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Flowering plants (Magnoliophyta)

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Abstract

Flowering plants (Magnoliophyta; angiosperms) are the predominant plants in modern terrestrial ecosystems. They include 270,000 known species distributed in eight major lineages. Amborellales, Nymphaeales, and Austrobaileyales are the earliest branches. A clade that includes Chloranthales and magnoliids, and another joining monocots, Ceratophyllales and eudicots form the core angiosperms. The molecular timetree places the origin of angiosperms at the onset of the middle Jurassic (175 million years ago, Ma) and its initial diversification during the middle Jurassic (167–159 Ma). Core angiosperms originated in the late Jurassic (150 Ma) and differentiated into five lineages by the latest Jurassic (148–146 Ma).

Flowering plants (Magnoliophyta, angiosperms) are among the most successful organisms in the history of life. Not only do they encompass an exceptionally vast morphological and phylogenetic diversity, but also they are the major determinants of ecological function and biotic composition in modern terrestrial ecosystems (Fig. 1). Angiosperms constitute a monophyletic group very well supported by molecular data and by a large number of unique traits. These traits include, for example, apical meristems with a two-layered tunica-carpus construction, circular bordered pits lacking margo and torus, and paracytic stomata. Angiosperms share numerous unique reproductive attributes, including the aggregation of pollen- and ovule-producing organs into structurally and functionally integrated units, that is, flowers, a bithecal and tetrasporangiate anther, a carpel enclosing the ovules, two integuments surrounding each ovule, a double fertilization process that results in embryo and endosperm, and several whole genome duplications. Concerted efforts among the international botanical community have led to the recognition of

the major clades within angiosperms and to an understanding of their relationships at all phylogenetic levels. Although a few families and genera remain to be phylogenetically placed, and particular regions of the angiosperm tree have for a long-time defied resolution, a solid understanding of the phylogenetic affinity of the majority of living angiosperms and of relationships among clades has been achieved. This phylogenetic knowledge has been translated into a classification that reflects current understanding of angiosperm evolutionary relationships (1). In this classification, major clades within the angiosperms are treated as orders, and informally named supraordinal clades are also recognized (1, 2).

Angiosperms include approximately 270,000 known species distributed in 457 families (2), but the real number of species may exceed 400,000 (3). Angiosperms are distributed in eight major lineages. Amborellales, Nymphaeales, and Austrobaileyales are the three earliest branches, which encompass only a minute proportion of their standing species richness (<0.1%). The great majority of living angiosperms belong to a clade referred to as core angiosperms or Mesangiospermae (4), which includes Chloranthales, magnoliids, monocotyledons,



Fig. 1 A tulip poplar (*Liriodendron tulipifera*). Credit: S. Magallón.

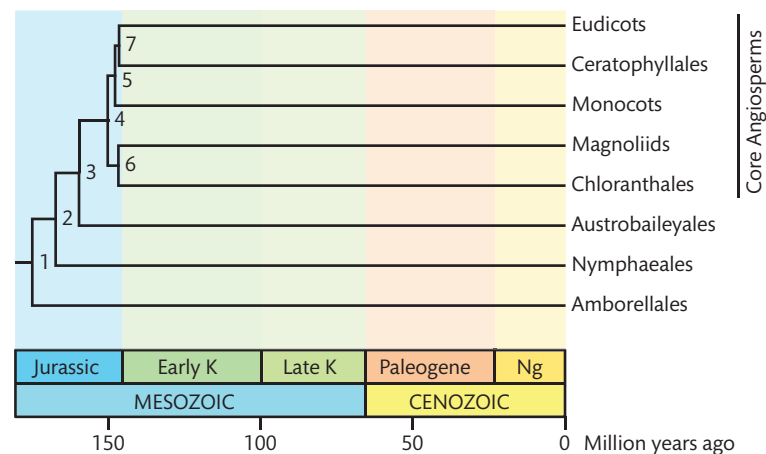


Fig. 2 A timetree of flowering plants. Divergence times are shown in Table 1. Abbreviations: K (Cretaceous) and Ng (Neogene).

