothwell & Serbet, 1994; Soltis & al., 2004).

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

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

Definition (apomorphy-based). — The most inclusive clade exhibiting a carpel synapomorphic with that in *Zea mays* L. 1753. A carpel is a structure that envelops one or more ovules and develops into a fruit after ovule fertilization.

Reference phylogeny. — None.

Composition. — /*Angiospermae* and any extinct carpel-bearing plants that lie outside the crown.

Synonymy. — The informal name "angiosperms" has been applied to the apomorphy-based clade originating with the origin of the carpel (e.g., Sun & al., 2002).

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; 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*.

Synapomorphies. — Unambiguous morphological synapomorphies for /*Mesangiospermae* are not yet known. One possibility is that plicate carpels sealed by postgenital fusion of the margins (see Endress & Igersheim, 2000) evolved at this point, but this depends on the ultimate placement of *Chloranthaceae*, which have ascidiate carpels sealed by secretion, comparable to those of *Amborella* and other members of the "ANITA" grade. Most recent molecular analyses have supported the nesting of *Chloranthaceae* within /*Mesangiospermae*, which would favor (but not guarantee; Soltis & al., 2005: Fig. 3.17) the view that plicate carpels and sealing by postgenital fusion are synapomorphies at the level of /*Mesangiospermae*. However, a combined molecular and morphological analysis (Doyle & Endress, 2000) and a recent molecular analysis (Qiu & al., 2005) supported the placement of *Chloranthaceae* as sister to all remaining /*Mesangiospermae*, in which case the ascidiate carpels of *Chloranthaceae* could be plesiomorphic, and plicate carpels sealed by postgenital fusion would be inferred to have evolved within /*Mesangiospermae.* In either case, some homoplasy would remain (e.g., reversals to ascidiate carpels in *Nelumbo* and *Berberidacaeae*; convergent origins of partially plicate carpels in *Illicium*; Doyle & Endress, 2000: Fig. 7; Soltis & al., 2005: Fig. 3.17). Finally, recent embryological studies (Williams & Friedman, 2002; Friedman, 2006) raise the possibility that the typical 7-celled, 8-nucleate *Polygonum* type embryo sac is a synapomorphy of /*Mesangiospermae*, assuming that the 9-nucleate embryo sac of *Amborella* was independently derived from the 4-nucleate type found in *Nymphaeales* and *Austrobaileyales*.

Synonymy. — None.

Magnoliidae Novák ex Takhtajan 1967: 51 [W.S. Judd, P.S. Soltis & D.E. Soltis], converted clade name.

Comments on name. — Magnoliidae, as circumscribed by Takhtajan (1997) or Cronquist (1988), are significantly different in composition from the clade given the informal name "magnoliids" or "eumagnoliids" in many recent publications (e.g., Judd & al., 2002; APG II, 2003; Hilu & al., 2003; Soltis & Soltis, 2004; Soltis & al., 2005; Qiu & al., 2006a; Simpson, 2006). However, the name Magnoliidae has been formally linked with this clade by Giulietti & al. (2005: 636), who stated "The dicotyledons, for present purposes including the Nymphaeales, Magnoliidae, and eudicotyledons (sensu APG [Angiosperm Phylogeny Group] II, 2003), are only partially listed in Table 2." This is the only preexisting scientific name for this clade.

Definition (node-based). — The least inclusive clade containing *Canella winterana* (L.) Gaertn. 1788 (*Canellales*), *Magnolia virginiana* L. 1753 (*Magnoliales*), *Cinnamomum camphora* (L.) J. Presl 1825 (*Laurales*), and *Piper betle* L. 1753 (*Piperales*).

Reference phylogeny. — Qiu & al. (2006a: Fig. 1). See also Mathews & Donoghue (1999), Qiu & al. (1999, 2000, 2005), Graham & Olmstead (2000), Soltis & al. (2000), Nickrent & al. (2002), Zanis & al. (2002, 2003), Hilu & al. (2003).

Composition. — *Canellales*, *Laurales*, *Magnoliales*, and *Piperales* (APG II, 2003)

Synapomorphies. — Possible synapomorphies include the phenylpropane compound asarone, the lignans galbacin and veraguensin, and the neolignan licarin (Hegnauer, 1962-1994; Soltis & al., 2005).

