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EARLY CRETACEOUS FOSSIL EVIDENCE FOR ANGIOSPERM EVOLUTION

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ABSTRACT

Morphological, stratigraphic, and sedimentological analyses of Early Cretaceous pollen and leaf sequences, especially from the Potomac Group of the eastern United States, support the concept of a Cretaceous adaptive radiation of the angiosperms and suggest pathways of their initial ecological and systematic diversification. The oldest acceptable records of angiosperms are rare monosulcate pollen grains with columellar exine structure from probable Barremian strata of England, equatorial Africa, and the Potomac Group, and small, simple, pinnately veined leaves with several orders of reticulate venation from the Neocomian of Siberia and the basal Potomac Group. The relatively low diversity and generalized character of these fossils and the subsequent coherent pattern of morphological diversification are consistent with a monophyletic origin of the angiosperms not long before the Barremian. Patuxent-Arundel floras (Barremian-early Albian?) of the Potomac Group include some pollen and leaves with monocotyledonous features as well as dicotyledonous forms. Patuxent angiosperm pollen is strictly monosulcate and has exine sculpture indicative of insect pollination. Rare Patuxent-Arundel angiosperm leaves are generally small, have disorganized venation, and are largely restricted to sandy stream margin lithofacies; the largest are comparable to and may include ancestors of woody Magnoliidae adapted to understory conditions. Patapsco floras (middle to late Albian?) contain rapidly diversifying tricolpate pollen and several new complexes of locally abundant angiosperm leaves. Ovate-cordate and peltate leaves in clayey pond lithofacies may include ancestors of aquatic Nymphaeales and Nelumbonales. Pinnatifid and later pinnately compound leaves with increasingly regular venation which are abundant just above rapid changes in sedimentation are interpreted as early successional "weed trees" transitional to but more primitive than the modern subclass Rosidae. Apparently related palmately lobed, palinactinodromous leaves which develop rigidly percurrent tertiary venation and become abundant in uppermost Potomac stream margin deposits (latest Albian-early Cenomanian?) are interpreted as riparian trees ancestral to the order Hamamelidales. Comparisons of dated pollen floras of other regions indicate that one major subgroup of angiosperms, tricolpate-producing dicots (i.e., excluding Magnoliidae of Takhtajan) originated in the Aptian of Africa-South America at a time of increasing aridity and migrated poleward into Laurasia and Australasia. However, the earlier (Barremian) monosulcate phase of the angiosperm record is represented equally in Africa-South America and Laurasia before marked climatic differentiation between the two areas. These trends are considered consistent with the hypothesis that the angiosperms originated as small-leafed shrubs of seasonally arid environments, and underwent secondary expansion of leaf area and radiated into consecutively later successional stages and aquatic habitats after entering mesic regions as riparian "weeds," as opposed to the concept that they arose as trees of mesic forest environments.

INTRODUCTION

In recent years, there has been a significant reawakening of interest in the old and vexing question of the origin and early evolution of the flowering plants. One stimulus for this interest has been the appearance of more natural systems of angiosperm classification which incorporate new lines of comparative evidence and are based on more explicit, and hence testable, phylogenetic assumptions (e.g., Cronquist, 1968; Takhtajan, 1969; Thorne, 1976). Another has been revival of the theory of continental drift as a corollary of the plate tectonic "revolution" in geology, which has led to attempts to formulate more realistic paleobiogeographic models for angiosperm distribution (e.g., Raven and Axelrod, 1974; Schuster, 1976). Equally important, however, has been clearer recognition of the potentials and implications of the fossil record in elucidating major events in the evolutionary history of plants, in part reflecting development of new techniques such as palynology. The most conspicuous and widely acknowledged recent successes of paleobotany have been in areas only indirectly related to the angiosperm problem: the Precambrian history of microscopic algal life (Schopf, 1970, 1975; Barghoorn, 1971; Cloud, 1976), the initial Silurian-Devonian radiation of land plants (Chaloner, 1967, 1970; Banks, 1968, 1970), and the origin and early evolution of the gymnosperms (Florin, 1951; Beck, 1960, 1970; Andrews, 1963; Pettitt and Beck, 1968; Scheckler and Banks, 1971; Mamay, 1976). Advances in understanding of the early angiosperm record have had less impact on other disciplines, perhaps because many of them have come from stratigraphic palynology, a field relatively unfamiliar to megafossil paleobotanists and systematic botanists alike. However, we believe their implications are no less fundamental.

Our emphasis on the fossil record arises not only from the fact that it is the only source of direct evidence on past stages in the evolution of life, but also from our conviction that its potential for elucidating the evolution of the angiosperms has for many years been grossly underestimated. In marked contrast to phylogenetic studies of vertebrates or mollusks, attempts to reconstruct the evolutionary history of the angiosperms have been dominated almost exclusively by inferences drawn from the comparative morphology and geographic distribution of modern forms. This neglect of fossil evidence largely reflects a deeply ingrained belief that the fossil record of angiosperms is significantly more biased and inadequate for phylogenetic purposes than is the record of other groups. One reason for this belief is the fact that, before the advent of palynology, the fossil record of angiosperms consisted mostly of leaves, which until recently have been considered of minimal use for systematic purposes, while flowers, traditionally the primary basis of angiosperm classification, are extremely rare. Equally important, however, have been the non-evolutionary perspective of early paleobotanists and their lack of attention to critical morphological detail (cf. Hughes, 1976). These led numerous early investigators, of whom Fontaine (1889), Lesquereux (1892), Hollick (1906), and Berry (1911a, 1911b) are only a few examples, to misidentify badly Cretaceous angiosperm megafossil remains, often assigning them to modern families or even genera on the basis of what are seen in hindsight as purely superficial resemblances (cf. Wolfe, 1972a, 1973; Dilcher, 1974; Wolfe et al., 1975; Doyle and Hickey, 1976). These misidentifications were perpetuated as recently as 1967 by Chesters et al. in their compilation of first records of angiosperm families, despite their recognition in the text of the questionable nature of this procedure. Such identifications have been repeatedly cited as proof that the first angiosperms to enter the fossil record belonged to already diverse and specialized modern groups, and hence as support for theories that the flowering plants had a long latent history in some geographically or ecologically restricted area before invading *en masse* the regions of the known fossil record in the Early Cretaceous (e.g., Seward, 1931; Axelrod, 1952, 1960, 1970; Němejc, 1956; Takhtajan, 1969). In this light, it is small wonder that even many recent authors have continued to consider the origin of the angiosperms nearly as much of an enigma as when Charles Darwin labeled it "an abominable mystery" nearly a century ago, or that those interested in angiosperm phylogeny have avoided paleobotany and concentrated exclusively on comparative studies of modern plants.

The first strong indications that the early fossil record of the angiosperms was in need of reinterpretation came as a result of stratigraphic palynological studies of the 1950's and early 1960's. Because of the extreme chemical inertness of the pollen exine and its transportability, the palynological record is generally more representative of the regional flora, including elements which may be far removed from the site of deposition, than is the megafossil record, and it is of corresponding value in both stratigraphic and evolutionary studies (cf. Kuyl et al., 1955; Muller, 1959, 1970). Hence, the consistent failure of palynologists to find distinctively angiospermous pollen types in Triassic, Jurassic, and earliest Cretaceous strata and the low morphological diversity of the first angiosperm pollen grains from the mid-Cretaceous were quickly recognized as evidence against the concept of extensive pre-Cretaceous angiosperm diversification and in favor of the alternative hypothesis of a Cretaceous radiation (Scott et al., 1960; Hughes, 1961a; Pierce, 1961; Pacltová, 1961; Brenner, 1963; Kemp, 1968). This interpretation has been further strengthened by more detailed morphologic and stratigraphic investigations of mid-Cretaceous pollen floras, which reveal a pattern of appearance and diversification of successively more differentiated angiosperm pollen types, as would be expected if a genuine evolutionary diversification was under way (Doyle, 1969, 1973; Muller, 1970; Pacltová, 1971; Dettmann, 1973; Jarzen and Norris, 1975; Laing, 1975, 1976; Wolfe et al., 1975; Hughes, 1976). These results, as well as the successes of Chaloner (1967, 1970) and Banks (1968, 1970) in their analyses of the Silurian-Devonian record of land plants, have in turn stimulated a critical re-evaluation of the early angiosperm leaf record using a comparable stratigraphic-morphologic approach, independent of supposed affinities with modern taxa (Pacltová, 1961; Wolfe, 1972b; Doyle and Hickey, 1972, 1976; Wolfe et al., 1975; Hughes, 1976). When viewed in this way, even the relatively sporadic leaf record reveals a diversification pattern consistent with a Cretaceous radiation, rather than the previously inferred sudden appearance of modern forms. Because trends in the early angiosperm pollen and leaf record carry with them clear implications on directions of morphological and ecological evolution of early angiosperms, and indirectly on the relative advancement and relationships of high-rank angiosperm taxa, they represent the first positive indication that the fossil record can achieve a primary role in the reconstruction of angiosperm phylogeny.

Our purpose in the present paper is to review aspects of the fossil record bearing on the origin and early evolution of the angiosperms and to discuss more speculative evolutionary and ecological models we have developed from them, relying extensively on our own studies of the Potomac Group of the eastern United States (Doyle and Hickey, 1972, 1976). We have concentrated on these strata not because we believe that eastern North America was an especially important center of early angiosperm evolution, but rather because they combine an excellent and intensively studied pollen sequence with the most complete succession of Lower Cretaceous megafossil localities yet known. In addition to analysis of the morphology of pollen, leaves, and to a lesser extent other plant organs, an important aspect of our study has been an attempt to draw inferences on the paleoecology of early angiosperms from the types of sediment in which their remains are preserved.

EARLIEST RECORDS OF THE ANGIOSPERMS

In attempting to establish the earliest appearance of a group in the fossil record, it is necessary to separate misidentifications and stratigraphically misplaced material from well dated occurrences which can be identified with reasonable assurance as members of the group in question. With the angiosperms, as with any other major taxon, evidence of a single character or organ is seldom decisive, but must be weighed in the light of evidence of other characters and organs in order to minimize the problems of convergence and mosaic evolution. In particular, care should be taken to use as criteria characters or combinations of characters that are both common to most or all members of the group and specialized over the situation in other, older groups, rather than characters found in only one of its subgroups, unless there is strong evidence from other characters that precisely the same subgroup is represented (cf. Wolfe et al., 1975).

A sufficient number of supposed pre-Cretaceous angiosperms have been

TABLE I

SUBDIVISIONS OF THE CRETACEOUS

(*Ages of series boundaries after Casey, 1964*)

System/Period	Series/Epoch	Stage/Age		Age in years
Tertiary				
				64-65 × 10^6
Cretaceous	Upper/Late	Maestrichtian	Senonian	
		Campanian		
		Santonian		
		Coniacian		
		Turonian		
		Cenomanian		
				ca. 100 × 10^6
	Lower/Early	Albian		
		Aptian		
		Barremian		
		Hauteriaian	Neocomian	
		Valanginian		
		Berriasian		
				136 × 10^6
Jurassic				

reported to give some credence to the idea that flowering plants were well established prior to that period (cf. Axelrod, 1952, 1960, 1970). However, none of these reports can be said to have stood up under critical morphological and stratigraphic examination. Fortunately, the recent detailed evaluation of such fossils by Hughes (1976), supplementing discussions by Scott et al. (1960), Hughes (1961a), Doyle (1973), and Wolfe et al. (1975), makes mention of more than a few highlights unnecessary.

At the present time, the earliest acceptable pollen records of angiosperms are monosulcate grains (*Clavatipollenites*, *Retimonocolpites*, *Stellatopollis*) from Barremian strata of England (Couper, 1958; Kemp, 1968; Hughes, this symposium) and putatively correlative horizons in the basal Potomac Group and in equatorial Africa (cf. Table I, and below). These grains lack such universally recognized angiospermous features as the multiple apertures and radial symmetry of slightly younger (Aptian) tricolpate and derived pollen types. However, they do have a type of exine structure — columellar, with radial rods or columellae connecting the continuous inner exine layer, or nexine, with the generally perforated outer layer, or tectum — which is so far known only in angiosperms (Van Campo, 1971), or a related type with no columellae but with a coarsely reticulate tectum (*Retimonocolpites* spp.: Doyle et al., 1975). Columellar exine structure contrasts both with alveolar structure, with a honeycomb-like or spongy system of partitions and chambers below the tectum, which is found only in gymnosperms such as Cycadales and saccate conifers (Van Campo, 1971), and with granular exine structure, with a layer of granules of sporopollenin below the tectum, which is found both in gymnosperms such as Gnetales and non-saccate conifers and in angiosperms such as porate "Amentiferae" and some Magnoliidae (Van Campo and Lugardon, 1973; Doyle et al., 1975; Walker, 1976). In addition, two of the lower Potomac monosulcates cited above and a related third species from Albian strata of the Potomac Group have been shown by transmission electron microscopy to resemble modern angiosperms in lacking the laminated structure of the endexine (chemically differentiated inner layer of the nexine) which is characteristic of all gymnosperms so far investigated (Doyle et al., 1975).

Although several authors have reported angiosperm pollen from pre-Barremian rocks, further investigation has shown that the forms concerned are contaminants, belong to non-angiospermous groups poorly known at the time they were described, or lack sufficiently diagnostic angiospermous features to determine whether they represent angiosperms or extinct members of other groups (cf. Scott et al., 1960; Hughes, 1961a, 1961b, 1976). For example, Jurassic grains identified as *Clavatipollenites* by Pocock (1962), Helal (1966), Schulz (1967), and Tralau (1968) have not been shown to have the columellae characteristic of the Early Cretaceous forms, and the published illustrations are in fact more suggestive of alveolar structure (cf. Doyle et al., 1975). A more widely cited case is the common Jurassic and Early Cretaceous genus *Eucommiidites*, described by Erdtman (1948) as tricolpate and hence probably dicotyledonous. However, later authors have demonstrated that *Eucommiidites* has bilateral symmetry rather than the radial symmetry of typical tricolpate dicots (Kuyl et al., 1955; Couper, 1958; Hughes, 1961b), and granular exine structure combined with a gymnospermous laminated endexine (Doyle et al., 1975; Scheuring, unpublished). Still more conclusive has been the discovery of *Eucommiidites* in the micropyles of seeds and in male cones of uncertain but clearly gymnospermous affinities (Hughes, 1961b; Brenner, 1963; Reymanówna, 1968; Van Konijnenburg-van Cittert, 1971).

The oldest megafossil remains which we consider definitely angiospermous are a very small (ca. 23 mm), pinnately veined, simple leaf from the Neocomian of Transbaikalian Siberia (Vakhrameev, 1973), and the variety of leaves described in detail below from probable Barremian-Aptian strata of the Potomac Group. These leaves combine normal dicotyledonous (and in one case monocotyledonous) major venation patterns with a more diagnostically angiospermous syndrome of several discrete vein orders, vein anastomoses between two

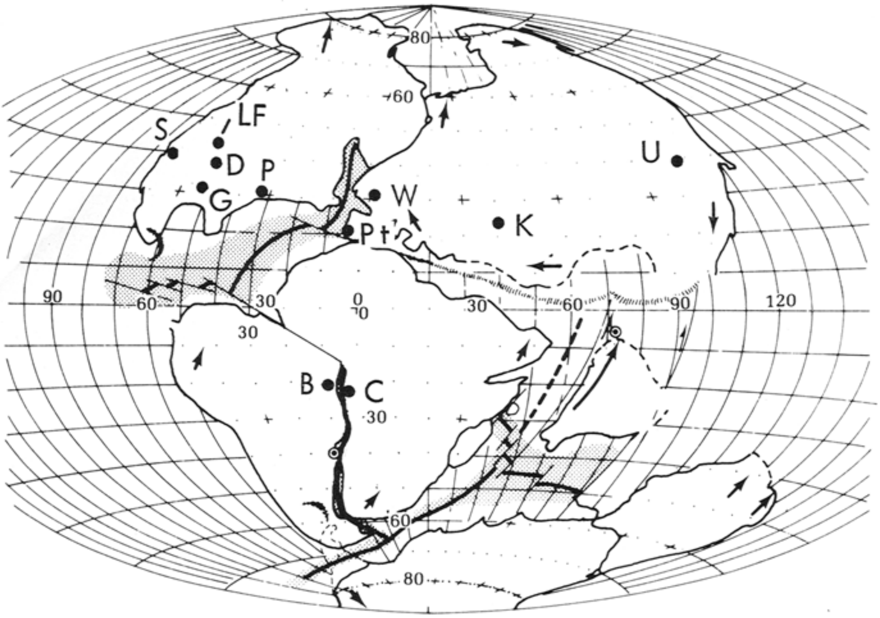

Fig. 1. Continental configuration at the beginning of the Cretaceous Period, 135 million years ago. North of the equatorial Tethys seaway lies the supercontinent of Laurasia, while to the south the former landmass known as Gondwanaland has already broken into several smaller fragments – a western part (Africa and South America), an eastern part (Australasia and Antarctica), and the Indian Plate. The geographical positions of several early and mid-Cretaceous stratigraphic units containing angiosperms mentioned in this paper are plotted on the map. These are identified as: *S*, Shasta Group; *LF*, Lakota and Fall River Formations; *D*, Dakota Group of central Kansas; *G*, Gulf coastal units such as the Fredericksburg Group of Oklahoma; *P*, Potomac Group; *W*, Wealden Group of southern England; *Pt*, Portugal; *K*, Kazakhstan; *U*, Ussuri River Basin; *B*, coastal basins of Brazil; *C*, Cocobeach sequence of Gabon and the Congo. (Base map modified from R. S. Dietz and J. C. Holden, 1970, Journal of Geophysical Research, 75: 4947, copyrighted by the American Geophysical Union.)

or more orders, and freely ending veinlets (cf. Hickey and Wolfe, 1975, and below), and they lack evidence of the fiber network characteristic of *Gnetum*, the gymnosperm genus which converges most closely to the dicot pattern (Wolfe, personal communication, and our observations).

Reports of older angiosperm megafossils fail to be convincing for reasons similar to those noted for the pollen. Thus, *Sanmiguelia*, a late Triassic leaf from Colorado compared by Brown (1956) with the palms because of its conspicuously plicate lamina, not only lacks such basic palm features as leaf or leaf-segment midveins (Read and Hickey, 1972) and a discrete petiole, but it also shows no evidence of such general monocot features as more than one vein order, apical vein fusion, and cross-veins (Doyle, 1973). Fossil palm wood and roots supposedly from Jurassic strata in Utah (Tidwell et al., 1970a, 1970b) have subsequently been shown to have been derived from overlying Tertiary strata (Scott et al., 1972).

Furcula granulifer, a Y-shaped leaf described by Harris (1932) from the Upper Triassic of Greenland, represents a more complex, intriguing case. Despite its strikingly dicot-like finer venation and cuticle structure, noted by Harris, its bifurcating midvein and lamina are reminiscent of many seed ferns (cf. Scott et al., 1960), and its secondary veins show a predominance of equal dichotomous branching quite unlike the asymmetric brochidodromous pattern of dicots (cf. Wolfe et al., 1975). Other characters of *Furcula* which are uncommon in dicots include the generally fairly acute angle of origin of third- and fourth-order veins and the absence of a fifth order of venation. In addition, the freely ending veinlets described by Harris are unbranched, and published photographs and drawings leave open the question of whether the vein endings are preservational discontinuities or true terminations (Hickey, personal observation). Hence, although *Furcula* shows a remarkable approach to the angiosperms in some characters, its large number of pteridospermous and otherwise anomalous characters indicate that it was far from a full-fledged angiosperm, and could well represent an extinct, purely convergent gymnosperm group.

In view of the absence of convincing angiosperm remains in pre-Cretaceous sediments, we have focused our attention on the earliest stages of the assured Cretaceous record of the angiosperms for evidence on their origin and early evolution. We believe that the evidence summarized in the following sections for rapid angiosperm diversification in the Early Cretaceous fully justifies this approach and renders superfluous the assumption that the angiosperms had a long pre-Cretaceous history.

GEOLOGIC AND GEOGRAPHIC SETTING

Vital to any discussion of the early history of the flowering plants is a realization of the differences between Early Cretaceous geography and that of the present (Fig. 1: cf. Raven and Axelrod, 1974; Cracraft, 1974; Schuster, 1976). By the time of appearance of angiosperms in the middle of the Early Cretaceous, continental rifting and seafloor spreading initiated in the Late Triassic had resulted in dissection of the Late Paleozoic supercontinent of Pangea by a nearly equatorial seaway, the Tethys, and an incipient Indian Ocean. To the north of the Tethys lay the continent of Laurasia, consisting of North America, Europe, and Asia minus India; to the south, the partially fragmented former continent of Gondwana, consisting of Africa-South America (West Gondwana), interrupted by a rift valley system destined to become the South Atlantic Ocean, the minor continents of Madagascar and India in uncertain spatial relation to each other and to the other blocks, and Antarctica-Australasia (East Gondwana), which remained united until the Early Tertiary. Depositional settings for sedimentary sequences containing early angiosperm floras included rift valleys soon to be invaded by marine waters, as in Brazil, Gabon, and the Congo (Bahia and Cocobeach sequences); coastal plains on the subsiding margins of earlier Mesozoic rift oceans, such as the Atlantic Coastal Plain (Potomac Group) and Gulf Coastal Plain (Fredericksburg and Tuscaloosa Groups) of United States and the coastal plain of Portugal; interior continental basins (the Wealden Group of England); margins of shallow epicontinental seas, as in the Western Interior of the United States (Cheyenne Sandstone and Dakota Group of Kansas; Lakota and Fall River Formations of the Black Hills) and in Kazakhstan; and older continental borders, such as the underthrust Pacific margin of North America (Shasta Group of California) and the Ussuri River region of maritime Siberia.

The Potomac Group, which serves as the focus for the present discussion, consists of a wedge of terrestrial sediments deposited on river flood plains and upper deltas, dipping seaward at approximately 1° ESE. It is exposed in a discontinuous belt up to 30 km wide extending from the Nottoway, Appomattox, and James Rivers south of Richmond, Virginia, through Fredericksburg, Virginia, Washington, D.C., Baltimore, Maryland, northeastern Maryland and adjacent Delaware, and an uncertain distance into New Jersey (Fig. 2; Glaser, 1969; Hansen, 1969; Owens and Sohl, 1969; Wolfe and Pakiser, 1971; Schluger and Roberson, 1975).

In its type area between Baltimore and Washington, the Potomac Group has been customarily divided into three or four formations (following Clark and Bibbins, 1897). The predominantly sandy Patuxent Formation at the base is overlain by the highly organic Arundel Clay, followed by the more heterogeneous Patapsco Formation. The generally sandy beds which overlie typical Patapsco strata in Maryland and Delaware were for many years misidentified

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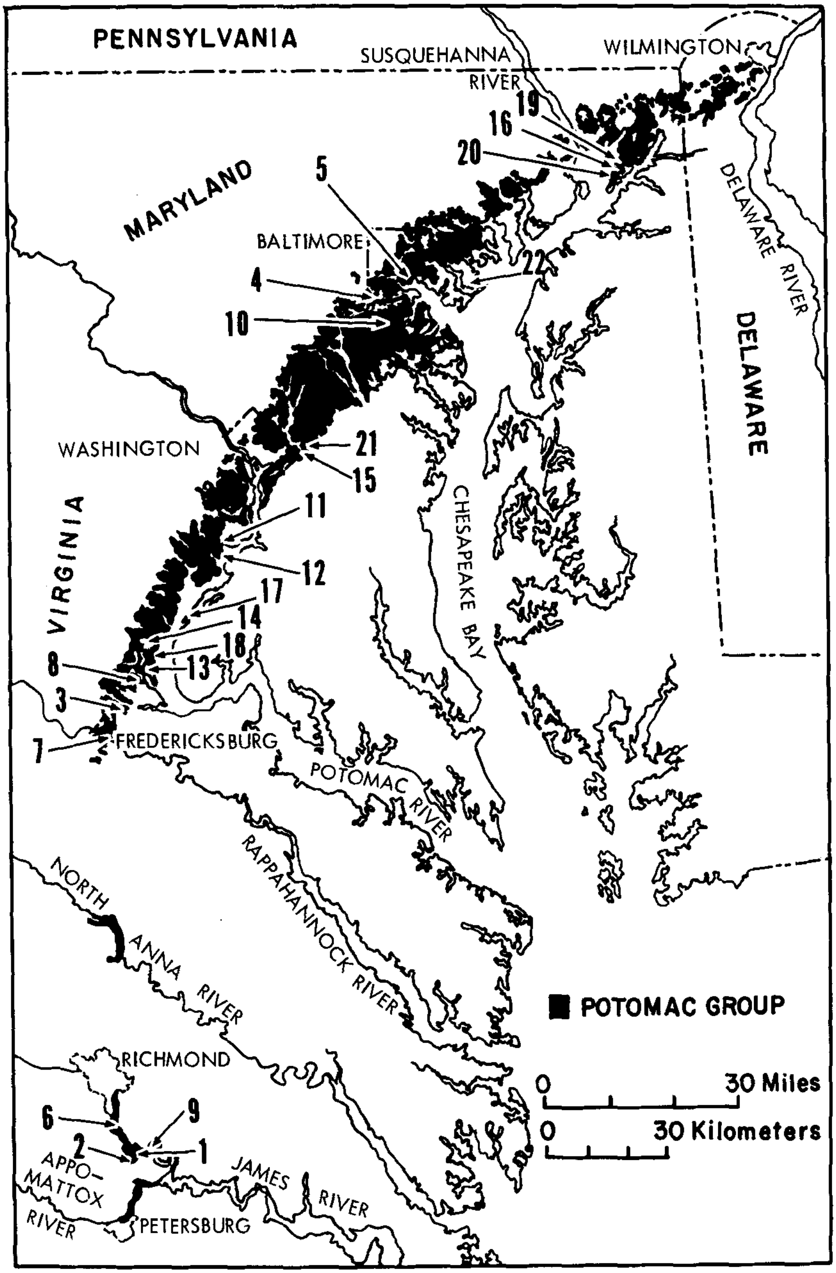
Fig. 2. Outcrop map of the Lower Cretaceous Potomac Group of Virginia, Maryland, and Delaware, not including Elk Neck beds. Localities mentioned in the text are identified by numbers in approximate stratigraphic order from oldest to youngest: 1, Dutch Gap Canal; 2, Trent's Reach; 3, Potomac Run; 4, Vinegar Hill; 5, Federal Hill in Baltimore; 6, Drewrys Bluff; 7, Fredericksburg; 8, Bank near Brooke; 9, Deep Bottom; 10, Wellhams; 11, Mount Vernon; 12, White House Bluff; 13, Aquia Creek; 14, Quantico; 15, West Brothers clay pit; 16, Red Point; 17, Stump Neck; 18, Widewater; 19, White Point; 20, Bull Mountain; 21, Brightseat; 22, Cedar Point. An additional locality, the Hylton pit, is located on Pennsauken Creek in northern Camden County, New Jersey. (Base map modified after Glaser, 1969.)


PENNSYLVANIA
SUSQUEHANNA RIVER
WILMINGTON
MARYLAND
BALTIMORE
DELAWARE RIVER
DELAWARE
WASHINGTON
VIRGINIA
CHESAPEAKE BAY
FREDERICKSBURG
POTOMAC RIVER
RAPPAHANNOCK RIVER
NORTH ANNA RIVER
RICHMOND
APPOMATTOX RIVER
PETERSBURG
JAMES RIVER
■ POTOMAC GROUP
0 30 Miles
0 30 Kilometers
1
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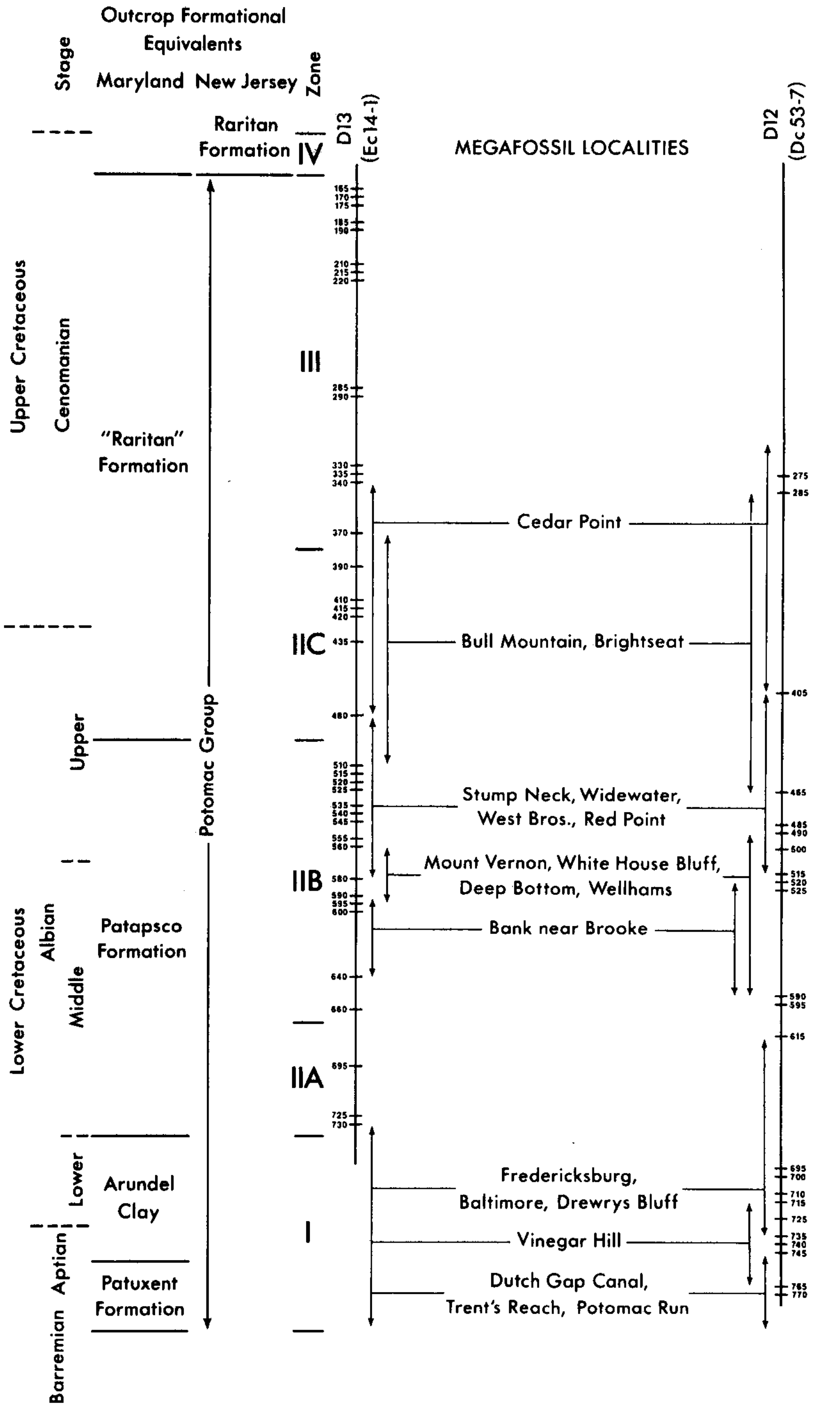
Outcrop Formational Equivalents
Stage
Maryland
New Jersey
Zone
D13 (Ec14-1)
MEGAFOSSIL LOCALITIES
D12 (Dc53-7)
Raritan Formation
IV
Upper Cretaceous
Cenomanian
"Raritan" Formation
III
IIC
Upper
Potomac Group
IIB
Lower Cretaceous
Albian
Middle
Patapsco Formation
IIA
Lower
Arundel Clay
I
Aptian
Patuxent Formation
Barremian
165
170
175
185
190
210
215
220
285
290
330
335
340
370
390
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435
480
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595
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640
660
695
725
730
Cedar Point
Bull Mountain, Brightseat
Stump Neck, Widewater, West Bros., Red Point
Mount Vernon, White House Bluff, Deep Bottom, Wellhams
Bank near Brooke
Fredericksburg, Baltimore, Drewrys Bluff
Vinegar Hill
Dutch Gap Canal, Trent's Reach, Potomac Run
275
285
405
465
485
490
500
515
520
525
590
595
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700
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770

with the younger and lithologically distinct Raritan Formation of New Jersey (e.g., McGee, 1888; Clark, 1897; Berry, 1916). As a result of sedimentological and palynological studies, these "Maryland Raritan" beds are now considered part of the Potomac Group (Weaver et al., 1968; Owens and Sohl, 1969; Wolfe and Pakiser, 1971). Wolfe and Pakiser (1971) have treated them simply as part of the Patapsco Formation, but we prefer to distinguish them informally as the Elk Neck beds (cf. Doyle and Robbins, in press). Outside the Baltimore-Washington area, where the Arundel Clay is not recognizable, there is no consistent way to subdivide the Potomac Group lithologically, and it is therefore referred to as the Potomac Formation.

