

EVOLUTION AND EXPANSION OF FLOWERING PLANTS

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FLOWERING PLANTS are a classic example of a group arising late in Earth history and yet achieving very high diversity, abundance, and ecological and morphological variety in a great array of environments and climatic conditions on all continents. Thus, the success of flowering plants raises basic questions about how new lineages become inserted into existing terrestrial ecosystems. To what degree did flowering plants replace older lineages competitively, and to what extent did their expansion depend on large-scale environmental disruption or extinction of older groups? Is the higher taxonomic diversity of flowering plants a consequence of higher rates of speciation, lower rates of extinction, or both? Have flowering plants expanded the total area and range of habitats occupied by terrestrial vegetation? What were the effects of the diversification and spread of flowering plants on the structure of habitats and the types of resources available to terrestrial heterotrophs?

Many "key innovations" have been hypothesized to be responsible for the high taxonomic diversity of flowering plants. These hypotheses tend to downplay the importance of environmental and historical factors, and generally have dealt with flowering plants as a whole. As research on the flowering plant radiation has progressed over the last three decades it has become clear that to better understand the hows and whys of the flowering plant radiation, it is necessary to examine patterns of diversification, abundance, and ecological spread at multiple scales spatially and taxonomically. Despite Darwin's infamous "abominable mystery" of flowering plant origins, the group arose and spread over a substantial interval of geological time. Within the group there is great variation in body plan, reproductive biology, edaphic and climatic requirements,

geographic distribution, and timing of sublineage origin. Explanations of the success of flowering plants based on single key innovations or unique environmental events are likely doomed by this variation. Different subclades of flowering plants have diversified at different times in different places and for different reasons. Generalization in the face of such diversity is difficult, but that is nevertheless what follows.

OUTLINE OF ANGIOSPERM PHYLOGENY

It will be helpful to review briefly the major outlines of angiosperm phylogeny before discussing the paleoecology of the group. Angiosperms almost certainly originated in the Mesozoic (see Sytsma and Baum, 1996 for a critical review of molecular clock studies indicating a Paleozoic origin), but the large number of unique apomorphies of extant angiosperms, and the present low diversity of other taxa of higher seed plants, make it difficult to understand their relationships. Recent phylogenetic analyses tend to support the hypothesis that angiosperms are related most closely to the Gnetales (extant but with only 3 genera), and two extinct groups, the Bennettiales and Pentoxylales (e.g., Crane, 1985; Doyle and Donoghue, 1986a, 1986b, 1987, 1993; Hamby and Zimmer, 1992; Nixon et al., 1994). Gnetales, Bennettiales, and angiosperms have been called "anthophytes" because they cluster their reproductive organs into flower-like structures, and enclose their seeds in more than one layer of tissue (Doyle and Donoghue, 1986b; Crane et al., 1995).

There is no consensus on the sister taxon of angiosperms (Fig. 1). Bennettiales, Gnetales, and Pentoxylales are all known from earlier in the Mesozoic than angiosperms. Gnetalean pollen

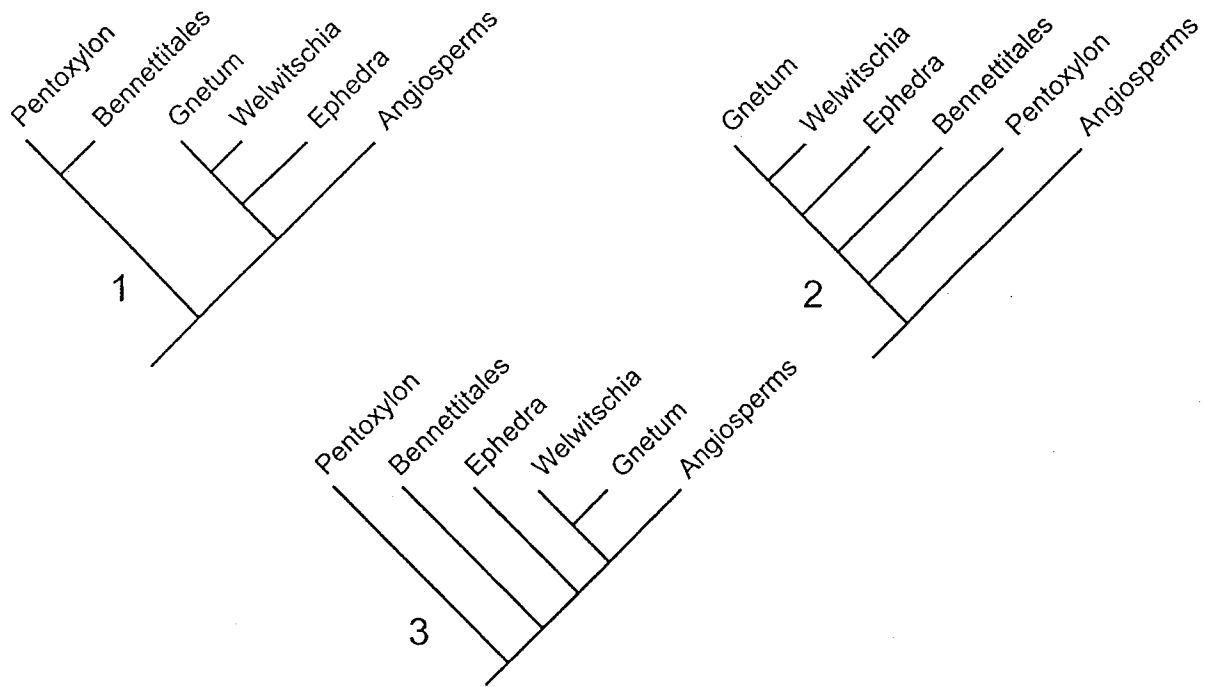


FIGURE 1.—Possible relationships of flowering plants to other anthophytes. 1, Cladogram from Crane (1985); 2, Cladogram from Doyle and Donoghue (1993); 3, Cladogram from Nixon et al. (1994). Phylogenies 1 and 2 imply that the angiosperm stem group existed through most of the Mesozoic, whereas phylogeny 3 is consistent with an Early Cretaceous origin.

occurs from the Triassic through the Cretaceous, and Gnetales may be as old as the Permian (Crane, 1988). Bennettitales are Late Triassic through mid-Cretaceous (Crane, 1987, 1988). Pentoxylales are known from the Early Jurassic and Early Cretaceous (Drinnan and Chambers, 1985; Doyle and Donoghue, 1993). The existence of all the probable sister taxa to the angiosperms by the Jurassic has led to the hypothesis that “stem angioophytes” were present in the early Mesozoic (Doyle and Donoghue, 1993). Stem angioophytes of the Late Triassic and Jurassic might have lacked many of the derived features of the crown group and, thus, be hard to recognize. Possible stem angioophytes include Late Triassic pollen grains with “angiospermoid” features (Cornet, 1989a), and the Late Triassic megafossil *Sanmiguelia* (Cornet, 1989b).

The putative long latent period between the divergence of the angioophyte line from other anthophytes and the radiation of the crown-group angiosperms in the Early Cretaceous seems to require an explanation, and two have been offered (Doyle and Donoghue, 1993). One, the features that lead to high diversity in the crown group were not present in stem angioophytes, and/or two, the diversification of angioophytes was inhibited during the Jurassic by environmental conditions or biotic interactions (Doyle and Donoghue, 1993). Sanderson and Donoghue (1994) have shown there is no increase in branching rate associated with characters that are reconstructed to appear near the base of the angiosperm phylogeny, which may reinforce the idea that many small factors rather than a few key innovations were involved in creating high diversity in crown angiosperms. The

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environmental explanation offered by Doyle and Donoghue (1993) has not been evaluated carefully.

One recent phylogenetic analysis of anthophytes does not require a latent period for angiosperms. Nixon et al., (1994) concluded that the extant gnetalean genera *Gnetum* and *Welwitschia* were the sister taxa to crown group angiosperms, with the third extant gnetalean, *Ephedra*, an outgroup to *Gnetum*, *Welwitschia* plus the angiosperms. Since the first appearance of *Gnetum*-like pollen is approximately coeval with the earliest angiosperm pollen (Brenner, 1996), this phylogeny implies that angiosperms originated in the Early Cretaceous, shortly before their diversification is recorded by fossils.

