

Molecular and Fossil Evidence on the Origin of Angiosperms

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Abstract

Molecular data on relationships within angiosperms confirm the view that their increasing morphological diversity through the Cretaceous reflected their evolutionary radiation. Despite the early appearance of aquatics and groups with simple flowers, the record is consistent with inferences from molecular trees that the first angiosperms were woody plants with pinnately veined leaves, multiparted flowers, uniovulate ascidiate carpels, and columellar monosulcate pollen. Molecular data appear to refute the hypothesis based on morphology that angiosperms and Gnetales are closest living relatives. Morphological analyses of living and fossil seed plants that assume molecular relationships identify glossopterids, Bennettitales, and *Caytonia* as angiosperm relatives; these results are consistent with proposed homologies between the cupule of glossopterids and *Caytonia* and the angiosperm bitegmic ovule. Jurassic molecular dates for the angiosperms may be reconciled with the fossil record if the first angiosperms were restricted to wet forest understory habitats and did not radiate until the Cretaceous.

INTRODUCTION

In the past 20 years, phylogenetic analyses of DNA sequence data have revolutionized thinking about the origin and evolution of many groups of organisms. The impact of molecular data has been especially profound in angiosperms, or flowering plants, which rose to dominance in most terrestrial ecosystems during the Cretaceous. By the late 1990s, analyses of multiple genes led the Angiosperm Phylogeny Group (1998) to propose a new higher-level phylogenetic classification of angiosperms, which has remained remarkably stable with studies of increasing numbers of genes (Angiosperm Phylogeny Group 2009), including nearly complete chloroplast genomes (Jansen et al. 2007, Moore et al. 2007). As in other taxa, molecular phylogenetic studies of angiosperms have revealed both agreements with previous ideas derived from the fossil record, which could be taken as reaffirming the value of both fossil and molecular data, and apparent conflicts, which raise questions about the interpretation of both lines of evidence.

This review explores areas of congruence and conflict and ways in which conflicts might be resolved (cf. Doyle 2001). I focus on the origin of angiosperms, as distinguished from their evolutionary diversification, emphasizing a phylogenetic framework. A successful solution to the problem would involve primarily an understanding of the origin of the distinctive new intrinsic features of angiosperms, or synapomorphies, by transformation of structures known in related plants, and secondarily an understanding of extrinsic aspects, such as when and where these changes occurred and under what environmental selective pressures.

STATUS OF THE PROBLEM PRIOR TO MOLECULAR SYSTEMATICS

Prior to the 1960s, the fossil record of the origin and rise of angiosperms was thought to be unusually mysterious, because of both the lack of fossil taxa intermediate between angiosperms and other groups and the character of the earliest angiosperm record in the Barremian, Aptian, and Albanian stages of the Early Cretaceous. The record then consisted largely of leaves, which had been identified or compared with diverse modern taxa. The resulting impression that angiosperms appeared “suddenly” in “modern form” led to suggestions, going back to Darwin in 1879 (Friedman 2009), that the group originated and diversified before the Cretaceous in some area with a poor fossil record. The best developed theory was that of Axelrod (1952, 1970), who postulated that angiosperms originated in tropical uplands in the Permian or Triassic and invaded lowland basins of deposition in the Cretaceous as a result of increasingly equable climates.

This picture began to change with studies of fossil pollen, which provided evidence on floras in geographic areas where plant megafossils were unknown and broader representation of taxa making up the vegetation. Despite nearly worldwide sampling, palynological studies failed to reveal angiosperm pollen before the mid-Early Cretaceous, whereas some should have been transported from the uplands if angiosperms were growing there, and found that Early Cretaceous angiosperm pollen was much less diverse than expected from fossil leaf identifications (Scott et al. 1960, Brenner 1963). Most significantly, the sequence of appearance of major angiosperm pollen types agreed with hypotheses on pollen evolution derived from comparative morphology of Recent plants (**Figure 1**) (Doyle 1969, 1978; Muller 1970). The first angiosperm pollen was monosulcate; that is, it had a single furrow for pollen tube germination, as in gymnosperms, monocots, and “magnoliid dicots,” which were thought to include the most primitive angiosperms. This pollen was identified as angiospermous by its columellar exine structure, with radial rods connecting the inner and outer wall layers (nexine and tectum, respectively). Such pollen is now known back to the Hauterivian or Valanginian (Trevisan 1988, Hughes 1994, Brenner 1996). Monosulcates were followed by tricolpate pollen, characterized by three longitudinal furrows,

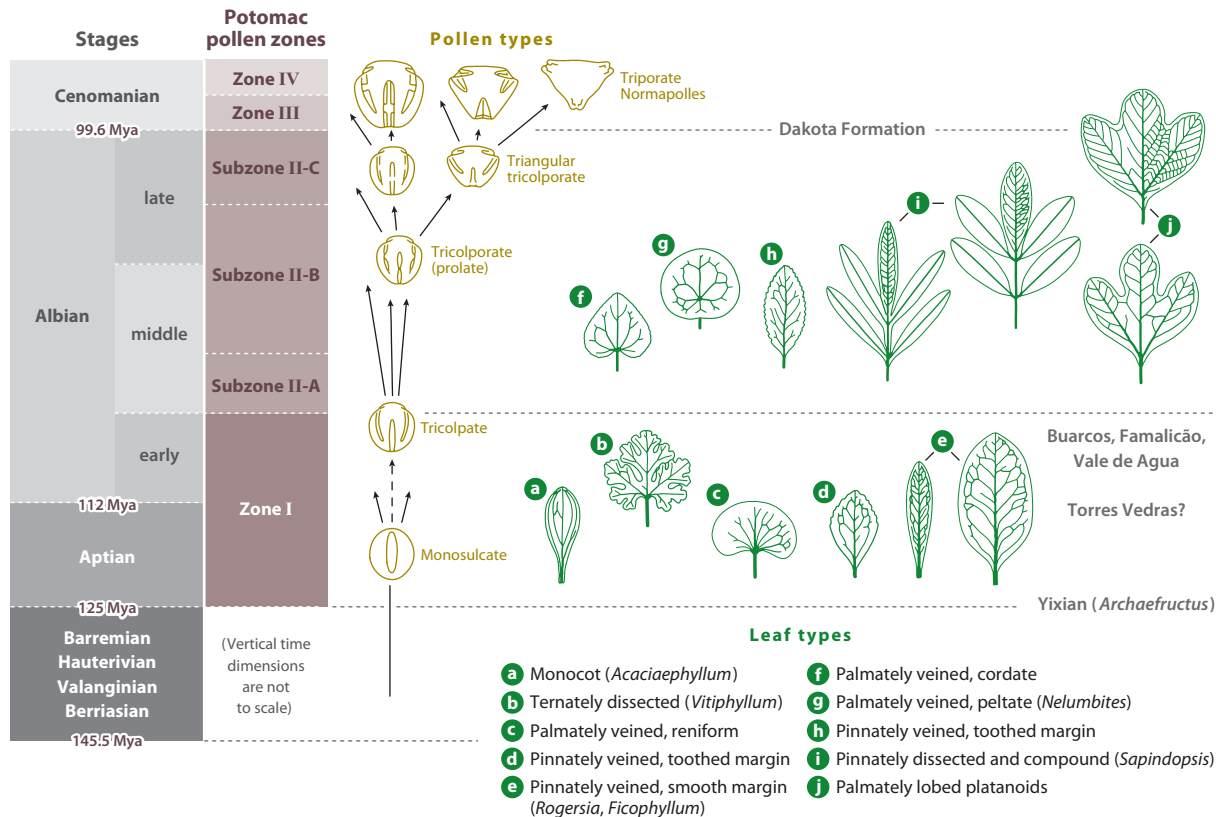


Figure 1

Stratigraphic sequence of major angiosperm pollen and leaf types in the Potomac Group of eastern North America (modified from Doyle & Hickey 1976), with correlations of plant-bearing localities in other geographic areas. Abbreviation: Mya, million years ago.

usually in the Albian at northern middle latitudes (Southern Laurasia). This is the basic pollen type for the vast majority of “dicots,” now known to form a clade named eudicots. Tricolpates appeared in the late Barremian or Aptian of South America, Africa, and the Middle East (Northern Gondwana), but there, too, they were preceded by monosulcates (Brenner 1976, 1996; Doyle et al. 1977; Schrank 1983; Penny 1986; Regali & Viana 1989; Doyle 1992; Ibrahim 2002; Schrank & Mahmoud 2002). Tricolpates were joined in the late Albian by tricolporate pollen, the most common type in living eudicots, with a pore in the middle of each furrow. Tricolporates were joined in the Cenomanian (Late Cretaceous) by triporate pollen of the Normapolles group, with three round apertures, as in wind-pollinated Fagales, which most botanists regarded as highly derived.

These observations led to a consensus that the main radiation of angiosperms occurred during the Cretaceous. Several authors noted that angiosperms might have existed earlier, but, if so, they must have been low in diversity and advancement to have escaped detection (e.g., Doyle 1969, Muller 1970). The congruence of the stratigraphic sequence of pollen types and their presumed evolutionary sequence would make no sense if angiosperms had already diversified in a hidden homeland area; there is no reason to expect that groups would migrate into better-known areas in the order in which they had evolved much earlier. Axelrod (1970) suggested that pollen evolution might have lagged behind the systematic diversification of angiosperms, but others argued that

this was inconsistent with the systematic congruence of pollen and classification (Muller 1970, Walker & Doyle 1975).

