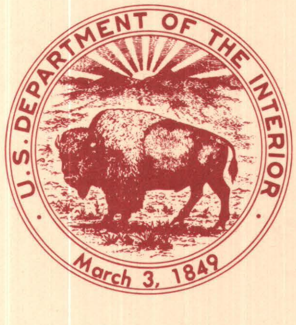
Cenomanian Angiosperm Leaf Megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, Southeastern Nebraska

U.S. GEOLOGICAL SURVEY BULLETIN 1915



AVAILABILITY OF BOOKS AND MAPS OF THE U.S. GEOLOGICAL SURVEY

Instructions on ordering publications of the U.S. Geological Survey, along with prices of the last offerings, are given in the current-year issues of the monthly catalog "New Publications of the U.S. Geological Survey." Prices of available U.S. Geological Survey publications released prior to the current year are listed in the most recent annual "Price and Availability List." Publications that are listed in various U.S. Geological Survey catalogs (**see back inside cover**) but not listed in the most recent annual "Price and Availability List" are no longer available.

Prices of reports released to the open files are given in the listing "U.S. Geological Survey Open-File Reports," updated monthly, which is for sale in microfiche from the U.S. Geological Survey, Books and Open-File Reports Section, Federal Center, Box 25425, Denver, CO 80225. Reports released through the NTIS may be obtained by writing to the National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161; please include NTIS report number with inquiry.

Order U.S. Geological Survey publications **by mail** or **over the counter** from the offices given below.

BY MAIL

Books

Professional Papers, Bulletins, Water-Supply Papers, Techniques of Water-Resources Investigations, Circulars, publications of general interest (such as leaflets, pamphlets, booklets), single copies of Earthquakes & Volcanoes, Preliminary Determination of Epicenters, and some miscellaneous reports, including some of the foregoing series that have gone out of print at the Superintendent of Documents, are obtainable by mail from

U.S. Geological Survey, Books and Open-File Reports
Federal Center, Box 25425
Denver, CO 80225

Subscriptions to periodicals (Earthquakes & Volcanoes and Preliminary Determination of Epicenters) can be obtained ONLY from the

Superintendent of Documents
Government Printing Office
Washington, D.C. 20402

(Check or money order must be payable to Superintendent of Documents.)

Maps

For maps, address mail orders to

U.S. Geological Survey, Map Distribution
Federal Center, Box 25286
Denver, CO 80225

Residents of Alaska may order maps from

Alaska Distribution Section, U.S. Geological Survey,
New Federal Building - Box 12
101 Twelfth Ave., Fairbanks, AK 99701

OVER THE COUNTER

Books

Books of the U.S. Geological Survey are available over the counter at the following Geological Survey Public Inquiries Offices, all of which are authorized agents of the Superintendent of Documents:

- **WASHINGTON, D.C.**--Main Interior Bldg., 2600 corridor, 18th and C Sts., NW.
- **DENVER, Colorado**--Federal Bldg., Rm. 169, 1961 Stout St.
- **LOS ANGELES, California**--Federal Bldg., Rm. 7638, 300 N. Los Angeles St.
- **MENLO PARK, California**--Bldg. 3 (Stop 533), Rm. 3128, 345 Middlefield Rd.
- **RESTON, Virginia**--503 National Center, Rm. 1C402, 12201 Sunrise Valley Dr.
- **SALT LAKE CITY, Utah**--Federal Bldg., Rm. 8105, 125 South State St.
- **SAN FRANCISCO, California**--Customhouse, Rm. 504, 555 Battery St.
- **SPOKANE, Washington**--U.S. Courthouse, Rm. 678, West 920 Riverside Ave..
- **ANCHORAGE, Alaska**--Rm. 101, 4230 University Dr.
- **ANCHORAGE, Alaska**--Federal Bldg, Rm. E-146, 701 C St.

Maps

Maps may be purchased over the counter at the U.S. Geological Survey offices where books are sold (all addresses in above list) and at the following Geological Survey offices:

- **ROLLA, Missouri**--1400 Independence Rd.
- **DENVER, Colorado**--Map Distribution, Bldg. 810, Federal Center
- **FAIRBANKS, Alaska**--New Federal Bldg., 101 Twelfth Ave.

Cenomanian Angiosperm Leaf Megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, Southeastern Nebraska

By GARLAND R. UPCHURCH, JR. and DAVID L. DILCHER

U.S. GEOLOGICAL SURVEY BULLETIN 1915

DEPARTMENT OF THE INTERIOR
MANUEL LUJAN, JR., Secretary

U.S. GEOLOGICAL SURVEY
Dallas L. Peck, Director

UNITED STATES GOVERNMENT PRINTING OFFICE: 1990

For sale by the
Books and Open-File Reports Section
U.S. Geological Survey
Federal Center
Box 25425
Denver, CO 80225

Library of Congress Cataloging-in-Publication Data

Upchurch, Garland R.
Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska / by Garland R. Upchurch, Jr., and David L. Dilcher.
p. cm.—(U.S. Geological Survey bulletin; 1915)
Includes bibliographical references.
Supt. of Docs. no.: I 19.3:1915.
1. Leaves, Fossil—Nebraska—Jefferson County.
2. Paleobotany—Cretaceous. 3. Paleobotany—Nebraska—Jefferson County. I. Dilcher, David L. II. Title. III. Series.
QE75.B9 *no. 1915*
[QE983]
557.3 s—dc20
[561′.2]CIP
90-2855

CONTENTS

PLATES

[Plates follow index]

PLATES

FIGURES

TABLES

Cenomanian Angiosperm Leaf Megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, Southeastern Nebraska

By Garland R. Upchurch, Jr. *and* David L. Dilcher[1, 2]

ABSTRACT

The leaves described in this report comprise the first assemblage of early flowering plant leaf megafossils to be accorded formal systematic treatment using modern methods of foliar architecture and cuticular anatomy. The 20 species of dicotyledonous leaves are described from a new locality in the Dakota Formation of Nebraska, near Rose Creek (Rose Creek locality). Seventy percent of the species represent either subclass Magnoliidae or forms with a similar grade of foliar architecture. Among Magnoliidae, species are assignable to the orders Magnoliales and Laurales, and one species shows resemblance to Illiciales. Although three species have strong similarities to one extant family (Lauraceae, or the laurel family), most species of Magnoliidae or magnoliid-grade foliage possess generalized features or combine the characteristics of two or more extant families. One species possesses unique features of foliar architecture that represent an unsuccessful "experimental" design. Two species of Rosidae are present in the flora, and these combine features of foliar architecture that today are restricted to either compound-leaved or simple-leaved families. The leaves examined in this study show little evidence for fragmentation prior to burial and are preserved in a sequence of rooted mudstones containing brackish-water bivalves (including one specimen in life position); thus, the leaves represent predominantly local, brackish-water vegetation. This indicates that flowering plants evolved the ability to tolerate greater-than-freshwater salinities by the Cenomanian. The vegetation represented by the Rose Creek leaf remains shows few similarities to modern mangrove swamps but instead is most analogous to brackish-water swamps that occur inland from mangrove swamps.

INTRODUCTION

The mid-Cretaceous was an important period in the history of the vascular land plants. During this time, the angiosperms began their adaptive radiation, and major extant lineages at the level of subclass, order, and family made their first appearance. (See, for example, Wolfe and others, 1975; Hickey and Doyle, 1977; Dilcher, 1979; Upchurch, 1984; Walker and Walker, 1984.) Associated with this adaptive radiation were progressive and broad-scale ecological displacements, wherein cycadophytes, ginkgophytes, and other dominant groups of gymnosperms declined in relative abundance and diversity and were replaced in most habitats and geographic regions by angiosperms, especially at lower and middle paleolatitudes (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Retallack and Dilcher, 1981, 1985; Crane, 1987; Upchurch and Wolfe, 1987b). Although some aspects of this transition have been elucidated by recent paleobotanical research, much remains unknown about this critical interval of Earth history, particularly with respect to the dynamics of angiosperm diversification and the establishment of major extinct and extant angiosperm lineages.

This state of ignorance is largely due to an inadequate taxonomic data base, a problem that is especially acute for angiosperm leaf megafossils. During the 19th and early 20th centuries, paleobotanists described numerous angiosperm leaf remains of Cretaceous age, but without a clear understanding of foliar architecture and the systematic distribution of foliar architectural features in extant flowering plants (Wolfe, 1973; Dilcher, 1974; Doyle and Hickey, 1976). Compounding the problem was an automatic assignment of most fossil leaves to extant families and genera, even if these leaves lacked one or more features found in the extant taxa. This "picture matching" (Wolfe 1973; Dilcher, 1974) gave the Cretaceous angiosperm record a falsely modern aspect,

---

Manuscript approved for publication, October 20, 1989.

[1] Department of Biology, Indiana University, Bloomington, Indiana, 47405.

[2] Address as of June 1990: Florida Museum of Natural History, University of Florida, Gainesville, Florida, 32611.

preventing the recognition of extinct evolutionary intermediates and disguising similarities that were the result of convergent evolution. As a result, even the oldest known angiosperm leaf assemblages were inferred to show affinities with both primitive and derived taxa, and few angiosperms were thought to represent extinct intermediate forms. While some authors explained this situation by proposing extremely rapid evolution of flowering plants during the Cretaceous (Scott and others, 1960), others proposed an extensive period of diversification prior to the group's appearance in the fossil record, either in remote geographic regions (Seward, 1931) or in upland regions, where preservation of pre-Tertiary sediments is minimal (Axelrod, 1952, 1970). These concepts were consistent with occasional reports of pre-Cretaceous flowering plants (for example, Harris, 1932; Erdtman, 1948; Kuhn, 1955; Brown, 1956; Tidwell and others, 1970), now either discounted or considered problematic on morphological or stratigraphic grounds (Read and Hickey, 1972; Scott and others, 1972; Wolfe and others, 1975; Hickey and Doyle, 1977).

The purpose of this study is to partially redress the systematic problem for early angiosperm foliage through analysis of leaf architecture and cuticular anatomy in well-preserved leaf remains from the mid-Cretaceous (uppermost Albian? to middle Cenomanian) Dakota Formation of southeastern Nebraska, along with a few related forms from the classic Dakota assemablages of Kansas. In this report we propose new species and genera that more accurately reflect the interrelationships of mid-Cretaceous angiosperms. We also discuss probable extant affinities at the level of family, order, and subclass, based on detailed consideration of foliar architecture and cuticular anatomy. These data will serve as a basis for elucidating the evolutionary status of early angiosperms during the early Cenomanian, approximately 20 million years into the angiosperm adaptive radiation.

ACKNOWLEDGMENTS

We thank Jack A. Wolfe (U.S. Geological Survey, Denver) for his discussions concerning the systematic affinities of the Rose Creek foliage, for discussions of the issues raised in this report, and for critical review of the manuscript. We thank James Basinger (University of Saskatchewan, Saskatoon) for his initial research on the Rose Creek leaf flora and for preparing most of the cuticles examined during this study. We also thank Roger Pabian (Nebraska Geological Survey) for discovery of the Rose Creek locality, help with geological problems, and field assistance, and Howard Reynolds (Fort Hays State University, Kansas) for initially informing us about the Rose Creek locality and for field reconnaissance. We thank Bruce H. Tiffney for careful and helpful review of the manuscript. Mr. and Mrs. Richard DeBoer granted permission to collect at the Rose Creek locality, and Roger Judd of the Endicott Clay Products Company provided the services of a bulldozer. Field assistance was provided by James Basinger, Charles Beeker, Margaret Bolick, Peter Crane, Peter Dilcher, Martin Farley, Karl Longstreth, Greg Retallack, and Michael Zavada. Insightful comments on the relationships of the Rose Creek leaf fossils were provided by Leo Hickey and Scott Wing. William Cobban and Douglas Nichols (U.S. Geological Survey, Denver) provided assistance with stratigraphic problems. The research for this report was completed while the senior author was a National Research Council Postdoctoral Research Associate at the U.S. Geological Survey, Denver. Fieldwork and the earlier stages of research were supported by National Science Foundation Grants DEB-79-10720 and BSR-83-00476 to David L. Dilcher at Indiana University, Bloomington. The final stages of data analysis and writing were supported by National Science Foundation Grant BSR-86-07298 to Garland R. Upchurch, Jr. and Erle G. Kauffman at the University of Colorado, Boulder, and by National Science Foundation Grant BSR-85-16657 and a Guggenheim Foundation Fellowship to David L. Dilcher at Indiana University, Bloomington.

MATERIALS AND METHODS

Nearly every specimen examined during this study was collected between June 1978 and October 1983. All distinctive leaf architectural types and all specimens with organic preservation were retained for laboratory analysis, and many of the organically preserved specimens were coated with Krylon crystal clear acrylic plastic spray to prevent cracking of the organic matter. All collected specimens were initially deposited in the Indiana University paleobotanical collections and given the locality prefix 15713-. These collections are now housed at the Florida Museum of Natural History in Gainesville, Florida.

Foliar architecture of fossils was studied through direct observation of specimens and through enhancement of details by line drawings and high-contrast photography with Kodak Technical Pan 2415 film. Leaf architectural terminology largely follows Hickey (1973, 1979) but incorporates the modifications suggested by Wolfe (1977) and Wolfe and Wehr (1987) with three exceptions. First, we have used Hickey's term "exmedial" instead of "abmedial," largely because abmedial is easy to confuse with admedial. Second, we have used "quaternary" and "quinternary" instead of "quatary" and "quintary." Third, we have avoided use of Hickey's terms "imperfect," "incomplete," and "lacking" for the description of areolation. These three conditions intergrade and represent a composite of characters (variation in areolar size, shape, and degree of branching of the freely ending veinlets), and we could not be confident that we were always using the terms in the manner intended by Hickey (1973, 1979). Instead, we have described areolation as well developed, moderately developed, or poorly developed, depending on the regularity in size and shape, and provided illustrations for the reader. We also have added descriptions of the general organizational tendencies in festooned brochidodromous secondary venation. Readers unfamiliar with venational terminology should obtain a copy of Hickey (1979) to use while reading species descriptions.

Cuticles were prepared for light microscopy with a combination of standard methods, such as those outlined in Dilcher (1974), using bleach for maceration and Safranin O for staining. When cuticular fragments were large, a piece of 100-mesh screen was sometimes used to transfer cuticle between solutions. All leaf cuticles were photographed with Kodak Technical Pan 2415 film on the Zeiss Photoscope I at the Paleontology and Stratigraphy Branch, U.S. Geological Survey, Denver, using brightfield and phase-contrast optics. Cuticular terminology follows Stace (1965) and Dilcher (1974), except when the use of terminology would potentially confuse the nonspecialist. "Upper" cuticle is used in place of "adaxial" cuticle and "lower" cuticle is used in place of "abaxial" cuticle. This is because the upper and lower cuticle in fossils are recognized by an ecologically controlled character (frequency of stomata), while abaxial and adaxial denote developmental position. (In the mature leaves of a few extant species, the lower surface actually represents the adaxial side of the developing leaf.) The term "cuticular flange" is used in place of "anticlinal cell wall" because the cuticular flanges are the only part of the anticlinal walls preserved in most cuticular preparations. All measurements of cell size are for unspecialized cells. Cells from modified areas of the epidermis in proximity to veins ("veinal areas") and stomata were not included in the measurements.

Because foliar architecture and cuticular anatomy in extant flowering plants have not been comprehensively described and illustrated, we have included illustrations of extant relatives of the Rose Creek taxa. Complete illustration of foliar architecture and cuticular anatomy in the extant relatives would be a major undertaking and was not attempted because of limited time and space; instead, we illustrated only representative taxa. Most photographic illustrations of foliar architecture are ×1 but can be magnified for observation of secondary, tertiary, and quaternary venation. Illustrations of tooth architecture are largely confined to line-drawings; the interested reader should consult Hickey and Wolfe (1975) for photographic illustrations of major tooth types in extant flowering plants.

CRITERIA FOR CLASSIFICATION

Angiosperm phylogeny is riddled with examples of convergent morphologies, and individual plant organs show a large degree of developmental independence relative to one another. Together these create the potential for strong mosaic evolution. Any classification based on a single organ has a greater potential for error than one based on a variety of organs, because whole plants contain a larger number of nondevelopmentally linked characters than single organs. Hence, the analysis of whole plants improves the chances of spotting convergent similarities. However, while leaves are the most abundant component of the megafossil record, foliar characters have traditionally played a small role in the classification of extant angiosperms, in contrast to reproductive structures. Although one solution to this problem would be to restrict the systematic analysis of angiosperm megafossils to taxa known from both reproductive and vegetative organs, this approach would greatly restrict information about the flora as a whole, given the dominance of isolated vegetative organs in the megafossil record.

Fortunately, comparative studies of extant angiosperms indicate that leaves show a number of features of systematic importance at the levels of genus, family, order, and subclass; (Wolfe, 1973; Hickey and Wolfe, 1975; Roth, 1981; Jones, 1984; Levin, 1986a, b). In particular, features, such as venation pattern, tooth structure, and leaf organization, show strong correspondence with recent angiosperm classifications based on more traditional botanical characters taken from a variety of plant organs. (See, for example, Cronquist, 1968, 1981; Takhtajan, 1969, 1980.) Studies of foliar architecture also have resolved the systematic placement of taxa whose classification proved problematic on the basis of reproductive organs. The most prominent example at the level of subclass is Euphorbiaceae, where foliar architecture (Hickey and Wolfe, 1975) strongly supports Takhtajan's (1969, 1980) placement of the family within Dilleniidae, rather than Rosidae, as proposed by Cronquist (1968, 1981). At lower taxonomic levels, the combination of foliar architecture and epidermal anatomy have resolved the systematic placement of various problematic taxa, including several genera within the subfamily Phyllanthoideae of the Euphorbiaceae (Levin, 1986a, b). Thus, foliar characters have much potential for the classification of fossil angiosperms, especially if venation is combined with anatomical features, such as stomatal structure and trichome type, which are routinely analyzed by systematic plant anatomists.

We followed four major principles to minimize potential error in our classification of fossil angiosperm foliage.

First, the only characters used to circumscribe fossil genera were those that have systematic significance in extant angiosperms at the level of genus or family. This was determined by direct study of the foliar architecture and epidermal anatomy of extant angiosperms and by examination of the literature on foliar architecture (for example, Hickey and Wolfe, 1975; Levin, 1986a, b) and anatomy (for example, Metcalfe and Chalk, 1950, 1979; Wilkinson, 1979). For members of the subclass Magnoliidae, this comparison was exhaustive and involved examination of over 260 extant genera. Approximately 4000 total extant species were examined for foliar architecture.

Second, new genera were erected only on the basis of several independent and congruent characters, so as to avoid the pitfalls of single character taxonomy. In order to be considered independent, two characters must have a different developmental origin or show distinctly different constructional principles. For example, both foliar venation and cuticular anatomy were used in diagnosing genera because the veins and cuticle have their developmental origins in different tissue layers of the leaf (Fahn, 1967). For another example, the presence of two or more vein orders with a particular venational pattern (such as reticulate tertiary and quaternary venation) was counted as only a single character, because this condition could easily result from the iteration of the same developmental pattern at different levels of the venational hierarchy. For the sake of completeness, potentially linked characters were listed separately in the descriptions of species.

Third, all leaf remains that formed the basis for generic diagnoses had to be known with at least three or four orders of preserved venation and be represented by sufficient specimens to understand the construction of the whole leaf. This insured that a large number of venational characters was considered before erecting a classification and that all diagnostic features were present in the type species. This also prevented erroneous assignment of fossil leaves to the most similar extant taxon, because many times the similarities seen between a fossil leaf and an extant taxon were in lower order architectural features and cuticular anatomy, rather than in fine venation.

Fourth, a leaf taxon had to show either probable congeneric relationship to other fossil species or a highly distinctive suite of features before being formally diagnosed at the generic level. If a fossil leaf type met only three of these criteria (for example, it was represented by an incompletely preserved specimen that had a distinctive suite of leaf architectural features unknown in any extant family), a generic level taxon was informally recognized, permitting diagnosis when better preserved specimens are found. If a leaf type was distinctive at the species level but had incompletely preserved venation or a generalized suite of venational features, the leaf was assigned to *Dicotylophyllum*.

In this report we make extensive comparisons between species in the Rose Creek flora and previously reported taxa. The discussion section following most species descriptions is divided into three parts. The first part compares the taxon with previously described fossil genera and discusses the validity of previous generic assignments, largely to justify the creation of new genera. The second part compares the Rose Creek species with previously described species of fossil angiosperm leaves, many of which were invalidly assigned to extant or fossil genera. This is done to justify creation of new species and to point out possible congeneric species from other floras. The third part provides the basis for assignments to extant taxa, starting at the level of class or subclass and working down the level of family.

Many discussion sections might seem lengthy by the standards of Tertiary paleobotany. This lengthiness is necessitated by the prior identification of species by some workers solely on the basis of shape and size and by widespread misidentification of mid-Cretaceous angiosperm foliage at generic and higher taxonomic levels, practices that, unfortunately, continue to the present day. We hope that these comparisons will suggest avenues for future research on the systematics of Cretaceous angiosperm foliage.

GEOLOGICAL SETTING AND DESCRIPTION OF FOSSIL PLANT LOCALITY

In central Kansas and adjacent regions, the mid-Cretaceous sequence comprises five distinct formations, considered to represent the early stages of the Greenhorn transgression by Kauffman (1969). In ascending stratigraphic order these units are as follows: (1) the Cheyenne Sandstone of middle to late Albian age, (2) the Kiowa Formation of late Albian age, (3) the Dakota Formation of latest Albian (?) to middle Cenomanian age, (4) the Graneros Formation of middle Cenomanian age, and (5) the Greenhorn Formation of late Cenomanian to Turonian age (Hattin, 1967; Kauffman, 1969; Franks, 1975; Ward, 1986). Although the full stratigraphic sequence is exposed in central Kansas, older units successively pinch out to the northeast, so that in southeastern Nebraska rocks of the Dakota Formation

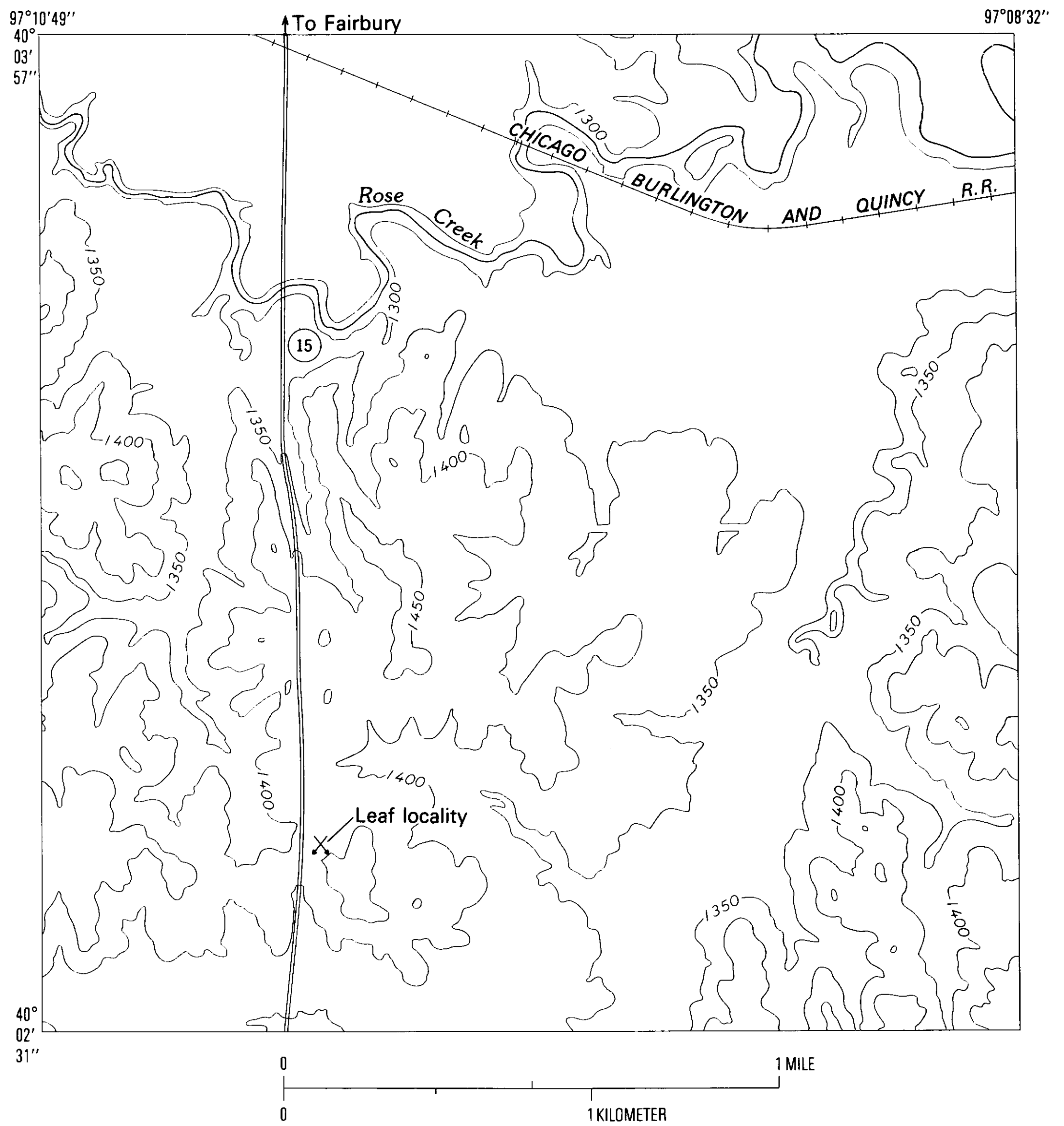


Figure 1. Map showing the location of the Rose Creek leaf megafossil locality (from the Fairbury SW 7.5-Minute Quadrangle, Nebraska-Kansas). The exact topography of the clay pit has changed somewhat since the publication of this map.

unconformably overlie rocks of Permian age (Franks, 1975). In southeastern Nebraska and north-central Kansas, the Dakota Formation is divided into two members (Plummer and Roemary, 1942): (1) the Terra Cotta Clay Member, which comprises largely sandstones and gray and red mottled claystones; and (2) the Janssen Clay Member, which comprises largely sandstones, gray claystones, and lignites. The estimated thickness of the Dakota Formation in southeastern Nebraska is 200–400 ft (Franks, 1975).

The leaf assemblage described in this report was collected from the upper half of the Janssen Clay Member in a clay pit located 6 miles south of Fairbury, Nebraska and 1.1 miles south of Rose Creek, approximately 50–100 m east of Nebraska State Highway 15, on the west-facing wall of the pit (W½NW¼SE¼ T. 1 N., R. 2 E., Fairbury SW 7.5' Quadrangle, Nebraska-Kansas) (fig. 1). Because of the proximity of the clay pit to Rose Creek, the megafloral locality is known as the "Rose Creek Locality." Field observations from near the study site indicate that the leaf megafossil beds are no more than 20 m stratigraphically below the contact between the Dakota and Graneros Formations and could be much closer. Unfortunately, the Dakota-Graneros contact could not be observed unequivocally at the study site due to vegetational cover.

Evidence from palynology, macroinvertebrates, and lithostratigraphic position indicate that the Rose Creek leaf remains are probably early to middle Cenomanian in age. Farley and Dilcher (1986) reported a palynoflora from a lignitic clay exposed a few meters above the leaf-bearing horizon at Rose Creek and concluded that this palynoflora and other assemblages from the Dakota Formation of Kansas indicate a Cenomanian age. Examination of the species list presented by Farley and Dilcher (1986) indicates a probable correlation with Zone III of the Atlantic Coastal Plain, considered early to middle Cenomanian in age by Doyle and Robbins (1977); in addition, some pollen species listed for Rose Creek have their first occurrences within the Western Interior in rocks dated as Cenomanian on the basis of marine invertebrates (see below). A Cenomanian age for the Rose Creek locality is indicated by the combined occurrence of (1) long-ranging spore and pollen taxa, such as *Appendicisporites*, *Gleicheniidites*, and *Classopollis*, which occur throughout most of the Cretaceous, (2) forms, such as *Rugubivesiculites rugosus* and *Tricolpites sagax*, which first appear in Subzone II-B (middle to late Albian) of the Atlantic Coastal Plain and in middle to upper Albian rocks of the Western Interior (Doyle and Robbins, 1977 and references cited therein), and (3) angiospermous pollen types such as *Tricolporopollenites aliquantulus* that are indicator species for Zone III of the Atlantic Coastal Plain and first occur within the Gulf Coastal Plain sequence in the Cenomanian Red Branch Member of the Woodbine Formation (Doyle and Robbins, 1977; Hedlund, 1966). Consistent with a Zone III age is the high diversity and high relative abundance of simple, pinnately veined angiosperm leaves at Rose Creek, because similar assemblages are not known from the Atlantic Coastal Plain until Zone III (Upchurch and Wolfe, 1987b).

Direct dating of Dakota rocks by macroinvertebrate fossils in Kansas and northeastern Nebraska indicate an age no younger than late-middle Cenomanian for the Rose Creek leaf locality. Macroinvertebrate assemblages described by Hattin (1967) from north-central Kansas indicate a middle Cenomanian age for the upper few meters of the Dakota Formation, and assemblages described by Cobban and Merewether (1983) from northeastern Nebraska place the Dakota-Graneros contact at the middle-upper Cenomanian boundary. An age no younger than early-middle Cenomanian is implied by the absence of Normapolles in palynofloras from Rose Creek and other Dakota localities (Farley and Dilcher, 1986), because Normapolles are first known from upper-middle Cenomanian rocks of Europe (Doyle and Robbins, 1977).

Sedimentological and paleontological data indicate that the Dakota Formation of central Kansas and southeastern Nebraska was deposited on a low-lying coastal plain under predominantly fluvial conditions, with estuarine conditions possibly present in the upper few meters of the formation (Hattin, 1967; Franks, 1975; Karl, 1976; Siemers, 1976). Deltaic environments may also have been widespread but not preserved due to extensive reworking of sediments by the transgressing Graneros sea (Franks, 1975). Karl (1976) provided evidence for predominantly fluvial conditions in the Dakota Formation of southeastern Nebraska, with major stratigraphic trends in stream sinuosity, grain size, and cross stratification related to a change in stream gradients from the transgressing Graneros sea. Karl (1976) suggested that the Janssen Clay Member was deposited by high-sinuousity meandering streams that were preserved as fine-grained, trough- and epsilon-cross-stratified, lens-shaped sandstone bodies. Higher-than-freshwater salinities for some parts of the Janssen Clay Member are indicated by (1) the occurrence *Brachidontes* bivalves in association with the leaf remains at Rose Creek, including one specimen in life position (Retallack and Dilcher, 1981), and (2) the occurrence of more fully marine molluscan assemblages and dinoflagellates 13 miles downdip to the northwest, a few meters below the contact with the Graneros Formation (Veatch, 1969). These assemblages are consistent with Hattin's (1967) postulation of extensive coastal swamps in the Dakota Formation of southeastern Nebraska. Farley and Dilcher (1986) proposed the possibility of deltaic conditions for the Janssen Clay Member in the Rose Creek area, based on (1) evidence for rapid sediment deposition, and (2) the occurrence of polymodal cross-bedding in a channel 2 m stratigraphically below and 2 km to the south of the Rose Creek pit.

The leaf remains at Rose Creek are confined to lowermost unit described by Farley and Dilcher (1986), which occurs several meters below the pollen-bearing horizon. Nearly all identifiable leaf remains occur within a 2-m-thick interval of light gray, jointed, overbank mudstones. A few identifiable leaf megafossils occur in an underlying dark gray mudstone that contains pyritic nodules and dispersed pyrite, but these were not analyzed because of poor preservation. The floral remains described by Basinger and Dilcher (1984) occur within a 0.3-m-thick zone in the middle part of the leaf-bearing horizon. Most leaf species show little evidence for fragmentation prior to burial; the bulk of fragmentation exhibited by the specimens results from extensive jointing of the mudstone after deposition of fossil leaves. Leaves sometimes occur in 1- to 2-cm-thick layers separated by much thicker layers of barren sediment. Roots occur in association with the leaves and are typically preserved as impressions. Rooted layers typically occur no more than 20 cm above a concentration of fossil leaves. Branch roots can penetrate right through a leaf vertically, producing little distortion (pl. 24, fig. 5). The low distortion of fossil leaves by penetrating roots indicates that sediment deposition was rapid, because low rates of sediment deposition would be characterized by extensive root bioturbation and high distortion and fragmentation of leaf remains. Penetration of the leaf bed by roots long after deposition seems unlikely, because the roots are concentrated in numerous layers (rather than one layer near the top of the sequence) and because no extensive tap roots indicative of deep rooting have been observed. The small size of the roots implies that the vegetation was of low stature (Retallack and Dilcher, 1981); however, the actual size of the plants is unknown because no trunks have been found attached to these roots. We interpret the leaf remains at the Rose Creek locality to largely represent local vegetation (some elements may have been transported in) that was fossilized approximately in place under conditions of rapid sediment deposition, a conclusion in accord with that of Retallack and Dilcher (1981) and Farley and Dilcher (1986).

FLORISTIC COMPOSITION

The leaf taxa in the list below occur at the Rose Creek locality. The scheme of classification follows Takhtajan (1980). This classification was chosen for two reasons. First, the classification of Takhtajan (1980) produces families that show relatively little variation in foliar architecture, while the classification of Cronquist (1981) produces families that can be strongly heterogeneous. This is especially pronounced for Laurales, which are well represented in the Rose Creek flora. Second, the foliar architecture of Chloranthaceae is more similar to that of certain Laurales (like Trimeniaceae) than that of Piperales, as would be predicted by the classification of Takhtajan (1980). All fossils are assigned to class, subclass, and order, when possible. Fossils are not assigned to subordinal taxa; instead, only the most similar modern families are designated. This is because (1) no species of fossil leaf examined here has all the characters that circumscribe an extant family, (2) published subordinal taxa of Magnoliidae are often heterogeneous with respect to foliar architecture, and (3) disagreement exists among authors with respect to the subordinal classification of Magnoliidae. When a fossil leaf genus shows some similarity to an extant taxon but cannot be included because it does not possess one or more diagnostic features, it is preceded by a "cf." designation.

- Magnoliophyta
  - Magnoliopsida
    - Magnoliidae
      - Magnoliales
        - cf. Winteraceae, Degeneriaceae, Eupomatiaceae, and Annonaceae
          - New genus A
- Magnoliophyta—Continued
  - Magnoliopsida—Continued
    - Magnoliidae—Continued
      - Laurales
        - cf. Chloranthaceae
          - *Crassidenticulum decurrens* (Lesquereux) new combination
          - *Densinervum kaulii* new genus and species
        - cf. Amborellaceae, Monimiaceae, Gomortegaceae, Hernandiaceae
          - *Landonia calophylla* new genus and species
        - cf. Atherospermataceae, Gomortegaceae, Gyrocarpaceae, Lauraceae, Hernandiaceae, and Hortoniaceae
          - *Pabiania variloba* new genus and species
        - cf. Lauraceae
          - *Pandemophyllum* new genus
            - *P. kvacekii* new species
            - *P. attenuatum* new species
            - *P.* sp.
      - cf. Illiciales
        - *Longstrethia varidentata* new genus and species
    - Magnoliidae order unknown; magnoliid-grade foliage
      - *Didromophyllum basingerii* new genus and species
      - *Acritodromum ellipticum* new genus and species
      - *Reynoldsiophyllum nebrascense* new genus and species
      - *Dicotylophyllum angularis* new species
      - New Genus B
    - Rosidae order unknown
      - *Anisodromum wolfei* new genus and species
      - *Citrophyllum doylei* new species
  - Magnoliopsida subclass unknown
    - *Dicotylophyllum myrtophylloides* new species
    - *D. rosafluviatilis* new species
    - *D. aliquantuliserratum* new species
    - *D. expansolobum* new species

Magnoliidae and magnoliid-grade foliage are by far the most important angiospermous element at Rose Creek, comprising 70% of the angiospermous species and over 90% of the collected angiospermous specimens. Rosidae and incertae sedis comprise 10% and 20% of the species, respectively, and each species in these categories is represented by fewer than 10 specimens. This situation contrasts with that for most of the classic "Dakota sandstone" leaf assemblages reported by Lesquereux (1892), where Hamamelididae are a conspicuous and abundant element. Among latest Albian to middle Cenomanian leaf megafloras, the dominance of

Magnoliidae and magnoliid-grade foliage at Rose Creek is most comparable to the situation for an undescribed leaf assemblage from Zone III (Cenomanian) of the Potomac Group of Maryland (the Malden Mountain assemblage of Wolfe and Upchurch, 1987b), which also comes from fine-grained facies.

The relationship of Rose Creek leaves to extant taxa is highly generalized, as might be expected during the early phases of angiosperm diversification. Although most species can be compared with an extant subclass, only half the species possess a suite of features that permits placement within an extant order. Further, practically no species possesses the full suite of features that circumscribes an extant family. This contrasts markedly with the situation for the late Paleocene and Eocene, 40 million years further into the adaptive radiation of flowering plants; at this time, most species of leaves have foliar architecture comparable to that of extant families. (See, for example, Wolfe, 1977, and Hickey, 1977.) The high percentage of extinct taxa relative to better known Tertiary leaf megafloras gives the Rose Creek flora a strongly archaic aspect.

EVOLUTIONARY CONSIDERATIONS

The high relative diversity of Magnoliidae at Rose Creek and good quality of preservation provide an opportunity to evaluate the evolutionary status of Magnoliidae during the early to middle Cenomanian, especially when other reports of Magnoliidae and leaf megafossils preserved only as impressions are taken into account. From a taxonomic standpoint, the Rose Creek assemblage indicates that the "core" alliance of Magnoliidae was well established by the Cenomanian: definite representatives of Magnoliales and Laurales occur, as well as one species with many points of resemblance to Illiciales. However, much variation exists between each of the three ordinal alliances in the degree to which individual species can be compared with modern families. Magnoliales, which are considered the most primitive order of flowering plants by Cronquist (1968, 1981) and Takhtajan (1969, 1980), are represented by fossils that show relatively low comparability with a single extant family and that show closest similarities to generally primitive extant taxa. For example, new genus A has the multistranded midrib and low venational regularity inferred to be primitive for the flowering plants as a whole (Hickey and Wolfe, 1975; Hickey and Doyle, 1977), plus a combination of features that is most similar to generalized magnolialean venation. *"Ficus" macrophylla*, a taxon originally described by Lesquereux (1892) from the Dakota Formation of Kansas, appears to represent a Late Cretaceous relative of the *Ficophyllum* complex, whose closest modern affinities lie with the primitive families Austrobaileyaceae, Magnoliaceae, and Winteraceae (Upchurch, 1983). The closest similarities found between an early Cenomanian megafossil taxon and an extant family of Magnoliales are those seen between the *Liriophyllum-Archaeanthus* complex and extant Magnoliaceae (Dilcher and Crane, 1984). Here, certain derived features indicate a possible close cladistic relationship, in particular the presence of a calyptra on the flowers. However, the overall floral structure of *Archaeanthus* is more primitive than that in Magnoliaceae, while foliar architecture in *Liriophyllum* is in some respects more advanced: each leaf is characterized by a primary vein that runs to the leaf apex and dichotomizes, a characteristic unknown in any extant Magnoliidae.

Fossil Laurales provide a marked contrast to fossil Magnoliales in comparability to extant families and inferred level of advancement. Although Laurales are thought to represent a more derived taxon than Magnoliales (Takhtajan, 1980; Cronquist, 1981), certain early Cenomanian Laurales can be compared closely with a single modern family (Chloranthaceae or Lauraceae), and members of the order as a whole show modern affinities that range from primitive to derived. For example, *Crassidenticulum decurrens* shows close similarities to extant Chloranthaceae (considered one of the primitive families of Laurales by Takhtajan [1980]), although its precise combination of venational features is not known from any extant genus. This is not surprising, because dispersed pollen and flowers comparable to extant genera of Chloranthaceae occur in older rocks (Walker and Walker, 1984; Friis and others, 1986). *Landonia* provides a possible evolutionary link between extant primitive Laurales that produce inaperturate pollen (Amborellaceae and Monimiaceae) and more derived members of the alliance because it combines (1) the pinnate venation and generally isodiametric intercostal regions characteristic of Amborellaceae and Monimiaceae, and (2) the generally transverse and sparsely branched intercostal tertiary venation with admedial branches characteristic of Gomortegaceae and certain Hernandiaceae (*Illigera*). *Landonia*, therefore, provides paleobotanical evidence in favor of the relationship postulated between Monimiaceae and Gomoregaceae on the basis of comparative morphology (Takhtajan, 1980). *Cocculophyllum*, *Pabiania*, and *Pandemophyllum* show their closest similarities to Lauraceae and allied families, and these three genera together can be interpreted as a series of related taxa that shows increasing similarity to extant Lauraceae in higher order venation and stomatal structure. Assuming that the remains examined in the course of our study comprise a representative sample, forms comparable to modern families apparently appeared much more rapidly in Laurales than in Magnoliales. Of course, much of this pattern also could reflect major diversification of Magnoliales in regions outside of North America, a concept consistent with the restriction to the Southern Hemisphere of certain advanced magnolialean pollen types, most notably permanent tetrads that have been compared to those of extant Winteraceae (Walker, Brenner, and Walker, 1983).

Illiciales are the only core order of Magnoliidae whose presence during the early Cenomanian is uncertain. Although dispersed cuticle similar to that of extant Illiciales occurs as early as late Aptian–early Albian (Upchurch, 1984), no known species of Cenomanian age has all the features characteristic of the modern order. *Longstrethia* has a combination of stomatal features that today is restricted to Illiciales (round stomata over 30 microns in length, curved lamellar cuticular thickenings on the guard cells, T-pieces, and laterocytic subsidiary cells), but pronounced striations on the cuticle are absent, and the venation is more poorly organized than that of extant Illiciales. This could simply reflect the small number of Cenomanian leaf taxa that are known in detail but is consistent with palynological evidence for the origin of Illiciales much later in the Cretaceous (Muller, 1981, 1984).

Most foliage from Rose Creek cannot be confidently assigned to an extant order. For certain taxa, such as *Dicotylophyllum angularis*, (1) this could be an artifact of incomplete preservation, and in particular the absence of preserved higher order venation and well-defined cuticular features. For other taxa, such as new genus B, (2) this may be the result of having highly irregular foliar venation with few or no obviously derived features. For some taxa, however, this situation results from having (3) a combination of features not observed in extant angiosperms, or (4) one or more foliar architectural features not found in extant angiosperms. A good example of situation 3 is *Acritodromum*, which combines secondary venation that is irregular in course and spacing with curved tertiary venation that is highly irregular in course and spacing but tends to be oriented parallel to the midvein. The prime example of situation 4 is *Didromophyllum*, where the primary veins give rise to secondary veins only on their apical sides, and the primary venation plays no role in defining planes of bilateral symmetry within the lamina. These last two examples, along with others provided by latest Cretaceous Magnoliidae (Upchurch and Wolfe, 1987a), indicate that extant Magnoliidae possess only a subset of the variation in foliar architecture that once existed within the subclass.

Within Rosidae, the two species present at Rose Creek show a level of advancement comparable to that found in early Cenomanian Rosidae as a whole (see data provided in Hickey, 1978), and each of the two species has features of foliar architecture that today are restricted to separate orders. *Anisodromum*, which comprises leaflets with slightly asymmetric secondary venation, has well-organized secondary and tertiary venation, a syndrome of features first seen in leaves of late Albian age (Hickey, 1978). *Citrophyllum*, which comprises simple leaves with morphological evidence of a compound-leaved ancestry (Hickey, 1978), has one of its oldest occurrences at Rose Creek. Both genera possess the thin, closely spaced, admedially oriented tertiary venation characteristic of extant simple-leaved orders, such as Rhamnales, Cornales, and Celastrales, rather than the thicker, more widely spaced, transverse tertiary venation characteristic of compound-leaved orders such as Sapindales and Rutales. This combination of fundamentally compound organization with tertiary venation most characteristic of simple-leaved Rosidae provides direct fossil evidence for a phylogenetic link between the two major divisions of Rosidae (Hickey and Wolfe, 1975), as predicted by comparative morphology.

Comparison of Rose Creek species of Rosidae with both late Albian rosid foliage (*Sapindopsis*) and extant, simple-leaved taxa of Rosidae such as Rhamnaceae indicates that the Rose Creek species occupy the middle region of a graded morphological series. One end starts with compound-leaved forms belonging to *Sapindopsis*, which possess (1) festooned brochidodromous secondary venation where each secondary vein shows eucamptodromous tendencies by forming its own series of brochidodromous loops, and (2) irregular tertiary venation that tends to be reticulate and admedially oriented. The other end of the series consists of simple-leaved taxa such as Rhamnaceae (especially the genera *Berchemia* and *Rhamnidium*), Celastraceae (*Bhesa*), and Olacaceae (*Coula*), which possess (1) truly eucamptodromous secondary venation, and (2) thin, closely spaced, percurrent, admedially oriented tertiary venation. The Rose Creek species combine the fundamentally compound organization characteristic of *Sapindopsis* with the eucamptodromous secondary venation characteristic of most simple-leaved rosids, and the tertiary venation present in the Rose Creek species is similar to that of the simple-leaved rosids but has more irregular organization. *Sapindopsis* has the most irregular vein organization of all taxa in the series, which implies that it represents the primitive end; this implies that compound leaves are primitive to many simple-leaved clades of Rosidae. Combined stratigraphic and phenetic evidence reinforces evidence from comparative morphology, because pinnately compound foliage of the *Sapindopsis* type is the most ancient and shows the closest morphological resemblance to angiosperm leaf taxa of Aptian to middle Albian age (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Hickey, 1978; Upchurch, 1984).

ECOLOGICAL CONSIDERATIONS

From an ecological standpoint, the Rose Creek flora provides the oldest well-documented occurrence of early angiosperms in brackish-water facies and indicates that angiosperms tolerated higher-than-freshwater salinities early in their evolutionary history (Retallack and Dilcher, 1981, 1985). Taphonomic evidence indicates that most Rose Creek taxa probably represent brackish-water plants, rather than the remains of freshwater plants transported into brackish-water environments. Most leaves were deposited whole and occur in a sequence of rooted mudstones in which the leaves can form dense mats separated by thicker intervals of barren sediment. This pattern implies that many of the leaf-bearing layers may represent leaf litter fossilized by the rapid and episodic deposition of overbank sediments. The small average leaf size of the Rose Creek flora relative to coeval assemblages from the Dakota Formation and elsewhere (Wolfe and Upchurch, 1987b) corroborates taphonomic evidence for brackish-water vegetation. In plants, saline habitats produce water stress similar to that of dry climates (Walter, 1973), which selects for small xeromorphic foliage (Walter, 1973; Givnish, 1979).

Consideration of the Rose Creek flora in conjunction with evidence on Cenomanian paleoenvironments in the Western Interior indicates that the closest modern analogue may be tropical vegetation that occurs inland from mangrove swamps in regions of low tidal amplitude but which lives under brackish conditions (Richards, 1952). First, the diversity of species and genera at Rose Creek is high relative to most extant mangrove swamps, which are characterized by a few species that form monodominant stands, but the diversity is similar to that of more inland brackish-water swamps (Richards, 1952). Second, biological and physical evidence indicates that the eastern margin of the Western Interior sea had very low tidal amplitudes, probably less than one meter (Kauffman and Ryer, 1980; Ryer and Kauffman, 1980); hence, there was probably little tidal dispersal of propagules, as occurs in extant mangroves (Richards, 1952). Third, the Western Interior seaway had lower salinity than the open ocean during the middle Cenomanian, especially in nearshore regions, as indicated by the following: (1) the dominance of agglutinated foraminifera in the Graneros Shale of Kansas (Eicher, 1965), (2) distributional patterns in Cenomanian calcareous nannofossils (Watkins, 1985), and (3) isotopic ratios indicative of significant freshwater input into the Western Interior sea (Pratt, 1985). Fourth, the molluscan assemblage from Rose Creek consists almost solely of *Brachidontes*, an assemblage type inferred to represent conditions of low marine influence (Siemers, 1976). More fully marine molluscan assemblages occur in the Dakota Formation 13 miles downdip to the northwest, less than 20 m stratigraphically above the Rose Creek locality (Veatch, 1969).

KEY TO LEAF TYPES AT ROSE CREEK

The determination of leaf types found at Rose Creek can be made using the following key.

