

Research Article

Accelerated evolution of early angiosperms: Evidence from ranunculalean phylogeny by integrating living and fossil data

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Abstract The new discovery of angiosperm remains in the Jehol Biota of northeastern China contributes to our understanding of the origin and early evolution of flowering plants. The earliest eudicot genus with reproductive organs, *Leefructus*, was recently documented from the Lower Cretaceous Yixian Formation at 125.8–123.0 Ma, and was reconsidered to be close to the extant family Ranunculaceae based on gross morphology. However, this hypothesis has not been tested using a cladistic approach. To determine the possible allies of *Leefructus* within extant eudicots, we constructed a 66 morphological data matrix. Molecular and morphological analyses of extant Ranunculales combined with the fossil suggest that it has an affinity with the Ranunculaceae. The earliest fossil record of the eudicots is 127–125 Ma based on tricolpate pollen grains. Thus, we suggest a hypothesis that the basal eudicots might have experienced an accelerated evolution and diversification during the latest Barremian and earliest Aptian, leading to the stem groups of at least six extant families or lineages, 10–15 Myr earlier than currently documented. Angiosperms have undergone multiple uneven pulses of radiation since their origin. Many key character innovations occurred in different stages that could have triggered those radiations in concert with various biotic and abiotic factors.

Key words: angiosperms, Cretaceous, diversification, paleobotany, phylogeny, Ranunculales.

Angiosperms are of exceptional evolutionary interest because of their diversity of over 250 000 species (Palmer et al., 2004) and their abundance as the dominant vegetation in most terrestrial ecosystems today. Their evolutionary history has been filled with uneven pulses of radiation since their Early Cretaceous origin (140–135 Ma) and their rapid radiations during the mid-Cretaceous (107–93 Ma) that has been documented in many research papers (e.g., Crepet et al., 2004; Anderson et al., 2005; Moore et al., 2007) and textbooks (e.g., Stewart & Rothwell, 1993; Willis & McElwain, 2002; Taylor et al., 2009). This was followed by further radiations as the result of fruit evolution in concert with radiations of birds and mammals (Dilcher, 2010).

The current molecular systematics of angiosperms (Palmer et al., 2004; Soltis et al., 2009, 2011; Qiu et al., 2010) recognizes the basalmost angiosperms and five major angiosperm lineages. The five lineages include the sister lineages Chloranthaceae and magnoliids, the monocots, *Ceratophyllum*, and the eudicots consisting of the basal eudicots and the core eudicots (Moore et al., 2007; Soltis et al., 2011). The eudicots now constitute more than 70% of all extant angiosperm species.

Our current understanding of the natural relationships of angiosperms is based mainly on molecular phylogenetic data

(e.g., Qiu et al., 1999, 2006, 2010; Soltis & Soltis, 2004; Doyle et al., 2008; Qiu & Estabrook, 2008; APG III, 2009; Wang et al., 2009b; Soltis et al., 2011). These data are most often presented in the form of cladograms showing stem and branch lineages that are derived from the analysis of large datasets including DNA sequences from chloroplast, mitochondrial, and nuclear genomes (Qiu et al., 1999; Palmer et al., 2004; APG III, 2009). Such cladograms have come to represent the evolutionary history of angiosperms while the branching points between the clades are considered to be constrained in time (Crepet et al., 2004; Anderson et al., 2005). The origin of flowering plants and the origins of major clades as constrained by time (Bell et al., 2005, 2010) are best revealed by the fossil record when available. It is the fossil record that holds the key to understanding the sequences and timing of the multiple radiations involved in flowering plant evolution (Crepet et al., 2004; Gandolfo et al., 2008). Whenever possible the angiosperm fossil record should be used to ground truth the systematic relationships and the time of the divergence and radiation of major clades of extant angiosperms as understood from molecular and morphological data (Crepet et al., 2004; Anderson et al., 2005; Gandolfo et al., 2008). However, the earliest known fossil records of angiosperms are rare, often incomplete, and difficult to interpret.