This picture was confirmed by studies on Cretaceous angiosperm leaves, which had been neglected since the early 1900s. Leaves were traditionally thought to have low systematic value, but this view was changing with more rigorous methods of analysis of leaf characters and surveys of their systematic distribution (Dilcher 1974, Hickey & Wolfe 1975, Doyle 2007). Studies of angiosperm leaves in the Potomac Group of the eastern United States (**Figure 1**) showed a pattern of morphological diversification through time comparable with that seen in the pollen record (Doyle & Hickey 1976, Hickey & Doyle 1977), bearing in mind that the section begins late in the monosulcate phase. In the lower Potomac (Zone I of Brenner 1963), probably Aptian to earliest Albian (Hochuli et al. 2006), angiosperm leaves are rare, simple, and usually pinnately veined, with unusually irregular venation. Similar features occur in Recent “woody magnoliid” groups with monosulcate pollen. A few are palmately veined, as in “herbaceous magnoliids.” Ternately dissected leaves (with threefold division of the blade), as in the eudicot order Ranunculales, appear along with the first rare tricolpate pollen (*Vitiphyllum*). More abundant and divergent leaf types appear in the upper Potomac (Zone II, middle and late Albian), many of which are comparable with living tricolpate groups, such as peltate leaves (*Nelumbites*) similar to the aquatic genus *Nelumbo* (lotus), palmately lobed “platanoids” compared with *Platanus* (sycamore), and pinnately dissected and compound leaves (*Sapindopsis*) now also known to be related to *Platanus* (Crane et al. 1993). Most of these leaves have more regular venation than those in the lower Potomac. Consistent sequences are known in western North America, Portugal, Kazakhstan, Colombia, Brazil, and Argentina (Doyle & Hickey 1976, Pons 1984, Mohr & Friis 2000, Archangelsky et al. 2009).

These advances did not have a great impact on discussions of the origin of angiosperms; they provided more indications on character polarity and timing of the radiation than on relationships with other seed plants. However, they did help refute older theories based on derived taxa, such as comparisons between Fagales and Gnetales, and favored those based on angiosperms with monosulcate pollen (Doyle 1978). Most discussions of the origin centered on so-called Mesozoic seed ferns such as glossopterids (actually Permian), corystosperms (Triassic), and *Caytonia* (mainly Jurassic), and possible homologies of the outer integument of the bitegmic angiosperm ovule with the seed-bearing cupule of these taxa (Gaussen 1946, Stebbins 1974, Doyle 1978, Retallack & Dilcher 1981).

Beginning in the 1980s, understanding of the Cretaceous angiosperm record was further revolutionized by discoveries of fossil flowers and fruits (Friis 1984; Friis et al. 2000, 2006a, 2010a,b, 2011), mostly in the mesofossil (millimeter) size range. Contrary to earlier assumptions, flowers are often well preserved as lignite or charcoal and can be extracted from sediments by sieving and studied with scanning electron microscopy or X-ray microtomography (Friis et al. 2009, Friis & Pedersen 2011). Flowers have been the mainstay of angiosperm systematics since Linnaeus, largely because they are so rich in characters. Furthermore, fossil flowers often have pollen in the stamens or on the stigma, which allows integration with the dispersed pollen record, and they can sometimes be associated with leaves and wood. Studies of fossil flowers have broadly confirmed the picture based on pollen and leaves, but they provide more detail on the actual clades present. However, palynology remains valuable because of its geographic and stratigraphic coverage, which increases confidence in inferred evolutionary patterns.

These advances were paralleled by the expansion of cladistic (parsimony) methods for phylogeny reconstruction, initially using morphological data. Although some morphological cladistic results have been refuted by molecular analyses, others that were controversial at first have been confirmed. In addition, the cladistic approach greatly clarified evolutionary questions by forcing

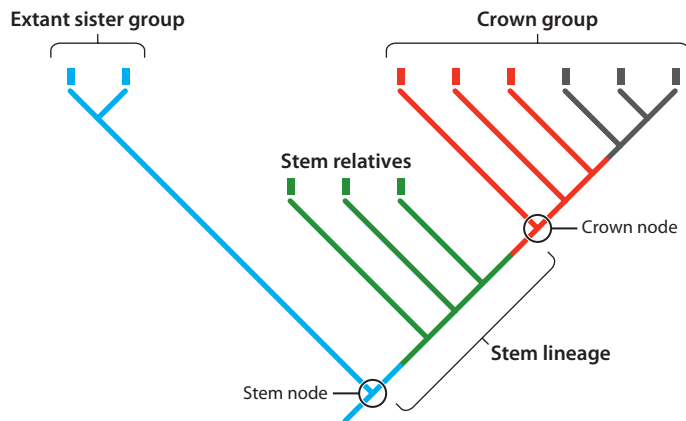


Figure 2

Concepts involved in relating fossil taxa and trees of living taxa and the use of parsimony optimization to reconstruct character states at the crown group node and on the stem lineage.

systematists to formulate more explicit hypotheses on phylogeny and its relation to character evolution, which is no less important in the present molecular era.

Molecular results concern only crown groups (a crown group consists of the most recent common ancestor of a living clade and all its derivatives), and not the stem lineages connecting crown groups with one another, or extinct branches (stem relatives) from these lineages (**Figure 2**) (Doyle & Donoghue 1993). From a phylogenetic point of view, the origin of angiosperms can be broken into two related problems, which are loosely comparable with the classic questions, “What were the first angiosperms like?” and “What did they come from?” The first problem is where the crown group tree is rooted, or which extant lines are most basal (attached to the most basal nodes). Basal does not necessarily mean primitive: Living representatives of basal lines are usually more or less specialized relative to the long-dead common ancestor (Crisp & Cook 2005). However, given the characters of living taxa and the tree topology, we can use the principle of parsimony (or related criteria) to optimize character states on the tree and estimate the ancestral state, even in the absence of data from outgroups (a top-down approach; Bateman et al. 2006). For example, if there are two or more lines with the same state branching in a series below the bulk of a clade, it is most parsimonious to reconstruct this state as ancestral. The second problem is what the closest outgroups of the angiosperms are (the nearest being the sister group). Again, outgroups may be more or less derived, but if several outgroups are known, it may be possible to reconstruct character states at nodes below the angiosperms and infer how new angiosperm features evolved from structures known in the outgroups (a bottom-up approach). These questions involve a risk of circular reasoning: Where the ingroup tree is rooted may depend on which taxa are considered the closest outgroups, and vice versa. This problem is best resolved by simultaneous analysis of both ingroup and outgroup taxa.

Most morphological cladistic analyses of seed plants indicated that angiosperms were most closely related to living Gnetales and Mesozoic Bennettitales and *Pentoxylon*—the anthophyte hypothesis, so named because all these taxa have flower-like reproductive structures. This recalled views of Arber & Parkin (1907), who also associated angiosperms with Bennettitales and Gnetales. However, some analyses linked anthophytes with Mesozoic seed ferns (Crane 1985, Doyle & Donoghue 1986), others associated them with coniferophytes (Nixon et al. 1994, Rothwell & Serbet 1994), and some moved *Caytonia* up to a position sister to the angiosperms (Doyle 1996, 2006, 2008; Hilton & Bateman 2006). Rootings of the angiosperms were also inconsistent; the

basal lines in some analyses had multiparted flowers (Magnoliales: Donoghue & Doyle 1989; Calycanthaceae: Loconte & Stevenson 1991; Nymphaeales: Doyle 1996), whereas those in other analyses had simple flowers (Chloranthaceae and/or Piperales: Nixon et al. 1994, Taylor & Hickey 1996).

Molecular studies provide no direct evidence on relationships of angiosperms with fossils, but they almost uniformly reject the main conclusion about their relationships with living taxa that morphological analyses agreed on, namely their connection with Gnetales. However, molecular data have essentially resolved the rooting problem and thereby greatly clarified the morphology of the first angiosperms. The next sections explore the status of these phylogenetic questions in light of molecular and fossil data and discuss the problem of the time and environment of the origin of angiosperms. Although the topic is the origin of angiosperms, I devote much space to the Cretaceous radiation because its interpretation is essential for reconstructing ancestral states and gaining perspective on conflicts between molecular and fossil evidence on the age of angiosperms.

