
A COASTAL HYPOTHESIS FOR THE DISPERSAL AND RISE TO DOMINANCE OF FLOWERING PLANTS

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INTRODUCTION

Few subjects in natural history have attracted so many diverse speculations as the origin of flowering plants. According to the most popular concept of early angiosperms, they were tropical, *Magnolia*-like, evergreen trees, pollinated by insects, their large seeds dispersed by animal ingestion (Takhtajan 1969; Regal 1977). The apparent lack of any fossil evidence for this concept was explained by Axelrod (1952, 1966), who postulated that angiosperms differentiated in tropical uplands, perhaps as long ago as 250 million years (during the Permian period) before invading lowland depositional environments about 110 million years ago (during the early Cretaceous period). Building on some aspects of Axelrod's work and also on a general observation made by Seward (1926, 1933), Raven (1977) suggested that the poleward spread of insect-pollinated tropical angiosperms was aided by climatic warming of coastal areas as a consequence of the dramatic mid-Cretaceous expansion of epeiric seas. Like most other views of early angiosperms, these are based largely on inferences drawn from the comparative anatomy, morphology, and distribution of living plants.

The most encouraging effect of the recent upsurge in research on angiosperm origins is the gathering recognition that the fossil record may furnish critical evidence for the origin and diversification of flowering plants, as it has for understanding the early history of amphibians, reptiles, birds, mammals, and humans. For example, Doyle and Hickey (1976; Hickey and Doyle 1977) have shown that the oldest angiosperm-like leaves and pollen

are not as advanced as Axelrod assumed. They have also found much support for Stebbins's (1974) hypothesis that some early angiosperms were small-leaved shrubs of seasonally arid environments which migrated into disturbed habitats of mesic regions as streamside weed trees.

In our own studies of the diverse and well-preserved fossil plants, soils, and sedimentary environments of the mid-Cretaceous Dakota Formation in Russell County, Kansas, we have been able to extend our observations to early angiosperm fructifications and to a variety of coastal sedimentary environments, in addition to coastal stream deposits. We agree with the general concept of pioneer early angiosperms, as presented by Stebbins, Doyle, and Hickey, but also believe that this view can no longer be reconciled with the traditional concept of upland, *Magnolia*-like ancestral angiosperms. Accordingly, we propose the following new hypothesis for the dispersal and rise to dominance of flowering plants, based primarily on early angiosperm fossils and their ancient environments.

Some of the earliest angiosperms were probably woody, microphyllous plants of the rift valley system joining Africa and South America during the Early Cretaceous. Some of these plants were evidently adapted to pioneering disturbed coastal environments and so were exceptionally widespread during the remarkable transgressions and regressions of epeiric seas during the mid-Cretaceous. In the North American interior, the first angiosperms penetrated from the Gulf Coast to as far north as Alberta, Canada, with the Late Albian marine transgression and sea temperature maximum. Angiosperms became dominant rapidly in temperate paleolatitudes and first appeared in Alaska during the latest Albian regression. As angiosperms became more abundant, characteristic Early Cretaceous mangroves (*Weichselia*, *Frenelopsis*, *Pseudofrenelopsis*), ferns of freshwater coastal swamps and marshes (*Tempskya* and other ferns), and levee plants of coastal streams (*Cycadeoidea*) became extinct, but conifers of floodplains and uplands were less affected. Globally dispersed populations of these pioneering angiosperms were increasingly isolated during the Late Cretaceous by continued continental drift and realignment, by the general retreat of the epeiric seas, by local dispersal of angiosperms into disturbed and depositional environments further inland, and by increasingly specialized coadaptation with local animal pollinators and seed dispersers.

PALEOECOLOGY OF THE DAKOTA FORMATION

The upper Dakota Formation in Russell County, Kansas (Fig. 2.1) was deposited about 92 to 94 million years ago (Obradovich and Cobban 1975) during the early Cenomanian age of the Cretaceous. These are sediments of a complex lagoonal and deltaic coastal plain disconformably overlying the

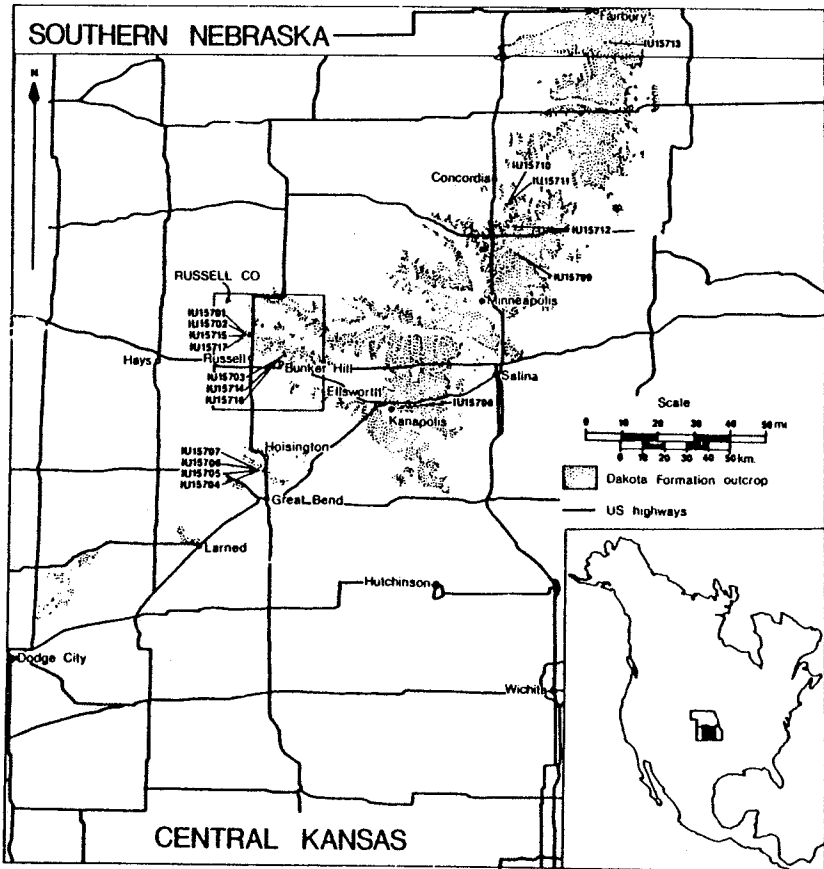


FIGURE 2.1. Mid-Cretaceous fossil plant localities (numbers prefixed by IU) in the Dakota Formation (stipple) in central Kansas and southern Nebraska.

Late Albian marine Kiowa Shale and older Paleozoic rocks, and formed as shallow mid-Cretaceous seas expanded over central North America. As discussed in more detail later in this chapter, angiosperms had only migrated into the interior of the United States a few million years before, during the Late Albian. This was also a time when the initial evolutionary radiation of early angiosperms was just beginning to wane (Doyle and Hickey 1976). Some of the oldest angiosperm leaf and pollen types, many of which became extinct soon after, were still present along with more modern types (Hickey, in press). Angiosperm fossils from the Dakota Formation are thus evidence of a critical phase in the early evolution and dispersal of flowering plants.

Perhaps more important, however, is the excellent preservation and abundance of the fossil plants, including common fructifications, and also the diversity of sedimentary paleoenvironments in the upper Dakota Formation (Table 2.1), which is not equaled by any older localities for early angiosperm fossils yet reported.

Shallow Marine Sands and Muds

The contact between the Dakota Formation and the overlying marine Graneros Shale can be arbitrarily drawn at the top of the highest sandstone, but represents a transition from nonmarine to marine sedimentation through a complex of coastal paleoenvironments. The uppermost sandstones of the Dakota Formation often contain marine fossils (Hattin 1967). One of these north of Russell (Figs. 2.2, 2.3) is a bed of ferruginized, bioturbated sandstone with molds and casts of disarticulated marine bivalves, probably deposited in a barrier or off-shore bar (in the sense of Shepard 1952). The invertebrate fauna of the lower Graneros Shale includes oysters (*Exogyra columbella*), venerid bivalves (*Aphronidina lamarensis*), brachiopods (*Lingula*), and arenaceous foraminifera. The fauna is sparse compared to that found in overlying marine sediments and was probably adapted to more brackish seawater near deltaic distributaries (Hattin 1965). Features such as these indicate that the Dakota Formation and Graneros Shale were produced by continuous sedimentation as the interior seaway expanded eastward into Minnesota.

Angiosperm Debris in Coastal Lagoons

The most diverse assemblages of fossil plants in the upper Dakota Formation are found in the shales of coastal lagoons. Fairly complete impressions of leaves and fructifications are common, along with trails of more thoroughly comminuted plant debris. These plant remains all appear to have been transported some distance from where the plants lived originally and are probably mixed from several former plant communities. *Sequoia*-like conifer shoots are common, but are far outnumbered by angiosperm remains of almost every taxon known from the Dakota Formation.

Remains of this kind are found at Indiana University plant locality IU15702, along the Saline River, near U.S. Highway 281, north of Russell (Figs. 2.2, 2.3). Sandy flaser and linsel interbeds within these lagoonal shales show opposed cross-bedding, indicating some tidal influence. Hattin (1965) found arenaceous foraminifera at two levels in this same unit only 100 m along strike to the north of the most productive fossil plant locality. Siemers (1971) found disarticulated valves of mussels (*Brachidontes arlingtonanus*)

at the base of the shaly unit near the fossil plant locality. Living species of *Brachidontes* are found in nearshore or lagoonal waters of brackish and fluctuating salinity (Siemers 1976; Scott and Taylor 1977), as also are arenaceous foraminifera (Hattin 1965).

At another locality (IU15707) in the clay pits south of Hoisington (Fig. 2.1), fossil plant fragments are scattered through shales near the top of the Dakota Formation with flaser and linsel interbeds, and also a variety of trace fossils. In the same shaly unit, some 150 m south along strike from this is a remarkable accumulation of diverse and complete impressions of plants (IU15706) in the C horizon of a very weakly differentiated paleosol. This fossil soil has only a few roots, scattered ferric mottles, and much relict bedding. The plant fossils were probably a mixed accumulation of plant debris near a lagoonal shoreline only intermittently and sparsely vegetated as the shoreline fluctuated.

As in modern lagoonal systems, salinity probably varied dramatically in time as well as in space, from fully marine salinities more usual near the opening into the sea to completely fresh water common in the innermost reaches of the lagoons (Phleger 1969). This is especially apparent from the paleoecology of invertebrate fossils of the upper Dakota Formation (Hattin 1967; Siemers 1976; Hattin, Siemers, and Stewart 1978). Low-diversity assemblages of bivalves (*Brachidontes* and *Ostrea*) and serpulid worm tubes, probably lived in brackish water, typical of the more inland portions of coastal lagoons. Other assemblages include brackish elements (*Brachidontes*, *Crassostrea*), and also a variety of more typically marine bivalves (such as *Breviarca*, *Cymbophora*, *Geltina*, *Laternula*, *Parmicorbula*, *Tellina*, and *Volsella*), which indicate normal marine salinity common in the outer (seaward) parts of lagoons.

Distributary Sands

The nature of the sandstones of the upper Dakota Formation is the key to understanding the mid-Cretaceous coastal geomorphology of Kansas, and its attendant suite of subenvironments.

The Rocktown channel sandstone has a distinctive sinuous outcrop pattern across Russell County (Fig. 2.2A). This quartz-sandstone lacks fossils and is conspicuously cross-bedded, with foresets dipping mainly to the west (Siemers 1976). It was probably deposited by a meandering coastal stream (Siemers 1976; Karl 1976).