Recently, Sun et al. (2011) reported a fossil eudicot genus with reproductive organs, *Leefructus*, from the Lower Cretaceous Yixian Formation at 125.8–123.0 Ma (Meng et al., 2008), and placed it as an extinct eudicot on the stem lineage of the extant family Ranunculaceae based on gross morphology (Fig. 1). However, *Leefructus* has not been included in a cladistic analysis or been shown to possess any previously defined synapomorphies for the eudicot total group, crown group, or any clade within the crown group, which prevents its use as a calibration constraint for a molecular clock (Clarke et al., 2011). In this study, 14 characters of *Leefructus* were coded based on the description of the fossil genus (Sun et al., 2011), and added into our previous established 65 morphological data matrix (Wang et al., 2009b) to determine the positions of the fossil *Leefructus* within eudicots.

Material and Methods

We added one beak character (present vs. absence) into our previous 65 morphological data matrix (Wang et al., 2009b). Fourteen characters of *Leefructus mirus* Sun et al. (2011) were coded based on the description of the fossil genus: beak (present), growth form (herbaceous), stipules (absent), leaf arrangement (spiral), major venation (palmate), blade shape (ovate), inflorescence (solitary), stamen arrangement (irregular), stamen fusion (free), carpel number (more than 3), carpel form (ascidiate up to stigma), carpel fusion (pseudo-syncarpous), ovule number (more than two), and fruit wall (dry). When a character was poorly known or unavailable for the species, it was coded as missing or inapplicable.

Phylogenetic analyses were carried out using maximum parsimony (MP) and Bayesian inference (BI) methods. These were used in PAUP* version 4.0b10 (Swofford, 2003) and MrBayes version 3.0b4 (Ronquist & Huelsenbeck, 2003), respectively. For MP analyses, we used the backbone constraint tree approach as in Endress & Doyle (2009). The tree is based primarily on the combined analysis of morphology, *rbcL*, *matK*, *trnL-F*, and 26S rDNA by Wang et al. (2009b), but with change in the position of Ceratophyllaceae based on more recent analyses. The plastid phylogenomic analyses of the whole angiosperm (Moore et al., 2007, 2010) and 17 genes from three genomes (Soltis et al., 2011) found *Ceratophyllum* sister to eudicots. The MP heuristic searches were carried out with 1000 random sequence addition replicates, tree bisection-reconnection branch swapping, MuTrees in effect, and steepest descent off. Bootstrapping was carried out with 1000 replicates, using a heuristic search strategy (five random addition replicates, saving five trees per replicate).

For BI analyses, the combined morphological and four DNA matrix by Wang et al. (2009b) was reconstructed, where the molecular data of *L. mirus* were coded as missing. The detailed analysis approach was described in Wang et al. (2009b).

Results and Discussion

The MP and BI analyses resulted in identical topology at the familial level (Fig. 2). Within Ranunculales, Eupteleaceae is the earliest-diverging family, followed by Papaveraceae; the other five families form a clade. These results are congruent with our previous study (Wang et al., 2009b). Significantly, all our

