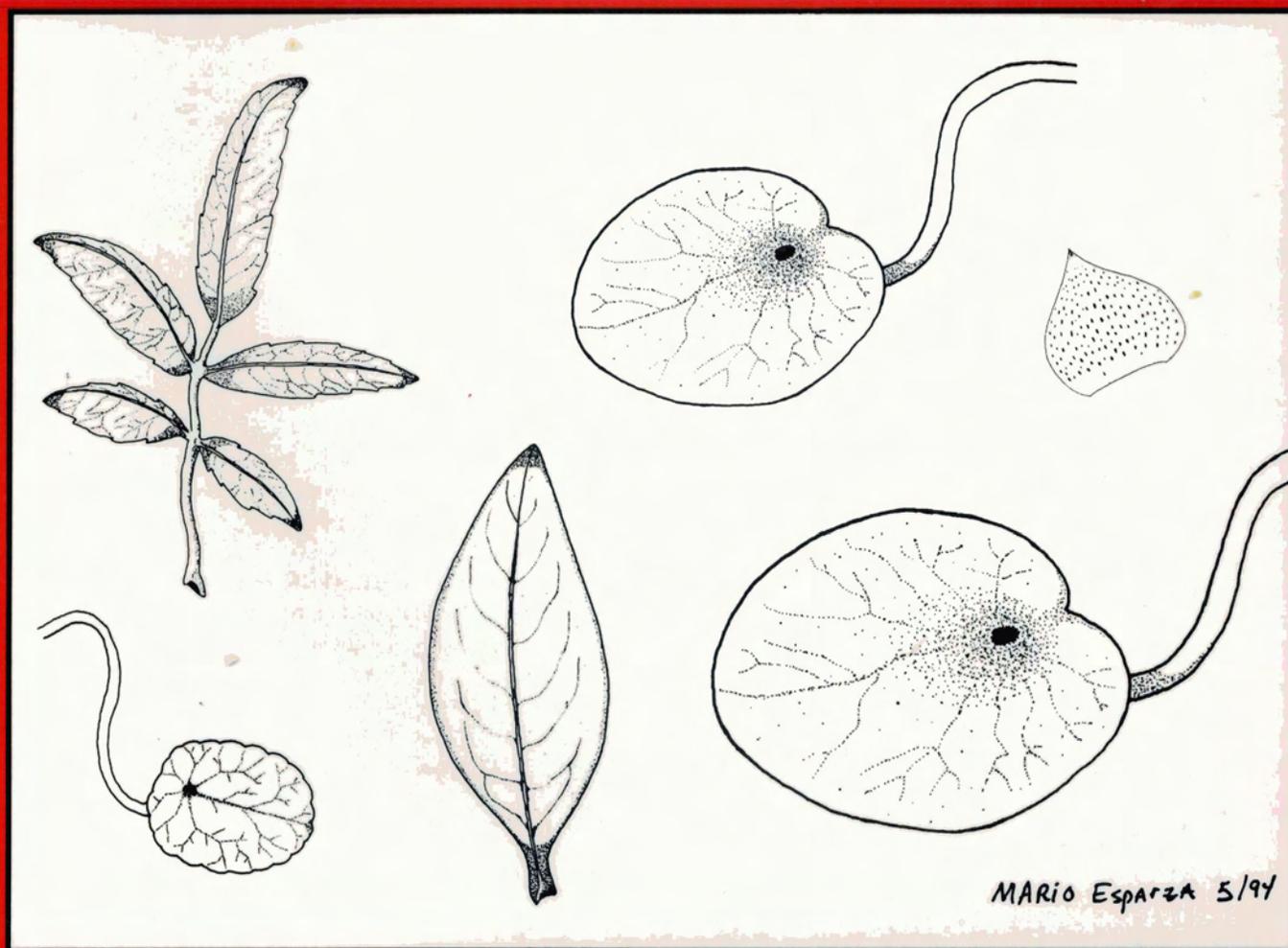


# The Megaf flora from the Quantico Locality (Upper Albian), Lower Cretaceous Potomac Group of Virginia

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Garland R. Upchurch, Jr.  
Peter R. Crane  
Andrew N. Drinnan

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Lower Cretaceous Potomac Group of Virginia

# The Megaflora from the Quantico Locality (Upper Albian), Lower Cretaceous Potomac Group of Virginia

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# THE MEGAFLORA FROM THE QUANTICO LOCALITY (UPPER ALBIAN), LOWER CRETACEOUS POTOMAC GROUP OF VIRGINIA

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Garland R. Upchurch, Jr., Peter R. Crane, and Andrew N. Drinnan

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## ABSTRACT

The megafloora documented in this paper from Quantico, Virginia, is one of the first assemblages of Lower Cretaceous angiosperm megafossils from North America to be described in detail using modern methods of foliar architectural analysis. The megafloora is of middle to early late Albian age and consists of 22 species of leaves/shoots and at least 5 species of reproductive structures. Three new species are described in this publication. Estimates of botanical diversity indicate the presence of at least 1 species of pteridophyte (*Equisetum*), 1 species of cycadophyte, 9 species of conifers, and 12 species of angiosperms (all dicotyledons). A minimum of 5 angiosperm species are referable to the dicot subclass Magnoliidae, including leaves with affinities to extant Laurales, and leaves and associated reproductive structures with affinities to extant Nelumbonaceae (placed in Ranunculidae by some authors). Also present are leaf megafossils with probable affinities to the dicot subclasses Rosidae and/or Hamamelididae (2 species of *Sapindopsis*), other possible Hamamelididae (1 species of "platanoid" leaf fragments), and specimens assigned to the form genus *Dicotylophyllum*. Evidence from sedimentology, megafossil preservation, and the morphology of the most abundant species (*Nelumbites extenuinervis*) indicates that the fossil-bearing beds at Quantico probably represent deposition in a pond or swale. The megafloora consists of both herbaceous aquatic angiosperms representing *in situ* elements and remains of woody gymnosperms and angiosperms transported from nearby terrestrial environments.

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## INTRODUCTION

The past two decades have witnessed a major resurgence of interest in the systematics and paleoecology of Cretaceous flowering plants. Prior to the 1970s, most botanists believed that the fossil record could contribute little evidence on the course and timing of angiosperm evolution, because even the oldest known fossils were thought to represent mostly modern families and genera of both primitive and advanced status (e.g., Axelrod, 1952,

1970). Subsequent studies have shown that many of these older generic and familial identifications are incorrect or cannot be substantiated (Dilcher, 1974) and that the major adaptive radiation of flowering plants probably began in the Early Cretaceous (e.g., Doyle, 1969; Wolfe et al., 1975; Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch and Dilcher, 1990). During the Cretaceous adaptive radiation of flowering plants, patterns of species diversity changed on both a global and regional scale and included a major increase in the diversity of flowering plants during the mid-Cretaceous (Crane, 1987; Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989; Upchurch and Wolfe, 1993). These and other studies indicate that combined systematic and paleoecological investigations of Cretaceous fossil floras can potentially provide much detailed information on the geographic, ecological, and phylogenetic history of major clades of angiosperms. The goal of this paper is to integrate paleoecological analysis with systematic analysis of foliar architecture in early angiosperms and associated remains.

This paper comprehensively describes and illustrates an Early Cretaceous angiosperm leaf megaflora, plus associated pteridophytes and gymnosperms, from a single Potomac Group locality at Quantico, Virginia. A formal systematic treatment of these remains is provided. Two objectives are to provide a general overview of structural diversity within a single megafloral assemblage during an early phase of the angiosperm diversification and to improve upon the descriptions and illustrations of early angiosperms and associated plants provided by earlier literature on Potomac Group megafloras.

## THE QUANTICO LOCALITY

The Quantico megafloral locality was discovered in 1971 by James A. Doyle in the course of his and Leo Hickey's reinvestigation of early flowering plant pollen and leaf remains from the mid-Cretaceous Potomac Group. Doyle and Hickey collected megafloral remains from the site during the early 1970s and performed preliminary analyses of angio-

sperm leaf systematics and paleoecology. Some of their results were reported in two papers that summarize features of early angiosperm evolution in North America (Doyle and Hickey, 1976; Hickey and Doyle, 1977). A comprehensive systematic treatment of the Quantico flora has never been published. Specimens from the Quantico locality preserve excellent gross morphology and venation but no cuticle.

Several hundred identifiable plant megafossils and a variety of arthropod remains are now known from the Quantico locality. These remains are archived at the U.S. National Museum of Natural History (USNM), the Field Museum of Natural History (FMNH), and the University of Michigan Museum of Paleontology (UMMP) (most UMMP specimens from Quantico are currently on loan to J. A. Doyle, University of California, Davis). Together these collections comprise one of the largest assemblages of Early Cretaceous angiosperm leaf megafossils known from a single locality in North America. Specimens from USNM and FMNH comprise a representative sample of the taxonomic and morphologic diversity present at the Quantico locality and were analyzed in detail.

The Quantico megafloral locality is located at the southern end of the U.S. Marine Corps base at Quantico, Virginia, approximately 30 miles southwest of Washington, D.C., and 75 miles north of Richmond, Virginia. The military base is accessed by taking Interstate Highway 95 to the southern exit for the Quantico Marine Base (the first exit south of Triangle, Virginia), then driving east on Russell Road to the south entrance gate. The fossil plant locality is located south of the U.S. Marine Corps air station, approximately 0.5 miles south of Chopawamsic Creek and 0.5 miles west of the Potomac River. It is located on the south side of Engineers Road, an east-west road running parallel to Chopawamsic Creek (38°29'36"N, 77°18'50"W, Widewater 7.5' Quadrangle, Virginia-Maryland). The fossiliferous horizon occurs on the west-facing wall of a gravel pit, which was actively mined in the 1970s, in claybeds exposed approximately 15 m above the base, near the top of the exposure.

## FLORISTIC COMPOSITION

The following taxa are recognized from the Quantico locality:

- Division EQUISETOPHYTA  
 Order EQUISETALES  
 Family EQUISETACEAE  
*Equisetum lyellii* Mantell  
 Rhizome of ?*Equisetum*
- Seed Plants, Division Unknown  
*Dichotozamites cycadopsis* (Fontaine) Berry
- Division CONIFEROPHYTA  
 Order CONIFERALES  
 Family CHEIROLEPIDIACEAE  
*Pseudofrenelopsis parceramosa* (Fontaine) Watson  
 Family ARAUCARIACEAE  
*Araucarites aquiensis* Fontaine  
 Family TAXODIACEAE  
*Athrotaxopsis* sp.  
*Sphenolepis sternbergiana* (Dunker) Schenk  
 Family PINACEAE  
 Indeterminate leaves (cf. *Abietites longifolius* [Fontaine] Berry)  
 Winged seed type 1  
 Winged seed type 2  
 Family UNKNOWN  
*Brachyphyllum crassicaule* Fontaine  
 Conifer shoot, genus undetermined
- Division MAGNOLIOPHYTA (Angiosperms)  
 Class MAGNOLIOPSIDA (Dicotyledons)  
 Subclass MAGNOLIIDAE  
 Order LAURALES  
 aff. *Pabiania* sp. 1  
*Landonia* cf. *L. calophylla* Upchurch & Dilcher  
*Dicotylophyllum ovato-decurrans* n. sp.  
 Subclass MAGNOLIIDAE or RANUNCULIDAE  
 Order NELUMBONALES  
*Nelumbites extenuinervis* n. sp.  
*Nelumbites* cf. *N. minimus* Vakhrameev  
 Associated stems and reproductive structures  
 aff. Subclass ROSIDAE and HAMAMELIDIDAE  
*Sapindopsis magnifolia/variabilis* Fontaine  
*Sapindopsis minutifolia* n. sp.  
 Subclass HAMAMELIDIDAE  
 Fragments of platanoid foliage

## Subclass UNKNOWN

### Leaves

*Dicotylophyllum* sp. 1 (cf. *D. argillaceum* [Velenovsky] Vakhrameev)

*Dicotylophyllum* sp. 2 (cf. "*Magnolia*" *amplifolia* Heer?)

*Dicotylophyllum* sp. 3 (aff. *Didromophyllum* Upchurch & Dilcher?)

*Dicotylophyllum* sp. 4

### Diaspores and miscellaneous

aff. *Kenella* Samylinia

Diaspore type 1

Diaspore type 2

Diaspore type 3

Diaspore type 4

The megafloral assemblage from Quantico consists of horsetails, cycadophytes, conifers, and flowering plants. The described and illustrated remains comprise a minimum of 22 distinct biological entities (recognized here as species), which include 1 species of horsetail, 1 species of cycadophyte, 8 species of conifers, and 12 species of angiosperms. Of the 8 species of angiosperms that can be at least tentatively referred to subclass, as many as 5 belong to taxa referred by at least some authors to subclass Magnoliidae, and in particular the orders Laurales and Nelumbonales. Conspicuously absent from the Quantico megafloral assemblage is a high diversity of ferns, other pteridophytes, and cycadophytes. This latter pattern of diversity characterizes Zone I megafloral assemblages from the Potomac Group and pre-late Albian megafloral assemblages from other parts of North America and Eurasia. The Quantico assemblage, therefore, fits the global pattern of a mid-Cretaceous decline in relative diversity for free-sporing plants and cycadophytes (Crane, 1987; Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989, 1990; Upchurch and Wolfe, 1993).

## AGE OF THE QUANTICO FLORA

Early age estimates for the Potomac Group were based on leaf megafossils (Ward, 1888, 1897; Fontaine, 1889) and dinosaur remains (e.g., Marsh, 1888, 1896). These early age estimates generated intense debate over whether the Potomac Group

and overlying coastal plain rocks were Jurassic or Cretaceous in age, with vertebrate paleontologists favoring a Jurassic age and paleobotanists favoring a Cretaceous age. Subsequent investigators concluded that the Potomac Group was Cretaceous in age but disagreed over more precise assignment. They based their Cretaceous age assignment on diverse lines of evidence, including species composition and patterns of relative abundance in plant megafossil assemblages, interpretations of regional geology, reinterpretations of fossil vertebrate assemblages, and age constraints provided by fossil invertebrates from the overlying Raritan Formation of New Jersey (e.g., Berry, 1911a; Lull, 1911; Gilmore, 1921; Spangler and Peterson, 1950; Dorf, 1952).

Biostratigraphic investigations of the Potomac Group over the past three decades have relied primarily on palynology (e.g., Brenner, 1963; Doyle, 1969, 1982, 1992; Wolfe and Pakiser, 1971; Doyle and Hickey, 1976; Doyle and Robbins, 1977; Hickey and Doyle, 1977; Reinhardt et al., 1980). Palynostratigraphic studies confirm plant megafossil evidence for a mid-Cretaceous age and provide a precise and reliable means of dating individual formations and informal stratigraphic units within the outcrop belt. Starting with the work of Brenner (1963), palynologists have proposed and refined a series of informal zones and subzones for the Potomac Group. These zones and subzones are based on changes in the taxonomic composition of pollen and spore assemblages, which are documented from both the outcrop belt and well cores drilled to the east of the outcropping Potomac Group. These zones and subzones can be correlated with the standard European zonation for the Cretaceous because they are recognizable in marine rocks dated by macroinvertebrates. Potomac Group palynozones and subzones have been recognized in rocks from the Gulf Coastal Plain and Western Interior of North America, Europe, and West Africa (e.g., Doyle and Robbins, 1977; Ward, 1986; Doyle, 1992; and references therein).

Three palynological zones currently are recognized for the Potomac Group, the middle of which is divided into three subzones. In ascending stratigraphic order, these zones and subzones are:

- Zone I* – early and middle Aptian age;
- Zone II* – late Aptian to late Albian age;
  - Subzone II-A* – late Aptian to possibly early Albian age;
  - Subzone II-B* – early Albian to early late Albian age;
  - Subzone II-C* – late Albian age;
- Zone III* – early to middle Cenomanian age.

Individual zones and subzones of the Potomac Group also have been subdivided into two or more parts, further increasing biostratigraphic resolution. Outcropping Potomac Group sediments have a maximum thickness of 230 meters and represent a time period of approximately 22 million years (Olsson et al., 1988), which indicates an average rate of deposition of about 11–12 meters per million years.

Palynological zonation of the Potomac Group has benefited studies of the megafloora in three major ways. First, palynostratigraphy has permitted evolutionary trends within leaf megafossils to be inferred independently of megafloreal zonation schemes, thereby avoiding circular reasoning. Second, palynostratigraphy has corrected correlation errors made by early workers on the basis of megafloreal remains. These errors resulted from lack of attention to leaf/facies relationships and to critical features of foliar morphology, as for example in Berry's (1911a) assignment of the Baltimore locality to the Patapsco Formation, rather than Arundel Formation (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch and Doyle, 1981). Third, palynostratigraphy has provided a check on intraformational correlations based on inferred lithostratigraphic position within the outcrop belt. This is important because the potential for error in lithostratigraphic correlation is greatest in a highly condensed stratigraphic sequence such as the outcropping Potomac Group, especially when faults and other structural features are present. Such is the case for the outcropping Potomac Group in northern and central Virginia (e.g., Mixon and Newell, 1977; Dischinger, 1987).

The fossiliferous clay bed at Quantico preserves little organic matter besides fusain (probable fossil

charcoal). No palynomorphs are known from the Quantico leaf beds, in contrast to most megafloral localities from the Potomac Group; thus, the Quantico leaf beds must be correlated on the basis of lithostratigraphic position within the outcrop belt and megafloral similarities with better-dated localities. We correlate the Quantico megaflora on the basis of the entire assemblage, rather than one or more indicator species, to minimize the effects of sporadic occurrence and preservation of taxa. Stratigraphic ranges of megafossil taxa within the Potomac Group are based on occurrence data listed in Berry (1911a), Doyle and Hickey (1976), Hickey and Doyle (1977), and Upchurch and Doyle (1981), with cross checks made against museum collections to minimize errors in identification. Occurrence data for other formations are listed where relevant. The relative palynostratigraphic placement of megafloral localities follows Doyle and Hickey (1976, fig. 2) and Hickey and Doyle (1977, fig. 3) as updated by Doyle (1992).

Overall taxonomic composition indicates that the Quantico megafloral assemblage correlates with Subzone II-B of Brenner (1963), and probably the upper part of Subzone II-B (middle to early late Albian; Doyle and Robbins, 1977). This correlation is indicated by: (1) the occurrence of stratigraphically long-ranging conifer taxa, such as *Pseudofrenelopsis parceramosa*, *Sphenolepis sternbergiana*, and *Brachyphyllum crassicaule*, which within the Potomac Group occur in megafloral assemblages ranging in age from Zone I to Subzone II-B or younger; (2) the occurrence of taxa, such as *Dichotozamites cycadopsis*, *Araucarites aquiensis*, and *Sapindopsis* foliage with pinnatifid organization, which within the Potomac Group occur in many megafloral assemblages of Subzone II-B age but are not known from older and younger assemblages; and (3) the occurrence of taxa, such as *Nelumbites* and leaves improperly assigned to extant *Sassafras*, which are not present in megafloral collections older than Subzone II-B in age. (Fontaine [1889] and Berry's [1911a] attribution of species in these groups to Zone I localities cannot be substantiated through analysis of USNM collections.) Consistent with a Subzone II-B age is the combined occurrence of: (4)

rare specimens belonging to *Athrotaxis*, a taxon previously reported only from Zone I of the Potomac Group; and (5) rare specimens comparable to *Landonia calophylla*, *Dicotylophyllum argillaceum*, and "*Magnolia*" *amplifolia*, previously reported only from the Cenomanian (Zone III) of North America and Eurasia (Vakhrameev, 1952, and references therein; Upchurch and Dilcher, 1990). A late Subzone II-B age (early late Albian) is implied by the occurrence of *Sapindopsis* foliage with truly pinnately compound organization, which within the Potomac Group first appears in megafloral assemblages younger than the Brooke assemblage of early to middle Subzone II-B age. Hickey and Doyle (1977) also favored a late Subzone II-B age for the Quantico locality, based on the occurrence of pinnately compound *Sapindopsis* and inferred lithostratigraphic position within the Potomac Group outcrop belt.

#### DEPOSITIONAL ENVIRONMENT AND PALEOECOLOGY

Previous sedimentological studies of outcropping and subsurface Potomac Group have concluded that the Potomac Group represents a complex of fluvial-deltaic rocks derived from source areas in the Piedmont and Appalachian regions (e.g., Glaser, 1969; Hansen, 1969; Owens, 1969; Reinhardt et al., 1980; Olsson et al., 1988). In the subsurface, Potomac Group sediments often show evidence for deposition under tidal influence and elevated salinities, as indicated by the occurrence of glauconite, marine to brackish-water mollusks, dinoflagellates, and various acritarchs suggestive of marine influence (Anderson, 1948; Richards, 1967; Reinhardt et al., 1980; Upchurch and Doyle, 1981). Marine influence generally increases toward the east in the subsurface. In contrast, outcropping Potomac Group sediments show strong evidence for deposition under nonmarine conditions, as indicated by sedimentary sequences, regional trends in the direction of crossbedding, evidence for anastomosing stream channels, and preservation of almost exclusively terrestrial flora and fauna (e.g., Fontaine, 1889; Berry, 1911a; Clark, 1911; Lull, 1911; Glaser, 1969; Johnston and Froelich, 1977; Up-

church and Doyle, 1981). Little evidence exists for elevated salinities in the outcropping Potomac Group except for a few localities that yield dinoflagellate cysts; spinose acritarchs; low-diversity floral assemblages characterized by dominance of *Classopollis* and *Exesipollenites* pollen, *Pseudofrenelopsis* shoots, and *Dionites* leaves; and invertebrate trace fossils referable to the genus *Chondrites* (Upchurch and Doyle, 1981). Previous reports for the outcropping Potomac Group of glauconite (e.g., Glaser, 1969) and brackish-water megafloras with angiosperms (e.g., Retallack and Dilcher, 1981) cannot be confirmed when examined closely (Upchurch and Doyle, 1981).

The Quantico plant locality and other exposures of Potomac Group rocks on the Quantico Marine base are characterized by a predominance of cross-bedded sands that show the fining-upward sequences characteristic of fluvial channels. The leaf-bearing beds at Quantico occur near the top of the exposure, in the upper part of a fining-upwards sequence, and show features characteristic of pond and swale environments, as suggested by Hickey and Doyle (1977). The megafossil-bearing exposure comprises approximately 16 m of sediment, the basal 14 m of which are fining-upwards cross-bedded sands and gravels that contain clay clasts. The fossiliferous horizon occurs about 15 m above the base of the exposure and consists of brown to gray, laminated clays deposited on a scoured surface. These clays are typically no thicker than 10–20 cm, have sharp contacts with the underlying and overlying sands, and are laterally continuous over a distance of at least 50 m. At the northern end of the exposure the clays form a single bed, but towards the south they split to form two clay beds separated by approximately 0.5 m of sand. The general fining-upwards sequence and the sharp scoured basal contact of the clay beds with the underlying sands indicate either the basal part of an abandoned channel-fill or a swale deposit. The splitting of the claybeds along the length of the exposure is more consistent with a swale interpretation, because the claybeds in abandoned channel fill deposits typically show stronger lateral continuity and do not split laterally.

The morphology of certain Quantico leaf taxa and probable growth habit in extant and fossil relatives indicates that the Quantico megaflora is a mixture of remains from two or more distinct communities. The probable *in situ* component comprises *Nelumbites* leaves (especially *N. extenuinervis*) and associated reproductive structures that may belong to *Nelumbites*. Leaves of *N. extenuinervis* have a morphology most characteristic of herbaceous aquatic plants that produce emerged and floating leaves. This, together with evidence for affinities to extant *Nelumbo*, implies an ecologically similar plant (for details see Table 1 and the discussion of *N. extenuinervis* in "Description of Remains"). Fossilization at or near the actual site of growth is implied by: (1) thin laminar texture and low stature, which together imply low transport potential relative to associated conifer and angiosperm remains, (2) strong tendencies for leaves of *Nelumbites* to occur in clusters along the length of the exposed claybeds, and (3) co-occurrence of probable herbaceous stem remains in association with *Nelumbites* foliage. These features indicate a low-diversity community of aquatic angiosperms with physiognomy similar to extant communities dominated by *Nelumbo*.

The allochthonous component of the Quantico leaf assemblages comprises leaves and shoots of conifers, other gymnosperms, and various angiosperms. Allochthonous derivation of these remains is based on evidence for woody growth habit (Table 1), low abundance of most species relative to *Nelumbites extenuinervis* (Table 2), and the low abundance of root remains in the fossil-bearing beds coupled with the absence of evidence for any large roots. The number of communities represented by the preserved leaf and shoot remains is unclear, because no detailed taphonomic analysis has been undertaken. However, more than one biotic community is probably present, because various rare elements of the Quantico megaflora dominate leaf assemblages from other localities and facies (cf. Hickey and Doyle, 1977; Upchurch and Wolfe, 1993).