MOLECULAR AND FOSSIL EVIDENCE ON THE FIRST ANGIOSPERMS

The first molecular analyses of angiosperms, based on single genes, gave inconsistent rootings. Ribosomal RNA identified Nymphaeales (water lilies) as the sister group of all other angiosperms (Hamby & Zimmer 1992), whereas the chloroplast gene *rbcL* placed the rootless aquatic *Ceratophyllum* in this position (Chase et al. 1993). However, since 1999, multigene analyses have yielded remarkably consistent and statistically well-supported results (Mathews & Donoghue 1999, Parkinson et al. 1999, Qiu et al. 1999, P.S. Soltis et al. 1999, D.E. Soltis et al. 2005), which are largely insensitive to choice of outgroups (Graham & Iles 2009). These analyses (see **Figure 3**) placed three lines containing ~175 species at the base of the tree, in the so-called ANITA grade: *Amborella*, a scrambling tree or shrub in New Caledonia; Nymphaeales; and Austrobaileyales, a clade of lianas, shrubs, and small trees, the most familiar being *Illicium* (star anise). (ANITA stands for *Amborella*, Nymphaeales, Illiciales, *Trimenia*, and *Austrobaileya*.) The remaining >99.9% of angiosperm species form a core group named mesangiosperms (Cantino et al. 2007), made up of five clades: Chloranthaceae, noted for their simple flowers; *Ceratophyllum*; Magnoliidae, in a new monophyletic sense, consisting of Magnoliales, Laurales, Canellaceae (including Winteraceae), and Piperales (including Aristolochiaceae); monocots; and eudicots, with tricolpate and derived pollen. Within eudicots, Ranunculales (poppies, buttercups) and several other lines form a basal grade with mostly tricolpate pollen below a vast core clade termed Pentapetalae, most of which have pentamerous flowers with a perianth differentiated into five sepals and five petals, as well as tricolporate pollen.

Some molecular results that contradicted older views were anticipated by morphological analyses, such as the monophyly of eudicots and the association of Aristolochiaceae with Piperales (Dahlgren & Bremer 1985, Donoghue & Doyle 1989). However, morphological studies grouped Piperales, Nymphaeales, and monocots in either a paraphyletic grade (Dahlgren & Bremer 1985) or a clade (Donoghue & Doyle 1989), rather than placing Nymphaeales in the ANITA grade and Piperales in the magnoliid clade. In these cases, morphology was overruled when morphological characters were combined with sequences of three genes (Doyle & Endress 2000). Persisting areas of uncertainty concern whether *Amborella* and Nymphaeales form two successive lines or a clade and the arrangement of the five mesangiosperm clades. In the combined analysis of Doyle & Endress (2000), carpel features retained from the ANITA grade overruled molecular data in placing Chloranthaceae at the base of mesangiosperms (**Figure 3**). Doyle & Endress (2000) did not include *Ceratophyllum*, but morphological data of Endress & Doyle (2009) linked it with

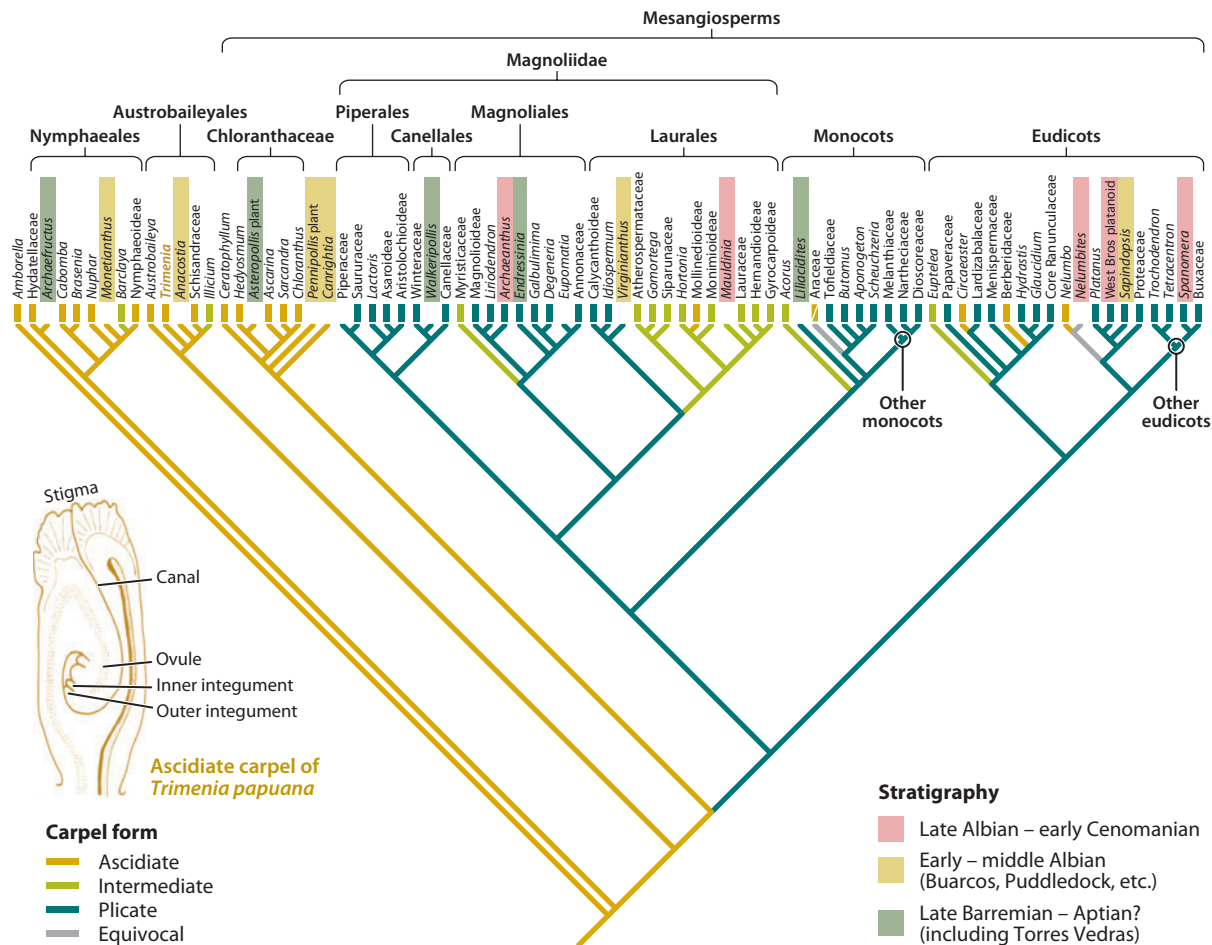


Figure 3

Phylogenetic tree of basal angiosperm relationships from Endress & Doyle (2009), based on molecular and morphological data, with fossil taxa placed at most parsimonious positions based on analyses of Doyle et al. (2008), Endress & Doyle (2009), Friis et al. (2009), Doyle & Endress (2010), and Friis & Pedersen (2011). Colors of branches indicate the most parsimonious course of evolution of carpel form. Probable positions of other monocots and eudicots are indicated. Colors behind names of fossils indicate stratigraphic positions of localities where taxa occur or have been described in most detail. Drawing of a longitudinal section of an ascidiolate carpel of *Trimenia* provided by P.K. Endress.

Chloranthaceae. In analyses of nearly complete chloroplast genomes (Jansen et al. 2007, Moore et al. 2007), *Amborella* and Nymphaeales formed two successive lines, Chloranthaceae were linked with magnoliids, and *Ceratophyllum* was linked with eudicots, but a study of mitochondrial genes (Qiu et al. 2010) linked *Amborella* with Nymphaeales and *Ceratophyllum* with Chloranthaceae. It is not clear whether these conflicts reflect bias in one or the other molecular data set or different evolutionary histories of chloroplasts and mitochondria, owing to ancient hybridization or lineage sorting (polymorphism in the common ancestor and loss of different copies in its descendants). However, an analysis of slowly evolving chloroplast genes (Moore et al. 2011), which were expected to be more reliable, found the *Ceratophyllum*-Chloranthaceae link, which might indicate biases in the whole chloroplast genome data sets.

These results provide an independent framework for the study of character evolution that helps overcome the problems of circularity and outgroup choice that plagued morphological analyses (Doyle & Endress 2000, Zanis et al. 2003, Endress & Doyle 2009). By placing three low-diversity lines below the bulk of angiosperms, the ANITA rooting presents a near-ideal situation for reconstruction of ancestral states. Using parsimony, the ancestral state for some characters is ambiguous owing to variation among the ANITA lines, such as whether floral parts were arranged in a spiral or in whorls of three, but many other ancestral states are clear. Thus, we can infer that the most recent common ancestor of angiosperms had vesselless wood, pinnately veined simple leaves (Doyle 2007), monosulcate pollen with columellar exine structure (Doyle 2005, 2009), more than two whorls or series of undifferentiated perianth parts (tepals), numerous stamens, and more than one ascidiate carpel containing a single pendent bitegmic ovule (**Figure 3**; terms discussed below) (Endress & Doyle 2009). The two arrangements of *Amborella* and Nymphaeales have little impact on these inferences.

The relation of these results to the Cretaceous record can be evaluated by optimizing individual characters of fossils on a molecular tree or by analyzing a data set that includes both fossil and living taxa. The ideal approach might be a total evidence analysis (Hermesen & Hendricks 2008), with a data set of morphological characters for both living and fossil taxa and molecular characters for living taxa, but so far most studies have used a molecular scaffold approach (Springer et al. 2001), in which a morphological data set for living and fossil taxa is analyzed with the arrangement of living taxa fixed to a backbone tree based on molecular data (Eklund et al. 2004, Doyle et al. 2008, Friis et al. 2009, Doyle & Endress 2010, Friis & Pedersen 2011). This seems justified on the grounds that fossils have relatively few characters and that most molecular relationships are robust enough that the addition of fossils would probably not affect the topology of living taxa, but these assumptions should be tested in the future.

