

Registration Number: 82

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

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

Reference Phylogeny: The primary reference phylogeny is Kenrick and Crane (1997: Fig. 7.10), where the clade *Pan-Spermatophyta* originates at the base of the branch leading to *Pertica*, *Tetraxylopteris*, and seed plants. For more detailed representation of the composition of *Pan-Spermatophyta* (but no outgroups), see Hilton and Bateman (2006: Fig. 10). For a broader view of outgroup relationships, see Kenrick and Crane (1997: Fig. 4.31), where *Pan-Spermatophyta* is the clade originating at the base of the branch that leads to *Pertica* and *Tetraxylopteris* (no extant pan-spermatophytes are shown).

Composition: *Spermatophyta* (this volume) and all extinct plants that share more recent ancestry with *Spermatophyta* than with any extant plants that do not bear seeds (e.g., *Monilophyta*, *Lycopodiophyta*). According to the reference phylogenies, stem spermatophytes that lacked seeds include *Tetraxylopteris*, *Archaeopteris*, *Cecropsis*, and possibly *Pertica*; for stem spermatophytes that possessed seeds, see *Apo-Spermatophyta* (this volume).

Diagnostic Apomorphies: Synapomorphies of most *Pan-Spermatophyta*, including

“progymnosperms” (a paraphyletic group) such as *Aneurophyton*, *Tetraxylopteris*, *Archaeopteris*, and *Cecropis* (Beck, 1960), include a bifacial vascular cambium that produces both secondary xylem and secondary phloem and probably a cork cambium that produces periderm (Scheckler and Banks, 1971). Kenrick and Crane (1997) listed three synapomorphies supporting inclusion of *Pertica* in this clade, but these are problematical. Synapomorphies proposed in their Table 4.6 were tetrastichous branching and presence of xylem rays (indicative of secondary xylem). However, tetrastichous branching is questionable because it occurs in *Tetraxylopteris* but not in other “progymnosperms,” and branching in *Pertica* is highly variable (Hotton et al., 2001). Xylem rays and other anatomical characters are actually unknown in *Pertica*, because its stems are not preserved anatomically, and Kenrick and Crane (1997) correctly scored these characters as unknown; their identification of rays as a synapomorphy appears to be a result of using accretan character optimization. However, secondary xylem with apparent rays has been described in a possibly related fossil, *Armoricaphyton* (Gerrienne and Gensel, 2016). In Table 7.2, Kenrick and Crane (1997) indicated that the clade including *Pertica*, *Tetraxylopteris*, and seed plants, designated *Radiatopses*, is united by tetrastichous branching and “a distinctive form of protoxylem ontogeny with multiple strands occurring along the midplanes of the primary xylem ribs” (“radiate protoxylem” of Stein, 1993), but again anatomical characters are unknown in *Pertica*, and *Armoricaphyton* has a presumably more plesiomorphic *Psilophyton*-like centrarch stele with unlobed xylem (Gerrienne and Gensel, 2016). In any case, it is equivocal whether radiate protoxylem is ancestral or derived within the

monilophyte-spermatophyte clade relative to the “permanent protoxylem” of early monilophytes.

Synonyms: The name *Radiatopses* (Kenrick and Crane, 1997: Tables 7.1, 7.2) is an approximate synonym. It has a “synapomorphy-based definition,” but its presumed composition may be identical to that of *Pan-Spermatophyta* if the latter includes *Pertica*. The name *Progymnospermopsida*, proposed for relatives of seed plants that have secondary xylem and phloem but lack seeds (Beck, 1960), may be a partial and approximate synonym in that it refers to a paraphyletic group that originated in approximately the same ancestor as *Pan-Spermatophyta* (see Comments).

Comments: Uncertainty about the status of *Progymnospermopsida* and the corresponding informal name “progymnosperms” as (partial) synonyms of *Pan-Spermatophyta* is related to the distinction between *Pan-Spermatophyta* and *Lignophyta*, an apomorphy-based clade (Donoghue and Doyle in Cantino et al., 2007) characterized by a bifacial vascular cambium that produces secondary xylem (wood) and phloem. If a close relationship to seed plants is more critical to the concept of “progymnosperms” than is the possession of secondary xylem and phloem, then the name “progymnosperms” is appropriately interpreted as a partial and approximate synonym of *Pan-Spermatophyta*. However, if the possession of secondary xylem and phloem is more critical to the concept, then the name is more appropriately interpreted as a partial and approximate synonym of *Lignophyta*.