Ceratophyllales, and eudicots, and are characterized by conduplicate carpels, an eight-nucleate embryo sac, and triploid endosperm (2). Chloranthales (one family, 75 species) are characterized by leaves with a distinctive kind of marginal teeth and small monosymmetric unisexual flowers with one apical anatropous ovule per carpel (2). Ceratophyllales (one family, six species) are aquatic herbs lacking roots, vessels, stomata, and endosperm (2). Magnoliids (19 families, 10,000 species) have entire leaf margins, hypostase, nucellar cap, and raphal bundles at the chalaza (2). Monocotyledons (monocots; 93 families, 62,000 species) have many distinctive characters including a single cotyledon, parallel-veined leaves not differentiated into petiole and lamina, scattered vascular bundles in stems, adventitious root system, and sympodial growth (2, 5). Eudicots (or tricolpates; 336 families, 198,000 species) are distinguished by a single but unequivocal morphological shared-derived character, the presence of tricolpate pollen grains (pollen with three longitudinal apertures) or derived from this condition (2, 6). Magnoliids, monocots, and eudicots comprise 3.1%, 22.8%, and 74.0% of living angiosperm species richness, respectively.

Eudicots encompass a vast phylogenetic, morphological, and ecological diversity. The deepest split within eudicots separates Ranunculales (seven families, 4450 species) from a lineage that includes the core eudicot clade (321 families, 191,000 species) that contains over 90% of eudicot species richness. A distinctive five-parted floral structural organization with a bipartite perianth consisting of a calyx and corolla is common among core eudicots (pentamerous eudicots); however, this

floral structure does not characterize core eudicots as a whole, and it is not clear if it evolved once or several times within the clade. Core eudicots are distributed in nine major lineages: Gunnerales (two families, 52 species); Berberidopsidales (two families, four species); Vitales (one family, 850 species); Dilleniales (one family, 300 species); Santalales (eight families, 2300 species); Saxifragales (16 families, 2400 species); Caryophyllales (33 families, 11,400 species); rosids (147 families, 80,000 species); and asterids (111 families, 95,000 species). Within rosids, species diversity is concentrated in two clades: the fabids (78 families, 51,000 species) and the malvids (39 families, 16,500 species). Asterids include four major clades: Cornales (seven families, 600 species), Ericales (25 families, 11,800 species), lamiids (39 families, 48,000 species), and campanulids (38 families, 34,000 species). Here, I review the phylogenetic relationships and divergence times of the eight major lineages of angiosperms.

Current understanding of angiosperm phylogeny has been reviewed in several recent works (5–7). A number of studies based on different molecular data, taxon sampling, and methodological approaches congruently identified Amborellales, Nymphaeales, and Austrobaileyales as the earliest divergent lineages within angiosperms (8–10). The identification of these three lineages as the most ancient among living angiosperms was corroborated in numerous subsequent studies (11–16), but questions remained regarding the composition of the earliest branch. According to some studies, the earliest branch consists only of Amborellales (8–10, 13–16), but in others, it includes Amborellales and Nymphaeales

Table 1. Divergence times (Ma) and confidence/credibility intervals among flowering plants.

| Timetree | | Estimates | | | | | |
|----------|-------|-----------|---------|-----------|---------|-----------|---------|
| Node | Time | Ref. (23) | | Ref. (28) | | Ref. (30) | |
| | | Time | CI | Time | CI | Time | CI |
| 1 | 174.9 | 169.7 | 170–169 | 170 | 182–158 | 185.1 | 185–184 |
| 2 | 167.3 | 163.4 | 164–163 | 164 | 175–153 | 174.6 | 175–174 |
| 3 | 159.5 | 154.8 | 155–154 | 158 | 169–147 | 165.6 | 166–165 |
| 4 | 150.1 | 143.9 | 144–143 | 153.7 | 164–143 | 152.7 | 157–148 |
| 5 | 147.8 | 143.1 | 143–143 | 147.7 | 156–139 | 152.7 | 157–148 |
| 6 | 146.6 | 140.4 | 141–140 | 149.3 | 159–140 | 150.1 | 156–144 |
| 7 | 146.3 | 141.4 | 141–141 | 149.7 | 159–140 | 147.9 | 156–140 |

Note: Node times in the timetree represent the mean of time estimates from different studies. Estimates from ref. (23) are the mean ages and confidence intervals of three different constraint implementations for major angiosperm lineages. Estimates from ref. (28) are the mean divergence times and confidence intervals derived from ACCTRAN, DELTRAN, and maximum likelihood-estimated branch lengths of major angiosperm lineages. Estimates from ref. (30) are the mean divergence times and confidence intervals from different gene and codon position partitions of major angiosperm lineages.

