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Flowering plant origins

Flowering plants (angiosperms) are the dominant plants in the world today, accounting for between 300 and 400 families and between 250 000 and 300 000 species (compared to approximately 10 000 species of pteridophytes and 750 species of gymnosperms). However, in evolutionary terms, flowering plants are relatively recent, with fossil evidence indicating their first appearance at around 140 million years ago in the early Cretaceous, followed by rapid diversification and radiation in the mid-Cretaceous. By the early Tertiary (~65 Ma), only 60 to 70 million years after their first appearance, angiosperms had attained ecological dominance in a majority of habitats and over a wide geographical area. As a group, therefore, even though they evolved some 300 million years later than the first vascular plants and 220 million years later than the first seed plants, they are of profound evolutionary interest. This chapter examines the evidence for the first flowering plants, considers various theories as to why their appearance was so late in the geological record and discusses the proposed evolutionary pathways leading to angiosperm evolution.

6.1 Evidence for the first angiosperms

Features used to separate extant angiosperms from other seed plants include the enclosed nature of the ovary (the carpel or carpels), the presence of flowers, specialized conducting cells in the xylem and phloem, ovules that have a double-layered seed coat (two integuments), and pollen with a distinctive grain wall made up of columellae. A number of characteristics of the angiosperm life cycle are also distinctive, including a process of double fertilization, whereby two sperms are released from the pollen tube into the ovary (which has one or several ovules inside it). One sperm fuses with the egg to form the zygote (which divides immediately after fertilization to form the embryo), and the other sperm fuses with the embryo sac to produce the primary endosperm (the storage tissue in the seed) (Figure 6.1). The angiosperms were traditionally divided into monocotyledons and dicotyledons; however, this division is no longer supported by recent systematic studies. Instead, two major monophyletic groups are now recognized, the monocots and the eudicots (which contain most, but not all, of the dicotyledons and are characterized by a pollen type with three apertures)

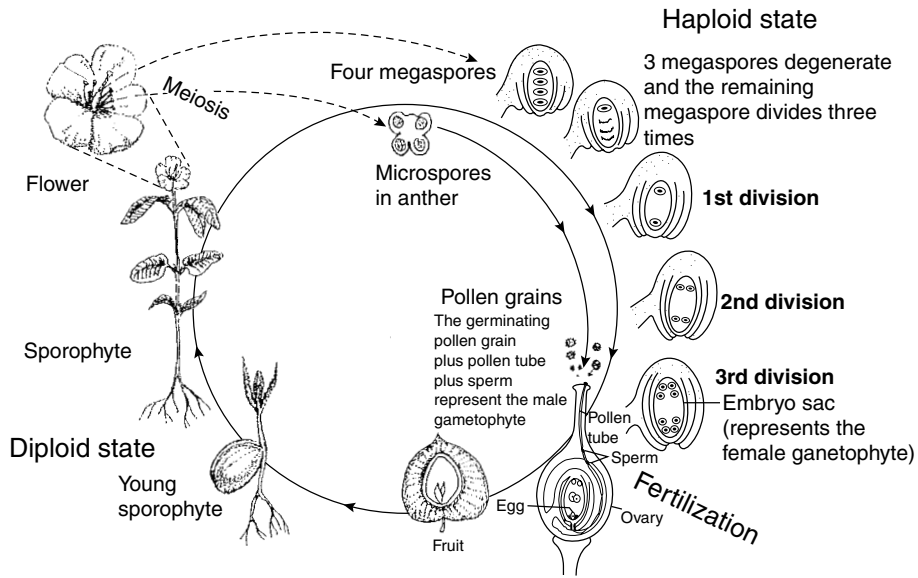


Figure 6.1 Simplified angiosperm life cycle.

Table 6.1 Distinguishing characteristics between monocotyledons and dicotyledons (redrawn from Raven, 1992; Magallon *et al.*, 1999)

Characteristic	Dicotyledons	Monocotyledons
Flower parts	In fours or fives (usually)	In threes (usually)
Pollen	Usually with three pores or furrows	Usually having one pore or furrow
Cotyledons	Two	One
Leaf venation	Usually netlike	Usually parallel
Primary vascular bundles in stem	In a ring	Complex arrangement
True secondary growth with vascular cambium	Commonly present	Commonly absent

(Crane *et al.*, 1995; Magallon *et al.*, 1999). The remaining dicotyledons constitute a third, smaller group, the magnoliids, which have pollen with a single aperture. Although the similarities between the two major groups are far greater than the dissimilarities, the features that group angiosperms as a division and separate monocots from eudicots (Table 6.1) appear to have persisted from early stages of angiosperm evolution (see Section 6.3). Evidence from the geological record suggests that angiosperms first appeared approximately 140 million years ago in the Valanginian, with their major radiation, leading to a global

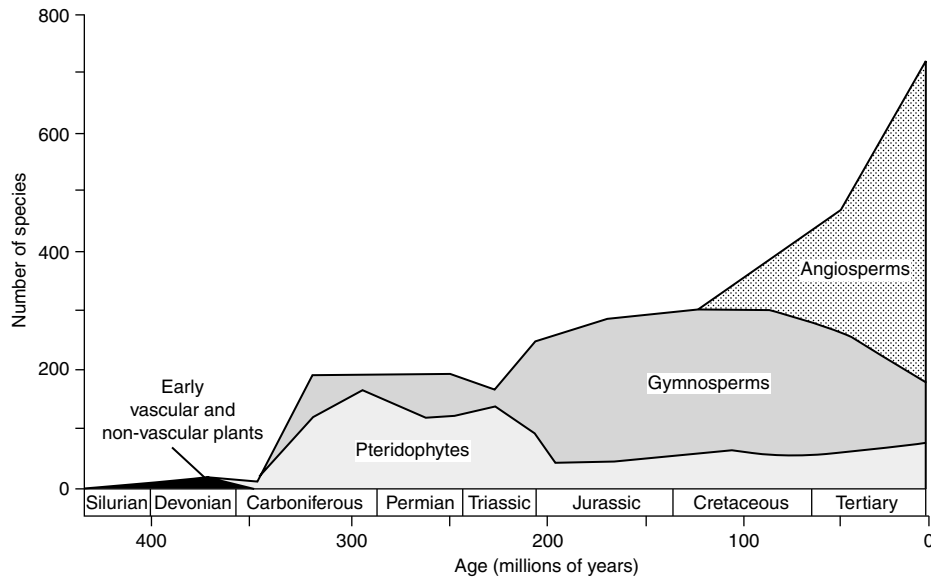


Figure 6.2 Evidence for the appearance and major expansion of the angiosperms from ~140 Ma and a dramatic increase in the number of angiosperms through the mid-Cretaceous (redrawn from Niklas *et al.*, 1983).

distribution, during the Albian–Cenomanian (~100–90 Ma) (Figure 6.2). The earliest fossil evidence for angiosperms is represented in the record as flower parts, fruits, leaves, wood, and pollen (Table 6.2).

Flower parts

Some of the earliest known fossil flowers, dating back to approximately 127–120 Ma, have been found in deposits from Portugal (Barremian or Aptian) (Friis *et al.*, 1999) and near Melbourne in Australia (Aptian) (Taylor and Hickey, 1990). The fossil flowers from Portugal show character combinations that indicate magnoliid or monocotyledonous affinity. Those from Melbourne appear to be similar in floral arrangement to extant perennial herbs in the Piperaceae family, and probably grew in marshy habitats. Although such early finds are rare (the majority of evidence for fossil angiosperm flowers dates back only to approximately 100 million years ago), they show the greatest potential for further insights on early angiosperm biology, ecology, and evolution (Endress, 1987; Crane *et al.*, 1995).

Most early fossil angiosperm flowers can be subdivided into two broad groups (Endress, 1987). Group (i) includes features such as relatively few flower parts (stamens, carpels, number of ovule/seeds per carpel, number of perianth members) and small (< 1 mm diameter), possibly unisexual flowers. Such flowers are compared to those of existing angiosperm families such as Chloranthaceae,

Table 6.2 Some of the earliest angiosperms in the fossil record

Order/family/species	Fossil evidence (leaves, pollen, flowers, wood)	Tree, shrub or herb	Fossil localities	Age (Ma)	Reference
Dicotyledons					
Magnoliales					
Lesqueria	Fruits, flowers	? Herbaceous	Kansas, USA	112(99 (AL)	Crane and Dilcher (1984)
Archaeanthus	Fruit, leaves	? Herbaceous	Kansas, USA	112–99 (AL)	Dilcher and Crane (1984)
Protomonimia	Reproductive organ, wood	Woody shrub or tree	Japan	112–99 (AL)	Nishida and Nishida (1988)
Prisca	Fruit, leaves, stem	Woody tree or shrub	Kansas, USA	99–93 (CE)	Retallack and Dilcher (1981)
Winteraceae					
Walkeripollis	Pollen, wood	Woody tree or shrub	Israel, California	121–99 (AP/AL)	Walker <i>et al.</i> (1983)
Laurales					
Amborellaceae	Fruit	? Shrub		121–112 (AP)	Friis <i>et al.</i> (1995)
Crassidenticulum	Leaves	? Woody tree/shrub	Nebraska, USA	99–93 (CE)	Upchurch and Dilcher (1990)
Mauldinia	Flowers	? Woody tree/shrub	North America	99–93 (CE)	Drimman <i>et al.</i> (1990)
Chloranthaceae					
Chloranthus	Flowers, pollen, seeds	? Herbaceous	North America	112–99 (AL)	Friis <i>et al.</i> (1986)

Table 6.2 (Continued)

Order/family/species	Fossil evidence (leaves, pollen, flowers, wood)	Tree, shrub or herb	Fossil localities	Age (Ma)	Reference
Hedyosmum-like	Flowers, pollen	Herbaceous	Portugal	127–112 (BA/AP)	Friis <i>et al.</i> (1999)
Piperales	Flowers, pollen	Herbaceous	Portugal	127–112 (BA/AP)	Friis <i>et al.</i> (1999)
Platanaceae					
<i>Platanus potomacensis</i>	Flowers, pollen	? Woody tree/shrub	North America, Sweden	112–99 (AL)	Friis <i>et al.</i> (1988)
Hamamelidales					
Hamamelidaceae	Leaves	? Herbaceous	Patagonia, Argentina	127–112 (BA/AP)	Romero and Archangelsky (1986)
Monocotyledons					
Pandanaceae	Leaves	?	?	71–65 (MA)	Jarzen (1978)
Palmae	Leaves, pollen, and stem	Tree/shrub	New Jersey	89–85 (CO)	Christophee (1979)

BA, Barremian; AP, Aptian; AL, Albian; CE, Cenomanian; TU, Turonian; CO, Coniacian; SA, Saxonian; CA, Campanian; MA, Maastrichtian.



Figure 6.3 Fossil *Archaeanthus linnenbergeri* (~100 Ma), indicating many similarities with members of extant Magnoliaceae (redrawn from Dilcher and Crane, 1984).

Piperaceae (the pepper family), and Platanaceae (the plane-tree family). In comparison, group (ii) has numerous flower parts and large, bisexual flowers (up to 65 mm in diameter). These flowers are compared with those of extant angiosperm families such as Magnoliaceae, Degeneriaceae, and Winteraceae (Friis and Crepet, 1987). An example of a fossil flower classified in this second group is *Archaeanthus* (Figure 6.3). This has a fossil record dating back to the Albian (~100 Ma) (Dilcher and Crane, 1984), and demonstrates many features in common with extant species of *Magnolia*, such as numerous stamens (between 50 and 60) and free carpels (between 100 and 130).

It was originally suggested that the first flowers to evolve were similar to extant *Magnolia*, with numerous bisexual flowers (therefore those classified above in group (ii)), and that group (i) originated either by extreme reduction in the floral parts from group (ii) or from two different sources in the gymnosperms (Endress, 1987). Fossil evidence, however, indicates that both types of flowers were present at around the same time (Friis and Crepet, 1987). Also, in extant orders of angiosperms, extreme variations in the number of floral organs are not restricted to comparatively unrelated orders or families, but can occur within a genus, and even a single species (Endress, 1987), thus indicating that floral organization is very plastic. It is highly probable therefore that the number and arrangement of floral organs changed many times during evolution, and that extremes in these features in the earliest angiosperms was not necessarily an expression of distant relationship.

Fruits

Earliest evidence for fossil angiosperm fruits dates back to the Aptian and Albian (~121 Ma), with examples from localities in Asia and North America, including fruits of ceratophyllales (Dilcher, 1989), juglandales (Krassilov and Dobruskina, 1995), and ranunculids (Friis *et al.*, 1995). Many of these early seeds were small (1–40 mm in length) in relation to later groups in the fossil record—a feature that is thought to be indicative of the ‘weedy’ stature of these early flowering plants (Tiffney, 1984). Comparison of seed sizes in extant floral groups, for example, broadly demonstrates that small propagules with thin seed walls and little storage material are associated with early successional plants that can be classified as ‘r’ strategists (weedy generalists) (Wing and Boucher, 1998).