Molecular results confirm that the stratigraphic order of appearance of angiosperm pollen types corresponds to their sequence of evolution (Doyle 2005, 2009). The inferred ancestral aperture state is monosulcate, as in the oldest recognizable angiosperm pollen. Prior to the ANITA rooting, a continuous tectum and granular exine structure were widely considered ancestral. Fossil pollen with these features would be difficult to distinguish from pollen of Bennettitales and might therefore have existed long before the Cretaceous without being recognized (Muller 1970, Doyle et al. 1975, Walker & Walker 1984). However, molecular trees imply that the ancestral exine structure was columellar, and although the tectum was originally continuous, a reticulate tectum arose at the node connecting Austrobaileyales and mesangiosperms. This suggests that Valanginian reticulate-columellar monosulcates may not be as far from the origin of angiosperms as thought. The continuous-tectate stage may be represented by Hauterivian pollen with a verrucate tectum reminiscent of *Amborella* (Hughes 1994; Doyle 2001, 2005; Hesse 2001).

Molecular trees imply that tricolpate pollen, the next major fossil type, evolved once from monosulcate on the line to eudicots. Tricolporate pollen was derived from tricolpate several times, as inferred from the varied sculpture of late Albian tricolporates (Doyle 1969, Furness et al. 2007). Most basal eudicots are tricolpate, but a few show isolated origins of tricolporate pollen (some Menispermaceae, Sabiaceae, Buxaceae). Among Pentapetalae, tricolpate pollen is retained in many Saxifragales and Caryophyllales, but Rosidae and Asteridae are basically tricolporate. Triporate pollen with granular exine structure, as in Cenomanian Normapolles, evolved from tricolporate within wind-pollinated Fagales (e.g., Betulaceae, Juglandaceae) and in the wind-pollinated subgroup of Rosales that was formerly called Urticales (Doyle 2009).

Similar congruence can be seen when characters of Cretaceous leaves are plotted on molecular phylogenies (Doyle 2007). The inferred ancestral venation was pinnate, as in most lower Potomac

angiosperms, but there were three early origins of palmate venation, in Nymphaeales, Piperales, and eudicots, consistent with the presence of a few palmately veined leaf types in the lower Potomac and their increasing diversity in the upper Potomac. Upchurch (1984) noted that stomatal patterns in lower Potomac leaves were most like those in *Amborella* and Austrobaileyales, 15 years before these taxa were recognized as basal.

Most phylogenetic analyses of Early Cretaceous angiosperms (see **Figure 3**) have involved fossil flowers. Some of the best-studied localities, from Portugal, were originally thought to be as old as Valanginian, but more recent correlations imply that most of them are late early Albian, with Torres Vedras probably being older (see **Supplemental Section 1**; follow the **Supplemental Materials link** from the Annual Reviews home page at <http://www.annualreviews.org>). Original descriptions of taxa that have been analyzed phylogenetically are referenced in **Supplemental Section 2**. Most of these fossils appear to belong on the stem lineages of living families or larger clades (see **Supplemental Section 3**).

Phylogenetic analyses show better evidence for Magnoliidae and other basal groups, beginning before and continuing alongside the radiation of eudicots. Doyle & Endress (2010) confirmed and refined comparisons of *Endressinia* (late Aptian, Brazil) and *Archaeanthus* (late Albian–early Cenomanian) with Magnoliales, *Virginianthus* (middle Albian) with basal Laurales and *Mauldinia* (late Albian–early Cenomanian) with Lauraceae and Hernandiaceae, and *Walkeripollis* pollen tetrads (late Barremian–early Aptian) with Winteraceae. Monocots are represented from the Aptian onward by *Liliacidites* pollen, with diagnostic graded sculpture (Doyle 1973, Walker & Walker 1984, Doyle et al. 2008); by *Acaciaephyllum*, a leafy stem whose assignment to monocots was questioned by Gandolfo et al. (2000) but confirmed by Doyle et al. (2008); and by inflorescences related to the near-basal monocot family Araceae (Friis et al. 2010b). At least two flowers are securely placed in the ANITA grade: *Monetianthus* (early Albian) in Nymphaeaceae (Friis et al. 2009) and *Anacostia* (early-middle Albian) in Austrobaileyales (Doyle et al. 2008). Other probable Nymphaeales are *Pluricarpellatia* from the late Aptian of Brazil (Mohr et al. 2008) and leaves from the Albian of Jordan (Taylor et al. 2008).

Doyle & Endress (2010) also confirmed affinities of middle and late Albian taxa with tricolpate eudicot lines: peltate leaves and fruits of *Nelumbites* with *Nelumbo*, heads of unisexual flowers and palmately lobed and pinnately dissected leaves (platanoids, *Sapindopsis*) with *Platanus*, and unisexual *Spanomera* flowers with Buxaceae. The first floral evidence for Pentapetalae is near the Albian–Cenomanian boundary (Basinger & Dilcher 1984), but they may be represented among the tricolporate pollen types that begin to proliferate in the late Albian. The relation of Late Cretaceous Normapolles pollen to Fagales is well established by association with fossil flowers (Friis 1984, Friis et al. 2006b).

Fossils related to the now-obscure family Chloranthaceae (or Chloranthaceae plus *Ceratophyllum* if these form a clade) are remarkably conspicuous in early angiosperm floras. These include monosulcate pollen with characteristic sculpture and a thick nexine (*Clavatipollenites*, *Asteropollis*, *Pennipollis*; Doyle 1969, Walker & Walker 1984, Doyle et al. 2008), leaves with chloranthoid teeth and stomata (Upchurch 1984), and extremely simple flowers with single uniovulate carpels (Pedersen et al. 1991, Friis et al. 2000, Eklund et al. 2004). Some have suggested that Chloranthaceae offer an alternative prototype for the angiosperm flower (Nixon et al. 1994, Taylor & Hickey 1996), but this conflicts with molecular data, which place the family securely in the mesangiosperms, implying that their floral simplicity is a result of reduction (Endress & Doyle 2009). This view is consistent with the coeval existence of more complex flowers and is further supported by *Canrightia* (Friis & Pedersen 2011), which resembled Chloranthaceae and *Ceratophyllum* in having one orthotropous ovule per carpel but retained bisexual flowers with several tepals, stamens, and carpels. Although Chloranthaceae may not be a key to the origin of angiosperms, they

are significant as the first common angiosperms, which bears on ecological causes for the rise of the group (Feild et al. 2004, Feild & Arens 2007).

Similar discussion was stimulated by the finding that Hydatellaceae, minute aquatic plants with linear leaves that were assumed to be monocots, are instead a basal branch of Nymphaeales (Saarela et al. 2007). Their reproductive structures have been interpreted as inflorescences of unisexual flowers consisting of one stamen or one carpel, but Rudall et al. (2009) suggested instead that they represent a nonfloral or prefloral state. However, the phylogenetic position of Hydatellaceae implies that their flowers are reduced (Endress & Doyle 2009).

A related case is *Archaeofructus*, an aquatic plant with finely dissected leaves and reproductive axes bearing single or paired stamens and carpels, from the Yixian lake beds of northeast China (Sun et al. 1998, 2002). *Archaeofructus* was first reported as the oldest known angiosperm (Sun et al. 1998), because the Yixian was thought to be Late Jurassic, but the beds have been redated radiometrically as Barremian or Aptian (Zhou et al. 2003). A cladistic analysis by Sun et al. (2002) placed *Archaeofructus* below all living angiosperms, which led them to suggest that it illustrates a prefloral stage before the perianth, stamens, and carpels were grouped into typical flowers. However, Friis et al. (2003) cited the fact that the stamens and carpels are often in pairs as evidence that the reproductive axes were inflorescences of reduced unisexual flowers. They also noted that the ternate pattern of leaf dissection resembles that of *Vitiphyllum* in the lower Potomac and Ranunculales in the eudicots. Phylogenetic analyses by Doyle (2008) and Endress & Doyle (2009) nested *Archaeofructus* in the angiosperm crown group with one of two taxa that have even simpler flowers, depending on the backbone tree: *Ceratophyllum*, if this plant is linked with eudicots, or Hydatellaceae. These results depend on the description of *Archaeofructus* as having monosulcate pollen, but Friis et al. (2003) questioned whether the remains figured by Sun et al. (2002) were pollen grains. If pollen characters of *Archaeofructus* are scored as unknown, its most parsimonious position is in Ranunculales (Endress & Doyle 2009). Under any of these hypotheses, *Archaeofructus* is too far from the base of the angiosperms to have a major impact on inferred ancestral states.