Synonymy. — None known.

Monocotyledoneae de Candolle 1817: 122 [W.S. Judd, P.S. Soltis, D.E. Soltis & S.W. Graham], converted clade name.

Comments on name. — There are four names that are commonly applied to this clade: *Monocotyledoneae*, *Monocotyledonae*, *Monocotyledones*, and *Liliopsida*. The *Kew Bibliographic Databases* (http://www.kew.org/kbd/searchpage.do) yielded far more links to *Monocotyledoneae* and *Monocotyledones* than the other two (175, 22, 159, and 22, respectively, as of April 10, 2007). We also prefer descriptive names based on distinctive synapomorphies to nondescriptive, rank-based names unless a name of the latter sort is much more widely used (see Methods: Choice of name). The corresponding informal names "monocots" and "monocotyledons" have been applied to this clade in nearly all recent phylogenetic treatments of angiosperms (e.g., APG II, 2003; Judd & al., 2002; Chase, 2004; Soltis & Soltis, 2004; Soltis & al., 2005; Simpson, 2006). Our choice of *Monocotyledoneae* over *Monocotyledones* is somewhat arbitrary, but the former appears to have been used in more post-1900 classifications, floras and textbooks.

Definition (node-based). — The least inclusive clade containing *Acorus calamus* L. 1753, *Gymnostachys anceps* R. Br. 1810, *Tofieldia glutinosa* (Michx.) Pers. 1805, and *Lilium superbum* L. 1762.

Reference phylogeny. — Chase & al. (2006), Graham & al. (2006). See also Chase & al. (1995a, b, 2000), Soltis & al. (2000), Stevenson & al. (2000), Hilu & al. (2003), Davis & al. (2004, 2006), and Givnish & al. (2006).

Composition. — *Acorus* and the total clade of /*Nartheciidae.*

Synapomorphies. — Embryo with single cotyledon; parallel-veined leaves (see Givnish & al. [2005] for secondary evolution of net venation); stem with scattered vascular bundles; sieve tube plastids with cuneate proteinaceous crystalloids. Monocot-like sieve tube plastids also occur in some *Piperales*, where they apparently evolved independently. Other possible synapomorphies (Judd & al., 2002; Stevens, 2006) include sheathing leaf base, mature plant with adventitious root system, and sympodial growth. All of these character states occur in other angiosperms and some of them do not occur in all monocots, but they may still be synapomorphies of /*Monocotyledoneae*, depending on outgroup and ingroup tree topology.

Synonymy. — See Comments on name.

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

Comments on name. — The name *Nartheciidae* is chosen in recognition of commentary on *Nartheciaceae* and associated taxa by Tamura (1998) and earlier authors cited therein, which foreshadowed our current phylogenetic understanding of the deepest phylogenetic relationships in /*Monocotyledoneae*. The clade has not been named previously, and the name *Nartheciidae* has not been applied to any other clade.

Definition (node-based with an external qualifier). — The least inclusive clade containing *Gymnostachys anceps* R. Br. 1810 (*Alismatales*) and *Narthecium ossifragum* (L.) Huds. 1762 (/*Petrosaviidae*), but not *Acorus calamus* L. 1753.

Comments on definition. — The name applies to a clade that includes all extant monocots except *Acorus*. An external qualifier is used to prevent the name from applying to any clade that includes *Acorus calamus*. For example, in the context of a phylogeny in which *Acorus* groups with *Alismatales* (Davis & al., 2004), the name /*Nartheciidae* is not applicable to any clade.

Reference phylogeny. — Tamura & al. (2004; Fig. 1). See also Chase & al. (2000, 2006), Givnish & al. (2006), and Graham & al. (2006). A conflicting grouping of *Acorus calamus* with *Alismatales* (Davis & al., 2004, 2006) may be an artifact of extensive rate heterogeneity in the mitochondrial genome (Chase, 2004).

Composition. — *Alismatales* and the total clade of /*Petrosaviidae*.

Synapomorphies. — Absence of oil cells in the mesophyll (Doyle & Endress, 2000) may be a synapomorphy. However, this depends partly on the outgroup relationships of /*Monocotyledoneae*, which remain poorly resolved.

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 /*Commelinidae*.

