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

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Eudicots

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Abstract

The eudicots comprise about three-quarters of all angiosperm species. They are characterized by the unique presence of tricolpate pollen grains, or derived types thereof. Palynological records indicate that eudicots first evolved in the Barremian and early Aptian (121 million years ago, Ma). Molecular age estimates indicate a slightly older emergence for eudicots (147–131 Ma) and suggest that the main lineages in this group evolved rapidly after the first diversification event (all were present around 100–90 Ma). Despite some discrepancies between molecular and fossil age estimates, both concord in supporting a rapid radiation in the early history of eudicots.

Much attention and effort have been devoted to the understanding of the early evolution of eudicots, a group comprising a large proportion of the angiosperm total species number (~75%, 1). They are characterized by the presence of tricolpate pollen grains (or derived from this type), a type of pollen grain with three pores set in apertures called colpi (Fig. 1). Eudicot taxa at the basal nodes of the tree consist of several small to medium-sized lineages in which the two most important groups of angiosperms, rosids and asterids, are nested. These two groups account for almost two-thirds of all angiosperm species (~88% of eudicot species; 1). In this chapter, relationships and divergence time estimates of early-diverging eudicots as well as the smaller lineages of core eudicots are reviewed. The rosid and asterid groups are discussed elsewhere in this volume.

Ranunculales is the first diverging group in eudicots, followed successively by Proteales, Sabiaceae, Buxaceae + Didymelaceae, and Trochodendraceae (2–6). Relationships in this sequence are not well supported, and other studies have proposed slightly different topologies (7–9). The remainder of the eudicots form a group principally characterized by strong support in various molecular phylogenetic analyses and has been labeled “core eudicots” (10).

Ranunculales comprise seven families and about 3350 species, of which the most species-rich are Ranunculaceae (~1500 species), Papaveraceae (665 species; now including Fumariaceae), Berberidaceae (630 species), and Menispermaceae (520 species). Berberidaceae and Ranunculaceae are cultivated as ornamentals (e.g., *Berberis*, *Aquilegia*) although in the latter some species are also weeds (e.g., some *Ranunculus* species). Menispermaceae consists of many species used as arrow poison (e.g., *Abuta*), contraceptives (e.g., *Cissampelos*), sweeteners (e.g., *Dioscoreophyllum*), and ornamentals (e.g., *Cocculus*). Papaveraceae comprises the genus *Papaver* from which opium is produced and many species cultivated for their horticultural value (e.g., *Dicentra*, *Sanguinaria*) (11).

In molecular-based studies, Ranunculales have consistently formed a monophyletic (inclusive) group, usually with strong support (2–8, 12, 13). It appears that floral morphology offers no clear character uniting Ranunculales, but several morphological, chemical, and anatomical features characterize this group (10). Within Ranunculales, Papaveraceae form the earliest diverging group followed by Eupteleaceae. The remaining families form two closely related groups, the first one comprising Lardizabalaceae and Circaeasteraceae and the second



Fig. 1 Lotus tricolpate pollen grains (*Nelumbo*) cultivated at Royal Botanic Gardens, Kew. Credit: H. Banks.