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Definition: The clade characterized by seeds as inherited by *Magnolia tripetala* (Linnaeus) Linnaeus 1759 (*Angiospermae*), *Podocarpus macrophyllus* (Thunberg) Sweet 1818 (*Coniferae*), *Ginkgo biloba* Linnaeus 1771, *Cycas revoluta* Thunberg 1782 (*Cycadophyta*), and *Gnetum gnemon* Linnaeus 1767 (*Gnetophyta*). This is an apomorphy-based definition. A seed is a fertilized ovule, the ovule being an indehiscent megasporangium surrounded by an integument (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., derived *Santalales*; Brown et al., 2010) in which the integuments have been lost. If only one of the two features is present, the presence of an integument rather than indehiscence will determine whether a structure is an ovule according to the definition used here. Abbreviated definition: ∇ apo seeds [*Magnolia tripetala* (Linnaeus) Linnaeus 1759 & *Podocarpus macrophyllus* (Thunberg) Sweet 1818 & *Ginkgo biloba* Linnaeus 1771 & *Cycas revoluta* Thunberg 1782 & *Gnetum gnemon* Linnaeus 1767].

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

Reference Phylogeny: Hilton and Bateman (2006: Fig. 10), where *Apo-Spermatophyta*

includes the entire illustrated tree except the “progymnosperms.” See also Rothwell and Serbet (1994: Fig. 3).

Composition: The crown clade *Spermatophyta* (this volume) and all extinct seed-bearing plants that lie outside the crown (e.g., Palaeozoic seed ferns such as *Elkinsia*, *Lyginopteris*, and *Medullosa*; for additional members, see Rothwell and Serbet, 1994; Hilton and Bateman, 2006).

Diagnostic Apomorphies: Ovules and seeds (see Definition and Comments for more detailed descriptions). Some associated apomorphies are listed under Comments.

Synonyms: The name *Spermatophytata* Kenrick and Crane (1997: Table 7.2) is an unambiguous synonym. It is defined based on two apomorphies—presence of an integument and only one functional megaspore—both of which characterize the ovule and the former of which we have used as the defining feature of an ovule for the purpose of our definition (see Comments). The name *Spermatophyta* as used by many earlier authors is also implicitly apomorphy-based, but we prefer to use it for the crown clade (see *Spermatophyta*, this volume). The name *Gymnospermae*, as used for living and fossil seed plants other than angiosperms, is a partial synonym; gymnosperms originated from the same immediate ancestor as *Apo-Spermatophyta* but are paraphyletic with respect to angiosperms. The informal names “pteridosperms” and “seed ferns” and corresponding formal names (e.g., *Cycadofilicales*, *Pteridospermales*, *Pteridospermopsida*) refer to a multiply paraphyletic group of extinct

seed plants that originated in the same ancestor as *Apo-Spermatophyta* but includes only a small fraction of its total diversity. Seed ferns, so named because they retained the fernlike foliage that appears to have been ancestral for *Apo-Spermatophyta*, include both stem relatives and plesiomorphic members of the crown clade *Spermatophyta*.

Comments: Some earlier workers (e.g., Arnold, 1948; Beck, 1966) suggested that seeds evolved more than once (ignoring the seedlike structures of some fossil lycophytes), specifically in “coniferophytes” (including cordaites, ginkgophytes, and conifers) and “cycadophytes” (including cycads, “seed ferns,” and bennettites). This hypothesis has not been supported by modern phylogenetic analyses, which nest “coniferophytes” among “seed ferns” (Crane, 1985; Doyle and Donoghue, 1986; Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006). However, our definition of *Apo-Spermatophyta* is constructed such that the name would not apply to any clade in the context of a phylogeny in which the seeds of the five extant subgroups are not homologous.

