Monilophyta P. D. Cantino and M. J. Donoghue in P. D. Cantino et al. (2007): E13 [J. A. Doyle, P. D. Cantino, and M. J. Donoghue], converted clade name

Registration Number: 67

Definition: The largest crown clade containing *Pteridium aquilinum* (Linnaeus) Kuhn 1879 (originally *Pteris aquilina*) (*Leptosporangiatae*) and *Equisetum hyemale* Linnaeus 1753 but not *Oryza sativa* Linnaeus 1753 (*Spermatophyta*) or *Huperzia lucidula* (Michaux) Trevisan de Saint-Léon 1875 (originally *Lycopodium lucidulum*) (*Lycopodiophyta*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Pteridium aquilinum* (Linnaeus) Kuhn 1879 & *Equisetum hyemale* Linnaeus 1753 ~ *Oryza sativa* Linnaeus 1753 ∨ *Huperzia lucidula* (Michaux) Trevisan de Saint-Léon 1875).

Etymology: From the Latin *monile*, meaning necklace, in reference to the "position and ontogeny of protoxylem in the lobed primary xylem of early fossil groups" (Kenrick and Crane, 1997: 248), and the Greek *phyton* (plant).

Reference Phylogeny: The primary reference phylogeny is Knie et al. (2015: Fig. 4). See also Rothfels et al. (2015: Fig. 1, the clade labeled "*Polypodiopsida*"), Pryer et al. (2001: Fig. 1, as "*Moniliformopses*"), Pryer et al. (2004: Fig. 3, as "ferns (monilophytes)"), Qiu et al. (2007: Fig. 1), and Wickett et al. (2014: Figs. 2, 3).

Composition: *Equisetum*, *Psilotophyta*, *Ophioglossales*, *Marattiales*, and *Leptosporangiatae*, their most recent common ancestor, and all of its other descendants. In addition to fossil representatives of the five listed crown subgroups, fossil members presumably include various taxa considered to be their stem relatives, such as *Sphenophyllales*, *Archaeocalamites*, and *Calamites* in the case of *Equisetum*; *Psaronius* in the case of *Marattiales*; and *Ankyropteris* in the case of *Leptosporangiatae* (see Doyle, 2013). Less can be said about other fossil members because most of the analyses that inferred the existence of this clade included only extant plants, and some analyses that included both fossils and extant plants did not infer the existence of this clade. Kenrick and Crane (1997: Table 7.1) included the fossil groups *Cladoxyliidae*, *Zygopteridae* (which may include additional stem relatives of *Leptosporangiatae*: see Galtier, 2010), and *Stauropteridae* within *Moniliformopses* (a clade that may be either equivalent to or slightly more inclusive than *Monilophyta*; see Comments). In contrast, Rothwell (1999) inferred that *Cladoxyliidae* and *Zygopteridae*, along with *Equisetum*, are more closely related to seed plants than to extant ferns (thus the clade *Monilophyta* as defined here does not exist on that phylogeny) and stauropterids are even more distant from extant ferns. Some of the analyses of Rothwell and Nixon (2006) inferred the existence of *Monilophyta* (as defined here) and others did not, but in those trees in which there is a clade that fits our definition of *Monilophyta*, all three of the above-mentioned extinct groups included in *Moniliformopses* by Kenrick and Crane lie outside *Monilophyta*.

Diagnostic Apomorphies: In the analysis of Kenrick and Crane (1997), the main synapomorphy is mesarch protoxylem confined to the outer lobed ends of the xylem strand (Crane and Kenrick, 1997); typically the protoxylem is parenchymatous, so that the metaxylem forms a conspicuous "peripheral loop" around a spongy protoxylem area. This feature occurs in fossil cladoxylopsids, zygopterids, and *Ankyropteris*, and it has been assumed that the spongy protoxylem areas were modified into the protoxylem canals of *Equisetum* and related fossil calamites; however, homologous structures have not been recognized in living ferns. Schneider et al. (2009), considering extant groups only, reported four unambiguous apomorphies: sporangia arranged in a sorus, presence of a pseudoendospore, centrifugal spore wall formation (also reported by Schneider et al., 2002), and plasmodial tapetum. However, it is not clear that the groups of sporangia in *Equisetum*, *Psilotophyta*, *Ophioglossales*, and many presumed fossil monilophytes are more comparable to the typical sori of leptosporangiate ferns than are the groups of sporangia and microsynangia of seed plant stem relatives ("progymnosperms," "seed ferns"). It is also not certain that the spore characters of monilophytes are derived relative to the pollen of living seed plants, which have more complex exine development, or to the more fern-like spores and "pre-pollen" of seed plant stem relatives, in which exine development is largely unknown.