1a. Primary venation consisting of two veins that run along the basal margins of the lamina and give rise to secondary veins only on their apical sides—*Didromophyllum basingerii*

1b. Primary venation always with a medial vein that gives rise to secondary veins on both sides—Go to 2

2a. Margin entire—Go to 8

2b. Margin non-entire, either serrate or crenate—Go to 3

3a. Teeth typically less than 2 mm wide, usually visible only under magnification—Go to 4

3b. Teeth greater than 2 mm wide, easily visible to the naked eye—Go to 5

4a. Primary venation palmate, lamina lobed, teeth widely spaced—*Dicotylophyllum expansolobum*

4b. Primary venation pinnate, lamina unlobed, teeth closely spaced—*Dicotylophyllum aliquantuliserratum*

5a. Lamina broadly deltoid, secondary veins straight and usually running directly into teeth, secondary veins in the basal part of the lamina often basally branched for at least half their length—*Dicotylophyllum rosafluviatilis*

5b. Lamina elliptic to oblong and usually elongate, secondary veins apically curved or connecting with an intramarginal vein before entering teeth, lacking tendencies for basal branching—Go to 6

6a. Teeth few (<10) per leaf, strongly asymmetrical, secondary venation pinnate with an intramarginal vein—*Longstrethia varidentata*

6b. Teeth many per leaf, tending toward symmetrical and crenate, secondary venation looping and/or curving apically before entering teeth—Go to 7

7a. Teeth <2 mm wide, secondary veins thin, enclosing exmedially elongate intercostal regions—*Crassidenticulum decurrens*

7b. Crenations 2–6 mm wide, secondary veins of moderate thickness, enclosing somewhat elongate to isodiametric intercostal regions—*Reynoldsiophyllum nebrascense*

8a. Lamina predominantly 3-lobed to occasionally unlobed, lobed forms with suprabasal palinactinodromous primary venation and sinuses braced by a lateral vein that originates from the midvein and bifurcates at the sinal margin, basilaminar secondary veins strongly developed in all specimens—*Pabiania variloba*

8b. Lamina always unlobed, venation always pinnate, basilaminar secondary veins weakly developed or absent—Go to 9

9a. Lamina showing evidence of leaflet homology, either by having secondary veins that originate at lower angles on one side of the midrib or by having an alate petiole that is constricted at the base of the lamina, secondary venation tending towards eucamptodromous—Go to 10

9b. Lamina showing no evidence of leaflet homology, secondary venation festooned brochidromous or pinnate with an intramarginal vein—Go to 11

10a. Petiole alate and constricted at base of lamina, secondary veins truly eucamptodromous (not forming loops near margin), originating at similar angles on both sides of the midrib—*Citrophyllum doylei*

10b. Petiol(ule) not alate, secondary veins forming some loops near the margin, originating at slightly lower angles on one side of the midrib—*Anisodromum wolfei*

11a. Brochidodromous loops flattened at least in the apical regions of lamina, in some species forming a well-developed intramarginal vein—Go to 12

11b. Brochidodromous loops not flattened, no intramarginal vein present—Go to 17

12a. Lamina strongly oblong in shape, intramarginal vein well developed for full length of lamina, tertiary venation reticulate and irregular in behavior, unoriented to somewhat admedially oriented—Go to 13

12b. Brochidodromous loops flattened in the apical regions of lamina and sometimes in other regions but not forming a full-fledged intramarginal vein, tertiary venation unbranched to reticulate and tending towards transverse—Go to 14

13a. Laminar width ⩽1 cm, intercostal regions apically elongate—*Dicotylophyllum myrtophylloides*

13b. Laminar width 1–2 cm, intercostal regions exmedially elongate to isodiametric—*Longstrethia varidentata*

14a. Lamina probably obovate, brochidodromous looping highly angular, tertiary venation strongly reticulate, with lateral branches of the tertiary veins gradually thinning, anastomosing, and giving rise to reticulate quaternary veins—New genus A

14b. Lamina elliptic to ovate, brochidodromous looping tending towards curved, tertiary venation often unbranched and with a well-developed transverse component, quaternary venation tending to be distinct and consisting of unbranched to admedially branched veins—Go to 15

15a. Lamina strongly ovate, with elongate attenuate apex—*Pandemophyllum attenuatum*

15b. Lamina elliptic to oblong, apex (when preserved) acute—Go to 16

16a. Lamina elliptic to slightly ovate or obovate, L/W ranging from 2–3, each secondary vein in the basal two-thirds of lamina forming its own series of excostal loops—*Pandemophyllum kvacekii*

16b. Lamina oblong, L/W probably well over 3, some secondary veins in the basal two-thirds of lamina forming flattened brochidodromous arches—*Pandemophyllum* sp.

17a. Each secondary vein forming its own series of apically arching excostal loops, margin with serrations visible only under magnification—*Dicotylophyllum aliquantuliserratum*

17b. Each secondary vein forming excostal loops, these loops not forming clearly defined series, margin entire—Go to 18

18a. L/W of intercostal regions 5–6, inner series of excostal loops exmedially elongate and rounded on the outer side—*Densinervum kaulii*

18b. L/W of intercostal regions less than 3, inner series of excostal loops irregular in shape—Go to 19

19a. Lamina oblong, inner series of excostal loops tending to join margin—Go to 21

19b. Lamina elliptic to ovate, inner series of excostal secondary loops not tending to join margin—Go to 20

20a. Secondary veins with highly irregular spacing and angles of origin, not making a distinctively sharp bend before looping, tertiary veins highly irregular in course and spacing but oriented 135°–180° to midrib—*Acritodromum ellipticum*

20b. Secondary veins with relatively regular spacing and angle of origin, making a sharp bend just before looping, tertiary venation not strongly oriented—*Dicotylophyllum angularis*

21a. Lamina <1 cm wide, intercostal tertiary venation highly irregular in behavior—New genus B

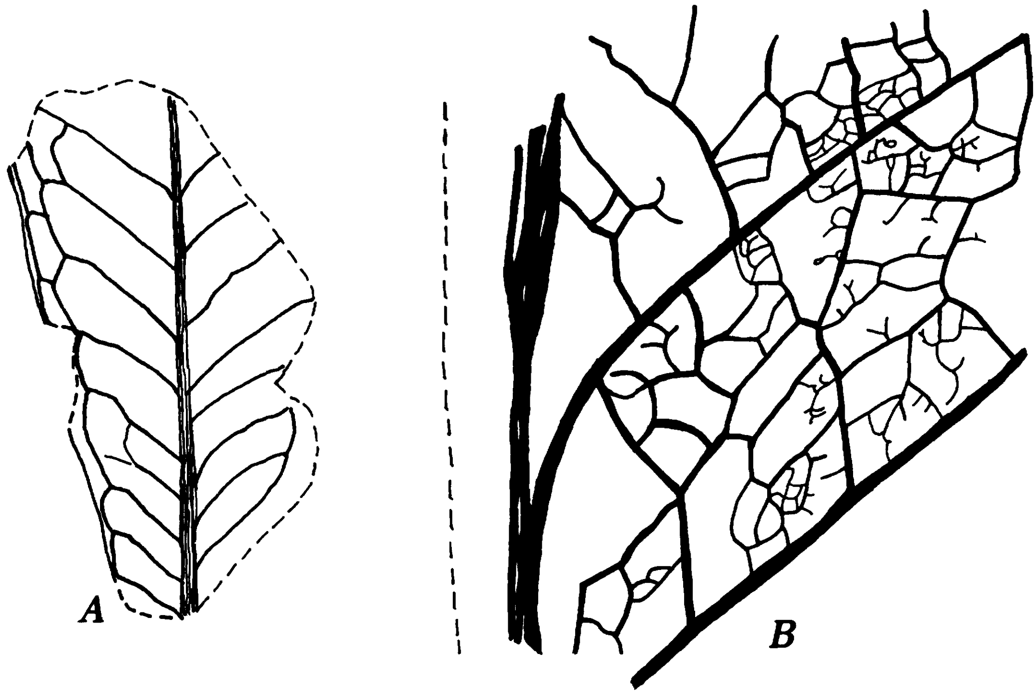


Figure 2. New genus A, 15713-4879, specimen shown on plate 1. *A*, General view of leaf, ×1. *B*, Tertiary and higher order venation, ×7.5. On the primary vein, only the vascular strands nearest the secondary veins have been drawn.

21b. Lamina 4–5 cm wide, intercostal tertiary venation tending to enclose transversely elongate regions—*Landonia calophylla*

SYSTEMATICS

Class MAGNOLIOPSIDA
Subclass MAGNOLIIDAE
Order MAGNOLIALES

New genus A

Plate 1, figures 1–4; text figure 2

Description.—Basal part of lamina preserved, L/W estimated to be over 1.5, lamina greater than 7 cm long by 4.6 cm wide (estimated width); apex and base unknown; margin entire, slightly sinuate under magnification, with mechanical reinforcement (nature of tissue unknown). Primary venation pinnate; primary vein stout, multistranded. Secondary venation irregularly brochidodromous; secondary veins thin relative to primary vein, more than 7 pairs, subopposite, somewhat irregularly spaced, decurrent on the primary vein, originating at a moderate acute angle, zig-zag in course and often slightly recurved just below junction with superadjacent secondary vein; both secondary veins of equal thickness at their junction and with the superadjacent secondary vein deflected apically, angle of junction strongly obtuse, brochidodromous arches flattened. Excostal tertiary venation poorly differentiated from secondary venation, irregularly looped. Excostal quaternary venation poorly differentiated from excostal tertiary venation, similar in behavior but forming smaller loops that tend to be strongly flattened. Intersecondary veins common, one per intercostal region, arising decurrently from primary vein and branching to form tertiary veins. Intercostal tertiary venation reticulate; tertiary veins thick relative to secondary veins, originating at variable angles but tending toward right-angled, irregular in course but tending toward transverse, enclosing roughly rectangular areas, producing thinner, non-orthogonal lateral branches that ramify, anastomose, and eventually thin into quaternary veins. Ultimate venation poorly preserved, possibly with freely ending veinlets. Marginal venation poorly preserved, either with a fimbrial vein or loops associated with mechanical tissue. Resin bodies present, interpreted as the remains of mesophyll secretory cells.

Cuticle not well preserved, no preparations made.

Number of specimens examined.—1.

Specimen number.—15713-4879.

Discussion.—New genus A is recognized on an informal basis because of fragmentary preservation. Despite this, New genus A clearly is distinct from all previously described taxa of Cretaceous angiosperm leaves. Among previously described taxa, New genus A resembles one specimen of "*Juglans*" *debeyana* Heer from the Dakota Formation of Kansas (Lesquereux, 1874, pl. 23, fig. 3), especially in the shape of the intercostal regions, angle of secondary vein origin, and pattern of tertiary venation, but it differs in having a much thicker midrib and a more uniform pattern of secondary vein branching. New genus A also resembles *"Ficus" macrophylla* from the Dakota Formation of Kansas (Lesquereux, 1892, pl. 11, fig. 1) in overall appearance, the shape of its intercostal regions, and pattern of tertiary venation but differs in having a much smaller size, better defined intercostal regions, and more regular pattern of secondary vein branching. Finally, New genus A resembles *Ficophyllum crassinerve* Fontaine from the Potomac Group (Fontaine, 1889, pls. 144–148) and similar species (*"Ficus" virginiensis* Fontaine, *Proteaephyllum ovatum* Fontaine, and certain specimens referred to *Ficophyllum tenuinerve* Fontaine) in general features, but it differs in having a more regular pattern of secondary vein looping, more obtuse angle of junction between adjacent secondary veins, intersecondary veins in every intercostal region, and thicker, more irregular tertiary and quaternary venation.

New genus A is inferred to represent an extinct taxon within Magnoliales, some extant members of which are illustrated on plate 2. An affinity to Magnoliidae is indicated by the high irregularity of the venation, the poor distinction of vein orders, and the presence of mesophyll resin bodies, which may be the remains of oil-filled cells. Within Magnoliidae, New genus A possesses a suite of features that characterizes several of the more primitive taxa within Magnoliales, including Winteraceae, Degeneriaceae, Magnoliaceae, and certain Annonaceae (pl. 2). These features include (1) an entire margin, (2) brochidodromous secondary venation that is zig-zag in course and encloses straight-sided, nearly symmetrical intercostal regions, (3) abundant intersecondary veins that branch to form tertiary veins and never number more than one per intercostal region, and (4) reticulate tertiary venation that has a tendency for transverse orientation, encloses predominantly rectangular areas, and gives rise to somewhat thinner, non-orthogonal lateral branches that eventually become quaternary veins. The probable obovate shape of New genus A is consistent with these other characters, because Magnoliales differ from other orders of Magnoliidae in showing strong tendencies for obovate leaf shape. Within the above group of families, New genus A most closely resembles Winteraceae in having a multistranded primary vein, irregularly spaced secondary veins that form a strong obtuse angle at their junction (for example, *Zygogynum* (pl. 2, fig. 5)), and marginal venation that consists of flattened brochidodromous loops. However, New genus A falls outside the range of variation shown by Winteraceae in having less decurrent secondary venation than is typical for the family and in having a slightly sinuate margin with well-developed mechanical tissue. Of the similarities shared with Winteraceae, none provides unambiguous evidence of a close relationship: the multistranded primary vein and irregular secondary venation are inferred to be primitive for the dicotyledons as a whole (Wolfe and others, 1975; Hickey and Doyle, 1977), and flattened brochidodromous loops occur in other families of Magnoliales, such as Annonaceae. New genus A and Winteraceae probably retain numerous features that were present in the common ancestor of Magnoliales, rather than derived features indicative of a close relationship.

Order LAURALES

Crassidenticulum new genus

Diagnosis.—Lamina elliptic to oblong; petiole with a decurrent wing of laminar tissue; margin predominantly non-entire, with numerous very small teeth that possess well-developed mechanical thickening along the margin; tooth construction of the chloranthoid type. Primary venation pinnate; primary vein stout to massive. Secondary venation showing strong craspedodromous tendencies but with the secondary veins curving apically and tending to form loops on the superadjacent secondary veins before entering teeth; secondary veins thin relative to the primary vein, numerous, closely spaced. Intersecondary veins present. Tertiary venation reticulate, not rigidly organized. Higher order venation irregularly reticulate.

Type species.—*Celastrophyllum decurrens* Lesquereux, 1892, p. 172, pl. 36, fig. 1—see pl. 4, fig. 1 of this report for a photograph of the holotype.

Derivation of name.—Latin, crassus = thick, denticulum = diminutive of tooth, referring to the well-developed structural reinforcement on the small teeth.

Crassidenticulum decurrens (Lesquereux) new combination

Plate 3; plate 4; text figure 3

Celastrophyllum decurrens Lesquereux, 1892, p. 172, pl. 36, fig. 1

Diagnosis.—As for genus.

Description.—Lamina narrowly elliptic to oblong, L/W 4–6, leaf 3–13 cm long by 0.5–4 cm wide; apex attenuate; base decurrent and occasionally flared immediately above petiolar region; petiolar region with a decurrent wing of laminar tissue; margin ranging from finely serrate to crenulate, often on the same leaf, very rarely entire; serrations and crenations approximately 1 mm wide by less than 1 mm tall, serrations typically straight-convex (B–1), intergrading with convex-convex

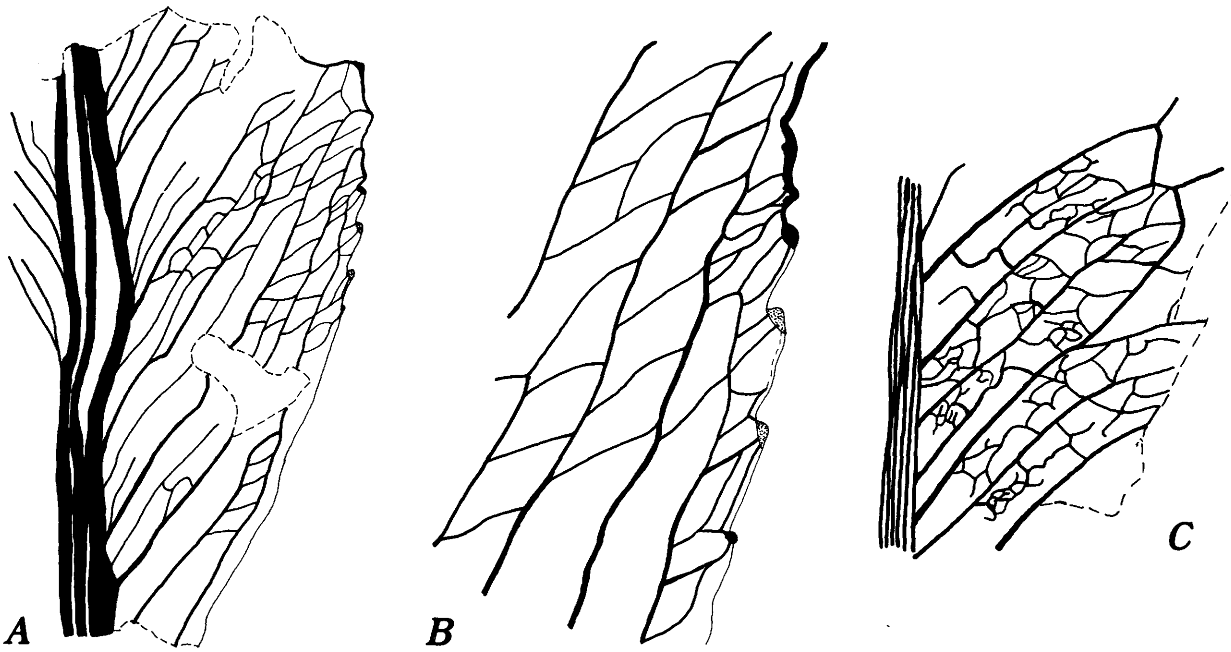


Figure 3. *Crassidenticulum decurrens* (Lesquereux) new combination. *A* and *B*, 15713-4730, specimen shown on plate 3, figures 1–3. *A*, Drawing of whole specimen, ×3. The midrib consists of three groups of coalesced vascular strands that separated when the leaf decayed. *B*, Details of margin, ×7.5. Stippled regions designate areas where the remains of the structural reinforcement have pulled away from the leaf. *C*, 15713-4746, specimen from plate 4, figure 6, higher order venation, ×7.5. The drawing of the midrib is schematic and only intended to show groups of vascular strands.

(A–1) crenulations. Primary venation pinnate; primary vein stout to massive, appearing to be multistranded in partially decayed specimens. Secondary venation fundamentally craspedodromous, but with the secondary veins curving apically and tending to form loops with the superadjacent secondary veins before entering teeth; secondary veins thin, numerous, closely spaced, decurrent on the primary vein and sometimes also giving off a decurrent branch just above the point of origin, diverging at predominantly narrow to moderate acute angles, showing an irregular pattern of variation in divergence angle, irregular to nearly regular in course, generally not much curved until at least halfway to margin, tending to form festooned brochidodromous loops on the superadjacent secondary veins, angle of the junction between secondary veins ranging from acute to obtuse, loops angular to rounded, excostal branches of the secondary veins either forming loops or running to the margin. Intersecondary veins common, mostly 1–3 per intercostal region, either arising from primary vein or arising from the exmedial side of secondary veins, intergrading with the secondary veins, irregular in course, either branching to form tertiary veins or joining with the secondary veins. Tertiary venation reticulate, often obscure; tertiary veins thick relative to the secondary veins, diverging at highly variable angles, course and spacing irregular but showing some tendency towards admedial orientation. Quaternary venation generally obscure or not preserved, irregularly reticulate; quaternary veins often curved. Areoles small, under 0.3 mm in diameter, somewhat variable in size and shape. Serrations glandular, conforming to the chloranthoid type of Hickey and Wolfe (1975), with a prominent, often thickened gland and a pair of accessory veins that run along the margin and fuse with the gland; crenulations tending toward nonglandular but with a similar arrangement of veins, usually with a zone of thickening that extends along the full width of the tooth. Thickening probably composed of scelerenchyma rather than vascular tissue, based on its tendency to be darker and show more relief than veins on the same leaf.

Cuticle poorly preserved, no successful preparations made.

Number of specimens examined.— > 100.

Holotype.—University of Kansas State Museum (UKSM) 7257.

Hypotypes.—15713-4723, 4728, 4730, 4732, 4732′, 4746, 4795a, 4938, 7817, 7818.

Discussion.—Pinnately veined, serrate-margined angiosperm foliage of Cretaceous age typically has been assigned to *Celastrophyllum* Goeppert, a form genus for leaves belonging to Celastraceae. However, this assignment appears to be invalid, at least for mid-Cretaceous leaves. The type species, *Celastrophyllum attenuatum* (Goeppert, 1854, p. 52, pl. 14, figs. 89, 91), is described and illustrated as having an entire margin and a

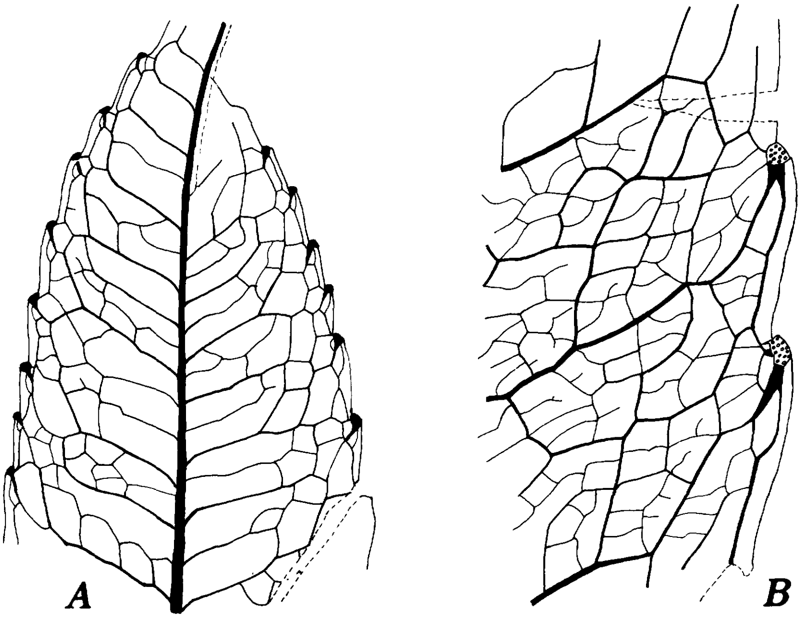


Figure 4. *Ascarina lanceolata* Hook f., U.S.G.S. Ref. Coll. no. 2327. *A*, Apical region of leaf, ×3. *B*, Details of teeth along lower right margin, ×7.5. Dotted region at the apex of each tooth designates differentially staining tissue.

distinct petiole. This combination of features is not present in the mid-Cretaceous species of *Celastrophyllum* examined by us, nor is it present in extant species of *Celastrus*. In extant angiosperms, margin type and petiolar construction typically separate genera and higher taxa. The discrepancy between the morphology of the type species and mid-Cretaceous remains has, in practice, been alleviated by many authors through expanding the concept of *Celastrophyllum* to include both entire- and non-entire-margined foliage with a general relationship to Celastraceae. This expansion of generic concept would appear logical, because extant Celastraceae range from entire-margined to toothed; however, the mid-Cretaceous species of *Celastrophyllum* examined by us do not possess features diagnostic of extant Celastraceae. Features missing from mid-Cretaceous foliage that diagnose extant Celastraceae include a distinct petiole, teeth with a glandular, non-deciduous seta directed into the sinus (a celastroid tooth), and subparallel tertiary venation with low-angle branching and perpendicular orientation to the midvein. Many individual species of *Celastrophyllum* differ from one another in features that typically segregate extant genera and families, including tooth construction, presence or absence of a structurally reinforced margin, size and structure of the primary vein, pattern of secondary venation, and details of tertiary and higher order venation. Thus, more than one genus is needed to accurately reflect the systematic relationships of pinnately veined, serrate-margined foliage traditionally assigned to *Celastrophyllum*.

Among other previously described genera that circumscribe only fossil leaves, none closely resembles the Rose Creek remains when comparison is restricted to the type species and similar forms. *Quercophyllum* Fontaine shows the closest resemblance, but the type species, *Q. grossidentatum* (Fontaine, 1889, pl. 156, fig. 9), has significantly larger teeth, no marginal thickenings, and a strongly attenuated primary vein.

Among previously described species of Cretaceous angiosperms that have incorrect generic assignments, *C. decurrens* shows similarities with many species but represents a distinct taxon. *C. decurrens* most closely resembles *"Myrica" zenkeri* (Ett.) Heer, illustrated in photographs by Vakhrameev (1952, pl. 11, figs. 1, 2; pl. 41, fig. 1), in laminar size and shape, the size and shape of the teeth, and the presence of strongly developed marginal thickenings over the teeth. However, all photographically illustrated specimens of *"M." zenkeri* have no venation visible above the first order, making determination of conspecificity of *C. decurrens* and *"M." zenkeri* impossible. *C. decurrens* closely resembles *"Myrtophyllum" torreyi* (Lesquereux) Dorf, such as specimens photographically illustrated by Brown (1962, pl. 50, figs. 1–4, 7–9), in nearly all preserved features but differs in having secondary veins that arch apically and directly enter the teeth, rather than connect with an intramarginal vein. Thus, while the two species may be congeneric, they are distinct. *Crassidenticulum decurrens* also resembles *Celastrophyllum hunteri* Ward from the Potomac Group of Virginia (Ward, 1905, pl. 4, fig. 9) in having a

Table 1. Comparison of *Crassidenticulum*, *Densinervum*, and related extant taxa

[NA. = not applicable]

Taxon	Midvein	Secondary venation	Intersecondary veins	Tertiary venation	Margin	Tooth type	Marginal thickening over teeth
Crassidenticulum	Multistranded	Fundamentally craspedodromous, but with tendency to form loops and/or curve apically.	Common, originate from midvein or secondary veins.	Irregularly reticulate.	Finely serrate to crenate, rarely entire.	Chloranthoid	Well developed.
Densinervum	Solid	Festooned brochididromous.	Common, originate from midvein or secondary veins.	Irregularly reticulate.	Entire	N.A.	N.A.
Ascarina	5 to 7-stranded at base of lamina.	Fundamentally craspedodromous, but with tendency to form loops and curve apically.	Present in some species, originate from midvein.	Irregularly reticulate, often exmedially oriented.	Serrate	Chloranthoid, sometimes with one accessory vein supressed.	Absent.
Hedyosmum	Usually 3- to 5-stranded at base, multistranded at base in one sp.	Fundamentally craspedodromous, usually curved apically.	Present in some species, originate from midvein.	Reticulate.	Serrate	Chloranthoid	Sclerenchyma over tooth apex in some species.
Chloranthus	5-stranded at base of lamina.	Festooned brochidodromous.	Weakly developed to absent, originate from midvein.	Transverse reticulate.	Serrate	Chloranthoid	Resistant tissue over tooth apex, not strongly developed as in *C. decurrens*.
Sarcandra	5-stranded at base of lamina.	Festooned brochidodromous.	Weakly developed to absent, originate from midvein.	Transverse reticulate.	Usually serrate.	Chloranthoid	Resistant tissue over tooth apex, not strongly developed as in *C. decurrens*.
Trimenia	3-stranded or coalesced strands.	Usually pinnate with an intramarginal vein, ± simple craspedodromous in *T. papuana*.	Absent	Admedially ramified and with a reticulate component.	Usually serrate.	Monimioid	Absent, but with opaque tissue over gland.
Piptocalyx	5-stranded	Pinnate with intramarginal vein.	Absent	Admedially ramified.	Entire	N.A.	N.A.

multistranded primary vein, a similar pattern of secondary venation, and a thickened, serrate margin, but differs in having more closely spaced and more rounded teeth that often are thickened only over the gland, and in having more strongly craspedodromous secondary venation. *Crassidenticulum decurrens* shows some similarity to two species of *Celastrophyllum* from the Upper Cretaceous Amboy clays of New Jersey, *C. angustifolium* Newberry (Newberry, 1895, pl. 14, figs. 11, 12, 14–16) and *C. crenatum* Heer (Berry, 1911b, pl. 22, fig. 9), especially in the size and shape of the lamina, pattern of secondary venation, and the size of the teeth, but it differs in having more regular and fundamentally craspedodromous secondary venation. *Crassidenticulum decurrens* resembles *"Salix" newberryana* Hollick (in Newberry, 1895, pl. 11, fig. 2) from the Upper Cretaceous of New Jersey in its size, shape, and number of intersecondary veins, but it differs in having no distinct petiole and in having less apically curved secondary venation. Finally, *C. decurrens* resembles *?Rogersia denticulata* from the Lower Cretaceous of the Soviet Union (Samylina, 1960, pl. 1, fig. 10, text fig. 6) in size, shape, and base, but it differs in having much smaller teeth and in having more apically curved and less obviously craspedodromous secondary veins. These similarities indicate that *Crassidenticulum* may have been a diverse genus during the Late Cretaceous, but detailed consideration of this possibility must await revision of other floras.

The modern affinities of *Crassidenticulum* appear to lie with Chloranthaceae, with additional affinities possibly to Trimeniaceae (table 1). The combination of a poorly differentiated petiole and blade, a multistranded primary vein, irregular secondary and higher order venation, and chloranthoid teeth is restricted to the subclass Magnoliidae, and in particular the orders Laurales and Illiciales. Between these two orders, fundamentally craspedodromous secondary venation is restricted to Laurales. Within Laurales, the exact pattern of secondary venation found in *Crassidenticulum* occurs only in the chloranthaceous genera *Ascarina* and *Hedyosmum* (pl. 7, figs. 2, 3; text fig. 4), and *Trimenia* (pl. 7, fig. 1) has a related pattern of secondary venation where the craspedodromous secondary veins are interconnected near the laminar margin by thinner lateral branches, which form a weak intramarginal vein. Among extant Chloranthaceae and Trimeniaceae, *Crassidenticulum* most closely resembles *Ascarina* and *Hedyosmum* in having closely spaced and apically curved secondary veins, common intersecondary veins, and small chloranthoid teeth. In addition, some species of *Hedyosmum* have sclerenchymatous tissue over the apex of each tooth (Richard Keating, oral comm., 1988). However, *Crassidenticulum* differs from *Ascarina* and *Hedyosmum* in having more irregular secondary venation, intersecondary veins that can arise either from a primary vein or the admedial side of a secondary vein, and irregular tertiary and quaternary venation, features postulated as primitive to the angiosperms as a whole (Doyle and Hickey, 1976; Hickey and Doyle, 1977). Thus, *C. decurrens* shows its closest similarities with extant Chloranthaceae but appears to represent a distinct genus.

Densinervum new genus

Diagnosis.—Lamina entire margined; margin with mechanical reinforcement; petiolar region distinct from lamina. Primary venation pinnate; primary vein moderate. Secondary venation "festooned" brochidodromous; secondary veins thin relative to the primary vein, enclosing exmedially elongate intercostal regions that are much longer than broad. Intersecondary veins common, arising from the primary vein or the exmedial sides of secondary veins, typically branching to form tertiary veins. Tertiary venation both reticulate and ramified, irregular, tending to enclose regions elongate parallel to the secondary veins. Quaternary venation irregularly reticulate; quaternary veins often curved.

Type species.—*Densinervum kaulii* new species.

Derivation of generic name.—Latin, densus = close, and nervis = nerve, referring to the closely spaced secondary veins.

Densinervum kaulii new species

Plate 5; text figure 5

Diagnosis.—As for genus.

Description.—Lamina ovate and in one specimen with a shallow indentation just above the widest part, L/W about 1.5–2, lamina approximately 3–5 cm long by 2–3 cm wide (estimated length and width); apex missing; base obtusely cuneate to rounded; margin entire, with structural reinforcement; petiole distinct, but in one specimen with a very narrow decurrent wing of laminar tissue along one side. Venation pinnate; primary vein moderate. Secondary venation "festooned" brochidodromous; secondary veins thin or moderate relative to the primary vein, numerous, opposite to alternate, irregularly and very closely spaced (7–8 veins per cm), sometimes slightly decurrent on primary vein, moderate acute, predominantly straight, with only slight undulation before looping; secondary veins bifurcating when forming loops, angle of brochidodromous junction acute; two series of excostal secondary loops present, inner series exmedially elongate, with rounded outer sides, outer series more or less isodiametric. Intersecondary veins common, usually 1–2 per intercostal region, intergrading with both the secondary and tertiary veins, decurrent on primary vein and sometimes originating from the secondary veins, generally oriented at an oblique angle to the secondary veins and unevenly dividing the intercostal region, branching to form tertiary veins or joining with the subadjacent secondary vein. Tertiary venation predominantly reticulate, but with some tertiary veins thinning to form quaternary veins; tertiary veins thick relative to the secondary veins, ranging from acute to obtuse on both sides of the secondary veins, tending to be widely spaced and admedially oriented. Quaternary venation irregular, curved, similar to tertiary venation in behavior; quaternary veins intergrading with the tertiary veins and originating from thin branches of the tertiary veins. Marginal venation looped, the loops tending to be flattened parallel to the margin.

Cuticle not preserved on specimens.

Number of specimens examined.—6.

Holotype.—15713-4841A, 4841A′ (part and counterpart).

Paratypes.—15713-4800, 4830, 7815.

Derivation of epithet.—In honor of Robert B. Kaul, and in recognition of his contributions to angiosperm phylogeny.

Discussion.—*Densinervum kaulii* is readily distinguished from all previously described taxa by the combination of (1) an entire margin, (2) very closely spaced secondary veins, (3) an inner series of exmedially elongate excostal loops, (4) common intersecondary veins that can arise from secondary veins, (5) irregular tertiary venation that tends to enclose elongate regions parallel to the secondary veins, and (6) curved quaternary venation. *D. kaulii* most closely resembles *Crassidenticulum decurrens* in having numerous thin and closely spaced secondary veins and a similar pattern of tertiary and quaternary venation. In addition, the origin of intersecondary veins from the exmedial side of the secondary veins is similar to the condition found in *C. decurrens*, where a secondary vein bifurcates shortly above its point of origin; this similarity in behavior and position implies that the two conditions are homologous. *D. kaulii* differs from *C. decurrens* in always having an entire margin (found on occasional specimens of *C. decurrens*), an obtusely cuneate to rounded base, a distinct petiole, a moderate primary vein, more irregular secondary vein looping, and an exmedially elongate inner series of excostal secondary loops. Among other previously described Cretaceous leaf types, *Densinervum kaulii* resembles entire-margined species of *Celastrophyllum* from Zone I (Aptian-lower Albian) of the Potomac Group such as *C. obovatum* (Fontaine, 1889, pl. 172, figs. 9, 10), *C. latifolium* (Fontaine, 1889, pl. 172, figs. 3, 6; pl. 173, fig. 13), and cf. *C. obovatum* of Upchurch

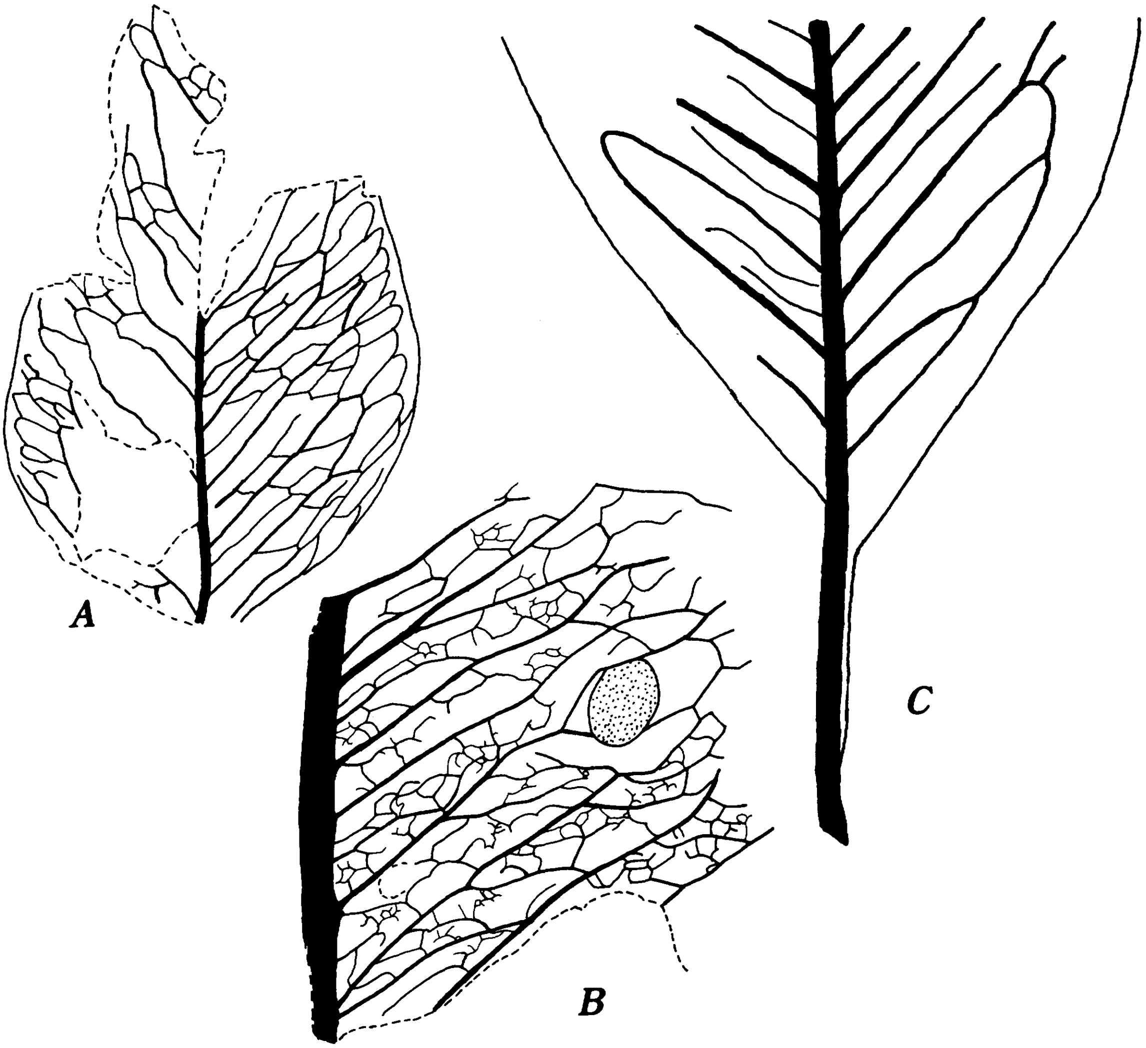


Figure 5. *Densinervum kaulii* new genus and species. *A*, 15713-4880, ×3. *B*, 15713-4841A, specimen shown on plate 5, figures 5 and 6, details of tertiary and higher order venation, ×7.5. The circular stippled region designates a fossil root that penetrates the leaf vertically. *C*, 15713-7815, specimen shown on plate 5, figure 2, ×7.

(1984, fig. 6) in shape, primary vein thickness, and angle of secondary vein divergence, but it differs in having a distinct petiole, in the shape of its excostal secondary loops, and in details of tertiary venation.

The irregular secondary and higher order venation of *Densinervum kaulii* are most characteristic of the extant subclass Magnoliidae. Within Magnoliidae, *D. kaulii* shows no close resemblance to any extant family. *D. kaulii* resembles some Canellaceae (certain species of *Cinnamodendron*) in secondary vein spacing and proportioning of the excostal secondary loops but differs in having a distinct petiole, less angular secondary vein looping, and less ramified higher order venation, features that are fairly uniform within extant Canellaceae. Among fossil Magnoliidae, however, *D. kaulii* closely resembles *Crassidenticulum decurrens*. This close resemblance implies a close relationship between the two taxa, which, by extension, would imply a relationship with extant Chlorathaceae. Thus, *Densinervum kaulii* represents an extinct taxon that may be related to extant Chloranthaceae but does not have all of the characters that circumscribe the extant family.

Landonia new genus

Diagnosis.—Leaf oblong; base decurrent; margin with mechanical reinforcement. Primary vein stout, multistranded. Secondary venation festooned brochidodromous, with the basalmost pairs of secondary veins closely spaced and the superadjacent pairs wider apart; secondary veins originating at broad acute or higher angles, tending toward sinuous; intercostal regions roughly isodiametric above the basalmost few centimeters of the leaf. Intercostal tertiary venation reticulate, consisting of thick, roughly transverse veins that give rise to somewhat thinner, admedially oriented lateral branches. Excostal tertiary venation admedially ramified.

Type species.—Landonia calophylla.

Derivation of name.—In honor of James Landon, and in recognition of his contributions to the paleobotany of Nebraska.

Landonia calophylla new species

Plate 6, figures 2–5; text figure 7

Diagnosis.—As for genus.

Description.—One side of the lamina preserved, laminar shape oblong, estimated L/W over 2, lamina well over 6.7 cm long by about 5 cm wide (estimated width); apex missing; base strongly obtuse but decurrent at the junction with the petiolar region; petiolar region at least 3 cm long; margin entire, with structural reinforcement. Primary venation pinnate; primary vein stout, multistranded. Secondary venation "festooned" brochidodromous, with some intracostal branching; secondary veins moderate to thick relative to the primary vein, possibly multistranded, numbering more than five pairs, irregularly spaced but with the basalmost two pairs very close to one another and the others much farther apart, these latter secondary veins enclosing roughly isodiametric intercostal regions; secondary veins decurrent on the primary vein for a short distance, originating at predominantly broad acute, rarely right, angles, with one of the secondary veins producing an intracostal branch on its admedial side and another of the secondary veins producing an intracostal branch on its exmedial side, secondary veins often sinuous in course, more strongly curved above their junctions with the subadjacent secondary veins, looping well within the margin; superadjacent secondary vein deflected apically, usually with each secondary vein of roughly equal thickness both below and above its junction with the subadjacent secondary vein, but in one case with the secondary vein of much greater thickness below the junction and appearing to bifurcate; excostal branches of the secondary veins forming a complete inner series and an incomplete outer series of loops, the loops of the inner series either confluent with the margin or with a highly irregular shape, giving rise to one or more admedial branches per loop. Intercostal tertiary venation with two components, the thicker component unbranched to reticulate,

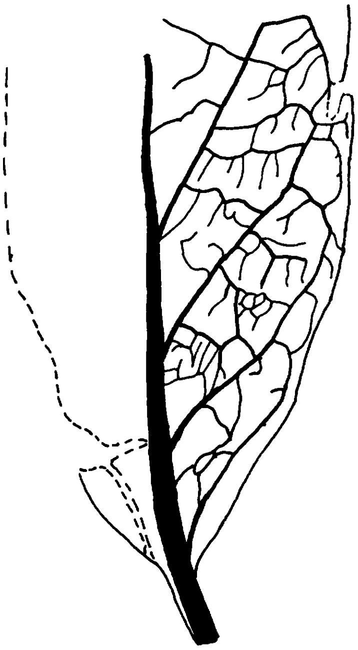


Figure 6. *Gomortega keule* (Mol.) Baill. (Gomortegaceae), U.S.G.S. Ref. Coll. no. 2462, leaf from plate 6, figure 1, and plate 7, figure 5, ×1.4. To facilitate comparison with the specimen in figure 7, only the venation on the right side of the leaf is illustrated.

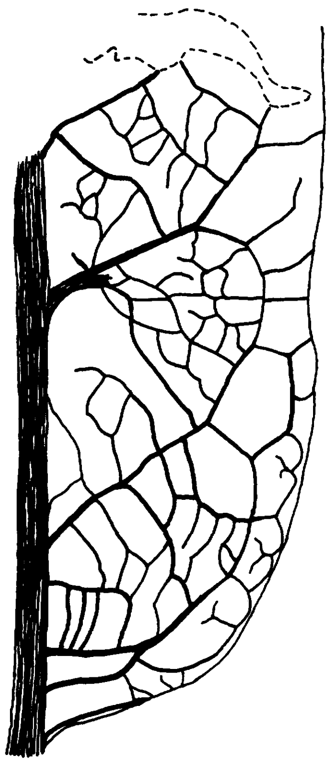


Figure 7. *Landonia calophylla* new genus and species, 15713-4881A, specimen shown on plate 6, figures 3–5, ×1.4. Note the similarity in tertiary venation to that of *Gomortega keule*, especially the tertiary venation in the uppermost intercostal region.

moderate to thick relative to the secondary veins, originating at predominantly acute to right angles on both sides of the secondary veins, subparallel, tending to enclose elongate regions, weakly transverse to oblique relative to the secondary veins, but in one intercostal region with a slight tendency to be admedially ramified; the thinner component originating as non-orthogonal lateral branches, typically from the admedial side of the thicker veins, branching, anastamosing, and eventually thinning to form quaternary veins. Tertiary venation of excostal secondary loops admedially ramified. Quaternary (and higher order?) venation poorly preserved. Small dark spots present on the lamina, interpreted as the remains of mesophyll secretory cells.

Cuticle poorly preserved, no preparations made.

Number of specimens examined.—1.

Holotype.—15713-4881A, 4881A' (part and counterpart).

Derivation of epithet.—Greek, kalos = beauty, and phyllon = leaf, referring to the beautiful appearance of the fossil.

Discussion.—Despite the fragmentary preservation of the one known specimen of *Landonia calophylla*, enough of the foliar architecture is preserved to indicate that it represents a distinct genus of Cretaceous angiosperms. The combination of features that distinguishes *Landonia* from all other genera of extant and fossil angiosperms includes (1) oblong shape, (2) widely spaced secondary veins that have an irregular course and enclose roughly isodiametric intercostal regions above the base of the lamina, (3) predominantly transverse intercostal tertiary venation that produces thinner and typically admedial lateral branches, and (4) presence of admedially ramified tertiary veins in the excostal secondary loops. Although these features may occur individually in one or more taxa, together they form a distinctive suite of features that permit identification of leaves even in a fragmentary state.

In addition, many of the individual venational features found in *Landonia* are unusual in the context of extant and fossil dicot leaves. Multistranded secondary veins are unknown in extant dicots and all previously described Cretaceous angiosperm leaves, even for species with multistranded primary veins and extremely irregular vein organization. Admedial intracostal branching of the secondary veins occurs in scattered extant taxa such as Canellaceae (*Capsicodendron*) and Theaceae (various genera), and in Early Cretaceous taxa such as *Quercophyllum tenuinerve* Fontaine (see Hickey and Doyle, 1977, figs. 5, 17); however, exmedial intracostal branching of the secondary veins has never been observed in any extant or fossil angiosperm. The high irregularity in the shape of the excostal secondary loops, in conjunction with the production of admedially ramified tertiary veins, is atypical of extant dicots, although present in the possibly related Gomortegaceae (see below). Finally, the high variation found in thickness of one secondary vein has no known extant counterpart. This secondary vein is significantly thicker than the other secondary veins at its point of origin and abruptly thins at two points of branching: (1) close to the midrib, where a short, stubby, intracostal branch originates on the exmedial side, and (2) at the point of junction with the subadjacent secondary vein, where the thick secondary vein appears to bifurcate. This unusual pattern of secondary vein behavior could simply represent a developmental abnormality (teratology), a distinct possibility considering the preservation of only one specimen. Alternatively, such variable behavior in secondary venation could reflect the low degree of vein organization that typifies many species of early angiosperms.

Landonia calophylla cannot be placed within an extant family but most closely resembles Laurales of primitive to intermediate advancement (table 2; pl. 6, fig. 1; pl. 7; text figure 6). Among extant dicots, the combination of irregular secondary and higher order venation and laminar secretory cells is restricted to subclass Magnoliidae. Within Magnoliidae, the features of secondary and tertiary venation found in *L. calophylla* occur only in Laurales but never within a single extant family. *Landonia* resembles Amborellaceae, Austrobaileyaceae, and Monimiaceae in having an ovate to oblong shape, clustering of the basalmost 2–3 pairs of secondary veins, and predominantly isodiametric intercostal regions above the base of the lamina; within this group, *Landonia* most closely resembles Monimiaceae such as *Ephippiandra* in having sinuous margins to the intercostal regions. In contrast, *Landonia* resembles Gomortegaceae in having the following set of venational features: (1) excostal secondary loops that have a highly irregular shape, (2) widely spaced intercostal tertiary veins that have a weakly transverse to oblique orientation (compare the tertiary veins from the uppermost intercostal region of *Landonia calophylla* in pl. 6, fig. 3, and text figure 7 with those of *Gomortega keule* (Mol.) Baill. in pl. 6, fig. 1, and text figure 6), (3) the tendency for these intercostal tertiary veins to give rise to thinner lateral branches, usually on their admedial sides, and (4) admedially ramified excostal tertiary veins. This mixing of features that today are restricted to separate families is of phylogenetic significance, because it provides an intermediate condition between what is found in extant Monimiaceae and extant Gomortegaceae (table 2). Thus, *Landonia calophylla* provides paleobotanical evidence for the close relationship postulated between Monimiaceae and Gomortegaceae on the basis of comparative morphology (Takhtajan, 1980).

Table 2. Comparison of *Landonia* and related extant taxa

Taxon	Shape of intercostal regions	Margins of intercostal regions	Margins of excostal secondary loops	Intercostal tertiary venation	Excostal tertiary venation
Landonia	Isodiametric above base of lamina.	Highly sinuous	Highly sinous	Transverse to oblique, with thinner and usually admedially oriented lateral branches, thicker branches sometimes with a tendency to be admedially ramified near midvein.	Admedially ramified.
Austrobaileyaceae	Isodiametric above base of lamina.	Curved	Curved	Reticulate and admedially oriented.	Reticulate.
Amborellaceae	Isodiametric above base of lamina.	Mostly straight-sided.	Straight-sided to sinuous.	Reticulate and admedially ramified near midvein.	Reticulate and admedially ramified.
Monimiaceae	Isodiametric above base of lamina in most genera.	Straight-sided to sinuous, depending on genus.	Straight-sided to moderately sinuous, depending on genus.	Usually reticulate and admedially ramified near midvein.	Reticulate to admedially ramified.
Gomortegaceae	Exmedially elongate	Slightly sinuous	Highly sinuous	Transverse to oblique, with widely spaced veins that produce admedially ramified lateral branches.	Admedially ramified.
Hernandiaceae	Exmedially elongate in leaves that have at least several pairs of secondary veins.	Straight-sided	Tending to be rounded, often slightly sinuous.	Transverse to oblique, usually reticulate, rarely as in Gomortegaceae.	Usually admedially ramified.

Pabiania new genus

Diagnosis.—Lamina predominantly 3-lobed rarely 2-lobed or unlobed; margin entire. Primary venation of lobed forms suprabasal palinactinodromous; lateral primary veins decurrent on midvein, at lower angle than superadjacent secondary veins. Basilaminar secondary veins strongly developed, at same angle as the lateral primary veins or (in unlobed forms) superadjacent pair of secondary veins. Sinus bracing accomplished by the lowest pair of secondary veins on the midvein, these running directly to the sinus and bifurcating at the laminar margin, with each branch of the bracing vein running subparallel to laminar margin and connecting with the secondary veins of the lobes. Tertiary venation irregularly branched; tertiary veins thin and oriented at right or low obtuse angles to primary veins. Quaternary venation non-orthogonal. Quinternary venation weak, irregular; quinternary veins highly branched and showing a strong tendency to ramify within the areoles.

