ORIGIN AND DIVERSIFICATION OF ANGIOSPERMS

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GLOSSARY

homology   Similarity due to common ancestry.
phylogeny   The evolutionary history of species and higher taxa.
synapomorphies   Shared characteristics that define a cladistic grouping or clade.

ONLY A FEW YEARS AGO, a meaningful understanding of angiosperm relationships and their diversification might have seemed out of reach and questions swirled around the origin with little focus. Recent stunning advances in molecular systematics (Palmer and Zamir, 1982), including those techniques that now allow rapid analysis of large molecular datasets (the "ratchet," Nixon, 2003), have resulted in remarkably well-resolved assessments of within-angiosperm relationships. These advances accompanied by a much improved fossil record of angiosperms now also allow us to estimate timing in their diversification. The origin of angiosperms, however, is another matter. Just a few years ago, the angiosperms were comfortably nested in a clade called "anthophytes" with living Gnetales and extinct Cycadeiodales (Bennettitales). The same advances in molecular systematics that have provided valuable insights into within-angiosperm relationships and timing in angiosperm history have challenged the integrity of the anthophytes removing Gnetales to the rest of the gymnosperms. Cycadeoidales, on a closer look, may also be more appropriately grouped with other gymnosperms. Thus, new methods have helped to focus our questions on angiosperm ancestry but have not answered them. There remains a gulf between angiosperms and their possible ancestors that is populated by fossil taxa with arguable transitional affinities based on logical but inconclusive assertions of connecting homologies. Nonetheless, new breakthroughs in the molecular genetics of development and exciting, if controversial, new fossils are improving the prospects for a near-term solution to what is debatably one of evolutionary biology's greatest remaining mysteries.

In summarizing our state of understanding of angiosperm origins and diversification, it is important to note at the onset that these areas of inquiry remain open to controversy even as exciting new modes of investigation and analysis have become available. Perhaps because of the importance and scope of the

questions that remain unresolved concerning angiosperm relationships and radiation, these questions often inspire passionate advocates of differing points of view. While a consensus is being approached on certain aspects of angiosperm history, and relationships among the angiosperms are better understood, others are open to controversy and change in the face of an increasing pace of investigation. Thus, this may be regarded as a *status quo* summary and change in our understanding of these important biological questions is highly probable in the near future.

I. THE FLOWERING PLANTS AND THE ABOMINABLE MYSTERY

The flowering plants are preeminent among vascular plants in numbers of species (250,000–300,000), they define terrestrial ecosystems at most latitudes, and exhibit more morphological diversity than any other group of plants. Economically, they are of primary importance as food, fodder, fiber, and building materials, in addition to serving as drug sources. It is thus interesting that, of all plant groups, they have the most elusive evolutionary history and, until recently, perhaps have been the most poorly understood with respect to their interrelationships.

The uncertainty surrounding angiosperm origin extends to the nineteenth century when early paleobotanical studies relied on gross morphological similarities for assigning affinities to angiosperm fossils. This approach resulted in skewed identifications, giving the appearance that apparently modern taxa were present relatively early in the fossil record, and suggesting a rather abrupt appearance of modern angiosperms. This apparent sudden appearance of modern taxa without any identifiable preceding ancestral lineage led Darwin to observe, in a now famously hackneyed quote from a letter to Heer that the origin of angiosperms was both an "abominable mystery" and "a perplexing phenomenon" (Darwin, 1903).

Since the nineteenth century, approaches to understanding the origin and diversification of the angiosperms have depended on paleobotany, systematics methodologies, and molecular genetics successively and, as they became available, in combination. New developments in each of these areas have increased our understanding of angiosperm diversification and relationships, but interestingly, have deepened the uncertainty surrounding angiosperm origin. Even with

valuable new techniques and methodologies, the angiosperm fossil record remains central to understanding their origin. Beyond certain generalizations, ancestral types cannot be reconstructed from phylogenetic trees either by character optimization on morphology/structure-based trees or by inference from trees based on molecular data alone (gene sequences). Yet, while the fossil record holds the best potential for identifying angiosperm ancestors, it has failed to resolve questions surrounding angiosperm origin. In addition, at its face value—that is based on the totality of literature on the angiosperm fossil record—it has been proven unreliable for documenting angiosperm diversification because, historically, the purported affinities of many angiosperm fossils have not been based on sufficiently rigorous analyses and are unreliable in estimating the timing (Crepet *et al.*, 2004).

A. Studies of Diversification

One must be selective in attempting to derive a reasonably accurate picture of angiosperm diversification from published fossil evidence. Criteria used to identify the affinities of particular fossil taxa should be as close as possible to those used in establishing the relationships among the living ones today, that is, fossils must have a sufficient number of key characters (synapomorphies) to warrant identification via phylogenetic analysis. Developments in both paleobotanical and systematic studies have made it practical to employ these criteria in confirming fossil affinities. Increasingly careful comparative analyses of angiosperm fossils began in earnest in the 1960s with emphasis on leaf venation, epidermal features, and pollen characters (Dilcher, 1974; Hickey, 1973; Walker and Doyle, 1975; Hickey and Wolfe, 1975). In the mid-1970s, fossil flowers, important because of their taxonomic and reproductive implications, became serious objects of study, resulting in a more informative fossil record of angiosperms and a better understanding of their diversification pattern (Crepet *et al.*, 2004).

B. Studies of Angiosperm Origin

In recent years, new analytical methods, new data sources, and newly discovered fossils have brought us much closer to an understanding of the origin of angiosperms. Nevertheless, the origin of angiosperms remains unresolved. For example, even though there has been a breakthrough in identifying a number of genes controlling floral development in angiosperms

and some of these genes have been identified in non-angiospermous taxa, such discoveries have not yet provided definitive insights into angiosperm origin. And so far, there have been no successful attempts to reconstruct transitional morphologies linking angiosperms to gymnospermous ancestors based on our understanding of genes controlling floral development. While phylogenetic studies using molecular data have refined our understanding of the relationships among and within all major clades of plants, including angiosperms, they have also separated gymnosperm and angiosperm lineages at the base of the phylogenetic tree of extant seed plants (e.g., Chaw et al., 2000). In doing so, these studies have distanced modern Gnetales (composed of the genera *Gnetum*, *Welwitschia*, and *Ephedra*) from the angiosperms. The Gnetales are now considered to be more closely allied to other gymnosperms despite the shared suite of morphological/structural characters that was once interpreted as evidence of a close relationship with angiosperms (e.g., Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Rothwell and Serbet, 1994). This complexity has further deepened the mystery of angiosperm relationships with other seed plants (angiosperm origins).