Direct dating of the Potomac sequence in terms of the standard European stages of the Cretaceous (Table I) is precluded by the absence of marine fossils below the Woodbridge Clay Member of the Raritan Formation, which is dated by mollusks as mid-Cenomanian (N. F. Sohl, unpublished, cited by Doyle, 1969; Wolfe and Pakiser, 1971). In addition, the rapid lithological changes characteristic of such fluvial strata, extremely limited outcrops, and the sporadic distribution of plant megafossils have long frustrated attempts at internal stratigraphic subdivision and correlation. This situation has improved markedly in the past two decades as a result of discovery and investigation of abundant pollen and spores in the Potomac Group. Thanks to published studies on remarkably similar successions and associations of pollen and spore types in faunally dated sediments elsewhere in North America and Europe, palynology has clarified age relations not only within the Potomac-Raritan sequence, but also with the European stages (Groot and Penny, 1960; Groot et al., 1961; Brenner, 1963, 1967; Doyle, 1969, 1973; Wolfe and Pakiser, 1971; Doyle and Robbins, in press).

An important aspect of these studies has been establishment of an informal palynological zonation, beginning with Brenner's (1963) proposal of Zone I and Subzones II-A and II-B as a result of work on well sections of the Patuxent through Patapsco Formations of Maryland. This scheme has been extended

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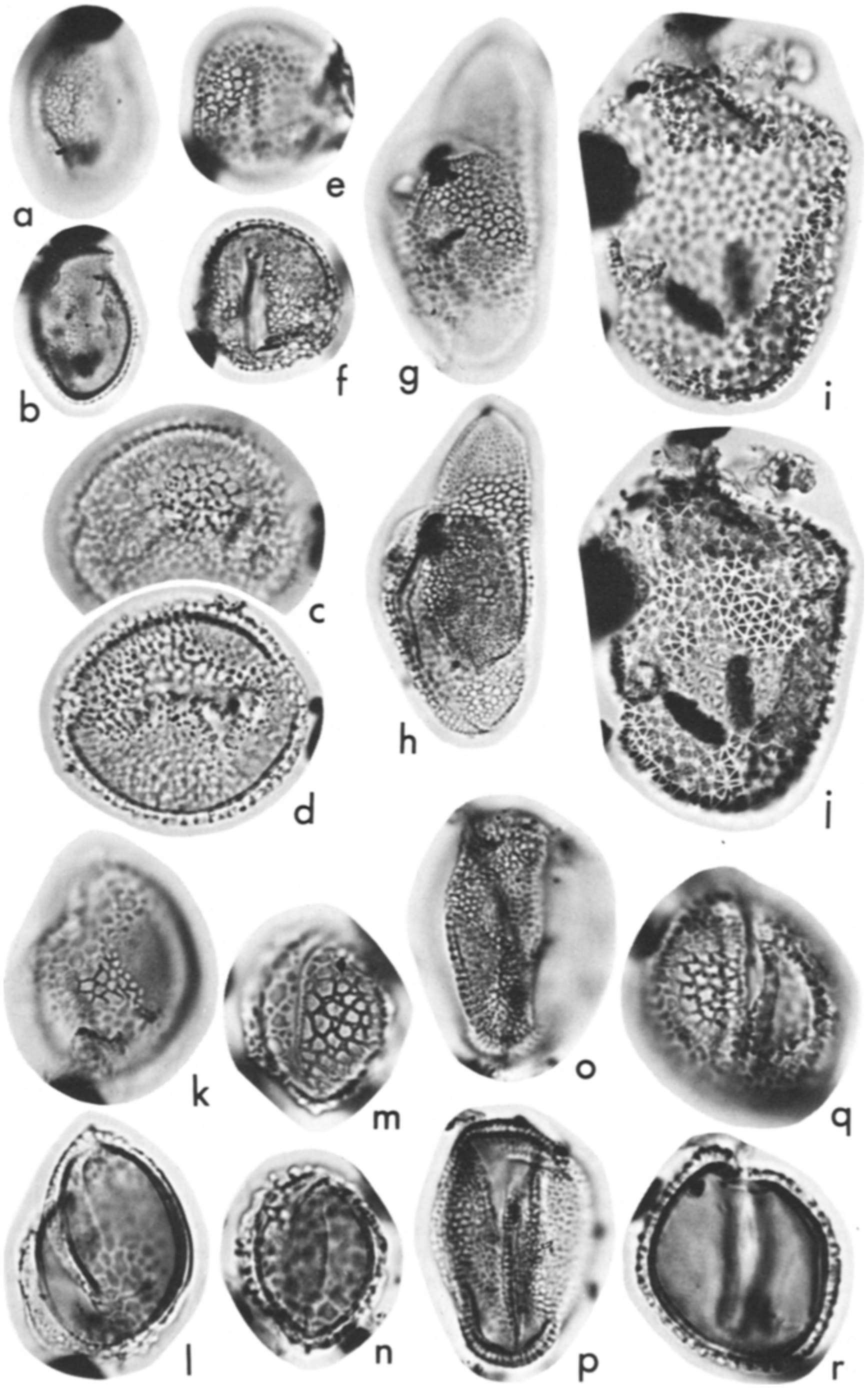
Fig. 3. Subdivisions of the Potomac Group and palynological correlations of its megafossil localities. Correlations are expressed (right) by comparison with two subsurface Potomac Group sequences near Delaware City, Delaware: well D13 (Ec14-1) and well D12 (Dc53-7). Double-headed arrows terminate above and below the depths (in feet) of well samples that are detectably older and younger than the outcrop sample (e.g., the age of Mount Vernon is bracketed as post-595', pre-560' in well D13). Overlaps of arrows (especially next to unsampled well intervals) do not necessarily indicate possible age equivalence. but rather reflect the fact that exact age limits cannot be defined where there is insufficient sampling in the reference section (e.g., Mount Vernon is considered definitely older than Stump Neck). Inferred correlations with the Potomac-Raritan palynological zonation, formational units, and the standard European series, stages, and substages are indicated to the left. (Modified after Doyle and Hickey, 1976.)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to younger beds by recognition of Subzone II-C and Zones III and IV, based on wells penetrating Potomac and Raritan strata in Delaware and southern New Jersey (Doyle, 1973; Wolfe et al., 1975; Doyle and Hickey, 1976; Doyle and Robbins, in press). Strictly speaking, these palynostratigraphic units are defined primarily on the stratigraphic distribution and associations of spore and pollen species, and secondarily on regional changes in relative abundance of major elements of the flora (Brenner, 1963; Doyle and Robbins, in press). However, for the present purposes they and the external correlations derived from them may be roughly characterized in terms of the first rare appearances and subsequent diversification of major angiosperm pollen types. Thus reticulate, columellar monosulcates comparable to those from the Barremian and Aptian of England (Couper, 1958; Kemp, 1968; Hughes, this symposium) occur throughout Zone I (Patuxent Formation and Arundel Clay and their equivalents) and younger units. Very rare reticulate tricolpates enter in the upper part of Zone I (Arundel Clay and equivalents), as in the early Albian of England (Kemp, 1968; Laing, 1975, 1976), and become regularly present and more diverse in Subzones II-A and II-B (Patapsco Formation), as in the middle and late Albian elsewhere (e.g., Hedlund and Norris, 1968). Tricolporoidates, with rudimentary ora in the centers of their colpi, appear and become more abundant in Subzone II-B; in Subzone II-C and Zone III (Elk Neck beds) they include increasing numbers of very small, smooth, and often triangular types similar to those first seen elsewhere near the Albian-Cenomanian boundary (Norris, 1967; Pacltová, 1971; Singh, 1971, 1975; Laing, 1975, 1976). Larger, definitely tricolporate forms are first recognizable in Zone III and become more common in Zone IV (lower members of the Raritan Formation of New Jersey), where they are joined by the first triangular triporates of the Normapolles complex, comparable to species which appear in the middle Cenomanian of Europe (Góczán et al., 1967; Pacltová, 1971;

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Fig. 4. Representative angiosperm pollen from Zone I of the Potomac Group (Barremian-early Albian?), light micrographs, × 1000. Coordinates: UMMP Zeiss RA microscope 4767359.

a, b: cf. *Clavatipollenites hughesii* Couper, Trent's Reach (71-8-1d, 17.2 × 101.1).

c, d: *Clavatipollenites* sp. A, Potomac Run (71-14-1b, 20.0 × 96.0).

e, f: *Retimonocolpites* sp. aff. "*Clavatipollenites*" *minutus* Brenner, Dutch Gap Canal (71-15-1b, 6.0 × 95.8).

g, h: *Liliacidites* sp. A, two grains, Trent's Reach (71-8-1d, 8.0 × 89.1).

i, j: *Stellatopollis* sp., Dutch Gap Canal (71-15-1b, 4.7 × 83.9).

k, l: *Liliacidites* sp. B, Trent's Reach (71-8-1d, 13.2 × 87.8).

m, n: aff. *Retimonocolpites peroreticulatus* (Brenner) Doyle, Dutch Gap Canal (71-15-1a, 8.6 × 87.3).

o, p: aff. *Tricolpites crassimurus* (Groot and Penny) Singh, Baltimore (71-6-1b, 10.1 × 83.1).

q, r: aff. *Retimonocolpites dividuus* Pierce, Fredericksburg (71-21-1c, 12.7 × 84.9).

Laing, 1975, 1976). The inferred ages of Zones I through III—from the Barremian or Aptian through the early Cenomanian—allow us to estimate the duration represented by the Potomac Group as approximately 15-20 million years.

MATERIALS AND METHODS

Our first step in integrating the Potomac Group angiosperm pollen and leaf records (Doyle and Hickey, 1972, 1976) was to correlate Potomac megafossil localities with the zonation scheme outlined above. This was accomplished by comparing the pollen and spore assemblages obtained from matrix samples of the classic Potomac megafossil collections of Fontaine (1889), Ward (1895, 1905), and Berry (1911a, 1916), as well as from several new localities, with reference sections consisting of two wells drilled through the Potomac Formation near Delaware City, Delaware (Brenner, 1967; Doyle and Robbins, in press). These correlations, documented in greater detail in our previous paper (Doyle and Hickey, 1976), are summarized in Figure 3.

This analysis shows that Potomac megafossil localities fall at five main stratigraphic levels, with an unfortunate gap in sampling in Subzone II-A and the base of Subzone II-B. Because pollen grains are so much more transportable than leaves, there are more conspicuous environmentally controlled, or facies, differences among megafossil assemblages from a single presumed horizon than among pollen assemblages. In some cases, notably that of Fredericksburg and Baltimore, these differences were incorrectly ascribed by earlier workers to age effects. Although each locality yields only a partial representation of the total leaf flora, the greater ease of palynological correlation between facies has allowed us to reconstruct what appears to be a fairly complete picture of the range of leaf morphology and ecological adaptations in the angiosperm flora for at least three horizons, namely upper Zone I and the middle and upper parts of Subzone II-B. In some cases, intensive col-

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Figs. 5-10. Angiosperm leaves from Zone I of the Potomac Group. These and all other line drawings of leaves are reproduced from Doyle and Hickey (1976) by permission of Columbia University Press. All figures × 1.

Fig. 5. *Rogersia angustifolia* Fontaine (USNM 192339), from Fredericksburg, Virginia.

Fig. 6. *Vitiphyllum multifidum* Fontaine (USNM 31824) from Baltimore, Maryland. Note the highly irregular venation and lack of venational bracing of the sinuses.

Fig. 7. *Acaciaephyllum spatulatum* Fontaine (USNM 175802A), bent axis with attached obovate, acrodromous leaves from Dutch Gap Canal near Richmond, Virginia.

Fig. 8. Leaf fragment belonging to the *Celastrophyllum latifolium* Fontaine complex from Baltimore, Maryland. Originally described and illustrated as *Celastrophyllum obovatum* Fontaine (in Ward, 1905, p. 560, Pl. 117, Fig. 2; USNM 31814).

Fig. 9. *Proteaephyllum reniforme* Fontaine (USNM 3915) from Fredericksburg, Virginia.

Fig. 10. *Proteaephyllum dentatum* Fontaine (USNM 31820) from Baltimore, Maryland.

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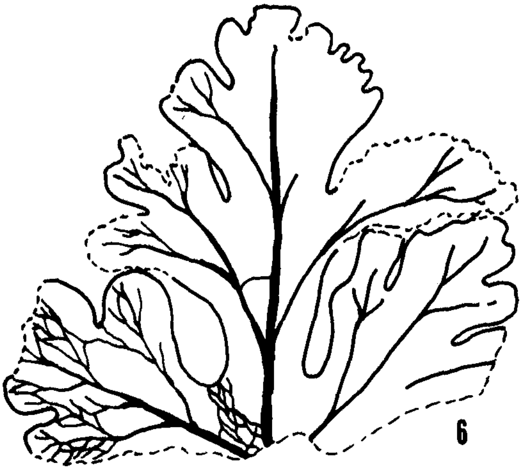

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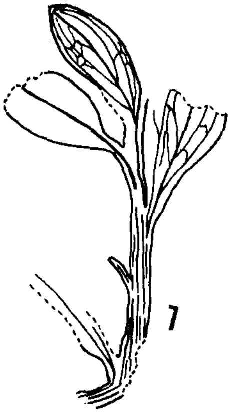

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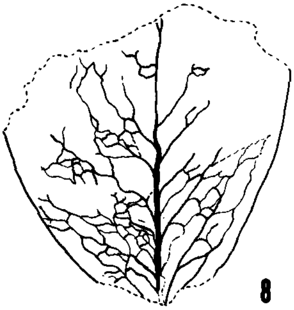

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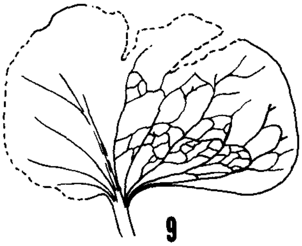

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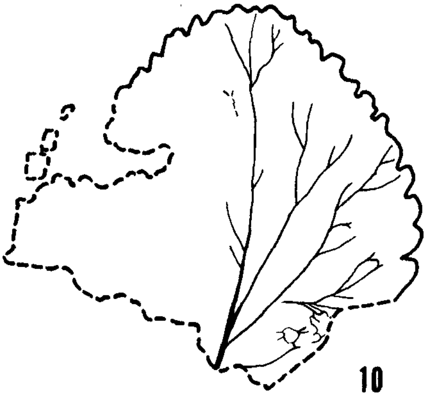

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lecting has revealed overlaps in the leaf assemblages from different facies which help to confirm the palynological correlations. While the greater facies restriction of leaves means that they are less reliable than the pollen for stratigraphic applications and elucidation of evolutionary series, our experience indicates that leaves are more valuable as indicators of ecological associations and habitat preferences of the early angiosperms.

Leaves of Potomac Group angiosperms are rarely complete and often show little contrast between areas of leaf tissue and the matrix. In order to prepare the line drawings for this and our previous report (Doyle and Hickey, 1976), we used a Wild dissecting microscope with a camera lucida attachment. Several days after the first drawing of a leaf was completed, a second drawing was executed on acetate. When this was finished, the two drawings were superimposed and areas of discrepancy resolved by further observation under the microscope.

We thought it highly desirable to provide photographic documentation of the leaf species discussed in this review. These illustrations were prepared either by photographing dry specimens on lithographic film such as DuPont Ortho A Litho or Kodalith Pan, or by photographing specimens immersed in kerosene or ethanol to increase contrast on standard 4 × 5 inch panchromatic film.

THE POTOMAC ANGIOSPERM SEQUENCE

Zone I

Throughout Zone I of Brenner (1963), corresponding to the Patuxent and Arundel Formations, palynofloras consist almost entirely of pteridophyte spores and gymnosperm pollen. In localities correlated with the lower part of the zone, such as Dutch Gap Canal, Trent's Reach, and Potomac Run, the only pollen grains of recognizably angiospermous affinities are several rare monosulcate forms distinguished from monosulcate gymnosperm pollen only on the exine structure criteria discussed above. Despite their rarity, sporadic species distribution, and uniform aperture condition, these angiospermous monosulcates show considerable diversity in size, shape, and exine sculpture. They include small, finely columellar grains with granular sulcus membranes (cf. *Clavatipollenites hughesii* Couper: Figs. 4a,b); similar but larger forms (*Clavatipollenites* sp. A: Figs. 4c,d); finely but distinctly reticulate forms (*Retimonocolpites* and *Liliacidites* species: Figs. 4e–h,k,l); much more coarsely reticulate grains with few or no evident columellae (*Retimonocolpites peroreticulatus* (Brenner) Doyle and related types: Figs. 4m,n); and rare and incompletely understood larger grains with a "crotonoid" or "stellate" sculpture pattern formed by triangular and rectangular projections on top of the tectum (*Stellatopollis* sp.: Figs. 4i,j).

Among living angiosperms, monosulcate pollen occurs only in monocots and in dicots of the putatively primitive subclass Magnoliidae, in the restricted sense of Takhtajan (1969). Most Zone I monosulcates have no characters that suggest affinities with one rather than the other of these two modern angiosperm subgroups. However, certain boat-shaped monosulcates assigned to the genus *Liliacidites* (*L.* sp. A: Figs. 4g,h) show a heterogeneous reticulate pattern with much finer sculpture at the ends of the grain and along the sulcus margins which is widespread in and apparently restricted to monocots today (Doyle, 1973; Walker and Doyle, 1975). Another species has areas of finer sculpture at the presumed proximal pole and along the sulcus margins (*Liliacidites* sp. B: Figs. 4k,l) which suggest a relationship to this complex, but we consider this species more problematically monocotyledonous because of the lack of close modern analogs.

The "crotonoid" sculpture pattern of *Stellatopollis* (Figs. 4i,j) may seem anomalous at this stage of the angiosperm record, since it is most commonly associated with supposedly advanced dicot groups such as Euphorbiaceae, Buxaceae, and Thymeleaceae (cf. Arkhangel'skiy, 1966). However, the fact that *Stellatopollis* is basically monosulcate while the modern groups cited are basically tricolporate or polyporate indicates that the similarity in sculpture patterns is a remarkable example of convergence rather than evidence of relationship. Interestingly, tendencies toward crotonoid sculpture are also seen in the monosulcate monocot genus *Lilium* (Erdtman, 1952; Muller, 1970; Krutzsch, 1970) and in the magnoliid dicot family Atherospermataceae (Doyle et al., 1975; Walker, 1976), where the aperture is an encircling ring furrow, apparently as a result of extension of a distal sulcus (Sampson, 1976). In fact, Zone I *Stellatopollis* is usually preserved as bowl-shaped fragments which suggest half-grains of the atherospermataceous type, but the fact that other *Stellatopollis* species are typically monosuclate (Barremian-Aptian forms from Africa and *S. barghoornii* Doyle from Subzone II-B of the Potomac Group) cautions against premature systematic comparisons with any living group. The likelihood of totally extinct, "experimental" angiosperm lines in the Early Cretaceous is underlined by the existence of coarsely reticulate, non-columellar forms such as *Retimonocolpites peroreticulatus* (Figs. 4m,n) which have no close analogs among modern plants (cf. Doyle et al., 1975).

Since our previous account of this sequence (Doyle and Hickey, 1976), Hughes (this symposium) has reported several reticulate monosulcates comparable to *Retimonocolpites* and crotonoid forms similar to *Stellatopollis* from the Barremian portion of the Wealden sequence in England, in addition to the previously known *Clavatipollenites hughesii* (Couper, 1958; Kemp, 1968). This leads us to revise our previous estimate of the age of the base of Zone I as Aptian, based largely on the supposedly greater diversity of angiospermous monosulcates than in the Wealden section, to possibly as old as Barremian.

Localities from the upper part of Zone I, such as Drewrys Bluff, Fredericksburg, and Baltimore, are marked by the appearance of the first very rare, medium-sized, reticulate tricolpate pollen grains [aff. *Tricolpites crassimurus*

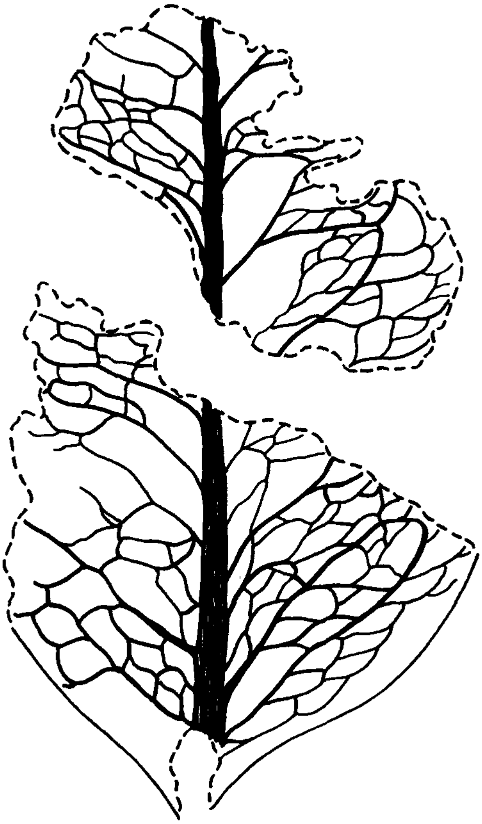

Fig. 11. Broken leaf of *Ficophyllum crassinerve* from Fredericksburg, Virginia (Zone I), × ¾. Apical portion originally described and illustrated as *Ficophyllum crassinerve* Fontaine (1889, p. 292, Pl. 157, Fig. 4; USNM 192347a) and the lower portion as *Proteaephyllum ellipticum* Fontaine (1889, p. 285, Pl. 142, Fig. 1, 1a; USNM 192347b). The fit of the margins of the two pieces of matrix containing this specimen is better seen in the photograph of the leaf in Fig. 13.

(Groot and Penny) Singh: Figs. 4o,p] and the distinctive reticulate monosulcate species aff. *Retimonocolpites dividuus* Pierce (Figs. 4q,r). The first appearance of probably conspecific forms ("*Retitricolpites*" *amplifissus* Laing, "*Clavatipollenites*" *rotundus* Kemp) in the marine lower Albian of England (Kemp, 1968, 1970; Laing, 1975, 1976) supports the suggestion of Wolfe and Pakiser (1971) that the top of Zone I is probably early Albian in age. It may be noted that no transitional forms between tricolpates and older pollen types are known from the Potomac or English sections, although the reticulate sculpture of the first tricolpates is consistent with their derivation from the *Clavatipollenites-Retimonocolpites* complex (cf. Doyle, 1969; Wolfe et al., 1975).

Like angiosperm pollen, angiosperm leaves make up only a very small portion of the total Zone I flora; in fact, whereas at least a few angiosperm pollen grains can be found in most Zone I samples, the leaves occur at only a few localities. The number of distinct leaf types is also low, increasing from approximately five species in the lower part of the zone to ten or twelve above. In addition, they exhibit a limited range of morphological diversity and several features which are unusual among modern angiosperms. We have seen no evidence to contradict the notion that all Zone I angiosperm leaves were simple: a few are known attached to stems (Figs. 7, 20, 22), and none show attachment to rachises or the pervasive asymmetry typical of leaflets of compound leaves, in contrast to the situation in Subzone II-B. Only the elliptic, ovate, and obovate shape classes are represented. Zone I leaves are generally small, most of them no more than 5 cm long, a character also noted for Albian leaves of the USSR by Vakhrameev (1952) and Samylina (1960, 1968). The most marked exception to this generalization is the genus *Ficophyllum* from the upper part of the zone (Figs. 11, 13, 16), some specimens of which exceed 20 cm in length.

The most unusual aspect of Zone I angiosperm leaves is their disorganized venation, as expressed in such characters as the irregular size and shape of the intercostal areas enclosed by the secondary veins, the poor differentiation between secondary and intersecondary veins, and the irregularly ramifying courses and poor differentiation of the tertiary and higher vein orders. The most regular venation is found in the largest *Ficophyllum* leaves (cf. Fig. 16). In addition, Zone I leaves frequently show poor differentiation of the petiole from the blade. These are the same characters that Hickey (1971) used in defining the "first rank" leaf architectural syndrome which a comparative analysis of modern leaves had led him to conclude was primitive for the dicots. These foliar characters, together with the presence of several orders of brochidodromous arches outside the secondary veins ("festooned brochidodromous" venation of Mouton, 1970) and of several apparently discrete strands in the proximal portion of the primary vein (also noted by Wolfe, 1972b), are largely restricted to magnolialian families such as Winteraceae, Himantandraceae, and Canellaceae today (cf. Wolfe et al., 1975; Hickey and Wolfe, 1975).

From a historical point of view, it is interesting that the "archaic" features of Zone I leaves were recognized as such by the earliest authors (Ward, 1888; Fontaine, 1889), but then generally ignored until Wolfe's studies. Reasons for this neglect presumably include the modern-looking names attached to the fossils in question, Berry's (1911a) unfounded suggestion that the Fredericksburg leaves represented *Gnetum* or ferns, and his misassignment of the other major Zone I locality, Baltimore, to the Patapsco Formation.


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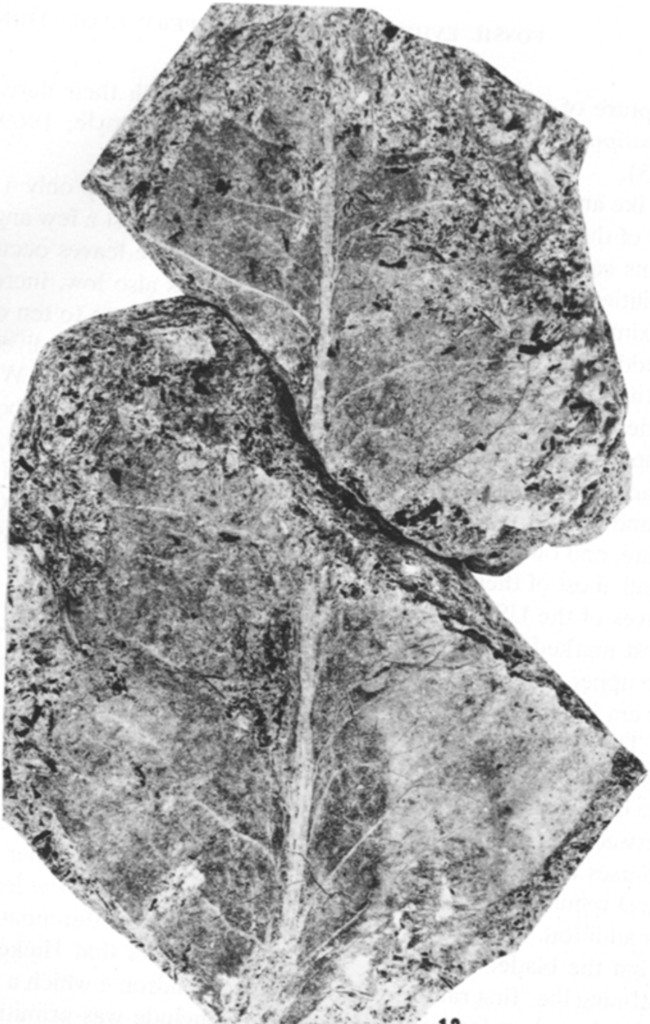
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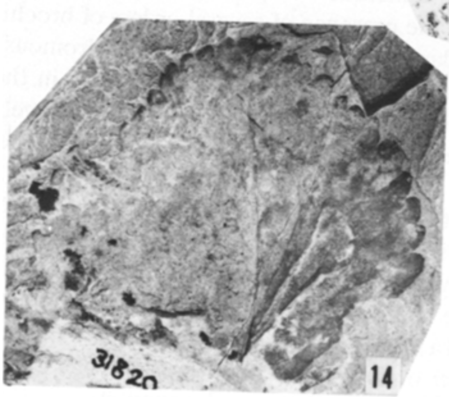

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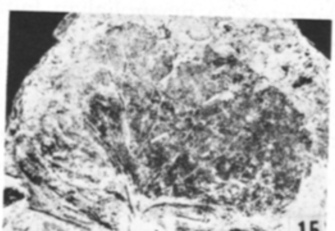
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Another aspect of the limited morphological diversity of Zone I angiosperm leaves is the fact that most species have entire margins. In addition to *Ficophyllum* (Figs. 11, 13, 16), other typical entire-margined leaves with highly irregular brochidodromous venation and poor separation of the blade from the petiole are the narrowly obovate *Rogersia angustifolia* Fontaine (Figs. 5, 12) and the more broadly obovate *Celastrophyllum latifolium* Fontaine (Figs. 8, 19–21), all from the upper part of the zone. Another important type from both lower and upper Zone I is *Proteaephyllum reniforme* Fontaine (Figs. 9, 15), which differs from other members of the flora in its broadly ovate to reniform shape and its tendency toward palmate venation: the crowded secondary veins radiate into the lamina from its base and nearly equal the midvein in thickness. These features and the tendency of the secondaries to dichotomize and loop well within the margin are suggestive of the cordate-peltate complex of Subzone II-B.