Advances in molecular systematics and the discovery of many new Cretaceous fossils have begun to clarify major lines within angiosperms. All recent analyses recognize two major monophyletic lineages: the monocots and the eudicots (Crane et al., 1995; Angiosperm Phylogeny Group, 1998). Less clear are the relationships of extant groups that retain a large number of primitive characters, e.g., *Amborella*, *Austrobaileya*, *Calycanthus*, Chloranthaceae, Illiciaceae, Winteraceae, Laurales, Magnoliales, Ceratophyllales, Nymphaeales, and Piperales. Nearly all of these have been proposed as the sister-taxon to the remainder of the angiosperms (Fig. 2). These hypotheses can be divided into two general categories: those that favor some type of woody magnoliid, and those that favor an herbaceous or aquatic sister to the rest of angiosperms. If the sister taxon is a magnoliid, this implies that basal angiosperms were woody plants; if the sister is herbaceous or aquatic, it implies that primitive angiosperms were small, possibly herbaceous plants (see reviews by Crane et al., 1995; Taylor and Hickey, 1996).

Although higher-level systematics of angiosperms remains in flux, some generalizations are likely to hold up. Some of these are summarized in the tree developed by the Angiosperm Phylogeny Group that is reprinted in Figure 3 (APG, 1998). Among eudicots (those with tri-aperturate pollen or pollen derived from this condition), the

Ranunculales (e.g., meadow-rue) appear to be relatively basal, as do Platanaceae or sycamores (grouped with the diverse Gondwanan family Proteaceae in Proteales), Buxaceae (e.g., boxwood), and several other extant clades that shift between basal nodes in various arrangements (e.g., compare APG, 1998 with Magallon et al., 1999). The "core eudicots" consist of two major sublineages: rosids and asterids. Geraniales are basal rosids, and the clade includes plants as diverse as beans (Fabales), oak trees (Fagales), and cucumbers (Cucurbitales). Dogwoods (Cornales) and heaths (Ericales) appear as basal members of the asterid lineage in many phylogenies; higher asterids range from hollies (Aquifoliales) to mints (Lamiales), to potatoes (Solanales), to asters (Asterales). Among monocots, a core derived group "commelinoids" is recognized that includes palms (Arecales), grasses (Poales), gingers (Zingiberales), and Commelinales proper (monkey flowers). Relationships of more basal monocots are not as well resolved, but lower monocots include the lily group (Lilliales) and a number of lineages of aquatic herbs. Most of the major angiosperm lineages depicted in Figure 3 are composed of many families, many of which have hundreds of genera and thousands of species displaying an enormous variety of life forms, reproductive and dispersal biology, climatic tolerances, and life history strategies.

TAXONOMIC DIVERSIFICATION OF CRETACEOUS ANGIOSPERMS

The oldest angiosperm fossils are inaperturate pollen grains from the late Valanginian - Hauterivian of Israel and are similar to those of extant Piperales (Brenner, 1996). By the late Hauterivian, pollen assemblages from Israel contain four types of angiosperms that may represent lineages allied with Winteraceae/Illiciaceae, Chloranthaceae, and monocots (Brenner, 1996). Pollen similar to Piperales and Chloranthaceae predate other types of angiosperm remains by as much as 4-5 million years, with winteraceous pollen appearing next. This pattern

of stratigraphic occurrence is more consistent with the "paleoherb" than the magnoliid hypothesis for basal angiosperms (Taylor and Hickey, 1996), but the difference in appearance times is not so great that it unambiguously favors either alternative (Doyle and Donoghue, 1993; Crane et al., 1995). Friis et al. (1994, 1999) have described diverse assemblages of three-dimensionally preserved reproductive structures from the Hauterivian(?)–Aptian of Portugal. These fusainized flowers, fruits, and seeds include representatives of Chloranthaceae, probable monocots, Nymphaeales, and Magnoliales. Pollen from the same deposits includes monosulcate types (magnoliids, Nymphaeales, or monocots) and tricolpate pollen of eudicots (Friis et al., 1999). If validated as Hauterivian, the tricolpate pollen would be the earliest record of eudicots, although rare dispersed tricolpate pollen has been described from the Barremian of England (Hughes, 1994). Also, if eudicots appeared essentially simultaneously with paleoherbs and magnoliids, this removes stratigraphic support for the paleoherb rooting of angiosperm phylogeny. Other proposed basal branches of the angiosperms, such as *Ceratophyllum* and Calycanthaceae, have first occurrences in the Aptian or Albian (Dilcher, 1989; Friis et al., 1994).

Regardless of which living taxa are most basal cladistically, there is no more than 10–12 million years between the first record of angiosperms and clear documentation of magnoliids, paleoherbs, monocots, and eudicots in the Aptian. During this initial radiation, angiosperm pollen grains were rare components of dispersed palynofloras, and megafossils of angiosperms also were uncommon (Doyle and Donoghue, 1993; Crane et al., 1995; Taylor and Hickey, 1996). The Portuguese mesofossil assemblages reported by Friis et al., (1999) are an important exception to this because they document local angiosperm diversity as high as that seen at many Cenozoic sites. The greater diversity and abundance of angiosperms in mesofossil assemblages than in dispersed pollen assemblages is consistent with the idea that early angiosperms are under-represented in most palynofloras because

they were pollinated by insects (Friis et al., 1999). The general rarity and small size of megafossil remains of early angiosperms is consistent with the plants being small, but their abundance at some Portuguese sites indicates they were, at least, locally common (Friis et al., 1999).

At both local and global scales, angiosperm diversity increased dramatically between the Albian and the Cenomanian (Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989, 1990; Lupia et al., 1999). The number of angiosperm species known from megafossils increased by approximately three-fold from the Albian to the Cenomanian (Fig. 4; Lidgard and Crane, 1988), and the mean percentage of taxa in local assemblages also increased rapidly. Recent analyses of pollen data from North America show the proportion of taxa that are angiosperms increasing most sharply at a somewhat later time—from the Cenomanian to the Campanian (Fig. 5; Lupia et al., 1999). During the interval that angiosperms were increasing as a proportion of taxa, ferns were declining and gymnosperms were holding more or less even.

The increase in angiosperm taxonomic diversity also was accompanied by the appearance of the major sublineages within the eudicots (Magallon et al., 1999). By the Maastrichtian there is pollen or megafossil evidence for relatively derived lineages such as Malvales, Urticales, Cornales, Aquifoliales, Apiales, Zingiberaceae, and Graminae (summarized by Muller, 1981; Collinson et al., 1993; Wing and Boucher, 1998; Magallon et al., 1999). However, the most derived asterid orders, such as Dipsacales, Gentianales, Lamiales, Solanales, and Asterales, did not appear until the Eocene or later. These are among the most diverse extant clades of angiosperms, and include both herbaceous (e.g., Lamiaceae [mints], Asteraceae [composites]) and woody (e.g., Rubiaceae, Apocynaceae, Bignoniaceae) plants. Poorly represented, though probably present, in the Cretaceous fossil record are Malvales and Fabales, which are among the most diverse orders of woody plants.

So many Cretaceous angiosperm fossils with affinities to extant families have been described in the last 15 years that it is quite possible that most

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angiosperm families will eventually be found to have originated in the Cretaceous. This is especially true because isolated fossil organs generally have not been assigned to extant families unless they have features that clearly demonstrate affinities to extant genera within a family (Collinson et al., 1993).

DEPOSITIONAL ENVIRONMENTS AND ABUNDANCE OF CRETACEOUS ANGIOSPERMS

The Valanginian-Hauterivian Helez Formation of Israel, which preserves the earliest angiosperm pollen, consists of shales, aeolian sands, limestones and dolomite deposited in near-shore marine and terrestrial environments; the pollen-bearing

sediments probably were deposited in lagoonal or fluvial settings (Brenner, 1996). Angiosperms are represented by fewer than two grains per thousand, but the rarity is not associated with poor preservation or marine conditions and probably indicates that the parent plants were insect pollinated (Brenner, 1996), or rare. Brenner (1996) inferred the climate of the earliest angiosperms to be humid tropical based on co-occurring conifer and fern palynomorphs.