The definition of “ovule” adopted here includes what some authors (e.g., Stewart and Rothwell, 1993) have referred to as preovules, with a ring of more or less free integumentary lobes surrounding the megasporangium, so that a micropyle is lacking, as in *Elkinsia* and *Genomosperma*. Such fossils have been described as seed plants. Various features are closely associated in the reproductive biology of seed plants (Stewart and Rothwell, 1993): e.g., an indehiscent megasporangium, an integument, pollination, and one functional megaspore (with derived exceptions in *Angiospermae* and *Gnetophyta*; Gifford and Foster, 1989). However, in order to apply the name *Apo-Spermatophyta* unambiguously, it is best for the definition 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*). Cantino et al. (2007) chose indehiscence of the megasporangium, on the grounds that it is “fundamental to the reproductive biology of seed plants,” but we prefer to use the presence of an integument because it is more consistent with the common definition of an ovule as an integumented megasporangium (e.g., Gifford and Foster, 1989; Stewart and Rothwell, 1993) and more readily applied in practice. Presence of an integument has been widely used to classify fossilized structures as ovules when the megasporangium character is unknown (Stewart and Rothwell, 1993). The two features are associated in all known fossils in which the characters are preserved, but if a fossil were to be found with an indehiscent megasporangium and no integument it would not be a member of *Apo-Spermatophyta*.

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Spermatophyta N. L. Britton and A. Brown 1896: 49
[P. D. Cantino, J. A. Doyle, and M. J. Donoghue],
converted clade name

Registration Number: 100

Definition: The smallest crown clade containing *Magnolia tripetala* (Linnaeus) Linnaeus 1759 (*Angiospermae*), *Podocarpus macrophyllus* (Thunberg) Sweet 1818 (*Coniferae/Cupressophyta*), *Ginkgo biloba* Linnaeus 1771, *Cycas revoluta* Thunberg 1782 (*Cycadophyta*), and *Gnetum gnemon* Linnaeus 1767 (*Gnetophyta*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Magnolia tripetala* (Linnaeus) Linnaeus 1759 & *Podocarpus macrophyllus* (Thunberg) Sweet 1818 & *Ginkgo biloba* Linnaeus 1771 & *Cycas revoluta* Thunberg 1782 & *Gnetum gnemon* Linnaeus 1767).

Etymology: Derived from Greek, *sperma* (seed) and *phyton* (plant) (Stearn, 1973).

Reference Phylogeny: The primary reference phylogeny is Qiu et al. (2007: Fig. 1). See also Burleigh and Matthews (2004: Fig. 5), Xi et al. (2013: Fig. 2), and Ruhfel et al. (2014: Fig. 5).

Composition: All extant seed plants and any fossils that are part of the crown, including *Pan-Angiospermae*, *Pan-Coniferae*, and the total clades (not named in this volume) of *Ginkgo*, *Cycadophyta*, and *Gnetophyta*. In the reference phylogeny and some other published trees, the total clade of *Gnetophyta* is contained within *Coniferae*, but there are other phylogenies in which these two clades are non-overlapping (see *Coniferae*, this volume).

Diagnostic Apomorphies: Possible apomorphies of this crown clade are endarch primary

xylem in the stem (assuming that the mesarch primary xylem in *Callistophyton* is a reversal, if this taxon is nested in the crown clade; Doyle, 2006), distal aperture position in the pollen (assuming that absence of a distal aperture in *Cordaitales* and *Emporia* represents a reversal to the state in early fossil seed plants (*Apo-Spermatophyta*), as implied by trees of Rothwell and Serbet, 1994 and Doyle, 2006), a linear tetrad of megaspores (Doyle and Donoghue, 1986; Doyle, 2006), honeycomb-alveolar infratectal structure of the pollen exine, and platyspermic ovules (Doyle, 2006). Because ovules of *Cycas* are platyspermic (biradial) but ovules of other cycads are radiospermic, the level at which platyspermy is synapomorphic is uncertain if the clade *Cycadophyta* is the extant sister group of the rest of *Spermatophyta* (e.g., Doyle, 2006: Fig. 6). Furthermore, Rothwell and Serbet (1994) questioned the distinction between radiospermic and platyspermic and divided ovule symmetry into four states.

The following are apomorphies of *Spermatophyta*, as defined here, relative to other crown clades (lycophytes and monilophytes) 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), axillary branching (reversed in living cycads), eustele, cataphylls, and a free-nuclear stage followed by alveolar cellularization in embryogeny (Doyle and Donoghue, 1986; Rothwell and Serbet, 1994; Doyle, 1998, 2006).

Synonyms: The name *Spermatophytatinae* sensu Jeffrey (1982) is an approximate synonym in that all listed subordinate taxa are extant. The “platyspermic clade” of Doyle and Donoghue (1986: 354) is an approximate synonym based on composition (independent of whether platyspermic ovules are a synapomorphy), but the name “platysperms” of Crane (1985) is not (because that taxon excludes *Cycadophyta*).