Marginal teeth do occur in two forms, *Proteaephyllum dentatum* Fontaine (Figs. 10, 14) from the upper part of Zone I, and the more widespread species *Quercophyllum tenuinerve* Fontaine (Fig. 17). These teeth are irregularly spaced and doubly convex in shape (A-1 of Hickey, 1973) and have a large glandular area near the apex, a combination of characters not found among living dicots, despite the suggestive generic names of the leaves in which they occur. The most highly lobate leaf in Zone I is *Vitiphyllum multifidum* Fontaine (Figs. 6, 18) from the upper Zone I locality at Baltimore; it has features such as highly irregular venation and a lack of bracing by veins of the sinuses between the lobes which suggest that it may have belonged to an herbaceous or aquatic plant.

The existence of features now restricted to monocots in some members of the Zone I pollen flora is paralleled by the occurrence of two monocot-like megafossils in a flora otherwise dominated by dicot-like leaf architectural patterns. The first of these is *Acaciaephyllum spatulatum* Fontaine, best represented by a specimen showing narrowly obovate, entire leaves with long sheathing bases attached helically to a bent and hence by inference herbaceous stem (Figs. 7, 22, 24). In addition to the elongate sheathing leaf bases, the low-angle acrodromous secondary veins fusing successively toward the apex and the fine, chevron-like cross-veins between them represent characters basic to modern monocots (cf. Kaplan, 1973; Doyle, 1973) but rare among dicots.

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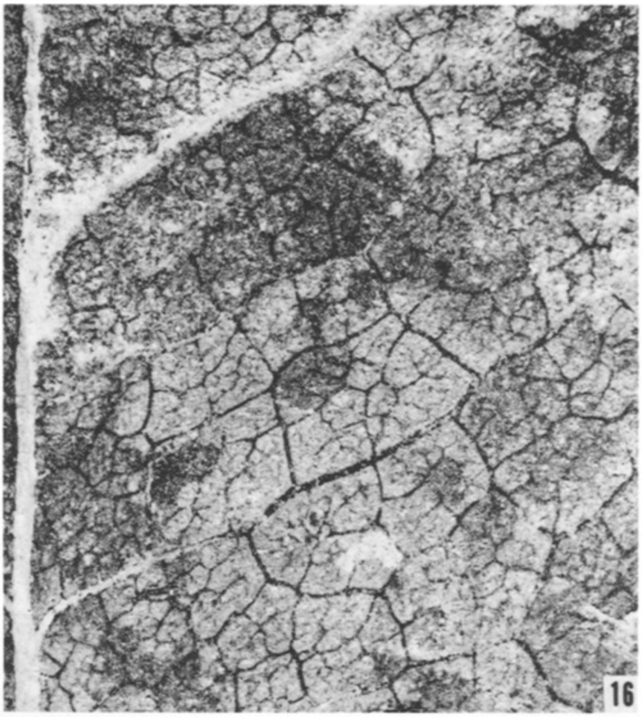
Figs. 12–15. Leaves from Zone I of the Potomac Group, × 1.

Fig. 12. *Rogersia angustifolia*, same specimen as in Fig. 5.

Fig. 13. *Ficophyllum crassinerve*, same specimen as in Fig. 11. Note fit of the two pieces of rock bearing the leaf impression.

Fig. 14. *Proteaephyllum dentatum*, same specimen as in Fig. 10.

Fig. 15. *Proteaephyllum reniforme*, same specimen as in Fig. 9.



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Linear, parallel-veined leaves apparently attached in a rosette make *Plantaginopsis marylandica* Fontaine from Baltimore (cf. Berry, 1911a, Pl. 79, Figs. 1–4; Pl. 80, Figs. 1, 2) a possible second early monocot, but almost no material of this form remains for critical examination.

Finally, *Eucalyptophyllum oblongifolium* Fontaine (Fig. 23) from Fredericksburg departs from other Zone I leaves in possessing an intramarginal vein. Although similar intramarginal veins occur in some modern dicot groups, such as Myrtales and Dilleniidae (cf. Hickey and Wolfe, 1975), the fern-like obliquely elongate areolation of *Eucalyptophyllum* is unlike that of modern dicots, suggesting that it either represents an extinct "experimental" group of early angiosperms (Wolfe et al., 1975) or is not an angiosperm at all.

Besides exhibiting a limited range of morphology, Zone I angiosperm leaf remains are almost entirely restricted to sandstone or sandy beds with cross-bedding or cross-lamination, or micaceous mudstone beds intimately associated with coarser sediment. In contrast, only conifer, cycadopsid, and fern remains are found in equivalent finer-grained, parallel-bedded units. The environmental interpretation of these deposits and its bearing on early angiosperm ecology are discussed below.

Subzone II-B

At the level represented by the next Potomac Group megafossil localities — Brooke, only slightly above the base of Subzone II-B, and Mount Vernon, White House Bluff, Wellhams, and Deep Bottom near the middle of the subzone — the number, total morphological diversity, and abundance of angiosperm pollen taxa have increased dramatically. New angiospermous monosulcate and derived types include large and coarsely reticulate monocotyledonoid forms (*Liliacidites* sp. D: Fig. 25a), definitely monosulcate grains with crotonoid sculpture (*Stellatopollis barghoornii* Doyle: Fig. 25b), and apparent derivatives of *Clavatipollenites* with a branched sulcus or several colpoid apertures (cf. *Asteropollis asteroides* Hedlund and Norris: Fig. 25c; *Stephanocolpites fredericksburgensis* Hedlund and Norris). The generally more abundant tricolpates range from small and finely reticulate [cf. *Tricolpites micromunus* (Groot and Penny) Burger: Figs. 25d,e], to similar but with larger tectal

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Figs. 16–18. Leaves from Zone I of the Potomac Group.

Fig. 16. Detail of the intercostal and ultimate venation of *Ficophyllum crassinerve* (USNM 192353) from Fredericksburg, Virginia, × 5.

Fig. 17. *Quercophyllum tenuinerve* Fontaine, a complete leaf from the west bank of Dutch Gap Canal, Virginia (UMMP specimen), × 2.5.

Fig. 18. *Vitiphyllum multifidum* Fontaine (USNM 222847) from Federal Hill (Covington Street) in Baltimore, Maryland, × 2.

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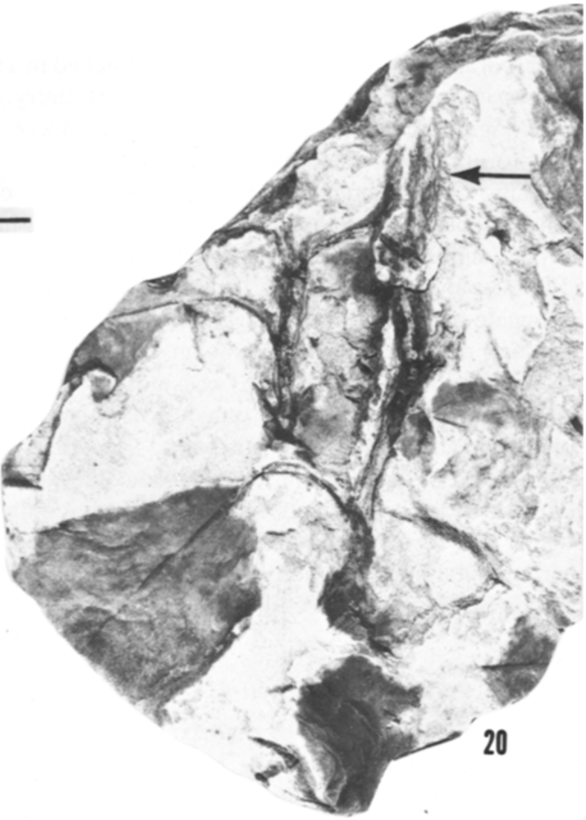

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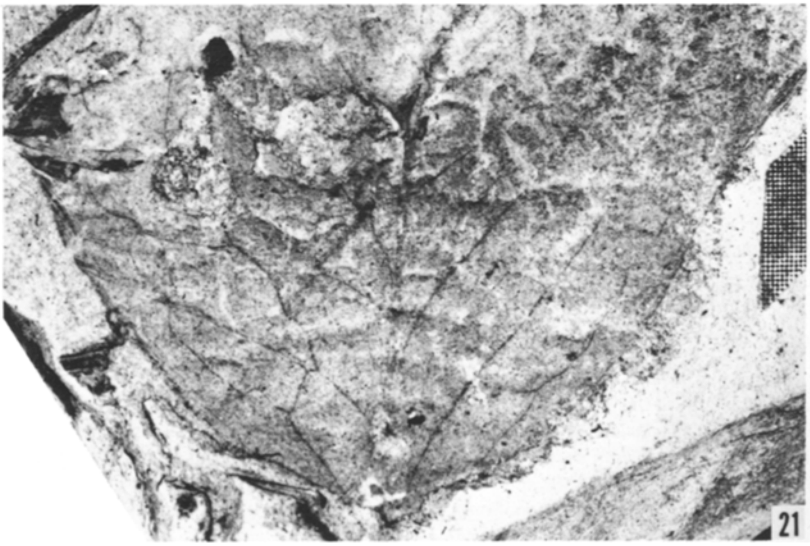

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perforations at the poles (cf. "*Retitricolpites*" *fragosus* Hedlund and Norris: Figs. 25f,g), small and tectate (cf. *Tricolpites albiensis* Kemp: Figs. 25l,m), very large ["*Retitricolpites*" *geranioides* (Couper) Brenner: Fig. 25j], rugulo-reticulate and striato-reticulate ("*Retitricolpites*" *vermimurus* Brenner: Figs. 25h,i; cf. "*Retitricolpites*" *paraneus* Norris), and oblate, thin-walled, and with three colpoid apertures and a thin spot at one pole (*Penetetrapites mollis* Hedlund and Norris: Fig. 25k). One of the most unusual elements is a species with triporoidate grains united in permanent tetrads (aff. *Ajatipollis* sp. A: Fig. 25n). In their detailed species composition, these floras, especially Mount Vernon, correlate closely with the flora described by Hedlund and Norris (1968) from Fredericksburgian strata of Oklahoma, whose nearby Texas equivalents are dated by ammonites as late middle Albian (Young, 1966). This correlation constitutes one of the strongest ties between the Potomac Group and the standard European stage sequence (cf. Doyle and Robbins, in press).

Pollen assemblages from the megafossil localities just cited vary markedly in the relative abundance of elements, with tricolpates especially abundant at Brooke and angiospermous monosulcates at Mount Vernon and White House Bluff. All three localities yield higher percentages of angiosperm pollen than most correlative and many younger outcrop and well samples. Since detailed comparisons of the species concerned indicate that Brooke, Mount Vernon, and White House Bluff correlate with only slightly different horizons in the Delaware City wells, these quantitative differences are presumably due to local environmental effects. This supposition is confirmed by the sedimentology of the localities and their leaf associations, as discussed below.

Megafossil localities correlated with the upper portion of Subzone II-B include Stump Neck, Widewater, and new localities at Red Point and the West Brothers clay pit. Pollen assemblages from these localities differ from those of middle Subzone II-B mostly in detailed species composition, notably the presence or greater abundance of very small, finely reticulate tricolporoidate grains closely related to older tricolpate species, such as aff. *Tricolpites micromunus* (Figs. 25o,p) and *Tricolpites minutus* (Brenner) Dettmann (Figs. 25q,r), and the disappearance of certain groups, such as the *Asteropollis*-*Stephanocolpites* complex. A few samples yield very rare, small, smooth tricol-

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Figs. 19–21. *Celastrophyllum obovatum* from Federal Hill in Baltimore, Maryland (Zone I).

Fig. 19. A portion of the axis, indicated by the arrow in Fig. 20, showing elliptical scars (arrow) in an apparent spiral arrangement, × 5.

Fig. 20. Two axes showing spiral attachment of leaves (USNM 222848), × 1. The left-hand axis with attached leaf base lies below the plane of the right-hand one.

Fig. 21. Detail of the base of the specimen illustrated in Fig. 8, showing secondary and tertiary venation, × 3.

poroidates showing the first hints of the tendency toward triangular shape which becomes prevalent in Zone III (aff. "*Tricolporopollenites*" *triangulus* Groot, Penny and Groot: Figs. 25s,t). As noted by Brenner (1963), younger Subzone II-B pollen floras also show a gradual increase in abundance of *Araucaria*-, *Phyllocladus*-, *Sciadopitys*-, and *Sequoia*-like conifer pollen types more characteristic of the Late Cretaceous, a trend which continues in Subzone II-C and Zone III.

In contrast to their sporadic occurrence and generalized morphology in Zone I, angiosperm leaves in Subzone II-B are locally abundant, consist of an increased number and diversity of morphological types, and are distributed in a wider variety of lithofacies. Furthermore, their leaf architecture is characterized by a general increase in vein regularity, or rank (Hickey, 1971).

Among the new groups appearing in Subzone II-B is an intergrading complex of palmately veined leaves which vary from ovate-cordate or lobate to peltate. A common feature of these leaves, recalling *Proteaephyllum reniforme* of Zone I, is the tendency of their radiating primary veins to dichotomize and form several orders of symmetrical loops well within the margin. The ovate-cordate to lobate group is best represented by "*Populus*" *potomacensis* Ward (Figs. 27, 30), with a base ranging from shallowly lobate to so deeply cordate as to appear peltate in imperfect specimens. Its actinodromous primary veins are highly regular. *Populophyllum reniforme* Fontaine (Figs. 29, 31) displays a similar variation in the depth of its basal lobation, but its venation is much less regular. Peltate leaves appear to be already represented at the Brooke horizon by *Menispermites virginiensis* Fontaine (Fig. 26), with up to ten moderately regular primary veins. However, because of the tendency for the leaf base to be folded, it cannot be determined whether this species is markedly peltate or has only a very narrow flange of laminar tissue passing around the adaxial side of the petiole attachment. Conspicuously peltate leaves, illustrated by *Menispermites* "*tenuinervis*" Fontaine (Fig. 28), are well established at the slightly younger Mount Vernon-White House Bluff horizon.

Several functional analogies with modern leaves and sedimentary associations (discussed further below) suggest an aquatic habit for at least the peltate members of this complex. Not only do they tend toward the circular shape and radiating venation pattern theoretically advantageous where support is of low

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Figs. 22–24. Leaves from Zone I of the Potomac Group.

Fig. 22. Axis of *Acaciaephyllum spatulatum* with attached leaves, × 1. Specimen illustrated in Fig. 7.

Fig. 23. *Eucalyptophyllum oblongifolium* Fontaine (USNM 3273) from Fredericksburg, Virginia, × 3. Note the intramarginal vein and the elongate, irregularly shaped areoles.

Fig. 24. *Acaciaephyllum spatulatum*, detail of the specimen in Fig. 22 showing the venation of the uppermost leaf, × 5.

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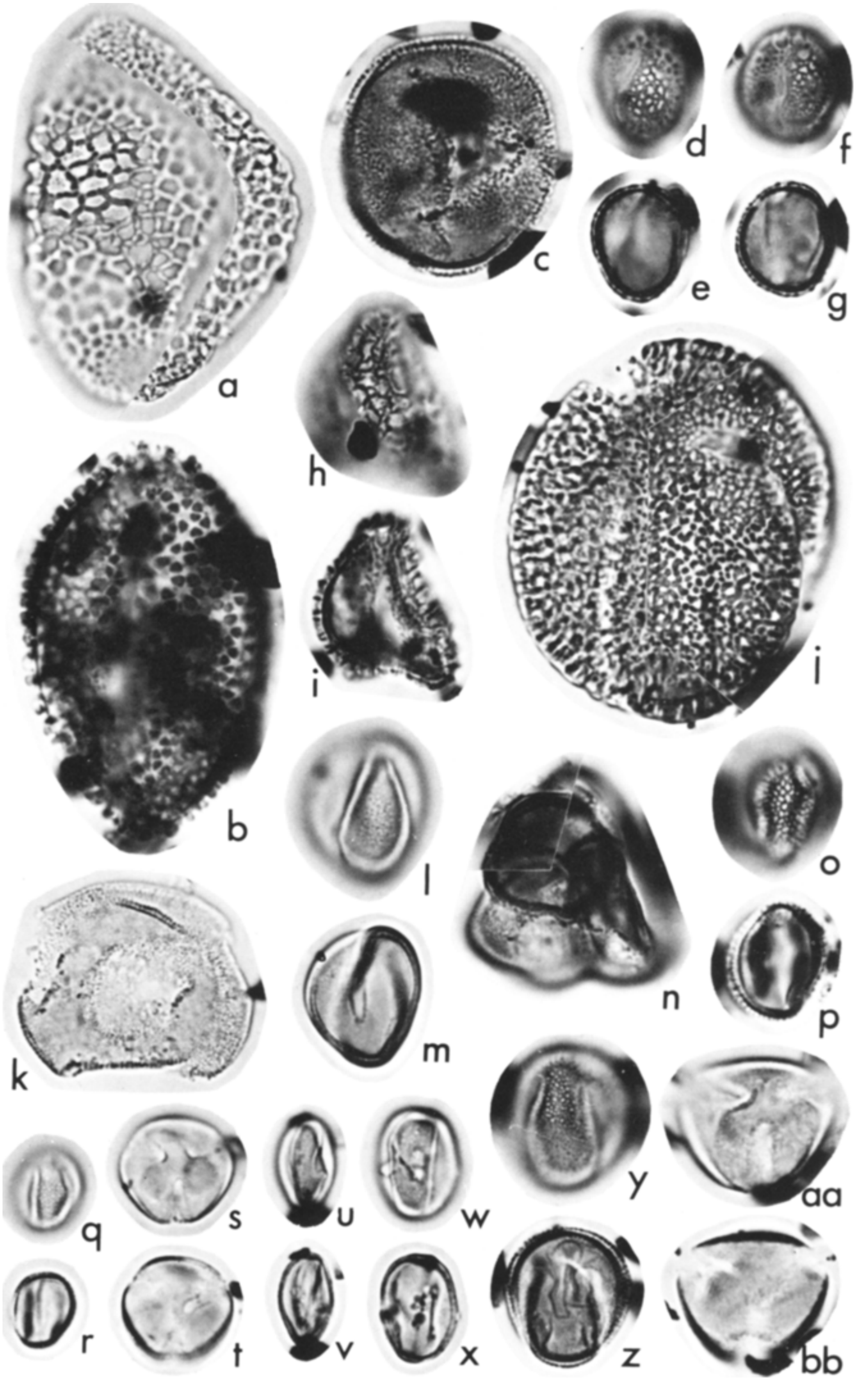
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priority (Givnish, 1976), but their characteristic tendency for repeated dichotomy and looping of the primary veins is also more analogous to the venation of such unrelated modern aquatics as Nymphaeales and *Nymphoides* than to the near-marginal camptodromous venation of peltate and cordate leaves of terrestrial herbs such as *Hydrocotyle* or lianas such as Menispermaceae. Other suggestive features are the long, apparently lax petioles of some species, and the characteristic variation between flat and funnel-shaped bases of both peltate and cordate forms (cf. Figs. 28, 29, 31), similar to the variation between floating and emergent leaves of *Nelumbo*. Another probable aquatic adaptation seen in Subzone II-B is the alveolar pattern of hexagonal air chambers on the surface of a less completely known leaf type, *Aristolochiaephyllum cellulare* Ward (Fig. 32). These inferences are strengthened by the occurrence of these leaves in parallel-laminated claystone and siltstone beds. At the Quantico locality, palynologically barren but believed to correlate with the upper part of Subzone II-B on geographic position and the presence of pinnately compound *Sapindopsis* leaves (cf. below), peltate leaves occur in clusters spaced about a meter apart along the outcrop of such a bed, suggesting growth in place in a pond habitat.

Simple, pinnately veined, first or second rank leaves, both entire and with

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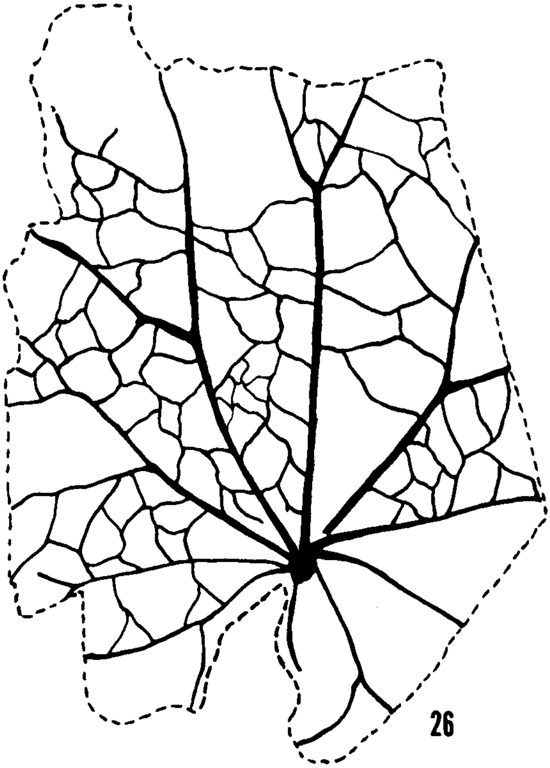
Fig. 25. Representative angiosperm pollen from Subzone II-B through Zone III of the Potomac Group (middle Albian-early Cenomanian?), light micrographs, × 1000. Coordinates: UMMP Zeiss RA microscope 4767359.

Lower-middle Subzone II-B (late middle Albian?):
a: *Liliacidites* sp. D, White House Bluff (71-5-1b, 21.2 × 88.1).
b: *Stellatopollis barghoornii* Doyle, Brooke (71-13-1a, 13.4 × 88.6).
c: cf. *Asteropollis asteroides* Hedlund and Norris, Brooke (71-13-1a, 17.0 × 97.9).
d, e: cf. *Tricolpites micromunus* (Groot and Penny) Burger, Brooke (71-13-1b, 6.9 × 85.2).
f, g: cf. *"Retitricolpites" fragosus* Hedlund and Norris, Brooke (71-13-1a, 11.6 × 95.5).
h, i: *"Retitricolpites" vermimurus* Brenner, Brooke (71-13-1b, 3.3 × 91.4).
j: *"Retitricolpites" geranoides* (Couper) Brenner, Mount Vernon (71-4-1b, 11.3 × 95.6).
k: *Penetetrapites mollis* Hedlund and Norris, White House Bluff (71-5-1b, 11.6 × 98.1).
l, m: cf. *Tricolpites albiensis* Kemp, White House Bluff (71-5-1b, 6.4 × 84.4).
n: aff. *Ajatipollis* sp. A, tetrad, Brooke (71-13-1a, 15.2 × 92.8).

Upper Subzone II-B (late Albian?):
o, p: aff. *Tricolpites micromunus*, tricolporoidate, Widewater (71-9-1a, 15.4 × 89.0).
q, r: *Tricolpites minutus* (Brenner) Dettmann, Stump Neck (71-18-1b, 7.7 × 101.7).
s, t: aff. *"Tricolporopollenites" triangulus* Groot, Penny and Groot, Widewater (71-9-1a, 13.1 × 100.1).

Subzone II-C and/or lower Zone III (latest Albian-early Cenomanian?):
u, v: cf. *Tricolporoidites subtilis* Pacltová, Bull Mountain (71-1-1a, 7.1 × 92.0).
w, x: cf. *"Tricolporopollenites" distinctus* Groot and Penny, Bull Mountain (71-1-1a, 16.5 × 87.6).
y, z: aff. *Tricolpites nemejci* Pacltová, Cedar Point (71-3-1b, 9.4 × 91.8).
aa, bb: *Tricolporoidites* sp. A, Cedar Point (71-3-1b, 5.1 × 85.3).



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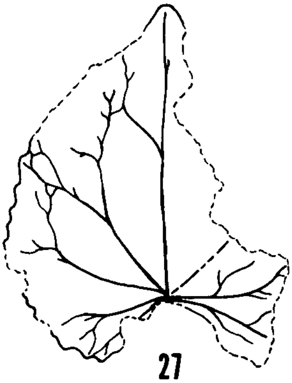

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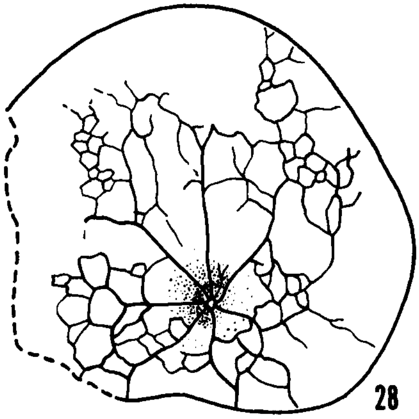

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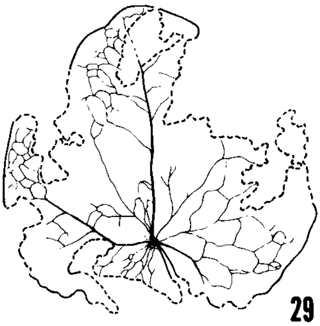

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doubly convex teeth, persist and diversify in Subzone II-B (cf. Doyle and Hickey, 1976). The only possibly monocotyledonous megafossil recognized from this interval is *Alismaphyllum Victor-Masoni* (Ward) Berry (cf. Ward, 1895, Pl. 3, Fig. 5; Doyle, 1973, Fig. 3f), an ovate, sagittate leaf with apically converging, campylodromous secondary veins.

The most striking innovation in the angiosperm megafossil flora of lower-middle Subzone II-B is the appearance of pinnately and palmately lobed leaves. At the Brooke locality, pinnatifid leaves here all assigned to *Sapindopsis magnifolia* Fontaine (Figs. 33–38) form a nearly continuous mat just above the base of a mudstone containing lignified conifer wood and charcoal fragments which abruptly overlies a sandstone (cf. Fig. 69 and below). These leaves are highly variable in their pattern of lobation, sometimes with two rather than three apical lobes (Fig. 37) and with varying degrees of decurrency of the lobes onto the rachis (Figs. 34, 35), but the rachis always bears at least narrow wings of laminar tissue which are continuous with the lobes. This contrasts with the situation in modern sapindaceous leaves with winged rachises with which *Sapindopsis* was originally compared, where the lamina of each leaflet and the rachial wing are constricted at the point where the leaflet is attached. The primary veins of the distal pair of lateral lobes branch from the midvein of the whole leaf at slightly different levels (i.e., palinactinodromously). The higher order venation is also irregular, ranging from high first to low second rank (Hickey, 1971), with closely spaced secondary veins forming irregular brochidodromous loops (Figs. 36, 38). These leaves are associated with apparent inflorescences consisting of an axis bearing small, head-like structures (Fig. 34, arrow), comparable to those associated with younger pinnately compound and palmately lobed leaves.

Leaves similar to Brooke *Sapindopsis* in their general lobation pattern but with marginal teeth—*Sapindopsis belviderensis* Berry—are known from middle or upper Albian strata of the Cheyenne Sandstone of Kansas (Berry, 1922)

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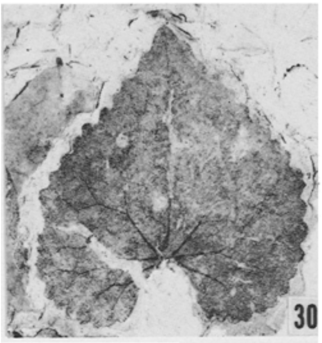
Figs. 26–29. Line drawings of peltate and cordate leaves from the middle part of Subzone II-B of the Potomac Group.

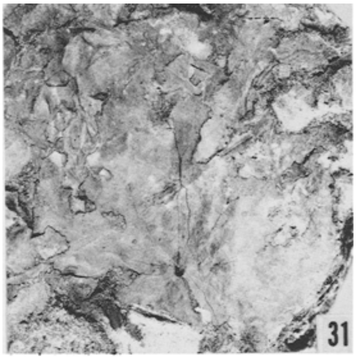
Fig. 26. *Menispermites virginiensis* Fontaine (USNM 3248) from Brooke, Virginia, × ¾. Fragment of a large, problematically peltate leaf showing the highest degree of vein regularity reached in this group.

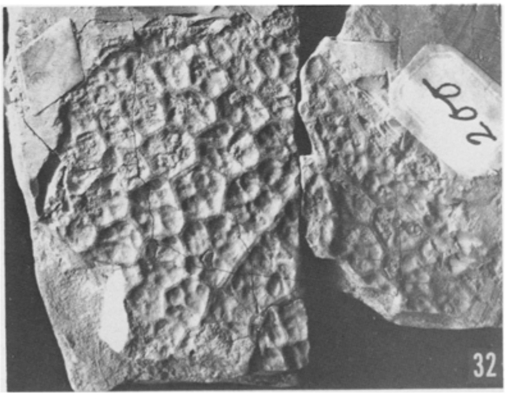
Fig. 27. "*Populus*" *potomacensis* Ward (USNM 205257), a shallowly cordate leaf from Mount Vernon, Virginia, × 1.