A more geographically extensive record of early angiosperms comes from Barremian through Cenomanian sediments in the South Atlantic Rift sequence (Doyle et al., 1982). These rift sediments contain large amounts of evaporites, consistent with a dry equatorial paleoclimate (Ziegler et al., 1987),

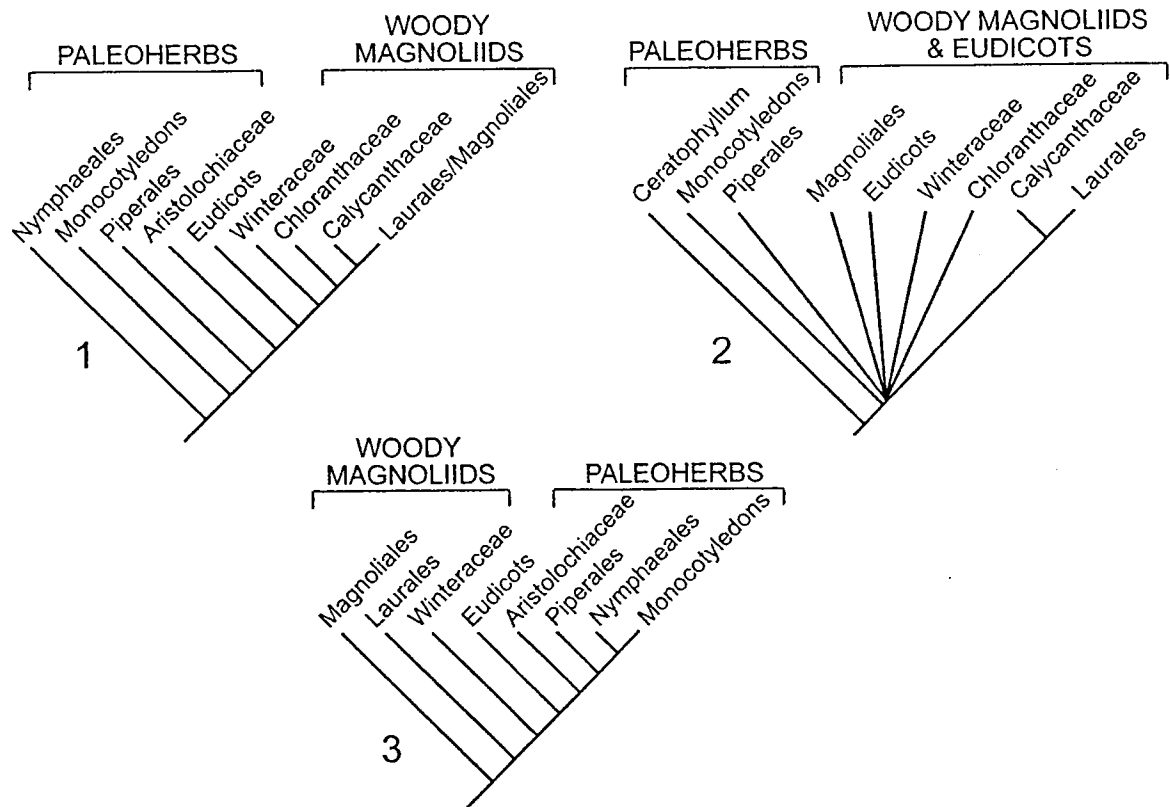


FIGURE 2.—Alternate phylogenies for major clades within angiosperms. 1, cladogram from Doyle et al., (1994); 2, Cladogram from Albert et al., (1994); 3 Cladogram from Doyle and Donoghue (1993). Magnoliid rooting as in 3 implies basal angiosperms were woody, whereas rootings in 1 and 2 imply basal angiosperms were herbaceous.

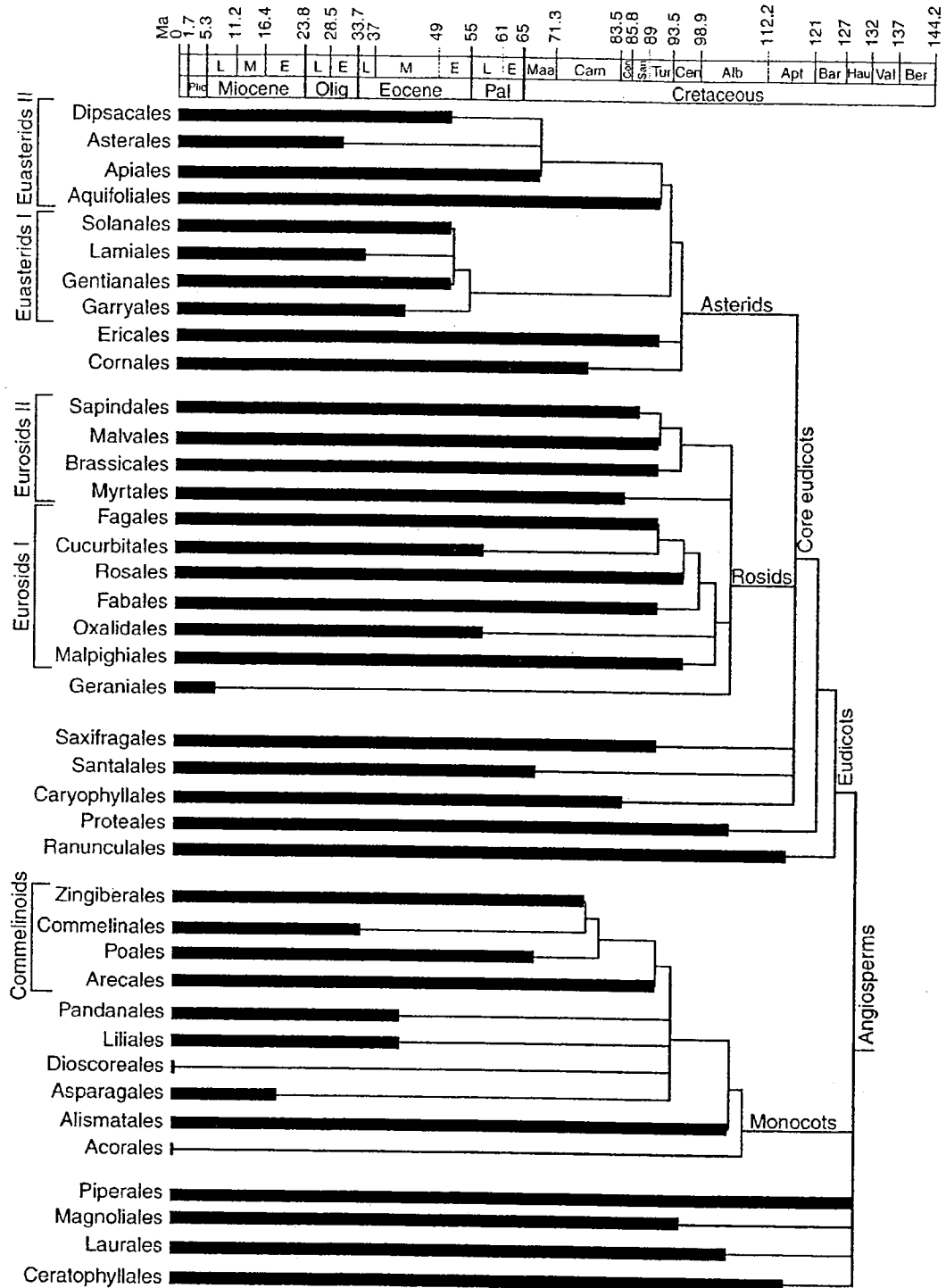


FIGURE 3.—Relationships of major angiosperm orders according to APG (1998). Black bars extend up from the earliest fossil record attributed to the order. Oldest fossil records are taken from Muller (1981), Collinson et al. (1993), and Wing and Boucher (1998).

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but the angiosperms in the Barremian part of this sequence are associated with sedimentary and palynological indicators of mesic rather than dry conditions (Doyle et al., 1982). By the Late Aptian, some species of *Clavatipollenites* (similar to extant Chloranthaceae) did occur in evaporitic sequences (Doyle et al., 1982). Both the Israel and West Africa records are consistent with angiosperms initially evolving in seasonal or moist tropical climates, then expanding into more arid climates within about ten million years.

The early Aptian-Cenomanian Potomac Group of eastern North America contains the earliest angiosperm megafossils with well-documented sedimentary context (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Taylor and Hickey, 1996). Angiosperms are rare, local, and undiverse in the early Aptian, and are found only in medium-to-very-fine sand with primary stratification indicating within- or near-channel deposition.

By the middle to late Albian, Potomac Group palynofloras contain a diversity of tricolpate pollen and angiosperms that are locally abundant in some leaf assemblages. Angiosperms also occur in a somewhat wider variety of facies (Doyle and Hickey, 1976). The first abundant angiosperm leaves are *Sapindopsis* and *Araliaephyllum*, genera in the Platanales (lower eudicots). As is true of angiosperms lower in the Potomac sequence, these genera are associated with fluvial deposits indicative of channel margin environments, and/or with burned plant material (Doyle and Hickey, 1976). Platanales are absent from backswamp deposits of this age, but floating aquatic angiosperms similar to extant Nymphaeales (water lilies) are found in depositional settings that indicate standing water. The increased range of depositional environments that preserve angiosperms suggests they occupied a slightly wider range of habitats than earlier in the Cretaceous. Abundant angiosperm remains in some channel and pond deposits suggest they were, at least, locally abundant in well-lit and well-watered settings that supported few other woody plants. The abundance of platanoids in stream margin environments continued throughout the Cretaceous

and Cenozoic, and is still seen in living *Platanus*, a striking example of habitat fidelity in a long-lived lineage.