Pollen

Angiosperm pollen is non-saccate (without bladders), and in the eudicots has numerous symmetrically arranged pores and furrows. In all angiosperms the pollen wall is divided into an outer layer (the tectum) supported on numerous short, radial structures (looking like columns and often referred to as columellae), which provide an extensive chamber system for the deposition of biologically active substances that act as ‘recognition substances’ on reaching the stigma (Traverse, 1988b; Hughes, 1994) (Figure 6.4).

The earliest unequivocal fossil angiosperm pollen has been found in late Valanginian (~130 million years ago) deposits of Israel (Brenner, 1996) and Morocco (Gubeli *et al.*, 1984). There are also reported occurrences of angiosperm pollen from older sediments in Libya (Berriasian, ~140 Ma) (Thusu *et al.*, 1988) and China (Hauterivian) (Li and Liu, 1994), but the ages of these sediments are not well constrained (Barrett and Willis, 2001).

All the earliest angiosperm pollen grains are small, between 10 and 50 μm in diameter, and distinguishable by their wall construction and the number and types of germination-furrows. Four morphological groups have been identified in the earliest angiosperm pollen, namely *Clavatipollenites*, *Pre-Afropollis*, *Spinatus*, and *Liliacidites* (Brenner, 1996). Those classified in the *Clavatipollenites* group have a characteristic columellate wall with usually one germination-furrow (Figure 6.5a). Those in the *Spinatus* group can be distinguished, along with other features, by short spines on the margin of the grain (Figure 6.5c). The *pre-Afropollis* group contains grains that are inaperturate (i.e. no furrows) but have a grain wall pattern that is described as wedge-shaped, with fluted walls (Figure 6.5b) (Brenner, 1996). Finally, those in the *Liliacidites* groups are distinguished by their larger size (up to 50 μm in diameter), their single germination-furrow, and a cell wall composed of very high columellae (Figure 6.5d).

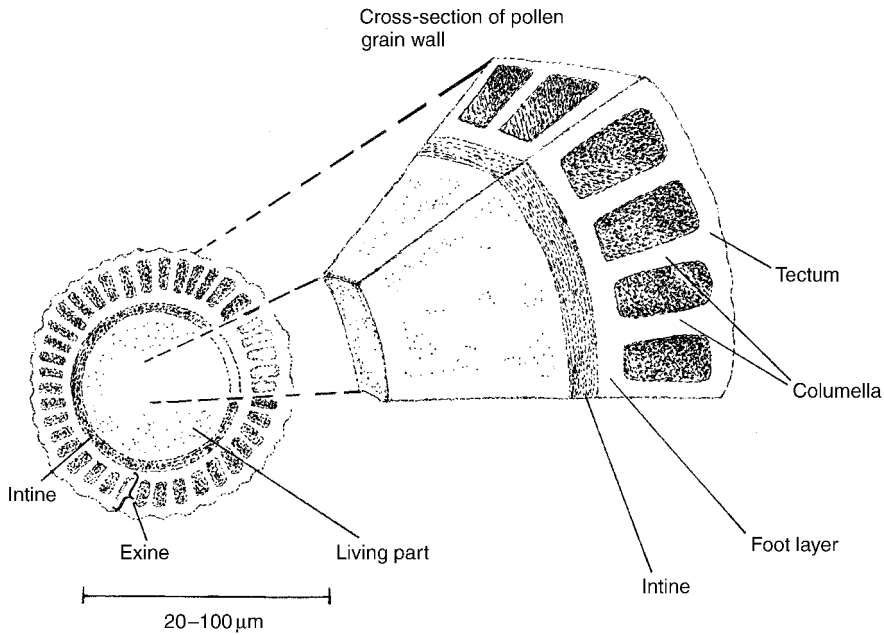


Figure 6.4 Distinguishing characteristics of fossil angiosperm pollen.

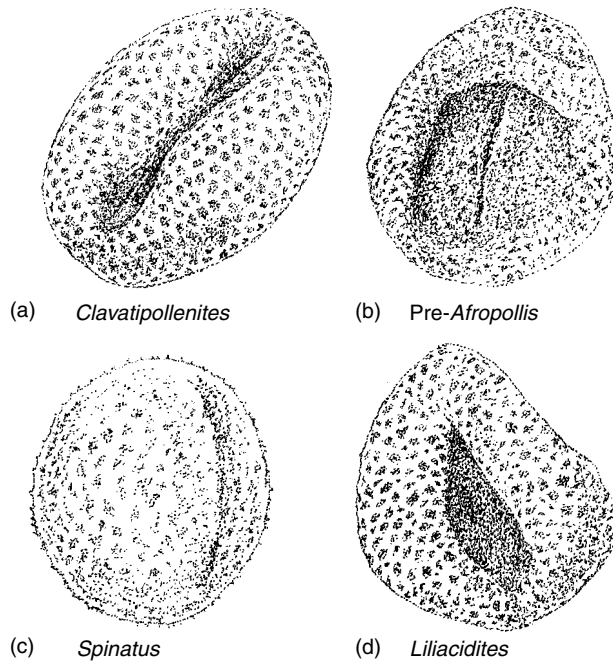


Figure 6.5 Four morphological types identified in the earliest fossil angiosperm pollen: (a) *Clavatipollenites*; (b) *Pre-Afropollis*; (c) *Spinatus*; and (d) *Liliacidites* (redrawn from Brenner, 1996). All are between 10 and 50 μm in diameter.

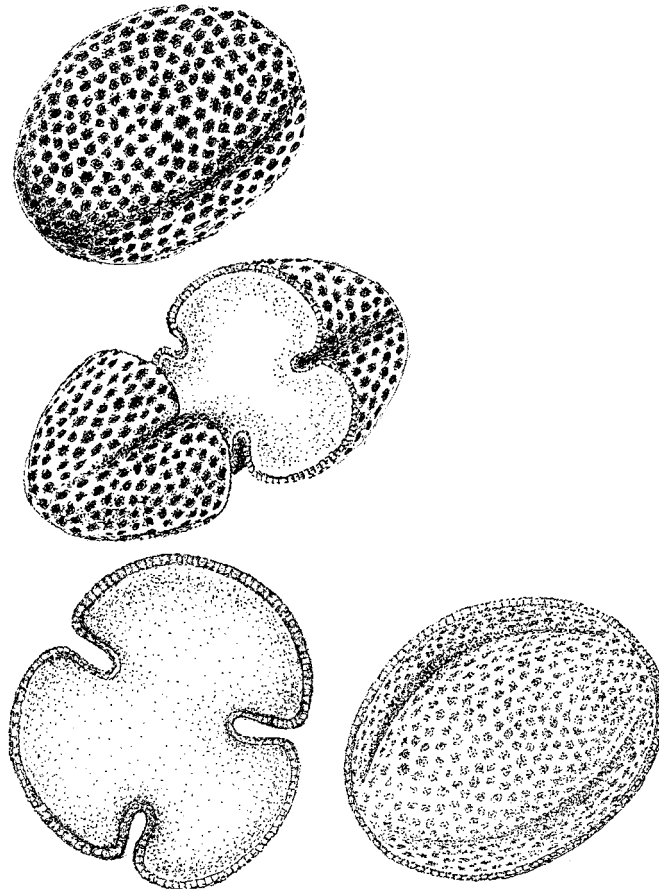


Figure 6.6 Fossil *Tricolpites* pollen, equatorial and transverse view (redrawn from Stewart and Rothwell, 1993). These grains were approximately 50 μm in diameter.

A number of associations have been made between the early fossil angiosperm pollen and extant types. The fossil grains of *Clavatipollenites*, for example, apparently bear a close morphological resemblance to pollen of the extant family Chloranthaceae (Traverse, 1988b). *Clavatipollenites* has also been found within fossil flowers identified as members of the Chloranthaceae family, supporting the suggestion that it is associated with this family (Crane *et al.*, 1995). Those in the *Liliacidites* group, in comparison, have an outer layer (the sexine) that is similar in structure to that of extant monocotyledons such as Liliaceae (Brenner, 1996).

In increasingly younger sediments (Barremian/Aptian boundary), there is the appearance of more complex fossil pollen grains with various arrangements of pores and furrows. One type, named *Tricolpites*, for example, had three symmetrically arranged furrows (often referred to as tricolpate; Figure 6.6).

Evolution of three furrows is thought to be an adaptation that facilitated germination on a stigmatic surface (Endress, 1987), as any orientation of a tricolpate grain would result in at least one germination furrow being positioned near or on the surface of the stigma. *Tricolpites* pollen grains have been found inside the anthers of fossil Platanaceae flowers (Friis and Crepet, 1987), indicating a probable association with this family. Another type of pollen grain to appear from the Cenomanian (~95 Ma) was spherical with numerous apertures resembling pores. These grains, known as polyporate, had pores either arranged around the equatorial margins of the grain or all over the surface of the grain, which presumably would also have facilitated germination (Muller, 1981, 1984).

Leaves

Angiosperm leaves are thought to be megaphyllous in origin. Distinguishing characteristics include reticulate venation, forming areoles on dicotyledon leaves, together with veins that end blind within the areoles, and parallel major veins arranged in sets of various sizes and interconnected by smaller veins on the lamina of monocotyledons (Stewart and Rothwell, 1993). In monocotyledons, the leaf is usually differentiated into a blade and sheath, whereas in dicotyledons the leaf is usually differentiated into a blade and petiole (Figure 6.7a).

Angiosperm leaves are first recorded in the fossil record from approximately 120 million years ago (Barremian). Fossil localities range from central Asia, the Russian far-east, Portugal, and the eastern United States (Hughes, 1994), and indicate broadly similar assemblages containing small leaves (approximately 2–4 cm in diameter) with expanded laminae and reticulate venation patterns (Figure 6.7b).

Attempts to characterize these earliest leaf types and compare them with extant leaves and their associated environmental conditions (based on features such as presence/absence of drip-tips, entire or dissected margins, size of leaf blade) has led to the suggestion that most were similar to plants that grow in streamside situations, semiaquatic habitats, or as an understory (Upchurch and Wolfe, 1987; Wolfe and Upchurch, 1987). In comparison, fossil leaves present in younger assemblages of Albian age (~110–100 Ma) possessed features characteristic of extant early successional plants, namely pinnately compound leaves, palmately lobed leaves, and shallow cordate leaves with serrated margins and palmate venation (Figure 6.8) (Hickey and Doyle, 1977; Taylor and Hickey, 1990). Leaves present in deposits of Cenomanian age (~100–90 Ma) included leaf physiognomies (shape and size) that in extant species are typical of late successional plants. These marked changes in angiosperm leaf physiognomy spanning the latter part of

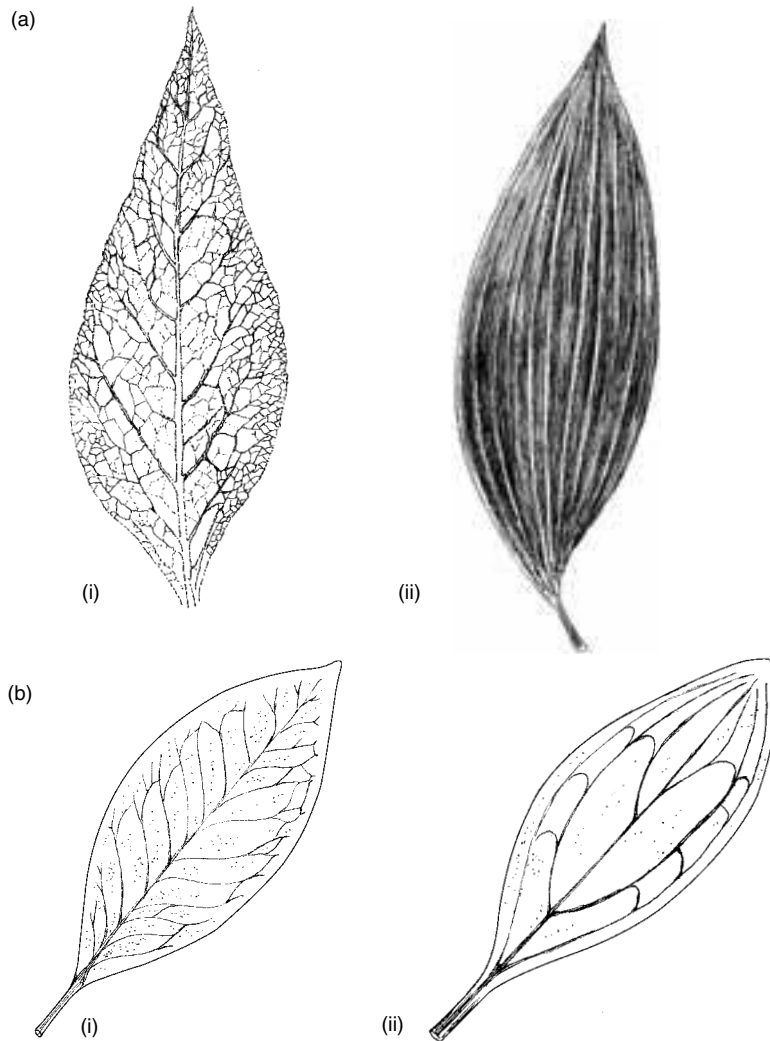


Figure 6.7 (a) Extant angiosperm leaves: distinguishing characteristics include (i) reticulate venation forming areoles on dicotyledon leaves, together with veins that end blind within the areoles, and (ii) parallel major veins arranged in sets of various sizes and interconnected by smaller veins on the lamina of monocotyledons (Friis *et al.*, 1987; Stewart and Rothwell, 1993). (b) Primitive angiosperm leaf types from the early Cretaceous: (i) dicotyledon, showing pinnate venation and entire leaf margin; (ii) monocotyledon, showing convergence of main veins at top of leaf and interconnecting veins.

the early Cretaceous has led to the suggestion that although angiosperms were initially early successional plants, within a matter of 20 million years they had formed the canopy of late successional forests (Doyle and Hickey, 1976).

