The origin and early diversification of angiosperms

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The major diversification of flowering plants (angiosperms) in the Early Cretaceous, between about 130 and 90 million years ago, initiated fundamental changes in terrestrial ecosystems and set in motion processes that generated most of the extant plant diversity. New palaeobotanical discoveries, combined with recent phylogenetic analyses of morphological and molecular data, have clarified the initial phases of this radiation and changed our perspective on early angiosperm evolution, though important issues remain unresolved.

ANGIOSPERMS dominate the vegetation of most terrestrial ecosystems and consist of roughly 250,000–300,000 extant species, more than all other groups of land plants combined. For almost 150 years, understanding the origin and early diversification of these dominant land plants was hindered by what was thought to be an uninformative fossil record, uncertain relationships among extant angiosperms, and apparently insuperable morphological 'gaps' between angiosperms and other seed plants (gymnosperms). The 1960s and 1970s saw notable progress toward breaking this impasse. Syntheses of data from extant angiosperms demonstrated that the subclass Magnoliidae is a phylogenetically basal assemblage[1-3] and studies of fossil pollen, leaves and reproductive structures documented a major diversification of angiosperms in the Early Cretaceous between about 130 and 90 million years before present[4-9].

Recently there has been renewed interest in the patterns and processes of early angiosperm evolution, and explicit phylogenetic analyses, based both on morphological and on molecular data, have clarified and revitalized many of the old debates[10-14]. In the fossil record, bulk sieving techniques have yielded diverse and exquisitely preserved Cretaceous flowers (both mummified and charcoalified) that have resolved the systematic relationships of many early angiosperms and identified the source of important dispersed Cretaceous pollen[15-19]. New information on floral form and reproductive biology in putatively basal extant groups has also catalysed comparative studies and enhanced the interpretation of fossil material[20-22]. Here we review how these developments have sharpened arguments over the relationships among basal angiosperms and their seed plant relatives, and have changed our perspective on early angiosperm evolution.

Origin of angiosperms and their flowers

Ideas on the origin of angiosperms have sometimes invoked polyphyly, have treated the pteridosperms (seed ferns) as a natural group, and have implicated almost all groups of fossil and living gymnosperms as potential angiosperm ancestors[9,23]. More recent work has emphasized cladistic discrimination of relationships among major clades of extant and extinct seed plants[10] (Box 1). Parsimony analyses, based on morphological data, have shown that angiosperms are one of the most strongly supported monophyletic groups in the plant kingdom (see Box 1) and that the pteridosperms (as traditionally defined) are a highly unnatural group[10,11]. However, the most striking result from recent phylogenetic analyses is the support for earlier ideas that identified Bennettitales (extinct) and Gnetales (extant; Fig. 5) as the seed plants that are most closely related to angiosperms (see Box 1). The resulting group (Bennettitales, Gnetales and angiosperms, plus *Pentoxylon* in some analyses) has been termed the 'anthophytes', to emphasize their shared possession of flower-like reproductive structures[11]. Among extant taxa, angiosperm monophyly and a close relationship between Gnetales and

angiosperms (to the exclusion of *Ginkgo*, conifers and cycads), is also supported by parsimony analysis of partial 18S and 26S ribosomal RNA sequence data[14,24] as well as analyses of combined morphological and molecular (*rbc*L, 18S, 26S) data[14,25].

Although all of the explicit cladistic studies conducted to date[10,11,26-28] broadly support the anthophyte concept, they differ markedly in their resolution of relationships within the clade, and in their identification of the closest relatives of anthophytes (see Box 1). In addition, the long-standing question of whether angiosperm flowers are derived from a simple branch (euanthial) or derived from multiple branches (pseudanthial) is still unresolved (Fig. 1). The origin of angiosperm stamens and carpels, and their homologies with structures in other seed plants also remain problematic[29]. Angiosperm stamens are both more regular and more simple than the pollen organs of the Bennettitales, Gnetales and most Mesozoic pteridosperms. In contrast, angiosperm carpels and bitegmic ovules are relatively complex compared to the ovulate structures of Gnetales and Bennettitales. Particular concerns are how the carpel and the outer layer of the typical angiosperm ovule should be compared to structures in related groups[30,31]. Current explanations are all inadequate, and lean heavily on critical interpretations of fossil specimens that are not well understood (such as *Caytonia*, corystosperms).

Such uncertainties highlight the need to clarify structural and developmental homologies among the reproductive structures of angiosperms and related groups; in many respects, the morphological gap between angiosperms and other seed plants remains as wide as ever. This gap can be closed most directly through renewed morphological documentation and phylogenetic analysis of well preserved fossil gymnosperm material from Mesozoic fossil floras[32,33]. Progress may also be possible by understanding how the genes controlling angiosperm stamen and carpel differentiation are expressed in the reproductive organs of extant gymnosperms (such as cycads, conifers, Gnetales)[29].

Angiosperm phylogeny and floral evolution

Current hypotheses of angiosperm evolution recognize two large clades (monocotyledons and eudicots) embedded within a poorly defined basal assemblage (grade) of magnoliid dicots (Magnoliidae[1]). The monocotyledons are defined as monophyletic by their single cotyledon and other features[34]. Eudicots are circumscribed by the production of triaperturate or triaperturate-derived pollen (convergent in Illiciaceae, Schisandraceae[35]).