By the late Albian-Cenomanian, pinnately compound leaves of *Sapindopsis* are abundant in fluvial channel sites or fusain-rich sediments (Doyle and Hickey, 1976; Hickey and Doyle, 1977). Platanoids are also common in channel deposits. Some latest Albian and early Cenomanian floras from finer-grained Potomac Group sediments have a moderate diversity of simple, pinnate leaves that may signal the importance of magnolialeans in stable flood basin areas (Doyle and Hickey, 1976). Upchurch et al. (1994) recognized three megafloreal assemblages consistent with the sedimentological observations of Hickey and Doyle (1977). Platanoid-dominated assemblages were found in coarse-grained channel deposits and contained few other floral remains. *Sapindopsis* leaves occurred as mono-specific assemblages in slightly finer-grained crevasse-splay or abandoned channel deposits. Laminated clays deposited in abandoned channels were dominated by nearly *in situ* floating aquatic *Nelumbites* and a variety of conifer foliage, with rarer magnolialean or lauralean leaves derived from surrounding floodplain trees.

Angiosperm pollen and megafossils are regular members of assemblages in the mid-latitudes by the middle of the middle Albian, and are widespread by the late middle Albian except in the far north; however, angiosperms are not abundant in many of these floras (Crabtree, 1987). One flora from 38° N paleolatitude that does show high dicot abundance is a dispersed cuticle assemblage from a coal in the upper Albian of eastern Kansas (Upchurch, 1995). Upchurch interpreted the regional vegetation as conifer-dominated, with abundant herbaceous or small woody dicots (Chloranthaceae and Laurales) in areas of the peat that had burned recently.

The importance of magnoliids on more stable substrates is reinforced by the Cenomanian Rose Creek flora from Kansas. This assemblage is derived from fine-grained Dakota Group

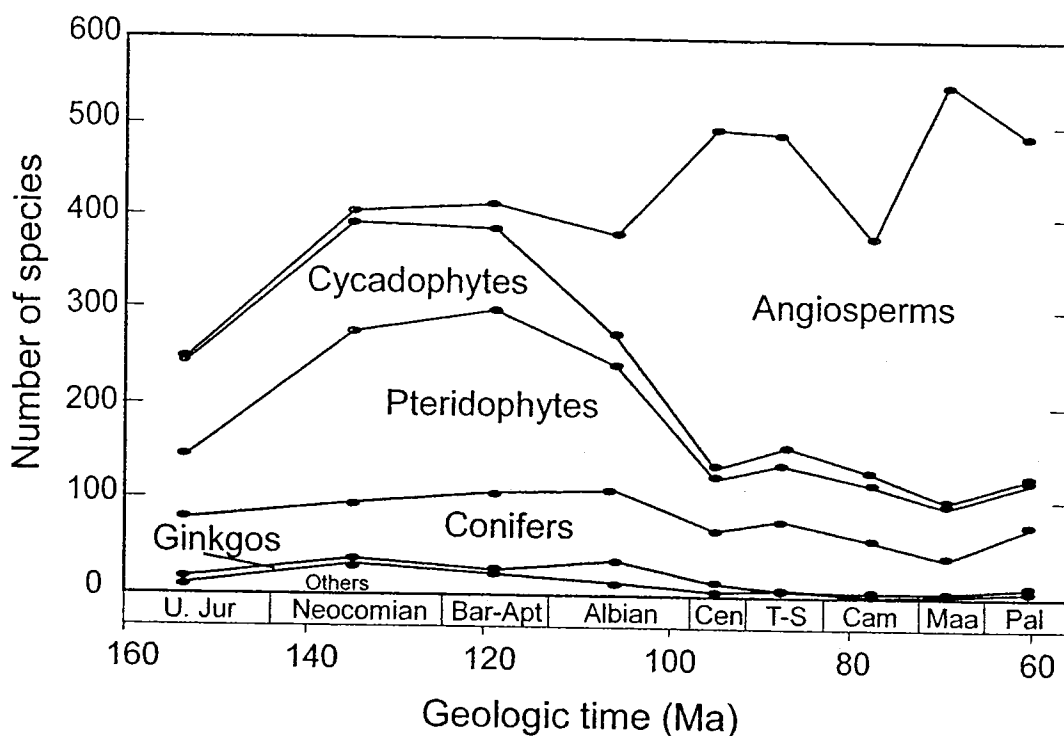


FIGURE 4.—Changing diversity of plant higher taxa through the Cretaceous modified from Lidgard and Crane (1988).

sediments; magnoliid or magnoliid-like leaves constitute 70% of the angiosperm species and 90% of the angiosperm specimens (Upchurch and Dilcher, 1990). 85 % of the leaf cuticle fragments in an associated lignite are lauralean (Upchurch, 1995). Rosid and *incertae sedis* dicot leaves are 20-30% of the angiosperm species and represented by few specimens. This contrasts sharply with the dominance of leaves of platanoids, other basal eudicots, and probable eurosids in the sandier Dakota floras described by Lesquereux (1892). Retallack and Dilcher (1981, 1986) recognized the same distinction: stream-side and lake margin assemblages dominated by platanoids, and swampier environments that have a higher abundance of magnoliids.

At high northern latitudes the tendency for angiosperm dominance to be low, except in channel-related or other disturbed environments, continued into the Late Cretaceous. Cenomanian assemblages from the North Slope of Alaska have

moderately abundant platanoids and rosids in channel and channel margin settings, but the distal floodplain areas were dominated by conifers, ferns, cycadophytes, and ginkgos (Spicer, 1987). Lower Campanian floras from Alberta and Montana contain abundant araucarian, taxodiaceous, and cupressaceous foliage, although dicots are the most diverse element of the flora (Crabtree, 1987). Swamp facies were dominated by taxodiaceous and cupressaceous conifers. Palms (commelinoids in Fig. 3) were abundant in the channel margin facies, and the levees and crevasses were dominated by dicots, especially trochodendroids (eudicots), cercidiphyllids (Saxifragales), and hamamelids (rosids). Other dicots constitute only about 10% of the leaves. Campanian leaf assemblages from Utah also have a greater dominance of angiosperms in channelmargin than in peat-accumulating swamp settings, where conifers and ferns were more abundant (Parker, 1975).

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Even in the early Maastrichtian of northern North America, some floras show a clear pattern of dicot dominance linked to disturbed sites. *in situ* assemblages from the Meeteetse Formation in central Wyoming are dominated by gleicheniaceus fern foliage where the substrate was highly organic, and dicots (chiefly platanoids, rosids, and basal eudicots) were abundant only near channels (Wing et al., 1993). Overall, although angiosperms were 80% of the species, they were only 12% of the material identified on bedding planes (Wing et al., 1993; Tiver et al., 1994). The one abundant angiosperm in these deposits was a species of coryphoid palm, perhaps indicating palm thickets growing on muck soils in this deltaic setting. An approximately coeval flora from southern Wyoming occurs in an ashfall within a coal, and is similar to the Meeteetse floras both in species composition and in dominance by non-angiosperms (Tiver et al., 1994). Megafloras from the Late Cretaceous of Alberta also are dominated by conifers (McIver and Aulenback, 1994). The early Maastrichtian pattern may have changed by the end of the Cretaceous; late Maastrichtian megafloras from North Dakota are dominated by dicots, with ferns and taxodiaceous conifers making up more than 5% of the specimens at only 2 of 15 sites (Johnson, 1992). The dominant dicot groups remained platanoids, cercidiphyllids, trochodendroids, and rosids. Well-preserved leaves were derived largely from channel and near-channel sedimentary environments (Johnson, 1992).

In contrast with the northern middle and high latitudes, late Campanian-early Maastrichtian floras from farther south in New Mexico (about 38° N paleolatitude) show dicots were dominant across a wide variety of flood plain habitats with the exception of some highly organic distal swamp environments (Boucher and Wing, 1997; Boucher et al., 1997). Only floras preserved in ashfalls within coals are dominated by ferns. Fossil wood also shows the importance of dicots in this area; fossil dicot wood is more abundant than coniferous wood, and some dicot trunks are 0.5-1 m in diameter (Wheeler et al., 1995), showing that dicots were large plants that dominated floodplain vegetation across a range of habitats. Late

Maastrichtian megafloras and dispersed cuticle assemblages from northern New Mexico are also dominated by angiosperms (Wolfe and Upchurch, 1987; Upchurch, 1995). Although ferns are absent from the cuticle assemblage, their importance in peat substrate vegetation may be indicated by the 25% abundance of their spores in coals (Upchurch, 1995). As with the Meeteetse megafloras, however, much of the angiosperm abundance was made up by just a few types of monocots (44% of fragments), while the much more diverse eudicots made up only 18% of the cuticle fragments across all samples (Upchurch, 1995). Magnoliid dicots were 38% of the cuticle sample and more than half the species (Upchurch, 1995).