These and other fossils with eudicot-like features pose problems for the congruence of the leaf, pollen, and flower records. The Yixian Formation also contains simple and ternate leaves associated with eudicot-like four- and five-carpellate fruits (*Sinocarpus*, *Leeifructus*: Leng & Friis 2006, Sun et al. 2011). *Vitiphyllum* occurs with the oldest tricolpate pollen in the Potomac (Doyle & Hickey 1976, Hickey & Doyle 1977), at a level that is probably earliest Albian (Hochuli et al. 2006), but the Yixian is Barremian or Aptian. Tricolpate pollen occurs in the latest Barremian and Aptian of Africa and South America (Doyle 1992, Brenner 1996, Heimhofer & Hochuli 2010), but only isolated pre-Albian tricolpate grains are known in Europe (Hughes 1994), and northeast China was at a higher paleolatitude, where tricolpates generally appeared later (Brenner 1976, Hickey & Doyle 1977, Crane & Lidgard 1989). Ternately lobed leaves also predate tricolpate pollen in the Aptian of Argentina (Archangelsky et al. 2009, Puebla 2009). One possibility is that some or all of these leaves are not eudicots, but rather extinct lines of Nymphaeales, as proposed for *Archaeofructus*. Another is that they represent taxa on the eudicot stem lineage, before the origin of tricolpate pollen. Parsimony analysis implies that dissected leaves arose within Ranunculales (Doyle 2007), but according to likelihood analysis (Geeta et al. 2012) they probably already existed in the ancestor of eudicots. Alternatively, it may be that tricolpate pollen occurs in the Yixian and Argentina but is rare because the first eudicots were low pollen producers. Wang et al. (2000) reported “prototricolpate” pollen from the Yixian, but it is not clear that these grains have three colpi; at least one (figure 21 of Wang et al. 2000) may be a crushed grain of the conifer *Classopollis*.

An important result of molecular studies concerns the original morphology of the carpel (Figure 3). The ANITA rooting refutes the older view that the ancestral carpel was plicate (conduplicate), like a leaf folded down the middle and sealed by fusion of the margins, as in some

Winteraceae and Magnoliales (Bailey & Swamy 1951). Instead, the ANITA groups, Chloranthaceae, and *Ceratophyllum* have ascidiate carpels, in which the arms of the U-shaped primordium are connected by a meristematic cross zone and the carpel grows up like a tube. The inside of the tube becomes a canal sealed with secretion, a remarkable “half-angiospermous” condition (Doyle & Endress 2000, Endress & Igersheim 2000). Because developmental data may be needed to distinguish ascidiate from plicate carpels (Endress 2005), this character is difficult to determine in fossils. However, many Aptian–early Albian carpels were barrel shaped and lack evidence for a ventral suture, which suggests that they were ascidiate (Friis et al. 2000, Doyle 2001).

With one ovule per carpel in *Amborella*, Hydatellaceae, some Austrobaileyales, Chloranthaceae, and *Ceratophyllum*, this condition can be reconstructed as ancestral (Endress & Doyle 2009). Uniovulate carpels predominate in Early Cretaceous mesofossil floras (Friis et al. 2010b). It is equivocal whether the ancestral ovule was anatropous (reflexed) or orthotropous (erect), because *Amborella*, Chloranthaceae, and *Ceratophyllum* are orthotropous and other near-basal taxa are anatropous. However, the fact that the outer integument of *Amborella* and Chloranthaceae is asymmetrical in development suggests that these taxa came from anatropous ancestors (Yamada et al. 2001). Both types occur in the Early Cretaceous, but anatropous seeds are more common (Friis et al. 2010b). Many have a hard exotestal layer, as in Nymphaeales and most Austrobaileyales, and sometimes an operculum, a synapomorphy of Nymphaeales (Friis et al. 2006a, 2010a; Mohr et al. 2008).

Traditionally, bisexual flowers have been considered ancestral, but this is equivocal on parsimony grounds because so many basal lines are unisexual (*Amborella*, Hydatellaceae, Schisandraceae, *Ceratophyllum*, and *Hedyosmum* and *Ascarina* in the Chloranthaceae). However, the presence of sterile stamens in female flowers of *Amborella* suggests a bisexual ancestry (Endress & Doyle 2009). Both bisexual and unisexual flowers are conspicuous in the oldest mesofossil floras (Friis et al. 2010b).

Since a survey of angiosperm distributions by Bews (1927), most botanists have viewed angiosperms as a basically tropical group. The fact that taxa then considered primitive (woody magnoliids and ANITA lines) are most diverse in Southeast Asia and Australasia led Takhtajan (1969) to conclude that the first angiosperms were trees of wet tropical forests. By contrast, Stebbins (1974) argued that the novel features of angiosperms, many related to acceleration of the life cycle, were more likely selected in unstable habitats in the drier tropics. Using evidence for aridity in the Early Cretaceous of Northern Gondwana (salt deposits, subordinate ferns, abundant dry-adapted conifers and Gnetales), Brenner (1976) argued that the poleward spread of tricolpate pollen supported this view. Although this argument was strictly relevant for eudicots only, the fact that monosulcate angiosperm pollen was also more abundant and diverse in Northern Gondwana suggested that it might be valid for angiosperms as a whole (Doyle et al. 1977). In the Potomac area, which was wet and subtropical, Doyle & Hickey (1976) and Hickey & Doyle (1977) argued that the morphology and facies distribution of angiosperm leaves (largely in coarser stream-margin facies) fit the view that they represented immigrants from the semiarid tropics that were preadapted to disturbed habitats. However, the geographic argument has been weakened by evidence that some parts of Northern Gondwana (Egypt, Israel, Colombia) were less arid (more abundant ferns, some coals) and that early angiosperm pollen was as common there as in dry regions, or more so (Doyle et al. 1982, Schrank 1983, Brenner 1996, Ibrahim 2002, Schrank & Mahmoud 2002). Early angiosperm leaves from Colombia (Pons 1984) are similar to those at middle latitudes. Taylor & Hickey (1996) argued that the first angiosperms were herbaceous, citing evidence for herbaceous angiosperms in the Early Cretaceous and the fact that Chloranthaceae and Piperales were basal in their phylogenetic analysis.

Molecular analyses have led to revision of these ideas. Feild et al. (2004) and Feild & Arens (2007) showed that the ANITA groups, except Nymphaeales, have adaptations to disturbance

(including small seeds) but grow in low-light understory habitats in wet tropical and subtropical forests, suggesting that this is the original niche of angiosperms—the “dark and disturbed” hypothesis. Chloranthaceae often grow in sunnier habitats, suggesting that new adaptations that allowed them to “break out” of the understory could explain why they were the first common angiosperms. Feild et al. (2004, 2009) argued that these inferences were consistent with the lower Potomac record, in which angiosperms are associated with evidence for disturbance but subordinate to conifers and ferns. Lower Potomac angiosperm leaves lack xeromorphic cuticle features, and their epidermal and venational similarities to ANITA taxa (Upchurch 1984, Feild et al. 2011) suggest that they had similar physiology. Evidence for open stream-margin habitats is seen later, in Albian platanoids.

The prominence of aquatic angiosperms in the Early Cretaceous (doubtless magnified by preservational bias) has led to suggestions that the first angiosperms were aquatic (Sun et al. 2002, Coiffard et al. 2007, Gomez et al. 2008). In addition to *Archaeofructus* (Sun et al. 2002), aquatics include *Monetianthus* (Friis et al. 2009), *Pluricarpellatia* (Mohr et al. 2008), Albian nymphaealean leaves (Taylor et al. 2008), *Montsechia* from Barremian lake beds in Spain (Martín-Closas 2003), late Albian–early Cenomanian *Ceratophyllum* relatives (Dilcher & Wang 2009), and *Nelumbites* (Samylina 1968, Hickey & Doyle 1977, Upchurch et al. 1994). However, all of these that have been analyzed phylogenetically have been linked with living taxa in which the aquatic habit is best interpreted as derived. Even if *Archaeofructus* were basal (Sun et al. 2002), in the absence of outgroups it would be equally parsimonious to assume that the first angiosperms were aquatic or terrestrial. An aquatic ancestry is implausible on anatomical grounds because it would probably entail loss of cambial activity, as in monocots, Nymphaeales, *Ceratophyllum*, and *Nelumbo* (Carlquist 2009), whereas *Amborella* and Austrobaileyales have a normal secondary xylem cylinder (Feild & Arens 2007). There are almost no cases in which relationships imply that terrestrial angiosperms were derived from aquatics (Cook 1999), with the conspicuous exception of monocots, which prove the rule by lacking a normal bifacial cambium. However, the early appearance of aquatics could support the idea that the first angiosperms had a growth habit (e.g., rhizomatous) that was more easily transformed into an aquatic one than would be expected if they were trees.

