Pan-Tracheophyta P. D. Cantino and M. J. Donoghue in P. D. Cantino et al. (2007): 830 [P. D. Cantino and M. J. Donoghue], converted clade name

Registration Number: 83

Definition: The total clade of the crown clade *Tracheophyta*. This is a crown-based total-clade definition. Abbreviated definition: total ∇ of *Tracheophyta*.

Etymology: From the Greek *pan-* or *pantos* (all, the whole), indicating that the name refers to a total clade, and *Tracheophyta* (see entry in this volume for etymology), the name of the corresponding crown clade.

Reference Phylogeny: Crane et al. (2004: Fig. 1; the clade stemming from the base of the branch labeled "Polysporangiophytes"). See also Kenrick and Crane (1997: Fig. 4.31).

Composition: *Tracheophyta* (this volume) and all extinct plants (e.g., *Aglaophyton*, *Horneophytopsida*, and *Rhyniopsida* sensu Kenrick and Crane 1997) that share more recent ancestry with *Tracheophyta* than with extant *Musci* (mosses), *Hepaticae* (liverworts), and *Anthocerotae* (hornworts).

Diagnostic Apomorphies: An independent sporophyte, multiple sporangia, and sunken archegonia are possible synapomorphies of *Pan-Tracheophyta*. All three were listed by Kenrick and Crane (1997: Table 7.2) as synapomorphies of *Polysporangiomorpha* ("polysporangiophytes" of Crane et al., 2004; a slightly less inclusive clade than *Pan-Tracheophyta*; see Comments). The order in which the three features evolved is not known. Moreover, sunken archegonia also occur in *Anthocerotae* (Kenrick and Crane, 1997: Fig. 3.33, pp. 63–64) and thus may be a synapomorphy of a more inclusive clade if *Anthocerotae* is the extant sister group of tracheophytes, a hypothesis that has received some molecular support (Kelch et al., 2004; Wolf et al., 2005; Qiu et al., 2006, 2007; however, see Wickett et al., 2014). Another possible synapomorphy of *Pan-Tracheophyta* is the production of a sporophyte stem, if Kato and Akiyama (2005) are correct that the stem is not homologous with the bryophyte seta.

Synonyms: The phylogenetically defined names *Polysporangiomorpha* (Kenrick and Crane, 1997) and *Polysporangiophyta* (Crane and Kenrick, 1997) have the same known composition as *Pan-Tracheophyta* but potentially refer to different clades (see Comments).

Comments: The definition of *Pan-Tracheophyta* is identical to the one we used when we first published the name (Cantino et al., 2007). The name *Polysporangiomorpha* (polysporangiophytes) sensu Kenrick and Crane (1997: Table 7.2, Fig. 4.31) has an apomorphy-based definition and thus is unlikely to be fully synonymous with *Pan-Tracheophyta*. Its currently known composition is the same as that of *Pan-Tracheophyta*, but there may have been pan-tracheophytes that preceded the evolution of multiple sporangia. Similarly, *Polysporangiophyta* sensu Crane and Kenrick (1997) has the same known composition as both *Pan-Tracheophyta* and *Polysporangiomorpha*, but its name has a node-based definition and thus the clade *Polysporangiophyta* may be less inclusive than either of the other two. The three names would no longer be synonyms if a fossil were to be found in the future that possesses

an intermediate combination of ancestral and derived states of the three characters mentioned above as possible synapomorphies (for example, a sporophyte that is dependent on the gametophyte throughout its life, as is the case in bryophytes, but has more than one sporangium).

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Apo-Tracheophyta P. D. Cantino and M. J. Donoghue in P. D. Cantino et al. (2007): E10 [P. D. Cantino and M. J. Donoghue], converted clade name

Registration Number: 15

Definition: The clade characterized by the apomorphy tracheids (i.e., differentially thickened water-conducting cells) as inherited by *Pinus sylvestris* Linnaeus 1753. This is an apomorphy-based definition. Abbreviated definition: ∇ apo tracheids [*Pinus sylvestris* Linnaeus 1753].