This separation between angiosperms and Gnetales is both interesting and perplexing because of the apparent conflict between the previous morphological analyses that consistently grouped Gnetales with angiosperms in the "anthophytes" (Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Rothwell and Serbet, 1994) and more recent analyses based on gene sequence data that separate all gymnosperms from angiosperms early in the diversification of the seed plants (Chaw et al., 2000). Thus, the characters in Gnetales that putatively linked them with angiosperms (e.g., including net-veined leaves, a form of double fertilization, "bisexual" reproductive structures (Fig. 1), the presence of vessels in the wood, and sterile structures surrounding ovules) are now regarded as parallel developments. Conversely, comparative studies of within-modern angiosperm relationships have also failed to illuminate angiosperm ancestry because the modern representatives of the earliest branching lineages of angiosperms *Amborella* or the Nymphaeales, depending on the analysis, do not have characters that provide insights into the relatives of angiosperms (i.e., they do not share significant characters with any nonangiospermous taxa). Given that no living links can be identified between the angiosperms and other seed plants, and that the reconstruction of such links based on our existing understanding of character
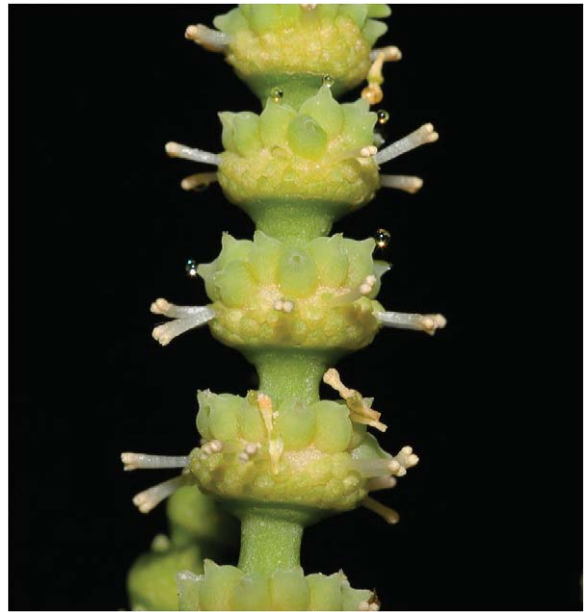

FIGURE 1 *Gnetum gnemon* pollen-bearing organs. Note that whorls of synangiate pollen-bearing organs subtend whorls of (sterile) ovules illustrating the juxtaposition of structurally male and female reproductive organs in the Gnetales. Photo courtesy of Nixon (2006), http://www.PlantSystematics.org

distribution and genes controlling floral development has not been possible, hope for a solution remains with the fossil record. Fossil evidence, however, is problematic and as with comparative studies of extant taxa, there are no obvious fossil intermediates between the gymnosperms and the angiosperms, leaving the field open to speculation and a variety of competing hypotheses.

C. Why the Fossil Record has Failed So Far

Why has the fossil record failed us with this most important group of plants despite the fact that it is replete with transitional mosaics (missing links) between other groups of vascular plants? There are no generally accepted fossil intermediates between angiosperms and other seed plants, and attempts to identify fossils that represent extinct taxa transitional to angiosperms are complicated by a number of issues. A traditional difficulty has been attempting to identify an angiosperm sister group on the basis of the preserved morphological/structural characters. A weakness to this approach lies in the possibility that underlying genetic changes could have been involved in such transformations without leaving a sequence of morphologically expressed connecting intermediates.

Thus, from the onset one must acknowledge the possibility that there were no morphoclines leading from gymnosperms to angiosperms, that is, that actual intermediates may not be recognizable on morphological grounds even if discovered in the fossil record. If so, clarification of angiosperm origin must await advances in understanding more completely the genetics underlying floral development, factors controlling gene expression, and the distribution of these genes in existing seed plants. But assuming that intermediacy was expressed in a morphological transition to angiospermy, and that fossils representing transitional taxa have either been undiscovered or gone unrecognized, there are a number of relevant questions including: What subset of characters is required to reasonably identify a potential angiosperm sister group and for that matter what subset might be necessary even in identifying a very early angiosperm? What combinations definitely indicate a relationship to the angiosperms? And, given that preservation is most often incomplete limiting the number of available characters, which characters are definitive indicators of angiosperms? Given these questions, it has been traditionally difficult to avoid subjective judgments in evaluating the significance of fossils that are possible angiosperm ancestors. However, questions regarding relationships of fossils can now be addressed more objectively by phylogenetic analysis, a methodology that precisely determines relationships among taxa and purportedly minimizes the influences of subjective interpretation. However, even with the advent of phylogenetic analysis, there has been no consensus on the closest fossil relatives of angiosperms.

There are a number of plausible reasons for this disappointing situation. First, in addition to the issues cited above, there are general problems inherent to fossil evidence: the record is incomplete, reflecting variation in optimum conditions for fossilization through time, and is undersampled. In addition, there have been only a few paleontologists and available fossil sites for investigation. Furthermore, the fossil record relatively has been poorly sampled in the time periods likely to be important in discovering extinct angiosperm relatives (Jurassic–Early Cretaceous). In addition, given the morphological gap between angiosperm reproductive structures and all the known gymnospermous ones (fossil and modern), and in the absence of a generally accepted transformation series (or morphocline) linking key nonangiospermous reproductive structures with angiospermous ones, it is difficult to identify characters in nonangiosperms that can be regarded as homologous with angiosperm

defining characters. For example, based on morphological transformation models, multistepped and tortuous transformations are necessary to support hypotheses linking various (and virtually all possibly "ancestral") fossil taxa to the angiosperms (e.g., *Cycadeoidea* (Bennettitales), Corystospermaceae, Glossopteridales, and Caytoniaceae (a good example is in the sometimes hypothesized transition from the caytonialean cupule to anatropous ovule + carpel of angiosperms)). Thus, while phylogenetic analysis has provided a powerfully objective tool for determining relationships, the assignment of character equivalencies needed for phylogenetic analysis (the determination of homologies) remains highly subjective in the absence of unequivocal links and so there is no consensus on extinct angiosperm relatives.

II. FOSSIL EVIDENCE—*STATUS QUO*

What is the *status quo* in our understanding of fossil evidence? In approaching the fossil record, as with evaluations of extant taxa that might be germane to angiosperm origin, we might consider what to look for in addressing the question of angiosperm origin and then consider appropriate fossils and the implications of these fossils. In general, there are two possible subgroups that would be relevant to angiosperm ancestry: fossil taxa that are clearly not angiosperms, but that have synapomorphies (shared derived characters) that may link them to angiosperms; and early angiosperm fossils that may possess characters linking them to nonangiospermous ancestors.

A. Potential Angiosperm Sister Groups ("Ancestors")

In the first category above (nonangiosperms), known fossils include principally:

The Mesozoic seed fern Caytonia (Fig. 2). *Caytonia* was originally described as an angiosperm because the ovule-enclosing cupules were confused with enclosed carpels (Thomas, 1925). Even after the discovery that the cupules were not closed led to the conclusion that *Caytonia* was a seed fern (Harris, 1940), the taxon continued to be linked with angiosperms. Some authors felt this because of a number of similarities such as net-veined leaves (although *Caytonia* veins are not hierarchical by size like those of the angiosperms), stomatal subsidiary cell configuration (paracytic—a generalized character occurring in a number of taxa)
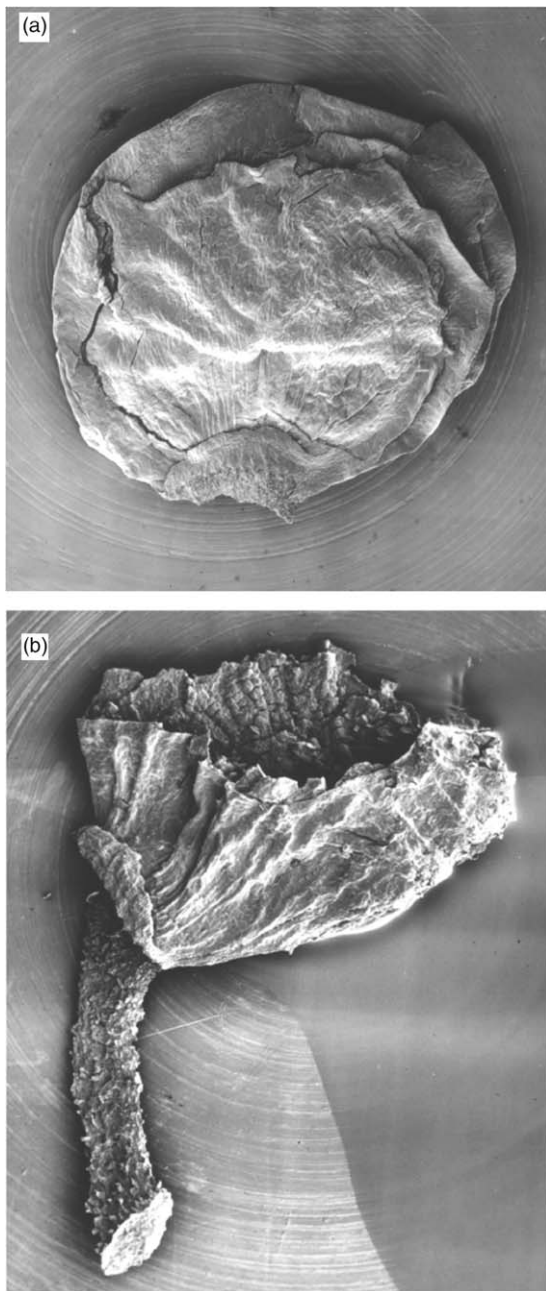
FIGURE 2 Continued