Synapomorphies. — No unambiguous synapomorphies known.

Synonymy. — None.

Commelinidae Takhtajan 1967: 514 [S.W. Graham & W.S. Judd], converted clade name.

Comments on name. — *Commelinidae* is the only scientific name that has been applied to this clade (Givnish & al., 1999; Thorne, 2000), which has been referred to informally in recent papers as "commelinoids" (e.g., Chase & al., 1995b, 2000; APG, 1998; Zona, 2001) and "commelinids" (e.g., APG II, 2003, Chase, 2004; Chase & al., 2006; Graham & al., 2006). The name *Commelinidae* was applied previously to various sets of taxa that excluded *Arecaceae* and *Dasypogonaceae* (Takhtajan, 1997) or *Arecaceae*, *Bromeliaceae*, *Dasypogonaceae*, and *Zingiberales* (Cronquist, 1981), in addition to other minor differences.

Definition (node-based). — The least inclusive clade containing *Dasypogon hookeri* J. Drumm. 1843 (*Dasypogonaceae*), *Commelina communis* L. 1753 (*Commelinales*), *Roystonea princeps* (Becc.) Burret 1929 (*Arecales*), and *Oryza sativa* L. 1753 (*Poales*).

Reference phylogeny. — Graham & al. (2006: Fig. 1B). See also Givnish & al. (1999, 2006), Chase & al. (2000, 2006), and Davis & al. (2004, 2006).

Composition. — *Arecales*, *Commelinales*, *Dasypogonaceae*, *Poales*, and *Zingiberales*.

Synapomorphies. — UV-fluorescent ferulic acid in cell walls is an unreversed synapomorphy (Dahlgren & Rasmussen, 1983; Clark & al., 1993; Givnish & al., 1999). "*Strelitzia* type" epicuticular wax sculpturing (the wax crystalloids aggregated into rod-like, often massive projections; Dahlgren & al., 1985: 65) is a probable synapomorphy, but there were many losses within the clade and a few presumed convergences outside it (Dahlgren & Rasmussen, 1983; Clark & al., 1993; Givnish & al., 1999). Starchy pollen (although apparently lacking in *Dasypogonaceae*) and starchy endosperm (lacking in *Arecales*) may also be synapomorphies (Dahlgren & Rasmussen, 1983; Zona, 2001); this depends in part on how currently uncertain relationships among the five clades in the composition list are resolved. Silica bodies may be a synapomorphy, but their diversity of shapes and tissue-level distribution patterns suggest that their occurrences may not all be homologous (Dahlgren & al., 1985: 63). Bracteate inflorescence is also cited as a possible synapomorphy by Givnish & al. (1999), with appropriate caveats about homology.

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; Doyle & Endress, 2000; APG II, 2003; 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* (below) 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; and 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 /*Eudicoyledoneae* 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 *Didymeles*), and /*Gunneridae.*

Synapomorphies. — /*Eudicotyledoneae* are characterized by tricolpate pollen grains and a wide array of evolutionarily derived forms. Tricolpate pollen appears to have originated on the line leading to crown eudicots from the monosulcate (and globose, columellar) grains that appear to be ancestral in angiosperms (Doyle, 2005). Loss of oil cells in the mesophyll and dry fruit wall have also been identified as synapomorphies of /*Eudicotyledoneae* (Doyle & Endress, 2000, Fig. 4), but this inference is sensitive to outgroup relationships.

Synonymy. — None.

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

Comments on name. — There is no preexisting scientific name for this clade. Published uses of the terms "eudicots" and "tricolpates" have not clearly distinguished whether they refer to the crown clade or to a clade originating with the evolution of an apomorphy. Our aim here is to separate the meanings associated with these names by applying *Eudicotyledoneae* to the crown clade (see above) and *Tricolpatae* (which refers to tricolpate pollen grains) to the apomorphy-based clade. We think that this distinction will be helpful in view of the substantial fossil record of pollen and the possibility of discovering plants within the tricolpate clade that fall outside of the crown. The appearance of tricolpate grains has taken on great importance in assessing the timing of angiosperm evolution (see Soltis & al., 2005). If only extant plants are considered, however, /*Eudicotyledoneae* and /*Tricolpatae* have the same membership.