MOLECULAR AND FOSSIL DATA ON ANGIOSPERM OUTGROUPS AND HOMOLOGIES

Molecular analyses of seed plants appear to refute the view that the closest living relatives of angiosperms are Gnetales, a key element of the anthophyte hypothesis. Early analyses of single genes gave highly varied trees (reviewed by Doyle 1998b, 2001; D.E. Soltis et al. 2005), but multigene analyses have narrowed these to a few main alternatives (**Figure 4**). Only a few studies of ribosomal DNA have grouped angiosperms and Gnetales, with negligible statistical support (Hamby & Zimmer 1992, Stefanovic et al. 1998, Rydin et al. 2002), and there is zero character support for this relationship in the chloroplast genes *rbcL*, *psaA*, and *psbB* (Sanderson et al. 2000, Sanderson & Doyle 2001). Many multigene analyses, beginning with Qiu et al. (1999), Bowe et al. (2000), and Chaw et al. (2000), nested Gnetales within conifers, usually as the sister group of Pinaceae—the gnepine hypothesis (**Figure 4a**). In most such trees, angiosperms are the sister group of extant gymnosperms (acrogymnosperms: Cantino et al. 2007). This does not mean that gymnosperms in the traditional sense of “plants with naked seeds” are monophyletic; all morphological analyses have placed various Paleozoic seed ferns, which are typologically gymnosperms, below the seed plant crown group. Trees with Gnetales in conifers but cycads linked with angiosperms (**Figure 4b**) were found in some analyses of Magallón & Sanderson (2002) and in the study by

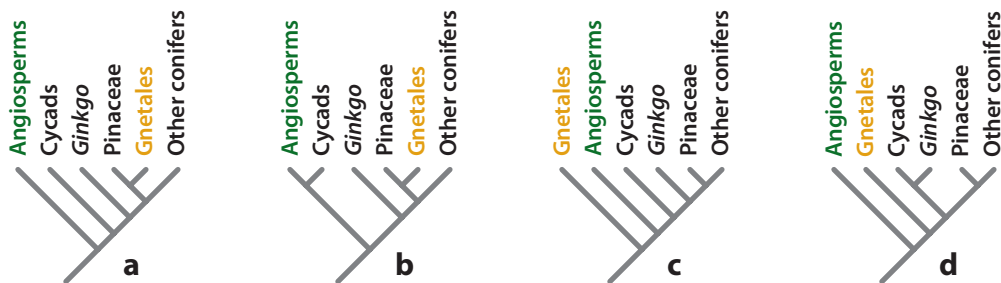


Figure 4

Main phylogenetic relationships among living seed plants found in molecular analyses. Panels *a* and *b* are gnetpine trees.

Mathews et al. (2010), in which phylogenies of genes derived from duplications on the seed plant stem lineage were used to root one another. In the most common alternative, Gnetales were the sister group of other seed plants—a Gnetales-basal tree (**Figure 4c**). In most such trees, angiosperms were sister to the remaining taxa, but in those of Rai et al. (2008), angiosperms were linked with cycads. In an analysis of ~1,200 genes but only 16 taxa (de la Torre-Bárcena et al. 2009), angiosperms were basal in seed plants and Gnetales were sister to other gymnosperms (**Figure 4d**). Trees of the last two types are less consistent with stratigraphy than either anthophyte or gnetpine trees because Gnetales and angiosperms are the last two seed plant lines to appear in the fossil record (Doyle 1998a, Burleigh & Mathews 2004).

These conflicts among trees do not inspire confidence in molecular data (cf. Rothwell et al. 2009), but studies using more statistical approaches help identify which results are due to long-branch effects (Felsenstein 1978), which occur when too much evolution on some lines results in convergences or reversals that outnumber true synapomorphies between lines (reviewed by Mathews 2009). First are comparisons of analyses of first and second codon positions (where most substitutions result in different amino acids) versus third positions (where most substitutions do not affect amino acid composition), which evolve more rapidly and are more subject to homoplasy. When analyses of all codon positions give Gnetales-basal trees, analyses of first and second positions give gnetpine trees, thus favoring the latter (Sanderson et al. 2000, Magallón & Sanderson 2002). Burleigh & Mathews (2004) obtained similar results by removing rapidly evolving sites, irrespective of codon position. Second are studies comparing parsimony, maximum likelihood, and Bayesian methods; the latter two are designed to compensate for multiple changes and should be less subject to long-branch effects. Data sets that give Gnetales-basal trees when analyzed with parsimony give gnetpine trees when analyzed with likelihood and Bayesian methods (Magallón & Sanderson 2002, D.E. Soltis et al. 2002, Burleigh & Mathews 2004). These results have led some to conclude that relationships among living seed plants are now resolved in favor of the gnetpine hypothesis, but this may be premature (Mathews 2009, Mathews et al. 2010).

Gnetpine trees were not a complete surprise from a morphological point of view. Before the advent of cladistics, many authors had noted possible homologies of Gnetales and coniferophytes in wood anatomy, leaf morphology, and organization of the strobili (Bailey 1925, 1953; Eames 1952; Bierhorst 1971; Doyle 1978). Weaknesses of characters thought to associate Gnetales and angiosperms were discussed by Donoghue & Doyle (2000), and additional anatomical similarities between Gnetales and conifers (e.g., pits with a torus) were documented by Carlquist (1996). In the morphological analysis of Doyle (2008), in which characters were rescored in accordance with these observations, trees with Gnetales in conifers and in an anthophyte clade became equally parsimonious.

Resolution of seed plant phylogeny in favor of a gnepine tree may seem like a Pyrrhic victory to those interested in the origin of angiosperms. Whereas the anthophyte hypothesis implied that Gnetales might preserve steps in the evolution of angiosperm features, such as double fertilization (Friedman & Carmichael 1996), trees in which angiosperms and acrogymnosperms are sister groups imply that no living outgroup is closer to the angiosperms than any other. If so, living plants provide no evidence on the homologies of new angiosperm features or their sequence of origin, except perhaps via studies on the phylogeny of genes involved in development (Frohlich & Chase 2007). If cycads are sister to the angiosperms (Mathews et al. 2010), the situation is not much better; the main step that cycads show toward angiosperms is partial simplification of the leaf from the fernlike frond of the first seed plants. Progress can come only from recognition of fossil stem relatives of the angiosperms, but these can be recognized only by analysis of morphology, and the reliability of morphology has been challenged by the molecular results. However, even if morphology was misleading in the case of angiosperms and Gnetales, it is not always misleading, as illustrated by the many cases in which molecular analyses have confirmed the results of morphological analyses (and precladistic views).

If gnepine trees are correct, the situation is analogous to that of amniotes, in which living mammals and reptiles (including birds) are sister groups that split in the Carboniferous (Gauthier et al. 1988, Meyer & Zardoya 2003). However, there is a long series of so-called mammal-like reptiles that are securely attached to the mammal stem lineage, whereas there is no consensus among paleobotanists that any known fossils are angiosperm stem relatives (cf. Taylor & Taylor 2009).

To evaluate potential stem relatives of angiosperms in the context of molecular results (Doyle 2006, 2008), I used a molecular scaffold approach, with relationships of living taxa constrained to a gnepine tree. Some justification for this approach was provided by the angiosperm analyses of Doyle & Endress (2000): Where the results of morphological and molecular analyses differed, the combined analysis agreed with molecular data (at least for the angiosperm taxa included in Doyle 2006, 2008), so a purely morphological analysis would be hard to defend. Furthermore, a total evidence analysis of first and second codon positions of four genes and the Doyle (2006) data set by Magallón (2010) gave the same series of fossil outgroups. From the base, these were glossopterids and *Pentoxylon*, then Bennettitales, and then *Caytonia* as the sister group of the angiosperms (**Figure 5**). In unconstrained trees with Gnetales in conifers (Doyle 2008), cycads were at the base of the angiosperm line, as in Magallón (2010) and Mathews et al. (2010). With this outgroup arrangement, it is most likely that aggregation of fertile parts into a flower occurred independently in angiosperms and Bennettitales, so I concentrate on the origin of the parts.

Considering female structures (**Figure 5**), the association of angiosperms with glossopterids and *Caytonia* is consistent with the hypothesis that the outer integument of angiosperms is homologous with the cupule in these fossils, which was itself derived from a leaf or a leaflet with ovules on the adaxial (upper) surface (versus the abaxial surface in cupules of peltasperms and corystosperms; Doyle 2006). The *Caytonia* cupule is like an angiosperm bitegmic ovule in being anatropous; it differs in containing several ovules, which would have to be reduced to one. There are problems in homologizing the cupule-bearing structures of glossopterids and *Caytonia*, although a relationship between the two taxa has also been found in analyses in which they had nothing to do with angiosperms (Nixon et al. 1994, Rothwell & Serbet 1994, Rothwell et al. 2009). In glossopterids, the cupule is most easily interpreted as a leaf (sporophyll) borne on an axillary branch that is adnate to the subtending leaf, whereas in *Caytonia* the cupules have been interpreted as leaflets borne along the rachis of a compound leaf (Harris 1940, Gaussen 1946, Stebbins 1974, Doyle 1978, Retallack & Dilcher 1981). One of several possibilities (Doyle 2008) is that the supposed rachis is actually a branch. Wang (2010a) interpreted an Early Cretaceous fossil with spirally arranged cupules