Guard cell pair elongate, elliptic to spindle shaped; lamellar cuticular thickenings present to absent, sometimes on the same leaf. Stomatal complex generally brachyparacytic, but with some leaves having rare laterocytic, hemiparacytic, and weakly cyclocytic to anomocytic stomata. Trichome bases (when present) consisting of an angular, heavily cutinized pore and associated cells that are scarcely modified but show a strong tendency to be radially oriented.

Type species.—Pabiania variloba Upchurch and Dilcher.

Derivation of generic name.—In honor of Roger Pabian, and in recognition of his discovery of the Rose Creek locality and other contributions to Nebraska geology.

Pabiania variloba new species

Plate 8; plate 9, figures 1–3; plate 11, figures 1–7;
text figures 8 and 9

Acerites multiformis Lesquereux, Retallack and Dilcher, 1981, fig. 4.

Diagnosis.—As for genus.

Description.—Phyllotaxy opposite and decussate. Leaf commonly trilobate, rarely bilobate or unlobed; base ranging from acute to obtuse and tending towards cuneate, with the basalmost portion of the lamina decurrent on the petiole; margin entire. Trilobed leaves with their widest part above the middle of the lamina, L/W 0.8–1.0; blade 2.5–5.7 cm long by 2–5.5 cm wide; medial lobes 0.7–2 cm long, sometimes with the widest part above the base; lateral lobes 0.6–1.6 cm long (measured from the sinus to lobe tip), oriented at acute angles to the medial lobe, with their apical sides oriented at broad

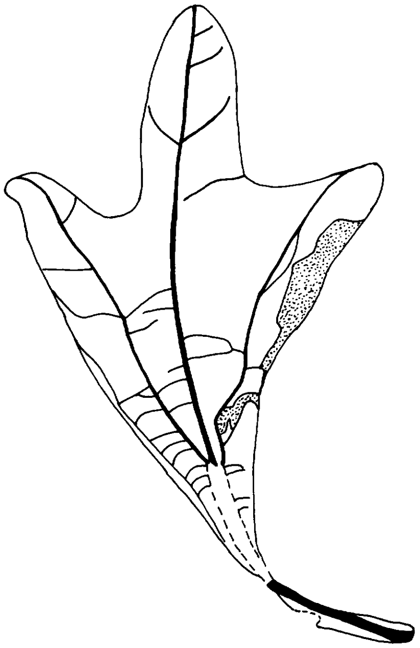


Figure 8. *Pabiania variloba* new genus and species, 15713-3327, specimen shown on plate 8, figure 4, ×3.

acute to right angles to the midvein; apex of lobes acute to rounded; petiole preserved in two isolated trilobed leaves, 3.5–4.2 cm long, shorter in leaves preserved on a shoot, but this possibly resulting from fossilization of the leaves in an immature state. Unlobed leaves broad elliptic to obovate, L/W 1–2; blade 1.5–3 cm long by 1.7–4 cm wide; apex rounded; petiole not preserved in any isolated unlobed leaves. Primary venation suprabasal palinactinodromous in 3-lobed leaves, pinnate in unlobed leaves; midvein moderate; lateral primary veins similar to midvein in thickness, at lower angle than superadjacent secondary veins and tending to be recurved, commonly decurrent on midvein, producing 1–3 festooned brochidodromous external branches. Secondary venation fundamentally festooned brochidodromous; secondary veins thin or moderate relative to primary veins, 3–6 pairs along midvein, with one pair of basilaminar secondary veins present in all leaves, alternate, moderate acute, straight to apically curved, looping tending to be festooned brochidodromous except near sinuses, where the secondary veins connect with a branch of the sinus-bracing vein; angle of brochidodromous junction right-angled to obtuse; excostal secondary loops curving apically. Intersecondary veins absent. Tertiary venation unbranched to bordering on reticulate; tertiary veins thin relative to secondary veins, opposite to alternate, closely but somewhat irregularly spaced, originating at acute to right angles, bending at points of branching and at junctions with other tertiary veins, oriented at 90°–110° to primary veins. Quaternary venation intergrading with tertiary venation, generally unbranched; quaternary veins opposite to alternate, non-orthogonal, enclosing somewhat elongate, 4-sided regions. Quinternary venation highly irregular, both ramified and reticulate, arising both from thick lateral branches of the quaternary veins and from the sides of lower order veins; quinternary veins weak, curved, often producing a series of H-shaped branches that can suddenly change orientation. Areolation poorly developed, average areolar size minute. Marginal venation consisting of a thin fimbrial vein.

Upper cuticle of medium thickness, with well-developed flanges; cell shape isodiametric to mixed, cells generally 4 to 5 sided, rarely 3 or 6 sided, 12–30 microns long by 6–22 microns wide, anticlinal wall contour commonly straight, more rarely curved; cells with sharp corners; external and internal sculpture smooth under light microscopy ×500. Trichome bases present on the upper cuticle of some specimens, consisting of a small, heavily cutinized pore and several associated cells; pore isodiametric to elongate, with straight to concave sides; associated cells tending to be radially oriented and underthrusting the outer rim of the pore. Two types of idioblasts observed on the upper cuticle; the first type of idioblast consisting of a single cell with the shape and cutinization of trichome bases, perhaps representing the basal cell of an abscissed trichome, common; the second type of idioblast similar to unmodified epidermal cells but with thin outer cuticle, adjacent cells with secondary divisions parallel to the anticlinal walls of the idioblast, found in only one specimen.

Lower cuticle ranging from medium to thin, usually thinner than the upper cuticle and often adhering to it in preparations; flanges typically present but sometimes only visible with phase-contrast microscopy; cell shape and number of sides as on upper cuticle; cells 12–38 microns long by 8–32 microns wide; anticlinal wall contour straight-curved, rarely undulate, when undulate with no more than one wavelength per cell side; external and internal sculpture smooth under light microscopy ×500. Guard cell pair usually elliptic, rarely rectangular or spindle-shaped, L/W usually 2–3, 15–30 microns long by 6–18 microns wide; stomatal poles flattened to truncate; lamellar cuticular thickenings present on the guard cells of many specimens, occurring on the outer walls and not extending the full length of stoma, not present in other specimens, but here with an elaborated cuticular flange adjacent to the subsidiary cells (this elaborated flange is similar to the lamellar cuticular thickenings in *Pandemophyllum*). Subsidiary cell arrangement usually brachyparacytic, but with rare laterocytic, hemiparacytic, and weakly cyclocytic to anomocytic stomata present on some leaves; subsidiary cells often with curved tangential walls and showing a tendency to be radially compressed, in a few specimens with thinner outer cuticle either over the entire subsidiary cell or in a

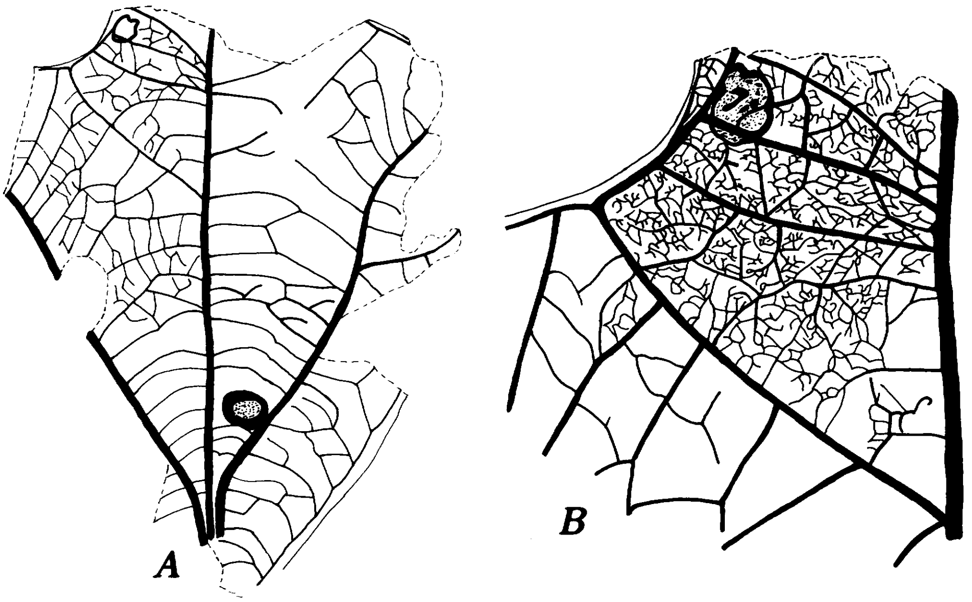


Figure 9. *Pabiania variloba* new genus and species, 15713-4845, specimen shown on plate 9, figure 2. The circular regions on the leaf represent galls. *A*, General view of venation, ×3. *B*, Closeup of sinus region (upper left corner of 9*A*) showing details of sinus bracing and higher order venation, ×7.5.

narrow zone adjacent to the guard cells. Trichome bases present on many specimens, structure as for upper cuticle. Idioblasts present on one specimen, identical to the first type observed on the upper cuticle. Mesophyll secretory bodies present in most cuticular preparations, spherical, similar in diameter to the epidermal cells, interpreted as the remains of secretory cells.

Number of specimens examined for foliar architecture.— > 100.

Number of specimens examined for cuticular anatomy.—16.

Holotype.—15713-3317, 3317′ (part and counterpart).

Paratypes.—15713-3316, 3318, 3320, 3320′, 3327, 3546, 4845, 4847, 7801, 7801′, 7838, 7839, 7840, 7841.

Derivation of epithet.—Latin, varius = variable, lobus = lobe, referring to the variable development of lobation.

Discussion.—The name *Pabiania* is proposed for predominantly 3-lobed foliage of Cretaceous age that traditionally has been assigned to Lauraceae. Typically, foliage of the *Pabiania*-type has been assigned to the extant lauraceous genera *Sassafras* and *Lindera*, which have a similar shape and pattern of sinus bracing. However, analysis of higher order venation indicates that these generic assignments, as well as an assignment to extant Lauraceae, are incorrect. All extant Lauraceae are characterized by quaternary venation that has at least tendencies for orthogonal rooting, and the majority of genera possess reticulate quinternary venation that forms a fairly regular network of areoles. (For examples, see pl. 9, fig. 5 and pl. 10, fig. 1.) This suite of features is interpreted to be derived within Laurales, because it is absent from the more primitive families of the order, such as Amborellaceae, Trimeniaceae, Idiospermaceae, Atherospermataceae, and Gomortegaceae, and occurs only in relatively derived families, such as Lauraceae and Gyrocarpaceae. *Pabiania*, in contrast, possesses the generalized features of higher order venation that characterize most families of Laurales; namely, quaternary venation that originates at variable angles and quinternary venation that is highly ramified and forms an irregular system of areoles. Although the occurrence of primitive higher order venation in the fossils does not in itself preclude a close common ancestry with Lauraceae, primitive higher order venation does preclude an assignment to extant genera of Lauraceae such as *Sassafras* and *Lindera*.

No previously described fossil taxon has a generic name that can validly be applied to the Rose Creek remains. *Acerites* Viviani, a name used for these same remains by Retallack and Dilcher (1981) and for similar Dakota remains by Lesquereux (1892), cannot be used because the type species, *Acerites ficifolia* (Viviani, 1833, p. 131, pl. 9, fig. 5), has a different pattern of primary venation and hence appears to belong to a different genus and family. *Araliaephyllum* Fontaine cannot be used because the type species, *A. obtusilobum* (Fontaine, 1889, p. 317, pl. 163, fig. 14; pl. 164, fig. 3) is five-lobed, with basally palinactinodromous primary venation and a different pattern of sinus bracing. No other previously described fossil genus has a suite of venational features similar to that of the Rose Creek remains.

Although *Pabiania variloba* was originally assigned to the species *"Acerites" multiformis* Lesquereux (Retallack and Dilcher, 1981), close examination of foliar architecture indicates that it represents a distinct, though similar, species. *P. variloba* differs from *"A." multiformis* in having the combination of suprabasal palinactinodromous primary venation, sinus bracing accomplished by a vein that originates from the midvein and bifurcates at the sinus margin, and (in trilobed leaves) the absence of subsidiary lobes on the middle lobe. *Pabiania variloba* shows close similarities to additional species of trilobed leaves known from uppermost Albian and Cenomanian strata; however, most of these species lack preserved venation above the first or second order, making detailed comparisons difficult. In terms of size and shape, *P. variloba* most closely resembles *"Sassafras" bradleyi* Brown from the mid-Cretaceous (upper Albian to lower Cenomanian) Aspen Shale of Wyoming (Brown, 1933, pl. 2, fig. 5); however, the two taxa are probably not conspecific because the sinus-bracing vein in *"S." bradleyi* appears to bifurcate within the margin. Further, *"S." bradleyi* lacks preserved venation above the second order. Among angiosperms from the Dakota Formation, *P. variloba* most closely resembles *"Lindera" venusta* (Lesquereux, 1892, pl. 16, figs. 1, 2) in size and shape but differs in having suprabasal lateral primary veins and possibly somewhat different sinus bracing. Other taxa of Late Cretaceous angiosperm leaves showing strong similarities to *P. variloba* in shape and lower order venational features include certain specimens of *"Sassafras" acutilobum* Lesq. as illustrated by Newberry (1895, pl. 25, figs. 1–10; excluding pl. 26, figs. 2–6) and *"Sassafras" progenitor* Newberry (1895, especially pl. 27, fig. 3). However, *P. variloba* differs from *S. acutilobum* in having stronger basal lobes and from *S. progenitor* in having suprabasal lateral primary veins.

Pabiania variloba also shows similarities to Albian species of angiosperm leaves invalidly assigned to Lauraceae, including *"Sassafras" bilobatum* Fontaine (1889, pl. 156, fig. 12; pl. 164, fig. 4) and *"S." potomacensis* Berry (1911a, pl. 94, fig. 1). Among these taxa, two specimens assigned to *"Sassafras" potomacensis* by Hickey and Doyle (1977, figs. 49–51) preserve features of higher order venation that indicate a close relationship with *Pabiania*. These two specimens not only resemble *Pabiania variloba* in size, shape, sinus bracing, and pattern of origin for external branches of the lateral primary veins, but they also resemble *Pabiania* in possessing tertiary and quaternary venation that is comparable in vein thickness and degree of organization. (Higher order venation is more reticulate and widely spaced in *"S." potomacensis*.) These strong similarities in both lower and higher order venation between *Pabiania variloba* and Early Cretaceous remains assigned to *"Sassafras" potomacensis* indicate that *Pabiania* probably originated from a trilobed complex of Early Cretaceous Laurales.

Among unlobed fossil angiosperm leaves, *Pabiania* shows strong similarities in foliar architecture and cuticular anatomy to the genus *Cocculophyllum* (especially those species illustrated by Němejc and Kvaček (1975) and Kvaček (1983) from the Upper Cretaceous of Czechoslovakia), implying a close relationship. Features shared by these two genera include decurrent and typically suprabasal lateral primary veins, closely spaced and irregularly branched tertiary veins, quaternary veins that originate at highly variable angles and are typically unbranched, elongate and sometimes spindle-shaped guard cells that have poorly developed lamellar thickenings, an arrangement of subsidiary cells that is predominantly brachyparacytic but has laterocytic and other stomatal types, and hair bases comprising an isodiametric polygonal pore with heavily cutininized anticlinal walls. These similarities also are shown by *Pabiania* and the latest Cretaceous species *"Cinnamomum" linifolium* Knowlton (1917, pl. 90, fig. 3), which was allied with the genus *Cocculophyllum* by Upchurch and Wolfe (1987a). The only consistent differences shown by *Pabiania* and *Cocculophyllum* are the strong tendency for lobation in *Pabiania*, a consistently higher L/W ratio in *Cocculophyllum*, and perhaps a more uniform arrangement of subsidiary cells in *Pabiania*. We interpret these differences as significant at the generic level by analogy to extant Lauraceae, where lobed leaves are restricted to certain genera.

The modern affinities of *Pabiania variloba* clearly lie with the order Laurales (table 3; see pl. 7, pl. 9, figs. 4, 5, and pl. 10 for illustrations of extant Laurales). A relationship to either Magnoliidae or very primitive families of non-magnoliid dicots is indicated by low degree of organization in the venation, lamellar cuticular thickenings on the guard cells, and the presence of mesophyll secretory cells. Within this group, only Laurales possess the combination of suprabasal palinactinodromous primary venation with decurrent lateral primaries; basilaminar secondary veins; sinus bracing accomplished by a secondary vein that originates from the midvein and bifurcates at the laminar margin; highly ramified quinternary venation composed of thin and curving veins; brachyparactyic subsidiary cells; and trichome bases composed of an isodiametric, heavily cutinized, polygonal pore and scarcely modified base cells. Among non-magnoliid dicotyledons, certain Araliaceae, such as *Gilbertia*, have primary and secondary venation and sinus bracing similar to that of *Pabiania*, which could be taken to indicate that *Pabiania* represents Araliaceae. However, Araliaceae are readily distinguished from

Table 3. Comparison of *Pabiania*, *Pandemophyllum*, and related extant taxa

Taxon	Lobation	Margin	Lateral primary veins	Basilaminar secondary venation	Intercostal tertiary venation	Quaternary venation	Areolation	Embedded guard cells?	Subsidiary cell arrangement
Pabiania	Present	Entire	Well developed, decurrent on midvein.	Well developed	Subparallel, irregularly branched and close-spaced.	Usually unbranched non-orthogonal.	Poorly developed, FEV's highly branched.	No	Paracytic.
Pandemophyllum	Absent	Entire	Absent	Weak pair of secondary veins near base of lamina.	Subparallel, irregularly branched, moderately spaced.	Unbranched to reticulate or ramified, at more regular angle.	Moderately developed, FEV's not present in all areoles.	Yes	Paracytic.
Atherospermataceae	Absent	Entire or with Monimioid teeth.	Absent	Absent	Usually reticulate can be strongly transverse.	Usually reticulate, can be strongly ramified.	Moderately to poorly developed, FEV's often highly branched.	No	Paracytic or anomocytic, depending on genus.
Gomortegaceae	Absent	Entire	Absent	Absent	Weakly transverse, widely spaced, with admedially ramified lateral branches.	Ramified	Poorly developed FEV's highly branched.	No	Paracytic, with a few laterocytic to cyclocytic stomata.
Gyrocarpaceae	Absent	Entire	Well developed, originating from base of lamina.	Present	Reticulate, oriented transverse to midvein.	Reticulate, tending to be orthogonal.	Moderately developed, FEV's branched.	No	Anomocytic.
Hernandiacee	Present in one sp. of Illigera.	Entire	Present in some species, can be decurrent on midvein.	Weakly developed to absent.	Reticulate, transverse to midvein or secondary veins.	Reticulate to ramified.	Poorly developed, FEV's highly branched.	No	Anomocytic.
Hortoniaceae	Absent	Entire	Well developed, decurrent on midvein.	Well developed	Reticulate, transverse to midvein.	Reticulate and ramified, rooting ± orthogonal	Moderately developed, FEV's highly branched.	No	Anomocytic.
Lauraceae	Present in some genera.	Entire	Well developed in some genera, point of origin varies.	Well developed in some genera.	Reticulate to percurrent, strongly organized.	Usually orthognal reticulate, unbranched and ramified in Eusideroxylon	Well developed in all genera, except Eusideroxylon, FEV's branched to absent.	Yes	Paracytic.

Pabiania by their cuticular anatomy, especially by having well-developed outer stomatal ledges on the guard cells and a ring of weakly specialized subsidiary cells. Within Laurales, the families Amborellaceae, Austrobaileyaceae, and Monimiaceae can be excluded from consideration by their combination of pinnate venation, intercostal regions that are isodiametric above the base of the lamina, and tertiary venation that is strongly reticulate or ramified (table 2). Among the remaining extant families of Laurales (table 3), *Pabiania* shows a pattern of tertiary and quaternary venation most comparable to that of Idiospermaceae (pl. 7, fig. 8) and one species of Atherospermataceae (*Siparuna decipiens*—pl. 9, fig. 4) and a low level of areolar organization characteristic of all Laurales except Austrobaileyacee, Gyrocarpaceae, and Lauraceae. This implies a level of advancement in tertiary and higher order venation comparable to that of Idiospermaceae and Atherospermataceae.

In terms of a possible cladistic relationship, *Pabiania* shows a probable common ancestry with Gyrocarpaceae, Hernandiaceae, Hortoniaceae, and Lauraceae. Evidence for this hypothesis is the presence of well-developed lateral primary veins within at least some species of each taxon. Lateral primary veins are probably derived within Laurales because they are absent from more primitive families in the order. The predominantly trilobed condition in *Pabiania* and the distinctive pattern of sinus bracing invites comparison with Lauraceae, as does the shape of the guard cells and the predominantly brachyparacytic arrangement of subsidiary cells. However, *Pabiania* appears to be more primitive than extant Lauraceae in having (1) the irregular areolation with highly branched freely ending veinlets characteristic of most primitive Laurales, (2) guard cells that show little evidence of being embedded in the subsidiary cells (a feature that, within Laurales, only occurs in Lauraceae), and (3) subsidiary cell arrangement that is more variable than that of Lauraceae. (See pl. 11, fig. 8, and pl. 17, figs. 5–7 for illustrations of extant Lauraceae.) Further, lobation is a character that typically varies on an individual plant in Lauraceae as well as between individual species, which indicates the possibility of parallel evolution, and most Lauraceae have alternate, rather than opposite and decussate, phyllotaxy. Thus, *Pabiania* shows a close relationship with intermediate to derived families of Laurales, with the closest relationship possibly being to Lauraceae.

Pandemophyllum new genus

Diagnosis.—Leaf simple; demarcation between petiole and blade indistinct; margin entire and with structural reinforcement. Primary venation pinnate. Secondary venation festooned brochidodromous but forming flattened brochidodromous arches in at least the apical quarter of the lamina; strong basilaminar secondary veins absent but with a thin pair of secondary veins present near the base of the lamina. Intersecondary veins present in some intercostal regions, branching to form tertiary veins. Tertiary venation unbranched to reticulate, often with a ramified component, irregularly transverse; tertiary veins irregularly spaced, enclosing regions no more than 2–3 times as long as wide. Quaternary venation unbranched to reticulate and ramified; quaternary veins non-orthogonally rooted, often irregularly transverse to the tertiary veins, irregularly spaced, tending to be admedially branched.

Cuticle of medium thickness, easy to prepare, flanges well developed. Guard cells typically spindle shaped, with well-developed lamellar thickenings along the boundary with the inner pair of subsidiary cells, strong lamellar thickenings developed over the inner pair of subsidiary cells in some species, lamellar cuticular thickenings often appearing to "float" in the stomatal complex under light microscopy. Stomatal complex brachyparacytic to amphibrachyparacytic. Trichome bases, when present, consisting of an angular to rounded pore with a heavily cutinized margin and several adjacent cells that often are radially oriented.

Type species.—Pandemophyllum kvacekii.

Derivation of name.—Greek, pandemos = common, phyllos = leaf, referring to the widespread occurrence of this leaf type during the Late Cretaceous.

Pandemophyllum kvacekii new species

Plate 12; plate 13, figures 1, 2; plate 15; text figure 10

Diagnosis.—Lamina narrow elliptic to narrow subrhombic, L/W 2.8–3.6, apex acute to attenuate with a rounded tip. Secondary veins oriented approximately 45° to primary vein, curving sharply near the margin just before forming loops, flattened brochidodromous arches present only near the tip of the leaf. Tertiary veins moderate relative to the secondary veins, unbranched to reticulate, ranging from roughly transverse to the secondary veins to nearly parallel to the primary vein, sometimes on the same leaf. Quaternary venation unbranched to reticulate, similar to tertiary venation in course and branching, generally enclosing elongate regions oriented transverse to the tertiary veins.

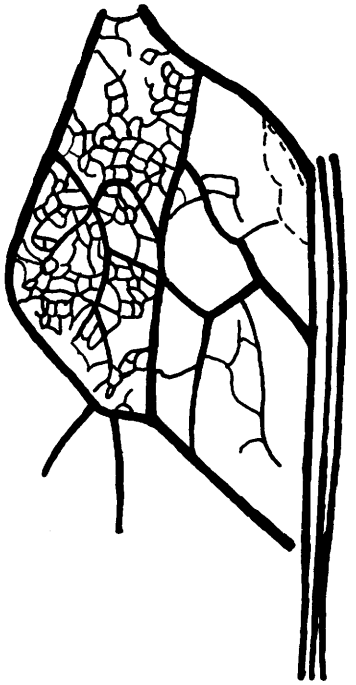


Figure 10. *Pandemophyllum kvacekii* new genus and species, 15713-4847, specimen shown on plate 13, figures 1 and 2. Note the separate strands in the midvein and the reticulate higher order venation, × 15.

Description.—Lamina elliptic to rhomboidal, L/W 2.8–3.6; lamina 6–16 cm long by 2.1–4.5 cm wide (maximum length estimated); apex acute and with a rounded tip; base acute to cuneate; boundary between petiole and blade not well defined, petiole 1.2 cm long (only one petiole completely preserved); margin entire, in many specimens somewhat darkened (structurally reinforced). Primary venation pinnate; primary vein stout to massive, sometimes curved near the base of the lamina, appearing to be composed of separate vascular strands. Secondary venation festooned brochidodromous, brochidodromous loops flattened only in the apical fourth of the lamina; secondary veins thin relative to the primary vein, ranging from 6 to over 10 pairs per leaf, predominantly opposite to subopposite, predominantly moderate (rarely narrow) acute; course more or less straight until forming loops, curving strongly just before forming loops near margin; intercostal regions always exmedially elongate but decreasing in length apically; brochidodromous junction formed by two veins of nearly equal thickness, the superadjacent vein deflected apically only where the costal loops are flattened, angle of brochidodromous junction broad acute to obtuse; one well-developed series of excostal secondary loops present, these apically oriented. Intersecondary veins rare, branching to form tertiary veins. Tertiary venation unbranched to reticulate; tertiary veins moderate relative to secondary veins, ranging from acute to obtuse on the exmedial side of the secondary veins and acute to right-angled on the admedial side, irregularly spaced, course somewhat irregular, orientation roughly transverse to nearly parallel to primary vein. Quaternary venation unbranched to reticulate, similar to the tertiary venation in behavior; quaternary veins thin or moderate relative to the tertiary veins, non-orthogonally rooted, tending to enclose elongate regions roughly transverse to tertiary veins. Quinternary venation poorly preserved on most specimens, irregularly reticulate; quinternary veins often curved. Areolation moderately developed, areoles typically quadrangular, isodiametric to elongate, minute, 0.1–0.2 mm in diameter, with straight or curved sides, freely ending veinlets possibly present adjacent to tertiary and quaternary veins, but difficult to distinguish from preservational artifacts. Marginal venation obscure.

Upper cuticle with well-developed flanges; cell shape mixed; cells 4–6 sided, 10–38 microns long by 10–22 microns wide; anticlinal wall contour a mixture of straight and curved; external and internal sculpture smooth under light microscopy ×500; trichome bases present, each comprising an isodiametric, angular pore with thickened walls and several base cells that are often radially arranged, pore usually less than 10 microns in diameter.

Lower cuticle somewhat thinner than upper cuticle but with well-developed flanges; cell shape mixed; cells 4–6 sided, 12–46 microns long by 5–20 microns wide; anticlinal wall contour a mixture of straight and curved; surface sculpture and internal sculpture smooth under light microscopy ×500. Guard cells elliptic to spindle-shaped; lamellar cuticular thickenings strongly developed at the junction with subsidiary cells, sometimes well developed over the inner pair of subsidiary cells, with intermediate conditions present; lamellar cuticular thickenings not extending the full length of the guard cell, under light microscopy often appearing to "float" in the stomatal complex; subsidiary cell arrangement brachyparacytic to more commonly amphibrachyparactyic, usually with two to three pairs of subsidiary cells but with up to four pairs observed; inner pair of subsidiary cells typically elongate parallel to the guard cells, up to 12 microns wide but usually much narrower; outer pairs of subsidiary cells less modified than inner pair, typically with curved tangential walls and often with thinner cuticle than unspecialized cells. Cells adjacent to stomatal complex often radially compressed (that is, elongate parallel, rather than perpendicular, to the stomatal complex), forming a weak ring of encircling cells. Trichome bases present, similar in structure to those of the upper cuticle, pore usually <10 microns in diameter. Idioblasts present, possibly related to trichome bases ontogenetically, each consisting of a small, angular cell with heavily cutinized walls. Spherical secretory bodies present in a few cuticular preparations, typically several times the diameter of the epidermal cells, interpreted as the remains of mesophyll secretory cells.

Number of specimens examined for foliar architecture.—70.

Number of specimens examined for cuticular anatomy.—13.

Holotype.—15713-7877.

Paratypes.—15713-3323b, 3667b, 3671b, 3671c, 3672, 4716, 4797, 4799, 4800a, 7851, 7877, 8300.

Derivation of epithet.—In honor of Dr. Zlatko Kvaček, and in recognition of his studies of the cuticular anatomy of Late Cretaceous angiosperm leaves.

Discussion.—Foliage of *Pandemophyllum*, along with similar leaf types known only as poorly preserved impressions, appears to be a common and diverse element in Late Cretaceous leaf floras from North America and Europe (see Němejc and Kvaček, 1975; Kvaček, 1983) and comprises the "protolaurels" of Wolfe and Upchurch (1987a). Traditionally, leaf impressions with the generalized lower order venation characteristic of *Pandemophyllum* have been assigned to a wide variety of extant dicotyledonous families belonging to Magnoliidae and other subclasses, presumably because of highly generalized foliar architecture. Some forms have been assigned to Lauraceae, including the extant genus *Laurus* (*Laurus plutonia* Heer as illustrated in Lesquereux, 1892, pl. 13, figs. 5, 6; pl. 22, fig. 5) as well as the form genera *Laurophyllum* Goeppert and *Daphnophyllum* Heer; however, the degree of differentiation between petiole and blade and pattern of higher order venation in *Pandemophyllum* indicates that an assignment to Lauraceae may be incorrect. Other forms have been placed within Magnoliaceae ("*Magnolia*" *pseudo-acuminata* Lesquereux, 1892, pl. 24, fig. 2) and a variety of non-magnoliid families such as Salicaceae ("*Salix*" *deleta* Lesquereux, 1892, pl. 3, fig. 8), Aquifoliaceae ("*Ilex*" *scudderi* Lesquereux, 1892, pl. 58, fig. 2), Ebenaceae ("*Diospyros*" *pseudoanceps* Lesquereux, 1892, pl. 22, fig. 1), Moraceae ("*Ficus*" *inaequalis* Lesquereux, 1892, pl. 49, figs. 6–8; pl. 50, figs. 3, 6), Ericaceae ("*Andromeda*" *paralatorii* Heer sensu Lesquereux, 1892, pl. 19, fig. 1; pl. 52, fig. 6) and Leguminosae (*Phaseolites formus* Lesquereux, 1892, pl. 55, figs. 5, 6, 12). None of these assignments of *Pandemophyllum*-like foliage to extant genera and families can be considered valid, because the suite of venational and cuticular features present in *Pandemophyllum* is not known from these modern relatives, and most previously described fossil species lack preserved venation above the third order, which is needed to identify leaves with such generalized foliar architecture.

No previously described fossil taxon has a generic name that can be applied to the Rose Creek foliage. Commonly, the names *Laurophyllum* Goeppert, *Litsaeophyllum* Deane, *Daphnogene* Unger, and *Daphnophyllum* Heer have been used for Cretaceous leaves of the *Pandemophyllum*-type; however, the use of these four names appears to be invalid. *Laurophyllum* Goeppert is an orthographic variant of the extant genus *Laurophyllus* Thunb. (Wolfe, 1977). *Litsaeophyllum* Deane cannot be used because the type species, *L. wingellense* (Deane, 1902, p. 64; pl. 17, fig. 4), has well-developed lateral primary veins, which are restricted to only some genera of Lauraceae. *Daphnogene* Unger could possibly be used because the type species, *D. cinnamomeifolia* (Brongiart) Unger (1845, p. 227), is pinnately veined. However, illustrations of the type species imply that only two orders of venation and no cuticle are preserved, which indicates that a separate taxon could be represented, especially considering the Tertiary age. *Daphnophyllum* Heer is an orthographic variant of the extant genus *Daphniphyllum* Blume because both names are based on the same Greek roots.

Other generic names used for foliage of the *Pandemophyllum* type show similar problems. For example, *Proteophyllum* has been used for certain species with lower order venation and cuticular anatomy similar to that of *Pandemophyllum* (*Proteophyllum laminarium* Velenovsky as illustrated in Němejc and Kvaček (1975; p. 40, pl. 6, figs. 1, 4, 6; pl. 7, figs. 1, 2, 4, 6; pl. 19, figs. 1–6)); however, *Proteophyllum* cannot be used because the type species, *P. bipinnatum* Friedrich (1883, p. 335; pl. 28, figs. 1, 2), is bipinnately compound, and hence belongs to a totally different subclass (Hickey and Wolfe, 1975). Certain species assigned to *Myrtophyllum* strongly resemble *Pandemophyllum* in cuticular anatomy (Kvaček, 1983) and higher order venation (unpublished observations), which implies a close relationship. However, all species assigned to *Myrtophyllum* possesses a distinct intramarginal vein that runs nearly the full length of the lamina, a distinction we think is significant at the generic level.

Among previously described species of fossil leaves, *Pandemophyllum kvacekii* shows strong similarities to *Daphnophyllum crassinerve* Heer (1869, pl. 7, fig. 2; pl. 11, fig. 5), reported from the Cenomanian of Czechoslovakia, in size, shape, and features of lower order venation. However, we hesitate to assign our fossils to this species because (1) no venation above second order was illustrated by Heer, and (2) the stomata of Czechoslovakian specimens assigned to this species by Kvaček (1983) differ from those in our specimens by showing the consistent development of lamellar cuticular thickenings on the inner pair of subsidiary cells and by possessing consistently thin cuticle over the outer pair of subsidiary cells. Organically preserved leaves assigned by Tanai (1979) to the species *Laurophyllum kujianum* differ from *P. kvacekii* in having stronger, more curved secondary veins, a better defined petiole, and possibly well-developed lamellar cuticular thickenings on the inner pair of subsidiary cells; this last character is difficult to interpret from the published photographs. Numerous other species of fossil leaves resemble *P. kvacekii*, but all differ in size and shape or lack enough preserved venation to indicate conspecificity.

Among extant angiosperms, the combination of simple, pinnate organization, lamellar cuticular thickenings on the guard cells, paracytic subsidiary cells, and the presence of spherical mesophyll secretory cells is restricted to Magnoliidae. Within Magnoliidae, the combination of basilaminar secondary veins and trichome bases consisting of a small, isodiametric, polygonal pore with scarcely modified adjacent cells is restricted to Laurales. Within Laurales, *Pandemophyllum* most closely resembles Lauraceae and Atherospermataceae in foliar architecture and stomatal structure (table 3). Among these two families, *Pandemophyllum* more closely resembles Lauraceae in having an entire margin and a combination of two postulated derived features restricted to the family: (1) moderately developed areolation, and (2) guard cells that have strong cuticular lamellae developed along their junction with the inner pair of paracytic subsidiary cells (see pl. 17, figs. 5–7 for extant Lauraceae). The stomatal structure found in *Pandemophyllum* could be taken as evidence for affinities with Myristicaceae, because extant Myristicaceae possess guard cells with strong lamellar cuticular thickenings along the junction with paracytic subsidiary cells; however, Myristicaceae also possess trichome bases that are distinct from those of Laurales (pl. 17, figs. 8, 9) but similar to those of many Magnoliales. *Pandemophyllum* closely resembles the lauraceous genus *Eusidereroxylon* (pl. 10, fig. 6) in having festooned brochidodromous secondary venation where the brochidodromous arches are flattened in the apical quarter of the lamina, a pair of weakly developed secondary veins near the base of the lamina, and a comparable (although slightly less regular) pattern of tertiary and quaternary venation. However, *Pandemophyllum* may be more primitive than any extant Lauraceae in having a less well differentiated petiole and blade and in having less rigidly organized tertiary venation and areolation than most Lauraceae. Determination of whether *Pandemophyllum* represents an extinct genus of Lauraceae or a closely related extinct family awaits discovery of its reproductive organs and future cladistic analysis of extant and fossil Laurales.

Pandemophyllum attenuatum new species

Plate 13, figures 3–5; plate 16, figures 1–6; text figure 11

Diagnosis.—Lamina lanceolate; apex long-attenuate. Secondary veins originating at about 45°, commonly curved for their entire length in the basal half of the lamina; flattened brochidodromous arches present in the apical half of lamina; intercostal regions exmedially elongate basally, becoming predominantly isodiametric and with apical attenuation in the apical half of lamina. Tertiary venation predominantly reticulate; tertiary veins moderate relative to the secondary veins.

Description.—Lamina lanceolate, L/W 5–8 (estimated); lamina 12–16 cm long (estimated) by 2–2.3 cm wide; apex strongly attenuate; base probably acute (only partial base observed); margin entire, with mechanical reinforcement. Primary venation pinnate; primary vein moderate. Secondary venation festooned brochidodromous, with flattened brochidodromous arches in the apical half of the lamina; secondary veins moderate relative to primary vein, > 6 pairs, alternate to subopposite, with somewhat irregular spacing, originating at about 45°, slightly deflected where they give rise to tertiary veins, curving over most of their length in the basal half of the lamina; intercostal regions in the basal half of the lamina exmedially elongate, intercostal regions in the apical half of the lamina isodiametric and with an apical prolongation near their exmedial sides; brochidodromous junction formed by two veins of equal thickness, the superadjacent secondary vein deflected apically only in the apical half of the lamina; angle of brochidodromous junction obtuse in the apical half of the leaf; one well-developed series of excostal secondary loops present, these apically oriented. Intersecondary veins present in some intercostal regions, branching to form tertiary veins. Tertiary venation predominantly reticulate; tertiary veins moderate relative to secondary veins, angle of origin variable, irregularly spaced, course somewhat irregular, tending to be oriented nearly parallel to the midrib. Quaternary venation poorly preserved, unbranched to reticulate, similar to the tertiary venation in behavior. Higher order and marginal venation obscure.

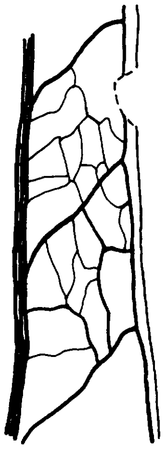


Figure 11. *Pandemophyllum attenuatum* new species, 15713-8305, specimen shown on plate 13, figure 5, illustrating details of the apex, ×3.

Upper cuticle of medium thickness, with well-developed cuticular flanges; flanges 2–3 microns wide; cell shape mixed; cells 4–5 sided, 18–40 microns long by 9–18 microns wide, tending to occur in clusters or linear groups, secondary divisions common; anticlinal wall contour tending towards curved; external and internal sculpture smooth under light microscopy ×500. Veinal areas consisting of rows of cells, these grouped into linear arrays of cells separated by thin cuticular flanges; linear arrays of cells following an undulatory path. Trichome bases present, each consisting of a small, concave-sided pore and several adjacent cells that tend to be radially oriented; pore heavily cutinized, possibly occluded.

Lower cuticle of medium thickness, somewhat thinner than upper cuticle, with well-developed flanges; flanges approximately 2 microns wide; cell shape mixed; cells 4–6 sided, 12–36 microns long by 10–22 microns wide; anticlinal wall contour ranging from straight to curved; external and internal sculpture smooth under light microscopy ×500. Veinal areas consisting of rows of cells, these often undulating over smaller veins, undulations difficult to see for cells beneath the larger veins. Guard cells spindle-shaped, 22–30 microns long by 3–10 microns wide, with well-developed lamellar cuticular thickenings along border with inner pair of subsidiary cells; subsidiary cell arrangement ranging from brachyparacytic to amphibrachyparactyic; the inner pair of subsidiary cells sometimes with well-developed lamellar cuticular thickenings, 2–10 microns wide; the unthickened subsidiary cells with cuticle of the same thickness as unspecialized cells. Trichome bases present, consisting of an isodiametric pore and several scarcely modified adjacent cells that tend to be radially oriented; pore ranging from angular to circular, up to 10 microns in diameter, heavily cutinized at the outer margin of hair; adjacent cells can be radially elongate.

Number of specimens examined for foliar architecture.—7.

Number of specimens examined for cuticular anatomy.—2.

Holotype.—15713-7845.

Paratypes.—15713-4698a, 4698b, 8305.

Derivation of epithet.—Latin, attenuatus = drawn out, referring to the apex.

Discussion.—*Pandemophyllum attenuatum* is distinguished from *P. kvacekii* by its lanceolate shape, attenuate apex, and different pattern of variation in the shape of the intercostal regions. Among previously described species of fossil angiosperm leaves, *P. attenuatum* most closely resembles *"Salix" deleta* Lesquereux (1892, pl. 3, fig. 8; see pl. 14, fig. 2 of the present report) in having an ovate shape, attenuate apex, and similar tertiary and quaternary venation but differs in having more apically prolonged intercostal regions in the apical half of the lamina and in having predominantly reticulate, rather than predominantly unbranched, tertiary and quaternary venation. *P. attenuatum* also closely resembles *Proteoides daphnogenoides* Heer (pl. 14, fig. 4 of the present report). However, the absence of preserved venation above the first order in type material of *Proteoides daphnogenoides* makes demonstration of conspecificity impossible; further, the genus *Proteoides* originally was proposed for leaves with poor preservation (Heer, in Capellini and Heer, 1866, p. 17). *P. attenuatum* also resembles *"Inga" cretacea* from the Dakota Formation of Kansas (Lesquereux, 1892, pl. 55, fig. 11; see pl. 14, fig. 1 of the present report) but differs in having well-developed intersecondary veins.

Pandemophyllum sp.

Plate 14, figures 5–6; plate 16, figures 7–9; plate 17, figures 1–3

Description.—Fragment of one leaf preserved; lamina apparently very narrow elliptic and bordering on oblong; L/W well over 2, length well over 2.6 cm, estimated width 1.5 cm; apex and base missing; margin entire, with mechanical reinforcement. Primary venation pinnate; primary vein stout. Secondary venation festooned brochidodromous; secondary veins moderate relative to the primary vein, at least 6 pairs, alternate, with somewhat irregular spacing, originating at somewhat irregular angles that are always narrow acute (less than 45°), slightly deflected where they give rise to tertiary veins, curving apically when more than halfway to the margin; secondary veins looping near the margin, with both secondary veins of equal thickness at their junction and the superadjacent secondary vein deflected apically; angle of the junction (when preserved) obtuse; brochidodromous loops tending to be flattened. Excostal secondary veins slightly thinner than their source veins, forming somewhat irregularly proportioned loops that are elongate parallel to the margin. Intercostal tertiary venation tending towards unbranched; tertiary veins thick relative to the secondary veins and poorly differentiated from the quaternary veins, irregularly spaced, originating at an obtuse angle on the exmedial side of the secondary veins and at an acute angle on the admedial side of the secondary veins, oriented roughly parallel to the primary vein. Quaternary venation arising from thick lateral branches of the tertiary veins, non-orthogonal; quaternary veins highly branched, the branching tending to be admedially oriented; some quaternary veins ramifying into quinternary veins. Quinternary venation obscure. Marginal venation probably looped, obscured by the remains of the mechanical tissue.

Upper cuticle medium, with well-developed flanges; flanges 2 microns wide; cell shape mixed; cells generally 4–6 sided, 12–24 microns long by 6–22 microns wide; anticlinal wall contour straight to curved. Veinal areas consisting of rows of cells; scattered stomata present adjacent to one observed veinal area. One trichome base observed, similar in construction to the trichome bases of other species.

Lower cuticle medium, with well-developed flanges; flanges 1–2 microns wide; cell shape mixed; cells 4–6 (rarely 3 or 7) sided, 18–40 microns long by 8–26 microns wide; anticlinal wall contour straight to curved. Veinal areas poorly developed on cuticle, cells tending to be in longitudinal files over primary vein, cells tending to be isodiametric, files of cells weakly undulate. Guard cell pair spindle-shaped, 20–34 microns long by 8–12 microns wide; stomatal poles truncate; guard cells with well-developed lamellar cuticular thickenings adjacent to inner pair of subsidiary cells; inner pair of subsidiary cells also with well-developed lamellar cuticular thickenings; subsidiary cell arrangement amphibrachyparacytic; inner pair of subsidiary cells 2–6 microns wide; outer pair of subsidiary cells broader, with curved tangential walls, tending to be radially compressed, outer cuticle always thinner than that of unspecialized cells. Trichome bases and idioblasts not observed.

Number of specimens examined for foliar architecture and cuticular anatomy.—1.

Specimen.—15713-4827, 4827′ (part and counterpart).

Discussion.—*Pandemophyllum* sp. clearly represents a distinct species of *Pandemophyllum*, but the fragmentary preservation of the one known specimen precludes formal diagnosis. *Pandemophyllum* sp. is readily distinguished from other species of *Pandemophyllum* by (1) its nearly oblong shape, (2) brochidodromous loops that are more flattened in the middle portion of the lamina, (3) thick tertiary veins, (4) quaternary veins that tend to be admedially ramified, and (5) stomatal complexes in which the inner pair of subsidiary cells always has strongly developed lamellar cuticular thickenings and the outer pair of subsidiary cells always has thinner outer cuticle than adjacent unspecialized cells.

cf. Order ILLICIALES

Longstrethia new genus

Diagnosis.—Lamina very narrow elliptic to oblong; petiolar region poorly differentiated from the lamina; margin ranging from entire to coarsely toothed. Primary venation pinnate. Secondary venation ranging from brochidodromous, with strongly flattened brochidodromous loops, to pinnate with an intramarginal vein; secondary veins numerous, decurrent, irregular in course and spacing. Intersecondary veins present, branching into tertiary veins. Tertiary venation irregularly reticulate, enclosing areas of variable shape. Higher order venation not present or poorly developed.

Cuticle with well-developed flanges. Guard cell pair broad-elliptic to circular, over 30 microns long; T-pieces present at the stomatal poles; each guard cell with a C-shaped lamellar cuticular thickening. Subsidiary cell arrangement predominantly laterocytic, sometimes also with polar subsidiary cells. Epidermal secretory cells present, each consisting of an isodiametric, polygonal cell surrounded by larger but several scarcely modified cells.

Type species.—Longstrethia varidentata.

Derivation of name.—In honor of Karl Longstreth, and in recognition of his assistance to our research on early angiosperms.

Longstrethia varidentata new species

Plate 18; plate 19; plate 20, figure 1; text figure 12

Diagnosis.—As for genus.

Description.—Lamina linear, L/W over 6 to at least 11; lamina 6–15 cm long by 1–2 cm wide; apex acute to abruptly rounded; base very narrow acute to cuneate; petiolar region poorly differentiated from the lamina and with a decurrent wing of laminar tissue; margin ranging from entire to having widely spaced teeth; teeth nonglandular, <1 mm to 2 mm tall by 2 to 9 mm wide, variable in shape but tending towards straight-straight (B–2) or convex-convex (A–1), often strongly asymmetrical; angle formed by sides of teeth ranging from acute to obtuse; apex of tooth rounded. Primary venation pinnate; primary vein massive. Secondary venation ranging from brochidodromous with strongly flattened brochidodromous arches to pinnate with an intramarginal vein; secondary veins thin relative to primary vein, numerous, opposite to alternate, irregularly spaced, decurrent, narrow acute; course of secondary veins irregular and often sinuous, sometimes recurved just below junction with intramarginal vein; angle of brochidodromous junction obtuse. Intersecondary veins present, branching into tertiary veins. Intercostal tertiary venation very irregular, reticulate; tertiary veins nearly as thick as the secondary veins, originating at highly variable but commonly acute angles on both sides of the secondary veins, irregularly but widely spaced, often curved. Ultimate venation possibly of fourth order, poorly differentiated from tertiary venation. Areolation moderately developed but of highly irregular shape, freely ending veinlets present in a few areoles, unbranched. Tooth venation consisting of a medial vein

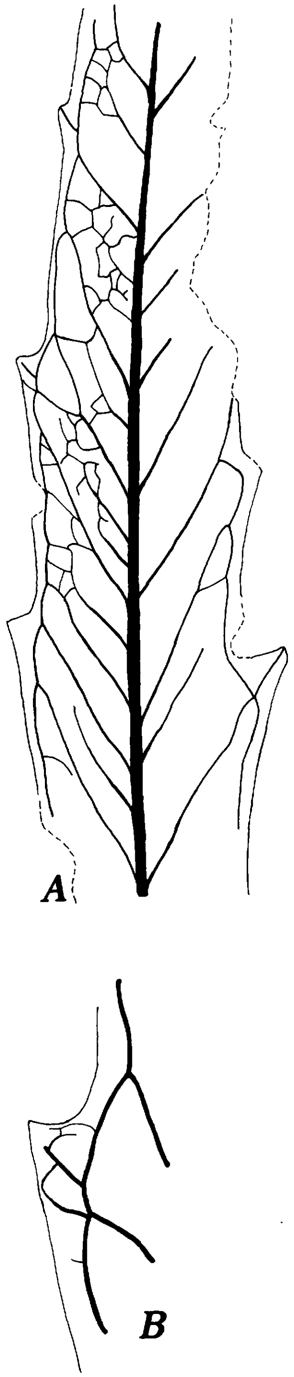


Figure 12. *Longstrethia varidentata*, new genus and species, 15713-4961b, specimen shown on plate 18, figure 4. *A*, Central region of leaf, ×3. *B*, Details of middle tooth, left margin, ×7.5. Note the absence of glandularity to the tooth.

that is sometimes associated with much thinner unmodified veins; teeth not conforming to any of the types recognized by Hickey and Wolfe (1975).

Upper cuticle thick, with well-developed flanges; cell shape mixed; cells 4–6 (rarely 5–7) sided, 30–90 microns long by 20–55 microns wide; anticlinal wall contour straight to curved; external and internal sculpture smooth under light microscopy ×500. Veinal areas consisting of cells in rows. One idioblast observed, consisting of a small, isodiametric cell with straight to concave sides, underthrust by unmodified adjacent cells; idioblast with thicker cuticle than the adjacent cells, possibly representing the basal cell of an abscissed hair.