Some Subzone II-B megafloras are characterized by dominant conifers and no angiosperms, while

others are characterized by dominant angiosperms. In the context of Subzone II-B megafloras as a whole, the megafloral remains from Quantico can be assigned to one of three distinct angiosperm-bearing biofacies, which we designate as "megafloral facies" because plant megafossils are the only abundant remains. Each megafloral facies represents a distinctive assemblage of plant megafossils that occurs in a limited range of lithologies. Each of these assemblages is characterized by distinctive patterns of taxonomic composition, relative abundance, and adaptation.

The three angiosperm-bearing megafloral facies that we recognize for Subzone II-B of the Potomac Group generally parallel Hickey and Doyle's (1977, fig. 68) lithofacies-based reference system for early angiosperm remains. However, we prefer to use a biologically based reference system because it emphasizes potential community patterns and because individual taxa often occur in more than one lithofacies. Our use of the term "megafloral facies" parallels Archibald's (1981) use of the term "faunal facies." Like Archibald (1981), we use the term in preference to "community" because it is more descriptive. In addition, "megafloral facies" does not connote patterns of lateral variation in the source vegetation. We use the term in preference to "florule" because the Potomac Group megafloral facies probably can be recognized in other parts of North America and Asia and range in age from Albian to Cenomanian.

The three angiospermous megafloral facies are designated:

1. The Platanoid megafloral facies;
2. The *Sapindopsis* megafloral facies;
3. The *Nelumbites/Populophyllum* megafloral facies.

The platanoid megafloral facies is characterized by abundant and diverse foliage showing features characteristic of extant Platanaceae (the "platanoids" of Doyle and Hickey, 1976). Conifers are typically rare or absent. Platanoid foliage is the most abundant and diverse element of the megafloral assemblage and can consist of both lobed

species (e.g., "*Sassafras*" *parviflorum* Berry) and unlobed species (e.g., platanoid #3 of Upchurch, 1984). *Sapindopsis* leaves are present in the platanoid megafloral facies and form the dominant element on some individual bedding planes, but their diversity and relative abundance are lower than that of platanoid foliage. Lobed leaves of Laurales characterized by palinactinodromous primary venation are present and can be confused with true platanoids (e.g., "*Sassafras*" *potomacensis* Berry as illustrated by Hickey and Doyle, 1977, fig. 49–52; possibly Platanoid #2 of Upchurch, 1984). Also present are enigmatic unlobed angiosperm leaves characterized by flabellate primary venation (*Menispermites* *potomacensis* Berry). The platanoid megafloral facies generally is restricted to coarse-grained fluvial sediments interpreted as channel and point-bar deposits (Doyle and Hickey, 1976; Hickey and Doyle, 1977). Megafloral assemblages belonging to the platanoid megafloral facies include Subzone II-B assemblages from Stump Neck and Widewater and Subzone II-C assemblages from Bull Mountain, Brightseat, and White Point.

The *Sapindopsis* megafloral facies is characterized by abundant pinnatifid or pinnately compound foliage referable to the genus *Sapindopsis* and less-common conifer shoots and seeds. Additional angiospermous leaf types, such as platanoids, are rare and of low diversity. The *Sapindopsis* megafloral facies characterizes fine-grained beds within crevasse-splay deposits and gray clays on floodplains that represent abandoned channel-fill deposits (cf. Hickey and Doyle, 1977; Hickey, 1984). In addition, the *Sapindopsis* megafloral facies can occur in sandy beds that represent near-channel depositional environments (a UMMP assemblage collected by G. Upchurch from Ft. Foote, Maryland). The *Sapindopsis* megafloral facies appears to be absent from environments of greater-than-freshwater salinity, because coeval lithofacies that show evidence for brackish-water salinities are characterized by a dominance of conifer shoots and pollen and an absence of angiosperm leaves (Upchurch and Doyle, 1981; Upchurch and Wolfe, 1993). Megafloral assemblages belonging to the *Sapindopsis* megafloral facies include Subzone II-B assemblages from West

Table 1.—Inferred growth habit, Quantico megafossils.

TAXON	GROWTH HABIT	EVIDENCE FOR INTERPRETATION	REFERENCES
<i>Equisetum lyellii</i>	Rhizomatous herb	Strong flattening of preserved aerial shoot, growth habit in extant <i>Equisetum</i>	Gifford & Foster (1989) This report
<i>Dichotozamites cycadopsis</i>	???		
<i>Pseudofrenelopsis parceramosa</i>	Tree	Anatomical similarities between leafy shoots and associated woods	Alvin et al. (1981) Alvin (1983)
<i>Araucarites aquiensis</i>	Tree	Growth habit in extant Araucariaceae	Krüssman (1960) Bailey (1978)
<i>Athrotaxopsis</i> sp.	Tree	Growth habit in extant Taxodiaceae	Krüssman (1960) Bailey (1978)
<i>Sphenolepis sternbergiana</i>	Tree	Anatomical similarities between leafy shoots and associated woods in <i>S. kurriana</i> , growth habit in extant Taxodiaceae	Harris (1953) Krüssman (1960) Bailey (1978)
Pinaceae	Tree or possibly shrub	Growth habit in extant Pinaceae	Krüssman (1960) Bailey (1978)
<i>Brachyphyllum crassicaule</i>	Woody plant, tree or shrub	Diameter of preserved shoots, depth of stem impressions in matrix, rigidity of preserved shoots as evidenced by the absence of bending.	This report
Unnamed conifer	Woody plant tree or shrub	Rigidity of one preserved shoot, depth of stem impression in matrix	This report
Aff. <i>Pabiania</i> sp.	Woody plant tree or shrub	Attachment of Cenomanian <i>Pabiania</i> leaves to a slender shoot, growth habit in extant Laurales	Cronquist (1981) Upchurch & Dilcher (1990)
<i>Landonia</i> cf. <i>L. calophylla</i>	Woody plant tree or shrub	Growth habit in extant Laurales	Cronquist (1981)
<i>Dicotylophyllum ovatodecurrans</i>	Woody plant tree or shrub	Growth habit in extant Laurales	Cronquist (1981)
<i>Nelumbites extenuinervis</i>	Aquatic herb	Functional morphology of leaves, association with probable herbaceous stems, taphonomy, growth habit in extant <i>Nelumbo</i>	Doyle & Hickey (1976) Hickey & Doyle (1977) This report
<i>Nelumibites</i> cf. <i>N. minimus</i>	Aquatic herb	As in <i>N. extenuinervis</i>	Samykina (1968) Doyle & Hickey (1976) Hickey & Doyle (1977)
<i>Sapindopsis variabilis/magnifolia</i>	Tree or shrub probably weedy	Functional morphology of leaves, tendency for monodominance in some assemblages, sedimentary associations	Doyle & Hickey (1976) Hickey & Doyle (1977)
<i>Sapindopsis minutifolia</i>	Probably shrub	Small leaf size relative to other dicots	This report
"Platanoid" leaf fragments	Tree or shrub early successional	Morphology of platanoid leaves, dominance of coeval platanoids in channel facies	Doyle & Hickey (1976) Hickey & Doyle (1977)
<i>Dicotylophyllum</i> spp. 1-4	Probably woody	Predominance of woody taxa in megafossil record, rarity relative to <i>Nelumbites</i> , absence of evidence for herbaceous habit	

Table 2.—Relative abundances of individual Quantico taxa.\*

TAXON	NO. OF SPECIMENS	PERCENT
<i>Equisetum</i> shoot + rhizome	1	1
<i>Dichotozamites cycadopsis</i>	2	2
<i>Araucarites aquiensis</i>	7	7
<i>Pseudofrenelopsis parceramosa</i>	7	7
<i>Athrotaxis</i> sp.	—	—
<i>Sphenolepis sternbergiana</i>	19	21
Pinaceae, leaves + seeds	6	6
<i>Brachyphyllum crassicaule</i>	10	11
Unnamed conifer	1	1
aff. <i>Pabiania</i> sp.	1	1
<i>Landonia</i> cf. <i>L. calophylla</i>	—	—
<i>Dicotylophyllum ovato-decurrens</i>	1	1
<i>Nelumbites extenuinervis</i>	32	36
<i>Nelumbites</i> cf. <i>N. minimus</i>	—	—
<i>Sapindopsis magnifolia/variabilis</i>	2	2
<i>Sapindopsis minutifolia</i>	—	—
Platanoid leaf fragments	—	—
<i>Dicotylophyllum</i> sp. 1	1	1
<i>Dicotylophyllum</i> sp. 2	1	1
<i>Dicotylophyllum</i> sp. 3	1	1
<i>Dicotylophyllum</i> sp. 4	1	1
TOTAL	93	100

\*All relative abundances are based on number of leaf specimens, not relative leaf area on the rock surface (i.e., cover abundance). Specimens are from the Field Museum of Natural History.

Table 3.—Major ecological groups, Quantico.\*

GROUP	PERCENT WOODY	PERCENT WOODY AND HERBACEOUS
Pteridophytes	0	1
Cycadophytes	3	3
Conifers	85	54
Angiosperms	12	43
TOTAL	100	100

\*Count is based only on number of specimens, not relative leaf area on the rock surface (i.e., cover abundance). Specimens are from the Field Museum of Natural History.

Brothers, Red Point, Severn Clay Mine, the upper beds at Bank near Brooke, and Ft. Foote.

The *Nelumbites/Populophyllum* megafloral facies is characterized by abundant angiosperm leaves that have deeply cordate to peltate bases and other features suggestive of an aquatic herbaceous habit. Other types of angiosperm leaves are rare, while conifers and other gymnosperms can form a common to dominant element of the woody megaflora (see Tables 2 and 3 for relative abundance data from the Quantico locality). The *Nelumbites/Populophyllum* megafloral facies typifies laminated clays indicative of shallow standing water, which are interpreted as the deposits of swales, ponds, and the basal units of abandoned channel-fill sequences. Potomac Group megafloral localities belonging to the *Nelumbites/Populophyllum* megafloral facies include Subzone II-B assemblages from Quantico, Mount Vernon, White House Bluff, the lower beds at Bank near Brooke, and an unpublished UMMP/ USNM assemblage from a claybed at Stump Neck, which is now inaccessible due to slumping.

## SYSTEMATICS

All identifiable megafossils in the paleobotanical collections of the U.S. National Museum (USNM) and Field Museum of Natural History (FMNH) are described and illustrated in the following section. Three additional leaf types are present but possess insufficient features for accurate identification. These leaf types are: (1) narrow, strap-shaped gymnospermous leaf fragments with one order of longitudinal parallel veins that may represent cycadophyte pinnules (?*Dioonites* Schimper?), (2) a lobate angiospermous leaf fragment with poorly preserved venation (?*Araliaephyllum* Fontaine?), and (3) the basal part of a low-rank angiosperm leaf with highly decurrent secondary and intersecondary veins. Type and illustrated specimens, largely from the USNM and FMNH collections, are listed following each species description.

Graded comparisons for some species are used because of taxonomic uncertainties due to poor preservation, small numbers of known specimens,

and morphologic differences between previously described taxa and Quantico leaf megafossils. These graded comparisons are derived from the scheme of Hughes and Moody-Stuart (1967) and Hughes (1976) as simplified by Doyle and Robbins (1977). A "cf." designation indicates one or a few minor quantitative differences between a published taxon and a Quantico species. An "aff." designation indicates general similarity between a published taxon and a Quantico species but greater morphologic differences, usually in one or two qualitative characters used to diagnose the taxon.

The terminology used to describe coniferous winged seeds and dicot leaf venation will be unfamiliar to many readers. Readers unfamiliar with this terminology should consult Wolfe and Schorn (1990, p. 6-7, fig. 1) for winged conifer seeds and Hickey (1973, 1979), Dilcher (1974), and Upchurch and Dilcher (1990) for general terminology of dicot leaf venation. For pinnatifid and other types of pinnately divided leaves, we follow the terminology of Hickey (1973, 1979) and Hickey and Doyle (1977), rather than Wolfe and Wehr (1988). The term "zig-zag" is used to describe veins that undergo sharp and repeated changes in course. "L/W" designates the ratio of length to maximum width for seeds and for the blades of leaves.

### Order EQUISETALES Family EQUISETACEAE Genus *Equisetum* Linnaeus

#### *Equisetum* cf. *E. lyellii* Mantell (Figure 1)

Description.—One shoot with two nodes preserved. Shoot unbranched, 8 to 9 mm wide, with at least 15 longitudinal ridges on the one preserved side, nodes slightly constricted; only one complete internode preserved, 28 mm long, subadjacent internode only partially preserved, > 28 mm long. Leaf sheath absent from preserved nodes.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446028.

Discussion.—The longitudinal ridges on the stem and distinct nodes indicate that this specimen can be assigned to *Equisetum*. The absence of a leaf

sheath at the nodes could indicate that the sheath was deciduous, as in certain extant species of *Equisetum*.

We compare the Quantico remains with *Equisetum lyellii* because *E. lyellii* is the only reported Potomac Group species of *Equisetum* with generally unbranched stems of large diameter (Fontaine, 1889; Berry, 1911a).

#### Rhizome of ?*Equisetum* (Figure 2)

Description.—Regularly segmented axes with a strong constriction between each segment. Each segment approximately 10 mm long; widest part of each segment approximately in the middle, 6 to 7 mm in diameter, narrowest part approximately 2 mm in diameter. Each segment elliptical in outline, producing much relief in rock.

Number of specimens examined.—2.

Illustrated specimen.—USNM 446022.

Other identified specimens.—FMNH PP43892.

Discussion.—These axes resemble the segmented rhizomes of certain *Equisetum* species. The relief of the specimens in the rock indicates that they were probably thick textured in life. The elliptical outline and thick texture together imply that each segment had an ovoid shape in life.

#### Seed Plants, Division Unknown Genus *Dichotozamites* Berry

##### *Dichotozamites cycadopsis* (Fontaine) Berry (Figure 3)

*Sequoia cycadopsis* Fontaine – Fontaine, 1889, p. 243, Pl. 112, figs. 9–11; Pl. 113, figs. 1–3.

*Sequoia cycadopsis* Fontaine – Fontaine in Ward, 1905, pp. 489, 533, Pl. 109, fig. 11.

*Dichotozamites cycadopsis* (Fontaine) Berry – Berry, 1911a, p. 365, Pl. 77, figs. 2, 3.

Description of Quantico remains.—Ultimate pinnatifid portions of much larger leaves preserved, largest specimen 3 cm long by 1.5 cm wide. Ultimate parts of leaf deeply pinnatifid, lobes linear, oriented at approximately 20° to rachis, >2 cm long by about 1 mm wide, L/W >20. Apex of lobes not preserved, base of lobes broadly decurrent on

rachis, arrangement of lobes on rachis tending toward opposite. Rachis with wing of laminar tissue 1–1.5 mm wide, rachis narrowest immediately above the zone of lobe divergence and widest immediately below the zone of lobe divergence, increase in width of rachis between lobes gradual. Ultimate lobes and rachis each with a single prominent midvein; midvein approximately 20 percent the width of the lamina, exact width difficult to measure because of small size, forming a distinct groove on one leaf surface and a distinct ridge on the other leaf surface. Faint transverse patterns visible on leaves (interpretation unclear).

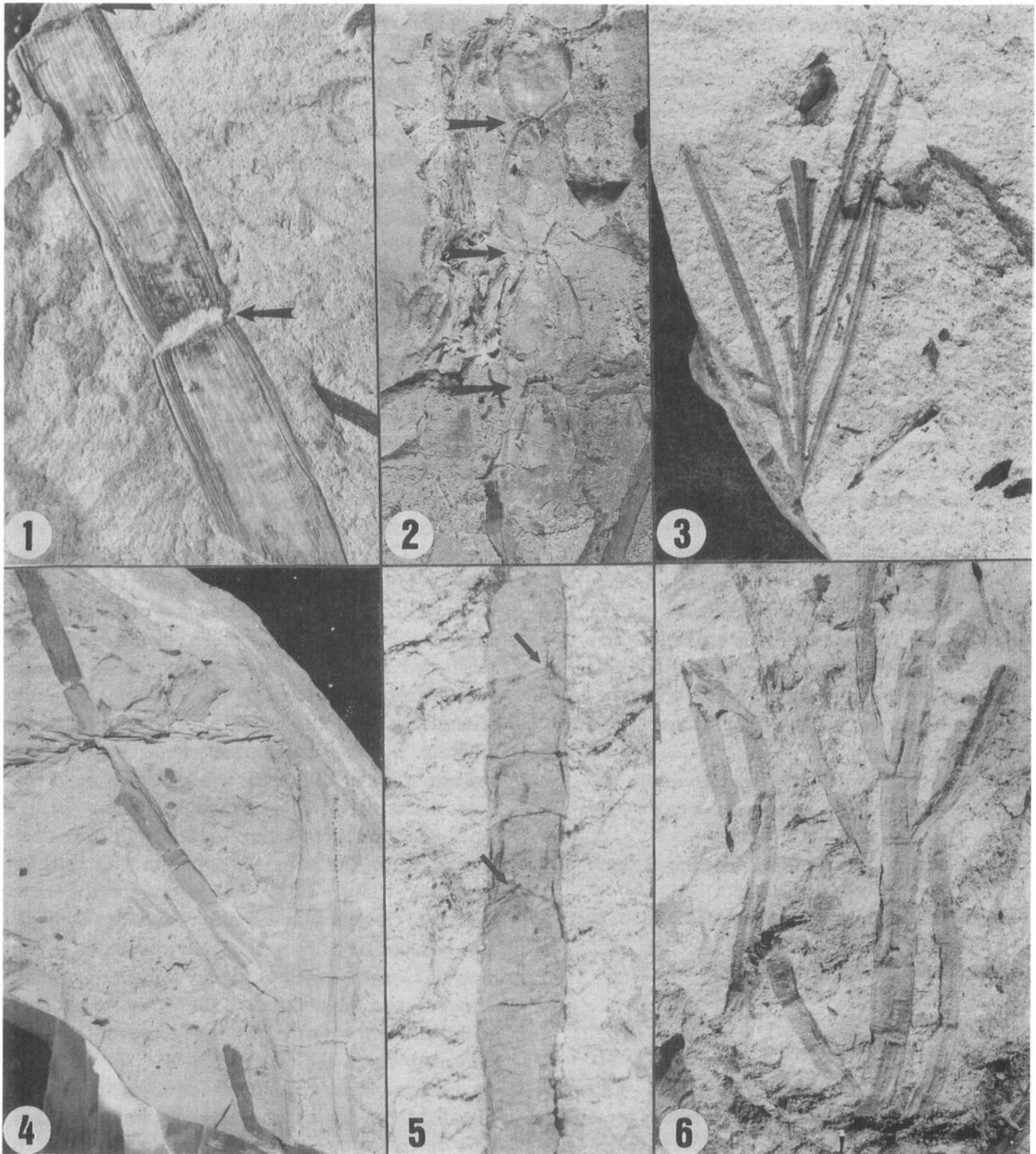
Number of specimens examined.—2.

Illustrated specimen.—FMNH PP43808.

Other identified specimens.—FMNH PP43893.

Discussion.—Although highly fragmentary, at least two specimens from Quantico can be assigned to *Dichotozamites cycadopsis* (Fontaine) Berry. *Dichotozamites* is distinguished from other genera of Potomac Group cycadophytes by its deeply pinnatifid organization, bifurcate winged rachis, and linear pinnules that are oriented at a very low acute angle to the rachis. The Quantico specimens match illustrated specimens of *D. cycadopsis* in all preserved features, including size, shape, pinnule orientation, and the occurrence of a prominent midvein, but they are not sufficiently complete to indicate whether the rachis was bifurcate, as in the type material. The Quantico specimens of *D. cycadopsis* also show no clear evidence for secondary veins within the ultimate lobes of the leaf, in contrast to Berry's (1911a) report for the type materials. However, details of venation are ambiguous, because no photographically illustrated specimen of *D. cycadopsis* has clearly visible secondary venation, and preservation of the Quantico remains is insufficient to rule out the presence of thin secondary veins.

*Dichotozamites cycadopsis* strongly resembles *Tenuiloba canalis*, an anatomically preserved leaf type described by Serlin (1982) from the lower to middle Albian Edwards Limestone of Texas. Known remains of *T. canalis* comprise the ultimate portions of a deeply pinnatifid leaf, which divides dichotomously and gives rise to linear lobes that are pin-



nately arranged along a winged rachis. Individual fragments of *T. canalis* measure as much as 5 cm long, with a winged rachis 1.7 mm wide and laminar segments 1 mm wide. Both the rachis and laminar segments have an adaxial groove and, judging by one photograph of certain leaf fragments (Serlin, 1982, Pl. 12, fig. 104), an abaxial ridge. Paradermal sections of *T. canalis* indicate the presence of weak secondary veins, which branch dichotomously near the margin and are reported to form brochidodromous loops. Stomata are restricted to two abaxial longitudinal grooves lined with dense trichomes; these stomata are reported to have paracytic subsidiary cells, but the one published photograph (Serlin, 1982, Pl. 12, fig. 108) indicates that subsidiary cell arrangement may be more variable. The morphological similarities between *Dichotozamites* and *Tenuiloba* indicate that *Tenuiloba* may be a junior synonym of *Dichotozamites*. However, we think that the generic separation should be maintained until more is known about the morphology and anatomy of Potomac Group *Dichotozamites*.

Little is known about the affinities of *Dichotozamites*. The apparently simple venation and bifurcation of the leaf rachis are suggestive of affinities with "seed fern" groups such as *Corystospermales* and *Peltaspermales*. However, *Tenuiloba canalis* is inferred by Serlin (1982) to be an Early Cretaceous angiosperm that has affinities with extant *Proteaceae* (the latter of which we consider suspect). If *Dichotozamites* has secondary and higher-order venation similar to that reported for *Tenuiloba*, then *Dichotozamites* may be an angiosperm.

Order CONIFERALES  
Family CHEIROLEPIDIACEAE  
Genus *Pseudofrenelopsis* Nathorst

*Pseudofrenelopsis parceramosa* (Fontaine)  
Watson (Figures 4–6)

Synonymy for North America only:

*Frenelopsis parceramosa* Fontaine – Fontaine, 1889, p. 218, Pl. 111, figs. 1–5; Pl. 112, figs. 1–5; Pl. 168, fig. 1.

*Frenelopsis parceramosa* Fontaine – Berry, 1911a, p. 425, Pl. 70, figs. 1–5.

*Manica parceramosa* (Fontaine) Watson – Watson, 1974, p. 428.

*Pseudofrenelopsis parceramosa* (Fontaine) Watson – Watson, 1977, p. 720, Pl. 85, figs. 1–4; Pl. 86, figs. 1–12; Pl. 87, figs. 3–7.

*Pseudofrenelopsis parceramosa* (Fontaine) Watson – Upchurch and Doyle, 1981, figs. 1a–1c, 3b, 3c.

Description of *Quantico* remains.—Shoots with as many as two orders of branching preserved. Branching alternate, lateral branches inserted at nodes, apparently axillary in origin. Ultimate branches 1–2.5 mm wide, bearing reduced scale-leaves, internodes 2–4 mm long, usually demarcated by transverse groove in the matrix; penultimate order of branching wider than ultimate order, as much as 7 mm wide. Phyllotaxy alternate and spiral, leaves scale-like, with sheathing base, free portion of leaf less than 1 mm long.

Number of specimens examined from *Quantico*.— >9.

Illustrated specimens.—FMNH PP43797, PP4381.

Other identified specimens.—FMNH PP43796, PP43871–PP43875.

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Facing page: *Figure 1*.—*Equisetum lyellii*, specimen showing longitudinal ribbing and two nodes (arrows). USNM 446028, x2. *Figure 2*.—Rhizome (of *Equisetum*?) showing characteristic constrictions (arrows). USNM 446022, x2. *Figure 3*.—*Dichotozamites cycadopsis* (Fontaine) Berry, leaf fragment showing ultimate divisions of frond and venation. FMNH PP43808, x2.25. *Figures 4–6*.—*Pseudofrenelopsis parceramosa* (Fontaine) Watson. *Figure 4*, thick stem giving rise to thinner lateral branch. FMNH PP44797, x1.8. *Figure 5*, close-up of shoot showing reduced scale leaves and one leaf per node. Two leaves have their tips visible (arrows). FMNH, x7. *Figure 6*, profusely branched shoot. FMNH PP, x2.