Etymology: From the Greek *apo-*, indicating that the name refers to an apomorphy-based clade, and *Tracheophyta* (see entry in this volume for etymology).

Reference Phylogeny: The primary reference phylogeny is Crane et al. (2004: Fig. 1; the clade labeled "Tracheophytes"). See also Kenrick and Crane (1997: Fig. 4.31; the clade labeled *Tracheophyta*).

Composition: Assuming that tracheids with S-type and G-type cell walls (see Kenrick and Crane, 1997: Fig. 4.26) are homologous, *Apo-Tracheophyta* includes *Tracheophyta* sensu Cantino and Donoghue (this volume) and *Rhyniopsida* sensu Kenrick and Crane (1997) (*Rhyniaceae* in the primary reference phylogeny). Under the alternative hypothesis that these tracheid types evolved independently, *Rhyniopsida* would not be part of *Apo-Tracheophyta*, and the currently known membership of *Apo-Tracheophyta* and *Tracheophyta* would be the same.

Diagnostic Apomorphies: Tracheids (see Definition), and possibly lignin deposition on the inner surface of the tracheid cell wall (Kenrick and Crane, 1997: Table 7.2, under *Tracheophyta*).

Synonyms: Based on composition, *Tracheophyta* sensu Kenrick and Crane (1997: Tables 7.1, 7.2, p. 236) is an approximate synonym. Although Kenrick and Crane (1997: 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 because they exclude *Apo-Spermatophyta* sensu Cantino and Donoghue (this volume).

Comments: Although the name *Tracheophyta* is often applied to this apomorphy-based clade, we opted here and previously (Cantino et al., 2007) to apply that name instead to the crown clade, following *PhyloCode* (version 6) Recommendation 10.1B, and a new name to the apomorphy-based clade.

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

Registration Number: 107

Definition: The smallest crown clade containing *Magnolia tripetala* (Linnaeus) Linnaeus 1759 (*Euphyllophyta*) and *Lycopodium clavatum* Linnaeus 1753 (*Lycopodiophyta*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Magnolia tripetala* (Linnaeus) Linnaeus 1759 & *Lycopodium clavatum* Linnaeus 1753).

Etymology: From the Latin *tracheida*, refering to the presence of tracheids (differentially thickened water conducting cells in the xylem), and the Greek *phyton* (plant).

Reference Phylogeny: The primary reference phylogeny is Qiu et al. (2007: Fig. 1). See also Kenrick and Crane (1997: Fig. 4.31; as "Eutracheophytes"), Pryer et al. (2001: Fig. 1), Wolf et al. (2005: Fig. 3), Qiu et al. (2006: Fig. 1), and Ruhfel et al. (2014: Figs. 5–7).

Composition: All extant vascular plants and their extinct relatives that fall within the crown clade. The crown clade is composed of two primary subclades, *Pan-Lycopodiophyta* and *Pan-Euphyllophyta* (see entries in this volume).

Diagnostic Apomorphies: The walls of the water-conducting cells in the xylem have a thick, lignified, decay-resistant layer. A 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 and Crane (1997: Table 7.2, pp. 114, 120) as synapomorphies of "eutracheophytes" (= *Tracheophyta* as defined here), but the extent of missing data for fossils combined with the apparent loss of these traits in all extant tracheophytes reduces confidence in their inferred originations.

Synonyms: "Eutracheophytes" sensu Kenrick and Crane (1997: 236) was described as "the tracheophyte crown group" and is thus an unambiguous synonym. Crane and Kenrick (1997) formalized this name as *Eutracheophyta* and defined it (node-based) using species of *Huperzia* and *Nymphaea* as specifiers; this is an unambiguous synonym. *Cormatae* Jeffrey (1982) is an approximate synonym; all listed subordinate taxa are extant.

