Cretaceous Angiosperm Invasion of North America

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G. J. Retallack and D. L. Dilcher. Cretaceous Angiosperm Invasion of North America. *Cretaceous Research* (1986), **7**, 227–252. Angiosperms appeared in the coastal plains of eastern North America during the latest Barremian or early Aptian, reaching California by the Albian, or perhaps as early as Aptian. In Alaska, however, they are found in sediments only as old as latest Albian. From their earliest Cretaceous appearance, and well into the Late Cretaceous, angiosperms were most abundant and diverse in coastal and fluvial depositional environments, conifers remaining dominant in well drained and inland soils. Extensive dispersal of pioneering, coastal angiosperms occurred at a time of extensive sea-level fluctuation and went hand in hand with their mid-Cretaceous diversification. The early successes of invading angiosperms can most easily be attributed to their ability to colonise disturbed sedimentary surfaces. It is unlikely that they were initially successful in high salinity or other unfavourable habitats, or that they could compete directly with pre-existing plants for nutrients, pollinators or other resources.

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1. Introduction

Flowering plants (angiosperms) are the most abundant and conspicuous living vascular plants. They have diversified to occupy most terrestrial and some marine habitats. Speculation on the origin of these important plants has long been the preserve of neobotanists. One encouraging effect of recent research on fossil angiosperms (Hickey and Doyle, 1977; Dilcher, 1979; Retallack and Dilcher, 1981a) is the growing role of the fossil record in providing critical evidence of their origin and early evolution. It is becoming apparent that not only the morphology and systematics of angiosperm fossils, but also the precise determination of their geological age, their paleoecology, and their ancient environments are important for a full understanding of early angiosperms. In this article, we review the geological background to their appearance and their diversification in North America during the Early and mid-Cretaceous. Many aspects of the Cretaceous appearance and rise to dominance of the angiosperms are very similar in various regions of North America (Figure 1). Although these similarities are important corroboration of a general pattern of angiosperm dispersal, our account stresses those aspects of the early history of angiosperms best understood in each region.

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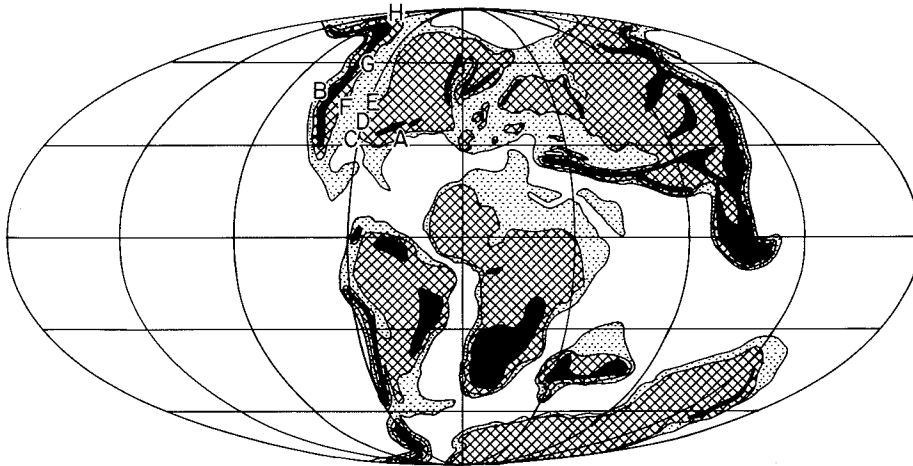
Figure 1. Mid-Cretaceous (Cenomanian) paleogeography (after Parrish *et al.*, 1982). Regions discussed include Virginia, Maryland, and New Jersey (A), northern California (B), Texas (C), central Kansas (D), Black Hills (E), Utah (F), western Alberta (G), and northern Alaska (H). (□: Deep sea; ▨: shallow sea; ▧: Low land; ■: High land).

2. Atlantic coastal plain

Cretaceous sediments in the central Atlantic Coastal Plain of the United States have a record of both the appearance of the earliest angiosperms to penetrate North America and their subsequent diversification. Also preserved is a record of pre-existing vegetation which was invaded and replaced by angiosperms.

2.1 *Earliest Angiosperm immigrants*

Within the Potomac Group and overlying Raritan Formation in Virginia, Maryland and New Jersey, angiosperm pollen (Walker and Walker, 1984) and leaves (Upchurch, 1984) first appear as rare fossils in Barremian or Aptian deposits and become more numerous in those of younger age (Figure 2). Doyle and Hickey (1976) and Hickey and Doyle (1977) attributed much of this diversification to evolutionary radiation of angiosperms. However, migration probably remained important in the subsequent diversification of angiosperms in the Potomac Group. For example, intermediate forms between monosulcate and tricolpate angiosperm pollen have not yet been found in North America, although they may be present in the Early Cretaceous rocks of Gabon and Congo (Doyle, 1979, 1980). Migration also explains the occurrence of other distinctive kinds of angiosperm pollen, such as *Afropollis*, in the Potomac Group, as well as Europe, Africa and South America (Doyle *et al.*, 1982).

2.2. *Angiosperms on estuary and river margins*

Where Early Cretaceous angiosperms have been collected in the outcropping Potomac Group, they appear to have lived largely on the freshwater parts of a

coastal plain. In addition to channel and levée sandstones, silstones and shales, the Patuxent and Patapsco Formations and Elk Neck Beds include a variety of red and variegated claystones (Fontaine, 1889; Clark *et al.*, 1911; Glaser, 1969), which have many of the characteristics of a sequence of former, well drained, wooded or forested soils (Ultisols, Alfisols or Spodosols, like those described by Retallack, 1976, 1977). Swamp deposits are best developed in the Arundel Clay, which consists of grey claystone, nodular and lenticular siderite and lignite (Clark *et al.*, 1911). These were in part sequences of swamp soils (Histosols and gleyed Entisols and Inceptisols). Among these various paleoenvironments of the Potomac Group, angiosperm leaf fossils are most common in levée deposits and were probably derived from streamside, weed-trees (Hickey and Doyle, 1977). The overwhelming abundance of conifer remains in shaly and coal-bearing sediments away from paleochannels and in the regional palynoflora are indications that the dominant trees of swamps and well drained soils were mostly conifers. Their dominance in well drained soils continued well into Cenomanian time, when angiosperms had become dominant in other parts of the landscape (Hickey and Doyle, 1977).

Angiosperm pollen grains also have been found in marine and near-marine rocks laterally equivalent to the Potomac Group and Raritan Formation 100 km down dip to the east in the deep boreholes of the Delmarva Peninsula (Doyle and Robbins, 1977). Angiosperms appear to have been a part of the vegetation of coastal regions as well as the freshwater coastal plain. They appear there at similar stratigraphic levels and their apparent step-wise diversification can be related to regional changes in sea-level and environments (Retallack and Dilcher, 1981*a*). Angiosperm fossils appear (in the Patuxent Formation) at a time of regression after at least two earlier marine transgressions. They are more diverse and abundant in deposits above the Arundel-Patapsco contact, which records a marked regional marine regression. Angiosperm megafossils dominate most sedimentary environments in the Elk Neck Beds, which were deposited during regression from one of the most extensive of Cretaceous marine transgressions (Figure 2).