Discussion.—The preserved features of these shoots all fall within the range of variation described by Watson (1977) and Upchurch and Doyle (1981) for organically preserved *Pseudofrenelopsis parceramosa*. Diagnostic features include highly reduced scale-leaves with a free tip less than 1 mm long, alternate and spiral phyllotaxy, and axillary branching. The ultimate order of branches in the Quantico materials is typically narrower (1–2.5 mm wide) than the ultimate order of branches in Zone I specimens of *P. parceramosa* from the Potomac Group (usually >3 mm wide). However, the ultimate order of branches in the Quantico specimens is similar to those in Zone III specimens of *Pseudofrenelopsis* from Bodkin Point, Maryland (Upchurch and Doyle, 1981, fig. 3c). This variation in average width between specimens of different ages warrants further study.

Family ARAUCARIACEAE  
Genus *Araucarites* Sternberg

*Araucarites aquiensis* Fontaine (Figure 7)

*Araucarites aquiensis* Fontaine – Fontaine, 1889, p. 264, Pl. 133, figs. 8–12.

*Araucarites aquiensis* Fontaine – Fontaine, in Ward, 1905, Pls. 489, 514, 528.

*Araucarites aquiensis* Fontaine – Berry, 1911a, Pls. 398–399.

Description of Quantico remains.—Isolated thick cone scales, outline broadly obovate and bordering on obdeltoid, one longitudinal keel and two weakly developed wings visible on some specimens. Cone scale narrowed to a stalked base, L/W 1.2–1.5, cone scales 2–2.4 cm long by 1.4–1.8 cm wide (maximum width), with a transverse thickening well developed at the widest part of each cone scale. Surface of most cone scales with approximately 15–20 longitudinal ridges (probably the remains of vascular and fiber bundles).

Number of specimens examined.—8.

Illustrated specimen.—USNM 446036.

Other identified specimens.—FMNH PP43884–PP43890.

Discussion.—The suite of preserved features is within the range of variation reported by Fontaine (1889, p. 264) for *Araucarites aquiensis*, a species originally reported from the Bank near Brooke locality of lower Subzone II-B age. Berry (1911a) collected cone scales from additional localities and reported that this species commonly occurs in megafloreal assemblages from the Patapsco Formation. Palynological correlations of Potomac Group megafloreal localities by Doyle and Hickey (1976) and Hickey and Doyle (1977) indicate that *A. aquiensis* ranges from lower to upper Subzone II-B.

The obovate shape of the cone scale and presence on some specimens of a weak longitudinal keel with two wings are features that imply possible affinities to extant Araucariaceae. Specimens of *A. aquiensis* always are preserved as isolated cone scales. This indicates that the cone scales of this species were deciduous (Fontaine, 1889), as in extant Araucariaceae.

Family TAXODIACEAE  
Genus *Athrotaxopsis* Fontaine

*Athrotaxopsis* sp. (Figures 8, 9)

Description of Quantico remains.—Terminal region of shoot with an attached female cone. Shoot unbranched, nearly 2 mm wide, with appressed scale leaves, phyllotaxy alternate and spiral. Leaves rhombic, L/W approximately 1, 1.5–2 mm long by 1.5–2 mm wide, dorsal keel weakly developed or absent, free portion of leaf approximately the same length as the attached portion.

Seed cone terminal on shoot; cone >10 mm long by 8 mm wide, with 9 cone scales visible on the specimen surface; no bracts visible. Cone scales peltate and with an expanded head; stalks not seen; head of each cone scale isodiametric, 2.5–3 mm in diameter, outer surface of head wrinkled but without a distinct invagination or groove.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446043.

Discussion.—The single fragmentary specimen

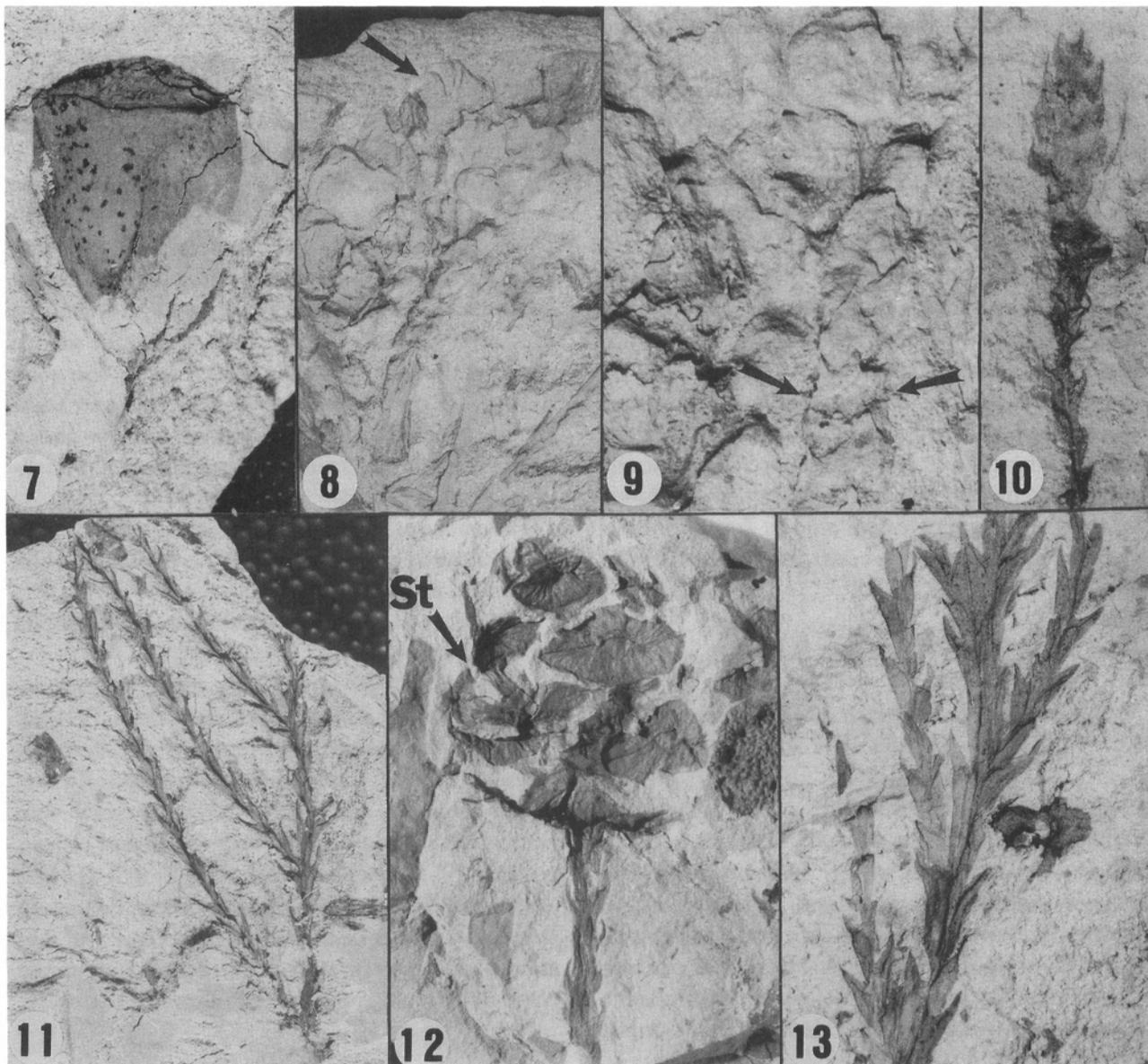


Figure 7.—*Araucarites aquiensis* Fontaine, isolated cone scale showing transverse thickening near apex and weakly developed lateral wings. USNM 446036, x2. Figures 8, 9.—*Athrotaxopsis* sp. USNM 446043. Figure 8, view of shoot showing terminal seed cone with ovuliferous scales, x3. Figure 9, view of shoot showing scale leaves (arrows), x8. Figures 10–13.—*Sphenolepis sternbergiana* (Dunk.) Schenk. Figure 10, shoot with attached male cone at tip, FMNH PP43900, x5. Figure 11, shoot with two orders of branching showing characteristic pseudoplanate arrangement of lateral branches, USNM 446026, x2.4. Figure 12, shoot with attached female cone at tip. Note the peltate cone scales with stalks (St) and transversely elongate heads showing wrinkles and transverse grooves. FMNH PP43801, x2.2. Figure 13, close-up of shoot showing the thick spreading leaves characteristic of species, FMNH PP43809, x3.5.

possesses a suite of features characteristic of the genus *Athrotaxopsis* Fontaine. These features include closely appressed rhombic scale leaves, small terminal seed cones, and peltate cone scales with an expanded head that is more or less isodiametric in surface view. Among the species of *Athrotaxopsis* recognized by Berry (1911a) for the Potomac Group, the Quantico remains most closely resemble *A. grandis* Fontaine in shoot diameter, leaf shape, weak development to absence of a keel on the leaves, and seed cone dimensions. However, poor preservation precludes unequivocal assignment to any previously described species.

The occurrence of *Athrotaxopsis* at Quantico represents a stratigraphic range extension for the genus within the Potomac Group. All previously reported Potomac Group localities with *Athrotaxopsis* are palynologically dated as Zone I or have an associated megaflora consistent with a Zone I age.

#### Genus *Sphenolepis* Schenk

##### *Sphenolepis sternbergiana* (Dunker) Schenk (Figures 10–13)

Description of Quantico remains.—Shoots preserving as many as two orders of branching, some shoots with attached cones. Branching pseudoplanate, restricted to one plane, superimposed on an alternate and spiral phyllotactic pattern. Penultimate shoots with as many as 4 branches per cm; ultimate shoots 2–4 mm wide, penultimate shoots often slightly wider. Leaves scale-like, with a dorsal keel, less than 1 mm wide in dorsal view; base of leaves decurrent on stem, 2–6 mm long and as much as 1 mm thick; apical part of leaves free from stem, shorter than the base, 1–2 mm long, with an acuminate shape and sharp tip, oriented at a narrow acute angle to the shoot axis, straight or apically curved.

One shoot with a pollen cone attached at or near the tip of a branch, precise mode of attachment not clear due to poor preservation. Pollen cone ovoid but tending toward cylindrical, 5 mm long by 2 mm wide. Phyllotaxy of microsporophylls

alternate and spiral. Microsporophylls rhombic and possibly with a terminal seta, L/W (excluding possible seta) approximately 1, microsporophylls 1 mm long by 1 mm wide. No pollen sacs observed.

One shoot with a well-preserved seed cone attached to the tip of a branch. Seed cone ovoid, 2 cm long by 2 cm wide, with approximately 8 cone scales visible on specimen; no bracts visible (inferred to have fused to the cone scale). Cone scales peltate, each with a distinct stalk and an expanded head; stalks 3–4 mm long by about 1 mm wide (two measured); heads of cone scales elliptic in surface view, with their long axis transverse to the cone axis, 8–10 mm wide by 5–6 mm tall (four measured), typically with a wrinkled surface and a distinct transverse groove. No seeds or seed attachment scars observed.

Number of specimens examined.—30.

Illustrated specimens.—USNM 446026; FMNH PP43801, PP43809.

Other identified specimens. — FMNH PP43846– PP43868.

Discussion.—Potomac Group remains of *Sphenolepis* were assigned to two species by Berry (1911a). The Quantico specimens have the relatively robust stems with thick, spreading leaves characteristic of *S. sternbergiana*, rather than the relatively thin stems with thinner, often appressed leaves characteristic of *S. kurriana*. We follow Berry's (1911a) taxonomic treatment of Potomac Group *Sphenolepis* largely as a matter of convenience, recognizing that studies of better preserved fertile remains could potentially change species delimitations.

#### Family PINACEAE

##### Undetermined leaves (cf. *Abietites longifolius* [Fontaine] Berry) (Figure 14, Lf)

Description.—One incomplete leaf preserved. Leaf needle-like, curved, > 15 cm long by < 1 mm wide.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446024.

Discussion.—This leaf has the shape of *Pinus* and *Prepinus* leaves. It is similar to *Abietites longi-*

*folius* (Fontaine) Berry in general form but is longer than the range of lengths reported for the species by Berry (1911a) (12–15 cm long). Intrafamilial affinities cannot be determined accurately without organic preservation or attachment to shoots.

#### Winged seeds of Pinaceae

Winged seeds with affinities to Pinaceae are associated with the above leaf type. At the species level, these seeds are distinct from previously described pinaceous winged seeds from the Potomac Group; at the generic level, they show a mosaic of features today restricted to separate genera of Pinaceae. (See Miller, 1977, for similar examples among anatomically preserved Cretaceous Pinaceae.) We recognize two morphotypes (Figures 15, 16) on the basis of size and shape but refrain from formal description pending more comprehensive revision of Cretaceous pinaceous winged seeds.

#### Winged seed type 1 (Figure 16)

Description.—Both adfacial and abfacial sides of seed preserved. Seeds 2 cm long by 1 cm wide, admedial margin of seed straight to gently curved, abmedial margin of seed strongly flared in the basal half, gradually curving toward admedial margin in apical half of seed. Widest part of seed midway between the base and apex, L/W 2. Wing of seed two to three times as long as the central body, admedial margin of wing attached near the apex of the seed body, abmedial margin of wing attached to the midpoint of seed body; apex of wing somewhat ragged (implying that it was torn from the cone scale). Wing without transversely oriented wrinkling; faint streaks possibly indicative of cellular pattern present, some of these streaks oriented obliquely to the admedial edge and connecting with the abmedial edge at an oblique angle; distinct resin vesicles not observed on wing. Body of seed distinctly ovoid in adfacial view, 6–8 mm long by about 4 mm wide, L/W 1.5–2, body of seed rounded to flattened along abfacial side.

Number of specimens examined.—2.

Illustrated specimen.—USNM 446038B.

Other identified specimens.—USNM 446038A (counterpart of 446038B); FMNH PP43804.

Discussion.—Winged seed type 1 differs from *Pinus vernonensis* Ward (1895, p. 497, Pl. 109, figs. 4–6), *Pinus schista* Ward (1895, p. 531, Pl. 112, figs. 13–15), and seeds doubtfully related to *Pinus* by Fontaine (1889, Pl. 170, fig. 4) in showing a distinct flaring of the abmedial margin of the wing near the base of the seed and in having a more asymmetrical shape. It differs from seeds of extant *Pinus* in showing no evidence for an undulatory cellular pattern on the wing parallel to the long axis, or wrinkling of the wing transverse to the long axis. These two characters readily distinguish the winged seeds of *Pinus* from the winged seeds of other extant Pinaceae (Wolfe and Schorn, 1990). Another difference separating winged seed type 1 from the seeds of extant *Pinus* is the probable tearing of the apical margin of the wing, which may indicate that a distinct abscission zone along the wing apex was absent. This is the probable generalized condition for winged seeds of Pinaceae, where tearing of the wing from the cone scale plays an important role in seed dispersal. In extant *Pinus*, however, a well-developed abscission zone forms at the margin of the seed wing (Wolfe and Schorn, 1990).

Winged seed type 1 possesses features intermediate between those used to differentiate extant genera of Pinaceae (see keys to the winged seeds of extant Pinaceae in Wolfe and Schorn, 1990, figs. 2 and 3). This situation is best illustrated by using the key for seeds with the abfacial face preserved (Wolfe and Schorn, 1990, fig. 3). In winged seed type 1, the abfacial side of the wings shows evidence for directing some of the cellular pattern toward the abmedial margin at an oblique angle; this characteristic segregates seeds of *Abies*, *Cedrus*, *Tsuga*, *Keteleeria*, and *Pseudolarix* from seeds of *Picea*, *Larix*, and *Pseudotsuga*. Within the first group of extant genera, *Abies* and *Cedrus* are segregated from *Tsuga*, *Keteleeria*, and *Pseudolarix* by having the widest part of the seed in the distal, rather than proximal, half; *Tsuga* is segregated from *Keteleeria* and *Pseudolarix* by having seeds that are <2 cm,

rather than  $> 2$  cm, long; *Keteleeria* is segregated from *Pseudolarix* by having the length of the wing relative to the seed body  $< 1.5$ , rather than  $> 2.5$ . Winged seed type 1, however, cannot be referred unambiguously to any of these modern genera because the widest part of the seed is located halfway between the base and apex, the seed is 2 cm long, and the wing of the seed is 2–3 times the length of the central body. Such a combination of features is consistent with the suggestion that most extant genera of Pinaceae did not appear until the Tertiary (Miller, 1977, 1988).

#### Winged seed type 2 (Figure 15)

Description.—Abfacial side of seed preserved. Seed 3 cm long by about 1 cm wide, admedial margin of seed straight, abmedial margin of seed gently flared in the basal half of seed, gradually curving toward the admedial margin in the apical half. Widest part of seed halfway between base and apex, L/W 3. Wing of seed 3 times as long as body, apex not fully preserved. Cellular pattern of wing not clearly visible on specimen but with faint brown streaks that may represent the remains of cellular pattern, some streaks oriented at an oblique angle to the abmedial margin of wing. Body of seed 10 mm long by 5 mm wide, L/W of body 2, body of seed strongly tapered to a point, possibly indicating an aborted seed.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446037B.

Other identified specimens.—USNM 446037A (counterpart of 446037B).

Discussion.—The absence of undulatory cellular pattern on the wing parallel to the long axis of the seed and the absence of wrinkles on the wing transverse to the long axis are features that distinguish this seed from seeds of extant *Pinus*. The presence of faint brown streaks on the wing, some of which are oblique to the abmedial margin, perhaps indicates cellular pattern, and hence affinities to *Abies*, *Cedrus*, *Tsuga*, *Keteleeria*, and *Pseudolarix*. As in winged seed type 1, the fact that the widest part of the seed is halfway between the base and apex precludes more detailed determination of

relationships.

The tapering of the seed body to a sharp point at the base of the seed may indicate that the specimen is atypical for the species (cf. Wolfe and Schorn, 1990, Pl. 3, figs. 5a–5f).

Family UNKNOWN

Genus *Brachyphyllum*

- Brachyphyllum crassicaule* Fontaine (Figure 17)  
*Brachyphyllum crassicaule* Fontaine – Fontaine, 1889, p. 221, Pl. 100, fig. 4; Pl. 109, figs. 1–3; Pl. 111, figs. 6, 7; Pl. 112, figs. 6–8; Pl. 168, fig. 9.  
*Brachyphyllum crassicaule* Fontaine – Fontaine, in Ward, 1905, pp. 529, 557, Pl. 113, fig. 6.  
*Brachyphyllum crassicaule* Fontaine – Berry, 1911a, p. 393, Pl. 164, figs. 1–6.

Description of Quantico remains.—Shoots with as many as 3 orders of branching preserved, phyllotaxy alternate and spiral, branching restricted to one plane, branches of each order untapered for most of their length. Branches of ultimate order 2–14 mm long by 1.5–3 mm wide, with rounded apex. Apex of ultimate branches sometimes bearing thick round bodies  $< 2$  mm in diameter, possibly representing buds. Branches of penultimate order longer and thicker than branches of ultimate order, 3–4 mm wide; branches of next lower order rarely preserved, 5 mm wide (one measured). Leaves scale-like, rhomboidal, closely appressed to stem, 2–4 mm long by 2–4 mm wide, L/W 1.

Number of specimens examined.— $> 11$ .

Illustrated specimen.—FMNH PP43812.

Other identified specimens from Quantico.—USNM 446021; FMNH PP43813, PP43876–PP43882, PP43899.

Discussion.—These shoots are referable to the Potomac Group species *Brachyphyllum crassicaule* Fontaine, which is known from both Zone I and Subzone II-B. Shoots of this general aspect are common in mid- to Late Cretaceous megafloras from the Atlantic Coastal Plain and Europe. These include *Brachyphyllum obesum* Heer (photographically illustrated in Texeira, 1948, Pl. 22, fig. 7; Pl. 23, figs. 1–4; Pl. 26, fig. 1; Pl. 36, figs. 1–3; Pl. 41,

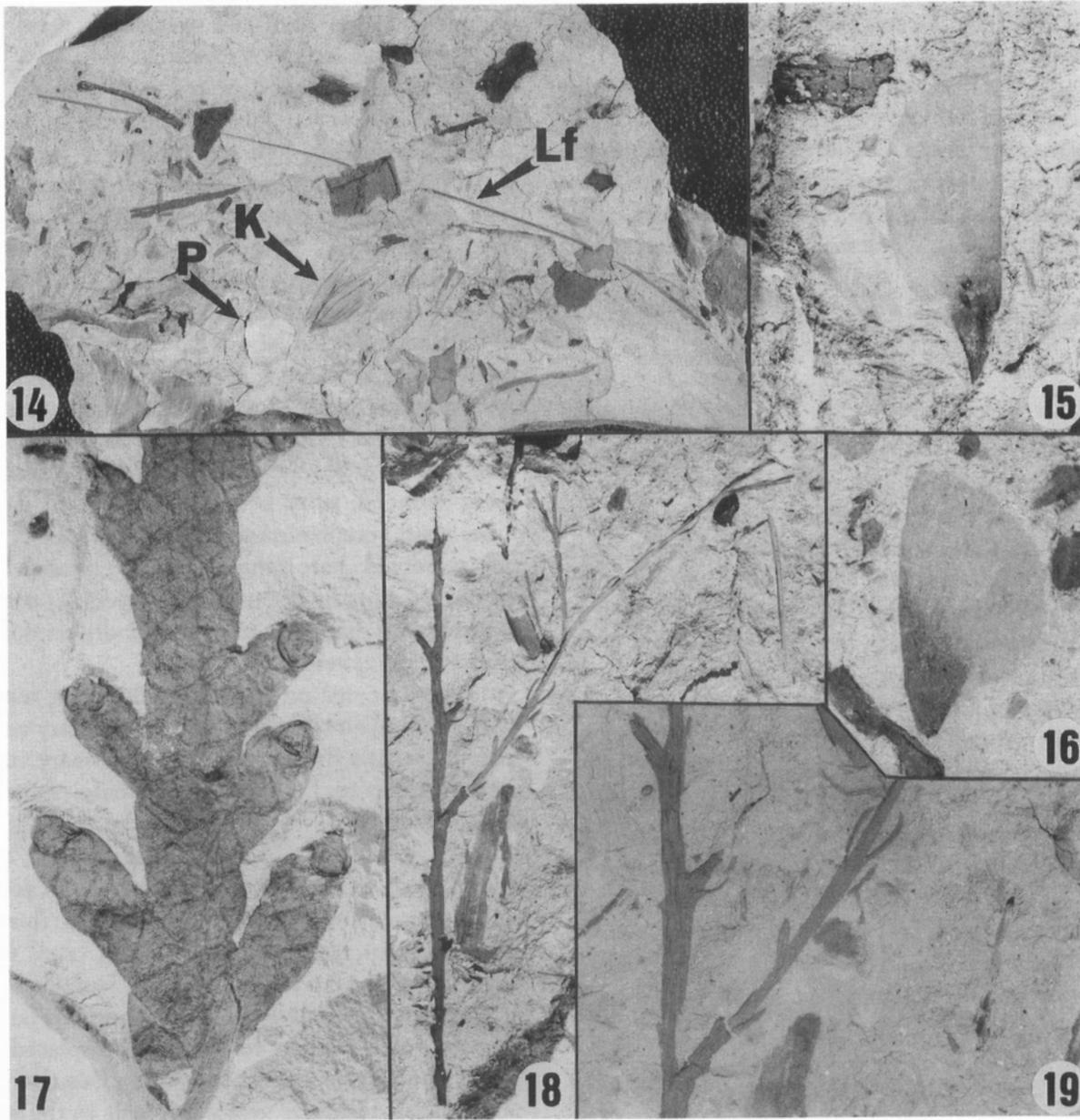


Figure 14.—Needle of Pinaceae (cf. *Abietites longifolius* [Fontaine] Berry) (arrow). Also note the specimen of aff. *Kenella* (K) and the cast of a pelycypod shell (P). USNM 446024, x0.75. Figure 15.—Winged seed of Pinaceae, type 2. USNM 446037B, x4. Figure 16.—Winged seed of Pinaceae, type 1. USNM 446038B, x5. Figure 17.—*Brachyphyllum crassicaule* Fontaine, specimen showing two orders of branching, scale leaves, and round terminal structures, interpreted as probable buds. FMNH PP43812, x4. Figures 18, 19.—Unnamed species of conifer, FMNH PP43800. Figure 18, general view of shoot, x1.5. Figure 19, close-up of shoot showing widely spaced, linear leaves, x3.

figs. 1, 2), *Brachyphyllum crassum* Lesquereux (1891, p. 32, Pl. 2, fig. 5), and *Brachyphyllum macrocarpum* Newberry (well illustrated in Berry, 1911b, Pl. 7, figs. 1–4). Detailed systematic revision of this species complex has not yet been attempted, and relationships within Coniferales are not well understood. Cretaceous species of *Brachyphyllum* are considered to belong to Araucariaceae or Cheirolepidiaceae (e.g., Watson, 1988; Raubeson and Gensel, 1991).