Fig. 28. *Menispermites* "*tenuinervis*" Fontaine (USNM 5392) from Mount Vernon, Virginia, × 1. A small, clearly peltate leaf with an apparently funnel-form base and somewhat less regular venation.

Fig. 29. *Populophyllum reniforme* Fontaine (USNM 201913) from Aquia Creek, Virginia, × 1. A very deeply cordate leaf with an apparently funnel-form leaf base.







Figs. 30–32. Members of the cordate and peltate leaf complex from the middle part of Subzone II-B of the Potomac Group, × 1.
Fig. 30. "*Populus*" *potomacensis* (USNM 5387) from Mount Vernon, Virginia.
Fig. 31. *Populophyllum reniforme* (USNM 201913) from Aquia Creek, Virginia.
Fig. 32. *Aristolochiaephyllum cullulare* Ward (USNM 31736) from Mount Vernon, Virginia, with the venation forming the framework for the well developed network of deeply impressed hexagonal cells or alveolae.

and the upper part of the Lakota Formation of the Black Hills of South Dakota and Wyoming (Figs. 39, 40). In the Black Hills the lithofacies relationships of this form, which is dominant where it occurs, are similar to those of *Sapindopsis* at Brooke and younger Potomac localities, namely, just above abrupt changes from sandstone to relatively coarse beds containing clay pebbles, lignified conifer axes, and charcoal (Hickey, personal observation).

The oldest member of the palmately lobed or "platanoid" complex, *Araliaephyllum obtusilobum* Fontaine from Brooke (Figs. 41, 42), is characterized by two (rarely one) large lateral lobes and palinactinodromous primary venation. Occasionally there is a small accessory lobe at the base of each of the

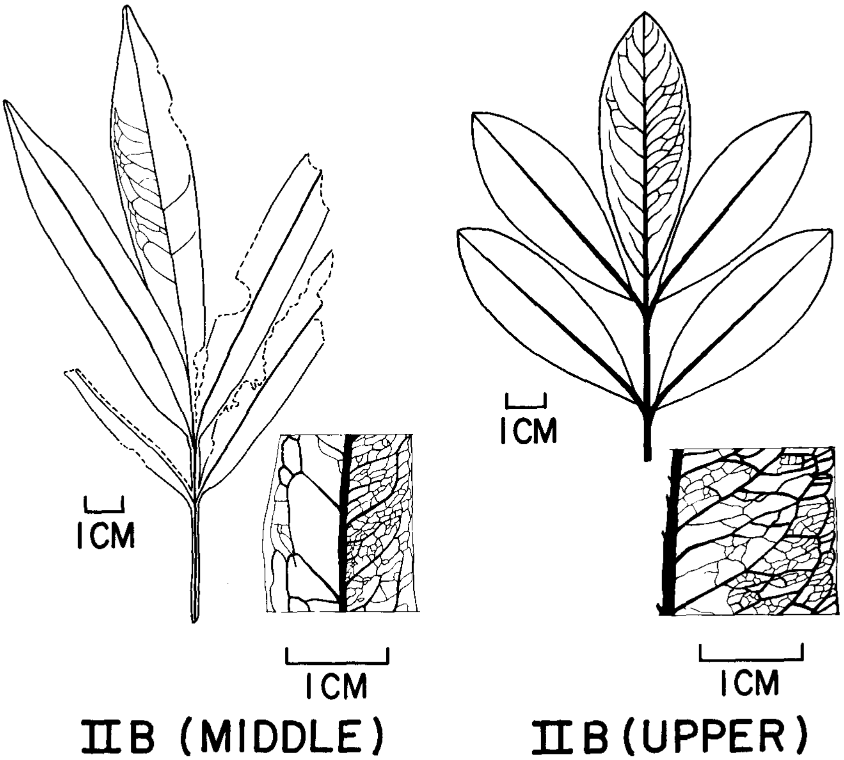
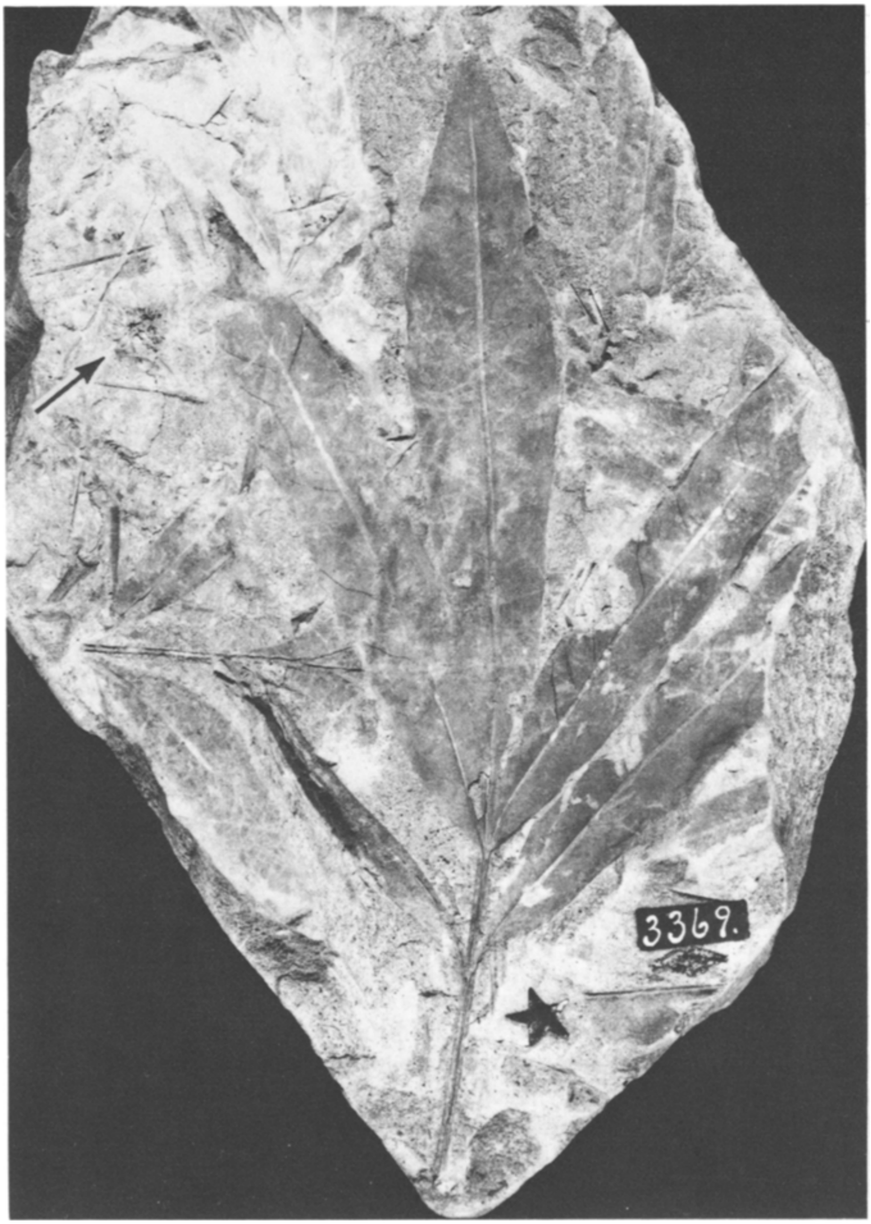


Fig. 33. The Potomac *Sapindopsis* sequence, illustrating the trend from pinnatifid to pinnately compound leaves and the increasing vein regularity found in this complex. The left-hand leaf is the same as that pictured in Fig. 34, and it and the leaf used to illustrate ultimate venation (USNM 201915) are from Brooke, Virginia. The pinnately compound leaf on the right is a modification of Berry's (1911a) Pl. 86, Fig. 1, and is actually a composite representing the general features of two species of *Sapindopsis*, based on numerous incomplete specimens from Red Point and the West Brothers clay pit in Maryland. The right-hand inset of the venation is from a new species of *Sapindopsis* from Red Point, Maryland (USNM 201919).

large lateral lobes. In contrast to younger platanoids, the secondary veins in this form are only moderately regular and its tertiaries are weak and irregular. Brooke and Deep Bottom platanoids show a tendency to occur in coarser-grained sediment than does *Sapindopsis*, but this effect is less pronounced than in higher units.

Although changes in the angiosperm pollen flora between middle and upper Subzone II-B are somewhat gradational, several important advances are recog-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nizable in the megafossil record. In addition to the Quantico peltates cited above, which represent a continuation of types seen at the Mount Vernon horizon, there are several new members of the peltate-cordate actinodromous complex. The most important of these is *Menispermites potomacensis* Berry (Fig. 43), an ovate leaf often with a shallowly lobate margin and with several primary veins fanning out from the decurrent base. Another is an irregularly lobate leaf from Quantico with low rank venation suggesting that of *Populophyllum reniforme* (Fig. 44). An important advance in the pinnately veined, simple-leafed component of the flora is the first occurrence of straight-convex (B-1) teeth in a small, oblong, closely serrate leaf from Red Point (Fig. 52).

Localities from the upper part of Subzone II-B also yield the first truly pinnately compound leaves, with each leaflet attached to the rachis by a distinct petiolule (Figs. 33, 45–48). Bases of the lateral leaflets vary from slightly to strongly asymmetrical. These leaves have more regular patterns of secondary and tertiary venation than did Brooke *Sapindopsis*, particularly a tendency for the tertiaries to be oriented perpendicularly to the leaflet midvein (cf. Fig. 33). Nevertheless, their similar patterns of variation in organization, such as variation between two and three apical leaflets and tendencies for palmate lobation of the terminal leaflet, and similarities in their fine venation and cuticle structure (Mersky, 1973; Upchurch, unpublished) support the concept that these compound leaves were derived from the pinnatifid complex represented at Brooke, which incidentally persists to this level as a rare element.

Other aspects of its leaf architectural variation indicate that the pinnately compound complex was evolving rapidly in late Subzone II-B times. Leaf architectural and cuticular analysis demonstrate at least one type with laminar resin glands and another without. Some specimens also show a transition from entire to toothed margins (Figs. 46–48). Investigation of these teeth is only in its preliminary stages, but they show a number of features such as concave-convex (C-1) shape, deflection and branching of the principal vein just before entering the tooth, converging higher order lateral veins, and suggestions of a glandular tooth apex with a possible apical process which are mainly found in the subclass Rosidae today (Hickey and Wolfe, 1975); however, a few of these features are also found in the Hamamelididae.

New members of the palmately lobed platanoid complex also showing

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Fig. 34. *Sapindopsis magnifolia* from Brooke, Virginia (USNM 3369), × 1. This specimen is characterized by a narrow wing of foliar tissue along the rachis. Note the associated globose "head" (at arrow) inferred to represent part of an inflorescence. The pencil lines approximating the courses of the secondary veins in two of the leaf segments are rendered in sharp detail by the current method of high contrast photography. These appear to have been added before the original plates of the specimens were made (Berry, 1911a, Pl. 81, Fig. 1).

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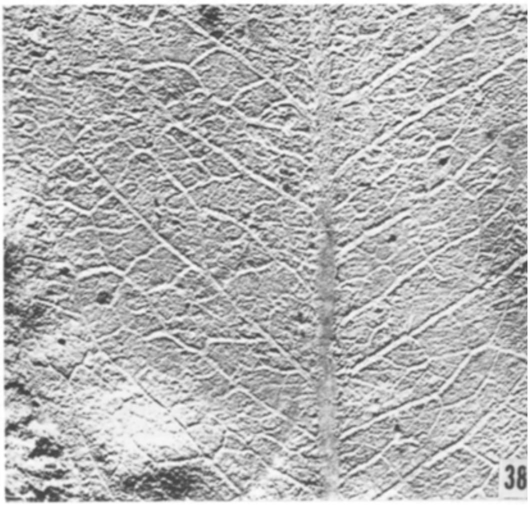

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moderately more organized venation and a tendency for larger numbers of lobes, typified by "*Sassafras*" *potomacensis* Berry, appear in coarser facies of upper Subzone II-B (Figs. 42, 49–51). Although the secondary and tertiary veins of "*Sassafras*" *potomacensis* are more regular than those of *Araliaephyllum obtusilobum* from Brooke, its secondaries are still thin, and its thin, only moderately regular, distantly spaced, oblique tertiary veins differ from the thick, perpendicularly percurrent, closely spaced tertiaries of later platanoids such as *Araliopsoides cretacea* (Newberry) Berry (cf. Fig. 42). Interestingly, many leaves of "*S.*" *potomacensis* bear round structures interpreted as the oldest known insect galls (Fig. 51).

Angiosperm leaves from Subzone II-B are closely analogous to those known from presumably contemporaneous middle and late Albian floras of many other parts of Laurasia. Peltate, lobate-cordate, palmately lobed, and both entire-margined and serrate low rank, simple leaves make up the angiosperm component of middle Albian floras of Portugal, Kazakhstan, and eastern Siberia (Teixeira, 1948; Vakhrameev, 1952; Samylina, 1960, 1968; Krassilov, 1967). In addition to many of the types just cited, pinnatifid leaves of the *Sapindopsis* type, sometimes with marginal teeth (*S. belviderensis*), occur in the middle or upper Albian of western Canada (Bell, 1956), the Cheyenne Sandstone of Kansas (Berry, 1922), and the upper Lakota and Fall River Formations of the Black Hills (cf. Figs. 39, 40). Truly pinnately compound leaves are known from upper Albian-Cenomanian deposits of Kazakhstan (*Anacardites neuburgae*: Vakhrameev, 1952) and the Dakota Group of Kansas (Lesquereux, 1892).

Subzone II-C and Zone III

Pollen floras from Subzone II-C localities such as Brightseat and Bull Mountain in the "Maryland Raritan" or Elk Neck beds are similar to those of Subzone II-B in most respects, but they can be distinguished on the rarity or absence of certain typical Subzone II-B species, such as "*Retitricolpites*" *vermimurus*, the presence of two species of the bizarre conifer *Rugubivesi-*

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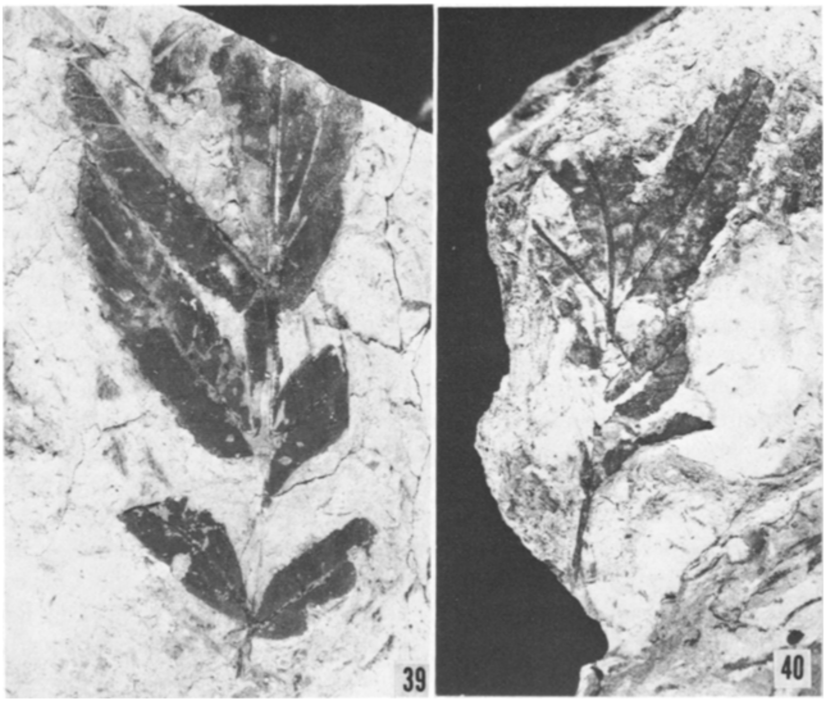
Figs. 35–38. *Sapindopsis magnifolia* from Brooke, Virginia (middle Subzone II-B).

Fig. 35. Terminal portion of a leaf showing characteristic lobing, × 1. The lateral primaries arise in palinactinodromous fashion and the primary vein is markedly thickened below this point.

Fig. 36. Marginal and ultimate venation of a relatively narrow leaflet (USNM 222849, originally described and figured as *S. variabilis* by Fontaine, 1889, Pl. 152, Fig. 2), × 5.

Fig. 37. Specimen showing bifurcation of the terminal lobe of the leaf, a mode which occurs as an occasional variant of the more typical lobing shown in Fig. 34 (USNM 222850, originally described and figured as *S. variabilis* by Fontaine, 1889, Pl. 155, Fig. 5), × 1.

Fig. 38. Detail of the venation of a relatively broad leaf lobe (USNM 201915), × 5.



Figs. 39, 40. *Sapindopsis belviderensis* Berry from the upper Lakota Formation on Oak Creek, Crook County, Wyoming, × 1.
Fig. 39. Relatively complete specimen showing pinnatifid part of the leaf (USNM 222851).
Fig. 40. Upper part of leaf showing characteristic lobing and palinactinodromous primary veins (USNM 222852).

culites, and the appearance of several new species of very small, smooth tricolporoidates, such as cf. *Tricolporoidites subtilis* Pacltová (Figs. 25u,v) and cf. "*Tricolporopollenites*" *distinctus* Groot and Penny (Figs. 25w,x). The Cedar Point locality has a few additional forms, such as slightly larger triangular tricolporoidates (*Tricolporoidites* sp. A: Figs. 25aa,bb) and characteristic small, prolate tricolpates with tall, thin columellae (aff. *Tricolpites nemejci* Pacltová: Figs. 25y,z) which suggest basal Zone III in the Delaware City wells and early Cenomanian floras of other regions (cf. Pacltová, 1971; Singh, 1971, 1975; Laing, 1975, 1976).

The angiosperm megafossil floras from these and palynologically undated but presumably correlative localities (e.g., White Point on Elk Neck) are dominated by new members of the palmately lobed platanoid complex, such as *Araliopsoides cretacea* (Newberry) Berry (Figs. 42, 53, 54), and apparently derived unlobed, pinnately veined leaves comparable to *Protophyllum*, *Betu-*

Fig. 41. A member of the *Araliaephyllum obtusilobum* Fontaine complex from Brooke, Virginia (USNM 201916), middle Subzone II-B, × 1. Specimen originally identified as *A. aceroides* by Fontaine (1889, p. 319, Pl. 162, Fig. 2). Note the weakness and irregularity of the second and third order veins.

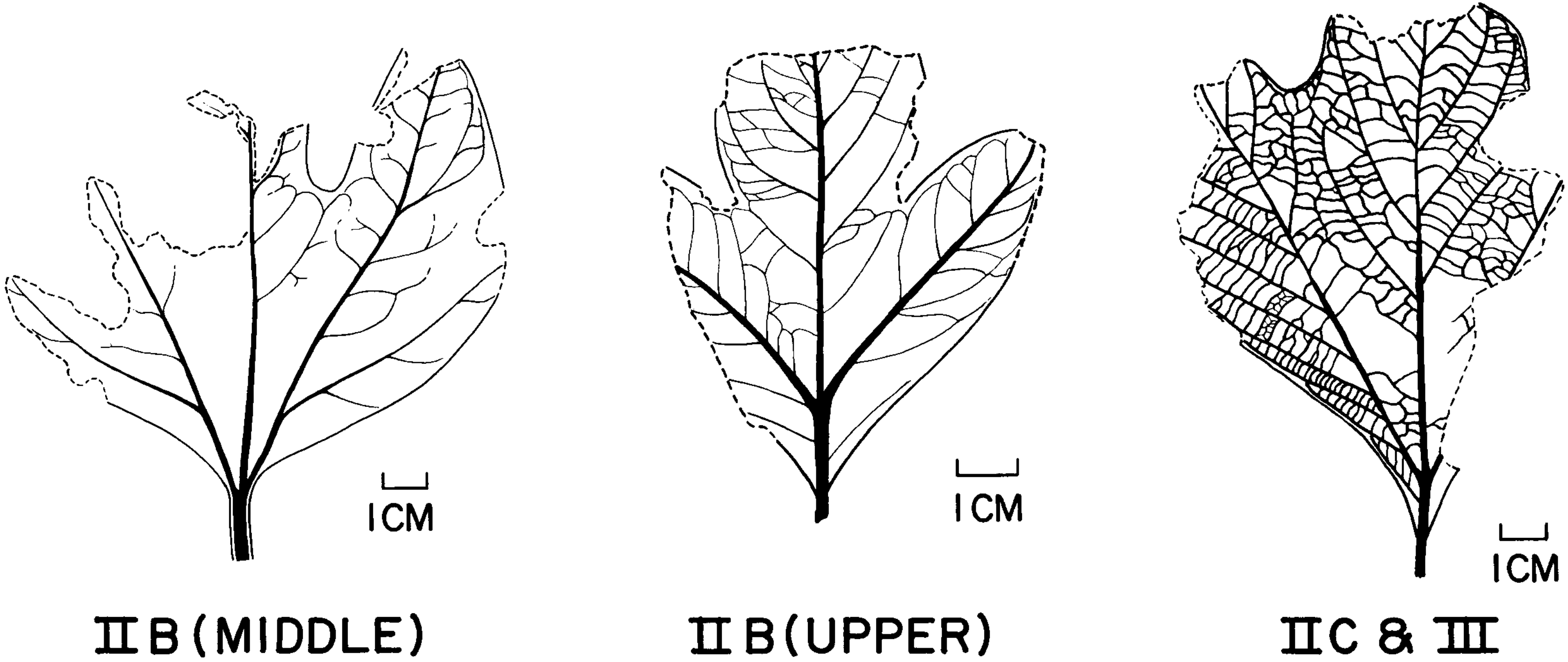
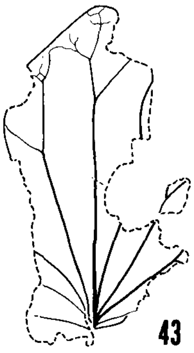


Fig. 42. The Potomac "platanoid" sequence, illustrating the progressive strengthening and increase in regularity of venation which takes place in representatives of the palmately lobed, platanoid leaf complex going upward in the Potomac section. Left-hand leaf, a member of the *Araliaephyllum obtusilobum* complex from Brooke, Virginia (Fig. 40); middle leaf, "*Sassafras*" *potomacensis* Berry from Stump Neck, Maryland (USNM 201920); right-hand leaf, *Araliopsoides cretaceae* (Newberry) Berry from Bull Mountain, Maryland (USNM 201921A). Note the change in scale in order to minimize the size differences between individual specimens.



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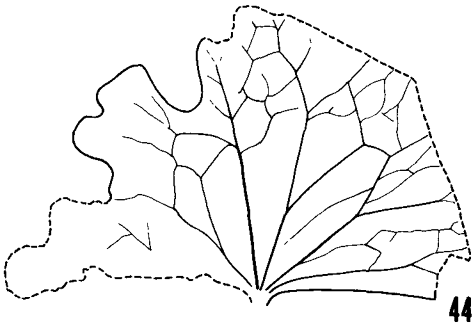

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Figs. 43, 44. Actinodromously veined leaves from the upper part of Subzone II-B of the Potomac Group, × 1.

Fig. 43. *Menispermites potomacensis* Berry (USNM 201919A) from near Widewater, Virginia.

Fig. 44. A new species of lobed leaf (USNM 201917) from Quantico, Virginia, similar to some members of the *Populophyllum reniforme* complex.

lites, and *Populites* from the Dakota Group of Kansas (cf. Lesquereux, 1892). The relationship of these two groups is inferred from the straight or slightly recurved courses of the lateral primary veins in the palmately lobed types and of the basal secondaries in the pinnate forms. Other indications of relationship include the frequent presence of a marked thickening or reinforcement of the midvein in the vicinity of the origin of the lateral primaries or basal secondaries, and close similarities in marginal teeth and higher order venation. All these leaves differ from older platanoids in having high third rank venation, with rigidly percurrent tertiary veins and "stitched intertertiaries" formed by branching and fusion of the alternating quaternary veins (cf. Fig. 42). Other noteworthy features of Subzone II-C and Zone III platanoids are their sometimes expanded petiole bases, suggestive of development of an abscission mechanism as in modern deciduous leaves, and their association with axes bearing small "heads" comparable to those found with Subzone II-B *Sapindopsis* (Fig. 55).

The apparent dominance of platanoid leaves and their allies in the upper part of the Potomac Group is in part a facies effect reflecting their association with the widespread beds of fluvial sandstone that predominate at this level. Many of these forms, including the very abundant *Araliopsoides cretacea*, the basally peltate genus *Aspidiophyllum*, and *Protophyllum*, are also typical of latest Albian to Cenomanian floras from similar facies in the Dakota Group (Lesquereux, 1892) and in Kazakhstan (Vakhrameev, 1952).

Our best sample of the angiosperm megafossil flora of fine-grained equivalents of the Elk Neck beds is a small collection of Berry (1911b) from the Hylton pit of southern New Jersey, which judging from the pollen assemblage


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reported by Wolfe and Pakiser (1971) probably falls in Zone III. This flora is of interest in containing a number of forms transitional to the flora of the Raritan Formation (cf. Newberry, 1895; Hollick, 1906; Berry, 1911b) and early Late Cretaceous floras elsewhere. These include a number of simple, entire-margined laminae, some of them asymmetric (Fig. 56), as well as the first representatives of the important Late Cretaceous genus *Liriodendropsis*, characterized by an emarginate apex (Figs. 58, 59), and a possible lobate forerunner of the palinactinodromously compound genus *Dewalquea* (Fig. 57).

IMPLICATIONS OF THE RECORD

Time and Place of Initial Angiosperm Diversification

Although the riddle of angiosperm origins seems still far from solved, we feel that the volume and quality of information reviewed above and summarized in Figure 60 sharply limit the range of permissible hypotheses on the course, timing, geographic framework, and causal aspects of early angiosperm evolution.

Our first and most important conclusion is that the primary adaptive radiation of the flowering plants took place during the Early Cretaceous. In their monosulcate aperture condition and other gross morphological features, *Clavatipollenites hughesii, Retimonocolpites,* and other members of the oldest well-documented angiosperm pollen floras (Barremian) are still relatively close to pollen of Cycadales, Bennettitales, Pentoxylales, Ginkgoales, and a few seed ferns (Peltaspermaceae). In fact, it is only details of their exine structure, such as the presence of columellae, tectal perforations, and granulate sulcus membranes, that allow them to be recognized as angiosperms at all. Some living monosulcate Magnoliales and Nymphaeales, as well as some putatively more specialized dicots, have non-columellar, granular or homogeneous exine structure distinguished from that of known gymnosperms on

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Figs. 45–48. Leaves of *Sapindopsis* spp. from the upper part of Subzone II-B of the Potomac Group.

Fig. 45. Terminal part of a pinnately compound leaf of a new species of *Sapindopsis* from the West Brothers clay pit, Maryland (USNM 222853A), × 1. The individual leaflets of this compound leaf have distinct petiolules and entire margins.

Fig. 46. Fragment of the same new species of *Sapindopsis* from the West Brothers pit (USNM 222854) chosen from the small portion of the population whose leaflets show the development of teeth, × 1.

Fig. 47. Leaf of a new species of *Sapindopsis* from Quantico, Virginia (USNM 222855A) with teeth and separate leaflets, × 2.

Fig. 48. Detail of the teeth and marginal venation shown in Fig. 46, × 5. Note the tooth shape and branching of the medial vein just before it enters the tooth.

TABLE II

BASES FOR ASSIGNMENT SCORES FOR ANALYSIS OF MORPHOLICAL EVOLUTION IN THE POTOMAC-RARITAN ANGIOSPERM POLLEN RECORD

(*Fig. 61; Doyle, in press*)

	Score				
CHARACTERS	0	1	2	3	4
MEAN SIZE	18–35 μm	< 18 μm > 35 μm			
APERTURE CONDITION	monosulcate	branched sulcus polycolpoidate			
		tricolpate	tricolporoidate triporoidate	tricolporate	triporate
SHAPE	bilateral, length > width	width ⩾ length (uniaperturates)			
		prolate (triaperturates)	oblate, spheroidal	oblate, triangular	oblate, concave sides
EXINE SCULPTURE	fine reticulate (meshes < 2 μm)	coarse reticulate (meshes ⩾ 2 μm) heterogeneous striate, rugulate			
		tectate, smooth	"blotchy" verrucate		
POLLEN UNIT	single grains	tetrads			

criteria visible solely with transmission microscopy, particularly the absence of a laminated endexine (Doyle et al., 1975; Walker, 1976). Hence, it is very probable that there existed still earlier angiospermous monosulcates which have not yet been recognized as such (cf. Doyle, 1969; Muller, 1970; Walker, 1976). However, the pattern of Early Cretaceous angiosperm radiation reviewed here makes it unnecessary to assume that such forms existed long before the Barremian until this has been demonstrated by careful TEM studies. Even if this is done, the possibility should not be ignored that the features tentatively considered criteria for angiospermous affinities arose independently in gymnospermous groups whose exine structure is not yet known, or in the angiosperm line before evolution of other angiosperm characters.