Planar-bedded sandstones are often associated with this and other channel sandstones in the upper Dakota Formation and form a prominent marker horizon throughout Russell County, Kansas (Figs. 2.2B,C, 2.3). Paleocurrents deduced from low-angle cross-bedding and ripple marks in these sandstones are bimodal or polymodal (Siemers 1976), indicating

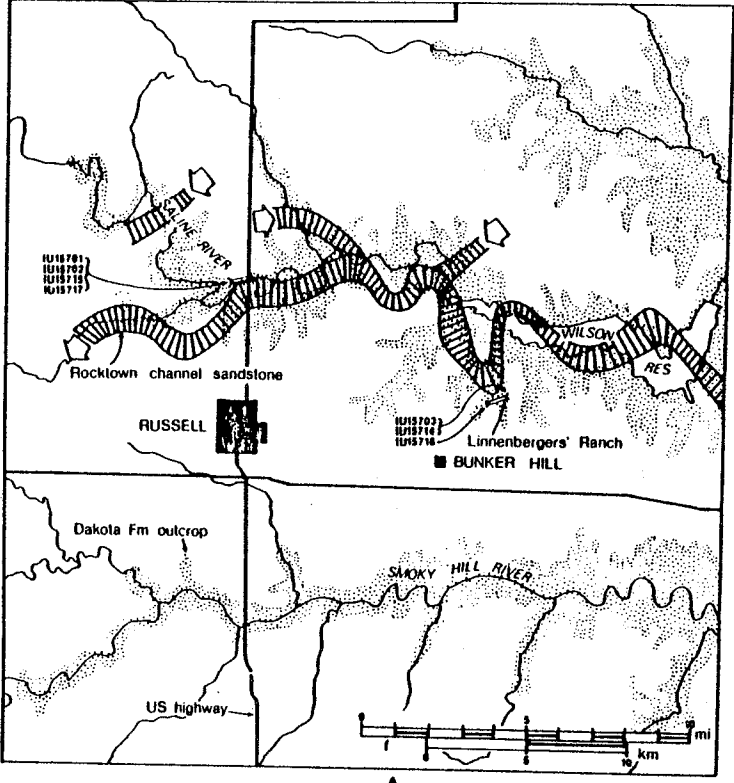
TABLE 2.1: Reconstructed Vegetation as Evidenced by Fossil Plant Assemblages, Soils, and Sedimentary Environments of the Mid-Cretaceous, Upper Dakota Formation in Kansas and Nebraska.

Reconstructed vegetation	plant debris drifted into coastal lagoons	mangroves of tidally influenced distributaries	swamp woodlands of lagoonal margins and interdistributary areas	levee scrub of coastal streams	lake margin scrub	floodplain forest
Sedimentary facies	linsel and flaser bedded shales with diverse trace fossils, arenaceous foraminifera and brackish to marine molluscs	massive gray mudstones and carbonaceous shale adjacent to channel sandstones	coal and carbonaceous shales	epsilon crossbeds with scour-and-fill and ferruginized sandstones	laminated shale with scattered plants and insects	redbeds (superimposed paleosols)

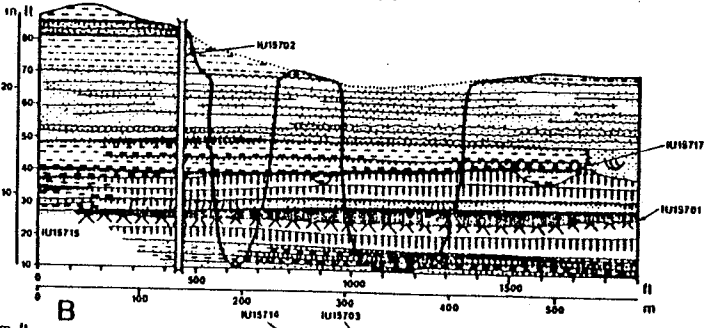
TABLE 2.1 (continued): Reconstructed Vegetation as Evidenced by Fossil Plant Assemblages, Soils, and Sedimentary Environments of the Mid-Cretaceous, Upper Dakota Formation in Kansas and Nebraska.

Paleosols	none	weakly differentiated clayey	coal-bearing (thick organic horizon)	weakly differentiated sandy	weakly differentiated sandy	well differentiated with reddish B horizon
Characteristic fossil plants	very diverse, fragments of nearly all plant taxa found in the Dakota Formation	" <i>Acerites multififormis</i> " of Lesquereux 1892	<i>Magnoliaephyllum</i> sp., <i>Sapindopsis</i> sp., <i>Liriophyllum</i> sp.	<i>Araliopsoides cretacea</i>	<i>Platanus</i> -like leaves and <i>Sequoia</i> -like conifer shoots	none preserved (likely habitat of conifers in drifted plant beds and regional pollen rain)
Representative localities (Fig. 2.1)	Hoisington (IU15706, IU15707), Saline River (IU15702)	Rose Creek (IU15713), Saline River (IU15717, IU15715)	Linnenbergers' Ranch (IU15703, IU15714, IU15716), Saline River (IU15701)	Hoisington (IU15704, IU15705), Kanapolis (IU15708)	Braun's Ranch (IU15709)	Saline River, Kanapolis. (areas where fossil soils have been found)

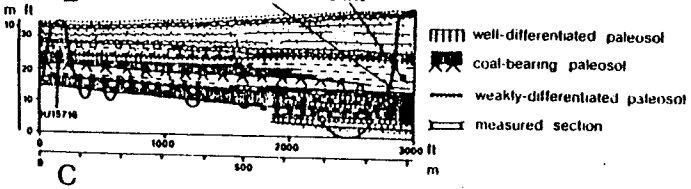
Source: Compiled by the authors.



A



B



C

considerable tidal influence. Most of the sandstone is more or less bioturbated, with trace fossils such as *Planolites*, *Skolithus*, *Arenicolites*, and *Chondrites*. They also contain brackish-adapted fossil bivalves (*Corbicula*) and serpulid worm tubes (Hattin, Siemers, and Stewart 1978).

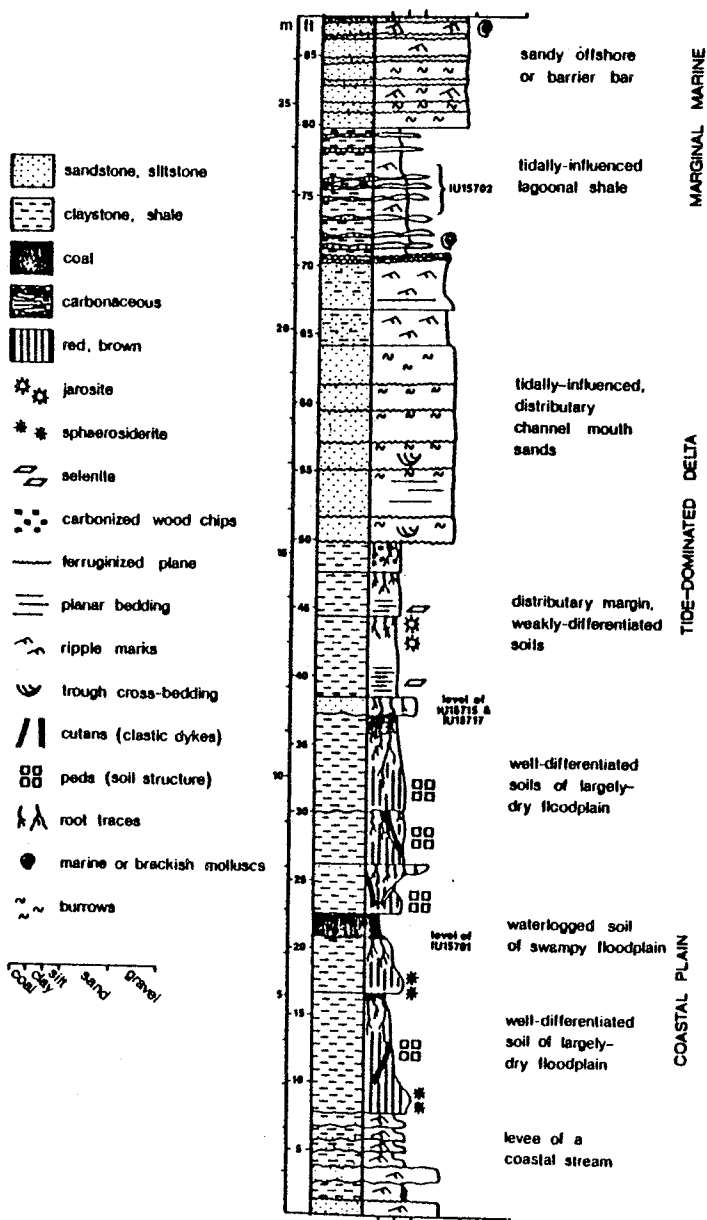
These marine-influenced sandstones were probably deposited in the wide shoaling mouths of distributaries of a tide-dominated delta, like the modern Klang Langat (Coleman, Gagliano, and Smith 1970), Ganges-Brahmaputra, and Mekong deltas (Morgan 1970). This is indicated especially by the close relationship of the channel and marine-influenced sandstones in Russell County, by the westward thickening of the marine-influenced sandstone at the expense of the channel sandstone, and by the restriction of marine fossils in the base of the marine-influenced sandstones to localities where the channel sandstone is also present (Siemers 1971, 1976; Hattin, Siemers, and Stewart 1978). The term *tide-dominated delta* is used here rather than estuary, to indicate that these sediments were part of a depositional landscape and sequence rather than lying on an older erosional land surface. Franks (1980) has interpreted the Longford Member of the Kiowa Formation (underlying the Dakota Formation in Kansas) as an estuarine coast. Such tide-dominated sedimentation was probably widespread in the stable low-relief coasts of the eastern margin of Cretaceous seaways in the interior of the United States.

Tide-dominated deltas may support different plant communities than river-dominated or digitate deltas, like the Mississippi delta (Shepard 1956; Frazier and Osanik 1969) or wave-dominated arcuate deltas, like the Grijalva-Usumacinta delta of Mexico (Thom 1967). The seaward flaring distributaries of tide-dominated deltas are marine-influenced for some distance inland and their margins are usually muddy and well vegetated. The various subenvironments of the tide-dominated deltas of India and Malaya are forested largely by different and diverse mangal communities (Blasco 1977; Chapman 1977b).

Mangal Paleosols of Distributary Margins

Weakly differentiated gray clayey paleosols are common in the uppermost Dakota Formation, associated with marine-influenced and channel sandstones. Many of these soils were probably marine influenced. Some

FIGURE 2.2. Geology of mid-Cretaceous fossil plant localities in the Dakota Formation, in Russell County, Kansas. A. Outcrop of the Dakota Formation and the Rocktown Channel Sandstone in Russell County. Paleocurrents are indicated by arrows. B and C. Geological cross-sections with considerable vertical exaggeration. Present topography indicated by heavy line. Lithological symbols are mostly as in Figure 2.3. B. North of the Saline River, near U.S. Highway 281, north of Russell. C. On Innenbergers's Ranch, northeast of Bunker Hill.



even contain brackish-adapted mussels in life position. Judging from the fossil roots and leaf litter found in these paleosols, they were vegetated by scrubby angiosperms, characterized by "*Acerites multiformis*" (of Lesquereux 1892; Figs. 2.4, 2.22K).

The clearest example of a mangal paleosol was found near Rose Creek, south of Fairbury, Nebraska (locality IU15713). Within this paleosol, Dr. J. F. Basinger found recently a specimen of *Brachidontes*, of normal size (25.5 mm long) and preserved articulated and closed, in life position (Fig. 2.5). This epibyssate bivalve evidently lived for some time in brackish water bathing mudflats near or within a stand of mangrove-like plants. Work is still in progress on the plant remains found in the leaf litter of this paleosol. Leaves of "*Acerites multiformis*" (Figs. 2.4, 2.22K) and radially symmetrical perfect flowers (Figs. 2.6, 2.7) are the most common fossils. A limited diversity of other angiosperm leaves was also found. Fern and conifer fragments are rare.