(8, 11, 16–18). The core angiosperm clade and its five lineages have been consistently recognized in phylogenetic studies (8–11, 13–16, 19), but the relationships among Chloranthales, Ceratophyllales, monocots, magnoliids, and eudicots have been unstable. Some studies have shown Chloranthales as closely related to monocots, and Ceratophyllales to eudicots (9, 15), but others show the opposite relationship (10, 14, 20). Whereas monocots and eudicots have each been almost ubiquitously supported solidly as a monophyletic group (9, 10, 14, 15, 19, 21, 22), the recognition of a well-supported magnoliid clade has depended on taxonomic sampling (10, 14, 15, 20). Nevertheless, recent studies seemingly provide enhanced resolution to these lingering questions (23, 24). There is now more solid evidence supporting Amborellales as the single member of the earliest branch within angiosperms, and within core angiosperms; Chloranthales and magnoliids are closest to each other; and monocots are most closely related to a clade formed by Ceratophyllales and eudicots (23, 24; Fig. 2).

Whereas monocots have traditionally been proposed as monophyletic and confirmed as such by molecular data (7), the eudicot clade was recognized only after explicit phylogenetic investigation (21). The eudicot clade receives very strong and uncontradicted support in molecular phylogenetic analyses (9, 10, 12, 14, 15, 20, 22), in addition to being distinguished in analyses including morphological data (19, 21) by the unequivocal presence of tricolpate pollen grains (or derived from

this condition). However, many of the lineages within eudicots have been recognized on the basis of molecular data alone. Some eudicot lineages largely correspond to traditional taxonomic groups, but many others represent unexpected associations from the standpoint of traditional taxonomy. Several eudicot clades share particular morphological or chemical attributes, some of which are cryptic, many have been identified only after clade recognition on the basis of molecular data, and the level of universality which some morphological attributes characterize is not well understood. Still, distinctive morphological characters for some core eudicot clades remain to be identified.

Ranunculales is the closest relative of all other eudicots (9, 10, 12, 19, 22–25). The lineage opposite to Ranunculales contains an early grade of depauperate branches, and the core eudicot (pentamerous eudicot) clade. The nine major lineages within core eudicots are well supported in molecular phylogenies, but, possibly except for the position of Gunnerales as closest relative of all other core eudicots (25, 26), phylogenetic relationships among them are unstable (9, 12, 15, 22). The nine core eudicot lineages differ vastly in the number of species each encompasses, for example, Gunnerales and Berberidopsidales each includes fewer than 60 species, whereas the rosoid and asterid clades each includes more species than the monocots. The rosoid clade is strongly supported by molecular data, but morphological distinctive characters are elusive. It encompasses two large subclades, the fabids

and the malvids, and two or three smaller independent lineages, but relationships among them are unstable (9, 12, 15, 17, 22). The asterid clade receives strong support in molecular phylogenies and largely corresponds to groups that have been associated on the basis of morphological syndromes, most particularly flowers with fused petals (sympetaly), and particular chemical pathways. In many phylogenies, Cornales is the closest relative of all other asterids, and Ericales is the closest relative of a core asterid clade, which is characterized by particular chemical pathways and a fixed floral structural plan onto which considerable architectural diversity is superimposed. Core asterids consist of two monophyletic clades, the lamiids, among which sympetaly usually arises from a meristematic ring, and the campanulids, in which sympetaly usually arises from the fusion of ontogenetically independent floral primordia (27).

Few studies have provided molecular estimates of age across the angiosperms. The most comprehensive study published so far (28; Table 1) is based on a phylogeny for over 500 angiosperm species corresponding to one of the most parsimonious trees obtained in a previous study (9). Branch lengths were obtained by optimizing the sequences of *rbcl*, *atpB*, and 18S nrDNA on the branches of the tree using parsimony with ACCTRAN and DELTRAN, and using maximum likelihood with a HKY85 model. Age estimates were obtained with a nonparametric rate smoothing method (29) with a single calibration of 84 Ma assigned to the divergence of Fagales and Cucurbitales, a node nested highly within the core eudicots (fabids, rosids; Table 1). The age of angiosperms was estimated as middle Jurassic (170 ± 12.2 Ma); the origin of core angiosperms as late Jurassic (153.7 ± 10.7 Ma); and magnoliids, monocots, and eudicots as late Jurassic (147.7 ± 8.8 , 147.7 ± 8.8 , and 149.7 ± 9.5 Ma, respectively).