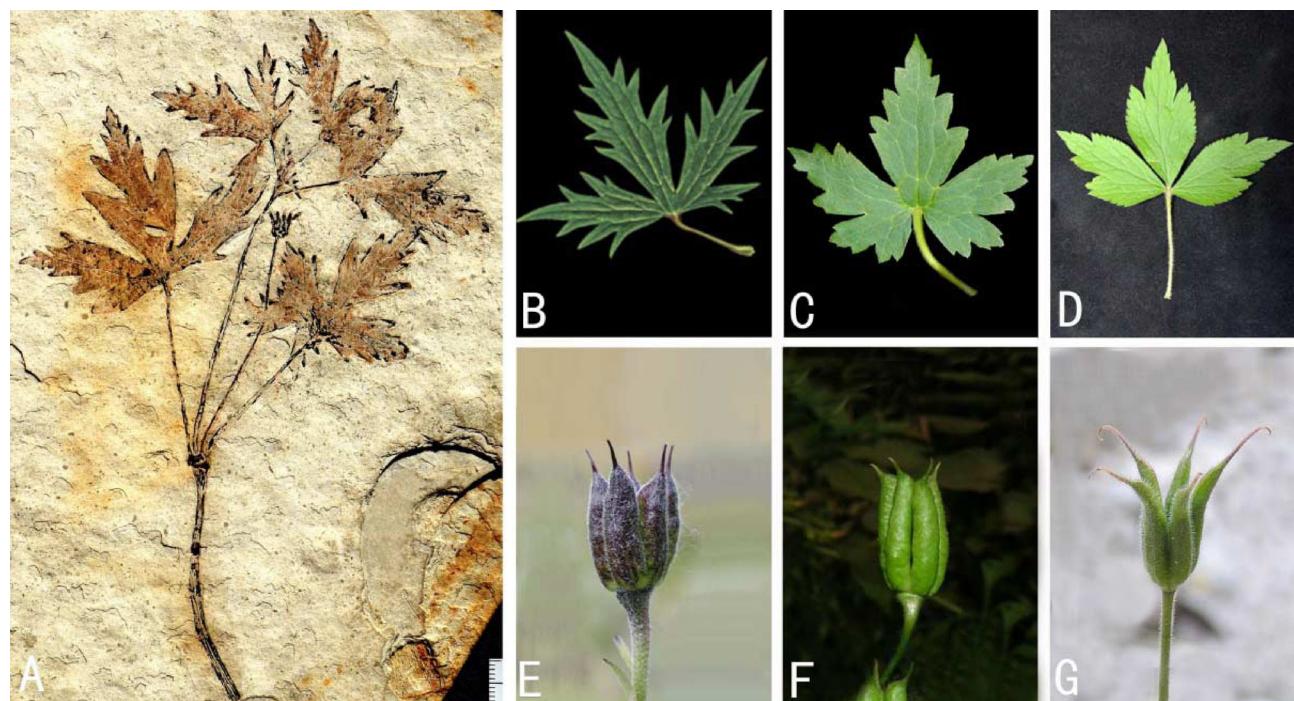


Fig. 1. Leaves and fruits of fossil (**A**) and extant Ranunculaceae species (**B–G**). **A**, *Leefructus mirus* Sun, Dilcher, Wang et Chen. **B**, *Delphinium* sp. **C**, *Aconitum hemsleyanum* Pritz. **D**, *Anemone virginiana* L. **E**, *Delphinium glaucum* S. Watson. **F**, *Aconitum kusnezoffii* Reichb. **G**, *Aquilegia einseleana* F. W. Schultz. Photograph A is from Sun et al. (2011). Photographs B–G were taken by S.-X. YU and used with permission.

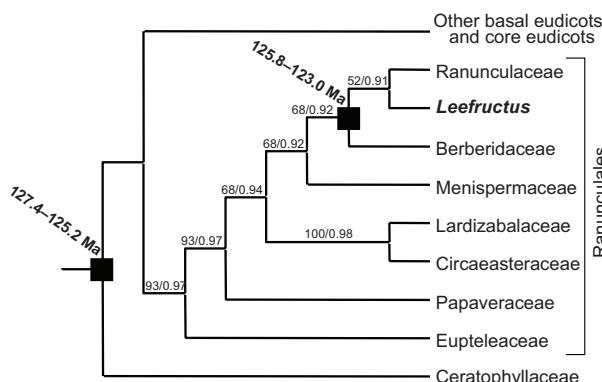


Fig. 2. Bootstrap tree obtained after addition of *Leefructus* to the tree of Wang et al. (2009b). Numbers at the nodes are bootstrap percentages and Bayesian posterior probabilities, respectively.

analyses indicate that *Leefructus* is sister to the Ranunculaceae (bootstrap support = 52%; posterior probability = 0.91). *Leefructus* shares many characters with the extant Ranunculaceae, including presence of herbaceous habit, palmate venation, free stamens, more than two ovules, stamens of irregular arrangement, and fruits with beaks. The leaves of *Leefructus* resemble the venation patterns and forms of *Delphinium* leaves (Fig. 1: B), typical of the Ranunculaceae, and the fruits of *Leefructus* resemble grossly those of *Aconitum* and *Delphinium* (Fig. 1: E, F). But *Leefructus* has some unique characters, such as leaves in spiral arrangement and syncarpous carpels (also in *Nigella* and some *Helleborus*). Thus, combining phylogenetic analyses, we are in agreement with Sun et al. (2011) that *Leefructus* belongs to the stem group of Ranunculaceae.