Comments: Although the clade *Spermatophyta* has very strong support from both morphological and molecular analyses, relationships among its principal extant subgroups (*Angiospermae*, *Ginkgo*, *Cycadophyta*, *Coniferae*, and *Gnetophyta*) remain unresolved in spite of intensive study (Doyle and Donoghue, 1986; Rothwell and Serbet, 1994; Bowe et al., 2000; Chaw et al., 2000; Magallón and Sanderson, 2002; Rydin et al., 2002; Soltis et al., 2002; Burleigh and Mathews, 2004; Doyle, 2006, 2008; Hilton and Bateman, 2006; Qiu et al., 2007; Mathews, 2009; Mathews et al., 2010; Lee et al., 2011; Xi et al., 2013; Ruhfel et al., 2014). Consequently, all five of these subgroups are represented by internal specifiers in our definition. Although there is disagreement as to whether the clade *Pinaceae* is more closely related to *Gnetophyta* or to *Cupressophyta*, both are represented in the reference phylogeny, so there is no need to include a specifier to represent *Pinaceae*.

Here and previously (Cantino et al., 2007) we have defined the name *Spermatophyta* to refer to the seed plant crown clade, following *PhyloCode* Recommendation 10.1B. This application is somewhat unconventional, since this name has more often been applied to the apomorphy-based clade originating with the origin of the seed. However, it has been implicitly applied to the crown in molecular studies. For example, Jager et 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, their statement implies application of the name *Spermatophyta* to the crown (see *PhyloCode* Note 10.1B.1). We are aware of only one other scientific name having been applied to the crown (see Synonymy), and only one use of it.

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

Registration Number: 11

Definition: The largest crown clade containing *Liquidambar styraciflua* Linnaeus 1753 but not *Cycas revoluta* Thunberg 1782 (*Cycadophyta*) and *Ginkgo biloba* Linnaeus 1771 and *Gnetum gnemon* Linnaeus 1767 (*Gnetophyta*) and *Pinus strobus* Linnaeus 1753 (*Coniferae*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Liquidambar styraciflua* Linnaeus 1753 ~ *Cycas revoluta* Thunberg 1782 & *Ginkgo biloba* Linnaeus 1771 & *Gnetum gnemon* Linnaeus 1767 & *Pinus strobus* Linnaeus 1753).

Etymology: Derived from Greek, *angeion* (vessel or case) and *sperma* (seed), referring to the enclosure of the ovules inside a carpel and, consequently, the seeds inside a fruit.

Reference Phylogeny: The primary reference phylogeny is Doyle (2008: Fig. 3C). See also Doyle (2008: Figs. 3A, 4), Soltis et al. (2011: Fig. 2), Ruhfel et al. (2014: Fig. 5), and Rothwell and Stockey (2016: Fig. 28).

Composition: The total clades corresponding to *Amborella*, *Nymphaeales* (including *Hydatellaceae*), *Austrobaileyales*, *Ceratophyllum*, *Chloranthaceae*, *Magnoliidae* (as defined in this volume), *Monocotyledoneae* (this volume), and *Eudicotyledoneae* (this volume); for summary of internal relationships, see Soltis et al. (2011). *Angiospermae* is a huge clade, with an estimated 271,500 extant species (Mabberley, 2008), a figure that is certain to increase as many new species continue to be described, particularly from the tropics. For information about the

composition of subgroups whose names are not defined in this volume, see Stevens (2001 onwards) and Mabberley (2008).

Diagnostic Apomorphies: The following are apomorphies relative to other crown clades, some of which also occur in fossil plants that may be stem relatives of *Angiospermae* (these are noted parenthetically): closed carpel, which develops into a fruit; ovule with two integuments; lack of an exinous megaspore membrane (also in *Caytonia*, *Bennettitales*, and *Pentoxylon*); highly reduced female gametophyte, most commonly with eight nuclei (potentially based on a module consisting of an egg, two synergids, and a polar nucleus, as seen in the four-celled, four-nucleate female gametophyte of *Nymphaeales* and *Austrobaileyales*; Friedman and Williams, 2003; Friedman and Ryerson, 2009); endosperm (either diploid or triploid) resulting from double fertilization; microgametophyte with three nuclei; scalariform pitting or perforations in secondary xylem (also in *Bennettitales*); apical meristem with tunica of two cell layers; more than two 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; anther wall with endothecium; pollen with unlaminated endexine; stamen with two pairs of pollen sacs (Crane, 1985; Doyle and Donoghue, 1986a, 1992; Rothwell and Serbet, 1994; Doyle, 1996, 2006, 2008; P. Soltis et al., 2004).