Lower cuticle thick, with well-developed cuticular flanges; cell shape mixed; cells mostly 4–6 sided, 20–72 microns long by 16–45 microns wide; maximum cell length and width on an individual cuticle usually no more than twice the minimum length and width; anticlinal wall contour usually straight to curved, rarely curved to undulate, when undulate with no more than 1½ wavelengths per cell side; external and internal sculpture smooth under light microscopy ×500. Epidermal secretory cells present; each secretory cell isodiametric, straight-sided, and usually smaller than the adjacent cells, sometimes with attached resinous remains; adjacent cells ranging from radially oriented to radially elongate. One idioblast observed, similar to that of the upper cuticle but showing no strong cutinization. Guard cell pairs circular to broadly elliptic, with regions of cuticle on the outer walls that are significantly thinner than the outer cuticle of unspecialized cells, 38–60 microns long by 32–57 microns wide; stomatal poles nearly always rounded, rarely slightly retuse; striations present on the stomata of a few specimens, concentric to the stomatal pore; lamellar cuticular thickenings well developed, those on the outer walls of the guard cells forming a ring concentric to the stomatal pore, those of the inner walls of the guard cells tending to be straight; T-pieces present on nearly every pair of guard cells, weakly to moderately developed; the upright present in all cases and sometimes flared towards the stomatal pores, up to several microns wide; crossbar present in some stomata, weaker than upright; subsidiary cell arrangement predominantly laterocytic, but with some stomata cyclocytic or intermediate between laterocytic and cyclocytic; number of lateral subsidiary cells predominantly 4–6, rarely 2 or 3. Mesophyll secretory bodies present in a few cuticular preparations, spherical, somewhat smaller in diameter than the epidermal cells, interpreted as the remains of oil cells.

Number of specimens examined for foliar architecture.—98.

Number of specimens examined for cuticular anatomy.—11.

Holotype.—15713-4962.

Paratypes.—15713-3668a, 3684b, 3691a, 3693a, 4715, 4893, 4893′, 4904, 4918, 4961a, 4961b, 4961c, 7806, 8301.

Derivation of name.—Latin, varius = variable, dentatus = toothed, referring to the variable development of teeth on the lamina.

Discussion.—Traditionally, foliage of the *Longstrethia* type has been assigned to the genera *Eucalyptus* and *Myrtophyllum* (entire-margined forms) and *Proteophyllum* and *Celastrophyllum* (toothed forms). However, *Longstrethia* cannot be assigned to *Myrtophyllum* because its tertiary venation differs from that of the type species, *M. geinitzii* (irregularly reticulate rather than transversely oriented), and its stomatal structure differs significantly from that of *M. angustifolium*, a probable congener of *M. geinitzii*. (See Kvaček, 1983.) *Longstrethia* cannot be assigned to *Proteophyllum* because the type species of *Proteophyllum* is bipinnately compound (Friedrich, 1883), and an assignment to *Celastrophyllum* is invalid because the type species of *Celastrophyllum* is entire-margined and has a distinct petiole (Goeppert, 1854). Finally, *Longstrethia* possesses a combination of features that invalidates an assignment to *Eucalyptus* and other extant Myrtales. These features include a decurrent wing of laminar tissue on the petiole, irregular intercostal venation with no preferred orientation, and lamellar cuticular thickenings on the guard cells, rather than outer stomatal ledges.

Longstrethia shows some similarities with two additional genera of fossil angiosperm leaves but is distinct with respect to foliar features that typically circumscribe genera of extant angiosperms. *Longstrethia* resembles *Rogersia* Fontaine (1889) from the Lower Cretaceous Potomac Group of Virginia in having small size, a narrow elongate shape, and highly irregular tertiary venation, but it differs in having teeth in some specimens and in having an intramarginal vein. *Longstrethia* also resembles *Eucalyptophyllum* Fontaine (1889) from the Potomac Group in having an elongate shape and an intramarginal vein, but it differs in having (1) predominantly unoriented, rather than exmedially elongate, regions enclosed by the tertiary veins, (2) large stomata with well-developed T-pieces, and (3) a pattern of subsidiary cell arrangement that typically ranges only from laterocytic to cyclocytic. (See Wolfe and others, 1975 and Hickey and Doyle, 1977 for illustrations of foliar architecture in *Eucalyptophyllum*; see Upchurch, 1984 for illustrations of stomatal structure.)

Longstrethia varidentata shows strong similarities with six species of Cretaceous age but cannot be assigned to any of them because of different foliar architecture and/or incomplete preservation of the previously described material. Among Early Cretaceous forms, *Longstrethia* most closely resembles "*Sapindopsis*" *elliptica* Fontaine (1889, pl. 147, fig. 3) from the Potomac

Group of Virginia. Characters shared by both species include an elongate and nearly oblong shape, highly irregular and decurrent secondary venation that is organized in a festooned brochidodromous pattern, brochidodromous arches that show a strong tendency to be flattened, common intersecondary veins, and tertiary and quaternary venation that is poorly differentiated and not strongly quadrangular. However, *L. varidentata* differs from "*S.*" *elliptica* in having a prominent intramarginal vein and in having teeth present in some leaves.

Longstrethia resembles two species described from the Dakota Group. *Longstrethia varidentata* resembles *Myrtophyllum warderi* Lesquereux (Lesquereux, 1892, pl. 53, fig. 10) in having an elongate shape, numerous thin secondary veins, and an intramarginal vein, but it differs in having a smaller size. In addition, no venation above the second order is visible on the holotype of *Myrtophyllum warderi*, which makes demonstration of conspecificity (and congeneric relationships) impossible because tertiary venation is one of the diagnostic features separating *Longstrethia* from *Myrtophyllum*. *L. varidentata* also resembles "*Eucalyptus*" *dakotensis* Lesquereux (1892, pl. 37, figs. 14–19) in size, shape, and presence of an intramarginal vein, but it differs in having intercostal regions that are flattened, rather than rounded, on their exmedial sides. In addition, the type specimens of "*E.*" *dakotensis* have no preserved venation above the second order.

Longstrethia also closely resembles three species reported from the Upper Cretaceous Raritan Formation of New Jersey. Serrate variants resemble "*Celastrus*" *arctica* Heer (Newberry, 1895, pl. 13, figs. 8–18) in having similar laminar shape, secondary venation, and tooth shape, but they differ in having a larger size and more widely spaced teeth. (On the basis of illustrations of the holotype, "*C.*" *arctica* Heer (1883, pl. 61, figs. 5d, 5e) differs from Raritan remains assigned to "*C.*" *arctica* in showing no intramarginal vein.) Entire-margined members of *Longstrethia* resemble "*Eucalyptus*" *angustifolia* Newberry (Newberry, 1895, pl. 32, figs. 1, 6, 7) in having an oblong shape and irregular secondary veins that connect with an intramarginal vein, but they differ in their larger size and less linear shape. *L. varidentata* also resembles two specimens of "*Eucalyptus*" *geinitzi* Heer (=*Myrtophyllum geinitzi* (Heer) Heer) illustrated by Newberry (1895, pl. 32, figs. 2, 12) in shape and secondary venation, but the absence of readily visible tertiary venation precludes assignment to this species, as does cuticular anatomy significantly different from that illustrated for *Myrtophyllum angustifolium* (a probable congener of *M. geinitzi*) by Kvaček (1983).

Among extant flowering plants, a relationship between *Longstrethia* and Magnoliidae is indicated by the combination of poor differentiation between petiole and blade, irregular venation, lamellar cuticular thickenings on the guard cells, epidermal secretory cells that are isodiametric and straight-sided, and mesophyll secretory cells. A possible relationship with Illiciales is indicated by the combination of oval stomata over 30 microns long, lamellar cuticular thickenings that form a ring concentric to the stomatal pore, T-pieces at the stomatal poles, and laterocytic subsidiary cells, a suite of features that distinguishes Illiciales from other Magnoliidae (see pl. 20, figs. 2–5). In spite of these similarities, *Longstrethia* differs from extant Illiciales in having an intramarginal vein (compare pl. 18, figs. 2, 7 to pl. 20, figs. 6–8), somewhat less quadrangular tertiary venation, and poorly developed striations on the cuticle. Also, Illiciales with only four orders of venation (*Illicium*, *Kadsura*) differ from *Longstrethia* in having highly branched freely ending veinlets (pl. 20, fig. 9), and most serrate-margined Illiciales have glandular teeth. However, a few Illiciales have only very weakly glandular teeth with poorly developed accessory venation (text figure 13), which indicates that tooth structure in *Longstrethia* may not preclude a relationship to extant Illicales

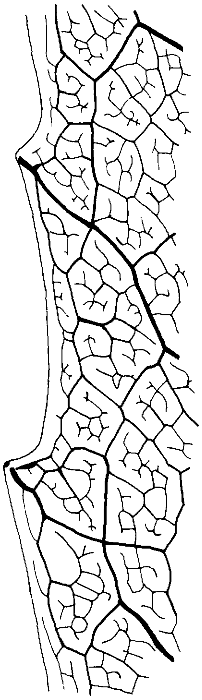


Figure 13. *Schisandra propinqua* (Wall.) Baill., U.S.G.S. Ref. Coll. no. 2384, details of weakly glandular teeth, ×7.5.

An alternative to the above scheme of relationships is a close relationship between *Longstrethia* and extant Trimeniaceae. This alternative is based on the presence of an intramarginal vein in both taxa, a derived feature that within Magnoliidae characterizes Trimeniaceae (Laurales). In addition, teeth of Trimeniaceae conform to the monimioid type of Hickey and Wolfe (1975), which

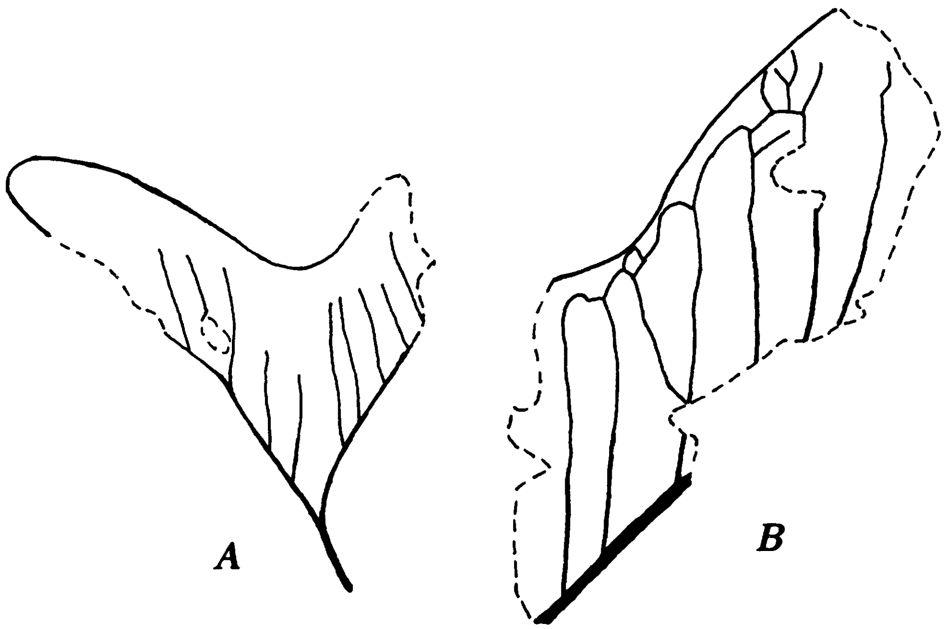


Figure 14. *Didromophyllum basingerii* new genus and species, ×1. *A*, 15713-4895, specimen shown on plate 21, figure 3, and pl. 22, fig. 2. *B*, 15713-4699b, specimen shown on plate 21, figure 1, fragment showing details of secondary venation.

differs from the tooth type of *Longstrethia* in being glandular but is similar in having one or no accessory veins. However, phenetic differences between the two taxa that typically segregate genera and families of extant Magnoliidae imply that the intramarginal vein and absence of accessory tooth venation in *Longstrethia* may have originated independently of those in Trimeniaceae. *Longstrethia* differs from Trimeniaceae in having (1) irregularly reticulate tertiary venation, (2) nonglandular teeth, and (3) large stomata with T-pieces that have predominantly laterocytic, rather than paracytic, subsidiary cells. Additional differences between *Longstrethia* and Trimeniaceae of ambiguous phylogenetic significance include (4) irregular tertiary venation (a presumed primitive feature) and (5) the presence of cuticular striations (which are readily evolved in separate extant families).

Longstrethia, therefore, represents an extinct taxon of Magnoliidae that shows a possible relationship to Illiciales or Trimeniaceae but differs from all extant members of Magnoliidae in at least several characters.

MAGNOLIIDAE order unknown and magnoliid-grade foliage

Didromophyllum new genus

Diagnosis.—Laminar units bilobed. Primary venation of each laminar unit consisting of two veins that originate from the top of the petiole(ule?) and run along the basal margins of the lamina. Secondary veins arising only from the apical sides of the primary veins, somewhat irregular in course and spacing, festooned brochidodromous. Tertiary and higher order venation irregularly reticulate, commonly deflected at points of branching.

Type species.—*Didromophyllum basingerii.*

Derivation of name.—Greek, di = two, dromos = course, phyllos = leaf, referring to the presence of two primary veins in each lamina.

Didromophyllum basingerii new species

Plate 21; plate 22, figures 1–2; text figure 14.

Diagnosis.—As for genus.

Description.—Lamina bilobate; distance from the base of the lamina to the apical sinus 3–4.5 cm; distance from the base of the lamina to the tip of each lobe 6–>10 cm; lobes 1.8–3.5 cm wide at the widest point; apex of lobes acute; apical sinus rounded; base of lamina acutely cuneate, poorly differentiated from the petiole(ule); one complete petiole(ule) preserved, 4.5 cm long; margin of lamina entire. Primary venation consisting of two primary veins that originate from the top of the petiole(ule); one primary vein commonly thicker than the other; the smaller primary vein usually somewhat decurrent on the larger one; both primary veins running along the basal margins of the lamina to the apex of the lobes; primary veins thick, diverging at an angle of 60–100°. Secondary venation originating only from the apical side of each primary vein, festooned brochidodromous; secondary veins thin relative to primary veins, at least 5–7 per lamina lobe, slightly decurrent on primary vein, narrow to moderate acute, tending to zig-zag;

brochidodromous junction formed by secondary veins of equal thickness, with the superadjacent secondary vein deflected apically; angle of brochidodromous junction ranging from acute to obtuse; excostal secondary loops irregular in size and shape; 1–2 orders of excostal loops present between costal loops and margin. Intercostal tertiary venation unbranched to reticulate, poorly differentiated from the higher order venation; tertiary veins thick relative to the secondary veins, diverging at acute to right angles on both sides of the secondary veins, deflected at points of branching, course and spacing variable. Higher order venation poorly differentiated from tertiary venation, originating from thin lateral branches of the tertiary veins, similar in behavior. Areolation well developed; areoles medium to large, 4–5 sided; freely ending veinlets in few, if any, of the areoles; freely ending veinlets possibly representing an artifact of decay. Marginal venation looped, margin with structural reinforcement.

Cuticle poorly preserved, no successful preparations made.

Number of specimens examined.—12.

Holotype.—15713-4895.

Paratypes.—15713-4699a, 4699b, 4699a′, 4699b′, 7863, 7865, 8302.

Derivation of epithet.—In honor of James Basinger, and in recognition of his contributions to this project.

Discussion.—Didromophyllum basingerii is a highly unusual leaf type. In all other angiospermous leaf types examined, primary venation conforms to a well-defined pattern of symmetry: laminar tissue occurs on both sides of a primary vein, and branch veins originate from opposite sides of each primary vein. Primary veins, therefore, define actual or potential planes of symmetry within the lamina. In *D. basingerii*, laminar tissue occurs only on the apical side of each primary vein, and higher order veins only originate from the apical side of each primary vein. Primary veins, therefore, do not define actual or potential planes of symmetry within the lamina.

The unusual primary venation of *Didromophyllum* shows some similarity to the venation of certain fern taxa that have several discrete orders of reticulate venation, and in particular Cheiropleuriaceae and Dipteridaceae. In these two families, the primary vein of each leaf exhibits one or more bifurcations, the secondary venation can show strong tendencies for looping (at least in the lobes), and the tertiary and higher order venation is generally strongly reticulate and encloses quadrangular areas. However, *Didromophyllum* possesses three sets of features that are anomalous among extant and fossil ferns and that together are more consistent with angiospermous affinities. First, the primary venation of *Didromophyllum* does not appear to be truly dichotomous, like that of Cheiropleuriaceae and Dipteridaceae, but it is fundamentally monopodial in organization: one of the two primary veins is nearly always thinner than the other, and this thinner vein arises from the thicker vein in a decurrent manner. This pattern is characteristic of various mid-Cretaceous angiosperms that have bilobed foliage, including "*Sassafras*" *bilobatum* Fontaine (1889, pl. 156, fig. 12; pl. 164, fig. 4) and "*Sterculia*" *snowii*, var. *disjuncta* Lesquereux (1892, pl. 58, fig. 6; see pl. 22, fig. 3 of the present report). Second, the secondary veins *Didromophyllum* are somewhat irregularly spaced, decurrent on the primary veins, and enclose regions of variable size and shape. This syndrome of features differs from that of Cheiropleuriaceae and Dipteridaceae, where the secondary venation is more regular and is not decurrent on the primary veins. Third, the tertiary and higher order venation of *Didromophyllum* is more irregular in its angle of origin and shape of enclosed regions than that of comparable ferns, which typically have strongly orthogonal tertiary and quaternary venation that encloses strongly quadrangular regions. These anomalies are consistent with the similarities found between *Didromophyllum* and the bilobed mid-Cretaceous genus *Liriophyllum* (elaborated below), which are taken as evidence of relationship.

The preservation of *Didromophyllum* precludes determination of whether each laminar unit represents a leaf or leaflet. Although each laminar unit shows the fundamentally symmetrical organization that characterizes leaves, no specimen preserves the base of the petiolar region. In addition, laminar units often occur in pairs on the same bedding plane, indicating that they might be part of some larger foliar structure. This possibility is strengthened by the occurrence of bifurcately compound taxa of Cenomanian age, such as *Haliserites* Sternberg, *Fontainea* Newberry (here considered a junior synonym of *Haliserites*), and "*Sterculia*" *snowii* var. *disjuncta* Lesquereux. The most similar of these taxa to *Didromophyllum* is *S. snowii* var. *disjuncta* (pl. 22, fig. 3 of this report), which consists of two bilobed laminar units connected to each other by the base of their petiolules. The primary venation of each laminar unit in *S. snowii* var. *disjuncta* is very similar to that of *Didromophyllum* in consisting of a distinct midvein and a somewhat thinner decurrent lateral primary vein and differs only in having laminar tissue basal to each primary vein. These similarities indicate that the unique pattern of primary venation in *Didromophyllum* may have arisen in the following manner: (1) origin of a lateral lobe with a decurrent lateral primary vein, then (2) supression of laminar development in the region basal to the two primary veins.

If the unique pattern of primary venation and possible bifurcately compound organization are excluded from consideration, the modern affinities of *Didromophyllum* appear to be with Magnoliidae, and possibly with primitive families of Magnoliales and Laurales.

Among extant angiosperms, the combination of irregular festooned brochidodromous secondary venation and irregularly reticulate tertiary and quaternary venation is most characteristic of Magnoliidae. Within Magnoliidae, the suite of venational features characteristic of *Didromophyllum* is most similar to that of the families Magnoliaceae and Austrobaileyaceae, primitive members of the orders Magnoliales and Laurales, respectively. Features shared by *Didromophyllum*, Magnoliaceae, and Austrobaileyaceae include reticulate tertiary venation that tends toward quadrangular, higher order venation that usually encloses quadrangular or isodiametric regions, and well-developed areolation. *Didromophyllum* more closely resembles Magnoliaceae in having exmedially elongate, predominantly straight-sided intercostal regions, tertiary venation with a stronger transverse than admedial component, and a margin with strong mechanical reinforcement (rather than a fimbrial vein), but *Didromophyllum* more closely resembles Austrobaileyaceae in having areoles with few freely ending veinlets. These similarities between *Didromophyllum*, Magnoliaceae, and Austrobaileyaceae are reinforced by similarities between *Didromophyllum* and two fossil genera: (1) *Ficophyllum*, a genus with close similarities in foliar architecture to extant Winteraceae, Magnoliaceae, and Austrobaileyaceae (Upchurch, 1983), and (2) *Liriophyllum*, a genus associated with floral remains showing strong similarity to the flowers of extant primitive angiosperms, such as Degeneriaceae, Magnoliaceae, and Austrobaileyaceae (Dilcher and Crane, 1984). In particular, the straight-sided, exmedially elongate intercostal regions and syndrome of tertiary and higher order venational features found in *Didromophyllum* resemble what is found in *Ficophyllum* and *Liriophyllum*, and *Didromophyllum* strongly resembles *Liriophyllum* in having a pattern of higher order venation that is similar in its degree of organization. Thus, *Didromophyllum* appears to represent a taxon of early angiosperms that may be related to primitive families of extant Magnoliales and Laurales, but it possesses a highly divergent, "experimental" pattern of foliar organization with no close modern counterpart.

Acritodromum new genus

Diagnosis.—Leaf simple, margin entire and with structural reinforcement, base acute. Primary venation pinnate. Secondary venation festooned brochidodromous, secondary veins irregular in their course and spacing. Tertiary venation reticulate; tertiary veins also irregular in course and spacing but showing a definite tendency to be closely spaced and oriented subparallel to the midrib, commonly curved or sinuous. Quaternary venation unbranched to reticulate, quaternary veins irregular in their behavior.

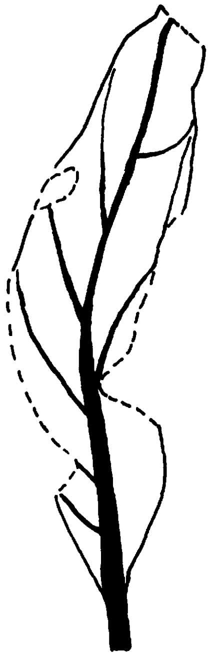


Figure 15. *Acritodromum ellipticum* new genus and species, 1571-4704, specimen shown on plate 23, figures 1–3, illustrating spacing of the secondary veins, ×1.

Type species.—*Acritodromum ellipticum.*

Derivation of name.—Greek, akritos = disorderly, dromos = course, referring to the irregular course and spacing of the secondary and higher order venation.

Acritodromum ellipticum new species

Plate 23, figures 1–3; text figure 15

Diagnosis.—As for genus.

Description.—Lamina elliptic but bordering on subrhomboidal, L/W over 4; lamina over 8 cm long by about 2 cm wide (estimated width); apex unknown (perhaps attenuate); base acute; petiole unknown; margin entire. Primary venation pinnate; primary vein massive, curved. Secondary venation festooned brochidodromous; secondary veins thin, more than four pairs, alternate, irregularly spaced and with the median 2 cm of the leaf having no secondary veins, diverging at narrow to broad acute angles in a non-uniform manner, irregular in course; basalmost pairs of secondary veins looping well within the margin, the others not looping until at least two-thirds of the way to the margin; the superadjacent secondary vein thicker than the subadjacent secondary vein at their junction and not deflected apically; angle of brochidodromous junction obtuse except in the basalmost pairs of secondary veins, where it is acute; excostal secondary loops irregular in size and shape. Intersecondary veins present, none or 1 per intercostal region, irregular in course, branching into tertiary veins. Tertiary venation irregularly reticulate; tertiary veins thick relative to the secondary veins, originating at obtuse angles on the exmedial side of the secondary veins and at acute angles on the admedial side, often curved, enclosing regions of highly variable shape that usually are elongate and oriented nearly parallel to the primary vein. Quaternary venation unbranched to reticulate, non-orthogonal; quaternary veins irregular in course and spacing, the few preserved unbranched veins tending to enclose regions that are slightly elongate and oriented oblique to nearly perpendicular to the tertiary veins. Marginal venation obscure, possibly consisting of a weak fimbrial vein formed from flattened loops.

No cuticular preparations made.

Number of specimens examined.—1.

Holotype.—15713-4704a.

Derivation of epithet.—Latin, ellipsis = ellipse, referring to the elliptical laminar shape.

Discussion.—*Acritodromum* differs from other Cretaceous taxa of elongate, entire-margined foliage by showing high variation in the spacing and angle of departure of secondary veins and by showing unique patterns of tertiary and quaternary venation. Among Early Cretaceous angiosperms, *Acritodromum* resembles *Rogersia* Fontaine (1889), *Saliciphyllum* Fontaine (1889), and "*Sapindopsis*" *elliptica* Fontaine (1889) in having festooned brochidodromous secondary venation organized in a highly irregular manner, but it differs in having wider intercostal regions, tertiary venation that shows a definite tendency to enclose elongate regions, and quaternary veins that tend to be unbranched. Among Cenomanian angiosperms, *Acritodromum* resembles *Pabiania* in having closely spaced tertiary veins that show tendencies to be parallel and resembles both *Pabiania* and *Pandemophyllum* in having an entire margin with structural reinforcement and non-orthogonally rooted quaternary veins that are typically unbranched. In addition, the subrhomboidal laminar shape found in *Acritodromum* is rarely encountered in extant angiosperms but is similar to what is found in some specimens of *Pandemophyllum kvacekii*. However, *Acritodromum* differs from these taxa in having much more irregular secondary and tertiary venation, and hence appears to be more primitive.

The modern affinities of *Acritodromum* appear to lie with Magnoliidae, but ordinal affinities within the subclass are unclear. Among extant angiosperms, the low regularity of venation found in *Acritodromum* characterizes Magnoliidae. Within Magnoliidae, no extant family or order possesses the suite of features found in *Acritodromum*. For example, curved primary veins occur in scattered Magnoliidae, such as Idiospermaceae, Canellaceae, and certain Winteraceae, but none of these groups possesses the suite of higher order venational features diagnostic of *Acritodromum*. The extremely variable course and spacing of the secondary venation found in *Acritodromum* is a syndrome of features postulated as primitive for the flowering plants as a whole (Wolfe and others, 1975; Hickey and Doyle, 1977) and hence cannot be used as evidence of phyletic relationship. The syndrome of tertiary and quaternary venational features in *Acritodromum* also has no close counterparts in extant flowering plants, although points of resemblance exist with Myristicaceae, particularly in the tendency for the veins to enclose elongate regions. The similarities previously noted between *Acritodromum* and the fossil genera *Pabiania* and *Pandemophyllum* could indicate a relationship with extant Laurales, but much more needs to be learned about this problematic taxon before relationships can be determined accurately.

Reynoldsiophyllum new genus

Diagnosis.—Leaf simple; base acute; petiole poorly differentiated from blade, less than 1 cm long; margin broadly crenate and with mechanical reinforcement. Primary venation pinnate. Secondary venation festooned brochidodromous; secondary veins zig-zag to sinuous in course; intercostal regions somewhat elongate exmedially but never more than several times as tall as broad; exmedial margins of the intercostal regions poorly demarcated by the secondary veins. Tertiary venation irregularly reticulate; tertiary veins thick relative to secondary veins, with a zig-zag course, dividing each intercostal region into a series of segments. Quaternary venation poorly differentiated from the tertiary venation, reticulate. Larger crenations typically with a medial vein and sometimes with a pair of accessory veins that converge on the margin and fuse with the thickening at the tooth apex.

Type species.—*Ilex masonii* Lesquereux (1892, p. 179, pl. 7, fig. 6; pl. 63, fig. 6)

Derivation of name.—In honor of Howard Reynolds and in recognition of his invaluable assistance to our research on Dakota angiosperms.

Reynoldsiophyllum masonii (Lesquereux) new combination

Plate 23, figures 4–6; text figure 16.

Ilex masoni Lesquereux, 1892, U.S. Geological Survey
Monograph 17, p. 179, pl. 6, fig. 6; pl. 63, fig. 6.

Emended diagnosis.—Leaf 4–5 cm wide, L/W 3–4; crenations 2–10 mm wide by up to 4 mm tall; marginal thickening most strongly developed at the apex of each crenation. Secondary veins moderate relative to primary veins; superadjacent secondary vein always thicker than the subadjacent secondary vein at their point of junction; angle of brochidodromous junction ranging from broad

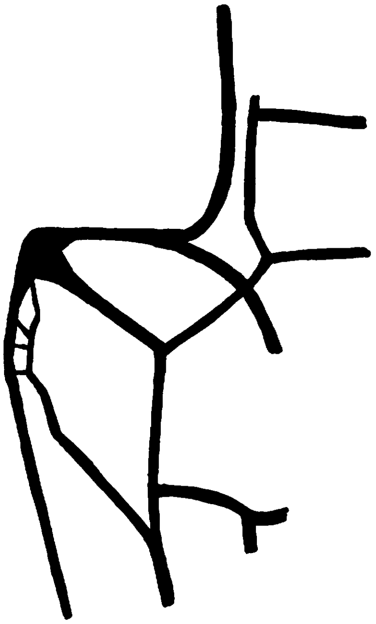


Figure 16. *Reynoldsiophyllum masonii* (Lesquereux) new combination, USNM 50077, details of tooth shown on plate 23, figure 5, ×7.5.

acute to obtuse. Orientation of tertiary venation ranging from transverse to nearly perpendicular to midvein; tertiary veins distinctly thinner than secondary veins.

Description.—Lamina oblong, L/W 3–4; leaf 12–15 cm long (estimated) by about 4.5 cm wide; apex obtuse; base acutely cuneate; margin broadly crenate; crenations 2–10 mm wide by up to 4 mm tall; sinuses broad, obtuse, rounded, and tending to be asymmetric in shape. Primary venation pinnate; primary vein stout to massive. Secondary venation festooned brochidodromous; secondary veins thin to moderate relative to primary vein, 9–10 pairs, subopposite to alternate, irregularly spaced, originating at predominantly moderate to broad acute angles, with a non-uniform pattern of variation in divergence angle, zig-zag to somewhat curved in course, looping well within the margin; subadjacent secondary vein thinner than the superadjacent secondary vein at their point of junction, with the superadjacent secondary vein often deflected apically; angle of brochidodromous junction broad acute to obtuse; excostal branches of secondary veins tending to form discrete series of loops parallel to the superadjacent secondary vein; exmedial sides of excostal secondary loops ranging from strongly angular to curved. Intersecondary veins absent. Tertiary venation irregularly reticulate; tertiary veins half to two-thirds the thickness of the secondary veins, tending to divide the intercostal regions into transverse to oblique segments, originating at acute to right angles on the exmedial side of the secondary veins and broad acute to obtuse angles on the admedial side, course irregular, giving rise to thinner lateral branches. Marginal reinforcement strongly developed, probably consisting of a fimbrial vein, marginal thickening usually widest and thickest at the apex of each crenation, suggesting that the apex of each crenation may be glandular. Each crenation with a medial vein, some of the large crenations with one or two accessory veins that converge on the margin and fuse with the thickened apex; tooth architecture possibly representing a variant of the chloranthoid type of Hickey and Wolfe (1975).

Cuticle not preserved on specimens.

Number of specimens examined.—2.

Holotype.—USNM 50077.

Paratype.—USNM 2779.

Locality.—Near Pipe Creek, Cloud County, Kansas (locality from Lesquereux, 1892).

Discussion.—Lesquereux originally assigned this species to the genus *Ilex* (Aquifoliaceae). However, detailed examination of foliar architecture indicates that this assignment is incorrect. In extant Aquifoliaceae, the leaf margin is either entire or serrate (never strongly crenate), the secondary veins are less zig-zag in course, the intercostal regions have much better defined exmedial margins, and the tertiary venation shows features different from those in *Reynoldsiophyllum.* Further, serrate-margined leaves of Aquifoliaceae have teeth that either are symmetric and spinose (for example, *Ilex dipyrena*) or are strongly asymmetric, with an eccentric medial vein, no accessory veins, and a non-deciduous glandular seta on the tooth apex (most species of *Ilex).* These patterns conform to the spinose and celastroid tooth types of Hickey and Wolfe (1975), respectively. The tooth architecture of *Reynoldsiophyllum* differs in several features and conforms most closely to the chloranthoid tooth type of Hickey and Wolfe (1975).

Reynoldsiophyllum masonii is distinct from all previously described taxa but shows similarities with four species. *R. masonii* resembles *"Myrica" aspera* Lesquereux (1892, p. 66, pl. 2, fig. 11) in shape and marginal pattern but is larger and has more prominent crenations; further, *"Myrica" aspera* preserves no venation above the first order. *R. masonii* resembles *"Celastrophyllum" crenatum* Heer, a species reported from the Patoot flora of Greenland (Heer, 1874, p. 41, pl. 62, fig. 1) and the Raritan Formation of New Jersey (Newberry, 1895, p. 99, pl. 48, figs. 1–19), and *Celastrophyllum undulatum* Newberry from the Raritan Formation of New Jersey (Newberry, 1895, p. 102, pl. 38, figs. 1–3), in shape and general pattern of secondary venation, but *R. masonii* differs in having more widely spaced secondary veins that enclose broader intercostal regions and show a more zig-zag course. In terms of tooth architecture, *R. masonii* strongly resembles *Crassidenticulum decurrens* in having a fundamentally chloranthoid pattern of venation combined with well-developed mechanical thickening at

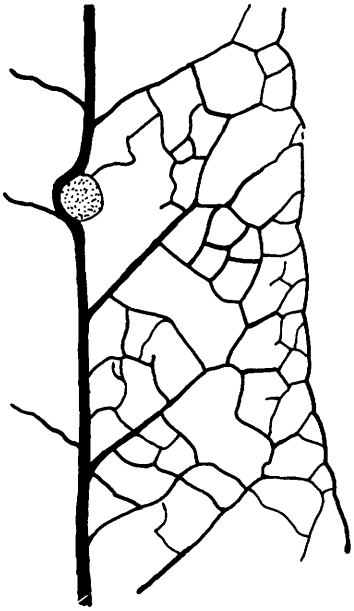


Figure 17. *Reynoldsiophyllum nebrascense* new species, 15713-4876, specimen shown on plate 24, figures 3 and 5, ×3. The stippled circular area adjacent to the midrib represents a fossil root that penetrates the leaf vertically.

the apex. However, *R. masonii* differs from *C. decurrens* in having broader intercostal regions, no intersecondary veins, and tertiary venation that tends to divide each intercostal region into a series of segments.

Because the tertiary and quaternary venation are better preserved in *Reynoldsiophyllum nebrascense*, modern affinities are discussed under that species.

Reynoldsiophyllum nebrascense new species

Plate 24; text figure 17

Diagnosis.—Lamina under 4 cm wide, L/W over 4; crenations 3–4 mm wide by less than 1 mm tall; marginal reinforcement showing no variation in width along the length of each crenation. Secondary veins thin relative to primary vein; superadjacent secondary vein usually equal in thickness to the subadjacent secondary vein at their point of junction, forming an acute angle. Orientation of tertiary venation typically transverse; tertiary veins nearly as thick as the secondary veins.

Description.—Lamina narrow elliptic, nearly oblong, L/W well over 4; lamina well over 8 cm long by about 1.8–2.5 cm wide; apex not fully preserved but probably obtuse or rounded; base acutely cuneate; petiole poorly differentiated from the blade; margin broadly crenate and with mechanical reinforcement; crenations 3–4 mm wide and less than 1 mm tall; sinuses broadly obtuse, rounded. Primary venation pinnate; primary vein stout. Secondary venation predominantly festooned brochidodromous, but intergrading with the condition where the secondary veins curve apically, thin, and merge with the tertiary venation; secondary veins thin relative to the primary vein, more than 8 pairs, subopposite to alternate, irregularly spaced, predominantly moderate to broad, rarely narrow, acute; course apically curved and often with deflection at points of branching; brochidodromous junction formed by two secondary veins of equal thickness, with the superadjacent secondary vein often deflected apically; angle of brochidodromous junction almost always acute; excostal secondary veins forming a complete inner and incomplete outer series of loops, these poorly differentiated from the tertiary venation, outer sides of loops tending towards rounded, in the outermost loops appearing to merge with the marginal thickening. Intersecondary veins absent. Tertiary venation irregularly reticulate; tertiary veins thick relative to the secondary veins and in excostal regions often difficult to distinguish from secondary veins, tending to divide the intercostal regions into a series of transverse segments, originating at acute to right-angled on the exmedial side of the secondary veins and obtuse to right-angled on the admedial side, composed of trunk veins and thick lateral branches that anastomose in an unpredictable pattern. Quaternary venation poorly differentiated from the tertiary venation, reticulate; quaternary veins often curved.

Cuticle poorly preserved, no preparations made.

Number of specimens examined.—4.

Holotype.—15713-7805, 7805′ (part and counterpart).

Paratype.—15713-4876, 4876′ (part and counterpart).

Derivation of epithet.—Referring to the occurrence of this species in Nebraska.

Discussion.—Four specimens from Rose Creek belong to *Reynoldsiophyllum nebrascense.* The holotype preserves nearly a complete leaf. The paratype comprises the middle portion of a leaf and lacks an apex and base, and the other specimens lack an apex, base, and margin but are identical to the first two specimens in preserved venational features. *Reynoldsiophyllum nebrascense* is distinguished from *R. masonii* by its smaller size (especially width), smaller and less prominent crenations, thinner secondary veins that are of equal thickness and form predominantly acute angles at their brochidodromous junctions, narrower intercostal regions, and thicker tertiary veins that have a more transverse orientation. *R. nebrascense* strongly resembles "*Myrica*" *aspera* in its size and shape but appears to have more numerous crenations; further, *M. aspera* preserves no venation above the first order, making demonstration of conspecificity impossible. *R. nebrascense* also resembles *Celastrophyllum crenatum* and *C. undulatum* in general shape and marginal type but is smaller and more elongate.

The modern affinities of *Reynoldsiophyllum* appear to lie with Magnoliidae, and similarities in tooth architecture with *Crassidenticulum decurrens* imply possible affinities with Chloranthaceae. Among extant angiosperms, the combination of pinnate organization, festooned brochidodromous secondary venation that has irregular course and spacing, and irregularly reticulate tertiary venation are most consistent with an assignment to Magnoliidae, although none of the characters represents a derived feature restricted to the subclass. Within extant Magnoliidae, the combination of transverse reticulate tertiary venation and chloranthoid teeth is restricted to Illiciales and certain Chloranthaceae (*Chloranthus* and *Sarcandra*). However, *Reynoldsiophyllum* does not possesses the curved and highly ramified quaternary venation that characterizes extant Illiciales with comparable venational regularity, and *Reynoldsiophyllum* differs from Illiciales in having well-developed marginal reinforcement over the teeth. *Reynoldsiophyllum* also is unlike *Chloranthus* and *Sarcandra* in quaternary venation (significantly thicker and not as strongly ramified), tooth shape (more rounded), and marginal thickenings (significantly better developed and not restricted to the region over the gland); however, many of these features occur in other genera of Chloranthaceae, indicating a possible relationship. This possibility is strengthened by similarities between *Reynoldsiophyllum* and the fossil taxon *Crassidenticulum decurrens*, especially with respect to features of systematic importance in extant flowering plants at higher taxonomic levels. These include pinnate organization, a tendency for the exmedial sides of the intercostal regions to be poorly demarcated by secondary veins, excostal secondary loops that range from angular to strongly curved on their exmedial sides, reticulate tertiary and quaternary venation, commonly curved quaternary veins, and teeth with chloranthoid venation that can be strongly crenate and have well-developed structural reinforcement, especially at the tooth apex. Of these features, the syndrome of tooth characters is unusual within extant angiosperms and, together with the other similarities, provides evidence for a close relationship between the two taxa. Thus, *Reynoldsiophyllum* may show affinities with Chloranthaceae but differs from extant members of the family in several foliar features, most notably the occurrence of mechanical reinforcement over the entire length of the tooth.

Dicotylophyllum angularis new species

Plate 25, figures 2–3; text figure 18

Diagnosis.—Lamina ovate, L/W 2.7 to at least 3; lamina >5 cm long by 1.8–3 cm wide; apex attenuate; base acutely cuneate. Primary venation pinnate; primary vein consisting of separate strands. Secondary venation festooned brochidodromous; secondary veins sharply changing course when forming loops; intercostal regions more or less isodiametric above the base of the lamina. Laminar resin bodies present.

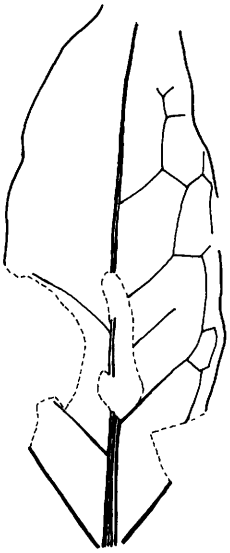


Figure 18. *Dicotylophyllum angularis*, 15713-4882A, specimen shown on plate 25, figures 2 and 3, ×1.

Description.—Lamina symmetric or more rarely slightly asymmetric, ovate, L/W 2.7 to at least 3; lamina >5 cm long by 1.8–3 cm wide; apex attenuate; tip of leaf not preserved; base acutely cuneate; petiolar region poorly differentiated from blade; margin entire, with structural reinforcement. Primary venation pinnate; primary vein moderate to stout, usually several-stranded at base, with fewer strands apically. Secondary venation festooned brochidodromous; secondary veins thin relative to primary vein, about as thick as an individual primary vein strand, at least 5 pairs, generally alternate, with wide but irregular spacing, with predominantly moderate acute divergence angles, curving little until at least halfway to the margin, typically making a sharp bend just before connecting with the superadjacent secondary vein; secondary vein looping tending towards angular, brochidodromous junction formed by two secondary veins of equal thickness, with the superadjacent secondary vein deflected apically; intercostal regions mostly isodiametric; excostal branches of the secondary veins forming a complete series of loops. Higher order venation poorly preserved. Laminar resin bodies present, interpreted as the remains of secretory cells.

Cuticle preserved along the margin and midvein of some specimens, but with the upper and lower cuticle adhering together tightly in preparations, making observation of cellular features impossible.

Number of specimens examined for foliar architecture.—5.

Number of specimens examined for cuticular anatomy.—1.

Holotype.—15713-4882A.

Derivation of epithet.—Latin, angularis = diminutive of angulus, or corner, referring to the sharp bend made by the secondary veins before forming loops.

Discussion.—Despite incomplete preservation *Dicotylophyllum angularis* is distinct from previously described species of Cretaceous angiosperms. Among Rose Creek forms it most closely resembles *Landonia calophylla*, from which it differs in shape and details of venation. *D. angularis* shows little resemblance to any previously described species of angiosperm leaves, despite the small number of preserved features.

Dicotylophyllum angularis appears to represent Magnoliidae, although few preserved features can be used for systematic placement. In particular, the combination of a several-stranded midvein and laminar resin bodies appears to be restricted to Magnoliidae. If an assignment to Magnoliidae is accepted, then *Dicotylophyllum angularis* probably belongs to Laurales, because the combination of a strongly ovate shape and isodiametric intercostal regions only occurs in Laurales of primitive to intermediate status, such as Amborellaceae, Austrobaileyaceae, and Monimiaceae. More definite consideration of the systematic position of *Dicotylophyllum angularis* awaits discovery of better preserved specimens.

New Genus B

Plate 25, figures 4–6; text figure 19

Description.—Lamina symmetric to slightly asymmetric, oblong, L/W well over 3; lamina well over 3 cm long by 1–2.4 cm wide (estimated maximum width); apex and base missing; margin entire, with structural reinforcement. Primary venation pinnate; primary vein massive, possibly multistranded. Secondary venation festooned brochidodromous; secondary veins thin, more than 5 pairs, ranging from alternate to subopposite, irregularly spaced, decurrent on primary vein, with irregular divergence angles ranging from narrow to broad acute, often sinuous, looping near the margin; loops often flattened parallel to margin; brochidodromous junction formed by secondary veins of equal thickness, with the superadjacent secondary vein deflected apically; intercostal regions highly variable in shape; excostal branches of the secondary veins poorly preserved but appear to extend to margin. Intersecondary veins present, 0 or 1 per intercostal region, branching to form tertiary veins. Tertiary venation irregularly reticulate; tertiary veins thick relative to the secondary veins, originating at acute to right angles on both sides of the secondary veins, course and spacing highly irregular but with a slight tendency for transverse orientation.

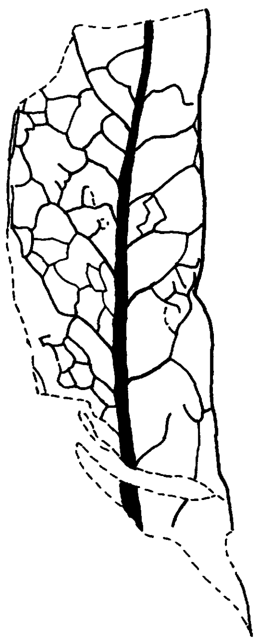


Figure 19. New genus B, 15713-4850, specimen shown on plate 25, figures 4 and 6, ×3.

Cuticle not preserved, no preparations made.

Number of specimens examined.—2.

Specimens.—15713-4831, 4831′ (part and counterpart), 4850.

Discussion.—Although this taxon differs from all previously described species of mid-Cretaceous angiosperms, fragmentary preservation precludes formal diagnosis. Among previously described fossil genera, New genus B resembles *Rogersia* Fontaine (1889) in size, shape, and venational regularity but differs in having less apically oriented secondary veins. New genus B also resembles *Eucalyptophyllum* Fontaine and *Myrtophyllum* Heer in having an oblong shape but differs in having secondary veins that form loops (rather than connect with an intramarginal vein) and in having less strongly oriented tertiary venation.

The high irregularity of the secondary and tertiary venation in New genus B is suggestive of magnoliid affinities, but incomplete preservation and predominance of generalized venational features makes systematic placement difficult.

Subclass ROSIDAE

Anisodromum new genus

Diagnosis.—Leaf compound, lamina of each leaflet elliptic, base acute, with a distinct petiolule present on each leaflet, margin entire. Primary venation pinnate. Secondary venation tending toward eucamptodromous but with tendencies to form brochidodromous loops; secondary veins originating at an angle greater than 45°, distinctly asymmetric in behavior, with the secondary veins on one side of the lamina either diverging from the midvein at a higher angle or curved for a greater proportion of their length; each secondary vein producing its own series of weakly formed brochidodromous loops that extends to near the margin. Tertiary venation weakly percurrent; tertiary veins thin, closely spaced, with low angle branching, oriented at nearly a right angle to the midrib.

Type species.—*Anisodromum wolfei* new species.

Derivation of name.—Greek, anisos = unequal, dromos = course, referring to the asymmetry of the secondary venation.

Anisodromum wolfei new species

Plate 26; text figure 20

Diagnosis.—As for genus.

Description.—Leaf compound, with at least three leaflets; lamina of leaflets narrow elliptic, L/W over 2; lamina >4.5 cm long by 2–4 cm wide; apex unknown; base acutely cuneate; petiolule present, up to 2 cm long; margin entire, with structural reinforcement. Primary venation of each leaflet pinnate; primary vein stout. Secondary venation smoothly curving and gradually thinning near margin but showing a tendency to form loops (therefore, predominantly eucamptodromous but with brochidodromous tendencies), asymmetric in behavior, with the secondary veins on one side of the lamina diverging from the primary vein at a higher angle and/or curving for a greater proportion of their length; secondary veins moderate relative to the primary vein, more than 8 pairs, subopposite, tending to be evenly spaced, moderate to broad acute, apically curved, extending to near the margin. Intersecondary veins absent. Tertiary venation percurrent; tertiary veins thin relative to the secondary veins, usually forming an acute angle on the exmedial side of the secondary veins and right or obtuse angle on the admedial side, typically branching at narrow acute angles, in most specimens oriented at nearly right angles to the midvein of the leaflet.

Cuticle not preserved.

Number of specimens examined.—6.

Holotype.—15713-7803.

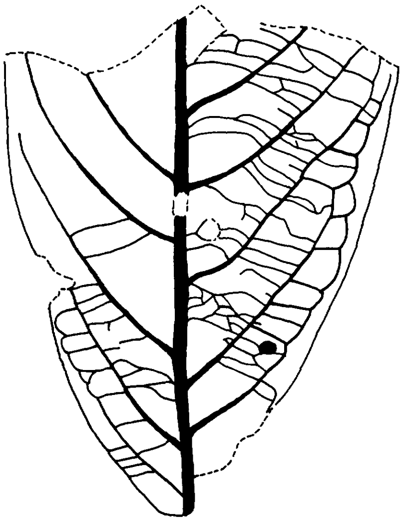


Figure 20. *Anisodromum wolfei* new genus and species, 15713-7866, ×2. The dark circular region on the lower right represents a fossil root that penetrates the leaflet vertically.

Paratypes.—15713-7802, 7866.

Derivation of epithet.—In honor of Jack A. Wolfe and in recognition of his assistance to this project.

Discussion.—Among previously described genera of fossil angiosperms *Anisodromum* most closely resembles *Sapindopsis*, especially pinnately compound leaves assigned to this genus by Doyle and Hickey (1976) and Hickey and Doyle (1977), in shape and general pattern of venation. However, *Anisodromum* differs in having secondary venation that shows asymmetric behavior and much less brochidodromous looping, much more percurrent and closely spaced tertiary venation, and a structurally reinforced margin. We interpret these differences as significant at the generic level by analogy to extant pinnately compound Rosidae, where genera are distinguished on the basis of secondary venation, tertiary venation, and marginal characteristics.

