

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

Registration Number: 47

Definition: The smallest crown clade containing *Gnetum gnemon* Linnaeus 1767, *Ephedra distachya* Linnaeus 1753, and *Welwitschia mirabilis* J. D. Hooker 1862. This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Gnetum gnemon* Linnaeus 1767 & *Ephedra distachya* Linnaeus 1753 & *Welwitschia mirabilis* J. D. Hooker 1862).

Etymology: Derived from *Gnetum* (the name of an included genus) and the Greek *phyton*, meaning "plant." The name *Gnetum* is apparently derived from the same word as the specific epithet *gnemon* (i.e., *genemo*, the vernacular name for *Gnetum gnemon* in the Molucca Islands; Markgraf, 1951).

Reference Phylogeny: The primary reference phylogeny is Rydin et al. (2002: Fig. 1). See also Hou et al. (2015: Fig. 2).

Composition: *Ephedra* (40 species), *Gnetum* (30 species), and *Welwitschia* (1 species) (species numbers from Mabberley, 2008). For descriptions of these three taxa, see Kubitzki (1990).

Diagnostic Apomorphies: Synapomorphies relative to other crown clades include multiple axillary buds, opposite phyllotaxy, terminal ovules with one or two outer envelopes derived from opposite primordia, basally fused microsporophylls with terminal microsporangia, vessels in xylem (assuming these are not homologous with angiosperm vessels, as inferred even in analyses in which angiosperms and gnetophytes are extant sister groups: Doyle

and Donoghue, 1986; Doyle, 1996), compound microsporangiate strobili, striate pollen (modified to echinate in *Gnetum*; Yao et al., 2004), micropylar tube, and apical meristem with one tunica layer (Doyle and Donoghue, 1986, 1992; Crane, 1988; Rothwell and Serbet, 1994; Doyle, 2006).

Synonyms: *Gnetopsida* and *Gnetales* (see Comments); also *Gnetidae* (Chase and Reveal, 2009) and *Gnetatae* (Kubitzki, 1990). All four are approximate synonyms with the same composition.

Comments: The monophyly of *Gnetophyta* is very strongly supported by both molecular and morphological analyses (Crane, 1985, 1988; Doyle and Donoghue, 1986, 1992; Doyle et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996, 2006; Rydin et al., 2002; Soltis et al., 2002; Burleigh and Mathews, 2004; Hilton and Bateman, 2006; Zhong, 2010, 2011; Lu et al., 2014; Wickett et al., 2014). The names *Gnetophyta*, *Gnetopsida*, and *Gnetales* are widely applied to this clade (*Gnetidae* and *Gnetatae* much less frequently). Here and previously (Cantino et al., 2007), we have opted for the *-phyta* ending even though the name *Gnetales* is more frequently used, because, although *-phyta* is used to designate the rank of phylum (division) in botanical rank-based nomenclature, it also means "plants," whereas *-opsida* and *-ales* have no meaning other than indicating rank.

Literature Cited

Bessey, C. E. 1907. A synopsis of plant phyla. *Univ. Stud.*, University of Nebraska, 7:275–373.