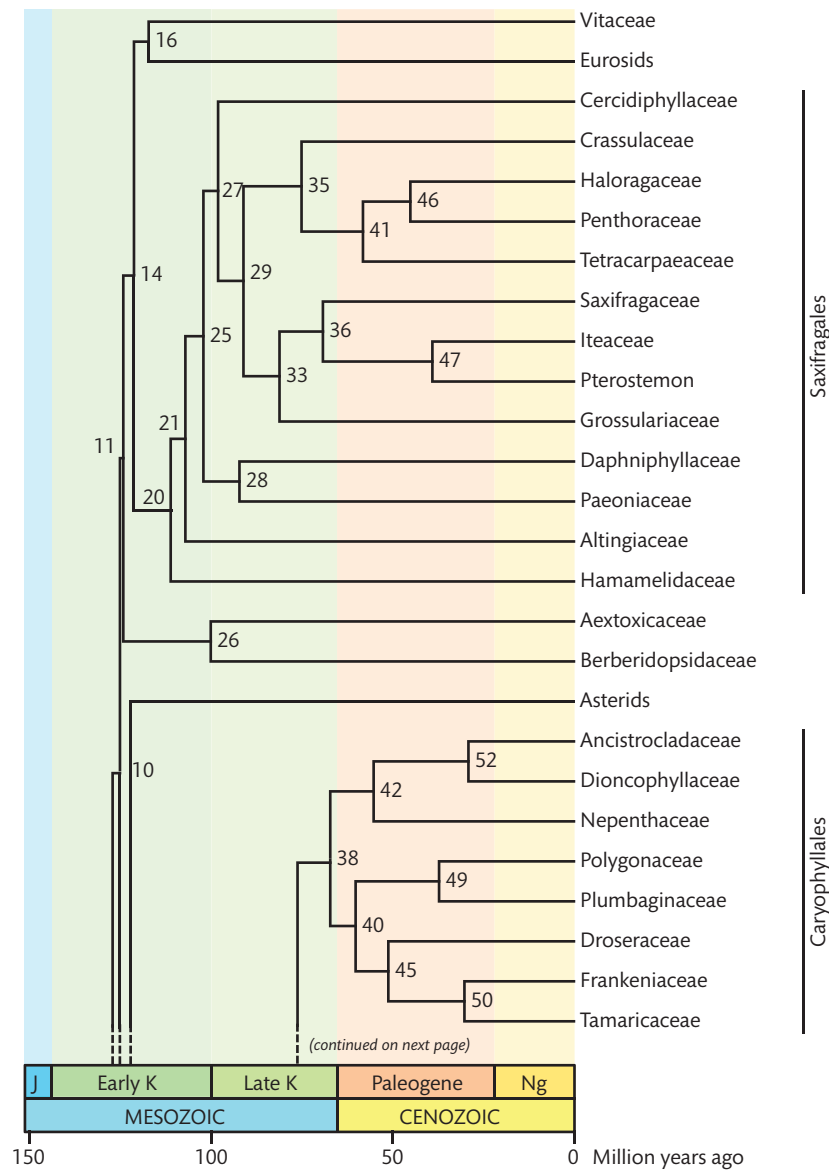


Fig. 2 Continues

Ranunculaceae, Berberidaceae, and Menispermaceae (3, 4, 7).

Wikström and colleagues based on an analysis using a phylogenetic tree reconstructed from *rbcL* sequences, the nonparametric rate smoothing method (14), and a single calibration point obtained estimates ranging from 140 Ma to 126 Ma for the first lineage split within Ranunculales (15), values somewhat older than those obtained by Anderson *et al.* (16) using multiple calibration points (121–114 Ma; Table 1). These divergence times are older than estimates made from the fossil record.

The fossil record of Ranunculales is not extensive, but the oldest unequivocal remains of this group are fruits of Menispermaceae from the Maastrichtian (68.1 Ma). However, some fossils from the early Cretaceous could also be assigned to Ranunculales (1, 17) and would be more in line with the molecular estimates. The timetree indicates that the early diversifications in Ranunculales occurred at a slower pace than deeper nodes in the remainder of the eudicots (Fig. 2).

Among early-diverging eudicots, Proteales containing Nelumbonaceae (lotus family), Proteaceae (protea