Among previously described species of fossil angiosperm foliage *Anisodromum wolfei* resembles several species of pinnately compound leaves that have thin, apically curved secondary veins, including "*Rhus*" *powelliana* Lesquereux (1892, pl. 56, fig. 45), "*Rhus*" *uddeni* Lesquereux (1892, pl. 57, fig. 2) and "*Hymenaea*" *dakotana* Lesquereux (1892, pl. 55, figs. 2, 3; pl. 56, figs. 1, 2; pl. 62, fig. 2). *Anisodromum wolfei* differs from these species in having asymmetrical secondary venation and in having the following combination of features: (1) leaflets with a distinct petiolule, and (2) closely spaced tertiary veins that are oriented at nearly right angles to the midvein. *A. wolfei* also resembles isolated laminar units described as *Leguminosites hymenophyllus* Lesquereux (1892, pl. 55, figs. 7–9; pl. 56, fig. 3) but differs in having asymmetrical secondary venation.

A. wolfei strongly resembles isolated laminar units assigned to "*Rhamnus*" *prunifolius* Lesquereux (1874, illustrated in Lesquereux, 1892, pl. 35, fig. 14) in secondary and tertiary venation but has an elliptic, rather than ovate, shape and asymmetrical secondary venation. Finally, *A. wolfei* resembles isolated laminar units described as "*Andromeda*" *latifolia* by Newberry (1895, especially pl. 34, figs. 6–11) in shape and pattern of secondary and tertiary venation, but it differs from "*A.*" *latifolia* in having asymmetrical secondary venation that is oriented at a higher angle to the midrib.

The modern affinities of *Anisodromum* clearly lie with the subclass Rosidae. Among extant dicotyledons, compound foliage is restricted to the subclasses Ranunculidae, Rosidae, Dilleniidae, and Asteridae. Of these subclasses, only Rosidae has compound leaves where the secondary venation of each leaflet has distinct asymmetry. *Anisodromum* does not fit within any extant order of Rosidae because it combines features currently restricted to separate orders. *Anisodromum* has the compound organization characteristic of Sapindales, Rutales, and certain taxa of Saxifragales and Rosales; however, its pattern of tertiary venation is unknown in these groups. Instead, the general pattern of tertiary venation found in *Anisodromum* characterizes many simple-leaved members of Rosidae, most notably Cornales, Rhamnales, certain Celastrales (some Celastraceae and Icacinaceae) and Santalales (Olacaceae), and some simple-leaved families of Saxifragales (most notably Escalloniaceae and Iteaceae). These simple-leaved taxa typically have more widely spaced tertiary veins than *Anisodromum*, but some pinnately veined Rhamnaceae (*Berchemia*, *Rhamnidium*, and *Rhamnus*), Celastraceae (*Bhesa*), Icacinaceae (*Emmotum*) and Olacaceae (*Coula*) have tertiary venation with the same close spacing and orientation relative to the midrib, typically in association with strongly eucamptodromous secondary venation. The venational similarities between *Anisodromum* and extant Rhamnaceae are of particular interest because the flowers reported from the Rose Creek locality by Basinger and Dilcher (1984) combine generalized features found in Rosidae and other subclasses with specialized features most characteristic of Rhamnales (especially stamens opposite the petals and small tricolporate pollen grains with an oblate shape and psilate surface sculpture). This combination of features today found in different orders of Rosidae, when coupled with evidence for the derivation of *Citrophyllum* from a compound-leaved ancestor (described later), provides direct paleobotanical evidence for a phylogenetic link between the two major alliances of Rosidae (Hickey and Wolfe, 1975).

Citrophyllum Berry, 1911b.

Emended Diagnosis.—Leaf simple, lamina unlobed, petiole alate, constricted at the base of the lamina, margin entire, structurally reinforced. Primary venation pinnate. Secondary venation often faintly visible or absent on impressions; secondary veins originating at an acute angle greater than 45°; intercostal regions exmedially elongate, apically curved. Tertiary and higher order venation more or less immersed in the laminar tissue, when preserved at least in part reticulate.

Figure 21. *Citrophyllum doylei* new species, 15713-4894, specimen shown on plate 27, figures 1, 3, and 4, ×2. Note the eucamptodromous secondary veins and the closely spaced tertiary veins with low-angle branching. The raggedness of the margin results from differential preservation of the reinforcement tissue.

Type species.—*Ficus aligera* Lesquereux, 1892, p. 84, pl. 10, figs. 3–6.

Species included within Citrophyllum.—*C. aligerum* (Lesq.) Berry, 1911b, p. 169, pl. 21, figs. 1–8. Upper Cretaceous, Dakota and Raritan Formations, USA.

C. doylei new species. Upper Cretaceous, Dakota Formation, USA.

Citrophyllum doylei new species

Plate 27, figures 1, 3, 4; text figure 21

Diagnosis.—Lamina mesophyllous in size. Alation on petiole parallel-sided for nearly all its length, abruptly constricted at base of lamina.

Description.—Basal two-thirds of leaf preserved, L/W well over 2; lamina significantly longer than 8.5 cm by about 5 cm wide (estimated width); apex missing; base obtuse, bordering on rounded, slightly asymmetric, with the two sides of the lamina joining the midrib at slightly different levels; petiole at least 0.9 cm long by 0.3 cm wide, with margins that are more or less parallel up to the point of constriction. Primary vein stout, bordering on moderate. Secondary venation eucamptodromous; secondary veins moderate relative to the primary vein, more than 6 pairs, subopposite to alternate, sometimes slightly decurrent on the primary vein, originating at a broad acute angle, apically curved for most of their length. Tertiary venation at least in part reticulate; tertiary veins thin relative to the secondary veins, originating at an acute angle on the exmedial side of the secondary veins and an obtuse angle on the admedial side, oriented nearly perpendicular to the primary vein, closely spaced (about 10 veins per cm), subparallel, straight to slightly curved or sinuous, often branching at a low acute angle. Higher order venation poorly preserved.

Cuticle poorly preserved, no preparations attempted.

Number of specimens examined.—1.

Holotype.—15713-4894.

Derivation of name.—In honor of James A. Doyle and in recognition of his numerous contributions to our understanding of early flowering plants.

Discussion.—*Citrophyllum* is distinguished from other genera of Cretaceous angiosperm leaves by the combination of an unlobed lamina with a structurally reinforced margin, an alate petiole that is constricted at its junction with the lamina, and pinnate venation. Although the genus was assigned to Rutaceae and compared with exant *Citrus* by Berry (1911b), *Citrophyllum* does not possess the following features that characterize Rutaceae: (1) a joint at the junction of the petiole and blade in simple leaves, (2) straight-sided intercostal regions, (3) widely spaced tertiary venation, and (4) large laminar secretory cavities, which in fossil material would be preserved as dark spots or as empty regions around which the higher order veins ramify. Therefore, the assignment of *Citrophyllum* to Rutaceae is invalid.

The one specimen of *Citrophyllum doylei* known from Rose Creek represents a new species, which differs from remains assigned to *C. aligera* (Lesq.) Berry in having a larger size, a more abrupt constriction of the petiole, and more strongly curved secondary venation. The orientation of the tertiary venation in *Citrophyllum doylei* also differs from that illustrated by Lesquereux for the type species (Lesquereux, 1892, pl. 20, figs. 3–6), but the type specimens lack clearly observable tertiary venation. The type specimens of *C. aligera* examined from the Dakota and Raritan Formations can be divided into at least two groups based on the shape of the petiole and blade, which implies that three species of *Citrophyllum* may have been present in the earliest Late Cretaceous of North America.

The alate petiole of *Citrophyllum*, with its constriction at the base of the lamina, previously has been interpreted as the homologue of a rachis in a compound leaf and hence evidence of a compound-leaved ancestry (Berry, 1911b; Hickey, 1978). Some simple-leaved taxa of presumed compound-leaved ancestry, such as *Citrus* in the Rutaceae, have an alate petiole with a constriction at the lamina-petiole junction, similar to the constriction of the alate rachis of a compound leaf at points of leaflet origin. This comparison is supported by similarities in the secondary and tertiary venation of *Citrophyllum* and *Anisodromum*, the latter of which represents a compound leaf. The absence of a constriction at the junction of the petiole and blade in families, such as Winteraceae and Canellaceae, which are of presumed simple-leaved ancestry, adds further support to this interpretation. One potential problem with this scheme of homology is that all known specimens of *Citrophyllum* appear to lack a joint at the junction of the petiole and blade, a feature that is present in extant *Citrus* and is thought to be the homologue of the joint found at the base of each leaflet in a typical compound leaf. This absence could be explained by the absence of a joint at the junction of the leaflet and rachis in a compound-leaved ancestor, because Early Cretaceous taxa with pinnately compound leaves (such as *Sapindopsis*) do not appear to possess a joint at the junction of the leaflet and rachis (L.J. Hickey, oral comm., 1983; Garland Upchurch, unpublished observations). Although the absence of a joint in the leaves of *Citrophyllum* could reflect the evolution of the alate rachis through the fusion of stipules to the petiole, extant forms with this condition (such as many Rosaceae) almost always have stipules that are free from the petiole for part of their length. Thus, evidence favors a compound-leaved ancestry for *Citrophyllum*.

The modern affinities of *Citrophyllum* appear to be with subclass Rosidae. Within extant angiosperms, compound leaves occur in Ranunculidae, Rosidae, and a few Dilleniidae and Asteridae (Hickey and Wolfe, 1975). Among these subclasses, only Rosidae has members where the compound leaf possesses an alate rachis (many Sapindaceae, some Anacardiaceae) or where there is a simple leaf with an alate petiole constricted at the base of the lamina (some Rutaceae). The general pattern of tertiary venation found in *Citrophyllum* is consistent with an assignment to Rosidae, because it is found in only a few Dilleniidae (Thymeleaceae) but characterizes many families of simple-leaved Rosidae, including Iteaceae, Olacaceae, Mastixiaceae, Rhamnaceae, Celastraceae, and Icacinaceae. Within Rosidae, *Citrophyllum* cannot be assigned to an extant order. This is because it has the alate petiole suggestive of the alate rachis in compound-leaved taxa, such as Sapindales, Rutales, and certain Saxifragales (for example, Cunoniaceae), but it has the thin, weakly percurrent, admedially oriented tertiary venation characteristic of some genera in simple-leaved orders, such as Rhamnales, Celastrales, and Santalales. This combination of features today is restricted to separate groups of Rosidae, and thus provides fossil

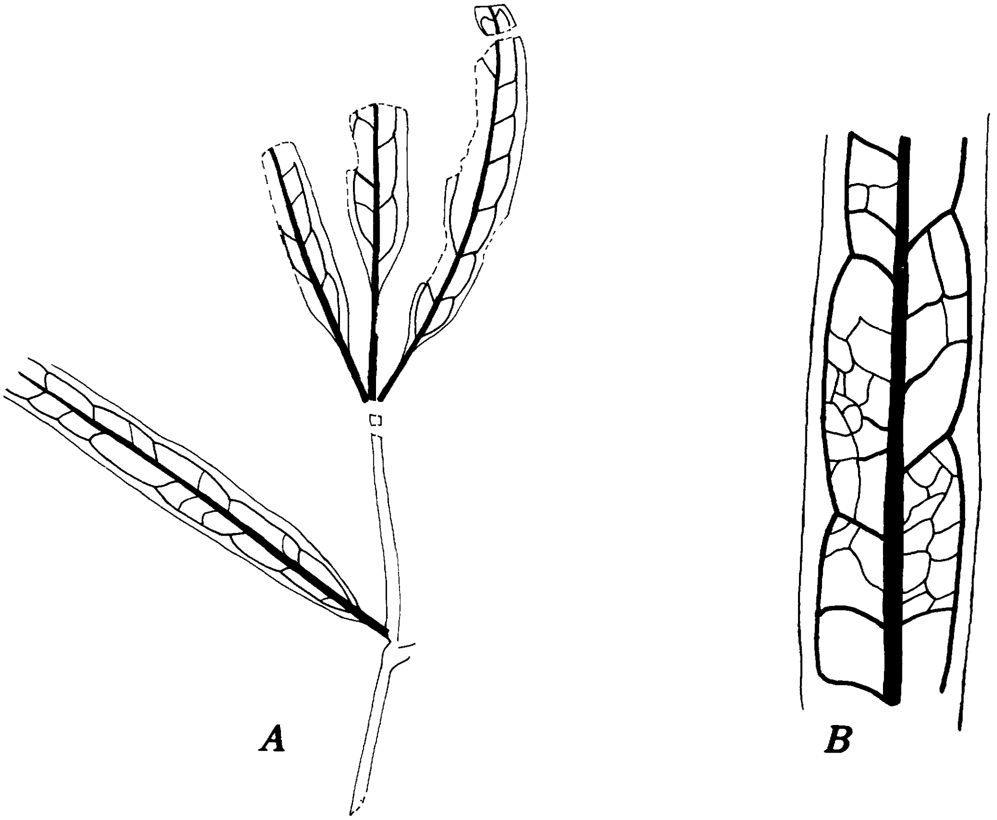


Figure 22. *Dicotylophyllum myrtophylloides* new species, 15713-8303, specimen shown on plate 28. *A*, General view of specimen, × 3. *B*, Enlargement of middle region, lower left leaf, × 10. Note the poorly organized tertiary venation.

evidence for phylogenetic link between the simple- and compound-leaved families of the subclass. The occurrence of more generalized venational features in earlier Cretaceous compound leaves belonging to Rosidae, along with the apparent absence of simple-leaved Rosidae from the Early Cretaceous, provides stratigraphic evidence in favor of compound leaves being primitive to the subclass, as proposed by Hickey and Wolfe (1975).

MAGNOLIOPSIDA subclass unknown

Dicotylophyllum myrtophylloides new species

Plate 28; text figure 22

Diagnosis.—Leaf linear. Primary venation pinnate. Secondary venation pinnate with an intramarginal vein; intramarginal vein arching between secondary veins; basalmost secondary vein at a lower angle than the superadjacent secondary veins; intercostal regions elongate parallel to midrib. Tertiary venation irregularly reticulate.

Description.—Leaves attached to stem, phyllotaxy appearing to be either opposite and decussate or whorled; stem approximately 0.5 mm in diameter, having no wing of flattened tissue and hence appearing to have little cortical tissue. Leaves simple, linear, L/W over 7; lamina over 2 cm long by 2–3 mm wide; apex unknown; base acute; petiole with a decurrent wing of laminar tissue; margin entire. Primary venation pinnate; primary vein massive, 0.3–0.4 mm wide at base of lamina. Secondary venation pinnate with an intramarginal vein, but with the intramarginal vein smoothly arching between secondary veins; secondary veins thin relative to primary vein, more than 8 pairs, with the basalmost pair at a lower angle than the superadjacent pairs, subopposite to alternate, irregularly spaced, diverging at moderate to broad acute angles, straight, connecting with intramarginal vein well within margin; intercostal regions apically elongate. Intersecondary veins present, none or 1 per intercostal region, branching to form tertiary veins. Tertiary venation irregularly reticulate; tertiary veins thin relative to secondary veins. Higher order venation not preserved.

Cuticle not preserved.

Number of specimens examined.—1 (4 leaves attached to one axis).

Holotype.—15713-8303.

Derivation of epithet.—From the genus *Myrtophyllum*, referring to the superficial resemblance of *Dicotylophyllum myrtophylloides* to *Myrtophyllum*.

Discussion.—The one preserved specimen of *Dicotylophyllum myrtophylloides* clearly represents a new taxon of mid-Cretaceous angiosperms. Although leaves of this taxon might be assigned to the genus *Myrtophyllum* by some workers, *D. myrtophylloides* differs from the type species of *Myrtophyllum* (*M. geinitzi*) and obviously related forms (for example, *M. angustifolium*) in having intercostal regions that are elongate parallel, rather than perpendicular to, the midvein. In extant angiosperms, such pronounced variation in the shape of the intercostal regions typically segregates genera and families. (See table 2 for examples.)

Leaves of *D. myrtophylloides* resemble those of Myrtaceae in gross aspect, but details of secondary and tertiary venation preclude assignment to Myrtaceae. Most Myrtaceae have intercostal regions that are elongate at an angle to the midvein, rather than parallel to it, and the tertiary venation tends toward percurrent, rather than irregularly reticulate. Myrtaceae that have intercostal regions elongate parallel to the midvein, such as *Callistemon* and *Rhodamnia*, typically have two sets of associated features that are not present in *D. myrtophylloides*: first, the secondary veins are significantly thinner than the intramarginal vein and tend to intergrade with the tertiary veins, while the intramarginal vein is nearly the same thickness as the midvein and does not arch between the secondary veins; second, the tertiary venation is either reticulate and more highly organized than that of *D. myrtophylloides* or has a strongly ramified component. Thus, *Dicotylophyllum myrtophylloides* does not appear to represent Myrtaceae, despite a gross resemblance.

The one preserved specimen of *D. myrtophylloides* appears to represent four leaves attached to a slender axis, rather than a compound leaf. Evidence for this interpretation is the position and orientation of the laminar units in the matrix. In a compound leaf, all the leaflets typically are preserved on a single bedding plane, rather than at different levels, and petiolules are all oriented parallel to the bedding plane. In addition, the bases of the most apical pair of lateral leaflets do not overlap the base of the terminal leaflet. In contrast, the basalmost laminar unit of *D. myrtophylloides* is located at a significantly higher position in the matrix than the superadjacent laminar units (not readily apparent on plate 28), and its petiole is oriented at nearly a right angle to the bedding plane. The superadjacent laminar units are orientated much more parallel to the plane of bedding than the most basal laminar unit; however, each one of these superadjacent laminar units is oriented in a somewhat different plane from the others, and the base of the medial laminar unit looks as if it is somewhat obscured by the bases of the two lateral laminar units (pl. 28, fig. 3). The presence of a cluster of three laminar units at the tip of the axis implies that phyllotaxy was whorled. Also possible is that the leaves were arranged in an opposite and decussate manner and that the fourth leaf was preserved only on the now missing counterpart.

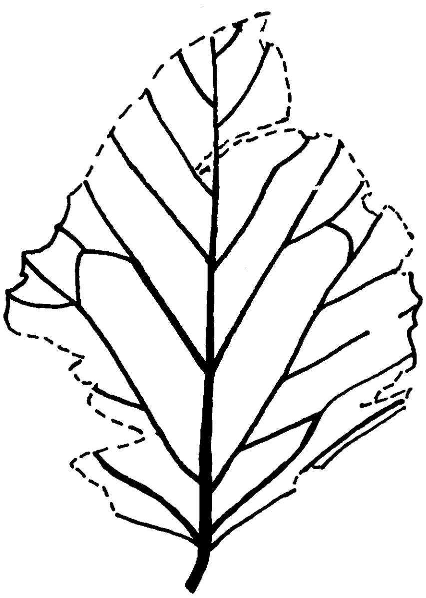


Figure 23. *Dicotylophyllum rosafluviatilis* new species, 15713-4698, specimen shown on plate 29, figures 1, 2, 4, and 5, illustrating secondary venation, ×1.

Incomplete preservation of venation precludes assignment of *D. myrtophylloides* to any extant order of angiosperms. The inferred pattern of leaf arrangement and details of secondary venation imply that *D. myrtophylloides* could be related to either Laurales (*Myrtophyllum geinitzii* and *M. angustifolium*) or Myrtales. If the inferred pattern of phyllotaxy is wrong, then affinities to Dilleniaceae (*Hibbertia*) are also possible (Rury and Dickison, 1977). Precise systematic placement awaits discovery of better preserved materials.

Dicotylophyllum rosafluviatilis new species

Plate 29; text figure 23

Diagnosis.—Lamina ovate, but with the sides of the lamina tending toward straight-sided rather than curved; base cuneate; petiole distinct; margin denticulate. Primary venation pinnate, but with one pair of secondary veins producing exmedial branches for most of its length. Secondary venation craspedodromous, with each secondary vein running directly to a tooth; some secondary veins interconnected by an additional set of loops; basilaminar secondary veins present. Tertiary venation thin, subparallel, tending to be admedially oriented near the apex.

Description.—Lamina ovate but with the sides of the lamina tending towards straight-sided rather than curved, L/W = 1.5 (estimated); lamina 7.5 cm long (estimated length) by 5.2 cm wide; apex probably attenuate (tip missing); base obtusely cuneate; distinct petiole present; margin denticulate and with structural reinforcement; teeth tending towards straight-straight (B-2), broad, with rounded apex, 2–3.5 mm wide by < 1 mm tall; sinuses broadly obtuse, rounded. Primary venation pinnate; primary vein moderate. Secondary venation simple craspedodromous, with additional brochidodromous loops connecting some adjacent secondary veins; secondary veins thick relative to the primary vein, crowded at the base of the leaf, at least 8 pairs, subopposite in the basal half of the lamina, alternate above, narrow acute; basilaminar secondary veins thin, unbranched, and retroflexed; second pair thicker but similar in behavior; third pair of secondary veins thick, straight, and with external branches for most of their length; the superadjacent secondary veins successively thinner and with external branches for less than half their length; external branches of the secondary veins always at a narrow acute angle to source vein. Tertiary venation percurrent; tertiary veins thin relative to secondary veins, arising at an acute angle on the exmedial side of the secondary veins and an acute to right angle on the admedial side, joining the primary vein at an acute to right-angle, convex. Quaternary venation unbranched to reticulate; quaternary veins thick relative to tertiary veins, without strong orthogonal rooting, irregular in spacing and course. Teeth showing no evidence of strong glandularity (but preservation is poor); medial vein symmetric; accessory venation obscure but obviously not strongly developed; features of teeth difficult to discern because of decay and the darkened remnants of the reinforcement tissue along the margin.

Number of specimens examined.—1.

Holotype.—15713-4698, 4698′ (part and counterpart).

Derivation of epithet.—Latin, rosa = rose, fluviatilis = of a stream, referring to the occurrence of this species at the Rose Creek locality.

Discussion.—Dicotylophyllum rosafluviatilis represents a distinct taxon of mid-Cretaceous angiosperm foliage. If the teeth and higher order venation were better preserved, the specimen probably would be the basis for a new genus. However, because poor preservation makes confident assignment to a subclass impossible, we have assigned the specimen to *Dicotylophyllum*. Among previously described species of mid-Cretaceous angiosperm foliage, *D. rosafluviatilis* most closely resembles "*Crataegus*" *lacoei*? Lesquereux (1892, pl. 64, fig. 14; pl. 66, fig. 2) and "*Viburnum*" *lesquereuxii* Ward var. *longifolium* (in Lesquereux, 1892, pl. 53, fig. 1) in shape and pattern of secondary venation. *D. rosafluviatilis* differs from "*C.*" *lacoei*? in having a distinct petiole and from "*V.*" *lesquereuxii* var. *longifolium* in having more closely spaced tertiary veins that tend to be admedially oriented in the apical part of the lamina. The unusual pattern of secondary venation shared by these three species implies that they are possibly congeneric, but confirmation of this suggestion awaits study of better preserved materials.

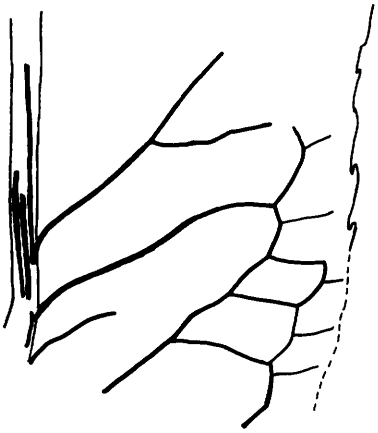


Figure 24. *Dicotylophyllum aliquantuliserratum* new species, 15713-4707, specimen shown on plate 30, figure 2, details of brochidodromous looping and margin, ×5.

The general pattern of secondary venation found in *Dicotylophyllum rosafluviatilis* occurs in many families of dicotyledons but is most characteristic of subclass Hamamelididae. The exact pattern of secondary venation found in *D. rosafluviatilis* (with a pair of basilaminar secondary veins, a superadjacent pair of recurved, sparsely branched secondary veins, and a third pair of craspedodromous secondary veins that are branched for most of their length) has only been observed in Eupteleaceae. Although this could indicate a relationship between *D. rosafluviatilis* and Eupteleaceae, tooth structure is not well enough preserved in *D. rosafluviatilis* to determine affinities. Further, Eupteleaceae differ from *D. rosafluviatilis* in having a margin without structural reinforcement, larger teeth, less branched and more regular tertiary venation, and quaternary venation that encloses quadrangular regions of fairly regular size and shape. Thus, *Dicotylophyllum rosafluviatilis* may belong to Hamamelididae, but better preserved specimens are needed to accurately determine modern affinities.

Dicotylophyllum aliquantuliserratum new species

Plate 30; text figure 24

Diagnosis.—Lamina narrow elliptic, margin with minute serrations that are generally visible only with magnification. Primary venation pinnate. Secondary venation festooned brochidodromous; secondary veins numerous, closely spaced, moderate to broad acute; brochidodromous junction formed by secondary veins of equal thickness, with the superadjacent vein deflected apically; each secondary vein forming an apically arching series of excostal loops. Tertiary veins admedially oriented.

Description.—Lamina elliptic, L/W over 3; lamina at least 4.5–5.5 cm long by 1.4–1.8 cm wide; apex acute and tending toward rounded at the tip; base missing; margin minutely serrate. Primary venation pinnate; primary vein stout. Secondary venation festooned brochidodromous; secondary veins thin relative to the primary vein, numerous, closely but somewhat irregularly spaced, slightly decurrent, moderate to broad acute, with only a few of the secondary veins showing significant differences in divergence angle; course somewhat irregular, not curving apically until looping, forming loops at irregular distances from the margin; brochidodromous junction formed by secondary veins of equal thickness, the superadjacent secondary vein deflected apically; angle of brochidodromous junction acute to obtuse; each secondary vein gradually thinning and forming its own series of irregularly proportioned excostal loops that run to near the margin; excostal loops tending towards curved on their exmedial sides. Intersecondary veins occasionally present. Tertiary venation generally obscure, probably reticulate; tertiary veins (when preserved) forming an acute or right angle on the exmedial side of the secondary veins and an obtuse or right angle on the admedial side, oriented towards midvein. Discontinuities present in the lamina of one specimen, appearing to represent venation, if so, then higher order venation irregularly reticulate.

Cuticle not preserved.

Number of specimens examined.—5.

Holotype.—15713-4877A, 4877B.

Paratypes.—15713-4704, 7804.

Derivation of epithet.—Latin, aliquatulus = small, and serra = saw, referring to the small teeth that often can be seen only under the microscope.

Discussion.—These remains, though preserved as fragments, resemble leaflets of an entire-margined, pinnately compound leaf type from the Potomac Group of Maryland that was informally included within the genus *Sapindopsis* Fontaine by Doyle and Hickey (1976, figs. 23, 24), Hickey and Doyle (1977), and Upchurch (1984). Similarities include a narrow elliptic shape, stout primary vein, numerous secondary veins (each forming its own series of irregular excostal loops that extends to near the margin), excostal loops that are curved on their outer sides, and reticulate tertiary venation where the tertiary veins originate at acute to right angles on the exmedial sides of the secondary veins and right to obtuse angles on the admedial side. The Rose Creek fossils compare favorably with the Potomac Group leaves in other preserved features except for the minutely serrate margin, which is unknown in any of the leaves assigned to *Sapindopsis*. The Rose Creek fossils show points of similarity with "*Hymenaea*" *dakotana* Lesquereux from the Dakota Formation of Kansas (Lesquereux, 1892, pl. 55, figs. 2, 3; pl. 56, figs. 1, 2; pl. 62, fig. 2) but differ in their denticulate margin, less regular secondary venation, and less admedially oriented tertiary venation. *D. aliquantuliserratum* also resembles remains from the Cheyenne Sandstone of Kansas (improperly) assigned by Berry to *Sapindopsis variabilis* Fontaine and *S. magnifolia* Fontaine (Berry, 1922, p. 213–215, pl. 55, figs. 2–5; pl. 56, figs. 1–3), particularly in shape and secondary venation, but it differs in the character of its margin. Finally, *D. aliquantuliserratum* resembles various serrate leaf types that have pinnatifid and pinnately compound organization, such as *Sapindopsis belvederensis* Berry (1922) and *Anarcardites neuburgae* Vakhrameev (1952), in general pattern of secondary venation but differ in the details of the margin. These similarities are such that if the Rose Creek fossils were preserved as leaflets or lobes pinnately arranged along a rachis we would describe them as a new species of *Sapindopsis*. However, in the absence of better preserved materials, this leaf type is assigned to the form genus *Dicotylophyllum*.

Dicotylophyllum expansolobum new species

Plate 31; text figure 25

Diagonosis.—Leaf simple, five-lobed; lobes all diverging at approximately the same level on the leaf; each lobe widest above the base; margin with minute teeth that are difficult to see without magnification. Primary venation basally palmate; primary veins 5, stout/massive.

Description.—Leaf simple, five-lobed; lamina over 8.5 cm long by over 7.5 cm wide; lobes 0.4–0.8 cm wide at base, with a maximum width of 3.0 cm (estimated); apex of lobes missing; sinuses between lobes rounded; base of lamina obtusely cuneate; margin with both structural reinforcement and minute serrations; serrations ranging from concave to straight on the apical side and straight to convex on the basal side, less than 1 mm wide by less than 0.3 mm tall; distinct petiole present, over 1 cm long. Primary venation palmate, exact pattern difficult to discern because of poor preservation; primary veins stout or massive, 1 mm wide at base of leaf, with a straight course. Secondary and higher order venation obscure due to poor preservation; one secondary vein observed, thin, less than 0.2 mm wide.

Cuticle badly fragmented, no preparations made.

Number of specimens observed.—1.

Holotype.—15713-8304, 8304′ (part and counterpart).

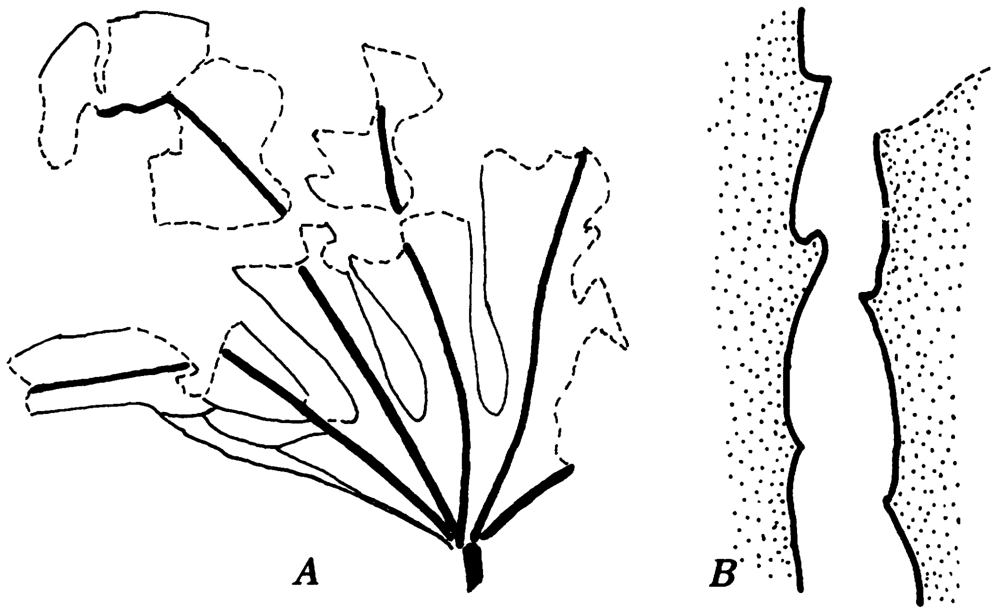


Figure 25. *Dicotylophyllum expansolobum* new species. *A*, 15713-8304′ (counterpart), specimen shown on plate 31, figure 1, ×1. *B*, 15713-8304 (part), specimen shown on plate 31, figures 2–4, teeth along the margin of two adjacent lobes, ×7.5. Areas of leaf tissue are stippled.

Derivation of epithet.—Latin, expansus = spread out, and lobus = lobe, referring to the expansion of the lobes above their base.

Discussion.—*Dicotylophyllum expansolobum* is clearly distinct from any previously described type of Cretaceous leaf, despite poor preservation. The surficial wrinkling and evidence for a structurally reinforced margin imply that this leaf was thick-textured in life. The primary veins of this leaf possess longitudinal striations, which were originally interpreted as evidence of a multistranded primary vein. However, the strong wrinkling found on other parts of the leaf indicate that this probably is an artifact of preservation.

Among previously described species of fossil angiosperms, *Dicotylophyllum expansolobum* most closely resembles several species of lobed leaves of Cenomanian age. These include *"Aralia" quinquepartita* Lesquereux (1871, p. 302; 1874, pl. 15, fig. 6) and *"Sterculia" lugubris* Lesquereux (1883, pl. 6, figs. 1–3), both from the Dakota Formation of Kansas. Similarities shared by these three taxa include palmate organization and similar shape to the lobes, sinuses, and laminar base. However, *Dicotlyophyllum expansolobum* differs from *"A." quinquepartita* in having small teeth and in having the sinuses between the inner and outer pairs of lobes occur at approximately the same level on the leaf, rather than at different levels; *D. expansolobum* differs from *"S." lugubris* in having small teeth and five lobes. Unfortunately, none of these species preserves venation above the first order well, precluding closer comparison.

The modern affinities of *Dicotlyophyllum expansolobum* are uncertain because of poor preservation. No extant species of Magnoliidae has pentalobate organization with basally palmate primary venation.

REFERENCES CITED

Axelrod, D.I., 1952, A theory of angiosperm evolution: Evolution, v. 5, no. 1, p. 29–60.

_____ 1970, Mesozoic paleogeography and early angiosperm history: Botanical Review (Lancaster), v. 36, p. 277–319.

Basinger, J.F., and Dilcher, D.L., 1984, Ancient bisexual flowers: Science, v. 224, no. 4648, p. 511–513.

Berry, E.W., 1911a, Systematic paleontology, Lower Cretaceous: fossil plants, *in* Clark, W.B., editor, Lower Cretaceous: Baltimore, Maryland Geological Survey, p. 214–508, pls. 22–97.

_____ 1911b, The flora of the Raritan Formation: Geological Survey of New Jersey Bulletin 3, 233 p., 29 pls.

_____ 1922, The flora of the Cheyenne Sandstone of Kansas: U.S. Geological Survey Professional Paper 129–I, p. 199–226.

Brown, R.W., 1933, Fossil plants from the Aspen Shale of southwestern Wyoming: U.S. National Museum Proceedings, v. 82, art. 12, 10 p., 2 pls.

_____ 1956, Palmlike plants from the Dolores Formation (Triassic) in southwestern Colorado: U.S. Geological Survey Professional Paper 274–H, p. 205–209, pls. 32, 33.

_____ 1962, Paleocene flora of the Rocky Mountains and Great Plains: U.S. Geological Survey Professional Paper 375, 119 p., 69 pls.

Capellini, Giovanni, and Heer, Oswald, 1866, Les phyllites cretacees du Nebraska: Societe Helvetique science naturelles, Nouvelle, Memoires, v. 22, p. 1–22.

Cobban, W.A., and Merewether, E.A., 1983, Stratigraphy and paleontology of mid-Cretaceous rocks in Minnesota and contiguous areas: U.S. Geological Survey Professional Paper 1253, 52 p., 15 pls.

Crane, P.R., 1987, Vegetational consequences of the angiosperm diversification, *in* Friis, E.M, Chaloner, W.G., and Crane, P.R., eds., The origins of angiosperms and their biological consequences: New York, Cambridge University Press, p. 107–144.

Cronquist, Arthur, 1968, The evolution and classification of flowering plants: Boston, Houghton Mifflin Co., 396 + x p.

______ 1981, An integrated system of classification of flowering plants: New York, Columbia University Press, 1262 + xviii p.

Deane, Henry, 1902, Notes on the fossil leaves from the Tertiary deposits of Wingello and Bungonia: New South Wales Geological Survey Records, v. 7, no. 2, p. 59–65.

Dilcher, D.L., 1974, Approaches to the identification of angiosperm leaf remains: Botanical Review (Lancaster), v. 40, no. 1, p. 1–157.

______ 1979, Early angiosperm reproduction: an introductory report: Review of Palaeobotany and Palynology, v. 27, p. 291–328.

Dilcher, D.L., and Crane, P.R., 1984, *Archaeanthus*: an early angiosperm from the Cenomanian of the Western Interior of North America: Annals of the Missouri Botanical Garden, v. 71, no. 2, p. 351–383.

Doyle, J.A., and Hickey, L.J., 1976, Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution, *in* Beck, C.B., ed., Origin and early evolution of angiosperms: New York, Columbia University Press, p. 139–206.

Doyle, J.A., and Robbins, E.I., 1977, Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment: Palynology, v. 1, p. 43–78.

Eicher, D.L., 1965, Foraminifera and biostratigraphy of the Graneros Shale: Journal of Paleontology, v. 39, no. 5, p. 875-909.

Erdtman, Gunnar, 1948, Did dicotyledonous plants exist in Early Jurassic times?: Stockholm, Geologiska Foereningens I Stockholm, Foerhandlingar, v. 70, p. 265–271.

Fahn, A., 1967, Plant anatomy: Oxford, Pergamon Press, 534 + viii p.

Farley, M.B., and Dilcher, D.L., 1986, Correlation between miospores and depositional environments of the Dakota Formation (mid-Cretaceous) of north-central Kansas and adjacent Nebraska: Palynology, v. 10, p. 117–134.

Fontaine, W.M., 1889, The Potomac or younger Mesozoic flora: U.S. Geological Survey Monograph 15, 377 p., 180 pls.

Franks, P.C., 1975, The transgressive-regressive sequence of the Cretaceous Cheyenne, Kiowa, and Dakota formations of Kansas, *in* Caldwell, W.G.E., ed., The Cretaceous system in the Western Interior of North America: Geological Association of Canada Special Paper 13, p. 469–521.

Friedrich, Paul, 1883, Beiträge zur Kenntniss der Tertiärflora der Provinz Sachsen: Abhandlungen der Preussen geologischen Landesanstalt, v. 4, no. 3, p. 159–463, pls. 1–31.

Friis, E.M., Crane, P.R., and Pedersen, K.R., 1986, Floral evidence for Cretaceous chloranthoid angiosperms: Nature, v. 320, no. 6058, p. 163–164.

Givnish, Thomas, 1979, On the adaptive significance of leaf form, *in* Solbrig, O.T., Jain, S., Johnson, G.B., and Raven, P.H., eds., Topics in plant population biology: New York, Columbia University Press, p. 375–407.

Goeppert, H.R., 1854, Die Tertiärflora auf der Insel Java: Elberfeld, Germany, A. Martini and Grüttefien, 162 p., 14 pls.

Harris, T.M., 1932, The fossil flora of Scoresby Sound, east Greenland—Part 2, Description of seed plants *incertae sedis*, together with a discussion of certain cycadophyte cuticles: Meddelelser om Groenland, v. 85, no. 3, p. 1–112, pls. 1–9.

Hattin, D.L., 1967, Stratigraphic and paleoecologic significance of macroinvertebrate fossils in the Dakota Formation (Upper Cretaceous) of Kansas, *in* Teichert, Curt, and Yochelson, W.L., eds., Essays in paleontology and stratigraphy, R.C. Moore commemorative volume: Lawrence, University of Kansas Department of Geology, Special Publication 2, p. 570–589.

Hedlund, R.W., 1966, Palynology of the Red Branch Member of the Woodbine Formation (Cenomanian) Bryan County, Oklahoma: Oklahoma Geological Survey Bulletin 112, 61 p.

Heer, Oswald, 1869, Beiträge zur Kreide-Flora—[Part] 1, Flora von Moletein in Mähren: Societe helvétique des sciences naturelles, Nouveaux Mémoires, v. 23, no. 2, p. 1–24, pls. 1–11.

______ 1874, Die Kreide-Flora der arctishen Zone, *in* Flora fossilis arctica, Band 3, Heft 2: Zurich, J. Wurster, p. 1–140, pls. 1–38.

______ 1883, Die fossile Flora der Polarlander, *in* Flora fossilis arctica, Band 7: Zurich, J. Wurster, p. 1–275, pls. 48–110.

Hickey, L.J., 1973, Classification of the architecture of dicotyledonous leaves: American Journal of Botany, v. 60, no. 1, p. 17–33.

______ 1977, Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North America: Memoir of the Geological Society of America 150, 183 p., 55 pls.

______ 1978, Origin of the major features of angiospermous leaf architecture in the fossil record: Courier Forschungs-Institut Senkenberg, v. 30, p. 27–34.

______ 1979, A revised classification of the architecture of dicotyledonous leaves, *in* Metcalfe, C.R., and Chalk, L., Anatomy of the dicotyledons, Second Edition, Volume I, Systematic anatomy of the leaf and stem, with a brief history of the subject: Oxford, Clarendon Press, p. 25–39.

Hickey, L.J., and Doyle, J.A., 1977, Early Cretaceous evidence for angiosperm evolution: Botanical Review (Lancaster), v. 43, no. 1, p. 3–104.

Hickey, L.J., and Wolfe, J.A., 1975, The bases of angiosperm phylogeny: vegetative morphology: Annals of the Missouri Botanical Garden, v. 62, no. 3, p. 538–589.

Jones, J.A., 1984, Leaf architectural and cuticular analyses of extant Fagaceae and "Fagaceous" leaves from the Paleogene of southeastern North America: Bloomington, Indiana University, unpublished Ph.D. dissertation, 328 p.

Karl, H.A., 1976, Depositional history of Dakota Formation (Cretaceous) sandstones, southeastern Nebraska: Journal of Sedimentary Petrology, v. 46, no. 1, p. 124–131.

Kauffman, E.G., 1969, Cretaceous marine cycles of the Western Interior: The Mountain Geologist, v. 6, no. 4, p. 227–245.

Kauffman, E.G., and Ryer, T.A., 1980, Paleobiologic evidence for Cretaceous tides, Western Interior Basin, North America: American Association of Petroleum Geologists Bulletin, v. 64, no. 5, p. 731.

Knowlton, F.H., 1917, Geology and paleontology of Raton Mesa and other regions in Colorado and New Mexico: U.S. Geological Survey Professional Paper 101, p. 223–349, pls. 30–113.

Kuhn, Oskar, 1955, Das erste Dicotyledonblatt aus dem deutschen Lias: Neues Jahrbuch für Geologie und Paläeontologie Monatsheft 1955, no. 11, p. 495–498.

Kvaček, Zlatko, 1983, Cuticular studies in angiosperms of the Bohemian Cenomanian: Acta Palaeontologica Polonica, v. 28, no. 1–2, p. 159–170.

Lesquereux, Leo, 1871, Paleontology, fossil flora, *in* Hayden, F.V., ed., U.S. Geological Survey of Montana and portions of adjacent territories, 5th Annual Report, Part III: p. 281–318.

______ 1874, Contributions to the fossil flora of the Western Territories—Part 1, the Cretaceous flora: U.S. Geological and Geographical Survey of the Territories Report 6: p. 1–136, pls. 1–31.

______ 1883, The Cretaceous and Tertiary floras: U.S. Geological and Geographical Survey of the Territories Report 8, 283 p., 57 pls.

______ 1892, The flora of the Dakota Group: U.S. Geological Survey Monograph 17, 256 p., 66 pls.

Levin, G.A., 1986a, Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus: Annals of the Missouri Botanical Garden, v. 73, no. 1, p. 29–85.

______ 1986b, Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis: Systematic Botany, v. 11, no. 4, p. 515–530.

Metcalfe, C.R., and Chalk, L., 1950, Anatomy of the dicotyledons: Oxford, Clarendon Press, 1500 +xiv p.

______ 1979, Anatomy of the dicotyledons, Second Edition, Volume I, Systematic anatomy of leaf and stem, with a brief history of the subject: Oxford, Clarendon Press, 276 +viii p., 18 pls.

Muller, Jan, 1981, Fossil pollen records of extant angiosperms: Botanical Review (Lancaster), v. 47, no. 1, p. 1–142.

______ 1984, Significance of fossil pollen for angiosperm history: Annals of the Missouri Botanical Garden, v. 71, no. 2, p. 419–443.

Němejc, František, and Kvaček, Zlatko, 1975, Senonian plant macrofossils from the region of Zliv and Hluboká (near Česká Budějovice) in south Bohemia: Prague, University Karlova Praha, 82 p., 24 pls.

Newberry, J.S., 1895, The flora of the Amboy Clays: U.S. Geological Survey Monograph 26, 137 p., 58 pls.

Plummer, Norman, and Romary, J.F., 1942, Stratigraphy of the pre-Greenhorn Cretaceous beds of Kansas: Kansas Geological Survey Bulletin, v. 41, no. 9, p. 313–348.

Pratt, L.M., 1985, Isotopic studies of organic matter and carbonate in rocks of the Greenhorn marine cycle, *in* Pratt, L.M., Kauffman, E.G., and Zelt, F.B., eds., Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway: evidence of cyclic sedimentary processes: Society of Economic Paleontologists and Mineralogists Field Trip Guidebook No. 4, 1985 Midyear Meeting, Golden, Colorado, p. 38–48.

Read, R.W., and Hickey, L.J., 1972, A revised classification of fossil palm and palmlike leaves: Taxon, v. 21, no. 1, p. 129–137.

Retallack, Greg, and Dilcher, D.L., 1981, A coastal hypothesis for the dispersal and rise to dominance of flowering plants, *in* Niklas, K.J., ed., Paleobotany, paleoecology and evolution: New York, Praeger, v. 2, p. 27–77.

______ 1985, Cretaceous angiosperm invasion of North America: Cretaceous Research, v. 7, no. 3, p. 227–252.

Richards, P.W., 1952, The tropical rainforest: an ecological study: New York, Cambridge University Press, 450 + viii p.

Roth, John, 1981, Epidermal studies in the Annonaceae and related families: Bloomington, Indiana University, unpublished Ph.D. dissertation, 218 p.

Rüffle, Ludwig, and Knappe, Hartmut, 1977, Entwicklungsgeschichte und ökologische Aspecte zur Oberkreide-Flora: Zeitschrift für Geologische Wissenshaften, v. 5, no. 3, p. 269–303.

Rury, P.M., and Dickison, W.C., 1977, Leaf venation patterns of the genus *Hibbertia* (Dilleniaceae): Journal of the Arnold Arboretum, v. 58, no. 3, p. 209–241, pls. 1–15.

Ryer, T.A., and Kauffman, E.G., 1980, Physical evidence for Cretaceous tides, Western Interior Basin, North America: American Association of Petroleum Geologists Bulletin, v. 64, no. 5, p. 778–779.

Samylina, V.A., 1960, The angiosperms from the Lower Cretaceous of the Kolyma Basin: Botanicheski Zhurnal SSSR, v. 45, no. 3, p. 335–352, 4 pls. (in Russian with English summary).

Scott, R.A., Barghoorn, E.S., and Leopold, E.B., 1960, How old are the angiosperms?: American Journal of Science, v. 258A, p. 284–299.

Scott, R.A., Williams, P.L., Craig, L.C., Barghoorn, E.S., Hickey, L.J., and MacGinitie, H.D., 1972, "Pre-Cretaceous" angiosperms from Utah: evidence for Tertiary age of the palm woods: American Journal of Botany, v. 59, no. 9, p. 886–896.

Seward, A.C., 1931, Plant life through the ages: Cambridge, Cambridge University Press, 601 p.

Siemers, C.T., 1976, Sedimentology of the Rocktown Channel Sandstone, upper part of the Dakota Formation (Cretaceous), central Kansas: Journal of Sedimentary Petrology, v. 46, no. 1, p. 97–123.

Stace, C.A., 1965, Cuticular studies as an aid to plant taxonomy: Bulletin of the British Museum (Natural History) Botany, v. 4, no. 1, p. 3–78.

Takhtajan, Armen, 1969, Flowering plants: origin and dispersal [translation by C. Jeffrey]: Washington, D.C., Smithsonian Institution Press, 310+x p.

——— 1980, Outline of the classification of flowering plants (Magnoliophyta): Botanical Review (Lancaster), v. 46, no. 3, p. 225–359.

Tanai, Toshimasa, 1979, Late Cretaceous floras from the Kuji district, northeastern Honshu, Japan: Journal of the Faculty of Science, Hokkaido University, Series IV, v. 19, nos. 1–2, p. 75–136.

Tidwell, W.D., Rushforth, S.R., Reveal, J.L., and Behunin, H, 1970, *Palmoxylon simperi* and *Palmoxylon pristina*: two pre-Cretaceous angiosperms from Utah: Science, v. 168, no. 3933, p. 835–840.

Unger, Franz, 1845, Synopsis plantarum fossilium: Leipzig, 330 p.

Upchurch, G.R., Jr., 1983, *Ficophyllum* leaves from the Lower Cretaceous Potomac Group: evidence for possible affinities with Magnoliales and Austrobaileyaceae: American Journal of Botany, v. 70, no. 5, Part 2, p. 81.

——— 1984, Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland: Annals of the Missouri Botanical Garden, v. 71, no. 2, p. 522–550.

Upchurch, G.R., Jr., and Wolfe, J.A., 1987a, Foliar diversity in latest Cretaceous Laurales: American Journal of Botany, v. 74, no. 5, p. 693.

——— 1987b, Mid-Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and woods, *in* Friis, E.M., Chaloner, W.G., and Crane, P.R., eds., The origins of angiosperms and their biological consequences: New York, Cambridge University Press, p. 75–106.

Vakhrameev, V.A., 1952, The stratigraphy and the fossil flora of the Cretaceous deposits of western Kazakhstan: Moscow, Regional Stratigraphy of the U.S.S.R., v. 1, 340 p., 44 pl. (in Russian).

Veatch, M.D., 1969, Ground-water occurrence, movement and hydrochemistry within a complex stratigraphic framework, Jefferson County, Nebraska: Palo Alto, California, Stanford University, unpublished Ph.D. dissertation, 201 p.

Viviani, Vino, 1833, Sur les restes des plantes fossiles traves dans les gypses tertiares de la Stradella, pres Paris: Paris, Memoires de la Societe Geologique de France, no. 1 p. 129–134, pls. 9, 10.

Walker, J.W., Brenner, G.J., and Walker, A.G., 1983, Winteraceous pollen in the Lower Cretaceous of Israel: early evidence of a magnolialean angiosperm family: Science, v. 220, no. 4603, p. 1273–1275.