Comments: The vascular plants, or tracheophytes, have long been recognized as a clade based on their possession of tracheids as a synapomorphy, and the crown clade is strongly supported by DNA analyses (Nickrent et al., 2000; Pryer et al., 2001; Qiu et al., 2006, 2007; Ruhfel et al., 2014; Wickett et al., 2014). Here and previously (Cantino et al., 2007: 829) we have defined the name *Tracheophyta* to refer to the crown clade, following *PhyloCode* Recommendation 10.1B. This application is somewhat unconventional in that this name has more often been applied to the slightly more inclusive clade originating with the evolution of tracheids (i.e., *Apo-Tracheophyta* in this volume). Sinnott (1935) introduced the name *Tracheophyta* for the vascular plants but the Latin diagnosis required by the botanical code (Turland et al., 2018) was first provided by Cavalier-Smith (1998: 251).

We earlier (Cantino et al., 2007) used a maximum-crown-clade definition with external specifiers representing liverworts, mosses, and hornworts, because we thought this definition would provide greater compositional stability than a simple node-based definition. However, in view of the very strong support for the basal dichotomy within *Tracheophyta* in recent molecular analyses (Qiu et al., 2006, 2007; Wickett et al., 2014), we are opting here for a simpler minimum-crown-clade definition with the two internal specifiers representing the two clades originating from the basal split: *Pan-Lycopodiophyta* and *Pan-Euphyllophyta*.

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Pan-Lycopodiophyta P. D. Cantino and M. J. Donoghue in P. D. Cantino et al. (2007): E11 [P. D. Cantino and M. J. Donoghue], converted clade name

Registration Number: 81

Definition: The total clade of the crown clade *Lycopodiophyta*. This is a crown-based total-clade definition. Abbreviated definition: total ∇ of *Lycopodiophyta*.

Etymology: From the crown clade name, *Lycopodiophyta* (see entry in this volume for its etymology), and the Greek *pan-* or *pantos* (all, the whole), indicating reference to a total clade.

Reference Phylogeny: Doyle (2013: Fig. 1.1). See also Crane et al. (2004: Fig. 1). In both of these phylogenies, the clade here named *Pan-Lycopodiophyta* is not labeled as such but is the most inclusive clade containing the lycophytes but not the euphyllophytes.

Composition: *Lycopodiophyta* (this volume) and all extinct plants that share more recent ancestry with *Lycopodiophyta* than with *Euphyllophyta* (this volume). According to the phylogenies of Kenrick and Crane (1997), Crane et al. (2004), and Doyle (2013), extinct taxa outside of the crown include (not an exhaustive list): the relatively apical stem groups *Asteroxylon*, *Drepanophycus*, *Baragwanathia*; the zosterophylls; and the relatively basal stem groups *Renalia*, *Yunia*, *Uskiella*, *Sartilmania*, and *Cooksonia cambrensis*. The inclusion of some other species of *Cooksonia* is uncertain because of their unresolved position on these trees.

Diagnostic Apomorphies: A possible synapomorphy is sporangium dehiscence by a transverse, apical slit. Doyle (1998, 2013) showed this character as arising at or near the base of the (unnamed) lycopodiophyte total clade. Kenrick and Crane (1997: Table 4.6) cited it as a possible synapomorphy of their node 52, which is near the base of the total clade. Crane and Kenrick (1997) listed the following additional potential synapomorphies for their *Lycophytina* (which is somewhat less inclusive than the total clade but much more inclusive than the crown; see Comments): reniform sporangia; marked sporangial dorsiventrality; inconspicuous cellular thickening of the dehiscence line; sporangia on short, laterally inserted stalks; and exarch xylem differentiation. However, the more taxonomically comprehensive analysis of Kenrick and Crane (1997: Fig. 4.32 and Table 4.6) suggests that some of these characters may be synapomorphic for more inclusive clades than *Lycophytina* within the total clade (also see Doyle, 2013).