FIGURE 2 (a–c) *Caytonia*. (a, b) SEM photographs of the seed-bearing cupules. (c) Line drawing of cupule-bearing axis. (d) *Caytonia* leaf (*Sagenopteris*) venation pattern. (e, f) *Caytonia* pollen-bearing organs (*Caytonanthus*). (e) A synangia-bearing frond. (f) Several synangia showing that they are composed of four fused and radially arranged pollen organs. (c, d) Redrawn from Thomas (1925), and (e, f) redrawn from Harris (1937).

and, most significantly, by a superficial similarity between the adaxially incurved cupules containing numerous seeds and the anatropous ovule characteristic o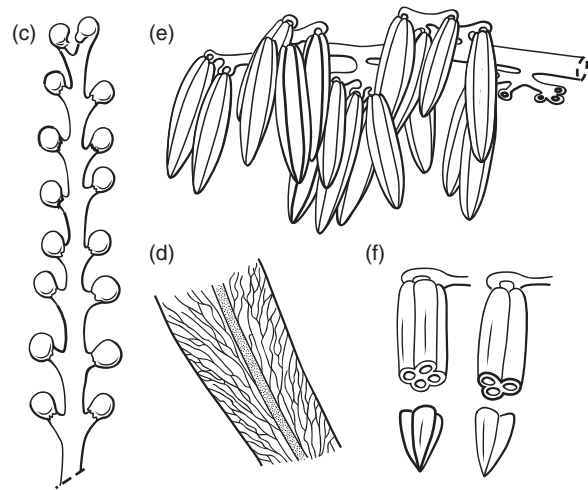f many, but not all angiosperms (interestingly not found in *Amborella*, the taxon at the base of most recent angiosperm phylogenies). The proposal equating the cupule of *Caytonia* with an anatropous angiosperm ovule posits that the cupule itself represents the second integument of the angiosperm ovule (even though not all angiosperms are bitegmic), and requires several additional morphological changes, including the reduction of ovules within the cupule to one, and the *de novo* origin of the carpel. Thus, beyond what we observe in *Caytonia*, there are several steps needed for the transformation, and yet there is no fossil evidence of any intermediates to support the hypothesized transformation. Furthermore, the combination of ovules with adaxially disposed micropyles and subtending sterile structures evocative of anatropy is not unique to the Caytoniaceae in gymnosperms or even among Mesozoic seed ferns. Thus, while plausible and possible depending on underlying genetics, this proposed homology is not compelling enough to be regarded as solving the issue of angiosperm origins, especially given the distinctly pinaceous saccate pollen found in *Caytonia* (adding additional steps to any transformation).

The Cycadeoidales (or Bennettitales, *Fig. 3*). This is the other major fossil group often associated with angiosperms. One of the principal genera of the order, *Cycadeoidea* (Fig. 3), was thought to be a link between angiosperms and gymnosperms when it was first found to have bisexual reproductive structures (Fig. 3). Subsequently, its relationship to angiosperms has been debated. While the Cycadeoidales are part of the "anthophyte" clade recognized in morphology-based phylogenetic analyses, the integrity of the group is in
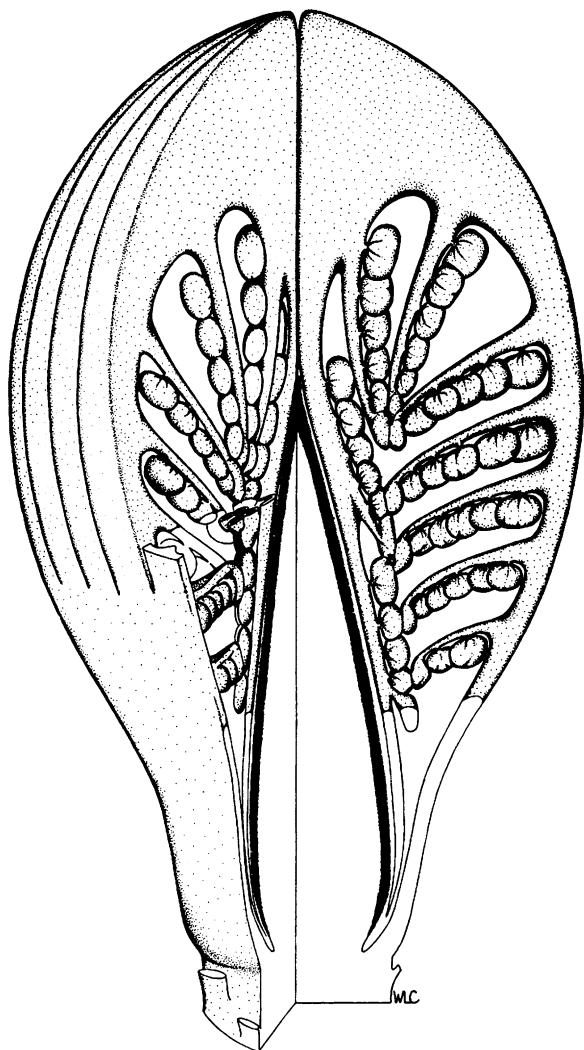
FIGURE 3 A reconstruction of the bisporangiate cone of the genus *Cycadeoidea* showing pollen-bearing organs subtending a conical ovule-bearing receptacle. This arrangement of pollen-bearing organs and ovules is unique to cycadeoids, angiosperms, and is approached in Gnetales.

question based on molecular systematics analyses mentioned above. Nonetheless, as with *Caytonia*, there are some appealing similarities between angiosperms and Cycadeoidales. The cycadeoidalean genera *Cycadeoidea*, *Wielandiella*, and *Williamsoniella* each have bisporangiate cones with an ovulate receptacle subtended by variously pinnate microsporophylls bearing synangiate pollen organs that are in turn subtended by sterile bracts. The parallel between this arrangement of organs and the succession found in the typical angiosperm flower (carpels surrounded by stamens surrounded by sterile petals/sepals) raises the question of affinities—homology or parallel evolution.