Following the appearance of angiospermous monosulcates in the Barremian, the angiosperm pollen record shows a progressive increase in total abundance, number of species, and the spectrum of morphological types, with tricolpates, tricolporates, and triporates appearing in that order. The subjective impression that this pattern is consistent with the orderly diversification of a monophyletic group beginning with monosulcates comparable to those in lower Zone I, but not with either markedly polyphyletic origin or random immigration of already advanced and differentiated types from some other area, is graphically confirmed by the semiquantitative analysis of morphological evolution summarized in Figure 61 (Doyle, in press, suggested by Simpson, 1953, pp. 22–25). Here each distinct angiosperm pollen type (essentially species) in the Delaware City Potomac sequence (Doyle and Robbins, in press) was assigned an "advancement index" obtained by adding scores for the degree of departure in five characters from the conditions in an "average" lower Zone I reticulate monosulcate grain (Table II). In some cases where there are especially good intermediates between pollen types, it was possible to recognize several stages of modification from the supposed ancestral state on the basis of a comparative analysis (thus avoiding the trap of circularity which would have resulted from reliance on stratigraphic position alone). When histograms of the number of species with each advancement index are plotted for seven successive intervals in the Delaware Potomac sequence, we see that not only the number of species but also the mean and maximum advancement indices and the total range of advancement increase steadily with time. Other noteworthy phenomena are the occurrence of the highest rates of increase in mean advancement near (though not at) the beginning of the sequence, and the persistence of certain relatively unmodified types even at the highest levels (peaks at 1 and 4 in upper Zone III). Both are common features of adaptive radiation and subsequent "intrazonal" evolution in other groups (cf. Simpson, 1953; Doyle, in press). By the end of the Potomac sequence (mid-Cenomanian), some of the most advanced pollen types had reached an evolutionary grade comparable to that of some inter-

TABLE III

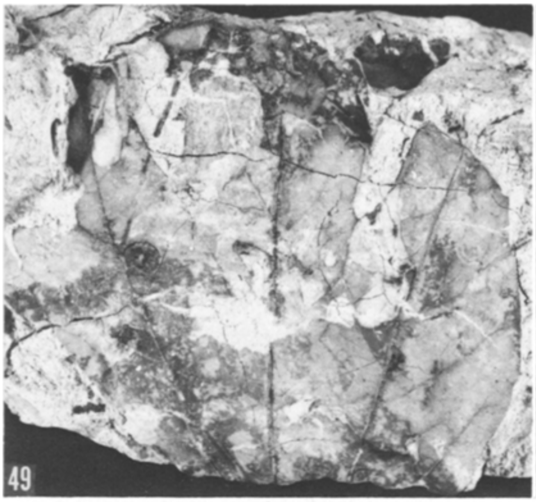
BASES FOR ASSIGNMENT OF ADVANCEMENT SCORES FOR ANALYSIS OF MORPHOLOGICAL EVOLUTION IN THE POTOMAC-DAKOTA ANGIOSPERM LEAF RECORD
(*Fig. 62*)

CHARACTERS	Score			
	0	1	2	3
LENGTH	0–5 cm	5–10 cm	10–20 cm	> 20 cm
LEAF RANK	1st	2nd	3rd	4th
TEETH	absent	doubly convex (A-1)	straight-convex (B-1) concave-convex (C-1) convex-concave (A-3)	doubly concave (C-3)
PETIOLE	poorly differentiated from blade	well differentiated		
MAJOR VENATION	pinnate	palmate actinodromous flabellate palinactinodromous parallelodromous	secondarily pinnate	
SECONDARY VENATION	brochidodromous in two or more orders: "festooned"	brochidodromous in one order		
		semicraspedodromous	craspedodromous	acrodromous
SHAPE	simple, elliptic	simple, peltate	simple, asymmetric	simple, apex emarginate
	ovate	ovate-cordate		
	obovate	ovate-truncate		
		palmately lobed	palmately lobed with basilaminar lobe	loss of palmate lobation
		pinnately lobed	pinnately compound	secondarily simple

mediate-level modern dicots, such as more primitive tricolporate Rosidae and Dilleniidae. However, even these most advanced types were well below the grade of many modern groups, such as triporate Amentiferae, and the flora as a whole was strikingly more primitive than that of today (cf. Scott et al., 1960; Pierce, 1961; Doyle, 1969; Muller, 1970).

Although less complete for the reasons stated above, a similar pattern of increasing advancement and diversity emerges from the leaf data, supporting the idea that the primary adaptive radiation of the angiosperms was under way. In Zone I, angiosperm leaves constitute less than 2% of the total flora, and they exhibit a limited range of morphological variation: apparently always simple, mostly entire, relatively undiverse in shape, and characterized by unusually irregular pinnate venation, frequently accompanied by such features as poor differentiation of the blade from the petiole and multistranded midveins. The one lobate form has unbraced sinuses, and those with nonentire margins all have doubly convex teeth (A-1, in the terminology of Hickey, 1973). By the middle of Subzone II-B, angiosperm leaves have become locally abundant and include new lobate-cordate, peltate, and both pinnately and palmately lobed shape classes. Most leaves from this horizon show a moderate increase in the regularity of their venation, especially the primary and secondary vein orders. In the upper portion of Subzone II-B, pinnately compound leaves appear; both these and the associated palmately lobed forms have somewhat more regular tertiary venation than their assumed precursors. Greater diversity in tooth shape appears in both simple and pinnately compound leaf types, with straight-convex (B-1) and concave-convex (C-1) classes both represented. In Subzone II-C and Zone III, the palmately lobed leaves and their apparent unlobed derivatives show further increase in morphological diversity and the development of a regular vein network extending to the fourth order. These trends are paralleled by a marked increase in the range of sedimentary lithofacies occupied by angiosperms; the specific ecological implications of this phenomenon are discussed further below, but its general evolutionary implications are clearly compatible with those based on morphology.

A morphological advancement analysis of the mid-Cretaceous leaf record (Fig. 62) yields results analogous to those obtained from the pollen record, despite the more sporadic distribution of leaves and clear evidence of lithofacies influences. Here advancement indices were calculated as percentages based on degree of approach to the most advanced state in each character observed out of seven (Table III), in order to overcome the lack of data on some characters in some species. The mean advancement index for the whole flora and histograms of the number of species falling in each of ten 10% advancement index classes were then plotted for six horizons in the Potomac Group and for the Dakota Group of Kansas (cf. Lesquereux, 1892), roughly equivalent to Zone III and possibly Zone IV.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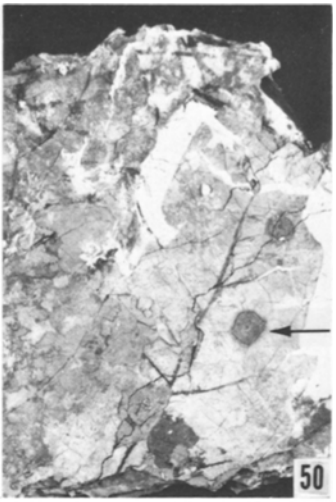
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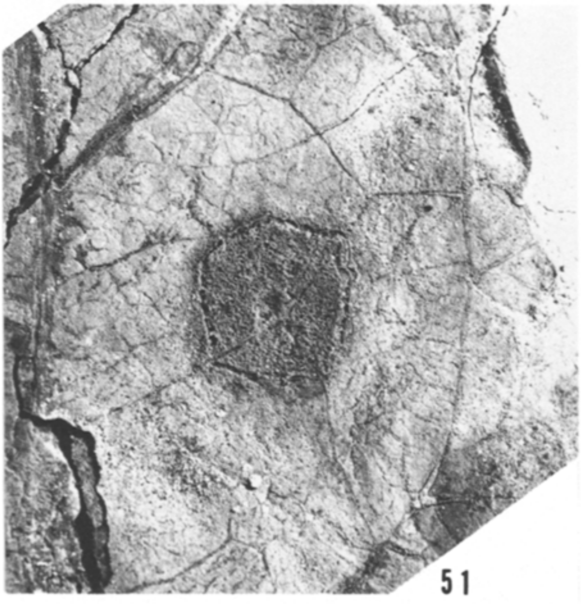
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Figs. 49–52. Leaves from the upper part of Subzone II-B of the Potomac Group.

Fig. 49. "*Sassafras*" *potomacensis*, fragment of the middle and upper parts of a three lobed leaf (USNM 222810) from Stump Neck, Maryland, × 1. The remains of several inferred galls can be seen on the leaf tissue.

Fig. 50. Part of the middle and lateral lobes of "*Sassafras*" *potomacensis* (USNM 222811)

This analysis confirms the very narrow morphological spectrum covered by the angiosperm leaf flora in Zone I and the stratigraphic trend for appearance of progressively more advanced leaf types. The effect of lithofacies manifests itself in the decrease in the value of the most advanced class in the middle of Subzone II-B (Mount Vernon) and the pronounced bimodality of the curve for Subzone II-C and Zone III. This reflects the fact that the general advancement level tends to remain lower in the finer-grained lithofacies represented at Mount Vernon and the Hylton pit, while the highly advanced platanoid complex predominates in the cross-bedded, sandy lithofacies seen at White Point. Although this is not as obvious as for the pollen, the leaf diagram also shows the persistence of relatively primitive morphological types in later Potomac and Dakota times.

Similar secular trends are also seen in a plot for leaf rank (Fig. 63), an expression of the general regularity with which the structural elements of the leaf—principally the venation—are organized (Hickey, 1971). Further implications of the leaf ranking trend for the origin of the angiosperm leaf will be treated below.

These indications of a coherent pattern of morphological diversification in both pollen and leaf records support the hypothesis that we are observing a true evolutionary radiation rather than simply immigration of forms which had already undergone most of their diversification elsewhere. This is not to say that there are no migrational effects in the Early Cretaceous angiosperm record, only that they are not great enough to prevent reading general evolutionary trends from the order of appearance of major types in Laurasian sections such as the Potomac Group. Actually, comparisons of pollen floras from independently correlated horizons in different geographic areas, attempted in greatest detail by Brenner (1976), reveal significant migrational effects which yield important clues on areas of origin and direction of spread of major angiosperm subgroups, and indirectly on the original climatic preferences of the angiosperms as a whole.

These data may be summarized by plotting the first records of both monosulcate and tricolpate angiosperm pollen against paleolatitude (Fig. 64), as was done by Axelrod (1959) for leaves and Brenner (1976) for tricolpate pollen. Despite the uncertainties in independent dating and estimates of paleolatitude, the resulting curves clearly support Axelrod's (1959) hypothesis of poleward migration of the early angiosperm flora, but with several important qualifications and exceptions.

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showing several circular structures interpreted as insect galls, × 1.

Fig. 51. Detail of one of the structures in Fig. 49 (arrow) inferred to be the earliest record of insect galls on angiosperm leaves, × 5. Note depressed rim and central portion as well as the spongy texture of the limonite making up the structure.

Fig. 52. Fragment of an inferred simple leaf with closely spaced teeth (USNM 222856) from Red Point, Maryland, × 2.

Early Cretaceous floras of other parts of the United States, Europe, and Central Asia show close similarities to those of the Potomac Group in their great diversity of ferns, especially Schizaeaceae, Cyatheaceae-Dicksoniaceae, and Gleicheniaceae, and of gymnosperms, including Cupressaceae-Taxodiaceae, Pinaceae, Araucariaceae, Cycadales, a few probable ephedraceous precursors, and extinct groups such as Cheirolepidiaceae (*Classopollis*), Caytoniaceae, and Bennettitales (cf. Brenner, 1963; Kemp, 1970; Hughes, 1976). These similarities led Brenner (1976) to assign all these areas to a single palynofloristic unit, his Southern Laurasian province. Although independent checks on the simultaneity of events in the angiosperm pollen record in the Potomac Group and elsewhere are difficult because of the absence of marine fossils below the Raritan Formation (middle Cenomanian), the remarkable consistency of the detailed sequence and associations of angiosperm species in the Potomac area, the Western Interior and Gulf Coastal Plain of the United States, and Europe supports the concept that geographic and climatic barriers and migrational lags were minimal within this province (cf. Doyle and Robbins, in press). The climate of the Potomac area appears to have been moist and probably at least as warm as subtropical, considering its relatively low paleolatitude (McElhinny, 1973), its position on the north shore of the east-west, nearly circumequatorial Tethys seaway (Luyendyk et al., 1972), the abundance of plant material, and the great diversity of both ferns and gymnosperms, many of them with large, broad leaves (cf. Brenner, 1963, 1976). Indeed, recent deep sea drilling and seismic reflection studies have revealed suggestive, though still controversial, evidence for a more or less continuous reef system along the eastern continental margin of North America from the Bahamas to the vicinity of the Grand Banks during the Aptian-Albian (Scientific Party for Leg 43 of the Deep Sea Drilling Project, 1975; Grow et al., 1976).

One significant deviation from the Southern Laurasian angiosperm sequence ascribable to migrational and climatic effects is the distinctly later appearance of angiosperm pollen in higher latitude areas of both hemispheres. In western Canada, which we consider a transition zone between Southern Laurasia and the Northern Laurasian province of Brenner (1976), tricolpate and monosulcate angiosperm pollen types generally enter together in sediments of middle

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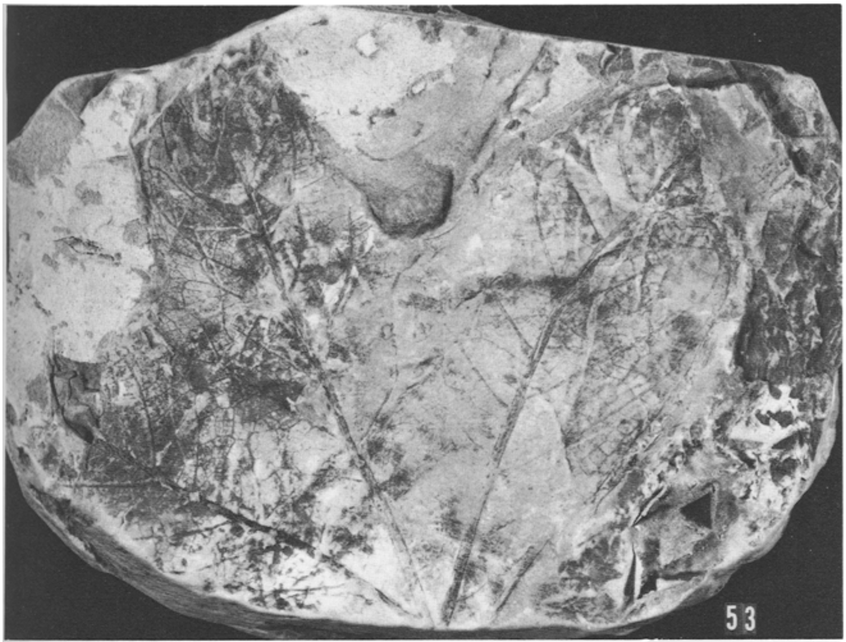
Figs. 53–55. *Araliopsoides cretacea* and associated remains from Subzone II-C of the Potomac Group, × 1.

Fig. 53. A three lobed leaf fragment (USNM 222857) from Brightseat, Maryland.

Fig. 54. Petiole and leaf base (USNM 222858) of a leaf from White Point, Maryland. Note the expanded base of the petiole.

Fig. 55. Presumed inflorescence axis bearing head-like structures associated with leaf remains of *A. cretacea* (USNM 222859).



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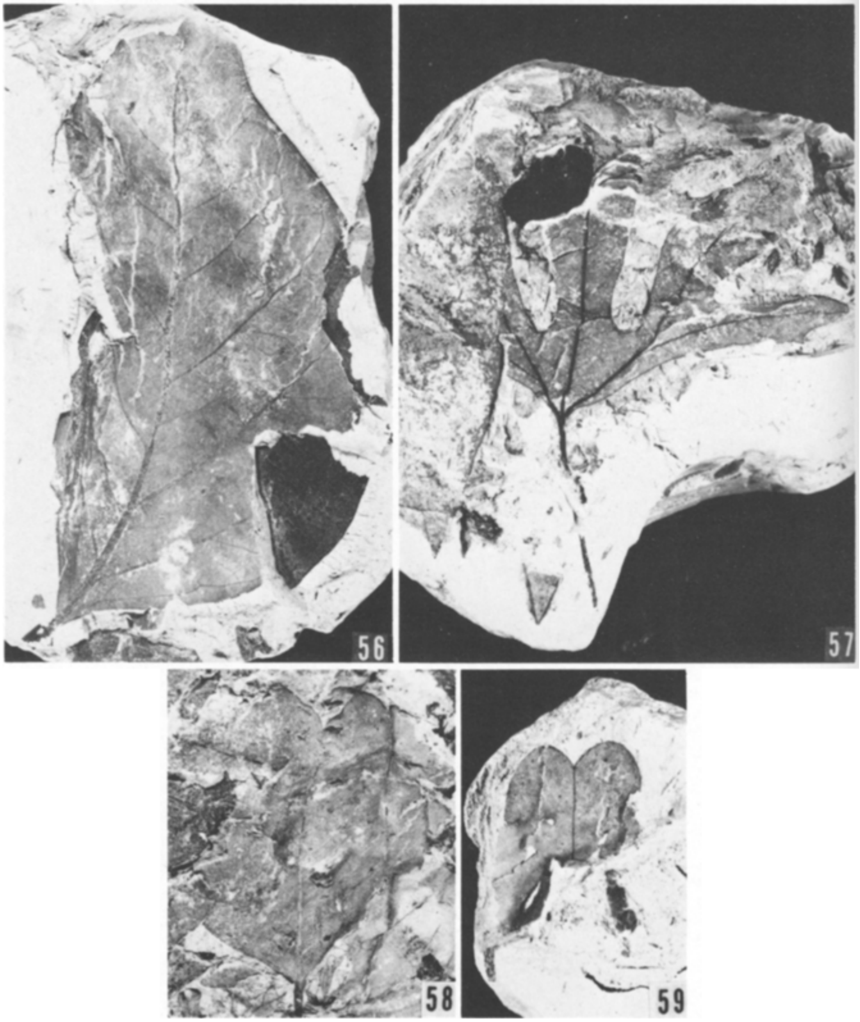


Figs. 56–59. Leaves from the Hylton pit, New Jersey, probably lying in Zone III of the Potomac Group, × 1.

Fig. 56. Leaf similar to "*Andromeda*" *parlatorii* Heer (USNM 222860A).

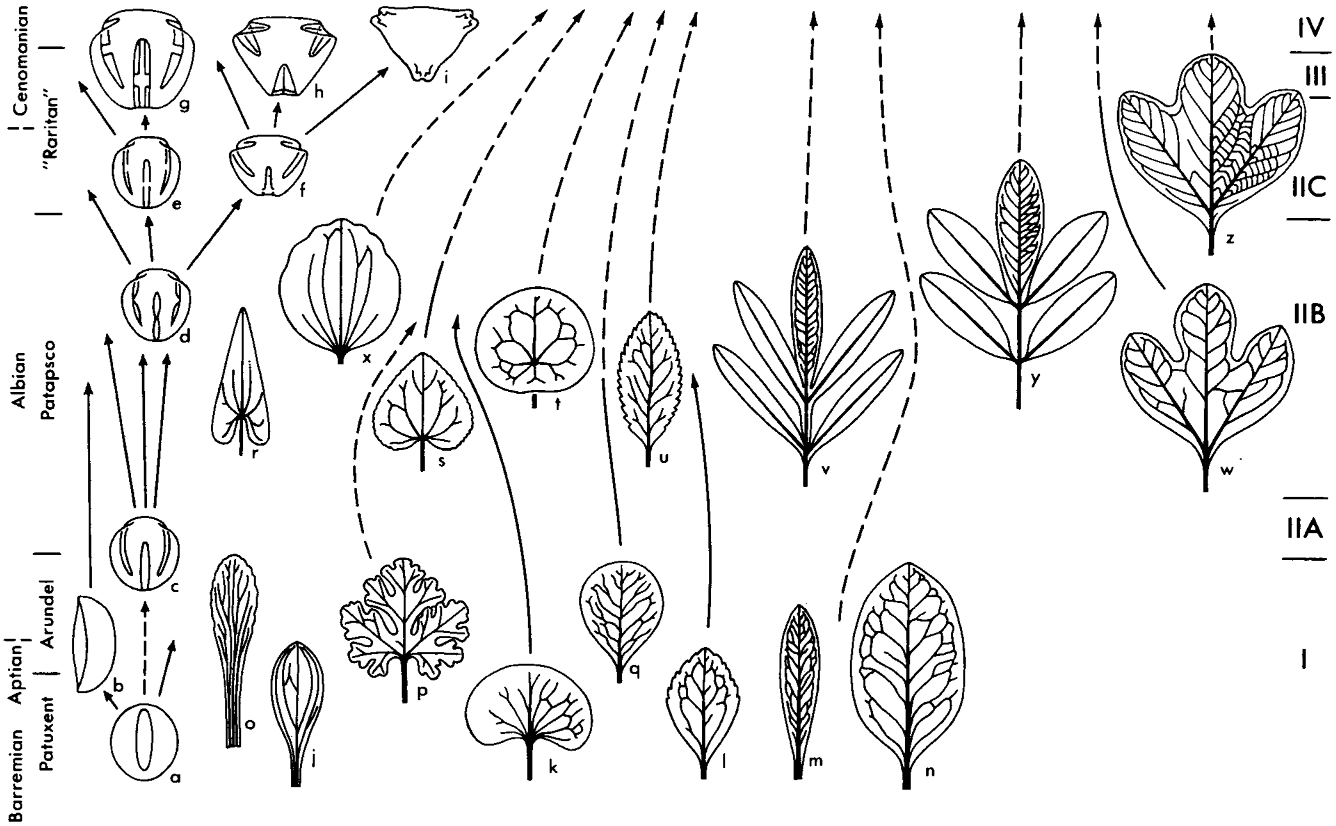
Fig. 57. "*Aralia*" *quinquepartita* Lesquereux (USNM 38500).

Fig. 58. Damaged leaf of *Liriodendropsis* sp. (USNM 222861).

Fig. 59. Apical part of a *Liriodendropsis* leaf showing the characteristic emarginate apex (USNM 222862).

or late Albian age (Norris, 1967; Singh, 1971, 1975; Jarzen and Norris, 1975). There are no reports of the Barremian-early Albian monosulcate phase of the angiosperm pollen record which is recognized in Southern Laurasia, except for one occurrence of *Clavatipollenites* in the Aptian of the District of Mackenzie (Brideaux and McIntyre, 1975, not included in Fig. 64), and perhaps a less securely dated monosulcate assemblage from the Swan River Group of Saskatchewan (Playford, 1971). In the Canadian Arctic and northern Alaska (Brenner's Northern Laurasian province proper), tricolpate pollen does not appear until the Cenomanian, and angiospermous monosulcates are only sporadically reported (Brenner, 1976). In comparison with Southern Laurasia, the non-angiospermous component of the Arctic flora is also markedly depauperate: it contains abundant bissaccate pinaceous pollen, but far fewer spores (except for those of the *Sphagnum* type!), and little or no *Classopollis* and ephedroid pollen (Brenner, 1976). In Australia and New Zealand, part of Brenner's Southern Gondwana province, present data indicate that tricolpate pollen first appears with or even slightly before angiospermous monosulcates in the middle or late Albian, much as in western Canada (Couper, 1953, 1960; Burger, 1970, 1973; Dettmann, 1973). These data confirm Axelrod's (1959) conclusion that there was a significant lag in migration of angiosperms into higher latitude areas, presumably because time was required for evolution of physiological adaptations to cooler climates (Brenner, 1976).

In contrast, palynological studies on the Cretaceous of Africa and South America exclusive of Patagonia (the Northern Gondwana province of Brenner, 1976) show distinctly earlier records and greater diversity of angiosperm pollen types than in Laurasia. This effect is especially clear for the tricolpates, which first appear in both Brazil (Müller, 1966; Regali et al., 1974; Brenner, 1976) and equatorial Africa (Jardiné et al., 1974b; Doyle et al., 1976, in press) in beds well below salt deposits overlain by carbonates containing late Aptian and early Albian ammonites (Reyment and Tait, 1972), and in beds in Israel indirectly dated as Barremian-early Aptian (Brenner, 1976). The same strata also contain endemic angiospermous monosulcates with no close analogs in Laurasia (Doyle et al., 1976, in press). The precise age of these occurrences cannot be determined in the absence of associated marine animal fossils, although associated palynomorphs in Africa suggest an early Aptian rather than Barremian age (Doyle et al., in press), but they are all clearly bracketed as at least a stage older than the oldest well dated Laurasian tricolpates from the lower Albian of England (Kemp, 1968; Laing, 1975, 1976). Thus, tricolpate-producing plants appear to have originated and begun their diversification in Northern Gondwana, and their early Albian appearance in Southern Laurasia probably reflects their first dispersal across the Tethys rather than evolution in place (cf. Brenner, 1976). During the Albian, angiosperm floras of Africa-South America continued to be more diverse than those of Laurasia, contain-

Barremian
Aptian
Albian
Cenomanian
Patuxent
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IIA
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Fig. 60. Summary of Potomac leaf and pollen sequence. Principal leaf and pollen types are plotted against Atlantic Coastal Plain lithologic units and their presumed equivalents in the standard stage sequence (left) and the Potomac-Raritan pollen zonation (right). In the case of the pollen, arrows indicate both evolutionary transformations and stratigraphic range extensions. The dashed arrow indicates that the inferred transition from monosulcate to tricolpate is not directly documented in the Potomac sequence. In the case of the leaves, solid arrows indicate upward extensions of morphological complexes within the Potomac sequence; dashed arrows, range extensions inferred from other areas.

Pollen types indicated: (**a**) Generalized tectate-columellar monosulcates (*Clavatipollenites, Retimonocolpites, Stellatopollis*). (**b**) Reticulate monocotyledonoid monosulcates (*Liliacidites*). (**c**) Reticulate to tectate tricolpates (*Tricolpites*). (**d**) Reticulate to tectate tricolporoidates (*Tricolpites, Tricolporoidites*). (**e**) Small, generally smooth-walled prolate tricolporoidates (*Tricolporoidites*). (**f**) Small, generally smooth-walled, oblate-triangular tricolporoidates (*Tricolporoidites, Perucipollis*). (**g**) Larger, smooth-walled to reticulate prolate tricolpor(oid)ates (*Tricolporopollenites*). (**h**) Larger, generally smooth-walled, oblate-triangular tricolpor(oid)ates (*Tricolporopollenites*). (**i**) Early members of the triangular triporate Normapolles complex (*Complexiopollis, Atlantopollis*).

Leaf types indicated: (**j**) Acrodromous, narrowly obovate, monocotyledonoid (*Acaciaephyllum*). (**k**) First rank, pinnately veined, reniform (*Proteaephyllum reniforme*). (l) First rank, serrate (*Quercophyllum*). (**m**) First rank, narrowly obovate (*Rogersia*). (**n**) First rank, broadly elliptical (*Ficophyllum*). (**o**) Parallelodromous, elongate (*Plantaginopsis*). (**p**) Lobate reniform (*Vitiphyllum*). (**q**) First rank, obovate (*Celastrophyllum*). (**r**) Campylodromous, sagittate (*Alismaphyllum*). (**s**) Actinodromous ovate-cordate-lobate ("*Populus*" *potomacensis, Populophyllum reniforme*). (**t**) Actinodromous, peltate (*Menispermites* "*tenuinervis*", (**u**) Pinnately veined, serrate (*Celastrophyllum*). (**v**) Second rank, pinnatifid (*Sapindopsis magnifolia*). (**w**) Second rank, palinactinodromous, palmately lobed (*Araliaephyllum*). (**x**) Acrodromous, lobate elliptical (*Menispermites potomacensis*). (**y**) Third rank, pinnately compound, sometimes serrate (*Sapindopsis* spp.). (**z**) Third rank, palinactinodromous, palmately lobed (*Araliopsoides*, "*Sassafras*", etc.). (Reprinted from Doyle and Hickey, 1976, Fig. 28, p. 178, with permission of Columbia University Press.)

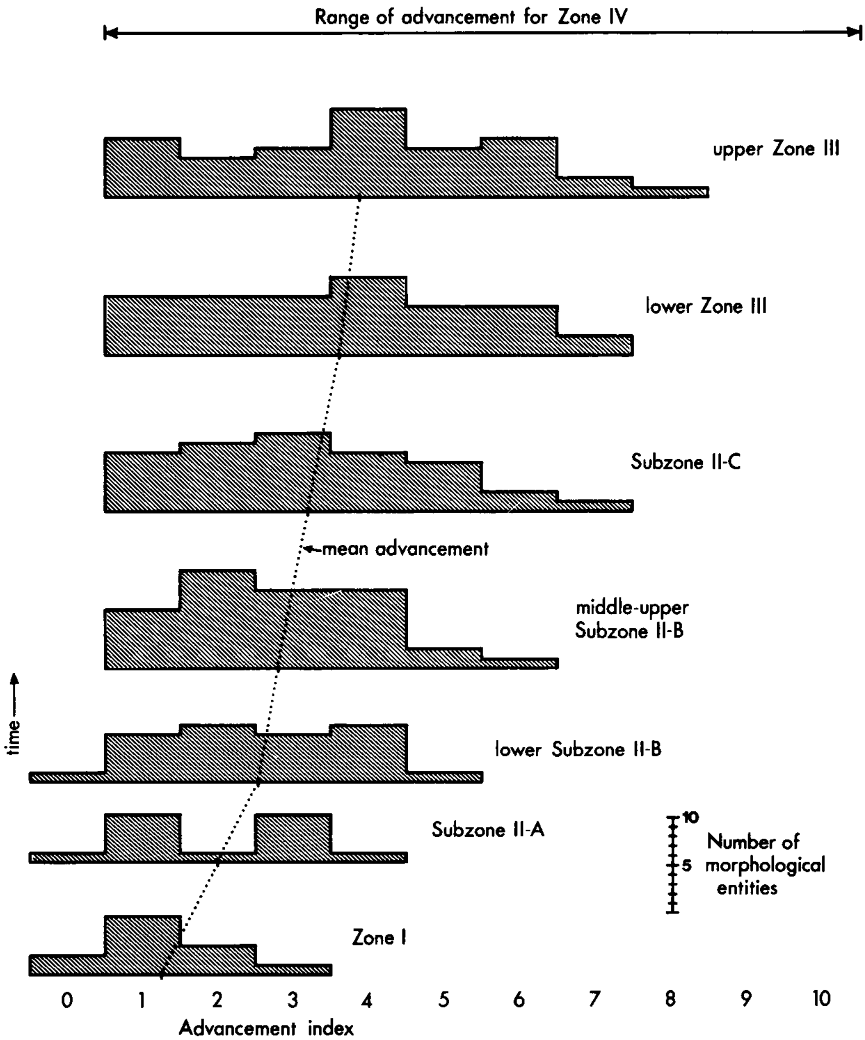


Fig. 61. Analysis of morphological advancement in Potomac-Raritan angiosperm pollen (modified from Doyle, in press). Histograms show numbers of morphological entities with particular advancement indices (Table 2) at each of seven stratigraphic intervals of the Potomac Formation in wells near Delaware City, Delaware (Doyle and Robbins, in press). The morphological entities generally correspond to palynological species, except when species are so broadly defined that they include variants with more than one advancement index.

