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the **TIMETREE** *of* **LIFE**

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Magnoliids

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Abstract

With ~8000 species in 20 families, magnoliids are one of the most important groups of basal living angiosperms. Most DNA-based phylogenetic analyses show that magnoliids form a strongly supported clade and, although debated by some, show that the four orders form two closely related groups, Magnoliales + Laurales and Piperales + Canellales. Monophyly of each order is well supported in molecular studies and corroborated by numerous morphological, anatomical, and chemical characters. Few studies have examined divergence times in this group, but the first divergence in this clade has been estimated to be 149–137 million years ago (Ma).

The magnoliid clade attaches to one of the basal-most nodes in the angiosperm tree and comprises four orders, Magnoliales, Laurales, Piperales, Canellales, and a total of ca. 8000 species grouped in 20 families, of which Piperaceae (black pepper family; 3000 species), Lauraceae (laurel family; 2500 species), and Annonaceae (custard-apple family; 1200 species) are by far the largest (1). Many species in this group are widely cultivated as ornamentals (e.g., *Magnolia*, Magnoliaceae (Fig. 1); *Peperomia*, Piperaceae) for spices and flavorings such as nutmeg (*Myristica*, Myristicaceae), cinnamon (*Cinnamomum*, Lauraceae), and bay (*Laurus*, Lauraceae), and for their fruit (e.g., avocado; *Persea*, Lauraceae) (2). Representatives of this clade have various habits ranging from trees and shrubs to lianas and herb, and are widespread in tropical and temperate regions of the world (3). Here, relationships and divergence times of the four orders and 20 families forming the magnoliids are reviewed.

The monophyly of magnoliid clade has been generally well supported in several phylogenetic analyses (4–9) and is recognized in the classification of the Angiosperm Phylogeny Group (10). Studies of relationships within this group have generally identified two closely related clades,

Magnoliales + Laurales and Piperales + Canellales (4, 7, 11, 12). Although relationships between orders are generally well understood, some studies presented results conflicting with this view. For example, an analysis based on morphological data (13) found that Magnoliales + Laurales were closest relatives of Canellales, with Piperales not related to the other three orders, but instead part of a large unresolved clade with monocots, Nymphaeaceae, and several lineages of eudicots. A three-gene analysis of angiosperm relationships (9) showed that Piperales is the first diverging lineage in magnoliids followed by Laurales which is the closest relative of Magnoliales + Canellales. A more recent study using the same data set but analyzed under a Bayesian framework showed the same relationships (5). These contradictory results had only little or no support.

Morphological characters defining the magnoliids and relationships between the four orders forming this group are sparse and difficult to characterize accurately. However, morphological traits characterizing each of the four orders are numerous (1). Magnoliales is well defined by anatomical (e.g., stratified phloem), palynological (e.g., continuous tectum), and seed (e.g., multiplicative testa) characters. Similarly, Canellales shares



Fig. 1 *Magnolia* (*Magnolia sprengeri* var. *diva*) from China, in cultivation at the Royal Botanic Gardens in Kew. Credit: F. Forest.