Synonyms: *Moniliformophyta* Crane and Kenrick 1997 is an unambiguous heterodefinitional synonym in the context of some phylogenetic hypotheses but not others (see Comments).

Moniliformopses sensu Lecointre and Guyader (2006) is a possible synonym (see Comments). The names *Filicophyta*, *Filicopsida*, *Polypodiophyta*, *Pterophyta*, and *Pteropsida* are partial synonyms of *Monilophyta* in the context of some phylogenies (e.g., Pryer et al., 2001) in that they have been commonly applied to the paraphyletic group ("ferns") originating from the same ancestor as the clade *Monilophyta* but excluding *Equisetum* and usually (but not always; e.g., Bierhorst, 1971) *Psilotophyta*. However, in the context of other phylogenies (e.g., Wickett et al., 2014; Knie et al., 2015; Rothfels et al., 2015), where *Equisetum* is sister to all other monilophytes, names such as *Filicophyta* are not synonyms of *Monilophyta* but instead apply to a major subclade comprising the "ferns" and *Psilotophyta*.

Comments: Kenrick and Crane (1997) first proposed the existence of a clade that includes ferns and *Equisetum* (represented in the tree shown in their Figure 4.32 by the presumed fossil ferns *Pseudosporochnus*, a "cladoxylopsid," and *Rhacophyton*, a "zygopterid," and the presumed fossil sphenopsid *Ibyka*) but excludes *Lycopodiophyta* and seed plants. Ferns and *Equisetum* do not form a monophyletic group in several other morphological studies (Bremer et al., 1987; Rothwell, 1999; Rothwell and Nixon, 2006), but the two groups (also including *Psilotophyta* or "whisk ferns") are strongly supported as a clade by molecular analyses (Nickrent et al., 2000; Pryer et al., 2001, 2004; Wikström and Pryer, 2005; Schuettpelz et al., 2006; Qiu et al., 2007; Ruhfel et al., 2014; Wickett et al., 2014; Knie et al., 2015; Rothfels et al., 2015) and weakly supported by a morphological analysis of extant taxa by Schneider et al. (2009).

A maximum-crown-clade definition usually has only one internal specifier, but a second internal specifier is included here in order to disqualify the name under certain conditions. In the context of a phylogenetic hypothesis in which extant ferns share more recent ancestry with seed plants than with *Equisetum* (Bremer et al., 1987: Fig. 1), or one in which *Equisetum* shares more recent ancestry with seed plants than with extant ferns (Rothwell, 1999: Fig. 2; Rothwell and Nixon, 2006: Fig. 3A), the name *Monilophyta* would not apply to any clade. Abandonment of the name would be appropriate in such cases because it is universally associated with the hypothesis that ferns (including *Psilotophyta*) and horsetails form a clade exclusive of seed plants and lycopodiophytes. The maximum-crown-clade definition that we have adopted here and the slightly different definition of Cantino et al. (2007) both capture the essence of this hypothesis. The two definitions differ in the specifiers chosen to represent *Equisetum*, *Spermatophyta*, and *Lycopodiophyta*, with each definition using species included in the respective primary reference phylogeny.

When we phylogenetically defined the name *Monilophyta* as referring to this crown clade (Cantino et al., 2007), we selected this name because it closely approximates the informal name "monilophytes," which is often used for this clade (e.g., Judd et al., 2002, 2008; Simpson, 2006). The name *Monilophyta* was applied to this clade in a field guide (Cobb et al., 2005) but without a description or diagnosis, so it did not qualify as a preexisting name. Another candidate name, *Moniliformopses* Kenrick and Crane (1997: Table 7.1), was apparently apomorphy-based (1997: Table 7.2), and it is unclear whether subsequent uses of this name (e.g., Lecointre and Guyader, 2006) refer to the crown or an apomorphy-based clade. A third candidate name, *Moniliformophyta* (Crane and Kenrick, 1997), was given a "node-based" (minimum-clade) definition using a species of *Equisetum* and a leptosporangiate fern as the specifiers. In the context of those authors' reference phylogeny, our primary reference phylogeny (Knie et al., 2015), and others (e.g., Wickett et al., 2014; Rothfels et al., 2015) in which *Equisetum* is sister to the rest of the clade, *Moniliformophyta* refers to the same crown clade as does *Monilophyta*, but in the context of other molecular phylogenies (e.g., Pryer et al., 2001; Wikström and Pryer, 2005; Schuettpelz et al., 2006; Qiu et al., 2007), in which *Equisetum* is nested deeper within the clade, *Moniliformophyta* applies to a less inclusive crown clade than *Monilophyta*; i.e., the ophioglossoid ferns and whisk ferns (*Psilotophyta*) are part of *Monilophyta* but lie outside of *Moniliformophyta*.