Conifer shoot, genus not determined  
(Figures 18, 19)

Description.—One shoot with two orders of branching preserved. Branching alternate, apparently in one plane; ultimate order of branches < 1 mm wide, 0.5–2.1 cm apart; penultimate order of branches 0.9–1.5 mm wide. Phyllotaxy alternate and spiral, leaves sparse on stem, 2–8 leaves per cm. Leaves linear, 1–3 mm long by 0.2–0.4 mm wide, with a decurrent base; base of leaf < 1 mm long; free part of leaf spreading from stem, straight or apically curved, not tapered for most of length, tip poorly preserved, possibly sharp.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43800.

Discussion.—This species of conifer is extremely rare at Quantico, and the one known shoot is poorly preserved. It does not resemble any previously described species of conifer from the Potomac Group. Poor preservation precludes formal taxonomic recognition.

Division MAGNOLIOPHYTA  
Class MAGNOLIOPSIDA  
Subclass MAGNOLIIDA  
Order LAURALES  
Genus *Pabiania* Upchurch and Dilcher

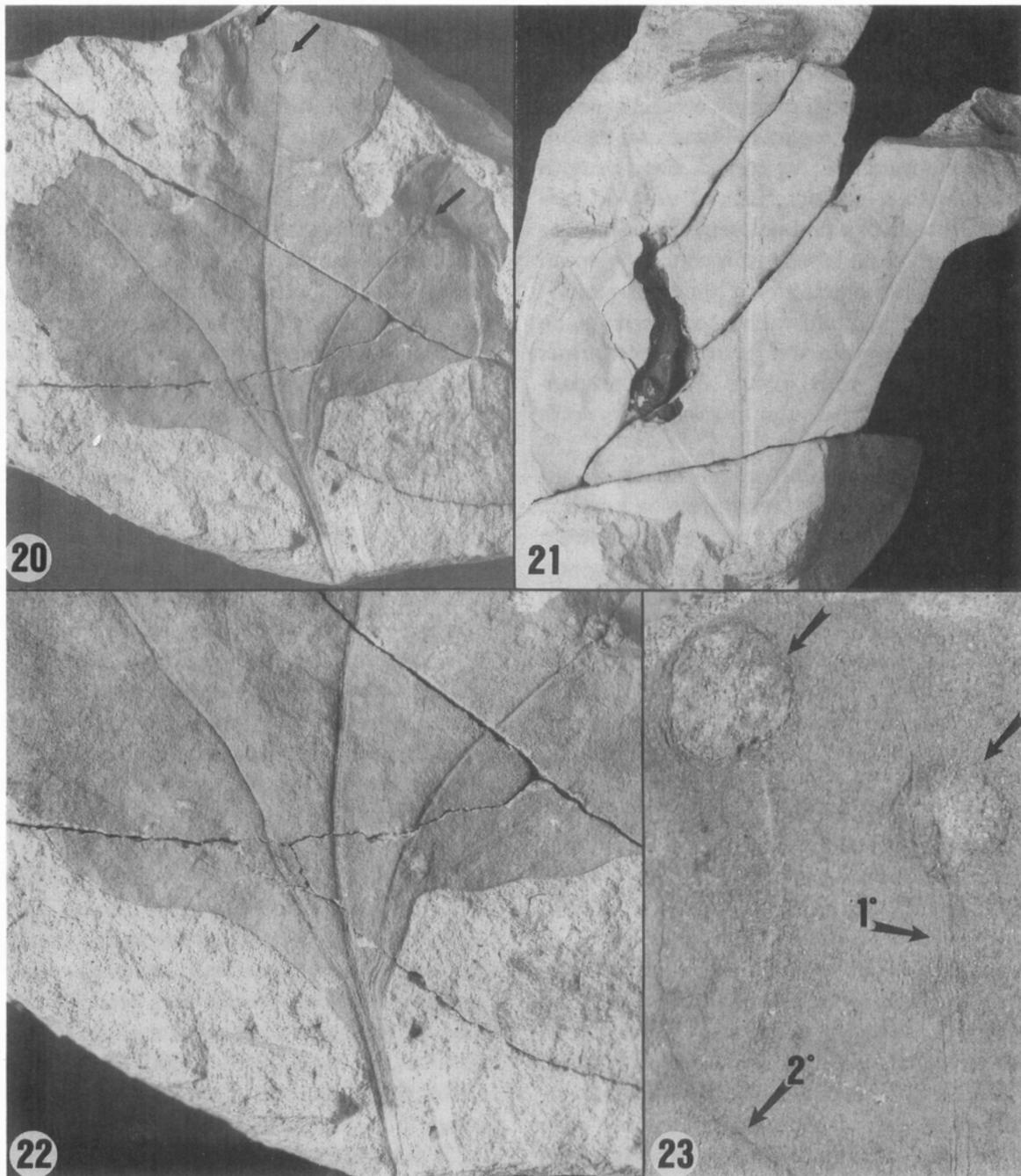
Type species – *Pabiania variloba* Upchurch and Dilcher (1990), p. 21, Pl. 8; Pl. 9, figs. 1–3; Pl. 11, figs. 1–7; text figs. 8, 9).

aff. *Pabiania* sp. 1 (Figures 20–27)

Description of Quantico remains.—Two nearly complete leaves and two fragments preserved. Lamina > 6 cm long by 4 to 6.5 cm wide, L/W 1 to > 1.5. Lamina bilobed or trilobed. Bilobed leaf with a large medial lobe and a smaller, shorter lateral lobe; medial lobe incomplete, > 3 cm long by 2.5 cm wide (estimated width), widest above base, apex not preserved; lateral lobe 1.5 cm long by 1.2 cm wide, curved towards medial lobe. Trilobed leaves with a medial lobe and two lateral lobes of nearly equal size, leaf 5 to 8 cm long by 5 to 8 cm wide; medial lobe > 2.3 cm to > 3 cm long by 2.3 to > 3 cm wide, widest above base; lateral lobes oriented at < 45° to medial lobe, free portion of lateral lobes > 1.5 cm long by 1.6 to > 2.2 cm wide, lateral lobes widest at base. Apex of lateral lobes rounded, sinus between medial and lateral lobes acute, predominantly rounded. Apex of leaf not preserved; base ranging from right-angled to obtuse but broadly decurrent onto petiole; petiole > 1 cm long; margin entire, structurally reinforced with a fimbrial vein.

Primary venation palinactinodromous, with a midvein and pair of decurrent lateral primary veins; midvein slightly thicker than lateral primary veins, moderate, up to 1.5 mm wide at base, thinning little in the basal 75 percent of the leaf; lateral primary veins decurrent on midvein, distinct from midvein between the top of the petiole and points of divergence from the midvein, slightly thinner than midvein, up to 1 mm wide at base, each lateral primary vein in an individual leaf diverging at a slightly different level than the other, lateral primary veins straight to recurved, displaced towards the side of the lateral lobe closest to the medial lobe, thinning noticeably only in the most apical 20–30°, giving rise to 5 or more exmedial branches at narrow to broad acute angles. Exmedial branches of the lateral primary veins thin to moderate relative to source veins, the basalmost exmedial branch sometimes running directly to margin and connecting with a fimbrial vein, the other exmedial branches always forming loops; the angle between each pair of lateral primary veins < 90°.

Secondary venation probably brochidodromous (exact pattern difficult to discern because of preser-



Figures 20–23.—*aff. Pabiania* sp. Figure 20, nearly complete trilobed leaf showing recurved lateral primary veins and galls (arrows). UMMP 66621, x1.5. Figure 21, specimen of a larger trilobed leaf showing less recurved lateral primary veins and secondary veins on the medial lobe. UMMP 66622, x1. Figure 22, base of specimen in Figure 20 showing truncate base that is decurrent onto the petiole and decurrent lateral primary veins that are separate into the petiole. UMMP 66621, x2.5. Figure 23, medial lobe of specimen in Figures 20 and 22 showing primary vein (1°), a secondary vein (2°), and two galls (arrows). UMMP 66621, x5.

vation); secondary veins thin to moderate relative to primary veins, at least 4 pairs present on midvein, originating at moderate to broad acute angles, zig-zag on one specimen, strongly curved near the margin and less often near base; intercostal regions exmedially elongate, apically curved. Basal margins of lamina with a distinct fimbrial vein or dark regions suggestive of a fimbrial vein. Sinus-bracing vein consisting of the basalmost secondary vein on the midvein; sinus-bracing vein bifurcating inside the leaf margin; each bifurcation connecting to an adjacent secondary vein and giving rise to thinner exmedial branches, these exmedial branches connecting with the fimbrial vein. Intersecondary veins not observed.

Tertiary venation faint on specimens, apparently irregularly reticulate, tending to be oriented towards primary veins; tertiary veins moderate relative to secondary veins, closely spaced, originating at acute to obtuse angles from the admedial sides of the secondary veins and generally acute angles on the exmedial sides, tending to enclose exmedially elongate regions. Higher order venation obscure. Marginal venation probably consisting of a fimbrial vein, based on the darkening and thickening of the leaf margin and the termination of lower-order veins at the leaf margin.

Number of specimens examined.—4.

Illustrated specimens.—USNM 446025; FMNH PP43791, PP43791' (part and counterpart); UMMP 66621, 66622.

Discussion.—Four leaves from Quantico possess features that diagnose *Pabiania*, an extinct genus of Laurales proposed by Upchurch and Dilcher (1990) for lobed leaves of Cenomanian age. Features characteristic of *Pabiania* include: (1) lobate shape, (2) palinactinodromous primary venation with lateral primary veins that are decurrent into the petiole, (3) thin/moderate secondary veins that originate at moderate to broad acute angles, (4) tertiary veins that are (apparently) closely spaced, irregular in pattern, and oriented towards the primary veins, and (5) marginal venation that consists of a fimbrial vein. *Pabiania* possesses a combination of features unknown in any extant family of Laurales, but the greatest number of

individual features occur in Atherospermataceae, Gyrocarpaceae, Hernandiaceae, Hortoniaceae, and Lauraceae (Upchurch and Dilcher, 1990). Such a generalized relationship to extant Lauraceae is plausible given the occurrence of distinctly lauraceous flowers in Potomac Group rocks of Zone III (Cenomanian) age (Drinnan et al., 1990).

The Quantico remains and Cenomanian *Pabiania* differ most noticeably in details of sinus bracing. In the Quantico leaves the sinus-bracing vein bifurcates inside the leaf margin. Each branch of this bifurcation connects with an adjacent secondary vein, and exmedial branches of these bifurcations connect with the margin. In Cenomanian *Pabiania* the basalmost secondary veins on the midvein run directly to the sinuses and bifurcate at, rather than inside, the leaf margin. Each branch of a bifurcation connects with an adjacent secondary vein, as in the Quantico specimens, but no exmedial branches are produced. Although these two patterns of sinus bracing are distinct, they show an underlying similarity in the branching and position of the bracing vein. Both patterns occur in extant Lauraceae. The Quantico pattern is probably the more primitive, because it more closely resembles the brochidodromous secondary venation of unlobed Laurales and occurs in fossils that are older than type *Pabiania*.

The Quantico specimens of aff. *Pabiania* resemble other three-lobed leaves of Albian to early Cenomanian age in primary venation, sinus bracing, and (where preserved) marginal venation. Formally described species that preserve at least three of its diagnostic features include "*Sassafras*" *bilobatum* Fontaine (1889, p. 290, Pl. 156, fig. 12; Pl. 164, fig. 4) from the Lower Cretaceous Potomac Group, "*Sassafras*" *bradleyi* Brown (1933, p. 7, Pl. 2, fig. 5) from the mid-Cretaceous (upper Albian to Cenomanian) Aspen Shale of Wyoming (also illustrated in Crabtree, 1987, fig. 40), and *Araliaephyllum paluxyense* Ball (1937, p. 530, figs. 1–4) from the upper Albian Paluxy Sandstone of Texas.

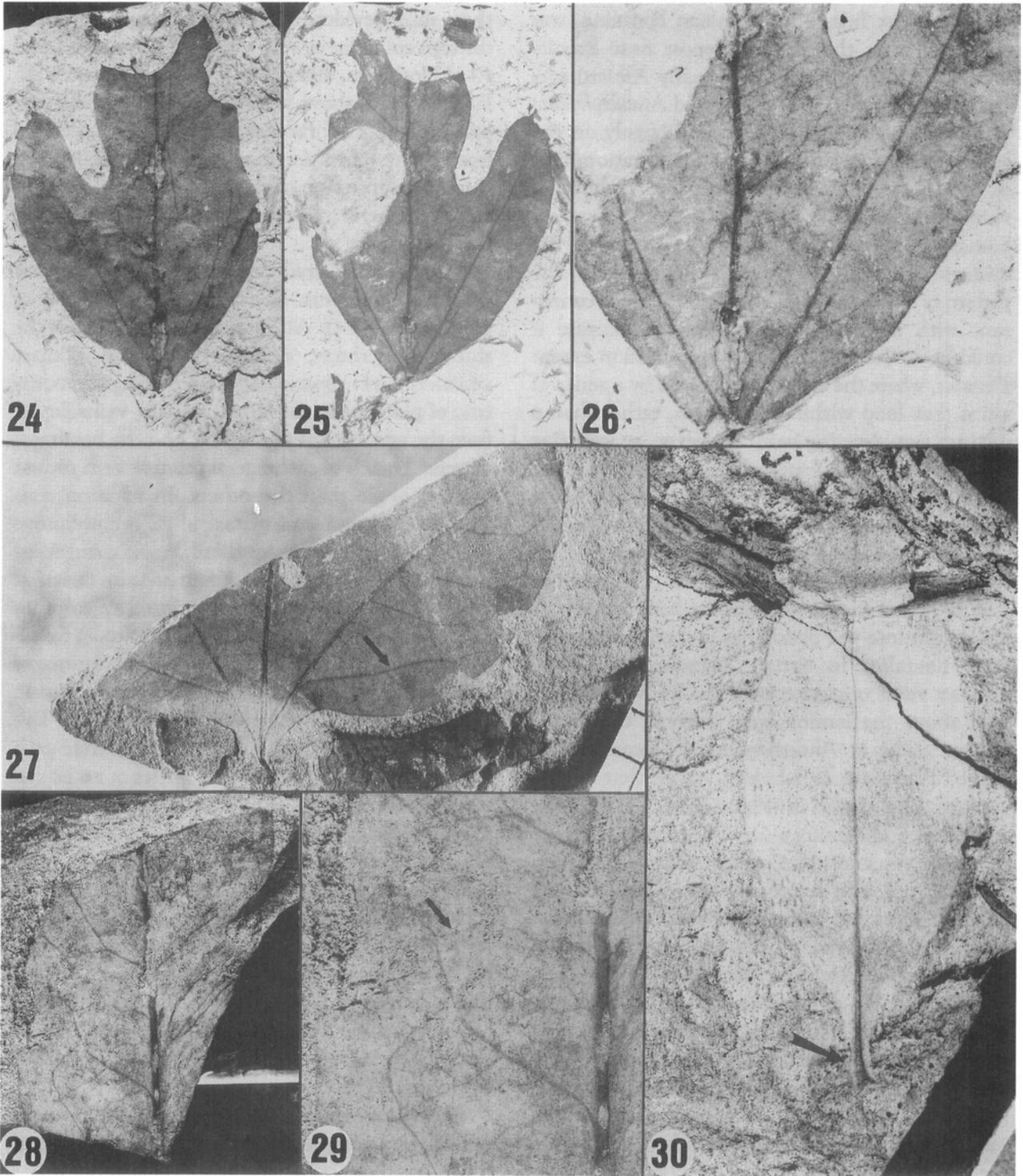
Comparison of aff. *Pabiania* from Quantico with three-lobed Potomac Group "platanoids" analyzed by Hickey and Doyle (1977) and Upchurch (1984) indicates that at least two taxa were probably

misassigned to the platanoid complex and represent Laurales. The first, *Araliaephyllum* Fontaine, was described from the 72nd Milepost near Brooke locality of lower Subzone II-B (early Albian) age. Hickey and Doyle (1977) interpreted *Araliaephyllum* as a three- to five-lobed platanoid largely on the basis of palinactinodromous primary venation; that is, the lateral primary veins depart from the midvein at different levels, and the first external branch of the lateral primary veins forms the midvein in the lower pair of lateral lobes. The pattern of sinus bracing in *Araliaephyllum* is consistent with a platanoid interpretation because it conforms to the unspecialized type found in extant *Platanus*, where the sinuses are braced by a series of veins that loop within the margin, rather than a distinct sinus-bracing vein. However, at least five sets of venational features in *Araliaephyllum* are better interpreted as features of Laurales and imply that the *Platanus*-like sinus bracing simply represents the primitive state for lobed leaves of Laurales. First, *Araliaephyllum* has lateral primary veins that diverge at the very base of the lamina and may be distinct into the petiole, as in many extant and fossil Laurales. In extant *Platanus*, the lateral primary veins originate from the midvein usually well above the lamina base. Second, the lateral primary veins in *Araliaephyllum* are sometimes recurved like those in Laurales, rather than always straight like those in Platanaceae. Third, the secondary and tertiary veins of *Araliaephyllum* are the same thickness as those in *Pabiania* and aff. *Pabiania*, but thin relative to the secondary and tertiary veins in later platanoids. Fourth, the darkening of the margin near the leaf base and in the sinuses of *Araliaephyllum* (e.g., Hickey and Doyle, 1977, fig. 41) implies that it had a fimbrial vein like many Laurales, rather than looped marginal venation like extant *Platanus*. Finally, each lateral primary vein in *Araliaephyllum* produces a series of external branches, the basalmost of which runs at a lower angle than the others and terminates at the margin or at the apex of a small lobe. This pattern of behavior is not typical of either

most extant *Platanus* or mid-Cretaceous platanoids that show evidence for platanaceous affinities through cuticular anatomy (e.g., platanoids #1 and #3 of Upchurch, 1984), but it does characterize aff. *Pabiania*. The above features imply that the three-lobed leaves of aff. *Pabiania* may have been derived from a five-lobed ancestor such as *Araliaephyllum* through suppression of the basalmost pair of lobes and strengthening of the secondary veins that brace the sinuses.

The second mid-Cretaceous platanoid that probably represents Laurales is platanoid #2 of Upchurch (1984). Although platanoid #2 has the three-lobed shape, palinactinodromous primary venation, and unspecialized sinus bracing characteristic of platanoids, the lateral primary veins depart from the very base of the lamina, and the basalmost external branch of each lateral primary vein runs at a lower angle than the others. In addition, two anatomical features of platanoid #2 are unknown within extant Platanaceae and well-characterized fossil relatives but are common within Laurales. First, the mesophyll tissue in platanoid #2 contains numerous spherical secretory cells that resist oxidative maceration and have the same appearance as secretory cells in fossil Laurales (e.g., compare Upchurch, 1984, fig. 60 with Upchurch and Dilcher, 1990, Pl. 11, figs. 1 and 3). Second, each trichome base in platanoid #2 consists of an isodiametric pore with a heavily cutinized rim as in most Laurales, rather than a cutinized basal cell that is positioned above the other epidermal cells as in other platanoids and Platanaceae. Consistent with a lauralean interpretation are other less systematically reliable epidermal features shared by platanoid #2 and *Pabiania* that differ from those of other mid-Cretaceous platanoids. These more plastic features include small isodiametric epidermal cells and stomata that are large relative to unspecialized epidermal cells.

The above discussion underscores the need for critical and comprehensive systematic revision of mid-Cretaceous palmately lobed foliage.



Genus *Landonia* Upchurch and Dilcher*Landonia* cf. *L. calophylla* Upchurch and Dilcher (Figures 28, 29)

Description.—Middle portion of one lamina preserved. Shape probably oblong, apex and base missing, lamina >6.2 cm long by about 4.5 cm wide (estimated width), preserved portion of margin entire, with a slight darkening (suggestive of mechanical reinforcement). Primary venation pinnate; primary vein stout, composition of primary vein difficult to observe because of poor preservation. Secondary venation “festooned” brochidodromous, with one intracostal branch observed; secondary veins moderate relative to the primary vein, more than four pairs, irregularly spaced, occasionally decurrent on primary vein but more often not, originating from primary vein at moderate to broad acute angles; secondary veins slightly sinuous in course, curving mostly near the margin, deflected at points of branching, each secondary vein forming festooned brochidodromous loops with the superadjacent secondary vein, with both secondary veins of similar thickness at their junction, angle of brochidodromous junction broad acute to obtuse; intercostal regions roughly isodiametric in shape, exmedial sides of intercostal regions tending to be curved, the other sides tending towards straight. Excostal branches of the secondary veins forming irregular series of loops (exact arrangement and number of series of loops unclear). Intersecondary veins present, 0–1 per intercostal region, branching to form tertiary veins. Intercostal tertiary venation

consisting of two components, each of which typically gives rise to thinner branches; the thicker component almost as thick as the secondary veins, somewhat irregular course but tending to be transverse to the secondary venation, forming zig-zags when giving rise to lateral branches, these lateral branches forming the thinner component of the tertiary venation; thinner component of tertiary venation nonorthogonally rooted but tending to be transverse to the source veins. Higher-order venation poorly preserved. Small dark spots present on the lamina, possibly representing the remains of secretory bodies.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446018B.

Other identified specimens.—USNM 446018A (counterpart of 446018B).

Discussion.—One fragmentary leaf from Quantic preserves most features that diagnose *Landonia*, an extinct genus of Laurales proposed by Upchurch and Dilcher (1990, p. 18) for remains from the Cenomanian Rose Creek locality in the Dakota Formation of Nebraska. Preserved features diagnostic of *Landonia* include: (1) a probable oblong shape, (2) an entire margin with possible mechanical reinforcement, (3) pinnate primary venation, (4) a stout primary vein, (5) irregularly spaced secondary veins of moderate thickness that tend to have a sinuous course and enclose roughly isodiametric intercostal regions in the middle part of the lamina, (6) intracostal branching of the secondary venation, and (7) sparsely branched tertiary venation, which comprises a thicker component that tends to be transverse to the source veins and a thinner compo-

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Facing page: Figures 24–27.—aff. *Pabiania* sp. Figure 24, leaf showing bilobate shape and small, apically curved lateral lobe with rounded tip. FMNH PP43791, x1. Figures 25, 26, counterpart of Figure 24, FMNH PP43791'. Figure 25, general view, x1. Figure 26, close-up of sinus showing pattern of sinus bracing, dark basal margins of lamina (evidence of basilaminar secondary veins?), and faint intercostal tertiary venation. Also note darkening of leaf margin at sinus, taken as evidence for a possible fimbrial vein, x2. Figure 27, basal part of leaf showing decurrent base and decurrent origin of lateral primary veins. The basalmost branch of the right lateral primary vein (arrow) is oriented at a lower angle than the superadjacent branches. USNM 446025, x1.5. Figures 28, 29.—*Landonia* sp. USNM 446018B. Figure 28, general view of leaf, x1. Figure 29, close-up of lower intercostal regions showing the intracostal branch of a secondary vein (arrow) and intercostal tertiary venation consisting of a thicker and thinner component, x2. Figure 30.—*Dicotylophyllum ovato-decurrans* new species, specimen showing ovate laminar shape and decurrent wing of laminar tissue on petiolar region (arrow). USNM 446013B, x1.

ment that tends to be transverse to the thicker component. In addition, the Quantico specimen strongly resembles the Rose Creek specimen of *Landonia* in features not used to diagnose the genus, including overall leaf size and the tendency for the lamina to preserve dark spots, which may represent the remains of secretory bodies. *Landonia* cf. *L. calophylla* is most similar to species assigned to Fontaine's (1889) genera *Ficophyllum* and *Proteaphyllum* but differs in three features: (1) secondary venation that has common intracostal branching, (2) intercostal regions that are uniformly isodiametric above the base of the leaf, and (3) tertiary venation that has two distinct orientations and thicknesses.