Generalizations developed around the turn of the century emphasized large multiparted flowers like those of extant *Magnolia* (Figs 1a and 2A) as a starting point for angiosperm floral evolution[36,37]. Recent ideas accept that plants in the subclass Magnoliidae retain a broad array of probable unspecialized angiosperm features[20,22] (such as parts generally free, lack of differentiation within the perianth), and have also documented

FIG. 1 Extremes of floral diversity in extant basal (magnoliid) angiosperms. *a*, Large multiparted flower of extant *Magnolia stellata* (Magnoliaceae), showing nine tepals and numerous stamens and carpels; magnification, ×1. *b*, Small few-parted flowers of *Sarcandra glabra* (Chloranthaceae); each flower consisting of a single bract, carpel and stamen (photograph courtesy of P. K. Endress) ×3.8. Interpretations based on recent phylogenetic results[14] suggest that flowers of *Magnolia* and *Sarcandra* are, respectively, elaborated and reduced compared to the basic angiosperm condition. More radical interpretations of floral evolution suggest that all angiosperm flowers may not be homologous, and that the simple flowers of some (such as *Sarcandra*) are equivalent only to parts of flowers in others (such as *Magnolia*)[44,86].
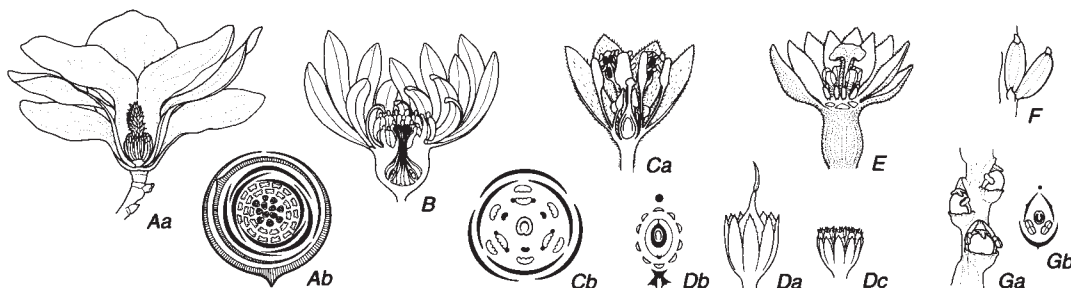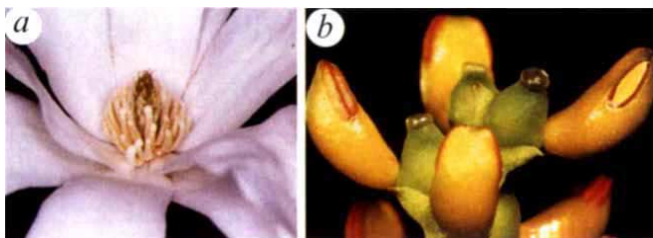

FIG. 2 Floral diversity in extant basal (magnoliid) angiosperms, illustrating variation in the number of carpels, stamens and perianth parts per flower. Generalized floral diagrams are shown in *Ab*, *Cb*, *Db* and *Gb*. *A*, *Magnolia* (Magnoliaceae); *B*, *Calycanthus* (Calycanthaceae); *C*, *Cinna-momum* (Lauraceae); *D*, *Ceratophyllum* (Ceratophyllaceae) (*a*, pistillate; *c*, staminate flowers); *E*, *Hazomalania* (Hernandiaceae); *F*, *Ascarina* (Chloranthaceae), showing two staminate flowers; *G*, *Piper* (Piperaceae), showing three flowers.

several previously unrecognized floral features that are general among extant magnoliids (such as valvate anther dehiscence[38], ascidiate carpel development[39]). Modern studies have emphasized the great diversity of floral form, biology and structure among magnoliids[22,40]. Variation in the number and arrangement of floral parts is extreme (Fig. 2), and both large, multiparted bisexual flowers and small, simple, frequently unisexual flowers are widespread[22,40] (Fig. 1).

Identifying the likely basic condition of angiosperm flowers is therefore intimately connected with the recognition of phylogenetic patterns among magnoliids (Box 2). Unfortunately, the substantial morphological differences that separate angiosperms from all other seed plants, combined with uncertain relationships
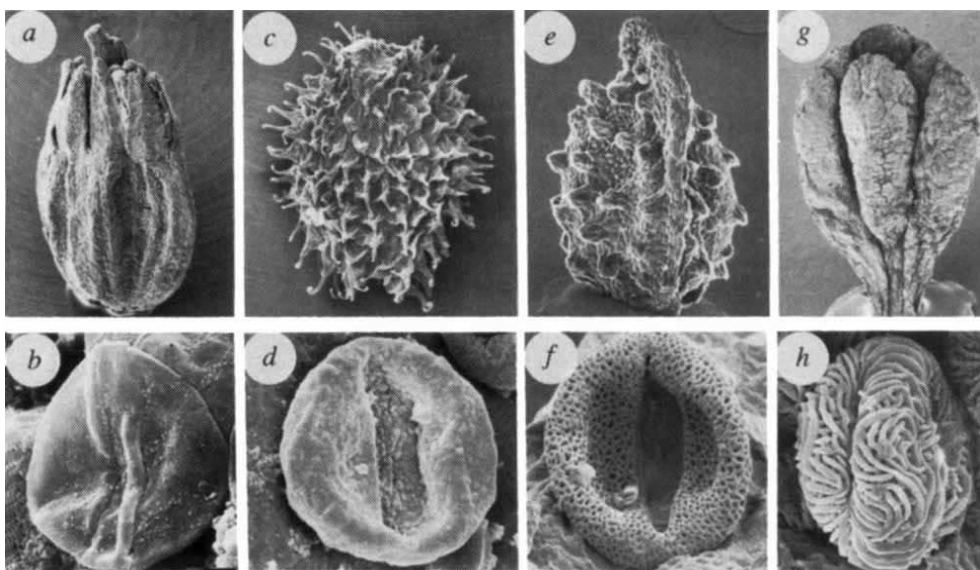
among the anthophytes, makes it difficult to 'polarize' many of the crucial characters. This, in turn, complicates attempts to 'root' the angiosperm tree and contributes to the instability of current phylogenetic results[12,14,41]. Among the studies currently available, there is emerging agreement that undue attention has focused on extant Magnoliaceae and its allies, and combined morphological and molecular results tend to favour phylogenetic models in which taxa with small, trimerous or even more simple flowers are basal in angiosperms[14,42–45] (see Box 2).