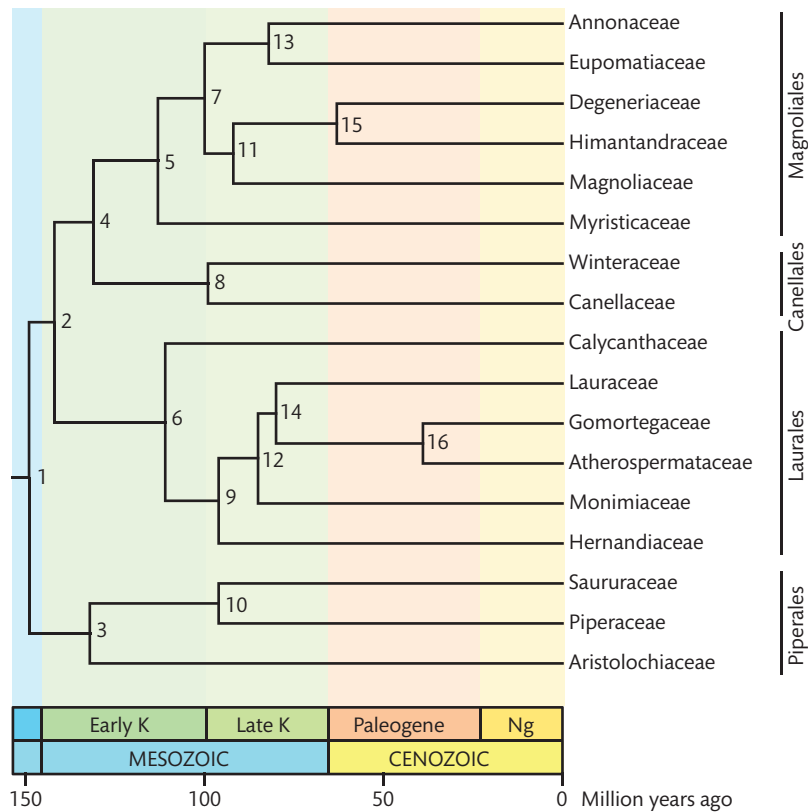


Fig. 2 A timetree of magnoliids. Divergence times are shown in Table 1. *Abbreviations:* K (Cretaceous) and Ng (Neogene).

pollen, seed (e.g., presence of palisade exotesta), leaf venation, and anatomical (e.g., nodal structure) characters, whereas Piperales is defined by distichous phyllotaxis, a single prophyll and oil cells. Laurales is defined by an array of morphological features, but it is best-characterized by its perigynous flower with a gynoeceum generally nested in a fleshy receptacle (1).

The most recent and extensive attempt at estimating divergence times within magnoliids was part of a wider survey of angiosperm diversification times (14). This dating exercise was done using one of the most parsimonious trees found in the analysis of Soltis *et al.* (9). This phylogenetic tree presents unsupported relationships between magnoliid orders as well as contradicting other more recent phylogenetic studies. In light of this evidence, existing divergence estimates between orders within this group should be considered tentative until more data are made available. Laurales and some members of Magnoliales have been studied in more detail (15, 16).

Magnoliids diverged from their closest relatives 145–139 Ma and started to diverge soon thereafter, between

149 and 137 Ma, at the end of the Jurassic (Fig. 2). These estimates are slightly older than the earliest known fossil remains for this group, but considering the incompleteness of the fossil record, these molecular estimates lie in a plausible time interval. The oldest fossils of magnoliids are from the early Cretaceous (late Barremian; 127–121 Ma), more specifically from the Family Winteraceae (17, 18). Magnoliales diversification started 113–108 Ma, which tallies with the earliest remains for this order. Likewise, the first lineage split in Laurales took place 114–108 Ma, in accordance with the oldest remains from the fossil record. On the other hand, the molecular estimates obtained for Piperales (133–122 Ma) are much older than what is inferred from the fossil record (Turonian; 95.5–89 Ma), whereas the fossil record supports an older age for Canellales (Winteraceae fossils) than indicated by the molecular estimates (105–99 Ma). However, these Canellales fossils could be better placed along the lineage leading to living Canellales rather than among the group of extant taxa, in which case the molecular estimates (134–127 Ma) would broadly agree with the fossil remains for this group. The fossil record for magnoliids

Table 1. Divergence times (Ma) and confidence/credibility intervals (CI) among magnoliids.

Timetree		Estimates		
Node	Time	Ref. (14)(a) Time (CI)	Ref. (14)(b) Time	Ref. (14)(c) Time
1	149	149 (155–143)	147	137
2	142	142 (148–136)	141	133
3	132	132 (138–126)	133	122
4	131	131 (137–125)	134	127
5	113	113 (119–107)	113	108
6	111	111 (118–104)	114	108
7	100	100 (107–93)	101	97
8	99	99 (105–99)	105	99
9	96	96 (103–89)	100	90
10	96	96 (102–90)	89	95
11	92	92 (99–85)	95	93
12	85	85 (92–78)	78	91
13	82	82 (88–76)	91	86
14	80	80 (86–74)	74	87
15	63	63 (70–56)	73	71
16	39	39 (44–34)	50	51

Note: Node times in the timetree are based on branch lengths computed using ACCTRAN optimization in maximum parsimony (a). Also presented are estimates from ref. (14) that are based on DELTRAN optimization in maximum parsimony (b) and maximum likelihood method (c).

is discussed in more details elsewhere (15, 19–22); see also (18).

Few additional studies have proposed divergence times for clades within magnoliids. Bell and colleagues (6) obtained an assortment of estimates for the split of Laurales and Magnoliales using a Bayesian relaxed clock and several combinations of fossil calibration points. Based on a four-gene combined analysis, their estimates range from 84.0 ± 19.1 to 114.9 ± 2.0 Ma for the first split in the group. Magnoliales and Laurales are not closest relatives in the tree used by Wikström *et al.* (14). In summary, the timetree for magnoliids broadly agrees with the fossil

record and highlights the long history of this important group of morphologically archaic angiosperms.

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