One might argue that a name based on *Filico-*, *Ptero-*, or *Polypodio-* (see Synonyms) should have been chosen for this clade given that these partial synonyms are widely applied to the plants that are commonly called ferns. However, the name *Monilophyta* has already been phylogenetically defined for the clade of concern here (i.e., including *Equisetum*), unlike any of the alternatives, and it avoids the suggestion that the common ancestor of *Equisetum* and ferns was fernlike in having compound leaves, when it more likely had branch systems with dichotomous ultimate appendages, as in "cladoxylopsids" (which may include stem relatives of the whole clade and some of its subgroups). Names such as *Filicophyta* and *Polypodiophyta* are better reserved for a clade that excludes *Equisetum*, such as "fern clade 3" of Rothwell (1999: Fig. 2), or the clade including all monilophytes except *Equisetum* in Knie et al. (2015) and Rothfels et al. (2015). Indeed, the name *Polypodiophyta* has already been phylogenetically defined to apply in precisely that way (Cantino et al., 2007: E14); the three specifiers were species of *Ophioglossales*, *Marattiales*, and *Leptosporangiatae*, and if the sister-group relationship of *Psilotophyta* and *Ophioglossales* found in most molecular analyses is correct, this clade also includes *Psilotophyta*.

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Pan-Gnetophyta J. A. Doyle, M. J. Donoghue, and P. D. Cantino in Cantino et al. (2007): E22 [J. A. Doyle, M. J. Donoghue, and P. D. Cantino], converted clade name

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

Etymology: Derived from the Greek *pan*, meaning "all," in reference to the total clade, and *Gnetophyta*, the name of the corresponding crown clade (see *Gnetophyta* in this volume for the etymology of that name).

Reference Phylogeny: The primary reference phylogeny is Doyle (1996: Fig. 5). See also Rothwell and Serbet (1994: Fig. 8) and Doyle (2008: Fig. 3).

Composition: The crown clade *Gnetophyta* (this volume) and all extinct plants that share more recent ancestry with *Gnetophyta* than with any other extant seed plants. In Doyle's (1996) analysis, this total clade includes *Piroconites* and, on some (but not other) trees, *Bennettitales*, *Pentoxylon*, and *Glossopteridales*. However, the striate pollen character that suggested *Piroconites* was related to *Gnetophyta* was based on a misinterpretation (Osborn, 2000). *Gnetophyta* are nested within *Coniferae* in some trees in the morphological analysis of Doyle (2008), as found in many molecular analyses (e.g., Bowe et al., 2000; Chaw et al., 2000); in these trees, *Bennettitales*, *Pentoxylon*, and *Glossopteridales* are linked more closely with *Angiospermae* than with *Gnetophyta*, and no other fossil taxa are related to *Gnetophyta* (*Piroconites* was not included). A better candidate for a stem taxon is *Dechellyia* (Ash, 1972; Crane, 1996), represented by shoots bearing opposite, linear leaves and strobili containing striate pollen. An analysis by Friis et al. (2007) identified *Bennettitales*, *Erdtmanithecales*, and Cretaceous charcoalified seeds (subsequently described by Friis et al., 2009) as stem relatives of *Gnetophyta*; the charcoalified seeds were also associated with *Gnetophyta* by Rothwell et al. (2009). Rothwell and Stockey (2013) interpreted the female strobilus *Protoephedrites*, which differs from extant *Gnetophyta* in having two ovules rather than one per fertile short shoot, as a probable stem gnetophyte.

Diagnostic Apomorphies: The treatment of *Gnetophyta* in this volume lists many synapomorphies relative to other crown clades. It is not known where on the gnetophyte stem these synapomorphies evolved. Striate (polyplicate) pollen similar to that of *Ephedra* and *Welwitschia* occurs in the earliest fossils that have been interpreted as possible stem gnetophytes (Crane, 1988, 1996), so this character may have arisen near the base 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*, but because the ovules are usually borne in pairs it is also possible that the structure bearing them is homologous with a single short shoot with two lateral ovules in *Protoephedrites* (Rothwell and Stockey, 2013). The ovule of *Protoephedrites* has only a very short micropylar tube, which could mean that the long micropylar tube of extant *Gnetophyta* originated late on the stem lineage.

Synonyms: None that unambiguously apply to the total clade.

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