Fossil evidence of early magnoliid diversity. The variety of leaves and pollen in the Early Cretaceous[6,7] implies that magnoliids were diverse early in angiosperm evolution, and this is supported by the surprisingly rich, emerging record of fossil flowers

FIG. 3 Scanning electron micrographs of fossil early angiosperm flowers and carpels with their corresponding pollen. *a*, Epigynous flower showing tepals and protruding stamens, western Portugal, Early Cretaceous (Barremian or Aptian); magnification; ×20. *b*, Monocolpate pollen with striate exine ornamentation from stamens of above type of flower (see *a*); ×2,200. *c*, Unilocular fruiting unit covered with hooked unicellular hairs, and containing a single, orthotropous, pendulous seed; Potomac Group, Virginia, USA, Early Cretaceous (Early-Middle Albian); ×22. *d*, Monocolpate *Transitoripollis/Tucanopollis*-like pollen from the stigmatic surface of above type of fruiting unit (see *c*); ×1,680. *e*, *Couperites mauldinensis*, unilocular fruiting unit, showing protruding 'resin bodies', and containing a single pendulous,

anatropous seed; Potomac Group, Virginia, USA, Late Cretaceous (Early Cenomanian); ×44. *f*, Monocolpate *Clavatipollenites*-type pollen from the stigmatic surface of *Couperites mauldinensis* (see *e*); ×1,200. *g*, *Spanomera mauldinensis*, staminate flower with five tepals and five stamens; Potomac Group, Virginia, USA, Late Cretaceous (Early Cenomanian); ×47. *h*, Tricolpate *Retitricolpites*-type pollen from stamens of *Spanomera mauldinensis* (see *g*); ×1,825.


BOX 1 Hypotheses of relationship among angiosperms and related plants

Two contrasting hypotheses of phylogenetic relationships among anthophytes. Morphological characters supporting the anthophyte group include: the presence of an additional integumentary envelope, granular-columellate structure of the pollen wall and at least some stomata syndetocheilic[10,11,27]. Other potential defining characters include scalariform pitting in the secondary xylem, whorled or opposite arrangement of microsporophylls, apical meristems with tunica-corpus organization, wood with syringal lignin subunits (Mäule reaction) and (secondarily) non-saccate pollen[10,11,27]. New information on fertilization in *Ephedra* and *Gnetum*[88,89] also raises the possibility that double fertilization may be a general feature of anthophytes. Monophyly of the Bennettitales is supported by the distinctive interseminal scales, and the aggregation of pollen sacs into bivalved synangia (present in all Bennettitales except a few Triassic taxa)[10,72]. Monophyly of angiosperms is supported by sieve tubes and companion cells derived from the same initials, stamens with two pairs of pollen sacs, anthers with a hypodermal endothecium, microgametophyte of only three nuclei, carpel with stigmatic pollen germination, carpel enclosing a (probably) bitegmic ovule, megaspore wall lacking sporopollenin, megagametophyte with only eight nuclei and the formation of a triploid endosperm[10,11].

Uncertainty concerning relationships among anthophytes is introduced by: (1) possible secondary loss or transformation of critical morphological features (such as loss of syndetochelic stomata in *Ephedra* and many angiosperms; loss of granular exine in most angiosperms); (2) the homologous or convergent origin of certain angiosperm-like features in Gnetales (especially in *Welwitschia* and *Gnetum*, Fig. 5) and Bennettitales (such as bisexual flowers); (3) the ambiguous homology of the second integument in the three anthophyte groups and the 'cupule' of potentially related taxa (such as *Caytonia*, corystosperms); and (4) uncertainty regarding the basic condition of many characters among basal angiosperms (such as orthotropous versus anatropous ovules, one-seeded versus many-seeded carpel, few-parted versus many-parted flowers).

a, Hypothesis A[10,11,90]. Gnetales are monophyletic and the derived similarities of *Gnetum/Welwitschia* and angiosperms are interpreted as convergence (such as reticulate-veined leaves, reduction of male gametophyte, tetrasporic female gametophyte lacking archegonia and with free nuclei serving as eggs, cellular early embryogeny). This hypothesis is consistent with parsimony analyses of current molecular data (*rbc*L[13], rRNA[14,24]), as well as analyses of combined morphological and molecular data (morphology plus *rbc*L[25] and morphology plus rRNA[14]).

