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By JACK A. WOLFE and WESLEY WEHR

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Middle Eocene Dicotyledonous Plants From Republic, Northeastern Washington

By Jack A. Wolfe *and* Wesley Wehr

Abstract

Twenty-four dicotyledonous species of megafossil plants from radiometrically dated early middle Eocene lake beds are discussed and illustrated. Six taxa are only generically determined and 18 are assigned to species. Of the genera represented, seven are extinct. Six genera are new: *Langeria* (Hamamelidaceae), *Macginitiea* (Platanaceae), *Barghoornia* (Burseraceae), *Bohlenia* (Sapindaceae), *Tsukada* (Davidiaceae), and *Republica* (Incertae sedis). Nine new species are described and five new combinations proposed.

The Republic flora represents a microthermal Mixed Coniferous forest that grew in an upland region that had an estimated altitude of about 700–900 m. The flora has few species in common with coeval lowland floras but shares several species with other Eocene upland floras. Analysis of the stratigraphic ranges of the Republic species indicates that several are useful in defining a biostratigraphic framework for upland Eocene floral assemblages.

The Republic flora represents a mixture of groups that were common during the Paleocene and early Eocene and groups that are of modern aspect. Analysis of the Republic lineages indicates that evolution and extinction in montane coniferous forests has proceeded at a greater rate than previously thought. Few of the Republic lineages survived into the Neogene, although some distant relatives now survive in broadleaved forests.

INTRODUCTION

Since 1960, extensive application of radiometric dating techniques to volcanic rocks in parts of the western conterminous United States and adjacent Canada has shown that many floras once thought to be of Miocene age are of Eocene age (Axelrod, 1966). These floras occur in isolated depositional basins from British Columbia south into northeastern Washington, Idaho, western Montana, and northern Nevada—a region that was apparently a significant upland during at least part of the Paleogene.

Our knowledge of Western North American Eocene floras and vegetation has been generally based on lowland assemblages from coastal or near-coastal areas (Potbury, 1935; Sanborn, 1935; MacGinitie, 1941; Wolfe, 1968, 1977). We know little of the Eocene upland assemblages; indeed, only two Eocene upland assemblages, the late Eocene Ruby flora (Becker, 1961) and the late Eocene Copper Basin flora (Axelrod, 1966), have been described. Although some species from other upland Eocene floras have been described and tentative floral lists published, these floras have generally been neglected.

Of particular interest are two upland floras that have been radiometrically dated as middle Eocene: the Princeton flora and the Republic flora. The Princeton flora of southern British Columbia is based on a largely undescribed impression flora and a petrifaction flora that has received some attention. The majority of Eocene plant taxa in Western North America are, however, known from impressions, and previous concepts of floristics, evolution, and biostratigraphy are largely based on the impression floras. The second known early middle Eocene impression flora comes from rocks in and near the town of Republic in northeastern Washington.

In this report, we will document many of the angiosperm taxa present in the Republic flora and discuss their biostratigraphic, floristic, evolutionary, and climatic significance. The conifers, although generically determined, are under study by H. E. Schorn, and thus will not be treated in this report. Members of Ulmoideae are under study by Robyn Burnham and are also not dealt with here. Numerous other angiosperm taxa (particularly members of Rosaceae) are represented by fragmentary material; although further collections will undoubtedly produce material sufficient for systematic treatment of these taxa, as well as adding other genera and species, we think that new additions will not significantly alter the discussions presented here.

The first collection of fossil plants from the rocks exposed in the town of Republic, Wash., was made by Waldemar Lindgren in 1902. Although Lindgren submitted the fossils to F. H. Knowlton, no description of the Republic plants appeared until E. W. Berry's (1929) brief account of a few Republic species. R. W. Brown (1935, 1937, 1939) also treated some of the Republic flora in a series of short reports. In 1965, in conjunction with geologic mapping in the Republic area by R. C. Pearson, Wolfe made collections from two new localities (Resner Canyon and Graphite Creek). Since 1977, Wehr has made extensive collections at the main locality at Republic.

ACKNOWLEDGMENTS

Assisting Wehr were Kirk Johnson and Michael Spitz, as well as many of the local residents, in particular: Elaina and Terry Koepke and Chester ("Sam") and Julie Jenkins and their children. Significant additional material was obtained by Steve and Andy Mannery of Bellevue and Janet and John Nicholas of Issaquah. Guy Anderson has been a source of continual encouragement for Wehr's Republic work.

We wish to acknowledge the considerable assistance of Scott L. Wing. Wing has not only discussed many of the evolutionary problems involved in the study of the Republic flora, but he has also assisted in unraveling some of the taxonomic problems. We have also had many useful discussions with H. D. MacGinitie on problems relating to Eocene plants and interpretations of their paleoclimatic significance.

GEOLOGIC OCCURRENCE

The Paleogene sequence in the Republic region consists of, in ascending order, the O'Brien Creek Formation, Sanpoil Volcanics, and Klondike Mountain Formation (Pearson and Obradovich, 1977). The O'Brien Creek is largely water-laid tuffs and conglomerates, and marks the beginning of Tertiary volcanism in the region. The Sanpoil, which conformably overlies the O'Brien Creek, represents a widespread volcanic unit of flows and breccias that were derived from numerous vents. This period of extensive volcanism is radiometrically dated at about 51-52 m.y. (Pearson and Obradovich, 1977).

A period of erosion followed the eruption of the Sanpoil Volcanics. During this period, extensive faulting resulted in the formation of grabens (Muessig, 1967). The Klondike Mountain Formation represents rocks that were locally deposited into these grabens. The lower part of the Klondike Mountain generally contains lacustrine rocks, and the middle and upper parts contain flows and coarse pyroclastic deposits.

The three localities from which the Republic assemblage was collected are all in the lower part of the Klondike Mountain Formation (Pearson and Obradovich, 1977). In the vicinity of Republic, the basal unit of lake beds was recognized by Muessig (1967) as the Tom Thumb Tuff Member, but Pearson and Obradovich (1977) did not formally distinguish members in the Klondike Mountain in the region northwest of Republic.

The lacustrine rocks that form the lower part of the Klondike Mountain Formation are interpreted to represent sediments deposited in lakes that were formed by damming from gravity slide deposits of pre-Tertiary rocks (Pearson and Obradovich, 1977). The source of the pre-Tertiary rocks was apparently the horst that is located between the Republic and Torada grabens (fig. 1). This would indicate that, at

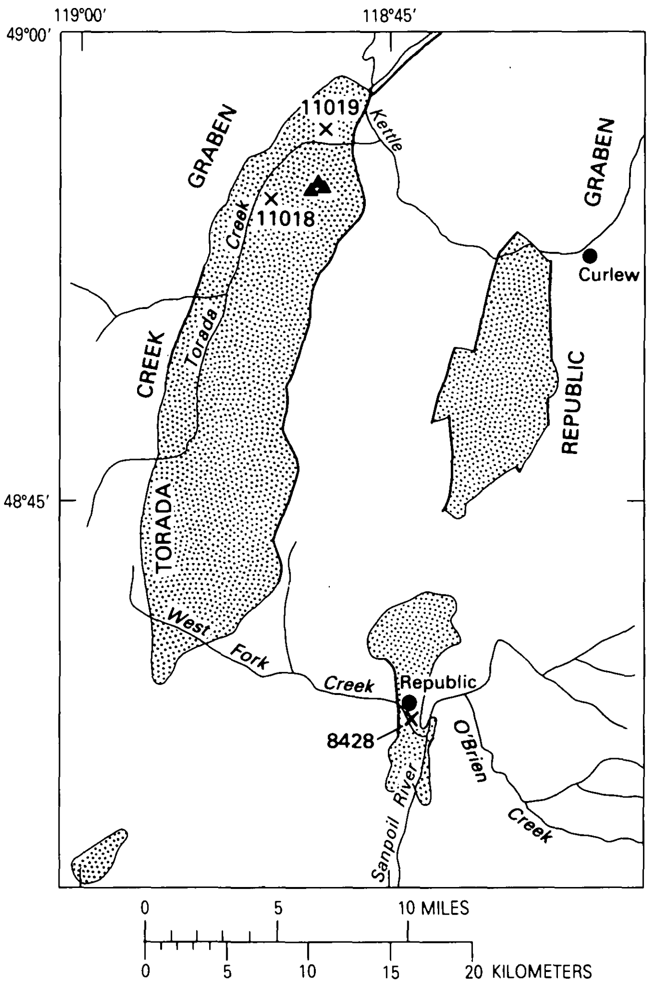

Figure 1. Location of Republic fossil localities. Stippled area denotes distribution of the Klondike Mountain Formation; heavy lines indicate contacts bounded by faults. Triangles represent localities at which radiometric samples were obtained. (Modified from Pearson and Obradovich, 1977.) Numbers refer to U.S. Geological Survey Paleobotanical Localities (Washington, D.C., catalog).

least locally, the horst was the site of mountains that had steep slopes. Additional evidence of considerable local relief is that in many areas the lacustrine rocks grade into nonvolcanic breccias and conglomerates.

Radiometric ages from the Klondike Mountain Formation range from 42.3 ± 2.0 to 50.3 ± 1.7 m.y. (Pearson and Obradovich, 1977). The three samples dated are from flows, and all samples came from the same stratigraphic position about 300 m above the plant-bearing unit in the Torada graben. Two of the samples had three analyses each; these analyses produced an average apparent age of 48.1 ± 1.8 m.y. for one sample and 49.4 ± 1.6 m.y. for the second sample. The third sample, on which two analyses were made, produced an average apparent age of 42.4 ± 1.8 m.y. The two older apparent ages are in close agreement and are accepted as the upper age limit for the Republic flora. Because the Sanpoil Volcanics are 51-52 m.y. old and are unconformable beneath the Klondike Mountain, the Republic flora is probably closer in age to 48-49 m.y. than to 51-52 m.y.

The radiometric age of 56 m.y. reported by Axelrod (1966) for the Republic flora is anomalously old. The sample dated, however, came from water-laid tuffs. The apparent age of Axelrod's is even older than that of the underlying Sanpoil Volcanics, and, as suggested by Pearson and Obradovich (1977), the sample dated probably contains contamination from pre-Tertiary rocks.

SYSTEMATIC LIST OF THE REPUBLIC FLORA

- Coniferophyta
  - Coniferae
    - Coniferidae
      - Taxales
        - Taxaceae
          - *Taxus*? sp.
          - Gen. indet.
      - Coniferales
        - Taxodiaceae
          - *Metasequoia occidentalis* (Newberry) Chaney
          - *Sequoia*? sp.
        - Cupressaceae
          - *Chamaecyparis* sp.
          - *Thuja* sp.
        - Pinaceae
          - *Abies milleri* Schorn and Wehr
          - *Picea* sp.
          - *Picea* sp.
          - *Pinus* sp.
          - *Pinus* sp.
          - *Pseudolarix americana* Brown
          - *Tsuga*? sp.
    - Ginkgoidae
      - Ginkgoales
        - Ginkgoaceae
          - *Ginkgo biloba* Linnaeus
- Magnoliophyta
  - Magnoliatae
    - Magnoliidae
      - Magnolianae
        - Laurales
          - Lauraceae
            - *Phoebe* sp.
            - *Sassafras hesperia* Berry
    - Hamamelididae
      - Hamamelidanae
        - Cercidiphyllales
          - Cercidiphyllaceae
            - *Cercidiphyllum obtritum* (Dawson) Wolfe and Wehr
        - Hamamelidales
          - Hamamelidaceae
            - *Langeria magnifica* Wolfe and Wehr
          - Platanaceae
            - *Macginitiea gracilis* (Lesquereux) Wolfe and Wehr
        - Urticales
          - Ulmaceae
            - *Ulmus* sp.
            - new genus aff. *Zelkova* sp.
        - Fagales
          - Fagaceae
            - *Fagopsis undulata* (Knowlton) Wolfe and Wehr
        - Betulales
          - Betulaceae
            - *Alnus parvifolia* (Berry) Wolfe and Wehr
            - *Betula leopoldae* Wolfe and Wehr
        - Myricales
          - Myricaceae
            - *Comptonia columbiana* Dawson
    - Dilleniidae
      - Dillenianae
        - Theales
          - Theaceae
            - *Ternstroemites* sp. "A"
            - *Ternstroemites* sp. "B"
      - Malvanae
        - Malvales
          - Tiliaceae
            - *Tilia johnsoni* Wolfe and Wehr
    - Rosidae
      - Rosanae
        - Saxifragales
          - Iteaceae
            - *Itea* sp.
        - Rosales
          - Rosaceae
            - *Crataegus* sp.
            - *Crataegus* sp.
            - *Crataegus* sp.
            - *Photinia pageae* Wolfe and Wehr

      - *Potentilla* sp.
      - *Prunus* sp.
      - *Prunus* sp.
      - *Prunus* sp.
      - *Sorbus* sp.
      - *Spiraea* sp.
  - Rutanae
    - Juglandales
      - Juglandaceae
        - *Carya*? sp.
        - *Pterocarya* sp.
    - Rutales
      - Anacardiaceae
        - *Rhus malloryi* Wolfe and Wehr
      - Burseraceae
        - *Barghoornia oblongifolia* Wolfe and Wehr
    - Sapindales
      - Aceraceae
        - "*Acer*" *arcticum* Heer
        - *Acer* sp.
      - Sapindaceae
        - *Bohlenia americana* (Brown) Wolfe and Wehr
        - *Koelreuteria arnoldi* Becker
        - gen. indet. (samaras)
  - Aralianae
    - Cornales
      - Davidiaceae
        - *Tsukada davidiifolia* Wolfe and Wehr
      - Cornaceae
        - *Cornus* sp.
  - Celastranae
    - Olacales
      - Olacaceae
        - *Schoepfia republicensis* (La Motte) Wolfe and Wehr
- Asteridae?
  - Lamianae?
    - Verbenales?
      - Verbenaceae?
        - "*Holmskioldia*" *speirii* (Lesquereux) MacGinitie
- Incertae sedis (Hamamelididae?)
    - *Republica hickeyi* Wolfe and Wehr

The above list is not complete. At least ten other dicotyledonous taxa are represented in our collections by fragmentary or poorly preserved material. At least three of these are represented by leaflets that are probably assignable to Rutanae, and one taxon is represented by a samara of apparent sapindaceous affinity (see p. 19). We have also excluded fragmentary sedgelike remains from the list.

Among the generically determined material listed previously, Rosaceae are particularly significant. Except for the *Photinia*, we have decided to defer detailed treatment of this family; this deferral is partly due to our wish to obtain more extensive material and partly due to our opinion that a detailed systematic treatment of the Republic Rosaceae should involve extensive reexamination of members of the family represented in other Eocene upland floras. The apparent modern aspect of the Republic and other Eocene Rosaceae at the generic level may be valid or may be an artifact of the lack of detailed comparative studies of fossil and extant rosaceous foliage.

BIOSTRATIGRAPHIC CONSIDERATIONS

Early workers generally considered the Republic flora to be part of the "Latah flora" and of Miocene age (Berry, 1929). Brown (1937), however, recognized that the Republic was perhaps more similar to the Bridge Creek flora; although then considered to be of early Miocene age, the Bridge Creek flora is now placed in the early Oligocene (Wolfe, 1981). Wolfe and Barghoorn (1960) suggested that the Republic flora was (1) older than the Bridge Creek and (2) correlative with both the Princeton, British Columbia, and Florissant, Colo., floras; although these are both Eocene floras, the Florissant (latest Eocene) is younger than the Princeton (middle Eocene). Axelrod (1966) considered the Republic to be approximately 56 m.y. old on the basis of the apparent age of a water-laid tuff in the Tom Thumb Tuff Member at Republic; if valid, the Republic flora would be of late Paleocene age.

Additional radiometric data indicate that (1) Axelrod's (1966) radiometric sample probably contains contaminants from underlying rocks, and (2) the Tom Thumb Tuff Member, which contains the Republic assemblages, is older than about 48-49 m.y., but younger than 51-52 m.y. The difficulties encountered in prior age assignments of the Republic flora (and similar microthermal assemblages) strictly on the basis of paleobotanical evidence involve three factors. First, the systematic treatments of the component species of these microthermal floras have been poor; the putative occurrence of known Miocene species in these floras has been based on superficial examinations of the material. Detailed morphologic analyses indicate that none of the Republic species is conspecific with a Miocene species. Second, as Axelrod (1966) noted, altitude was generally ignored; an upland assemblage such as the Republic might be significantly different in both vegetational aspect and floristic composition from isochronous lowland assemblages. Third, major temperature fluctuations during the Eocene (Wolfe, 1971, 1978) have also been ignored; two assemblages might be vegetationally and, to some extent, floristically similar but represent different cool intervals. If valid radiometric data on these upland assemblages are lacking, then the ages of these assemblages must be determined from careful systematic analyses of their component species. This report offers significant data on the occurrence of particular taxa and their stratigraphic distribution. Such data will allow us to understand the relative ages of fossil plant assemblages that represent Eocene upland vegetation in Western North America.

The Republic is one of two upland floras that have radiometric ages that place the floras in the early middle Eocene (Wolfe, 1981). The other is the Princeton (fig. 2) in southern British Columbia.

Figure 2. Location of some middle and late Eocene floras.

Underlying the Princeton lake beds are volcanic rocks that have been dated at 51–52 m.y. (Hills and Baadsgaard, 1967), and an ash in the lower third of the lake beds has an apparent age of 50 m.y. (Rouse and Matthews, 1961). Thus the Princeton and Republic floras are approximately coeval.

The following angiosperm taxa occur in both the Princeton and Republic floras:

Sassafras hesperia,
Cercidiphyllum obtritum,
Macginitiea gracilis,
Alnus parvifolia,
Betula leopoldae,
Comptonia columbiana,
Rhus malloryi, and
Tsukada davidiifolia.

The Princeton and Republic occurrences are the youngest known for *Macginitiea gracilis*, and the oldest for *Alnus parvifolia*. The other five species may prove to be indices for the middle Eocene in this region. *Cercidiphyllum obtritum* and *Comptonia columbiana* both occur at Quilchena, British Columbia, *Sassafras hesperia* and *Comptonia columbiana* both occur in the Challis Volcanics at Thunder Mountain, Idaho. *Sassafras hesperia* occurs at Joseph Creek, British Columbia (also with *Alnus parvifolia*).

The Yellowstone Park floras (Knowlton, 1899) are at about the early-middle Eocene boundary (MacGinitie, 1974). The younger assemblage contains *Fagopsis undulata*, which also occurs at Stump Lake, British Columbia. The Yellowstone floras represent warmer (lower altitude) vegetation than the Republic and similar floras, but even so some entities are conspecific. The following upland floras thus appear to be of middle Eocene age (fig. 3):

Republic, Wash.,
Thunder Mountain, Idaho,
Princeton, British Columbia,
Similkameen, British Columbia,
Quilchena, British Columbia,
Stump Lake, British Columbia, and
Joseph Creek, British Columbia.

The Joseph Creek assemblage may be somewhat younger (late middle Eocene) than the Republic. This suggestion is based on the occurrence in the Joseph Creek of *Bohlenia insignis*, which is thought to be descended from the Republic *B. americana*.

Upland floras of late Eocene age are known from the conterminous United States. Axelrod (1966) has described the Copper Basin, Nev., flora and also gave a preliminary generic list of the Bull Run, Nev., flora; both have apparent radiometric ages of about 40 m.y., which is early in the late Eocene.

The Salmon flora of the Challis Volcanics has been partially described (Brown, 1937). Although Axelrod (1966) considered the flora to be middle Eocene, the floral locality is several kilometers, and across a major river valley, from the sample Axelrod had radiometrically dated; the relative stratigraphic relations of the floral and radiometric samples are unknown. The floristic composition of the Salmon assemblage is indicative of a late Eocene age. The Salmon lacks the species that are considered in the preceding to be diagnostic of a middle Eocene age. Significant is the occurrence in the Salmon of *Mahonia* and section *Macrophylla* of *Acer*. The oldest occurrence of *Mahonia* is in mesothermal assemblages of late middle Eocene age (Green River flora); in microthermal assemblages, *Mahonia* first occurs in the late Eocene (Copper Basin). Section *Macrophylla* is otherwise known only in early Oligocene (Bridge Creek) and younger floras, although the Salmon species is clearly distinct from younger species of the section. The Salmon flora is possibly isochronous with the latest Eocene Florissant flora but is of cooler and more mesic aspect than the Florissant.

The age of the Ruby flora (Becker, 1961) has not been firmly determined. The occurrence in the Ruby of *Mahonia* and *Salix* may indicate an age no older than late Eocene, when both genera first appear in microthermal climates. At least two Republic dicotyledonous species occur in the Ruby: *Fagopsis undulata* and *Koelreuteria arnoldi.*

None of the floras of the Clarno Formation of north-central Oregon are very similar to the Republic flora. Although the lowest flora near Mitchell, Oreg., is probably correlative with the Republic, only a few genera (*Pinus*, *Ulmus*, *Rhus*) and species (*Alnus parvifolia*, *Macginitiea gracilis*, "*Holmskioldia*" *speirii*) are common to the two floras. The Mitchell flora contains numerous broadleaved evergreens and represents mesothermal lowland vegetation. Above the Mitchell flora is the West Branch Creek assemblage. This assemblage is overwhelmingly broadleaved evergreen and represents Paratropical Rain forest during the late middle Eocene. Still younger, the early late Eocene John Day Gulch flora (Wolfe, 1972, pl. 14) again has some broadleaved deciduous genera (but no species) in common with the Republic. The youngest Clarno flora, the latest Eocene Iron Mountain assemblage, represents Paratropical Rain forest (see Wolfe, 1971, for physiognomic analyses) and is also floristically dissimilar to the Republic.