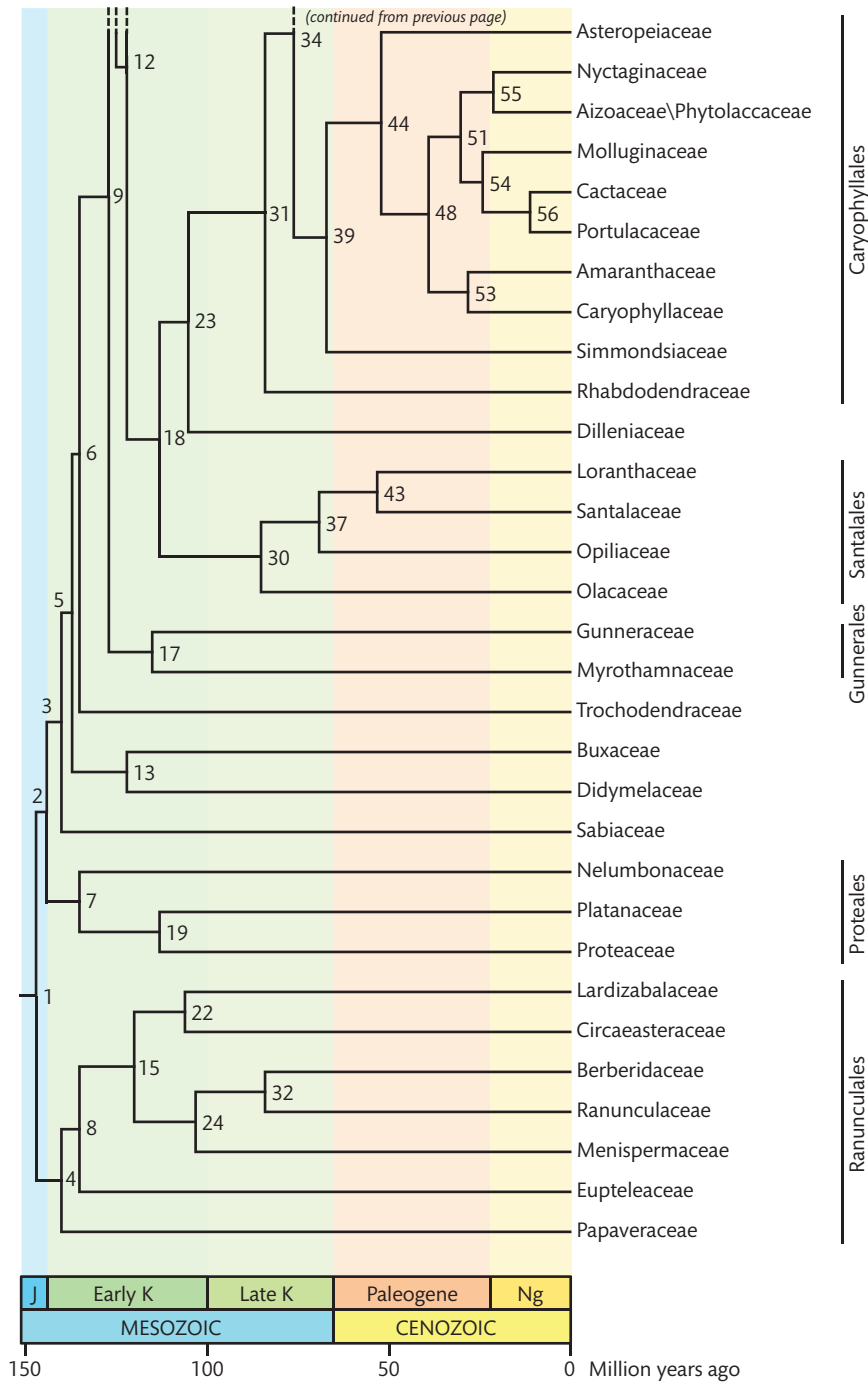


Fig. 2 A timetree of eudicots. Divergence times are shown in Table 1. Abbreviations: J (Jurassic), Ng (Neogene), and K (Cretaceous).

family), and Platanaceae (plane family) is the most unexpected grouping because of the highly dissimilar morphologies of the three families. Proteaceae is a relatively large family (~1050 species) of evergreen trees and shrubs found mainly in the Southern Hemisphere,

whereas Platanaceae comprises a single genus (*Platanus*, plane tree) of eight species of deciduous trees from the Northern Hemisphere. Nelumbonaceae also consists of a single genus (*Nelumbo*, lotus) of two widespread species of aquatic herbs (11, 18). Sabiaceae is a small family of