Walker, J.W., and Walker, A.G., 1984, Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants: Annals of the Missouri Botanical Garden, v. 71, no. 2, p. 464–521.

Walter, Heinrich, 1973, Vegetation of the Earth in relation to climate and the eco-physiological conditions: New York, Springer-Verlag, 237+viv p.

Ward, J.V., 1986, Early Cretaceous angiosperm pollen from the Cheyenne and Kiowa formations (Albian) of Kansas, U.S.A.: Palaeontographica, Abteilung B, v. 202, nos. 1–6, p. 1–50.

Ward, L.F., 1905, Status of the Mesozoic floras of the United States: U.S. Geological Survey Monograph 48, 616 p., 119 pls.

Watkins, D.K., 1985, Biostratigraphy and paleoecology of calcareous nannofossils in the Greenhorn marine cycle, *in* Pratt, L.M., Kauffman, E.G., and Zelt, F.B., Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway: evidence of cyclic sedimentary processes: Society of Economic Paleontologists and Mineralogists Field Trip Guidebook no. 4, 1985 Annual Midyear Meeting, Golden, Colorado, p. 151–156.

Wilkinson, H.P., 1979, The plant surface, *in* Metcalfe, C.R., and Chalk, L., Anatomy of the Dicotyledons, Second Edition, Volume I, Systematic anatomy of leaf and stem, with a brief history of the subject: Oxford, Clarendon Press, p. 97–165.

Wolfe, J.A., 1973, Fossil forms of Amentiferae: Brittonia, v. 25, no. 4, p. 334–355.

——— 1977, Paleogene floras from the Gulf of Alaska region: U.S. Geological Survey Professional Paper 997, 108 p.

Wolfe, J.A., Doyle, J.A., and Page, V.M., 1975, The bases of angiosperm phylogeny: paleobotany: Annals of the Missouri Botanical Garden, v. 62, no. 3, p. 801–824.

Wolfe, J.A., and Upchurch, G.R., Jr., 1987a, Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado: Proceedings of the National Academy of Sciences, U.S.A., v. 84, p. 4096–5100.

——— 1987b, North American nonmarine climates and vegetation during the Late Cretaceous: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 61, no. 1, p. 33–77.

Wolfe, J.A., and Wehr, Wesley, 1987, Middle Eocene dicotyledonous plants from Republic, northeastern Washington: U.S. Geological Survey Bulletin 1597, 25 p., 16 pl.

INDEX

[Italic page numbers indicate major references]

☆U.S. GOVERNMENT PRINTING OFFICE: 1990—773-047/06,063 REGION NO. 8

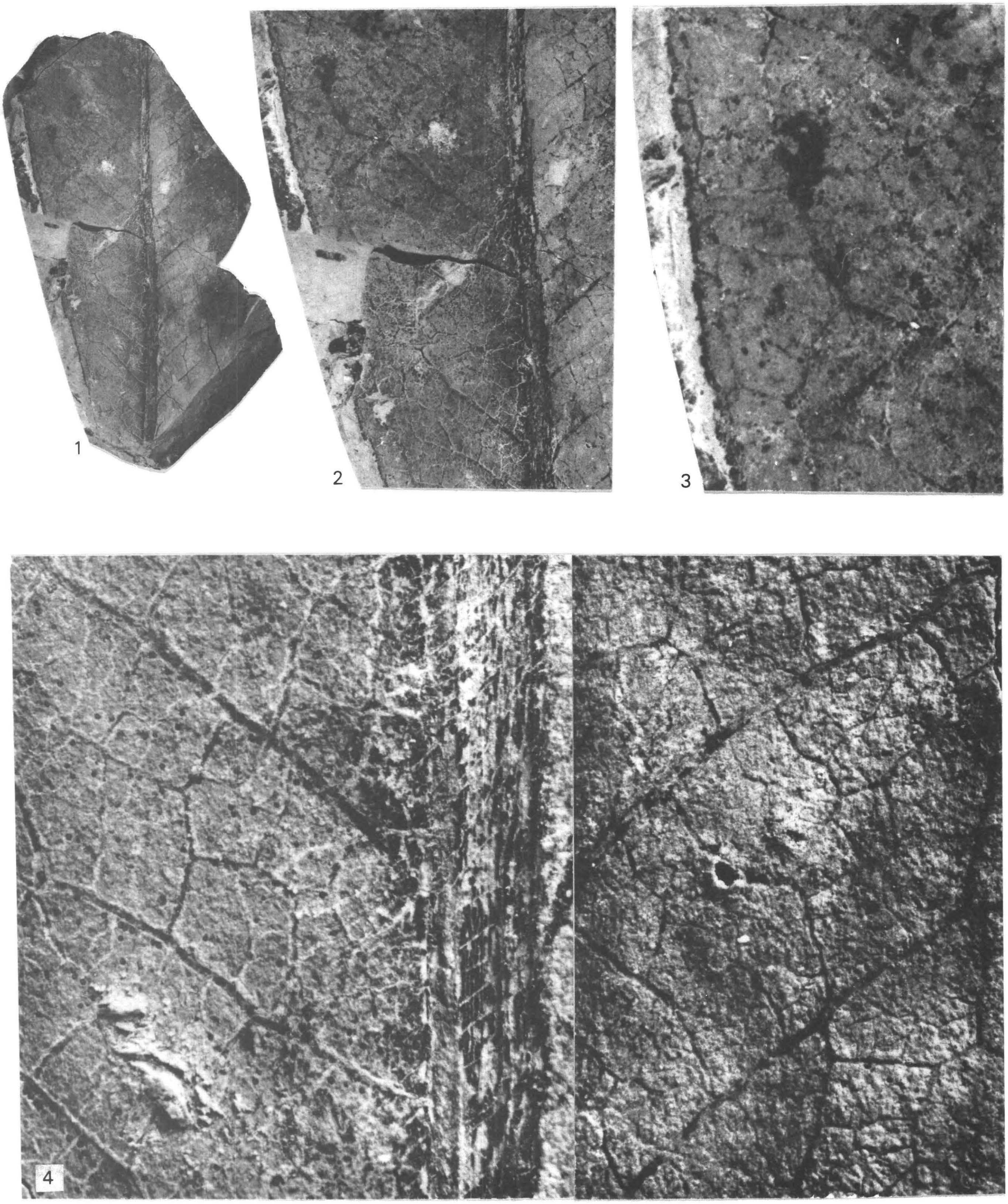
PLATES 1–31

[Contact photographs of the plates in this report are available, at cost, from the U.S. Geological Survey Photographic Library, Federal Center, Denver, Colorado 80225.]

PLATE 1

Figures 1–4. New genus A, 15713-4879A (p. 12)

1. General view, × 1.
2. Middle portion of leaf, showing origin of secondary veins, × 2.
3. Left side of leaf, showing the slightly sinuate margin with structural reinforcement (dark area), × 10.
4. Lower portion of leaf, showing the multistranded midrib, reticulate tertiary venation, and numerous laminar resin bodies to the left of the midvein, × 10.



NEW GENUS A

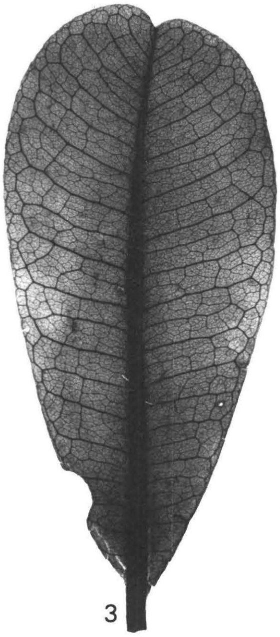
PLATE 2

[All figures ×1 except where indicated]

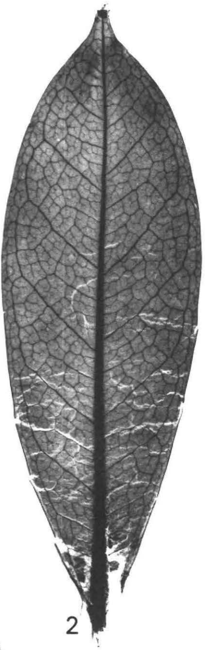
Figures 1–8. Foliage of select extant Magnoliales

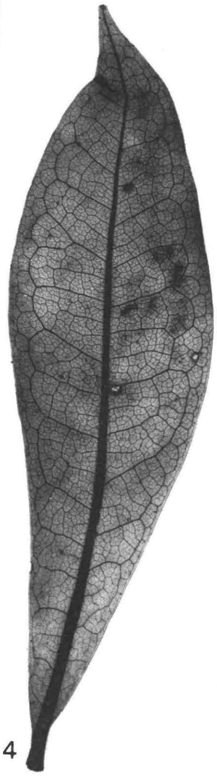
1. *Manglietia hookeri* (Magnoliaceae). U.S.G.S. Ref. Coll. no. 1144a.
2. *Manglietia fordiana* Oliv. (Magnoliaceae). U.S.G.S. Ref. Coll. no. 1067a.
3. *Bubbia* aff. *argentea* A.C. Smith (Winteraceae). U.S.G.S. Ref. Coll. no. 8889.
4. *Drimys* cf. *dictyophlebia* Diels (Winteraceae). U.S.G.S. Ref. Coll. no. 7847.
5. *Zygogynum balansae* v. Tiegh. (Winteraceae), basal half of leaf. U.S.G.S. Ref. Coll. no. 2314b.
6. *Sageraea laurifolia* (Annonaceae). U.S.G.S. Ref. Coll. no. 3927.
7. *Degeneria vitiensis* Bailey & A.C. Smith (Degeneriaceae). U.S.G.S. Ref. Coll. no. 750.
8. *Bubbia* sp. (Winteraceae), closeup of venation. USNM Cleared Leaf no. 237, ×5.

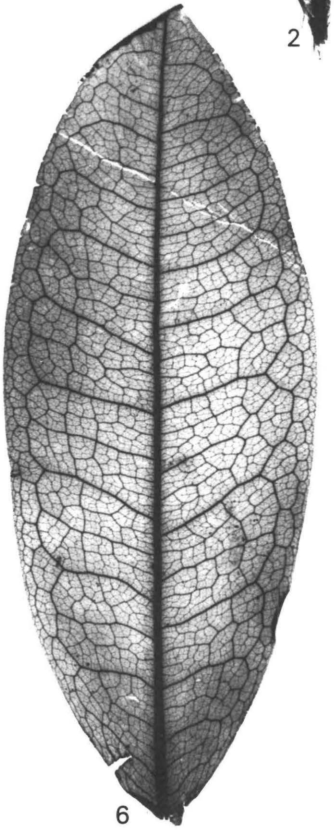

1

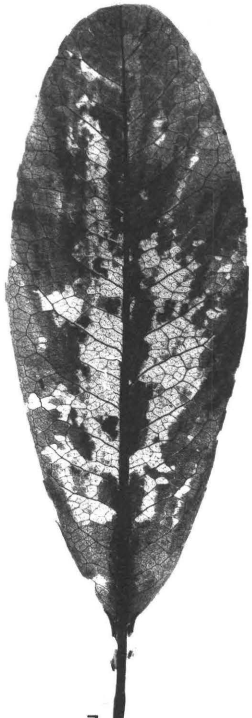

3

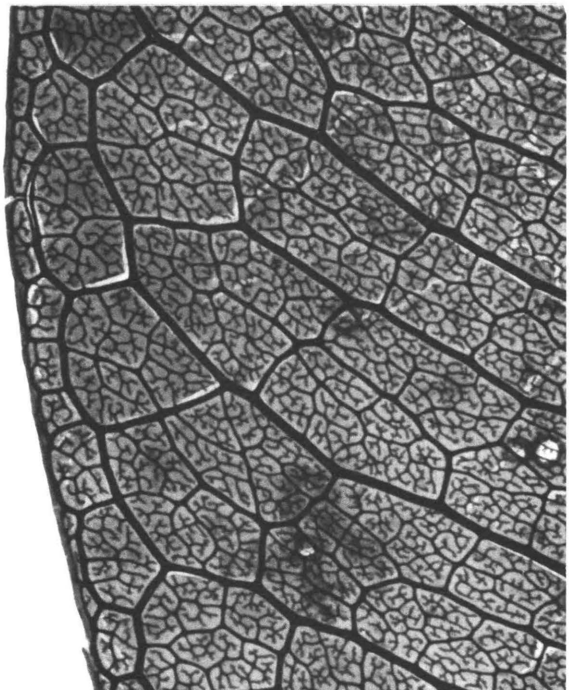

5


2


4


6


7


8

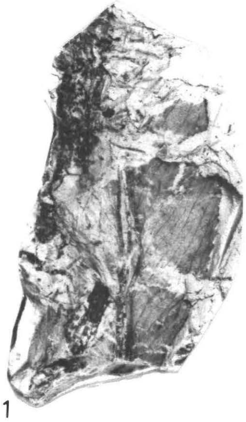
EXTANT MAGNOLIALES

PLATE 3

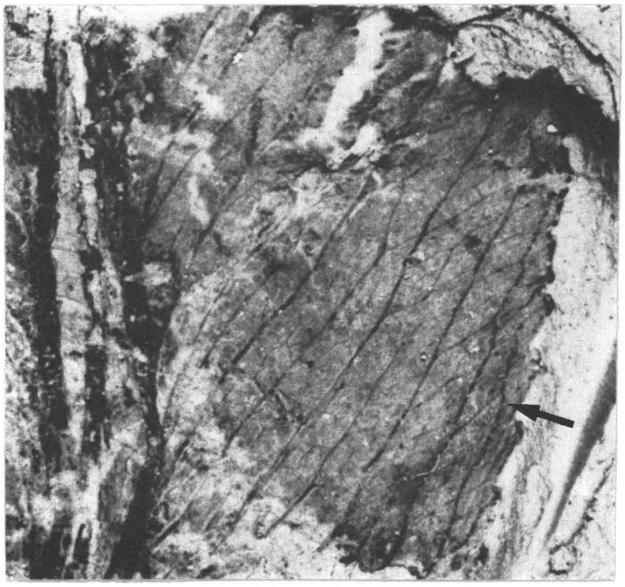
[All figures ×1 except where indicated]

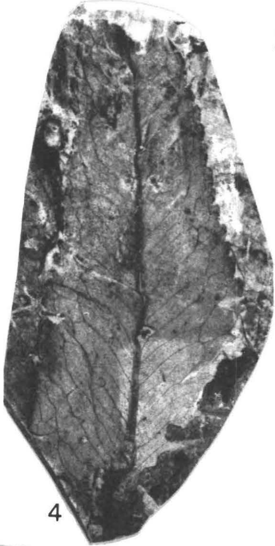
Figures 1–8. *Crassidenticulum decurrens* (Lesquereux) new combination (p. 13)

- 1–3. 15713-4730.
  - 1. General view of fragment preserving basal portion of a leaf.
  - 2. Enlargement of figure 1 showing the thin, apically curved secondary venation, ×2.
  - 3. Enlargement of figure 2 showing a secondary vein terminating in a tooth (arrow) and the structural reinforcement of the margin (dark regions along edge of leaf), ×5.
- 4, 7. 15713-4746.
  - 4. General view of specimen preserving apical portion of leaf, ×2.
  - 7. Enlargement of figure 4 showing well-developed brochidodromous looping of the secondary veins, ×5.
- 5. 15713-4723. Specimen showing decurrent laminar base and flaring of the base immediately above petiolar region, ×2.
- 6. 15713-7818. Specimen showing entire margin.
- 8. 15713-7817. Specimen preserving the basal two-thirds of lamina.


1


2


3


4


5


6


7


8

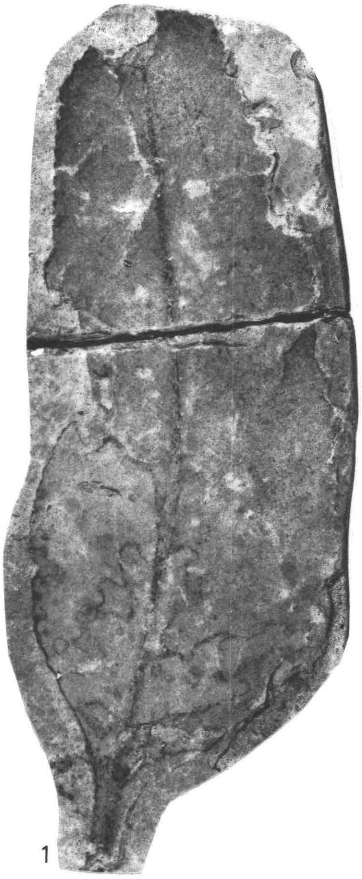
CRASSIDENTICULUM DECURRENS (LESQUEREUX) NEW COMBINATION

PLATE 4

[All figures × 1 except where indicated]

Figures 1–6. *Crassidenticulum decurrens* (Lesquereux) new combination (p. 13)

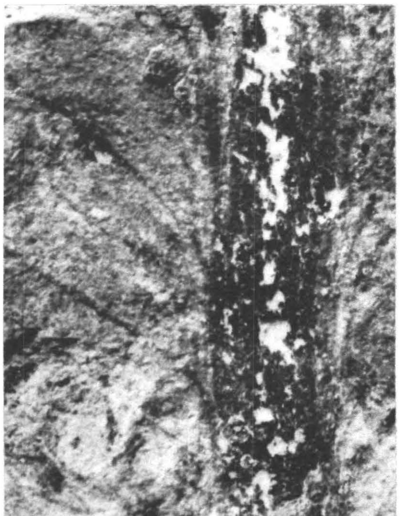
1. UKSM 7257. Holotype.
2. 15713-4732′. Specimen preserving basal half of lamina and numerous leaf mines in top half.
3. 15713-4728. Specimen preserving large dark circular galls, × 2.
4. 15713-4938. Specimen with crenate margin showing structural reinforcement along entire length of each tooth, × 5.
5. 15713-4795A. Closeup of multistranded midvein and decurrent secondary veins, × 10.
6. 15713-4746. Enlargement of lower right-hand region of specimen illustrated on plate 2, figure 4. Note the intersecondary vein (arrow) and poorly organized tertiary and quaternary venation, × 10.

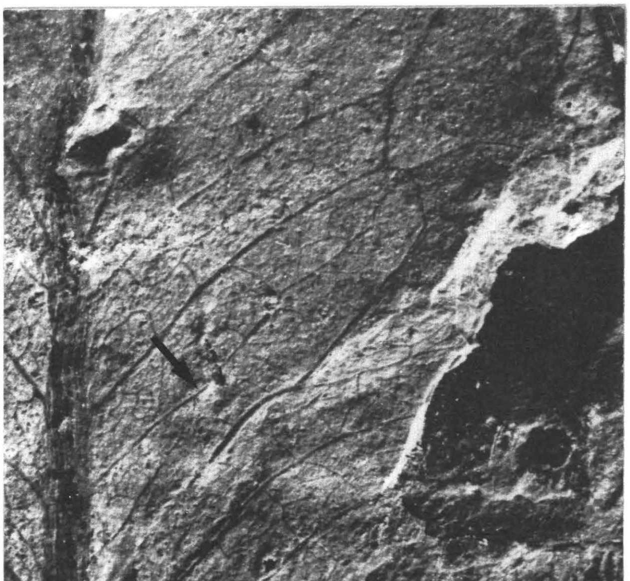

1


2


3


4


5


6

CRASSIDENTICULUM DECURRENS (LESQUEREUX) NEW COMBINATION

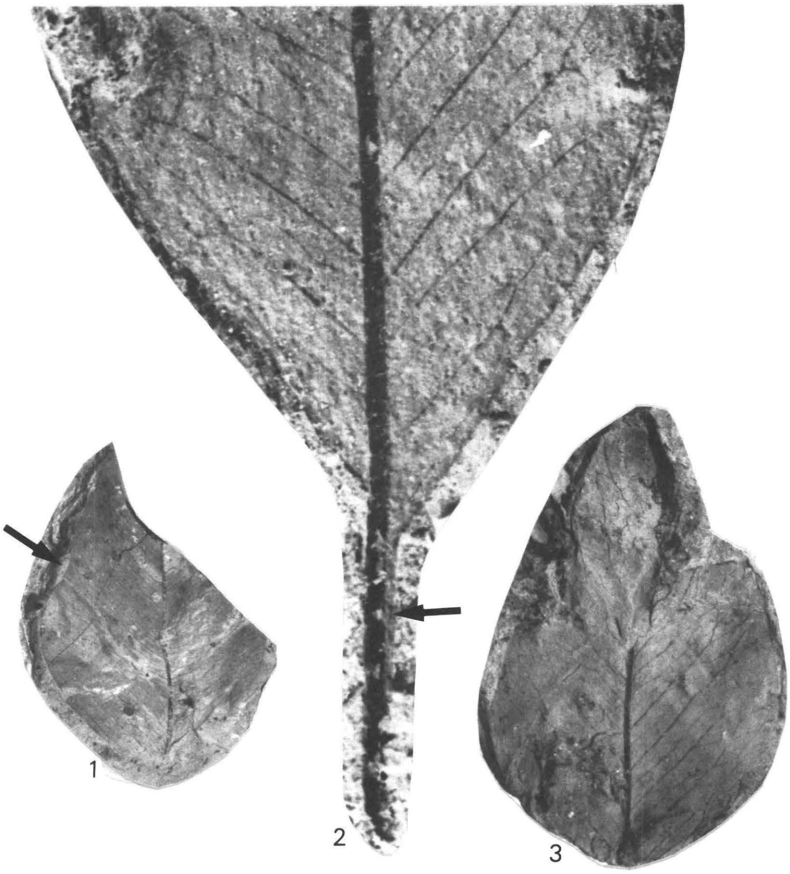
PLATE 5

[All figures ×1 except where indicated]

Figures 1–6. *Densinervum kaulii* new species (p. 17)

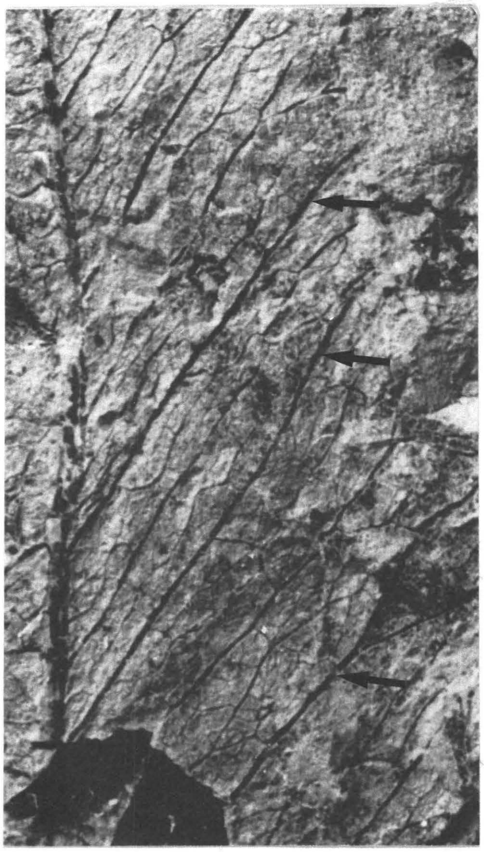
1. 175713-4841A′. Specimen showing indentation of the lamina above the widest part (arrow).
2. 15713-7815. Specimen showing petiolar region with wing of laminar tissue along right side (arrow), ×7.
3. 15713-4800A. Specimen showing ovate shape and closely spaced secondary veins, ×2.
4. 15713-4830. Specimen showing secondary veins (arrows) and weak, irregular higher order venation, ×10.

5, 6. 15713-4841A.
   5. Basal part of specimen showing closely spaced secondary veins, exmedially elongate brochidodromous loops near margin, and reticulate tertiary venation (bottom of specimen), ×5.
   6. Enlargement of figure 5, showing flattened brochidodromous arches by margin and structural reinforcement of margin (darkened region), ×10.


1

2

3


4


5

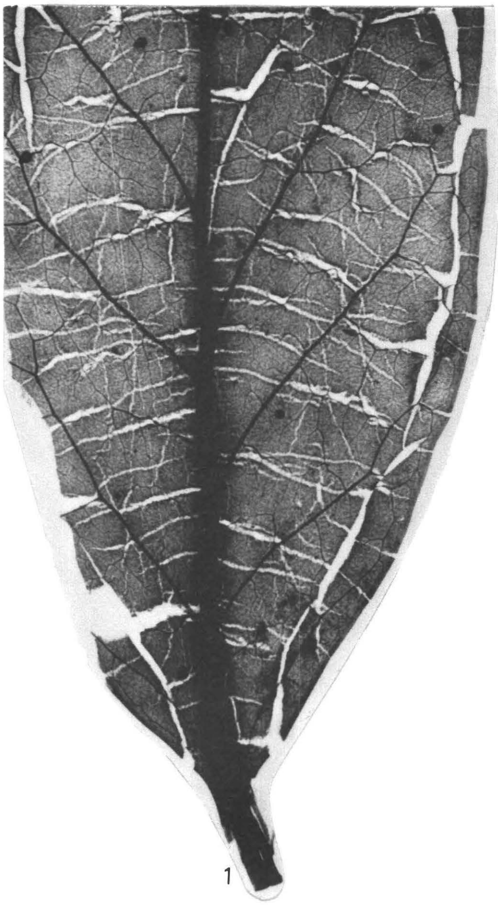

6

DENSINERVUM KAULII NEW SPECIES

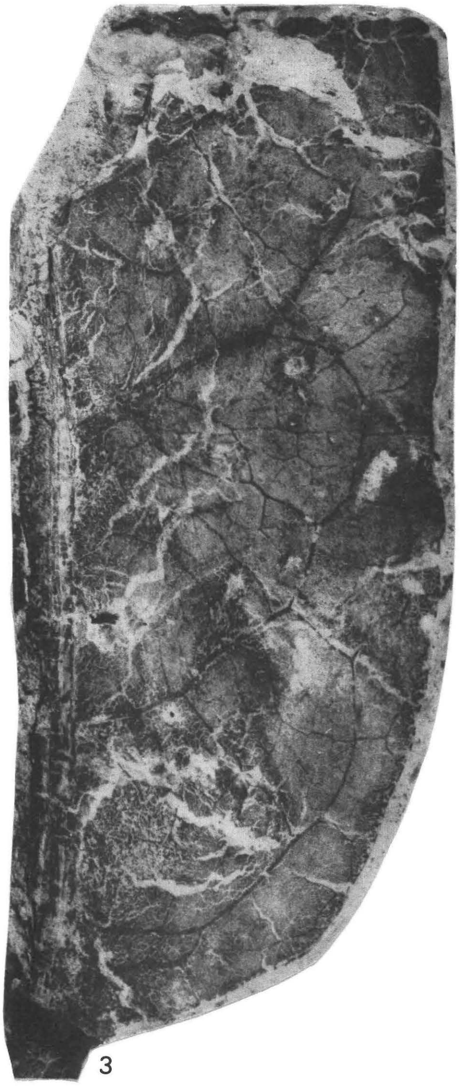
PLATE 6

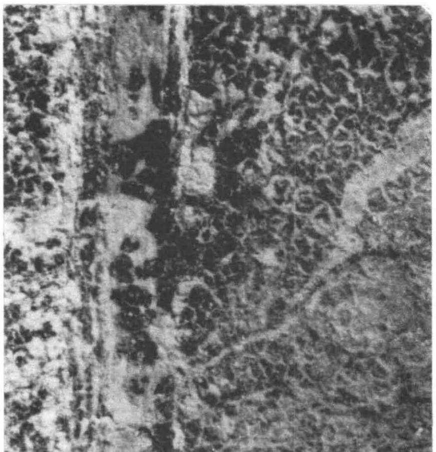
Figure 1. *Gomortega keule* (Mol.) Baill. (Gomortegaceae), U.S.G.S. Ref. Coll. no. 2462, ×2. Note irregularly transverse tertiary venation with admedially ramified lateral branches.

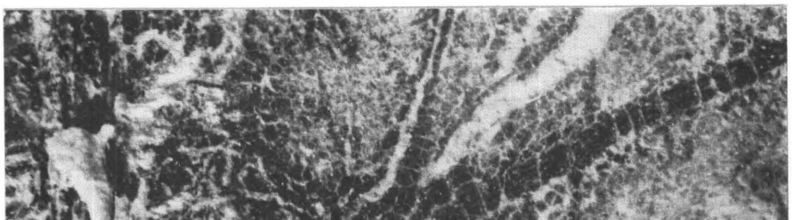
2–5. *Landonia calophylla* new species (p. 19)
  2. 15713-4881A′, counterpart showing elongate petiolar region, ×1.
  3–5. 15713-4881A.
    3. General view of specimen showing secondary and tertiary venation, ×2.
    4. Closeup of midrib showing multistranded nature, ×7.5.
    5. Closeup of thick secondary vein at its origin. Note short exmedial branch of the secondary vein (arrow), ×10.


1


2


3


4


5

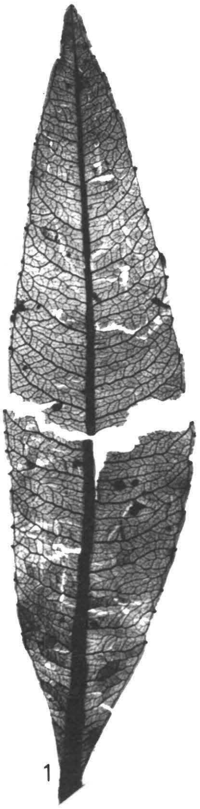
GOMORTEGA KEULE AND *LANDONIA CALOPHYLLA* NEW SPECIES

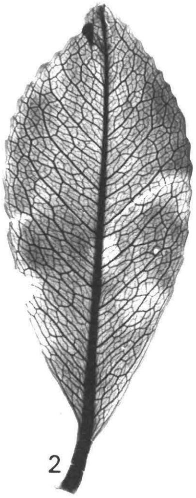
PLATE 7

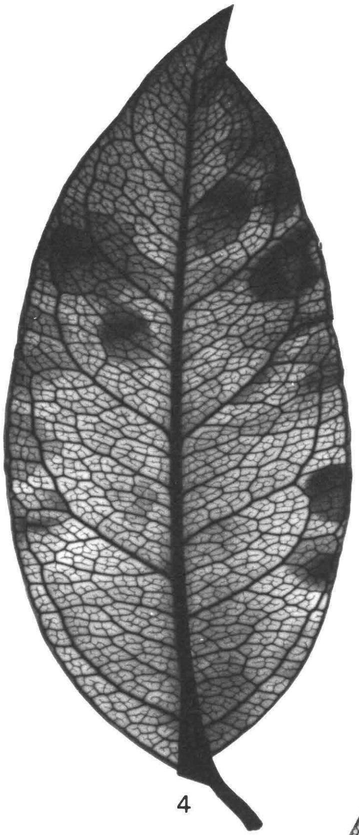
[All figures × 1]

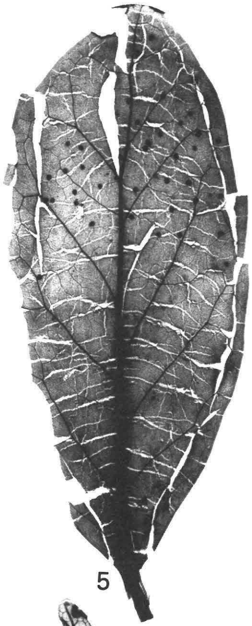
Figures 1–8. Foliage of extant Laurales

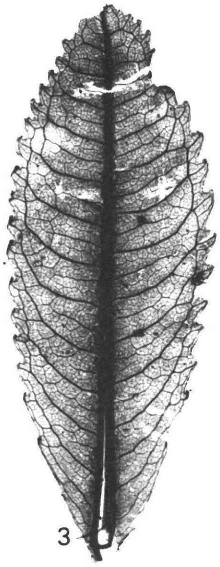
1. *Trimenia weinmanniaefolia* Seem. (Trimeniaceae), U.S.G.S. Ref. Coll. no. 2320.
2. *Ascarina philippensis* C.B. Rob. (Chloranthaceae), U.S.G.S. Ref. Coll. no. 11211.
3. *Hedyosmum arborescens* Sw. (Chloranthaceae), U.S.G.S. Ref. Coll. no. 2330.
4. *Austrobaileya scandens* C.T. White (Austrobaileyaceae), USNM Cleared Leaf no. 6415.
5. *Gomortega keule* (Mol.) Baill. (Gomortegaceae), U.S.G.S. Ref. Coll. no. 2462.
6. *Amborella trichopoda* Baill. (Amborellaceae), USNM Cleared leaf no. 4455.
7. *Hedycarya denticulata* (A. Gray) Perk. & Gilg. (Monimiaceae), U.S.G.S. Ref. Coll. no. 10592.
8. *Idiospermum australiense* (Diels) S.T. Blake (Idiospermaceae), U.S.G.S. Ref. Coll. no. 9650b, 9650c.

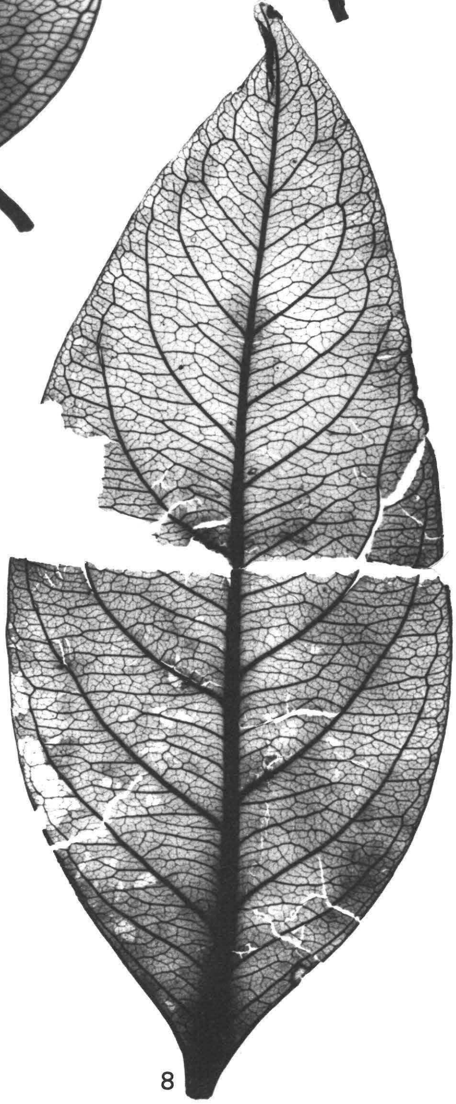

1

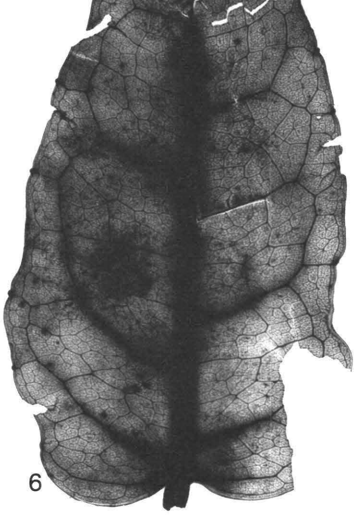

2

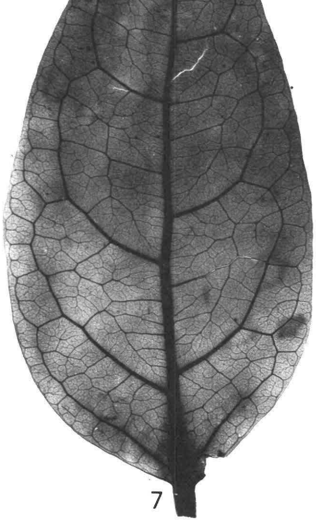

4


5


3


8


6


7

FOILAGE OF EXTANT LAURALES

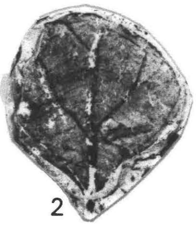
PLATE 8

[All figures ×1 except where indicated]

Figures 1–7. *Pabiania variloba* new species (p. 21)

1. 15713-3546A. Typical trilobed leaf with well-preserved petiole.
2. 15713-3320. Unlobed leaf with pinnate venation.
3. 15713-3317′. Holotype.
4. 15713-3327. Small trilobed leaf.
5. 15713-3318, ×2. Small unlobed leaf showing well-developed lateral primary veins.
6. 15713-4847, ×2. Trilobed leaf showing numerous galls (dark circular areas).
7. 15713-3316, ×2. Fragmentary specimen showing the decurrent base and basilaminar secondary veins (arrows).

1

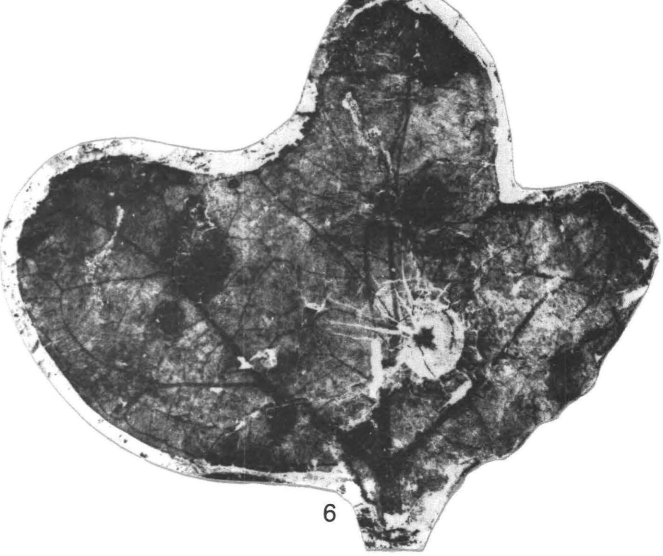


2

3

5

4



6

7

PABIANIA VARILOBA NEW SPECIES

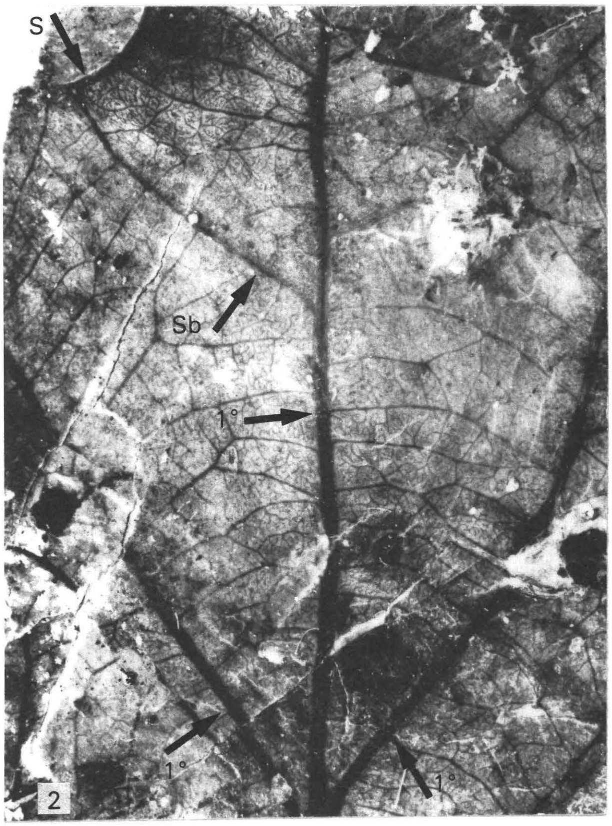
PLATE 9

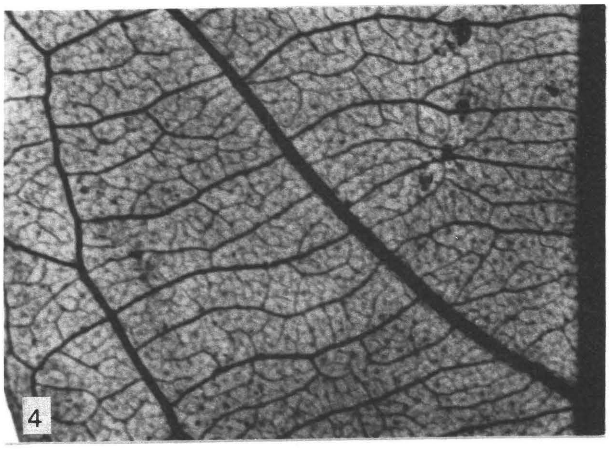
Figures 1–3. *Pabiania variloba* new species (p. 21)

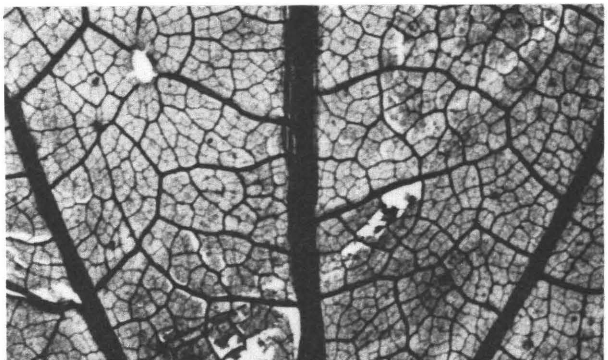
- 1, 3. 15713-7801′.
  - 1. General view of shoot with attached leaves, ×2.
  - 3. Closeup of figure 1 showing two successive nodes bearing opposite leaves. The leaves of each node are labeled in acropetal sequence, ×4.
- 2. 15713-4845, ×5. Closeup of trilobed leaf preserving primary veins (1°), sinus (S), sinus bracing vein (Sb), and tertiary and higher order venation.

4, 5. Higher order venation of select extant Laurales, ×4

- 4. *Siparuna decipiens* (Tul). A.Dc. (Atherospermataceae), U.S.G.S. Ref. Coll. no. 9203. Note strong venational similarities to *Pabiania*.
- 5. *Sassafras albidum* (Nutt.) Nees. (Lauraceae), U.S.G.S. Ref. Coll. no. 772. Note the uniform divergence angles for the quaternary and quintary venation and the regularity in areolar size and shape. This syndrome of features characterizes both *Sassafras* and *Lindera*.







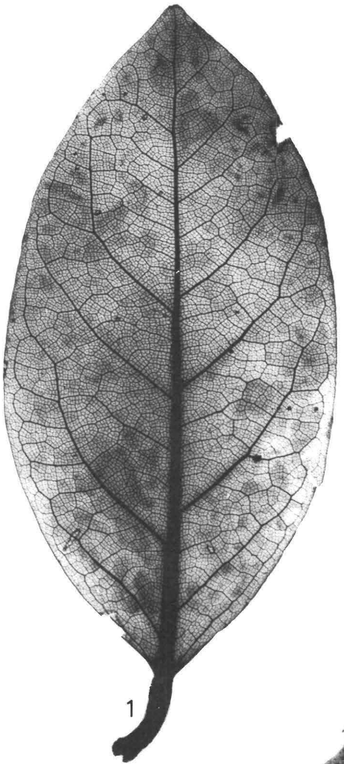
PABIANIA VARILOBA NEW SPECIES AND SELECT EXTANT LAURALES

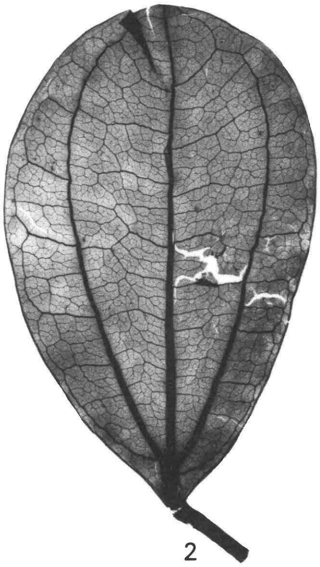
PLATE 10

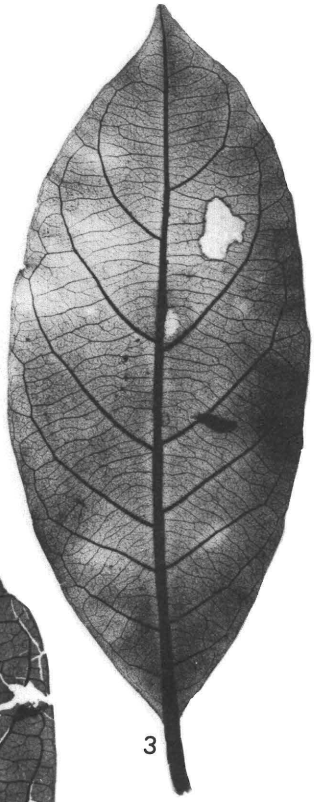
[All figures × 1]

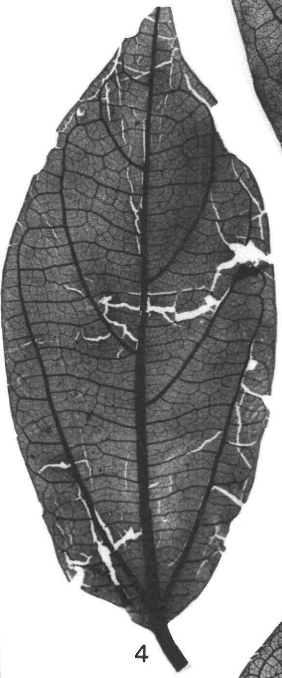
Figures 1–7. Foliage of extant Laurales with similarities to *Pabiania* and *Pandemophyllum*

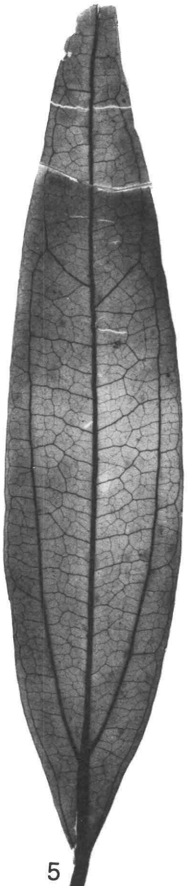
1. *Appolonias canariensis* (Lauraceae), U.S.G.S. Ref. Coll. no. 9615b. Note the strong distinction between petiole and blade and the orthogonal reticulate higher order venation, in contrast to *Pandemophyllum*.
2. *Illigera vespertilla* (Benth.) Baker f. (Hernandiaceae), U.S.G.S. Ref. Coll. no. 2828b. Note the well-developed lateral primary veins and the irregular higher order venation.
3. *Siparuna decipiens* (Tul) A.Dc. (Atherospermataceae), U.S.G.S. Ref. Coll. no. 9203.
4. *Sparattanthelium tupiniquinorum* Mart. (Gyrocarpaceae), U.S.G.S. Ref. Coll. no. 9091.
5. *Hortonia angustifolia* (Thw.) Trim. (Hortoniaceae), U.S.G.S. Ref. Coll. no. 4492.
6. *Eusideroxylon zwageri* T. & B. (Lauraceae), U.S.G.S. Ref. Coll. no. 3266a, 3266b. Note general similarities in secondary and tertiary venation to *Pandemophyllum*.
7. *Sassafras albidum* (Nutt.) Nees (Lauraceae), U.S.G.S. Ref. Coll. no. 771.