The pattern of lower angiosperm-megafoossil abundance at higher latitudes is seen in mirror image in the southern hemisphere. Most Albian and Cenomanian-Campanian floras on the Antarctic Peninsula are dominated by ferns and/or conifers (Truswell, 1990; Rees and Smellie, 1989; Chapman and Smellie, 1992; Cantrill, 1996; Cantrill and Nichols, 1996). Detailed paleoecological study of *in situ* late Albian megafloras from Alexander Island near the Antarctic Peninsula has demonstrated the presence of fern thickets with subdominant conifers (Cantrill, 1996); angiosperms occurred in significant abundance (40% of specimens) at only three localities out of 76 (Cantrill and Nichols, 1996). These three localities offer sedimentological evidence of overbank deposition adjacent to channels (Cantrill and Nichols, 1996). At somewhat lower paleolatitude, the Cenomanian Winton Formation flora from the Eromanga Basin in central Queensland, Australia, is derived from a low-energy fluvio-lacustrine setting. The flora is mixed ferns, conifers, Pentoxylales, and angiosperms, and seven of the eight angiosperm taxa are of hamamelid (eudicot) affinities (McLoughlin et al., 1995).

Angiosperm-dominated palynofloras and megafloras are not common at high southern latitudes until the Campanian-Maastrichtian (Truswell, 1990; Dettmann and Jarzen, 1988; Askin, 1988;

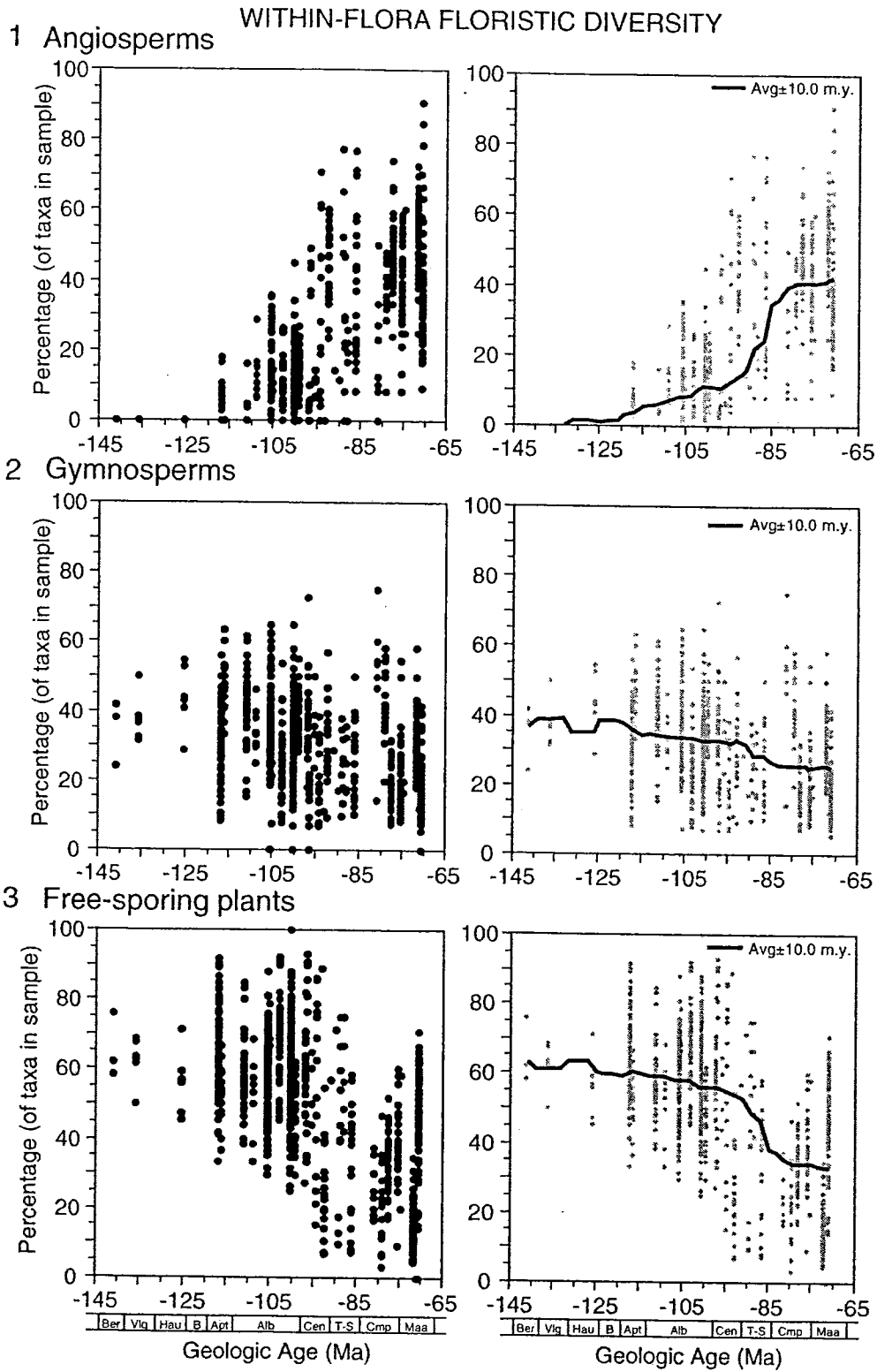


FIGURE 5.—Proportional diversity of major groups in North American palynofloras. Reprinted with permission from Lupia et al. (1999).

Zastawniak, 1994; Hill and Scriven, 1995). A probable Campanian megaf flora from King George Island off the Antarctic Peninsula is dominated in both species and specimens by a range of dicots including probable Fagaceae, platanoids, magnoliaceans, and lauraceans (Zastawniak, 1994), although the lack of information on depositional environment and the small sample size of only 102 specimens casts doubt on the generalizability of these observations. Santonian-Maastrichtian pollen and spore assemblages from southeast Australia and Antarctica have been interpreted to represent tall, open forest containing conifer and angiosperm canopies with shrubby understory angiosperms, cryptogams, and waterlogged sites dominated by pteridophytes (Specht et al., 1992).

Although the number of detailed studies of the sedimentary context of Cretaceous angiosperms is still relatively small, preliminary generalizations can be made. Early Cretaceous angiosperms were clearly tied to disturbed sites. By the late Albian or early Cenomanian, the magnoliid clades, in particular, had established themselves in some abundance on more stable floodplain sites. Rosids, platanoids, and trochodendroids appear to have remained centered in disturbed, fluvial settings. The distribution of angiosperms across gradients of soil type and disturbance frequency also interacted with their distribution on a larger scale. At lower latitudes, flowering plants not only appeared and became abundant earlier, they also were more important in more kinds of habitats, particularly those that were less disturbed. It is worth noting that even now angiosperms are less important in the vegetation of high latitudes and altitudes than they are in areas of warmer climate. The slow increase in angiosperm abundance at higher latitudes in the Cretaceous clearly indicates that they were limited by aspects of their biology that changed through evolution, rather than by slow rates of migration caused by physical barriers.

ECOMORPHOLOGY OF CRETACEOUS ANGIOSPERMS

So far the taxonomic diversification of flowering plants has been recapped, and examples have been provided of how they were deployed on local landscapes based on their distribution and abundance in various sedimentary environments. A third way of assessing the flowering plant radiation is to examine how their ecomorphological traits change through time. The chief areas of plant biology that can be evaluated through morphological characteristics of fossils are pollination (from pollen and flowers), dispersal (from fruits and seeds), size and growth rate (from wood), and photosynthesis/water use efficiency (from leaves).

Pollination.—Insect pollination is thought to have been widespread in angiosperm relatives such as Gnetales and Bennettitales (Crepet et al., 1991), and even the earliest known angiosperm pollen is of a size and has sculptural characteristics that are consistent with insect pollination (Doyle and Hickey, 1976; Brenner, 1996). The earliest known flowers with tricolpate pollen grains (eudicots) have pollen that is too small for effective wind pollination (Friis et al., 1994; Crane et al., 1995). Furthermore, pollen found *in situ* in one Early Cretaceous flower has a substance like the pollen kitt that sticks pollen together in some living insect-pollinated plants (Crepet et al., 1991). Insect pollination in early angiosperms was not associated with morphological specializations for particular insect vectors. Barremian-Albian flowers are small, simple, and tend to be aggregated into inflorescences (Taylor and Hickey, 1990; Crane et al., 1986, 1989; Crepet et al., 1991). No specimens are known that indicate large numbers of floral parts or showy bracts or petals to attract insect pollinators; Early Cretaceous angiosperms probably attracted pollinators with pollen and possibly brightly colored or odoriferous connective tissue in the stamens (Crepet et al., 1991). Even the early relatives of some wind-pollinated extant forms like Platanaceae may have been insect pollinated.