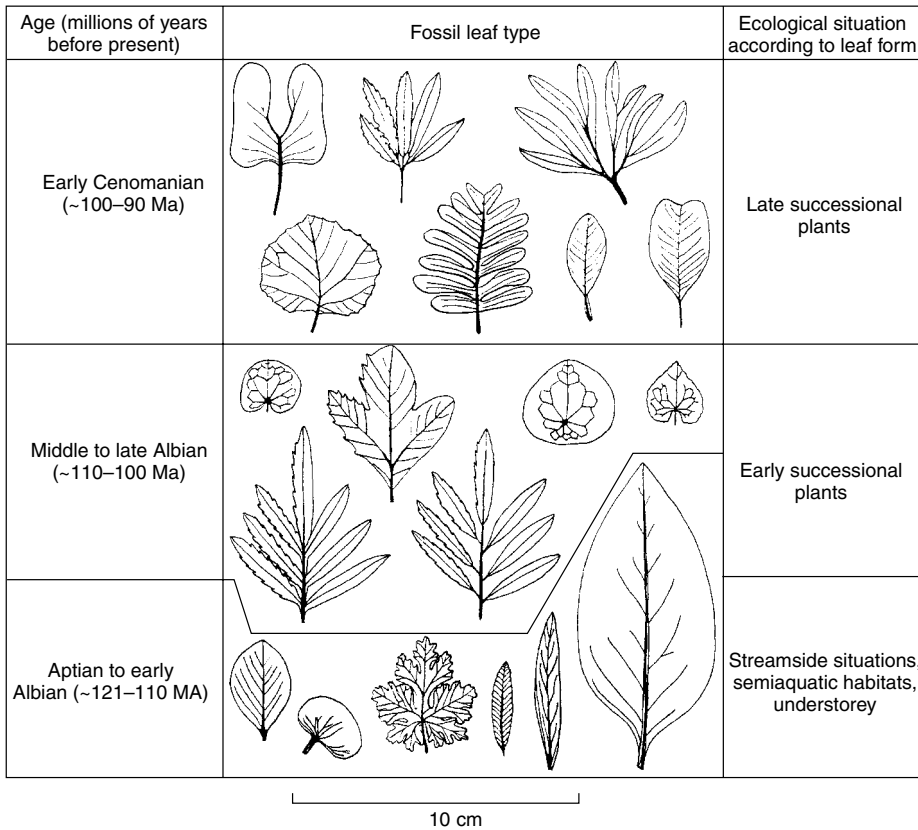


Figure 6.8 Trends in the earliest fossil angiosperm leaves through the Cretaceous and classification of their probably ecological situation according to leaf form (after Upchurch and Wolfe, 1987).

6.2 Nature and distribution of the earliest Angiosperms

Trees, shrubs, or herbs?

Various lines of evidence from the fossil record, including fossil flowers, fruits, leaves, pollen, and also wood, suggest that by 100 million years ago (Albian/Cenomanian) there was an increasing diversity of angiosperms in the global flora (Table 6.3). There is some difficulty, however, based on the available fossil evidence, in determining whether the earliest angiosperms were trees, shrubs, or herbs. Many of the earliest fossil families (i.e. Chloranthaceae, Piperaceae, Platanaceae, Magnoliaceae, Degeneriaceae, and Winteraceae) have both arborescent and non-arborescent forms. Hence, many competing hypotheses on the likely vegetative morphology of ancestral angiosperms have been proposed. These fall broadly into three schools of thought. According to the first, the

Table 6.3 Diversification and radiation of aborescent angiosperms between 100 and 70 Ma (adapted from Wing and Boucher, 1998)

Family/species	Dicot./ monocot. (tree, shrub, herb, vine)	Present-day distribution	Earliest fossil evidence
Hamamelidaceae	Dicot. (T and S)	Chiefly subtropical, especially E. Asia	~93–89 Ma (Turonian)
Platanaceae	Dicot. (T)	N. hemisphere (7 species); S.E. Asia (1 species); S.E. Europe (1 species); N.E. America (1 species) 168	~112–99 Ma (Albian)
Myrothamnaceae	Dicot. (S)	S. Africa and Madagascar	~99–93 Ma (Cenomanian)
Ulmaceae			
<i>Ulmus</i>	Dicot. (T and S)	N. temperate to N. Mexico	~71–65 Ma (Maastrichtian)
<i>Celtis</i>	Dicot. (T)	Tropical (70 species); temperate (4 species)	~93–89 Ma (Turonian)
Fagaceae			
<i>Castanea</i>	Dicot. (T)	N. temperate	~85–83 Ma (Santonian)
<i>Northofagus</i>	Dicot. (T)	S. hemisphere	~85–83 Ma (Santonian)
Betulaceae			
<i>Alnus</i>	Dicot. (T)	N. temperate; S.E. Asia; Andes	~85–83 Ma (Santonian)
<i>Betula</i>	Dicot. (T)	N. hemisphere	~85–83 Ma (Santonian)
Myricales			
<i>Myrica</i>	Dicot. (S)	Cosmopolitan except Mediterranean and Australia	~85–83 Ma (Santonian)
Juglandaceae	Dicot. (T and S)	Temperate and warm N. hemisphere to S. America and Malaysia	~83–71 Ma (Campanian)
Theaceae	Dicot. (T, S, and V)	Tropical (520 species) with few warm temperate	~93–89 Ma (Turonian)
Moringaceae	Dicot. (T)	Semi-arid Africa to Asia	~93–89 Ma (Turonian)
Actinidiaceae	Dicot. (T, S, and V)	Tropical and warm Asia mountains	~83–71 Ma (Campanian)
Clethraceae	Dicot. (T and S)	Tropical America; Asia; N. America	~71–65 Ma (Maastrichtian)
Ericaceae	Dicot. (T and S)	Cosmopolitan except deserts (and scarce in Australasia)	~93–89 Ma (Turonian)

Diapensiaceae	Dicot. (S and H)	Arctic and N. temperate to Himalayas	~83–71 Ma (Campanian)
Symplocaceae	Dicot. (T)	Tropical and warm America	~71–65 Ma (Maastrichtian)
Sapotaceae	Dicot. (T and S)	Tropical	~71–65 Ma (Maastrichtian)
Bombaceaceae	Dicot. (T)	Old World Tropical	~71–65 Ma (Maastrichtian)
Buxaceae	Dicot. (T)	Nearly cosmopolitan	~112–99 (Albian)
Araliaceae	Dicot. (T)	Tropical; America, few temperate	~71–65 Ma (Maastrichtian)
Cornaceae	Dicot. (T)	N. temperate; rare in Tropics and S. temperate	~71–65 Ma (Maastrichtian)
Rhamnaceae	Dicot. (T)	Cosmopolitan especially tropical and warm N. temperate	~71–65 Ma (Maastrichtian)
Rosaceae	Dicot. (T, S, and H)	Subcosmopolitan but especially temperate and warm N.	~71–65 Ma (Maastrichtian)
Sabiaceae	Dicot. (T and S)	S.E. Asia; Malasia; tropical America	~71–65 Ma (Maastrichtian)
Caesalpiniaceae	Dicot. (T and S)	Tropical; warm America	~93–89 (Turonian)
Myrtaceae	Dicot. (T and S)	Tropical, warm and temperate	~85–83 (Santonian)
Onagraceae	Dicot. (T and S)	Cosmopolitan, especially temperate and warm America	~71–65 Ma (Maastrichtian)
Combretaceae	Dicot. (T and S)	Tropical and warm, especially Africa	~83–71 (Campanian)
Gunneraceae	Dicot. (T and S)	S. tropical and S. hemisphere	~93(89 (Turonian)
Sapindaceae	Dicot. (T, S, and H)	Tropical and warm, few temperate	~89–85 (Coniacian)
Malpighiaceae	Dicot. (T, S, and V)	Tropical and warm, especially S. America	~71–65 Ma (Maastrichtian)
Aquifoliaceae (e.g. <i>Ilex</i>)	Dicot. (T and S)	Almost cosmopolitan	~93–89 (Turonian)
Olacaceae	Dicot. (T, S, and V)	Tropical; S. Africa	~71–65 Ma (Maastrichtian)
Santalaceae	Dicot. (T, S, and H)	Subcosmopolitan, especially tropical and warm dry	~71–65 Ma (Maastrichtian)
Proteaceae	Dicot. (T and S)	Tropical and subtropical, especially S. hemisphere	~83–65 (late Cretaceous)
Palmae	Monocot. (T)	Tropical and warm	~112–99 (Albian)
Pandanaceae	Monocot. (T and S)	Old world tropical to New Zealand	~71–65 Ma (Maastrichtian)

T, tree; S, shrub; V, vine; H, herb.

earliest angiosperms were arborescent shrubs or small trees (Arber and Parkin, 1907). The second suggests that they were herbaceous and rhizomatous in habit, such as in extant Chloranthaceae or Piperaceae (Taylor and Hickey, 1996). A third intermediate hypothesis suggests that they were most probably herbaceous, weedy, small shrubs (Stebbins, 1974; Crane, 1987; Wing and Tiffney, 1987).

Increasingly, evidence from the fossil and molecular record appears to support the third hypothesis. Angiosperm wood is rare in the early Cretaceous fossil record compared with that of gymnosperm wood, and it is not until the late Cretaceous (~70 Ma) that a diverse angiosperm wood flora is apparent (Wing and Tiffney, 1987; Wheeler and Baas, 1993; Wing *et al.*, 1993). Most of the specimens of early Cretaceous angiosperm wood are also extremely small (< 10 cm in diameter) (Herendeen, 1991). It is generally assumed, therefore, that this lack of angiosperm fossil wood is a reflection of the herbaceous nature of the earliest angiosperms. This assumption is further supported by the fact that, in the fossil record, the earliest angiosperm seeds tend to be small (1–40 mm in length) with thin seed walls, and the leaves, small (2–4 cm in diameter) with expanded laminae and reticulate venation. All of these characteristics in extant plants are usually indicative of small, weedy plants with a rapid life cycle (Taylor and Hickey, 1996; Wing and Boucher, 1998; Friis *et al.*, 1999). This evidence therefore appears to also support a herbaceous hypothesis. However, recent molecular phylogenetic analysis, based on evidence from mitochondrial, plastid, and nuclear DNA in extant plants, has identified *Amborella*, a small shrub, as the basal branch of angiosperm phylogeny (Qui *et al.*, 1999). This finding therefore supports the intermediate hypothesis, that the earliest angiosperms were herbaceous, weedy, small shrubs. It is interesting to note, however, that the second most basal group identified by the molecular study of Qui *et al.* (1999) are Nymphaeales, which are aquatic rhizomatous herbs. These results therefore also lend support to the herbaceous origin hypothesis.

Dicotyledons or monocotyledons?

In the fossil record, the earliest flowers and most of the leaves and pollen appear to be from dicotyledons and, although several lineages of monocotyledons are now known from both the palynofloras and megafloras of Barremian–Albian age (127–112 Ma) (e.g. Friis *et al.*, 1999; Pole, 1999), early monocotyledon fossils are rare (Table 6.3). Various suggestions have been made as to why there is this apparent paucity of early monocotyledons. First, it has been suggested that the majority of the monocotyledons were herbaceous (as is the case for extant monocotyledons) and therefore would not have been as well preserved as the woody dicotyledons (Taylor and Taylor, 1993). A second suggestion is that, similar to the present-day situation, there were many more genera of dicotyledons than monocotyledons (Stewart and Rothwell, 1993). Presently there are approximately six times as many dicotyledons as monocotyledons in the world's flora, and it is possible that this had a major influence on

representation in the early fossil record of angiosperms (Daghlian, 1981). Thirdly, it is suggested that the monocotyledons evolved from the dicotyledons (Walker and Walker, 1984) and therefore were later in evolutionary terms. This last suggestion appears to be increasingly unlikely, however, in the light of a number of recent cladistic and phylogenetic studies (e.g. Davis, 1995; Stevenson and Loconte, 1995; Gandolfo *et al.*, 1998; Qui *et al.*, 1999). Recent estimates, based on a phylogeny of monocotyledonous angiosperms, suggest that the major radiation of monocotyledons occurred during the early Cretaceous (Bremer, 2000). Thus, their late appearance in the fossil record is most likely due to taphonomic bias rather than a later evolution.