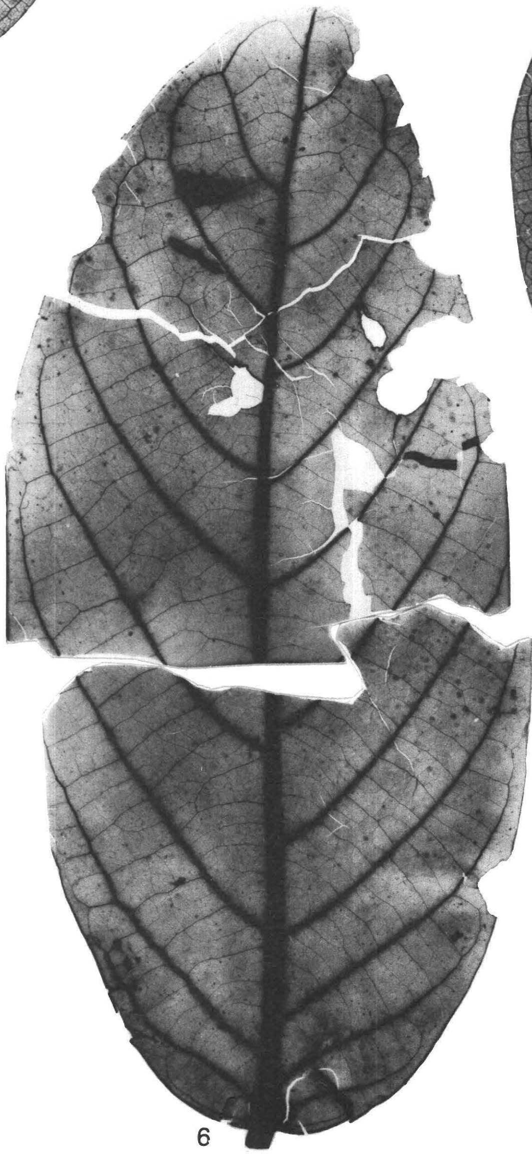

1


2


3


4


5


6


7

FOILAGE OF EXTANT LAURALES

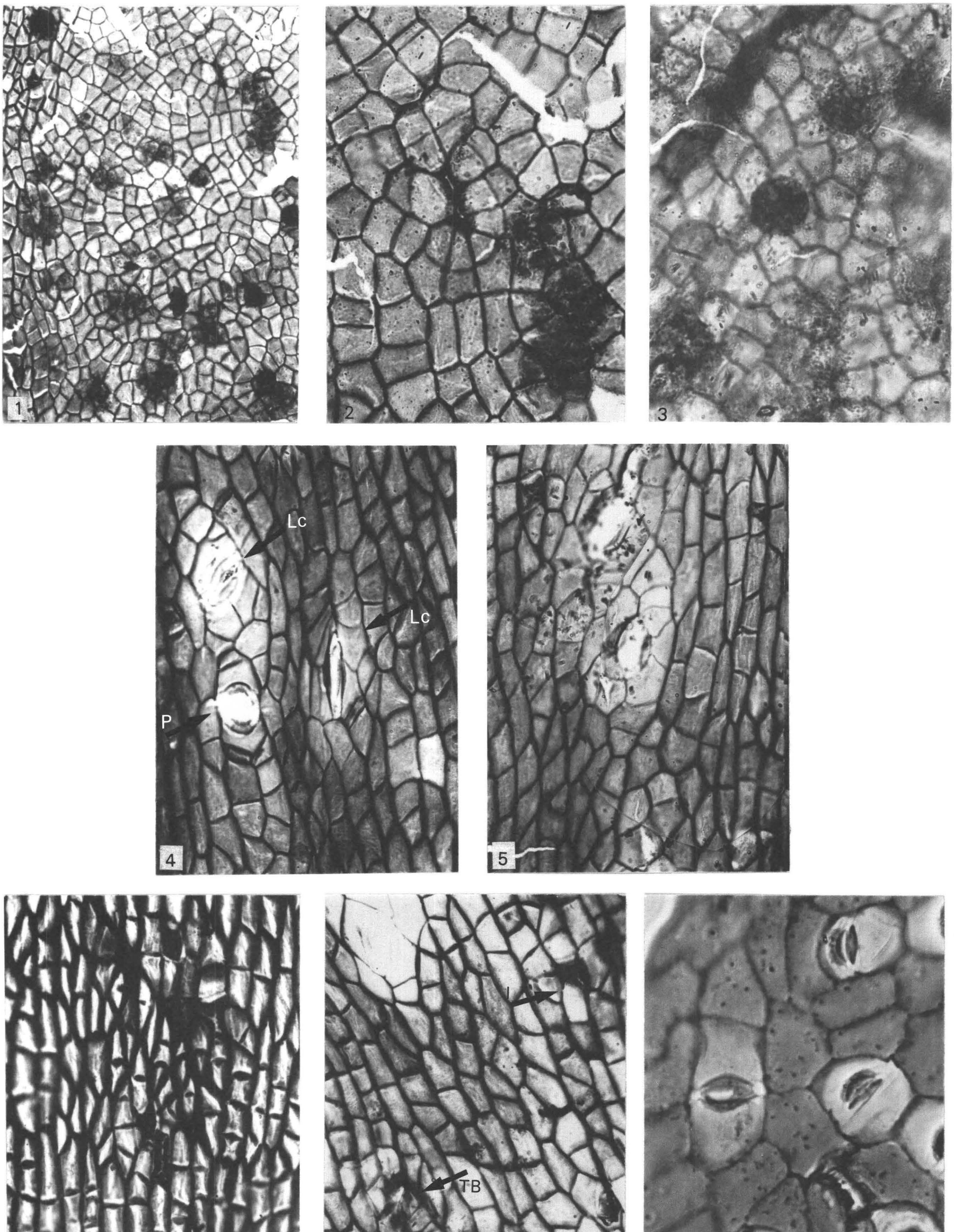
PLATE 11

[All figures ×400 unless otherwise indicated]

Figures 1–7. Cuticle of *Pabiania variloba* new species (p. 21)

- 1, 2. 15713-4875A.
  - 1. Upper cuticle showing two small trichome bases (arrows) and numerous laminar resin bodies, ×160.
  - 2. Closeup of trichome base in the upper right corner of figure 1, ×400.
- 3. 15713-4847A. Closeup of well-preserved laminar secretory body, ×512.
- 4–7. 15713-3314B.
  - 4. Three stomata showing paracytic (P) and laterocytic (L) subsidiary cell arrangement.
  - 5. Weakly cyclocytic stomatal complex (center).
  - 6. Region beneath primary vein, lower cuticle, showing numerous idioblasts (regions with thickened cuticle).
  - 7. Region beneath higher order vein, lower cuticle, with trichome base (TB) and idioblast (I).

8. Lower cuticle of *Sassafras albidum* (Nutt.) Nees (Lauraceae), University of Florida Modern Leaf Ref. Coll. no. 19, photographed under phase-contrast light microscopy, ×640. Note the general similarities to *Pabiania* in the construction of the stomatal complex but the more uniform arrangement of subsidiary cells.



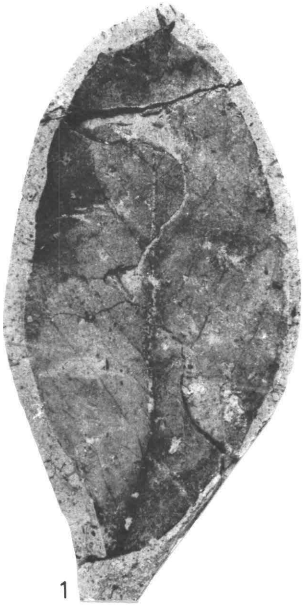
CUTICLES OF *PABIANIA VARILOBA* NEW SPECIES AND *SASSAFRAS ALBIDUM*

PLATE 12

[All figures ×1 unless otherwise indicated]

Figures 1–8. *Pandemophyllum kvacekii* new species (p. 26)

1. 5713-4800A. Specimen showing elliptic shape typical for species.
2. 15713-4797. Apical half of leaf showing subrhombiodal shape.
3. 15713-8300. Specimen showing somewhat ovate shape.
4. 15713-3672. Specimen showing petiole.
5. 15713-4716. Incomplete leaf showing transversely oriented tertiary venation.
6. 15713-7851, ×2. Small leaf showing gradation between petiole and blade.
7. 15713-4799, ×2. Base of leaf showing cuneate shape and weak development of basilaminar secondary veins. Note leaf mines in the upper right-hand corner of photograph.
8. 15713-7877. Holotype (leaf in center of photograph).


1


2

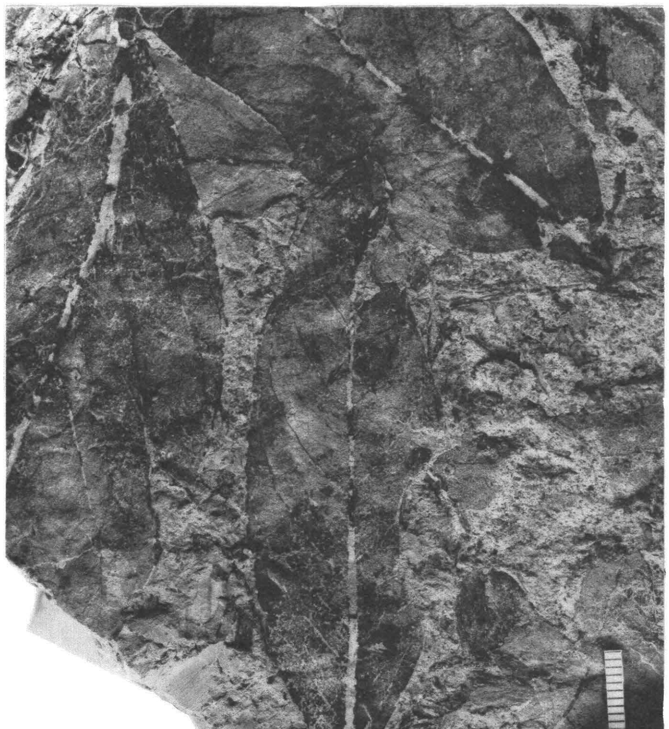

3


4


5


6


7


8

PANDEMOPHYLLUM KVACEKII NEW SPECIES

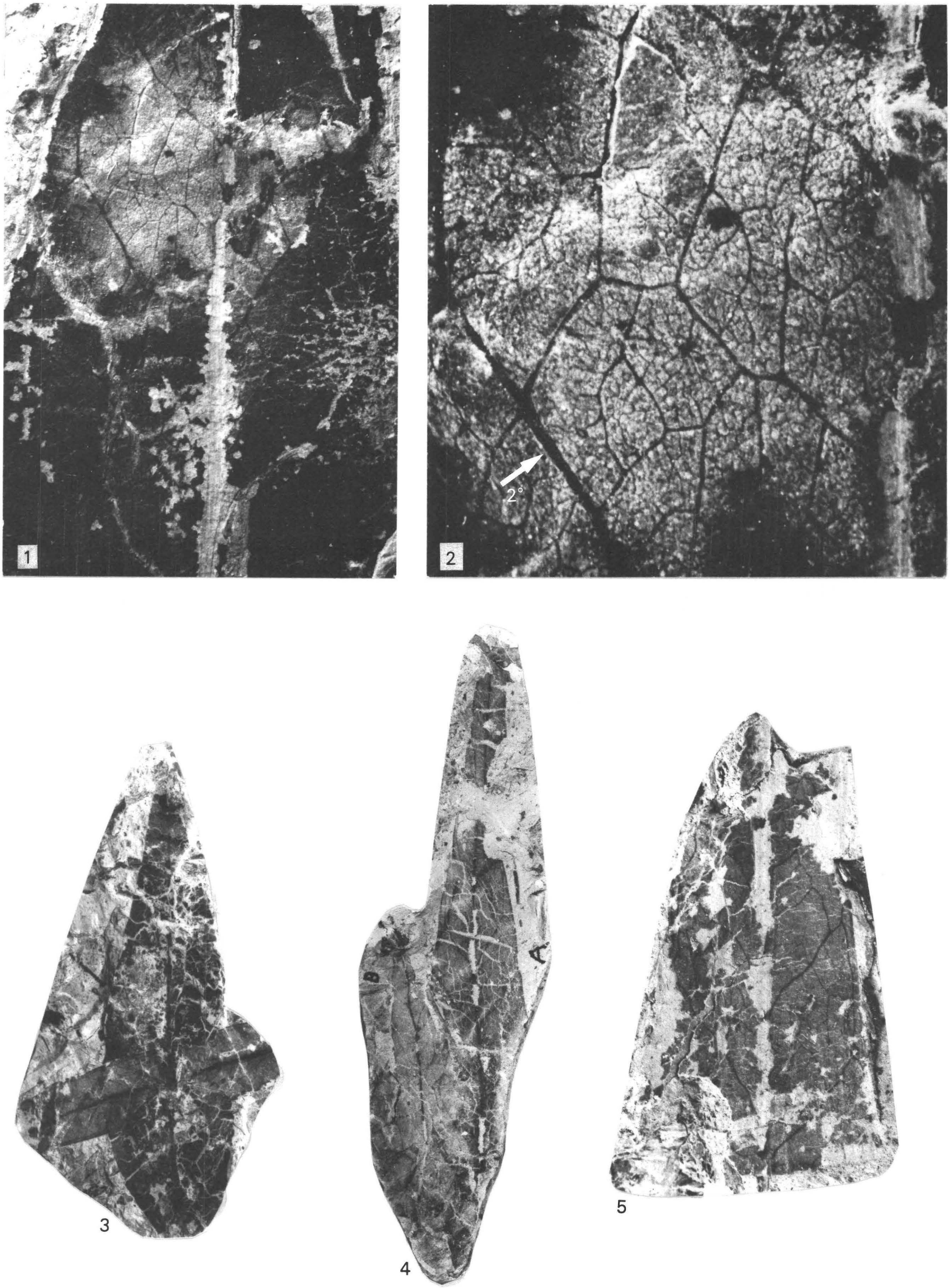
PLATE 13

Figures 1, 2. *Pandemophyllum kvacekii* new species, 15713-4797 (p. 26)

1. Apical region of specimen in plate 12, figure 2, × 5.
2. Enlargement of the upper left-hand region of figure 1, × 15. Note the secondary vein (2°), reticulate tertiary venation, and tendency for the quaternary veins to ramify. The quinternary veins show strong reticulate tendencies and enclose minute (0.1 mm diameter) areoles.

3–5. *Pandemophyllum attenuatum* new species. (p. 29)

3. 15713-7845, × 1. Holotype.
4. 15713-4898a, 4898b, × 1. Both specimens show the extremely long attenuate apex characteristic of this species.
5. 15713-8305, × 2. Fragment preserving apical region of leaf showing flattened brochidodromous arches.



PANDEMOPHYLLUM KVACEKII AND *PANDEMOPHYLLUM ATTENUATUM* NEW SPECIES

PLATE 14

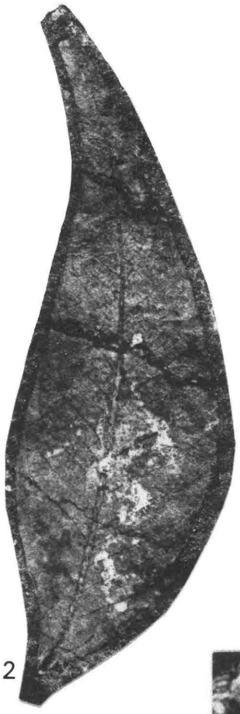
Figures 1–4. Fossil leaves with similarities to *Pandemophyllum*, ×1

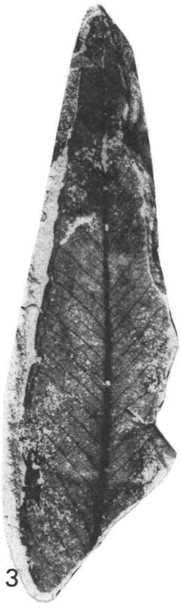
1. *"Inga" cretacea*, USNM 2767A. Dakota Formation, Kansas.
2. *"Salix" deleta*, USNM 50038. Dakota Formation, Kansas.
3. *Myrtophyllum geinitzii*, USNM 326818. Woodbine Formation, Texas.
4. *Proteoides daphnogenoides* Heer, paratype, USNM 665. Note the absence of well-preserved venation above the first order. Dakota Group, northeastern Nebraska.

5, 6. *Pandemophyllum* sp. 15713–4827 (p. 30)

5. General shot of single preserved leaf, ×2.
6. Closeup of figure 5 showing the flattened brochidodromous arches of the secondary veins and the thick, apically oriented tertiary veins, ×5.


1


2


3

4


5

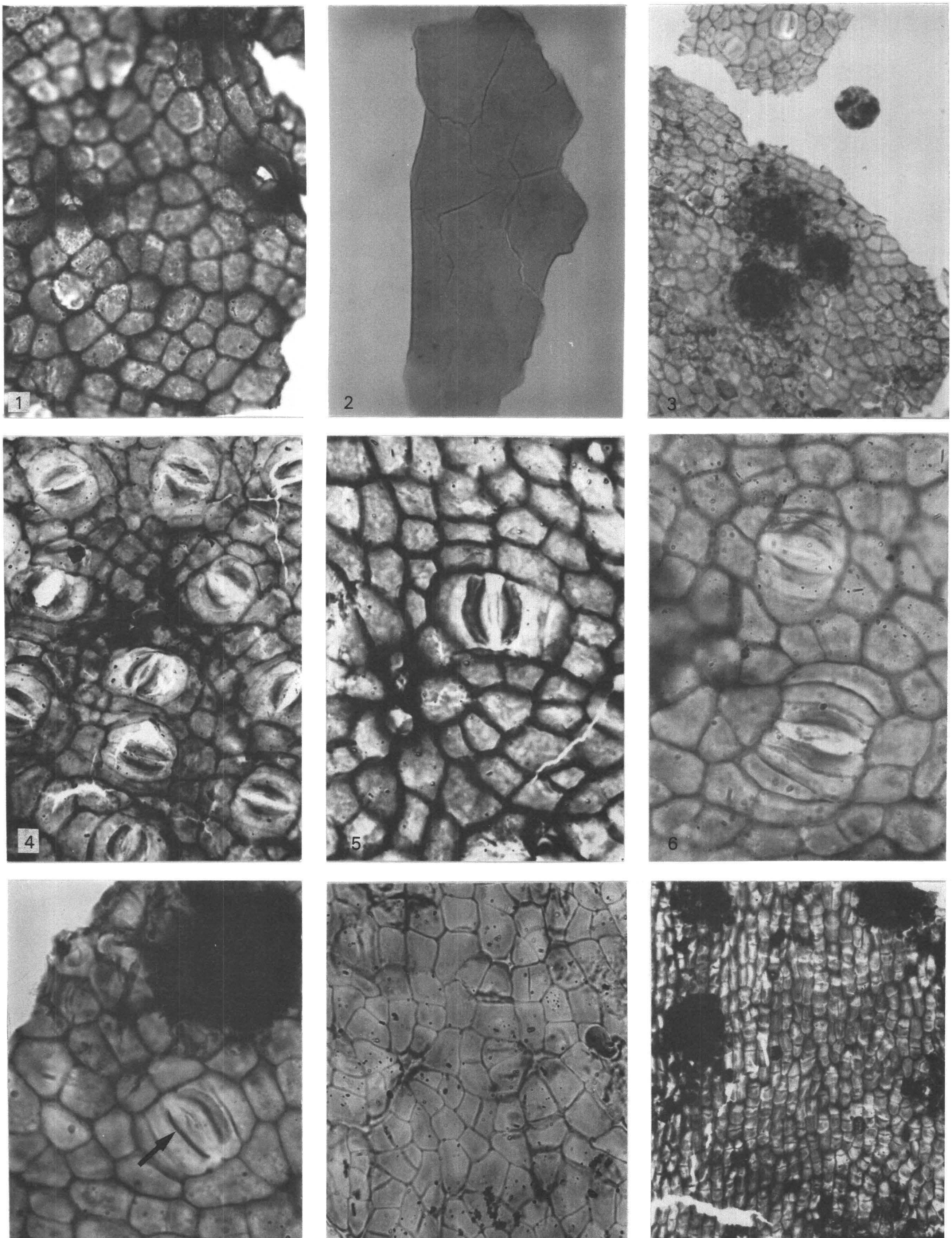

6

FOSSILS SIMILAR TO PANDEMOPHYLLUM, AND *PANDEMOPHYLLUM* SP.

PLATE 15

Figures 1–9. Cuticle of *Pandemophyllum kvacekii* new species (p. 26)

1. 15713-3671C(1), ×400. General shot of upper cuticle showing well-developed trichome bases.
2. 15713-3323B(2), ×160. Flake of wax.
3. 15713-3671B(2), ×160. Laminar resin bodies.
4. 15713-3667B(1), ×400. General view of lower cuticle showing numerous brachyparactytic stomatal complexes and a cluster of trichome bases (center of photograph).
5. 15713-3671C(2), ×640. Amphibrachyparacytic stomatal complex and associated trichome bases. Note how the lamellar cuticular thickenings are located only on the tangential walls of the guard cells and the inner pair of subsidiary cells.
6. 15713-3671B(1), ×512. Two stomatal complexes showing the weak development of lamellar thickenings over the inner pair of subsidiary cells..
7. 15713-3671B(1), ×512. Stomatal complex showing the development of one lamellar thickening only at the junction of the guard cell and inner subsidiary cell (arrow). Note large resin body in top right corner of photograph.
8. 15713-3323B(1), ×400. Upper cuticle over midvein showing numerous trichome bases.
9. 15713-3671B(1), ×160. Lower cuticle under midvein. Note large resin bodies in top half of photograph.



CUTICLE OF *PANDEMOPHYLLUM KVACEKII* NEW SPECIES

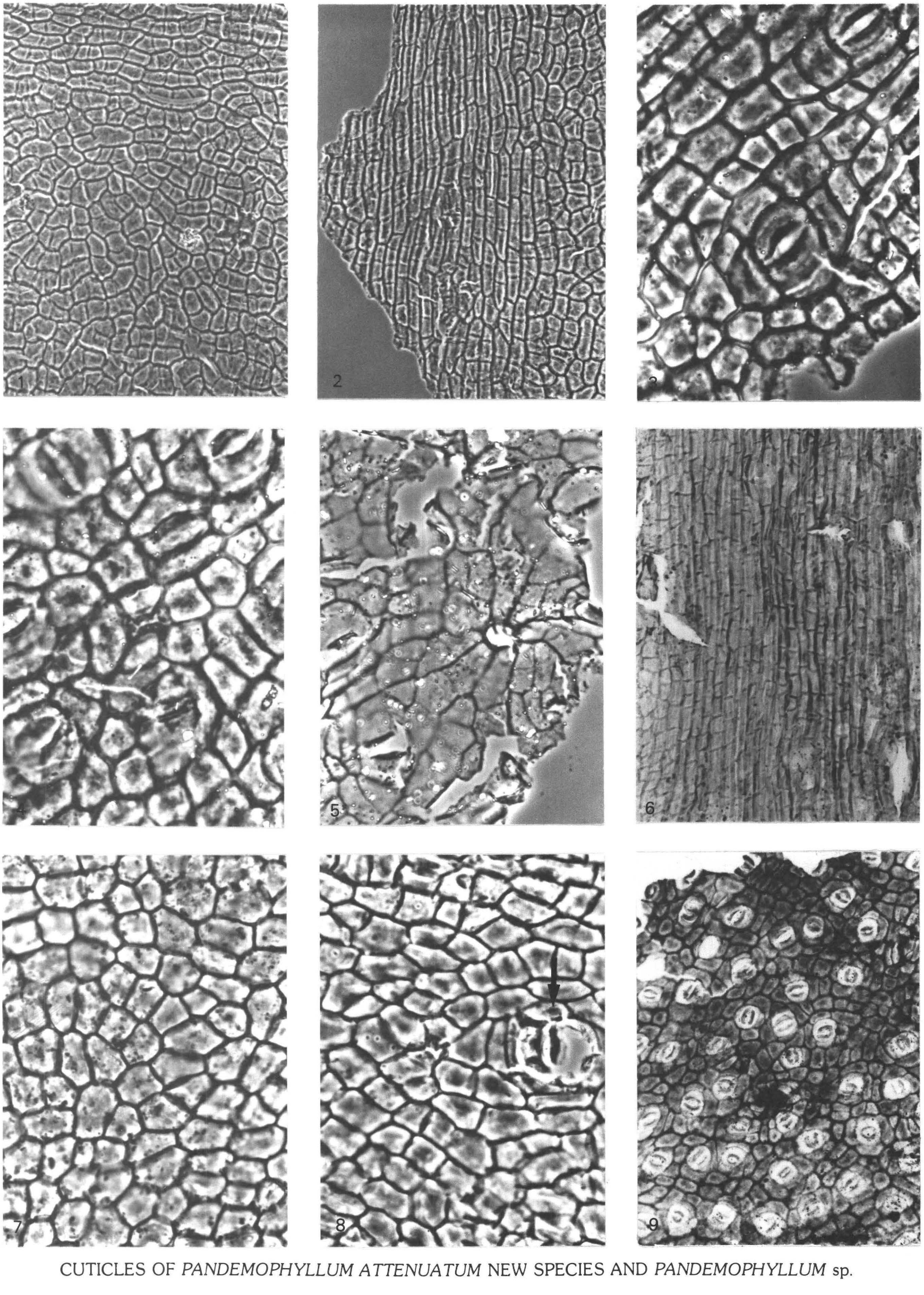
PLATE 16

Figures 1–6. Cuticle of *Pandemophyllum attenuatum* new species (p. 29)

- 1–4, 6. 15713-4698A.
  - 1. Phase contrast, general view of upper cuticle, ×160.
  - 2. Phase contrast, area over a higher order vein, upper cuticle, showing undulatory pattern characteristic of this species, ×160.
  - 3. Phase contrast, lower cuticle showing brachyparacytic stomatal complex. NOTE: The cuticle of the subsidiary cells is not thinner than that of the unspecialized epidermal cells, ×400.
  - 4. Phase contrast, trichome base with angular pore (arrow), ×400.
  - 6. Lower cuticle beneath primary vein. Note the weakly developed undulations, in contrast to the regions beneath higher order veins, ×160.
- 5. 15713-4898B. Phase contrast microscopy, lower cuticle, trichome base with circular pore, ×400.

7–9. Cuticle of *Pandemophyllum* sp. (p. 30)

- 7, 8. 15713-4827.
  - 7. Phase contrast microscopy, general view, upper cuticle, ×400.
  - 8. Phase contrast microscopy, stomatal complex on upper cuticle (arrow), ×400.
  - 9. 15713-4827′ (counterpart). General view of lower cuticle showing numerous brachyparacytic stomatal complexes with thin cuticle on the outer pairs of subsidiary cells, ×160.



CUTICLES OF *PANDEMOPHYLLUM ATTENUATUM* NEW SPECIES AND *PANDEMOPHYLLUM* sp.

PLATE 17

Figures 1–3. Cuticle of *Pandemophyllum* sp. 15713-4827′ (p. 30)

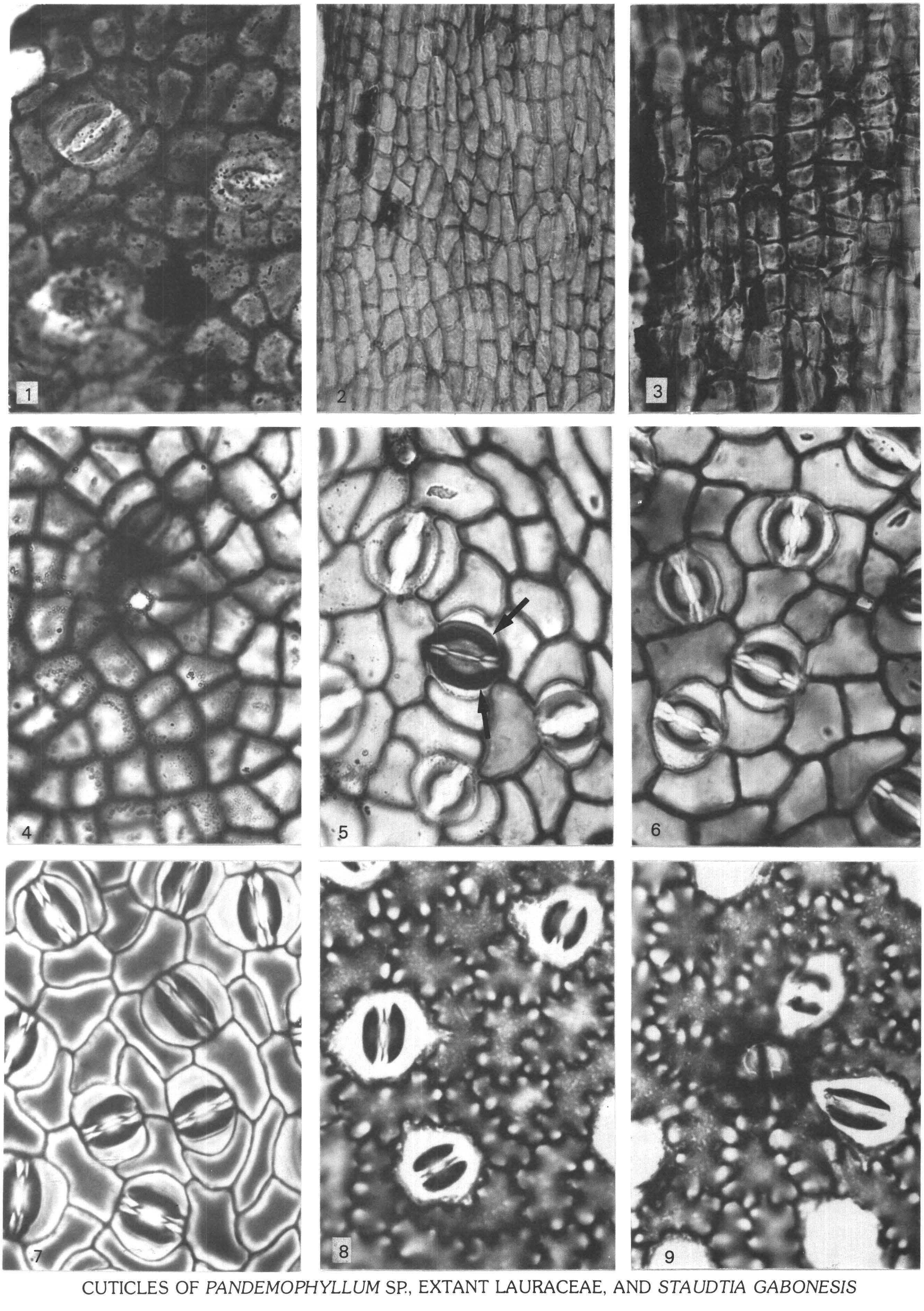
- 1. Stomatal complexes, ×512.
- 2. Upper cuticle above midvein showing cells organized into weakly defined rows and scattered idioblasts (heavily cutinized cells), ×160.
- 3. Lower cuticle beneath midvein with numerous idioblasts/trichome bases, ×400.

4–7. Cuticles of extant Lauraceae

- 4. *Ocotea tristis*, University of Florida Modern Leaf Ref. Coll. no. 182, upper cuticle showing trichome base of the *Pandemophyllum* type, ×512.
- 5, 6. *Ocotea bracteata*, University of Florida Modern Leaf Ref. Coll. no. 221, ×640.
  - 5. Partially macerated stomatal complex (center) showing narrow pair of inner subsidiary cells (arrows).
  - 6. Fully macerated stomatal complexes.
- 7. *Nectandra tarascensis*, University of Florida Modern Leaf Ref. Coll. no. 32, stomata showing well-developed lamellar cuticular thickenings on the guard cells, ×640.

8, 9. Cuticle of *Staudtia gabonensis* (Myristicaceae), U.S. National Herbarium no. 1750180, ×640

- 8. General view of stomata showing well-developed lamellar cuticular thickenings on the guard cells and brachyparacytic subsidiary cell arrangement.
- 9. Trichome base typical of Myristicaceae (center) showing a circular trichome abscission scar positioned over modified cells.



CUTICLES OF *PANDEMOPHYLLUM* SP., EXTANT LAURACEAE, AND *STAUDTIA GABONESIS*

PLATE 18

[All figures ×1 unless otherwise indicated]

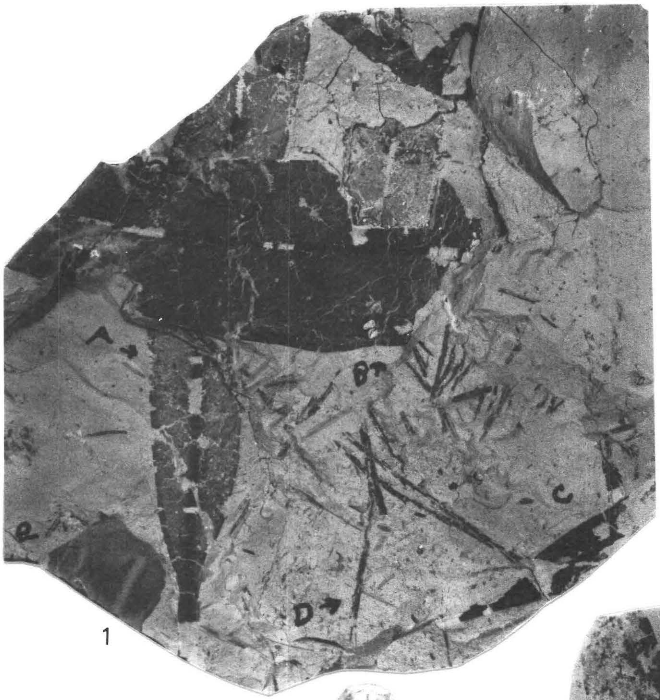
Figures 1–7. *Longstrethia varidentata* new species (p. 31)

1. 15713-4893A′, specimen showing gradually narrowed base of leaf and indistinct petiolar region.
2. 15713-4906a, 4906b. Note curvature in 4906a.
3. 15713-4715, ×2. Note teeth along right-hand margin of leaf.
4. 15713-4961a, 4961b, 4961c. Specimens showing coarsely dentate margins.

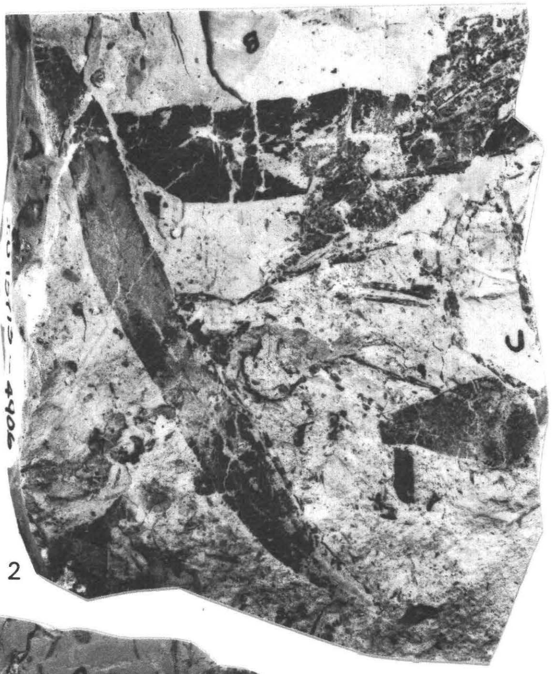
5, 6. 15713-8301.

   5. General view of specimen showing intramarginal vein, ×2.
   6. Closeup of apical region of specimen showing round, non-glandular tooth (left margin) and irregularly reticulate higher order venation, ×10.

7. 15713-7806, ×4. Specimen preserving tip of leaf and coarsely dentate margin.

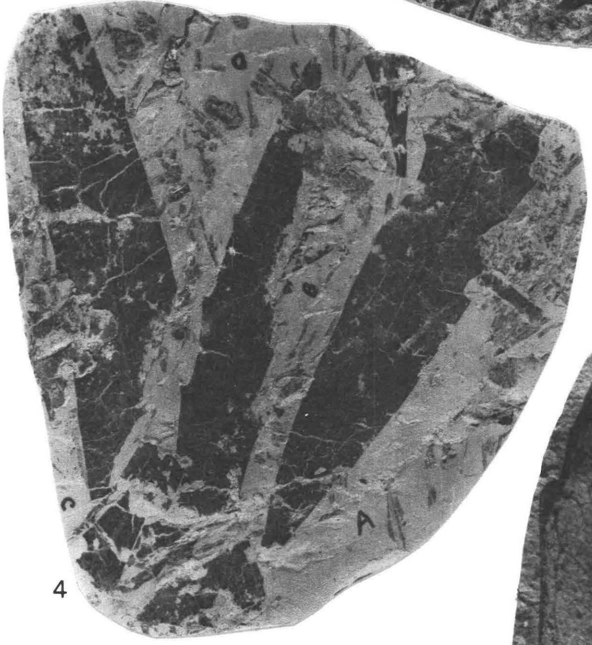


1

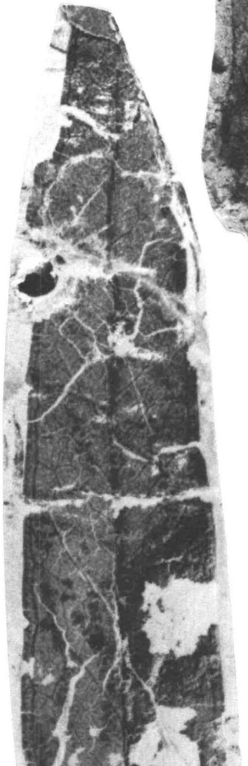


2

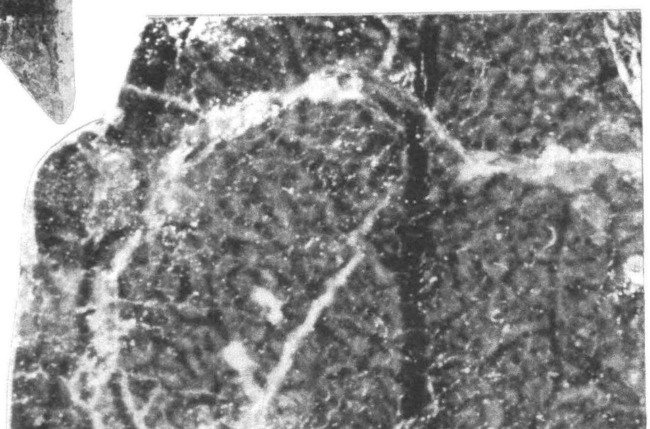
3



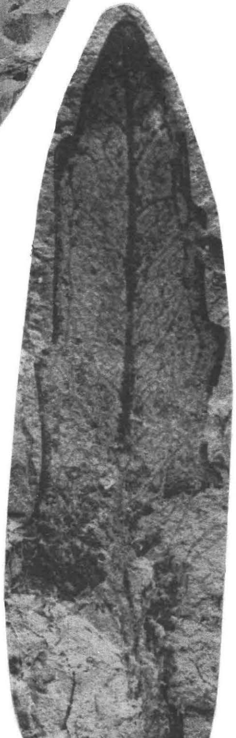
4



5



6



7

LONGSTRETHIA VARIDENTATA NEW SPECIES

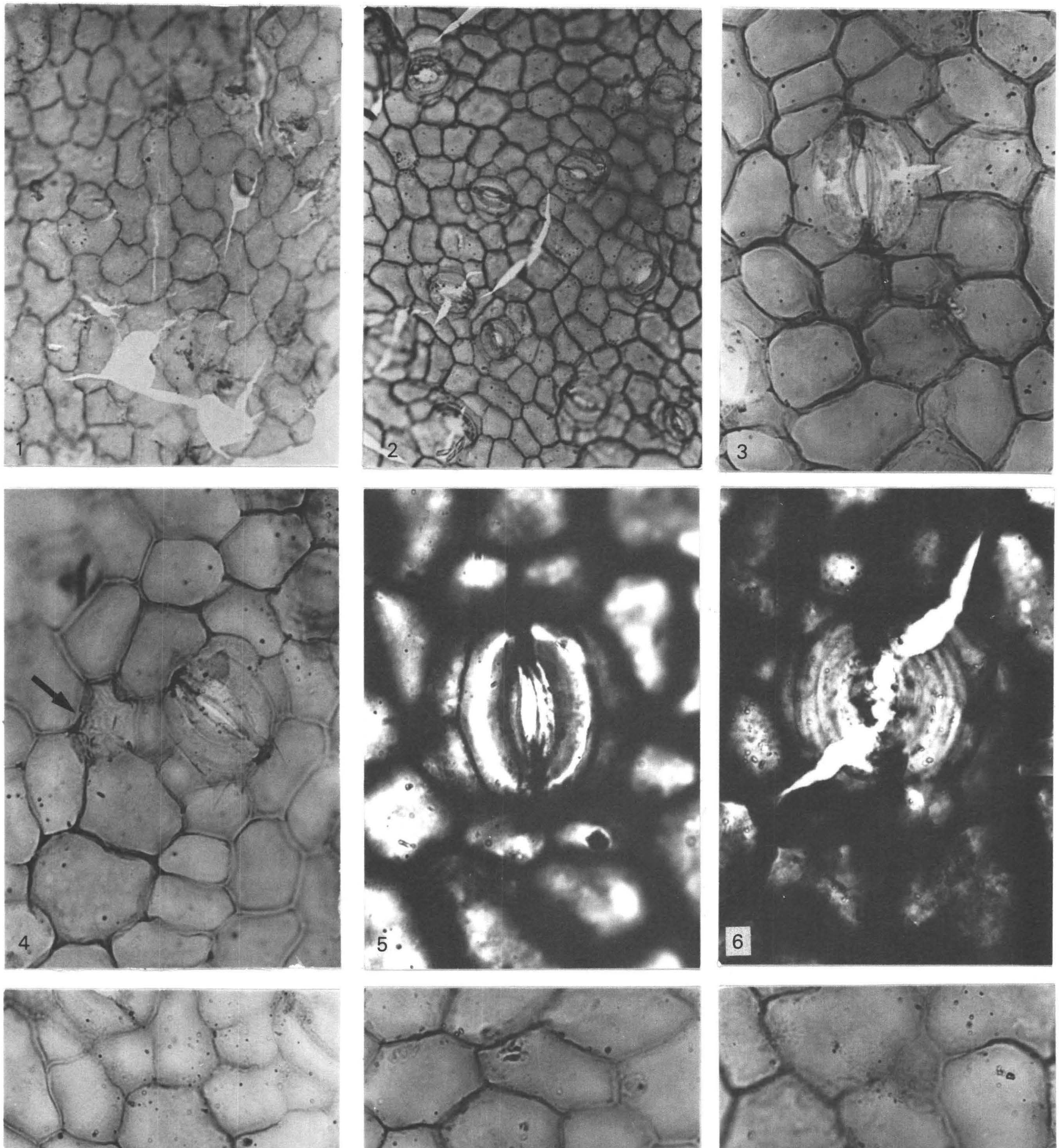
PLATE 19

Figures 1–9. Cuticle of *Longstrethia varidentata* new species (p. 31)

1, 2, 5, 7–9. 15713–3693A.

1. General view of upper cuticle, × 160.
2. General view of lower cuticle, × 160.
5. High-contrast photograph of stoma showing the curved lamellar cuticular thickenings on the guard cells, × 640.
7. Epidermal secretory cell (arrow) surrounded by 5 radially oriented unspecialized cells, × 400.
8. Epidermal secretory cell with attached resin body (arrow), × 512.
9. Laminar resin body, interpreted as mesophyll secretory cell, × 512.

3. 15713-3668A, × 512. Stomatal complex with tendency towards cyclocytic arrangement of subsidiary cells. Here only the upright portion of the T-piece is well developed, and the lower T-piece flares towards the stomatal pole.
4. 15713-3691A, × 400. Laterocytic stomatal complex and associated idioblast (arrow). In this stoma, both the upright and the crossbar of the T-piece are present.
6. 15713-3684B, × 640. High-contrast photograph of a stoma showing striations on the guard cells oriented concentric to the stomatal pore.

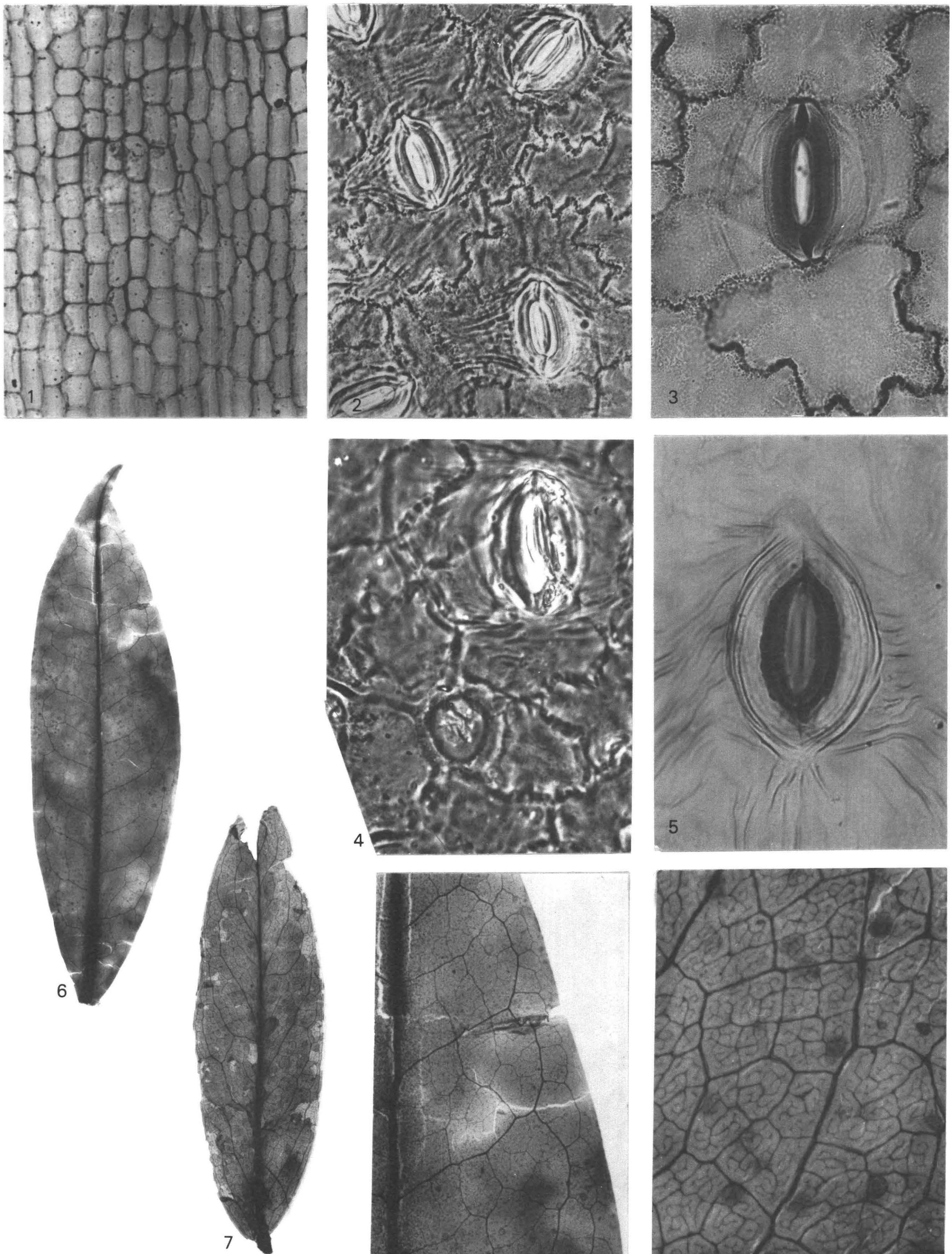


CUTICLE OF *LONGSTRETHIA VARIDENTATA* NEW SPECIES

PLATE 20

Figure 1. Lower cuticle of *Longstrethia varidentata* beneath midvein, 15713-3693A, ×160 (p. 31)

- 2–5. Cuticles of extant Illiciales.
  - 2, 3. *Illicium parviflorum* Michx (Illiciaceae), MICH, L.R. Holdridge no. 2124.
    - 2. Lower cuticle, phase contrast, ×256.
    - 3. Stoma with T-pieces, ×400.
    - 4. *Illicium floridanum* Ellis (Illiciaceae), MICH, A. Jewett no. 1046. Phase contrast, lower cuticle with secretory cell (lower left corner), ×400.
    - 5. *Kadsura japonica* Dun. (Schisandraceae), MICH, O. Yongsok no. 8209. Stoma showing oval lamellar thickenings on outer walls of guard cells and striations concentric to the stomatal pore, ×640.
- 6–9. Foliar architecture of extant Illiciales
  - 6, 8. *Illicium ternstroemoides* A.C. Smith (Illiciaceae), USNM Cleared Leaf no. 770.
    - 6. ×1.
    - 8. ×3.
  - 7, 9. Schisandraceae
    - 7. *Kadsura oblongifolia* Merr., USNM Cleared Leaf no. 784, ×1.
    - 9. *Kadsura phillipensis* Merr., USNM Cleared Leaf no. 403, closeup of secondary and higher order venation, ×5.



CUTICLES OF *LONGSTRETHIA VARIDENTATA*; CUTICLES AND VENATION OF EXTANT ILLICIALES

PLATE 21

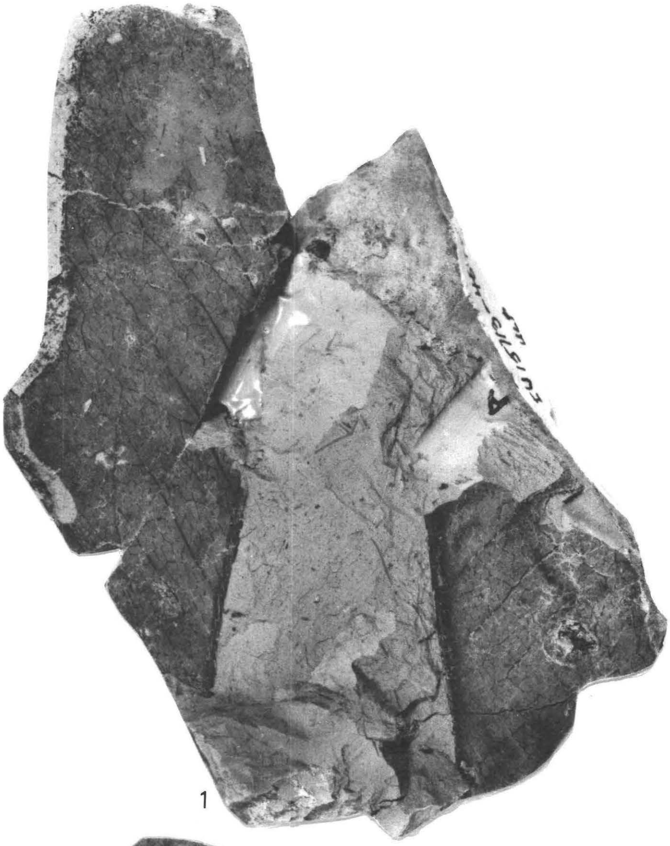
[All figures ×1 unless otherwise indicated]

Figures 1–5. *Didromophyllum basingerii* new species (p. 34)

1. 15713-4699a, 4699b. Specimen preserving a pair of laminar units on a single bedding plane.
2. 15713-7863. Nearly complete specimen showing characteristic asymmetry in the divergence of the two primary veins at the base of the lamina.
3. 15713-4895. Holotype.

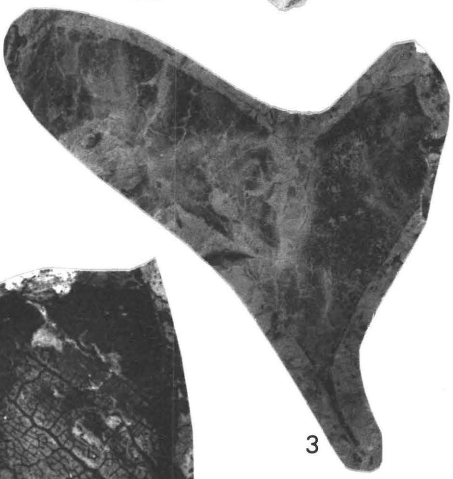
4, 5. 15713-7865.

   4. General view of specimen showing the tip of a lateral lobe (top), ×2.
   5. Closeup of specimen showing reticulate tertiary and higher order venation, well-developed areolation, and the apparent absence of freely ending veinlets, ×5.