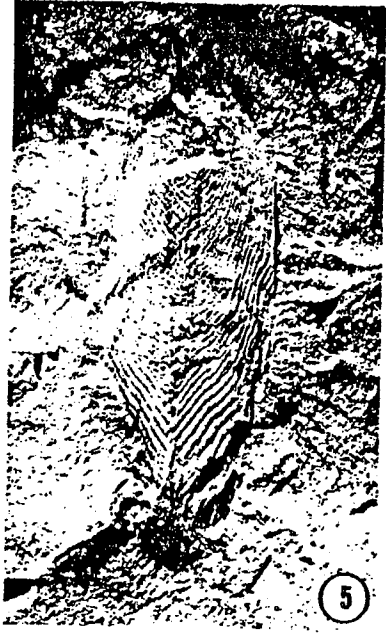
Comparable fossil soils are also found immediately underlying the marine influenced sandstones north of the Saline River and on Linnenbergers's Ranch, near Bunker Hill in Russell County, Kansas (Figs. 2.2, 2.3). The leaf litter of one of these (IU15717) contains small *Araliopsoides* leaves, leaflets of *Sapindopsis*, less common *Liriodendron*-like leaves, fragments of fern and cycadophyte leaves, and angiosperm fructifications. No brackish invertebrates have yet been found in these other paleosols, but like the Rose Creek paleosol, they too have conspicuous jarosite blooms, probably from the surficial weathering of pyrite and marcasite (Battey 1972). The apparent abundance of these sulfides in the leaf litter horizons of these fossil soils is comparable with that of marine-influenced coals (Mackowsky 1975; Carruccio and Geidel 1979). Large selenite crystals up to 7 cm long are also common in the B horizons of these and the Rose Creek paleosol, but, probably, do not indicate Cretaceous marine influence. Pyrite and marcasite have often been reported from drill cores and cuttings through the subsurface Dakota Formation, but gypsum has never been found in them (Rubey and Bass 1925; Landes 1930; Landes and Keroher 1938, 1939; Swineford and Williams 1945; Schoewe 1952; Merriam et al. 1959; Mack 1962; Siemers 1971). The selenite is probably not an original marine evaporite, but more likely precipitated in the present outcrops by ground water acidified by the weathering of iron sulfides (Hattin 1965).

Like the modern mangal, the vegetation of these clayey Cretaceous soils was apparently woody and adapted to fluctuating salinities of marine-influenced distributary margins. The analogy with modern mangroves

FIGURE 2.3. Stratigraphical section and interpreted paleoenvironments of the upper Dakota Formation at fossil plant locality IU15702, north of the Saline River, near U.S. Highway 281, north of Russell.



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should not, however, be taken too literally. There is no evidence in these Cretaceous fossils for such peculiarities as prop roots, air roots, or vivipary, found in a few of the more common genera of modern mangroves. There is no fossil record of any modern mangrove genera in rocks older than Eocene (Tralau 1964; Muller 1970; Churchill 1973). Before the Eocene, woody intertidal plants were very different taxonomically, and in their reproduction and adaptations to salinity, from modern mangroves. Extinct mangroves probably belonged to such diverse groups as lycopods (Retallack 1975), true ferns (Daber 1968), seed ferns (Harris 1966; Retallack 1977b), cordaites (Cridland 1964; Eggert et al. 1979), and conifers (Jung 1974).

Angiosperm Woodlands of Interdistributary Swamps

Many of the coals of the upper Dakota Formation contain large fossil roots, also extending into the underclay. Some of these swamp woodland paleosols also show evidence of abundant pyrite, probably indicating limited marine influence. They evidently formed in interdistributary depressions, in part fringing coastal lagoons and sheltered bays. From plant debris and pollen associated with the coals and from more complete larger remains in nearby subautochthonous accumulations, these swamps appear to have been wooded largely by angiosperms, commonly with leaves of *Magnoliaephyllum*, *Liriophyllum*, and *Sapindopsis*. There is also good evidence that these swamp woodlands had an extensive ground cover of true ferns.

On Linnenbergers's Ranch, near Bunker Hill in Russell County, Kansas (Figs. 2.1, 2.2), coal was mined as recently as 1927, but most of the old adits are now covered by slumps. Our excavations of the productive coal seam revealed numerous large carbonaceous roots in the underclay and also common jarosite blooms. Only indeterminate angiosperm leaf fragments were collected from the underclay (locality IU15716). Palynological preparations made recently from the coal by Michael Zavada (University of Connecticut, Storrs) contain abundant fern spores, common angiosperm pollen, and rare gymnosperm pollen. About 300 m northeast along strike from where the coal was mined, the coal passes laterally into fossiliferous shale filling a swale within levee deposits adjacent to the Rocktown channel sandstone and overlain by marine-influenced sandstone (localities IU15703, IU15714, Fig. 2.2). The fossil plants in this shale appear to have accumulated close to where the plants lived. This is indicated by the low taxonomic

FIGURES 2.4-2.7. Fossils from near Rose Creek, Nebraska (locality IU15713). 2.4. "*Acerites multiformis*" of Lesquereux 1892, a very common leaf at this locality. IU15713-3317. $\times 1.1$. 2.5. *Brachidontes*, a brackish water bivalve preserved in life position alongside plant fossils shown in Figures 2.4, 2.6, and 2.7. IU15713-3303. $\times 2.9$. 2.6 and 2.7. Remains of perfect flowers showing calyces, stamens, and a detached petal. Figure 2.6. IU15713-3429'. $\times 1.5$. Figure 2.7. IU15713-3429. $\times 1.5$.

diversity in our large fossil plant collection from here, by the excellent preservation of organic material in these remains, and by the mixture of leaves, fructifications, and logs, organs which would be sorted quickly during transport by wind and water. Angiosperm remains are most abundant, particularly leaves of *Magnoliaephyllum* (Figs. 2.9, 2.221), *Liriophyllum* (Figs. 2.14, 2.221), and *Sapindopsis* (Fig. 2.8) and a variety of fructifications which, on anatomical grounds, can be attributed to these same extinct angiosperms (Figs. 2.10, 2.11, 2.15). Ferns and *Brachyphyllum*-like conifer shoots are rare. These remains were probably derived from the vegetation of the adjacent coal-bearing paleosols. The composition of this megafossil assemblage is in broad agreement with the palynology of the coal. Many elements of the megafossil assemblage are also common in drifted plant accumulations of coastal lagoons, but few are common in levee vegetation better known from ferruginized sandstones of the Dakota Formation.

Another paleosol with a coaly organic horizon was found with associated angiosperm debris along the Saline River, north of Russell (IU15701, Figs. 2.2, 2.3). Similar paleosols are widespread in the Dakota Formation of Kansas and in other mid-Cretaceous rocks of the North American interior. Coals with autochthonous palynofloras dominated by angiosperms and ferns, and with rare conifers and microplankton have been found in mid-Cretaceous rocks of Arizona, Utah, Oklahoma, and Minnesota (Pierce 1961; Hedlund 1966; Agasie 1969; May and Traverse 1973; Romans 1975). The ferny understory of one of these mid-Cretaceous swamp woodlands has been remarkably well preserved by volcanic ash fall in a coal of the Dakota Formation in Utah (Rushforth 1971). As with coastal peats accumulating in modern deltas (Frazier, Osanik, and Elsik 1978), these swamp woodlands, probably vegetated interdistributary areas with fresh to brackish groundwater.

Sediments and Angiosperms of Coastal Streambanks

As in Cretaceous rocks of the eastern United States (Doyle and Hickey 1976; Hickey and Doyle 1977), there is good evidence in Kansas that scrubby pioneer angiosperms colonized levees and point bars of the freshwater reaches of coastal streams. From the relationships of sedimentary facies exposed in large clay pits, it seems that the leaf impressions of ferruginized sandy flagstones of Kansas, made famous by the pioneering monographs of Lesquereux (1874, 1883, 1892), are the remains of levee vegetation. The regional flora of these sandstones is very diverse, although few species were found at any one locality, perhaps an indication that the remains accumulated close to the living plants. Overall, *Araliopsoides cretacea* (Fig. 2.22G) is the most characteristic species of these angiosperm-dominated assemblages.

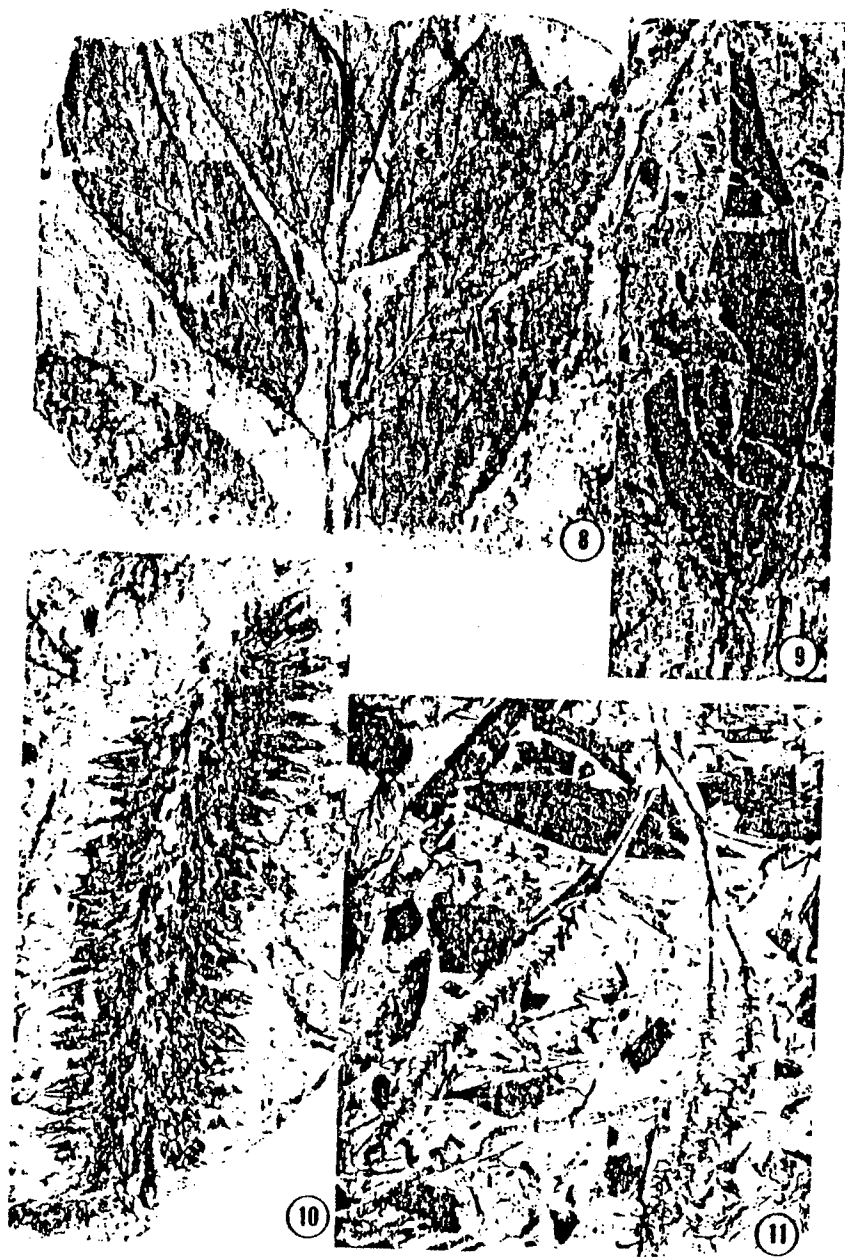
The sedimentary setting of these ferruginized sandstones is best seen in the clay pits south of Hoisington (Fig. 2.1). Underlying the lagoonal shales there are well-exposed deposits of a stream channel and its levee, overlying and partly eroding a well-differentiated floodplain paleosol. At the northern end of the northern clay pit is a trough cross-bedded, quartz sandstone, with numerous fossil logs. This passes southward along strike into a unit of finely interbedded sandstone and shale, cross-bedded at a very low angle and disrupted by several large scour-and-fill structures also containing finely interbedded sandstone and shale. The interbedded unit is an epsilon cross bed (as defined by Allen 1963), typical of levees of meandering streams (Retallack 1977a). This levee deposit includes beds of ferruginized sandstone (locality IU15705) with numerous impressions of *Araliopsoides* and other angiosperm leaves. Some of the shale beds are also fossiliferous (IU15704) with impressions of aquatic leaves, such as *Nelumbites* (Fig. 2.22H). These probably represent plants growing on levee tops and swales, respectively. Fossil soils are never well differentiated within these levee deposits, seldom showing more than small root traces and surficial ferruginization. The angiosperm-dominated levee vegetation was probably scrubby and (geologically) impermanent.