Synonyms: Based on its composition, the name *Lycopodiobiotina* Doweld (2001) is an approximate synonym. *Lycophytina* (Kenrick and Crane, 1997; Crane and Kenrick, 1997; Bateman et al., 1998) applies to a clade that is less inclusive than *Pan-Lycopodiophyta* (see Comments).

Comments: Our definition of *Pan-Lycopodiophyta* here is identical to that used when we published the name (Cantino et al. 2007). We chose the panclade name rather than its approximate synonym *Lycopodiobiotina* (Doweld, 2001), as permitted by *PhyloCode* Article 10.6, so that its application to a total clade would be evident. The name *Lycophytina* sensu Kenrick and Crane (1997: Fig. 4.31 and Table 7.2) has a "synapomorphy-based definition" (not a formal definition; perhaps better

described as an apomorphy-based conceptualization of the taxon, with six synapomorphies cited) and is somewhat less inclusive than *Pan-Lycopodiophyta*. The name *Lycophytina* sensu DiMichele and Bateman (1996) and Bateman et al. (1998) appears to be applied to a clade that, based on its synapomorphies and composition, is circumscribed similarly to *Lycophytina* sensu Kenrick and Crane (1997). *Lycophytina* sensu Crane and Kenrick (1997) has a minimum-clade definition and approximates *Pan-Lycopodiophyta* in composition if only the taxa in their cladogram are considered, but it is less inclusive than the total clade in the context of trees that include more stem fossils (e.g., Crane et al., 2004). For example, *Yunia* and *Renalia*, which were not included in Crane and Kenrick's (1997) tree, are part of *Pan-Lycopodiophyta* but outside of *Lycophytina* when Crane and Kenrick's (1997) definition of *Lycophytina* is applied in the context of the tree of Crane et al. (2004).

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

Registration Number: 160

Definition: The smallest crown clade containing *Lycopodium clavatum* Linnaeus 1753, *Huperzia selago* (Linnaeus) Schrank & Martius 1829 (originally described as *Lycopodium selago* Linnaeus 1753), *Isoetes lacustris* Linnaeus 1753, and *Selaginella apoda* (Linnaeus) Spring 1840 (originally described as *Lycopodium apodum* Linnaeus 1753). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Lycopodium clavatum* Linnaeus 1753 & *Huperzia selago* (Linnaeus) Schrank & Martius 1829 & *Isoetes lacustris* Linnaeus 1753 & *Selaginella apoda* (Linnaeus) Spring 1840).

Etymology: Based on the name *Lycopodium*, which is derived from Greek *lycos* and *podus*, meaning "wolf's foot", from a fancied resemblance (Fernald, 1970), and Greek *phyton* (plant) (Stearn, 1973).

Reference Phylogeny: The primary reference phylogeny is Korall et al. (1999: Fig. 2). See also Rydin and Wikström (2002: Fig. 2), Pryer et al. (2004b: Fig. 3; labeled "lycophytes"), Qiu et al. (2007: Fig. 1), Ruhfel et al. (2014: Fig. 6), and Wickett et al. (2014: Fig. 2).

Composition: The total clades of *Lycopodiaceae* (including *Huperziaceae*) and *Isoëtopsida* (*Isoëtes* + *Selaginella*; Cantino et al., 2007). According to current understanding of phylogeny (Doyle, 1998; Pryer et al., 2004a; Judd et al., 2016), the total clade of *Isoëtes* includes Palaeozoic arborescent forms such as *Lepidodendron*.