- Burleigh, J. G., and S. Mathews. 2004. Phylogenetic signal in nucleotide data from seed plants: implications for resolving the seed plant tree of life. *Am. J. Bot.* 91:1599–1613.
- Cantino, P. D., J. A. Doyle, S. W. Graham, W. S. Judd, R. G. Olmstead, D. E. Soltis, P. S. Soltis, and M. J. Donoghue. 2007. Towards a phylogenetic nomenclature of *Tracheophyta*. *Taxon* 56:822–846 and E1–E44.
- Chase, M. W., and J. L. Reveal. 2009. A phylogenetic classification of the land plants to accompany APG III. *Bot. J. Linn. Soc.* 161:122–127.
- Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Mo. Bot. Gard.* 72:716–793.
- Crane, P. R. 1988. Major clades and relationships in the “higher” gymnosperms. Pp. 218–272 in *Origin and Evolution of Gymnosperms* (C. B. Beck, ed.). Columbia University Press, New York.
- Doyle, J. A. 1996. Seed plant phylogeny and the relationships of *Gnetales*. *Int. J. Plant Sci.* 157 (suppl.):S3–S39.
- Doyle, J. A. 2006. Seed ferns and the origin of angiosperms. *J. Torrey Bot. Soc.* 133:169–209.
- Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev.* 52:321–431.
- Doyle, J. A., and M. J. Donoghue. 1992. Fossils and seed plant phylogeny reanalyzed. *Brittonia* 44:89–106.
- Doyle, J. A., M. J. Donoghue, and E. A. Zimmer. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Ann. Mo. Bot. Gard.* 81:419–450.
- Hilton, J., and R. M. Bateman. 2006. Pteridosperms are the backbone of seed-plant phylogeny. *J. Torrey Bot. Soc.* 133:119–168.
- Hou, C., A. M. Humphreys, O. Thureborn, and C. Rydin. 2015. New insights into the evolutionary history of *Gnetum* (*Gnetales*). *Taxon* 64:239–252.
- Kubitzki, K. 1990. *Gnetatae*. Pp. 378–391 in *Families and Genera of Vascular Plants*, Vol. 1 (K. U. Kramer and P. S. Green, vol. eds.). Springer-Verlag, Berlin.
- Lu, Y., J.-H. Ran, D.-M. Guo, Z.-Y. Yang, and X.-Q. Wang. 2014. Phylogeny and divergence times of gymnosperms inferred from single-copy nuclear genes. *PLOS ONE* 9(9):e107679.
- Mabberley, D. J. 2008. *Mabberley's Plant-Book*. 3rd edition. Cambridge University Press, Cambridge, UK.
- Markgraf, F. 1951. *Gnetaceae*. Pp. 336–347 in *Flora Malesiana*, Series 1, Vol. 4(3). (C. G. G. J. van Steenis, ed.). Noordhoff-Kolff, Djakarta.
- Rothwell, G. W., and R. Serbet. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Syst. Bot.* 19:443–482.
- Rydin, C., M. Källersjö, and E. Friis. 2002. Seed plant relationships and the systematic position of *Gnetales* based on nuclear and chloroplast DNA: conflicting data, rooting problems, and the monophyly of conifers. *Int. J. Plant Sci.* 163:197–214.
- Soltis, D. E., P. S. Soltis, and M. J. Zanis. 2002. Phylogeny of seed plants based on evidence from eight genes. *Am. J. Bot.* 89:1670–1681.
- Wickett, N. J., S. Mirarab, N. Nguyen, T. Warnow, E. Carpenter, N. Matasci, S. Ayyampalayam, M. S. Barker, J. G. Burleigh, M. A. Gitzendanner, B. R. Ruhfel, E. Wafula, J. P. Der, S. W. Graham, S. Mathews, M. Melkonian, D. E. Soltis, P. S. Soltis, N. W. Miles, C. J. Rothfels, L. Pokorny, A. J. Shaw, L. DeGironimo, D. W. Stevenson, B. Surek, J. C. Villarreal, B. Roure, H. Philippe, C. W. dePamphilis, T. Chen, M. K. Deyholos, R. S. Baucom, T. M. Kutchan, M. M. Augustin, J. Wang, Y. Zhang, Z. Tian, Z. Yan, X. Wu, X. Sun, G. K. Wong, and J. Leebens-Mack. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proc. Natl. Acad. Sci. USA* 111:E4859–E4868.
- Yao, Y., Y. Xi, B. Geng, and C. Li. 2004. The exine ultrastructure of pollen grains in *Gnetum* (*Gnetaceae*) from China and its bearing on the relationship with the ANITA group. *Bot. J. Linn. Soc.* 146:415–425.

Zhong, B., O. Deusch, V. V. Goremykin, D. Penny, P. J. Biggs, R. A. Atherton, S. V. Nikiforova, and P. J. Lockhart. 2011. Systematic error in seed plant phylogenomics. *Genome Biol. Evol.* 3:1340–1348.

Zhong, B., T. Yonezawa, Y. Zhong, and M. Hasegawa. 2010. The position of *Gnetales* among seed plants: overcoming pitfalls of chloroplast phylogenomics. *Mol. Biol. Evol.* 27:2855–2863.

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Mesangiospermae M. J. Donoghue, J. A. Doyle, and P. D. Cantino in
P. D. Cantino et al. (2007): 834 [M. J. Donoghue, J. A.
Doyle, and P. D. Cantino], converted clade name

Registration Number: 65

Definition: The largest crown clade containing *Platanus occidentalis* Linnaeus 1753 but not *Amborella trichopoda* Baillon 1869 and *Nymphaea odorata* Aiton 1789 (*Nymphaeales*) and *Austrobaileya scandens* C. T. White 1933 (*Austrobaileya*). This is a maximum-crown-clade definition. Abbreviated definition: max crown ∇ (*Platanus occidentalis* Linnaeus 1753 ~ *Amborella trichopoda* Baillon 1869 & *Nymphaea odorata* Aiton 1789 & *Austrobaileya scandens* C. T. White 1933).

Etymology: *Mesangiospermae* is a rough translation of “core angiosperms,” the informal name applied to this clade by Judd et al. (2002). The prefix *mes-* (Greek) means “middle” (Stearn, 1973), and *Angiospermae* (this volume) is the name of a larger clade.

Reference Phylogeny: The primary reference phylogeny is Qiu et al. (2005: Fig. 2). See also Soltis et al. (2011: Figs. 1, 2) and Wickett et al. (2014: Figs. 2, 3).

Composition: *Chloranthaceae*, *Ceratophyllum*, *Magnoliidae*, *Monocotyledoneae*, and *Eudicotyledoneae* (see entries in this volume for the last three clades).