Of particular interest is that the Republic flora includes taxa or lineages that in the lowland floras are not known to occur later than the early Eocene. *Macginitiea gracilis* occurs in the Paleocene and through the upper floral zone of the lower Eocene Willwood Formation (Wing, 1981). In the early middle Eocene, this species is apparently replaced by

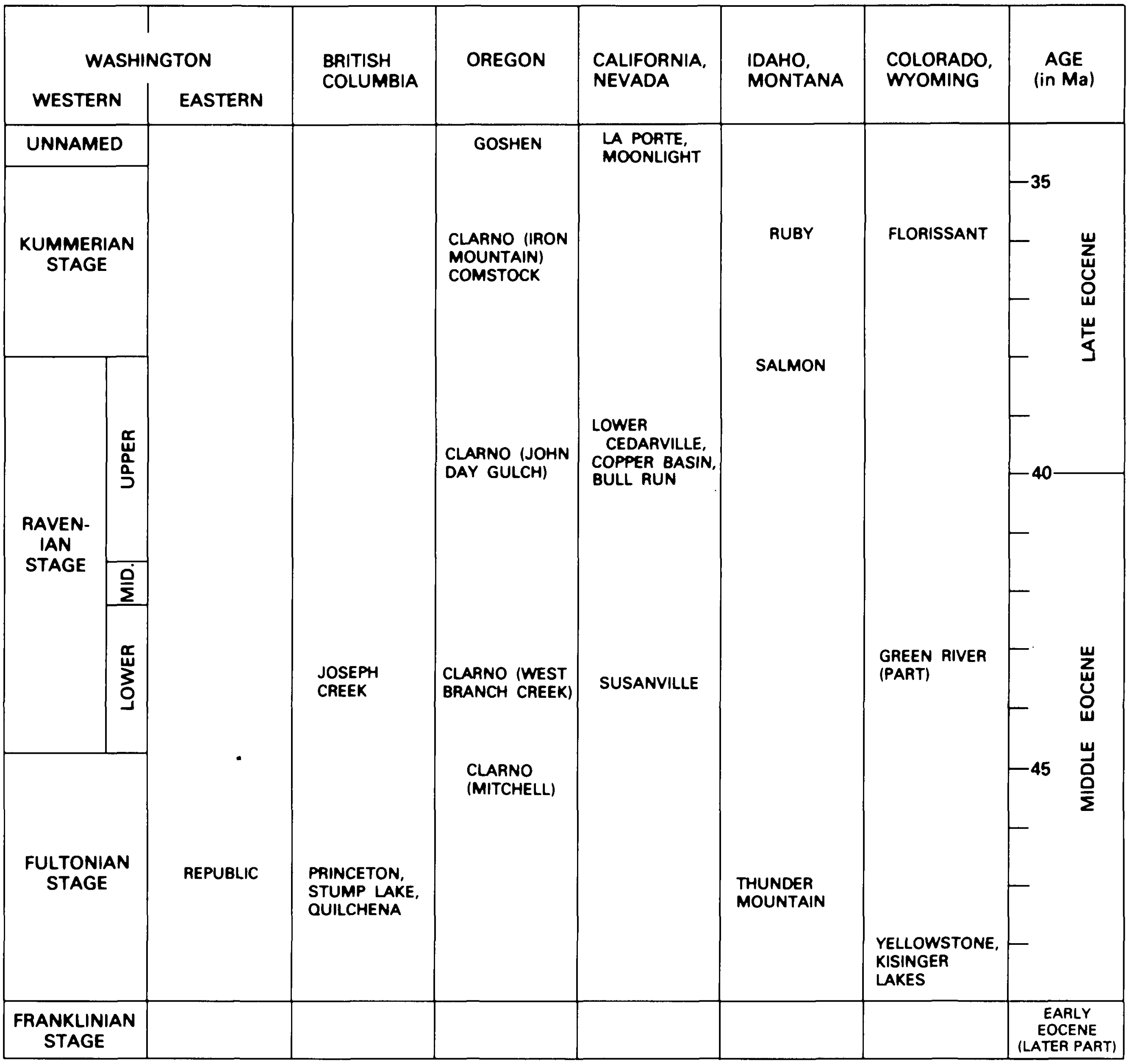

Figure 3. Suggested correlations of some middle and late Eocene floras. Radiometric ages suggested for epochal and subepochal boundaries follow Armentrout (1981).

"*Platanus*" (= *Macginitiea*) *browni* (MacGinitie, 1974) at low altitudes. *Cercidiphyllum genetrix* occurs in the Paleocene and into the upper floral zone of the Willwood (Wing, 1981); the genus is not found in floras such as the Kisinger Lakes (MacGinitie, 1974). In the Republic, *C. obtritum* is thought to be descended from *C. genetrix*. "*Ampelopsis*" *acerifolia* has a known range of Paleocene through the lowest floral zone of the Willwood (Wing, 1981), and the probably congeneric "*Acer*" *arcticum* is elsewhere known only from the early Eocene. The persistence of these lowland taxa in the Republic may indicate that upland areas served as refugia.

FLORISTIC AND EVOLUTIONARY CONSIDERATIONS

The relations of the Republic dicotyledonous flora to present floristic regions are ambiguous. Some Republic genera are now exclusively east Asian: *Cercidiphyllum*, *Pterocarya*, and *Koelreuteria*. At least one, however, is exclusively New World:

Comptonia. Additionally, *Bohlenia* is most closely related to extant New-World genera; *Tsukada* is related to the Old-World *Davidia.* Most extant Republic genera are today both Old and New World. On the subgeneric level, the relations are also ambiguous; *Tilia johnsoni* is most closely related to extant Eurasian species, but *Schoepfia republicensis* is most closely related to extant North American species.

The origins of most Republic dicotyledonous lineages are, at best, obscure. Some lineages were probably present in North American vegetation of moderate to low altitude during the Paleocene and early Eocene; members of this category include: *Cercidiphyllum obtritum, Macginitiea gracilis, Fagopsis undulata, Rhus malloryi, "Acer" arcticum, "Holmskioldia" speirii,* and *Republica hickeyi.* Other members of this category could include *Langeria magnifica, Alnus elliptica,* and *Betula leopoldae,* but the relationships of these taxa to older taxa are unclear.

The Republic dicotyledonous flora includes some taxa that represent the oldest megafossil occurrence of their respective genera and whose antecedents are unknown. Included in this category are: *Sassafras hesperia, Langeria magnifica, Tilia johnsoni, Itea* sp., *Photinia pageae, Barghoornia oblongifolia, Bohlenia americana, Koelreuteria arnoldi, Tsukada davidiifolia,* and *Schoepfia republicensis.* Many of the remaining unstudied Rosaceae probably also should be included in this category. The general mesothermal to megathermal affinities of some Republic genera, as well as the occurrences in the lowland palynological record of *Tilia* and *Anacalosidites,* indicate that the following taxa also probably represent the Paleocene to early Eocene lowland group: *Langeria magnifica, Tilia johnsoni, Barghoornia oblongifolia,* and *Schoepfia republicensis.* The lack of earlier megafossil records for these lineages, however, makes it impossible to determine whether these lineages entered microthermal climates during the middle Eocene or earlier. Also unknown is whether the lowland antecedents in the lineages were sufficiently morphologically similar to be considered congeneric with their descendants.

One significant aspect of the Republic flora is the inclusion of now dominantly megathermal to mesothermal groups. Some members of Lauraceae and Theaceae are today found in microthermal climates, so the inclusion in the Republic of *Phoebe* and *Ternstroemites* is not anomalous. Burseraceae, Sapindaceae, and Olacaceae, however, represent "paleoecological dissonance," to use Woodring's (1960) term; members of these groups today are dominantly megathermal with some mesothermal (but no microthermal) outliers. Both *Barghoornia* (Burseraceae) and *Bohlenia* (Sapindaceae) are extinct, a situation that might be expected for microthermal outliers of now dominantly megathermal groups.

Axelrod (1966, p. 53) considered the Republic and other upland floras to have a modern aspect, from which he suggested that little evolution has occurred in coniferous (or mixed broadleaved and coniferous) forests during the Tertiary. Of the broadleaved genera recognized by Axelrod (1966, p. 45) as occurring in the Republic, a few do have a somewhat modern aspect: *Sassafras* and *Comptonia.* Some other genera listed, however, represent misidentifications; for example, the "*Fagus*" represents the extinct *Fagopsis,* the "*Aralia*" represents the extinct *Macginitiea,* the "*Acer*" represents seeds of an as yet undetermined genus (perhaps Sapindaceae), the "*Dipteronia*" represents the extinct *Bohlenia,* and the "*Zelkova*" represents an extinct genus of Ulmoideae.

The Republic broadleaved taxa exhibit little morphologic similarity to extant taxa. *Cercidiphyllum obtritum* is related to species such as *C. genetrix*; these represent an extinct group that was coeval with a group morphologically similar to the extant *C. japonicum. Comptonia columbiana* is a unique doubly serrate form, unlike many older and younger (including the extant *C. asplenifolia*) species of the genus. *Tilia johnsoni* resembles species of the extant subsection Reticulares that inhabit broadleaved deciduous forests in eastern Asia but does not resemble extant North American species.

Floristic comparisons of the Republic assemblage to the present flora of the Low Montane Coniferous forest of North America (table 1) indicate few similarities. Among the Republic dicotyledons that we have studied, some genera and generic pairs are found in both Eocene and extant floras, but the respective lineages are not phyletically related (table 1). Indeed, of the 25 reliably determined Republic dicotyledonous genera, only 4 now occur in Mixed Coniferous forest in Western North America, and only 10 occurred in this vegetation in Western North America during the Neogene.

A thorough study of the Republic and other Paleogene Rosaceae will probably indicate a somewhat closer relationship between the Republic and younger microthermal floras than indicated in table 1. Indeed it is the numerous diverse rosaceous types in the Republic that give the flora a "modern" aspect. The sources for many Neogene rosaceous lineages may well have been in the Eocene uplands of Western North America, but this suggestion requires further evaluation by detailed systematic treatment of rosaceous fossils.

Table 1. Occurrences of Republic dicotyledonous genera or related genera in extant and Neogene Mixed Coniferous forests

Republic	Extant Mixed Coniferous forest, Western North America	Neogene Mixed Coniferous forest, Western North America
Phoebe	*Umbellularia*	*Laurophyllum*
Sassafras	---	*Sassafras*
Cercidiphyllum	---	*Cercidiphyllum*
Langeria	---	*Fothergilla*
Ulmus	---	*Ulmus*
"Zelkova"	---	*Zelkova*
Fagopsis	*Quercus*	*Fagus*
Alnus	*Alnus*	*Alnus*
Betula	*Betula*	*Betula*
Comptonia	*Myrica*	*Comptonia*
Ternstroemites	---	---
Tilia	---	*Tilia.*
Itea	---	---
Photinia	*Heteromeles*	*Heteromeles*
Pterocarya	---	*Pterocarya*
Rhus	*Toxicodendron*	*Toxicodendron*
Barghoornia	---	---
Acer	*Acer*	*Acer*
Bohlenia	---	---
Koelreuteria	---	---
Cornus	*Cornus*	*Cornus*
Tsukada	---	---
Schoepfia	---	---
Republica	---	---
Holmskioldia	---	---

The basic causative factor in the strong floristic difference between the Eocene and later Low Montane Mixed Coniferous forest is the major temperature shift at the end of the Eocene (Wolfe, 1978). This shift was to a high mean annual range of temperature (the warm-month temperatures were not significantly altered but the cold-month temperatures radically decreased), and led to the regional or total extinction of many woody broadleaved evergreen and broadleaved deciduous species and genera that were intolerant of intense and prolonged winters. The High Montane Mixed Coniferous forest was the predominant coniferous forest during the Oligocene and Miocene at high latitudes and at high altitudes at middle latitudes (for example, floras at Creede, Colo.). Only during the Miocene did areas suitable to Low Montane Mixed Coniferous forest become available as mean annual range of temperature decreased; floras of the later half of the Miocene on the Columbia Plateau (Blue Mountains, Thorn Creek, Trout Creek) and Cascade Range (Hidden Lake) represent this vegetation. The broadleaved deciduous trees and shrubs in the Miocene coniferous forest show little phyletic linkage to those of the Republic flora, although some genera are common to both assemblages. The persistent and important broadleaved deciduous adjuncts to the Miocene coniferous forest in the Pacific Northwest are *Platanus*, *Ulmus*, *Zelkova*, *Alnus*, *Betula*, *Fagus*, *Quercus*, *Populus*, *Salix*, *Carya*, *Pterocarya*, and *Acer*; half these genera are absent in the Republic flora.

Comparison of the Republic flora to late Eocene microthermal floras (Salmon, Copper Basin, Ruby Basin) indicates some continuity of lineages; for example, *Sassafras ashleyi* and *Bohlenia insignis* are probably derived from species represented in the Republic flora, and *Fagopsis undulata*, *Alnus parvifolia*, and *Koelreuteria arnoldi* are represented in both middle and late Eocene floras. On the other hand, lineages represented by the Republic *Langeria*, *Cercidiphyllum obtritum*, *Macginitiea*, *Comptonia columbiana*, and *"Acer" arcticum* are unknown later than the middle Eocene.

Some groups represented in the Republic flora survived into the Oligocene microthermal flora in Western North America. Such groups include *Bohlenia*, *Koelreuteria*, and *"Holmskioldia"*; none of these, however, are known in the Neogene of North America. Notable in the Republic flora is the absence of some groups that are now prominent in microthermal vegetation: for example, Ericaceae, Salicaceae, and Caprifoliaceae. In the instance of Ericaceae and Caprifoliaceae, these families are not conspicuous in microthermal vegetation until the later half of the Miocene. Salicaceae are present in mesothermal middle Eocene vegetation (MacGinitie, 1974), but they are first known in microthermal vegetation in the late Eocene (Wolfe, 1977).

The data strongly indicate that microthermal vegetation in Western North America experienced considerable floristic change during the Tertiary. Various lineages became extinct at various times. Other lineages entered microthermal vegetation at different times during the Tertiary, some lineages for brief periods and other lineages remained for long periods during which diversification occurred. The fact that one species of a genus occurs in an Eocene microthermal assemblage and a second species of the same genus occurs in Miocene or Holocene microthermal vegetation is, by itself, no proof of genetic continuity and an inferred low rate of either evolution or floristic change in microthermal vegetation. An understanding of evolutionary rates and floristic continuity should be based on detailed morphologic analyses.

PALEOCLIMATIC INFERENCES

The present distributions of the extant species most similar to the Republic taxa cannot be used reliably to estimate paleotemperatures. Genera such as *Ginkgo*, *Metasequoia*, *Cercidiphyllum*, *Sassafras*, and *Koelreuteria* are now represented only in dominantly broadleaved forests. Some Republic taxa are members of extinct genera (*Langeria*, one member of Ulmoideae, *Macginitiea*, *Fagopsis*, *Barghoornia*, *Bohlenia*, *Tsukada*, *Republica*) and others (*Ternstroemites*) can only be assigned to form genera. Other Republic genera (*Chamaecyparis*, *Abies*, *Pinus*, *Tsuga*, *Alnus*, *Acer*, *Tilia*) occur in both dominantly broadleaved and dominantly coniferous forests, and at least one genus (*Picea*) is now confined to coniferous forests. Indeed, almost half the known Republic genera are today extinct or are monotypic or bitypic, which makes the present distributions of related taxa of doubtful value.

The Republic assemblage represents Mixed Coniferous forest from two lines of evidence. First, palynological samples contain 70 to 80 percent bisaccate pollen of Pinaceae (Wolfe, unpub. data). Second, the megafossil assemblage contains a diversity of members of Cupressaceae and Pinaceae: *Chamaecyparis*, *Thuja*, *Abies*, *Picea*, *Pinus*, *Pseudolarix*, and *Tsuga*. However, the megafossil samples are at most localities dominated by dicotyledonous leaves, and thus the Republic assemblage could be inferred (for example, Axelrod, 1966) to represent broadleaved deciduous forest with an admixture of conifers. This dominance of dicotyledonous leaves, however, is probably related to most of the fossils having been obtained from fine-grained lacustrine rocks that were deposited a considerable distance from shore. The organs of higher specific gravity (cones and detached needles of conifers) would probably settle out close to the shore, and the organs of lower specific gravity (dicotyledonous leaves and winged seeds of both conifers and dicotyledons) would probably float a considerable distance out into the lake(s). If only winged seeds are considered, the Republic assemblage was decidedly coniferous: the seeds of Pinaceae are much more abundant than are the winged fruits or seeds of dicotyledons (Ulmoideae, Betulaceae, *Acer*, *Bohlenia*, *Koelreuteria*).

The apparent absence of vines in the Republic megafossil assemblage is also significant. Wang (1961) noted the absence or paucity of vines in coniferous forests in comparison to the abundance of climbers in broadleaved forests.

The most abundant dicotyledonous leaves at the main locality at Republic are *Alnus*, *Cercidiphyllum*, *Sassafras*, *Rhus*, Ulmoideae, *Macginitiea*, and *Comptonia*, all of which are represented by more than 20 specimens each. Represented each by 10 to 20 specimens are *Langeria*, "*Holmskioldia*," sapindaceous samaras, and *Bohlenia*. At the Resner Canyon locality (11018), the abundant dicotyledonous leaves are *Cercidiphyllum*, *Macginitiea*, and *Comptonia*. The Graphite Creek locality (11019) has abundant *Fagopsis* but few other dicotyledonous leaves. The Graphite Creek assemblage was obtained from more arenaceous rocks than the main Republic or Resner Canyon assemblages and hence represents deposition closer to shore. Significantly, foliage of *Chamaecyparis* and *Pinus* is at least as abundant as that of dicotyledons at Graphite Creek.

Broadleaved evergreens are a minor element in the Republic assemblage, and include *Phoebe*, *Ternstroemites* spp., *Photinia*, and *Republica*. These may represent small trees or shrubs in the coniferous forest. In contrast, many of the broadleaved deciduous taxa probably were trees of the moist bottomlands or lakeside to streamside habitats. This is particularly true of *Cercidiphyllum*, *Macginitiea*, Ulmoideae, *Fagopsis*, and *Alnus*; members of these groups are typically abundant in many Paleocene and Eocene assemblages, which is indicative of tolerance to moist ground habitats that occur close to depositional sites.

The Republic assemblage thus has the following physiognomic features: (1) a diverse and dominant coniferous element, (2) a subsidiary but diverse element—largely lakeside or streamside—of broadleaved deciduous and deciduous gymnospermous trees, (3) a minor forest element of broadleaved evergreen and broadleaved deciduous small trees and shrubs, and (4) no vines.

The temperature parameters for Mixed Coniferous forest (fig. 4) indicate that the mean annual temperature was <13°C and the mean of the warm month was <20°C (Wolfe, 1979). Further, the broadleaved evergreen element indicates a cold-month mean of >1° to -2°C, and the diversity of the broadleaved element indicates a warm-month mean of >15°C. That is, the Republic assemblage represents Low Montane Mixed Coniferous forest (Wolfe, 1979). In areas of this vegetational type, mean annual ranges of temperature are from 4° to 22°C (or to 19°C if the minimal cold-month mean is 1°C).

Any further refinement of the Republic paleotemperature estimates must be based on consideration of the temperatures estimated for coeval lowland assemblages. The Republic is approximately coeval with the assemblages from the type section of the Fultonian Stage of the Puget Group (Wolfe, 1981). The physiognomy of the assemblages from this stage indicates a mean annual range of temperature of 4° to 5°C (Wolfe, 1978). Assuming approximately the

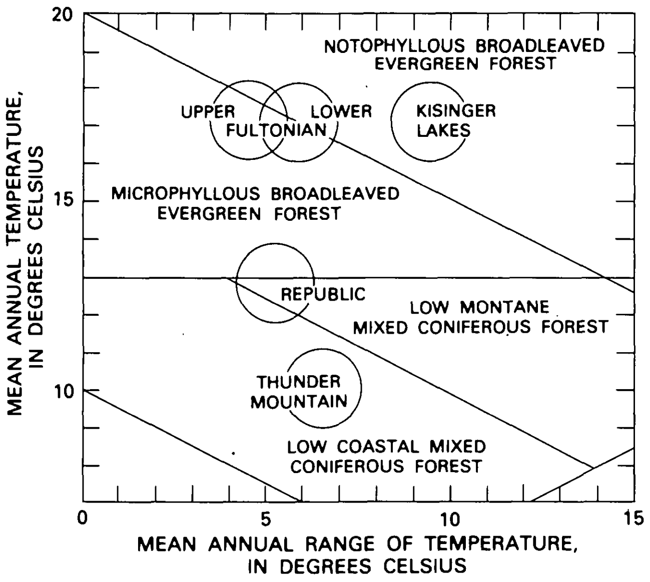

Figure 4. Suggested temperature parameters for some Eocene floras.

same mean annual range for the Republic area during the early middle Eocene appears justified; although the Republic area is about 250 km farther from the coast and about 1° of latitude farther north than the Puget area, mean annual range of temperature tends to decrease with increasing altitude (Axelrod, 1966; Wolfe, 1979, fig. 1). Whereas the first two geographic factors would yield a higher mean annual range for the Republic than for the Puget Fultonian assemblages, the altitudinal difference would tend to negate the geographic factors.