Definition (apomorphy-based). — The most inclusive clade exhibiting tricolpate (or derivative) pollen grains synapomorphic with those found in *Platanus occidentalis* L. 1753 (/*Eudicotyledoneae*). A tricolpate pollen grain is one having three elongate, furrow-like apertures (colpi) located at and running perpendicular to the equator.

Comments on definition. — The pollen of *Illicium* and *Schisandraceae* was scored as tricolpate by Donoghue & Doyle (1989), and then inferred to have evolved separately from the grains of the tricolpate clade. These grains also differ from standard tricolpate grains in that the colpi are located 60 degrees from those of the latter grains (i.e., according to Garside's Rule rather than Fischer's Rule; Huynh, 1976; Doyle & al., 1990) and usually fused at the distal pole (syntricolpate). Accordingly, they were scored as representing a separate state by Doyle & Endress (2000) and again (defined somewhat differently) by Doyle (2005). In any case, all relevant phylogenetic analyses clearly indicate that the three apertures of *Illicium* and *Schisandraceae* are not homologous with those of /*Tricolpatae*. Many different forms of pollen grains have evolved (in most cases multiple times) from the first tricolpate grains of this clade. These modifications include increases and decreases in the number of colpi (di-, tetra-, penta-, hexa-, and polycolpate forms) and the complete loss of apertures. Porate and compound-aperturate forms, especially tricolporate and triporate grains, appear to have originated frequently, and in some cases the position and/or orientation of the colpi or pores has shifted away from the equator of the grain (e.g., polyrugate and polyforate grains). The resulting multitude of pollen forms all appear to be modifications of the original grains of the /*Tricolpatae*.

Reference phylogeny. — Doyle (2005: Fig. 4). See also Doyle & Endress (2000: Fig. 4).

Composition. — /*Eudicotyledoneae* and stem taxa with tricolpate pollen. So far, all well-reconstructed Early Cretaceous (Albian) fossil taxa with tricolpate pollen (e.g., Friis & al., 1988; Drinnan & al., 1991; Crane & al., 1993) appear to be part of the crown group, /*Eudicotyledoneae*, but some dispersed tricolpate pollen types may represent stem taxa that are part of /*Tricolpatae* but not of /*Eudicotyledoneae*.

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*.

Synapomorphies. — /*Gunneridae* may be marked by gene duplications in a number of gene families that underlie flower development, including several duplications of MADS-box genes and in the TCP gene family (Lamb & Irish, 2003; Litt & Irish, 2003; Howarth & Donoghue, 2006). The presence of ellagic acid may also be synapomorphic (Soltis & al., 2005).

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* x *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 *Aetoxicaceae*; Hilu & al., 2003; Soltis & al., 2005), *Dilleniaceae*, *Santalales*, *Saxifragales*, *Vitaceae*, and the total clades of /*Asteridae*, /*Caryophyllales*, and /*Rosidae*.

Synapomorphies. — A possible synapomorphy is duplication of the *AP1*/*FUL* pair of MADS-box floral regulatory genes (Litt & Irish, 2003). There may have been related changes in developmental mechanisms that are correlated with the fixation of floral structures characteristic of this clade, i.e., the evolution of a pentamerous, highly synorganized flower with a differentiated perianth composed of distinct calyx and corolla (Soltis & al., 2003).

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

Caryophyllales Jussieu ex Berchtold & Presl 1820: 239 (as "Caryophyllaceae") [P.S. Soltis, W.S. Judd & D.E. Soltis], converted clade name.

Comments on name. — The name *Caryophyllales* was applied to this clade by APG (1998) and APG II (2003) and in many recent phylogenetic papers (e.g., Savolainen & al., 2000a; Soltis & al., 2000; Cuénoud & al., 2002; Hilu & al., 2003). However, this leaves the less inclusive clade that was long associated with the name *Caryophyllales* (e.g., Takhtajan, 1967, 1987, 1997; Cronquist, 1981, 1988; see also Judd & al., 2002 for a variant on this traditional circumscription) in need of a new name. The less inclusive clade was also commonly referred to as *Centrospermae* in mid-20th century literature (e.g., Lawrence, 1951; Engler & Harms, 1960; Melchior, 1964; Rendle, 1967). We suggest that *Centrospermae* be phylogenetically defined to apply to this smaller clade, but we do not do so here.