An investigation focused on the age of angiosperms included 62 taxa representing all living groups of vascular plants, including seven of the eight major angiosperm lineages (30). The data were the nucleotide sequences of four highly conserved protein-coding chloroplast genes, *atpB*, *psaA*, *psbB*, and *rbcl*, partitioned by gene and by codon position (first plus second, and third). Phylogenetic relationships were estimated with Bayesian analysis, and branch lengths were subsequently optimized with maximum likelihood. Divergence times were estimated with the semiparametric penalized likelihood method (31), by calibrating the tree with the age of the oldest vascular plant fossils at 419 Ma, and using 20 additional fossil ages across vascular plants as auxiliaries. Dates were

obtained for each gene partitioned by codon position, for the combined genes partitioned by codon position, and for the complete, unpartitioned data. Averaged estimates of age indicate that angiosperms originated in the early Jurassic (185.1 ± 0.2 Ma), and core angiosperms in the late Jurassic (152.7 ± 4.5 Ma). The times of divergence of monocots (152.7 ± 4.5 Ma), magnoliids (152.2 ± 3.7 Ma), and eudicots (147.9 ± 8.0 Ma) were also estimated as late Jurassic (Table 1).

A recent study was based on 61 chloroplast genes for 45 taxa representing the major angiosperm lineages and outgroups (23). Divergence times were based on a tree derived from maximum likelihood, and estimated with penalized likelihood by calibrating the tree at the seed plant node, but implementing three alternative constraint schemes. In the first one, only the seed plant calibration was imposed, and in the second and the third, the divergence and the diversification of eudicots were each assigned a minimum age of 125 Ma, respectively. On average, the origin of angiosperms was dated as middle Jurassic (169.7 ± 0.1 Ma), and the origin of core angiosperms as early Cretaceous (143.9 ± 0.1 Ma). Magnoliids (140.3 ± 0.1 Ma), monocots (143.1 ± 0.1 Ma), and eudicots (141.4 ± 0.1 Ma) were estimated to have diverged in the early Cretaceous (Table 1).

Other studies have dated divergences within major angiosperm clades, for example the monocots (32), the asterids (33), and the eudicots (34). Bell *et al.* (35) used penalized likelihood and a Bayesian relaxed molecular clock method (36) with different data partitions, calibration strategies, and temporal constraints on nodes to date divergences within angiosperms. Angiosperm age varied between early Jurassic (198 Ma) and early Cretaceous (Berriasian–Valanginian; 140 Ma), and eudicot age between Barremian–Aptian (early Cretaceous; 125 Ma) and Cenomanian–Turonian (late Cretaceous; 94 Ma), which is younger than many reliable eudicot fossils. Other ages published in this study are not directly comparable to nodes in Fig. 2.

The early angiosperm fossil record consists of an initially low, but rapidly increasing morphological and phylogenetic diversity and abundance, seemingly reflecting the evolutionary diversification of a newly established biological lineage. There is general congruence between the sequence of appearance of angiosperm lineages in the fossil record and the sequence of phylogenetic branching in molecular-based phylogenetic trees. The oldest fossils unequivocally identified as angiosperms are pollen grains from Hauterivian (Lower Cretaceous) sediments (37). In slightly younger sediments (late Barremian–early

Aptian) several major angiosperm lineages, including Nymphaeales, Chloranthales, magnoliids, monocots, and eudicots, are reliably documented (37). The sequence of phylogenetic branching and the fossil dates together imply that the eight major angiosperm lineages had differentiated by the Barremian–Aptian, apparently as the result of a rapid evolutionary radiation that took place during the Lower Cretaceous. Nevertheless, molecular estimates of angiosperm age, and of timing of divergence of major angiosperm lineages, suggest a radically different view of early angiosperm evolution by providing ages that substantially predate their earliest fossils, increasingly so in deeper nodes (23, 28, 30; Fig. 2).

The timetree indicates that the unique traits that characterize living angiosperms had originated by the beginning of the middle Jurassic (175 Ma). Angiosperms underwent a gradual initial diversification that extended through the middle Jurassic and the onset of the late Jurassic (167–159 Ma). Core angiosperms originated in the late Jurassic (150 Ma), and soon after underwent a rapid phylogenetic diversification that gave rise to Chloranthales, magnoliids, monocots, Ceratophyllales, and eudicots during the final part of the late Jurassic (148–146 Ma).

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