We thus infer that the mean annual range of temperature for the Republic assemblage was most probably 5°C (certainly no more than 6°C). Given the other temperature parameters of Low Montane Mixed Coniferous forest, mean annual temperature was about 12° to 13°C (certainly no lower than 11.5°C). Such temperatures occur today, for example, along the coast of southern Oregon and northern California (Wolfe, 1979, pl. 3), and, judging from data at lower altitudes, probably also occur in the Mixed Coniferous forest of Central America. Such areas rarely receive freezing temperatures.

The difference between the mean annual temperatures for the Republic (12°-13°C) and the coastal Puget Fultonian (17°C; Wolfe, 1978) assemblages allows an approximate estimate of the altitude of the Republic basin of deposition during the early middle Eocene. Assuming a lapse rate (that is, the rate of decrease in mean annual temperature with increasing altitude) of about 0.55°C/100 m, the Republic basin's altitude was between 727 and 909 m (2,375 to 2,970 ft).

In calculating estimated paleoaltitudes, most important is that upland assemblages be properly calibrated in time with lowland assemblages. For example, if the Republic were compared to assemblages such as those of the lower part of the type section of the Ravenian Stage and the Steel's Crossing, a much higher paleoaltitude would be suggested. Early Ravenian assemblages are estimated to have a mean annual temperature about 7° to 8°C higher than Fultonian assemblages in the same area. The coolness of the early middle Eocene in contrast to the warmth of the late middle Eocene is also indicated in the marine record (Wolfe and Poore, 1982). The coolness of the late Ravenian relative to either the early Ravenian or the Kummerian Stage is also indicated in both marine and nonmarine environments.

SYSTEMATICS

We have generally followed the system of terminology presented by Hickey (1973). In some respects we have not found the system entirely satisfactory for descriptive purposes, but the system is the most comprehensive that has been published. We have used "abmedial" in preference to Hickey's "exmedial" (to parallel abaxial and adaxial), and we prefer von Ettingshausen's (1861) "external secondary" vein or branch to Hickey's "secondary vein branch."

The specimens cited have been placed in the following institutions:

UCMP:	University of California Museum of Paleontology, Berkeley, Calif.
USNM:	United States National Museum, Washington, DC, and
UW:	University of Washington, Thomas Burke Memorial Washington State Museum, Seattle, Wash.

Family LAURACEAE
Genus PHOEBE Nees

Phoebe sp.

Plate 1, figures 3–6

Discussion.—In their typically linear shape the Republic leaves are similar to *Cinnamomophyllum kushtakensis* Wolfe. Venation below the fourth-order level is, however, indistinct, and we thus hesitate to assign the Republic leaves to any named species.

Most, if not all, species assigned to *Cinnamomophyllum* may represent *Phoebe.* This suggestion is based on Kostermans' (1961) conclusion that the tri-nerved species of extant *Cinnamomum* actually represent *Phoebe.*

These leaves differ from the unlobed leaves of *Sassafras hesperia* in three regards: in the *Phoebe*, the shape is more linear, the first major lateral veins depart proportionately farther from the base, and these veins typically extend only about half the distance to the apex.

Specimens.—USNM 32676–32679; UCMP 9263, 9264.

Occurrence.—Locality 8428.

Genus SASSAFRAS Trew

Sassafras hesperia Berry

Plate 1, figures 1, 2, 7; Plate 2, figures 1–7

Sassafras hesperia Berry, 1929, p. 259, pl. 59, fig. 2. Brown, 1937 (part), p. 174, pl. 53, fig. 8.

Sassafras selwyni auct. non Dawson. Berry, 1926, p. 114, pl. 14, figs. 1–4.

Discussion.—In the breadth of the lamina, shape of the lobes, and departure of the two major lateral veins close to the base, the leaves from the Eocene on Joseph Creek, British Columbia (Berry, 1926), are similar to our Republic specimens of *Sassafras hesperia.* As Brown (1937) noted, the type specimen of *S. hesperia,* although stated by Berry (1929) to be from the Latah Formation at Spokane, actually came from Republic. Axelrod (1966, p. 45), although calling the Republic flora Eocene, confused the issue of typology; in discussing *S. hesperia,* he (1966, p. 70) erroneously attributed this species to the Oligocene. This error is significant, because one of Axelrod's (1966) theses is that the Eocene montane species of a given genus are typically smaller leaved than Miocene species of the same genus, and he cited as one of his examples the size difference between the Eocene *S. ashleyi* Axelr. and the Miocene *S. columbiana* Chaney and Axelr. The leaves of *S. hesperia* are as large (indeed the lobe of one incomplete specimen is 13.5 cm long) as those of *S. columbiana* and larger than those of *S. ashleyi.*

Axelrod (1966, p. 70) suggested that the northern Eocene *Sassafras* may represent lobed *Lindera.* In lobed *Lindera,* a prominent secondary vein does not extend directly to the sinus; the vein entering the sinus is a branch of a tertiary vein.

The texture of *Sassafras hesperia* is typically very thick—thicker than the Copper Basin *S. ashleyi* or *S. columbiana.* The thick texture may indicate an evergreen habit for *S. hesperia.* Although both extant species of *Sassafras* are deciduous, both deciduous and evergreen habits are found in *Lindera* and *Litsea.* The evergreen habit must occur in the ancestry of *Sassafras,* because such a habit is basic to Lauraceae.

Sassafras hesperia is one of the most common dicotyledonous leaves at Republic. The species also occurs in the Princeton and Joseph Creek assemblages. We reject the occurrence at Florissant (MacGinitie, 1953); the specimen on which the citation is based has external veins that approach the margin more closely than do the external veins of *S. hesperia* in several features.

The late Eocene *Sassafras ashleyi* Axelr. differs from *S. hesperia* in several features. As noted by Axelrod (1966, p. 70), *S. hesperia* has lobes that tend to be shorter and more abruptly acute, although this character intergrades (compare Axelrod's pl. 15, fig. 7 to our pl. 2, fig. 3). More significantly, in *S. hesperia* the secondary veins and their external veins tend to loop farther from the margin, the secondary veins tend to be brochidodromous (in *S. ashleyi* the secondaries thin markedly and are hence eucamptodromous), the tertiary veins are stronger and more percurrent, and the pair of major lateral veins typically depart closer to the base. All these characters overlap somewhat, and we suggest that *S. ashleyi* is closely related and probably descended from *S. hesperia.*

Hypotypes.—USNM 32680; UCMP 9265–9269; UW 31241, 39709, 39710, 39715, 39717, 39720.

Occurrences.—Localities 8428, 11018, 11019.

Family CERCIDIPHYLLACEAE

Genus CERCIDIPHYLLUM Siebold and Zuccarini

Cercidiphyllumobtri obtritum (Dawson) Wolfe and Wehr, n. comb.

Plate 3, figures 1-8

Populus obtrita Dawson, 1890, p. 82, text–fig. 12.

Cercidiphyllum crenatum (Unger) Brown, 1935 (part), p. 575, figs. 1, 6.

Populus daphnogenoides auct. non Ward. Dawson, 1890, p. 83, text–fig. 13.

Supplementary description.—Leaves simple; shape symmetrical; form very wide ovate; apex rounded to obtuse; base typically shallowly cordate to truncate; margin serrate, apical angle acute, serration type A–1 to B–1, sinuses rounded to angular, spacing regular, teeth simple and with small apical glands; petiole normal, at least 4 cm long; primary venation actinodromous (basal to atypically suprabasal), perfect, reticulate, typically two strong and one weak pairs, midrib moderate, straight; first pair of lateral primaries curving smoothly or forking, extending at least three-fourths or more the distance to apex, typically slightly converging with medial secondary veins; second pair of lateral primaries curving smoothly, extending about one-third the distance to the apex, parallel to abmedial branches of first pair of primary veins; typically three pairs of medial secondary veins, three to five pairs of abmedial branches of first pair of primary veins, and two to four pairs of abmedial branches of second pair of primary veins; all lateral primary veins, secondary veins, and abmedial branches diverging at about 45° to their respective primary; angularly eucamptodromous; intersecondaries present; axillary bracing between midrib and first lateral primaries formed by tertiaries that are orthogonal to acute to midrib and orthogonal to laterals, and that form abmedially oriented chevrons; other intercostal tertiaries orthogonal, widely and irregularly spaced, forming a coarse reticulum; quaternaries orthogonal, forming a reticulum of three to five areas per tertiary area; quinternaries forming a quadrangular to pentagonal reticulum of areoles, about four to five areoles per fourth-order area; veinlets branching two or more times; typically at least two series of complete marginal loops; teeth entered medially to apically by veins of quaternary rank, flanked by weak accessory veins converging at apex of tooth (chloranthoid type).

Discussion.—One of the most diagnostic features of *Cercidiphyllum obtritum* is the broad base that is typically truncate to shallowly cordate. The majority of the leaves have this type of base, are small, and have small teeth (pl. 3, figs. 5–8). A few specimens (pl. 3, figs. 1, 2) are larger and have suprabasal primaries and large teeth; these specimens may represent shade leaves. In the Paleocene to early Eocene *C. genetrix* (Newb.) Hick., the margin and venation are similar but the base is typically acute and the leaf shape flabellate (Hickey, 1977).

Cercidiphyllum genetrix and *C. obtritum* are morphologically similar and constitute a distinct (and extinct) type within the genus. Some undescribed leaves of *Cercidiphyllum* from the Fort Union Formation and from early Eocene rocks on the Similkameen River (USGS loc. 11015) have the strongly cordate base, orbicular shape, and crenate teeth similar to Oligocene and younger *C. crenatum* (Ung.) R.W. Br. and the extant *C. japonicum* S. and Z. Thus *C. obtritum* is unlikely to be ancestral to any of the Oligocene and younger species of *Cercidiphyllum*.

Hypotypes.—UCMP 9270–9272 USNM 32681, 32682; UW 31242–31244, 31285, 39711.

Occurrences.—Localities 8428, 11018.

Family HAMAMELIDACEAE

Genus LANGERIA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves simple; venation pinnate; secondary veins mixed camptodromous to typically craspedodromous, broadly curving apically; intersecondary veins absent; tertiary veins orthogonal, percurrent, alternate or opposite; axillary tertiary veins parallel to other intercostal tertiaries on one side of midrib but tending to be aparallel on other side (that is, axillary tertiaries are on second side formed by the merging of a tertiary vein orthogonal to midrib and a tertiary vein orthogonal to secondary); quaternaries branching, forming a coarse, irregular reticulum; in basal half of lamina, departure angle of secondary veins decreasing so that veins diverge from one another; in apical half of lamina, departure angle of secondary veins approximately constant; teeth numerous, compound, serration type C–3; sinuses rounded; teeth entered centrally by external secondary branches or by branches from loops of external secondary branches.

Type species.—*Langeria magnifica* Wolfe and Wehr.

Derivation of name.—Susanne K. Langer was a major exponent and teacher of symbolic logic, which has had a major influence on the organization and analyses of scientific data. Both of us acknowledge the impact Mrs. Langer's writings have had on our work.

Langeria magnifica Wolfe and Wehr, n. sp.

Plate 4, figures 1–4; plate 5, figures 1–4

Description.—Leaves simple; shape elliptic to typically ovate, apex acute, base shallowly cordate to acute; petiole normal, as much as 6 cm long; margin serrate, apical angle acute, serration type C–2 or C–3, sinuses rounded, spacing regular, teeth simple to typically compound; venation pinnate; secondary veins 10 to 12 pairs, departing basally at high (70° to 90°) angles that diminish apically, broadly curved, typically craspedodromous; third through fifth pairs of secondary veins diverging from one another, with three to six conspicuous, craspedodromous external secondary branches; intersecondary veins uncommon; tertiary veins spaced at about 0.3 to 0.5 cm, orthogonal, straight to slightly sinuous, simple or forked, percurrent; quaternary veins orthogonal, forming a coarse branched reticulum; quinternary veins orthogonal, forming a weakly branched reticulum of areoles; veinlets branching two to three times.

Discussion.—The characters found in *Langeria* are characteristic of Hamamelidoideae, although not all characters are found in one extant genus. The high angle of divergence of the basal pairs of secondaries, the divergence from one another of the next two or three pairs (and the corresponding large number of external secondaries), and the curved sinuses are all indicative of the subfamilial assignment.

The specimen illustrated as plate 5, figures 2, 3, is probably an immature leaf. This is indicated by the close spacing of the tertiary veins and the small teeth.

Langeria is one of the many Hamamelidoideae that occur in the Paleocene and Eocene of Western North America. "*Fortunearia*" *weedi* (Knowlt.) Wolfe is similar to *L. magnifica* and may prove to be congeneric; "*F.*" *weedi* has fewer secondary veins, fewer external secondary veins (and thus teeth), and the teeth are typically coarser than *L. magnifica*.

Holotype.—UW 39713; UCMP 9273 (counterpart).

Paratypes.—UCMP 9274–9276; UW 31246, 31286–31289.

Occurrence.—Locality 8428.

Family PLATANACEAE

Genus MACGINITIEA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves simple; venation basally palinactinodromous; major veins extending to margin, each entering a lobe; some intersecondary veins; secondary veins numerous, smoothly and shallowly curving, but abruptly curving near margin and brochidodromous; tertiary veins percurrent, branched once or unbranched; quaternary veins forming a pronounced coarse reticulum; one series of marginal loops; axillary bracing between primary veins formed by secondary veins that depart from primaries at acute angles, curve, and merge to form a series of chevrons that point toward sinus; lamina lobed, sinuses between lobes curved.

Type species.—Macginitiea gracilis (Lesquereux) Wolfe and Wehr [*Liquidambar gracile*].

Discussion.—The placement of this type of leaf in Platanaceae was first clearly demonstrated by MacGinitie (1941), who referred them to *Platanophyllum*. The type species of *Platanophyllum*, *P. virginiensis* Font., is from the Albian of Virginia; although *P. virginiensis* is palinactinodromous, its clear relationship in Platanaceae has yet to be demonstrated. We prefer, therefore, to propose a new name for the Paleocene and Eocene leaves previously referred to *Platanophyllum*.

Both Brown (1962) and Hickey (1977) considered the "*Platanophyllum*" type of foliage to be referable to *Platanus*. The most obvious distinction between *Platanus* and *Macginitiea* is in the axillary bracing between the primary veins: in *Macginitiea* the bracing forms a series of conspicuous chevrons that point towards the sinuses, whereas in *Platanus* the bracing is formed (as in most actinodromous leaves) by veins that are orthogonal to their respective primaries, are straight, and join angularly. Further, the lamina on one side of the midrib is a virtual mirror image of the other side in *Macginitiea*, whereas the size of the lobes may vary greatly from one side to another in *Platanus*.

Most species of *Macginitiea* have lobes that lack teeth. If teeth are present, they are typically few and of uniform size. In *Platanus*, teeth are typically present and are of varying size on a given leaf. Whereas leaves of *Platanus* are typically suprabasally palinactinodromous, *Macginitiea* is basally palinactinodromous.

The leaves of *Macginitiea*, in comparison to *Platanus*, are regular in shape, margin, and venation. This could be interpreted as indicating a higher degree of specialization in *Macginitiea* than in *Platanus*.

Derivation of name.—We take great pleasure in naming this genus for Harry D. MacGinitie. His work over a period of 50 years represents a major contribution to the paleobotany and paleoclimatology of the Tertiary of Western North America.

Macginitiea gracilis (Lesquereux) Wolfe and Wehr, n. comb.

Plate 6, figures 1–4

Liquidambar gracile Lesquereux, 1872, p. 287.

Platanus dubia Lesquereux (non Ettingshausen), 1874, p. 406.

Aralia? *gracilis* Lesquereux, 1878, p. 236, pl. 39, fig. 1.

Aralia notata Lesquereux, 1878, p. 237, pl. 39, figs. 2–4.

Aralia republicensis Brown, 1937, p. 183, pl. 55, fig. 7.

Platanus appendiculata auct. non Lesquereux. Berry, 1929, p. 249, pl. 52, fig. 5.

Aralia whitneyi auct. non Lesquereux. Berry, 1929, p. 260.

Platanus nobilis auct. non Newberry. Brown, 1962 (part), p. 64, pl. 29, fig. 6. Hickey, 1977, p. 131, pl. 31.

Discussion.—As here conceived, the epithet *gracilis* is applied to leaves that (1) are typically five lobed, (2) have no teeth, (3) have broad lobes, and (4) have the veins that form the axillary chevrons approximately parallel to the brochidodromous secondary veins in the lobes. The types of *Platanus nobilis* are three lobed, are toothed, and the veins forming the axillary chevrons are typically not parallel to the brochidodromous secondary veins; these fossils represent a distinct species. The types of *Aralia digitata* are toothed and narrowly lobed; these represent a distinct species allied to the Eocene "*Platanus*" (or, more validly, *Macginitiea*) *browni* and "*Platanus*" *wyomingensis*.

In an unpublished manuscript, Brown transferred "*Aralia*" *republicensis* to *Platanus*. Brown (1937), however, did not furnish a description for "*A.*" *republicensis*, and hence this epithet has not been validly published. Arnold (1955) listed "*Aralia republicensis*" for the Princeton flora.

Hypotypes.—UCMP 9277-9279; UW 39714, 31247, 31290.

Occurrences.—Localities 8428, 11018.

Family FAGACEAE
Genus FAGOPSIS Hollick

Fagopsis undulata (Knowlton) Wolfe and Wehr, n. comb.

Plate 7, figures 1–9

Fagus undulata Knowlton, 1899, p. 700, pl. 85, figs. 4, 5.

Carpinus grandis auct. non Unger. Dawson, 1890, p. 87, text-fig. 21.

Fagopsis longifolia auct. non (Lesquereux) Hollick. Becker, 1961 (part), p. 59, pl. 16, figs. 9, 12.

Discussion.—The rounded teeth and shallow sinuses distinguish this species from the sharper and more deeply incised teeth of the late Eocene *Fagopsis longifolia* (Lesq.) Holl. *Fagopsis undulata* also can have more numerous secondary veins and teeth than *F. longifolia*; in this character, *F. undulata* is more similar to the Paleocene *F. groenlandica* (Heer) Wolfe.

One character of leaves of all three known species of *Fagopsis* that ally them to Fagaceae rather than Betulaceae is that the serration type is Hickey's (1973) A–1 and that the teeth are simple. In Betulaceae, the typical serration type is D–1 to D–4 (some are A–3 or A–4) and each lamina invariably has some compound teeth. Also of major significance is the branch of the secondary vein that departs near the margin and ascends apically into the adjacent tooth (pl. 7, fig. 1); this architecture is of wide occurrence in extant Fagaceae.

The two specimens from the main Republic locality are both larger than the Resner Canyon and Graphite Creek specimens and have about 15 pairs of secondary veins in comparison to the 10 to 13 pairs on the specimens from the other localities. We do not, however, consider these differences to be of systematic value.

At both the Resner Canyon and Graphite Creek localities, leaves of *Fagopsis undulata* are accompanied by pistillate cones that are similar to those of *F. longifolia* described by MacGinitie (1953) from Florissant. The Republic cones, however, are not as large as those of *F. longifolia.*

Lectotype.—Specimen illustrated as pl. 85, fig. 5, by Knowlton (1899).

Hypotypes.—UCMP 9280-9282; USNM 32683-32690; UW 39716.

Occurrences.—Localities 8428, 11018, 11019.

Family BETULACEAE
Genus ALNUS L.

Alnus parvifolia (Berry) Wolfe and Wehr, n. comb.

Plate 8, figures 1–8

Betula parvifolia Berry, 1926, p. 103, pl. 15, figs. 1–3.

Alnus elliptica Berry, 1929, p. 244, pl. 50, figs. 8–10.

Alnus cuprovallis Axelrod, 1966, p. 66, pl. 11, figs. 1–13. Wolfe, 1977, p. 58, p. 26, fig. 7; text–fig. 11.

Carpinus grandis auct. non Unger. Berry, 1926 (part), p. 104, pl. 15, figs. 4, 5.

Alnus corralina auct. non Lesquereux. Brown, 1937 (part), p. 170, pl. 48, fig. 3.

Discussion.—The abundant material from Republic indicates that the base of this *Alnus* ranges from shallowly cordate to acute; such variation is typical in many extant species of *Alnus.* In the acute-based specimens, the teeth are typically small, as in Berry's (1926) Joseph Creek specimens assigned by him to *Carpinus grandis* (?).

As noted by Wolfe (1977), this species belongs to the same group as the extant *Alnus incana*, of subgenus *Alnus*, although *A. parvifolia* has only a slight tendency for the teeth to be grouped. Axelrod (1966) compared *A. cuprovallis* to the extant *A. crispa* (Alt.) Pursh of subgenus *Alnobetula*, but *A. parvifolia* has none of the characters diagnostic of that group; *Alnobetula* does occur, however, in some Alaskan Eocene assemblages.

The associated cones (pl. 8, fig. 5) are tentatively assigned to *Alnus parvifolia.* The cones are the only type of *Alnus* cone and *A. parvifolia* is the only type of *Alnus* leaf at Republic.

Hypotypes.—UCMP 9283-9285; USNM 32691, 32692; UW 31253-31255, 31291,39721.

Occurrence.—Locality 8428.

Genus BETULA L.

Betula leopoldae Wolfe and Wehr, n. sp.

