Pan-Coniferae P. D. Cantino, M. J. Donoghue, and J. A. Doyle in P. D. Cantino et al. (2007): E20 [J. A. Doyle, P. D. Cantino, and M. J. Donoghue], converted clade name

Registration Number: 77

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

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

Reference Phylogeny: The reference phylogeny is Doyle (2006: Fig. 8).

Composition: *Coniferae* (this volume) and all extinct plants that share more recent ancestry with *Coniferae* than with any other extant seed plants. Morphological homologies between extant and Palaeozoic conifers and *Cordaitales* proposed by Florin (1951) could be evidence that the cordaites belong in *Pan-Coniferae*, but this is uncertain, because Florin (1949) adduced similar evidence that *Ginkgo* and related fossils are also related to *Cordaitales*. In phylogenetic analyses that include fossils, depending in part on the position of *Ginkgo*, *Pan-Coniferae* may include *Cordaitales*, Palaeozoic conifers such as *Emporia* and *Lebachia*, both, or neither (Crane, 1985; Doyle and Donoghue, 1986; Rothwell and Serbet, 1994; Doyle, 1996, 2006, 2008; Hilton and Bateman, 2006). Because of uncertainty whether the clade *Gnetophyta* is part of *Coniferae* (see *Coniferae* in this volume), *Pan-Coniferae* may, similarly, include or exclude *Gnetophyta*.

Diagnostic Apomorphies: Based on a phylogenetic tree that included *Gnetophyta* within *Coniferae*, Doyle (2006: Fig. 11) listed the following synapomorphies for the clade labeled "Conifers" (including *Emporia* but not *Cordaitales* and corresponding roughly to *Pan-Coniferae* as defined here): leaves with a single vein (modified to several-veined within some groups such as *Agathis* and *Nageia*), compound female strobili but simple male strobili, bilateral (dorsiventral) symmetry in ovuliferous short shoots (modified into cone scales in extant taxa), inverted ovules, and sarcotesta absent or uniseriate. Of these, the sarcotesta character is questionable because it is unclear whether a sarcotesta is present or absent in the immature ovules of *Emporia* (Mapes and Rothwell, 1984).

Synonyms: The names *Pinopsida*, *Coniferophyta*, *Coniferopsida*, and *Coniferales*, which are listed as approximate synonyms of *Coniferae* (this volume), as well as *Coniferae* itself, could equally well be considered to be approximate synonyms of *Pan-Coniferae*, since authors have rarely made it clear whether these names apply to the crown, the total clade, or an intermediate clade.

Comments: We prefer the name *Pan-Coniferae* rather than its approximate synonyms because the name *Coniferae* (as defined in this volume) is unambiguous and neither *Coniferae* nor *Pan-Coniferae* has any implication of rank. As discussed in the entry on *Coniferae* (this volume), the names *Pinopsida*, *Coniferophyta*, and *Coniferopsida* have been used in broader senses. Moreover, the endings *-opsida* and *-ales* imply class and ordinal rank, respectively.

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

Registration Number: 31

Definition: The smallest crown clade containing *Pinus strobus* Linnaeus 1753, *Cupressus sempervirens* Linnaeus 1753, *Podocarpus macrophyllus* (Thunberg) Sweet 1818 (originally described as *Taxus macrophylla* Thunberg 1783), and *Taxus baccata* Linnaeus 1753. This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Pinus strobus* Linnaeus 1753 & *Cupressus sempervirens* Linnaeus 1753 & *Podocarpus macrophyllus* (Thunberg) Sweet 1818 & *Taxus baccata* Linnaeus 1753).

Etymology: Derived from Latin, *conus* (cone) and *ferre* (to carry or bear).

Reference Phylogeny: The reference phylogeny is Rydin et al. (2002: Fig. 1). See also Rai et al. (2008: Figs. 1, 2), Leslie et al. (2012: Fig. S4), Lu et al. (2014: Fig. 1), and Ruhfel et al. (2014: Fig. 5).