The similarities are even more compelling in light of other shared characteristics including some pollen characters, stomatal subsidiary cell configuration, and dicotyledonous embryos, although such embryos are not unique to angiosperms + cycadeoids and not even ubiquitous within angiosperms. And, transformation of a cycadeoid "flower" would be complex and once more require the *de novo* evolution of a carpel, dramatic reduction of the microsporophylls and a change in symmetry in both pollen organs and ovule-bearing structures. Moreover, careful comparisons between Cycadales and Cycadeoidales reveal more similarities and fewer differences than previously recognized in analyses leading to the identification of an anthophyte clade. This observation raises the possibility of closer ties between Cycadales and Cycadeoidales and might make the phylogenetic position of the Cycadeoidales near the angiosperms less secure. In contrast, even if Cycadeoidales turned out to be more closely related to Cycadales than previously thought, a link between these lower seed plants and angiosperms might not be out of the question in the context of the early split in seed plants between the angiosperm and gymnosperm lineages, that is, any group at the base of gymnosperms could plausibly be the one most closely related to angiosperms.

The Corystospermaceae. These Mesozoic seed ferns have been the focus of an attempt to synthesize knowledge of MADS Box floral development genes and fossil evidence in hypotheses on angiosperm origin that suggest ways that corystosperm pollen-bearing organs might be transformed into bisexual angiosperm flowers. This hypothesis draws attention to the importance of underlying genetics and to the possibility that transitional morphologies have not been discovered in the fossil record because they never existed. This general approach will become more important as details of genes controlling floral development are increasingly revealed and when there is a better understanding of the distribution and nature of these genes among extant taxa (Frohlich and Parker, 2000).

Glossopteridales. The seed-bearing structures of glossopterids were known for a long time from only relatively poorly preserved impression fossils. These fossils were alluringly carpel-like in appearance and quite variable in morphology. They are now more completely understood based on careful studies of well-preserved petrified fossils from Australia and Antarctica (e.g., Gould and Delevoryas, 1977). Although early suggestions that glossopterids might have been related to the angiosperms were based on putative homologies between the seed-bearing organs

of *Glossopteris* and the carpels of angiosperms and on their superficially common net-veined leaves (Retallack and Dilcher, 1981), glossopterids have not been placed near angiosperms in comprehensive phylogenetic analyses (e.g., Crane, 1985; Doyle and Donoghue, 1986; Nixon *et al.*, 1994).

In summary, there is no clear consensus on the closest fossil relatives of angiosperms, with unavoidably subjective assessments of homology clouding the results of the various, sometimes conflicting phylogenetic analyses. As it stands, there are a number of possibilities that cannot be definitively ruled out because the genetics underlying the development of key reproductive structures is poorly understood and available evidence does not favor one fossil taxon over another.

B. Early Angiosperms—Imagined and Real

The second category of potentially informative fossils relevant to angiosperm origin, that is, early putative angiosperm fossils, includes a number of taxa. Some of the better known ones are interesting, but they are not understood well enough to be unequivocally regarded as angiospermous because the fossils have too few characters to be convincingly placed with angiosperms in phylogenetic analysis. Notable among these fossils are several of Triassic age, and thus they are older than the earliest generally accepted angiosperm fossils (these are Lower Cretaceous). Such fossils include *Furcula*, an organ taxon for dichotomous leaves with net venation (Harris, 1932), isolated pollen grains with angiospermous pollen characteristics (Cornet, 1989a), and a taxon first described from leaves (*Sanmiguelia*) but later descriptions included purportedly related reproductive structures (*Axelrodia*) as well as almost entire plants (Brown, 1956; Cornet, 1986, 1989b; Tidwell *et al.*, 1977). *Sanmiguelia* is intriguing because the plicate fan-shaped leaves are similar to those of some extant monocots (e.g., Liliaceae). The fossils, however, are poorly preserved and the reproductive structures have been unconvincingly reconstructed. In the absence of sufficient data and analyses, there is no consensus on their significance at this time.

A relatively recently discovered fossil, *Archaefructus*, is one of the most potentially important of the known fossil angiosperms. While there is no doubt of its angiospermous nature, there is a debate as to its phylogenetic position. The question at issue: is it the sister group to all remaining angiosperms or is it nested within an extant taxon? (Friis *et al.*, 2003). *Archaefructus* is significant because it is completely preserved with reproductive organs attached to the vegetative part of the plant and because it comprises an unusual set of characteristics. Initially reported as Jurassic in age, it is now regarded as Lower Cretaceous and while early for an angiosperm, it is not uniquely the oldest of generally accepted angiosperm fossils. From specimens preserved in their entirety, it is obvious that *Archaefructus* was an aquatic plant (the leaves have air bladders), and that it lacked the typical organization of angiosperm flowers because naked carpels are only subtended by stamens along elongate axes. There is no evidence of any kind of floral envelope. *Archaefructus* has been interpreted both as an angiosperm that is a sister group to the rest of the angiosperms (Sun *et al.*, 1998, 2002) or as an aberrant member of the Nymphaeales, morphologically distinct from any modern member of that group with flowers that are so highly reduced that there is no evidence of usual angiosperm floral organization (Friis *et al.*, 2003). The latter interpretation is based on a phylogenetic reanalysis of the Sun *et al.* (2002) character matrix (Friis *et al.*, 2003). However, this reanalysis included a mistake in coding of a significant character (leaves) in a taxon that was added to the original analysis (*Cabomba*). When the matrix is corrected to reflect actual variation in *Cabomba* leaf morphology, subsequent analyses uniformly indicate that *Archaefructus* is the earliest branch in the angiosperm lineage. Once again it becomes a sister group to the angiosperms in 100% of the shortest trees. It is never placed with *Cabomba* or in the Nymphaeales, thus conforming with the results of Sun *et al.* (2002) and supporting original interpretations of its reproductive structures as innately simple and not simple owing to the process of evolutionary reduction that might have been associated with adaptation to an aquatic environment. Even so, it is likely that more characters (details of pollen structure, etc.) and subsequent supporting analyses will be needed to achieve a consensus view on the phylogenetic significance of *Archaefructus*. If confirmed as representing the earliest branch in the angiosperm lineage, *Archaefructus* would provide some unique insights into the nature of early angiosperms, but based on our present understanding of its morphology, would not unambiguously link angiosperms to any group of nonangiospermous seed plants. In a general aspect, *Archaefructus* is evocative of seed ferns, but the gap between known seed fern reproductive structures and those of *Archaefructus* is significant and evidence for transformations such as those invoked in the putative transition from *Caytonia* to an angiosperm is missing from the fossil record.

Should additional characters and analyses continue to support the phylogenetic placement of *Archaefructus* on the stem lineage below all other angiosperms, the implications of the aquatic habit in *Archaefructus* and questions as to whether an aquatic bottleneck was involved in the consolidation of angiospermous reproductive features will undoubtedly be pursued (e.g., did carpels evolve in response to selection for protecting developing ovules while still submerged? is insect pollination more efficient at the water level? what are the implications for identifying possible angiosperm "ancestors"? were there earlier stem lineage angiosperms that were not aquatics?).

III. CONCLUSIONS—ANGIOSPERM ORIGIN

There is no convincing evidence as to the closest group of nonangiospermous seed plants living or fossil. Recent developments have raised questions and revealed aspects of seed plant relationships that narrow the search and pose questions that can be foci of more intense investigations. Fossil studies have the potential for identifying the ancestral angiosperm lineage, especially in the context of molecular genetics, but, in spite of exciting new developments, the issue of angiosperm origin remains unresolved.