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

Timetree		Estimates					
Node (Fig. 2)	Time (Ma)	Ref. (15)(a)		Ref. (15)(b)	Ref. (15)(c)	Ref. (16)(a)	Ref. (16)(b)
		Time	CI	Time	Time	Time	Time
1	147.0	147	153-141	144	131	120	122
2	144.0	144	150-138	141	130	119	121
3	140.0	140	145-135	140	128	118	122
4	140.0	140	146-134	138	126	114	121
5	137.0	137	142-132	136	124	117	121
6	135.0	135	140-130	134	123	116	120
7	135.0	135	141-129	137	125	115	121
8	135.0	135	141-129	132	122	111	120
9	127.0	127	132-122	127	116	115	112
10	125.0	125	130-120	123	114	-	-
11	124.0	124	129-119	122	114	-	-
12	122.0	122	127-117	121	112	112	112
13	122.0	122	128-116	124	113	99	118
14	121.0	121	125-117	119	111	108	108
15	120.0	120	126-114	120	111	-	-
16	117.0	117	121-113	115	108	112	112
17	115.0	115	120-110	118	108	90	55
18	113.0	113	117-109	118	111	113	115
19	113.0	113	120-106	117	108	110	119
20	111.0	111	116-106	92	100	102	102
21	107.0	107	112-102	87	98	-	-
22	106.0	106	112-100	115	108	107	116
23	105.0	105	109-101	111	104	114	116
24	103.0	103	109-97	113	103	105	116
25	102.0	102	107-97	85	96	-	-
26	100.0	100	107-93	98	90	-	-
27	98.0	98	103-93	81	92	-	-
28	92.0	92	97-87	78	88	-	-
29	91.0	91	96-86	78	88	-	-
30	85.0	85	90-80	97	87	101	108
31	84.0	84	88-80	90	83	99	102
32	84.0	84	90-78	100	87	90	104
33	81.0	81	86-76	73	81	-	-
34	76.0	76	80-72	82	76	-	-
35	75.0	75	80-70	69	77	-	-
36	69.0	69	74-64	67	76	-	-
37	69.0	69	74-64	80	76	-	-
38	67.0	67	71-63	75	69	-	-
39	67.0	67	71-63	72	69	-	-
40	60.0	60	64-56	71	65	-	-

Table 1. *Continued*

Timetree		Estimates					
Node (Fig. 2)	Time (Ma)	Ref. (15)(a)		Ref. (15)(b)	Ref. (15)(c)	Ref. (16)(a)	Ref. (16)(b)
		Time	CI	Time	Time	Time	Time
41	58.0	58	62–54	53	58	-	-
42	55.0	55	59–51	67	62	-	-
43	53.0	53	57–49	67	65	-	-
44	52.0	52	56–48	61	58	-	-
45	51.0	51	54–48	66	62	-	-
46	45.0	45	49–41	43	47	-	-
47	39.0	39	44–34	43	46	-	-
48	39.0	39	42–36	47	46	-	-
49	37.0	37	40–34	52	42	-	-
50	30.0	30	33–27	43	40	-	-
51	30.0	30	33–27	40	39	-	-
52	29.0	29	32–26	47	38	-	-
53	28.0	28	30–26	40	38	-	-
54	24.0	24	26–22	35	34	-	-
55	21.0	21	23–19	28	26	-	-
56	11.0	11	13–9	18	18	-	-

Note: Node times in the timetree are based on branch lengths computed using (a) ACCTRAN optimization in maximum parsimony (a) in ref. (15). Other estimates from ref. (15) are obtained using (b) DELTRAN optimization in maximum parsimony and (c) maximum likelihood method. Time estimates from ref. (16) are obtained using (a) the penalized likelihood method (36) and (b) the nonparametric rate smoothing method (14).

~100 species of trees, shrubs, and lianas found in South East Asia and tropical South America. Buxaceae is a widespread family of ~100 species (mainly shrubs) of which the best-known member is the boxwood because of its value as ornamental and timber. Buxaceae is closely related to Didymelaceae, a family of two species of evergreen trees endemic to Madagascar. Trochodendraceae was a small family of only two genera and two species of evergreen trees found in Asia, which was considered as two distinct families in earlier treatments (e.g., 19).

The Order Gunnerales is the first diverging lineage in the core eudicots and comprises the Families Gunneraceae (one genus of ~40 species of herbs found mainly in the Southern Hemisphere) and Myrothamnaceae (one genus of two species of small shrubs found in southern Africa and Madagascar). First identified in earlier studies but with weak support, the close relationship of these two families was later shown to be strongly supported in subsequent analyses in addition to their isolated status within the core eudicots (2, 9). Deep relationships among major

clades of core eudicots remain unclear; these groups include Berberidopsidaceae + Aextoxicaceae, rosids + Vitaceae + Saxifragales, Santalales, Dilleniaceae + Caryophyllales, and asterids (4).

Aextoxicaceae comprises only one species of dioecious tree endemic to Chile, whereas Berberidopsidaceae comprises two genera of vines and shrubs found in South America and Australia. Both of these families had been difficult to position in earlier classifications and were thought to be more closely related to other groups, depending on the treatment. Although they are now shown convincingly to be closely related, the determination of their position in core eudicots will require additional data (4, 10, 11).