Paleosols, Sediments, and Angiosperms of Lake Margins

Shales of freshwater coastal lakes also contain abundant angiosperms, particularly *Platanus*-like leaves (Figs. 2.12, 2.22F) and their likely fructifications (Fig. 2.13), but also common *Sequoia*-like conifer shoots. Such shales are exposed for a distance of about a mile in gullies and a small quarry on Braun's Ranch, southeast of the intersection of highways 81 and 24, Kansas (IU15709, Fig. 2.1). Unlike the lagoonal shales of the upper Dakota Formation, there is no indication of tidal influence or marine fauna in these shales. Angiosperm leaves and conifer shoots are well preserved in the even shale partings along with fructifications and insects. No rocks were seen to overlie the shales here, but they are probably somewhere in the middle of the Dakota Formation, judging from their location in the middle of the outcrop area of this westerly dipping formation. Underlying the shales are sandstones with carbonized wood chips, low angle cross bedding, and ferruginized bedding planes, probably, the deposit of a lakeside beach. The sandstones overlie a well-differentiated reddish paleosol, formed in a largely dry floodplain. Fossil plants in the shale were probably derived from lake margin communities, as well as the floodplain forests.

Conifer Forested Floodplains

No fossil plant remains other than root traces are preserved in or associated with the thick well-differentiated reddish paleosols characteristic



of the middle Dakota Formation (Figs. 2.2, 2.3). Their clear differentiation into a gray or yellowish A horizon and a reddish brown B horizon indicates that they were forested soils of floodplains in which the water table was more or less permanently at or below about a meter from the surface. As conifer remains are abundant in mixed debris of coastal lagoons and lakes and dominated the regional pollen rain, they were probably prominent in these floodplain forests. The most common megafossil remains of conifers in the Dakota Formation of Kansas are *Sequoia*-like shoots. A number of other studies (Pierce 1961; Hedlund 1966; Agasie 1969; Burgess 1971; May and Traverse 1973; Romans 1975; Hickey and Doyle 1977) also indicate that conifer dominance of inland and floodplain vegetation of North America persisted well into the Late Cretaceous.

Overview

The mid-Cretaceous coastal plain of Kansas consisted of a variety of environments, including offshore and barrier bars, large coastal lagoons, tide-dominated deltas, lakes, and largely dry floodplains. Within this varied landscape, scrubby angiospermous mangal, characterized by "*Acerites multiformis*," evidently colonized distributary margins of tide-dominated deltas. Swamp woodlands extending inland from lagoons and interdistributary bay margins were also dominated by angiospermous trees, with leaves of *Magnoliaephyllum*, *Liriophyllum* and *Sapindopsis*, shading a ferny understory. Scrubby angiosperms such as *Araliopsoides*, and aquatic angiosperms such as *Nelumbites*, vegetated levees and swales of freshwater coastal streambanks. Angiosperms with *Platanus*-like leaves were common around freshwater lakes. However, the largely dry floodplains were forested mainly by conifers.

Angiosperms were most abundant in a variety of unstable depositional environments. Many were probably early successional plants. These conclusions are also supported by the nature of early angiosperm reproductive organs, discussed in the following section.

EARLY ANGIOSPERM REPRODUCTION

Structurally preserved early angiosperm fructifications are few. Our material from the Dakota Formation (Dilcher et al. 1976; Dilcher 1979) is

FIGURES 2.8-2.11. Leaves and unisexual reproductive organs of two mid-Cretaceous plants common at both Linnenbergers's Ranch (IU15703) and Hoisington (IU15706). These organs are attributed to the same original plants on the basis of anatomical evidence and their occurrence together. **2.8.** Leaflets of *Sapindopsis* sp. IU15703-2494. $\times 1.1$. **2.9.** Leaf referred to as *Magnoliaephyllum* sp. IU15703-2455. $\times 0.6$. **2.10.** Pollen-bearing florets of *Sapindopsis* sp. IU15703 2751. $\times 1.75$. **2.11.** Raceme of multifollicular axes of *Magnoliaephyllum*. IU15706-3402. $\times 0.7$.



among the oldest. Vachramev and Krassilov (1979) have also described a compressed fructification from Middle Albian rocks of western Kazakhstan. These few well-preserved fructifications allow a better understanding of a variety of poorly preserved fructifications from Early and mid-Cretaceous rocks. As our investigations into these remains continue, we are forming a concept of early angiosperm reproduction which can no longer be reconciled easily with traditional views.

Pollination

The interpretation of pollination syndromes from the morphology of dispersed pollen grains is difficult. Hickey and Doyle (1977) regarded the exine structure of early angiosperm-like pollen as "strong evidence that the plants which produced them were insect pollinated." On the other hand, Walker (1976) compared this same pollen to that of the living Chloranthaceae, which he regarded as wind pollinated. This is probably not a true dilemma. Both are likely, but only to a degree.

The oldest angiosperm-like pollen to appear in most regions have features which are not optimal for either wind or insect pollination. Plants producing these pollen were probably generalists, pollinated both by wind and by a variety of insects, like living *Salix* and *Rhizophora* (Faegri and van der Pijl 1966; Muller and Caratini 1977; Tomlinson, Primack, and Bunt 1979). This kind of pollination is best suited to early successional plants and communities (Proctor 1978). Fossil angiosperm-like pollen appearing at slightly higher stratigraphic levels show a dramatic adaptive radiation of pollen into additional types adapted more clearly to either wind or insect pollination. Much of the later evolution of angiosperms was, probably, a result of increasingly specialized methods of pollination.

The oldest angiosperm-like pollen appearing in both southern England and the eastern United States (*Clavatipollenites hughesii*) during the Barremian may well have been produced by a generalist. Its size (12 to 30 μm , according to Kemp 1968) is on the boundary of the optimum range for wind pollination (20 to 40 μm , according to Whitehead 1969). The exine of *Clavatipollenites* is tectate-perforate to semitectate, so it is unclear if these are true sculptural elements or whether the depressions between them were filled with substances involved in compatibility mechanisms, in adhering to the stigma or in preventing water loss, as in modern angiosperms (Heslop-

FIGURES 2.12-2.15. Leaves and reproductive organs of mid-Cretaceous plants common at Linnenbergers's Ranch (IU15703), Hoisington (IU15704), and Braun's Ranch (IU15709). These organs are attributed to the same original plants on the basis of anatomical evidence and their occurrence together. 2.12. *Platanus*-like leaf. IU15709-3135. $\times 0.5$. 2.13. *Platanus*-like reproductive axis. IU15709-3165. $\times 0.34$. 2.14. *Liriophyllum* sp. leaf. IU15706-3188. $\times 0.40$. 2.15. Reproductive axis of *Liriophyllum*. IU15706-3084. $\times 0.73$.

Harrison 1976). Even if regarded as sculpture, it is much finer than that usual in the modern pollen dispersed by insects studied by Skvarla and Larson (1965). If *Clavatipollenites* were dispersed in clumps (also argued by Hickey and Doyle 1977), then these remain to be found. Finally, the monosulcus, as in *Clavatipollenites*, is a feature which has developed independently in pteridosperms, *Ginkgo*, cycads, cycadeoids, and angiosperms (Townrow 1960; Wodehouse 1935). As argued by Heslop-Harrison (1976), the monosulcus is largely a mechanism to prevent desiccation, which is more critical for wind pollination than for specialized insect pollination.

Soon after the appearance of the first generalist angiosperm-like pollen in Barremian rocks of England and the United States, angiosperm-like pollen diversified to include types better suited either to wind or insect pollination. *C. rotundus*, first found in Lower Albian rocks of England, is similar to *C. hughesii*, but larger (20 to 32 μm), with a more conspicuous sulcus and more rounded outline (Kemp 1968). These may well have been dispersed by wind. Larger monosulcate grains with a more prominent stellate exine sculpture, but only 29 to 39 μm long, appear in rocks of latest Barremian to Early Aptian age in England (Hughes, Drewry, and Laing 1979). These may indicate a tendency toward more frequent or more specialized insect pollination. The large size (36 to 73 μm) and prominent stellate exine sculpture of *Stellatopollis barghoornii*, first appearing in Middle to Late Albian rocks of the eastern United States (Doyle, van Campo, and Lugardon 1975) are fully comparable with the pollen of modern insect-pollinated angiosperms. Very small (9 to 17 μm), finely reticulate pollen also first appear in Middle to Late Albian rocks of southern England (Kemp 1968) and the eastern United States (Doyle et al. 1975; Hickey and Doyle 1977). Pollen of this size would be deflected easily around the stigma by boundary layers of air flow, and was probably also dispersed by insects.

The first angiosperm-like pollen appeared in Australia during the Middle Albian (Dettmann 1973), and may also have been produced by generalists. The most common of these, *Phimopollenites pannosus*, is tricolporoidate, prolate to subspheroidal, 13 to 28 μm in size and microreticulate, appearing almost smooth in the light microscope. The other of the oldest angiosperm-like pollen, *Rousea georgensis*, is tricolpate, 15 to 24 μm in size and also microreticulate. During the Late Albian there was a greater diversity of angiosperm-like pollen, including likely generalists (*Clavatipollenites* sp., 17 to 26 μm), as well as pollen possibly dispersed by wind (*Phimopollenites aughathellaensis*, 22 to 40 μm) and by insects (*Tricolpites minutus*, 10 to 16 μm , and also found in dispersed tetrads; Dettmann 1973).

A greater variety of pollination syndromes may be represented by the earliest angiosperm-like pollen found in Gabon, west Africa. These include small, weakly-sculptured *Clavatipollenites*, medium-sized moderately sculp-

tured *Retimonocolpites*, and larger stellately sculptured *Stellatopollis* (Doyle et al. 1977). If this is indeed near the center of origin for angiosperms (Hickey and Doyle 1977), there may have been a variety of pollination syndromes there. The generalist pollination of early angiosperms best applies to those which emigrated to achieve one of the most dramatic revolutions of the world flora in the geological history of plants. Unfortunately, further details of these very ancient angiosperm-like pollen have not yet been published.