IV. ANGIOSPERM DIVERSIFICATION

A. Analytical Techniques Relevant to Understanding Diversification

Ideally, increasingly complete and reliably identified fossil evidence and advances in molecular systematics can be combined with the aim of improving our understanding of angiosperm diversification. While timing was once taken at face value from the fossil record, today we recognize that such an approach is compromised by a literature that is replete with misidentifications based largely on superficial comparisons between fossil angiosperms and the corresponding organs of modern angiosperm taxa. A selective approach to fossil evidence focusing on accurately identified fossils would improve our understanding of angiosperm history and would provide a better understanding of the diversification of the angiosperms than an uncritical review of the literature. However, the fossil record is incomplete and such a strict interpretation of

the literature would leave many gaps in our understanding of the timing of events in angiosperm radiation. The advent of molecular systematics provides better ways to estimate both diversification pattern and timing, especially now that it has engendered a growing consensus on the relationships among modern angiosperm taxa. There are a number of ways to combine phylogenies based on gene sequence data and the fossil record of angiosperms to reveal timing in angiosperm diversification. Different methods have produced different estimates and a lively debate is underway as to which promises to be the most accurate. A "consensus phylogeny" may be used either with selected fossil evidence in molecular clock-derived models (e.g., Sanderson, 1997; Sanderson *et al.*, 2004) or alternatively, in conjunction with the carefully screened entire fossil record of angiosperms in the "minimum-age node mapping" methodology (Crepet *et al.*, 2004). Depending on the details of the applications, the two methods "can" produce dramatically contrasting estimates of timing in angiosperm history or within particular clades. Depending on the model and the analysis, there is considerable variation in the estimation of timing in angiosperm history and some of this variation is related to the specific methods used to calculate timing and some to the choice of fossils used in calibration. For these reasons, estimates based on molecular clock-derived models have been subjected to intense scrutiny and criticism (Graur and Martin, 2004), but these clock-based methods are still evolving with different approaches showing promise (Sanderson *et al.*, 2004; Lavin *et al.*, 2005). The results of certain analyses are roughly congruent with timing suggested by fossil evidence alone, but timing estimates based on other analyses project much greater ages for various lineages or for the entire angiosperms than that revealed by the fossil record (Savolainen *et al.*, 2000). These discrepancies in timing angiosperm diversification have significant implications because differences in perceived timing affect our understanding of important events in angiosperm evolution and therefore of factors that may have been relevant to angiosperm success (e.g., possible synergy with insect pollination, animal fruit dispersal, and climatic conditions). Such differences also affect our understanding of angiosperm biogeography (timing, for example, is important in evaluating the potential significance of various land bridges to angiosperm biogeography or in estimating the effects of vicariance; Tiffney, 2006).

One of the major criticisms of analyses that have predicted greater ages for taxa than those verifiable by fossil evidence is that these discrepancies have not been satisfactorily explained except by the untested

premise that the record itself lags the pattern of evolution, often dramatically. This notion is based on the assumption that there is a significant delay between the origin of a new taxon and its first appearance in the fossil record owing to the time it takes a new taxon to reach a population size and distribution that make deposition, preservation, and discovery likely. This explanation of lagging fossil evidence is unconvincing because the time needed for population size to grow to the point where preservation and, ultimately, fossil discovery is likely is going to be miniscule relative to geologic time. Thus, discrepancies in timing on the scales projected by some clock-based models (tens of millions of years in some cases) seem unlikely given that a new taxon may have increased in population size and range to the point where preservation in the fossil record was likely in an interval that would be essentially instantaneous in the frame of geologic time (Burnham, 2006). There are cases where preservation seems unlikely—in widely dispersed herbaceous taxa that are insect-pollinated, for example, and instances such as these are partially responsible for gaps in the fossil record that may be addressed by the methods discussed above.

As molecular clock-based models continue to be refined and are becoming more accurate, an alternative and complementary way to combine fossil evidence with molecular systematics-generated phylogenies of living taxa already exists in "minimum-age node mapping" (Crepet *et al.*, 2004). Minimum-age node mapping methodology is based on the straightforward premise that, in phylogenetic context (and the success of the method depends on the framework of an accurate phylogeny for angiosperms made possible through molecular systematics such as that of Soltis *et al.*, 2000), a taxon's immediate ancestor (i.e., the taxon represented by the node proximally subtending the taxon) has to be as old or older than that taxon. By plotting reliably identified fossils on a consensus molecular systematics phylogeny, this methodology provides minimum times of appearance even for taxa that do not have fossil records (of course, such predictive power is also a goal of variously modified molecular clock models).

While some clock-based estimates of timing in angiosperm evolution seem outlandish when compared with the fossil record, others, using reliably identified fossils and refined methodologies (e.g., Lavin *et al.*, 2005; Magallón-Puebla *et al.*, 1999; Sanderson *et al.*, 2004), have generated results that are more consistent with those of minimum-age node mapping. As increasing numbers of reliably identified fossil taxa are used in calibrating such models, and as the models

themselves become further refined, results might be expected to converge with the fossil record of angiosperms and might also be effectively used for filling in gaps in understanding timing in particular clades that have relatively good fossil records (as in Lavin *et al.*, 2005). Currently, the results of node mapping methodology provide the most conservative assessment of timing in angiosperm radiation. Given the interest in improving molecular clock-based timing models, however, and their popularity (easy to use, appealing (especially rate smoothing) premise, fill in the gaps in the record), assessments of timing are likely to be in flux and somewhat controversial in the near future.

B. Major Features of Angiosperm Diversification

As consensus is approached in estimates of the timing and pattern of angiosperm diversification, major events in the evolution and radiation of the flowering plants can be conservatively, but reliably, placed in a temporal perspective allowing for the evaluation of various ecological/evolutionary hypotheses that have been proposed to explain angiosperm success.

1. Early Angiosperm Diversification

Timing and diversification in angiosperm history is summarized in the phylogenies presented in Figs. 4–6 based on a subset of carefully identified angiosperm fossils plotted according to minimum-age node mapping methodology using the phylogeny of Soltis *et al.* (2000) and Crepet *et al.* (2004). The early radiation of *bona fide* angiosperms illustrated in Figs. 4 and 5, began in, and then characterized the Lower Cretaceous. In Fig. 4, the emphasis is more on "basal" angiosperms followed closely and overlapping temporally with the subsequent radiation of the remaining tricolpate pollen-bearing clades (the "eudicots") illustrated in Fig. 5. The numbers in the figures represent ages of the clades in millions of years. Numbers on a terminal branch represent the age of the terminal taxon (e.g., Chloranthaceae 98). Terminals on unnumbered branches or clades without numbers (e.g., *Hedycarya* + *Peumus*) have the same minimum ages as the node below. *Archaefructus* is not included in the cladogram, but as a sister group to the rest of the angiosperms, a position now favored by the preponderance of available evidence, it would push back the timing of angiosperm radiation (still within the

Cretaceous) based on *bona fide* fossil evidence but would not affect the timing in the rest of the phylogeny.

The estimates illustrated in Figs. 4 and 5 suggest extensive diversification in several important angiosperm clades during the Lower Cretaceous to Turonian interval that included magnoliids, monocots, and several tricolpate clades. The possibility of an Early Cretaceous monocot diversification is supported by the presence of Triuridaceae floral evidence in the Turonian (because the triurids represent a derived taxon), but Early Cretaceous monocot diversification is not reflected by the mega or meso fossil records. While many reports of pre-Turonian monocot pollen are based on characters that are not exclusive to monocots (Gandolfo *et al.*, 2000), a recent report of dispersed but distinctive Araceae-like pollen (Friis *et al.*, 2004) suggests that at least some Early Cretaceous palynomorphs represent monocots, a finding

that would be consistent with node mapping projections of monocot minimum ages (Fig. 4).