Plate 9, figures 8–11

Description.—Leaves simple; shape narrowly ovate, apex acuminate, base obtuse; margin serrate, apical angle acute, serration types typcially D–2 to D–4, sinuses angular, spacing regular, teeth compound with typically two subsidiary teeth on basal flank of major teeth; petiole normal, 0.8 cm long; venation pinnate; about 12 pairs of secondary veins, departing at a 45° angle, straight, craspedodromous, entering teeth centrally in basal and medial parts of lamina and entering teeth basally in apical part then bending sharply toward apex; typically two external secondary veins per secondary, craspedodromous; intersecondary veins absent; tertiary veins spaced about 0.8 cm apart, percurrent, opposite or alternate, slightly convex; quaternaries forming an irregularly polygonal mesh; quinternaries forming irregularly polygonal areoles; veinlets stout, branching once or twice.

Discussion.—The sharp apical bend of the apical secondary veins on entering the teeth (pl. 9, fig. 8) is indicative of *Betula*, *Carpinus*, or *Ostrya*. Both *Carpinus* and *Ostrya* have typically large, quadrangular areoles, most of which have no veinlets. In extant *Betula*, as in the fossils (pl. 9, fig. 10), the areoles are small and have branching veinlets.

No other described *Betula* leaves from the Tertiary of Western North America are highly similar to *B. leopoldae*. The other described species are either more finely serrate than *B. leopoldae* or they have fewer secondary veins (as in the *B. papyrifera* complex). Leaves of *B. leopoldae* are present in the U.S. Geological Survey's collection from Princeton, British Columbia.

Holotype.—UW 39722; UCMP 9286 (counterpart).

Paratype.—UW 31256.

Occurrence.—Locality 8428.

Family MYRICACEAE
Genus COMPTONIA L'Heritier

Comptonia columbiana Dawson

Plate 9, figures 1–3

Comptonia columbiana Dawson, 1890, p. 81, text–fig. 10.

Comptonia hesperia auct. non Berry. Brown, 1937 (part), p. 169, pl. 46, figs. 12–14.

Myrica (Comptonia) cuspidata auct. non Lesquereux. Dawson, 1890, p. 80, text–fig. 9.

Discussion.—The Republic specimens are doubly serrate and compare well to Dawson's (1890) illustration of *Comptonia columbiana*. The Republic material also represents a simple leaf, and thus cannot represent the leaflet of the somewhat similar *Lyonothamnus*. The doubly serrate foliage of *C. columbiana* is unique in the genus; all other described fossil species and the one extant species are singly serrate.

Hypotypes.—UCMP 9287–9289; USNM 32693, 32694; UW 39723.

Occurrences.—Localities 8428, 11018, 11019.

Family THEACEAE
Genus TERNSTROEMITES Berry

Ternstroemites sp. "A"

Plate 9, figures 4–7

Discussion.—Two narrowly elliptic leaves have small closely appressed teeth that are furnished with small triangular glands (probably setae). The intercostal areas are of irregular size and shape, the secondary veins are festooned brochidodromous, and the tertiary veins are irregularly spaced but tend to be percurrent. Tertiary veins that have a similar pattern occur, for example, in *Gordonia*; as well, *Gordonia* tends to have curved secondary veins, which closely approach the margin before looping (as in the fossils). These fossil leaves thus represent a theaceous taxon, but the limited material and its lack of preservation of the higher vein orders does not warrant naming.

Specimens.—UCMP 9290; UW 31259, 39724.

Occurrence.—Locality 8428.

Ternstroemites sp. "B"

Plate 10, figures 1–4, 6

Discussion.—These leaves share two significant sets of characters with the preceding taxon: low rank secondary venation that is festooned brochidodromous and the small, closely appressed teeth that have apparent setae. Thus, these leaves also represent Theaceae, but they differ from *Ternstroemites* "A" in their elliptic shape, higher angle of departure of the secondary veins, and lower rank (more irregular) tertiary vein system. The irregularity of the tertiary vein system and the distance from the margin at which the secondary veins loop is most similar to *Cleyera*, a small genus that is dominantly New World but with one species in Asia. As with *T.* "A", we consider the current material to be insufficient for naming.

Specimens.—UW 31292, 31293, 39719.

Occurrence.—Locality 8428.

Family TILIACEAE
Genus TILIA L.

Tilia johnsoni Wolfe and Wehr, n. sp.

Plate 10, figures 5, 7

Description.—Leaf simple; venation perfectly and basally actinodromous, three pairs of lateral primary veins; lamina symmetrical, shape orbiculate, apex acuminate, base cordate; margin serrate to dentate, serration type A–3 to C–3, sinuses curved to broadly angular, spacing regular, first pair of lateral primary veins parallel to medial secondary veins, broadly curving, giving off three external craspedodromous branches that are parallel to next pair of lateral primaries; four pairs of medial secondary veins, shallowly curving, craspedodromous, forking and giving off one or two external branches that may also fork; tertiary veins orthogonal, closely and uniformly spaced, most percurrent; quaternary venation orthogonal, forming a quadrangular to pentagonal reticulum; higher order venation obscure.

Discussion.—The few pairs of medial secondary veins and the equidistant extension towards the apex of both the first lateral primary veins are indicative of section *Anastraea* and particularly subsection Reticulares. This section was considered to have the least specialized floral morphology in *Tilia* (Engler, 1909).

Tilia johnsoni represents the oldest valid megafossil record of the genus. Pollen referable to *Tilia* first appears near the Paleocene-Eocene boundary (E. B. Leopold, oral commun., 1982), and Reid and Chandler (1933) have described a fruit from the early Eocene as *Eotilia*. The first pollen of *Tilia* is in assemblages that are mesothermal, and *Eotilia* is in a megathermal assemblage. Indeed Tiliaceae are, except for *Tilia*, exclusively megathermal to mesothermal, and presumably *Tilia*, which is both mesothermal and microthermal, evolved from some mesothermal genus. What is of interest is that in less than 10 million years after *Tilia* first appeared in the palynological record, well-defined foliage is found in a microthermal assemblage.

We take pleasure in naming this species for Kirk Johnson, who has assisted in collecting much of the new material from Republic.

Holotype.—UW 39712; UCMP 9291 (counterpart).

Occurrence.—Locality 8428.

Family ITEACEAE
Genus ITEA L.

Itea sp.

Plate 11, figures 1–3

Discussion.—Three fragments—all representing foliar apices—have the characters diagnostic of *Itea*: (1) strongly eucamptodromous, strongly curving secondary veins, (2) somewhat sinuous tertiary veins that are all approximately perpendicular to the midrib, and (3) a finely serrate margin that has teeth that are uniformly spaced and markedly point apically.

Today *Itea* is an east Asian/east American vicariant, with about 10 species in east Asia and 1 in the Eastern United States. The genus is primarily mesothermal, although a few species extend into microthermal climates. This is the oldest known, as well as the first American, record of the genus as a fossil.

Specimens.—UW 31262, 39725.

Occurrence.—Locality 8428.

Family ROSACEAE
Genus PHOTINIA Lindley

Photinia pageae Wolfe and Wehr, n. sp.

Plate 11, figures 4–6

Description.—Leaf simple; lamina symmetrical, shape narrowly ovate to elliptic, apex acuminate, base symmetrically decurrent to cuneate; margin serrate, apical angle acute, serration type B–1 to B–2, sinuses narrowly rounded to acute, spacing regular; teeth of very unequal size but not compound, about two per secondary vein; petiole normal; venation pinnate; secondary veins brochidodromous departing at an angle of about 70°, straight to somewhat zigzag, some aparallel, forming intercostal areas of somewhat differing size and shape, looping angularly close to margin, giving off craspedodromous external branches that enter teeth centrally; intersecondary veins common and conspicuous; tertiary veins at acute angles to secondary veins, forming a random reticulation; quaternary veins randomly reticulate; quinternary veins randomly reticulate, forming areoles; veinlets irregularly ramified.

Discussion.—The acutely angled and irregularly and conspicuously random third-order reticulum, irregular intercostal areas, and serration type place these leaves in *Photinia* (s.s., excluding *Heteromeles).*

Photinia pageae is both the oldest and first American occurrence of the genus as a fossil. *Photinia* is typically mesothermal and is primarily in the Notophyllous Broadleaved Evergreen forest in both Central America and eastern Asia, although some species extend into microthermal climates in Asia.

We take pleasure in naming this species in recognition of Virginia M. Page's contributions to Cretaceous and Tertiary xylotomy.

Holotype.—UW 39188.

Paratypes.—UCMP 9292; UW 39195.

Occurrence.—Locality 8428.

Family ANACARDIACEAE
Genus RHUS L.

Rhus malloryi Wolfe and Wehr, n. sp.

Plate 12, figures 1, 2, 6, 7, 12

Dipteronia americana Brown, 1935 (part, nontypic), p. 580, pl. 67, fig. 12.

Description.—Leaflets symmetrical but base asymmetrical; shape narrowly elliptic to lanceolate, apex acute, base acute; margin serrate, apical angle acute, serration type A–1; sinuses acute, spacing regular; teeth simple, one per secondary vein; short petiolule; venation pinnate; secondary veins gradually curved, craspedodromous to semicraspedodromous, entering teeth centrally or ending in sinuses, some bifurcating and sending the apical branch to next most apical tooth; some weak intersecondary veins; external secondary branches forming loops that thin abmedially; tertiary veins orthogonal to acute, tending to thin midway between secondary veins; higher orders of venation indistinct.

Discussion.—The tendency to thinning of the tertiary veins and the loops of the external secondary veins is diagnostic of Anacardiaceae. The serrate margin and variable behavior of the secondary veins are, moreover, indicative of *Rhus* (s.s.).

The early Eocene *Rhus mixta* (Lesq.) MacG. is more linear than *R. malloryi*, has stronger secondary veins, and has longer and more conspicuous intersecondary veins.

We take pleasure in naming this species for V. S. Mallory, who, as chairman of the Geology and Paleontology Division of the Burke Memorial Museum, has encouraged the present study.

Holotype.—UW 39718.

Paratypes.—UCMP 9293, 9294; UW 31270, 31294, 31295.

Occurrence.—Locality 8428.

Family BURSERACEAE

Genus BARGHOORNIA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves presumed pinnate; leaflets asymmetrical; venation pinnate; margin serrate, teeth irregularly spaced, simple; secondary veins pronouncedly and sharply curving near margin, semicraspedodromous; tertiary venation forming a coarse, irregular reticulum; sinuses supplied with veins originating on abmedial sides of secondary vein loops and from craspedodromous external secondary veins.

Type species.—*Barghoornia oblongifolia* Wolfe and Wehr.

Discussion.—See under *B. oblongifolia.*

Derivation of name.—In recognition of his multitudinous contributions to paleobotany—Precambrian through Quaternary—we name this genus for the late Elso S. Barghoorn.

Barghoornia oblongifolia Wolfe and Wehr, n. sp.

Plate 12, figures 3-5

Description.—Leaflets asymmetrical; shape narrow oblong, apex acute, base acute; long-petiolulate; margin coarsely serrate, apical angle acute, serration type A–4 to D–4, sinuses angular, spacing irregular; about two teeth per secondary vein, simple; petiolule about 7 mm long; venation pinnate; eight pairs of secondary veins, lowest pair departing at 70°, other pairs at 80°, straight, looping sharply near margin to make an almost quadrangular intercostal area, semicraspedodromous; external secondary branches entering teeth typically centrally but some apically; tertiary veins orthogonal, few forming a large irregularly polygonal reticulum; quaternary veins orthogonal, forming a quadrangular to pentagonal reticulum.

Discussion.—The single specimen (and its counterpart) has pronounced asymmetry, both at the base and in the medial part of the lamina; this is a strong indication of a leaflet of a pinnately compound leaf. The strong veins terminating in the sinuses, as well as the probable pinnately compound organization, are indicative of Rosidae.

Among pinnately compound Rosidae, the Republic leaflet is unique. Particularly peculiar is the consistently semicraspedodromous venation. In toothed, pinnately compound Rosidae, semicraspedodromy is found in only one family, Burseraceae; indeed, five genera of Burseraceae have semicraspedodromous venation consistently present in some species. The tertiary venation of the fossil, however, is most similar to that of the craspedodromous *Bursera*, which has broad A–1 (almost crenate) serrations. Some Burseraceae also have long petiolules. All major characters of *Barghoornia* occur in Burseraceae, and we thus consider the familial assignment secure.

Holotype.—USNM 32695A, B.

Occurrence.—Locality 8428.

Family ACERACEAE

Genus ACER L.

"Acer" arcticum Heer

Plate 12, figures 11, 16

Acer arcticum Heer, 1876 (part), p. 86, pl. 22, figs. 1, 3–7; pl. 23, figs. 1–9; pl. 24, figs. 1–3.

Discussion.—The Republic leaves have the shallow lobes and rounded teeth that characterize Heer's material from the early Eocene of Spitzbergen. The validity of the generic reference, however, is problematic.

Almost all Eocene leaves of *Acer* have axillary bracing of the type shown in plate 12, figure 11: the tertiary veins join a vein midway between the primary and secondary veins and this vein thins as it approaches the axil. Such venation is not found in any extant species of *Acer* but is found in other families of Sapindales and particularly in Rutales. This type of axillary bracing in Eocene *Acer* could thus be considered to represent the retention of a primitive character.

The rounded teeth of "*Acer*" *arcticum* are not found in any extant species of *Acer*, and we are thus not totally convinced that these leaves represent *Acer*. That these leaves have a large number of characters in common with *Acer* is also certain. A strong resemblance is also evident between "*A*" *arcticum* and "*Ampelopsis*" *acerifolia* Newb. from the Paleocene and early Eocene (Hickey, 1977); other than overall architecture, the similarities include the rounded (some are emarginate in "*Ampelopsis*" *acerifolia*) teeth and tendency for the tertiary veins to form a V-shaped pattern pointing apically.

No samaras of valid *Acer* have been found with "*Ampelopsis*" *acerifolia*; commonly, however, these leaves occur with a samara of apparent sapindaceous affinity (Wing, 1981). These samaras were attached the opposite of *Acer*: the strongly veined "back" of the samara was medial rather than marginal as in *Acer*. These apparent sapindaceous seeds have not been found attached to one another, so it is unknown whether they were borne in threes as in Sapindaceae. The same type of sapindaceous samara also occurs with the leaves of "*Acer*" *arcticum* at Republic. If the sapindaceous samaras (and not the *Acer* samaras reported below) are the seeds of "*Acer*" *arcticum* then some interpretations are as follows:

1. "*Acer*" *arcticum* and "*Ampelopsis*" *acerifolia* represent an extinct genus of Sapindaceae. Arguing against this interpretation is that actinodromy does not occur in extant Sapindaceae.
2. "*Acer*" *arcticum* and "*Ampelopsis*" *acerifolia* represent an extinct genus and family of Sapindales. This interpretation would be particularly attractive if the seeds were borne in threes as in Sapindaceae; this extinct family would be a sister group of Aceraceae.
3. "*Acer*" *arcticum* and "*Ampelopsis*" *acerifolia* represent an extinct genus of Aceraceae. This interpretation would be supported if the seeds were borne in twos.

We think that "*Acer*" *arcticum* and "*Ampelopsis*" *acerifolia* are closely related. The fact that no *Acer* samaras have been found associated with "*Ampelopsis*" *acerifolia* strongly argues against either *Ampelopsis acerifolia* or "*Acer*" *arcticum* being members of *Acer*. We thus suggest that either interpretation 2 or 3 will prove to be valid.

Hypotypes.—UCMP 9295; UW 39726 (counterpart).

Occurrence.—Locality 8428.

Acer sp.

Plate 12, figures 9, 13–15

Discussion.—These samaras vary in the shape of the wing but all have the same angle between the distal side of the samara and line of dehiscence. The seed itself was inflated. The closest similarities are to seeds of section *Macrantha*.

Specimens.—UCMP 9296, 9297; USNM 32696; UW 31272, 39728, 39191.

Occurrences.—Localities 8428, 11018.

Family SAPINDACEAE

Genus BOHLENIA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves apparently pinnately compound; leaflets with serrate margin, serration type A–1, teeth compound or simple; venation pinnate; secondary veins with uniform angle of departure, alternate pairs of secondary veins craspedodromous, entering teeth centrally; other pairs of secondary veins bifurcating just before reaching sinuses between major teeth, apical branch extending parallel to basal side of lobe immediately apical, basal branch extending parallel to apical side of major tooth immediately basal; tertiary veins acute to secondary veins, straight to curved and merging midway between secondaries.

Fruit, a three-parted samara; pedunculate; samaras joined for about half the proximal margin along a vascularized stalk, vascularization extending across samara to a centrally located seed; samara fully enclosing seed; distal side of samara forming three-fourths of a circle; samara vascularized by a reticulum of veins that branch at acute angles.

Type species.—Bohlenia americana (Brown) Wolfe and Wehr [*Dipteronia americana* Brown].

Discussion.—See under *Bohlenia americana.*

Derivation of name.—This genus is named for Anne Bohlen of Portland, Oreg. Miss Bohlen is an inspiring teacher in biology, as evidenced by her being named Oregon's High School Biology Teacher of the Year. She was also instrumental in guiding and encouraging the senior author's early training.

Bohlenia americana (Brown) Wolfe and Wehr, n. comb.

Plate 13, figures 1–8

Dipteronia americana Brown, 1935 (part), p. 580, pl. 67, fig. 6.

Comptonia insignis auct. non Lesquereux. Berry, 1929, p. 241, pl. 50, fig. 5.

Supplementary description.—Leaf pinnately compound; leaflets ovate symmetrical, base obtusely asymmetrical, apex acute to acuminate; margin serrate, lobed, apical angle acute, serration type A–1; lobes typically with two teeth on basal side; venation pinnate; about eight pairs of secondary veins, angle of departure uniformly about 50°; alternate pairs of secondary veins craspedodromous, broadly curving, entering lobes centrally; other secondary veins bifurcating just before reaching sinuses between lobes, apical branch extending parallel to basal side of lobe immediately apical, basal branch extending parallel to apical side of lobe immediately basal; tertiary veins straight to curved and merging midway between secondaries, originations on secondaries acute; higher order venation obscure.

Discussion.—The leaflet illustrated by Brown (1935) as *Dipteronia americana* represents *Rhus malloryi* and is thus excluded from this discussion. Brown, however, also included in *D. americana* the two leaflets assigned by Berry (1929) to *Comptonia insignis*. These leaflets apparently represent, from their position on the matrix, part of the same leaf. Brown (1935) did not designate a holotype, and thus we choose as the lectotype the two leaflets illustrated by Berry.

The lectotype of "*Dipteronia*" *americana* has large teeth that have one or two subsidiary teeth on their basal flanks, and pairs of craspedodromous secondary veins that alternate with pairs of secondary veins that prominently bifurcate just before reaching the sinuses. This bifurcation does not occur in *Dipteronia,* in which the sinuses are connected to the secondary veins by an external secondary vein. The tertiary veins are orthogonal in *Dipteronia.*

Bifurcating secondary veins similar to those of *Bohlenia americana* occur in members of Sapindaceae, particularly in *Cardiospermum* and *Serjania*; both genera are members of Eupaullinieae. In species of these extant genera, however, the secondary vein typically forks at the sinus, or, if forking before reaching the sinus, the basal branch is weak and extends to the sinus before passing into the tooth. We therefore consider the Republic leaflets to represent an extinct genus.

That the fruits here assigned to *Bohlenia americana* represent Sapindaceae is indicated by the one specimen (pl. 13, figs. 4–6) that demonstrates that the samaras were borne in threes (samaras in Aceraceae are borne in twos). In *Dipteronia,* moreover, the samaras are typically not fused to one another (or for only a short distance) and the vascular strand extends from the peduncle straight to the seed.

Fruits of four of the five genera of Eupaullinieae and of the sole genus of Thinouieae (these two subtribes comprise the Paullinieae) analyzed indicate some basic similarities to fruits of *Bohlenia,* other than the trilocular condition basic to Sapindaceae. In our analysis we assume that the distal branching of the placental axis in *Bohlenia* is advanced and that the ancestor of *Bohlenia* would have had the seeds borne proximally. Refusion of the placental branches would probably produce apically borne seeds; the position of the seeds in *Bohlenia* is fundamentally apical—the branches are at the apical end of the central axis. Thus, *Bohlenia* is most similar to *Serjania* (fig. 5) in having apically borne seeds and a samara. The venation in the samara of *Bohlenia* is formed of acutely branching and typically open veins (pl. 13, fig. 2); this is similar to *Serjania* and *Thinouia.* In *Cardiospermum* and *Urvillea,* the venation is closed, forming a reticulum. In *Cardiospermum,* the fruit is an inflated capsule and the seeds are borne midway along the central axis; this last feature is shared with *Urvillea,* which, however, has a much less inflated capsule than *Cardiospermum.* In *Thinouia,* the seeds are borne basally and the wing is apical. *Paullinia* has a decidely sclerified fruit. The morphology of the fruits here assigned to *Bohlenia* is indicative of a relationship to *Serjania.*

The association of the leaflets and samaras of *Bohlenia americana* at Republic is not in itself sufficient grounds for the inclusion of both organs in the same taxon. We consider, however, the association at Florissant to be strongly indicative that the types of leaflet and samara here named *Bohlenia* represent the same genus; MacGinitie (1953) noted that the leaflets and samaras of "*Dipteronia*" *insignis* (= *Bohlenia insignis*) occur in association at all Florissant localities. The Republic occurrence represents the association of the same type of leaflet and samara (although specifically distinct from the Florrissant taxon). Yet a third such association occurs in the Joseph Creek flora; Berry (1926) assigned a leaflet of *Bohlenia* morphology to *Myrica uglowi,* and "*Dipteronia*" (= *Bohlenia*) samaras are present in later collections from the Joseph Creek locality housed in the Geological Survey of Canada's collections in Ottawa. We think that all these joint occurrences of leaflets and samaras are sufficient grounds for the inclusion of both organs in the same genus.