Diagnostic Apomorphies: Unambiguous morphological apomorphies for *Mesangiospermae* are not yet known. One possibility is plicate carpels sealed by postgenital fusion of the margins (see Endress and Igersheim, 2000), but this interpretation depends on the placement of two of the groups of *Mesangiospermae*, *Chloranthaceae*, and *Ceratophyllum*, which have

ascidiate carpels sealed by secretion, comparable to those of *Amborella trichopoda* and other members of what Qiu et al. (1999) called the “ANITA” grade (i.e., *Amborella*, *Nymphaeales*, and *Austrobaileyales*, later extended to include *Hydatellaceae*: Saarela et al., 2007). Most molecular analyses have indicated that *Chloranthaceae* and *Ceratophyllum* are nested within *Mesangiospermae*, and with some topologies (Endress and Doyle, 2009: Fig. 8B) it is equally parsimonious to assume either that plicate carpels and sealing by postgenital fusion are apomorphies at the level of *Mesangiospermae*, with reversals in some lines, or that these features originated more than once within the clade. However, with other topologies (Soltis et al., 2005: Fig. 3.17) the latter scenario is more parsimonious. Combined molecular and morphological analyses (Doyle and Endress, 2000; Endress and Doyle, 2009) and some molecular analyses (Qiu et al., 2005, 2010) supported the placement of *Chloranthaceae* or a clade consisting of *Chloranthaceae* and *Ceratophyllum* as sister to all remaining *Mesangiospermae*, in which case it could be inferred that the ascidiate carpels of *Chloranthaceae* (with or without *Ceratophyllum*) are plesiomorphic and plicate carpels sealed by postgenital fusion evolved once within *Mesangiospermae*. In all these cases, some homoplasy would remain (e.g., reversals to ascidiate carpels in *Nelumbo* and *Berberidaceae*; convergent origins of partially plicate carpels in *Illicium*; Doyle and Endress, 2000: Fig. 7; Soltis et al., 2005: Fig. 3.17). Finally, recent embryological studies (Williams and Friedman, 2002; Friedman, 2006) raise the possibility that the typical 7-celled, 8-nucleate *Polygonum*-type embryo sac is an apomorphy of *Mesangiospermae*, assuming that the 9-nucleate

embryo sac of *Amborella* was independently derived from the 4-nucleate type found in *Nymphaeales* and *Austrobaileyales*.

Synonyms: The informal names “euangiosperms” (Qiu et al., 2000) and “core angiosperms” (Judd et al., 2002) are approximate synonyms.

Comments: Until we published the name *Mesangiospermae* (Cantino et al., 2007), there was no preexisting scientific name for this large and well-supported clade, which includes the vast majority of living angiosperms. In most recent analyses of the basal angiosperm problem (e.g., Mathews and Donoghue, 1999; Doyle and Endress, 2000; Qiu et al., 2000; Zanis et al., 2003; Xi et al., 2014), which have focused on resolving relationships among *Amborella trichopoda*, *Nymphaeales*, and *Austrobaileyales*, the clade comprising the remaining angiosperms has not been named, with the exception that Qiu et al. (2000: S7) referred to it as “euangiosperms.” It did not receive even an informal name in several phylogenetic studies of the angiosperms as a whole (e.g., Soltis et al., 2000; Hilu et al., 2003) or in summary treatments (e.g., APG II, 2003; Soltis et al., 2005) despite rather high levels of support, though one text (Judd et al., 2002: 178) referred to the clade as the “core angiosperms.” More recent editions of this text (e.g., Judd et al., 2008, 2016) use the name *Mesangiospermae* (citing Cantino et al., 2007) as well as “core angiosperms.” The Angiosperm Phylogeny Group (APG IV, 2016) used the informal name “Mesangiosperms” in its appendix.

Because outgroup relationships are better resolved than basal relationships within *Mesangiospermae*, compositional stability can be achieved more simply with a maximum-crown-clade definition than a minimum-crown-clade definition. Relationships among five clades at the base of *Mesangiospermae* (*Chloranthaceae*, *Ceratophyllum*, *Magnoliidae*, *Monocotyledoneae*,

and *Eudicotyledoneae*) remain unclear. Some analyses have suggested that *Chloranthaceae* (e.g., Doyle and Endress, 2000; Qiu et al., 2005; Fig. 1) or a clade comprising *Chloranthaceae* and *Magnoliidae* (Saarela et al., 2007; Fig. 2) is the sister group of the rest of *Mesangiospermae*. Others have supported *Ceratophyllum* alone (e.g., Zanis et al., 2003; Fig. 4), *Monocotyledoneae* alone (Qiu et al., 2005; Fig. 2), or a clade consisting of *Ceratophyllum* and monocots (Qiu et al., 2005; Fig. 3C; Zanis et al., 2003; Fig. 3) as sister to the rest (see Soltis et al., 2005, for discussion). In still other analyses *Ceratophyllum* has been linked instead with eudicots (Hilu et al., 2003; Qiu et al., 2005; Fig. 2; Graham et al., 2006; Jansen et al., 2007; Moore et al., 2007; Saarela et al., 2007) or with *Chloranthaceae* (Qiu et al., 2005; Fig. 3A,B; Qiu et al., 2006; Fig. 3; Qiu et al., 2010; Endress and Doyle, 2009; Moore et al., 2011; Zhang et al., 2012; Zeng et al., 2014). By using a maximum-crown-clade 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 interrelationships. 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.