The antiquity of *Leefructus* requires a revision of some ages suggested for the age of the basal eudicots. An estimate for the diversification of the eudicots, a major clade of flowering plants, is 124.8 (± 3.2) Ma based on the molecular analysis of 61 plastid genomes (Moore et al., 2007). Based on 36 minimum age constraints treated as exponential distributions, Bell et al. (2010) suggested that the crown age of the eudicots is 129 Ma (123–134 Ma). Based on the plastid *rbcL* data, Anderson et al. (2005) used multiple fossil calibration points and placed the diversification of Ranunculales at an age of 114 Ma and the Ranunculaceae/Berberidaceae divergence from the Menispermaceae at 105 Ma. In this study, we suggest that the Ranunculaceae/Berberidaceae divergence from the Menispermaceae took place nearly 20 Myr earlier.

The term eudicot was proposed in 1991 (Doyle & Hotton, 1991) as a “putatively monophyletic group” using tricolporate pollen to define the clade. This clade was recognized at the Barremian–Hauterivian boundary from sediments in Gabon (Doyle et al., 1977) and from the early Albian of the Potomac Group in North America (Endress & Doyle, 2009). Hughes & McDougall (1990) and Hughes (1994) recognized tricolporate pollen from Bed 35 at the base of the Vectis Formation that Hughes considered “Phase 4,” which was at the Barremian–Aptian boundary. This current understanding of the fossil record placed the earliest fossils of the eudicots at this Barremian–Aptian boundary age of ca. 125 Ma (<http://www.stratigraphy.org/ICSchart/ChronostratChart2013-01.pdf>). The

distribution of this pollen type from cores taken off the coast of Gabon and from England suggests that plants belonging to this eudicot pollen type were already distributed widely by ca. 125 Ma and might have had an earlier origin. *Prototricholites* pollen was described from the Jianshangou Bed (127.4–125.2 Ma) of the Yixian Formation, which extended both the age and distribution of the basal eudicots (Wang et al., 2000).

If the first appearance of basal eudicots based on the occurrence of tricolporate pollen is at ca. 127–125 Ma or slightly earlier and the morphological characters for *Leefructus* have placed it firmly as an extinct form on the stem lineage of the Ranunculaceae at 125.8–123.0 Ma, then there might have been a time of accelerated evolution of the basal eudicots during the latest Barremian and early Aptian. This evolution needed to require an accelerated rate of evolution within the basal eudicot clade during the Early Cretaceous. The early fossil record of basal eudicot evolution is incomplete so each fossil that can be placed in this clade provides new and important information about early angiosperms. Previous fossil angiosperms reported from the Yixian Formation included *Archaeefructus* and *Hyrcantha decussata* (Sun et al., 1998, 2002; Dilcher et al., 2007). It is possible that *Hyrcantha* could also be considered as a stem lineage of the Ranunculaceae (Leng & Friis, 2003, 2006; Dilcher et al., 2007). Additionally, Jud & Hickey (2013) recently reported a fossil eudicot genus with leaf organs, *Potomacapnos*, from Aptian sediments of the Potomac Group exposed at the Dutch Gap locality in Virginia, USA, and tentatively placed it in Papaveraceae of Ranunculales based on leaf architecture.

The cladogram of Wang et al. (2009b) is presented in Fig. 2 with the addition of the fossil data. We accept the presence of the earliest tricolporate pollen in the fossil record as the time when eudicots can be firmly documented (Doyle et al., 1977, 2008; Hughes & McDougall, 1990; Doyle & Hotton, 1991; Doyle, 1992; Hughes, 1994) (mid-Barremian, Isle of Wright) and is placed at ca. 127–125 Ma. *Leefructus* is recognized at 125.8–123.0 Ma. This means less than 5 Myr from the initial recognition of the basal eudicots to the recognition of the stem lineage of the Ranunculaceae. The minimum age node mapping method (Crepet et al., 2004; Hermsen & Hendricks, 2008), as applied to a cladogram containing fossils, proposes that each node of the cladogram is at least as old as the oldest descendant. This leads to us concluding that the extant families of the basal eudicots came into existence between 127–125 and 125–123 Ma. In order to emphasize this rapid evolution, we suggest the hypothesis of an “accelerated angiosperm evolution” for the basal eudicots at a time much earlier than previously recognized by Anderson et al. (2005).