The occurrence of numerous platanoid fossil leaves, flowers, fruits, and pollen among the oldest representatives of the "tricolpate" clade (or "eudicots" of some authors) at about 100 Ma is consistent with, and even slightly younger, than the age of the sister clade of the tricolpates + *Ceratophyllum* based on fossil evidence of winteraceous pollen (Walker *et al.*, 1983) from the Early Cretaceous of Israel (>105 MyBP).

Minimum-node mapping methodology, like molecular clock-based models, can calculate minimum ages for the "stem groups" of some families that lack a fossil record revealing that the minimum calculated ages for some families are greater than the ages of the oldest known fossils for the group. Sabiaceae, for example, has a calculated minimum age of 98 MyBP for its divergence from other extant angiosperms, based on fossils assignable to other families (Fig. 5), even
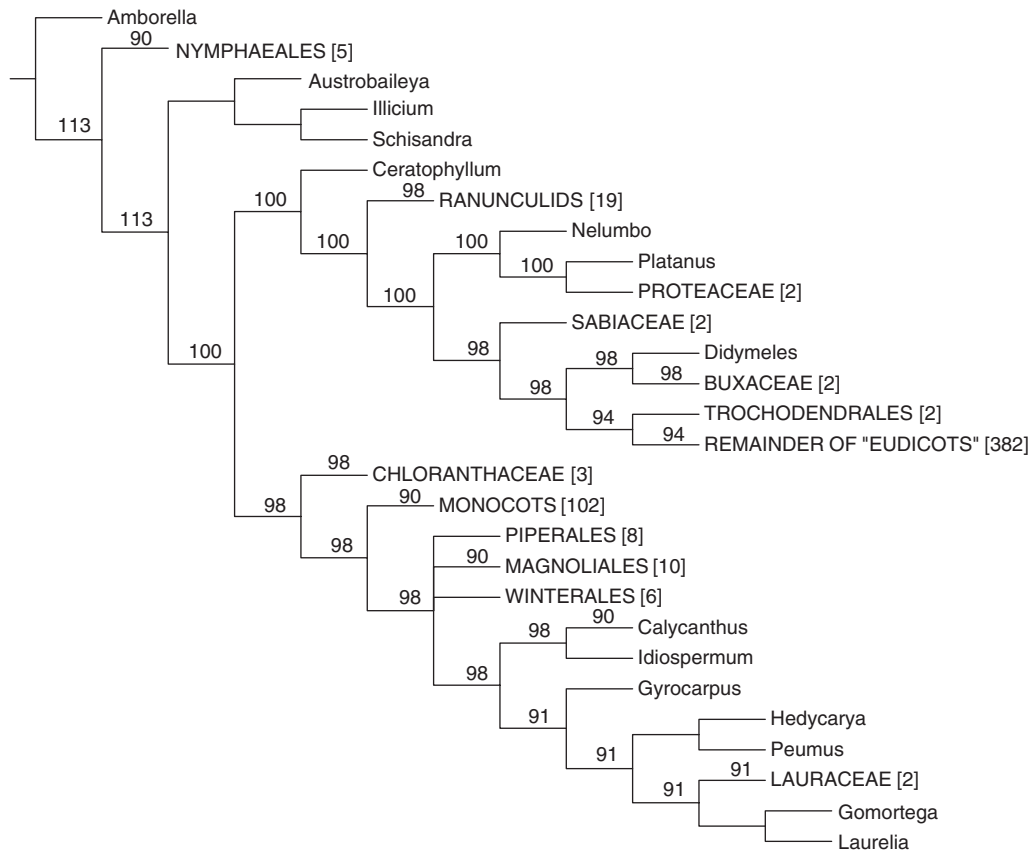

FIGURE 4   Minimum ages for major "basal" lineages of angiosperms (113–90 MyBP) based on the best available fossil evidence mapped onto the 3-gene 560 angiosperm tree (Soltis *et al.*, 2000). The tree has been collapsed to show major clades of interest. Numbers in brackets following a name indicate the number of distinct sequences that were used in the original molecular analysis.
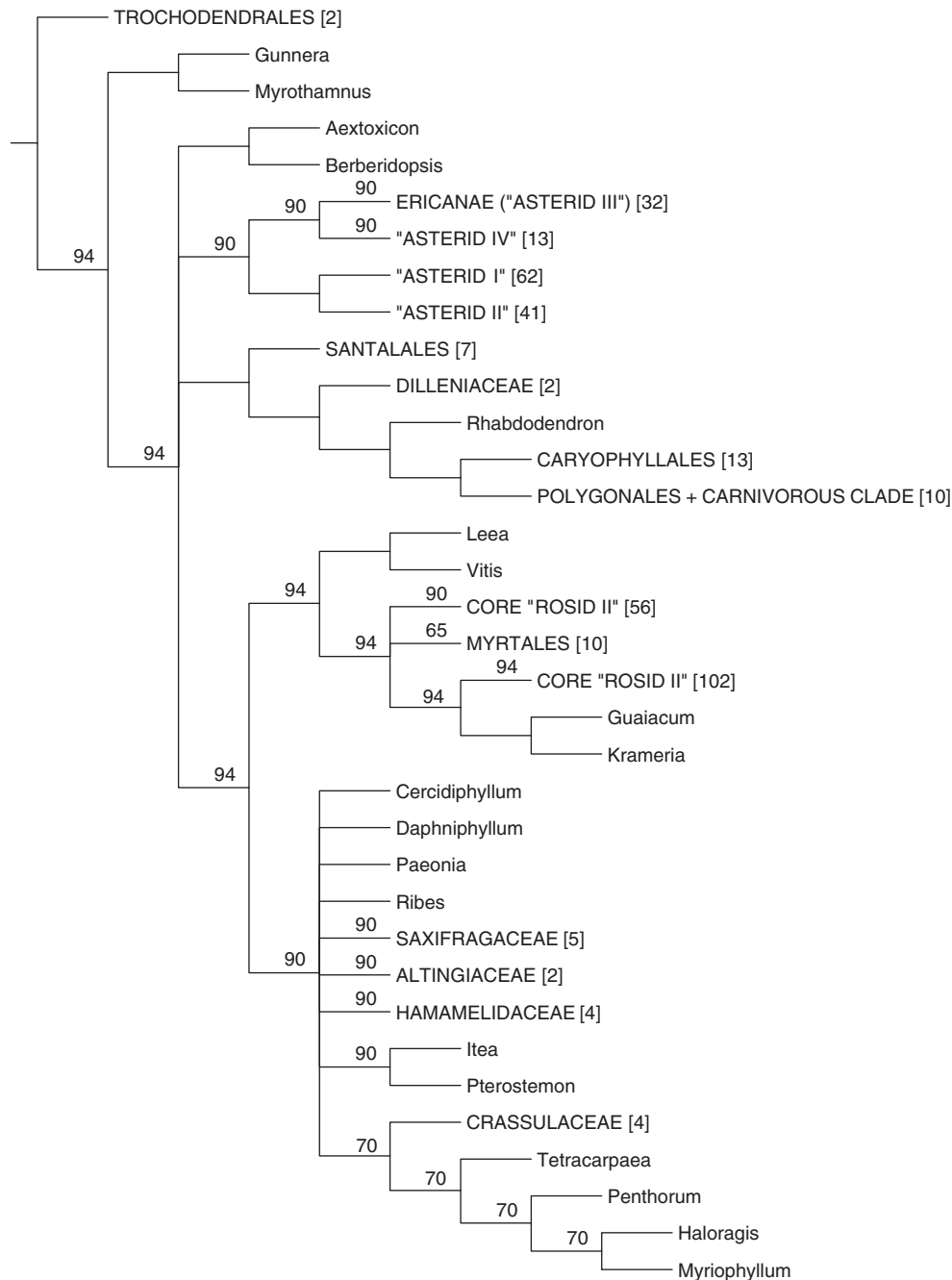
FIGURE 5 Minimum ages in million years before present for major lineages within the tricolpate or "eudicot" clade (some collateral groups not shown, such as Platanaceae, Buxaceae; see Fig. 4).