b, Hypothesis B[27]. Gnetales are paraphyletic, with *Gnetum* and *Welwitschia* the sister group to angiosperms. This hypothesis interprets the derived similarities of *Welwitschia*, *Gnetum* and angiosperms as homologous.
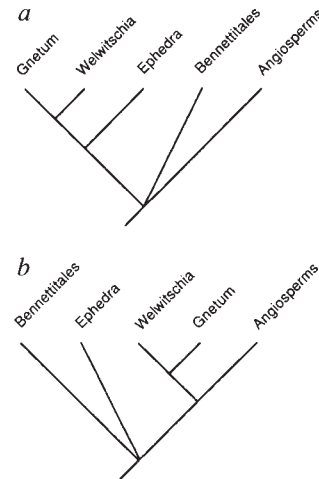
(Fig. 3 and Box 3). In the extensive assemblages of Early Cretaceous angiosperm reproductive structures from Portugal and eastern North America, all of the fossils described so far are small (frequently less than 2 mm in length), and because they occur with larger fossils of other plants (such as conifers) it seems unlikely that this is a result of depositional bias. The flowers are generally few-parted and often with an undifferentiated perianth. Stamens generally have small pollen sacs with valvate dehiscence, and a relatively large apically expanded connective[46]. Carpels generally have a poorly differentiated stig-

matic surface. Among magnoliids, the fossil record indicates that several extant families were already differentiated by about the Turonian (Box 3).

Fossil evidence of early monocot diversity. Among extant plants monocotyledons comprise only about 22% of angiosperm species. Over half of this diversity is accounted for by four families (Orchidaceae, orchids; Poaceae, grasses; Cyperaceae, sedges; Arecaceae, palms). The Cretaceous fossil record of monocotyledons is depauperate compared to that of contemporary magnoliids and eudicots, and perhaps reflects a variety of biases working


BOX 2 Hypotheses of relationships among basal angiosperms

Two of several published hypotheses of relationships among basal angiosperms. Taxa placed in a basal position by different recent studies include *Ceratophyllum*[13,42] Idiospermaceae-Calycanthaceae[43], Chloranthaceae/Piperales[44,45] and Nymphaeales[14].

a, Hypothesis A[14]. Phylogenetic analysis of combined morphological and rRNA data showing relationships among extant Gnetales and basal angiosperms. Under this interpretation angiosperms are 'rooted' close to Nymphaeales, monocots are interpreted as an early branch in angiosperm evolution, and basal magnoliids are various more or less herbaceous taxa with basically simple flowers (secondarily complex in derived Nymphaeaceae). Magnoliales (including Annonaceae,

Degeneriaceae, Magnoliaceae, Myristicaceae) are placed in a relatively derived position. Eudicots are monophyletic and diverge from the basal magnoliid assemblage below Laurales/Magnoliales. Note that an alternative 'rooting' in the vicinity of Magnoliales would imply a relatively late divergence of monocotyledons from magnoliids.

b, Hypothesis B[25]. Phylogenetic analysis of combined morphological and *rbc*L data showing relationships among extant Gnetales and basal angiosperms. Under this interpretation *Ceratophyllum* is the basal angiosperm lineage (not considered in hypothesis A) and eudicots are monophyletic, most other relationships are unresolved. Aristolochiaceae are not considered.
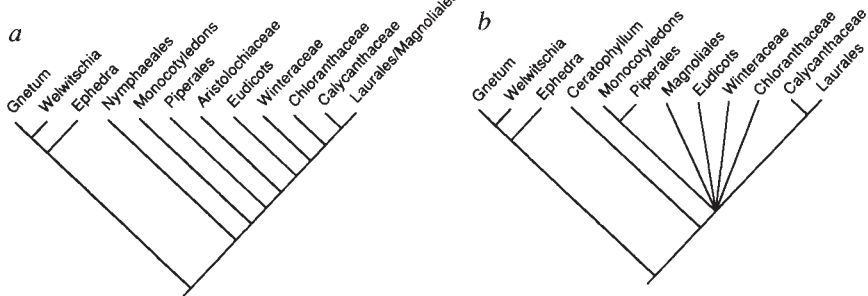
### BOX 3 Fossil evidence of floral diversity among early angiosperms

THE most extensive information on Early and mid-Creta-
ceous angiosperm reproductive structures is from western
Portugal (1–14)[19] and the Atlantic Coastal Plain of eastern
North America (15–32)[18] which together provide a
sequence of floras ranging in age from Valanginian(?)–
Hauterivian(?) to earliest Cenomanian.

Valanginian(?)–Aptian (1–14). Although only partially
described, the angiosperm component of the earliest
floras (Aptian and older, for example, 1–14) is dominated
by small, simple flowers and flower parts. Epigynous
flowers of possible lauralean affinity (such as 2, 3, 6, 7)
and unilocular, single-seeded fruits or fruitlets with mono-
colpate pollen (such as 8, 9, 11–14) are especially com-
mon and diverse[19]. Clavatipollenites-type pollen, for which
a chloranthoid affinity has been inferred[91], occurs on the
stigmatic surfaces of some of these fruits. Clavatipollenit-
es-type pollen is also known in situ within distinctive
angiosperm stamens and is widespread in dispersed
pollen floras from the Early Cretaceous[4,9]. Triaperturate
pollen diagnostic of eudicots is also present[19]. Other put-
ative angiosperm macrofossils from Aptian and older
rocks include probable magnoliid leaves[92] and horned
(?Ceratophyllum-like) fruits of uncertain systematic
affinity[93]. One small specimen with attached leaves and
reproductive structures, which is reported to show a
mosaic of chloranthoid and piperalean features[94], is too
poorly preserved for detailed study of the flowers, fruits,
stamens or pollen. In addition, dispersed pollen grains
from Aptian and older rocks include forms perhaps related
to extant Winteraceae[35] and Magnoliales[95].