Effects of changes in sea-level on Early Cretaceous vegetation of the Atlantic coast are likely to have been complex, because it probably was deeply embayed by large estuaries and lagoons, as it is now (Clark and Bibbins, 1902; Glaser, 1969). This would be expected considering the control on the landscape exerted by Early Cretaceous igneous intrusions and the buried underlying rift valley topography, as revealed by seismic surveys and deep drilling (Schlee *et al.*, 1976, 1977; Mattick and Bayer, 1980). The present outcrops of the Potomac Group were generally beyond or near the limit of penetration of estuarine brackish water during the Early Cretaceous and evidence for marine influence there has been disputed. Grain size distribution of Potomac paleochannels cannot be considered definitive evidence for estuarine conditions (Groot, 1955; Glaser, 1969). Glauconite, reported from the Potomac Group by Glaser (1969), is now thought to belong to the onlapping marine rocks of the Paleocene Aquia Formation (Hazel, 1969; Upchurch and Doyle, 1981). The acritarch *Schizosporis* has been found at only a few localities in the Potomac Group (Brenner, 1963). It has been compared with modern freshwater protists (Brenner, 1963; Pierce,
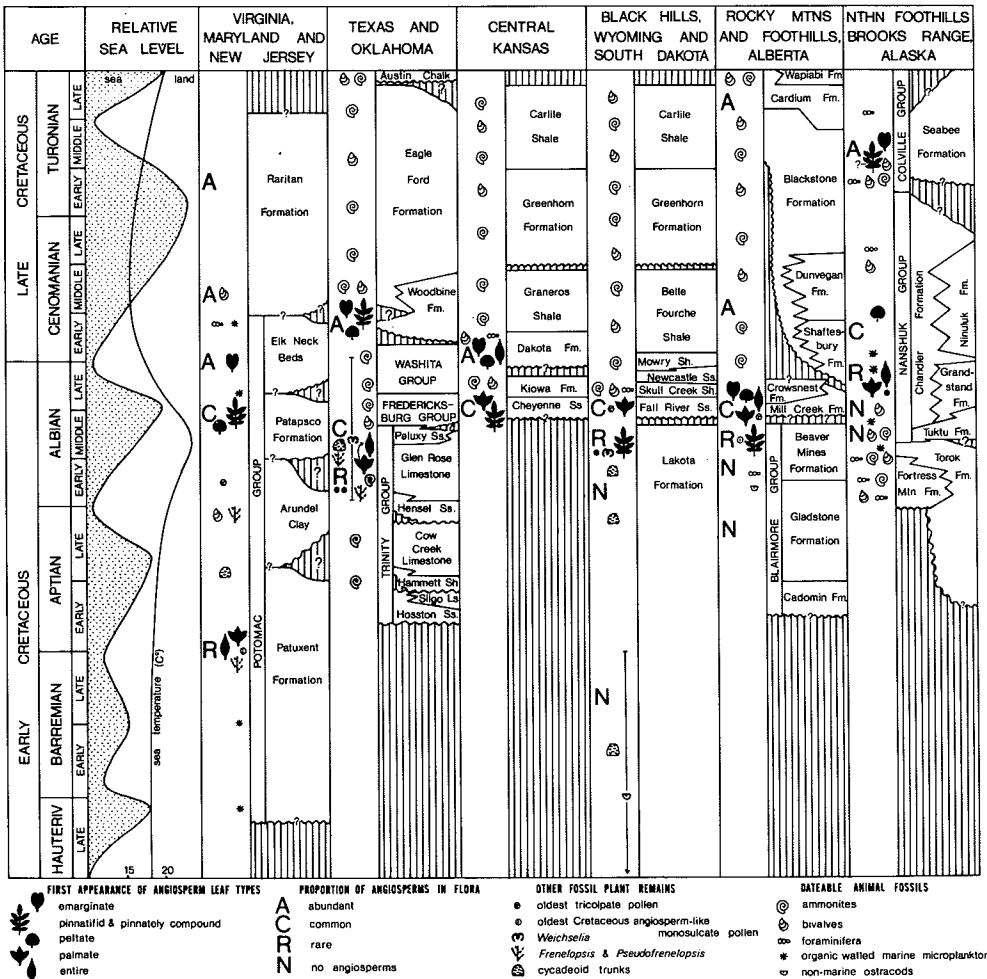
Figure 2. A correlation chart for rock formations of regions of North America with a good fossil record of Early and mid-Cretaceous angiosperm fossils. Sea level and sea temperature curves are based on data largely from the interior seaway (Kauffman, 1977b). The time scale is from Van Hinte (1976).

1977), but is a form widespread in both non-marine and fully marine mid-Cretaceous rocks all over the world (Pierce, 1976). Other possible marine microplankton (smooth and spiny acritarchs) have been found in small numbers at a few localities (Upchurch and Doyle, 1981). Nevertheless, the sea was not far away and brackish water penetrated well into the area of the outcropping Potomac Group during an extensive later (mid-Cretaceous or Cenomanian) marine transgression. A diverse molluscan fauna has been found in the Woodbridge Clay Member of that age in the Raritan Formation of New Jersey. Fully marine invertebrates, such as belemnites, ammonites and echinoids are conspicuously absent in this fauna of brackish-adapted bivalves and gastropods (Richards, 1958, 1962).

Perhaps the best evidence that the outcropping Potomac Group was near the limit of penetration of estuarine waters during the Early Cretaceous is

provided by fossil plant assemblages largely composed of *Pseudofrenelopsis parceramosa* (Figure 3–26). Smooth and spiny acritarchs (possible marine microplankton) are most prominent (up to 2% of the palynoflora) at localities also yielding *Pseudofrenelopsis*. Similar acritarchs are also present in lesser abundance (up to 0·5%) at localities yielding another xeromorphic cheirolepidiaceous conifer, *Frenelopsis ramossissima* (Figure 3–17; Upchurch and Doyle, 1981). Both genera usually dominate the fossil assemblages in which they are found, *Pseudofrenelopsis* more so than *Frenelopsis*. This is also true of their pollen, *Classopollis,* compared to associated pollen and spores (Upchurch and Doyle, 1981). Both *Frenelopsis* and *Pseudofrenelopsis* were probably trees (Alvin, 1982). They are associated with fossil wood and *Frenelopsis* shoots have been found attached to woody branches up to 2 cm wide (Gray Herbarium, Harvard University collections). Both genera have numerous morphological features found in modern plants of nutrient poor, dry or saline environments: jointed stems, succulent shoots, reduced sheathing leaves, thick papillate cuticles and sunken stomatal openings. Both genera also are associated with sediments of paleochannels, either of estuaries or of streams. It seems likely that *Pseudofrenelopsis parceramosa* vegetated the margins of brackish inland reaches of estuaries.

Frenelopsis ramossissima, on the other hand, was part of a more diverse, less marine-influenced vegetation of nutrient-poor and well drained substrates. Upchurch and Doyle (1981) have suggested that these substrates may have been either rock outcrops or quartzose, sandy soils. Rock outcrops or boulders are unlikely considering the exceptionally deep, weathered mantle of clayey, forested paleosols (which we interpret as former Oxisols or Ultisols) developed on pre-Cretaceous rocks throughout the piedmont and coastal plain of the central eastern United States (Cleaves, 1968; Glaser, 1969; Hunt, 1972; Tiefke, 1973; Blank, 1978). Colonisation of quartzose, sandy soils is in accord with sedimentological features of one of the most productive localities (Fredericksburg) for large, branched, shoots of *Frenelopsis*. These were found in a silty lens above a thin conglomeratic layer within fluvial sandstones (Fontaine, 1889). This and Fontaine's other localities (such as the clay lens at Baltimore) were probably abandoned stream beds or bars, like similar examples described by McDonnell (1974). Colonisation of nutrient poor, sandy, stream beds, bars, levées and beach ridges is characteristic of several kinds of xerophytic vegetation found today in the tropics (such as the padang vegetation of southeast Asia; Richards, 1941, 1952), which Upchurch and Doyle (1981) suggest was analogous to vegetation including *Frenelopsis* during deposition of the lower Potomac Group.