Place of origin and radiation

There is much discussion in the literature on where exactly angiosperms originated. Currently, the most favoured hypothesis suggests that angiosperms originated in the palaeotropics (0–30°), radiating out to colonize higher-latitude environments some 20 to 30 million years later (Hickey and Doyle, 1977; Crane and Lidgard, 1989; Drinnan and Crane, 1990; Hughes, 1994; Lupia *et al.*, 1999; Barrett and Willis, 2001). This hypothesis is based primarily on the evidence in the fossil pollen record (Figure 6.9). The earliest well-dated angiosperm pollen has been found in late Valanginian (~135 Ma) fossil localities in Israel (Brenner, 1996) and Morocco (Gubeli *et al.*, 1984). During the early Cretaceous these regions lay between the palaeoequator and 25°N (Smith and Littlewood, 1994) (Figure 6.9a). Angiosperms then appear to have spread relatively rapidly into the higher latitudes, with evidence for slightly younger (Hauterivian, ~132 Ma) pollen grains from fossil localities in England (Hughes and McDougall, 1987, 1994) and China (Li and Liu, 1994). By the Barremian (~127 Ma), angiosperms appear to have been widespread, with fossil localities in central Africa, Australia, Europe, and China (Barrett and Willis, 2001 and references cited therein).

Although angiosperms appear to have spread relatively quickly, they did not become floristically prominent in the low palaeolatitudes (between ~30°N and 30°S) until the Aptian (~120 Ma), and in higher palaeolatitudes (between 40 and 65°S) until the Cenomanian (~100 Ma) (Crane and Lidgard, 1989; Drinnan and Crane, 1990; Lidgard and Crane, 1990) (Figure 6.9b). However, differences in both diversity and abundance between the low and high latitudes persisted for at least another 30 million years. In the Maastrichtian (~70 Ma), for example, angiosperms dominated low latitude pollen assemblages, accounting for 60–80% of pollen, whereas in the high latitudes, they accounted for only between 30 and 50% of the total pollen (Crane, 1987). The remaining percentage of pollen in high-latitude floras was made up of gymnosperms and pteridophytes. The apparent paucity of early angiosperms in these high-latitude environments is thought to be due, in part, to limitations of light and temperature for a substantial part of the year. Such environmental conditions would have offered few opportunities for the replacement of existing well-adapted vegetation,

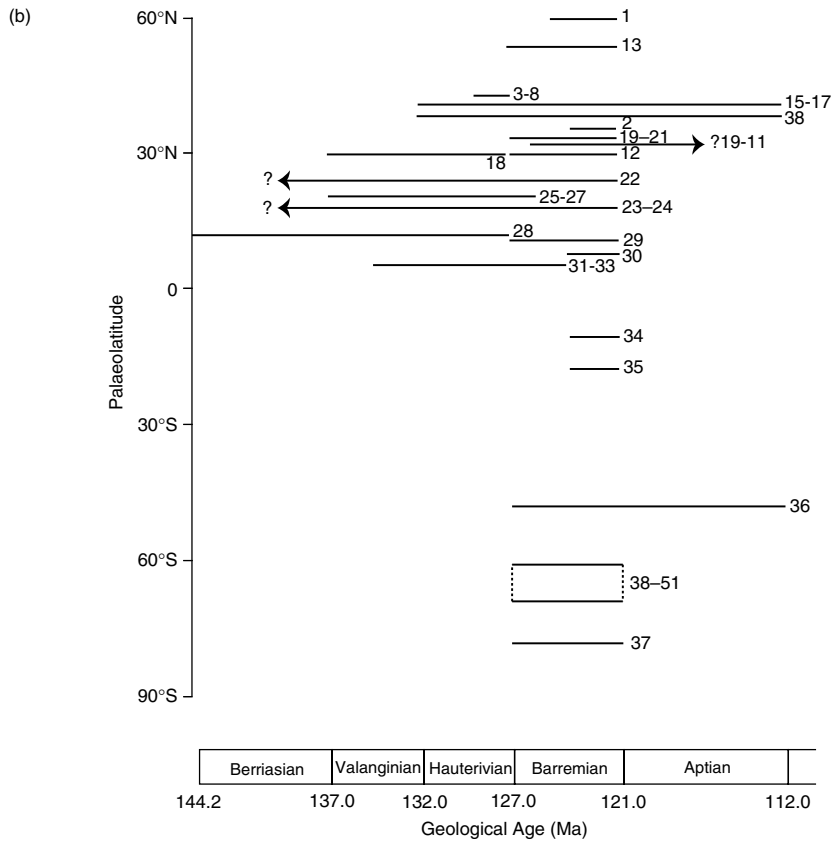
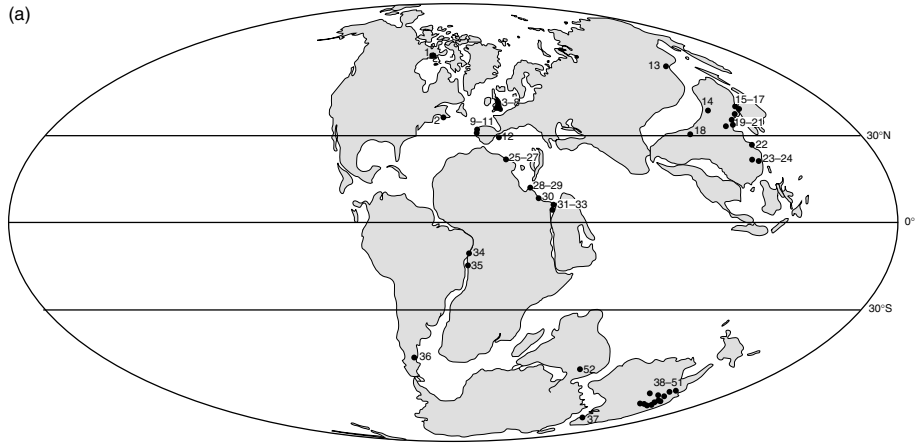


Figure 6.9 (a) Global distribution of earliest angiosperm occurrences (pre-Aptian, < 121 Ma) recorded in the fossil pollen record, plotted onto a palaeogeographical map of age 135 Ma (Valanginian). (b) Graphical representation of the data presented on the map above. Horizontal lines represent the temporal ranges suggested for the specific angiosperm taxa, the numbers correspond to the localities listed on the map (redrawn from Barrett and Willis, 2000 and references cited therein).

dominated by conifers and ferns, by ‘weedy’ angiosperms (Wing and Boucher, 1998).

Angiosperm diversity and abundance in the high latitudes increased slowly through the early and mid-Cretaceous, most probably as a function of their biology rather than due to slow migration rates (Wing and Boucher, 1998). Even today in the tundra and boreal biomes of the high-latitude regions of North America and Eurasia, for example, angiosperms are of relatively low abundance compared to gymnosperms, in particular the conifers (Nikolov and Helmisaari, 1992; Sirois, 1992).

Although the early angiosperms were not an invasive element in the high-latitude environments, for later angiosperm groups the high-latitudes appear to have been centres of origin. Southern Gondwana, in particular, appears to have been a centre of origin for *Nothofagus* (Dettmann and Jarzen, 1990; Dettmann *et al.*, 1990; Dettmann, 1992; Cantrill and Nichols, 1996). *Nothofagus* is presently an important element of the southern hemisphere flora, and according to the fossil record of this genus, evolved in southern high latitudes during the Maastrichtian (~70 Ma) (Hill and Scriven, 1995).

6.3 Why so late?

Even though angiosperms were present from as early 140 Ma (Berriasian–Valanginian), in plant evolutionary terms this is late. The first unequivocal evidence for angiosperms in the fossil record is up to 300 million years later than the first vascular land plants, and, as a group, they are therefore the most recent. The ‘enigma of angiosperm origins’ and their late arrival in the fossil record have long been areas of palaeobotanical interest and research (Hughes, 1994). There are a number of hypotheses as to why they appear so late in the fossil record. These include bias in the fossil record (therefore they evolved much earlier but went undetected), and the suggestion that their evolution was triggered by a particular set of environmental conditions, and/ or biotic interactions (such as co-evolution with faunal groups). A broad overview of these different hypotheses will be considered in the following section.

Nature of the fossil evidence

One commonly cited explanation for the late appearance of angiosperms is due to taphonomy. It is suggested that there is a bias in the fossil record against the preservation of the earliest angiosperm vegetative or reproductive parts. Thus it is argued that angiosperms may have been part of the global vegetation much earlier than the Cretaceous, but were situated in dry upland environments, where preservation potential would have been poor (Axelrod, 1952; Taylor and

Taylor, 1993). Both fossil and molecular evidence exists to support this hypothesis, although neither is particularly convincing.

Fossil evidence for a pre-Cretaceous origin of angiosperms is based on early examples of angiosperm-like pollen, fruiting axes, and leaves. Angiosperm-like pollen, recognized by a tectate pollen wall, has been found in deposits dating as far back as the Triassic (~ 220 Ma) and includes several species of grains with a single furrow that have been classified loosely in the *Crinopolles* group (Traverse, 1988). However, many discount this evidence since this early 'pollen' has never been found within angiosperm flowers. In addition, other morphologically similar types of early pollen, originally classified as angiosperm-like, have since been demonstrated to belong to earlier groups (i.e. gymnosperms or pteridophytes), or be contained in deposits that were stratigraphically misplaced and much younger than originally thought (Hughes, 1994).

Fossil evidence for angiosperm fruiting axes has been described recently from a late Jurassic (~145 Ma) fossil locality in China (Sun *et al.*, 1998). The angiosperm megafossil named *Archaeofructus liaoningensis*, and placed within the Magnoliophyta division, displays a number of key angiosperm features, including, for example, ovules (seeds) that are completely enclosed in carpels, and leaf-like structures subtending each axis, which are probably flowers. However, there has been much debate about the age of the formation in which this 'early' angiosperm is preserved. The fossil was extracted from the lower part of the Yixian Formation of the Liaoning Province, China, which has been dated by biostratigraphical correlations to late Jurassic (~145 Ma) (Sun *et al.*, 1998). However, other lines of evidence, including radiometric dating (^{40}Ar - ^{39}Ar) and palaeontological evidence, suggest that the lower part of the Yixian Formation is of late early Cretaceous age (~125 Ma) (Luo, 1999; Swisher *et al.*, 1999; Barrett, 2000), casting some doubts on the claim that this is the first unequivocal pre-Cretaceous angiosperm megafossil.

Angiosperm-like leaves have been found in deposits dating back to the late Triassic (~ 210 Ma), the most commonly cited being a leaf-type named *Furcula*. This leaf appears to have a typical angiosperm-like venation pattern (Stewart and Rothwell, 1993). However, *Furcula* leaves also display forking laminae (Figure 6.10), which are much more common in certain pteridosperms (Harris, 1932; Stewart and Rothwell, 1993). The classification of this leaf type as angiospermous therefore remains ambiguous, and from the fossil evidence alone (pollen, fruiting axes, and leaves) there is a justifiable scepticism concerning the pre-Cretaceous occurrence of angiosperms (Crane *et al.*, 1995).

However, evidence from molecular analyses has rekindled some support for a pre-Cretaceous origin for angiosperms. Construction of a molecular clock, based on the number of substitutions that have occurred since the divergence of monocotyledons from dicotyledons, suggests that this event may have occurred as early as 300 million years ago in the late Carboniferous (Martin *et al.*, 1989). Thus by inference, this study suggests that angiosperm origins must have occurred much earlier in plant evolutionary history. But a note of caution must

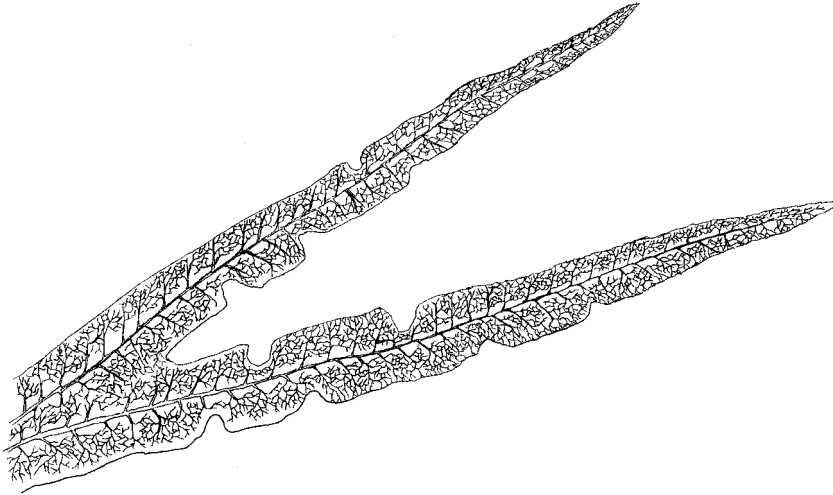


Figure 6.10 Fossil *Furcula* leaf (redrawn from Stewart and Rothwell, 1993). The typical angiosperm-like venation pattern seen in this fossil, which has been found in deposits dating back to the late Triassic (~210 Ma), led to the suggestion that this was an early angiosperm and therefore supports a pre-Cretaceous origin of this group.

be added since the method used in this study compared the number of substitutions that occurred in DNA of a slowly evolving glycolytic enzyme in nine extant species. When the same question (i.e. divergence of monocotyledons from dicotyledons) was asked using DNA from chloroplast sequences of extant species (Li *et al.*, 1989), the molecular clock suggested a date of between approximately 250 and 200 million years ago (Triassic). Both studies therefore suggest an earlier date for angiosperm origin than supported by the fossil evidence, but with up to a 100 million year discrepancy. However, the results of these molecular studies have not only been questioned on this discrepancy, but also on a number of other accounts. It is argued that their phylogenetic methodology is flawed (Crane and Lidgard, 1989), that the assumption that rates of molecular evolution in angiosperms has remained relatively constant through time is not adequately justified, and that the results are not supported by the angiosperm fossil record (Barrett and Willis, 2001).