Albian (15–27). In Albian floras (such as 15–27) small
epigynous flowers (such as 15–17) and unilocular single-
seeded fruits or fruitlets (such as 21, 23, 24) remain com-
mon. One of the most distinctive of these (24) appears
to combine characters of Piperales, Chloranthaceae and
perhaps Circaeasteraceae (Ranunculidae)[18]. A variety of
other taxa are also present, including probable flowers of
Lauraceae (22)[18] and Calycanthaceae[96], possible mag-
nolialean fruits (such as 18) and stamens[18], and possible
fruits of Ceratophyllaceae[93]. Flowers of basal eudicots
become a distinctive component of Cretaceous floras from the mid-
Albian onwards and several lineages of 'lower' hamamelidids can be
recognized during the mid-Cretaceous phase of angiosperm divers-
ification, including Platanaceae[16,52] (such as 25, 31) and perhaps
trocho-dendroids[6,7,51,52] and buxoids[52,97] (such as 32) (see Fig. 3g, h).

Earliest Cenomanian (28–32). By the early part of the Late Creta-
ceous the magnoliid groups include chloranthoids[98], and Lauraceae
(such as 28)[99], both of which were apparently geographically wide-
spread. Probable Magnoliaceae[100] were also present. Eudicots of this
age include a variety of platanoids[16,53], rosiids[17] and other taxa[20].

Fossils illustrated are from the Valanginian(?)–Hauterivian(?) of
Torres Vedras, western Portugal (1–5); the Barremian or Aptian of
Catefica, western Portugal (6, 12), Famalicão, western Portugal (13,
14), and Vale de Agua, western Portugal (7–11); the Early or mid-
Albian of Puddledock, Virginia (15–22, 24), Bank near Brooke, Virginia
(25), and Kenilworth, Maryland, (23); the Late Albian of West Brothers,
Maryland (26, 27, 30, 31); and the Early Cenomanian of Mauldin
Mountain, Maryland (28, 29, 32). 1, Four-angled fruit or seed in lateral
(a) and apical (b) view. 2, Epigynous (?) flower with monocolpate,
reticulate pollen. 3, Epigynous Hedyosmum-like flower in apical (a)
and lateral (b) view. 4, Floral structure with several whorls of stamens
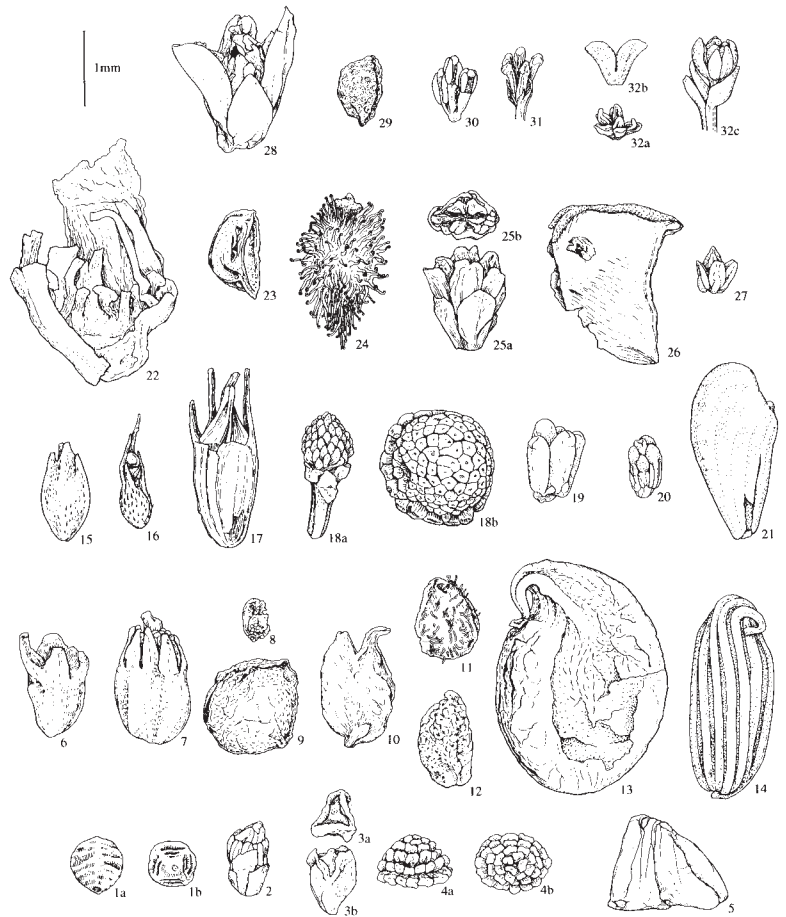
(?unistaminate flowers) in lateral (a) and apical (b) view. 5, Group of
seeds. 6, Four-angled, epigynous structure[18,19]. 7, Epigynous flower
with monocolpate, finely striate Cabomba-like pollen (see Fig. 3a, b)[19].
8, 9, 11, Unilocular single-seeded fruiting units with strengthening
tissue in seed wall; 8 and 11 have adhering Clavatipollenites-type
pollen. 10, Bicarpellate fruit. 12–14, Unilocular single-seeded fruiting
units with strengthening tissue in fruit wall. 15–17, Epigynous floral
structures. 18, Multiparted floral structure; smaller specimen in lateral
view (a), larger specimen in apical view (b). 19, Apocarpous pistillate?
flower. 20, Staminate flower. 21, Unicarpellate fruit with strengthening
layer in fruit wall. 22, Fragment of lauralean flower. 23, Unilocular
single-seeded fruiting unit with strengthening tissue in the seed wall
and with monocolpate pollen. 24, Spiny, unilocular and single-seeded
fruiting unit (see Fig. 3c, d). 25, Pistillate flowers of Platanocarpus
brookensis in lateral (a) and apical (b) view[53]. 26, 27, Fruitlet (26) and
staminate flower (27) of Spanomera marylandensis[98]. 28, Trimerous
flower of Mauldinia mirabilis[99]. 29, Fruit of Couperites mauldinensis
with adhering Clavatipollenites-type pollen (Fig. 3e, f)[91]. 30, Chloran-
thoid androecium[98]. 31, Pistillate flower of Platanocarpus maryland-
ensis[16]. 32, Staminate (a) and pistillate (b, c) flowers of Spanomera
mauldinensis (Fig. 3g, h)[97].