The generalist pollination of early angiosperms is supported only in an indirect way by known early angiosperm reproductive organs, as most of these are fruits rather than flowers. The oldest structurally preserved angiosperm fructification is a branched catkin-like aggregate of multifollicles (*Caspicarpus paniculiger* Vachrameev and Krassilov 1979) in the axils of leaves (*Cissites* sp. cf. *C. parvifolius*). Although Vachrameev and Krassilov refer this Middle Albian fossil to the Ranunculales, there is no evidence of any stamens, perianth parts, or scars from their previous attachment. We have studied a comparable raceme of multifollicles from the Dakota Formation (Fig. 2.11), for which we have about 100 specimens, many of them beautifully preserved and with a complete covering of cuticle. These also show no evidence of stamens, petals, sepals, or nectaries. Apparently apetalate unisexual multifollicles are the most common Early Cretaceous angiosperm fructifications. These include Late Barremian to Aptian remains referred to as "*Carpolithus*" *virginiensis*, "*C.*" *geminatus*, "*C.*" *sessilis*, and "capsules sp." of Fontaine (1889) from the eastern United States (Dilcher 1979), Early Albian remains referred to as "*Carpolithus*" *ternatus* and "*C.*" *fascicularis* by Fontaine (1889) from eastern North America (geological ages after Doyle and Hickey 1976), and Middle Albian remains referred to as "*Carpolithus*" *karatcheensis* by Vachrameev (1952) from western Kazakhstan (age discussed by Vachrameev and Krassilov 1979). Similar fructifications, apparently also derived from unisexual flowers, are common in Late Cretaceous and Tertiary floras of the North Hemisphere. These have been called *reproductive axes* by Dilcher et al. (1976; Dilcher 1979), "*Carpolithus arcticus*" by Hickey (1977), *Trochodendrocarpus* by Krassilov (1973a, 1977), *Jenkinsella* by Chandler (1961), and *Cercidiphyllum* by Brown (1939, 1962), Becker (1961, 1969, 1973), Chandrasekharam (1974), and Crane (1978). The absence of any evidence for features usually associated with insect pollination, such as nectaries, stamens, petals, and sepals in these fructifications may be because they were pollinated by wind or were generalists.

Other Early Cretaceous angiosperm-like fructifications also lack evidence of nectaries, stamens, petals, and sepals. These are terminal clusters of free follicles, including the Late Barremian to Aptian *Callitris* sp. and the Early Albian *Carpolithus conjugatus* and "indet. plant e" of Fontaine (1889) from eastern North America (Dilcher 1979; geological age from Doyle and

Hickey 1976) and the Albian *Ranunculaecarpus quinquecarpellatus* from the far eastern U.S.S.R. (Samylina 1968; Takhtajan 1969). As in modern flowers (van der Pijl 1972), the radial symmetry of these reproductive organs would have been recognized more easily by animals. This was unlikely to have been a specialized animal interaction, as the most similar modern flower is that of *Cercidiphyllum*, which is wind pollinated (Lawrence 1951).

A variety of angiosperm fructifications has been found in mid-Cretaceous rocks, although diversity is still low. In the Dakota Formation in Kansas, these include elongate multifollicles, catkin-like inflorescences, globular *Platanus*-like fructifications, and five-lobed flower calyxes (Figs. 2.6, 2.7, 2.10, 2.11, 2.13, 2.15; Dilcher et al. 1976; Dilcher 1979). In the Woodbridge Clay Member of the Raritan Formation in the eastern United States, there are terminal clusters of multifollicles, catkin-like inflorescences, and five-lobed flower calyxes (Newberry 1895; geology after Doyle and Robbins 1977). In the Elk Neck Beds of the upper Potomac Group, globular *Platanus*-like fructifications are found (Hickey and Doyle 1977; Doyle and Robbins 1977). In Cenomanian rocks of Czechoslovakia, there are also globular *Platanus*-like fructifications, arranged in spikes and in the axils of leafy shoots, and also spikes of five-lobed flower calyxes (Velenovsky 1889). Some of the catkin-like inflorescences may have been generalists or wind pollinated. Recent studies of one of the five-lobed flower calyxes from the Dakota Formation (Dilcher and Basinger work in progress) have shown that these are bisexual flowers with conspicuous petals and stamens containing very small, weakly-ornamented pollen. These were probably pollinated by insects.

In summary, many early angiosperms, including the first to migrate into many regions, were probably generalists, pollinated by wind and a variety of insects, like many modern early successional plants. Once these pioneering plants were established, their adaptive radiation very soon included species pollinated exclusively by wind or by insects, as well as persistent generalists.

Seed Dispersal

A variety of Early Cretaceous and Jurassic fossil plant propagules have been identified as angiospermous, largely on the basis of their various adaptations for animal dispersal, such as strong spines and pitted or ribbed, thick stony layers. These have been called *Nyxidium*, *Kenella*, *Ievlevia*, *Onoana*, *Lappacarpus*, and *Tyrmocarpus* (by Chandler and Axelrod 1961; Krassilov 1967, 1973a, 1973b; Samylina 1968; Douglas 1969). As also indicated by Wolfe, Doyle, and Page (1975) and by Hughes (1976b), none of these fossils have any definitive angiospermous character. They could

equally be considered propagules of extinct gymnosperms, so they need not be considered further here.

Spines and stony and fleshy layers are not found in any of the Cenomanian and older angiosperm fructifications already discussed. Instead, these appear to have been without exception, dry, dehiscent follicles with numerous small seeds. The Middle Albian *Caspiocarpus paniculiger* is a catkin-like aggregation of hundreds of follicles, each about 1 mm long, and containing about six ovate seeds about 0.8 x 0.5 mm in size (Vachrameev and Krassilov 1979). The follicles are fully cutinized inside and out and appear neither fleshy nor woody. Individual follicles from a Cenomanian fructification in Kansas are similar (Fig. 2.11). This fructification is a raceme of at least four multifollicles, each with 50 to 90 helically arranged follicles. These follicles average 2.0 x 2.7 mm and each contains two to six seeds, averaging 0.8 x 0.5 mm in size. The lax catkin-like form of these and similar fructifications would have been a poor visual attractant to animals. Neither the seeds nor the follicles have stony layers to withstand ingestion by animals. Nor do they have well-developed wings, like the modern winged fruits of *Engelhardia* and *Acer*, adapted to wind dispersal. The large number of small seeds could probably float or be blown considerable distances. They were probably dispersed in several ways, mainly by wind and water.

The apparent generalist pollination, large number of small seeds, wind and water dispersal, and lack of any evident interdependence on specific animal pollinators or dispersers are a syndrome of features found today largely in weeds and other early successional plants (Rorison 1973; Heinrich 1976). Early angiosperms appear to have had a potential for colonizing clearings, open woodland, fluvial and deltaic levees and crevasse splays, and tidal flats.

VEGETATIVE FEATURES OF EARLY ANGIOSPERMS

The woody and small-leaved nature of the oldest angiosperms has long been proposed from studies of the comparative morphology of living plants (Cronquist 1968; Takhtajan 1969). Both these features are also well in evidence from the fossil record of early angiosperms. These additional constraints serve to refine our concept of the habit and habitat of early angiosperms.

Woody Early Angiosperms

Comparison of woody and herbaceous forms within different orders, families, and genera of living plants, has almost universally led to the conclusion that herbaceous angiosperms were derived from woody ancestors

(Takhtajan 1969). The woody nature of most early angiosperms is also evident from their fossils. Most of the early angiosperm fructifications already discussed are attached to woody peduncles. In the Early Cenomanian Dakota Formation of Kansas, abscission scars have been found on several twigs and angiosperm leaves. This indicates that these plants were woody perennials and shed their leaves naturally. It is not yet certain, however, whether leaf fall was seasonal. Fossil soils and root traces in the Dakota Formation also indicate that much of the angiosperm-dominated vegetation consisted of shrubs and trees.

Some possible herbaceous early angiosperm fossils are notable for their antiquity: an Aptian or latest Barremian leafy shoot of *Acaciaephyllum spatulatum* from the eastern United States (Doyle 1973) and a Middle Albian fertile leafy shoot bearing catkins of *Caspiocarpus paniculiger* and leaves of *Cissites* sp. cf. *C. parvifolius* (Vachrameev and Krassilov 1979). Perhaps some early angiosperms were indeed herbaceous or perhaps these are merely young shoots. More detailed studies of these older plants and associated sediments and soils are needed. Herbaceous aquatic angiosperms, such as "*Menispermites*" and *Vitiphyllum*, are common in Albian and younger rocks (Doyle and Hickey 1976; Hickey and Doyle 1977).

As we have demonstrated, the reproduction of early angiosperms was most like that of modern early successional plants, most of which are now herbaceous weedy plants. Perhaps a better comparison is with modern larger woody plants of a similar early successional nature, such as the river colonizing species of *Platanus* (Moore 1972), and *Casuarina* (Beadle, Evans, and Carolin 1972) and the mangrove *Rhizophora* (West 1977).

Microphyllous Ancestors

The earliest angiosperm-like leaves in many regions are smaller than later angiosperm-like leaves in the same region (Vachrameev 1952; Samylina 1968; Krassilov 1973). The weakly organized venation of some of the oldest angiosperm-like leaves has been interpreted by Doyle and Hickey (1976) as evidence that their ancestors had even smaller leaves. They attribute the rapid size increase of early angiosperm leaves to the Early Cretaceous innovation of intercalary meristem in angiosperm leaves, thus enabling the expansion of formerly microphyllous leaves before the regularity of higher venation was determined genetically. It is also likely that most of the blade of parallel-veined monocotyledonous leaves was derived from a phyllode of ancestral plants (Kaplan 1973). Microphyllous was probably only one of a number of features developed in stressful environments during the early evolution of angiosperms. Other features include the closed carpel, reduced gametophyte stages, double fertilization, shortened reproductive cycle, and long dormancy of the seeds (Stebbins 1974).

The selective pressure producing such an hypothetical microphyllous

ancestral angiosperm has been thought to have been a locally or regionally arid habitat (Stebbins 1974; Hickey and Doyle 1977). On botanical grounds, this is at least as likely to have been an adaptation to the physiological aridity of tidally-influenced mudflats and hypersaline lagoons. Considering all the existing geological evidence, discussed in the next section of this chapter, the so-called *xeromorphic bottleneck* in angiosperm evolution (Hickey and Doyle 1977) was perhaps more likely induced by near marine rather than arid environments.

EARLY DISPERSAL OF ANGIOSPERMS

The Early Cretaceous dispersal and rise to dominance of angiosperms was a remarkable phenomenon. In only ten million years they had spread over coastal areas of the earth from the equator to the poles, apparently immune to oceanic barriers, different soils and climates, and competition from preexisting local vegetation, all of which prevented dispersal of many other plants. It is probably not a coincidence that the widespread dispersal of angiosperms coincides with maximum oscillations of epicontinental seas during the Aptian, Albian, and Cenomanian. Widespread changes in sea level would have presented a unique opportunity for pioneering coastal angiosperms with generalized methods of pollination and dispersal. This is indicated especially by the geological record of early angiosperm dispersal.

Evidence of Angiosperm-like Pollen

Palynological research provides a good overview of the early migrations of angiosperms and is in broad agreement with the appearance of angiosperm-like megafossils (as discussed by Axelrod 1959; Teslenko, Golbert, and Poliakova 1966). According to Hickey and Doyle (1977), the earliest angiosperm-like monosulcate pollen dispersed "instantaneously" around tropical Tethyan coasts during the Barremian, as it is found in deposits of roughly similar age in the eastern United States, western Africa, England, Israel, and Patagonia. The first angiosperm-like tricolpate pollen appeared in Brazil and western Africa during the Aptian and may be as old as the Barremian in Israel. It evidently reached England, the eastern United States, and Siberia by the Early Albian, penetrated the North American interior as far north as Alberta, Canada, and also south and east to Australia by the Middle Albian, and finally reached Alaska by the Cenomanian. From the precocious appearance and diversity of tricolpate and other angiosperm-like pollen in Early Cretaceous rocks of Brazil and western Africa, Hickey and Doyle also suggest that this region of west Gondwanaland was the center from which angiosperms dispersed.