Cheirolepidiaceous conifers, such as *Frenelopsis* and *Pseudofrenelopsis*, are now known to have vegetated a variety of stressful habitats (Alvin, 1982), in addition to mudflats flanking estuaries (Oldham, 1976), brackish lagoons (Doludenko, 1978) and reef-bound, hypersaline, tropical lagoons (Daghlian and Person, 1977; Perkins *et al.*, 1979). Although the Cheirolepidiaceae as a whole were ecologically diverse, individual species may be useful paleoenvironmental indicators.
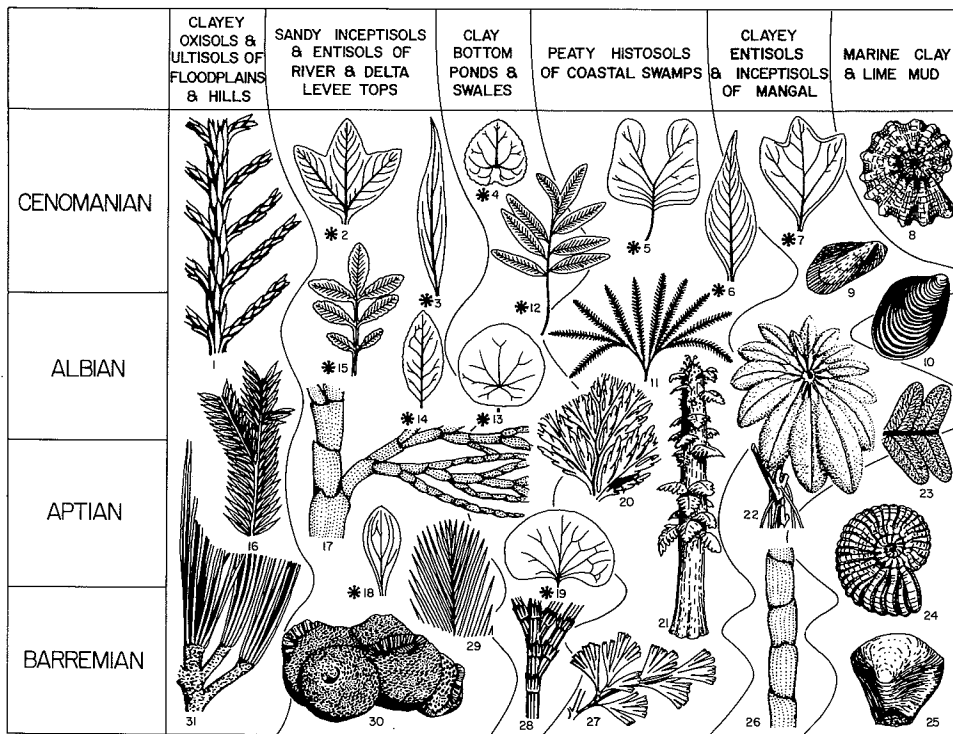
Figure 3. Representative North American megafossils and their likely paleoenvironments during Cretaceous time. Angiosperms are indicated by asterisks. Illustrated are: 1, *"Sequoia" condita* Lesquereux, conifer (natural size), after Berry (1922*b*); 2, *Araliopsoides cretacea* (Newberry) Berry, angiosperm (× 0.25), after Lesquereux (1874); 3, *"Andromeda Pfaffiana* Heer,"* angiosperm (× 0.25), after Lesquereux (1892); 4, *Nelumbites* sp., angiosperm (× 0.25), Indiana University collections (IU15706); 5, *Liriophyllum kansense* Dilcher and Crane, angiosperm (× 0.25), after Dilcher *et al.* (1978); 6, *Magnoliaephyllum* sp., angiosperm (× 0.5), Indiana University collections (IU15703-2262); 7, *"Acerites multiformis"* Lesquereux, angiosperm (× 0.5), Indiana University collections (IU15713-3317A); 8, *Acanthoceras amphibolum* Morrow, marine ammonite (× 0.13), after Kauffman (1977*a*) and Hattin *et al.* (1978); 9, *Brachidontes filisculptus* Stephenson, brackish-adapted mussel (× 0.5), after Hattin *et al.* (1978); 10, *"Inoceramus" comancheanus* Cragin, marine bivalve (× 0.25), after Kauffman (1977*a*); 11, *Matonidium brownii* Rushforth, fern (× 0.25), after Rushforth (1970); 12, *"Rhus" powelliana* Lesquereux, probably *Sapindopsis*, angiosperm (× 0.12) after Dilcher *et al.* (1978); 13, *Nelumbites virginiensis* (Fontaine) Berry, angiosperm (× 0.25), after Hickey and Doyle (1977); 14, *"Celastrophyllum" acutidens* Fontaine, angiosperm (× 0.25), after Hickey and Doyle (1977); 15, *Sapindopsis belviderensis* Berry, angiosperm (× 0.17), after Berry (1922*b*); 16, *Cephalotaxopsis brevifolia* Fontaine, conifer (× 0.5) after Fontaine (1889); 17, *Frenelopsis ramossissima* Fontaine, conifer (× 0.5), after Fontaine (1889); 18, *Acaciaephyllum spatulatum* Fontaine, angiosperm (× 0.5) after Hickey and Doyle (1977); 19, *Proteaephyllum reniforme* Fontaine, angiosperm (0.5) after Hickey and Doyle (1977); 20 *Onychiopsis goeppertii* (Schenk) Berry, fern (× 0.5), after Fontaine (1889); 21, *Tempskya*, reconstructed fern (× 0.05), after Andrews and Kern (1947); 22–23, *Weichselia reticulata* (Stokes et Webb) Fontaine, reconstructed fern (× 0.1) after Alvin (1971) and pinnules (× 2), after Fontaine in Ward (1899); 24, *Dufrenoyia justinae* (Hill) Burckhardt, marine ammonite (× 0.5), after Humphrey (1949); 25, *Anodontopleura speciosa* Felix, tropical marine, rudist bivalve (× 0.06), after Perkins and Coogan (1969); 26, *Pseudofrenelopsis parceramosa* (Fontaine) Watson, conifer (× 1), after Fontaine (1889); 27, *Acrostichopteris pluripartita* (Fontaine) Berry, fern (× 0.5), after Fontaine (1889); 28, *"Equisetites" burchardtii* Dunker, generic name debated by Jongmans (1914) and Boureau (1964), equisetalean (× 0.5), after Fontaine (1889); 29, *Zamites buchianus* (Ettingshausen) Seward, cycadophyte leaf (× 0.17), after Fontaine (1889); 30, *Cycadeoidea marshiana* Ward, cycadeoid trunk (× 0.1), after Wieland (1906); 31, *"Abietites" longifolius* (Fontaine) Berry, perhaps better referred to *Pityocladus* as understood by Harris (1969), conifer (× 0.5), after Fontaine (1889).