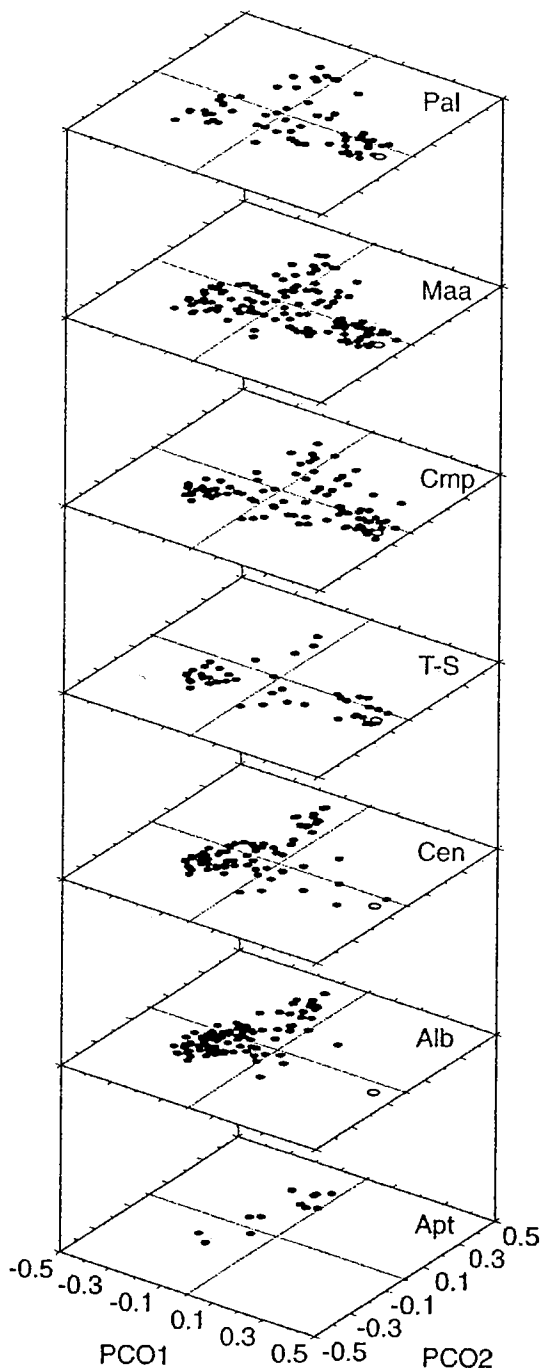


FIGURE 6.—Changes in angiosperm pollen morphospace from the Aptian to the Paleocene. Reprinted with permission from Lupia (1999). Note that the boundaries of angiosperm pollen morphology are reached early in the Cretaceous.

Some floral specializations for insect pollination appear to have evolved by the Cenomanian, including bisexuality, some differentiation of petals and sepals, and larger flowers (Basinger and Dilcher, 1984; Crepet et al., 1991). Still, most flowers were small, had few parts, and an open, radial form. One lauraceous flower had modified stamens that may have served as pollinator rewards (Drinnan et al., 1990), and in some rosids the attractive function may have been taken over by the corolla of the flower, but pollen was still probably the main reward in magnoliids and hamamelids (Crepet et al., 1991).

Diversity of floral form increased greatly in the Turonian-Maastrichtian as both groups of eurosids and basal asterid lineages radiated. Floral features such as sympetally, clawed petals/nectary complexes, bilateral symmetry, prolonged calyx tubes, elongate stamen filaments, inverted anthers, pseudoterminal short-slit anther dehiscence, anther appendages, viscin threads, polyads, and nectar and resin rewards appeared by the Turonian and probably reflect specialization for pollination by bees (Crepet, 1996). Many-parted flowers of magnoliaceans from the Turonian may indicate the evolution of specialized beetle pollination in this group. Most fossil flowers of this age were small, however. The presence of higher commelinoid monocots like Zingiberales in the Campanian-Maastrichtian (Hickey and Peterson, 1978; Friis, 1988) may indicate mammalian pollination because that is inferred to be the primitive state for this order of plants (Kress, 1990). Specialized wind-pollinated angiosperms, such as the eurosid Fagales, also diversified during the Late Cretaceous. Interestingly, although the increase in floral complexity seems most noticeable in the Cenomanian-Campanian, the morphological complexity of angiosperm pollen increased rapidly during the early radiation of flowering plants and did not change dramatically during the Late Cretaceous (Fig. 6; Lupia, 1999).

Dispersal and establishment.—Seed size is one of the most ecologically revealing traits of plants. Seed size is correlated directly with seedling growth rate under heavily shaded conditions and

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inversely correlated with death rate (e.g., Grime, 1979). Thus, large seeds are strongly associated with the ability to establish seedlings under a forest canopy, although there are small-seeded species that regenerate in forest gaps created by windfalls or other disturbance. Small seed size is also highly positively correlated with invasive behavior in trees (Marzluff and Dial, 1991).

The seed-size distribution of Cretaceous angiosperms only encompasses the smallest part of the size range seen in Paleocene through Recent flowering plants, and there was relatively little change in angiosperm seed size during the Cretaceous (Fig. 7; Tiffney, 1984). This is consistent with weedy biology and abiotic dispersal for the majority of Cretaceous flowering plants. The morphology of young fruits and winged seeds also suggests that seed dispersal was largely passive or by wind prior to the Turonian. Among tricolpate taxa, a large number of capsular fruits with small winged seeds have been found (Crepet and Nixon, 1994). The evolution of larger seed size in many angiosperm lineages during the early Cenozoic indicates that this was the time when animal dispersal and shade-tolerant life history strategies became common among flowering plants (Tiffney, 1984; Wing and Tiffney, 1987). Most new discoveries of Early Cretaceous flowers and fruits continue to be in small size categories (e.g., Friis et al., 1999). There may well be a taphonomic bias in fusainized assemblages (the main source of Early Cretaceous reproductive material) against larger plant parts, but even lignitized assemblages from the Cretaceous do not preserve large angiosperm seeds (Tiffney, 1984).

Size and growth rate.—Angiosperm wood is generally rare in the Cretaceous. Wheeler and Baas (1991) surveyed the fossil record of dicotyledonous wood worldwide and tabulated approximately 1200 records; fewer than 100 (8%) of these were from the Cretaceous, although the Cretaceous represents about 40% of the duration over which records were tabulated. Almost all of the Cretaceous records were from the Maastrichtian or Campanian, with only a small number from the Albian through Cenomanian (e.g., Cahoon, 1972; Serlin, 1982; Thayne et al., 1983, 1985). There is no dicot wood

reported from the Hauterivian-Aptian. Even in Late Cretaceous flora angiosperms wood is a rare component in conifer-dominated assemblages (e.g., Ramanujan, 1972). This pattern continues into the Maastrichtian in northern North America; in areas farther south, dicot wood is at least locally more abundant (Wheeler et al., 1987; Boucher and Wing, 1997; Boucher et al., 1997, *unpublished data*). Taken at face value, the rarity of dicot wood in the Cretaceous implies that large dicot trees were less common in the Cretaceous than they were during the Cenozoic. No taphonomic biases have been proposed to explain the preferential non-preservation of angiosperm wood in the Cretaceous.

In general, wood of Cretaceous dicots is anatomically distinct from that of Cenozoic dicots (Wheeler and Baas, 1993). Cretaceous woods generally do not have growth rings, a characteristic of less seasonal climates, but they also have small diameter vessels, which are associated with cool or dry climates in the Recent (Wheeler and Baas, 1993). This apparent conflict between characters suggests substantial functional differences between Cretaceous and post-Cretaceous dicot vascular function. Cretaceous wood anatomy suggests less efficient, more vulnerable vasculature, and less division of function among different cell types (Wheeler, 1991; Wheeler and Baas, 1991, 1993). Wheeler and Baas (1993) suggest that the more efficient vascular systems of Cenozoic dicots is consistent with taller-statured vegetation.

Growth form and phenology.—Aptian to earliest Albian dicot leaves are small (< 5 cm long), thin-textured, and poorly organized; some are highly lobed, others are indefinite pinnate/palmate, while others are pinnate and entire with poorly organized venation. Doyle and Hickey (1976) interpreted the disorganized, pinnately-veined leaves as being of magnolialean "grade," but not necessarily Magnoliales. Indefinite pinnate/palmate leaves may represent Saururaceae/Piperaceae or other paleoherb taxa (Taylor and Hickey, 1996). The morphology of the reniform and lobate leaves is consistent with herbaceous form (Taylor and Hickey, 1996), as are some leaves from the Early Cretaceous of Portugal

(Friis et al., 1999). Monocot leaves of this age also indicate an herb-growth form. A single type of dicot leaf from the early Albian of the Potomac sequence has features consistent with tree-growth form; *Eucalyptophyllum* has a leaf margin reinforced by a vein, a thick cuticle with sunken stomata, and an elongate shape (Upchurch and Wolfe, 1993).