Despite close similarities between the Quantico and Dakota remains assigned to *Landonia*, we are reluctant to assign the Quantico specimen to the Cenomanian species *Landonia calophylla*. We prefer to use a "cf." designation because the Quantico leaf does not preserve all the diagnostic features present in the Rose Creek specimen, including the leaf base and petiole, the structure of the midvein, the intercostal secondary venation from the basal part of the leaf, and the excostal secondary and tertiary venation. Also, the secondary veins of the Quantico specimen diverge at a somewhat lower angle than those known from Rose Creek foliage, but the significance of this difference is difficult to assess because only two specimens of *Landonia* are known. Adequate resolution of species-level taxonomy awaits the collection of new specimens.

*Landonia* shows features indicative of a relationship to Laurales of primitive to intermediate advancement (especially the families Monimiaceae and Gomortegaceae) but has a combination of venational features not known in any extant family

(Upchurch and Dilcher, 1990). The occurrence of *Landonia* at Quantico represents a stratigraphic range extension for the genus and indicates that it originated no later than late Albian.

#### Genus *Dicotylophyllum* Saporta

##### *Dicotylophyllum ovato-decurrens* new species (Figures 30–35)

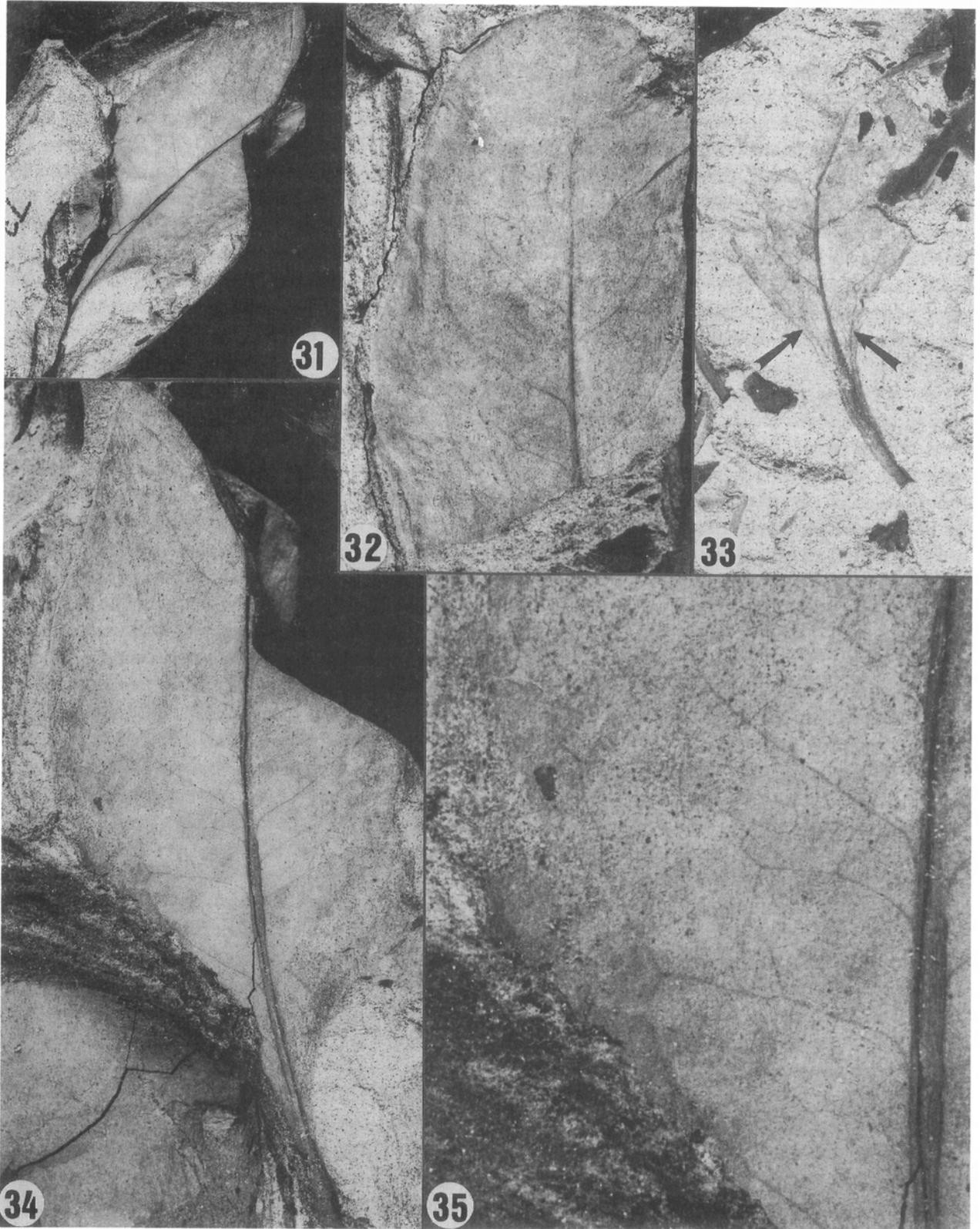
Diagnosis.—Lamina ovate, falling in the microphyll or notophyll size class, L/W 2 to 3; apex acute; base decurrent; margin entire; petiolar region with a well-developed decurrent wing of laminar tissue. Primary venation pinnate; primary vein thinning noticeably between the base and apex. Secondary venation festooned brochidodromous, with each secondary vein forming its own apically arching series of loops; secondary veins thin to moderate, often decurrent on midvein, basalmost pair of secondary veins decurrent into petiolar region. Intersecondary veins, when present, branching to form tertiary veins.

Derivation of specific epithet.—From the botanical terms "ovate" and "decurrent," referring to the ovate laminar shape and the decurrent wing of laminar tissue on the petiolar region.

Description.—Leaf ovate, 9.5 cm long (one leaf measured) by 3.5 to 4 cm wide, L/W approximately 2.5 (one leaf measured); apex acute; base decurrent; margin entire, in one specimen slightly darkened (implying mechanical reinforcement); petiolar region 10 mm long by 1 to 4 mm wide (two measured), with a well-developed wing of laminar tissue. Primary venation pinnate; primary vein moderate, markedly thinning between the base and apex of the leaf. Secondary venation festooned

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Facing page: *Dicotylophyllum ovato-decurrens* new species. Figure 31.—Basal part of lamina. USNM 446014A, x1. Figure 32.—Apical half of lamina showing apically curving secondary veins. USNM 446015, x2. Figure 33.—Basal part of lamina showing petiolar region, midvein, and pairs of secondary veins. Note that the basalmost pair of secondary veins (arrows) is close to the basal margin of the lamina and decurrent into the petiolar region. USNM 446019, x2.5. Figures 34, 35.—Close-up of specimen in Figure 31. USNM 44601A. Figure 34, view of whole lamina showing apical curvature of thin secondary veins and intersecondary veins, x2. Figure 35, close-up of intercostal regions on the lower left side of leaf showing how the intersecondary veins branch to form tertiary veins. The faintly visible tertiary and higher-order venation is suggestive of an irregularly reticulate pattern, x5.



brochidodromous; secondary veins moderate or thin relative to primary vein, at least 7 pairs, ranging from alternate to opposite, 7 to 10 mm apart, often decurrent on primary vein, forming predominantly moderate to broad acute angles with the primary vein except in the basalmost part of the leaf, where they form a lower angle, tending to be curved for most of their length, especially in the apical half of the lamina; each secondary vein appearing to form its own apically arching series of brochidodromous loops, but this feature difficult to discern because of poor preservation; intercostal regions exmedially elongate and apically curved. Possible basilaminar secondary veins present in one specimen. Intersecondary veins present, 0 to 1 per intercostal region, often decurrent on midvein, branching to form tertiary veins. Tertiary venation poorly preserved in specimens, appearing to be irregularly reticulate; angle of tertiary vein origin appearing to be highly variable. Quaternary venation obscure, possibly forming a reticulum.

Number of specimens examined.—7.

Holotype.—USNM 446014A, B.

Paratypes.—USNM 446013A, B; 446015; 446019.

Discussion.—*Dicotylophyllum ovato-decurrans* comprises a distinct species of early angiosperm leaf. Few species of mid-Cretaceous angiosperms show closely similar foliar architecture, largely because few species combine an entire margin, ovate shape, and moderate L/W ratio with a decurrent wing of laminar tissue on the petiolar region, pinnate venation, decurrent secondary veins, and irregularly reticulate tertiary venation. One of the more similar species of early angiosperms is *Dicotylophyllum angularis* from the Cenomanian Dakota Formation of Nebraska (Upchurch and Dilcher, 1990, p. 40, Pl. 25, figs. 2, 3, text fig. 18). However, *D. angularis* differs from *D. ovato-decurrans* in having a narrower wing of laminar tissue on the petiolar region and in having more widely spaced secondary veins that define intercostal regions of different size and shape.

Among previously described fossil genera, *Dicotylophyllum ovato-decurrans* could be assigned to either *Ficophyllum* or *Proteaephyllum*, given the range of variation circumscribed by the species des-

cribed in Fontaine (1889). However, we prefer to assign our species to the genus *Dicotylophyllum* because the taxonomy of *Ficophyllum* and *Proteaephyllum* is in a state of confusion. For example, the specimen of *Ficophyllum crassinerve* illustrated by Hickey and Doyle (1977, figs. 11, 13) consists of two pieces. One piece was described by Fontaine (1889) as *Ficophyllum crassinerve*, while the other piece was described as *Proteaephyllum ellipticum*. As a second example, the one specimen of *Ficophyllum tenuinerve* illustrated by Wolfe et al. (1975, fig. 46) differs from other specimens assigned to *F. tenuinerve* by Fontaine (1889) in having an auriculate base, a primary vein of several discrete strands, and secondary veins congested at the base of the lamina; these features define the species *Proteaephyllum reniforme*. As a third example, patterns of relationships between *Ficophyllum*, *Proteaephyllum*, extant Magnoliales, and extant Laurales do not reflect the genus and species assignments of individual fossil specimens. Many specimens assigned to *F. crassinerve* and *F. tenuinerve* have a pattern of venation most similar to that of Magnoliales: the secondary veins loop irregularly and enclose exmedially elongate intercostal regions; the tertiary venation is irregularly reticulate, forms zig-zags at points of branching, and tends towards transverse orientation; and the higher order venation forms zig-zags at points of branching and encloses regions that tend towards isodiametric or rectangular. However, other specimens assigned to *F. crassinerve* and *F. tenuinerve*, and specimens assigned to species of *Proteaephyllum* such as *P. ovatum*, have venation that more closely resembles Austrobaileyaceae and other primitive Laurales: the secondary veins are more widely spaced, tend towards curved, and enclose isodiametric regions above the base of the lamina; and the tertiary venation has tendencies towards admedial orientation.

Despite preservation of only three orders of venation, *Dicotylophyllum ovato-decurrans* possesses sufficient features to warrant tentative placement in Laurales. Among extant angiosperms, the combination of simple organization, a decurrent wing of laminar tissue on the petiole, and relatively

low-rank venation is most characteristic of subclass Magnoliidae. Within Magnoliidae, the combination of distinctly ovate foliage with pinnate venation and basilaminar secondary veins appears to be restricted to the order Laurales. Consistent with lauralean affinities for *D. ovato-decurrans* is a pattern of secondary venation similar to that of *Pandemophyllum* (cf. Upchurch and Dilcher, 1990), an extinct genus of Laurales that differs from *D. ovato-decurrans* in having a distinct petiole. More detailed consideration of modern affinities awaits collection of better-preserved specimens.

Order NELUMBONALES  
Genus *Nelumbites* Berry

Emended diagnosis.—Lamina generally orbicular; base peltate, but with the margin of the lamina showing a shallow indentation or flattening below the level of petiole insertion; petiole generally inserted in the basal half of the lamina, rather than centrally; margin entire or crenate. Primary venation actinodromous, consisting of a midvein and several pairs of lateral primary veins, radial in organization; midvein running to leaf apex and giving rise to two or more pairs of secondary veins, otherwise similar to the lateral primary veins; all primary veins predominantly straight, forming a series of festooned brochidodromous loops; innermost series of loops (here termed the intercostal primary loops) radially elongate, tending to be shorter in the basal part of the lamina. Secondary veins arising from midvein, similar to the primary veins in pattern but producing less-elongate intercostal loops. Primary and secondary veins together forming at least one series of excostal loops, veins of excostal loops similar in thickness to their source veins, looping angular. Tertiary venation (where known) reticulate, pattern of organization irregular. Ultimate venation (where known) reticulate; areoles polygonal and of various shapes.

Type species.—*Menispermites virginiensis* Fontaine (designated herein).

Discussion.—The name *Nelumbites* was first proposed by Berry (1911a) for leaves that had been previously referred to *Menispermites* but showed a

close resemblance to extant *Nelumbo*. However, Vakhrameev (1952) first formally diagnosed the genus. Translated from Russian, his diagnosis states, "Leaf generally rounded, rarely oval, with either an entire or wavy margin. Point of petiole attachment in central part of leaf, or, more commonly, somewhat displaced towards its lower margin. Venation radially organized, camptodrome." Our emendation expands upon Vakhrameev's diagnosis and incorporates features of foliar architecture now known to be systematically significant within extant angiosperms.

Although *Nelumbites* was originally proposed as an organ genus for leaves related to extant *Nelumbo*, comparison of mid-Cretaceous *Nelumbites* leaves with those of extant *Nelumbo* indicates that the two genera are distinct. Leaves of extant *Nelumbo* consistently differ from those of mid-Cretaceous *Nelumbites* in seven features: (1) leaf shape is always orbicular, (2) the margin is always entire, (3) the petiole is always positioned in the center of the lamina, (4) the medial primary vein only gives rise to secondary veins immediately beneath the leaf apex, (5) the intercostal primary loops are fairly uniform in size and shape, (6) the tertiary venation is very regular and transversely oriented, and (7) the areolation shows strong tendencies towards hexagonal shape. Most differences in foliar architecture between extant *Nelumbo* and mid-Cretaceous *Nelumbites* could be interpreted as differences in advancement, because *Nelumbites* shows character states closer to those that would occur in a hypothetical common ancestor characterized by a cordate base and low-rank actinodromous venation. However, relationships between *Nelumbites* and extant Nymphaeales/Nelumbonales remain to be investigated in detail.

Berry (1911a) designated no type species for the genus *Nelumbites*, and to our knowledge no subsequent author has designated a type species. When first proposing the genus *Nelumbites*, Berry (1911a) transferred two species from the genus *Menispermites* Lesquereux: *M. virginiensis* Fontaine (1889, p. 321–322, Pl. 161, figs. 1, 2), a taxon originally proposed from two leaves collected at the Brooke locality of lower Subzone II-B age, and *M. tenui-*

*nervis* Fontaine (1889, p. 322, Pl. 172, fig. 8), a taxon originally proposed from a single poorly preserved leaf collected at the Baltimore locality of Zone I age. Peltate angiosperm leaves collected from the Potomac Group after 1889 were automatically assigned to one of these two species, and often incorrectly; as a result, both species have served as repositories for unrelated taxa. Reexamination of the two syntypes assigned to *M. virginensis* by Fontaine (1889), along with subsequently collected specimens showing similar features of foliar architecture, indicates that *M. virginensis* clearly possesses a peltate base and actinodromous primary venation, features that led Berry (1911a) to propose affinities with extant *Nelumbo*. In contrast, reexamination of the holotype for *M. tenuinervis* indicates a poorly preserved leaf with a possibly cordate base and pinnate venation (L. J. Hickey, personal communication, 1979), not a peltate base and actinodromous primary venation as in most specimens assigned to this species after 1889. We propose that *Menispermites virginensis* Fontaine serve as the type species for the genus *Nelumbites* and that *M. tenuinervis* Fontaine be transferred to another genus, perhaps *Dicotylophyllum* or *Phyllites*.

*Nelumbites extenuinervis* new species  
(Figures 36–40, 43)

*Menispermites virginensis* Fontaine (non type) – Ward, 1895, p. 360, Pl. 4, fig. 7 (non fig. 8).

*Menispermites tenuinervis* Fontaine (non type) – Fontaine, in Ward, 1905, pp. 496, 557, Pl. 109, figs. 2, 3.

*Nelumbites tenuinervis* (Fontaine) Berry (non type) – Berry, 1911a, pp. 464, 465, Pl. 87, figs. 1, 2.

*Menispermites virginensis* Fontaine (non type) – Doyle and Hickey, 1976, fig. 14.

*Menispermites "tenuinervis"* Fontaine – Hickey and Doyle, 1977, fig. 28.

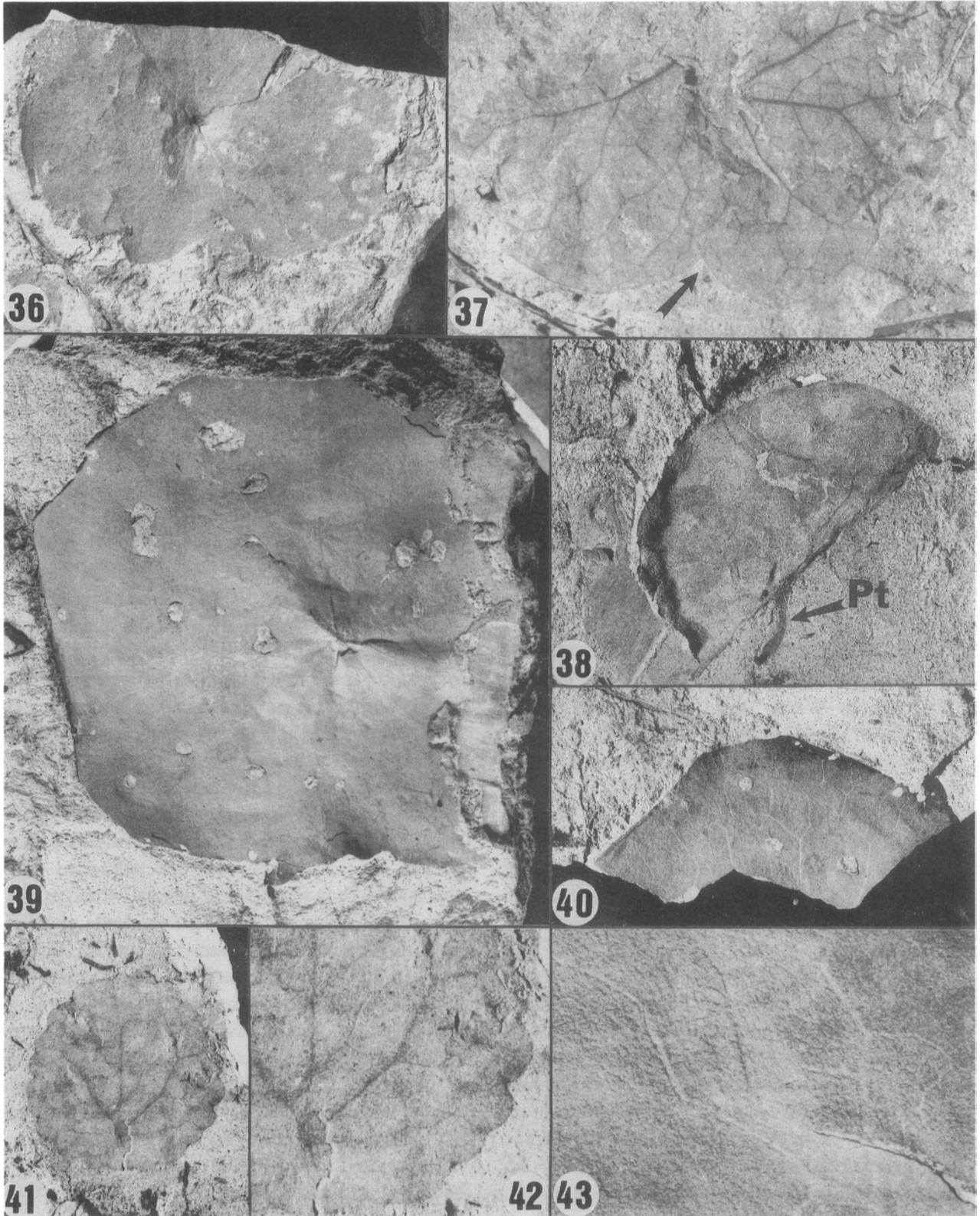
Diagnosis.—Lamina typically falling in the notophyll size class; margin generally entire, rarely crenate. Three complete series of excostal loops present; the innermost series of excostal loops tending toward radially elongate; the middle series of excostal loops tending toward isodiametric; the outermost series of excostal loops often radially compressed (i.e., elongate parallel to the margin), tending to be confluent with the margin.

Description.—Lamina falling in the notophyll, or more rarely mesophyll, size class. Lamina tending toward orbicular, commonly funnel-form, 3.5 to 10 cm in diameter, L/W 0.75 to 1, lamina easily folded during fossilization and producing little relief in the rock; apex rounded; base peltate but typically with an indentation basal to the point of petiole attachment, indentation obtuse-angled, up to 2 cm deep, shape of indentation ranging from sharp to gently rounded; margin usually entire, rarely crenate; petiole inserted in the basal half of lamina, > 2 cm long by 1 to 2 mm wide, oriented at nearly a right angle to lamina.

Primary venation actinodromous, with a medial primary vein and 4 to 5 pairs of lateral primary veins; primary veins typically thin, straight, radially oriented, branching well within the margin to form a series of angular intercostal primary loops; intercostal primary loops radially elongate, L/W of intercostal primary loops greatest in the part of the lamina apical to the point of petiole attachment

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Facing page: Figures 36–40.—*Nelumbites extenuinervis* new species. Figure 36, basal part of lamina showing peltate petiole attachment and radially oriented primary venation. Note how the lamina has a funnellform shape in the region of petiole attachment. FMNH PP43792, x1.25. Figure 37, basal part of lamina showing basal indentation below the point of petiole attachment (arrow), radially oriented primary veins that form several series of angular loops, and reticulate intercostal tertiary venation. This lamina has a non-funnelform shape. FMNH PP43793, x2. Figure 38, folded leaf showing portion of petiole (arrow). USNM 446029, x1.75. Figure 39, large, nearly complete lamina showing funnellform base. USNM 446020B, x1. Figure 40, fragment of counterpart of Figure 39 showing three complete series of excostal loops and margin. USNM 446029A, x1. Figures 41, 42.—*Nelumbites* cf. *N. minimus* Vakhrameev. USNM 446031A. Figure 41, general view of leaf showing crenate margin and actinodromous primary venation, x2. Figure 42, close-up of right side of leaf showing details of primary vein looping and the crenate margin, x4. Figure 43.—*Nelumbites extenuinervis* new species, details of faintly visible higher-order venation and areolation. FMNH PP, x7.5.



and lowest in the part of the lamina basal to the point of petiole attachment.

Secondary venation festooned brochidodromous; secondary veins originating from the medial primary vein, similar in thickness, forming angular loops, intercostal secondary loops less elongate than intercostal primary loops. Primary and secondary venation together forming three complete series of angular excostal loops; innermost series radially elongate; middle series radially elongate to isodiametric; the outer series isodiametric to radially compressed, often confluent with margin.

Tertiary venation reticulate, enclosing regions ranging from isodiametric to somewhat radially elongate; tertiary veins thick relative to source veins, forming predominantly acute to right angles on both sides of the source veins, tending to form zig-zags at points of branching. Quaternary venation poorly differentiated from tertiary venation, similar in pattern. Areolation well developed but often preserving poorly; areoles of medium size, tending towards 4-sided, no freely ending veinlets observed. Marginal venation consisting of brochidodromous loops confluent with the margin.

Number of specimens examined.— > 100.

Holotype.—USNM (Mount Vernon locality; illustrated by Ward, 1895, Pl. 4, fig. 7; and by Fontaine in Ward, 1905, Pl. 109, fig. 2).

Paratypes.—USNM (Mount Vernon locality; illustrated by Fontaine in Ward, 1905, Pl. 109, fig. 3); USNM 446020A, B; 446029; 446031A, B; FMNH PP43792, PP43793.

Derivation of specific epithet.—Latin, *ex* = out or away from, *tenuinervis* = thin-nerved, referring to the segregation of this species from *Menispermites tenuinervis*.

Discussion.—*Nelumbites extenuinervis* is by far the most abundant species at Quantico, comprising at least one-third of all collected remains. It also occurs at the Mount Vernon locality of middle Subzone II-B age in association with *N. virginensis*, the other large-leaved species of *Nelumbites* from the Potomac Group. Despite similarities in leaf size and general features of primary venation, *N. extenuinervis* is readily distinguished from *N. virginensis* in at least two features: (1) the margin is

generally entire in *N. extenuinervis*, rather than strongly crenate as in *N. virginensis*, and (2) three complete orders of excostal loops are present in *N. extenuinervis*, rather than only one as in *N. virginensis*. In extant angiosperm species, these two features together do not show the range of variation present in large-leaved *Nelumbites* from the Potomac Group. This and the absence of known intermediates indicate the presence of two distinct species.