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against both their preservation and recognition. During the mid-
Cretaceous, monocots are probably represented by several
leaves[47], and more equivocally by dispersed pollen[48,49]. However,
evidence of rapid monocot diversification is provided later in
the Cretaceous by fruits of Zingiberales (gingers and their allies),
and leaves and stems of palms[34]. By the Early Tertiary many
monocot groups had differentiated[34,50] (Fig. 4).

Fossil evidence of early eudicot diversity. Eudicots comprise
about 75% of extant angiosperm species, and are recognized
as a monophyletic group in phylogenetic analyses of combined
morphological and molecular data[14,25]. Triaperturate pollen,
which is diagnostic of the group, is first recorded in dispersed

palynological assemblages around the Barremian–Aptian
boundary (about 125 Myr) or perhaps slightly earlier.

Basal groups in the eudicot clade include the ranunculids
(Ranunculidae, sometimes included in the Magnoliidae) and
also the 'lower' hamamelidids[51,52]. Embedded within this basal
eudicot assemblage are the diverse groups that comprise the
bulk of extant angiosperms, including the 'higher' hamamelidids
along with the subclasses Rosidae, Caryophyllidae, Dilleniidae
and Asteridae, which contain many highly diverse extant families
(such as Asteraceae, the sunflower family). Among the eudicots
that can be recognized during the mid-Cretaceous diversification
are several 'lower' hamamelidid lineages and a diversity of

FIG. 4 Simplified phylogenetic tree showing the relative stratigraphic ranges of selected angiosperm groups and putative close gymnosperm relatives. The fossil record of Gnetales is based primarily on diagnostic dispersed ribbed pollen, with supporting evidence from rare Triassic[72,87] and Cretaceous[72] macrofossils. The fossil record of *Eucommiidites* is based primarily on dispersed pollen, with seeds and pollen organs known from the Jurassic and Cretaceous[32]. The combined evidence suggests that *Eucommiidites*-producing plants are closely related to the anthophyte group[32]. Crinopolles pollen is reported from the Late Triassic[57] but other organs of the plant are not known. Bennettitales have an extensive fossil record based on leaves and reproductive structures[10,72]. The bennettitalean flower-like reproductive structure illustrated is *Williamsoniella*. Monocolpate pollen is the basic condition in angiosperms that is retained by monocots and magnoliid dicots. Triaperturate pollen is diagnostic of eudicots. Dillen, Dilleniidae; Cary., Caryophyllidae.
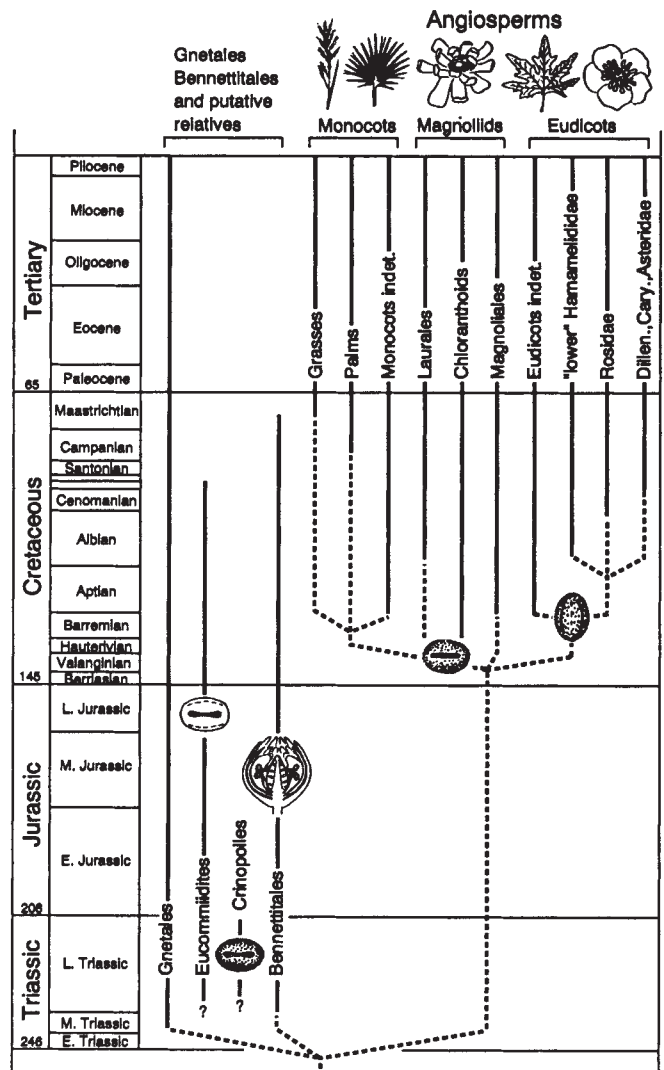
generalized rosiid types (Fig. 4). By around the Campanian, eudicots were very diverse[20,50,52].