These migrations would not be so remarkable if angiosperms were

polyphyletically derived from a number of gymnospermous groups, as Krassilov (1977) has argued. However, the oldest angiosperm-like pollen is similar everywhere, morphologically conservative and low in diversity. This and the orderly evolutionary radiation of angiosperm-like pollen in younger rocks are additional support for the existing floral, morphological, and embryological evidence that angiosperms are monophyletic (Doyle 1978). As a group, these plants seem to have been undeterred by oceanic barriers, such as the deep equatorial Tethyan ocean and several meridional epicontinental seas and embayments. The successful crossing of the Tethys sea by two successive waves of angiosperm-like pollen was most remarkable, as considerations of plate tectonics (Dietz and Holden 1970; Dewey et al. 1973; Spencer 1974), marine faunal interchange (Ager 1967; Dillely 1973; Kauffman 1973; Stevens 1973), and likely oceanic circulation (Luyendyk, Forsyth, and Phillips 1972; Gordon 1973), indicate continuous oceanic separation of the northern from the southern continents during the Early Cretaceous. These early angiosperms also appear to have been little affected by climatic zonation which restricted the distribution of preexisting flora and fauna (Bergquist 1971; Sohl 1971; Vachrameev 1978). Angiosperms probably migrated largely in coastal regions, where the climate was more uniform.

Although the oldest cosmopolitan angiosperm-like pollen are of limited diversity, they became increasingly provincial and diverse during the Late Cretaceous (Brenner 1976). By the end of the Cretaceous, the rudiments of modern floristic provinces and higher taxonomic groups of angiosperms, including several modern families, had already appeared (Muller 1970; Raven and Axelrod 1974; Pacltova 1978; Martin 1977). Even the marine angiospermous seagrasses seem to have originated during the Late Cretaceous (Brasier 1975).

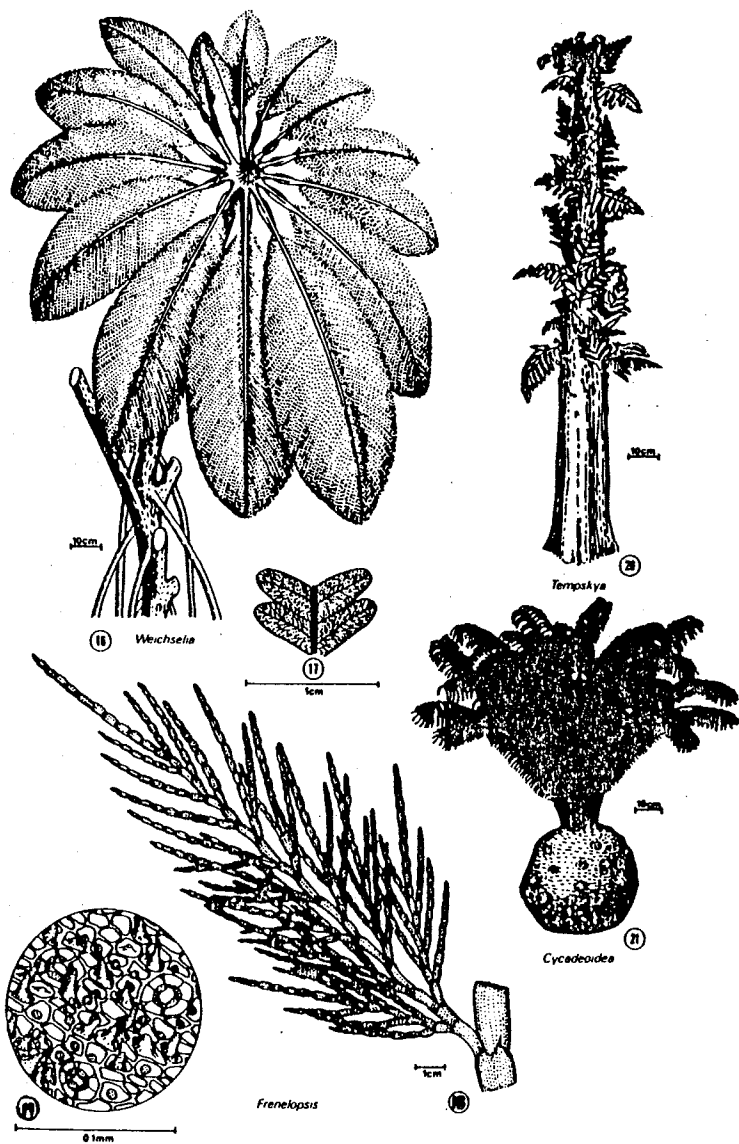
According to our hypothesis, regional differences in the widely dispersed early angiosperms would have been initiated as their range extended along the world's coastlines. Once dispersed, these pioneer angiosperms appear to have adapted to other unstable environments, such as river levees (Hickey and Doyle 1977). These environments may have served as secondary dispersal routes to other disturbed habitats further inland. Continued continental drift culminated in the increased separation of continents by deep meridional oceans (Dietz and Holden 1970), a geographic configuration which has induced provinciality even in modern mangroves (van Steenis 1962). The general retreat of epeiric seas by the end of the Cretaceous (Kauffman 1977a) may have left isolated populations of coastal angiosperms in inland areas. Finally, coevolution of angiosperms with local animal pollinators and dispersers has proceeded to extraordinary levels in modern angiosperms and evidently has been a major factor in the speciation of both angiosperms and animals (Faegri and van der Pijl 1966; van der Pijl 1972).

Early Angiosperms in the Rift Valleys of West Gondwanaland

Several authors (Brenner 1976; Doyle et al. 1977) have argued, from the record of angiosperm-like pollen in the Early Cretaceous rift valley sediments which connected Africa and South America, that regional aridity was a stimulus to angiosperm evolution. However, what evidence there is for regional aridity in west Gondwanaland is not only too late to explain the origin of the oldest angiosperm-like pollen there, but also inextricably linked with marine transgression. The main evidence of aridity is the widespread Aptian evaporites which accumulated in restricted embayments and coastal lagoons as marine transgression proceeded into the rift valley system (Reyre 1966; Reyre et al. 1966; Brognon and Verrier 1966; Hourcq 1966; Reymont and Tait 1972). Angiosperm-like pollen first appear in sediments stratigraphically below the evaporites at levels where there is little evidence of aridity. Just below the evaporites, bisaccate pollen and fern spores become much less abundant at the expense of *Classopollis* and *Ephedripites* (Jardiné, Kieser, and Reyre 1974; Doyle et al., 1977). In Gabon, angiosperm-like pollen becomes spectacularly diverse in rocks underlying and interbedded with the salt (Doyle et al. 1977). It is difficult to determine whether these changes are due to increasing aridity, salinity, or both. At least one genus of the bizarre extinct pollen found in Early Cretaceous rocks of this region, *Classopollis*, is known to have been produced by halophytic conifers whose shoots are referred to as *Frenelopsis* (Figs. 2.18, 2.19) and *Pseudofrenelopsis* (Oldham 1976; Daghlian and Person 1977; Hluštik and Konzalová 1976; Alvin, Spicer, and Watson 1978). Further studies of the palynofloras and further work on the Early Cretaceous megafossil floras (additional to that of Axelrod and Raven 1978; Batton 1965; Plumstead 1969; Berry 1939, 1945) of west Gondwanaland are needed, particularly in view of the possibility outlined by Hickey and Doyle (1977) that this was the center of origin for the angiosperms.

English Coastal Lagoons

Angiosperm-like pollen first appears in Barremian (middle Early Cretaceous) rocks of England within the Weald Clay (Hughes 1976a, 1977; Hughes et al. 1979). At this level, Wealden rocks accumulated largely in estuaries and coastal lagoons of laterally variable and temporally fluctuating salinity, with brackish water fossils, redeposited marine fossils, and interbeds of glauconitic sandstone (Kilenyi and Allen 1963; Allen 1976; Allen et al. 1973; Kennedy 1978). Angiosperm-like megafossils have not yet been recognized in Wealden rocks, although megafossil plants are common on many lower horizons, nor have angiosperm-like pollen been found in older Wealden palynofloras (Hughes 1976a, 1977; Hughes and Moody-Stuart



FIGURES 2.16–2.21. Characteristic Early Cretaceous warm temperate to tropical, coastal plants which became extinct as angiosperms became abundant. 2.16, 2.17. *Weichselia reticulata* (Stokes et Webb) Fontaine in Ward 1899. 2.16. Reconstruction (after Alvin 1971, with permission). 2.17. Detail of pinnules, with characteristic reticulate venation (after Fontaine in Ward 1899). 2.18, 2.19. *Frenelopsis ramosissima* Fontaine 1889. 2.18. Partially reconstructed shoot (after Fontaine 1889). 2.19. Strongly papillate cuticle with thickly cutinized and sunken stomata (after Berry 1910). 2.20. *Tempskya*, a reconstruction. (Source: Andrews, H. N., and Kern, E. M. *Ann. Miss. Bot. Gard.* 34:119–186, 1947, with permission.) 2.21. *Cycadeoidea*, a reconstruction (Source: Delevoryas, T., *Proc. Nth. Am. Paleont. Conv.* 11:1672, 1971, with permission.)

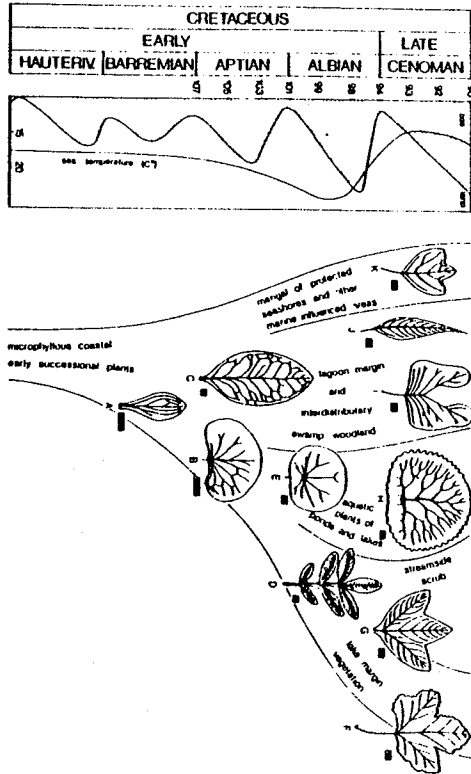


FIGURE 2.22. A coastal hypothesis for the dispersal and rise to dominance of angiosperms, based largely on the geological record of early angiosperms in later Early and earliest Late Cretaceous rocks of North America. The radiometric time scale, marine transgressions, and regressions are based largely on studies on the North American interior (Kauflman 1977a, 1977b). Fossil angiosperm leaves are: A, *Acaciaephyllum spatulatum* Fontaine 1889 (after Doyle and Hickey 1979); B, *Proteaephyllum reniforme* Fontaine 1889 (after Doyle and Hickey 1976); C, *Ficophyllum crassinerve* Fontaine 1889 (after Doyle and Hickey 1976); D, *Supindopsis belviderensis* Berry 1922b (after Berry 1922b); E, *Nelumbites virginensis* (Fontaine) Berry 1911 (after Doyle and Hickey 1976); F, *Platanus*-like leaf (Indiana University collections, Dakota Formation); G, *Araliopsoides cretacea* (Newberry) Berry 1916b (after Lesquereux 1874); H, *Nelumbites* sp. (Indiana University Collection); I, *Liriodaphnium* sp. (Indiana University Collection); J, *Magnoliaephyllum* sp. (Indiana University Collection); K, "*Acerites multififormis*" of Lesquereux 1892 (Indiana University Collection). Scale bars are all 1 cm.

1967). Angiosperm-like pollen reaches its highest concentrations (up to 10 percent in the shallow marine and prodeltaic Atherfield Clay of the overlying Greensand and persists in concentrations somewhat less than 1 percent in overlying marine rocks of Aptian to Albian age (Casey 1961; Kemp 1968;

Hughes 1976b; Middlemiss 1976). It is notable that angiosperm-like pollen first appears rarely in the marine-influenced upper portion of a terrestrial sequence well-known for fossil plant remains, is most common in shallow marine prodeltaic sediments, and persists in younger marine rocks. Considering this timing and observations of Churchill (1973) and Hughes (1976b) on distinguishing coastal vegetation from regional pollen rain into the sea, it is likely that these early angiosperms were most abundant along the coast, but less prominent, if present at all, further inland.