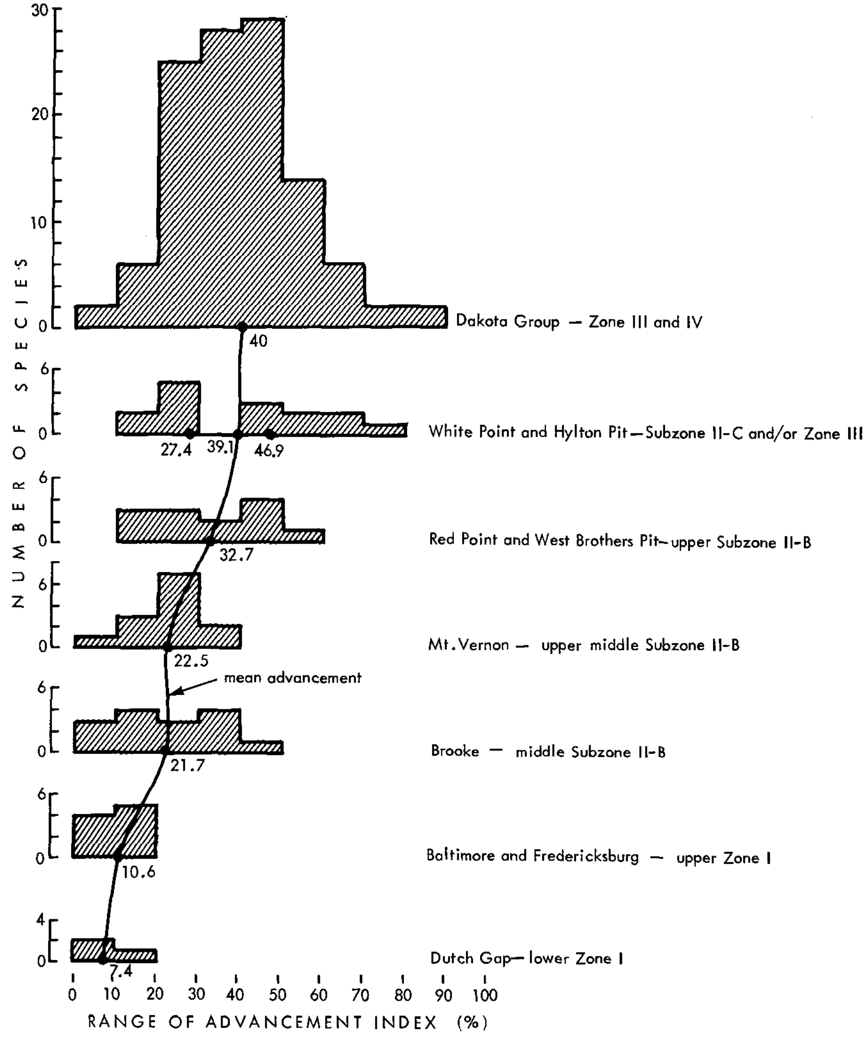


Fig. 62. Analysis of morphological advancement in leaves of the Potomac and Dakota Groups. Histograms show numbers of leaf species with advancement indices (Table 3) falling in each 10% advancement class at each of six levels in the Potomac Group and for the Dakota Group as a whole. Only a randomly selected sample comprising approximately one-third of the described leaf species from Dakota strata was analyzed. Advancement indices were calculated as percentages rather than absolute scores in order to include leaf species of which all specimens lack a particular character.

ing endemic elements such as polyporates, not known until the Cenomanian in Laurasia (Pacltová, 1971), and tricolpodiorates (with two ora per colpus), which are quite unknown elsewhere (Jardiné and Magloire, 1965; Müller, 1966; Brenner, 1968, 1976; Herngreen, 1973, 1974; Jardiné et al., 1974b). Tricolporates and triporates, however, appear in the same order and at roughly the same time as in Laurasia (middle or late Albian and later Cenomanian, respectively: cf. Herngreen, 1974).

These features of the Aptian-Albian angiosperm pollen record of Northern Gondwana are matched by equally striking differences in composition of the non-angiospermous dominants, which together with geological evidence suggest hotter and drier climates than in Southern Laurasia (cf. Kuyl et al., 1955; Brenner, 1968, 1976; Jardiné et al., 1974a; Herngreen, 1974). The total diversity of palynomorphs is much lower: the bisaccate and cupressaceous-taxodiaceous conifer pollen so abundant in Laurasia is absent, and fern spores, notably Schizaeaceae, are much less common and diverse. The two dominant groups are *Classopollis,* known to have been produced by cheirolepidiaceous conifers with markedly xeromorphic vegetative features (but which did exist in mesic areas: cf. Hughes, 1976), and striate ephedroid pollen, whose most probable modern descendants are the xerophytic genera *Ephedra* and *Welwitschia.* Finally, the salt deposits cited earlier constitute unequivocal evidence of at least semiarid conditions when marine waters first entered the South Atlantic rift in the Aptian.

Although Brenner (1976) considered these data further evidence for Axelrod's (1959) poleward migration theory and for Stebbins' (1974) concept that the angiosperms originated under semiarid rather than mesic conditions (cf. also Raven and Axelrod, 1974; Doyle and Hickey, 1976), it must be realized that they apply directly to only one subgroup of the angiosperms, the tricolpate dicots, and cannot automatically be extended to the angiosperms as a whole. In fact, recent palynological studies of the stages preceding the appearance of tricolpates in Gabon and the Congo (Doyle et al., 1976, in press) have revealed a monosulcate phase in the angiosperm record which has geographic and paleoecological implications quite different from those drawn from the tricolpates (contrast the monosulcate and tricolpate curves in Fig. 64). The angiosperm element in these beds consists of rare *Clavatipollenites, Retimonocolpites,* and *Stellatopollis* species close to and no more advanced than those from Wealden beds of England (Hughes, this symposium) and the basal Potomac Group. Significantly, despite the rather wide margins of uncertainty in independent dating, the best estimate of the age of all three floras is the same, Barremian. Furthermore, the non-angiospermous component of the flora in which monosulcate angiosperms appear is much more like that found in Wealden and lower Potomac strata, with abundant bisaccate conifer pollen and more diverse fern spores. The marked disparity between the floras

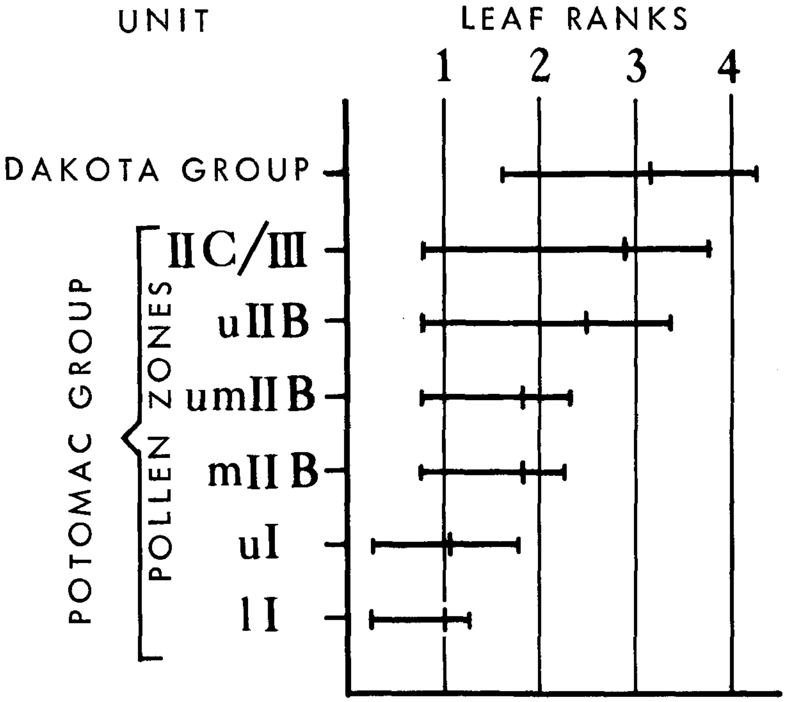
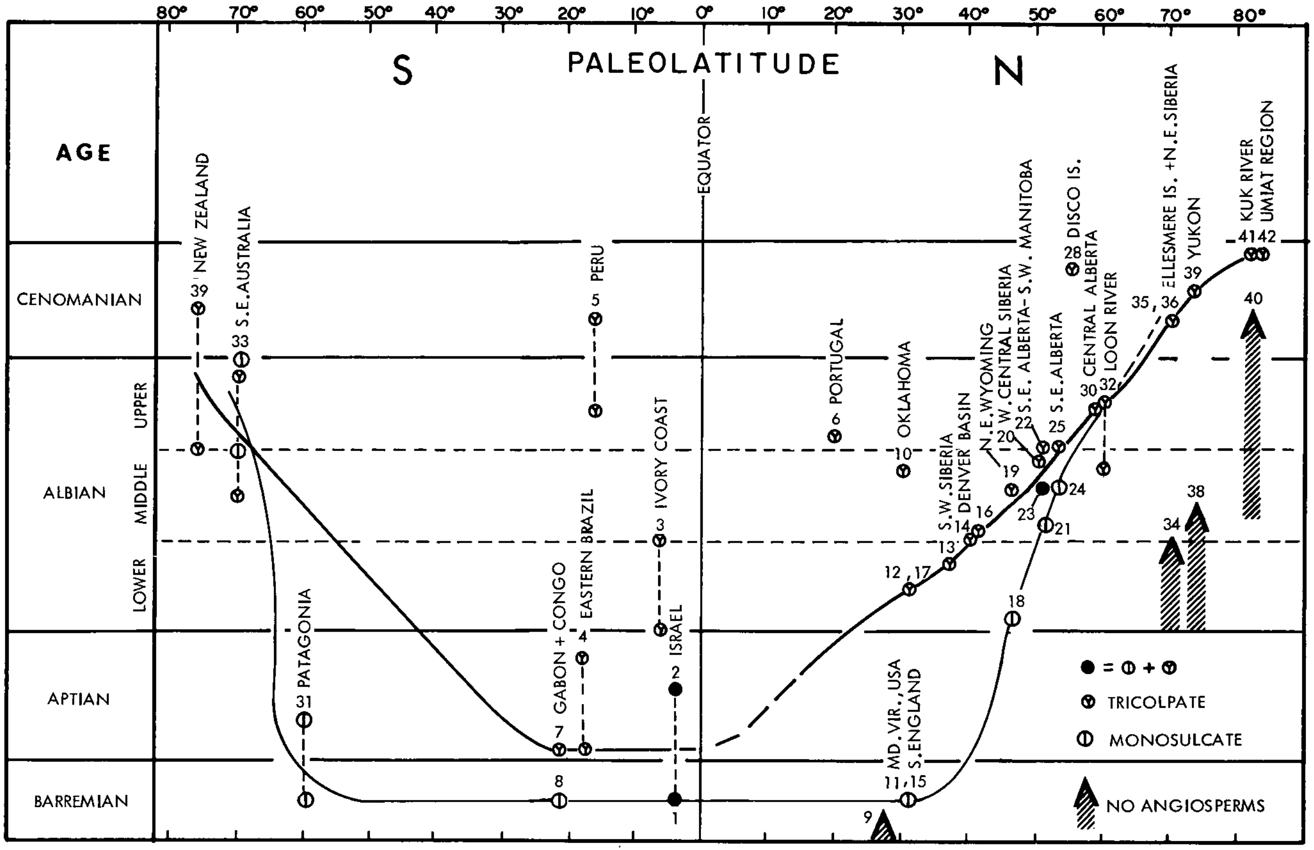


Fig. 63. Change in the range of leaf ranks shown by the Potomac and Dakota angiosperm floras. The cross-bar represents the average value. The levels shown are the same as those in Fig. 62.

of the two sides of the Tethys develops near the presumed Barremian-Aptian transition. In Gabon and the Congo, the changes involved — extinction of bisaccates, decline in fern spores, and a shift from lacustrine to fluvial sedimentation — are all consistent with increasing aridity, *after* the appearance of angiosperms (Doyle et al., 1976, in press).

These new observations indicate that whereas tricolpate-producing dicots may have originated in Africa-South America at a time of increasing aridity and subsequently migrated poleward into Laurasia and Australasia, the earlier monosulcate angiosperms were able to disperse "instantaneously" throughout a broad belt on both sides of the Tethys at a time when both areas were still relatively mesic. In the following sections, we will argue that morphological features of early angiosperm leaves and sedimentological evidence on the sorts of habitats they first occupied in the Potomac basin strongly favor Stebbins' (1965, 1974) concept that the first angiosperms were "weedy" shrubs which arose under selective pressures of a seasonally dry climate. It is now



PALEOLATITUDE
S
N
80° 70° 60° 50° 40° 30° 20° 10° 0° 10° 20° 30° 40° 50° 60° 70° 80°
EQUATOR
AGE
CENOMANIAN
ALBIAN
UPPER
MIDDLE
LOWER
APTIAN
BARREMIAN
39 NEW ZEALAND
33 S.E.AUSTRALIA
31 PATAGONIA
5 PERU
7 GABON + CONGO
8
4 EASTERN BRAZIL
3 IVORY COAST
2 ISRAEL
1
6 PORTUGAL
10 OKLAHOMA
9
11,15 MD.VIR.,USA S.ENGLAND
12,17
13 S.W.SIBERIA
14 DENVER BASIN
16
18
19 N.E.WYOMING
20 W.CENTRAL SIBERIA
22 S.E. ALBERTA-S.W. MANITOBA
21
23
24
25 S.E.ALBERTA
28 DISCO IS.
30 CENTRAL ALBERTA
32 LOON RIVER
34
35,36 ELLESMERE IS. +N.E.SIBERIA
38
39 YUKON
40
41 42 KUK RIVER UMIAT REGION
● = Ⓘ + Ⓨ
Ⓨ TRICOLPATE
Ⓘ MONOSULCATE
▲ NO ANGIOSPERMS

Fig. 64. Latitudinal spread of angiosperm pollen during the mid-Cretaceous. Note the clear poleward spread of tricolpate pollen; contrast with the lack of evidence for directions of migration of angiospermous monosulcates until the middle Albian, when they begin to spread into high latitude areas of both hemispheres at the same time or somewhat after tricolpate pollen. Where there is considerable uncertainty in the date of first appearance the earliest and latest possible dates are connected by a dashed line. Lines for first appearances are plotted within the limits given by the authors so as to give the smoothest possible curve. Locality details, stratigraphic units (in some cases), and references are given by the number of the occurrence, as follows: 1, 2: Northern Negev, Zeweira Fm. (Brenner, 1976); 3: Jardiné and Magloire (1965); 4: Alagoas and Sergipe Basins (Müller, 1966; Regali et al., 1974; Brenner, 1976); 5: Montaña region (Brenner, 1968); 6: Nazaré area (Groot and Groot, 1962); 7, 8: Jardiné et al. (1974b), Doyle et al. (1976, in press); 9: Jura Mountains (Millioud, 1967, cited in Hughes, 1976); 10: Antlers Sand and Walnut Clay (Hedlund and Norris, 1968); 11, 12: Potomac Group (Brenner, 1963; Doyle, 1969; Wolfe et al., 1975; Doyle and Hickey, 1976); 13: Southwestern Lowlands of Siberia (Vakhrameev et al., 1970); 14: Fall River Fm. (Pannella, 1966, cited in Brenner, 1976); 15: Wealden Group (Couper, 1958; Kemp, 1968; Hughes, this symposium); 16, 17: Lower Greensand (Kemp, 1968, 1970; Laing, 1975, 1976); 19: Fall River Fm. (Davis, 1963, cited in Brenner, 1976); 20: West Central Siberia (Vakhrameev et al., 1970); 21, 22: Swan River Group (Playford, 1971); 23: Norris (1967), Singh (1971, 1975); 24, 25: Youngstown area (Jarzen and Norris, 1975; Norris et al., 1975); 28: Atane Fm. (Brenner, 1976); 30: McMurray Fm. (Vagvolgyi and Hills, 1969); 31: Baqueró Fm. (Archangelsky and Gamerro, 1967); 32: Singh (1971); 33: Alluru Mudstone (Burger, 1970, 1973; Dettmann, 1973); 34: Brenner (1976); 35: Hassel Fm. (Brenner, 1976); 36: Stanley (1967); 37: Brenner (1976); 38: Peel Plateau (Brenner, 1976); 39: Northeast South Island, Clarence Series (Couper, 1953, 1960); 40: Corwin Fm. (Brenner, 1976); 41: Corwin Fm. (Stanley, 1967; Brenner, 1976); 42: Prince Creek Fm. (Stanley, 1967).

clear that the poleward spread of tricolpate pollen has no direct bearing on this question. Nevertheless, the fact that the Aptian aridization of Northern Gondwana was followed by the origin and remarkable radiation of tricolpate and endemic monosulcate angiosperms may constitute indirect support for Stebbins' hypothesis, since it suggests that early angiosperms were preadapted to dry conditions to a far greater degree than would have been expected under the more conventional postulate that they were forest trees of mesic environments (e.g., Bews, 1927; Axelrod, 1952; Cronquist, 1968; Takhtajan, 1969; Thorne, 1976).

Morphological Features of Early Angiosperms

Considering the key role of pollen in the life cycle of flowering plants, a functional analysis of pollen-morphological features of early angiosperms might be expected to yield important evidence on their reproductive biology. Although functional correlations have not yet received the attention they deserve from students of modern pollen morphology and pollination biology, a few preliminary inferences seem justified.

First, we interpret the well-developed reticulate exine sculpture of *Clavatipollenites, Retimonocolpites, Liliacidites,* and *Stellatopollis* from the basal Potomac Group and the Barremian of England as strong evidence that the flowering plants which produced them were insect-pollinated (Doyle and Hickey, 1976). This supposition is based on the general correlation between exine sculpture and insect pollination in living plants (cf. Faegri and van der Pijl, 1966; Heslop-Harrison, 1971), presumably reflecting the fact that surface irregularities allow the grains to stick to each other and to the body of their insect vector. Another functional aspect of typical angiospermous exine structure is the role of infratectal cavities and tectal perforations in storage and release of proteins involved in intra- and interspecific incompatibility mechanisms and stigma recognition (Heslop-Harrison, 1976; Walker, 1976). These functions are related to one of the most important advances of the angiosperms over gymnosperms, germination on a stigma, and the resulting unprecedented possibilities for the development of isolating mechanisms. Unfortunately, there is not yet enough information to determine whether the exine features of Barremian angiosperms were primarily adaptive for pollen transfer, stigmatic interactions, or both; this is an area where future comparative research on modern monosulcates might yield interesting results.

More convincing evidence for germination of pollen on a stigma and, by extension, for carpel closure is the appearance of tricolpate pollen in the Aptian of Africa-South America. The tricolpate condition is the most important example of a general centrifugal trend for the development of more than one pollen germination aperture found throughout the angiosperms (cf.

Muller, 1970; Sporne, 1972; Walker, 1974; Walker and Doyle, 1975). Only the rarest analogs of this trend occur among gymnosperms: e.g., the "pseudo-tricolpate" Mesozoic genus *Eucommiidites*, in which two furrows are narrower than the third and perhaps functioned in compensation for volume changes (harmomegathy) rather than germination. One might expect that possession of more than one aperture would have little advantage in most gymnosperms, where the pollen grain germinates slowly within the moist, protected pollen chamber of the ovule. However, grains with several apertures would have a distinct advantage over those with only one on the exposed surface of an angiosperm stigma, where germination must be rapid and intraspecific competition is intense, and where much of the time a monosulcate grain would land with its aperture facing out into the air (cf. Hughes, 1961a, 1976; Walker, 1971; Doyle and Hickey, 1976). The appearance of tricolpate pollen only slightly later than Barremian monosulcate pollen with reticulate exine sculpture strengthens the concept that the first angiosperms to enter the record already had closed carpels and other basic angiospermous reproductive adaptations, rather than acquiring many such features later in the course of their radiation (e.g., Hughes, 1976). Direct evidence for carpel closure comes from 5-folliculate fruits from the Albian of Siberia (*Ranunculaecarpus*: Samylina, 1960, 1968), and elongate axes bearing conduplicate carpels from the Cenomanian Dakota Group of Kansas (Dilcher et al., 1976).

Like Muller (1970), we would suggest that the great diversity of later trends and character combinations in size, shape, sculpture, and aperture structure in both monosulcate and triaperturate groups in some way reflects adaptive radiation in floral and pollination-biological themes, as well as perfection of various compromises between the germinational and harmomegathic functions of apertures (e.g., the tricolporate condition). However, we feel it would be premature to propose specific adaptive explanations for most characters and trends.

The pollen grains of wind-pollinated angiosperms provide some of the clearest examples of the interrelationships of functional and morphological characters (cf. Faegri and van der Pijl, 1966; Whitehead, 1969). Their size, generally between 20 and 40 μm, is small enough for buoyancy but large enough to prevent deflection of the grain around the stigma in the air stream. Their smooth, dry exine surface prevents cohesion and ensures separate dispersal. There is also a strong tendency for reduction of furrows to pores, perhaps to reduce desiccation, in groups such as the grasses, with one pore; the "Amentiferae," with three or more pores; and the Chenopodiaceae, Amaranthaceae, and Plantaginaceae, with many pores. These characters first occur together in the triporate Normapolles of the middle Cenomanian (Zone IV). The presumed ancestors of the Normapolles, the smooth, triangular tricolporates of Zone III, are generally below the 20–40 μm size range and have their closest analogs today in insect-pollinated groups (e.g., Saxifragales). This suggests a reversion to wind pollination at just about the time that angiosperms were becoming regionally dominant, and hence when wind pollination, favored in dense stands of deciduous trees (Whitehead, 1969), would first be advantageous. This interpretation is consistent with evidence that the Normapolles include the ancestors of many if not all Tertiary and modern triporate Amentiferae (Góczán et al., 1967; Doyle, 1969; Wolfe, 1973; Wolfe et al., 1975). However, tendencies toward the round shape typical of modern Amentiferae do not become evident until later (Turonian?), and the thick exines and aperture specializations of many younger Normapolles (e.g., *Trudopollis, Oculopollis*) cast doubt on the assumption that they were all wind-pollinated.

Somewhat more detailed inferences concerning the vegetative habit and adaptations of early angiosperms are possible from the leaf record, based on studies on the developmental and ecological significance of leaf architectural features in modern plants by Pray (1955, 1960, 1962, 1963), Slade (1957), Givnish (1976, in press), and Givnish and Vermeij (1976).

A comparison of the leaf architecture of Zone I angiosperms with that of both gymnosperms and later angiosperms in the light of developmental studies recently led us to propose a speculative model for the origin of the typical dicot leaf (Doyle and Hickey, 1976). Only the salient points of the arguments then presented will be reviewed here.

Because the dicot leaf is such a familiar structure, it is easy to overlook the uniqueness of its basic reticulate venation pattern, characterized by generally more than three discrete orders of venation, extensive anastomoses between veins of both the same and different orders, and the presence of freely ending veinlets. This syndrome of features, already well-established in the oldest Zone I angiosperm leaves, stands out as a conspicuous innovation in the Early Cretaceous plant world, which was dominated by ferns and gymnosperms with a relatively restricted range of stereotyped leaf architectural patterns (cf. Hughes, 1976). The Permian and Mesozoic gymnosperms *Glossopteris* and *Sagenopteris* (Caytoniaceae), often cited as approaching angiospermous reticulate venation, are actually quite different, since their reticulum is formed of veins of essentially a single order. Closer but still usually incomplete convergences occur in leaves of the putative Triassic gymnosperm *Furcula*; Mesozoic and Recent Dipteridaceae; Cheiropleuriaceae, *Tectaria*, and a few other specialized Recent ferns; and most notably the Recent gymnosperm genus *Gnetum*.

The differences between the mature venation patterns of angiosperm leaves and those of lower groups are underlined when we consider that they are matched by equally major differences in developmental processes, particularly the greatly augmented role of intercalary meristematic activity. Ontogenetic studies (Pray, 1960, 1962) show that two phases of meristematic activity are involved in development of fern leaves with open dichotomous venation (*Nephrolepis*, *Regnellidium*): (1) an apical phase, during which the petiole and rachis are produced by activity of an apical meristem; and (2) a marginal phase, during which the pinnules are produced by rows of meristematic cells arising along the sides of the embryonic rachis. The entire dichotomous venation pattern differentiates outward, or progressively, from cell lineages established by these marginal meristems. In contrast, typical simple, pinnately veined dicot leaves go through three overlapping phases of meristematic activity (Esau, 1953; Pray, 1955, 1963; Slade, 1957): (1) a brief apical phase, producing a minute, peg-shaped leaf primordium and procambium destined to become the midrib; (2) a brief marginal phase, during which two marginal meristems produce an embryonic lamina and the pinnately arranged, outward-differentiating secondary veins; and (3) a prolonged phase of diffuse intercalary, or plate, meristematic activity, during which most of the leaf area is produced and all higher vein orders differentiate sequentially within the expanding areas blocked out by already-formed lower order veins. Pray (1960, 1962) and Slade (1957) go on to suggest that the predominance of marginal vs. intercalary growth is causally responsible for the difference between open dichotomous and reticulate venation. However, since Hara (1964) has shown that the *Sagenopteris*-type, simple reticulate venation of the fern *Onoclea* is initiated during strictly marginal growth, we would specify that the most direct leaf architectural expression of the predominance of intercalary growth in angiosperms is not the presence of anastomoses *per se*, but rather the existence of a hierarchy of internally differentiated, successively finer vein orders.

Unfortunately, appropriate studies on the relationships between ontogeny and leaf architecture in gymnosperms have not yet been carried out. For the purpose of the present argument, we have assumed that similar processes are involved in gymnosperm leaves to those described in fern leaves with similar architecture. This and many other assumptions and predictions of our model are testable by future ontogenetic studies of living plants.

In the light of these correlations, the peculiarly disorganized, irregular first rank venation of Zone I angiosperms takes on special interest, since it suggests some major reorganization of developmental processes — perhaps the origin of plate meristematic activity itself — not long before the angiosperms entered the fossil record. In our previous paper (Doyle and Hickey, 1976), we proposed a model for the specific ecological and developmental processes involved in this transformation, inspired in part by a more general discussion by Němejc (1956). We postulated first a phase of profound reduction from the pinnately organized frond of the hypothetical cycadopsid gymnosperm ancestor of the angiosperms to a simple, xeromorphic leaf with only a midrib and a vestige of laminar venation, followed by secondary expansion of leaf area by

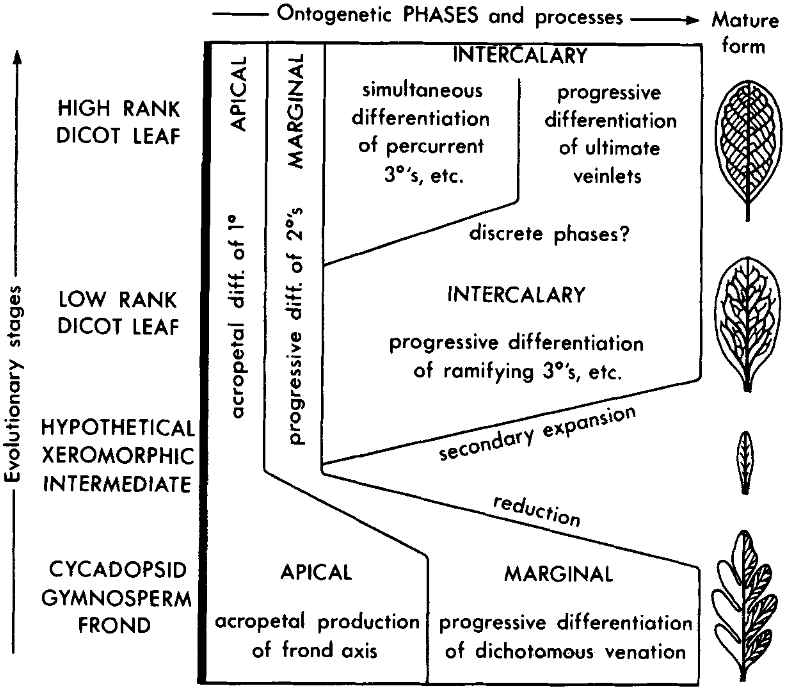


Fig. 65. Model for the origin of the dicot leaf and the subsequent trend for increased regularity of successively higher vein orders ("ranking") in terms of ontogenetic and phylogenetic processes. Successive phases of meristematic activity, their relative duration, and the process of vein differentiation known or assumed to be operative in each case are indicated from left to right. Transformation of a pinnately compound, cycadopsid gymnosperm (seed fern?) leaf, with dichotomous pinnule venation and with a growth pattern assumed to be analogous to that seen in ferns, into a dicot leaf, with several orders of venation and relatively brief phases of apical and marginal meristematic activity, is postulated to have occurred as a result of evolutionary reduction associated with semixerophytism, followed by a secondary expansion of leaf area mediated by a new developmental process, intercalary growth. The trend observed in the Potomac sequence for increase in rank (especially for percurrency of tertiary and higher vein orders) is interpreted as having resulted from the gradual addition of new developmental processes, specifically simultaneous rather than progressive differentiation of tertiary and higher vein orders, and perhaps discrete phases of vein differentiation. (Reprinted from Doyle and Hickey, 1976, Fig. 30, p. 193, by permission of Columbia University Press.)

a new or recently augmented process of intercalary growth (Fig. 65). We proposed adaptation to a semiarid climate as an explanation for the hypothetical leaf reduction phase, and we equated the secondary expansion phase with reinvasion of mesic areas such as the Potomac basin.

As one argument in support of this scheme, we cited Brenner's (1976) evidence for origin of tricolpate pollen and generally greater diversity of angiosperm pollen in the Aptian-Albian of Africa-South America, associated with indications of regional aridity. However, in view of the new evidence cited above for similarity of the earlier, Barremian monosulcate phase in the angiosperm record on both sides of the Tethys, predating the onset of arid conditions in Africa-South America, we now believe it was premature to imply that Northern Gondwana was the semiarid area where leaf reduction occurred. Rather, we would envision a wider range of possible sites, such as unspecified earlier Neocomian or Jurassic semiarid regions in either Laurasia or Gondwana (cf. Vakhrameev, 1952), or locally or physiologically arid habitats within a generally mesic region (cf. Axelrod, 1972).