Literature Cited

- APG II (Angiosperm Phylogeny Group II). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141:399–436.
- APG IV (Angiosperm Phylogeny Group IV). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181:1–20.

- Cantino, P. D., J. A. Doyle, S. W. Graham, W. S. Judd, R. G. Olmstead, D. E. Soltis, P. S. Soltis, and M. J. Donoghue. 2007. Towards a phylogenetic nomenclature of *Tracheophyta*. *Taxon* 56:822–846 and E1–E44.
- Doyle, J. A., and P. K. Endress. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *Int. J. Plant Sci.* 161:S121–S153.
- Endress, P. K., and J. A. Doyle. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *Am. J. Bot.* 96:22–66.
- Endress, P. K., and A. Igersheim. 2000. Gynoecium structure and evolution in basal angiosperms. *Int. J. Plant Sci.* 161:S211–S223.
- Friedman, W. E. 2006. Embryological evidence for developmental lability during early angiosperm evolution. *Nature* 441:337–340.
- Graham, S. W., J. M. Zgurski, M. A. McPherson, D. M. Cherniawsky, J. M. Saarela, E. S. C. Horne, S. Y. Smith, W. A. Wong, H. E. O'Brien, V. L. Biron, J. C. Pires, R. G. Olmstead, M. W. Chase, and H. S. Rai. 2006. Robust inference of monocot deep phylogeny using an expanded multigene plastid data set. Pp. 3–20 in *Monocots: Comparative Biology and Evolution (Excluding Poales)* (J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson, eds.). Rancho Santa Ana Botanic Garden, Claremont, CA.
- Hilu, K. W., T. Borsch, K. Müller, D. E. Soltis, P. S. Soltis, V. Savolainen, M. W. Chase, M. P. Powell, L. A. Alice, R. Evans, H. Sauquet, C. Neinhuis, T. A. B. Slotta, J. G. Rohwer, C. S. Campbell, and L. W. Chatrou. 2003. Angiosperm phylogeny based on *matK* sequence information. *Am. J. Bot.* 90:1758–1776.
- Jansen, R. K., Z. Cai, L. A. Raubeson, H. Daniell, C. W. dePamphilis, J. Leebens-Mack, K. F. Müller, M. Guisinger-Bellian, R. C. Haberle, A. K. Hansen, T. W. Chumley, S.-B. Lee, R. Peery, J. R. McNeal, J. V. Kuehl, and J. L. Boore. 2007. Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. *Proc. Natl. Acad. Sci. USA* 104:19369–19374.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. *Plant Systematics—A Phylogenetic Approach*. 2nd edition. Sinauer Associates, Sunderland, MA.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2008. *Plant Systematics—A Phylogenetic Approach*. 3rd edition. Sinauer Associates, Sunderland, MA.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2016. *Plant Systematics—A Phylogenetic Approach*. 4th edition. Sinauer Associates, Sunderland, MA.
- Mathews, S., and M. J. Donoghue. 1999. The root of angiosperm phylogeny inferred from duplicate phytochrome genes. *Science* 286:947–949.
- Moore, M. J., C. D. Bell, P. S. Soltis, and D. E. Soltis. 2007. Using plastid genome-scale data to resolve enigmatic relationships among basal angiosperms. *Proc. Natl. Acad. Sci. USA* 104:19363–19368.
- Moore, M. J., N. Hassan, M. A. Gitzendanner, R. A. Bruenn, M. Croley, A. Vandeventer, J. W. Horn, A. Dhingra, S. F. Brockington, M. Latvis, J. Ramdial, R. Alexandre, A. Piedrahita, Z. Xi, C. C. Davis, P. S. Soltis, and D. E. Soltis. 2011. Phylogenetic analysis of the plastid inverted repeat for 244 species: insights into deeper-level angiosperm relationships from a long, slowly evolving sequence region. *Int. J. Plant Sci.* 172:541–558.
- Qiu, Y.-L., O. Dombrowska, J. Lee, L. Li, B. A. Whitlock, F. Bernasconi-Quadroni, J. S. Rest, C. C. Davis, T. Borsch, K. W. Hilu, S. S. Renner, D. E. Soltis, P. S. Soltis, M. J. Zanis, J. J. Cannone, R. R. Gutell, M. Powell, V. Savolainen, L. W. Chatrou, and M. W. Chase. 2005. Phylogenetic analyses of basal angiosperms based on nine plastid, mitochondrial, and nuclear genes. *Int. J. Plant Sci.* 166:815–842.
- Qiu, Y.-L., J.-Y. Lee, F. Bernasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, Z. Chen, V. Savolainen, and M. W. Chase. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* 402:404–407.
- Qiu, Y.-L., J.-Y. Lee, F. Bernasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, E. Zimmer, Z. Chen, V. Savolainen, and M. W. Chase. 2000. Phylogeny of basal angiosperms: analyses of five genes from three genomes. *Int. J. Plant Sci.* 161:S3–S27.