Recent molecular phylogenetic studies of 106 extant angiosperms, however, have yet again reopened this whole debate (Qui *et al.*, 1999). This study analysed gene sequences for all three plant genomes (mitochondrial, nuclear, and chloroplast DNA), thereby avoiding the problems associated with single genome analysis (as above) (Kenrick, 1999a). Results from this study suggest that the split between gymnosperms and angiosperms may have occurred as early as the late Carboniferous (~290 Ma) (Qui *et al.*, 1999), therefore also supporting a pre-Cretaceous origin of the angiosperm lineage (Kenrick, 1999a).

Environmental considerations

Another hypothesis for the late appearance of angiosperms is related to the effects of major global environmental changes, including oceanic anoxia, increased tectonic activity, and sea-floor spreading, occurring in the mid-Cretaceous (~140–80 Ma). While there is no clear evidence (as yet) that the diversification and radiation of angiosperms was triggered by these environmental events, a number of floristic changes in mid-Cretaceous vegetation do correlate broadly with them (Lupia *et al.*, 1999). It is suggested that these major environmental changes may have conferred competitive advantages to the angiosperms at the expense of the previously dominant gymnosperms and pteridophytes.

In particular, the period between 124 and 83 million years ago (Aptian to Campanian) saw a dramatic change in continental configurations. Although the supercontinent Pangea had started to break up by the early Jurassic (~200 Ma) (Erwin, 1993), a period of rapid plate spreading was initiated in the Aptian (~124 Ma) until the Cenomanian (~83 Ma) (Sheridan, 1987, 1997). This resulted not only in changing continental configurations (the continents of Africa and South America were formed, and India, Australia, and Antarctica were distinguishable as attached plates), but also a 50–100% increase in the Earth's ocean crust production. Large-scale changes in global sea levels and atmospheric composition would have been associated with continental break-up. Geological evidence indicates that this entire period of major environmental perturbation is most probably attributable to an extraordinary upwelling of heat and material from the Earth's core–mantle boundary, known as a superplume episode (Larson, 1991a, b).

The effect of these geological events would have had a significant impact on global environments. It is estimated, for example, that a 100-m rise in long-term eustatic sea level occurred (Valentine and Moores, 1970; Haq *et al.*, 1987; Hallam, 1992), resulting in the formation of extensive epicontinental seas covering the interiors of North America, southern Europe, Australia, Africa, and South America (Briggs, 1995; Condie and Sloan, 1998). In addition, increased volcanism, which accompanied the plate movements, would have pumped greenhouse gases into the atmosphere, most notably CO₂ (Figure 6.11). Carbon cycle modelling indicates that CO₂ levels were 4–5 times greater than those of the present day (Tajika, 1999). This could have raised global temperatures by as much as 7.7°C (Caldeira and Rampino, 1991). Evidence from various palaeoclimatic indicators also supports the suggestion that this was a time of global climate warming (Figure 6.12). Coral reefs, for which warm water is essential for survival and growth, increased their ranges as much as 1500 km closer to the poles, and isotopic analysis of deep ocean sediments ($\delta^{18}\text{O}$) suggests that deep ocean water, presently hovering near freezing, was 15°C warmer. There is also no evidence for polar ice during this period of time (Barron and Washington, 1984; Condie and Sloan, 1998).

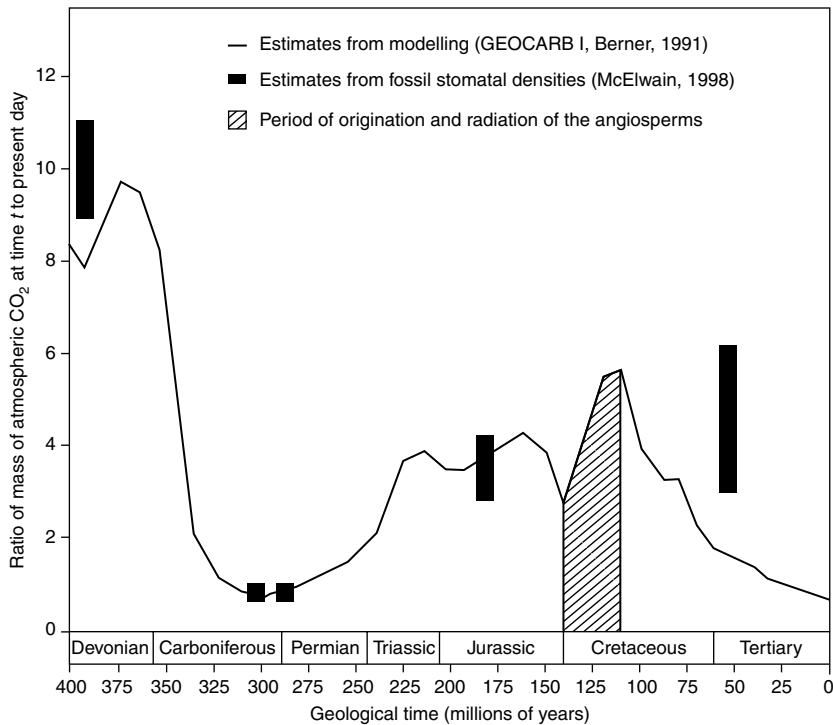


Figure 6.11 Estimated variations in atmospheric CO₂ during the past 400 million years (redrawn from Berner, 1991; GEOCARB I). The general direction of the trends are supported by independently derived results from carbon isotope analysis of palaeosols (e.g. Mora *et al.*, 1996) and stomatal densities on fossil leaves (e.g. McElwain, 1998). For comparison, the latter are indicated on the graph. Both are plotted against ratio of mass of atmospheric CO₂ at time *t* to present day (where present day is taken at the pre-industrial value of 300 p.p.m.v.). The early to mid-Cretaceous rise in atmospheric CO₂ is highlighted, along with the major change apparent in the plant fossil record during this time.

But why should increasing warmth promote angiosperm evolution or favour their diversification and radiation? A number of key innovations are recognizable among angiosperms which may have made them more drought resistant and therefore at a competitive advantage. These include tough, leathery leaves that were commonly reduced in size; a tough, resistant seed coat that protected the young embryos from drying out; vessel members providing much more efficient water-conducting cells than in previous groups; and a deciduous habit (Taylor and Taylor, 1993). The latter characteristic would have been critical in periods of drought but is not, however, unique to angiosperms. For instance, a number of gymnosperms (e.g. glossopterids, Ginkgoales, and Cycadales) are thought to have been deciduous, particularly at higher latitudes. The predominance of drought-resistant features, as well as a weedy life history and rapid reproduction, in the early angiosperms may have given them a competitive advantage in increasingly disturbed environmental conditions and warm

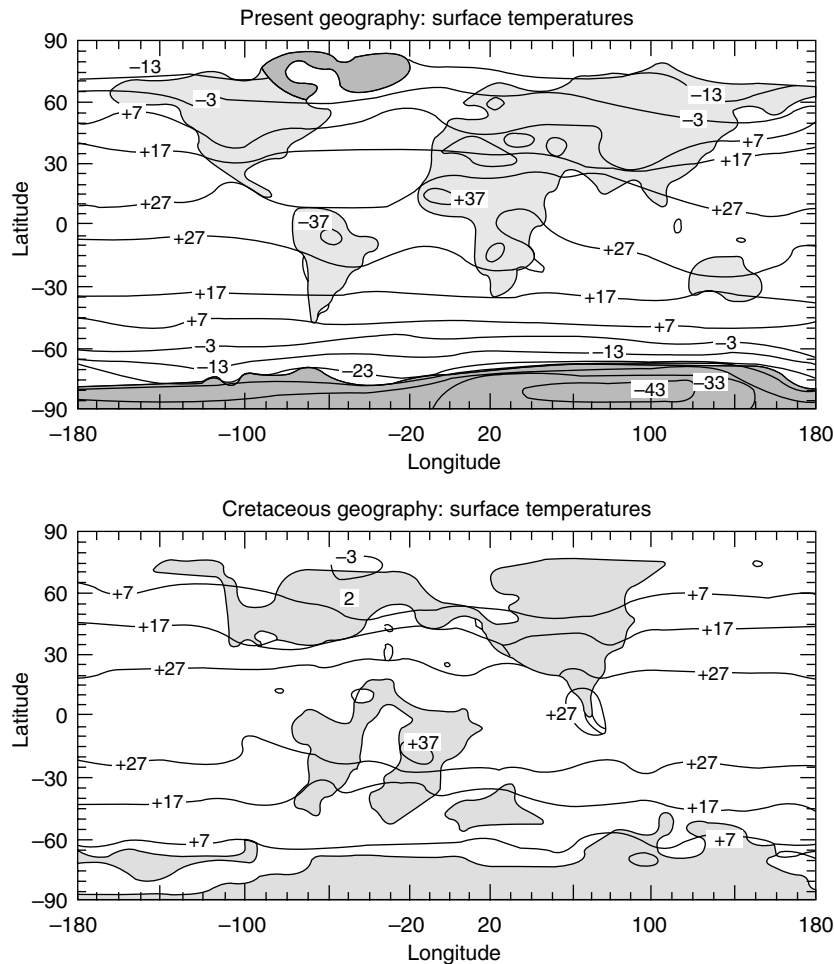


Figure 6.12 Computer-simulated model of mid-Cretaceous surface temperatures (~ 100 Ma) compared to present (redrawn from Barron and Washington, 1984). The model used predictions of Cretaceous topography, ice cover (stippled), continental positions, and sea-level in comparison with the present day in order to determine global surface temperatures. From this model it is predicted that the average global temperature during the Cretaceous was approximately 4.8°C warmer than present. Temperatures are contoured in $^\circ\text{C}$.

climate. An alternative explanation, is that dramatically accelerated speciation rates, which are characteristic of the angiosperms (Doyle and Donoghue, 1986), simply led to an overwhelming diversity of adaptive types (Lupia *et al.*, 1999).

Biotic interactions

Dinosaur–angiosperm coevolution

One hypothesis proposed for the late appearance of the angiosperms is that their evolution was closely associated with the large-scale radiation of certain groups

of tetrapods, and that dinosaur feeding behaviour promoted the evolution of flowering plants (Bakker, 1978, 1986). This hypothesis is based on apparent evidence in the fossil record to suggest that a change in herbivore communities from high to low browsers occurred at approximately the same time as the initial evolution and radiation of angiosperms. Dinosaur fossil evidence suggests, for example, that approximately 160 million years ago, in the late Jurassic, 95% of the preserved biomass of dinosaurs was made up of sauropods and stegosaurus (Figure 6.13). These were high-browsing herbivores with a diversity of cranial and dental adaptations indicating a diet of a wide range of conifer tissue. It is argued that these high-browsing forms would have put intense pressure on the canopies of the mature trees, but permitted the development of gymnosperm saplings. However, from approximately 144 million years ago (Jurassic/Cretaceous boundary) the herbivore communities changed considerably and new groups of big, low-browsing ornithischian dinosaurs (Figure 6.13) appeared in the fossil record. It is suggested that these intense low-browsing dinosaurs would have increased mortality among the gymnosperm seedlings and thinned out the forest structure, thus creating gaps in the canopy and highly disturbed environments (Bakker, 1978, 1986). Early angiosperm traits, such as small

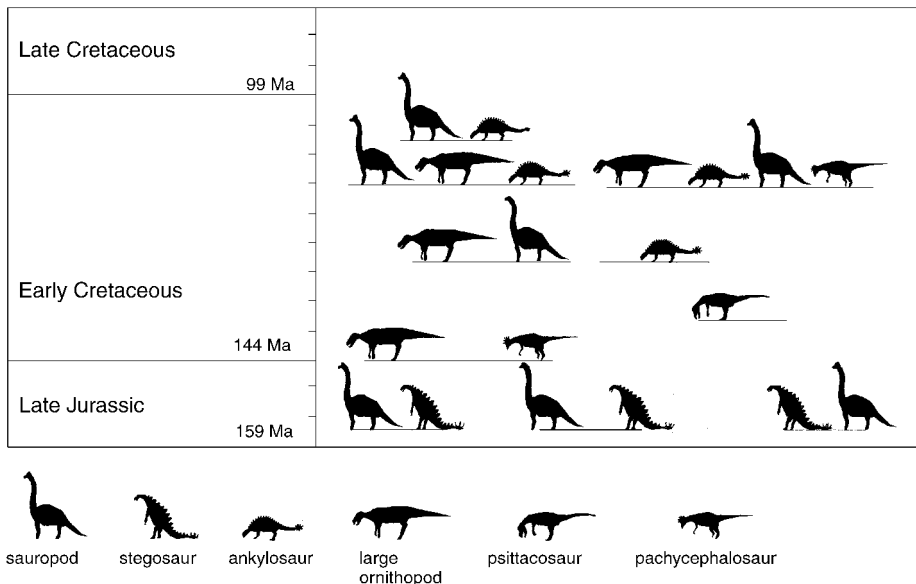


Figure 6.13 Stratigraphic record of herbivorous dinosaurs through the late Jurassic/early Cretaceous (redrawn from Bakker, 1978, 1986). It is proposed that the transition from high-browsing forms to low browsers in the early Cretaceous resulted in increased mortality among the gymnosperm seedlings and thinned out the forest structure, thus creating gaps in the canopy and highly disturbed environments (Bakker, 1978, 1986). Early angiosperm traits, such as small structure, rapid life cycle, and high colonizing ability, would have given them the competitive advantage on these disturbed substrates, thereby promoting their radiation.

structure, rapid life cycle, and high colonizing ability, would have given them the competitive advantage on these disturbed substrates, thereby promoting their radiation (Bakker, 1978; Wing and Tiffney, 1987).