Into the Interior of North America

The coincidence between sea level changes and the appearance and rise to dominance of angiosperms is seen most strikingly in the geological record of early flowering plants in North America.

The oldest generally accepted angiosperm-like remains in North America have been found in the Aptian or perhaps latest Barremian portion of the lower Potomac Group of the eastern United States (Doyle and Hickey 1976; Hickey and Doyle 1977). As the fossiliferous outcrops are about 100 km west of laterally equivalent marine rocks intersected in deep boreholes (Doyle and Robbins 1977), only a limited number of largely fluvial environments are preserved in the outcropping Potomac Group. As in the Dakota Formation in Kansas, the floodplains of the Potomac Group were forested largely by conifers, while angiosperms were most common on fluvial levees (Hickey and Doyle 1977). Even though inland, some of the major changes in the appearance and abundance of fossil angiosperms correlate with sea level changes better documented in deep drill cores of equivalent rocks to the east (Vokes 1948; Stephenson 1948; Doyle and Robbins 1977). Angiosperm-like fossils appear within the Patuxent Formation, at a time of regression after at least two earlier marine transgressions. They became more common and diverse above the contact between the Arundel Clay and the Patapsco Formation, at a time of marked local regression. They became abundant in the Elk Neck Beds and Raritan Formation, during the most pronounced fluctuations of sea level. There are also indications that some large coastal estuaries, like those of the modern mid-Atlantic coast of North America, may have penetrated even as far inland as the outcropping Potomac Group during the Cretaceous. Such an irregular topography would be expected, considering the Early Cretaceous intrusions and underlying rift valley systems of basement rocks revealed by recent deep drilling (Schlee et al. 1976, 1977; Scholle 1977). More direct evidence includes the estuarine grain size distribution of some outcropping sandstones of the Potomac Group (Groot 1952; Glaser 1969) and estuarine molluscan faunas in outcrops of the

overlying Raritan Formation (Wolfe and Pakiser 1971). This may also explain the local abundance of *Frenelopsis* and *Pseudofrenelopsis* at several fossil plant localities and stratigraphic levels in the Potomac Group, such as Trents Reach, Fredericksburg, Fort Washington, and Chinkapin Hollow of Fontaine (1889), Knowlton (1919), and Doyle and Hickey (1976). Almost monodominant assemblages of these species in other parts of the world have been interpreted usually as the remains of estuarine gallery or lagoonal margin mangal (Oldham 1976; Daghlian and Person 1977; Doludenko 1978). It is likely that *Pseudofrenelopsis*, *Frenelopsis*, and early angiosperms dispersed inland along estuaries and coastal streams which deeply dissected vegetation dominated by ferns, cycadeoids, and conifers.

In marine rocks of the northwestern Great Valley of California, fossil plant remains indicate that angiosperms had dispersed right around the southern shoreline and up the west coast of the United States by the Albian (when most of Central America was not yet attached to North America). Most of the supposed angiosperms from these marine rocks (reported by Fontaine in Ward 1905; Diller 1908; Chandler and Axelrod 1961) cannot be considered definitively angiospermous (Wolfe, Doyle, and Page 1975; Hughes 1976b; examination by Dilcher). However, the fragments reported by Fontaine (in Ward 1905) from Elder Creek, west of Red Bluff (locality 23 of Ward 1905; interval 9500-10,000' of Diller and Stanton 1894) probably are angiospermous, although unidentifiable. These are in the Albian or Aptian portion of the succession. Angiosperms are again found more commonly in conglomerates of Late Albian or Cenomanian age in the same region (Diller and Stanton 1894; Murphy 1965; Popenoe, Imlay, and Murphy 1960).

Angiosperms do not appear to have penetrated the interior of North America until the great meridional epeiric sea was established, linking the western Tethyan and the Arctic oceans during the Middle to Late Albian stand of high sea level. The Early Cenomanian and Early Furonian high sea level stands were of successively greater extent and were followed by lesser oscillations of sea level until the sea retreated for the last time from the North American interior by the latest Cretaceous (Kauffman 1977a).

These epeiric seas were characterized by dramatic sea level changes and probably also significant tidal fluctuations. Active uplift and volcanism on the hilly western margin contrasted with the stable coastal plains and low hills of the eastern margin. Kauffman (1977a) has argued that, during times of high sea level, warm currents from the south increased the salinity and temperature of the interior seaway. During low stands the waters were not only colder, but probably also had a low-density layer of brackish water on the surface and near the coasts. The Late Albian transgression and temperature maximum, during which marine temperatures at midlatitudes were

raised as much as 5°C, appear to have been the most critical time for wide dispersal of angiosperms into the North American interior.

In Texas and Oklahoma, along what was then the Gulf Coast, a Middle Albian fossil flora of conifers and cycads, and the likely mangrove, *Freneopsis*, has been found in the Glen Rose Limestone (Daghlian and Person 1977; Perkins, Langston, and Stone 1979). A single loose nodule containing another likely extinct mangrove, *Weichselia* (Figs. 2.6A,B) (Daber 1968; Alvin 1971; Batten 1975) may have come from this or a younger Albian limestone (Berry, 1928). The oldest angiosperm fossils in the region are found in the later Middle Albian, marginal-marine Paluxy Sandstone, and equivalents (Ball 1937; Hedlund and Norris 1968). During the latest Middle to earliest Late Albian, angiosperms appear in fossil floras as rare elements throughout the interior as far north as Alberta, Canada. In both the Beaver Mines Formation in Alberta and in the upper Lakota Formation of the Black Hills of western South Dakota and eastern Wyoming, these pioneer angiosperms, represented largely by *Sapindopsis* leaf fossils, are rare elements of the fossil flora and occur in successions with older Albian fossil floras lacking angiosperms. In the Black Hills, angiosperms appear with *Weichselia* (Ward 1899; geology also discussed by Cobban and Reeside 1952; Gookey et al. 1972; Hickey and Doyle 1977). In Alberta, angiosperms appear soon after a minor marine transgression, evidenced by fossil foraminifera in the lowest Beaver Mines Formation (Bell 1956; Mellon 1967; Stott 1974; Jeletsky 1978). During the Late Albian, angiosperms became common in fossil floras of the Cheyenne Sandstone in Kansas (Berry 1922b; Scott and Taylor 1977), the Fall River Sandstone in the Black Hills (Ward 1899), and the Mill Creek Formation in Alberta (Bell 1956). Only by latest Albian times do the first rare angiosperms appear in the Chandler Formation in the northern foothills of the Brooks Range, Alaska (Scott and Smiley 1979). The Chandler Formation has also yielded older Albian nonangiospermous fossil floras in its lower part and was apparently deposited by a series of large river-dominated marine deltas (Ahlbrandt et al. 1979). Following widespread earliest Cenomanian regression, angiosperms came to dominate coastal depositional environments rapidly, as preserved in the Woodbine Formation of Texas and Oklahoma (Berry 1922a; MacNeal 1958; Kauffman, Hattin, and Power 1977) and in the Dakota Formation in central Kansas (Dilcher et al. 1976; Dilcher, Potter, and Reynolds 1978; Dilcher 1979). Similar dominance was not achieved in Alaska until the Turonian, when the marginal marine Seabee Formation was deposited (Smiley 1969).

Two features of the fossil record of early angiosperms in North America should be noted. Firstly, nonangiospermous mangroves, prominent in Albian and older fossil floras, become rare or extinct as angiosperms become more abundant. Secondly, the introduction and rapid increase in abundance of angiosperms are coincident with episodes of marine influence. This is

most striking in areas where there is a good fossil record of preexisting inland nonangiospermous floras.

Early Cretaceous Coasts of the Far Southeastern U.S.S.R.

Judging from Krassilov's (1973c) description of floral changes in the far southeastern U.S.S.R., the appearance of angiosperms there was in many ways similar to that of the North American interior. The first rare angiosperms appear in the Sutschan Basin at a level where oyster fossils occur for the first time in a largely nonmarine sequence with abundant older nonangiospermous fossil floras. Higher in the sequence, a more pronounced marine transgression is recorded by deposition of the "*Trigonia* sandstones" and overlying, marginal-marine black shales. Plant fossils, including more common angiosperms, "occur occasionally in the *Trigonia* beds as well as in the black shales. More numerous and better preserved specimens come from the fine-grained coaliferous sandstones, 70 m thick, which are transitional between marine and lacustrine deposits" (Krassilov 1973c).

Along the Seashores of Central Australia

In Australia, angiosperm-like pollen first appears in coastal and marine sediments of Late Middle Albian age. As in Early Cretaceous rocks of England, angiosperm-like pollen are more abundant (up to 60 percent of the total palynological assemblage) in nearshore and lagoonal deposits than in marine rocks further offshore (Dettmann 1973). The transgression of Albian epeiric seas into Australia also introduced several cosmopolitan marine mollusks into endemic faunas remaining from older epeiric seas (Day 1969), and coincides with a diversification of newly introduced gleicheniaceae and schizaeaceous fern spores (Dettmann and Playford 1969) and perhaps also, with rising marine temperatures (Stevens 1971). This was a particularly appropriate time for the immigration of tropical coastal vegetation.

The oldest angiosperm-like leaves in Australia are found in Albian sediments of coastal basins of Victoria (Medwell 1954) and Queensland (Walkom 1919). Angiosperm-like pollen have not yet been found in these sediments (Dettman 1963; Dettmann and Playford 1969), but palynological preparations from several interbedded horizons contain abundant microplankton (de Jersey 1960; Douglas 1969). Other Early Cretaceous angiosperm-like fossils (as reported by Douglas 1963, 1965, 1969) cannot be regarded as convincing records of angiosperms.

For the later history of early angiosperms in Australia, both palynological (Dettmann 1973) and megafossil (Berry 1916a; Douglas 1969; Senior, Mond, and Harrison 1978) records are in agreement. Angiosperms become

rapidly dominant following withdrawal of epeiric seas during the Cenomanian.

COMPETITIVE REPLACEMENT OF PREEXISTING VEGETATION

The key elements of the Cretaceous floral revolution were the appearance and rise to dominance of angiosperms and a synchronous decline and even extinction of characteristic earlier Cretaceous true ferns, seed ferns, cycadeoids, and ginkgo-like plants (Delevoryas 1971; Scott and Smiley 1979). The nonangiospermous plants affected most by these changes were those most prolific in lowland and coastal environments. However, conifers which were abundant in upland and floodplain environments (Pierce 1961; May and Traverse 1973), were relatively unaffected in either abundance or diversity by Early Cretaceous invasions of angiosperms (Delevoryas 1971; Miller 1977). The more dramatic overturn of other kinds of plants could be due to competitive replacement of preexisting lowland and coastal plants by angiosperms adapted better to pioneering similar disturbed coastal environments. Such an interpretation is particularly evident from the case histories of four prominent and characteristic Early Cretaceous plants. Each of these became extinct just as angiosperms were becoming common, and each vegetated specific coastal environments.