- Qiu, Y.-L., L. Li, T. A. Hendry, R. Li, D. W. Taylor, M. J. Issa, A. J. Ronen, M. L. Vekaria, and A. M. White. 2006. Reconstructing the basal angiosperm phylogeny: evaluating information content of mitochondrial genes. *Taxon* 55:837–856.
- Qiu, Y.-L., L. Li, B. Wang, J.-Y. Xue, T. A. Hendry, R.-Q. Li, J. W. Brown, Y. Liu, G. T. Hudson, and Z.-D. Chen. 2010. Angiosperm phylogeny inferred from sequences of four mitochondrial genes. *J. Syst. Evol.* 48:391–425.
- Saarela, J. M., H. S. Rai, J. A. Doyle, P. K. Endress, S. Mathews, A. D. Marchant, B. G. Briggs, and S. W. Graham. 2007. *Hydatellaceae* identified as a new branch near the base of the angiosperm phylogenetic tree. *Nature* 446:312–315.
- Soltis, D. E., S. A. Smith, N. Cellinese, K. J. Wurdack, D. C. Tank, S. F. Brockington, N. F. Refulio-Rodriguez, J. B. Walker, M. J. Moore, B. S. Carlswald, C. D. Bell, M. Latvis, S. Crawley, C. Black, D. Diouf, Z. Xi, C. A. Rushworth, M. A. Gitzendanner, K. J. Sytsma, Y.-L. Qiu, K. H. Hilu, C. C. Davis, M. J. Sanderson, R. S. Beaman, R. G. Olmstead, W. S. Judd, M. J. Donoghue, and P. S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *Am. J. Bot.* 98:704–730.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot. J. Linn. Soc.* 133:381–461.
- Soltis, D. E., P. S. Soltis, P. K. Endress, and M. W. Chase. 2005. *Phylogeny and Evolution of Angiosperms*. Sinauer Associates, Sunderland, MA.
- Stearn, W. T. 1973. *Botanical Latin*. David & Charles, Newton Abbot, Devon.
- Wickett, N. J., S. Mirarab, N. Nguyen, T. Warnow, E. Carpenter, N. Matasci, S. Ayyampalayam, M. S. Barker, J. G. Burleigh, M. A. Gitzendanner, B. R. Ruhfel, E. Wafula, J. P. Der, S. W. Graham, S. Mathews, M. Melkonian, D. E. Soltis, P. S. Soltis, N. W. Miles, C. J. Rothfels, L. Pokorny, A. J. Shaw, L. DeGironimo, D. W. Stevenson, B. Surek, J. C. Villarreal, B. Roure, H. Philippe, C. W. dePamphilis, T. Chen, M. K. Deyholos, R. S. Baucom, T. M. Kutchan, M. M. Augustin, J. Wang, Y. Zhang, Z. Tian, Z. Yan, X. Wu, X. Sun, G. K. Wong, and J. Leebens-Mack. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proc. Natl. Acad. Sci. USA* 111:E4859–E4868.
- Williams, J. H., and W. E. Friedman. 2002. Identification of diploid endosperm in an early angiosperm lineage. *Nature* 415:522–526.
- Xi, Z., L. Liu, J. S. Rest, and C. C. Davis. 2014. Coalescent versus concatenation methods and the placement of *Amborella* as sister to water lilies. *Syst. Biol.* 63:919–932.
- Zanis, M., P. S. Soltis, Y.-L. Qiu, E. Zimmer, and D. E. Soltis. 2003. Phylogenetic analyses and perianth evolution in basal angiosperms. *Ann. Mo. Bot. Gard.* 90:129–150.
- Zeng, L., Q. Zhang, R. Sun, H. Kong, N. Zhang, and H. Ma. 2014. Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. *Nat. Commun.* 5:4956.
- Zhang, N., L. Zeng, H. Shan, and H. Ma. 2012. Highly conserved low-copy nuclear genes as effective markers for phylogenetic analyses in angiosperms. *New Phytol.* 195:923–937.

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[M. J. Donoghue, J. A. Doyle, and P. D. Cantino], converted clade name

Registration Number: 108

Definition: The most inclusive clade exhibiting tricolpate (or derivative) pollen grains synapomorphic with those found in *Platanus occidentalis* Linnaeus 1753 (*Eudicotyledoneae*). A tricolpate pollen grain is one having three elongate, furrow-like apertures (colpi) located at and oriented perpendicular to the equator. This is an apomorphy-based definition. Abbreviated definition: ∇ apo tricolpate pollen [*Platanus occidentalis* Linnaeus 1753].