Five families are currently recognized in the Order Santalales, in which members are hemiparasites: Olacaceae, Opiliaceae, Loranthaceae (the mistletoe family), Misodendraceae, and Santalaceae (includes Viscaceae) (20). Olacaceae is considered to be the first diverging lineage of Santalales, but because some

evidence indicates that this family could be paraphyletic (not forming an inclusive group; 21), several of the first early-diverging lineages in Santalales are currently assigned to Olacaceae.

Essentially, the basis of today's Caryophyllales is a group of plants formerly known as the Centrospermae in which several additional families were included following DNA-based studies. Caryophyllales is a diverse group, both in phenotype (e.g., pigment production, pollen morphology) and ecology (e.g., adaptation to xeric environments, carnivory) (10). Of particular interest is the production of betalain pigments in most of the core families of the order (except Molluginaceae and Caryophyllaceae) instead of anthocyanins as in the rest of the angiosperms. As currently circumscribed, Caryophyllales comprises about 11,000 species in 29 families, of which the largest are Caryophyllaceae (carnation family; 2300 species), Amaranthaceae (amaranth family; 2250 species), Aizoaceae (stone plant family; 1850 species), and Cactaceae (cactus family; 1400 species).

The closest relative to Caryophyllales is still ambiguous and several candidates have been proposed in previous phylogenetic studies: Dilleniaceae (3, 4, 8), Dilleniaceae + Vitaceae (7), Aextoxicaceae + Berberidopsidaceae (5), asterids (9), Saxifragales (2), Santalales (22), Cornaceae (22). Because the timetree presented here is based on the three-gene analysis of Soltis *et al.* (4) in which Dilleniaceae is the closest relative to Caryophyllales, we treat Dilleniaceae with Caryophyllales in this chapter. Dilleniaceae is a family of 12 genera and about 300 species of pantropical distribution concentrated in Southeast Asia and Australasia (11, 23). The members of this family vary greatly in habit, from trees or shrubs to herbs or lianas. Some are cultivated for their edible fruits whereas others are used as ornamentals and timber (11, 23).

The most extensive phylogenetic analysis of Caryophyllales is from Cuénoud *et al.* (22) and will be discussed here. The timetree, which comprises 19 of the 29 families circumscribed in the order, differs in some respects from this study, and these discrepancies will be highlighted later. The first diverging lineage within Caryophyllales comprises the Families Polygonaceae, Plumbaginaceae, Tamaricaceae, and Frankeniaceae (22), which are closely related to a group of families characterized by the evolution of carnivory. This group comprises the families Droseraceae (sundew family), Nepenthaceae (pitcher plant family), Drosophyllaceae, Ancistrocladaceae, and Dioncophyllaceae. In the timetree, these two groups are not recovered (15). The ability to capture insects and digest them has appeared only once in the evolution of

Caryophyllales and was subsequently lost in Ancistrocladaceae and some species of Dioncophyllaceae (24). The following lineages comprise the “core Caryophyllales” in which the most species-rich families of the order are found (22). The first diverging lineages in the core Caryophyllales is a group formed by Simmondsiaceae and Rhabdodendraceae followed by Asteropeiaceae (22). In other studies, Rhabdodendraceae is found to be the first diverging lineage in Caryophyllales, but with weak support (4, 5, 7). The next lineages consist of Caryophyllaceae, followed by Achatocarpaceae + Amaranthaceae. In the timetree, Caryophyllaceae is closely related to Amaranthaceae, and Achatocarpaceae is not included. The remainder of the order is found in two groups recovered in both the timetree and analysis of Cuénoud *et al.* (22). The first one comprises Portulacaceae, Didiereaceae, Basellaceae, Halophytaceae, and Cactaceae whereas the second one includes Phytolaccaceae, Aizoaceae, Gisekiaceae, Barbeuiaceae, Agdestidaceae, Sarcobataceae, and Nyctaginaceae. Members of the Family Molluginaceae are scattered in both groups whereas one genus is found in neither of them, but rather diverged before the split between these two groups. Members of Families Phytolaccaceae and Portulacaceae are found in several unrelated positions in their respective groups (22).