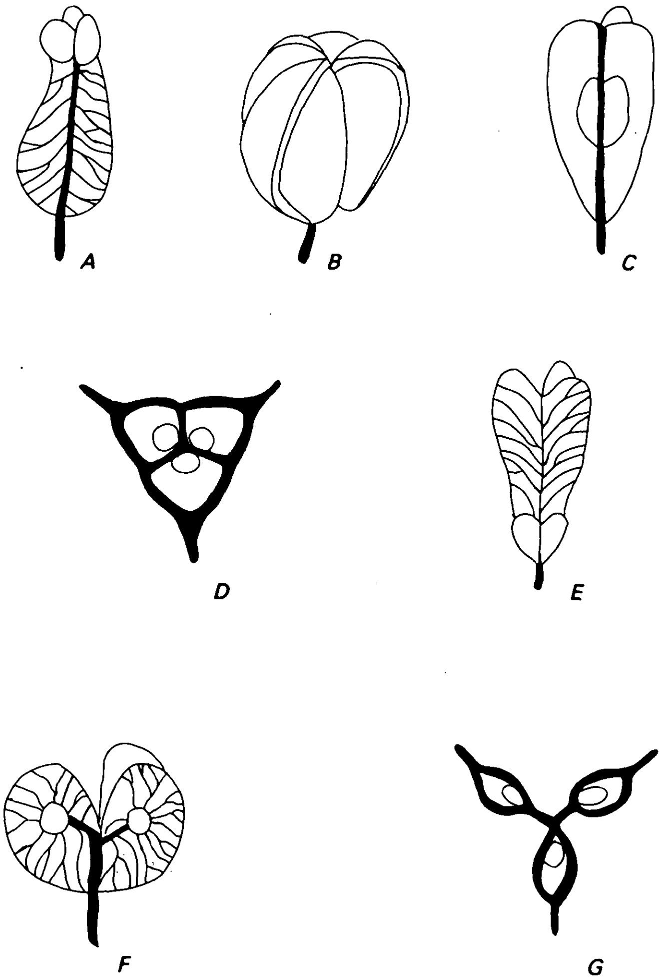

Figure 5. Fruits of Sapindaceae. *A, Serjania. B, Cardiospermum. C, Urvillea. D, Urvillea* (diagrammatic representation of cross section, after Radlkofer, 1933). *E, Thinouia. F, Bohlenia. G, Bohlenia* (diagrammatic interpretation of cross section).

The Paullinieae are today basically neotropical, with two genera (*Lophostigma* and *Urvillea*) endemic to South America. Also of interest is that Paullinieae were considered by Radlkofer (1933) to be the least advanced extant Sapindaceae (and *Serjania* the least advanced of Eupaullinieae). Although the present distribution could be interpreted as indicating a South American origin for the family, the occurrence of *Bohlenia*, which was probably derived from a *Serjania*-like ancestor, strongly indicates the possibility of a boreotropical origin and diversification for the family.

Lectotype.—USNM 38094.

Hypotypes.—UCMP 9298–9300; UW 31278, 31298, 39192, 39729.

Occurrences.—Localities 8428, 11018.

Genus KOELREUTERIA Laxmann

Koelreuteria arnoldi Becker

Plate 12, figures 8, 10

Koelreuteria arnoldi Becker, 1961 (part), p. 83, pl. 27, figs. 1–4.

Discussion.—In their small size and pattern of wing venation, the Republic fossils are similar to the Ruby types of *Koelreuteria arnoldi* Beck. The holotype contains three seeds, but none of the four Republic specimens shows the presence of seeds within the capsule. As noted by Becker, the capsules of *K. arnoldi* appear to have been almost flat, unlike the inflated capsules of extant *Koelreuteria*.

Hypotypes.—UCMP 9301; UW 39189, 39190.

Occurrence.—Locality 8428.

Family CORNACEAE
Genus CORNUS L.

Cornus sp.

Plate 14, figures 1–4

Discussion.—The strongly and apically arched eucamptodromous secondary veins and widely spaced tertiary veins oriented perpendicular to the midrib indicate that these fragmentary leaves represent *Cornus*. The margins of the fossils are slightly erose as in *Cornus*.

Although the generic assignment seems certain, the limited material does not warrant naming. The Republic specimens do not appear assignable to any previously described species from the North American Tertiary.

Specimens.—UW 31276, 39193, 39734.

Occurrence.—Locality 8428.

Family DAVIDIACEAE

Genus TSUKADA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves simple; venation pinnate; secondary veins craspedodromous, broadly curving apically; intersecondary veins absent; tertiary veins acute to secondary veins (AO pattern), some branched; axillary tertiary veins tending to be parallel to other intercostal tertiaries; quaternaries branching, forming a coarse, dominantly quadrangular reticulum; three most basal pairs of secondary veins crowded near base, giving an almost actinodromous appearance; external secondary veins more numerous on three most basal pairs of secondary veins than on more apical pairs; external secondary veins craspedodromous to camptodromous; teeth entered medially and with lateral bracing veins that loop; weakly developed sinal knot; teeth at least one per secondary vein; serration type broadly A–1; ill-defined glandular area on apex of teeth.

Type species.—*Tsukada davidiifolia* Wolfe and Wehr.

Derivation of name.—We take pleasure in naming this genus for Matsuo Tsukada in recognition of his extensive work in Quaternary paleoecology and biogeography.

Tsukada davidiifolia Wolfe and Wehr

Plate 14, figures 5, 6; plate 15, figures 1–4

Description.—Leaf simple; shape symmetrical wide elliptic, apex acuminate, base narrowly and shallowly cordate; margin typically serrate (a few teeth dentate), apical angle acute, spacing regular, teeth simple; petiole normal; venation pinnate; secondary veins six pairs, (except for basal pair) departing at an angle of 45°, broadly curving, craspedodromous, entering teeth centrally, giving off one craspedodromous or camptodromous external branch except for most basal of the six pairs, which has seven external branches; most basal pair of secondary veins weak, departing at an angle 80°, broadly curving, semicraspedodromous; tertiary veins orthogonal, percurrent, alternate or opposite, uniformly spaced; higher vein orders indistinct.

Discussion.—The serration type, slightly cordate base, broadly curving and craspedodromous secondary veins, and crowded basal secondary veins are characters that are combined in the extant *Davidia involucrata* S. and Z., which is the sole extant member of Davidiaceae. In contrast to *Davidia* leaves, however, the leaves of *Tsukada* have an AO (rather than an RR) tertiary vein orientation, they have a weakly developed sinal knot, and they also differ in details of dental morphology and venation. In *Davidia*, the lateral bracing veins are strong and typically approximately straight, the external secondary branches are consistently craspedodromous, and the dental apices have a clearly defined and elongated gland; in *Tsukada*, the lateral bracing veins form distinct loops, the external secondary branches can be camptodromous (as well as craspedodromous), and the dental apices have a poorly developed and short gland.

Tsukada, in some characters, is morphologically intermediate between *Davidia* and some members of Escalloniaceae. The AO tertiary vein orientation, weak sinal knot, narrowly rounded teeth, and presence of some camptodromous external secondary branches of *Tsukada* are characters that are found in some Escalloniaceae but are absent in *Davidia*. If *Tsukada* represent a low grade of foliar morphology in Davidiaceae, then Davidiaceae are closely related to Escalloniaceae but not to Cornaceae (and should thus be excluded from Cornales).

Holotype.—UW 71095.

Paratypes.—UW 39187, 71081; UCMP 9302 (counterpart of UW39187).

Occurrence.—Locality 8428.

Family OLACACEAE
Genus SCHOEPFIA Schreber

Schoepfia republicensis (LaMotte) Wolfe and Wehr, n. comb.

Plate 16, figures 1-3

Cornus acuminata Berry, 1929, p. 260, pl. 59, fig. 3.
Cornus republicensis LaMotte, 1944, U.S. Geol. Survey Bull. 924, p. 126.

Discussion.—Berry's (1929) original specimen lacks a base but has the pronounced acrodromy of the two specimens illustrated here. In *Cornus*, acrodromous veins depart from the midrib about halfway the distance to the apex and are typically the fourth pair of secondary veins, in contrast to the Republic specimens in which the acrodromous veins depart near the base and are the second pair of secondary veins.

A tendency for acrodromous secondary veins and tertiary veins oriented perpendicular to the midrib is evidenced in Olacaceae, particularly in *Anacalosa* and even more pronounced in *Schoepfia*. One critical character is the decurrency of the lamina to form an alate petiole; two pairs of veins—one weak pair and the most basal pair of secondary veins—depart from the midrib along the petiole and extend along the wing to flare out in the lamina. This characteristic architecture is totally lacking in *Cornus* but is found in *Schoepfia*.

Olacaceae are predominantly megathermal with some mesothermal representatives, among which is *Schoepfia*. Acrodromy is more pronounced in the extant American than in the extant Asian species of *Schoepfia*, and thus *S. republicensis* is apparently most closely related to the extant American species. The pollen type referred to as *Anacalosidites* includes the morphology of *Schoepfia*, and this pollen type is known in mesothermal Eocene assemblages in North America (Leopold *in* MacGinitie, 1974) to marginally microthermal Miocene assemblages (Wolfe, 1962).

The epithet "*acuminata*" was preoccupied in *Cornus*, as recognized by LaMotte (1944), who proposed the epithet *Republicensis*.

Hypotypes.—USNM 32683; UW 39194.

Occurrence.—Locality 8428.

INCERTAE SEDIS (HAMAMELIDIDAE?)

Genus REPUBLICA Wolfe and Wehr, n. gen.

Diagnosis.—Leaves simple; shape symmetrical; margin entire; venation pinnate; secondary veins several, irregularly spaced, departure angle high on most basal pair (which are also weak), departure angle low on medial pairs and gradually increasing toward apex, broadly curving in basal and medial parts of lamina and narrowly curving in apical part, eucamptodromous, extending to margin before looping; conspicuous external secondary veins in basal half of lamina, departing at acute angles and forming a series of ladderlike loops; more apical intercostal areas conspicuously narrowing toward margin; intersecondary vein typically absent; tertiary veins orthogonal, percurrent, or branched; axillary tertiary bracing orthogonal; quaternary veins orthogonal, branched, forming a conspicuous reticulum.

Type species.—*Republica hickeyi* Wolfe and Wehr.

Derivation of name.—For Republic, Wash.

Republica hickeyi Wolfe and Wehr, n. sp.

Plate 16, figures 4, 5

Description.—Leaf simple; shape symmetrical, wide elliptic, apex broadly acute, base acute; margin entire; texture coriaceous; petiole thick; venation pinnate, midrib thick at base, thinning markedly toward apex, straight; secondary veins eight on one side, nine on other; two most basal pairs of secondary veins departing at angle of 50°, somewhat irregular and weak, eucamptodromous; more apical secondary veins departing at angles of 45° to 55° (increasing apically), broadly (basally) to narrowly (apically) curving, eucamptodromous at the margin; a single series of conspicuous external secondary loops in basal two-thirds of lamina, formed by external branches that typically depart at low (about 30°) angles and that loop at margin to create a ladderlike effect; more apical intercostal areas conspicuously narrowing towards margin; intersecondary veins typically absent; tertiary veins uniformly spaced, orthogonal, percurrent or branched; axillary tertiary bracing orthogonal; quaternary veins orthogonal, branched, forming a quadrangular to pentagonal reticulum;

quinternary veins randomly reticulate forming areoles; veinlets typically once-branched.

Discussion.—The affinities of this well-preserved, highly coriaceous (and thus almost certainly evergreen) leaf are not certain. The absence of weak lateral veins at the laminar base excludes Lauraceae, despite the superficial resemblance to some species of Lauraceae. Some evergreen Central American species of *Clethra* also have a superficial resemblance, but these do not have the many external secondary branches in the medial and few or none in the apical parts of the lamina.

Republica has several points of resemblance to the ulmaceous *Girroniera*. Leaves of this extant genus typically lack strong external secondary veins (although a few occur in some leaves); if an external secondary vein is present, the angle of departure is acute as in *Republica*, but the loops formed apical to this external vein are bounded basally and apically by veins that are perpendicular to the midrib. In all other architectural features, however, *Republica* and *Girroniera* are similar. If strong and numerous external secondary veins were known in genera closely allied to *Girroniera*, we would not hesitate to assign *Republica* to Ulmaceae. The pattern of strong, numerous external secondary veins is common in Hamamelididae, and we suggest that *Republica hickeyi* is almost certainly related to the leaves (1) originally called *Laurophyllum litseafolia* MacG., which were transferred to *Artocarpoides* (Wolfe, 1968) and finally to *Dicotylophyllum* (Wolfe, 1977) and (2) of *D. kummerensis* (Wolfe) Wolfe. *Republica hickeyi* can be readily distinguished from these other two species by the external secondary loops that extend to the margin; in the other species a second small series of loops is present between a given major external secondary loop and the margin.

The specific epithet honors Leo J. Hickey's contributions to the comparative foliar morphology of the angiosperms, both fossil and extant.

Holotype.—USNM 32697A, B.

Occurrence.—Locality 8428.

SYSTEMATIC CHANGES IN OTHER EOCENE FLORAS

Sassafras ashleyi Axelrod

Sassafras ashleyi Axelrod, 1966, p. 70, pl. 15, figs. 1–9.

Sassafras hesperia auct. non Berry. Brown, 1937 (part), p. 174, pl. 53, fig. 10. MacGinitie 1953, p. 113, pl. 35, fig. 1.

Discussion.—See under *Sassafras hesperia.*

Bohlenia insignis (Lesquereux) Wolfe and Wehr, n. comb.

Myrica insignis Lesquereux 1878, p. 135, pl. 65, figs. 7, 8.

Dipteronia insignis (Lesquereux) Brown, 1937, p. 181, pl. 59, figs. 10–12. MacGinitie, 1953, p. 142, pl. 58, figs. 3, 6; pl. 72, fig. 5.

Myrica uglowi Berry, 1926, p. 100, pl. 18, fig. 1.

Discussion.—The leaflets of "*Dipteronia*" *insignis* have pairs of craspedodromous secondary veins that alternate with pairs of conspicuously bifurcating secondary veins; these leaflets thus conform to *Bohlenia.* The leaflets of *B. insignis* are, however, simply serrate and have more convex teeth than *B. americana.* The samaras assigned to "*Dipteronia*" *insignis* are also similar to those of *B. americana* in having an attachment scar about half the length of the proximal side, along which extends the vascular supply for the seed.

We are uncertain as to whether the Ruby "*Dipteronia*" *insignis* (Becker, 1961) is valid or represents *Bohlenia americana*; the illustrations are insufficient. The Bridge Creek "*Dipteronia*" *(Brown, 1959) also represents Bohlenia,* but the size of the samara is larger than any specimen of either *B. americana* or *B. insignis.* The Bridge Creek leaflet assigned to *Dipteronia* (Brown, 1940) is poorly preserved but appears to represent *Rhus.*

Republica kummerensis (Wolfe) Wolfe and Wehr, n. comb.

Artocarpoides kummerensis Wolfe, 1968, p. 19, pl. 4, figs. 1, 7, text–fig. 12.

Dicotylophyllum kummerensis (Wolfe) Wolfe, 1977, p. 86, pl. 25, fig. 7; pl. 30, fig. 11.

Discussion.—see p. 23

Republica litseafolia (MacGinitie) Wolfe and Wehr, n. comb.

Laurophyllum litseafolia MacGinitie, 1941, p. 116, pl. 18, figs. 2, 3; pl. 19, figs. 1, 2; pl. 22, fig. 2.

Artocarpoides litseafolia (MacGinitie) Wolfe,1968, p. 19.

Dicotylophyllum litseafolia (MacGinitie) MacGinitie, 1969, p. 130.

Discussion.—see p. 23

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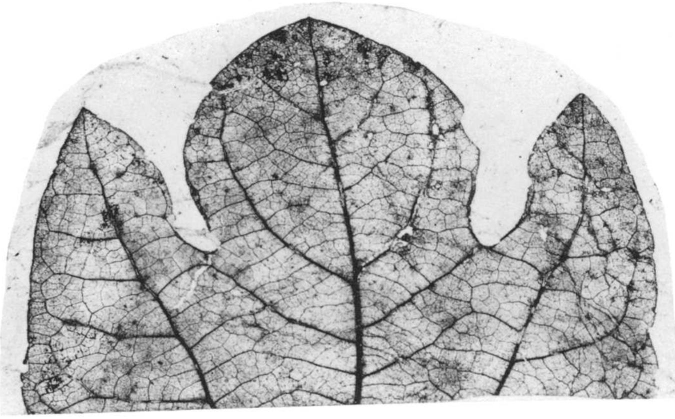
PLATES 1–16

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

PLATE 1

[All natural size]

Figures 1, 2, 7. *Sassafras hesperia* Berry (p. 12)
Hypotypes UW 31241, 39715, 39717; loc. 8428.
3–6. *Phoebe* sp. (p. 11)
Specimens USNM 32676–32679; loc. 8428.



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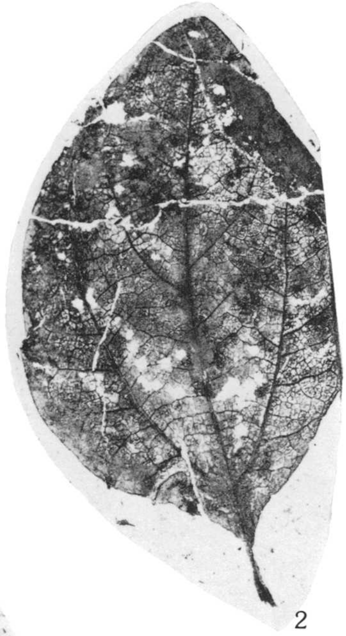

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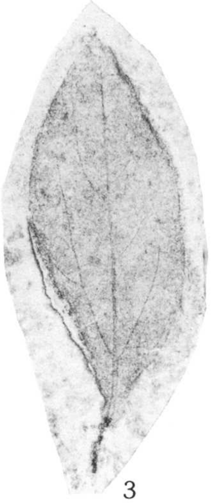

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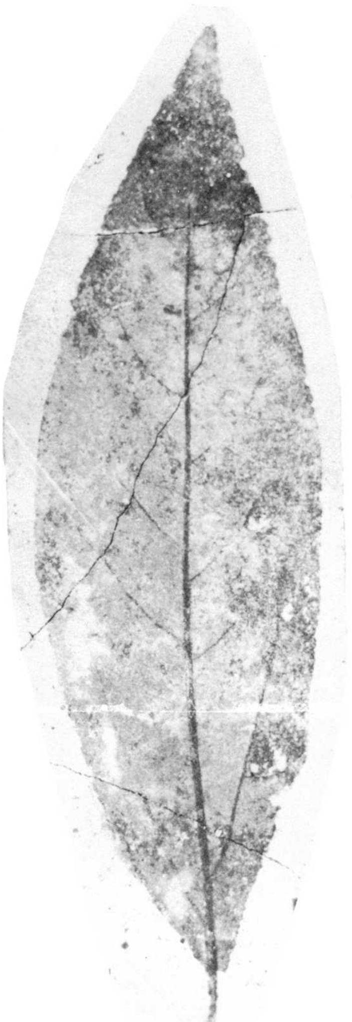

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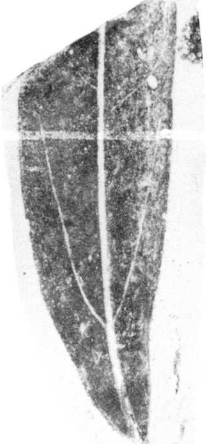

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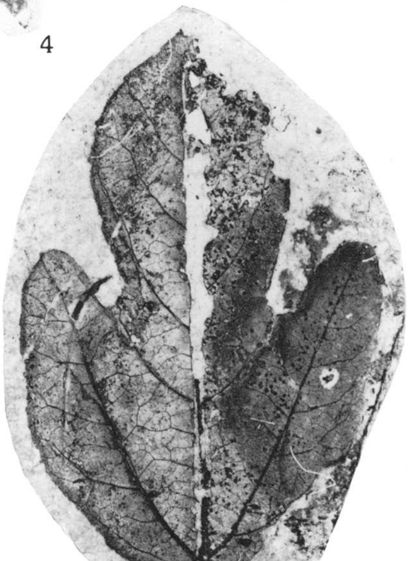

7

PHOEBE AND *SASSAFRAS*

PLATE 2

[All natural size unless otherwise indicated]

Figures 1–7. *Sassafras hesperia* Berry (p. 12)

Hypotypes UW 39709, 39710; USNM 32680; UW 39720; UCMP 9265–9267. Loc. 8428. Figs. 6, 7, × 4. Fig. 6 is counterpart of fig. 2; fig. 7 is counterpart of pl. 1, fig. 2.