Definition (node-based). — The least inclusive clade containing *Dianthus caryophyllus* L. 1753, *Polygonum sachalinense* F. Schmidt ex Maxim. 1859, *Simmondsia chinensis* (Link) C.K. Schneid. 1907, and *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber 1909.

Reference phylogeny. — Soltis & al. (2000: Fig. 5) and Cuénoud & al. (2002: Fig. 2); see also Hilu & al. (2003).

Composition. — *Caryophyllales* sensu AGP II (2003); *Caryophyllales* and *Polygonales* sensu Judd & al. (2002) plus *Rhabdodendraceae* (not covered by Judd & al.).

Synapomorphies. — Unknown; more studies are needed but perhaps anther with outer parietal cells developing directly into the endothecium (Stevens, 2006).

Synonymy. — *Caryophyllidae* sensu Soltis & Soltis (2003: 1793) is a synonym, and *Caryophyllidae* sensu Takhtajan (1967, 1987, 1997) and Cronquist (1981, 1988) are partial synonyms; some taxa placed by the latter authors in *Dillenidae*, *Rosidae*, and *Hamamelidae* are part of */Caryophyllales*.

Rosidae Takhtajan 1967: 264 [W.S. Judd, P.D. Cantino, D.E. Soltis & P.S. Soltis], converted clade name.

Comments on name. — *Rosidae*, as circumscribed by Takhtajan (1997) or Cronquist (1988), are significantly different in composition from the clade given the informal name "rosids" or "eurosids" in many recent phylogenetic studies (Savolainen & al., 2000a, b; Soltis & al., 2000, 2003, 2005; Hilu & al., 2003; Judd & Olmstead, 2004; Soltis & Soltis, 2004), classifications (APG, 1998; APG II, 2003), and texts (Judd & al., 2002; Simpson, 2006). However, the name *Rosidae* has been formally linked with this clade by Fukuda & al. (2003: 589), who stated, "we focus on the legume family (*Fabaceae*), which belongs to another large group of core dicotyledons, the subclass *Rosidae* (Chase & al. 1993; APG, 1998)" and by Soltis & Soltis (2003: 1793), who stated, "Cronquist's concepts of *Rosidae*, *Asteridae*, and *Caryophyllidae* must be expanded and revised to correspond to monophyletic groups; these clades are the rosids, asterids, and *Caryophyllales* sensu APG II (2003)." *Rosidae* is the only preexisting scientific name for this clade.

Definition (branch-modified node-based). — The most inclusive crown clade containing *Rosa cinnamomea* L. 1753 but not *Berberidopsis corallina* Hook. f. 1862 (*Berberidopsidales*) or *Dillenia indica* L. 1753 (*Dilleniaceae*) or *Gunnera manicata* Linden ex André 1873 (*Gunnerales*) or *Helianthus annuus* L. 1753 (*/Asteridae*) or *Saxifraga mertensiana* Bong. 1832 (*Saxifragales*) or *Stellaria media* (L.) Vill. 1788 (*/Caryophyllales*) or *Viscum album* L. 1753 (*Santalales*).

Comments on definition. — Because the position of Vitaceae has varied in phylogenetic studies (see Soltis & al., 2005: 171 for a summary), it has been included in the rosid clade in some recent classifications (Judd & al., 2002; APG II, 2003) and excluded in others (APG, 1998; Stevens, 2006). The definition of */Rosidae* is agnostic about the inclusion of *Vitaceae*. Because the definition is branch-modified, and the external specifiers do not include any species of *Vitaceae*, */Rosidae* will include *Vitaceae* in the context of some phylogenies (e.g., Soltis & al., 2000) but exclude it in the context of others (e.g., Hilu & al., 2003). Additional studies will presumably resolve this issue, but the definition can accommodate either outcome. Similarly, the definition is agnostic about the inclusion of *Picramniaceae*, though the little evidence available (Fernando & al., 1995; Savolainen & al., 2000a, b) weakly supports its inclusion (see also discussion in Fernando & Quinn, 1995).

Reference phylogeny. — Soltis & al. (2000: Fig. 5). See also Savolainen & al. (2000a), Hilu & al. (2003), and Soltis & al. (2003).