In any case, assuming that the pre-angiosperms had lost the capacity to produce a compound frond, secondary expansion effected by augmentation of intercalary rather than marginal growth would have functional advantages of its own. In particular, the resulting hierarchy of thick secondary trunk bundles and internally ramifying finer veins would permit more rapid diffusion of fluids to and from the margin and the laminar areas than would the single order of fine secondary veins expected with marginal growth, as illustrated by the late Paleozoic and Mesozoic cycadopsid *Taeniopteris*.

This model also provides a rationale for the leaf ranking trend seen in the Potomac record. While the control of vein differentiation might still have been rudimentary during the early stages of secondary expansion, selection would tend to favor accumulation of developmental mechanisms resulting in such improvements as a more rigid and efficient support and supply network and the prevention of marginal tearing. There is indirect evidence from modern leaves that one of the most conspicuous expressions of the ranking trend, evolution of percurrent tertiaries, did in fact involve origin of new developmental mechanisms. In the one low rank leaf investigated (*Aucuba*: Pray, 1963), the irregularly ramifying tertiary and higher order veins fill the intercostal areas by the same process of progressive, acropetal differentiation as the secondaries and freely ending veinlets, whereas in the more numerous high rank leaves studied (Pray, 1955, 1963), the percurrent tertiaries arise by a different process, namely simultaneous differentiation into procambium of a whole row of cells from one secondary to the next.

The plausibility of our model is supported by analogies with modern groups where there is comparative evidence for leaf reduction and secondary expansion: for example, the several orders of reticulate venation in the simple, spatulate leaves of the fern genus *Ophioglossum*, whose nearest relative, *Botrychium*, shows an apparent reduction series from typical fern fronds to nearly linear leaves (Wagner, 1964); and the remarkably dicot-like leaves of *Gnetum*, which anatomical and embryological evidence indicates is related to but more specialized than the xerophytic genera *Ephedra* and *Welwitschia* (cf. Bierhorst, 1971). Other evidence is the small size of many early angiosperm leaves, also regarded as an indication of xerophytic ancestry by Vakhrameev (1952), as well as the spatulate shape and poor petiole differentiation of such forms as *Rogersia*. Finally, considering the general evidence for a cycadopsid rather than coniferopsid ancestry of the angiosperms (Bailey, 1949; Cronquist, 1968; Takhtajan, 1969; Bierhorst, 1971), it is noteworthy that a tendency for leaf reduction among cycadopsid gymnosperms may be inferred from a comparison of highly compound Pennsylvanian neuropterids (medullosan seed ferns) with apparently related Pennsylvanian-Permian simple-leafed taeniopterids (early Cycadales, according to Mamay, 1976), or of pinnately compound early Mesozoic seed ferns (Peltaspermaceae, Corystospermaceae) with younger palmately compound forms (*Sagenopteris*: Caytoniaceae), and perhaps the *Glossopteris*-like simple-leafed genus *Mexiglossa*, recently described from the Jurassic of Mexico by Delevoryas and Person (1975).

The concept of a xeromorphic "bottleneck" in angiosperm evolution might of course help explain the continued non-recognition of angiosperm precursors, and it may have broader implications for interpretation of other peculiarities of angiosperm morphology and biology (cf. Stebbins, 1974; Doyle and Hickey, 1976). For example, Stebbins (1974) has argued that the unrivaled vegetative flexibility of angiosperms and many of the condensations and transfers of function in their reproductive structures, exemplified by reduction of the female gametophyte, double fertilization, and triploid endosperm formation, may have arisen under selective pressures for more rapid growth and reproduction in seasonally dry environments. Many of the "juvenile" features of the angiosperms regarded by Takhtajan (1969, 1976) as evidence of neoteny, such as scalariform pitting in the secondary wood and the closed carpel, might be explained in similar terms.

At first examination, the concept that the angiosperms evolved under semiarid conditions seems to be contradicted by Carlquist's (1975) observations that vesselless dicots and vesseliferous dicots with relatively primitive scalariform perforation plates are essentially restricted to mesic areas today (cf. Thorne, 1976). In the first case, Carlquist argues that this distribution reflects lower conduction rates in tracheids than in vessels; in the second, the increased sensitivity of vessels to air embolisms, not compensated by sufficiently increased conduction rates. This might seem to imply, as Thorne (1976) argues, that invasion of dry areas by angiosperms could not occur until evolution of vessels with simple perforations, where increased conduction capacity outweighs the problem of embolisms. However, Carlquist's arguments apply only to modern broad-leafed vesselless dicots and vesseliferous forms, and they in no way rule out the possible existence of still earlier vesselless dicots in dry areas, provided they had small leaves or other devices to reduce transpiration

(Carlquist, personal communication). In any case, the ability of early angiosperms to survive in particular environments must be evaluated in terms of their ability to compete with Early Cretaceous gymnosperms and ferns, not with higher dicot types which had not yet evolved.

In our previous paper, we also proposed a model for the subsequent vegetative adaptive radiation of mid-Cretaceous angiosperms, based in part on sedimentary associations and in part on functional-morphological analysis of trends in the Potomac leaf record (Fig. 66). We stressed mechanical considerations and relations between light gathering strategies and ecological succession, following arguments presented by Horn (1971, 1975). Many of Horn's inferences should now be refined and reformulated in terms of a more comprehensive theory of the adaptive trade-offs involved in leaf architecture developed by Givnish (1976, in press) and Givnish and Vermeij (1976).

One of the main conclusions of our analysis is that the general pattern of the Potomac leaf record is more consistent with our secondary expansion hypothesis and Stebbins' (1965, 1974) concept that the first angiosperms were shrubs of semixerophytic origin which entered mesic areas as colonizers of unstable habitats — the "weeds" of the Early Cretaceous — than it is with the more conventional postulate that they were broad-leafed, mesic forest trees comparable to living Magnoliales (e.g., Bews, 1927; Cronquist, 1968; Takhtajan, 1969; Thorne, 1976). Sedimentological evidence that small-leafed Zone I angiosperms were adapted to disturbed habitats, specifically stream margins, is presented below. Here we will only remark that their small size, poor petiole differentiation, and disorganized venation are more consistent with low, highly branched shrubs growing in sunny habitats, where small leaf size is favored (cf. Givnish and Vermeij, 1976), than with arborescent stature. The occurrence of apparently herbaceous monocot-type leaves from the beginning of the Potomac record is also easier to explain if one postulates that the first angiosperms were low shrubs rather than trees.

In functional terms, the most notable variants from the norm among Zone I angiosperms are the large, broad, undissected, low rank leaves of the *Ficophyllum* type. Such leaves suggest Horn's (1971) monolayer light gathering strategy, where photosynthetic tissue is arranged in a single layer to catch all available light. Since such a strategy is advantageous in poorly lit situations, we proposed (Doyle and Hickey, 1976) that these leaves belonged to some of the first angiosperms to enter conifer-dominated Early Cretaceous forests, not as direct competitors of the conifers but as understory trees. This would have been a relatively minor step from our hypothetical shrubby prototype. Although Givnish and Vermeij (1976) question some of Horn's assumptions regarding light gathering strategies, their analysis of trade-offs between transpirational losses and photosynthetic gains also leads to the conclusion that large, undissected leaves should be favored at intermediate levels of the understory. Horn

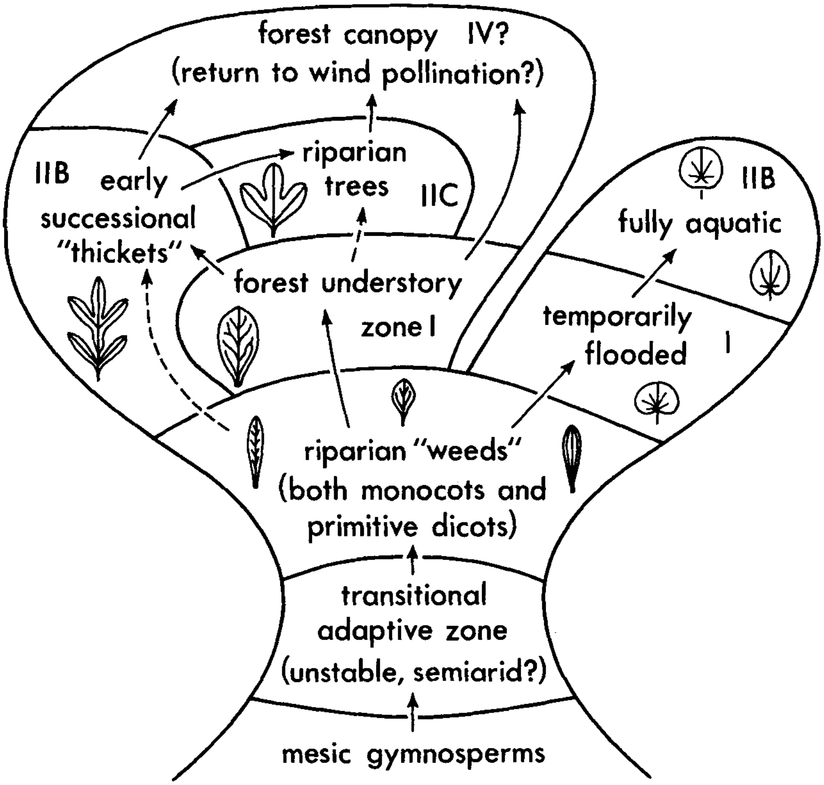


Fig. 66. Model for early ecological-adaptive evolution of the angiosperms (reprinted from Doyle and Hickey, 1976, Fig. 28, p. 186, by permission of Columbia University Press). We argue that trends in the Early Cretaceous leaf and pollen records are consistent with Stebbins' (1965, 1974) hypothesis that angiosperms arose from mesic gymnospermous ancestors (seed ferns?) under pressures for efficient reproduction in an unstable, semiarid environment, as opposed to the concept that they arose as trees of mesic forest habitats. We infer that the primary adaptive radiation of the angiosperms followed perfection of their distinctive reproductive features and coincided with their reinvasion of mesic regions such as the Potomac basin, first as "weedy" shrubs of disturbed stream margin habitats. The course of ecological evolution from "riparian weeds" onward is based on functional interpretations of observed trends and sedimentological associations of Potomac Group leaves. Alternative interpretations for certain trends, such as the possibility that the pinnately and palmately lobed groups originated as dry-season deciduous plants of tropical regions before entering mesic areas as early successional "weed trees", are discussed in the text. Roman numerals (I, IIB, IIC, and IV) refer to Atlantic Coastal Plain pollen zones by which particular adaptive types are inferred to have evolved.

(1971, 1975) argues that a monolayer strategy is also advantageous for climax forest canopy trees; however, observations by Hickey (unpublished) show that virtually no modern canopy species match the low degree of vein regularity or petiole differentiation displayed by Zone I leaves. This is probably related to the mechanical disadvantages of irregular vein networks in the high wind and rain stresses experienced at the canopy level. Also consistent with an understory habit for *Ficophyllum* is the fact that it is most abundant in the rich fern-gymnosperm flora from Fredericksburg, but even there it makes up only a small proportion of the total flora.

In our previous discussion, we suggested that the appearance of pinnatifid, pinnately compound, and palmately lobed leaves in Subzone II-B represents evolution of early successional "weed trees" from understory or shrubby ancestors. Following Horn (1971), we argued that lobation, by decreasing internal leaf diameter and hence the length of full shadows cast by leaves, allows lower leaves to be stacked in the partial shadows of higher leaves in a multilayer configuration that makes more efficient use of full sunlight. Again, although Givnish (1976, in press) points out that Horn does not explain why lobate or compound leaves are superior to branches bearing collections of small, narrow leaves, he too concludes that lobed and compound leaves are advantageous for early successional trees. Givnish argues that in pioneer tree species competing to fill a space as rapidly as possible, natural selection should tend to maximize the amount of photosynthetic laminar tissue and minimize the amount of slower-growing, non-productive support tissue.

One solution to the problem of obtaining the most laminar tissue using the least support tissue is exemplified by Subzone II-B and II-C "platanoids"—a large, lobate leaf in which thin laminar tissue is stretched like fabric on the ribs of an umbrella between the primaries radiating from the leaf base, rather than supported by numerous pinnate secondary veins. Considering the resultant tensional stresses on the laminar tissue between the major veins, it is not surprising that the platanoids are the first group to develop rigid percurrent tertiary venation running perpendicularly from one secondary to the next.

Another solution to the same problem is the pinnately compound or pinnatifid *Sapindopsis*-type leaf, which escapes the necessity for extensive internal bracing by developing a large amount of foliar tissue supported mainly by the rachis and leaflet midveins, while keeping the size of the individual laminae relatively small. The smaller size of contiguous laminar areas may well be the reason why the leaf ranking trend in the *Sapindopsis* complex lags behind that in the platanoids. The pinnately compound leaf, which can be regarded functionally as a cheap "throwaway" branch system, represents an especially advantageous solution for an early successional tree, where rapid upward growth is more important than the capacity for true lateral branching.

Givnish (1976, in press) argues that pinnately compound leaves are also

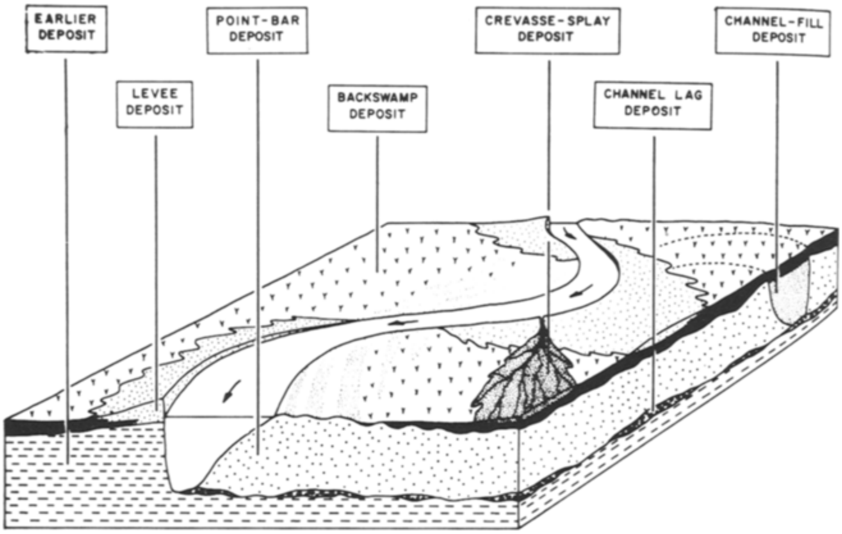


Fig. 67. Lithofacies relationships in the floodplain deposits of a meandering river illustrated by an idealized block diagram. (Reprinted from Allen, 1964, Fig. 4, p. 168, by permission of Elsevier Publishing Company.)

advantageous for dry-season deciduous trees of tropical areas, since the ability to shed their ultimate support framework along with the leaflets allows them to eliminate a major source of transpirational water loss. This explanation is not directly applicable to leaves from the Potomac Group, where the climate appears to have been moist and subtropical and there is sedimentological evidence in favor of the early successional interpretation. However, it is possible that the pinnatifid-leafed *Sapindopsis* complex originated in the tropics in response to seasonal drought, and was preadapted to early successional habitats upon later entering mesic areas, rather than *vice versa* (cf. below).

A final aspect of Givnish's (1976) synthesis which applies to our analysis of the early angiosperm record is his prediction that in leaves where there is no requirement for the veins to fill a support function, the blade should tend to become circular about the supply entry point (petiole attachment), and the veins should assume a roughly radial configuration. A somewhat similar solution for an optimal transport network with major trunk lines radiating from a central but elongate supply line was derived by Sen (1971). In addition, Givnish and Vermeij (1976) argue that whereas a cordate shape best resolves mechanical stresses in liana leaves with petioles held at an angle, a peltate form is favored when the petiole is held vertically. These observations further support the interpretation of actinodromously veined Subzone II-B peltate leaves as floating- or emergent-leafed aquatics, though they do not resolve the question of the habit of the related cordate forms. Both groups, however, show a tendency for extensive dichotomy and looping of the radiating primary veins well within the margin, a feature which is typical of aquatic leaves of both Nymphaeales and unrelated groups such as the genus *Nymphoides*, but which contrasts with the tendency for primary veins or their branches to run directly to the margin or an intramarginal vein in lianas such as Menispermaceae. It may be noted that the early appearance of aquatic angiosperms is easier to explain if the first angiosperms were weedy shrubs, especially if they occupied stream margin habitats, rather than mesic trees.

Sedimentological Evidence on Ecology of Early Angiosperms

In addition to providing an integrated suite of micro- and megafloral remains, the Potomac Group supplies important sedimentological insights into the paleoecology of early angiosperms. The unit consists of lenses of sandstone interbedded with claystone and mudstone and is comparable to ancient and modern sedimentary sequences laid down by meandering river systems on flood plains. Analysis of such fluvial deposits has advanced rapidly during the past 20 years, allowing the development of a rather detailed picture of sedimentary environments and the genesis of constituent rock types (Moore and Scruton, 1957; Allen, 1964, 1965, 1970; Beerbower, 1965; Laming, 1966; Cotter, 1971; Rigby and Hamblin, 1972; Blatt et al., 1972). Because of the importance of the fluvial environment as our window on early angiosperm evolution, we feel that a brief description of its sedimentology will be of value in understanding the fossil record.

The deposits of a meandering river are coarsest near the channel and become finer with increasing distance from the stream (Fig. 67). On the inner, or convex, side of the channel-meander the river lays down point-bar deposits. These consist of lenses of cross-bedded sand becoming finer-grained and horizontally stratified upward. Episodes of lateral accretion as the river channel shifts toward the outside of the meander alternate with quiet water intervals, leaving the upper surface of the point-bar deposit marked by a series of concentric ridges separated by swales. The swales tend to be occupied by standing water where accumulation of parallel-laminated, organic-rich beds of clay or mud takes place, especially on the portion of the point bar away from the stream. Natural levees, made up of cross-bedded and cross-laminated silt and fine-grained sand, are laid down on the stream margins as the river overflows its banks during times of flood, especially on the outer, or concave, portion of the meander-loop. The low-lying back-swamp areas behind the point bars and levees receive much finer sediment which settles from suspension as flood

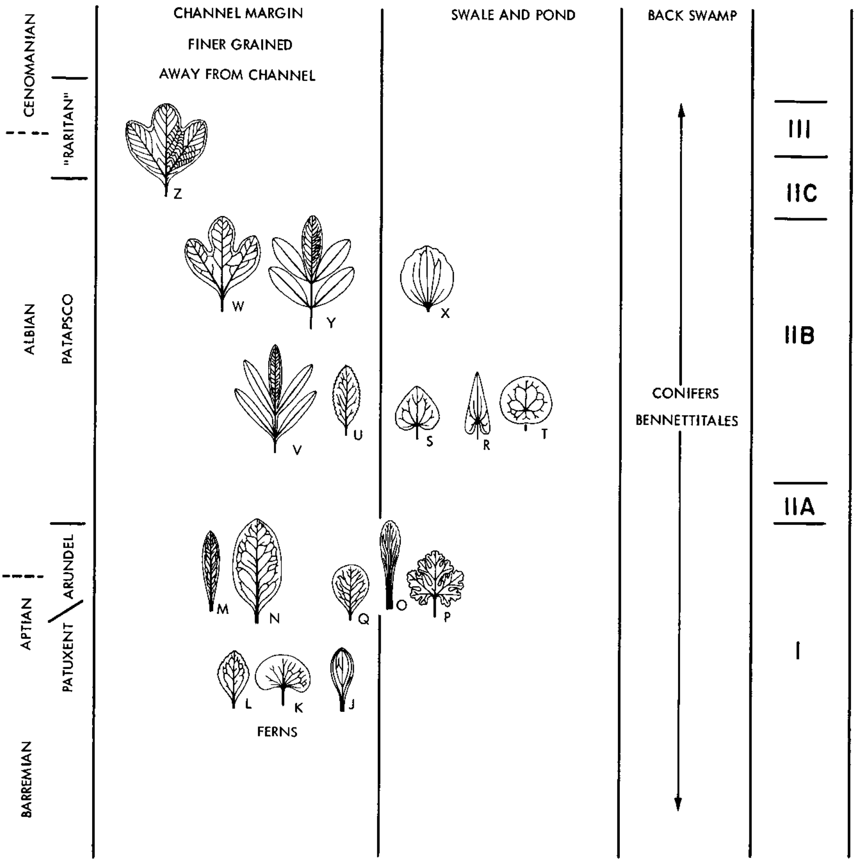


Fig. 68. Relationship of certain leaf types to the sedimentary lithofacies of the Potomac Group. Distance from the left-hand margin of the diagram is roughly correlated with decrease in grain size of the enclosing sediments and increase in features indicating lower energy deposition. The channel-margin lithofacies includes point-bar, levee, and crevasse-splay deposits. The letters identifying the various leaf types are the same as in Fig. 60 except for W, indicating "*Sassafras*" *potomacensis*.

waters recede; they are characterized by massive to parallel-laminated mud and clay with a high content of organic matter. During times of flood, the levee may be breached and fine-grained, cross-laminated sand or silt carried into the back-swamp to form what are called crevasse-splay deposits.

During our megafossil collecting in the Potomac Group, we noted a strong correlation between sedimentary lithofacies and the types of plants encountered. In fact, these observations often allowed us to predict whether a bed was likely to yield fossil leaves, to specify the assemblage we would encounter, and to assign previously collected material to a general facies. Figure 68 shows the principal Potomac angiosperm leaf types placed within one of three major fluvial lithofacies based on the characteristics of the enclosing sediments. Relative distance from the stream channel is indicated by increasing distance of the leaf sketches from the left-hand side of the diagram. The channel-margin lithofacies includes point-bar, levee, and crevasse-splay deposits. Preliminary observations on lithofacies associations of early angiosperm leaves in Kazakhstan and the Western Interior of the United States lead us to believe that the correlations illustrated are typical of the early angiosperm record in at least the Southern Laurasian area.

First, this analysis demonstrates the striking localization of Zone I angiosperm leaf remains to relatively coarse, channel-margin sediments. In any specific case, it cannot be determined whether these leaves represent plants that were actually growing on the stream margin site where they were preserved, or plants whose leaves were transported from some distance upstream. However, this distance could not have been great if they were to escape mechanical degradation. Furthermore, their almost complete absence from finer-grained back-swamp deposits even where these are extremely rich in ferns, cycadopsids, and conifers supports the notion that Zone I angiosperms occupied only areas relatively close to stream courses.

In middle Subzone II-B, the majority of angiosperm leaves, including *Sapindopsis* and the platanoids, continue to occur in channel-margin deposits, but in contrast to the situation in Zone I they are locally abundant and tend to extend into finer-grained sediments. The presence of a nearly pure mat of *Sapindopsis magnifolia* just above the contact between a horizontally bedded sandstone and a mudstone in the inferred crevasse-splay deposit at Brooke (Fig. 69), associated with lignitized and charred fragments of conifer wood, is dramatic evidence of both its ability to form dense stands and the instability of the local environment in which it grew. This agrees well with our functional-morphological arguments that *Sapindopsis* was a "weed tree" adapted to early successional conditions. Later members of the *Sapindopsis* complex with pinnately compound leaves are often found in the same sort of setting (e.g., just above a clay-pebble conglomerate with abundant charcoalized wood at the West Brothers pit). However, by the top of Subzone II-B and in Subzone II-C *Sapindopsis* and the platanoids have begun to show an imperfect segregation into different lithofacies, with the platanoids especially abundant in the coarser channel-margin facies (e.g., White Point), recalling the riparian habitat of modern *Platanus*, and *Sapindopsis* sometimes occurring in quite fine, clayey sediments (e.g., Red Point, Severn Clay Mine).

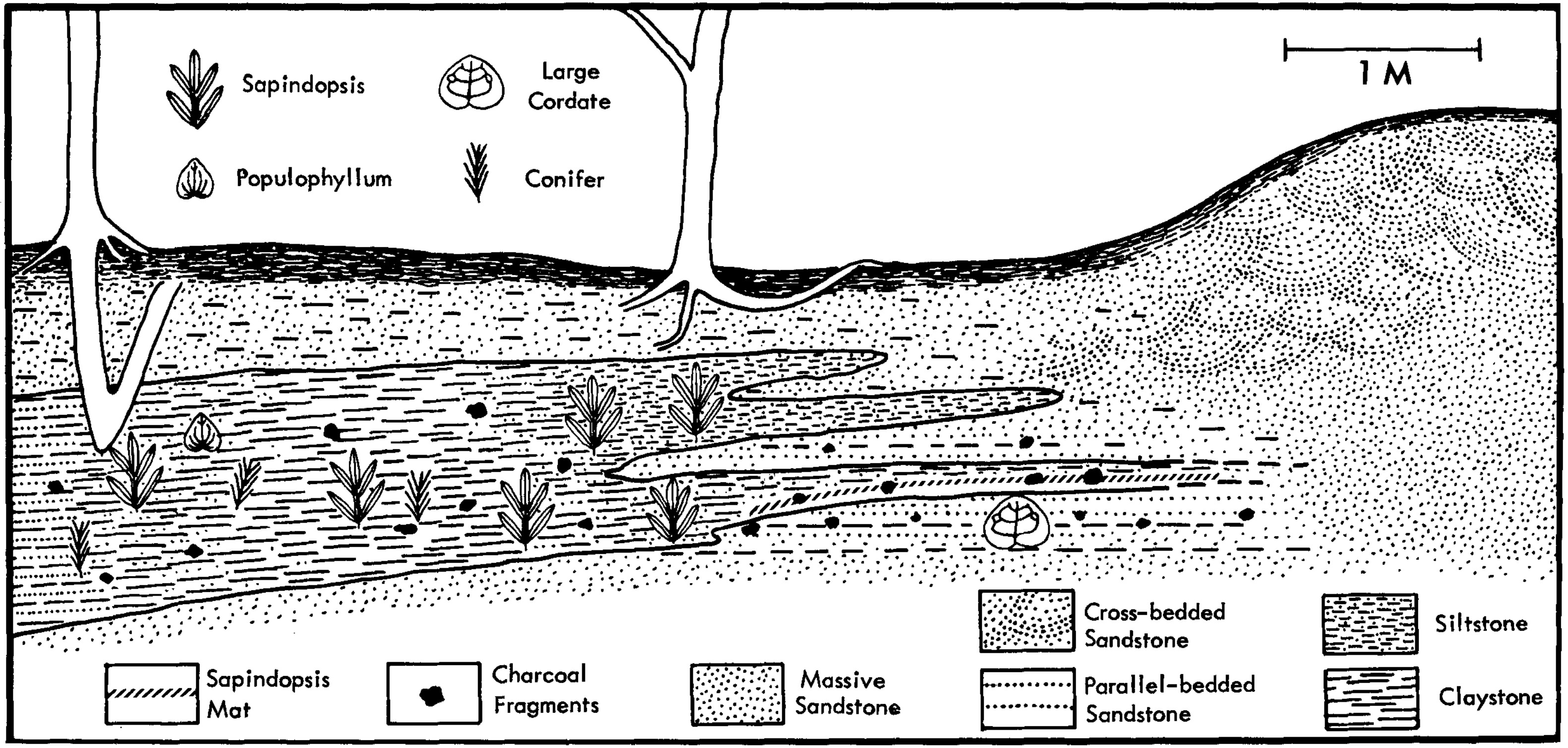


Fig. 69. Sketch of sedimentary facies at the Brooke, Virginia locality showing the major leaf types found in them. Note the symbol indicating the mat of *Sapindopsis magnifolia* leaves near the base of the lowest claystone unit at the right, and the general decrease in grain size and the increase in conifer material toward the left.

Another important development seen in the middle of Subzone II-B is the appearance of cordate and peltate actinodromous leaves in fine-grained beds that are often thin and interbedded with sandstone. The inference that at least the peltate forms were growing in place in the standing water of swale or pond environments is supported by the generally parallel lamination of their enclosing sediments, as well as by the leaf architectural features mentioned above. In one such deposit, at Quantico, the peltate leaves occur in clusters spaced about a meter apart along the outcrop, suggesting a rooted aquatic habit.

Even in upper Subzone II-B and in Zone III, we have found fine-grained deposits containing mostly ferns and gymnosperms, suggesting that many environments well removed from the stream channels remained dominated by non-angiospermous groups throughout deposition of the Potomac Group. Such observations agree with pollen evidence, noted as early as 1961 by Pierce, that even in the Cenomanian, gymnosperms continued to play a greater role in the regional vegetation than had been inferred from the abundance of angiosperm leaves in some contemporaneous fluvial facies, such as the sandstones of the Dakota Group of Kansas.

The results of this sedimentological analysis reinforce our functional-morphological inferences concerning early evolution of the angiosperm vegetative body. In particular, the gradual spread of angiosperms from coarse-grained channel-margin deposits agrees with Stebbins' (1965, 1974) hypothesis that the first angiosperms were "weedy" semixerophytic shrubs preadapted to disturbed habitats, rather than mesic trees comparable to modern Magnoliales. Stream margins are the least stable sites in a flood plain environment, where plants are subjected to periodic inundation, flood-training, and rapid sedimentation, and the areas where closed-canopy conifer forests would have the least chance to develop. In addition, when viewed in terms of the time-scale and dynamics of ecological succession, the evolutionary trends inferred in the subsequent angiosperm leaf record make sense as responses to selective pressures operating in a stream margin situation. On the one hand, the repeated cycles of lateral migration of the channel and return to more stable back-swamp conditions which are typical of a fluvial system would place plants growing on stream margins under selective pressure to adapt to later successional stages. *Sapindopsis* and the platanoids are interpreted as examples of such a trend. On the other hand, periodic flooding and shifting of the borders between stream margin and swale or pond habitats would favor adaptations for partially and eventually fully aquatic habit, as inferred for the peltates. If correct, this picture constitutes a remarkable example of Margalef's (1968) concept that in most groups evolutionary trends should tend to parallel changes realized in succession, except when unusual evolutionary events (e.g., neoteny) allow groups to "drop back" to earlier successional stages.