Additional work on plant–herbivore interactions adds further detail to the above in suggesting that it was the mechanics of chewing among herbivores that aided angiosperm evolution during the Cretaceous. In particular, the radiation of ornithischian dinosaurs between 160–120 million years (mid-Jurassic–mid-Cretaceous) may have played an important role, since these were the first group of herbivores to develop a transverse chewing motion (which ground the food before passing it into the gut), thereby enabling these animals to exploit more fully the newly evolving plant resource (Weishampel and Norman, 1989).

However, recent work comparing the timing and location of the evolution of angiosperms with major events in the evolution of dinosaur herbivory has rejected this hypothesis, for a number of reasons (Barrett and Willis, 2001). First, the fact that angiosperms did not comprise a significant proportion of the global flora until the late Cretaceous suggests that it is highly unlikely that they formed a major constituent of dinosaur diets during the early Cretaceous. Secondly, detailed examination of the timing of the dinosaur fossil record suggests that no major event in the evolution of herbivorous dinosaurs can be correlated with angiosperm origins. Innovations in chewing and the onset of factors such as low browsing, for example, either precede or post-date the appearance of the first angiosperms in the fossil record. In addition, changes in dinosaur browsing behaviour at the Jurassic–Cretaceous boundary may not have been so marked as previously suggested. Thirdly, fossil evidence currently available suggests that there was no spatial overlap between the earliest angiosperms and the major clades of herbivorous dinosaurs. Most early Cretaceous dinosaur localities, for example, were situated at palaeolatitudes higher than 30°N and 30°S, with only around 10% of the total number within 20° of the palaeoequator, where the earliest angiosperms occurred (Barrett and Willis, 2001).

Insect–angiosperm coevolution

Another proposed biotic interaction of importance is that of angiosperm–insect coevolution. Early and mid-Cretaceous flowers contained many features to suggest that they were insect pollinated, including stamens with small anthers and low pollen production, and pollen grains often covered with pollenkitt-like material, and they were larger than the most effective size for wind dispersal (Crepet and Friis, 1987; Crane *et al.*, 1995).

Insect pollination would have been highly advantageous to the early angiosperms, enabling genetic exchange between widely spaced individuals or small populations. Furthermore, the suggestion that self-incompatibility mechanisms were present in the earliest angiosperms makes processes such as insect pollination even more critical for cross-pollination (Zavada, 1984). It is therefore suggested that the late evolution of angiosperms is closely related to that of insect evolution.

Fossil evidence for the coevolution of pollinating insects with angiosperms is ambiguous (Barrett and Willis, 2001). There is some fossil evidence for insect herbivory on Cretaceous angiosperms, such as leaf mines and other damage to leaves caused by feeding (Scott *et al.*, 1992; Labandeira *et al.*, 1994; Labandeira, 1998; Wilf *et al.*, 2000). However, comparison of the times of appearance of innovations in insect feeding systems with the timing of angiosperm radiation does not indicate a strong relationship (Labandeira, 1997). The advanced pollinator groups, including some *Hymenoptera* (certain wasps that are the sister group of the bees) and *Lepidoptera* (butterflies and moths), indicate a certain amount of synchronicity between their first fossil appearance (from approximately 140 million years ago) and that of angiosperms (Crepet and Friis, 1987; Labandeira and Sepkoski, 1993) (Figure 6.14). However, other early groups such as *Diptera* (e.g. crane flies and fungus-gnats), *Coleoptera* (beetles), and some *Hymenoptera* (e.g. saw-flies) have a fossil record indicating that their first appearance pre-dates that of the angiosperms, whereas other species of *Hymenoptera*, including the *Apoidea* (honeybees), have a fossil record that only extends as far back as the Albian (~100 Ma). Moreover, in analysis of insect familial-level diversity through time there is no marked increase in insect diversity with the time of angiosperm origin (Labandeira and Sepkoski, 1993) (Figure 6.15). There is increasing evidence to suggest, therefore, that advanced pollinators (wasps, bees, and moths) may have played an important role in the coevolution and major radiation of certain groups of flowering plants (Crepet, 1996; Grimaldi, 1999), but that the timing of angiosperm evolution as a whole cannot be explained by insect coevolution alone.

6.4 Evolutionary trends: gymnosperms to angiosperms?

Two questions that inevitably arise when discussing angiosperm origins are, from which lineage did they evolve, and when and how did divergence of the monocotyledons from the dicotyledons occur? Originally these questions were tackled by examination of only the fossil record, but more recent techniques, including morphological and molecular phylogenetic analyses of extinct and extant groups, have allowed the construction of detailed evolutionary relationships between the gymnosperms and angiosperms, and the monocotyledons and dicotyledons.

Despite early suggestions that angiosperms were of a polyphyletic origin (a number of different ancestors), almost all recent evidence (morphological and molecular) suggests that angiosperms were derived from a single common ancestor (that is they had a monophyletic origin) (Doyle and Donoghue, 1986). Two of the earliest suggestions for possible evolutionary pathways between gymnosperms and angiosperms were via the Bennettitales (Arber and Parkin, 1907, 1908) and Gnetales (Von Wettstein, 1907).

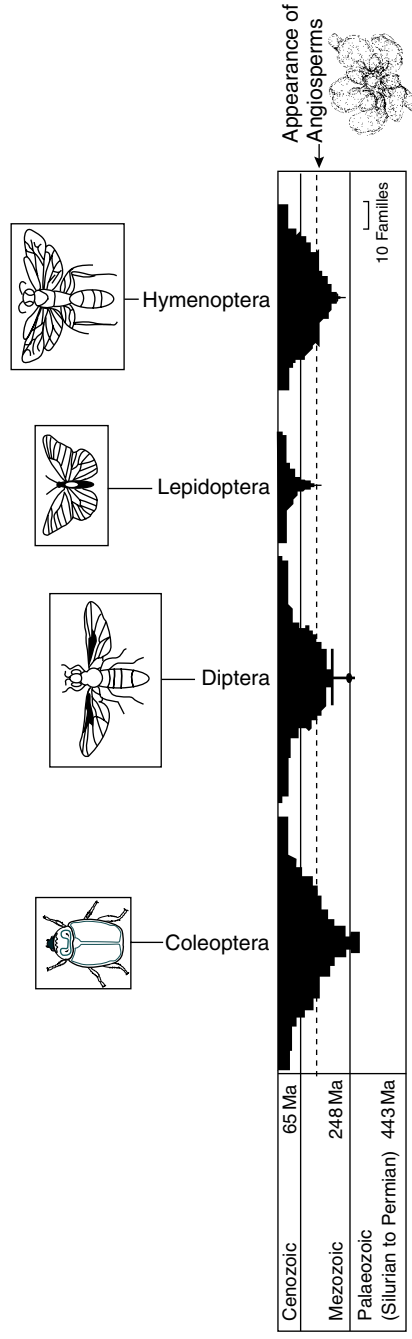


Figure 6.14 Spindle diagrams to display diversity of fossil insect families Diptera, Coleoptera, Lepidoptera, and Hymenoptera from the Silurian (~443 Ma) to present. The temporal position of the first appearance of angiosperms in the fossil record is also indicated (redrawn from Labandeira and Sepkoski, 1993).

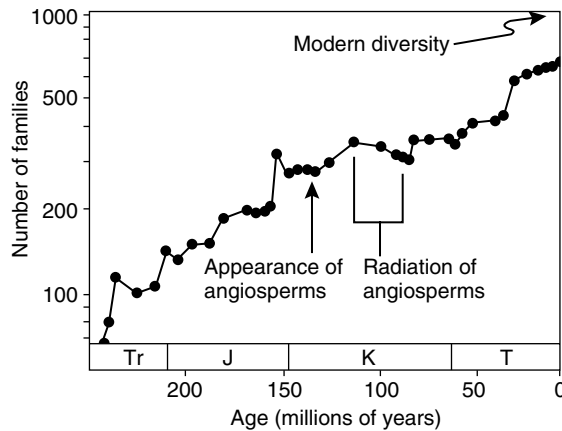


Figure 6.15 Insect familial diversity from the Triassic (~248 Ma) to present, plotted on a semi-logarithmic scale. The temporal position of the first appearance of angiosperms in the fossil record, and their subsequent radiation, are also indicated. (Redrawn from Labandeira and Sepkoski, 1993.)

Evidence for Bennettitales as the precursor to early angiosperms was based upon the fact that certain species in this fossil group had flower-like bisexual reproductive organs and similar wood anatomy. One species in particular that is often cited is *Williamsoniella*. This late Jurassic fossil plant had a reproductive organ that consisted of a bisexual reproductive axis bearing naked ovules above a series of pollen-bearing structures, the whole enclosed by large bracts (Stewart and Rothwell, 1993; Taylor and Taylor, 1993). These large bracts were thought to be the equivalent to petals in an angiosperm flower. Also, the position of the reproductive organ, erect and at the end of the branch, bore some similarities to extant insect-pollinated flower structures. *Coleoptera* and *Diptera* flies have been suggested as pollinators for this plant (Crepet and Friis, 1987).

Gnetales are present in the fossil record from the early Cretaceous (~140 Ma). The group has three extant genera in biogeographically distinct regions of the world: *Ephedra* (35 species), which exists in arid and semiarid regions, including parts of the Mediterranean, Asia, and the Americas (Bell, 1992); *Welwitschia mirabilis*, which is restricted to the Namibian desert (Figure 6.16); and *Gnetum* (30 species), which is exclusively tropical, occurring in Asia, Africa, and South America.

Morphological similarities between many species of Gnetales and angiosperms first led to the suggestion that they were probably close in evolutionary terms. These include, for example, reproductive organs that are bisexual (in some species), the presence of vessels, leaves with a venation pattern closely approximating that of dicotyledons, and a pollen wall (e.g. in certain species of



Figure 6.16 A model of extant *Welwitschia mirabilis* (courtesy of The Field Museum, neg. # B83079c).

Ephedra) that is tectate (Doyle and Donoghue, 1986). Some extant Gnetales are also insect pollinated (Friedman, 1996). Phylogenetic analysis based on these shared characteristics, in both extant and extinct species (Hill and Crane, 1982; Crane, 1985; Doyle and Donoghue, 1987), also confirmed a close relationship between angiosperms and Gnetales (Figure 6.17).

More recent cladistic analyses, which also include the molecular characteristics of extant species, are in agreement with the earlier morphological analysis and demonstrate a close relationship between Bennettitales, Gnetales, and the earliest angiosperms (Doyle *et al.*, 1994; Crane *et al.*, 1995). The phylogenetic trees obtained from these analyses (Figure 6.17) indicate that angiosperms from a clade with Bennettites and/or Gnetales but also sometimes with an extinct group, the Pentoxylales. However, the majority of studies suggest that the Gnetales are the most likely closest living relative of angiosperms.

There are a number of hypothesis as to which of the earliest angiosperms forms an evolutionary link with the Gnetales (Figure 6.18 a, b, c). Most suggest that early members of the Nymphaeales and Piperales were the evolutionary link between Gnetales and angiosperms (Taylor and Hickey, 1992; Doyle *et al.*, 1994); others have suggested a single genus, *Ceratophyllum*, within the Nymphaeales (Les *et al.*, 1991), and members of the Laurales (Loconte and Stevenson, 1991; Loconte, 1996). However, there is also strong support for woody Magnoliales (for a review, see Wing and Boucher, 1998).