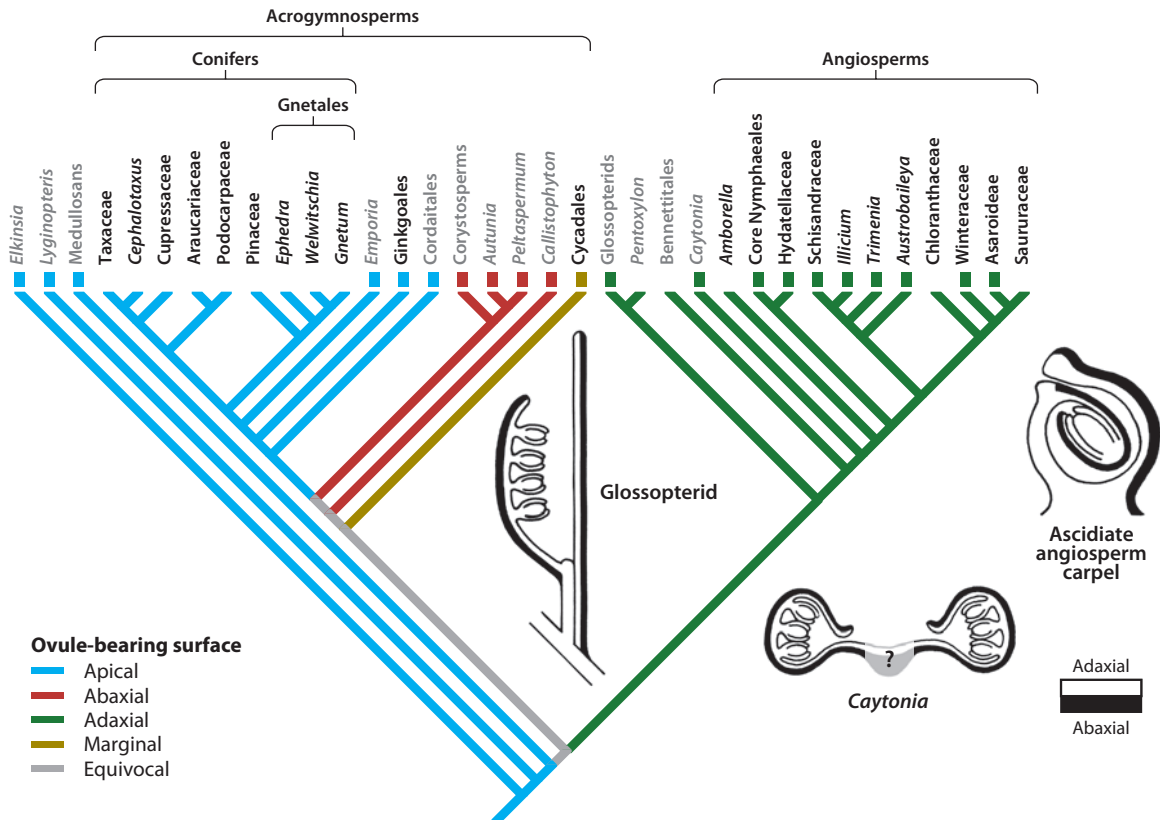


Figure 5

Representative seed plant tree from analysis of the morphological data set of Doyle (2008) with the arrangement of living taxa fixed with a gnetpine molecular backbone tree, showing the inferred evolution of ovule position. Diagrams show ovulate structures in glossopterids and *Caytonia* and an ascidiace angiosperm carpel, with abaxial surfaces indicated in black. Names of Recent taxa are indicated in black; those of fossil taxa, in gray.

as support for this possibility, but its relationship to *Caytonia* is questionable. If a glossopterid-like structure existed on the line to angiosperms, this might be consistent with reconstruction of the ancestral angiosperm as having one bitegmic ovule on the cross zone of an ascidiace carpel (Endress & Doyle 2009). The carpel wall could be homologous with the subtending leaf, whereas the position of the ovule could be compared with that of the cupule on the axillary branch.

The weakest link in this scenario may be Bennettitales, which have been associated with angiosperms in all morphological analyses, because their female structures show no obvious relation to either a glossopterid or an angiosperm plan. Current controversies on the interpretation of bennettitalean organs and suggestions that they show homologies with Gnetales are discussed in **Supplemental Section 4**.

Homologies between the angiosperm stamen and male structures in the outgroups are harder to recognize. Because the stamen has four microsporangia, Thomas (1925) compared it with the tetrasporangiate synangia (fused sporangia) of *Caytonia*, which were borne on a branched sporophyll, but as noted by Harris (1937), the stamen differs in being bilateral, with two fused sporangia on either side of the sterile connective. Gaussen (1946) suggested that the stamen was instead derived from a whole *Caytonia*-type sporophyll by reduction to two synangia. On the

basis of the ANITA rooting, the sporangia were originally lateral or adaxial (Endress & Doyle 2009). In this respect, the stamen is comparable with male structures in glossopterids, which had a sporangium-bearing branch on the adaxial side of a leaf, or with those in Bennettitales, which had synangia on the adaxial side of a sporophyll (Doyle 2008).

In the vegetative sphere, the trees of Doyle (2006, 2008) imply that the angiosperm leaf was derived from a simple pinnate type (as defined by Doyle & Donoghue 1986), with one order of laminar venation, either dissected into leaflets with one or more equal veins (most cycads and Bennettitales) or undivided (glossopterids plus fossil cycads, *Pentoxylon*, and Bennettitales with leaves of the *Taeniopteris* type). The palmately compound leaves of *Caytonia* would be an autapomorphy. The simple reticulate venation of glossopterids and *Caytonia*, made up of one vein order, could be a first step toward the complex reticulate venation of angiosperms. A subsequent step would be origin of a hierarchy of vein orders, which has been related to a shift from marginal to diffuse meristematic activity (Doyle & Hickey 1976, Boyce & Knoll 2002).

This review illustrates how many aspects of the morphology of critical fossil taxa are not yet understood. In the lack of consensus on whether any known taxa are angiosperm stem relatives, it may be that recognition of closer outgroups is needed to solve these problems. It may be that such outgroups exist among fossils that have been proposed as pre-Cretaceous angiosperms, which are evaluated in the next section.

TIME AND ENVIRONMENT OF ORIGIN

Analyses that use divergence in DNA sequences to date the splitting of extant lines have reopened the question of the age of the angiosperms. Molecular trees in which angiosperms are sister to living gymnosperms (acrogymnosperms) imply that the stem lineages of the two groups split some time before the oldest known fossil acrogymnosperms, namely Cordaitales in the Early Pennsylvanian and stem conifers in the Middle Pennsylvanian. This split was probably significantly younger than the oldest known seed-bearing plants in the Late Devonian, such as *Elkinsia*, because phylogenetic analyses place these several nodes below the seed plant crown node (Rothwell & Serbet 1994; Doyle 1996, 2006; Hilton & Bateman 2006) and because Mississippian seed plants also appear to be stem relatives. The origin of the angiosperm crown group could be anywhere between divergence of the stem lineage and the first crown group fossils in the Valanginian. Molecular dating offers a means of estimating the absolute time between the stem and crown nodes.

Molecular dating requires absolute fixed calibration points or minimum or maximum ages of nodes (imposed as constraints or parametric distributions) based on fossils. Such fossils should ideally be integrated into the phylogeny of living groups by phylogenetic analysis of their characters (Doyle & Donoghue 1993, Crepet et al. 2004, Magallón 2004), a condition that is not always met. Minimum ages are relatively easy to obtain, but analyses normally also require at least one fixed calibration or maximum age. Establishing these is more problematic because it assumes that the record of fossils with a synapomorphy of the group in question is dense enough that older occurrences are unlikely to have been missed. The most popular basis for a fixed or maximum age in angiosperms is the appearance of tricolpate eudicot pollen, discussed further below.

Whereas studies of the Cretaceous record were consistent with an origin of the angiosperm crown group near the Valanginian, molecular analyses have dated the crown node as either somewhat or much older than the Cretaceous. The first such analyses used the assumption of a molecular clock—that the rate of divergence in DNA sequences is stochastically constant over time and across branches. Such studies were reviewed by Sanderson & Doyle (2001), who evaluated errors due to a variety of factors, such as the stochastic nature of the substitution process, variation in rates with codon position, effects of tree topology, and variation in rates among lineages. This analysis

showed that the oldest dates for angiosperms [319–292 million years ago (Mya), Pennsylvanian; Martin et al. 1989, 1993] could be an artifact of sampling grasses and other herbaceous taxa that have high rates, possibly due to short generation times, and incorrect rooting on the grass lineage. Clock-based analyses with broader taxon sampling and more plausible topologies gave ages of 143–141 Mya (earliest Cretaceous) for *rbcL* and 188 Mya (Early Jurassic) for 18S ribosomal DNA.

Statistical tests in this and earlier studies (see Sanderson & Doyle 2001) showed that molecular data violated the assumption of a clock at the level of seed plants. Such cases stimulated the development of dating methods that do not assume a clock (see Magallón 2004, Sanderson et al. 2004). Examples include autocorrelated relaxed clock methods that assume that rates change gradually from one branch to the next, and Bayesian methods that use a probability distribution to model rate changes and introduce constraints as probabilistic prior distributions. However, when the data violate a clock, methods that do not assume a clock will not necessarily be more accurate; they make assumptions of their own that may or may not be valid. The most recent Bayesian analyses have continued to provide a wide range of dates for the angiosperm crown group. Bell et al. (2010) obtained estimates of 183–147 Mya (Early to Late Jurassic), but dates of Smith et al. (2010) centered on 228–217 Mya (Late Triassic), and Magallón (2010) obtained ages ranging from 275 Mya (Early Permian) to 221.5 Mya (Late Triassic). Setting aside the relative merits of different methods, a matter of much debate, it may be useful to consider how these dates relate to the fossil record.