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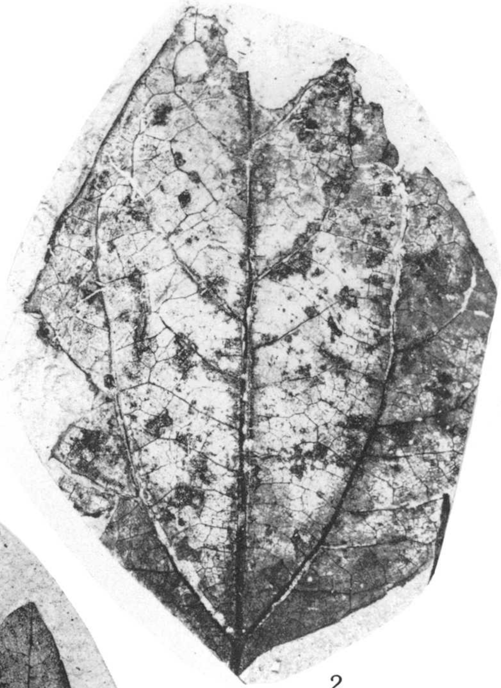

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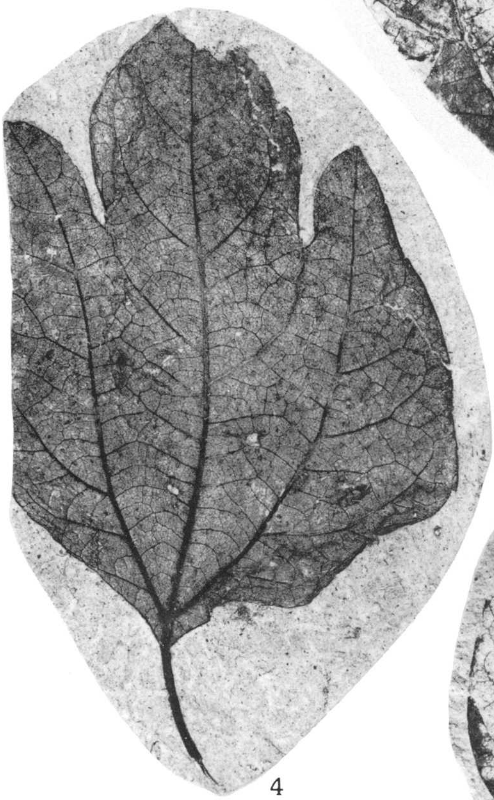

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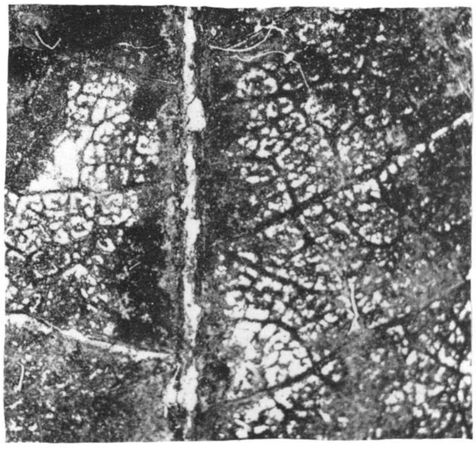

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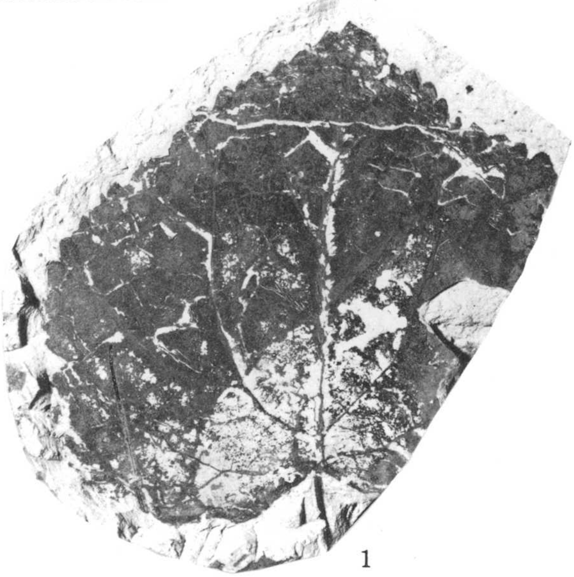
7

SASSAFRAS

PLATE 3

[All natural size unless otherwise indicated]

Figures 1–8. *Cercidiphyllum obtritum* (Dawson) Wolfe et Wehr (p. 12)
Hypotypes UW 31242, 31243; USNM 32681; UW 31244, 31285, 39711; USNM 32682. loc. 8428.
Figs. 4, 7, × 4. Fig. 7 is enlargement of
fig. 6.



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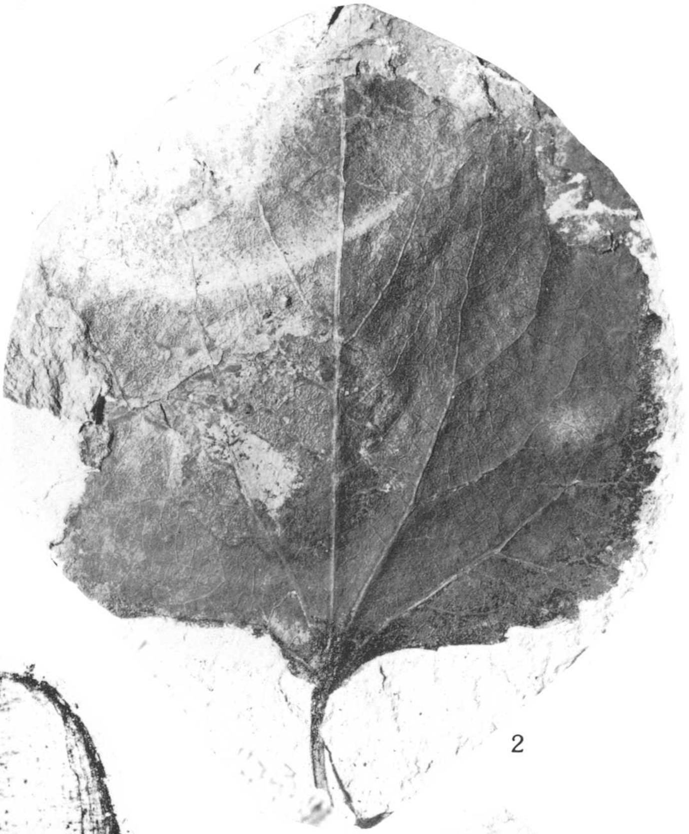

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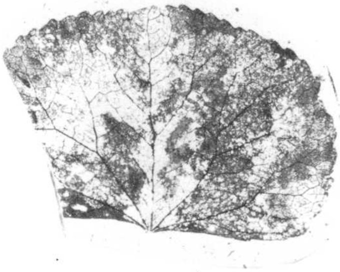

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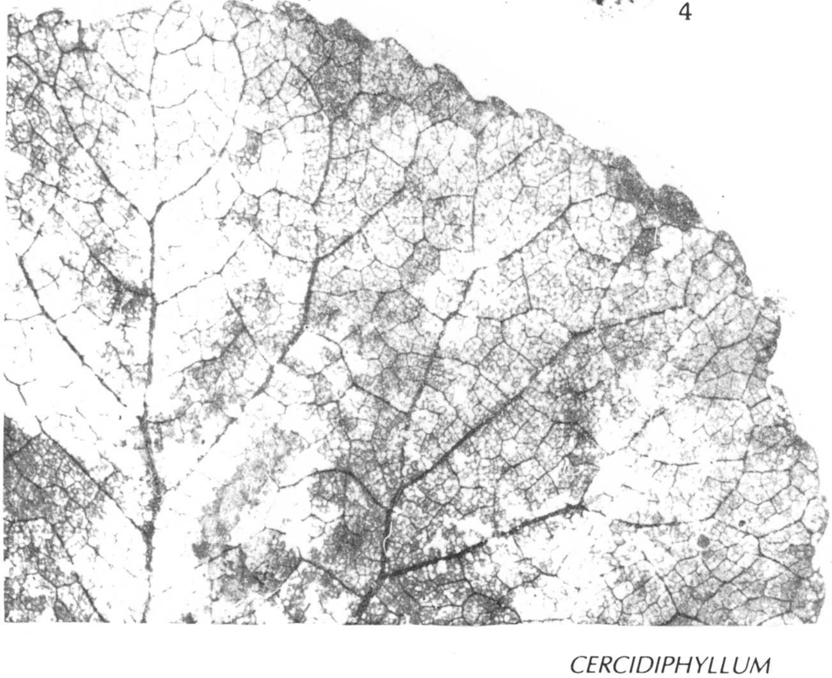

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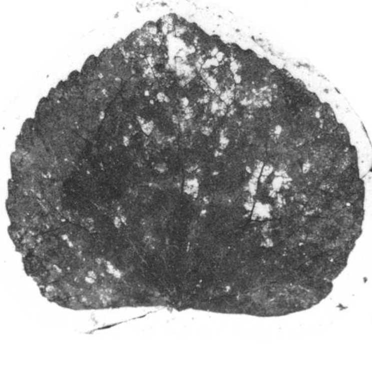

8

CERCIDIPHYLLUM

PLATE 4

[All natural size unless otherwise indicated]

Figures 1–4. *Langeria magnifica* Wolfe et Wehr (p. 13)

1, 4. Paratypes UW 31246, 31286. Loc. 8428. 2, 3. Holotype UW 39713; loc. 8428. Fig. 2, × 4.

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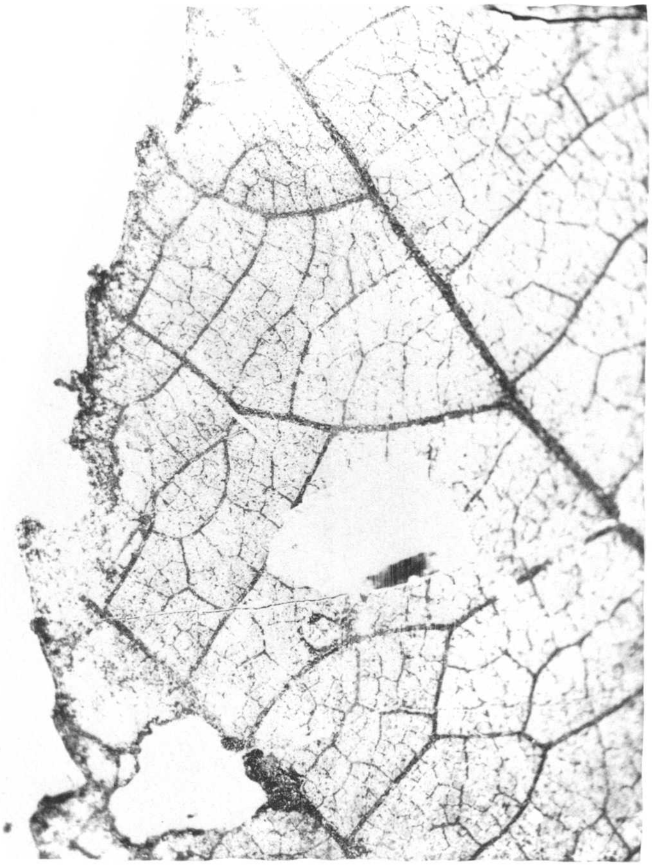

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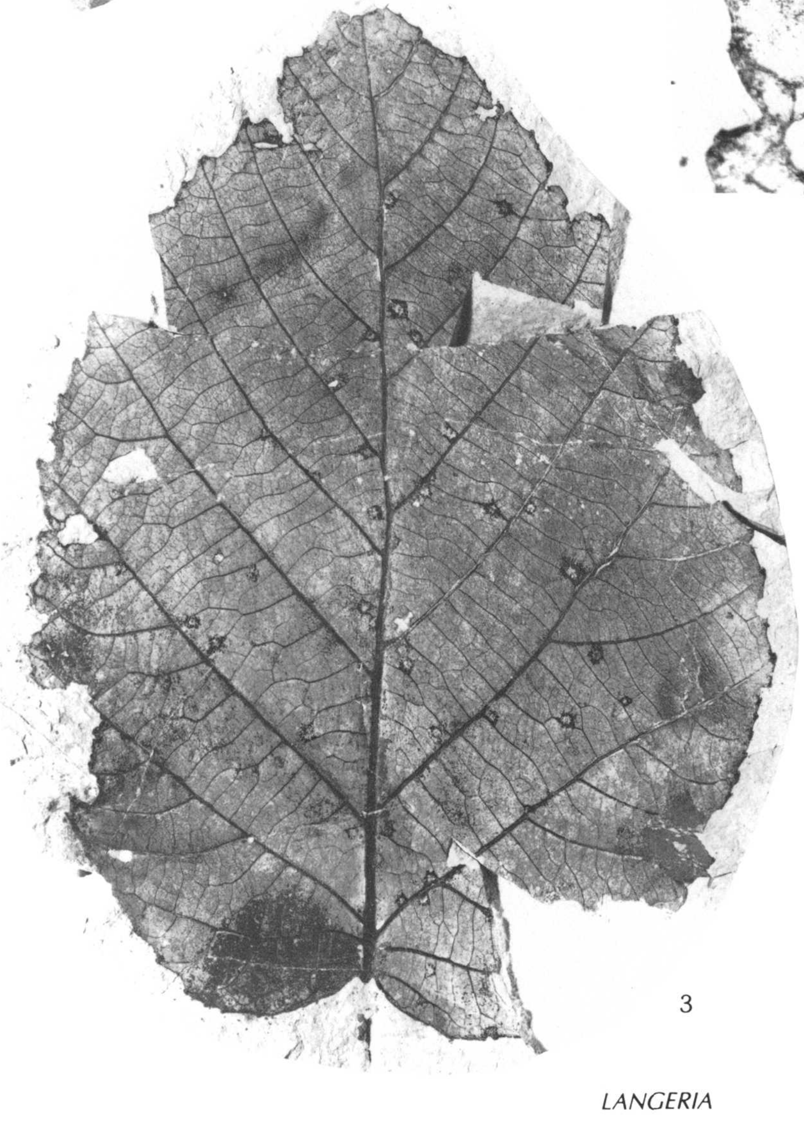

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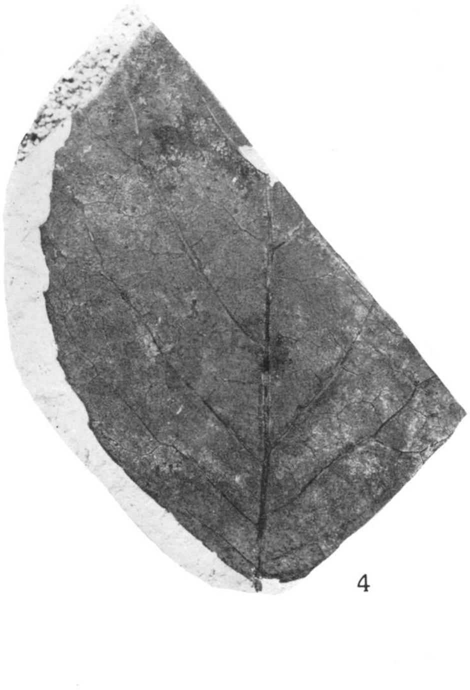

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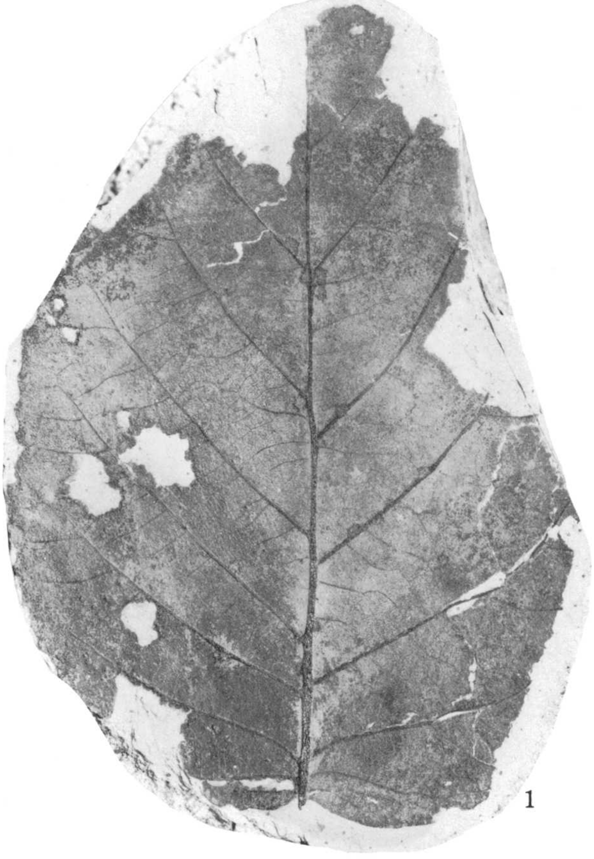
LANGERIA

PLATE 5

[All natural size unless otherwise indicated]

Figures 1–4. *Langeria magnifica* Wolfe et Wehr (p. 13)
Paratypes UW 31287–31289. Fig. 3, × 4 (enlargement of fig. 2). Loc. 8428.



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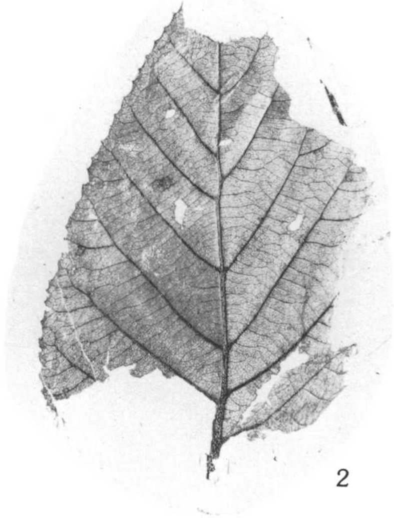

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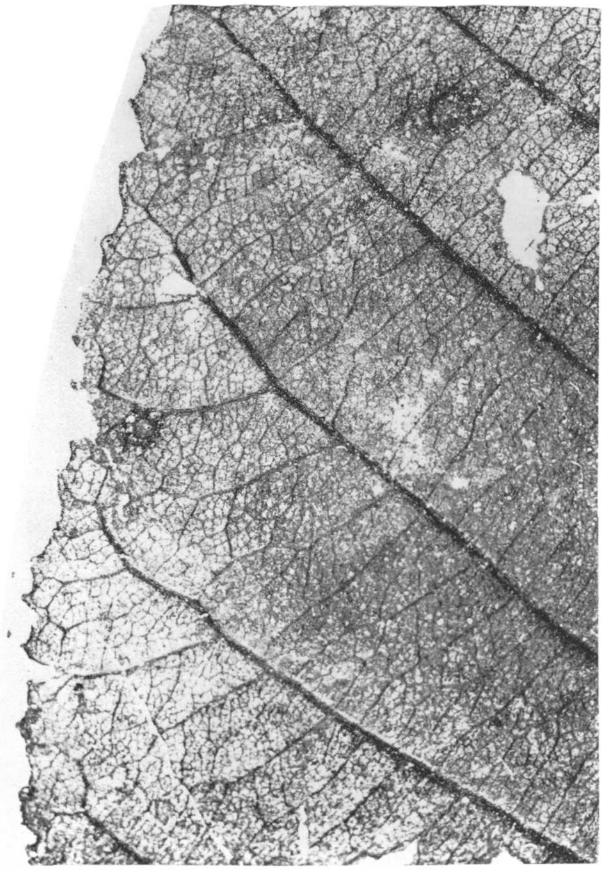

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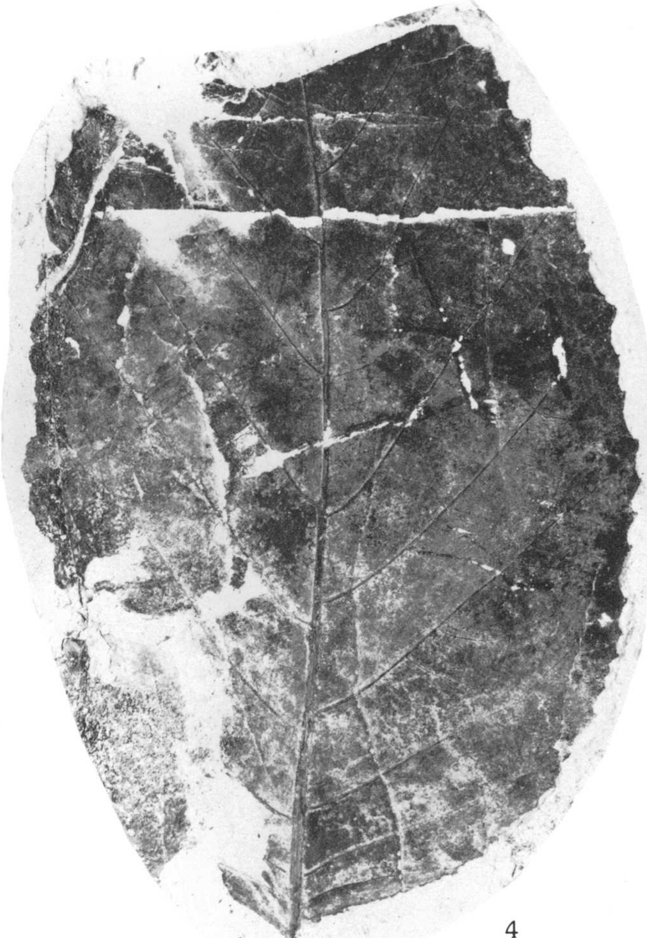

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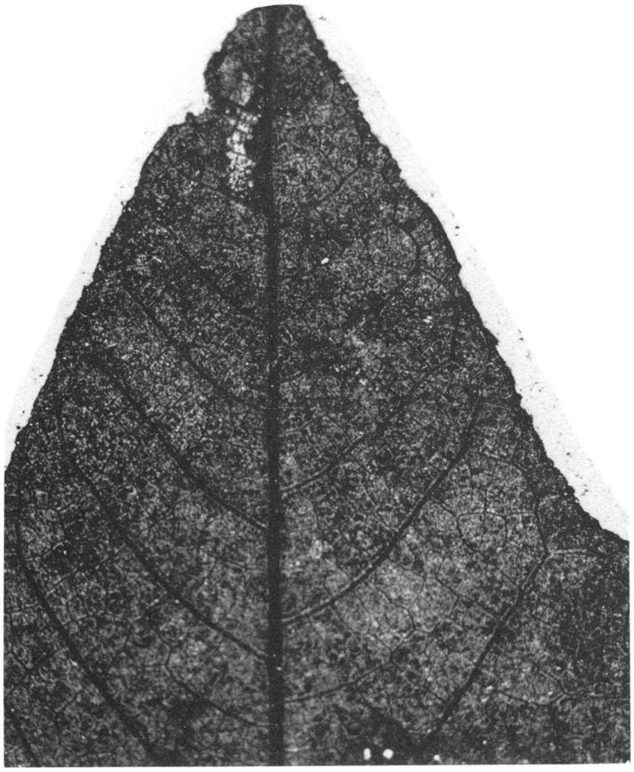
LANGERIA

PLATE 6

[All natural size unless otherwise indicated]

Figures 1–4. *Macginitiea gracilis* (Newberry) Wolfe et Wehr (p. 14)
Hypotypes UW 39714, 31247, 31290; loc. 8428. Fig. 1, × 4 (enlargement of fig. 2).