Diagnostic Apomorphies: Kenrick and Crane (1997: Table 6.3 and Fig. 6.19; node 35), Crane and Kenrick (1997: Table 9; "*Lycopsida*"), Doyle (1998), and Gensel (1992) listed the following synapomorphies for the crown clade: close developmental 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 for a more inclusive clade); crescent-shaped root xylem (but there are a lot of missing data for fossils outside the crown). The following are synapomorphies of this crown clade relative to other crowns but are known to be apomorphic at a more inclusive level when stem fossils are considered (Kenrick and Crane, 1997: Fig. 6.18 and Table 7.2; Doyle, 2013: Fig. 1.1): microphylls ("lycophylls"; Schneider et al., 2002; Pryer et al., 2004a); exarch xylem differentiation in stem (Kenrick and Crane, 1997; Doyle, 1998; Schneider et al., 2002); stellate xylem strand in stem; reniform sporangia with transverse dehiscence (Doyle, 1998). This list is not exhaustive; see Kenrick and Crane (1997: Table 7.2) and DiMichele and Bateman (1996) for other synapomorphies listed under *Lycophytina* and *Lycopsida*.

Synonyms: *Lycophyta*, *Lycopsida*, and *Lycopodiopsida* are approximate synonyms (see Comments below). *Lycopsida* sensu Crane and Kenrick (1997) is an unambiguous synonym in that it was phylogenetically defined as applying to the same crown clade, but the definition

conflicts with the labeling of the reference phylogeny (see Comments).

Comments: The monophyly of this clade is strongly supported by molecular data (Korall et al., 1999; Pryer et al., 2001, 2004b; Qiu et al., 2006, 2007; Ruhfel et al., 2014; Wickett et al., 2014) as well as by numerous morphological synapomorphies (detailed above). One study (Garbary et al., 1993) based solely on male gametogenesis characters found this group to be polyphyletic, with *Selaginella* sharing closer ancestry with bryophytes than with *Lycopodium*, but this hypothesis has not been supported by any other analysis.

While the monophyly of the morphologically distinctive taxa *Selaginella* and *Isoëtes* is not in question, the monophyly of *Lycopodiaceae* (including *Huperziaceae*) is supported by only one possible morphological synapomorphy (foveolate-fossulate microspore wall; Kenrick and Crane, 1997). Although there is molecular support for its monophyly, those studies either were based solely on *rbc*L (Korall et al., 1999) or included too small a sample of *Lycopodiaceae* to be convincing (Qiu et al., 2006, 2007; Wickett et al. 2014). We remain concerned that *Huperzia* could end up being sister to the rest of *Lycopodiophyta*. Consequently, the clade *Lycopodiaceae* is represented by two specifiers (*Lycopodium clavatum* and *Huperzia selago*) in the definition of *Lycopodiophyta*.

The names *Lycophyta*, *Lycopodiophyta*, *Lycopsida*, and *Lycopodiopsida* have historically applied to the same set of clades (from crown to total), but most phylogenetic studies have instead used the informal equivalents, "lycophytes" and "lycopsids". Since *Lycophyta* and *Lycopsida* are apparently based on the name *Lycopodium*, they should be corrected to *Lycopodiophyta* and *Lycopodiopsida* under the botanical code (Turland et al., 2018; Art. 16.1). We are narrowing our choice to the latter pair of names in the interest of promoting consistency between rank-based and phylogenetic nomenclature. We prefer the *-phyta* ending because it means "plant" while *-opsida* is solely an indicator of (class) rank, and we have therefore chosen *Lycopodiophyta*, as in our previous paper (Cantino et al., 2007). We also follow that paper (p. E11) in applying the name explicitly to the lycopodiophyte crown clade. The clade *Lycopsida* sensu Kenrick and Crane (1997) is somewhat larger in that it includes fossils such as *Asteroxylon* and *Baragwanathia* that are shown (p. 239; see also Pryer et al., 2004a: Fig. 10.3) as being outside the crown clade. The same is true of *Microphyllophyta* sensu Bold (1957) and Bold et al. (1980), *Lepidophyta* sensu Smith (1955), and *Lycopodiopsida* sensu Bierhorst (1971). Crane and Kenrick (1997) gave *Lycopsida* a minimum-clade definition with extant species of *Huperzia* and *Isoetes* as the specifiers, thereby effectively (but not explicitly) applying the name to the crown clade. However, in the accompanying cladogram and classification, they applied this same name to a larger clade by including an extinct stem group (*Drepanophycales*); thus, their conceptualization of the name was ambiguous.