The first divergence event in Caryophyllales took place from 90 to 83 Ma, a estimate somewhat younger than the one obtained by Anderson and colleagues (102–99 Ma) (16), but in line with inferences made from the relatively limited fossil record of the group, which places the first split in the Santonian–Campanian, 83.5 Ma ago (1, 17). The timetree presented here is one of the latest attempts at estimating ages in Caryophyllales, but because many families are not represented in it, additional data will be necessary to clarify relationships within this order and provide more robust divergence times.

The Order Saxifragales, as currently recognized by the Angiosperm Phylogeny Group (20), have been dubbed by many as one of the major surprises unveiled by DNA-based phylogenetic studies (10, 25). Saxifragales present a wide array of morphological variation, which would explain in part why the members of this group, first identified as a distinct clade in early phylogenetic analyses based on molecular data (26, 27), have been previously positioned in various unrelated lineages by earlier workers (19, 28, 29). This group now contains 11 families and about 2560 species, of which more than half are assigned to Crassulaceae (stonecrop family). The other larger families are Saxifragaceae (saxifrage family) with 584 species, Grossulariaceae (gooseberry family)

with 150 species, and Haloragaceae (water milfoil family) with 145 species. Some members of these families are cultivated as ornamentals (*Bergenia*, Saxifragaceae; *Kalanchoe*, *Sedum*, and *Crassula*, Crassulaceae), aquarium plants (*Myriophyllum*, Haloragaceae), and fruits (currants and gooseberry, *Ribes*, Grossulariaceae) (11). Although not as species-rich as the families mentioned earlier, other families in this group are well known because of their economic importance, especially in horticulture, such as peonies (Paeoniaceae) and witch hazel (Hamamelidaceae).

Some uncertainty remains regarding the position of Saxifragales in relation to other core eudicot lineages. However, many studies indicate, with reasonable support, that Saxifragales is closely related to a group comprising eurosids and Family Vitaceae (3, 4). Although the monophyly of the order is strongly supported in most, if not all, molecular-based analyses (3, 25, 30), relationships between families within the order remain unclear, despite the use of five DNA regions in some studies (25, 30). This lack of resolution in deeper nodes of Saxifragales has been interpreted as the footprint of a rapid diversification of the main lineages in the early history of the group (25).

Based on the timetree, the first diversification event in Saxifragales took place between 100 and 90 Ma, an estimate similar to the one inferred from the fossil record, that is flowers from the Turonian of New Jersey (91.2 Ma; 17). Other studies obtained similar results (102 Ma, 16; 90 Ma, 31). Relationships between families of Saxifragales are in general poorly resolved or weakly supported, thus inferring reliable age estimates could prove to be difficult. One exception to this is the well-supported relationship of Crassulaceae and Haloragaceae + Penthoraceae + Tetracarpaeaceae, which split 77–69 Ma.

The uniqueness of the tricolpate pollen type coupled with the high preservation potential of pollen grains in fossil deposits supports the hypothesis that the age estimate for the appearance of eudicots is possibly the most reliable of any angiosperm group (10). The earliest remains of tricolpate pollen grains are from the late Barremian–early Aptian and correspond to an estimate of 121 Ma for the first lineage split in eudicots (17, 32). Several angiosperm studies using molecular dating methods have used this estimate as calibration point (fixed age, minimum constraint, or maximum constraint) (16, 33, 34). In studies that did not use the earliest remains of tricolpate pollen grains as a calibration point, the estimated age for the first split in eudicots varies, but in general approximate the 121 Ma estimated from

the fossil record (15, 35). In the timetree based on the molecular dating study of Wikström *et al.* (15) presented here, the age estimate for the first split in the eudicots is 147–131 Ma, slightly older than the estimate inferred from the palynological record.

All the main lineages in eudicots evolved rapidly after the first diversification mentioned earlier, and all were present 100–90 Ma ago (Fig. 2, Table 1). In general, the age estimates inferred from the DNA-based phylogenetic tree for these lineages are older than their earliest fossil remains. One exception is Platanaceae, which splits from its closest relative, Proteaceae, 113–108 Ma; the earliest fossils are from the Albian (108.8 Ma; 17). However, the exact timing of the appearance of each of these lineages is difficult to assess in the current phylogenetic framework because several deeper nodes in eudicots are weakly supported. Nevertheless, estimates made from molecular studies and conclusions drawn from the fossil record concord in supporting a rapid radiation in the early history of eudicots.

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