Etymology: From Greek, *tri-* (three) and *kolpos* (a fold, lap, hollow, or bay, here an elongate longitudinal aperture in a pollen grain).

Reference Phylogeny: The primary reference phylogeny is Doyle (2005: Fig. 4). See also Doyle and Endress (2000: Fig. 4).

Composition: *Eudicotyledoneae* (this volume) and stem taxa with tricolpate pollen. So far, all well-reconstructed Early Cretaceous (Albian) fossil taxa with tricolpate pollen (e.g., Friis et al., 1988; Drinnan et al., 1991; Crane et al., 1993; Mendes et al., 2014; Friis et al., 2017) appear to be part of the crown group, *Eudicotyledoneae* (see Doyle and Endress, 2010), but some dispersed tricolpate pollen types may represent stem taxa that are part of *Tricolpatae* but not of *Eudicotyledoneae*.

Diagnostic Apomorphies: Tricolpate pollen (see Definition).

Synonyms: None (but see Comments).

Comments: Until we published the name *Tricolpatae* (Cantino et al., 2007), there was no 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 more inclusive clade originating with the evolution of tricolpate pollen. Here, as in our 2007 paper, we separate the meanings associated with these names by explicitly applying *Eudicotyledoneae* to the crown clade and *Tricolpatae* 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 eudicot crown. However, if only extant plants are considered, *Eudicotyledoneae* and *Tricolpatae* have the same composition.

The reference phylogenies and definition require comment. The pollen of *Illicium* and *Schisandraceae* was scored as tricolpate by Donoghue and Doyle (1989) and then inferred to have evolved separately from the grains of the tricolpate clade. However, these grains differ from standard tricolpate grains in that the colpi are located 60 degrees from those of the latter grains (Huynh, 1976; Doyle et al., 1990) and usually fused at the distal pole (syntricolpate). Accordingly, they were scored as representing a separate state by Doyle and 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

the clade *Tricolpatae*. These modifications include increases and decreases in the number of colpi (di-, tetra-, penta-, hexa-, and polycolpate forms). Compound-aperturate and porate 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). In other cases, apertures have been lost completely (inaperturate pollen). The resulting multitude of pollen forms all appear to be modifications of the original grains of *Tricolpatae*.

Literature Cited

- Cantino, P. D., J. A. Doyle, S. W. Graham, W. S. Judd, R. G. Olmstead, D. E. Soltis, P. S. Soltis, and M. J. Donoghue. 2007. Towards a phylogenetic nomenclature of *Tracheophyta*. *Taxon* 56:822–846 and E1–E44.
- Crane, P. R., K. R. Pedersen, E. M. Friis, and A. N. Drinnan. 1993. Early Cretaceous (early to middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of eastern North America. *Syst. Bot.* 18:328–344.
- Donoghue, M. J., and J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationship of *Hamamelidae*. Pp. 17–45 in *Evolution, Systematics and Fossil History of the Hamamelidae*, Vol. 1 (P. Crane and S. Blackmore, eds.). Clarendon Press, Oxford.
- Doyle, J. A. 2005. Early evolution of angiosperm pollen as inferred from molecular and morphological phylogenetic analyses. *Grana* 44:227–251.
- Doyle, J. A., and P. K. Endress. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *Int. J. Plant Sci.* 161:S121–S153.
- Doyle, J. A., and P. K. Endress. 2010. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: *Magnoliidae* and eudicots. *J. Syst. Evol.* 48:1–35.
- Doyle, J. A., C. L. Hotton, and J. V. Ward. 1990. Early Cretaceous tetrads, zonosulculate pollen, and *Winteraceae*. II. Cladistic analysis and implications. *Am. J. Bot.* 77:1558–1568.
- Drinnan, A. N., P. R. Crane, E. M. Friis, and K. R. Pedersen. 1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. *Am. J. Bot.* 78:153–176.
- Friis, E. M., P. R. Crane, and K. R. Pedersen. 1988. Reproductive structures of Cretaceous *Platanaceae*. *Biol. Skr. Dan. Vid. Selsk.* 31:1–55.
- Friis, E. M., K. R. Pedersen, and P. R. Crane. 2017. *Kenilanthus*, a new eudicot flower with tricolpate pollen from the Early Cretaceous (early-middle Albian) of eastern North America. *Grana* 56:161–173.
- Huynh, K.-L. 1976. L'arrangement du pollen du genre *Schisandra* (*Schisandraceae*) et sa signification phylogénique chez les Angiospermes. *Beitr. Biol. Pflanz.* 52:227–253.
- Mendes, M. M., G. W. Grimm, J. Pais, and E. M. Friis. 2014. Fossil *Kajanthus lusitanicus* gen. et sp. nov. from Portugal: floral evidence for Early Cretaceous *Lardizabalaceae* (*Ranunculales*, basal eudicot). *Grana* 53:283–301.