Composition: *Araucariaceae*, *Cephalotaxaceae*, *Cupressaceae* (including "*Taxodiaceae*"), *Pinaceae*, *Podocarpaceae*, *Taxaceae*, and *Sciadopitys*. The clade *Gnetophyta* (this volume) is included within *Coniferae* in some trees based on molecular data (Bowe et al., 2000; Chaw et al., 2000; Sanderson et al., 2000; Gugerli et al., 2001; Magallón and Sanderson, 2002; Burleigh and Mathews, 2004; Zhong et al., 2010, 2011; Xi et al., 2013; Lu et al., 2014; Ruhfel et al., 2014), but not in others (Sanderson et al., 2000; Magallón and Sanderson, 2002; Rydin et al., 2002; Burleigh and Mathews, 2004; Rai et al., 2008). The chloroplast-DNA structural mutation that characterizes conifers (see Diagnostic Apomorphies) is absent in *Gnetophyta* (Raubeson and Jansen, 1992). Most analyses based on morphology (see Comments) have not supported inclusion of *Gnetophyta*, but the clade *Gnetophyta* is nested in *Coniferae* in some most-parsimonious trees in the morphological analysis of Doyle (2008). Although *Emporia* (a Palaeozoic conifer) or *Emporia* and *Cordaitales* are part of *Coniferae*, as defined here, in some of the trees of Rothwell and Serbet (1994: Figs. 2a,b), this is not the case in their other equally parsimonious trees (Figs. 1, 2c,d), or in those of other authors (Miller, 1999; Doyle, 1996, 2006, 2008; Hilton and Bateman, 2006).

Diagnostic Apomorphies: Synapomorphies relative to other crown clades include one-veined needlelike leaves (modified to several-veined in some groups), resin canals, compound female strobili but simple male strobili, tiered proembryos, siphonogamy (Doyle and Donoghue, 1986; Rothwell and Serbet, 1994; Doyle, 2006, 2008), and loss or extreme reduction of one copy of the inverted repeat in the chloroplast genome (Raubeson and Jansen, 1992; Wakasugi et al., 1994). Siphonogamy in *Coniferae* is not homologous with that in angiosperms and gnetophytes if phylogenies such as those of Crane (1985), Doyle and Donoghue (1986), and Doyle (1996) are correct, but it may be homologous with siphonogamy in the latter groups in phylogenies that link *Coniferae* with angiosperms and gnetophytes (Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 2006: Fig. 6), and it is presumably homologous with siphonogamy in *Gnetophyta* if the latter are nested in *Coniferae*.

Synonyms: *Pinopsida*, *Coniferophyta*, *Coniferopsida*, and *Coniferales* are approximate synonyms (see Comments).

Comments: Many molecular analyses (e.g., Stefanovic et al., 1998; Bowe et al., 2000; Chaw et al., 2000; Gugerli et al., 2001; Magallón and Sanderson, 2002; Rydin et al., 2002; Soltis et al., 2002; Rai et al., 2008; Zhong et al., 2010, 2011; Leslie et al., 2012; Lu et al., 2014; Ruhfel et al., 2014) 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, phylogenetic analyses based on morphology have variously suggested that the clade *Taxaceae* is the extant sister to the rest (Miller, 1988, 1999; Rothwell and Serbet, 1994), that a clade comprising *Podocarpaceae* and *Pinaceae* occupies this position (Doyle, 1996; Hilton and Bateman, 2006), or that the position of *Podocarpaceae* is unresolved relative to *Pinaceae* and the rest of the conifers (Doyle, 2006: Fig. 6, 2008)—hence our inclusion of species of *Taxus* and *Podocarpus* as internal specifiers. Because no member of *Gnetophyta* is an internal or external specifier, our definition permits application of the name *Coniferae* in the context of the "gnepine hypothesis" (Bowe et al., 2000; Zhong et al., 2011), or of the "gnecup hypothesis" (Ruhfel et al., 2014), in which case the clade *Gnetophyta* is nested within (and therefore part of) *Coniferae*, but it does not require inclusion of *Gnetophyta*.