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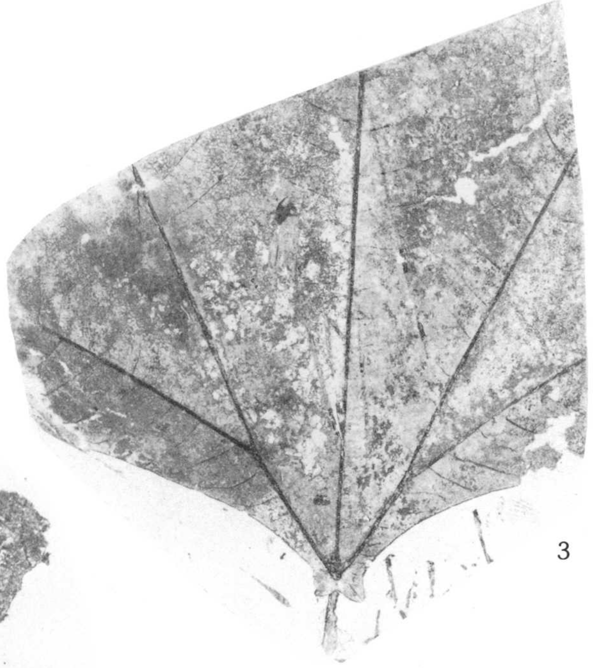

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MACGINITIEA

PLATE 7

[All natural size unless otherwise indicated]

Figures 1–9. *Fagopsis undulata* (Knowlton) Wolfe et Wehr (p. 15)

Hypotypes UCMP 9280; USNM 32684; UW 39716; USNM 32685–32690. Fig. 1, ×4 (enlargement of counterpart of fig. 3), loc. 8428. Figs. 2, 4–7, loc. 11019. Figs. 3, 8, loc. 8428. Fig. 9, ×5, loc. 11019.


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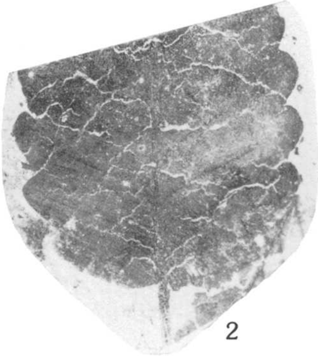
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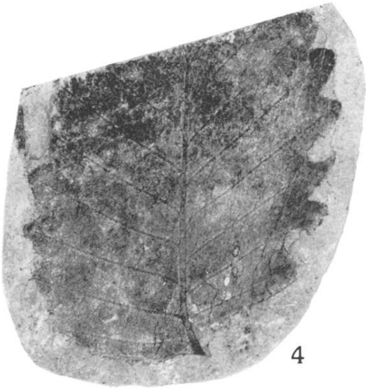
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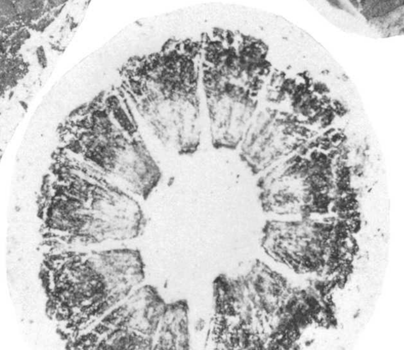
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FAGOPSIS

PLATE 8

[All natural size unless otherwise indicated]

Figures 1–8. *Alnus parvifolia* (Berry) Wolfe et Wehr (p. 15)

Hypotypes USNM 32691, 32692; UW 39721, 31253, 31255, 31254; USNM 32691; UW 31291; loc. 8428. Figs. 7, 8, × 4. Fig. 7 is enlargement of fig. 1.


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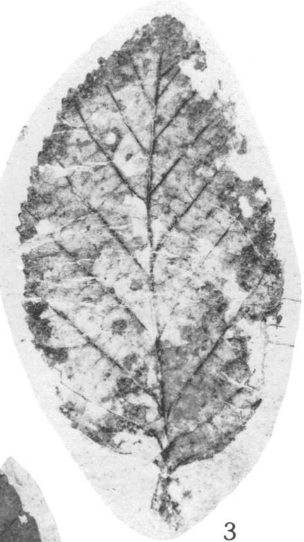
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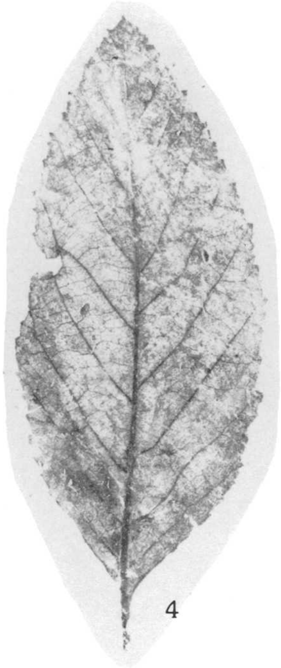
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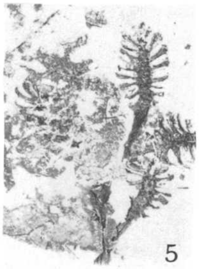
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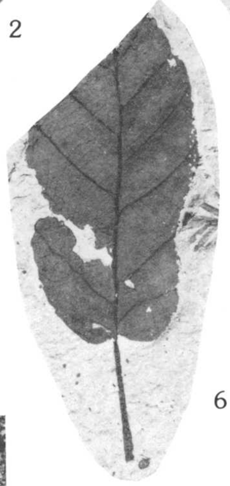
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8

ALNUS

PLATE 9

[All natural size unless otherwise indicated]

Figures 1–3. *Comptonia columbiana* Dawson (p. 16)

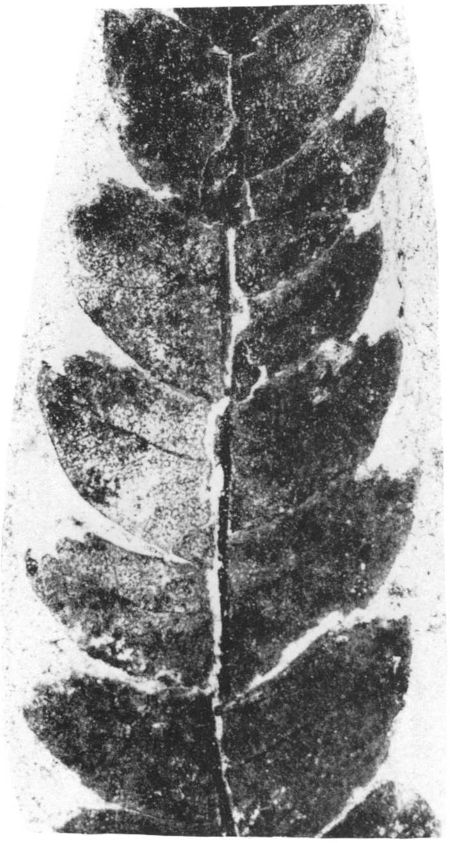
Hypotypes USNM 32693, 32694; UW 39723. Fig. 1, × 4, loc. 11018. Figs. 2, 3, loc. 8428.

4–7. *Ternstroemites* sp. "A" (p. 16)

Specimens UCMP 9290 (counterpart UW 39724); UW 39724, 31259; loc. 8428. Fig. 5, × 4 (enlargement of fig. 4).

8–11. *Betula leopoldae* Wolfe et Wehr (p. 15)

8–10. Holotype UW 39722; loc. 8428. Fig. 8, × 4; fig. 10, × 7. 11. Paratype UW 31256, × 4, loc. 8428.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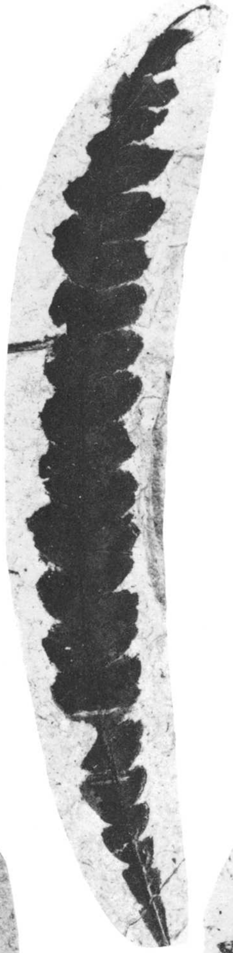
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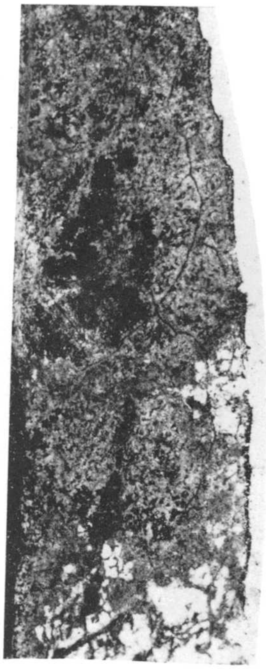
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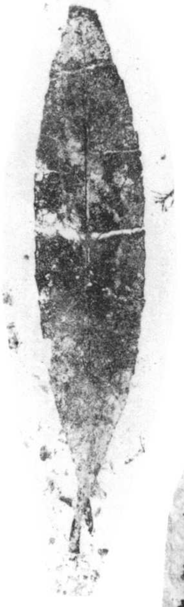
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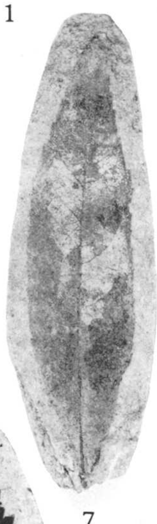
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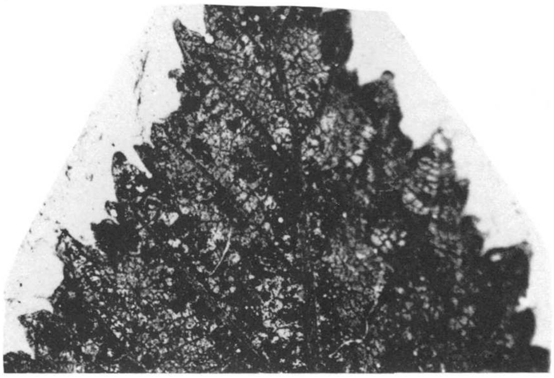
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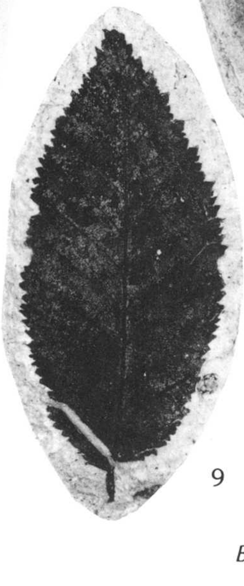
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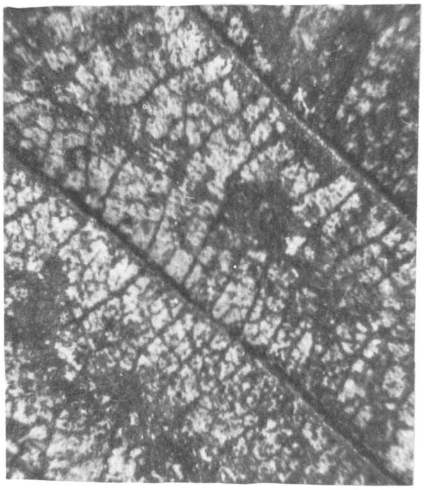
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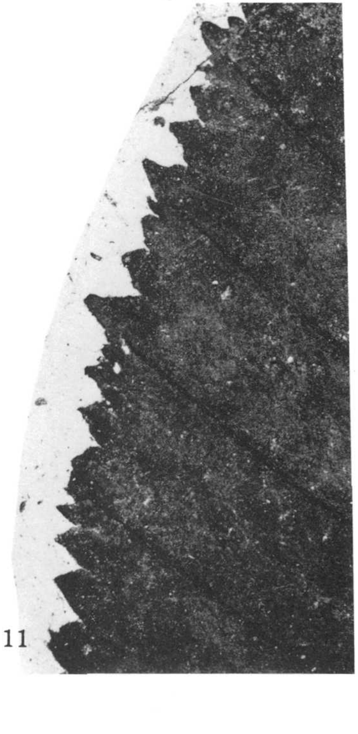
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BETULA, COMPTONIA, AND *TERNSTROEMITES*

PLATE 10

[All natural size unless otherwise indicated]

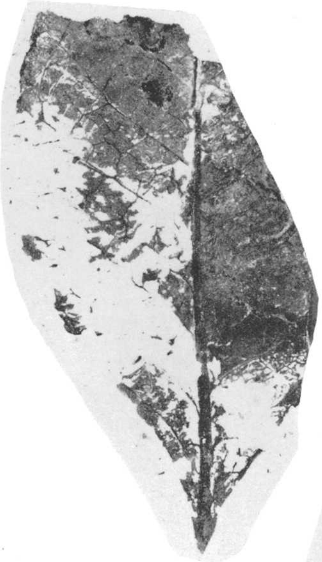
Figures 1–4, 6. *Ternstroemites* sp. "B" (p. 16)

Specimens UW 39719, 31292, 31293; loc. 8428. Fig. 1, × 4 (enlargement of fig. 3). Fig. 6, × 4 (enlargement of fig. 2).

5, 7. *Tilia johnsoni* Wolfe et Wehr (p. 16)

Holotype UW 39712, UCMP 9291 (counterpart); loc. 8428. Fig. 5, × 4.


1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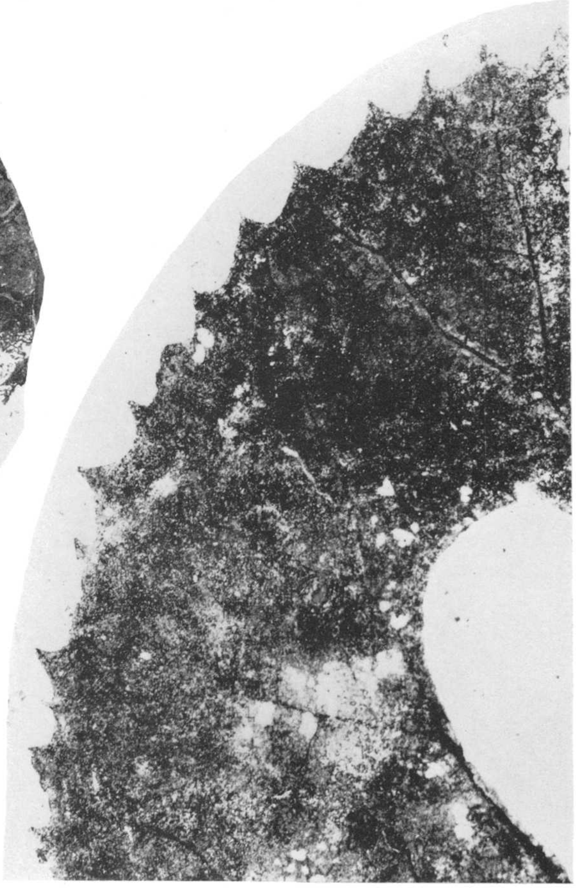
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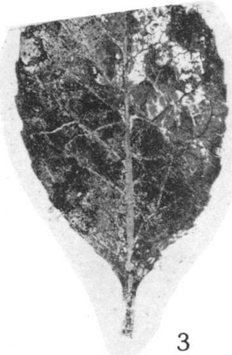
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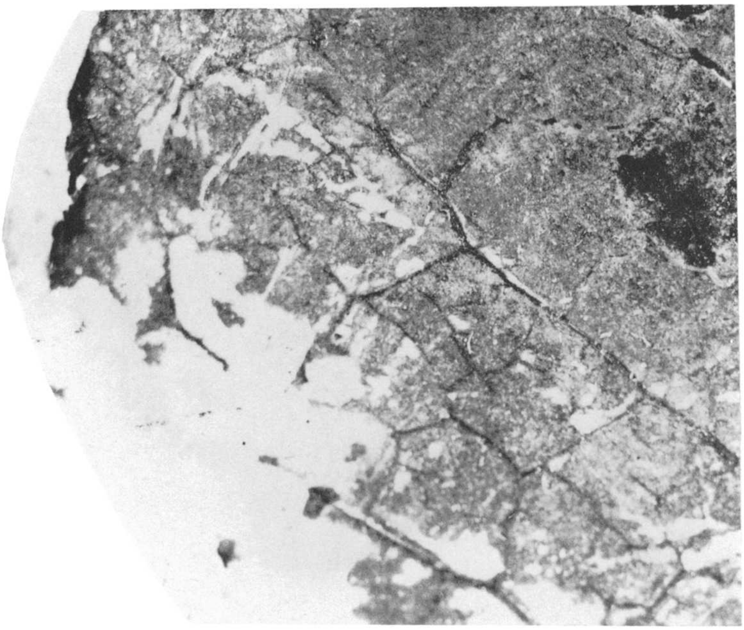
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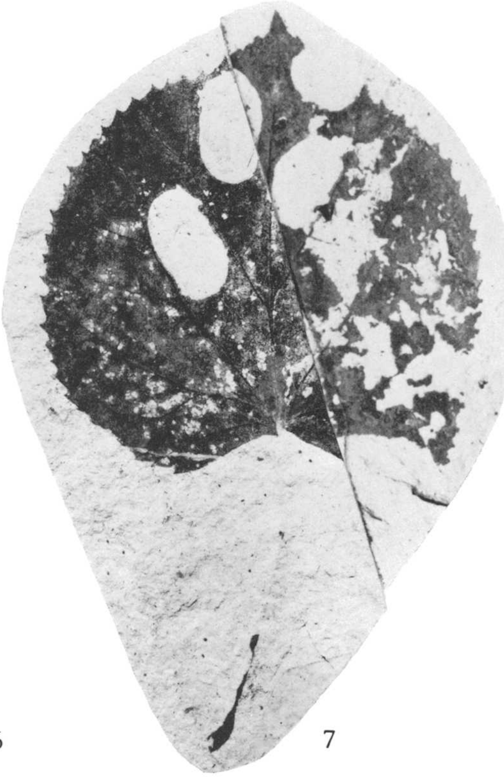
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TERNSTROEMITES AND *TILIA*

PLATE 11

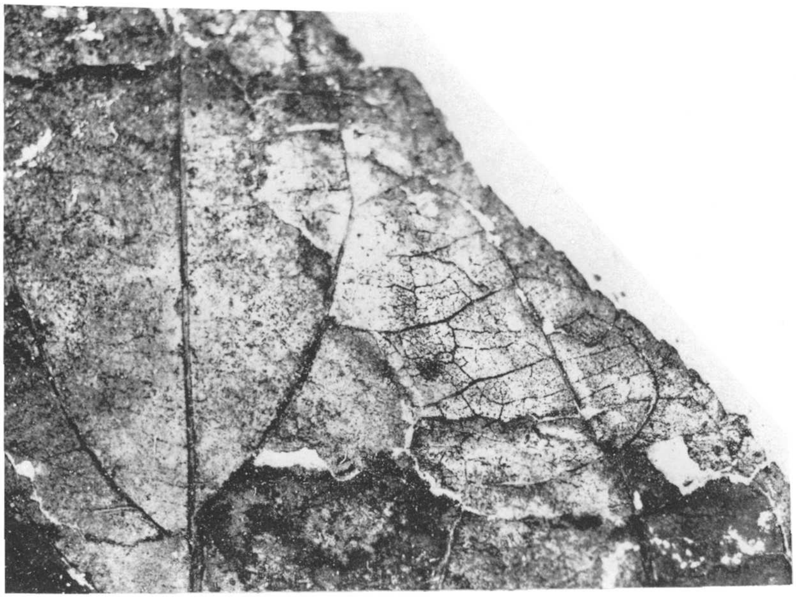
[All natural size unless otherwise indicated]

Figures 1–3. *Itea* sp. (p. 17)

Specimens UW 39725, 31262; loc. 8428. Fig. 1, × 4 (enlargement of fig. 3).