though the oldest putative fossils known for Sabiaceae, seeds from the Late Cretaceous, are at least 27 My younger (Knobloch and Mai, 1986). As with all minimum ages for clades predicted by minimum-age node mapping or other (molecular clock-based) models, this does not imply that the "crown group," in this instance modern Sabiaceae, had diverged by this time, but that the divergence of Sabiaceae from other extant angiosperms occurred at least 98 Ma. In fact, and again a good example for similar instances with other clades, the modern family may have diverged much more recently, and the perceived hiatus may be explained by numerous factors, including lack of identifiable features of modern Sabiaceae in the early members of the
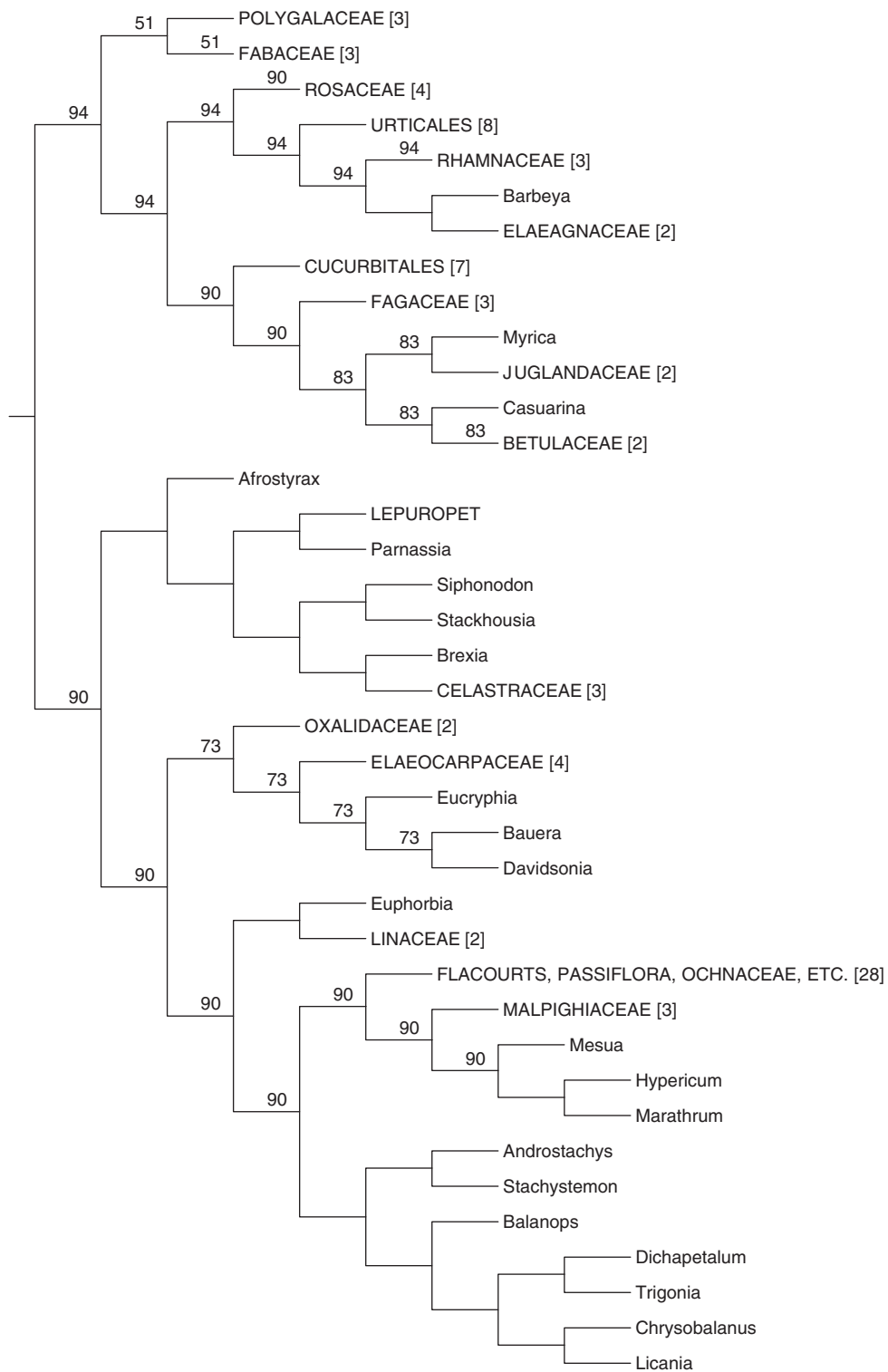
FIGURE 6 Minimum ages in million years before present of taxa within the "Rosid I" (sensu APG II, 2003) clade.

clade (e.g., as in legumes), preservational bias owing to morphology, mode of pollination, ecological distribution, or random events influencing the preservation of fossils (Crepet *et al.*, 2004).

2. Rosid 1 Clade Diversification

One of the most impressive aspects of angiosperm diversification is the rapid radiation of the Rosid 1 Clade—the clade that includes Rosaceae, Malpighiaceae, and a host of other families traditionally placed in either the Rosidae or the "Higher Hamamelididae" (Fig. 6). Beginning at least by the mid-Cretaceous, Rosid 1 diversity was already well established by the Turonian with the existence of two firmly identified fossils in the lower part of this subtree (Cunoniaceae and Clusiaceae) allowing estimates of the minimum divergence times for the stem lineages of several families owing to the pectinate topology. The divergence of the stem groups for Oxalidaceae, Elaeocarpaceae s.s., Eucryphiaceae, and Cunoniaceae can be estimated at 73 MyBP, and thus, any modern species in those families has a minimum divergence of 73 MyBP from any other angiosperm species not in the same family. Likewise, a minimum age of 90 MyBP for the divergence of the stem group of Malpighiaceae can be estimated based on Clusiaceae fossils from the Turonian of New Jersey (Fig. 7; Crepet and Nixon, 1998; also note Fig. 8 for an example of the kind of preservation that has improved our understanding of fossil floral history).

Another important clade within the "Rosid I" group includes Rosaceae, Fabaceae, Urticales, Cucurbitales,

and the families formerly included in the "Higher Hamamelididae" (e.g., Fagaceae, Nothofagaceae, Juglandaceae, Myricaceae, Betulaceae, and Casuarinaceae). This clade includes a diverse assemblage of economically important taxa with an exceptional fossil record. The minimum age of the stem group of the clade that includes Rosaceae and Fagales but excludes Fabaceae and Polygalaceae is estimated at 94 MyBP, while the first identifiable fossil of Fabaceae is from the Tertiary, ca. 51 MyBP (Herendeen and Crane, 1992), or at least 40 My after the minimum estimated divergence for the clade. It should be noted in this context that strongly zygomorphic flowers are not present in the best known Late Cretaceous deposits, and the radiation of both Polygalaceae and

FIGURE 8   An example of the exquisite preservation by charcoalification that has added so much to our understanding of the angiosperm fossil record. This 90 My old flower, related to modern Theales, is three dimensionally preserved and shows the preservation of delicate petals and stamens. Courtesy of Crepet and Martinez Millan, photo by J. Svitko.