Synonyms: Approximate synonyms include *Magnoliophyta* sensu Cronquist (1981) and

many other authors (see Comments), *Anthophyta* sensu Bold (1957) and *Magnoliopsida* sensu Jeffrey (1982), Scagel et al. (1984), and Thorne and Reveal (2007). However, the name *Magnoliopsida* is more widely applied to the paraphyletic group “dicots” (e.g., Takhtajan, 1987, 1997; Cronquist, 1981; and many texts that adopted Cronquist’s system).

Comments: The monophyly of *Angiospermae* is very strongly supported by both molecular and morphological analyses (Magallón and Sanderson, 2002; Rydin et al., 2002; Soltis et al., 2002; Doyle, 2006, 2008; Xi et al., 2014), and the clade has many morphological apomorphies (see Diagnostic Apomorphies). In various phylogenetic analyses, the extant sister group of the angiosperm crown clade has been inferred to be either *Gnetophyta* (Crane, 1985; Doyle and Donoghue, 1986a,b, 1992; Loconte and Stevenson, 1990; Doyle et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996, 2006, 2008: Fig. 3A; Stefanovic et al., 1998; Rydin et al., 2002: Fig. 3; Hilton and Bateman, 2006), a clade comprising *Gnetum* and *Welwitschia* (Nixon et al., 1994), all extant gymnosperms (Bowe et al., 2000; Chaw et al., 2000; Gugerli et al., 2001; Magallón and Sanderson, 2002; Soltis et al., 2002: Figs. 2, 4–6; Qiu et al., 2006, 2007; Xi et al., 2013; Ruhfel et al., 2014; Wickett et al., 2014), a clade comprising conifers, cycads, and *Ginkgo* (Hamby and Zimmer, 1992; Magallón and Sanderson, 2002; Rydin et al., 2002: Figs. 1, 2; Soltis et al., 2002: Fig. 3; Rai et al., 2003), a clade comprising conifers and *Gnetophyta* (Hill and Crane, 1982; Soltis et al., 2002: Fig. 1), or *Cycadophyta* (Doyle, 2006: Fig. 7; Doyle, 2008: Fig. 3C; Mathews et al., 2010). Because of this disagreement about outgroup relationships, four external specifiers are used here. A minimum-clade definition with three specifiers, two of which would be *Amborella trichopoda* and any species of *Nymphaeales* or *Hydatellaceae*,

would be simpler and is consistent with the results of recent molecular analyses (e.g., Soltis et al., 2011; Wickett et al., 2014; Xi et al., 2014; Zeng et al., 2014). 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 kind of definition. Regardless of how confident one may currently feel about the position of *Amborella*, one must consider the possibility that some other species that has to date not been included in a molecular analysis may turn out to be sister to the rest of *Angiospermae*. The discovery (Saarela et al., 2007) that the taxon *Hydatellaceae*, formerly thought to be part of the monocot clade, is related to *Nymphaeales* near the base of the angiosperm tree illustrates this point. Furthermore, some genome-based phylogenies (Goremykin et al., 2003, 2004; but see D. Soltis et al., 2004) suggest that monocots (represented only by grasses in Goremykin’s papers), rather than *Amborella*, are sister to the rest of the angiosperms (i.e., a basal split between monocots and dicots). Compositional stability is better served by a maximum-crown-clade definition with the relatively few candidates for the extant sister group represented by external specifiers.

Angiospermae and *Magnoliophyta* are the principal names for this clade. Here and previously (Cantino et al., 2007), we have adopted the name *Angiospermae* because we prefer to avoid names with rank-based endings if there is a reasonable alternative, and it appears to be the more widely used of the two names. We attribute the name *Angiospermae* to Lindley (1830). Although Lindley published this name as a tribe that contains orders, and thus it was not validly published by Lindley according to the botanical code (Art. 37.6; Turland et al., 2018), this does not disqualify Lindley as the earliest author of the preexisting name *Angiospermae* under the *PhyloCode* (Rec. 9.15A).

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