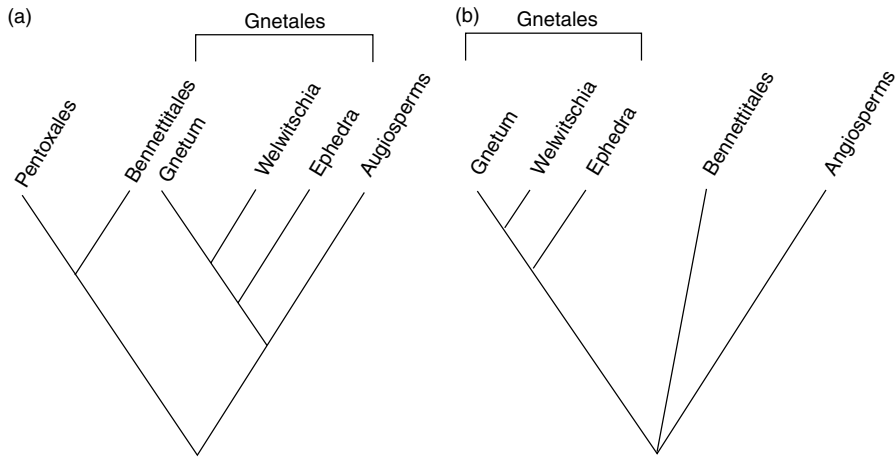


Figure 6.17 Phylogenetic trees showing two alternative relationships between angiosperms and related seed plants, (a) supports the hypothesis that Gnetales are the closest relative of the angiosperms and (b) supports the hypothesis that Bennettitales are the closest relative of the angiosperm (adapted from Crane (1985) and Doyle *et al.* (1994).

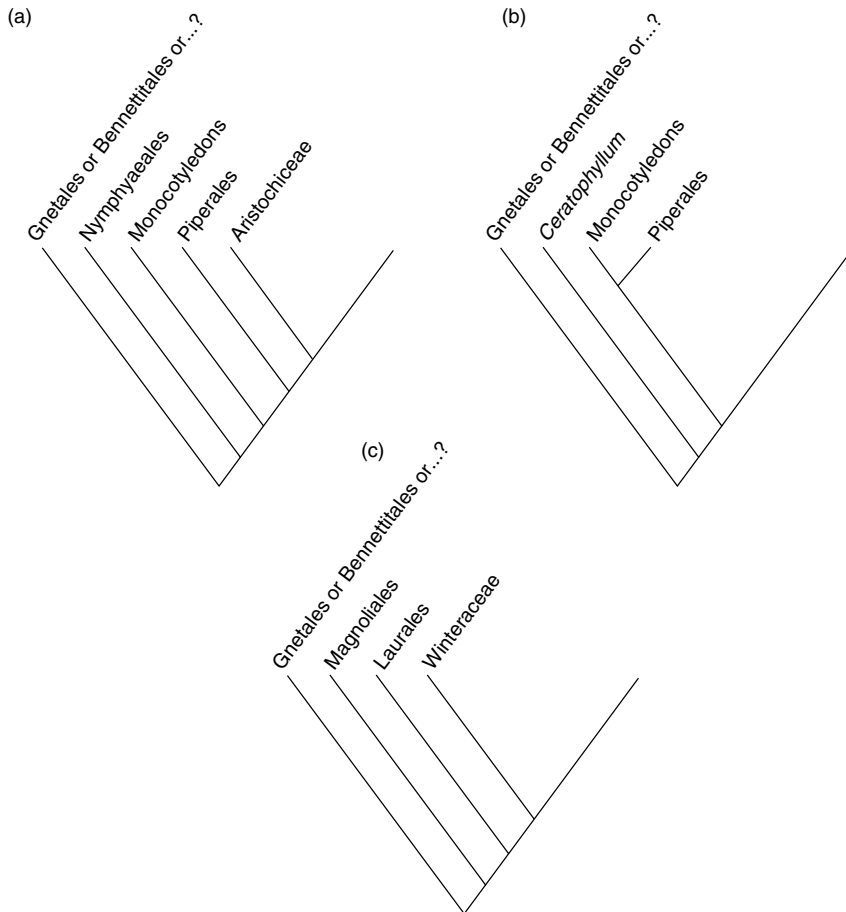


Figure 6.18 (a–c) Phylogenetic trees (from Wing and Boucher, 1998) to indicate alternative relationships for major basal clades within the angiosperms.

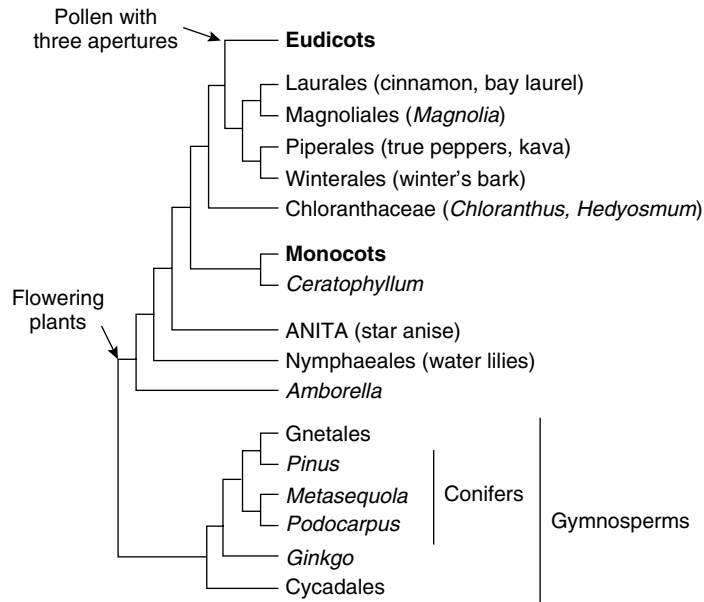


Figure 6.19 Phylogenetic tree based on recent molecular studies of angiosperms (redrawn from Qui *et al.*, 1999).

More recent and extensive molecular studies of angiosperm phylogenetics have, however, turned a number of these relationships on their head (Qui *et al.*, 1999; Soltis *et al.*, 1999). In the first instance, the results of both studies do not support the hypothesis that the Gnetales are the closest living relatives of the angiosperms. Instead, these analyses group the Gnetales with the conifers (Figure 6.19). Secondly, the results do not agree with any of the existing ideas about which angiosperms are most primitive. Instead, the analyses indicate that *Amborella trichopoda*, the only extant species of Amborellaceae, represents the most primitive (basal group) of all flowering plants (Qui *et al.*, 1999; Soltis *et al.*, 1999). This is followed by the Nymphaeales, and then a group including Illiciaceae, Trimereniaceae, *Austrobaileyaceae*, and Schisandraceae. Together they have been referred to as ANITA.

Evidence from the various cladistic analyses described above have also indicated the relationship between early monocotyledons and dicotyledons. Again, the analyses support the fossil evidence in suggesting that monocotyledons were an early branch in angiosperm evolution (Crane *et al.*, 1995; Niklas, 1997; Soltis *et al.*, 1999). However, the species or group that forms the evolutionary link between the monocotyledons and dicotyledons is still under debate.

6.5 Biogeographical distribution of global vegetation during the late Cretaceous (~84–65 Ma)

During the late Cretaceous (~100–65 Ma) angiosperms increased in both species number and diversity (Figure 6.20). Angiosperm trees and shrubs evolving during this time (Table 6.3) included a number of families that constitute a significant part of the present-day global flora. Evidence from the fossil record suggests, for example, that a number of extant northern and southern hemisphere families appeared for the first time. These include Ulmaceae (including evidence for *Ulmus*), Betulaceae, Juglandaceae, Fagaceae (especially *Nothofagus*), and Gunneraceae (Table 6.3). The striking number of angiosperm fossils present by the late Cretaceous with close affinities to extant families has led to the suggestion that eventually it will be discovered that all angiosperm families originated during this remarkable period (Wing and Boucher, 1998).

The majority of trees to appear in the late Cretaceous (~100–65 Ma) have a present-day distribution that is mainly tropical or subtropical (Table 6.3). It is interesting to note that most present-day angiosperm families are basically tropical in their requirements, with over one-half of angiosperm families confined to tropical regions and over three-quarters of all angiosperm families attaining optimum development and diversity in a tropical environment (Axelrod, 1966). Therefore, although many may now be classified as northern/southern temperate species by their distribution, it is probable that they still possess the traits that would enable them to survive in conditions similar to those characteristic of the early environments where they originated.

Detailed ‘biome level-analyses’ of global plant biogeography and palaeoclimate have been carried out for the late Cretaceous (Maastrichtian, ~71–65 Ma)

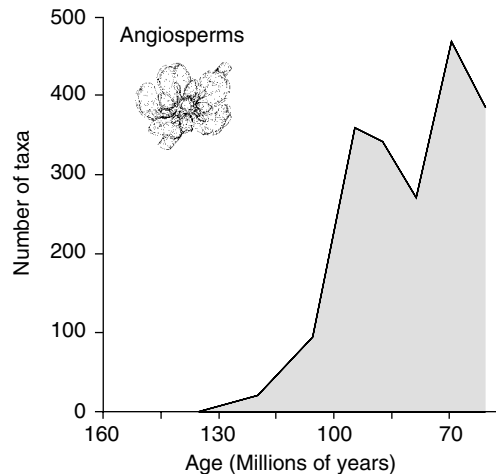
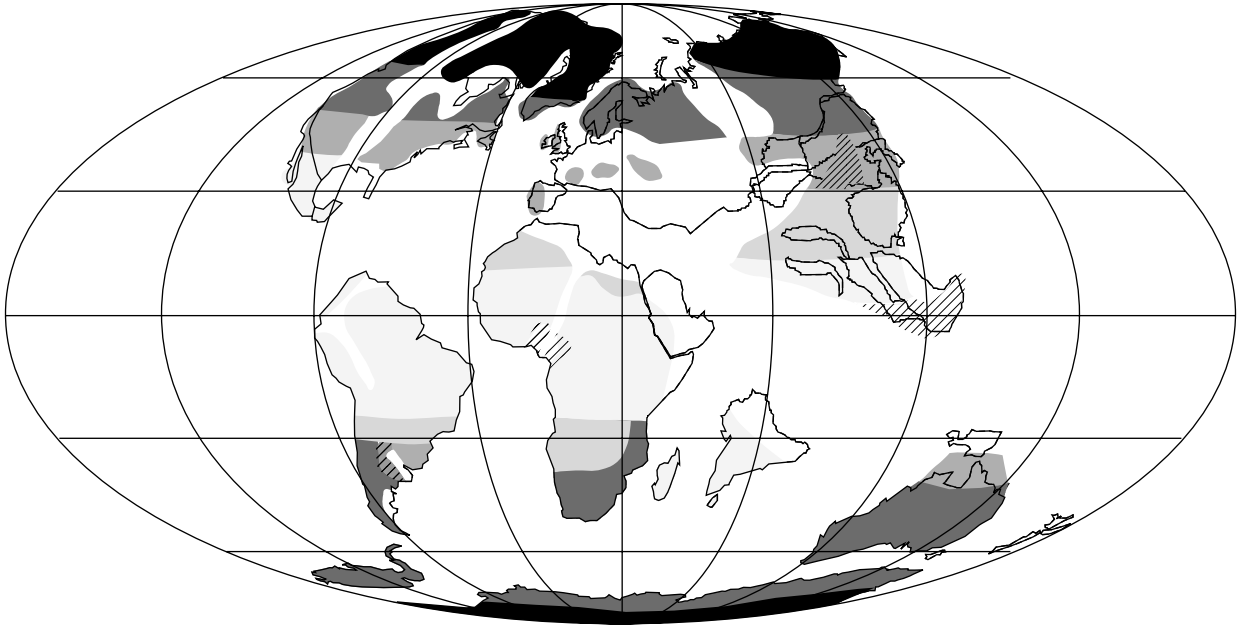


Figure 6.20 Evidence from fossil leaf assemblages (summed genus and species diversity) indicating the major expansion of the angiosperms from ~140 Ma and a dramatic increase in the absolute number (summed diversity) of angiosperms through the mid-Cretaceous (~10 Ma). Data taken from 147 late Jurassic to Palaeocene macrofossil floras (redrawn from Lidgard and Crane, 1988; Lupia *et al.*, 2000).

Late Cretaceous (70 Ma)



(Horrell, 1991; Upchurch *et al.*, 1999). Six global biomes are recognized, as follows (Figure 6.21).