The features of foliar architecture preserved in *Nelumbites extenuinervis* are consistent with postulated affinities to extant Nelumbonaceae and indicate similar leaf physiognomy (see subsequent paragraphs). Particular features, which in combination are restricted to the orders Nymphaeales and Nelumbonales and the genus *Nymphoides* (subclass Asteridae, family Menyanthaceae), are: (1) an orbicular shape, (2) actinodromous primary venation with strongly radial organization, (3) branching of the lateral primary veins and secondary veins well within the margin to form a series of angular brochidodromous loops, (4) the formation of several series of excostal loops well within the laminar margin, (5) reticulate tertiary venation, (6) looped marginal venation, and (7) well-developed areolation. Within this group of taxa, the occurrence of a peltate, rather than deeply cordate, leaf base is restricted to the floating and emersed leaves of Nelumbonaceae and Cabombaceae (here taken to include the genera *Brasenia* and *Cabomba*). Within this group of taxa, *Nelumbites extenuinervis* does not possess any of the obvious specializations that characterize individual extant genera, which makes systematic placement solely on the basis of foliar features difficult. Such specializations for extant genera include an oval, rather than orbicular, leaf shape (*Brasenia* and some species of *Cabomba*); possession of finely divided submersed leaves (*Cabomba*); and hexagonal areolation (*Nelumbo*) (Sculthorpe, 1967; Hickey, 1977). However, general features of foliar physiognomy are consistent with affinities to extant *Nelumbo*, as is the structure of associated reproductive remains, which are described in detail below.

Physiognomic analysis of *Nelumbites extenui-*

*nervis* foliage from Quantico indicates that this species probably had a growth habit similar to that of extant *Nelumbo*, a conclusion also reached by Doyle and Hickey (1976) and Hickey and Doyle (1977). Three lines of evidence support this conclusion. First, the leaf lamina shows strong tendencies toward orbicular shape, the point of petiole attachment is displaced towards the center of the leaf, and the petiole attaches to the blade at a high angle. Within extant angiosperms, this combination of features occurs in herbaceous angiosperms where essentially the petiole is held upright and the lamina is horizontal. Extant plants with this morphology include aquatic taxa with floating leaves, such as *Brasenia* and *Cabomba* (subclass Magnoliidae, orders Nymphaeales), *Nelumbo* (subclass Magnoliidae or Ranunculidae, order Nelumbonales), and *Nymphoides* (subclass Asteridae, order Solanales); and terrestrial herbs, such as *Podophyllum* (subclass Ranunculidae, order Berberidales) and *Hydrocotyle* and *Tropaeolum* (subclass Rosidae, orders Apiales and Geraniales). From a theoretical standpoint, orbicular peltate leaves are best adapted to situations of low wind or water-current activity, which produce little directional stress on the lamina and permit laminar support tissue to be positioned in the most economical manner (Givnish, 1976, 1979). Wind tunnel experiments also indicate that leaves with a circular shape convect heat more poorly at intermediate wind velocities than leaves with more lobed shapes (Vogel, 1970). Together these data indicate that plants with orbicular leaves should preferentially inhabit terrestrial environments with low wind stress, such as the forest understory, and aquatic habitats with little water-current activity, where abundant water supply readily permits evaporative cooling of the lamina.

A second line of evidence on growth habit in *Nelumbites extenuinervis* is provided by features of primary and secondary venation, which occur in a combination typical of floating-leaved aquatics but not terrestrial herbs. The primary venation shows strong radial organization, the primary and secondary veins bifurcate well within the margin, several series of excostal loops are developed within the margin (intramarginal loops of Hickey and Doyle,

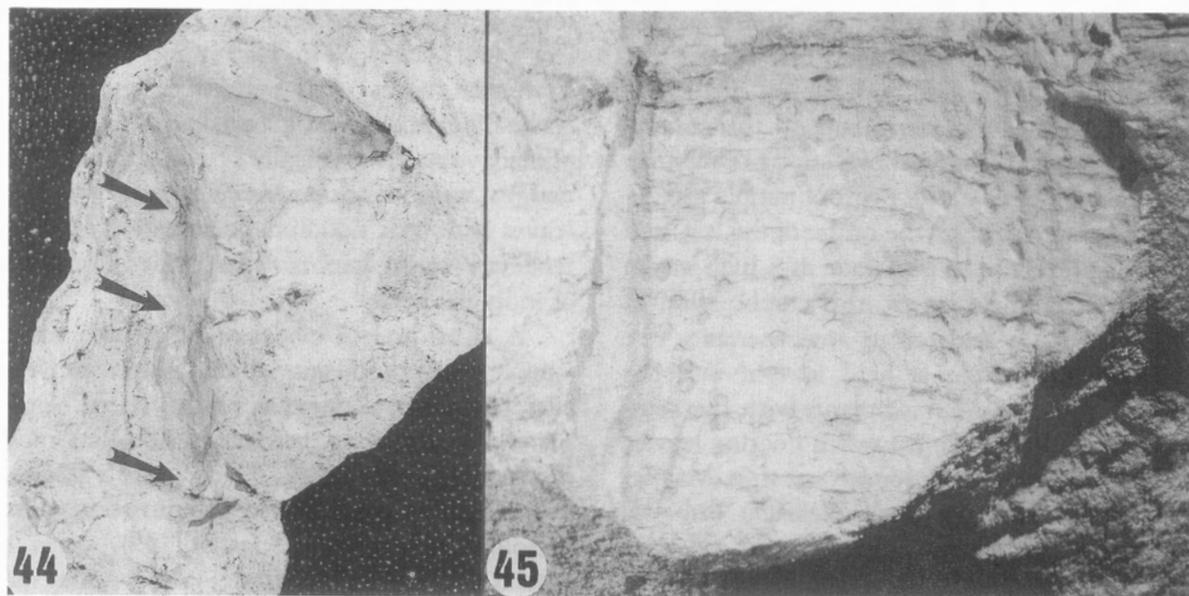
1977), and the lamina is frequently divided into a series of cells by the venation (Sculthorpe, 1967; Doyle and Hickey, 1976; Hickey and Doyle, 1977). Terrestrial herbs with peltate or pseudopeltate leaves differ from floating leaved aquatics in having primary veins that typically run directly to the leaf margin, weak development of excostal looping in leaves with brochidodromous venation, and little tendency for the lamina to be divided into a series of individual cells.

A third line of evidence on growth habit is laminar shape in the vertical dimension. In *Nelumbites extenuinervis*, laminar shape in the vertical plane shows strong tendencies for dimorphism (Hickey and Doyle, 1977): one leaf type has a funnel-form laminar shape adjacent to the point of petiole attachment (Figures 36, 39), while the second leaf type lacks a funnel-form laminar shape and appears to be flat (Figure 37). This dimorphism occurs in extant *Nelumbo*, which has both emergent and floating leaves. The lamina of emergent leaves typically is funnel-form in shape, while the lamina of floating leaves typically is flat.

Evidence from taphonomy is consistent with evidence from foliar physiognomy for growth habit in *Nelumbites extenuinervis*. In the leaf-bearing beds at Quantico, the abundance and preservation of *N. extenuinervis* shows the patchy pattern of lateral variation expected of a plant with a *Nelumbo*-like growth habit. In the Quantico leaf beds, foliage of *N. extenuinervis* typically preserves either as isolated leaves that are subordinate in abundance to the other elements of the megafloora or as clusters of leaves that are the most abundant element. Such lateral variation implies that isolated leaves of *N. extenuinervis* were transported from the site of growth prior to fossilization, while clusters of leaves represent remains of plants that were fossilized at or very near the site of growth.

#### Associated Stems (Figures 44, 45)

Abundant impressions of plant axes occur in association with leaf impressions of *Nelumbites extenuinervis*. Most appear to represent woody plants, based on their large diameter and tendencies



Figures 44, 45.—Probable herbaceous stems associated with *Nelumbites*. Figure 44, stem type showing numerous longitudinal folds and irregular changes in diameter (arrows). USNM 446034, x1. Figure 45, stem type showing numerous small rounded depressions on surface, interpreted as probable attachment scars of roots. FMNH PP43814, x3.

to produce strong relief in the rock. (These stems are poorly represented in museum collections, probably because they are discarded on the outcrop.) Two types of associated axes show evidence for probable herbaceous habit and are large enough to have borne the leaves of *N. extenuinervis*.

The more common type (Figure 44) is approximately 1 cm wide and shows no evidence of root attachments. These axes produce little relief on the rock surface, which indicates little or no woody tissue. In addition, most axes of this type preserve numerous longitudinal folds and show irregular changes in diameter (Figure 44, arrows). This implies that the stem lost much of its rigidity before or shortly after deposition and underwent shrinkage and distortion during compaction and dewatering of the clays. Although extensive decay of the stem could allow such marked shrinkage and distortion to occur, most other preserved stem types show little evidence for extensive decay. Instead, high

volumes of aerenchyma tissue provide the most straightforward explanation for this shrinkage and distortion, because the stem would lose most of its rigidity and ability to resist distortion immediately after loss of turgor in the aerenchyma cells.

The less-common type of herbaceous axis (Figure 45) is wider and has numerous dark round regions that may represent the attachment scars of roots. This type of axis (probably a rhizome) also produces little relief on the rock surface but differs from the first type in showing little or no folding. One specimen shows an abundance of probable root-attachment scars on both the part and counterpart, which indicates that the axis bore roots on all sides and, therefore, was subterranean in life.

Whether or not the above two stem types belong to the same plant is uncertain. If they do represent the same plant, then they imply stem morphology similar to that of extant *Brasenia* and *Nymphoides*, where the rhizome produces elongate

branches that grow above the substrate and ascend through the water column (cf. Sculthorpe, 1967). In extant *Nelumbo*, all stems are strictly subterranean rhizomes. Comparison with the growth habit of other herbaceous Magnoliidae and Ranunculidae implies that the production of ascending branches is probably primitive relative to the production of strictly subterranean rhizomes.

#### Associated Reproductive Remains (Figures 46–53)

The inferred structural and ecological similarities between *Nelumbites extenuinervis* and extant *Nelumbo* are reinforced by the occurrence at Quantico of isolated reproductive organs similar to those of *Nelumbo* (Figures 46–53). These reproductive structures consist of laminar units with similarities in venation, shape, and preservational features to tepals (Figures 46–48, 50) and axial structures with similarities to *Nelumbo* floral receptacles at fruiting stage (Figures 49, 51–53).

Isolated tepal-like structures are a common component of the Quantico megaf flora (Figures 46–48, 50). They vary considerably in size and shape, which is consistent with their interpretation as tepals from a large flower with numerous floral parts. These structures can be related to each another readily by intergradation in size and shape, by similarities in venation, and by possession of numerous dark spots that tend to occur in longitudinal rows on the laminar surface. These dark spots are < 1 mm in diameter, have a somewhat irregular shape that ranges from isodiametric to elongate, and possess margins that are irregularly angular, rather than smooth. Based on this irregularity we interpret these dark spots as the remnants of sclerenchyma clusters, rather than the remnants of resin bodies, which commonly occur in mid-Cretaceous angiosperm foliage with affinities to Magnoliidae. Extant *Nelumbo* has no oil cells, and its tepals contain nests of sclerenchyma.

The tepals range in shape from broadly deltoid and scale-like (Figure 46) to elongate and obovate (Figure 48) and measure 1 to > 4 cm long by 0.8 to 2.5 cm wide. L/W ranges from 1.2 to > 3, with the

shortest tepals typically showing the lowest L/W. The apex of the lamina ranges from acute to rounded, with a sharp tip (Figures 46, 48), while the base of the lamina gradually narrows to a broad flat area, which we interpret as the zone of attachment to the parent axis (Figures 46, 47). No evidence exists for a sheathing leaf base, which would be expected if these laminar structures represented the photosynthetic foliage of monocotyledons. The laminar margin is entire, and most remains have a robust appearance, which indicates that they probably were thick-textured in life.

A series of longitudinal parallel veins originates from the base of each tepal and runs towards the apex. The exact number of veins per tepal is difficult to determine because of poor preservation, but as many as 11 longitudinal parallel veins have been observed. In the narrower tepals, the longitudinal veins are essentially parallel or show only slight tendencies to change spacing (Figures 46–48). In the largest tepals, however, the longitudinal veins diverge above the base of the lamina. In the largest tepal examined, the medial longitudinal vein forms a distinct midvein that gives rise to lateral veins (Figure 50). Higher-order cross-veins originate at mostly acute (rarely right) angles from the longitudinal veins. In the largest tepals, the cross-veins form a reticulum (Figure 50). In smaller tepals, the cross-veins are unclear because of poor preservation. In at least one tepal, some of the longitudinal parallel veins gradually thin and merge with the network of cross-veins (Figure 50). Because of poor preservation, the organization of the venation at the apex of the lamina is poorly understood. The venation in these fossil tepals is similar to that in tepals of extant *Nelumbo* but less complex, perhaps due to their smaller size.

Additional reproductive structures comprise three impressions that preserve features suggestive of a floral axis (Figures 49, 51–53). No specimen is complete, but two are known from both part and counterpart (Figures 49, 51), which permits partial reconstruction of three-dimensional shape. These two specimens measure 1 and 2 cm long; they obviously represent structures that were thick in life because significant space exists between the surface

of the part and counterpart from which organic matter has been removed by decay. The surface of each specimen is covered with a number of closely spaced protuberances, which clearly represent cavities in the surface of the original plant organ that are now filled with sediment. Near the edge of one specimen (Figures 49, 51), where they are oriented at an angle to bedding, the protuberances have been distorted by compaction of the sediment but are otherwise circular in surface view and occur on all surfaces of parts and counterparts.

Each protuberance measures 2 to 3 mm in diameter by about 1 mm deep and has a roughly cylindrical shape. At the apex of each protuberance (i.e., the base of each cavity) is a distinct circular ridge and groove (Figures 52, 53) and a centrally positioned pit (Figures 49, 51).

Detailed interpretation of the structure of the floral receptacle is precluded by the absence of more complete specimens preserving anatomical details or showing the attachment scars of floral organs. However, the structures preserved may be readily interpreted in terms of the characteristic morphology of fruiting receptacles of *Nelumbo*. Under such an interpretation, the protuberances represent sediment-filled cavities homologous to the cavities that occur on the flat distal portion of a *Nelumbo* receptacle. In *Nelumbo*, each cavity leads

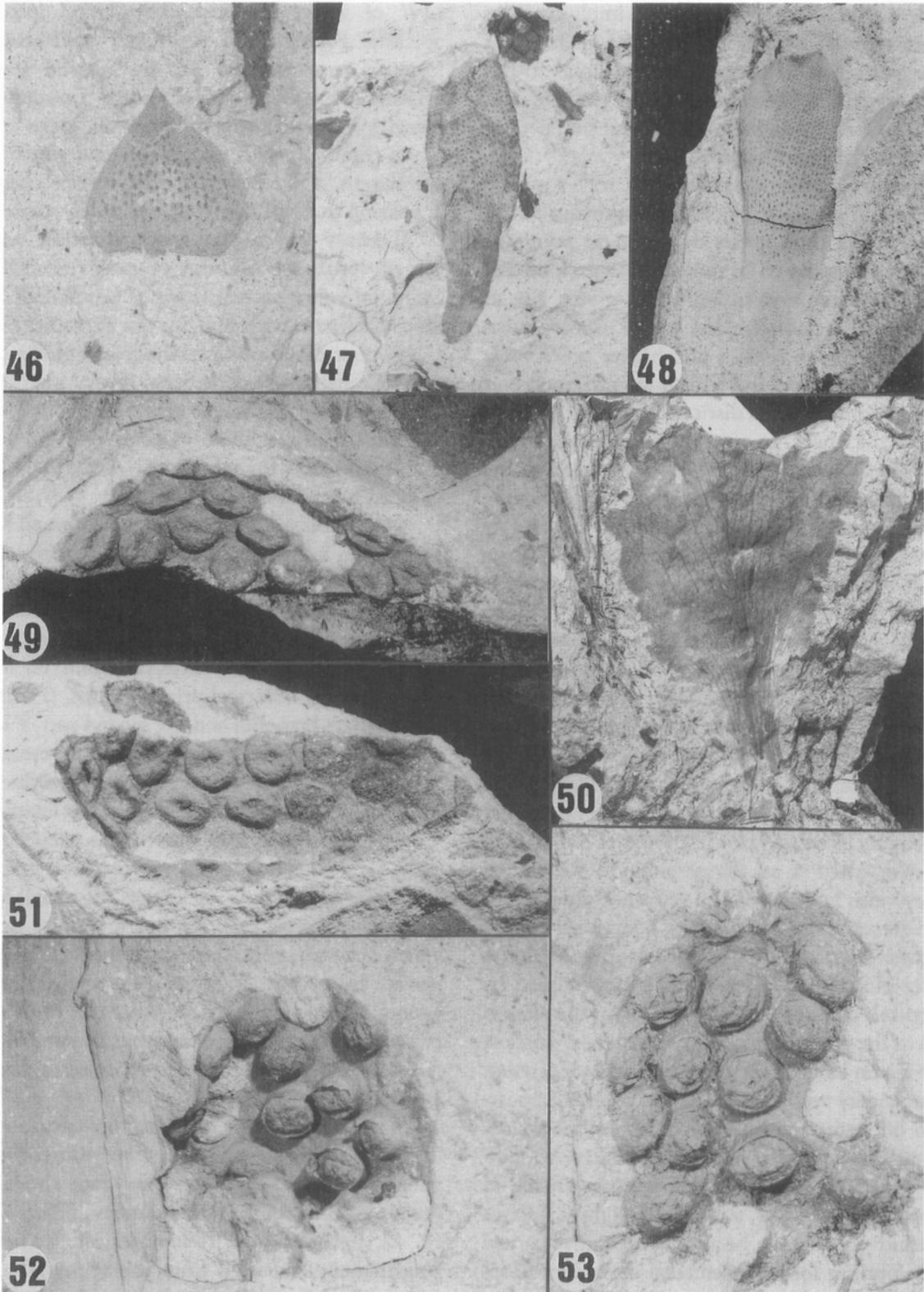
to the apex of a single achene embedded in the receptacle. The ridge and groove at the apex of each protrusion in the fossil may have been produced by the separation that occurs in *Nelumbo* between the receptacle and the apex of each embedded fruit. The central depression at the tip of each protrusion would be a cavity produced by the persistent style base at the apex of each achene. The only significant difference between features preserved in the fossils and features of *Nelumbo* is the distribution of protrusions (cavities) over the surface of the receptacle. In *Nelumbo* the receptacle is obconic, and cavities and achenes occur only on the flat distal surface. In the fossil material the receptacle was not strongly obconical, and cavities (presumably corresponding to achenes) were not confined to a particular region of the surface. Comparison with the receptacles of other Magnoliidae and Ranunculidae implies that the condition seen in the fossil material is more primitive than the specialized condition of extant *Nelumbo*.

*Nelumbites* cf. *N. minimus* Vakhrameev  
(Figures 41, 42)

Description of Quantico materials.—Lamina falling in the microphyll size class. Lamina orbicular, 1.7 cm in diameter, L/W 1, surface of lamina

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Facing page: Figures 46–48, 50.—Tepal-like remains associated with *Nelumbites*. Figure 46, small, short specimen showing broad base, acute apex with sharp tip, and numerous dark spots on lamina. FMNH PP, x3. Figure 47, elongate specimen showing probable elliptic to obovate shape and dark spots on lamina. Note portion of floral receptacle at the top of the block. FMNH PP43798, x1. Figure 48, partially inrolled specimen showing longitudinal parallel veins (light regions) and dark spots on lamina. USNM 446035, x1. Figure 50, large tepal showing numerous longitudinal parallel veins at base, lateral veins that diverge at narrow acute angles, and higher-order cross-veins. FMNH PP43795', x1.5. Figures 49, 51–53.—Probable floral receptacles with similarities to those of extant *Nelumbo*. Figures 49, 51, part and counterpart showing numerous protrusions, each with a central pit. Note that the protrusions on the two surfaces show no one-to-one correspondence, and that many protrusions along the unbroken edges are preserved in oblique or side views. This indicates that the protrusions represent infilled cavities that were distributed over most surfaces of the receptacle. Note the single small depression at the center of each protrusion. Each depression is interpreted as a raised region, most probably a beak on a fruit. Figure 49, USNM 446044A, x3. Figure 51, USNM 446044B, x3. Figures 52, 53, part and counterpart showing numerous surface protrusions. Note the absence of a one-to-one correspondence of protrusions on part and counterpart. Also note the collar on each protrusion. Figure 52, USNM 446045A, x4. Figure 53, USNM 446045B, x6.



slightly convoluted by sediment, implying thin laminar texture; apex rounded; base peltate but with a flattening of laminar outline basal to the point of petiole attachment; margin crenate, crenations 2 to 3 mm long by <1 mm tall; petiole inserted in the basal half of lamina.

Primary venation actinodromous, with a medial primary vein and 3 pairs of lateral primary veins, primary veins thin, often deflected at points of branching, tending to be radially oriented; medial primary vein running to leaf apex, giving rise to secondary veins on both sides; lateral primary veins only giving rise to tertiary and higher order veins on both sides, branching within margin, each pair of lateral primary veins distinct from the others in terms of thickness, course, and branching; innermost pair of lateral primary veins as thick as the midvein, with a slight tendency to arch apically, connecting with the basalmost pair of secondary veins to form loops, producing thin external branches at moderate to broad acute angles, external branches oriented at approximately 90° to the midvein; second pair of lateral primary veins much thinner than innermost pair of lateral primary veins, similar in thickness to the external branches of the innermost pair of lateral primary veins, straight until forming loops, not producing external branches, oriented at approximately 90° to the medial primary vein; third pair of lateral primary veins similar to second pair in thickness and behavior but oriented at an obtuse angle to the medial primary vein; lateral primary veins and their basalmost external branches forming a series of angular intercostal primary loops, intercostal primary loops radially elongate, L/W 2 to 3, area occupied by intercostal primary loops greatest in the region apical to the point of petiole insertion and smallest in the region basal to the point of petiole insertion.

Secondary venation difficult to observe, appearing to be festooned brochidodromous; secondary veins arising from midvein, thick relative to midvein, 3 pairs, opposite to subopposite, arising at moderate acute angles, straight to slightly sinuous near midvein, often becoming apically curved before forming loops, intercostal secondary loops ranging from isodiametric to exmedially elongate,

L/W of intercostal secondary loops decreasing apically. Primary and secondary veins together forming one complete and one partial series of excostal loops, excostal loops often confluent with margin, exmedial side of excostal loops curved when confluent with margin, angular when inside of margin. One intersecondary vein observed, appearing to branch into higher order veins.

Tertiary and higher order venation not observed, probably because of poor preservation. Marginal venation consisting of brochidodromous loops confluent with margin, the exmedial sides of these loops conforming to the shape of the crenations. Crenations nonglandular, medial vein absent.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446031A.

Other identified specimens.—USNM 446031B (counterpart of 446031A).

Discussion.—The one specimen of small-leaved *Nelumbites* known from Quantico is easily distinguished from *N. extenuinervis*, the larger-leaved and more abundant species, on the basis of at least four size-independent features. These features include: (1) production of thin external branches by the innermost pair of lateral primary veins, (2) orientation of these branches and the second pair of lateral primary veins at approximately 90° to the medial primary vein, (3) significant differences in thickness between the innermost pair of lateral primary veins and the other two pairs, and (4) the occurrence of only one complete series of excostal loops. In addition, the single specimen of small-leaved *Nelumbites* from Quantico has a crenate margin, which occurs in only a few specimens of *N. extenuinervis*. In extant angiosperms these differences generally distinguish species; this and the absence of intermediate forms indicate that the small-leaved *Nelumbites* represents a distinct species from *N. extenuinervis*.

The small-leaved species of *Nelumbites* from Quantico shows strong similarities with *Nelumbites minimus* Vakhrameev, reported from the middle Albian of Kazakhstan (Vakhrameev, 1952, p. 183, Pl. 12, figs. 5–8) and *Nelumbites* aff. *N. minimus* Vakhrameev, reported from the upper Albian of Siberia (Samylina, 1968, p. 208, Pl. 1, figs. 14, 15;

text-figs. D–E). Both taxa have small ( $\leq 20$  mm in diameter) peltate leaves characterized by orbicular shape, somewhat crenate margins, and actinodromous primary venation that typically branches within the margin; they are distinguished from each other by the number of lateral primary veins and (judging from the published illustrations) the degree of radial organization to the primary venation. Based on the illustrations available, the Quantico specimen is more similar to *N. minimus* in having only 3 pairs of lateral primary veins, a strong tendency for apical curvature in both the innermost pair of lateral primary veins and the secondary veins, and external branches of lateral primary veins that are oriented at approximately  $90^\circ$  to the medial primary vein. However, the Quantico leaf differs from illustrated specimens of *N. minimus* in showing a marked distinction between the thickness of the innermost pair of lateral primary veins and the thickness of the other pairs, and a marked distinction between the thickness of the innermost pair of lateral primary veins and the thickness of its external branches. Because of these differences between the Quantico and Kazakhstan materials, affinities to *N. minimus* are designated by “cf.”