The size and range of morphology of angiosperm leaves increases through the Albian and Cenomanian in the Potomac Group (Hickey and Doyle, 1977). Later Albian dicots have more organized venation than earliest Albian forms, indicating better developmental control of venation, enhanced resistance to shredding and, perhaps, a wider range of life forms including tree and shrub architecture (Hickey and Doyle, 1977). Pinnately and palmately lobed leaves, such as those seen in *Sapindopsis* and other platanoids, are associated with rapid growth and early successional habitats in living dicots (Givnish, 1979). Hence, it seems likely that these taxa were deciduous early successional shrubs or small trees (Hickey and Doyle, 1977). Such leaves remained a common element of Cretaceous megaflores through the Maastrichtian (e.g., Crabtree, 1987). Peltate and deeply cordate leaves reflect terrestrial herbs or floating aquatic plants (Hickey and Doyle, 1977; Upchurch et al., 1994), indicating that by the Albian, flowering plants occupied open, sunny, wet habitats and perhaps shaded understory areas.

New types of dicot leaves evolved during the late Albian or Cenomanian: strongly bilobed forms, bifurcately compound leaves, and simple pinnately veined leaves with emarginate apices (Upchurch and Wolfe, 1993). This latter leaf type, and the increased diversity of other simple, pinnate leaves, have been taken to indicate the expansion of dicots into late-successional habitats (Upchurch and Wolfe, 1993). One Cenomanian assemblage from the Dakota Group has leaves that have been interpreted as vines or lianas (Upchurch and Wolfe, 1993). Hence, it appears that all of the major functional types of dicot leaves were present by the Cenomanian in North America, although liana-type leaves were rare throughout the Late Cretaceous, perhaps an indication that complex,

rainforest vegetation was rare or absent (Wolfe and Upchurch, 1987). Late Cretaceous angiosperms from lower middle latitudes also retained small leaves relative to those of extant tropical and subtropical floras, which has been interpreted as a response to a subhumid climate rather than reflecting the evolutionary advancement or ecological strategies of flowering plants at that time (Wolfe and Upchurch, 1987). The early "saturation" of dicot-leaf morphospace may not be surprising given how convergent gross-leaf morphology is among a wide range of living dicots with different growth architectures and ecological strategies.

The occupation of cuticle morphospace during the Cretaceous angiosperm radiation is only beginning to be studied (e.g., Upchurch, 1984, 1995; Upchurch and Wolfe, 1993). However, cuticles of *Sapindopsis* and early platanoids are "mesomorphic," showing no particular features to retard water loss (Upchurch, 1984). Leaf cuticles of Albian and Cenomanian lauraleans and chloranthoids are thick, as is typical of broad-leaved evergreens (Upchurch and Dilcher, 1990; Upchurch, 1995), and have some features related to reducing water loss, possibly indicating water-stressed or nutrient-limited habitats. A middle Albian (?) plant assemblage from central Texas is dominated by conifers, ferns, and seed ferns, but also contains a few angiosperms that show xeromorphic features such as thick leaves, stomata restricted to the underside of the leaf, and dense hairs (Serlin, 1982). This may be the oldest record of a highly xeromorphic angiosperm.

DISCUSSION

It is now possible to begin to place the Cretaceous radiation of flowering plants in a context that includes a preliminary understanding of the phylogeny of the group, some knowledge of its diversity history, the abundance and environments of growth of various lineages within flowering plants, and a partial ability to interpret the biology of Cretaceous angiosperms from the morphology of their reproductive and vegetative parts.

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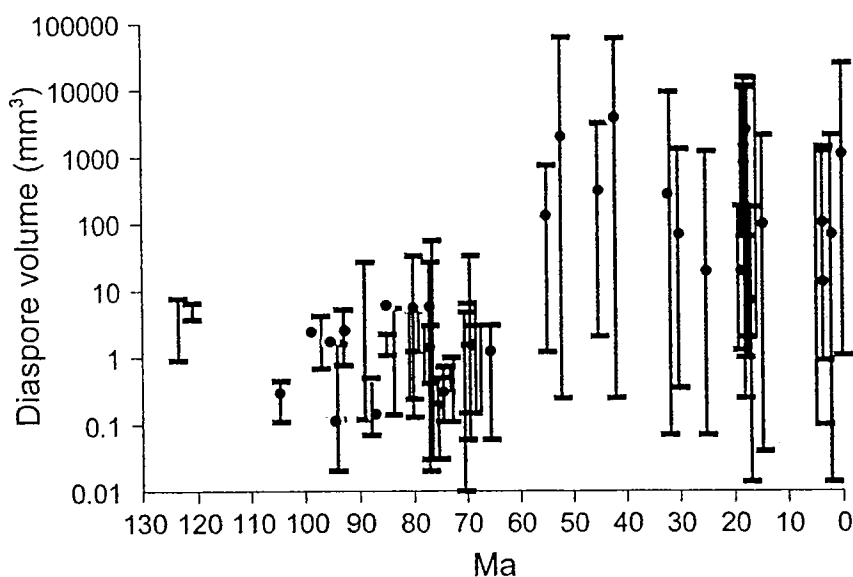


FIGURE 7.—Changes in angiosperm diaspore volume through time. Data from Tiffney (1984), with additions by Wing and Boucher (1998). Note increase in mean size and size range from Cretaceous to Cenozoic.

An ecological framework for considering plant evolution.— In order to grow and reproduce all plants need water, nutrients, space, and time. All also require light, except for a few parasites. Light and space are available in all terrestrial environments except where access to them is limited by the growth of other plants. Water, nutrients, and time for growth are in short supply at some places at some times, and different species have different capacities to tolerate shortages of these resources. Three primary gradients for terrestrial habitats can be identified: a gradient from greater to lesser supply of nutrients and/or water, a gradient from greater to lesser time for growth and reproduction, and a gradient from greater to lesser density of plants.

Habitats chronically lacking the levels of nutrients or water that most of the plants of a given epoch require are considered to be stressed. Modern stressed environments include peat bogs, white sand and other low-nutrient soils, and serpentine barrens, all places where major nutrients are continually sub-optimal for most plants. Arctic and high alpine climates also can be considered stress-inducing, because continuously low temperatures

inhibit photosynthesis and nutrient release from decay of organic matter (Grime, 1979). Low seasonality deserts (i.e. those without even irregular rainy periods) are also stressed environments.

Habitats that are frequently perturbed in a way that removes plant tissue or interferes with establishment of plants are disturbed. Disturbed habitats include stream channel margins subject to frequent flooding, areas prone to fires or mass wasting, and also most deserts. Deserts might seem naturally to be stressed habitats because they lack water. However, low annual precipitation is associated with short, intense episodes of precipitation, and water is abundant in most deserts for short periods of time (MacMahon, 1985). Hence, deserts are similar to disturbed habitats in having short periods of abundant resources. Other disturbed habitats include marshlands with variable water level, sea shores subject to large tidal fluctuation, and many grasslands (Grime, 1979).

Both stress and disturbance are defined by reference to the plants that live at a given time in a given region. That is, the most stressed habitats are those in which the fewest species are able to grow because of limiting resources. There are some

areas now that are so stressful that they lack land plants (e.g., rock surfaces in Antarctica). The most disturbed habitats are those in which physical destruction is so frequent that only a few of the available species can complete a life cycle. By definition, therefore, less disturbed and/or less stressed habitats support more species. Because more species can grow and reproduce in less stressed and less disturbed habitats, competition between plants for space and light is more severe. The inter-relationships between stress, disturbance, and competition give rise to three end-member habitat types: stressed, disturbed, and competitive. Of course, the three types of environments intergrade with one another: nutrient levels may be low in a tropical forest where other resources are abundant, peat bogs occasionally burn, temporarily releasing nutrients that are otherwise limiting.

Grime (1977, 1979) recognized three basic types of plant life history strategies: ruderal, competitive, and stress-tolerating. These strategies are better suited to disturbed, competitive, and stressed environments, respectively. Ruderals have short life spans, low investment in individual offspring, high potential growth rate, and little ability to withstand low resource levels except as seeds. Ruderals excel at growing where there is frequent partial or total destruction of plant biomass, but where resources may be plentiful between perturbations. Competitors tend to have longer life spans, greater investment in individual offspring, high potential growth rate, and respond rapidly through differential growth to changes in critical resources such as light and water. Competitive plants are able to succeed in physically stable habitats where light and space are limited by the growth of other plants. Stress tolerators have variable life spans, variable investment in offspring, low potential growth rate, and high tolerance of low light or low nutrient conditions. Stress tolerators exist in relatively stable environments with chronically low availability of some of the resources necessary for photosynthesis. Grime (1979) considered all shrubs and trees to be competitors or stress tolerators compared with herbs, but ecological strategies vary enormously within woody plants. Some trees appear to be

ruderal, at least relative to other woody plant.