Cool temperate biome

The cool temperate biome in the Maastrichtian coincides roughly with the present-day Arctic circle, comprising Canada, Greenland, and Siberia in the northern hemisphere and Antarctica in the southern hemisphere (Horrell, 1991). The vegetation of the cool temperate biome has also been referred to as polar deciduous forest (Upchurch *et al.*, 1999) and was clearly one of three remaining biomes in the late Cretaceous not dominated by angiosperms. Instead, vegetation in this region was dominated by deciduous and evergreen conifers with ferns and ginkgos. Angiosperms are believed to have been present as understorey and included members of the Betulaceae and Juglandaceae. The prevalence of leaf-shedding among the angiosperm species (Vakhrameev, 1991), relative low-diversity floras, evidence for growth rings (Spicer and Parrish, 1990), and the presence of some, but not abundant, coals, supports the suggestion of seasonality, typical of a cool temperate climate (Horrell, 1991). Members of the Pinaceae and Taxodiaceae (*Sequoia* and *Taxodium*) were common conifers, and the fossil record also includes evidence for ‘modern’ genera such as *Pinus* and *Abies*. Other conifers, widely spread but less significant in terms of their representation, included Cupressaceae and Araucariaceae. In the southern

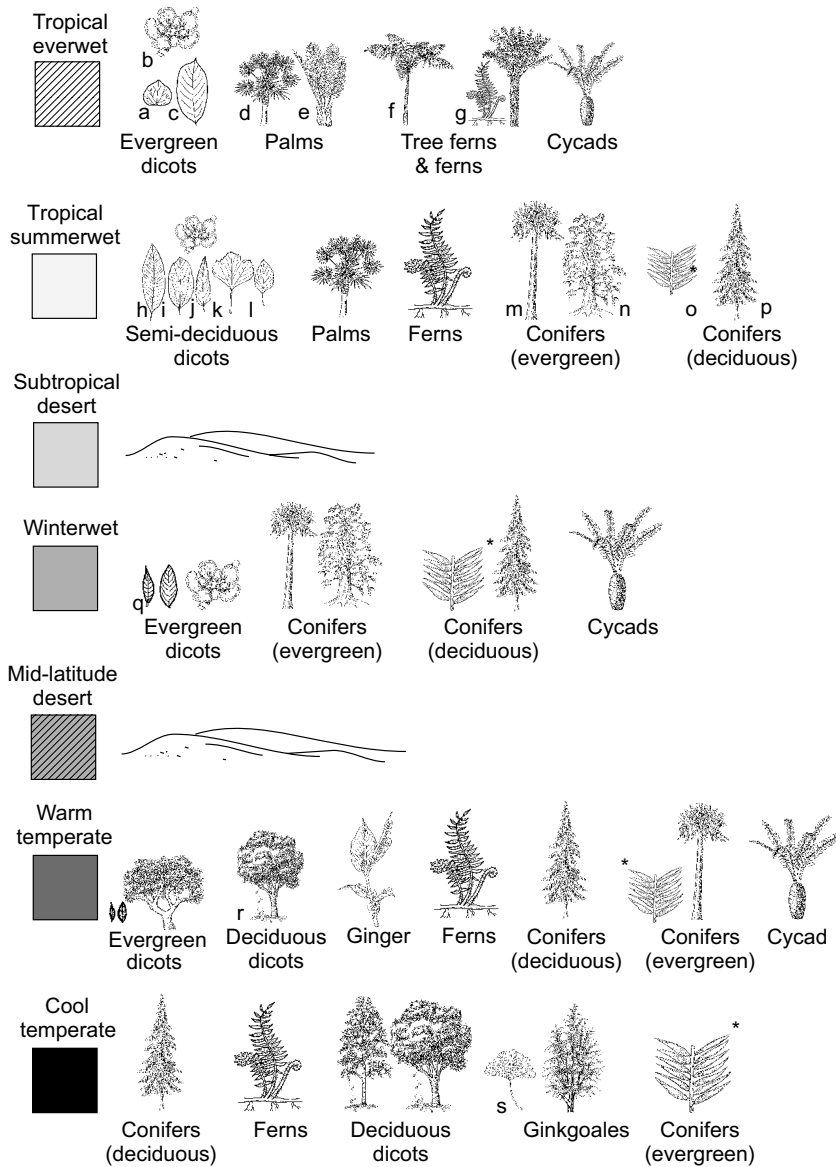


Figure 6.21 Suggested biomes for the late Cretaceous (84–65 Ma) (modified from Horrell, 1991; Upchurch *et al.*, 1999), with representatives of the most abundant and/or dominant fossil plant taxa shown. The biomes are superimposed on a global palaeogeographic reconstruction for the Maastrichtian (~70 Ma) (courtesy of A. M. Ziegler, PaleoAtlas Project). (a) and (c) Stylized megaphyllous leaves; (b) generalized Cretaceous flower; (d) *Sabalites* palm; (e) *Nypa* palm; (f) *Cyathea*; (g) *Dicksonia*; (h) *Myrica* leaf; (i) *Ficus* leaf; (j) *Dryophyllum* leaf; (k) *Viburnum* leaf; (l) *Grewiopsis* leaf; (m) *Araucaria*; (n) Cheirolepidaceous tree; (o) *Podocarpus* leaves; (p) Taxodiaceae conifer; (q) stylized microphyllous leaves; (r) generalized deciduous tree; (s) *Ginkgo* leaf. See Appendix 5 for sources of plant reconstructions and line drawings. * Dominant or abundant in the southern hemisphere.

hemisphere, the cool temperate biome was characterized by an abundance of podocarpacean and araucarian conifers and the angiosperm dicot genus *Nothofagus* (southern beech). The abundance of *Nothofagus* pollen has led to the suggestion that the climates of Antarctica and southern Australia were cooler and drier than those of the southern hemisphere lower latitudes (Herngreen and Chlonovo, 1981).

Warm temperate biome

The warm temperate biome between 45° and 65° palaeolatitude, encompassed present-day northern North America, southern Greenland, parts of western Europe, Russia, and northern China in the northern hemisphere, and Australia and coastal Antarctica in the southern hemisphere (Horrell, 1991). The vegetation characteristic of this biome included abundant dicotyledonous and monocotyledonous angiosperms, evergreen and deciduous conifers, ferns, and cycads. Upchurch *et al.* (1999) have referred to the vegetation of this region as ‘sub-tropical broad-leaved evergreen forest and woodland’ as many of the fossil leaf shapes are common among modern subtropical plants. However, due to the palaeolatitudinal position of this region, well outside the subtropics, Horrell’s climatic assessment and interpretation of this region as warm temperate rather than subtropical is used here (Figure 6.21). Common angiosperms included members of the Fagaceae (e.g. *Castanea*), Betulaceae (e.g. *Betula*), Juglandaceae (e.g. *Juglans*), Ulmaceae (e.g. *Ulmus*, *Zelkova*), Proteaceae (southern hemisphere only), and Winteraceae among the dicotyledons and corphoid palms were abundant monocotyledons. Conifers included Araucariaceae and Taxodiaceae.

The high diversity of angiosperm dicotyledons in fossil floras from this region was thought to indicate their dominance. However, detailed analysis of a fossil flora from Wyoming, preserved *in situ* by an ash fall, has shown that although dicotyledons constituted 61% of the total floral diversity, they accounted for a mere 12% of cover, compared with 49% by ferns (Wing *et al.*, 1993). It is apparent, therefore, that although angiosperms had reached a dominant position in stream-side vegetation of the warm temperate biome by the Maastrichtian (~70 Ma), ferns still maintained dominance in certain habitats, even after 30 million years of angiosperm diversification and radiation (Wing *et al.*, 1993). This study also demonstrates the complexity and mosaic of different habitats that exist within each individual biome, and highlights the importance of taking into account preservational biases when undertaking biogeographical analyses.

Winterwet biome

The vegetation between palaeolatitudes of approximately 30° and 45° was markedly less diverse than that of the warm temperate biome, and is characterized mainly by the occurrence of evergreen dicotyledons together with both evergreen and deciduous conifers with some cycads. A notable feature of the

vegetation of this region was the relatively lower abundance of monocotyledons. Floras from the winterwet biome indicate the presence of abundant *Araucaria* and cheirolepidaceous conifers, and evidence from fossil wood suggests that angiosperms may have formed part of an understorey of both shrubs and small trees rather than large canopy trees (Upchurch and Wolfe, 1987).

In the southern hemisphere, Patagonian floras contained abundant ferns and angiosperm families such as Lauraceae. The presence of huntite, a mineral which today is only formed in warm environments with high rates of evaporation, typical of Mediterranean climates, together with an absence of clear growth rings in fossil woods, provides good support for the designation of a winterwet biome to this region (Horrell, 1991). However, this is not supported unanimously and Upchurch *et al.* (1999) suggest that the absence of fossil leaves with spinose margins, which are typical of the modern winterwet biome vegetation, questions whether this biome really existed during the late Cretaceous. It is worth noting, however, that despite the absence of one vegetative characteristic, a number of model simulations of the late Cretaceous climate indicate that a Mediterranean (i.e. 'winterwet') climate may indeed have prevailed in certain areas during this time.

The northern limit of the winterwet biome in the northern hemisphere is marked by coals, whereas to the south it is marked by the presence of evaporites, indicating humid and arid conditions, respectively. It is thought therefore that this biome represents a transition between the arid desert biomes of the lower latitudes and the humid biomes of the higher-latitude temperate belts (Horrell, 1991).

Subtropical desert biome

Evidence for extensive evaporite deposits during the late Cretaceous (~70 Ma), indicating high rates of evaporation over precipitation, mark the subtropical desert biome (Horrell, 1991). These deposits occur in a northern hemisphere belt which incorporates present-day north Africa, China, and the Yukatan peninsula, and in the southern hemisphere include present-day south-western Africa and southern South America. No fossil floras have yet been found in these biomes, most probably reflecting both the low diversity and productivity which would have been apparent, but also the low preservation potential of fossil plants in arid environments.

Tropical summerwet biome

The tropical summerwet biome incorporates the majority of present-day Africa, South America, and India, from palaeolatitudes 0° to 25° (Horrell, 1991; Upchurch *et al.*, 1999) and is characterized by a 'tropical semi-deciduous forest' type vegetation. Common elements in the vegetation of this region include

dicotyledons and monocotyledons, ferns, conifers, and cycads. Evidence from fossil pollen and wood suggest that common conifers included members of the Araucariaceae, Cheirolepidaceae, and Podocarpaceae. India contained floral elements typical of both the southern hemisphere (e.g. *Notofagus*, Proteaceae, and Podocarpaceae) and also elements of the northern hemisphere vegetation, leading to the suggestion that by the late Cretaceous, the Indian plate was already part of the equatorial biogeographical region, even though in terms of palaeogeography it was still 30°S (Briggs, 1995).

The combined evidence from fossil floral composition, leaf physiognomy, and sedimentological indicators suggests that this region was characterized by a hot, subhumid to semiarid climate typical of present-day summerwet or savannah regions (Horrell, 1991).

Tropical everwet biome

The tropical everwet biome of the late Cretaceous was much reduced in comparison with the present-day extent of tropical rain forest, and was restricted to an area including present-day subequatorial west Africa and Malaysia (Horrell, 1991) and possibly Somalia, in east Africa and Colombia in South America (Upchurch *et al.*, 1999). Palynological assemblages recovered from these areas suggest that during the late Cretaceous the equatorial region was dominated by species of Arecaceae (palms) (Vakhrameev, 1991), including the extant genus *Nypa* (Figure 6.21). Other angiosperms present included Proteaceae and many other dicotyledon groups, while ferns and tree ferns were also abundant (Meyen, 1987). A striking feature of this biome is the almost complete absence of evidence for either evergreen or deciduous conifers, with the exception of Araucariaceae in Malaysia.

Comparison of the biogeographical patterns present in the late Cretaceous (~70 Ma) with those from the early Carboniferous (~360 Ma), middle Permian (~267 Ma), and early Jurassic (~196 Ma) reveals a consistent pattern, whereby the tropical everwet biome is either absent or severely restricted in extent. This phenomenon has also been observed for the early Cretaceous (~137 Ma) (Ziegler *et al.*, 1987). In contrast, however, the extent of the tropical everwet biome during the late Carboniferous (~300 Ma) spans from the equator to approximately 25°, similar to the observed extent of this biome today. It is noteworthy that the features common to both the upper Carboniferous and present day are the presence of polar ice caps, high latitudinal temperature gradients and comparatively low atmospheric CO₂ concentration. It can therefore be suggested that these characteristics may be important global environmental prerequisites to the development of an extensive 'tropical rain-forest' biome.

Summary

1. The first flowering plants (angiosperms) appeared in the fossil record from approximately 140 Ma (early Cretaceous). Rapid diversification from ~100 Ma led to their global dominance by the early Tertiary (~65 Ma).
2. Evidence for the first angiosperms includes fossil flowers, fruits, pollen, and leaves.
3. The earliest angiosperms originated in the palaeotropics (0–30°), radiating out to colonize higher latitudes some 20–30 million years later.
4. In evolutionary terms, the angiosperms are the most recent group to appear in the fossil record, approximately 300 million years later than the first vascular plants, and 220 million years later than the first seed plants.
5. Various hypotheses have been suggested to account for their relatively late appearance in the fossil record, including a bias in the fossil evidence, a particular suite of environmental conditions and/or biotic interactions that led to their later evolution.
6. Two biotic interactions that are of particular interest are the coevolution of flowering plants with low-browsing dinosaurs and with pollinating insect groups.
7. There is increasing evidence to support the suggestion that the earliest angiosperms were herbs or small shrubs.
8. Molecular phylogenies indicate that monocotyledons probably evolved from dicotyledons early in angiosperm evolution.
9. Examination of cladistic analyses based on morphological and molecular traits of both extant and fossil material indicates that angiosperms were probably derived from a single common ancestor.
10. Traditionally the suggested precursor to the angiosperms included members of the Bennettitales and/or Gnetales. However, recent phylogenetic analyses have indicated that *Amborella trichopoda* (which is a small shrub and the only extant species of Amborellaceae) is the most primitive of all angiosperms.
11. Reconstruction of the biogeographical distribution of vegetation during the Maastrichtian (~71–65 Ma) indicates that six global biomes can be recognized during this period, with all but the highest latitudes dominated by angiosperms.