2.3. *Ecology of early angiosperms*

Angiosperm fossils are evidence that these invaders were early successional plants of disturbed coastal environments. The oldest angiosperm pollen appearing in the Potomac Group is of a size and exine structure like that of modern weedy, early successional plants of disturbed areas, which rely on several methods of pollination rather than just one (Retallack and Dilcher, 1981*a*; Walker and Walker, 1984). Only by the Albian do angiosperm pollen of both larger and smaller size, as well as more varied exinal structure and sculpture, appear adapted to more constant modes of pollination by wind or insects. From Cenomanian rocks, there is palynological evidence of widespread angiospermous pollination by wind, perhaps an indication that angiosperms had come at last to dominate the canopy of some kinds of backswamp and floodplain forests (Hickey and Doyle, 1977).

The oldest angiosperm leaf fossils in the Potomac Group are small and simple like those of "low, highly-branched shrubs of sunny habitats" (Hickey and Doyle, 1977, p. 73). Compound and pinnatifid (*Sapindopsis*) leaves appear by Middle Albian time and are similar to leaves of living, early successional shrubs. Peltate leaves (*Nelumbites*; Figure 3–13) similar to those of living aquatic angiosperms, also appeared by Middle Albian time. Some large late Aptian or early Albian leaves (such as *Ficophyllum crassinerve*) may have "belonged to some of the first angiosperms to enter conifer-dominated Early Cretaceous forests, not as direct competitors of the conifers but as understory trees" (Hickey and Doyle, 1977, p. 73). If these interpretations are correct, then initial weedy invading angiosperms were later followed by angiosperms adapted to a variety of specific environments.

2.4. *Nature and replacement of pre-existing vegetation*

The kinds of plants which appear to have been replaced by angiosperms are also a guide to the ecology and nature of these early immigrants. The genera *Pseudofrenelopsis* and *Frenelopsis* were widespread in Early Cretaceous vegetation of tropical regions, including eastern North America. Although they persisted into Late Cretaceous time in some parts of the world, there is no good evidence of them in North American rocks younger than Cenomanian (Berry, 1911*b*, 1916; Upchurch and Doyle, 1981; Alvin, 1982). Declining abundance and extinction of these plants also is seen in the fossil pollen *Classopollis*, which was produced by these as well as a variety of other cheirolepidiaceous conifers (Alvin, 1982). *Classopollis* wanes dramatically in abundance and diversity in North America after Aptian time (Brenner, 1963) and is not found in North American Cretaceous rocks younger than Turonian (Srivastava, 1976). This may have been due to competitive exclusion of these peculiar conifers from their habitats by invading angiosperms. At Barremian to Aptian localities, angiosperm leaves are not found with *Pseudofrenelopsis* and their pollen is very rare with it. Monodominant stands of *Pseudofrenelopsis* appear to have been flanked by other conifers and cycadeoids, judging from associated pollen (at Drewry's Bluff and Oak Grove (drill core) localities of Upchurch and Doyle, 1981). By the early

Albian, angiosperms still had not dispersed into either estuarine gallery woodlands, or forests of *Pseudofrenelopsis*, or into the vegetation dominated by cycadophytes on levees (in evidence at Dutch Gap Canal localities of Fontaine, 1889; Upchurch and Doyle, 1981). At about this time, angiosperms were becoming prominent in the early successional vegetation of sandy soils (at Fredericksburg and Baltimore localities of Fontaine, 1889; Upchurch and Doyle, 1981). Later in the Albian, levées of freshwater streams were dominated by angiosperms, as *Frenelopsis* and cycadeoids had declined in abundance and disappeared (at Brooke of Hickey and Doyle, 1977). Some estuarine margin vegetation was still largely composed of *Pseudofrenelopsis* even as late as the Cenomanian, although by this time it was flanked largely by angiosperms (as indicated by pollen at Bodkin Point of Upchurch and Doyle, 1981). The persistence of *Pseudofrenelopsis* in nearly pure stands, compared to mixed vegetation including *Frenelopsis*, is also evident from a number of other localities within the Potomac Group (Fontaine, 1889; Ward, 1905). Although angiosperms ultimately occupied the habitats of both genera, it took a considerable length of time and angiosperms were more effective in diluting and displacing *Frenelopsis* earlier than *Pseudofrenelopsis*. If our ideas concerning the ecology of these conifers in the Potomac Group are correct, it would appear that early angiosperms were more effective at colonising disturbed sedimentary surfaces than other plants, but were less effective at penetrating undisturbed plant communities. In the terminology of Grime (1979), early angiosperms can be envisaged as ruderals (weedy and ecologically opportunistic plants), rather than stress tolerators or competitors.

Cycadeoids are another common Early Cretaceous group of plants which became extinct as angiosperms became more abundant and widespread (Retallack and Dilcher, 1981a). Silicified trunks (Figure 3–30) found in place in the Patuxent Formation in Maryland (Ward, 1905, p. 405), are amongst the youngest reliably documented occurrences of cyadeoids. As with other Early Cretaceous cycadeoid trunks found in place (Ward, 1899; Wieland, 1906, p. 23; Tidwell *et al.*, 1976), these were in growth position in streamside levée deposits. Trunks of cycadeoids have been found unbroken, upright and intact, even though decayed, internally disorganised, bored and with partially collapsed crowns (Wieland, 1906, p. 23; Crepet, 1974). Thus, they were not transported. Cycadophyte leaves (Figure 3–29) and pollen are also most abundant in levée deposits (at the Aptian locality at Dutch Gap Canal, Virginia; Fontaine, 1889; Upchurch and Doyle, 1981). As can be seen from younger Cretaceous localities (such as Brooke of Hickey and Doyle, 1977), angiosperms had displaced cycadeoids from the margins of freshwater coastal streams by Middle Albian time. Neither leaves nor trunks of cycadeoids are found in Cenomanian or younger deposits of the Atlantic coastal plain (Berry, 1911b, 1916; Retallack and Dilcher, 1981a).

Also associated with the rise of angiosperms in the Potomac Group were extinctions of many kinds of ferns (Brenner, 1963; Glaser, 1969), which were characteristic of Early Cretaceous coastal swamps and marshes throughout the world (Seward, 1933; Oishi, 1940; Rushforth, 1970). Among these was the tree fern *Tempskya* (Figure 3–21), petrified false stems of which have been found in the Patapsco Formation of the Potomac Group (Berry, 1911a).

The plants least affected during this time of angiosperm invasion and rise to dominance in North America, were conifers, especially those of the extant families Taxodiaceae and Pinaceae (Brenner, 1963; Glaser, 1969; Delevoryas, 1971; Miller, 1977). Throughout the Potomac Group, fine grained sediments deposited away from stream channels contain predominantly ferns and conifers. Some of these deposits of backswamps and floodplains as young as Cenomanian still contain few angiosperm fossils (Hickey and Doyle, 1977). The persistent abundance of conifer pollen in the regional palynoflora of the Potomac Group (Doyle and Robbins, 1977; Upchurch and Doyle, 1981) is an indication that conifers remained dominant in the deeply weathered soils (Oxisols and Ultisols) of the crystalline Appalachians, as well as on river terraces and valley bottoms seldom swept by floods.