Composition. — *Crossosomatales* s.l. (i.e., including *Aphloiaceae*, *Geissolomataceae*, *Ixerbaceae*, and *Strasburgeriaceae*; Stevens, 2006), *Geraniales*, *Myrtales* and the total clades of */Fabidae* and */Malvidae*; probably also *Picramniaceae* and possibly *Vitaceae*.

Synapomorphies. — No non-DNA synapomorphies known.

Synonymy. — None known.

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*), *Guaiacum 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 *Afrostyrax* 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*.

Synapomorphies. — No non-DNA synapomorphies discovered.

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).

Synapomorphies. — No non-DNA synapomorphies discovered.

Synonymy. — None.

Asteridae Takhtajan 1967: 405 [R.G. Olmstead & W.S. Judd], converted clade name.

Comments on name. — *Asteridae* was first used by Takhtajan (1967) for a group of plants that mostly shared a suite of floral characters including sympetalous corollas, stamens adnate to the corolla and arranged alternately with the corolla lobes, and two fused carpels. Circumscription of that group included *Asterales* and *Dipsacales* sensu APG II (2003) and */Lamiidae* with some minor differences. Takhtajan (1987, 1997) later recognized a much reduced *Asteridae*, which approximated *Asterales* sensu APG II (2003). The name *Asteridae* was linked formally to the clade of concern here by Olmstead & al. (1992; Fig. 2), who stated (p. 258): "The third major clade of higher dicots is the *Asteridae* sensu lato, which include several taxa traditionally placed in the *Rosidae* or *Dilleniidae*." This expanded concept of *Asteridae* has been accepted (as *Asteridae* or "asterids") in all recent phylogenetic analyses and classifications (e.g., Olmstead & al., 2000; Soltis & al., 2000; Albach & al. 2001b; Bremer & al., 2002; Hilu & al. 2003; APG II, 2003; Judd & Olmstead, 2004; Soltis & al., 2005).

Definition (node based). — The least inclusive clade containing *Lamium purpureum* L. 1753 (*/Garryidae*), *Cornus mas* L. 1753 (*Cornales*), *Aster amellus* L. 1753 (*/Campanulidae*), and *Erica carnea* L. 1753 (*Ericales*).

Reference phylogeny. — Soltis & al. (2000: Figs. 10–12), Bremer & al. (2002: Fig 1). See also Olmstead & al. (2000), Albach & al. (2001b), and Hilu & al. (2003).

Composition. — *Cornales*, *Ericales*, and the total clade of */Gentianidae*.

Synapomorphies. — Possible synapomorphies include tenuinucellate and unitegmic ovules, sympetaly, and iridoid compounds, but all of these traits may be synapomorphic at a less inclusive level (Albach & al., 2001a; Judd & al., 2002).

Synonymy. — None known.

Gentianidae 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 "euasterids" (Olmstead & al., 2000; Savolainen & al., 2000a; Bremer & al., 2002; APG II, 2003; Stevens, 2006) and "core asterids" (Judd & al., 2002; Hilu & al., 2003; Judd & Olmstead, 2004). Its composition is somewhat similar to that of *Asteridae* sensu Takhtajan (1980) and Cronquist (1981) but also includes *Apiales*, *Aquifoliales*, *Garryales*, and *Icacinaceae*.

Definition (node based). — The least inclusive clade containing *Gentiana lutea* L. 1753 (/*Garryidae*) and *Campanula elatines* L. 1759 (/*Campanulidae*).

Reference phylogeny. — Soltis & al. (2000: Figs. 10–12), Bremer & al. (2002: Fig 1). See also Olmstead & al. (2000), Savolainen & al., (2000a), Albach & al. (2001b), and Hilu & al. (2003).

Composition. — The total clades of /*Garryidae and /Campanulidae.*

Synapomorphies. — Possible synapomorphies include stamens epipetalous, equaling (or less than) the number of corolla lobes (Judd & al., 2002; Stevens, 2006), 2 fused carpels (Judd & al., 2002, Soltis & Soltis, 2005), and unitegmic ovules (Albach & al., 2001a), but it is not clear whether any of these characters is synapomorphic at this level.