Systematic Affinities of Early Angiosperms

In our previous report (Doyle and Hickey, 1976), we deliberately stressed a comparative and stratigraphic analysis of Potomac fossil pollen and leaves independent of possible systematic relationships with modern taxa. We made comparisons with living plants primarily in order to evaluate existing hypotheses on the relative advancement of modern groups in the light of fossil trends, as a source of functional analogies, and to refute the contention of some authors (e.g., Axelrod, 1970; Stebbins, 1974) that the level of advancement of Early Cretaceous leaves requires major deficiencies in the pollen record or a significant lag of pollen evolution behind leaf evolution. We felt this course was necessary in order to counteract the tendency that has so long plagued angiosperm paleobotany for misidentification of Cretaceous fossils with modern families and genera. The result has been a legacy of unjustified conclusions on the advancement of Cretaceous angiosperms, based on characters not actually seen in their fossil remains but simply assumed to be present from analogy with their supposed modern relatives (cf. Wolfe, 1972a, 1973; Dilcher, 1974; Wolfe et al., 1975; Doyle and Hickey, 1976; Hughes, 1976). However, thanks to increasingly comprehensive recent surveys of the distribution of leaf architectural and pollen characters at the higher categorical levels among modern angiosperms (Hickey and Wolfe, 1975; Walker and Doyle, 1975; Van Campo, 1976), we believe it is now theoretically and practically justifiable to hypothesize that certain Potomac leaf and pollen types represent early records of a number of orders and subclasses of flowering plants, provided we recognize that such plants may have possessed other characters different from or more primitive than those of any living members of the groups in question.

This picture of early angiosperm evolution parallels the rapid appearance and diversification of invertebrate phyla and classes in the Cambrian, of classes of lower vascular plants in the Devonian, and of orders of placental mammals in the Paleocene-Eocene. Most recent authors (e.g., Cloud, 1948; Simpson, 1953; Chaloner, 1967, 1970; Banks, 1968, 1970; Stanley, 1976) no longer take such patterns as evidence for long prior evolutionary history. Valentine and Campbell (1975) have recently described mechanisms to explain such rapid diversification, first involving attainment of new levels of complexity by elaboration of new systems of regulatory, as opposed to structural, genes, followed by exploitation of the potentialities thus achieved by rearrangement of sequences of gene activation into a number of particularly adapted patterns. Since it is mostly the timing of already existing developmental processes that would be affected (e.g., as in neoteny), it is quite conceivable that integration of vital functions might be maintained even during radical transformations of ground plans.

Many of the most distinctive innovations of angiosperms over gymnosperms are suggestive of just such a major reorganization and elaboration of regulatory gene systems controlling the pattern of developmental processes. These include telescoping and rearrangment of events in the life cycle, epitomized by double fertilization, which ensures that the embryo-nourishing tissue (endosperm) functionally comparable to the megagametophyte of gymnosperms is elaborated after fertilization instead of before; the various other abbreviations and neotenous features cited by Takhtajan (1969, 1976); and the expanded role of intercalary meristematic activity in both leaves and other organs (cf. Stebbins, 1974). The common selective advantage of these features might be increased reproductive efficiency and vegetative vigor and flexibility, as argued by Stebbins (1974).

Plausible examples of Valentine and Campbell's (1975) subsequent phase of rapid evolution of basic adaptive patterns by reshuffling of sequences of gene action may include the very early appearance of the distinctive leaf architectural types which Hickey and Wolfe (1975) have shown tend to characterize whole dicot subclasses or large portions of them (Fig. 70). By considering the close relationships between leaf architecture, growth habit, and ecology inferred by Horn (1971, 1975), Givnish (1976, in press), and Givnish and Vermeij (1976), it may be possible to interpret the occurrence of several of these patterns in the Early Cretaceous record as evidence of very early achievement of particular vegetative adaptive syndromes which tended to channelize the course of diversification of lines that are recognized in retrospect as subclasses or orders.

Contrary to Hughes (1976), we consider the presence of typically monocotyledonous specializations in both pollen and leaves from Zone I — the heterogeneous sculpture pattern of *Liliacidites*, and the apically fusing venation and sheathing leaf bases of *Acaciaephyllum* — evidence that the lines leading to monocots and dicots had already diverged by the earliest appearance of angiosperms in the fossil record. The fact that the leaf blade develops from a different part of the leaf primordium in modern members of the two groups — the upper leaf zone in dicots, the lower leaf zone in monocots (cf. Kaplan, 1973) — would even be consistent with separation of these lines at the pre-angiospermous stage characterized by highly reduced, xeromorphic leaves which we hypothesize preceded invasion of mesic habitats. On the other hand, the significant similarities between Zone I monocot- and dicot-type leaves and pollen, as well as the presence of the leaves in similar channel-margin lithofacies, suggest that this divergence may have been relatively recent.

Although Zone I monocotyledonoid forms appear herbaceous, they show no evidence of close relationship to the aquatic subclass Alismidae, considered primitive in many theories of monocot evolution (e.g., Cronquist, 1968; Takhtajan, 1969). Furthermore, their occurrence well before the earliest probable nymphaealian precursors with convincing aquatic specializations in Subzone II-B casts doubt on the related notion that the Nymphaeales are the closest surviving dicot sister-group of the monocots. From Potomac times on, evolution of the monocots seems to have emphasized variations on the herbaceous habit and exploitation of the possibilities of narrow leaves developed from the lower leaf zone. The present fossil data support the concept that the tree habit was a secondary development within monocots; in fact, the palms, the most important modern group of arborescent monocots, are not documented until some 30 million years later, in the second half of the Late Cretaceous (Muller, 1970; Read and Hickey, 1972; Doyle, 1973).

Features such as large, pinnately veined, low rank leaves with multistranded primary veins, festooned brochidodromous secondary veins (Mouton, 1970), and intersecondary veins which branch in a characteristic manner within the intercostal areas are consistent with derivation of woody members of the subclass Magnoliidae, particularly the order Magnoliales, from the complex of larger, elliptical-leafed dicots represented in Zone I (Wolfe, 1972b; Wolfe et al., 1975; Hickey and Wolfe, 1975). Of these features, at least the characteristic intercostal venation, large size, and associated tendencies for increase in rank can be reasonably interpreted as shared advances, and hence evidence for true phyletic relationship, rather than generalized characters residual from the common ancestry of all angiosperms.

Today woody Magnoliidae survive principally as subcanopy trees and shrubs in highly mesic subtropical and montane tropical environments (cf. Takhtajan, 1969; Carlquist, 1975), a habit very similar to that we have inferred for large-leafed Zone I forms. Divergence of the ancestors of woody Magnoliidae by Zone I time is consistent with pollen evidence, since the modern forms have exclusively monosulcate and derived pollen types. Some of these are roughly comparable to Zone I columellar monosulcates (e.g., Canellaceae, Chloranthaceae, Atherospermataceae), but others (e.g., Degeneriaceae, some Annonaceae) lack columellae and are thus considered more primitive by Walker (1976; cf. also Van Campo and Lugardon, 1973; Doyle et al., 1975). Despite their retention of these and other undoubtedly primitive characters, such as vesselless wood in Winteraceae, we re-emphasize our conclusion that the woody Magnoliidae do not make a plausible prototype for the spectrum of divergent trends and sedimentary associations seen in the Potomac record, and are presumably specialized in their own ways over the first angiosperms. Besides the habital and leaf architectural features cited, we would suggest the generally large size of their pollen as an especially good candidate for an advanced character of modern Magnoliales (contrary to Walker and Doyle, 1975).

Similarly, leaf architectural advances such as shape, repeated dichotomy of the actinodromous primary veins, and formation of a series of secondary loops

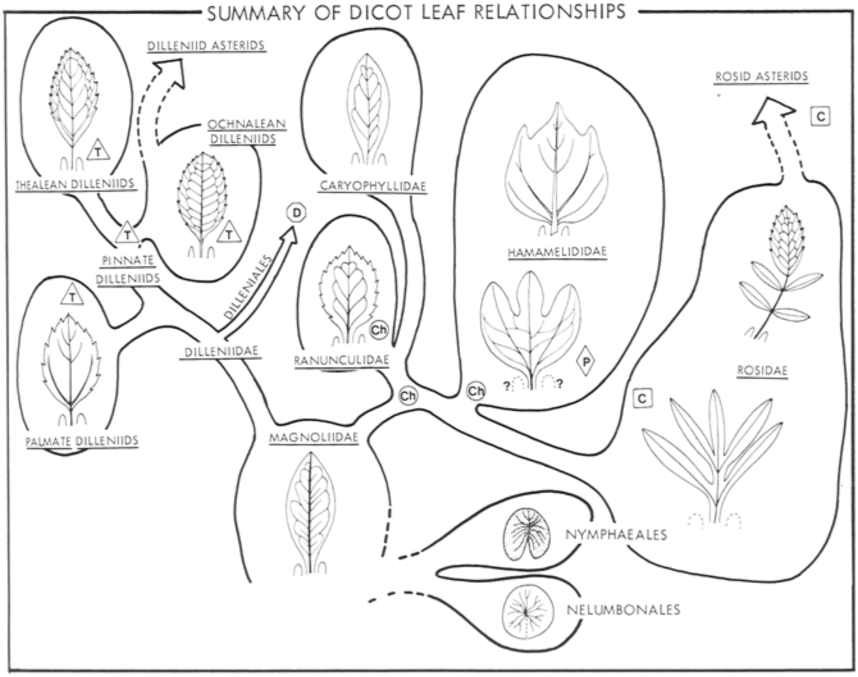


Fig. 70. General relationships between leaf morphology and the dicot subclasses of Takhtajan (1969) and Cronquist (1968), as interpreted by Hickey and Wolfe (1975). The emphasis here is on the types of leaf architecture that appear to be basic to or serve as the ground plan for the systematic groups without stressing their precise systematic boundaries or composition and without necessarily supporting the phylogenetic relationships indicated. The letters inside the symbols represent the occurrence of marginal teeth having specific combinations of morphological characters. These are: **Ch** = Chloranthoid, **P** = Platanoid, **C** = Cunonioid, **D** = Dillenioid, **T** = Theoid. The platanoid leaf of Early Cretaceous age described in this report is shown as the precursor of the basically palmately lobed, palinactinodromous part of the subclass Hamamelididae, while the pinnately organized *Sapindopsis* is shown as primitive for the Rosidae.

well within the margin are consistent with origin of the aquatic orders Nymphaeales and Nelumbonales (subclass Nymphaeidae of Walker, 1976) from the complex of cordate and peltate leaves which diversified in Subzone II-B. We have noted sedimentary and functional-morphological evidence that at least the peltate members of this complex were already aquatic. Differentiation of ancestral Nymphaeidae in the Albian (or earlier) would be consistent with the level of pollen advancement in their modern representatives (monosulcate and derived types, such as zonasulculate, in Nymphaeales, tricolpate in *Nelumbo*: cf. Walker, 1974; Walker and Doyle, 1975), with their retention of putatively primitive floral characters, and with their lack of vessels (cf. Takhtajan, 1969). Modern Nymphaeidae are more specialized than Subzone II-B forms in many aspects of their leaf architecture, including larger size, higher rank venation, and more stereotyped shape. Continued elaboration of a whole syndrome of highly specialized aquatic adaptations would of course be expected once the peltate-cordate line had entered aquatic environments.

Leaf architectural arguments can also be advanced that the pinnately lobed to compound and palmately lobed leaves of Subzone II-B—*Sapindopsis* and the platanoids—are representatives of an ancestral complex from which arose the subclass Rosidae and at least the order Hamamelidales (Hamamelidaceae, Platanaceae) of the subclass Hamamelididae of Cronquist (1968) and Takhtajan (1969) (cf. Hickey and Wolfe, 1975). With the exception of the Juglandales, regarded as Rosidae by the latter authors, certain of the Asteridae, and the Ranunculidae, which differ in their ternate organization, the Rosidae are the only major group of dicots with pinnately compound leaves, and according to Hickey and Wolfe (1975) they are primitively so. The Hamamelidales, especially the Platanaceae, share with the early platanoids their unusual palinactinodromous primary venation, strongly and closely percurrent tertiary veins, and "stitched intertertiary" veins formed by fusion of quaternaries; we interpret the unlobed, pinnately veined condition in many Hamamelidaceae as a secondary deviation from this pattern, on the basis of evidence for the same trend in Cenomanian platanoid-derived leaves (e.g., *Betulites*). Although Cronquist (1968) and Takhtajan (1969) do not consider the Rosidae and Hamamelidales closely related, the *Sapindopsis* and platanoid complexes show many tendencies for morphological intergradation with each other and evidence for relationships with both modern groups. Among such features are the palinactinodromous primary venation and lobed terminal leaflets of some *Sapindopsis* specimens from Brooke, the West Brothers pit, the Cheyenne Sandstone, and the Lakota Formation; the presence of a tooth type in a new species of *Sapindopsis* from the West Brothers pit having features of teeth of both modern groups; similarities in cuticle structure between Brooke *Sapindopsis* and platanoids from Stump Neck and Bull Mountain (Mersky, 1973; Upchurch, unpublished); and the association of both with the same type of inflorescence bearing small "heads."

Comparison of the levels of pollen and leaf advancement at the time of appearance of *Sapindopsis* and the platanoids is also consistent with the concept that they represent pre-rosids and pre-hamamelidalians, respectively (cf. Doyle and Hickey, 1976). Hamamelidales have basically reticulate tricolpate pollen corresponding roughly to the grade of advancement of many Subzone II-B species, but the Brooke platanoid leaves are at least slightly lower rank than any living members of the order. On the other hand, the most primitive pollen type in living Rosidae appears to be tricolporoidate, assuming that the absence of ora in some undoubtedly specialized herbaceous groups such as *Saxifraga* is the result of secondary loss (Hideux and Ferguson, 1976). Tricolporoidate pollen becomes abundant only in upper Subzone II-B and higher, and is represented at Brooke only by occasional individual variants of tricolpate species. The resulting inference that the earliest *Sapindopsis* plants produced tricolpate pollen, also supported by the unusual abundance of tricolpates at Brooke, is of course consistent with the concept that their pinnatifid leaves exemplify a truly transitional stage in the origin of the pinnately compound leaf which is no longer represented in the modern flora and which preceded evolution of other rosid features.

Interestingly, these considerations would also support the hypothesis that modern Rosidae with simple leaves, including the Escalloniaceae, Brexiaceae, and other Saxifragales, and the Cornales, Celastrales, and Myrtales, had compound-leafed ancestors. Such a derivation of these simple-leafed groups is consistent with their basically tricolporoidate or tricolporate pollen, often of the smooth, triangular, angulaperturate type not seen until Subzone II-C and first abundant in Zone III (early Cenomanian). The alternative would be to assume that the simple-leafed rosids actually belong in another subclass (as suggested for the Myrtales and Celastrales by Hickey and Wolfe, 1975), a possibility contradicted by their close palynological links with pinnately compound Saxifragales (cf. Walker and Doyle, 1975; Hideux and Ferguson, 1976; Van Campo, 1976) and by further clarification of the relations of rosid tooth types by Hickey (unpublished).

In this context, our sedimentary and functional-morphological inferences on the ecology of *Sapindopsis* and the platanoids suggest intriguing but unresolved alternative explanations for the adaptive basis of the divergence between Rosidae and Hamamelidales. As is discussed above, Givnish (1976, in press) has argued that pinnately compound leaves (and their pinnatifid precursors?) can be regarded functionally as cheap "throwaway" branchlets which are favored over permanent leafy branches in two situations: for minimization of stem transpiration during the dry season in deciduous trees of tropical climates, and for optimal use of resources for rapid growth in "weed trees" of early successional habitats in mesic areas. Clearly, the evidence summarized here favors the second interpretation of Potomac *Sapindopsis*. However, assuming that *Sapindopsis* and the platanoids were tricolpate groups, the geographic evidence reviewed above for poleward spread of the first tricolpates from Africa-South America raises the possibility that the ancestors of the *Sapindopsis*-platanoid complex originated in response to increasing seasonal moisture stress in that area during the Aptian, and only secondarily moved into early successional habitats in mesic areas of Laurasia, rather than *vice versa.* Obviously, discovery of angiosperm leaves associated with the Aptian tricolpates of Africa-South America and in Subzone II-A of the Potomac Group is essential to test this highly speculative hypothesis. In any case, subsequent evolution of the Rosidae has involved much variation on both these themes and alternation between them. For instance, rosid weed trees such as *Acer negundo*, *Ailanthus*, and *Rhus* are typical of many early successional habitats in the temperate zones, and legumes, Sapindales, and Rutales are important in drier and exposed canopy situations in the tropics.

On the other hand, Givnish's (1976) arguments would indicate that lobate leaves constructed on the broad, thin platanoid plan are more specifically adapted to mesic, seasonal temperate climates. Here leaves can be large without causing disadvantageously high water loss, but are shed in the winter and should therefore be produced cheaply. Hence, it is suggestive that Subzone II-C platanoids have expanded petiole bases comparable to those of modern deciduous leaves. In a temperate climate, tendencies for wind pollination, which is particularly advantageous when no leaves are present in the spring to baffle wind currents (cf. Whitehead, 1969), would be reinforced as such deciduous plants began to form dense stands. Such a pattern of adaptive radiation would explain well the distribution and features of the Hamamelidales, which are largely temperate deciduous trees and shrubs with strong tendencies for wind pollination and floral reduction. Remarkably, the genus *Platanus*, with leaf architecture closest to the presumed basic plan for the order and inflorescences suggesting highly reduced versions of those associated with both *Sapindopsis* and the platanoids, grows today in stream margin habitats similar to those inferred sedimentologically for its distant mid-Cretaceous precursors.

It might seem reasonable to interpret the evolution of the wind-pollinated porate "Amentiferae" of the temperate zones as simply a linear continuation of this "hamamelidalian" trend, and such a relationship is in fact assumed by Cronquist (1968), Takhtajan (1969), and many other authors. However, palynological evidence indicates that the history of the Amentiferae was more complex (cf. Wolfe, 1973; Wolfe et al., 1975; Walker and Doyle, 1975). Their granular exine structure (Van Campo and Lugardon, 1973; Doyle et al., 1975) and often clearly compound pororate apertures are several steps removed from the reticulate tricolpate pollen of the middle Albian or of modern Hamamelidales, and mid-Cretaceous fossil evidence suggests that the intermediate steps included early Cenomanian triangular tricolporates of rosid, rather than hamamelidalian, aspect, and the bizarre triangular triporate Normapolles (cf. Doyle, 1969; Wolfe et al., 1975; Walker and Doyle, 1975). A rosid ancestry for at least the Juglandaceae and Rhoipteleaceae is supported by their pinnately compound leaves and cunonioid teeth (Wolfe, 1973; Hickey and Wolfe, 1975). Forms such as Betulaceae have leaves which are more similar to those of the Hamamelidaceae (Wolfe, 1973; Hickey and Wolfe, 1975). However, the functional arguments presented here are at least as consistent with the possibility that these leaf similarities reflect convergent later invasion of the temperate deciduous adaptive zone by rosids as they are with the possibility that the equally striking normapolloid or juglandaceous pollen characters of the Betulaceae arose independently.

As yet, no leaf types having specializations characteristic of the subclass Dilleniidae of Cronquist (1968) and Takhtajan (1969) have been recognized in the Early Cretaceous record. The genus *Eucalyptophyllum* from Fredericksburg (Fig. 23) possesses an intramarginal vein in common with several dilleniid groups, but because of its totally distinct intercostal venation, we agree with Wolfe et al. (1975) that it more likely represents an extinct line of equal rank to the Magnoliales.

We would stress that until Early Cretaceous leaf and pollen types have been linked with Tertiary and Recent taxa by careful and critical tracing of lines through the Late Cretaceous, the ideas on systematic relationships presented here can be considered no more than preliminary hypotheses. Furthermore, we would re-emphasize that even if these hypotheses are correct, it would be dangerous and in many cases surely false to assume that Early Cretaceous representatives of lines we can recognize today were as distinct from each other or had all the same character combinations as even their most primitive living representatives. To an observer deprived of our retrospective viewpoint on the ultimate importance of incipient trends, the angiosperm line at some early point in its history might appear as only an aberrant species of cycadopsid distinguished by unusual reproductive biology, ecology, or embryological features detectable only by histological study rather than by gross morphological features recognizable on an herbarium sheet. The first angiosperms to enter the fossil record in the Barremian might still not be accorded the status of more than a family or order of cycadopsid seed plants. Even by the end of the Early Cretaceous, although the importance of the angiosperms as a major new group might have become evident, the separation between monocots and dicots might be considered of only ordinal magnitude, with the dicot lines destined to become subclasses, as well as others now extinct, classified as families.

One possibly surprising corollary of our analysis is that divergent adaptations in the vegetative sphere may have had a much greater role in determining the initial course of adaptive radiation and differentiation of higher angiosperm taxa than has been generally appreciated. This perhaps reflects a traditional overemphasis on reproductive characters in the systematics of Recent angiosperms and a too ready assumption that the vegetative structures of angiosperms are so plastic that their modifications have had little relation to major trends. The trend toward wind pollination in the Hamamelidales is especially suggestive of a case where establishment of particular vegetative adaptations may have tended to channelize trends in the reproductive sphere rather than *vice versa.* On the other hand, by permitting greatly increased speciation rates, the unique potentialities of the angiosperm reproductive system for new isolating mechanisms (specific insect pollinators, stigma recognition systems, etc.) may have had a decisive role in the success of the angiosperms by allowing them to realize an unprecedented array of combinations of both vegetative and reproductive features (cf. Stanley, 1976).

CONCLUSIONS

Although the very earliest phases of angiosperm origin and evolution are still unknown, evidence on the primary adaptive radiation of the angiosperms from Early Cretaceous fossil sequences is now strong enough that paleobotany can begin to assume a central role in formulation and testing of hypotheses on angiosperm phylogeny and in narrowing the previously wide range of speculation on their origin. Obviously, the interpretations and models we have proposed here are not necessarily the only ones that can be derived from the present data. However, many of the trends and regularities which we have noted are so solidly based on observations not only on the Potomac Group but also on many other geological sections that they must be incorporated into any future comprehensive theory of angiosperm evolution.

One theory which we consider already conclusively ruled out by fossil data is that the "Amentiferae," with superficially gymnospermous reproductive structures, represent a primitive group linking gymnosperms and angiosperms. Fossil evidence indicates that the triporate pollen type of most Amentiferae arose only in the Late Cretaceous as the result of a long series of intermediate stages from monosulcate pollen to triporate pollen of the Normapolles type, and that fourth rank leaves as rigidly organized as those of most Amentiferae had not yet evolved even in the Cenomanian. This is in full agreement with the interpretation of the Amentiferae as a highly specialized group whose simple, unisexual flowers are the result of secondary reduction associated with reversion to wind pollination (cf. Cronquist, 1968; Takhtajan, 1969; Thorne, 1976). In general, the fossil record makes implausible all theories of angiosperm evolution which regard as primitive groups with exclusively tricolpate or derived pollen types (including Dilleniaceae, contrary to Stebbins, 1974), high rank or compound leaves, or other characters which do not appear until well into the Cretaceous angiosperm diversification sequence. Similar considerations apply to theories that attempt to salvage a primitive role for the Amentiferae by postulating that they are one of several lines derived polyphyletically from a heterogeneous gymnospermous ancestry (e.g., Meeuse, 1966, 1975). The fact that the early angiosperm record is consistent with a coherent radiation from an initial monosulcate stock with simple, low rank leaves is just the sort of data taken elsewhere in paleontology as evidence for monophylesis, and leaves little room for theories that the angiosperms are markedly polyphyletic (e.g., Meeuse, 1966, 1970; Krassilov, 1973, 1975; Hughes, 1976). Similarly, while an eventual glossopterid ancestry for the angiosperms cannot be excluded, the Cretaceous record offers no support for Melville's (1962, 1963, 1969) arguments for such a relationship. Not only is there a gap of two geological periods between the last glossopterids and the first primitive angiosperms, but Melville's supposed glossopterid venational syndrome occurs today only in unrelated angiosperm groups which are highly advanced in other features, and it is lacking in the earliest Cretaceous angiosperms. At the same time, the Cretaceous evidence on primitive characters among angiosperms provides strong general support for "classical" or "ranalian" theories based on the assumption that the monosulcate Magnoliidae *s. str.* retain a greater number of primitive characters than any other living dicot group (e.g., Cronquist, 1968; Takhtajan, 1969; Thorne, 1976; Walker, 1976). However, we would add the qualification based on our analysis of early divergent trends (e.g., to monocots and Nymphaeales) that the woody order Magnoliales should not necessarily be considered archetypic for the angiosperms as a whole, but represents only one of several early lines of specialization.

Those working under the assumptions of the monophyletic, magnoliid theory may well ask what paleobotany has shown about angiosperm evolution that was not known already. First, it should be recognized that paleobotany has revealed direct historical evidence for this theory that did not exist previously. Second, it permits specific conclusions on the timing and ecological context of phylogenetic events where several alternative conjectures would be equally plausible on comparative evidence. For example, the hypothesis that the monocots and the aquatic dicot orders Nymphaeales and Nelumbonales were very ancient branches of the angiosperm line is fully consistent with their retention of monosulcate pollen and other supposed primitive characters (cf. Cronquist, 1968; Takhtajan, 1969; Thorne, 1976; Walker, 1976). However, without fossil evidence for their existence at the earliest stages of the angiosperm record it would be possible to maintain that they arose much later from one or another persisting woody monosulcate dicot group. Third, the existence of fossil groups with character combinations and intermediate conditions no longer surviving in the modern flora provides new evidence for hypotheses on relationships between higher angiosperm taxa which would otherwise be speculative and controversial. Thus, the morphological intergradation seen in the *Sapindopsis*-platanoid complex supports the concept of a sister-group relationship between the Rosidae and the Hamamelidales (accepted by Thorne, 1976, and Walker, 1976, but not Cronquist, 1968, or Takhtajan, 1969). Fourth, the Cretaceous record strongly hints that early angiosperms, like Florin's (1951) earliest Permo-Carboniferous conifers, had certain unexpected characters subsequently lost or modified in all living "primitive" groups, such as small leaves with disorganized venation and an apparent "weedy," stream margin growth habit. Fifth, it leads to conclusions on directions of geographic spread and ecological preferences of early angiosperms which depart significantly from conventional extrapolations from distributions of modern taxa, such as the inference that tricolpate-producing dicots originated in Africa-South America and that increasing aridity acted as a stimulus for their evolution. In contrast, the modern distribution of tricolpate dicots (lower Hamamelididae and Ranunculidae) would suggest a mesic, Laurasian origin. These last two conclusions are consistent with Stebbins' (1965, 1974) hypothesis that the first angiosperms were shrubs which originated under pressures of a semiarid environment, as opposed to the more conventional view that they were magnolialian trees of mesic forests (e.g., Bews, 1927; Cronquist, 1968; Takhtajan, 1969; Thorne, 1976).

Although the first Barremian fossils which can be related to the angiosperms appear to be fully angiospermous in their visible pollen and leaf characters and do not point unambiguously toward any one gymnospermous *group* as their ancestors, they do have features which have intriguing implications on *processes* involved in the origin of angiosperms. For example, the evidence from exine sculpture that Barremian angiosperms were insect-pollinated supports the concept that insect-plant interactions played a key role in origin of the angiosperm flower and its component structures (cf. Takhtajan, 1969), as well as in the subsequent unprecedented diversification of the angiosperms. Likewise, the indirect indications that angiosperms had stigmatic pollen germination soon after their first appearance supports the notion that the origin of defining angiosperm reproductive features was a crucial event which preceded, rather than followed, their initial expansion. Finally, when considered in the light of comparative developmental studies on modern plants, the small size and disorganized venation of early angiosperm leaves suggests the possibility of a reduction phase in the origin of the angiosperms, possibly related to adaptation to a seasonally dry environment as proposed by Stebbins (1974). Such a phase might also be responsible for the apparently juvenile or neotenous characters recognized in many angiosperm organs by Takhtajan (1969, 1976). Interestingly, these possibilities tend to widen rather than narrow the range of gymnosperm groups which can be considered as potential angiosperm ancestors. For example, if Takhtajan (1969, 1976) is correct in believing that scalariform pitting in the secondary wood of modern vesselless angiosperms is the result of prolongation of metaxylem pitting patterns, it is no longer valid to argue that only gymnosperms with scalariform pitting in their secondary wood (Cycadales, Bennettitales, and their hypothetical ancestors) could have given rise to angiosperms. Only groups which have no scalariform pitting at all, even in the metaxylem, can be eliminated (Coniferales, Ginkgoales, and Gnetales).

The rapid progress in Cretaceous paleobotany clearly shows that the problem of angiosperm origins is no longer an "abominable mystery," but rather a tractable scientific problem capable of solution by paleobotanical and coordinated comparative studies. Because of the tradition of excessive speculation in this field, it is worth emphasizing that theory must be balanced by collection and critical analysis of new data. In order to understand fully the significance of the Early Cretaceous record, more work is needed on already studied sedimentary sequences using new techniques such as TEM studies of pollen ultrastructure, cuticle analysis, and isolation of reproductive structures from plant debris beds (cf. Hughes, 1976), while in more poorly known but critical geographic areas such as Africa-South America and eastern Asia the basic pollen and leaf records remain to be elucidated. Expansion of these investigations will inevitably proceed in two directions. On the one hand, improved knowledge of Early Cretaceous angiosperms will help focus the search for still earlier angiosperms and their ancestors in Neocomian and Jurassic rocks. However, the identification of any Jurassic plants as proangiosperms (as attempted by Krassilov, 1973, 1975) will probably be a difficult task requiring a detailed comparative analysis of all organs as rigorous as that which was required to establish the relationship between cordaites and conifers (Florin, 1951), or the role of Devonian Aneurophytales and Archaeopteridales as progymnosperms (Beck, 1960, 1970, 1976; Scheckler and Banks, 1971). On the other hand, bridging the poorly known Late Cretaceous interval by detailed tracing of angiosperm lineages and changes in their adaptive strategies should prove to be an equally rewarding field for investigations over the next 20 years. In the light of the initial successes of such methods, their extension has the potential of leading to systems of angiosperm phylogeny and classification as firmly based in fossil evidence as those of any animal group.

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