Although invading angiosperms migrated into areas vegetated mainly by gymnosperms and ferns, this was different from modern vegetation of conifers and ferns. The lateral continuity and thickness of well differentiated paleosols and lignites in the Potomac Group (Fontaine, 1889; Clark *et al.*, 1911) are indications that these forests were luxuriant and dense. Many fern spores were probably dispersed by wind and water, and many conifers released their bisaccate pollen and winged seed to the wind, as related plants do today. There are also indications that insects and dinosaurs found in these deposits (Clark *et al.*, 1911; Hickey and Doyle, 1977) and perhaps other creatures not found, may have played more of a role in the propagation of this vegetation than is usual in extant vegetation of ferns and conifers. The large pollen grains and bored fructifications of *Cycadeoidea* are compatible with beetle pollination for these plants (Crepet, 1974). *Classopollis*, the pollen of *Frenelopsis* and *Pseudofrenelopsis* is also of a size usual in insect-pollinated plants, and is commonly found in larger, permanent tetrads (Upchurch and Doyle, 1981). Ginkgoalean or cycadophyte seeds up to 15 mm long with well-differentiated fleshy and stony layers (Fontaine, 1889; Berry, 1911*a*) are like modern fruits which can withstand ingestion by animals. These were stable, subtropical forests, rich in species and in methods of reproduction.

3. California

Although the fossil record of Cretaceous angiosperms in California is poor, it is evidence of early dispersal of angiosperms around southern and western coastal regions of North America, at a time before much of Central and South America were attached (Figure 1).

3.1. *Early dispersal in western and southern coastal regions*

Angiosperms first appeared in the northern Great Valley of California during the Aptian or Albian. They are represented by fragments of leaves in shallow marine siltstones and mudstones of a large embayment between the former land masses now represented by the Coast Range and Sierra Nevada. As is usual for plant debris in marine rocks, all these fossils are fragmentary and poorly preserved. Some of these fossils, once regarded as angiosperms, such as *Onoana californica* (Chandler and Axelrod, 1961) and *"Acaciaephyllum"*

ellipticum (Fontaine in Ward, 1905), are older than Aptian (Murphy, 1956, 1975; Popenoe *et al.*, 1960). However, neither of these fossils have any definitive angiospermous features (Wolfe *et al.*, 1975; Hughes, 1976; Dilcher, personal observations). Other fragmentary fossils, such as *"Proteae-phyllum californicum," "Populus? ricei," "Sapindopsis oregonensis,"* and undescribed remains from the South Fork of Cottonwood Creek (Fontaine in Ward, 1905; Diller, 1908, p. 397), are similarly unconvincing as records of angiosperms. The only Early Cretaceous fossil plants from California here accepted as angiospermous, although not identifiable to a genus, are fragments from Elder Creek, west of Red Bluff (locality 23 of Fontaine in Ward, 1905, in interval 9500–10 000 feet in the measured section of Diller and Stanton, 1894). These are rare fossils similar to early angiosperm leaves of the Potomac Group. They are also younger than fossil plant assemblages lacking angiosperms (locality d of Diller and Stanton, 1894, probably the same as locality 9 of Ward, 1905), at lower stratigraphic levels in the thick sequence of marine rocks exposed in Elder Creek, where there are Valanginian (very Early Cretaceous) marine fossils. At higher stratigraphic levels in the same sequence, there are conglomerates with more abundant angiosperm leaves of likely late Albian or Cenomanian age (Popenoe *et al.*, 1960).

4. Texas and adjacent states

Although much of Texas and the nearby Gulf States was inundated by shallow seas during the Early Cretaceous, marine and near marine rocks in this region contain plant fossils relevant to both the appearance and early habitats of angiosperms.

4.1. *Angiosperms on beach ridge plains*

Angiosperms may not have penetrated the Gulf Coast region by the time of the Aptian-Albian boundary. No evidence of them has been found among pollen and spores of about that age in Arkansas (Bond, 1972). The oldest angiosperm fossils in the region are rare monosulcate and tricolpate pollen from the Early to Middle Albian Glen Rose Limestone of Texas (Figure 2; Young, 1974; Perkins *et al.*, 1979). The Glen Rose Limestone and associated sandstone units were deposited in a system of tropical reefs, bays and hypersaline lagoons (Nagle, 1968; Stricklin and Amsbury, 1974; Perkins, 1974).

In the overlying and partly equivalent Middle Albian Paluxy Sandstone, there are palmately-lobed and entire-margined angiosperm leaves (Ball, 1937) similar to angiosperm remains from the Patapsco Formation of the eastern United States (Hickey and Doyle, 1977). The fossil angiosperm leaves come from that part of the Paluxy Sandstone interpreted as a strand-plain (Caughey, 1977), formed from extensive sheets of coalescent beach sands interstratified with marine and coastal lake muds, as in the modern Nayarit coast of western Mexico. Rocks of equivalent age in Oklahoma contain a limited diversity of monosulcate and tricolpate pollen (Hedlund and Norris, 1968) and in Louisiana, monosulcate angiosperm pollen (Phillips and Felix, 1971*a, b*).

Much of the Gulf Coast region was inundated by the sea until the early Cenomanian, as limestones of the Fredericksburg and Washita Groups accumulated (Young, 1967). A well preserved fossil flora from chert nodules in the Edwards Limestone of the Fredericksburg Group represents vegetation fringing a reef-bound tropical lagoon. It includes *Weichselia, Frenelopsis* and several other conifers together with a new species each of seed fern and angiosperm (Serlin, 1982). The angiosperm leaves are quite different from all other Early Cretaceous angiosperm leaves yet reported in their several xeromorphic features; small size, coriaceous nature, highly divided filiform segments, stomata restricted to the strongly re-curved underside of the leaf and protected by hairs. This is an indication that by this time some angiosperms had already evolved into stress tolerators, as that category is defined by Grime (1979). The presence of other angiosperms, similar to those elsewhere in North America, is indicated by angiosperm pollen found throughout the Fredericksburg Group (Srivastava, 1981).

These marine limestones are overlain disconformably by the Early to early Middle Cenomanian Woodbine Formation which accumulated in a large marine delta. Like wave-dominated deltas of the modern Surinam coast, this ancient delta probably included extensive beach ridge plains (Oliver, 1971). The Woodbine Formation has yielded diverse assemblages of fossil angiosperm leaves (Berry, 1912, 1922a; MacNeal, 1958) and pollen (Hedlund, 1966, 1967). Comparable assemblages of angiosperm leaves (Berry, 1919) and pollen (Phillips and Felix, 1971a, b) have been found in the Cenomanian Tuscaloosa Formation of Mississippi, Louisiana and Alabama.

Much of the Gulf Coast was again submerged during the Late Cenomanian by the most extensive marine transgression into the continental interior during the Cretaceous, culminating in Early Turonian time (Kauffman *et al.*, 1977). Lateral movements of the shoreline have been calculated to have been as fast as 585 km per million years (or 0.6 m/yr) by Hancock and Kauffman (1979).

4.2. Replacement of non-angiospermous coastal vegetation

Pseudofrenelopsis varians was abundant around hypersaline lagoons during deposition of the Glen Rose Formation (Daghlian and Person, 1977; Watson, 1977) and *Cycadeoidea* was still common in coastal deposits of the Paluxy Sandstone (Wieland, 1931; Perkins *et al.*, 1979). As in the Potomac Group of the eastern United States and elsewhere in the world, these plants appear to have become extinct by the Cenomanian and their habitats were occupied by increasingly abundant angiosperms.