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; Savolainen & al., 2000a; Soltis & al., 2000; Albach & al., 2001b, Hilu & al., 2003; APG II, 2003) and "lamiids" (Bremer & al., 2002; Judd & Olmstead, 2004).

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 (Sereno, 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*.

Synapomorphies. — No non-DNA synapomorphies discovered.

Synonymy. — None.

Lamiidae Takhtajan 1987: 228 [R.G. Olmstead & W.S. Judd], converted clade name.

Comments on name. — *Lamiidae* was first used by Takhtajan (1987) for a group that differs in circumscription in some details. Takhtajan included a description of *Lamiidae* in Russian, but the name was not properly validated according to the *ICBN* until Reveal (1993) provided a Latin description. The name *Lamiidae* was linked formally to the clade to which it is applied here by Olmstead & al. (1992: 259), who stated that this clade "corresponds to Takhtajan's (1987) subclass *Lamiidae*, including orders *Gentianales*, *Lamiales*, *Scrophulariales*, *Solanales*, and *Boraginales*." See also Olmstead & al. (1993: Fig. 3). This is the only preexisting scientific name for this clade. However, the informal clade name "lamiids" was used by Bremer & al. (2002) and Judd & Olmstead (2004) for the more inclusive clade herein named /*Garryidae*.

Definition (node based). — The least inclusive clade containing *Lamium purpureum* L. 1753 (*Lamiales*), *Nicotiana tabacum* L. 1753 (*Solanales*), *Gentiana procera* T. Holm 1901 (*Gentianales*), *Borago officinalis* L. 1753 (*Boraginaceae*), and *Vahlia capensis* (L. f.) Thunb. 1782 (*Vahliaceae*).

Reference phylogeny. — Bremer & al. (2002: Fig 1), Soltis & al. (2000: Fig. 11). See also Olmstead & al. (2000), Albach & al. (2001b), Hilu & al. (2003).

Composition. — *Gentianales*, *Solanales*, *Lamiales*, *Boraginaceae*, and *Vahliaceae.*

Synapomorphies. — Vessels with simple perforations (Baas & al., 2003; Stevens, 2006); perhaps corolla tube initiation late, but sampling very limited (Leins & Erbar, 2003; Stevens, 2006).

Synonymy. — None known.

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 *RPB*2 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).

Synapomorphies. — We know of no unambiguous synapomorphies. Stevens (2006) cited several characters for this clade, including vessel elements with scalariform perforations, small flowers, valvate corollas, short styles, copious endosperm, and short embryos. Several of these characters are poorly sampled; others are ill-defined or highly variable both within and outside of this clade (e.g., flower size, style length). Erbar & Leins (1996) showed that "early sympetaly" is largely restricted to this clade, but its correlation with inferior ovary and reduced calyx should be explored further (Endress, 2001), and its placement on the tree remains uncertain (e.g., it may be a synapomorphy of the less inclusive clade */Apiidae*, as suggested by Stevens [2006]).

Synonymy. — None.

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

Comments on name. — There is no preexisting name for this clade. The name *Apiidae* draws attention to the inclusion of *Apiales*, which have been widely separated from *Asterales* and *Dipsacales*, and even from *Asteridae*, in many earlier classifications (e.g., Cronquist, [1981] placed *Apiales* in *Rosidae*).

Definition (branch-modified node-based with internal qualifiers). — The most inclusive crown clade including *Apium graveolens* L. 1753 (*Apiales*), *Helianthus annuus* L. 1753 (*Asterales*), and *Dipsacus sativus* (L.) Honck. 1782 (*Dipsacales*), but not *Ilex crenata* Thunb. 1784 (*Aquifoliales*) or *Cardiopteris quinqueloba* Hassk. 1855 (*Aquifoliales*) or *Garrya elliptica* Douglas ex Lindl. 1834 (*Garryales*) or *Lamium purpureum* L. 1753 (*/Lamiidae*).