A Mangrove Fern

Weichselia (Figs. 2.16, 2.17) was one of the most common and characteristic fossil ferns along Tethyan and Proto-Atlantic seashores, from North America to Japan on the north shore and from Peru to north central India on the south shore. It is most common and widespread in rocks of Early Cretaceous age, and a useful index fossil for rocks of that age, although there are a few doubtful records of fragments of leaves and of similar petrified axes from Jurassic and Late Cretaceous rocks (Sahni 1936; Berry 1945; Batton 1965; Jongmans and Dijkstra 1965; Alvin 1971). *Weichselia* is strikingly different from other matoniaceous ferns: its leptosporangia are enclosed tightly by interlocking peltate indusia which form tight soral clusters; its cuticle is exceptionally thick for a fern; its pinnules are strongly recurved; and its many-branched stems bear numerous aerophores and probably formed tangled thickets supported by numerous prop roots (Fig. 2.16). *Weichselia* is found commonly in monospecific fossil associations in marine or near-marine sediments. Batten (1975) suggested that it may have been either a coastal dune-binder or a mangrove. Considering its occurrence in an evidently waterlogged humic paleosol (Daber 1968), the

latter interpretation seems more likely. Thus, *Weichselia* probably formed a pantropical mangal during the Early Cretaceous.

Conifer Mangroves

Frenelopsis (Figs. 2.18, 2.19) and *Pseudofrenelopsis* are fossil genera for distinctive jointed shoots with reduced sheathing leaves. They were evidently woody trees or shrubs (Watson 1977), which thrived along the northern coasts of the Tethys and Proto-Atlantic oceans from Texas to China and also in northern Africa (Boureau 1953; Batton 1965; Jongmans and Dijkstra 1973; Alvin et al. 1978; Vachrameev 1978; Doludenko 1978). They were most common during the Early Cretaceous, but persisted in a few places into the Late Cretaceous (Jongmans and Dijkstra 1973; Alvin 1977; Pons and Broutin 1978). The Late Cretaceous decline of these conifers is seen more clearly from the pollen produced by the same plants, *Classopollis* (Hluštík and Konzalová 1976; Alvin et al. 1978) and *Classoidites* (which differs only in detail from *Classopollis*; Pons and Broutin 1978). As this pollen has also been found in several cheirolepidiaceae conifer cones (Srivastava 1976; Miller 1977), its decline may indicate the decreasing importance of a whole group of plants, as well as *Frenelopsis* and *Pseudofrenelopsis*. *Classopollis* wanes dramatically in abundance in North America after the Aptian (Brenner 1976), when angiosperms first appear. It is extinct almost everywhere by the Turonian (Srivastava 1976), when angiosperms appear to have dominated coastal vegetation. *Classopollis* appears only to have persisted into the later Cretaceous in south central Asia (Vachrameev 1978).

The shoots of *Frenelopsis* and *Pseudofrenelopsis* are strongly vascularized, so evidently belonged to woody shrubs or trees (Watson 1977). They also have a distinctly succulent appearance, compared by several paleobotanists (Zeiller 1882; Reymanówna and Watson 1976) with the extant chenopodiaceous angiosperm *Salicornia*, which is a dominant plant of many modern salt marshes and hypersaline mudflats (Chapman 1977a). The geological occurrence of these shoots also indicates that these plants were coastal halophytes. Their shoots and dispersed cuticles commonly form monodominant fossil associations in near-channel and prodelta sediments. Oldham (1976) has suggested that they may have been comparable to the almost monospecific gallery mangals lining seashores, estuaries, and coastal streams in Florida today. Low-diversity assemblages of *Frenelopsis* or *Pseudofrenelopsis* have also been found in hypersaline lagoonal deposits (Daghlian and Person 1977) and with a variety of marine trace fossils and pectinid bivalves of a coastal lagoon or estuary (Doludenko 1978). A small branch, about 3 cm in diameter, has been found in an almost monodominant assemblage of *Pseudofrenelopsis* shoots, with a perfectly symmetrical

encrustation of serpulid worm tubes (Perkins, Langston, and Stone 1979). This branch was evidently vertical, and probably living, when bathed in brackish water. *Frenelopsis* and *Pseudofrenelopsis* appear to have been the shoots of woody shrubs or trees which colonized estuarine shorelines, and tidally-influenced and hypersaline mudflats throughout the tropical coasts of southern Laurasia and parts of northern Africa.

Ferns of Freshwater Coastal Swamplands

Tempskya is a characteristic and distinctive fern false stem, representative of a number of widespread ferns of Early Cretaceous coastal regions (Fig. 2.20). It is found north of the Tethys and Proto-Atlantic oceans, from Oregon through much of the United States and Europe to southern central U.S.S.R. and Japan (Jongmans and Dijkstra 1965; Banks et al. 1967; Endo 1926). In North America, *Tempskya* was extinct by the end of the Albian (Read and Ash 1961). It evidently persisted in parts of Europe, at least until the middle Late Cretaceous (Jongmans and Dijkstra 1965). *Tempskya* has been found preserved in growth position in pyritic-carbonaceous shale which accumulated in a freshwater swamp (Tidwell, Thayne, and Roth 1976). Petrified *Tempskya* false stems penetrated by angiosperm stems, could also be interpreted as evidence of direct competition (Tidwell et al. 1977). Considering the paleogeography of Cretaceous epeiric seas and Early Cretaceous tectonics (particularly of Oregon and Idaho; Jones, Silberling, and Hillhouse 1977), *Tempskya* appears to have been restricted to coastal plain areas. A widespread and diverse assemblage of ferns evidently thrived in Early Cretaceous freshwater peat swamps of these coastal plains (see Oishi 1940; Pierce 1961; Hedlund 1966; Agasie 1969; Rushforth 1970, 1971; May and Traverse 1973; Hughes 1976a). *Tempskya* was evidently an integral part of these Early Cretaceous fern brakes throughout freshwater coastal swamps of southern Laurasia.

Cycadeoids of Coastal Streamsides

Cycadeoidea (Fig. 2.21) was one of the last of a very important Mesozoic group of gymnosperms. These distinctive squat, silicified fertile trunks are found in Early Cretaceous rocks throughout North America and Europe, from California to Czechoslovakia (Jongmans and Dijkstra 1958). *Cycadeoidea* probably did not survive into the Late Cretaceous. Records of Late Cretaceous *Cycadeoidea* are based on outdated ideas of the geological age of sediments (Andrews and Kern 1947; Read and Ash 1961); on small fragments found loose on the surface, often in areas of marine rocks (Wieland 1906, p. 19, 1916, pp. 121, 122, 1934, p. 94; Leriche 1909); on

fragments lacking the diagnostic cones of *Cycadeoidea* (Chrysler 1932; Endo 1953; Baikovskaya 1956; Wieland 1928b); or on specimens whose locality is uncertain, such as those gained from Navajo Indians and archaeological excavations in New Mexico (Wieland 1928a, 1934; Delevoryas 1959). *Cycadeoidea*, apparently, became extinct just as angiosperms were becoming common in North America and Europe.

Only in a few places has *Cycadeoidea* been collected in place and reported by trained geologists. These are in the Lakota Formation of the Black Hills, eastern Wyoming and western South Dakota (Ward 1899; Wieland 1906, p. 23), in the Cedar Mesa Sandstone near Moab, Utah (Tidwell, Thayne, and Roth 1976) and in the uppermost Patuxent Formation in Maryland (Ward 1905, p. 405). All these were in streamside or levee deposits. This can be seen especially well from the better known occurrences from the Black Hills. Near Piedmont, South Dakota, on the eastern margin of the Black Hills, Ward (1899, p. 564) found cycadeoids in place in a soft yellowish sandstone and sandy shale, with occasional interbeds of reddish clay. Near Matias Peak ("Matties Peak" of Ward, 1899, p. 555) on the southern margin of the Black Hills, the unit (bed 12 of Ward) containing numerous upright cycadeoids is now known to be gray claystone, with numerous interbeds of red and orange-yellow, very fine grained sandstone (from stratigraphic drilling by Silver King Mines, Edgemont, South Dakota, courtesy of Mr. E. Faulkner). Both these occurrences are probably in deposits of levees, unlike the nearby cross-bedded sandstones of in-channel bars, including common large silicified conifer logs (Ward 1899). Unfortunately, the roots of these cycadeoids have never been found to prove that they were in growth position (Wieland 1906, p. 208). It is likely that the clayey material seen under some trunks (Wieland 1906, p. 224) was impervious to silicifying solutions which preserved the rest of the plant. Other evidence that they may have been in place is the rapid silicification of delicate young ovules and embryos in some of these trunks (Crepet and Delevoryas 1972; Crepet 1974). Like modern pachycaul trunks, such as the Australian *Macrozamia* and *Xanthorrhoea*, *Cycadeoidea* would also have disintegrated if transported any distance by streams. However, the fossil cycadeoids are still intact, even though some trunks are in advanced stages of decay, indicated by internal disorganization of tissue, conspicuous insect borings (Crepet 1974), and collapsed crowns ("birds nest" form described by Wieland 1906, pp. 22, 23). Also compatible with a levee habitat for *Cycadeoidea*, is the likelihood that they were self-pollinating (Crepet 1974). This is a common adaptation among pioneer plants of disturbed habitats (Stebbins 1977, p. 55), such as streambanks. *Cycadeoidea* was evidently a prominent plant of coastal streambanks and levees in North America and Europe, which also became extinct as angiosperms were becoming common in similar habitats.

A SCENARIO

The conclusions discussed in previous sections are summarized here into a possible scenario for the dispersal and rise to dominance of angiosperms (Fig. 2.22).

A variety of plants related to the ancestral complex of angiosperms may have flourished in the rift valley systems of west Gondwanaland during the Mesozoic. Some of these plants were evidently microphyllous and adapted to coastal environments. These plants were probably woody, both wind and insect pollinated and their numerous small seeds dispersed largely by wind and water. Such generalized pollination and dispersal strategies, independent of local animal and plant communities, made these plants ideal for long-range dispersal by pioneering fresh sedimentary surfaces of coastal deltas, lagoons, and tidal flats.

As the extent of marine transgression and regression began to increase during the Early Cretaceous, these pioneering early angiosperms or angiosperm ancestors began to disperse along coastlines out of the rift valley system of west Gondwanaland. By the Aptian, these plants had dispersed to a limited extent into tropical Tethyan and Proto-Atlantic coasts. Their opportunist reproduction enabled them to exploit rapidly a variety of unstable coastal depositional environments, such as the shores of estuaries, river levees, coastal lagoons, and swamps. Initial morphological diversification of these plants went hand in hand with their early exploitation of a variety of coastal environments.

The most extensive dispersal of these early angiosperms was largely a result of the remarkable transgression and regression of epeiric seas during the Late Albian and earliest Cenomanian. In the interior of North America, the first rare angiosperms were distributed from the Gulf Coast to as far north as Alberta, Canada, during the Late Albian marine transgression and sea temperature maximum. During the latest Albian regression, they became dominant in the central interior and first reached Alaska. By the end of the Albian they had dispersed widely to Siberia and Australia.

At this time, many common and characteristic Early Cretaceous plants of mangrove (*Weichselia*, *Frenelopsis*, *Pseudofrenelopsis*), freshwater coastal swamp (*Tempskya*), and fluvial levee environments (*Cycadeoidea*) began to wane in abundance and even become extinct as increasing numbers of angiosperms competed more and more effectively for the same coastal depositional environments.

Regional differences in the far-flung initial complex of angiosperms must have been initiated as their range extended to the far corners of the world's coasts. By the end of the Albian, diversification of this once-conservative group of plants was also encouraged by several other factors. Angiosperms were then globally dispersed and living in a variety of different local environments and climates. Angiosperm dominance of coastal stream-

sides was well established and this served as an additional dispersal route to other disturbed and depositional environments further inland. By this time also many angiosperms were becoming increasingly coadapted for pollination and dispersal by local animals. Diversification was further enhanced during the Late Cretaceous by continental breakup and realignment due to continued sea-floor spreading. The general retreat of epeiric seas may have allowed the persistence of coastal vegetation in more inland locations. By the end of the Cretaceous most lowland vegetation was dominated by angiosperms and many major taxonomic groups and floral provinces (evident in modern angiosperms) were established.

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