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 et al., 1972; Jones and Luchsinger, 1986; Meyen, 1987; Fedorov, 1999; Woodland, 2000). In accordance with our preference for names that are descriptive or end in *-phyta* (meaning plants) rather than having an ending that is meaningless except in indicating rank, *Coniferae* and *Coniferophyta* are the best candidate names for this clade. Here and previously (Cantino et al., 2007), we have chosen *Coniferae* over *Coniferophyta* because the informal names "coniferophytes" and "coniferopsids" (generally used synonymously) traditionally referred to a hypothesized larger group that includes *Ginkgo* and *Cordaitales* as well as conifers (e.g., Coulter and Chamberlain, 1910; Chamberlain, 1935; Foster and Gifford, 1974). The name *Coniferophyta*, which is not defined in this volume, is best reserved for this larger group in the context of phylogenies in which it is a clade (e.g., Crane, 1985; Doyle and Donoghue, 1986; Doyle, 1996, 2008).

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Pan-Angiospermae P. D. Cantino and M. J. Donoghue in Cantino et al. (2007): 833 [J. A. Doyle, P. D. Cantino, and M. J. Donoghue], converted clade name

Registration Number: 75

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

Etymology: Derived from the Greek *pan-* or *pantos* (all, the whole), indicating that this is a total clade, and *Angiospermae*, the name of the crown (see *Angiospermae*, this volume, for etymology of that name).

Reference Phylogeny: The primary reference phylogeny is Doyle (2008: Fig. 3C). See also Doyle (2006: Figs. 6, 8), Doyle (2008: Figs. 3A, 4), Rothwell et al. (2009: Fig. 30), and Rothwell and Stockey (2016: Fig. 28).

Composition: *Angiospermae* (this volume) and all extinct plants that share more recent ancestry with *Angiospermae* than with *Gnetophyta*, *Coniferae*, *Cycadales*, or *Ginkgo*. In the primary reference phylogeny and in the analysis of Hilton and Bateman (2006), *Caytonia*, *Bennettitales*, *Pentoxylon*, and *Glossopteridales* are pan-angiosperms. However, in some other phylogenies, in which *Gnetophyta* are more closely related to *Angiospermae*, only *Bennettitales* and *Pentoxylon* are stem relatives of angiosperms (Rothwell et al., 2009: Fig. 30), only *Bennettitales* (Rothwell and Serbet, 1994: Fig. 2a; Doyle, 2006: Fig. 6; Doyle, 2008: Fig. 3A), only *Caytonia* (Doyle, 1996), or only *Petriellales* (Rothwell and Stockey, 2016: Fig. 28), or there are no known stem relatives of angiosperms (Crane, 1985; Doyle and Donoghue, 1986, 1992; Rothwell and Serbet, 1994: Fig. 1).

Diagnostic Apomorphies: The crown clade has many apomorphies relative to other crown clades (see *Angiospermae*, this volume), some of which also occur in fossil plants (listed under Composition) that may be part of *Pan-Angiospermae*. Because of uncertainty about which fossils lie within *Pan-Angiospermae* and incomplete information on characters in fossils, it is difficult to identify apomorphies that arose near the base of this total clade. With the reference phylogeny and dataset of Doyle (2008), two unequivocally optimized apomorphies uniting putative stem relatives of angiosperms with members of the crown are absence of a lagenostome at the apex of the nucellus (a condition that arose independently in *Coniferae*) and a thick nucellar cuticle. Other apomorphies that are largely or entirely restricted to *Pan-Angiospermae* (not including those known only in extant angiosperms) but are equivocally optimized are ovule(s) borne on the adaxial surface of a foliar structure (potentially ancestral in crown *Spermatophyta*) and absence of an exinous megaspore membrane (a megaspore membrane is absent in *Pentoxylon*, *Bennettitales*, *Caytonia*, and *Angiospermae*, but present in *Glossopteridales*).

Synonyms: *Magnoliophyta* sensu Doweld (2001) is an approximate synonym; its inclusion of extinct, non-carpel-bearing seed plants such as *Caytonia* and *Leptostrobus* suggests that it was conceptualized as a total clade. Although not a scientific name, "angiophytes" (Doyle

and Donoghue, 1993: 146) is an unambiguous synonym.

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