Comments on definition. — Because basal relationships in */Apiidae* are poorly known, a standard node-based definition would require a long list of internal specifiers. We therefore prefer a branch-modified node-based definition. However, uncertainties regarding the relatives of */Apiidae* prompt us to use four external specifiers. Within *Aquifoliales* sensu APG II (2003), there are two well-supported clades (Kårehed, 2001): *Cardiopteridaceae*+*Stemonuraceae* and *Aquifoliaceae*+*Helwingiaceae*+*Phyllonomaceae*. Although it currently appears that *Aquifoliales* are a clade, we have used representatives of both subclades as external specifiers (i.e., species of *Ilex* and *Cardiopteris*) to guard against the possibility that *Ilex* and its immediate relatives are more closely related to */Garryidae* than to */Apiidae*, potentially leaving *Cardiopteridaceae*+*Stemonuraceae* alone as sister to */Apiidae*. There is some indication that this may be the case based on *RPB*2 duplications (Oxelman & al., 2004), but *Ilex* was sampled in that study while *Cardiopteridaceae* and *Stemonuraceae* were not. Similarly, we have included both *Garrya* and *Lamium* of */Garryidae* as external specifiers to guard against the possibility that */Lamiidae* and *Garryales* are eventually dissociated (see */Garryidae* treatment, above). A branch-modified node-based definition normally has only one internal specifier. Two other internal species are included here as qualifiers (Sereno, 2005). In the unlikely event that *Apiales*, *Asterales*, and *Dipsacales* turn out not to be closely related, the name */Apiidae* will not apply to any clade.

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

Composition. — The clade */Apiidae* includes three major subclades—*Apiales*, *Asterales*, and *Dipsacales* (sensu APG II, 2003)—plus several smaller subclades whose relationships remain uncertain: *Bruniaceae* (including *Berzelia*), *Columelliaceae* (including *Desfontainia*), *Escalloniaceae* sensu lato (including *Anopterus*, *Eremosyne*, *Forgesia*, *Polyosma, Tribeles*, and *Valdivia*), and *Paracryphiaceae* (including *Quintinia* and probably *Sphenostemon*; see Lundberg, 2001 and Bremer & al., 2002). In classifications developed before DNA data became extensively used (e.g., Cronquist, 1981), *Apiales* and these smaller groups were not associated with *Asterales* and *Dipsacales*.

Synapomorphies. — Possible synapomorphies cited by Stevens (2006) include early sympetaly (see Erbar & Leins, 1996; Leins & Erbar, 2003), a gynoecium of two or three carpels, and an inferior ovary. In addition, polyacetylenes are mentioned by Judd & Olmstead (2004). However, corolla tube development and polyacetylenes are still poorly sampled, and the gynoecial characters appear to show considerable homoplasy. A noteworthy tendency in */Apiidae* is the aggregation of small flowers into more conspicuous, head-like inflorescences.

Synonymy. — None.

Other comments. — Under any phylogenetic hypothesis in which /*Campanulidae* and /*Apiidae*, as defined above, are synonyms, we intend /*Campanulidae* to have precedence; see /*Campanulidae* treatment.

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 different clades (or non-monophyletic groups) in different classifications (Griffiths, 1976; de Queiroz & Gauthier, 1994; de Queiroz, 1997b; 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, *Euphyllophytina* 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 this situation, 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 important 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*, */Equisetum*, */Pinaceae*, */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.

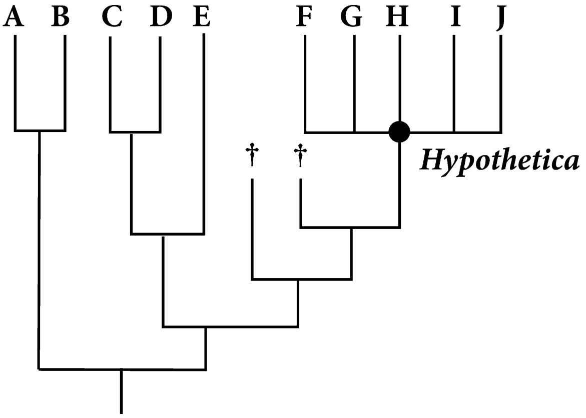

Fig. 2. A reference phylogeny (adapted from Lee, 1998) for the crown clade "*Hypothetica*" with a poorly resolved basal topology but well-resolved outgroup relationships. All resolved crown clades have high support values. Capital letters A–J designate extant clades, and lower case a–j (in definitions, 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.

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*, 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 & Thollesson, 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 & Thollesson, 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*. 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* 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), 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 in this paper, so neither automatically has 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, we have encountered a variety of tree topologies, degrees of support, 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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