Following the *PhyloCode* (Version 6, Rec. 9.15A), we attribute the preexisting name *Lycopodiophyta* to Cronquist et al. (1966), but under the botanical code (Turland et al., 2018; Art. 16.3), the name is attributed to Scott (1909), who spelled it *Lycopsida* (Hoogland and Reveal, 2005).

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Pan-Euphyllophyta P. D. Cantino and M. J. Donoghue in P. D. Cantino et al. (2007): E12 [P. D. Cantino and M. J. Donoghue], converted clade name

Registration Number: 78

Definition: The total clade of the crown clade *Euphyllophyta*. This is a crown-based total-clade definition. Abbreviated definition: total ∇ of *Euphyllophyta*.

Etymology: From the Greek *eu-* (true, original, primitive), *phyllon* (leaf), and *phyton* (plant), plus *pan-* or *pantos* (all, the whole), indicating that this is a total clade. Euphylls (also known as megaphylls; i.e., leaves that usually have more than one vein and are thought to have evolved from branch systems) are characteristic of the crown clade *Euphyllophyta*.

Reference Phylogeny: Crane and Kenrick (1997: Fig. 1, the clade labeled *Euphyllophytina*) (see Synonyms).

Composition: *Euphyllophyta* (this volume) and all extinct plants that share more recent ancestry with *Euphyllophyta* than with *Lycopodiophyta*. The stem euphyllophytes are often classified as trimerophytes, a paraphyletic group that has been named at various ranks (see Synonyms). The trimerophytes include species of *Psilophyton* and *Eophyllophyton*, which lie outside the euphyllophyte crown (Crane and Kenrick, 1997; Kenrick and Crane, 1997; Doyle, 2013), but *Pertica* (which is also classified as a trimerophyte; Stewart and Rothwell, 1993; Taylor, 1981) is thought to lie within the crown (Kenrick and Crane, 1997: Figs. 4.31, 7.10).

Diagnostic Apomorphies: Several synapomorphies were listed by Crane and Kenrick (1997: Table 9) and Kenrick and 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 (Kenrick and Crane, 1997: 109, 359; Doyle, 2013) (although if the fernlike leaves of early seed plants were derived from pseudomonopodial branch systems of more basal lignophytes (Doyle, 1998, 2013), the axillary monopodial branching of seed plants and the pseudomonopodial branching of more basal lignophytes may not be homologous; Doyle, 2013); helical arrangement of branches (Kenrick and Crane, 1997: 110, 360); dichotomous appendages (Kenrick and Crane, 1997: 113, 361); recurved branch apexes (Kenrick and Crane, 1997: 112–113, 360); paired sporangia grouped into terminal trusses (Kenrick and Crane, 1997: 121–122, 364); sporangial dehiscence along one side through a single longitudinal slit (Kenrick and Crane, 1997: 125, 366); Doyle, 2013; and radially aligned xylem in larger axes (Crane and Kenrick, 1997). Kenrick and 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 less inclusive group than the total clade (Kenrick and Crane, 1997: 120, 363, Fig. 7.10).

Synonyms: *Euphyllophytina* Kenrick and Crane (1997: Table 7.1) and Crane and Kenrick (1997) may be an approximate synonym (see Comments). *Trimerophytophyta* sensu Bold et al. (1980), *Trimerophytina* Banks 1968, *Trimerophytopsida* Foster and Gifford 1974 have been applied to a paraphyletic group originating in approximately the same ancestor as *Pan-Euphyllophyta* according to the phylogenies of

Kenrick and Crane (1997: Figs. 4.31, 4.32) and Crane and Kenrick (1997: Fig. 1) and therefore are partial (and approximate) synonyms.