Weichselia (Figures 3–22, 23) is another common and widespread Early Cretaceous plant which became extinct at about this time (Alvin, 1971; Barale, 1979; Harris, 1981; Retallack and Dilcher, 1981a). In Texas, this fossil plant has been found in chert nodules thought to be from the Edwards Limestone of the Fredericksburg Group (Berry, 1928; Serlin, 1982). *Weichselia* has a number of xerophytic features peculiar for a matoniaceous fern; sori protected by interlocking peltate indusia, thick cuticles, fleshy recurved pinnules, aerophores on the stem, a tangle of prop roots, leaves which appear to have burned to charcoal rather than ash (Alvin, 1971; Harris,

1981). It is commonly found in monospecific assemblages in coastal sediments. Of Batten's (1975) suggestions that it was either a coastal dune-binder or a mangrove, the latter seems more likely considering its abundance in the leaf litter of a humic, presumably waterlogged, estuarine paleosol (Daber, 1968). In its xeromorphism and geological occurrence *Weichselia* is similar to *Pseudofrenelopsis* and *Frenelopsis* and it is occasionally found along with these genera (Berry, 1939; Barale, 1979). Like the modern vegetation of estuarine banks, intertidal flats, salt pans, dune tops and interdune swales, these genera probably preferred one or more of these effectively xeric, coastal sedimentary environments.

5. Kansas

Although there is a poor record of Cretaceous vegetation before the invasion of angiosperms in Kansas, the paleoecology and reproductive biology of mid-Cretaceous angiosperms from this region are becoming especially well understood.

5.1. *Penetration of angiosperms and seas into the continental interior*

The oldest angiosperm fossils in Kansas are in the oldest Cretaceous sediments in the state, the Cheyenne Sandstone (Scott and Taylor, 1977). The Cheyenne Sandstone is disconformably overlain by marine shell lags of the basal Kiowa Formation (Franks, 1979, 1980), but contains no marine or near-marine fossils, and was deposited by freshwater streams (Latta, 1946). The sea was not far away, because the Cheyenne Sandstone and correlative estuarine deposits across the border in Oklahoma are interpreted as remnants of coastal plains inundated by Late Albian marine transgression of the Interior Seaway from the south and west (Scott, 1970). Angiosperm fossils from the Cheyenne Sandstone include deeply pinnatifid leaves (*Sapindopsis*, Figure 3–15), similar to the oldest angiosperm leaves at several localities along the margins of the Interior Seaway (Figure 2). As at similar stratigraphic levels in the Potomac Group, angiosperm leaves are far less numerous than associated conifer shoots (Knowlton, 1919; Berry, 1922*b*) and are found in interbedded shales and sandstones (Berry, 1922*b*) similar to sediments forming levees of modern streams.

As the sea retreated from Kansas during the latest Albian, angiosperms were already widespread. Angiosperm leaves are abundant in the lower Dakota Formation (Twenhofel, 1924, p. 28; Tester, 1931, p. 266). They are also abundant in the upper Dakota Formation (Lesquereux, 1874, 1883, 1892; Retallack and Dilcher, 1981*a*, *b*; Dilcher and Crane, 1984). This part of the formation was deposited in marine deltas of the tide-dominated kind, in which there were extensive estuarine and lagoonal mudflats. This coast was ultimately overwhelmed by continued marine transgression westward during Early and Middle Cenomanian time (Siemers, 1976; Hattin *et al.*, 1978; Retallack and Dilcher, 1981*a*, *b*).

5.2. Varied coastal habitats of angiosperms

From our own studies of extensive new fossil plant collections and fossil soils in the uppermost Dakota Formation, has emerged the following reconstruction of mid-Cretaceous (Early Cenomanian) vegetation. Weakly differentiated, clayey fossil soils (sulfidic, gleyed Inceptisols), containing remains of brackish-adapted mussels in life position, were once mangal soils of the tidal reaches of coastal streams. The fossil leaf litter of these marine-influenced paleosols is dominated by a distinctive, palmately-lobed leaf ("*Acerites multiformis*"; Figure 3–7). Other fossil leaf litters are evidence that angiospermous shrubs, mainly with large palmately-lobed leaves (*Araliopsoides cretacea*; Figure 3–2) colonised weakly developed sandy soils (Psamments and perhaps some Spodosols), and that there were angiospermous swamp woodlands in peaty soils (Histosols) of interdistributary depressions. Three common angiosperm leaves have been found associated with these swamp deposits: entire-margined leaves (*Magnoliaephyllum*; Figure 3–6), large leaves with an emarginate apex (*Liriophyllum*; Figure 3–5) and pinnately compound leaves (*Sapindopsis;* Figure 3–12). Pollen and spores in the organic horizons (now lignites) of these swamp soils are an indication that ferns were also abundant in these swamp woodlands, probably as an understorey (Farley, 1982; Zavada, pers. comm.). Ferns are uncommon as megafossils in association with these swamp deposits. Similarly plant debris accumulating in modern lakes and ponds seldom includes understorey plants from adjacent woodlands (Roth and Dilcher, 1978). Well developed red paleosols (probably Alfisols or Ultisols) of the Dakota Formation probably formed under well drained forests, like generally similar fossil soils discussed by Retallack (1976, 1977). These fossil soils were too oxidising for preservation of fossil plants (Retallack, 1984). Conifers probably dominated these forests because they are rarely preserved as megafossils in other paleosols of the Dakota Formation, but are abundantly represented in the fossilised regional pollen rain and among drifted megafossil plant remains which accumulated in coastal lagoons and lakes.

As for the Potomac Group and elsewhere, our studies confirm the occurrence of angiosperms in a variety of unstable, coastal, depositional environments. There is also evidence of angiospermous mangal vegetation. Considering the absence of *Weichselia, Frenelopsis* and *Pseudofrenelopsis* in the Dakota and younger formations, it appears that angiosperms by this time had occupied the varied, nutrient-poor, dry and saline habitats formerly vegetated by these genera. There is also evidence of angiosperm dominance of coastal swamps.

5.3. Reproductive biology of early angiosperms

Angiosperm leaves and pollen in the upper Dakota Formation are generally similar to those of comparable stratigraphic levels in the uppermost Potomac Group and Raritan Formation, but from the Dakota Group there is additional evidence of the nature of these plants from a variety of well preserved fructifications (Retallack and Dilcher, 1981*a, b*; Crane and Dilcher, 1984; Dilcher and Crane, 1984; Basinger and Dilcher, 1984). The

fructifications are mainly those of extinct plants and are limited in diversity. They are similar to a variety of poorly preserved and imperfectly understood Early Cretaceous fructifications in the Potomac Group (Dilcher, 1979), as well as to well-preserved Early Cretaceous fructifications from elsewhere in the world (Krassilov, 1984).

Some of the flowers are small, apparently unisexual and arranged in catkin-like or globose inflorescences. Other flowers are large, bisexual and have showy petals. The former may have been pollinated by a combination of methods (generalist) or by wind (Retallack and Dilcher, 1981*a, b*). The latter are most like modern insect pollinated flowers (Crane and Dilcher, 1984; Dilcher and Crane, 1984; Basinger and Dilcher, 1984). Many of the fructifications have numerous small seeds, like those of modern weedy plants (Retallack and Dilcher, 1981*a, b*; Dilcher and Crane, 1984). None have yet been found with large propagules of the kind which are now dispersed by animals (Tiffney, 1984).

Indications of insect pollination are found in Kansan fossil flowers of angiospermous mangal and swamp woodland vegetation. These habitats are less frequently disturbed than stream, lagoon and lake margins, and were vegetated by some plants interacting with local animals in their reproduction. Generalised mechanisms of pollination and dispersal characterised other fossil angiosperms of disturbed habitats, as they still do in modern vegetation (Heinrich, 1976).

6. Utah and adjacent states

The appearance and rise to dominance of angiosperms in Utah is similar in many respects to that in Kansas and elsewhere in the North American interior. At one locality, volcanic ash has preserved an exceptional record of the structure of mid-Cretaceous angiosperm-fern swamp woodlands, again illustrating differential replacement of various elements of pre-existing vegetation.