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Eudicotyledoneae M. J. Donoghue, J. A. Doyle, and P. D. Cantino in
P. D. Cantino et al. (2007): 835 [M. J. Donoghue,
J. A. Doyle, and P. D. Cantino], converted clade name

Registration Number: 250

Definition: The smallest crown clade containing *Ranunculus acris* Linnaeus 1753 (*Ranunculales*) and *Helianthus annuus* Linnaeus 1753 (*Asterales*). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Ranunculus acris* Linnaeus 1753 & *Helianthus annuus* Linnaeus).

Etymology: From the Greek *eu-* (true) and the name *Dicotyledoneae* (the name of a more inclusive taxon that is now understood to be paraphyletic). *Dicotyledoneae* is derived from the Greek *di-* (two) and *kotyledon* (seed leaf).

Reference Phylogeny: The primary reference phylogeny is Soltis et al. (2011: Figs. 1, 2). See also Doyle and Endress (2000: Fig. 4), Soltis et al. (2000: Figs. 1, 5), Hilu et al. (2003: Fig. 2), Soltis et al. (2003: Fig. 2), Kim et al. (2004: Fig. 4), Zeng et al., (2014: Fig. 3), and Sun et al. (2016: Fig. 2).

Composition: *Ranunculales* (sensu APG II, 2003) and its presumed sister clade, the latter including *Proteales* (*Proteaceae*, *Platanus*, and *Nelumbo*), *Sabiaceae*, *Trochodendraceae* (including *Tetracentron*), *Buxaceae* (including *Didymeles*), and *Gunneridae* (as defined in this volume).

Diagnostic Apomorphies: Members of *Eudicotyledoneae* are distinguished from other extant angiosperms by having pollen grains that are tricolpate or have aperture conditions that were derived from the tricolpate condition. 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 apomorphies of *Eudicotyledoneae* (Doyle and Endress, 2000: Fig. 4), but this inference is sensitive to outgroup relationships.

Synonyms: The informal names “eudicots” and “tricolpates” are approximate synonyms (see Comments).

Comments: Until we phylogenetically defined the name *Eudicotyledoneae* (Cantino et al., 2007), there was no scientific name for this crown clade, which has been referred to informally as either “eudicots” or “tricolpates.” It was originally recognized based on morphology by Dahlgren and Bremer (1985) and Donoghue and Doyle (1989), although only equivocally supported in the latter study, and subsequently strongly supported by molecular data (cited under Reference Phylogeny). This clade was originally referred to as the “tricolpates” (Donoghue and Doyle, 1989). Doyle and Hotton (1991) later coined the name “eudicots” (“true dicots”) to signify that this very large subset of “dicots” (dicotyledonous angiosperms—a paraphyletic group) forms a 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 and Endress, 2000; Hilu et al., 2003; APG II, 2003; Soltis et al., 2003, 2005; Soltis and Soltis, 2004; APG III, 2009; APG IV, 2016), as well as in textbooks (e.g., Judd et al., 2002, 2008, 2016; Soltis et al., 2005, 2018; Simpson, 2006).

Although cogent arguments have been made in favor of reverting to use of the name tricolpates (Judd and Olmstead, 2004), we chose *Eudicotyledoneae* for the crown clade owing to the widespread use of the name eudicots, which now extends well beyond the plant systematics literature. We have defined the name *Tricolpatae* (this volume and Cantino et al., 2007) for the more inclusive clade based on the apomorphy of tricolpate pollen. Pollen grains are well represented in the fossil record, and the appearance of tricolpate grains has taken on great importance in assessing the timing of angiosperm evolution (see Soltis et al., 2005). It is not clear that all early fossil tricolpate pollen grains represent members of *Eudicotyledoneae*, but they can be confidently assigned to *Tricolpatae*.

Cantino et al. (2007) defined the name *Eudicotyledoneae* using six internal specifiers (*Ranunculus trichophyllus* Villars 1786, *Platanus occidentalis* Linnaeus 1753, *Sabia swinhoei* W. B. Hemsley 1886, *Trochodendron aralioides* P. F. Siebold and Zuccarini 1838, *Buxus sempervirens* Linnaeus 1753, and *Helianthus annuus* Linnaeus 1753). Six specifiers were used because at the time measures of support for basal and near-basal eudicot relationships were variable, and in some cases low (e.g., see Soltis et al., 2000; Soltis et al., 2003; Hilu et al., 2003; and Kim et al., 2004). However, more recent analyses have provided strong support for the hypothesis that the members of *Ranunculales* form a clade that is sister to a clade containing the remaining eudicots (Soltis et al., 2011; Zeng et al., 2014; Sun et al., 2016). Consequently, a simpler minimum-crown-clade definition with only two specifiers can be used.