Little direct evidence on growth habit is available for *Nelumbites* cf. *N. minimus* from Quantico. However, published illustrations of *N. aff. N. minimus* from Siberia show preserved clusters of leaves, some of which are attached to small-diameter stems by flexuous petioles. This indicates a probable herbaceous growth habit for *N. cf. N. minimus*, similar to that inferred for *N. extenuinervis*.

aff. Subclass ROSIDAE and HAMAMELIDIDAE  
Genus *Sapindopsis* Fontaine

Pinnatifid and pinnately compound foliage forms a low-abundance element in the Quantico megafauna. Recent studies of Potomac Group angiosperm foliage (e.g., Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch, 1984; Crane et al., 1993) have referred such leaves to *Sapindopsis*, a taxon proposed by Fontaine (1889, p. 296) for foliage with general affinities to extant Sapindaceae. Leaves referred to *Sapindopsis* in recent

studies of Potomac Group angiosperms all show a consistent suite of features that includes: (1) deeply pinnatifid to pinnately compound organization, (2) tendencies in some species for a bilobed to trilobed lamina at the leaf apex, (3) at least 5 lobes or laminar segments per leaf, (4) thin secondary veins that tend to have a zig-zag course and festooned brochidodromous organization, and (5) irregularly reticulate tertiary venation. Where preserved, stomatal complexes on an individual leaf range from laterocytic and paracytic to weakly cyclocytic, and epidermal secretory structures have a highly variable yet distinctive pattern of organization with respect to shape, surface sculpture, and positioning relative to underlying cells (Upchurch, 1979, 1984). In extant angiosperms, these features typically segregate genera, families, and higher taxa, which indicates that the Potomac Group forms all may be more closely related to one another than to coeval taxa with different patterns of foliar organization.

Fontaine (1889) designated no type species when naming *Sapindopsis*. This is unfortunate, because more recent analyses of foliar architecture indicate that the species assigned by Fontaine (1889) to *Sapindopsis* are strongly heterogeneous in terms of foliar architecture and may be related to at least two different subclasses on the basis of venational features alone (Wolfe et al., 1975; Hickey and Doyle, 1977). We, therefore, base our assignment of deeply pinnatifid and pinnately compound leaves to *Sapindopsis* on our interpretation of Fontaine's diagnosis, which appears to indicate a deeply pinnatifid to pinnately compound leaf and appears to exclude leaves with simple organization. Our interpretation agrees with that of Dilcher and Basson (1990), who designate *Sapindopsis magnifolia* as the type species of the genus.

Pinnatifid to pinnately compound organization is present in most species referred to *Sapindopsis* by Fontaine, Berry, and subsequent workers. These species include *S. magnifolia* Fontaine, *S. variabilis* Fontaine, *S. brevifolia* Fontaine, *S. belvederensis* Berry, and undescribed species that were illustrated by Hickey and Doyle (1977). Pinnatifid to pinnately compound organization cannot be demonstrated for *S. cordata* and *S. elliptica*, the first two of

eight species described by Fontaine (1889) under the name *Sapindopsis* and excluded from the genus by Berry (1911a) and Dilcher and Basson (1990). Both of these species appear to be simple unlobed leaves, rather than leaflets, because they show no attachment to a rachis and no venational asymmetry that would indicate derivation from a compound leaf. This absence of evidence for leaflet or lobe homology is reinforced by the Zone I age for *S. cordata* and *S. elliptica*, which is older than the Subzone II-B or younger age documented for pinnatifid and pinnately compound species of *Sapindopsis*. In addition, inferred affinities of *S. cordata* and *S. elliptica* are with extant Magnoliidae (Wolfe et al., 1975), rather than with extant Rosidae or Hamamelididae, as is the case for pinnatifid and pinnately paracompound species of *Sapindopsis* (Hickey and Wolfe, 1975; Hickey and Doyle, 1977; Crane et al., 1993).

Although the genus *Sapindopsis* was placed within extant Sapindaceae by Fontaine (1889) and related to the genus *Sapindus*, detailed analysis of foliar architecture and cuticular anatomy indicates that *Sapindopsis* does not possess a suite of features that circumscribes extant Sapindaceae. Particularly important is the fact that extant Sapindaceae show a distinct pinnately compound organization in which the leaflets form a visible joint where they connect with the rachis. In addition, leaves with a winged rachis have a marked constriction where the leaflets attach to the rachis. This contrasts with the morphology of the type species of *Sapindopsis*, other Potomac Group species of *Sapindopsis*, and *S. anhouryi* from the Cenomanian of Lebanon. In these fossil species the individual lobes or leaflets do not form a joint where they attach to the rachis, and species with a winged rachis show no constriction at points of lobe divergence (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Dilcher and Basson, 1990). Other points of difference between extant Sapindaceae and Potomac Group *Sapindopsis* include: (1) the presence in extant Sapindaceae of more regular secondary and tertiary venation, (2) the presence in extant Sapindaceae of stomata where the guard cells are overthrust by weakly laterocytic subsidiary cells that show a fairly

uniform degree of specialization, and (3) the presence in extant Sapindaceae of trichome bases and trichomes that are far more regular in their organization than the trichome bases and trichomes of *Sapindopsis*. There is no evidence that fossil *Sapindopsis* is more closely related to extant Sapindaceae than to numerous other groups of Rosidae. Fossil reproductive structures associated with *Sapindopsis* from the Potomac Group and elsewhere are most similar to the reproductive structures of extant *Platanus* (Crane, 1989; Friis et al., 1989; Crane et al., 1993), and many features of foliar architecture and cuticular anatomy in fossil *Sapindopsis* show states that could be ancestral to those in extant Rosidae and Platanaceae (Hickey and Wolfe, 1975; Hickey and Doyle, 1977; Upchurch, 1984; Upchurch and Dilcher, 1990).

*Sapindopsis* cf. *S. magnifolia/variabilis* Fontaine  
(Figures 54–57)

Synonymy for Potomac Group only:

*Sapindopsis magnifolia* Fontaine – Fontaine, 1889, p. 297, Pl. 151, figs. 2, 3; Pl. 152, figs. 2, 3; Pl. 153, fig. 2; Pl. 154, figs. 1, 5; Pl. 155, fig. 6.

*Sapindopsis variabilis* Fontaine – Fontaine, 1889, p. 298, Pl. 151, fig. 1; Pl. 152, figs. 1, 4; Pl. 153, fig. 3; Pl. 154, figs. 2–4.

*Sapindopsis variabilis* Fontaine – Berry, 1911a, p. 469, Pl. 83; Pl. 84; Pl. 85.

*Sapindopsis magnifolia* Fontaine – Berry, 1911a, p. 471, Pl. 88 (non Pl. 86, figs. 1, 2; Pl. 87, fig. 1).

(Synonymy incomplete.)

Description of Quantico remains.—Terminal portion of deeply pinnatifid leaf and isolated lobes preserved. Leaf with up to 7 or more lobes, whole leaf > 6 cm long by > 5 cm wide (estimated width), terminal portion of lamina deeply and irregularly trilobed, becoming decurrent basally; rachis with a narrow wing of laminar tissue. Lateral lobes > 5 cm long by about 1.2 cm wide, L/W > 3; apex of lobes not preserved; base of lobes narrowing before attaching to rachis, width of attachment narrowing basally, lobe base typically asymmetric, forming a narrow acute angle with the midvein on the side closer to the leaf apex and a broad acute to obtuse angle on the side closer to the leaf base; margin

entire. Primary venation of lobes pinnate; primary vein stout. Secondary and higher-order venation preserved only in one fragment assigned to this species. Secondary venation apparently festooned brochidodromous, pattern of looping only preserved for one intercostal region; secondary veins thin relative to midvein, subopposite, sometimes slightly decurrent on midvein, diverging at moderate acute angles, somewhat zig-zag in course, showing little or no apical curvature until forming loops. Intersecondary veins present, 0 to 1 per intercostal region, branching to form tertiary veins. Intercostal tertiary venation irregularly reticulate; tertiary veins thick relative to secondary veins, originating at acute to obtuse angles on the admedial side of the secondary veins and predominantly acute angles on the exmedial side, somewhat zig-zag in course, enclosing regions of variable size and shape. Quaternary venation poorly differentiated from tertiary venation, similar in pattern.

Number of specimens examined.—3.

Illustrated specimens.—USNM 446023A, B; FMNH PP43816.

Other identified specimens.—FMNH PP43817.

Discussion.—These leaves are similar in preserved features to leaves classified as *Sapindopsis magnifolia* and *S. variabilis*. Features indicative of such an assignment include an entire margin, pinnatifid organization, a wing of laminar tissue along the rachis, elongate lobe shape, and details of the secondary, tertiary, and quaternary venation. The terminal region of one Quantico leaf has trilobed organization; this combined with the small size of the lobes is most characteristic of syntypes assigned by Fontaine (1889) to *Sapindopsis variabilis*, rather than *S. magnifolia*. However, we cannot find any additional character that clearly distinguishes the type specimens of *S. variabilis* and *S. magnifolia*, which implies that the two species recognized by Fontaine (1889) may represent a single, morphologically variable entity. Pending comprehensive systematic revision of the genus *Sapindopsis*, we designate our remains *Sapindopsis* cf. *S. magnifolia/variabilis*.

A noticeable feature of *Sapindopsis* cf. *S. magnifolia/variabilis* from Quantico is the strongly deve-

loped asymmetry of lobe bases, which is absent from *Sapindopsis variabilis* and *S. magnifolia* leaves from the older Brooke locality. This strong asymmetry is presumably derived within pinnatifid *Sapindopsis*, based on its younger stratigraphic occurrence and its occurrence in species of *Sapindopsis* that have pinnately compound organization (Hickey and Doyle, 1977, figs. 45, 47; Upchurch, 1984, fig. 29). The occurrence in *S. cf. S. magnifolia/variabilis* from Quantico of strong asymmetry at the base of the lateral lobes implies that the strong asymmetry found at the base of lateral "leaflets" is primitive within pinnately compound *Sapindopsis*, rather than derived.

Pinnatifid foliage of *Sapindopsis* generally occurs at localities of lower to middle Subzone II-B age (e.g., Bank near Brooke), where it can dominate the assemblage, but is generally absent from localities of upper Subzone II-B age (Hickey and Doyle, 1977). Pinnatifid *Sapindopsis* at Quantico constitutes one of its youngest well-documented occurrences in the Potomac Group.

*Sapindopsis minutifolia* new species  
(Figures 58, 59)

New species of *Sapindopsis* from Quantico, Va. — Hickey and Doyle, 1977, fig. 47.

Diagnosis.—Leaf pinnately compound. Leaflets small, falling in the nannophyll size class; lateral leaflets sessile, with acute asymmetric bases; margin serrate; teeth concave to straight on the apical side and straight to convex on the basal side; sinuses between teeth forming an angle of about 90°, rounded rather than sharp. Secondary venation semicraspedodromous, weak, irregular; secondary veins thin, forming zig-zags and angular loops.

Description.—Pinnately compound leaf with at least 5 leaflets preserved. Leaf >2.8 cm long by about 2.5 cm wide, distance between the terminal leaflet and the adjacent pair of lateral leaflets less than the distance between the two pairs of lateral leaflets; rachis without a distinct wing of laminar tissue. Terminal leaflet with a symmetric base, contracted at rachis, rachis prolonged 1 to 2 mm beyond lateral leaflets; lateral leaflets sessile, each

with an asymmetric base that narrows at its attachment to the rachis; basal pair of lateral leaflets incompletely preserved; terminal and lateral leaflets otherwise similar in size and shape. Leaflets approximately 15 mm long by 3–4 mm wide, exact length difficult to determine because the apex of most is missing, estimated  $L/W$  3.5 to 4; apex of one leaflet almost complete, probably acute; base of leaflets acute to decurrent, without a joint at the point of attachment to the rachis; margin serrate, serrations straight to concave on the apical side and convex to straight on the basal side, strongly asymmetric, minute, 1 to 2 mm long by <1 mm tall. Primary venation of leaflets pinnate; primary vein massive. Secondary venation of leaflets poorly preserved, appearing to be semicraspedodromous; secondary veins very thin relative to primary vein, opposite, > 10 pairs (estimated), irregularly spaced, diverging at moderate acute angles, often sinuous to zig-zag in course, showing little apical curvature until approaching margin, each secondary vein typically branching near margin to form two veins, with the admedial branch connecting with the superadjacent secondary vein to form a brochidodromous loop and the exmedial branch terminating at the apex of a tooth; intercostal regions of variable size and shape, looping angular. Tertiary venation poorly preserved, appearing to be irregularly reticulate; tertiary veins appearing to originate at acute to obtuse angles. Teeth with sharp tips, showing no

clear evidence for glandularity, perhaps lost in preservation, placement of medial vein appearing to be symmetric, no accessory veins observed.

Number of specimens examined.—1.

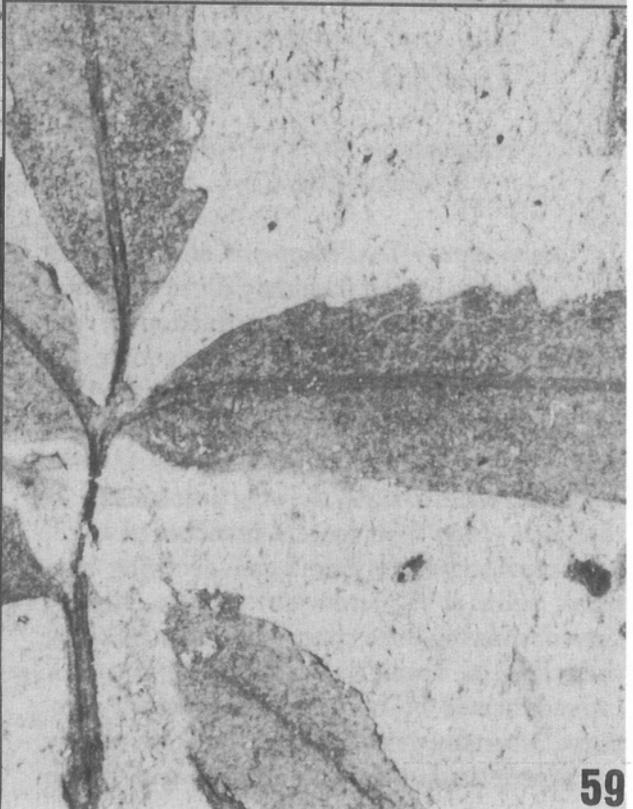
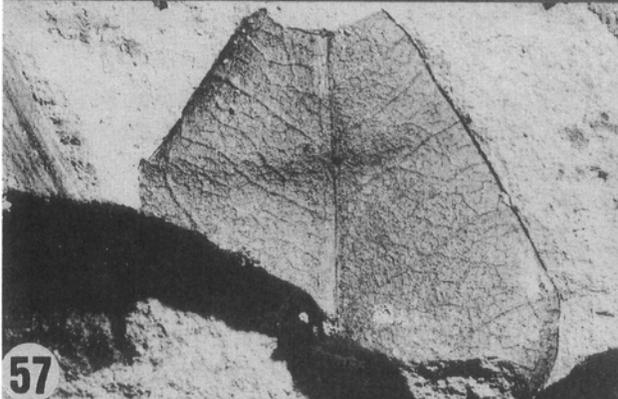
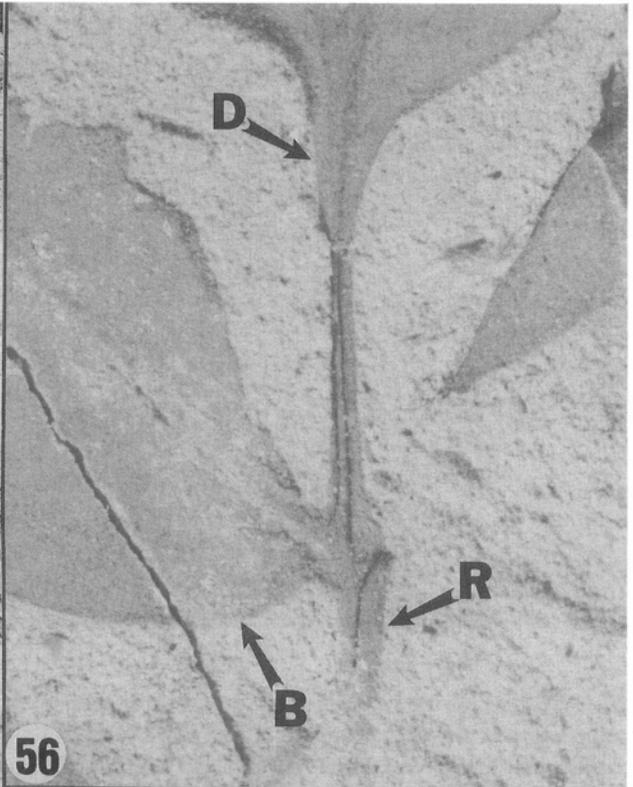
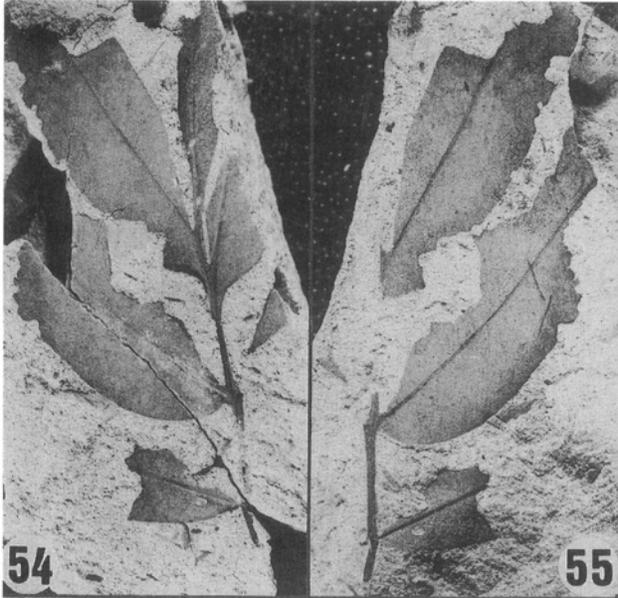
Holotype.—USNM 222855A, B (part and counterpart).

Derivation of specific epithet.—Latin, *minute* = small, *folius* = leaved, referring to the small leaves.

Discussion.—The specimen illustrated herein is USNM 222855B, which is the counterpart of the specimen illustrated in Hickey and Doyle (1977, fig. 47). Despite preservation of only one specimen, *Sapindopsis minutifolia* is sufficiently distinct from previously described species of *Sapindopsis* to warrant description as a new species. *S. minutifolia* most closely resembles *S. belvederensis* Berry (1922, p. 216, Pl. 49, figs. 1–7; Pl. 53, fig. 1; Pl. 54, fig. 1), a species known from the Western Interior of North America, in having a serrate margin, teeth of similar shape, and craspedodromous secondary venation. However, *S. minutifolia* is readily distinguished from *S. belvederensis* by pinnately compound organization that extends over the entire length of the leaf, rather than just near the base; smaller overall leaf size; laminar segments that fall in the nannophyll, rather than microphyll, size class; and much thinner secondary venation that has a more zig-zag course and more readily forms loops.

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Facing page: Figures 54–57.—*Sapindopsis magnifolia/variabilis*. Figure 54, specimen showing trilobed terminal region and lateral lobes. USNM 446023A, x1.25. Figure 55, counterpart of specimen in Figure 54. USNM 446023B, x1.25. Figure 56, enlargement of specimen in Figure 54 showing wing of laminar tissue along rachis (R), asymmetric base to a lateral lobe (B), and decurrent base to the trilobed terminal region (D). USNM 446023A, x5. Figure 57, inrolled leaf fragment assignable to *S. magnifolia/variabilis* showing midvein, secondary veins, and irregularly reticulate higher order venation. FMNH PP43816, x5. Figures 58, 59.—*Sapindopsis minutifolia* new species, holotype. USNM 222855B. Figure 58, general view of specimen showing one terminal and two pairs of lateral pinnatisect laminar units, x3. Figure 59, enlargement showing absence of laminar wing on rachis and the constriction of laminar units to vasculature where they connect with the rachis. Note the thin, zig-zag secondary venation in the horizontally oriented laminar unit, x7.5.



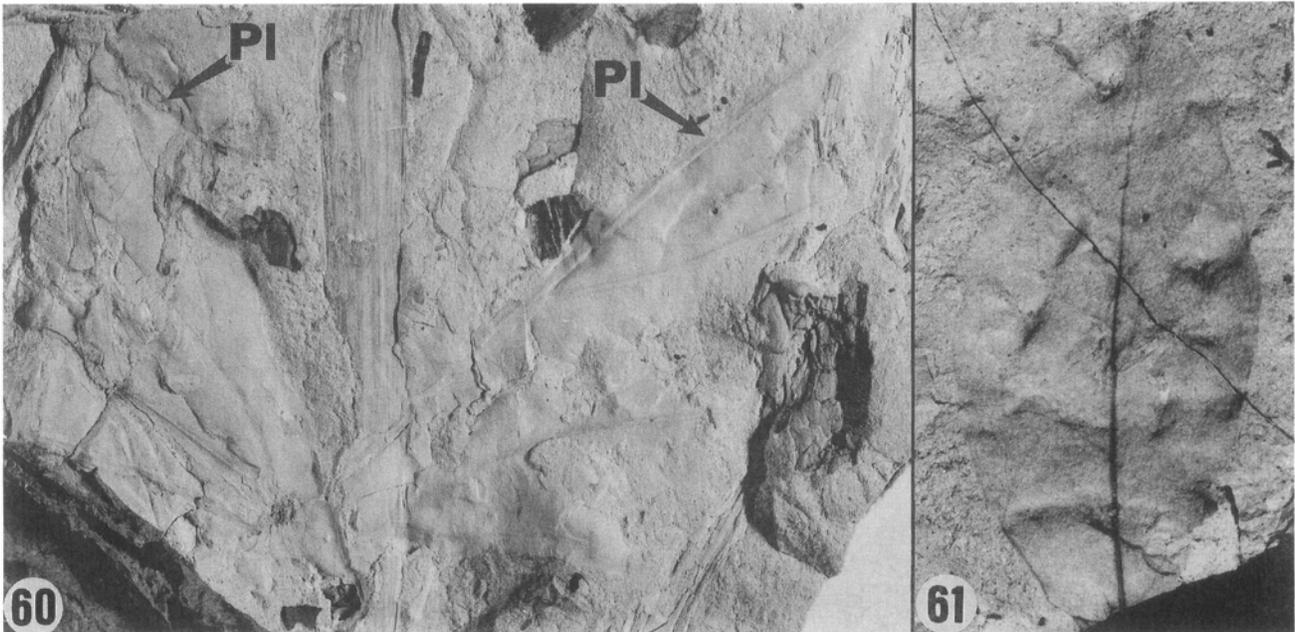


Figure 60.—Slab containing a fragmentary impression of a vertically oriented stem (center) and two fragmentary impressions of probable platanoid foliage (PI). USNM 446018A, x1. Figure 61.—*Dicotylophyllum* sp. 1 (cf. *Dicotylophyllum argillaceum* [Heer] Vakhrameev). FMNH PP43794, x2.

Subclass ?HAMAMELIDIDAE  
Order ?HAMAMELIDALES

Fragments of platanoid foliage  
(Figures 60, 62)

Description.—Two fragments of a large leaf type preserved. Largest fragment 10 cm long by 4 cm wide, representing only a fraction of the original leaf. Apex, base, margin, and petiole not preserved. Thickest veins producing branches on the one side, interpreted as the lateral primary veins of a palmately veined leaf; trunk veins 1–1.5 mm wide, straight, showing little change in thickness along their length; branches of trunk veins usually no wider than 1 mm, diverging from trunk veins at a narrow acute angle, slightly curved, showing little change in thickness along their length. Trunk veins and their branches interconnected by numerous thin veins (interpreted as tertiary veins); tertiary venation weakly percurrent; tertiary veins thin relative to source

veins, closely spaced (1 vein every 2 mm), originating at broad acute to right angles, curved to sinuous, either connecting with another source vein or anastomosing with other tertiary veins, enclosing regions many times longer than wide. Quaternary venation reticulate; quaternary veins without orthogonal rooting, often curved to sinuous, enclosing regions of variable size and shape. Quinary venation reticulate; quinary veins without orthogonal rooting, often curved. Areoles well developed, medium to small, well-defined freely ending veinlets not observed.