6.1. *Familiar patterns of immigration and replacement.*

The Aptian or Albian Cedar Mountain Sandstone and equivalent rock units in Utah, Colorado and New Mexico were deposited largely by streams draining east into the Interior Seaway (Young, 1960). These rocks contain only a few species of angiosperm wood (Tidwell *et al.*, 1976; Thayn and Tidwell, 1984; Thayn *et al.*, 1983, 1985), leaves and fructifications (these last similar to *Platanus*; Dilcher and Erickson, 1983), as well as other plants which are common and widespread in Early Cretaceous, but not found in younger rocks, such as *Pseudofrenelopsis varians*, cycadeoid trunks (*Cycadeoidea* and the closely allied *Monanthesia*) and false stems of *Tempskya*. Slender stems of angiosperms have been found within false stems of *Tempskya* (Tidwell *et al.*, 1977). These various non-angiospermous plants became extinct as angiosperms became more abundant.

Angiosperms are common megafossils in Late Albian and Cenomanian rocks of Wyoming (Knowlton, 1917; Berry, 1929; Brown, 1933; Andrews and Pearsall, 1941). A palynological study of these rocks (Burgess, 1971) indicated that conifers still dominated regional vegetation. Similar domin-

ance of conifer pollen has been reported for mid-Cretaceous rocks in the eastern United States (Hickey and Doyle, 1977), Minnesota (Pierce, 1961; Hall, 1963), Oklahoma (Hedlund, 1966), Utah (May and Traverse, 1973), Arizona (Agasie, 1969), Colorado and Nebraska (Pannella, 1966). Several of these studies have also found different assemblages in coals than in the adjacent shales and siltstones, which are dominated by conifer pollen. Few conifer pollen are found in coals, which contain instead a limited diversity of angiosperm pollen, fern spores and occasional marine microplankton. As in Kansas, angiosperms were prominent and widespread in coastal environments such as swamps, but conifers were more abundant in inland vegetation.

6.2. *Angiosperms of swamplands*

The angiosperm and fern vegetation of a mid-Cretaceous coastal swamp has been remarkably well preserved in a bed of volcanic ash within a coal of the upper Dakota Formation in central easternmost Utah (Rushforth, 1971). This thin (26 cm) ash preserved fronds and rhizomes of the ferny understory of these swamp woodlands in growth position. The thin, uppermost silty portion of the ash contains a more diverse assemblage of fossil plants, including angiosperm leaves. These were probably contributed by canopy trees represented by three cradle knolls (disturbed ground around rotted or felled trees) recently discovered disrupting the ash in the new road cutting 8 km northwest of Westwater Ranger Station (Retallack and Dilcher, 1981b). Thus, there were understories of ferns in mid-Cretaceous angiospermous swamp woodlands of the North American interior.

7. Black Hills

The appearance of angiosperms in the uparched rim of the Black Hills of western South Dakota and eastern Wyoming is well constrained because fossil floras older than those with the oldest angiosperms also are preserved. In other respects angiosperm appearance and rise to dominance followed a pattern similar to that seen in other parts of the continental interior.

7.1. *Inland persistence of non-angiospermous vegetation*

Although the lowest part of the Lakota Formation in the Black Hills may be as old as Valanginian (Sohn, 1979), the formation continued to accumulate until the Middle Albian (Waage, 1959). Cycadeoids, conifers and ferns (Ward, 1899; Wieland, 1906, 1916; Delevoryas, 1971) vegetated broad, northeasterly sloping valleys of this inland region (Waage, 1959; Chisholm, 1963). This vegetation without angiosperms persisted until well after the dispersal of angiosperms throughout eastern and southern coastal plains of North America.

7.2 *Familiar patterns of immigration and replacement*

The oldest angiosperm fossils in the Black Hills are rare and of limited diversity. They include monosulcate pollen grains (Davis, 1963) and leaves,

largely of *Sapindopsis*, found in the Fuson Shale Member of the upper Lakota Formation (Ward, 1899). As in the eastern United States, *Sapindopsis* is dominant where it occurs, and closely associated with stream channel deposits (Hickey and Doyle, 1977, p. 36, figs. 39, 40). As elsewhere in the North American interior, angiosperms appeared at a time of marine influence. Approach of the sea, presumably during the Middle Albian, may have been responsible for the higher water table, evidenced by coal and freshwater limestone in the upper (but not lower) Lakota Formation. Marine influence is also indicated by the appearance of the likely mangal fern *Weichselia* in the upper Lakota Formation (Fontaine in Ward, 1899).

The overlying Fall River Formation was deposited in a series of marine deltas (Dondanville, 1963). Considering the rarity of fully marine fossils and the sedimentological observations of Campbell and Oaks (1973), these were most like modern tide-dominated deltas (as discussed by Elliott, 1978). Such deltas were widespread on the low-relief, eastern coasts of the interior seaway (Franks, 1980; Retallack and Dilcher, 1981*a, b*). The Fall River Formation contains common angiosperm leaves in places (Ward, 1899; collections of the South Dakota School of Mines, Rapid City, Numbers 484–507) and the oldest tricolpate pollen in the region (Davis, 1963). Other kinds of fossil plants are less common. Cycadeoids and *Weichselia* appear to have become extinct by this time. Marine fossils of the Fall River Formation are too rare and poorly preserved to be of value in determining age (Dondanville, 1963).

The overlying shallow marine Skull Creek Shale and Newcastle Sandstone contain diagnostic Late Albian marine fossils (Grace, 1952; Waage, 1959; Skolnick, 1958), as well as rare angiosperm leaf fossils (Stanton, 1922).

8. Alberta

In the Rocky Mountains and foothills of Alberta, the first appearance of angiosperms is very similar to that of the Black Hills, but for better evidence of late Early Albian marine transgression.

8.1. *Sea-level change and angiosperm establishment*

The Early Cretaceous Blairmore Group of Alberta is largely varicoloured, non-marine sandstone, and has abundant non-angiospermous fossil floras in its lower part (Figure 2; Mellon, 1967). In the middle of the group, at the top of the Gladstone Formation, there is a freshwater limestone containing charophytes, molluscs and ostracods. This is overlain by shale containing marine foraminifera at the base of the Beaver Mines Formation (Loranger, 1954; Mellon, 1967). This widespread marine incursion is of late Early Albian age (Stott, 1974). Higher within the Beaver Mines Formation, the first angiosperm leaves are rare elements in fossil assemblages which consist largely of ferns, *Gingko*-like and conifer leaves (the "lower Blairmore flora" of Bell, 1956). Only one kind of angiosperm leaf (*Sapindopsis*) has been identified from the Beaver Mines Formation. It is similar to the earliest Cretaceous *Sapindopsis* leaves found farther south in the Black Hills and Kansas. In deep drill holes into marine rocks in other parts of Alberta, the first angiosperm monosulcate pollen appears during the Middle Albian and

the first tricolpate pollen in the earliest Late Albian, both ages judged from associated marine microplankton (Jarzen and Norris, 1975).