Literature Cited

- APG (Angiosperm Phylogeny Group). 1998. An ordinal classification for the families of flowering plants. *Ann. Mo. Bot. Gard.* 85:531–553.
- APG II (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141:399–436.
- APG III (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161:105–121.
- APG IV (Angiosperm Phylogeny Group). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181:1–20.
- Cantino, P. D., J. A. Doyle, S. W. Graham, W. S. Judd, R. G. Olmstead, D. E. Soltis, P. S. Soltis, and M. J. Donoghue. 2007. Towards a phylogenetic nomenclature of *Tracheophyta*. *Taxon* 56:822–846 and E1–E44.
- Dahlgren, R., and K. Bremer. 1985. Major clades of angiosperms. *Cladistics* 1:349–368.
- Donoghue, M. J., and J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of *Hamamelidae*. Pp. 17–45 in *Evolution, Systematics, and Fossil History of the Hamamelidae*, Vol. 1 (P. Crane and S. Blackmore, eds.). Clarendon Press, Oxford.
- Doyle, J. A. 2005. Early evolution of angiosperm pollen as inferred from molecular and morphological phylogenetic analyses. *Grana* 44:227–251.
- Doyle, J. A., and P. K. Endress. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *Int. J. Plant Sci.* 161:S121–S153.
- Doyle, J. A., and C. L. Hotton. 1991. Diversification of early angiosperm pollen in a cladistic context. Pp. 165–195 in *Pollen and Spores: Patterns of Diversification* (S. Blackmore and S. H. Barnes, eds.). Clarendon Press, Oxford.
- Hilu, K. W., T. Borsch, K. Müller, D. E. Soltis, P. S. Soltis, V. Savolainen, M. W. Chase, M. P. Powell, L. A. Alice, R. Evans, H. Sauquet, C. Neinhuis, T. A. B. Slot, J. G. Rohwer, C. S. Campbell, and L. W. Chatrou. 2003. Angiosperm phylogeny based on *matK* sequence information. *Am. J. Bot.* 90:1758–1776.

- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. *Plant Systematics—A Phylogenetic Approach*. 2nd edition. Sinauer Associates, Sunderland, MA.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2008. *Plant Systematics—A Phylogenetic Approach*. 3rd edition. Sinauer Associates, Sunderland, MA.
- Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2016. *Plant Systematics—A Phylogenetic Approach*. 4th edition. Sinauer Associates, Sunderland, MA.
- Judd, W. S., and R. G. Olmstead. 2004. A survey of tricolpate (eudicot) phylogenetic relationships. *Am. J. Bot.* 91:1627–1644.
- Kim, S., D. E. Soltis, P. S. Soltis, M. J. Zanis, and Y. Suh. 2004. Phylogenetic relationships among early-diverging eudicots based on four genes: were the eudicots ancestrally woody? *Mol. Phylogenet. Evol.* 31:16–30.
- Simpson, M. G. 2006. *Plant Systematics*. Elsevier, Amsterdam.
- Soltis, D. E., A. E. Senter, M. Zanis, S. Kim, J. D. Thompson, P. S. Soltis, L. P. Ronse De Craene, P. K. Endress, and J. S. Farris. 2003. *Gunnerales* are sister to other core eudicots: implications for the evolution of pentamery. *Am. J. Bot.* 90:461–470.
- Soltis, D. E., S. A. Smith, N. Cellinese, K. J. Wurdack, D. C. Tank, S. F. Brockington, N. F. Refulio-Rodriguez, J. B. Walker, M. J. Moore, B. S. Carlswald, C. D. Bell, M. Larvis, S. Crawley, C. Black, D. Diouf, Z. Xi, C. A. Rushworth, M. A. Gitzendanner, K. J. Sytsma, Y.-L. Qiu, K. H. Hilu, C. C. Davis, M. J. Sanderson, R. S. Beaman, R. G. Olmstead, W. S. Judd, M. J. Donoghue, and P. S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *Am. J. Bot.* 98:704–730.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot. J. Linn. Soc.* 133:381–461.
- Soltis, D. E., P. S. Soltis, P. K. Endress, and M. W. Chase. 2005. *Phylogeny and Evolution of Angiosperms*. Sinauer Associates, Sunderland, MA.
- Soltis, D. E., P. S. Soltis, P. Endress, M. Chase, S. Manchester, W. Judd, L. Majure, and E. Mavrodiev. 2018. *Phylogeny and Evolution of the Angiosperms: Revised and Updated Edition*. University of Chicago Press, Chicago, IL.
- Soltis, P. S., and D. E. Soltis. 2004. The origin and diversification of angiosperms. *Am. J. Bot.* 91:1614–1626.
- Sun, Y., M. J. Moore, S. Zhang, P. S. Soltis, D. E. Soltis, T. Zhao, A. Meng, X. Li, J. Li, and H. Wang. 2016. Phylogenomic and structural analyses of 18 complete plastomes across nearly all families of early-diverging eudicots, including an angiosperm-wide analysis of IR gene content evolution. *Mol. Phylogenet. Evol.* 96:93–101.
- Zeng, L., Q. Zhang, R. Sun, H. Kong, N. Zhang, and H. Ma. 2014. Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. *Nat. Commun.* 5:4956.

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