Number of specimens examined.—1 (2 fragments on 1 block).

Illustrated specimen.—USNM 446018A, B (part and counterpart).

Discussion.—These leaf fragments show a suite of features indicative of probable affinities with the platanoid complex, an informally recognized group of leaves with inferred affinities to extant Platanaceae and allied families (Doyle and

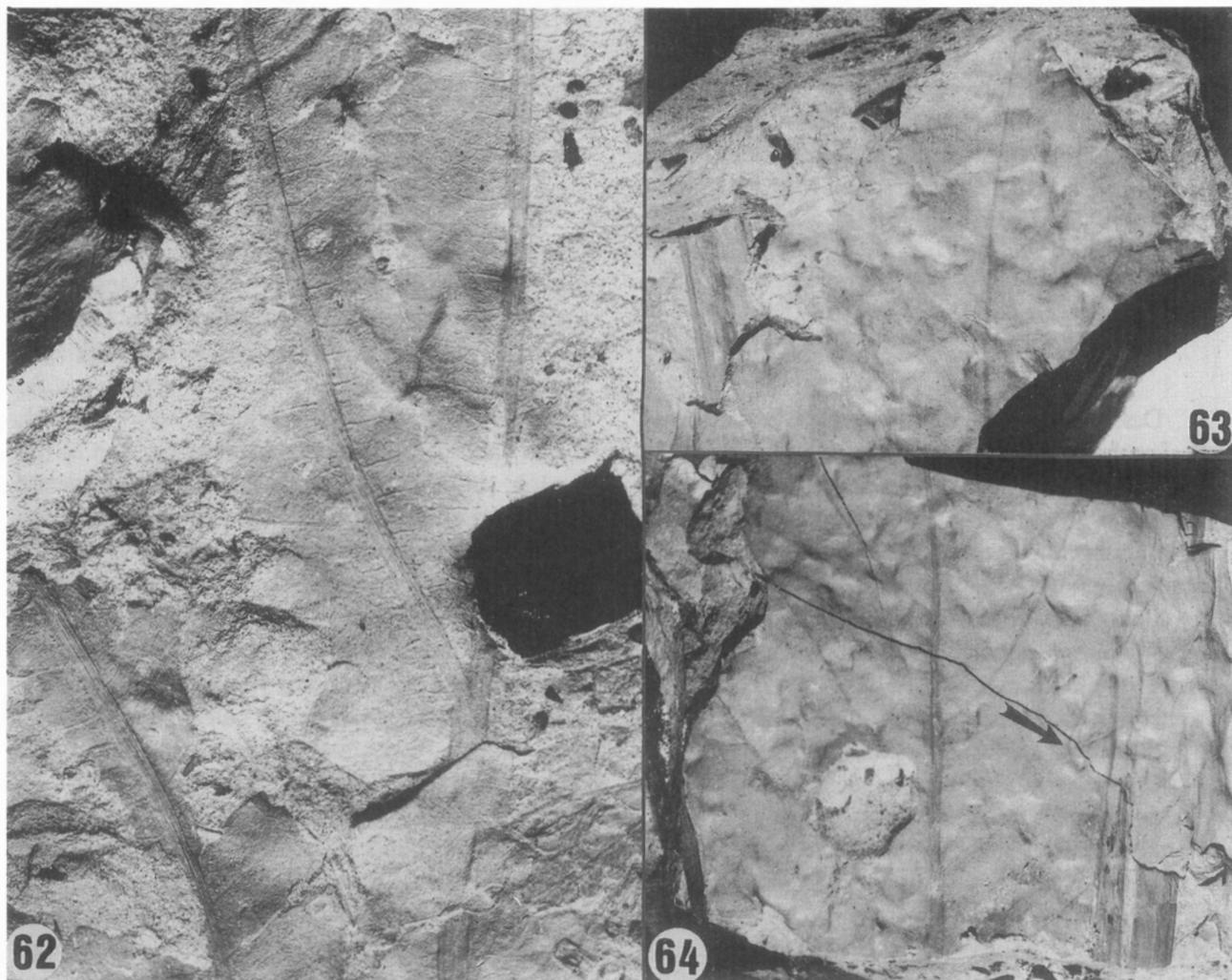


Figure 62.—Fragment of probable platanoid foliage showing vertically oriented trunk vein with two lateral veins, numerous closely spaced percurrent tertiary veins, and reticulate higher-order venation with non-orthogonal rooting. USNM 446018B, x2.5. Figures 63–64.—*Dicotylophyllum* sp. 2 (cf. “*Magnolia*” *amplifolia* Heer). Figure 63, apical region of counterpart showing acute apex. FMNH PP43790', x1. Figure 64, part showing medial region of leaf. Note midvein and secondary veins. Also note the branching of one secondary vein to the right of the midvein (arrow). FMNH PP43790, x1.

Hickey, 1976; Hickey and Doyle, 1977; Upchurch, 1984). Reproductive structures similar to those of extant Platanaceae occur in association with these leaves at many localities (Crane, 1989; Friis et al., 1989; Crane et al., 1993). Features in the Quantico leaf remains suggestive of mid-Cretaceous “platanoids” include the thickness, course, and pattern of branching of the trunk veins (which show the same

features as the lateral primary veins of platanoid leaves), percurrent tertiary venation, and reticulate quaternary and quinternary venation. These features also are suggestive of the Potomac Group species *Aristolochiaephyllum crassinerve* Fontaine, a large-leaved taxon known only from highly fragmentary specimens. No previously described species of Potomac Group angiosperms has tertiary and

higher-order venational features that exactly match those of the Quantico leaves in terms of vein thickness, vein course, and vein spacing. Thus, while the Quantico remains show comparable regularity in tertiary and higher-order venation to coeval platanoid foliage, they cannot be assigned to any previously described species.

#### Subclass UNKNOWN

##### *Dicotylophyllum* sp. 1 (Figure 61)

Description.—One nearly complete leaf preserved. Leaf probably elliptic, >4 cm long by 2.5 cm wide, L/W >2; apex acute but with tendencies for a rounded tip; base not preserved; margin entire. Primary venation pinnate; primary vein moderate, thinning noticeably near apex. Secondary veins thin relative to primary vein, originating at moderate acute angles, possibly curving apically (secondary venation poorly preserved).

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43794.

Discussion.—This leaf type is too poorly preserved to determine affinities accurately. Among previously described species of angiosperms, *Dicotylophyllum* sp. 1 from Quantico shows similarities in size and shape to *Dicotylophyllum argillaceum* (Velenovsky) Vakhrameev, known from the Cenomanian of Bohemia and Kazakhstan (Velenovsky, 1884; Vakhrameev, 1952), and *Dicotylophyllum* sp. B of Samylina (1960), known from the Lower Cretaceous of Siberia. The Quantico leaf strongly resembles the one specimen of *Dicotylophyllum argillaceum* illustrated

by Vakhrameev (1952, Pl. 43, fig. 5), but poor preservation of the Potomac Group and Kazakhstan specimens precludes closer comparison.

##### *Dicotylophyllum* sp. 2 (Figures 63, 64)

Description.—Part and counterpart preserved. Lamina probably falling in the mesophyll size class (exact size difficult to determine because of fragmentary preservation). Shape unknown, leaf >11 cm long by about 9 cm wide (estimated width); apex probably acute; base not preserved; margin entire. Primary venation pinnate; primary vein moderate, 2 mm wide in the lowest preserved portion of the lamina, slightly curved, gradually thinning toward apex. Pattern of secondary venation not possible to discern because of poor preservation; secondary veins moderate in thickness relative to primary vein, ≥8 pairs, alternate or opposite on midvein, 1 to 2 cm apart, originating at mostly moderate acute angles, slightly curved, one secondary vein producing a narrow acute exmedial branch about halfway to margin.

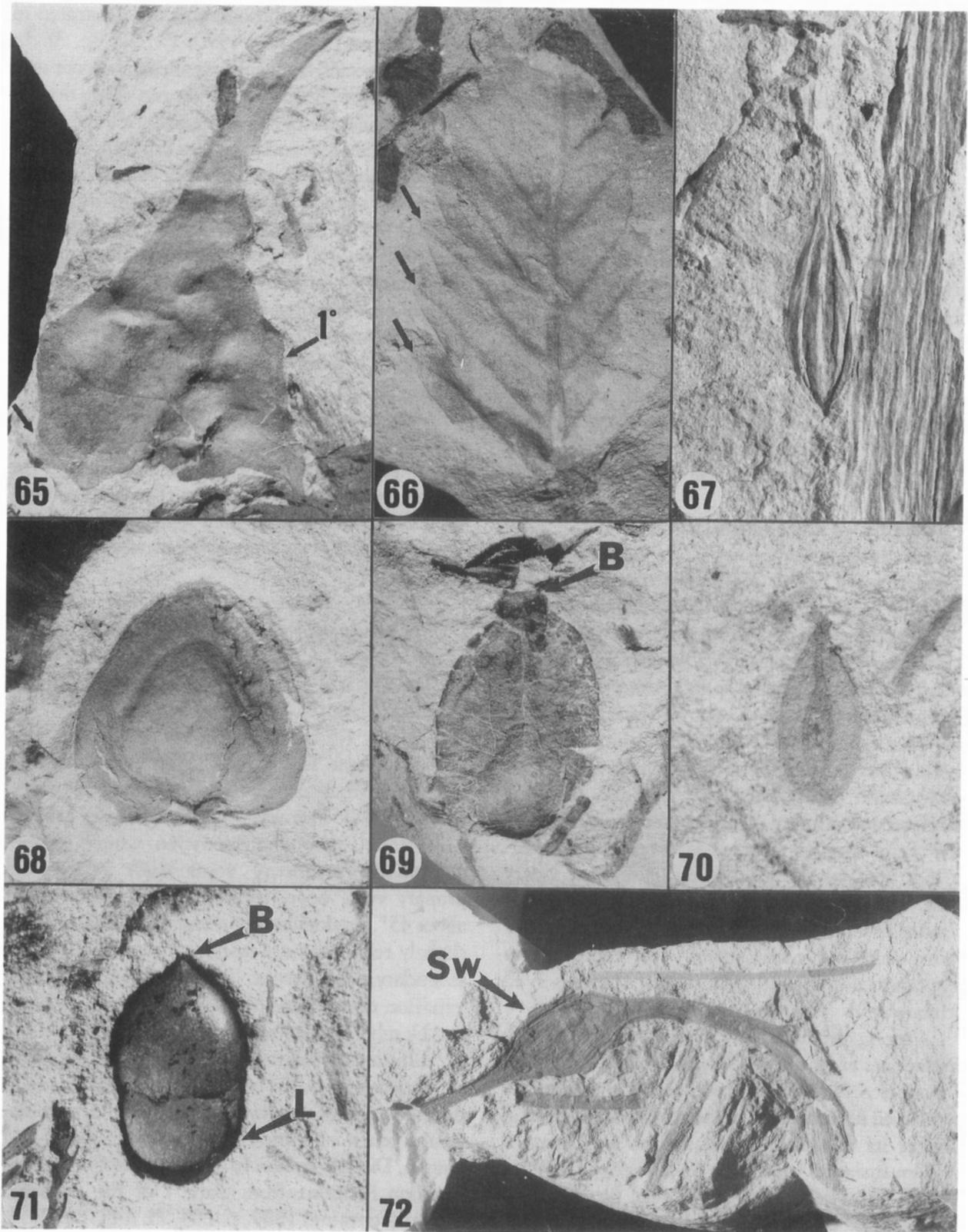
Number of specimens examined.—1 (part and counterpart).

Illustrated specimen.—FMNH PP43790, PP43790' (part and counterpart).

Discussion.—*Dicotylophyllum* sp. 2 is represented by a part and partially overlapping counterpart. It obviously represents a large leaf, but exact size cannot be determined because of poor preservation. Among previously described species of mid-Cretaceous angiosperm leaves, *Dicotylophyllum* sp. 2 closely resembles "*Magnolia*" *amplifolia* Heer (photographically illustrated in Vakhrameev, 1952, Pl.

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Facing page: Figure 65.—*Dicotylophyllum* sp. 3, leaf fragment with venation possibly similar to *Didromophyllum* Upchurch and Dilcher. One of the inferred primary veins (1°) runs along the right margin of the lamina and terminates in the narrow elongate lobe in the upper right corner of photograph. Note the blind termination of a secondary vein (unlabeled arrow) at a tear in the lamina. FMNH PP43807, x2. Figure 66.—*Dicotylophyllum* sp. 4, specimen showing midvein and simple craspedodromous secondary veins that slightly recurve when they enter teeth (arrows). FMNH PP43806, x3.5. Figure 67.—cf. *Kenella*, specimen to left of vertically oriented stem impression. Specimen shows at least 4 longitudinal ribs. USNM 446041, x2. Figure 68.—Diaspore type 1, specimen showing central body and marginal wing. FMNH PP43819, x4. Figure 69.—Diaspore type 2. Note truncate beak (B) at apex of specimen. FMNH PP43820, x3. Figure 70.—Diaspore type 3. Note smaller body inside larger one. FMNH PP, x10. Figure 71.—Diaspore type 4. Note beak (B) at apex of specimen and lobed structures (L) at base. USNM 446039, x3. Figure 72.—Stem with intercalary swelling (Sw). FMNH PP43799, x1.



13, fig. 2) in size, probable shape, and preserved features of venation. However, poor preservation of the Quantico remains precludes more detailed systematic comparisons.

*Dicotylophyllum* sp. 3 (Figure 65)

Description.—Leaf fragment roughly triangular in outline, with concave sides, length of sides measuring 8.5, >7.5, and >5.5 cm. Exact pattern of primary venation unknown; one primary vein observed, 1.5 mm wide at its base, running near the margin and terminating at the tip of a narrowly elongate lobe. Secondary venation appearing to be brochidodromous (poorly preserved), originating from one side of the primary vein, one secondary vein producing an external branch. Tertiary venation poorly preserved, possibly with transverse orientation.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43807.

Discussion.—The one known specimen of this leaf type has an intriguing morphology, but poor preservation makes conclusive determination of the venational pattern difficult. The primary venation seems to consist of one (or more) primary veins, the exact number of which cannot be determined. The one preserved primary vein runs near the laminar margin and terminates at the tip of a lobe. The organization of the secondary venation indicates that a second primary vein may have been basal to one of the marginal tears but is not preserved. This is indicated by the thickening of one secondary vein as it approaches a marginal tear, where it blindly terminates (Figure 65, 2°). The secondary veins, which curve and appear to form loops, seem to originate from only one side of the preserved primary vein.

Among previously described species of mid-Cretaceous angiosperm foliage, *Dicotylophyllum* sp. 3 most closely resembles two species characterized by bilobed laminar units, reinforcing our interpretation of its venation. These species are *Didromophyllum basingerii* Upchurch and Dilcher (1990, p. 34, Pl. 21; Pl. 22, figs. 1, 2; text fig. 14), and "*Sterculia*" *snowii* var. *disjuncta* Lesquereux (1891, p.

184, Pl. 58, fig. 6; photographically illustrated in Upchurch and Dilcher, 1990, Pl. 22, fig. 3). In these two species, the venation of each laminar unit consists of two primary veins that run along or near the basal margins of the leaf and terminate at the tips of the lobes. Secondary veins typically originate from only one side of each primary vein. If a similar pattern of venation is present in the Quantico leaf, the right-hand side of the lamina in Figure 65 represents one of the two basal margins, and the one preserved primary vein (1°) runs near this margin and terminates at the tip of a narrowly attenuate lobe. The other basal margin and its associated primary vein would then be missing (Figure 65, 2°).

More specimens of this taxon must be collected and analyzed to accurately determine the systematically important features of foliar architecture. If the Quantico leaf fragment can be related unambiguously to *Didromophyllum*, then it will constitute the oldest record of the *Didromophyllum* clade in North America.

*Dicotylophyllum* sp. 4 (Figure 66)

Description.—One nearly complete lamina preserved. Lamina tending toward oblong, >2.6 cm long by 1.5 cm wide, L/W >2; apex and base missing; margin serrate, teeth 3 to 4 mm long by 1 to 2 mm high, apical and basal sides tending toward convex (A-1). Primary venation pinnate; primary vein stout. Secondary venation simple craspedodromous; secondary veins thick relative to primary vein, opposite, >6 pairs, originating at about 45°, predominantly straight but tending to be slightly recurved near margin, unbranched. Inter-secondary veins absent. Tertiary and higher-order venation not preserved.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43806.

Discussion.—Although *Dicotylophyllum* sp. 4 is distinctive, poor preservation precludes determination of generic affinities. In terms of size, shape, and margin, *Dicotylophyllum* sp. 4 resembles *Ficophyllum serratum* Fontaine from Zone I of the Potomac Group (Fontaine, 1889, p. 294, Pl. 145, fig. 2; Pl.

149, fig. 9) but differs in having much thicker primary and secondary venation. *Dicotylophyllum* sp. 4 also resembles *Quercophyllum grossidentatum* Fontaine from Subzone II-B of the Potomac Group (Fontaine, 1889, p. 307, Pl. 156, fig. 6) but differs in showing little attenuation of the primary vein and in having more secondary veins. *Dicotylophyllum* sp. 4 resembles some specimens assigned to *Sapindopsis belvederensis* by Berry (1922) in terms of shape and simple craspedodromous secondary venation. Because of poor preservation, comparisons with other taxa, such as *Ulmiphyllum* Fontaine, are possible.

### REPRODUCTIVE STRUCTURES OF UNKNOWN AFFINITIES

The Quantico locality yields numerous reproductive structures of gymnospermous or angiospermous affinity. Preservation often precludes determination of whether a particular reproductive body represents a seed, a single-seeded fruit, or other type of seed-dispersal unit. We refer to each reproductive body as a *diaspore* when it obviously represents a fruit or seed and probably functioned as the unit of seed dispersal. Although systematic analysis of these reproductive structures contributes no new information about relationships at higher taxonomic levels, we illustrate and describe these remains to document their range of structural diversity and to provide data for future studies.

#### Genus *Kenella* Samylina

Type species. — *Kenella harrisiana* Samylina (1968, p. 212, figs. 11–13, text-fig. 2G).

#### aff. *Kenella* (Figure 67)

Description.—Bodies preserved solely as impressions; identity as seeds, fruits, or possibly floral buds uncertain. Bodies elongate-ovate, about 25 mm long by 6 mm wide, gradually becoming narrow at base and apex. Surface of structure smooth, without hairs, bristles, or spines; four elongate longitudinal ribs present on one preserved surface of each specimen, implying that the structure had

about 8 ribs in life. Narrow-elongate end of structure (here interpreted as apex) tending to splay apart in one specimen.

Number of specimens examined from Quantico.—3.

Holotype.—USNM 446041.

Other identified specimens.—USNM 446024, 446042.

Discussion.—Two specimens from Quantico have a shape and pattern of ribbing characteristic of the genus *Kenella*, an enigmatic taxon described by Samylina (1968) from the Cretaceous of Siberia. Remains similar to cf. *Kenella* from Quantico also occur in an unreported leaf assemblage from the Stump Neck locality, palynologically dated by Doyle and Hickey (1976) as upper Subzone II-B in age. The absence of evidence for hairs, bristles, and spines distinguishes the Potomac Group remains from *Kenella harrisiana*, the type species. This distinction is supported by the larger size of the Quantico remains (25 mm versus 16 mm long). Although it is tempting to describe a new species of *Kenella*, poor preservation makes it uncertain whether the type and Potomac Group specimens represent fruits, seeds, floral buds, or vegetative structures. Until the morphology of type *Kenella* is better understood, we think that no useful purpose would be served by describing additional species.

In her description of *Kenella harrisiana* from Siberia, Samylina (1968) noted that the species occurred separate from coeval species of angiosperm foliage. In the Potomac Group, however, remains of cf. *Kenella* are only known from localities with abundant angiosperm foliage, and in particular abundant *Nelumbites* foliage. At Stump Neck, cf. *Kenella* occurs in a restricted claybed characterized by a monodominant assemblage of matted *Nelumbites* cf. *N. minimus* leaves. At Quantico, cf. *Kenella* occurs in association with abundant *Nelumbites extenuinervis* and rare *N. cf. N. minimus*. The significance of these different associational patterns in Siberia and North America is uncertain.

#### Diaspore type 1 (Figure 68)

Description.—Specimen somewhat flattened in

surface view, with a central body and a marginal wing, body and wing together 1 cm in diameter, L/W 1, outline subtriangular and with rounded corners. Surface of specimen showing no evidence for hairs, bristles, or spines. Central body 7 mm long by 7 mm wide.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43819.

Discussion.—This diaspore is probably a seed. The flattening of the diaspore, in combination with the subtriangular shape and the central body, are suggestive of seeds in extant Taxodiaceae. However, seeds of extant Taxodiaceae are typically much smaller, and the cone scales of associated taxodiaceous seed cones are too small to have borne this seed type.

#### Diaspore type 2 (Figure 69)

Description.—Ovate, flattened body 13 mm long by 9 mm wide with an apical projection, specimen flattened in preservation, with a longitudinal groove possibly representing a septum. Apical projection with a truncate tip, 1 mm long by 3 mm wide.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43820.

Discussion.—This diaspore may be a fruit, but poor preservation precludes determination of its structure and systematic affinities. Although the shape of diaspore type 2 is similar to that of achenes in extant *Nelumbo*, diaspore type 2 is much too large to have been borne in the floral receptacles associated with *Nelumbites* foliage.

#### Diaspore type 3 (Figure 70)

Description.—Seed or fruit with a wing and an inner body, producing little relief in the matrix. Diaspore ovate, 3 mm long by ca. 1.5 mm wide, L/W 2. One end (base?) rounded, the other end (apex?) pointed. Wing ca. 0.5 mm wide, width more or less constant through length of diaspore. Central body darker than wing, 2.5 mm long by 0.5 mm wide. Central body with an ovate basal portion and an elongate terminal beak; ovate basal portion 1.5

mm long by 0.5 mm wide, L/W 3; terminal beak 1 mm long by 0.2 mm wide, L/W 5, extending to apex of diaspore.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43800B.

Discussion.—This taxon may be a winged seed or winged fruit, but details of its structure and systematic affinities are obscure. No venation is preserved in the wing.

#### Diaspore type 4 (Figure 71)

Description.—Diaspore producing strong relief in matrix, obovoid, 13 mm long by 8 mm wide, surface smooth, with no evidence of hairs, bristles, or spines. Apical projection present, ca. 1 mm long. Pair of structures subtending apical part of diaspore, 4 mm tall by 7 mm wide, possibly fleshy in life, perhaps representing arils or paired bracts.

Number of specimens examined.—1.

Illustrated specimen.—USNM 446039.

Discussion.—Preservation of one specimen as a cast precludes determination of whether this diaspore represents a fruit or seed.

### MISCELLANEOUS

#### Stem with intercalary swelling (Figure 72)

Description.—Stem curved, with intercalary swelling. Stem 2 to 4 mm wide in unswollen part, over 9 cm long, curved, surface longitudinally striate. Swollen part of stem 2 cm long by 1.4 cm wide, ovoid.

Number of specimens examined.—1.

Illustrated specimen.—FMNH PP43799.

Discussion.—Details of the structure and systematic affinities of this fossil are obscure.

### ARTHROPOD REMAINS (Figure 73)

Associated with the plant remains at Quantico are a variety of impressions of fossil insects, none of which have been analyzed in detail. Most of these consist of isolated wings, but a few preserve most or

all of the body. The most impressive specimen collected to date consists of a large nymph that has been tentatively identified as a stonefly (order Plecoptera) (Figure 73). The nymph is approximately 5.5 cm long and preserves the head (H), at least three legs (L), both cerci (C), and one wing bud (Wb). Features suggestive of the order Plecoptera include large size, long thick legs that show little difference in size between pairs, and long cerci. The occurrence of a possible stonefly nymph at Quantico is consistent with a swale or pond origin for the fossil bed.

Fossil insects from Quantico and other Potomac Group localities have not been formally described taxonomically, nor are they currently under investigation. Studies of these fossil insects would be most welcome.



Figure 73.—Insect nymph tentatively assigned to the order Plecoptera. Note head (H), legs (L), wing bud (Wb), and cerci (C). USNM 446017A, x2.

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