1

2



3

4

5

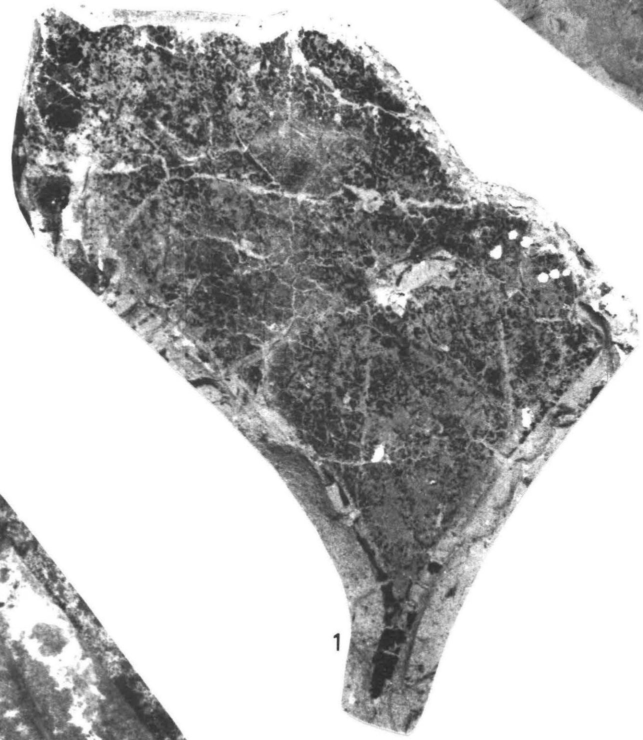
DIDROMOPHYLLUM BASINGERII NEW SPECIES

PLATE 22

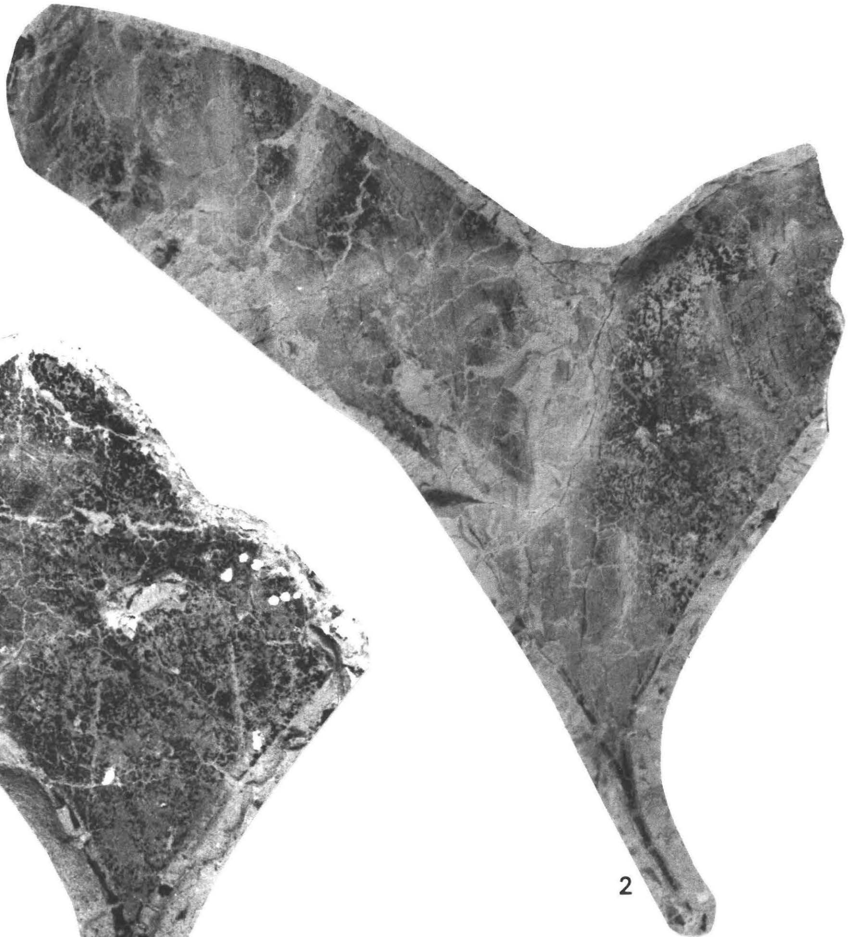
Figures 1, 2. *Didromophyllum basingerii* new species (p. 34)

1. 15713-8302. Specimen shows the decurrent origin of one of the two primary veins at the base of the lamina.
2. 15713-4895, × 2. Specimen illustrated on plate 21, figure 3, showing the nearly symmetrical bifurcation of the vascular tissue in the petiol(ul)e to form the two primary veins.

3. "*Sterculia*" *snowii* var. *disjuncta* Lesquereux, USNM 2745, × 1. Note the similarity in the general organization of each laminar unit to that found in *Didromophyllum* and the connection of the two laminar units at the base of the specimen.



1



2

3

DIDROMOPHYLLUM BASINGERII NEW SPECIES AND "*STERCULIA*" *SNOWII* var. *DISJUNCTA*

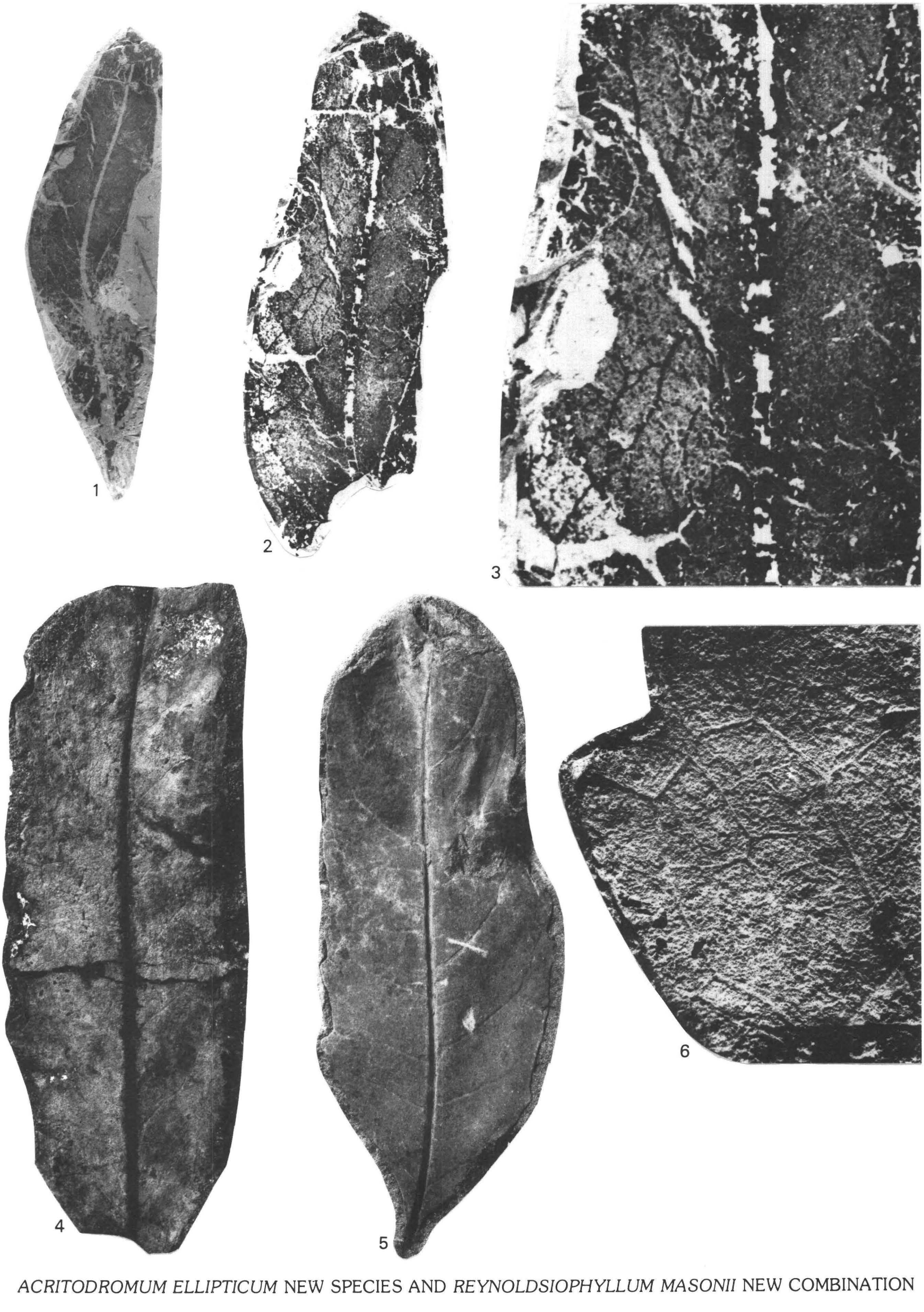
PLATE 23

Figures 1–3. *Acritodromum ellipticum* new species, 15713-4704 (p. 36)

1. General view of specimen after excavating basal region, ×1.
2. High-contrast photograph of specimen taken before excavating basal region showing details of secondary and tertiary venation, ×2.
3. Enlargement of figure 2, showing the irregular, sinuous tertiary venation and faint quaternary veins oriented at nearly right angles to the tertiary veins, ×5.

4–6. *Reynoldsiophyllum masonii* (Lesquereux) new combination (p. 37)

- 4, 6. USNM 50077.
  - 4. General view of specimen, ×1.
  - 6. Closeup of tooth, ×10.
- 5. USNM 2779, ×1.



ACRITODROMUM ELLIPTICUM NEW SPECIES AND *REYNOLDSIOPHYLLUM MASONII* NEW COMBINATION

PLATE 24

[All figures × unless otherwise indicated]

Figures 1–5. *Reynoldsiophyllum nebrascense* new species (p. 39)

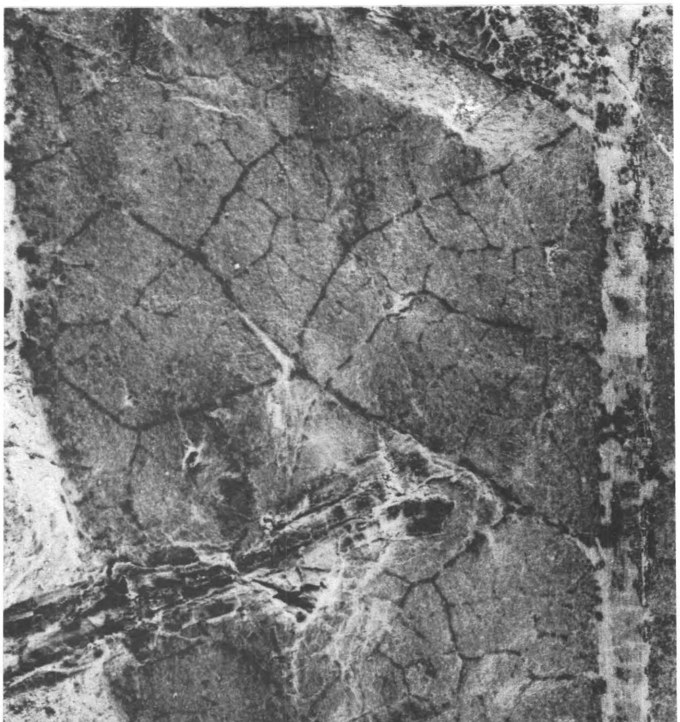
- 1, 2, 4. Holotype (part and counterpart).
  - 1. 15713-7805′.
  - 2. 15713-7805.
  - 4. 15713-7805′, ×5. Enlargement showing transversely oriented tertiary veins and curved, reticulate quaternary veins.
- 3, 5. 15713-4876.
  - 3. ×1.
  - 5. ×5. Note the uniform thickness of the structural reinforcement of the margin and the root penetrating the midvein of the leaf (arrows).


1

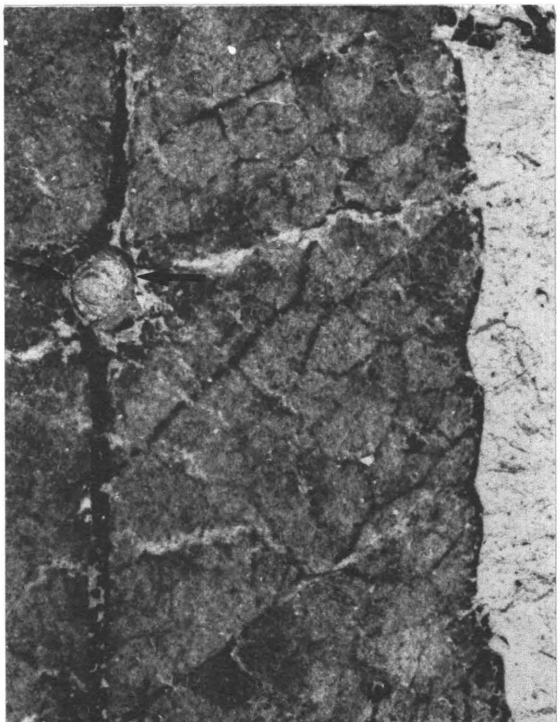

2


3

4



5

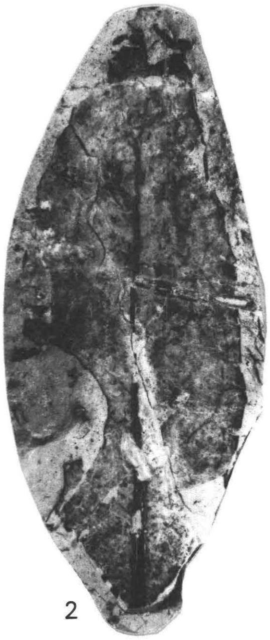


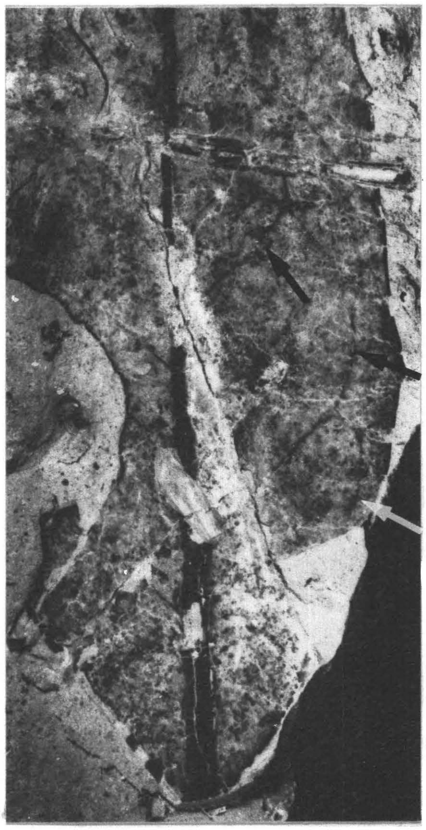
REYNOLDSIOPHYLLUM NEBRASCENSE NEW SPECIES

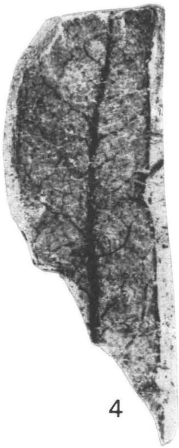
PLATE 25

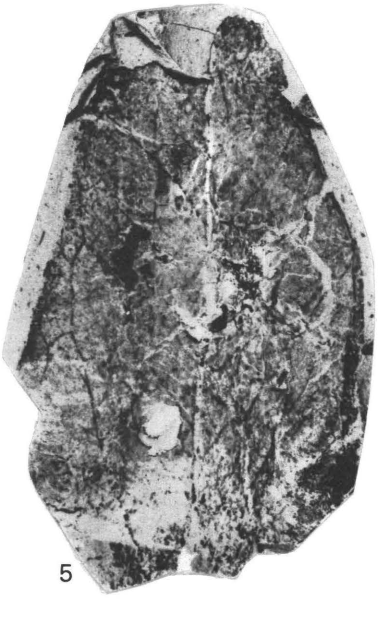
Figure 1. *"Elaeodendron" speciosum* Lesquereux, UKSM DT-13, ×1
- 2, 3. *Dicotylophyllum angularis*, 15713-4882A (p. 40)
  - 2. ×1.
  - 3. Closeup of basal part of leaf showing cuneate base and thin secondary veins (arrows), ×2.
- 4–6. New genus B (p. 41)
  - 4, 6. 15713-4850.
    - 4. General shot, ×2.
    - 6. Closeup showing irregular secondary venation that forms loops near the margin and irregularly reticulate higher order venation, ×5.
  - 5. 15713-4831′, ×2.

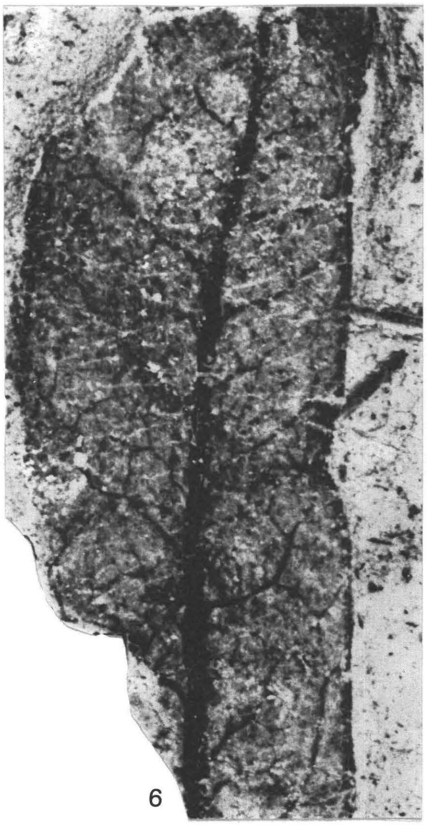

1


2


3


4


5

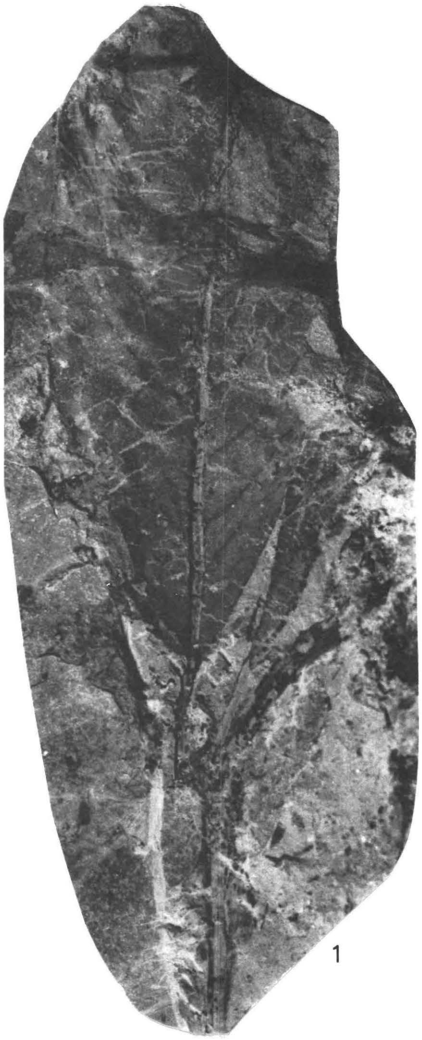

6

"*ELAEODENDRON*" *SPECIOSUM*, *DICOTYLOPHYLLUM ANGULARIS*, AND NEW GENUS B

PLATE 26

Figures 1–4. *Anisodromum wolfei* new genus and species (p. 42)

- 1, 2. 15713-7803.
  1. General view of holotype showing three leaflets attached to the rachis, ×2.
  2. Closeup of attachment of leaflets to rachis, ×5. Note darkening along laminar margins, interpreted as the remains of structural reinforcement.
- 3, 4. 15713-7802.
  3. General view of leaflet showing slight asymmetry to secondary venation, ×2.
  4. Closeup of middle portion of leaflet showing thin, sparsely branched, admedially oriented tertiary venation (poorly preserved), ×5.



1

2

3

4

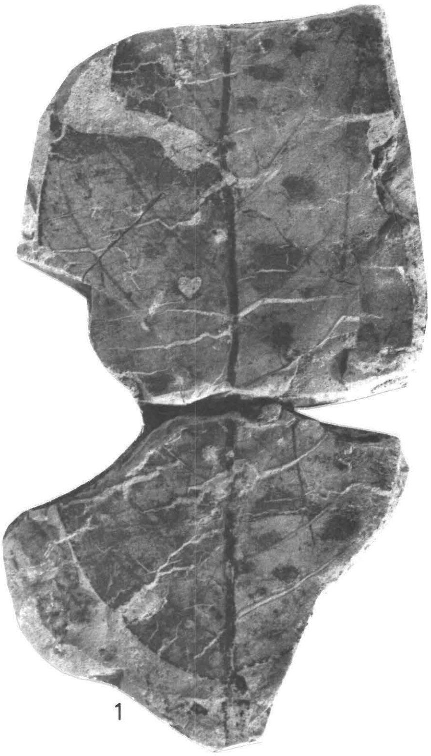
ANISODROMUM WOLFEI NEW GENUS AND SPECIES

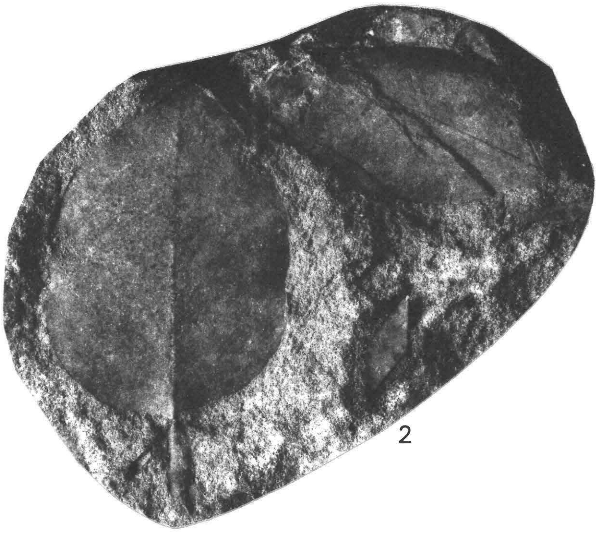
PLATE 27

Figures 1, 3, 4. *Citrophyllum doylei* new species, 15713-4894 (p. 43)

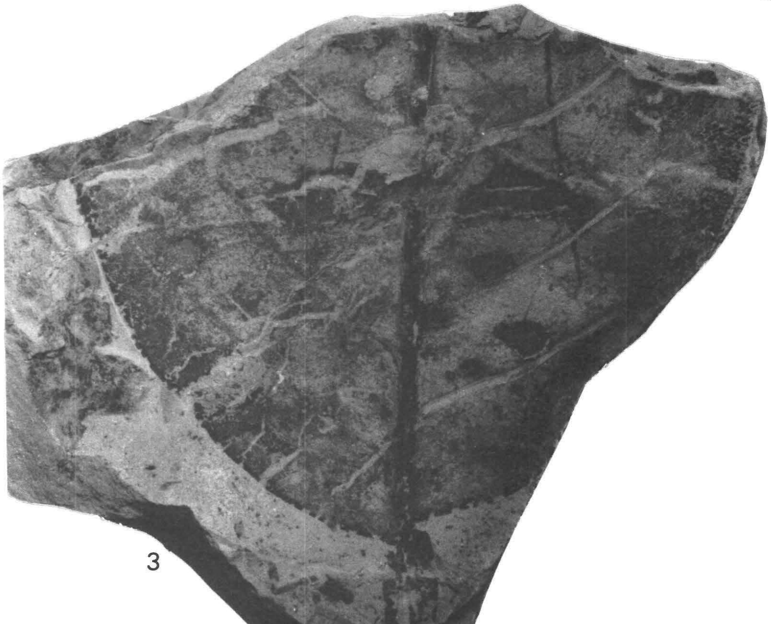
1. General view of holotype, × 1.
3. Closeup of base, showing alate petiole constricted at base of lamina, ×2
4. Enlargement of upper left region of leaf showing curved eucamptodromous secondary veins and thin, sparsely branched, admedially oriented tertiary venation (poorly preserved), ×3.

2. *Citrophyllum aligerum* (Lesquereux) Berry, USNM 50128, ×1.


1


2


4


3

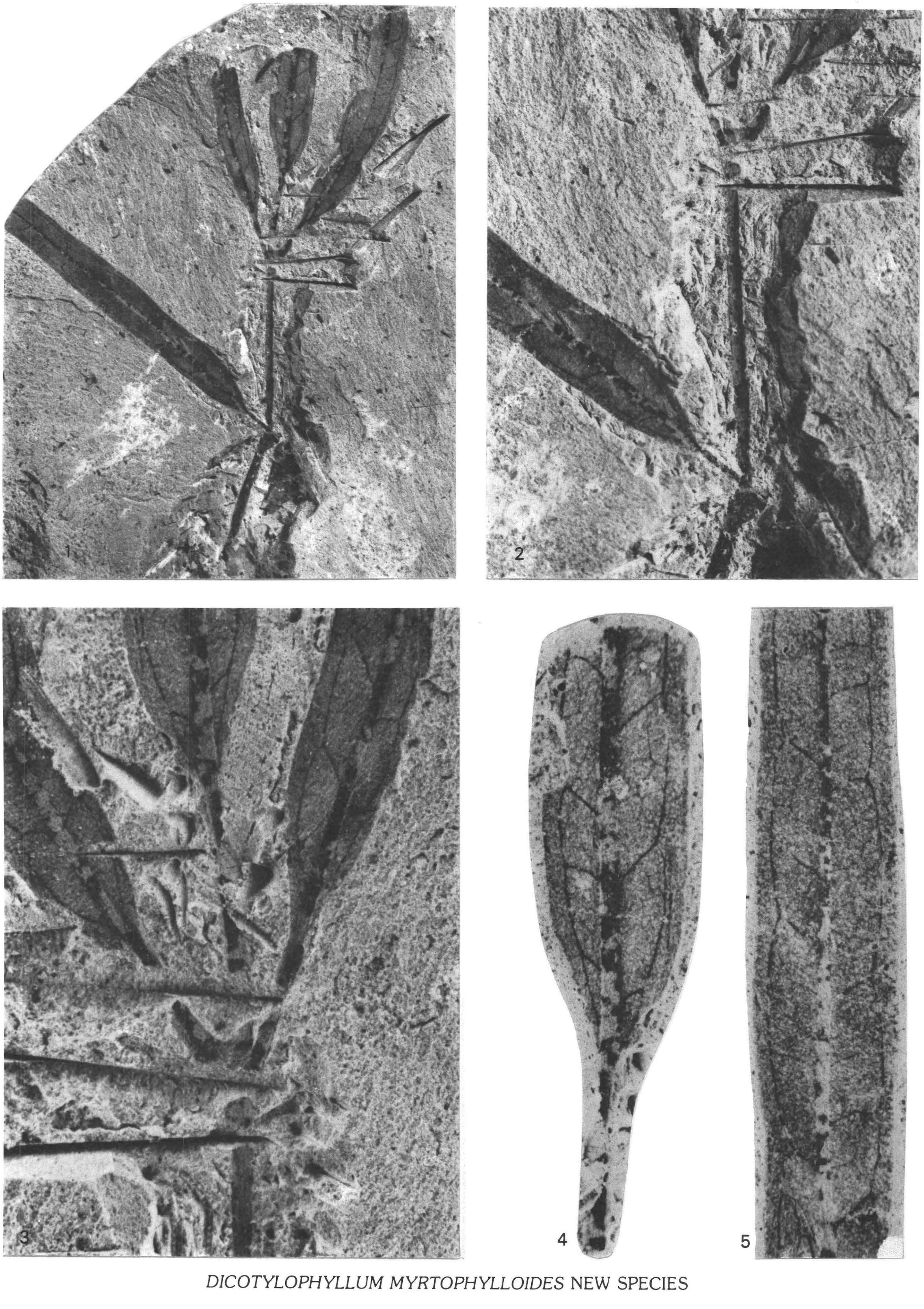
CITROPHYLLUM DOYLEI NEW SPECIES AND *CITROPHYLLUM ALIGERUM*

PLATE 28

Figures 1–5. *Dicotylophyllum myrtophylloides* new species, 15713-8303 (p. 45)

1. General view of specimen showing four leaves attached to axis, × 3.
2. Enlargement of figure 1 showing attachment of basal leaf to axis, × 6.
3. Enlargement of apical region showing attachment of terminal three leaves to axis, × 10. The linear markings are gouged areas in the matrix.

4, 5. Enlargements of different leaves showing details of secondary venation and poorly preserved, irregularly reticulate tertiary venation, × 10.



DICOTYLOPHYLLUM MYRTOPHYLLOIDES NEW SPECIES

PLATE 29

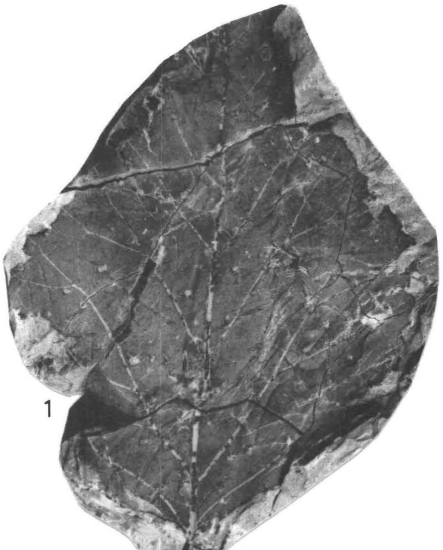
Figures 1–5. *Dicotylophyllum rosafluviatilis* new species (p. 46)

1, 2, 4, 5. 15713-4698.

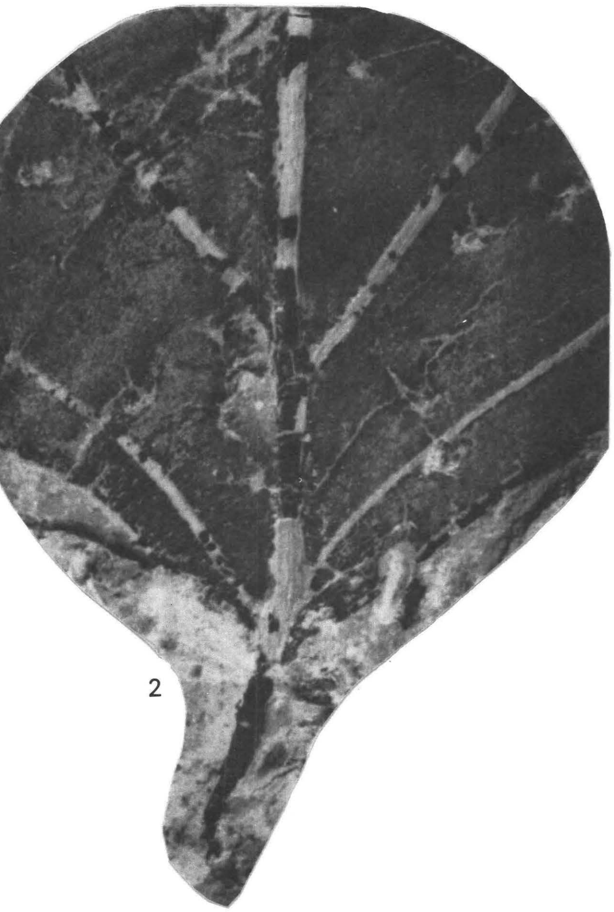
1. General view of holotype, × 1.
2. Closeup of base showing petiole, basilaminar secondary veins, and recurved superadjacent pair of secondary veins, × 5.
4. Closeup of highly branched secondary vein on right side of specimen showing exmedial branch of secondary vein (arrow), tertiary veins, and irregular quaternary venation (poorly preserved), × 10.
5. Margin showing darkened region and teeth, × 10.

3. 15713-4698′ (counterpart). Apical region showing thin, admedially oriented tertiary venation, × 5.

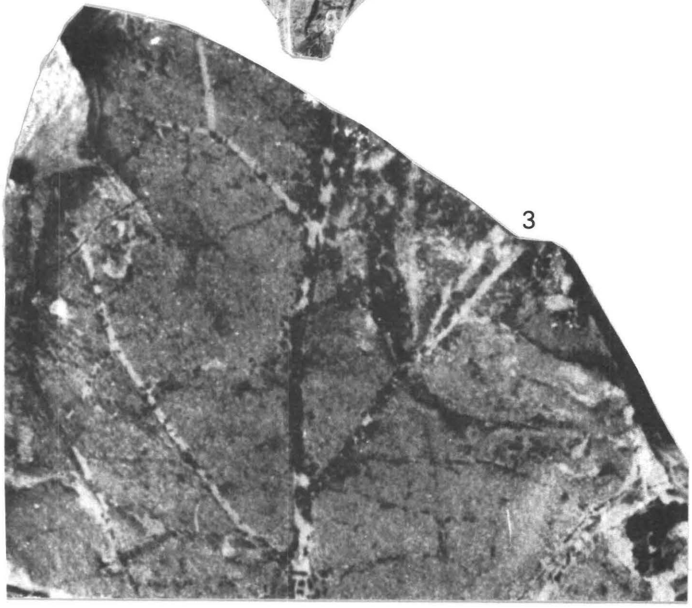
1



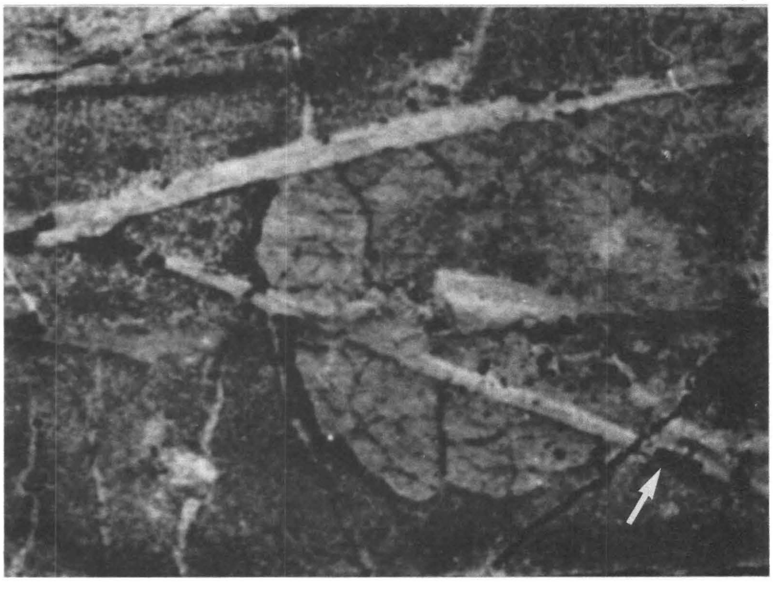
2



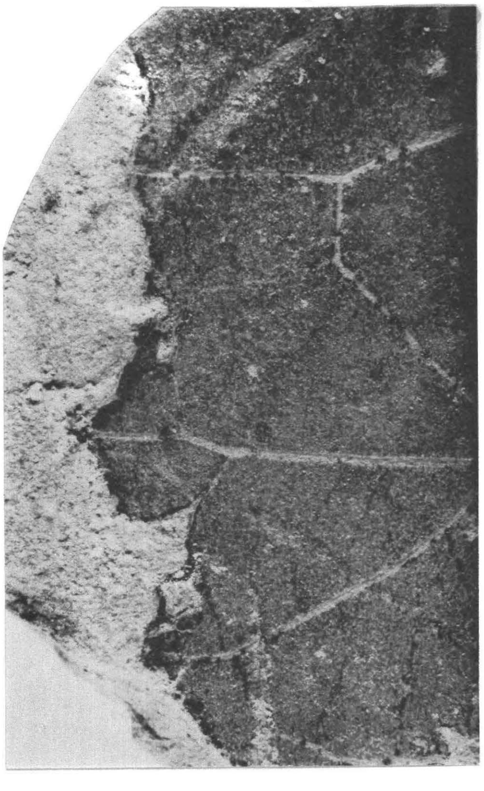
3



4



5



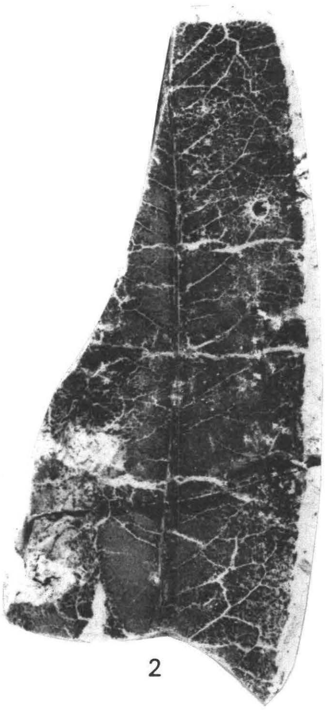
DICOTYLOPHYLLUM ROSAFLUVIATILIS NEW SPECIES

PLATE 30

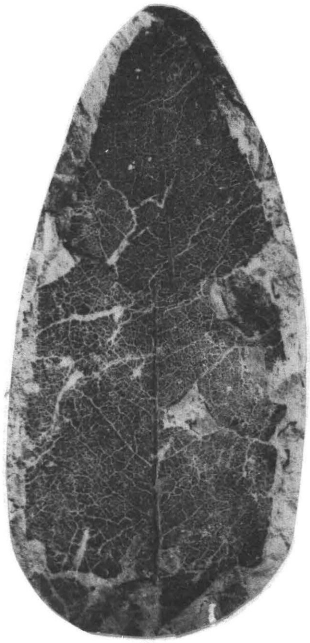
Figures 1–5. *Dicotylophyllum aliquantuliserratum* new species (p. 47)

- 1, 4. 15713-4877A, 4877B, holotype.
  - 1. Pair of laminae on bedding plane, ×1.
  - 4. Closeup left lamina showing crenate margin and thinning of secondary veins near margin, ×10.
- 2. 15713-4707, ×2. Note tendency for each secondary vein to form its own series of brochidodromous loops.
- 3, 5. 15713-7804.
  - 3. General view of specimen, ×2.
  - 5. Enlargement of apical region showing serrate margin and breaks in the lamina that may represent venation, ×10.

1



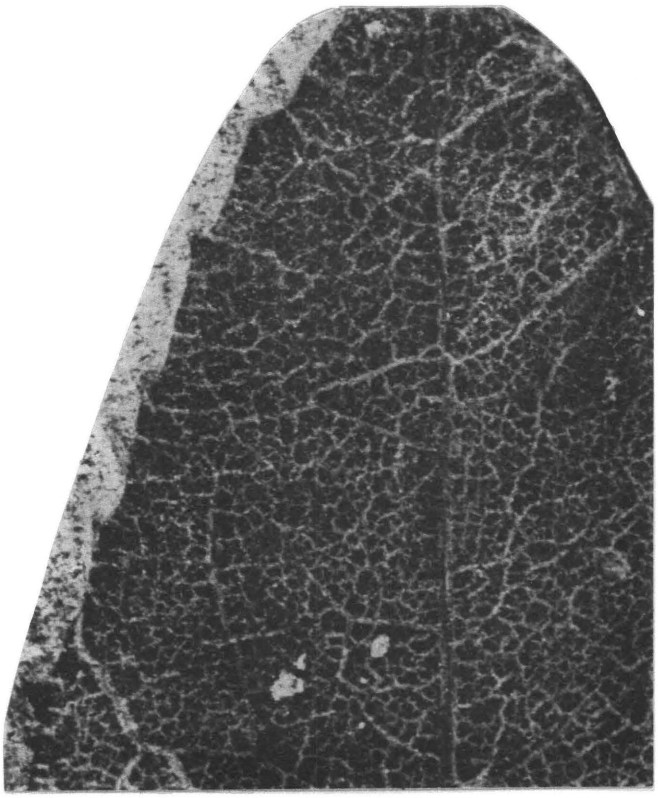
2



3

4

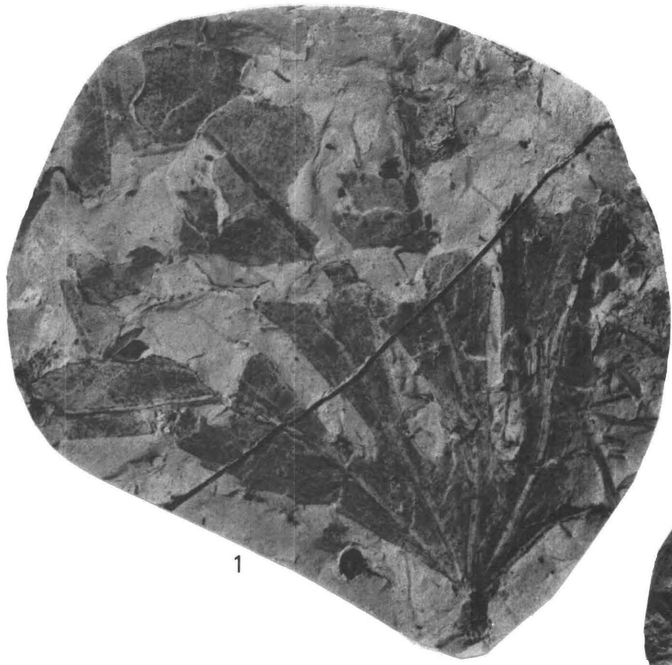
5



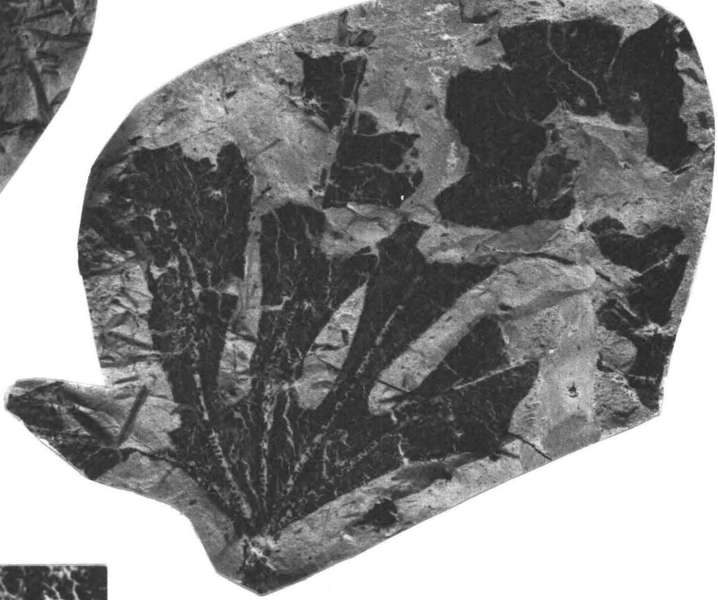
DICOTYLOPHYLLUM ALIQUANTULISERRATUM NEW SPECIES

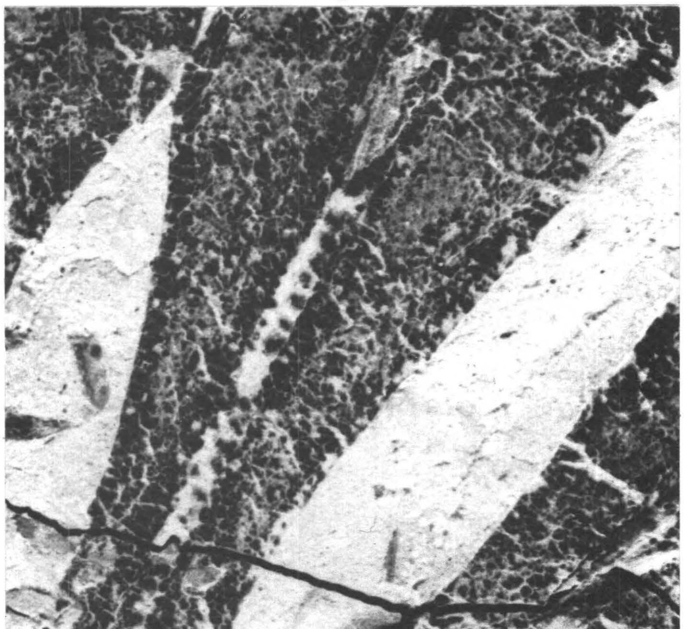
PLATE 31

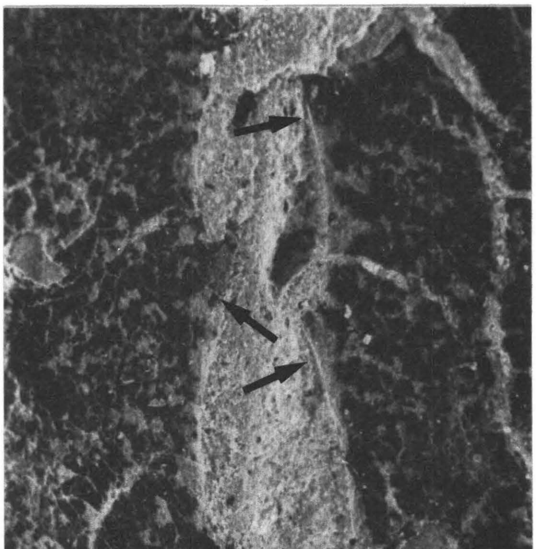
Figures 1–4. *Dicotylophyllum expansolobum* new species (p. 48)
- 1. 15713-8304′, counterpart, ×1.
- 2–4. 15713-8304.
  - 2. ×1.
  - 3. Enlargement of middle sinus showing shape and darkened region along margin, interpreted as structural reinforcement, ×5.
  - 4. Enlargement of two vertical lobes in figure 2 showing small teeth along margin (arrows), ×10.


1

2


3


4



DICOTYLOPHYLLUM EXPANSOLOBUM NEW SPECIES

SELECTED SERIES OF U.S. GEOLOGICAL SURVEY PUBLICATIONS

Periodicals

Earthquakes & Volcanoes (issued bimonthly).
Preliminary Determination of Epicenters (issued monthly).

Technical Books and Reports

Professional Papers are mainly comprehensive scientific reports of wide and lasting interest and importance to professional scientists and engineers. Included are reports on the results of resource studies and of topographic, hydrologic, and geologic investigations. They also include collections of related papers addressing different aspects of a single scientific topic.

Bulletins contain significant data and interpretations that are of lasting scientific interest but are generally more limited in scope or geographic coverage than Professional Papers. They include the results of resource studies and of geologic and topographic investigations; as well as collections of short papers related to a specific topic.

Water-Supply Papers are comprehensive reports that present significant interpretive results of hydrologic investigations of wide interest to professional geologists, hydrologists, and engineers. The series covers investigations in all phases of hydrology, including hydrogeology, availability of water, quality of water, and use of water.

Circulars present administrative information or important scientific information of wide popular interest in a format designed for distribution at no cost to the public. Information is usually of short-term interest.

Water-Resources Investigations Reports are papers of an interpretive nature made available to the public outside the formal USGS publications series. Copies are reproduced on request unlike formal USGS publications, and they are also available for public inspection at depositories indicated in USGS catalogs.

Open-File Reports include unpublished manuscript reports, maps, and other material that are made available for public consultation at depositories. They are a nonpermanent form of publication that may be cited in other publications as sources of information.

Maps

Geologic Quadrangle Maps are multicolor geologic maps on topographic bases in 7 1/2- or 15-minute quadrangle formats (scales mainly 1:24,000 or 1:62,500) showing bedrock, surficial, or engineering geology. Maps generally include brief texts; some maps include structure and columnar sections only.

Geophysical Investigations Maps are on topographic or planimetric bases at various scales; they show results of surveys using geophysical techniques, such as gravity, magnetic, seismic, or radioactivity, which reflect subsurface structures that are of economic or geologic significance. Many maps include correlations with the geology.

Miscellaneous Investigations Series Maps are on planimetric or topographic bases of regular and irregular areas at various scales; they present a wide variety of format and subject matter. The series also includes 7 1/2-minute quadrangle photogeologic maps on planimetric bases which show geology as interpreted from aerial photographs. Series also includes maps of Mars and the Moon.

Coal Investigations Maps are geologic maps on topographic or planimetric bases at various scales showing bedrock or surficial geology, stratigraphy, and structural relations in certain coal-resource areas.

Oil and Gas Investigations Charts show stratigraphic information for certain oil and gas fields and other areas having petroleum potential.

Miscellaneous Field Studies Maps are multicolor or black-and-white maps on topographic or planimetric bases on quadrangle or irregular areas at various scales. Pre-1971 maps show bedrock geology in relation to specific mining or mineral-deposit problems; post-1971 maps are primarily black-and-white maps on various subjects such as environmental studies or wilderness mineral investigations.

Hydrologic Investigations Atlases are multicolored or black-and-white maps on topographic or planimetric bases presenting a wide range of geohydrologic data of both regular and irregular areas; principal scale is 1:24,000 and regional studies are at 1:250,000 scale or smaller.

Catalogs

Permanent catalogs, as well as some others, giving comprehensive listings of U.S. Geological Survey publications are available under the conditions indicated below from the U.S. Geological Survey, Books and Open-File Reports Section, Federal Center, Box 25425, Denver, CO 80225. (See latest Price and Availability List.)

"Publications of the Geological Survey, 1879- 1961" may be purchased by mail and over the counter in paperback book form and as a set of microfiche.

"Publications of the Geological Survey, 1962- 1970" may be purchased by mail and over the counter in paperback book form and as a set of microfiche.

"Publications of the U.S. Geological Survey, 1971- 1981" may be purchased by mail and over the counter in paperback book form (two volumes, publications listing and index) and as a set of microfiche.

Supplements for 1982, 1983, 1984, 1985, 1986, and for subsequent years since the last permanent catalog may be purchased by mail and over the counter in paperback book form.

State catalogs, "List of U.S. Geological Survey Geologic and Water-Supply Reports and Maps For (State)," may be purchased by mail and over the counter in paperback booklet form only

"Price and Availability List of U.S. Geological Survey Publications," issued annually, is available free of charge in paperback booklet form only.

Selected copies of a monthly catalog "New Publications of the U.S. Geological Survey" available free of charge by mail or may be obtained over the counter in paperback booklet form only. Those wishing a free subscription to the monthly catalog "New Publications of the U.S. Geological Survey" should write to the U.S. Geological Survey, 582 National Center, Reston, VA 22092.

Note.--Prices of Government publications listed in older catalogs, announcements, and publications may be incorrect. Therefore, the prices charged may differ from the prices in catalogs, announcements, and publications.