FIGURE 7   Reconstruction of the fossil flower *Paleoclusia chevalieri* (Crepet and Nixon, 1998). Illustration courtesy of M. Rothman.

zygomorphic Fabaceae (i.e., papilionoid and ca-esalpinoid flowers) may have been a Tertiary event, possibly in response to selective pressures associated with the increased availability of specialized hymenopteran pollinators (apparently available at some level since at least Turonian times, Crepet, 2000). It is likely that members of the "stem group" subtending Polygalaceae–Fabaceae were actinomorphic and closely resembled modern Rosaceae, and thus identification of such taxa would be problematic without extensive characters for evaluation as might not be available in fossils (Lavin *et al.*, 2005).

The extensive record of the *Normapolles* palynomorphs in the Late Cretaceous (e.g., Christopher, 1979; Schönenberger *et al.*, 2001) seems to reflect diversification of the Juglandales lineage which is well nested within the "Fagales" (sensu the APG II, 2003). While *Normapolles* palynomorphs are diverse and difficult to place taxonomically from the characters of the pollen alone and there are only a few cases where pollen has been found in inflorescences, there is little doubt that at least some of the *Normapolles* palynomorphs are correctly placed in the broad clade that includes Juglandaceae, Betulaceae, and Myricaceae (Crepet *et al.*, 2004), implying a minimum age for the clade of 83 MyBP. Megafossils identifiable to those particular families do not occur until later, with the exception of cupulate Fagaceae from the Turonian of New Jersey (Crepet *et al.*, 2001; Nixon *et al.*, 2001).

Notably absent are fossils of the Cucurbitales clade, which is mostly herbaceous, and for which the "stem group" should have been present at least by 90 MyBP. The pattern within these clades nicely illustrates the probable effect of depositional, preservational, and ecological bias in the fossil record. The largely herbaceous and insect-pollinated Cucurbitales is essentially without a fossil record (with the exception of Tertiary fossils of the woody genus *Tetrameles* (Datiscaceae), Lakhanpal and Verma, 1966), while the concomitant "Fagales" group, which is entirely woody and mostly wind-pollinated has one of the most extensive fossil records for angiosperms, in terms of leaf, pollen, and reproductive structures, beginning in the Late Cretaceous and extending throughout the Tertiary (Crepet and Nixon, 1989a, b). Another factor that might contribute to the abundance of fossil Fagaceae and other members of the woody "Fagales" clade is their tendency to form extensive dominant forests (or riparian forests), while the Cucurbitales (e.g., Cucurbitaceae and Begoniaceae in particular) are generally scattered individuals with far less cumulative biomass.

3. Ericanae ("ASTERID III") and "ASTERID IV" Clades Diversification

The Ericales are well represented in the Turonian deposits of New Jersey (Crepet, 2000; Nixon and Crepet, 1993), providing an estimate of 90 MyBP for the minimum divergence of that group as well as for the broader group known as "ASTERID III" in recent works. The term "Ericanae" is used in Fig. 5 in place of Asterid III because it is more descriptive of the families that were not initially placed in Asteridae that, for the most part, lack fused corollas. The "Asterid IV" group includes Hydrangeales known from well-established fossils from Turonian deposits in New Jersey providing an estimate of ca. 90 MyBP for the divergence of this group.

4. "ASTERID I" and "ASTERID II" Clades Diversification

These groups include families that were traditionally grouped under Asteridae (Asteraceae, Solanaceae, Lamiaceae, Rubiaceae, and a host of other families that together include enormous species diversity, particularly in the tropics, Cronquist, 1981), and that typically have gamopetalous and often tubular and/or zygomorphic flowers. They are not reliably represented in Cretaceous deposits. The diversification of these asterids, with the associated floral features and various correlated often highly specialized pollination syndromes, very likely took place in the Tertiary unless early asterids were herbaceous, characterized by low population densities and were insect-pollinated and thus have gone undetected in the fossil record. Nonetheless, the apparently parallel radiation of legumes, a group with generally similarly specialized pollinators, is consistent with a radiation of asterids in the Tertiary (e.g., Herendeen and Crane, 1992; Lavin *et al.*, 2005), possibly for similar reasons.

Various complex pollination syndromes were likely to have been present by 90 MyBP given the diversity of Turonian floral morphologies (Crepet, 2000; Crepet and Nixon, 1998; Gandolfo *et al.*, 1998a, b; Nixon and Crepet, 1993). These morphologies have characteristics that imply high pollinator specificity, such as viscin threads (Nixon and Crepet, 1993), enclosed floral chambers that imply entrapment pollination (Gandolfo *et al.*, 2004), nonnectar floral rewards (Crepet and Nixon, 1998) and at least some sympetaly (Nixon and Crepet, 1993). The absence of strongly zygomorphic or bilabiate flowers at this time suggests that floral zygomorphy was, and remains, an ultimate refinement in pollination syndrome that followed

the development of other features. It is worth noting that the groups that later developed zygomorphy (again, probably almost entirely in the Tertiary based on current evidence) have become some of the most diverse and successful clades of modern angiosperms, including a large portion of the "asterids" (I and II) as well as the papilionoid and caesalpinoid legumes. Just as striking, however, is the success and persistence of numerous clades in which zygomorphic floral presentation is absent or rare, and which generally have less-stringent pollinator specificity (or passive pollination syndromes), such as the majority of rosid and ranunculid lineages, including the mimosoid legumes.

V. CONCLUSIONS—DIVERSIFICATION PATTERN

Conservative estimates of timing in angiosperm history suggest a rapid diversification of angiosperm groups between 113 and 80 MyBP, or alternatively, indicate an earlier diversification that left an extremely poor, even invisible fossil record.

The observed timing in angiosperm diversification has potential implications for understanding angiosperm success and distribution. For example, timing is critical in evaluating possible reasons for the rapid mid-Upper Cretaceous radiation of the tricolpate pollen-bearing angiosperms (the "eudicots"). This radiation appears to have been related to the availability of efficient pollinators; a relationship suggested by the timely appearance in the fossil record of characteristic floral morphologies, pollen characters, and taxa that are today specifically associated with such pollinators (Crepet, 2000; Crepet and Nixon, 1998; Gandolfo et al., 1998a, b; Nixon and Crepet, 1993). This coincidence has been addressed in numerous papers and is consistent with the possibility that insect pollinators, especially those likely to demonstrate pollinator fidelity, have been important in at least one major diversification of flowering plants and ultimately in establishing their dominance in a number of species (Crepet, 2000; Grimaldi and Engel, 2005).

It appears that angiosperms that developed zygomorphy, and extensively fused corollas went through a second major radiation with highly specific insect pollinators almost entirely during the Tertiary. These groups have become some of the most diverse and successful clades of modern angiosperms and they include a large portion of the "asterids" (I and II) as well as the papilionoid and caesalpinoid legumes.

Just as striking, however, is the success and persistence of numerous clades in which zygomorphic floral presentation is absent or rare, and which generally have less-stringent pollinator specificity (or passive pollination syndromes), such as the majority of rosid and ranunculid lineages, including the mimosoid legumes. In the same vein, it is interesting that other major groups radiated rapidly during the Tertiary and for apparently different reasons. Monocots with a spotty Cretaceous record nonetheless demonstrate considerable diversity by the end of the Cretaceous and an ensuing radiation during the Tertiary that includes palms and grasses. While Juglandales/Fagales were apparently insect-pollinated early in their history (Friis, 1983), they diversified in the Tertiary in association with climatic change and significant adaptation to wind pollination.

See Also the Following Articles

PHYLOGENY • POLLINATORS, ROLE OF • SYSTEMATICS, OVERVIEW

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