Comments: *Euphyllophytina* (Crane and Kenrick, 1997; Kenrick and Crane, 1997) referred to a clade that is similar in composition to *Pan-Euphyllophyta*. However, there is conflict within and between these two papers regarding whether the name *Euphyllophytina* applies to a node-based, apomorphy-based, or branch-based clade. Kenrick and Crane (1997) gave the name a "synapomorphy-based definition" in Table 7.2, but they described the clade (p. 240) as the sister group of *Lycophytina*, suggesting that both of these clades were conceptualized as originating from their point of divergence rather than from the origin of a particular apomorphy. In contrast, the same authors (Crane and Kenrick, 1997) used a "node-based" (minimum-clade) definition for *Euphyllophytina* with *Eophyllophyton bellum* and *Nymphaea odorata* as the specifiers. In any case, the composition of *Euphyllophytina*, as shown on the reference trees in these two papers by Crane and Kenrick, seems to approximate that of *Pan-Euphyllophyta* as defined here. However, there could be undiscovered fossil pan-euphyllophytes that lie outside the node-based *Euphyllophytina* of Crane and Kenrick.

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Euphyllophyta G. Lecointre and H. Le Guyader 2006: 181 [P. D. Cantino and M. J. Donoghue], converted clade name

Registration Number: 43

Definition: The largest crown clade containing *Ginkgo biloba* Linnaeus 1771 (*Spermatophyta*) and *Pteridium aquilinum* (Linnaeus) Kuhn 1879 (originally described as *Pteris aquilina* Linnaeus 1753) (*Leptosporangiatae*), but not *Selaginella apoda* (Linnaeus) Spring 1840 (originally described as *Lycopodium apodum* Linnaeus 1753) (*Lycopodiophyta*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Ginkgo biloba* Linnaeus 1771 & *Pteridium aquilinum* (Linnaeus) Kuhn 1879 ~ *Selaginella apoda* (Linnaeus) Spring 1840).

Etymology: From the Greek *eu* (true), *phyllon* (leaf), and *phyton* (plant). Megaphylls (sometimes referred to as euphylls; e.g., Simpson, 2006; Schneider et al., 2009), which are leaves that usually have more than one vein and are thought to have evolved either from dichotomously forking lateral branches or from branch systems bearing such units, are characteristic of this clade though probably not a synapomorphy (see Diagnostic Apomorphies).

Reference Phylogeny: The primary reference phylogeny is Pryer et al. (2001: Fig. 1, the clade labeled *Euphyllophytina*). See also Kenrick and Crane (1997: Fig. 7.10), Pryer et al. (2004: Fig. 3), Qiu et al. (2007: Fig. 1), Schneider et al. (2009: Figs. 1 and 2), Ruhfel et al. (2014: Figs. 6 and 7), and Wickett et al. (2014: Figs. 2 and 3).

Composition: All extant seed plants (*Spermatophyta*), ferns (*Leptosporangiatae*, *Ophioglossales*, and *Marattiales*), horsetails (*Equisetum*), and whisk ferns (*Psilotaceae*), as well as their extinct relatives that fall within the crown clade. The crown clade is composed of two primary subclades, *Pan-Spermatophyta* (see entry in this volume) and the unnamed total clade of *Monilophyta*.

Diagnostic Apomorphies: Apomorphies relative to other crown clades include roots with monopodial branching and endogenous lateral roots (Schneider et al., 2002); sporangia terminal on lateral branches (Pryer et al., 2004a) and dehiscing longitudinally (Doyle, 1998, 2013) (these features characterize the earliest members of *Pan-Euphyllophyta* and were modified in most extant representatives); lobed, mesarch primary xylem strand (Stein, 1993; Kenrick and Crane, 1997: Fig. 7.10 and p. 241; Doyle, 1998, 2013), which has been modified in the stems of most extant members; multiflagellate spermatozoids (apparently convergent in *Isoëtes*) (Garbary et al., 1993; Kenrick and Crane, 1997: 240, 275); a 30-kb inversion in the chloroplast genome (Raubeson and Jansen, 1992). Megaphylls are sometimes cited as a synapomorphy of this clade (Schneider et al., 2002), but analyses that include fossils suggest that megaphylls of monilophytes and seed plants evolved independently (Stewart and Rothwell, 1993; Kenrick and Crane, 1997; Doyle, 1998, 2013; Boyce and Knoll, 2002; Friedman et al., 2004; Galtier, 2010). Even within *Lignophyta* (i.e., *Spermatophyta* and their stem relatives that have a bifacial vascular cambium; phylogenetically defined by Donoghue and Doyle in Cantino et al., 2007), the small, wedge-shaped leaves of *Archaeopteris* may not be homologous with the whole fernlike fronds of "seed ferns" (a non-monophyletic assortment of extinct seed plants with more or less fern-like leaves), but rather with individual leaflets of such fronds (Doyle and Donoghue, 1986;