As Smith et al. (2010) noted, their analysis challenged the use of the age of the oldest known tricolpate pollen (~125 Mya) as a maximum age for the eudicot crown node, which they dated as 153 Mya (Late Jurassic). By contrast, Bell et al. (2010) obtained eudicot ages of 130–129 Mya (Hauterivian–Barremian); this node was fixed in Magallón (2010). Tricolpate pollen has the advantage of being a unique synapomorphy of a large clade, being conspicuous in the fossil state, and having a dense fossil record. As discussed above, rare tricolpate grains are first known from the latest Barremian of both Southern Laurasia and Northern Gondwana (Doyle 1992, Hughes 1994), and although there are few Aptian records from Laurasia, tricolpates are present throughout the Aptian in Northern Gondwana (e.g., Heimhofer & Hochuli 2010) and ubiquitous in the Albian of both provinces. Smith et al. (2010) questioned the assumption that the oldest tricolpates were close to the origin of eudicots because they showed “considerable structural variety” (Friis et al. 2006a, p. 274) and occurred in widely separated geographic areas. However, the diversity of the first tricolpates is only a fraction of that in the Albian, and the cosmopolitan distribution of many Cretaceous pollen types suggests that intercontinental dispersal was relatively easy. Furthermore, Friis et al. (2006a) may have overestimated the diversity by considering not only late Barremian but also Aptian palynofloras (e.g., with striate tricolpates) and early Albian mesofossil floras. However, the presence of leaves with eudicot-like characters in Aptian beds with no reported tricolpate pollen is cause for caution.

The analysis of Smith et al. (2010) also indicated that Pentapetalae (core eudicots) began to diversify in the Barremian, but there is no record of the tricolporate pollen or the pentamerous, dicyclic perianth characteristic of most Pentapetalae until the late Albian. If there were already basal eudicots in the Late Jurassic and Pentapetalae in the Barremian, the temporal sequence of monosulcate, tricolpate, and tricolporate pollen and its congruence with the evolutionary series inferred from molecular phylogenies would be a mystery. It is also difficult to imagine why angiosperms would remain hidden for so long if they had already diversified into clades that rose so rapidly in the mid-Cretaceous.

Together with phylogenetic evidence on the ancestral ecology of angiosperms, molecular dating has led to resurrection of a moderated version of the pre-Cretaceous homeland theory of Axelrod (1952, 1970). In arguing that the first angiosperms were physiologically restricted to

dark, wet, and disturbed (sub)tropical understory habitats, Feild et al. (2004, 2009) noted that this might explain the lack of a Jurassic fossil record of angiosperms if they existed at that time but did not diversify beyond the level of the ANITA grade. This is because ever-wet tropical environments were highly restricted in the Jurassic, when most of the tropical belt was arid and/or monsoonal (Rees et al. 2000, Ziegler et al. 2003). The idea that ANITA-grade angiosperms might have persisted without radiating is consistent with analyses by Magallón & Sanderson (2001), who inferred that rates of diversification were initially low and only increased in the mesangiosperms. The Cretaceous rise of angiosperms might therefore mark the radiation of mesangiosperms that broke out of the dark and disturbed niche, as suggested for Chloranthaceae. However, this must be weighed against evidence that ANITA-grade Nymphaeales and Austrobaileyles were also radiating in the Early Cretaceous.

This scenario would be consistent with 146–130 Mya (latest Jurassic–Hauterivian) ages for mesangiosperms inferred by Bell et al. (2010), but not with the 184 Mya (Early Jurassic) date of Smith et al. (2010). Feild et al. (2009) argued that “ancestral xerophobia” persisted into the mesangiosperms, to Canellales (Winterales) in the magnoliid clade; this scenario might increase the plausibility of ecologically restricted Jurassic mesangiosperms. However, there is reason to suspect that it was not difficult for early mesangiosperms to shift to drier habitats. By the Barremian, monosulcate angiosperm pollen (probably a mixture of ANITA lines, Chloranthaceae, and magnoliids) was more common and diverse in semiarid Northern Gondwana than in Laurasia (Doyle et al. 1977, 1982; Schrank 1983; Brenner 1996). Some of this pollen may represent plants of local wet and upland sites (Feild et al. 2009), but it is so common that this is probably not the whole story. In the Aptian of Brazil, *Endressinia* (Mohr & Bernardes de Oliveira 2004) appears to be a member of the Magnoliales that was dry-adapted, judging from its small leaves and associated climatic indicators (Doyle & Endress 2010).

In view of these results, it is time to reexamine supposed pre-Cretaceous fossil evidence for the angiosperm line. Many fossils have been proposed as pre-Cretaceous angiosperms (older ones listed by Axelrod 1952, 1970), but critical reviews, beginning with Scott et al. (1960), have shown that most of these were incorrectly dated (*Archaeofructus* is a recent example; Zhou et al. 2003), belonged to poorly understood gymnosperm groups, or lacked sufficient diagnostic features (Doyle 1978, Doyle & Donoghue 1993, Hughes 1994). Here I concentrate on fossils that are most resistant to refutation or recently reported. An intriguing possibility is that some of these are angiosperm stem relatives. Some authors seem curiously determined to prove that pre-Cretaceous fossils are crown group angiosperms, but for understanding most aspects of the origin of angiosperms (other than their age), close stem relatives would be far more significant. Novel crown group members could alter inferences on ancestral states, but only stem relatives could reveal events in the hidden history of the angiosperm line.

Among pre-Cretaceous angiosperm-like fossils, the most widespread are monosulcate pollen types described by Cornet (1989) from the Late Triassic of Virginia as the *Crinopolles* group and similar pollen from the Triassic elsewhere (Doyle & Hotton 1991, Hochuli & Feist-Burkhardt 2004). *Crinopolles* have a strikingly angiosperm-like outer exine, with a reticulate tectum supported by columellae. However, transmission electron microscopy (Cornet 1989, Doyle & Hotton 1991) shows that the inner exine layer (nexine) differs from that of monosulcate angiosperms in consisting of a uniformly thick, darker-staining endexine, as in gymnospermous groups (Doyle & Hotton 1991). This suggests that *Crinopolles* may represent plants on the angiosperm stem lineage. This hypothesis would conflict with the older view that granular exine structure was ancestral in angiosperms, but it is more plausible now that columellar structure appears to be ancestral (Doyle 2005). However, the affinities of *Crinopolles* will remain speculative until they are associated with other organs.

A much-discussed pre-Cretaceous megafossil is *Sanmiguelia*, based on pleated leaves from the Late Triassic, which Brown (1956) described as palm-like. Closer examination showed that these leaves differed from those of palms and most other monocots in lacking a midvein, and the preservation was too poor to show cross veins, an expected feature of monocots (Doyle 1973; Doyle et al. 2008). However, Cornet (1986) described new material with apparent cross veins, plus associated reproductive structures. He interpreted the female structures as having angiosperm-like carpels, but morphological details are difficult to discern (Crane 1987). The male structures appear to be strobili with sessile pairs of pollen sacs, more reminiscent of ginkgophytes than angiosperms, and the smooth monosulcate pollen has no angiosperm features. These characters suggest a position either on the angiosperm stem lineage or in some group with no close relationship to angiosperms (Doyle & Donoghue 1993).

Early Jurassic fossils named *Schmeissneria*, which were originally assumed to be reproductive axes of a ginkgophyte, were reinterpreted by Wang (2010b) as bearing units made up of two fused carpels with enclosed seeds. Because carpel fusion evolved several times within angiosperms, this character would support a position in the crown group, but the associated leaves, male strobili, and pollen are typically ginkgophytic (van Konijnenburg-van Cittert 2010). One possibility is that the female units are homologous with the so-called bivalved capsules of the ginkgophyte order Czekanowskiales. *Schmeissneria* is unlikely to be a link between angiosperms and ginkgophytes because *Ginkgo* may be the only seed plant group that no molecular or other analysis has ever associated with angiosperms.

Vesselless woods with scalariform pitting, termed *Sabnioxylon*, were once compared with angiosperms, but judging from the form of whole stems, they are probably Bennettitales (Bose & Sah 1954, Philippe et al. 1999). Philippe et al. (2010) argued that Early-Middle Jurassic vesselless wood named *Ecpagloxyton* was more likely related to angiosperms because it had additional detailed features shared with *Amborella* (in which vesselless wood is presumably primitive) and the eudicots *Tetracentron* and *Trochodendron* (in which the absence of vessels is apparently due to reversal; Doyle & Endress 2000). However, given that such wood may be ancestral in angiosperms, it is unclear whether *Ecpagloxyton* is a member of the crown group or a stem relative, if it is most closely related to angiosperms.

Perhaps most tantalizing is a 36-mm elliptical leaf described by Seward (1904) as *Phyllites* sp. from the Middle Jurassic Stonesfield Slate of England (refigured by Cleal & Rees 2003), which had trinerved-palmate major venation and outer secondary veins. Such venation is common in angiosperms and not known elsewhere, but no finer veins are preserved, so it cannot be determined if the leaf had the typical hierarchical reticulate vein pattern of angiosperms. Because molecular trees imply that the ancestral venation in angiosperms was pinnate, and palmate venation arose independently in Nymphaeales, Piperales, and eudicots (Doyle 2007), this character would tend to place *Phyllites* within the crown group. A relationship with Nymphaeales would be consistent with the hypothesis that Jurassic angiosperms were still at the ANITA grade. However, without preservation of the finer venation or cuticle, any assignment to the angiosperms must remain tentative.

Despite how much we have learned about the first angiosperms from fossil and molecular data, the inconclusive results of phylogenetic analyses of seed plants and the problems of interpretation of pre-Cretaceous records show how much we have yet to learn about the origin of angiosperms. However, better information on the morphology of known or new outgroups could have a dramatic effect on our understanding.

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