Does taxonomic diversity indicate ecological expansion?—For the last 20 years views of Cretaceous angiosperm paleoecology have been shaped strongly by the ideas of Doyle and Hickey (1976) and Hickey and Doyle (1977), who proposed that early angiosperms were small, ruderal trees that grew in riparian corridors. Retallack and Dilcher (1981, 1986) largely concurred with these views, and added that early angiosperms might have been centered along coastal corridors. Retallack and Dilcher also applied Grime's terminology of ecological strategies, referring to early angiosperms as ruderals. More recently, Taylor and Hickey (1992, 1996) have argued that basal angiosperms were perennial herbs rather than ruderal trees, but still disturbed environments and ruderal life history are seen as critical to their early diversification. The paleoecological settings and floral morphologies recently reported by Friis et al. (1999) continue to support the hypothesis that basal angiosperms were ruderal and insect pollinated.

The ecological strategies and environmental settings of Late Cretaceous angiosperms are less clear, and two divergent interpretations of the record have been made. One interpretation is that the range of angiosperm ecological strategies and growth forms expanded at about the same rate as their taxonomic diversity. The alternate is that the range of angiosperm ecological strategies and growth forms lagged considerably behind their taxonomic diversification, not accelerating until the latest Cretaceous or early Cenozoic. Congruency was implied by Hickey and Doyle (1977) when they concluded that some angiosperms were late successional canopy trees by the Cenomanian. Retallack and Dilcher (1986) cited examples of angiosperm stress-tolerators and competitors from the Cenomanian, also implying that the range of life history strategies increased congruently with taxonomic diversity. Upchurch and Wolfe (1993) also argued that some Cenomanian fossil assemblages represented angiosperm-dominated rainforest vegetation. Crane (1987) thought that vegetational dominance was concurrent with the taxonomic radiation of angiosperms.

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Delayed ecological expansion has been argued based on the small size of angiosperm diaspores throughout the Cretaceous (Tiffney, 1984; Wing and Tiffney, 1987), on the rarity, small size, and inefficient anatomy of Cretaceous angiosperm wood (Wing and Tiffney, 1987; Wheeler and Baas, 1991), and on the tendency, even in the Late Cretaceous, for angiosperm fossils to be most abundant in disturbed habitats (Wing et al., 1993; Tiver et al., 1994; Taylor and Hickey, 1996; Wing and Boucher, 1998).

Whether or not ecological and taxonomic diversification were congruent, the radiation of flowering plants clearly involved many distinct lineages evolving through time, across geographic and climatic zones, while occupying particular habitats on local environmental/edaphic mosaics. The appearance of congruence, or lack thereof, between taxonomic radiation and ecological expansion, may, in part, be the result of looking at different parts of a complex pattern, with different sublineages pursuing different strategies in different regions and local environments.

The data reviewed above show that angiosperm abundance expanded across both paleolatitude (low to high) and local environments (disturbed to mesic or stressed). These two gradients have an underlying similarity in that potential rates of growth decrease from higher- to lower-nutrient sites and from lower to higher latitudes. Equatorial regions with high levels of solar insolation, high temperatures, and adequate precipitation are favorable to ruderal strategies except in areas where soil nutrient levels are low (Grime, 1979). If the Cretaceous tropics were seasonally wet rather than ever wet (Ziegler et al., 1987), then ruderal strategies might have been even more advantageous in the tropics than they are today. This could be because tree biomass production would have been less and the structure of vegetation more open. The success of Early Cretaceous angiosperms in the tropics may have been related not only to their ability to maintain dispersed populations and avoid species specific predation/parasitism, but also to their rapid growth rates and life cycles (Bond, 1989; Midgely and Bond, 1991; Taylor and Hickey, 1996).

The slow movement of angiosperms into higher-latitude vegetation is consistent with the generally more stressed conditions that pertain in regions where temperature and/or light limit growth through a substantial part of the year. In these conditions, the existing conifer and fern vegetation would have offered few opportunities for growth to ruderals, which explains the strong tendency for angiosperms to be restricted to freshly disturbed areas at higher latitudes. High growth rates are basic to the ruderal strategy, and require habitats with high levels of light, water, and nutrients. Such habitats are, almost by definition, unstable or disturbed environments because stable habitats with ample resources develop a heavy cover of plants that reduces the availability of resources through competition (Grime, 1979). Plants that grow faster and have shorter generational times succeed in disturbed habitats because they use the resources of the open patch quicker, and are better able to locate the next patch through rapid reproduction and high fecundity.

Ruderals are, by definition, unable to do well in the most nutrient and light limited habitats, which may explain why stressed environments can become "museums" that retain older lineages; groups with slower metabolic rates persist because under stressed conditions high growth rates are not advantageous (Grime, 1977; Vermeij, 1987). As long as these stressed environments have a continuous distribution in space and through time, their stress-tolerant and competitive incumbents would be difficult to displace. The failure of angiosperms to diversify strongly into stress-tolerant or competitive strategies during most of the Cretaceous, and the apparently rapid development of these strategies in many distantly related angiosperm lineages during the early Cenozoic suggest that environmental disturbance near the K/T boundary may have been important for breaking the dominance of older stress-tolerant and competitive lineages (Wing and Tiffney, 1987). If this is a general pattern, then episodes of mass extinction or environmental disruption should precede periods during which escalated groups of plants take over more stressed environments, a pattern that has also been seen in Carboniferous

and Permian swamp forests (DiMichele et al., 1987).

Generalizing to other land plants.—The strategies outlined above have profound implications for patterns of diversification and clade replacement in terrestrial plants because plant body size appears to be correlated with speciation rate. A number of studies have documented positive correlations between herbaceousness and species diversity of angiosperm families (e.g., Ricklefs and Renner, 1994), and ferns, which are dominantly herbaceous, are frequently noted as the most diverse group of non-flowering plants. More recently these correlational studies have been refined by taxonomic contrasts between sister taxa (Dodd et al., 1999), in which a strong correlation between herbaceousness and diversity has been found to still hold true.

A general process for the diversification of land plants could be outlined as follows:

(1) Small body size and rapid life cycle are typical adaptations of ruderals that occupy disturbed habitats. They also are correlated with higher rates of speciation, probably because there are more generations per unit time (there is at least a 20-30 fold difference in generation times among angiosperm subgroups).

(2) Lineages that live in disturbed habitats will evolve ruderal strategies and will increase in diversity faster than competitive or stress-tolerant lineages with larger body size and longer generational time (assuming more or less equivalent extinction rates).

(3) As a radiation of ruderals proceeds, even the disturbed habitats in a particular region and time will become more saturated with species.

(4) Higher species diversity will lead to more competition for light and space (particularly among species with a recent common ancestor). Greater competition will favor evolution of plants with more competitive strategies, which tend to involve larger body size and longer generational times.

(5) As a result, ruderal lineages eventually give rise to competitive and stress-tolerant forms, but these will have lower rates of speciation.

(6) Stress tolerant plants that evolved from ruderal ancestors will be stranded as low-diversity

clades in habitats that are difficult for newly evolving ruderals from other lineages to invade.

CONCLUSIONS

(1) Basal angiosperms were probably tropical, insect-pollinated, ruderal plants.

(2) The diversification of angiosperms in the Barremian-Cenomanian produced many species, but limited expansion into different ecological strategies. The magnoliid clade evolved tree-growth form and stress-tolerant life histories relatively early, but most eudicots retained their ancestral ruderal life histories, even though they became woody.

(3) By the end of the Cretaceous, angiosperms were far more diverse than other groups of plants, but they probably did not have the biomass dominance of global vegetation and range of ecological strategies that they achieved during the Cenozoic. They were least important in stressed or competitive habitats and, on a global scale, they were least important at latitudes higher than 40-45°. This is probably because their success was related to fast growth and high rates of resource use.

(4) The angiosperm radiation provides a major example of decoupling of taxonomic diversity and ecological dominance. The tendency, seen also in extant plants, for herbaceous groups with ruderal life histories to have high diversity suggests that species diversity in the fossil record is likely to be a poor predictor of ecological importance. Angiosperms may not have displaced older groups of land plants competitively, but largely through replacement following preferential extinction of other groups and/or through higher rates of speciation.

(5) The angiosperms may be an example of a general phenomenon in plants in which successive major groups evolved first as small ruderals, and only later in their evolutionary history invaded competitive and stressed habitats. The continued dominance of earlier-evolving, presumably less escalated taxa, in stressed settings is consistent with the advantages of incumbency in environments where rapid growth and reproduction is not tenable.

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