Doyle, 1998, 2013). The single-veined leaves of *Equisetum* may be characterized as microphylls or megaphylls, depending on whether one's definition of these terms is based on structure (specifically, presence of only one vein in the case of microphylls) or evolutionary origin (specifically, from dichotomously forking branches or branch systems in the case of megaphylls versus from unvascularized enations [or possibly from sterilized sporangia; Kenrick and Crane, 1997] in the case of microphylls). Some fossil relatives of *Equisetum* such as *Sphenophyllum* had multiple-veined leaves that apparently evolved from dichotomous branches (reviewed by Doyle, 2013), suggesting that the one-veined leaves of *Equisetum* would qualify as megaphylls if the definition is based on origin.

Synonyms: There are no synonyms; *Euphyllophytina* (Kenrick and Crane, 1997; Crane and Kenrick, 1997) refers to a more inclusive clade (see Comments).

Comments: A group composed of 'ferns' (excluding *Equisetum* and *Psilotophyta*) and seed plants has been recognized on morphological grounds for many years (Banks, 1968), and the monophyly of this group, when *Equisetum* and *Psilotophyta* are included, is strongly supported by molecular data (Pryer et al., 2001, 2004; Qiu et al., 2007; Wickett et al., 2014). However, there was no scientific name for the crown clade until we explicitly applied the name *Euphyllophyta* to it (Cantino et al., 2007). We incorrectly referred to it as a new name, rather than converted, because we were unaware of its use by Lecointre and Le Guyader (2006). The latter authors were not explicit about the clade to which the name *Euphyllophyta* was intended to apply, but their inclusion of *Psilophyton* indicates that it was more inclusive than the crown (see Kenrick and Crane, 1997: Fig. 4.32).

Euphyllophytina Kenrick and Crane (1997: Table 7.1 and Fig. 7.10) referred to a more inclusive clade than the crown, though it is unclear whether the name was applied to an apomorphy-based or a total clade. The name was given a "synapomorphy-based definition" in Table 7.2, but the clade was described (p. 240) as the sister group of *Lycophytina*, suggesting that both of these clades were conceptualized as originating from their point of divergence rather than from the origin of a particular apomorphy. In contrast, the same authors (Crane and Kenrick, 1997) used a "node-based" (minimum-clade) definition for *Euphyllophytina*. Although there is conflict within and between these two papers as to whether the name *Euphyllophytina* applies to a minimum, apomorphy-based, or total clade, all three are more inclusive than the crown clade to which we apply the name *Euphyllophyta* here.

A maximum-crown-clade definition requires only one internal specifier, but two are used here in order to disqualify the name under certain conditions. In the context of a phylogeny in which either 'ferns' or seed plants share more recent ancestry with lycophytes than they do with each other (e.g., Rothwell and Nixon [2006: Fig. 6]; Ruhfel et al. [2014: Fig. 5]), the name *Euphyllophyta* would not apply to any clade. In our earlier definition (Cantino et al., 2007), we included a species of *Equisetum* as a third internal specifier, but we have omitted it here because it is unnecessary. To the best of our knowledge, *Euphyllophyta* has the same composition with either definition in the context of all recently published phylogenies.

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