The Beaver Mines Formation is disconformably overlain by the Mill Creek Formation, sandstones and varicoloured shales which pass transitionally into the overlying pyroclastic Crowsnest Formation (Mellon, 1967; Stott, 1974; Jeletzky, 1978). This disconformity represents latest Albian marine regression, after which angiosperms become more common and diverse (the "upper Blairmore flora" of Bell, 1956). Fossil floras similar to those from the Mill Creek and Crowsnest Formations are found also in the Pasayten Group, Kingsvale Group and Commotion Formation of British Columbia. These floras also have a variety of palmately-lobed, peltate-shaped, apically-emarginate and entire-margined angiosperm leaves (Bell, 1956). Angiosperms remain common in the deltaic Cardium Formation of Middle to Late Turonian age (Stott, 1965) and in palynofloras of this age elsewhere in Canada (Jarzen and Norris, 1975).

9. Northern Alaska

Angiosperms reached northern Alaska later than more southerly parts of North America and their rise to dominance of megafossil floras there was also later. Some of these angiosperms may have dispersed north from the interior seaway, but there are also reasons to suspect eastward dispersal from Siberia.

9.1. *Late appearance and rise to dominance of angiosperms in polar regions*

In the northern foothills of the Brooks Range, non-angiospermous fossil plant assemblages have been found in Middle Albian shallow marine sediments of the Tuktu Formation and the deltaic lower Chandler Formation of the lower Nanushuk Group (Figure 2; Imlay, 1961; Smiley, 1967, 1969*a, b*; May, 1979; Sliter, 1979). The deltaic Nanushuk Group overlies and is partly equivalent to deep sea sediments (Torok and Fortress Mountain Formations), which may be as old as Aptian (Bird and Andrews, 1979; Mull, 1979).

The oldest angiosperm leaf fossils from Alaska are from the late Albian part of the Chandler Formation (Scott and Smiley, 1979). They include entire leaves, sometimes found in a whorl or close helix ("cf. *Ampelopsis*"), dissected leaves ("*Cissites*") and palmately lobed leaves ("cf. *Platanus*"). Tricolpate pollen also appears at comparable stratigraphic levels (Scott and Smiley, 1979). At this level the Chandler Formation was deposited in a western river-dominated digitate delta and a separate eastern deltaic complex with more conspicuous beach deposits (Alhbrandt *et al.*, 1979; Huffman and Alhbrandt, 1979).

Regional regression at about the time of the Albian-Cenomanian boundary is represented by a tongue of the non-marine Chandler Formation separating the marine Grandstand Formation from the overlying Ninuluk Formation (Jones and Gryc, 1960; Imlay, 1961; Detterman, 1973; Sliter, 1979; May, 1979). Angiosperms became more common and diverse after this marine regression. Conifers are well represented in Alaska by pollen, but conifer

megafossils are less abundant, an indication that conifers forested adjacent highlands (Scott and Smiley, 1979).

Angiosperms dominate the megafossil flora of the Seabee Formation of Turonian age (Smiley, 1969a), finally attaining a level of prominence found in Cenomanian deposits farther south in North America. The Seabee Formation overlies the Nanushuk Group with a marked angular discordance (Jones and Gryc, 1960; Cobban and Gryc, 1961; Detterman et al., 1963), probably caused by continued deformation and emplacement of granites in the Brooks Range to the south (Mull, 1979).

9.2 Possible eastward entry of angiosperms

The first angiosperms not only reached Alaska later but were different plants from the oldest Cretaceous angiosperms found farther south in North America. Considering this and the remarkable similarities of Early Cretaceous Alaskan fern, cycadophyte, Gingko-like and conifer leaves with those of Siberia (Smiley, 1976), eastward entry of angiosperms into Alaska is perhaps more likely than northward from North America.

10. Conclusions

The geological occurrence of early and mid-Cretaceous angiosperm fossils reveals much about the nature and early dispersal of these plants. They appear to have migrated first into the Atlantic coast from the south and east during Barremian or Aptian time. They reached California by Aptian or Albian time, presumably via coastal regions of southern North America. When the Interior Seaway was established linking the Carribean region with the Arctic during Middle Albian time, angiosperms dispersed as rare elements of coastal vegetation as far north as Alberta. The first angiosperms reached Alaska during latest Albian marine regression, but are perhaps more likely to have reached Alaska from the west than from the south. Angiosperms dominate megafossil floras of Cenomanian and younger age in most of North America, but are comparably abundant as megafossils in Turonian and younger rocks in Alaska.

The appearance and rise to dominance of angiosperms in coastal depositional environments is striking. Preservational biases may be mitigated by comparing fossil soils, transported plant debris and pollen. From these considerations, it appears that little disturbed coniferous vegetation of well-drained soils was not greatly affected by the initial invasion of angiosperms into open habitats of coastal areas. However, a variety of common and widespread plants of coastal, depositional and disturbed environments (Weichselia, Frenelopsis, Pseudofrenelopsis, Cycadeoidea and Tempskya) became extinct as angiosperms became dominant in the same habitats (Figure 3).

The appearance and increases in diversity of early angiosperms occur at times of both marine regression and transgression. The extent of eustatic sea-level changes increased in magnitude as angiosperms spread more widely

from Aptian to Cenomanian times. However, dispersal of angiosperms does not appear to have been uniquely related to changes in sea-level. Maximum rates of shoreline movement of only 0.6 m per year were such that vegetation could readily adjust to changing shorelines. Locally disturbed environments, such as beach ridges and deltaic levées, and their greater extent during times of change in sea-level, were probably more significant for migration of early angiosperms.

A predilection for disturbed coastal habitats is in evidence from the nature of early angiosperm leaves, pollen, fructifications and their paleoenvironments. Initially in various parts of North America, angiosperms appear to have preferred disturbed open habitats, where generalised methods of pollination and seed dispersal are needed. Later in the Cretaceous, they colonised more stable habitats and evolved more specialised methods of reproduction. The earliest angiosperms in North America do not appear to have been specifically adapted to tolerate exceptionally dry, saline or otherwise unfavourable environments. Nor do they seem to have been direct competitors of pre-existing plants. Rather, they appear to have been able to colonise fresh sedimentary surfaces more readily than other plants. This was presumably because of their abbreviated reproductive cycle, a consistent feature distinguishing modern angiosperms from gymnosperms (Stebbins, 1974). There is little evidence of specialised methods of reproduction or overall plasticity of vegetative structure among angiosperms until the Late Cretaceous and Tertiary (Crepet, 1984; Tiffney, 1984). These features of modern angiosperms are unlikely to have played an important role in the early migrations of angiosperms.

Two hypotheses for the rise to dominance of angiosperms are not supported by the North American fossil record. Early angiosperms are unlikely to have dispersed downhill into coastal regions after prior evolution in mountainous refugia (Axelrod, 1976; Niklas et al., 1980). This view was initially based on 19th century identifications of early angiosperm leaves now known to be incorrect and misleading. Early angiosperms were extinct plants whose leaves and pollen were remarkably similar in distant coastal deposits flanked by geographically-isolated uplands. Angiosperms are consistently found in coastal deposits of Early and mid-Cretaceous age. They are initially absent in inland deposits and regional palynofloras, and remain rare in both well into the Late Cretaceous.

Hypotheses that the early successes of angiosperms were due to specialised coevolution with animals (Regal, 1977) lack support in the North American fossil record. Seeds and fruits of angiosperms clearly adapted for dispersal by animals have not been found in association with Early Cretaceous angiosperm pollen and leaves (Tiffney, 1984).

The geological and other evidence discussed supports the view that angiosperms dispersed widely and rose to dominance by colonising disturbed open spaces in coastal regions (Retallack and Dilcher, 1981a). Although the Early to mid-Cretaceous fossil record of angiosperms is still imperfectly and unevenly understood, the degree to which it can be used to test such hypotheses is a testimony to its quality.

Acknowledgments

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