This “accelerated angiosperm evolution” between 127–125 and 125–123 Ma is presented as a hypothesis here because there are limited data at present to support it. The presence of *Leefructus*, *Hyrcantha*, and *Potomacapnos*, which have been suggested as having possible Ranunculales/Ranunculaceae affinities, documents basal eudicot evolution early in angiosperm history. To date, more than 12 putative early eudicot megafossils reported from the Aptian to mid-Albian have been compared with or assigned to eudicots or Ranunculales (Jud & Hickey, 2013, and references therein). Why did such rapid radiations take place so quickly?

The “accelerated angiosperm evolution” hypothesis occurred at a post-Jurassic and Early Cretaceous time when there

was rapid evolution of a variety of insect pollinators active with gymnospermous seed plants (Ren et al., 2009). These pollinators must have transferred to the new angiospermous plant sources of pollen and nectar easily and rapidly. They were also joined by diverse lineages of insect pollinators that could play key roles in flowering plant evolution during the Barremian, Aptian, and Albian. The coevolutionary nature of the early angiosperms was well documented in the Albian when pollen clumps occurred (Hu et al., 2007), indicating continuation and further accommodation of flowering plants to insect pollination.

Accelerated angiosperm evolution has also been observed for particular clades such as the rosids, which might have diversified rapidly in perhaps as little as in 4–5 Myr (Wang et al., 2009a), and the Saxifragales, which diversified rapidly in as little as 6 Myr (Jian et al., 2008). Chaloner (1970) showed that the occurrence of spores preceded the finding of abundant megafossils of early land plants by at least 10–15 Myr. This suggests that spores and pollens might be found long before abundant angiosperm megafossils or mesofossils, and were common in sediments such as the Barremian, Aptian, and Albian angiosperm explosive diversity. Martínez-Millán et al. (2009) noted that the presence of the Ericales in the Turonian in the Late Cretaceous followed their earlier diversification during the Early Cretaceous by a few million years. The presence of tricolporate pollen followed by the burst of evolution of basal eudicots during the earliest Barremian preceded the conspicuous radiation of angiosperm diversity by approximately 20 Myr, during the late Albian (Dilcher & Eriksen, 1983; Pedersen et al., 1994; Magallón-Puebla et al., 1997; Mohr & Friis, 2000; Crepet et al., 2004; Mohr & Bernardes-de-Oliveira, 2004; Friis et al., 2006a, 2006b, 2009; Mohr et al., 2008; Dilcher & Wang, 2009; Taylor et al., 2009). Some of the basal eudicot fossil taxa known from the Albian have very modern features and are identified with extant taxa such as Platanaceae (Dilcher & Eriksen, 1983; Pedersen et al., 1994; Magallón-Puebla et al., 1997), Cabombaceae (Wang & Dilcher, 2006), Buxaceae (Pedersen et al., 2007), Priscaceae (Retallack & Dilcher, 1981), and Lauraceae (Drinnan et al., 1990), as well as sister taxa to the basal eudicots such as Ceratophyllaceae (Dilcher & Wang, 2009). The initial major lineages of basal eudicot evolution took place rapidly beginning during the Barremian and continued during the Aptian and early Albian. This is a time of insect radiation (Labandeira & Sepkoski, 1993; Grimaldi & Engel, 2005; Hu et al., 2007; Labandeira & Conrad, 2013) and early modifications for wind pollination. Based on the fossil record presented by Sun et al. (2011), it is evident that the Barremian and the early Aptian were important times of accelerated angiosperm evolution.

During the evolution of angiosperms, many important character changes occurred over many millions of years. The closed carpel has been proposed as the defining feature of angiosperms (Sun et al., 1998), which allows for biochemical incompatibility of pollen and ovule. Bisexual axis (fertile shoot) with ovules and pollens (male = pollen, ovule = female), occurred at ca. 125 Ma (Sun et al., 1998, 2002, 2011). The flowers of angiosperms with four whorl organs and fragrances and/or nectar first occur later, and the shift from radial to bilateral flowers happened at 70 Ma, which functioned for attracting potential pollinators (Dilcher, 2010). Fruits of angiosperms that are attractive to birds and mammals evolved

in the Late Cretaceous and early Cenozoic (Dilcher, 2010), which aided dispersal. Flowering plants have experienced multiple radiation pulses since their origin. The appearance of many important character innovations of the flowering plants, associated with coevolution in a biotic environment, is responsible for their radiations during different epochs. Thus, the accelerated evolution of the early eudicots, documented in this study, is just the initial example of the various radiation bursts that have continued throughout their long history.

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