Pre-Cretaceous angiosperms?

Current studies of the fossil record show an orderly sequence of appearance of angiosperm remains beginning with putative magnoliid pollen in the Valanginian, and triaperturate pollen of eudicots around the Barremian–Aptian boundary (or slightly earlier). By the early Cenomanian there are diverse magnoliids, a variety of hamamelidids and a few rosiids, which show clearly that several angiosperm families had already differentiated. By the Campanian, Maastrichtian and Palaeocene, many extant angiosperm families in all subclasses had already differentiated[34,50 54].

Claims of pre-Cretaceous angiosperms need to confront this orderly sequence, and although the literature on angiosperm origins is replete with putative pre-Cretaceous angiosperms, most have been shown to be stratigraphically misplaced, unrelated to angiosperms, lacking in diagnostic characters, or too poorly preserved for reliable determination[55]. Recently, however, there has been renewed discussion of the possibility of pre-Cretaceous angiosperms stimulated by the anthophyte hypothesis (which implies that the lineage leading to angiosperms diverged from other known groups of seed plants before the Late Triassic)[10,11,41], the description of new and potentially relevant fossils from Jurassic and Triassic rocks[56,57]; and calculations of divergence times based on molecular clock assumptions[58 60]. These developments have highlighted the

importance of distinguishing clearly between the timing of angiosperm divergence (splitting of the stem lineage from its sister groups) and the timing of angiosperm diversification (splitting of the crown group into extant clades)[41].

In our view, the absence of distinctive triaperaturate pollen grains in numerous, rich, Triassic and Jurassic palynofloras from both hemispheres precludes the long cryptic period of evolution implied by some estimates of rates of molecular evolution, at least for eudicots[61]. The systematic affinities of recently described putative Jurassic and Triassic angiosperms[56,57,62,63] are either clearly with other groups (such as dipteridaceous ferns[64]) or remain equivocal (such as Triassic *Sanmiguelia*-like plants and Crinopolles-type pollen grains[64,65]). Although some of these fossils may be attributable to the anthophyte clade, they highlight the difficulties of accurate systematic determination based on inadequate material. Most defining features of angiosperms (Box 1) are unlikely to be preserved in the fossil record. The most useful diagnostic morphological features of angiosperms are stamens with two pairs of pollen sacs, and a carpel enclosing the ovule. Both can only be observed in well preserved fossil material.

Coevolutionary interactions

Angiosperm diversification has often been linked to the diversification of pollen and nectar-collecting insects on the supposition that insect pollination provides new possibilities for reproductive isolation and therefore elevation of speciation rates[66 68]. Compared to wind pollination, which is widespread in other seed

FIG. 5 Gnetales consist of only three extant genera: *Ephedra* (*a*, about 40 species in arid and semiarid areas); *Welwitschia mirabilis* (*b*, one species restricted to the Namibian Desert); and *Gnetum* (*c*, about 30 species of tropical rainforest lianes and small trees). Despite the obvious morphological differences the group is widely regarded as monophyletic (Box 1) and is united by multiple axillary buds, opposite/decussate phyllotaxis (also reflected in the reproductive structures), circular bordered pits in the protoxylem, vessels (?derived independently to those in angiosperms) and a feeder in the embryo[10,11]. In addition, *Welwitschia* and *Gnetum* share several derived characters that are thought to be convergent with similar features in angiosperms[10,11] (see Box 1).

plants, insect pollination may also permit effective outcrossing at lower population densities and in a greater range of environments, perhaps thereby reducing extinction rates[66–68]. These factors may explain the diversity of some of the most speciose angiosperm families (such as orchids), but the extent to which they provide a general explanation for the massive mid-Cretaceous increase in angiosperm diversity is uncertain[69,70]. In the Bennettitales, flower-like reproductive structures provide indirect evidence of insect pollination from the Late Triassic to Late Cretaceous[71,72], and insect pollination may also have been established in some Mesozoic pteridosperms[33]. The size and morphology of diverse mid-Cretaceous gnetalean pollen, combined with evidence from extant taxa[73], is also suggestive of insect pollination in the Gnetales. Early angiosperms may therefore have coopted pollinators from previously established relationships with other groups of seed plants.

Whatever the effect of insect pollination on the initial angiosperm diversification, discoveries of Early and mid-Cretaceous flowers leave no doubt that early members of the group were insect pollinated. Stamens in fossil flowers have small anthers with low pollen production, anther dehiscence is valvate, pollen grains are often covered with a pollenkitt-like material, stigmatic surfaces are generally unelaborated and pollen grains are often smaller than the most effective size for wind dispersal[18,19]. Comparison with modern relatives suggests that these flowers were probably pollinated by pollen-collecting or pollen-eating insects. Flowers pollinated by nectar-collecting Hymenoptera and Lepidoptera occur in more derived groups of angiosperms and appear later in the fossil record[17].

Although Early Cretaceous angiosperms may have been very similar to their living relatives in pollination syndrome, modes of fruit and seed dispersal were probably substantially different[22]. Cretaceous angiosperm fruits and seeds are generally very small compared to their modern relatives, and there is no evidence of specialized mammal or bird dispersal. Among basal groups, as in angiosperms as a whole, the evolution of fleshy fruits, arillate seeds and other apparent adaptations for animal dispersal, seems to be correlated with the evolution of frugivorous/granivorous birds and mammals, perhaps during the latest Cretaceous, but most strikingly during the Early Tertiary. The only suggestion of animal dispersal of angiosperms in the Early Cretaceous is provided by a single species of small fruits covered with hooked spines (Box 3, Fig. 3*c*).

Rise to ecological dominance

The mid-Cretaceous diversification of angiosperms marks the transition from Mesozoic ecosystems dominated by ferns, conifers, cycads and Bennettitales to more modern Late Cretaceous and Tertiary ecosystems dominated by angiosperms[74,75]. In the palaeobotanical record this change is much more profound than that occurring at the Cretaceous–Tertiary boundary and is also reflected in the transition from sauropod-dominated to ornithopod-dominated dinosaur faunas[76]. Data on the floristic composi-

tion of both macrofloras and microfloras show that angiosperms had attained diversity levels of about 50–80% by the end of the Cretaceous[74], but there is evidence that angiosperm abundance still remained subordinate to gymnosperms and ferns in some habitats, perhaps over large geographical areas[77,78]. The extent to which this is a general phenomenon is currently uncertain but it is supported in part by the palynological data and by the prominence of certain open-habitat ferns in some Late Cretaceous floras. These considerations emphasize the value of complementary macrofossil-based, and pollen/spore-based, assessments of diversity and abundance in evaluating the rate and magnitude of the angiosperm radiation. They also raise the possibility that disturbance by herbivorous dinosaurs may have been a significant ecological factor in the first half of angiosperm history[76].

Problems of large-scale stratigraphic resolution make it difficult to resolve geographic patterns in the angiosperm radiation but compilations of palynological data, especially from the Northern Hemisphere, show that the initial increase in angiosperm diversity occurred in low palaeolatitude areas[75,77]. This result is of biogeographic interest for understanding the current distribution of relictual magnoliid families, and also has significant ecological implications. During the Early Cretaceous, low latitude areas experienced semiarid or seasonally arid conditions that may have promoted a weedy life history with precocious reproduction (progenesis)[1,11,41]. Associated effects may have included simplification and aggregation of sporophylls to form a flower, enclosure of ovules in a carpel, truncation of the gametophyte phase of the life cycle, and major reorganization of leaf and stem anatomy. In turn, several of these features may have contributed to angiosperm 'success' through elevated speciation rates[11,41,79] and/or more rapid and more flexible vegetative growth[80,81]. It remains uncertain, however, whether such effects were manifested at the base of the angiosperm clade or within one or more angiosperm subgroups[82,83].

Interestingly, the Gnetales, which show many remarkable structural and biological convergences to angiosperms (Fig. 5), also diversified during the mid-Cretaceous in low palaeolatitude areas, although they never became significant at middle and high palaeolatitudes and experienced rapid decline during the earliest Late Cretaceous[75,77]. The temporal, palaeogeographic, and perhaps ecological, parallels between this radiation of Gnetales and angiosperms implies a common response to changing environmental conditions. Explanations of angiosperm diversification may therefore have underemphasized the effects of environmental changes during the Early and mid-Cretaceous, which included high rates of sea-floor spreading, high sea-level stands and probably high global temperatures[84].

Future directions

The five living groups of seed plants are a poor sample of the total historical diversity of the seed plant clade and thus additional molecular phylogenetic analyses are likely to lead only to

limited progress in evaluating the phylogenetic relationships of angiosperms. However, reducing the gap between angiosperms and their gymnosperm relatives is important because of its implications for rooting the angiosperm tree. Renewed palaeobotanical efforts with the early members of the Gnetales, Bennettitales, angiosperms and other potentially closely related groups are therefore a high priority. Recognition of 'stem group' taxa, with some but not all of the defining features of the 'crown group' has been possible in other studies of land plant phylogeny, and would help to resolve several outstanding problems.

Current data from the fossil record and combined morphological/molecular phylogenies of extant taxa challenge the view that earliest members of the angiosperm clade were large, woody plants with *Magnolia*-like flowers. Instead they suggest a very different concept of early angiosperms as perhaps herbaceous plants of small stature. Flowers would have been small, simple (perhaps unisexual) and probably lacking clear differentiation into sepals and petals (suggesting that molecular genetic models of floral morphogenesis developed for the eudicots *Arabidopsis* and *Antirrhinum*[85] may require modification among magnoliids).

Stamens would have had a poorly developed filament and a well developed anther with valvate dehiscence. Pollen would have been small, monocolpate, tectate with a weakly developed endexine in non-aperturate areas. The gynoecium would have been composed of one or more unilocular carpels containing one or two ovules. The stigmatic surface would have been unelaborated.

Ecologically, the early diversity of angiosperms at low palaeolatitudes, and the parallel Aptian–Cenomanian radiation of angiosperm and gnetalean pollen in these areas, suggest that both groups responded in similar ways to the same environmental cues. Possible linkages between mid-Cretaceous climatic, tectonic and other environmental changes, and their possible impact on terrestrial ecosystems need to be explored. Early Cretaceous fossil plants from low palaeolatitudes are likely to be particularly informative. □

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