4–6. *Photinia pageae* Wolfe et Wehr (p. 17)

Holotype UW 39188; loc. 8428. Fig. 5, × 4; fig. 6, × 7.



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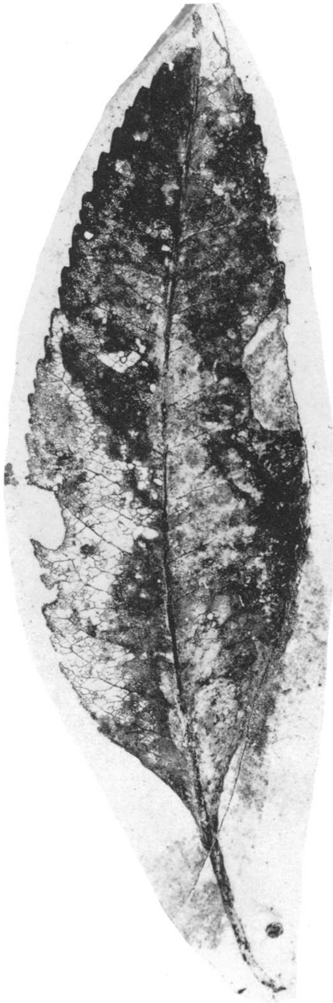

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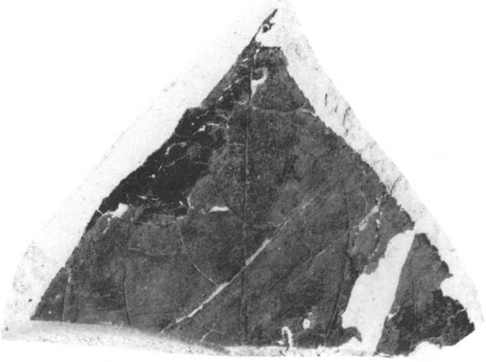

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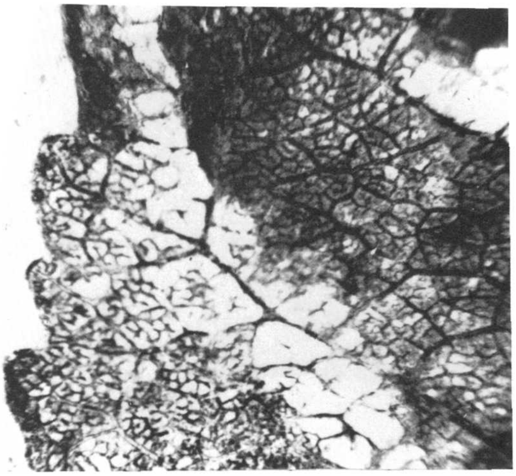

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ITEA AND *PHOTINIA*

PLATE 12

[All natural size unless otherwise indicated]

Figures 1, 2, 6, 7, 12. *Rhus malloryi* Wolfe et Wehr (p. 17)
    1, 12. Holotype UW 39718; loc. 8428. Fig. 12, × 4. 2, 6, 7. Paratypes UW 31270, 31294, 31295; loc. 8428.
3–5. *Barghoornia oblongifolia* Wolfe et Wehr (p. 18)
    Holotype USNM 32695A, B; loc. 8428. Fig. 5, × 4.
8, 10. *Koelreuteria arnoldi* Becker (p. 21)
    Hypotypes UW 39189, 39190; loc. 8428. Fig. 10, × 5.
9, 13, 14. *Acer* sp. (p. 19)
    Specimens UW 39728, 31272; USNM 32696. Figs. 9, 13, 15, loc. 8428; Fig. 14, loc. 11018.
11, 15. "*Acer*" *arcticum* Heer (p. 18)
    Hypotype UW 39726; loc. 8428. Fig. 11, × 4.


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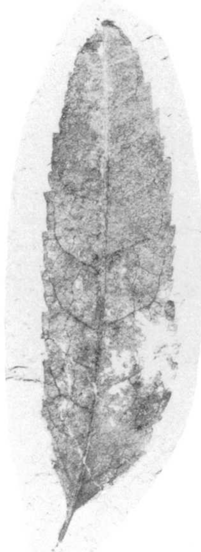
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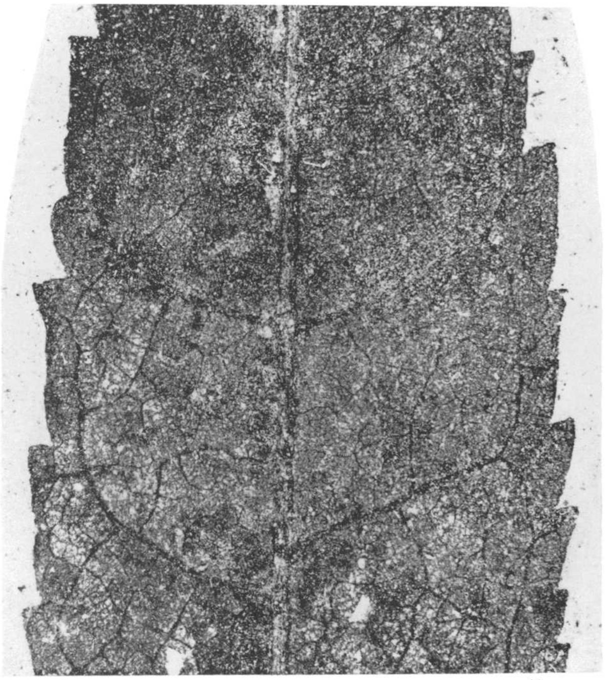
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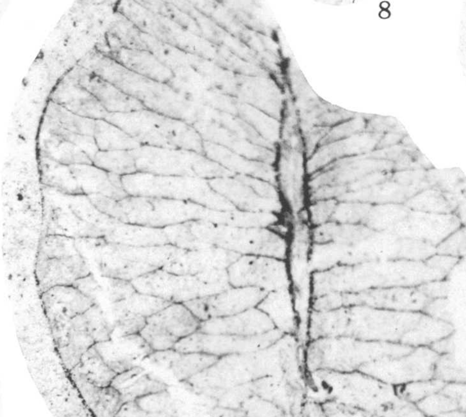
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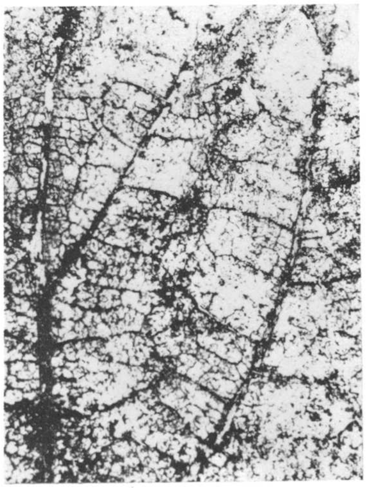
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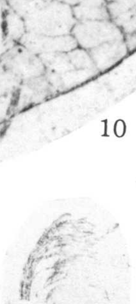
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15

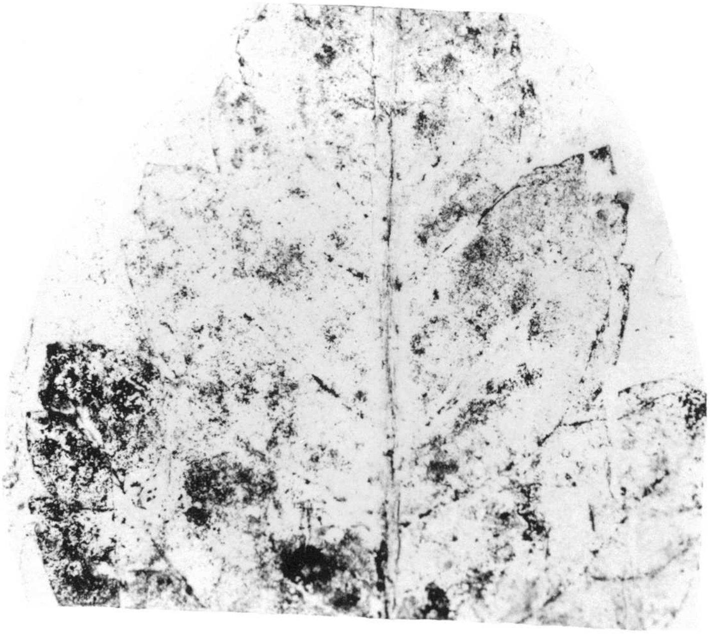
RHUS, BARGHOORNIA, KOELREUTERIA AND *ACER*

PLATE 13

[All natural size unless otherwise indicated]

Figures 1–8. *Bohlenia americana* (Brown) Wolfe et Wehr (p. 19)

Hypotypes, loc. 8428. 1,4. UCMP 9298; UW 39192 (counterpart). Fig. 1, × 4. 2, 7, 8. UW 31278, 39736, 31298. 4–6. UCMP 9299; UW 39729 (counterpart). Figs. 5, 6, × 4. Fig. 6 is enlargement of fig. 4.



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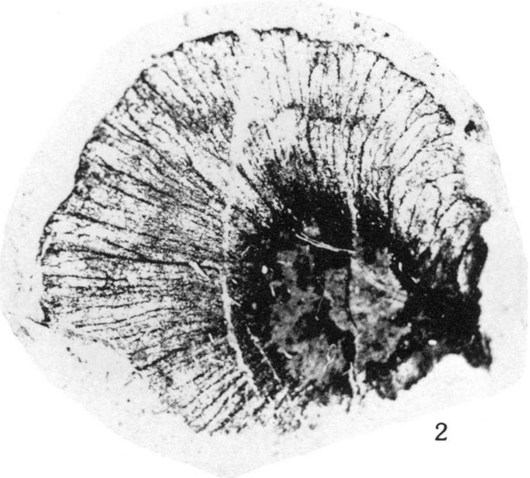

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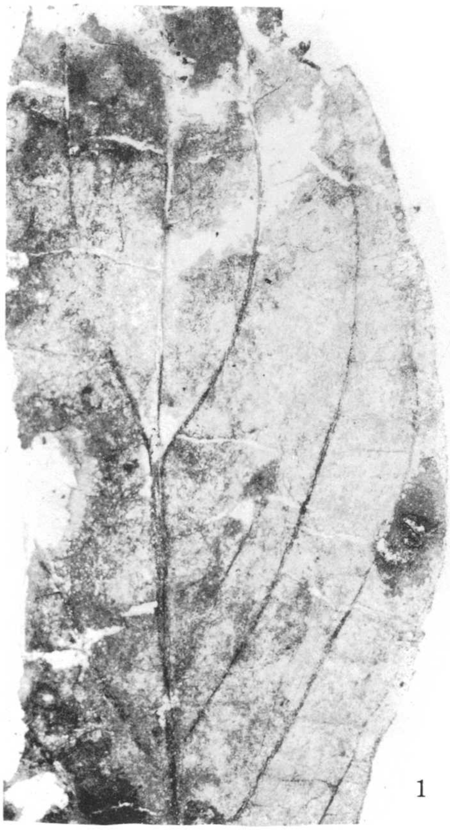
BOHLENIA

PLATE 14

[All natural size unless otherwise indicated]

Figures 1–4. *Cornus* sp. (p. 21)
Specimens UW 39734, 31276, 39193. Fig. 1, × 4 (enlargement of fig. 2). Loc. 8428.

5, 6. *Tsukada davidiifolia* Wolfe et Wehr (p. 21)
Paratype UW 39187. Fig. 5, × 4. Loc. 8428.



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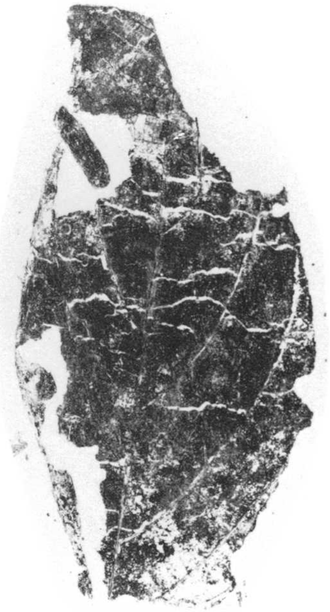

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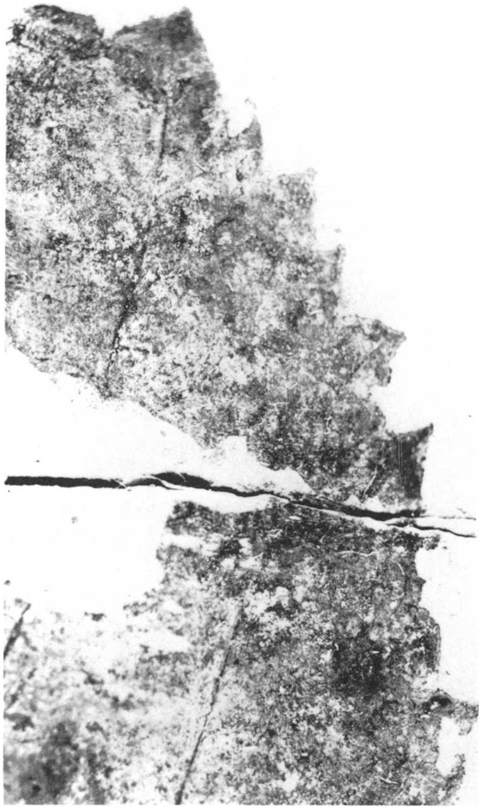

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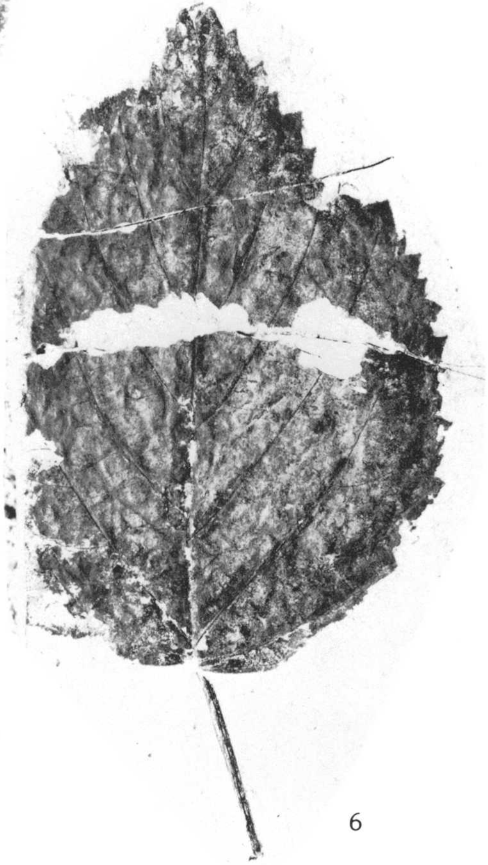

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CORNUS AND *TSUKADA*

PLATE 15

[All natural size unless otherwise indicated]

Figures 1–4. *Tsukada davidiifolia* Wolfe et Wehr (p. 21).

1, 2, 4. Holotype UW 71095. Figs. 2, 4, × 7.5. 3 Paratype UW 71081. Loc. 8428.

5. *Davidia involucrata* S. et Z. (introduced for comparison). *Wolfe*, s.n., USGS reference coll. 82. × 7.5.

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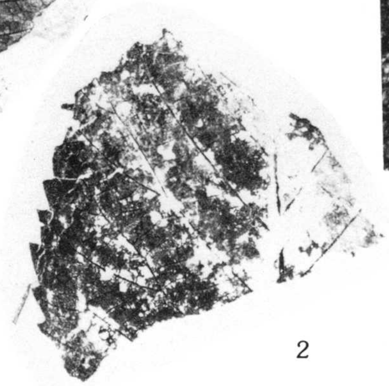

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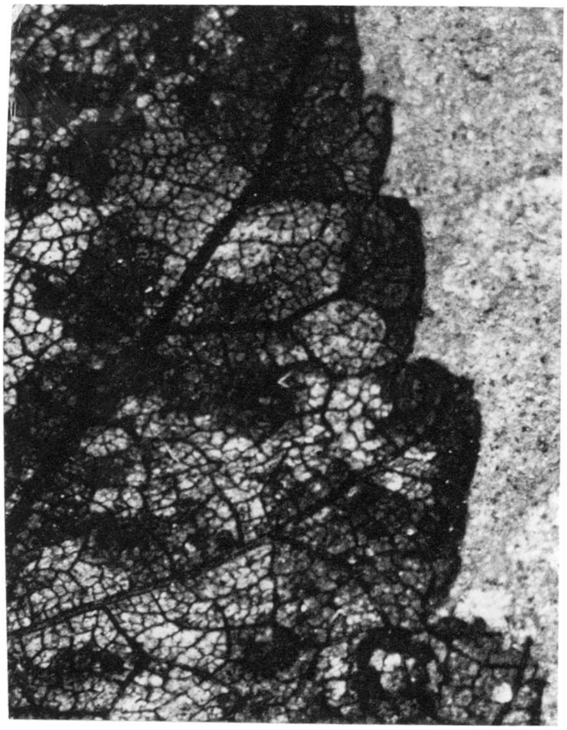

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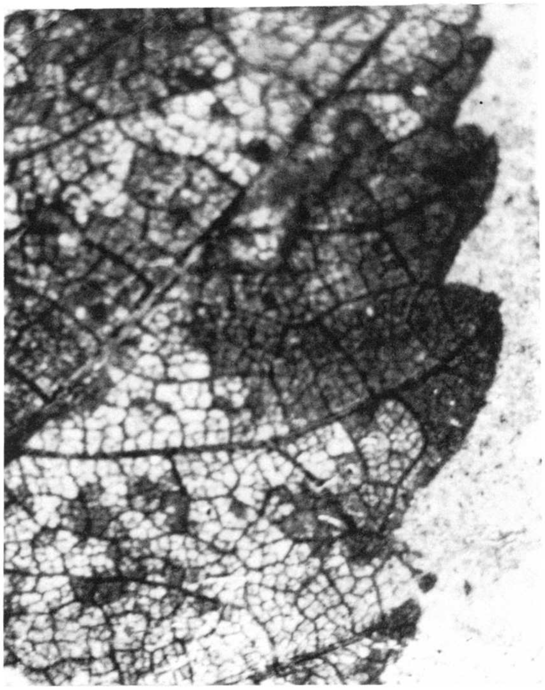

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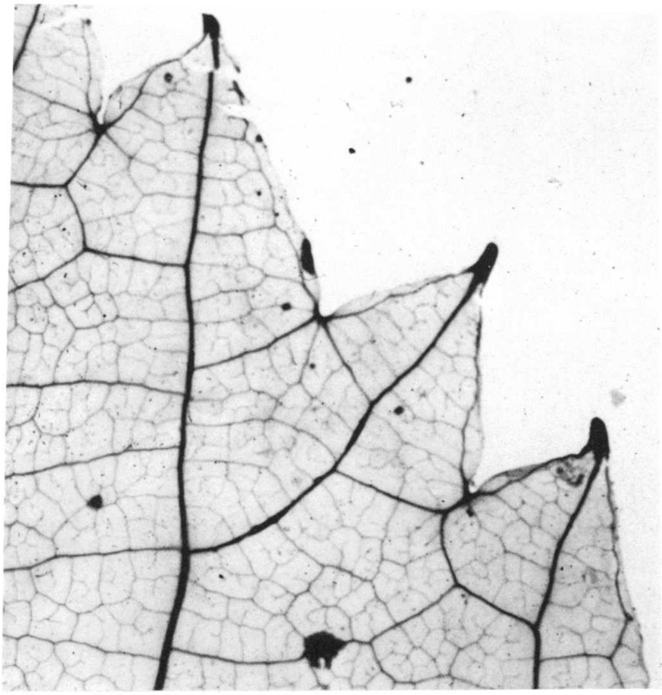

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TSUKADA

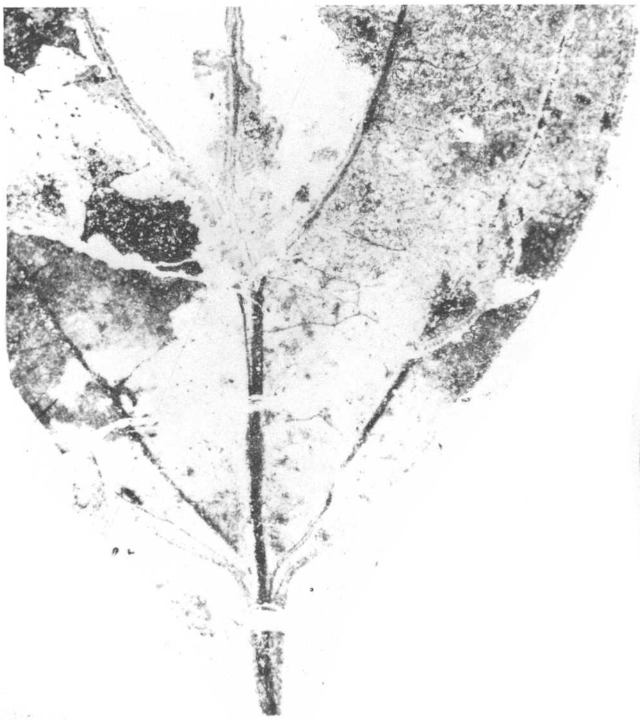
PLATE 16

[All natural size unless otherwise indicated]

Figures 1–3. *Schoepfia republicensis* (La Motte) Wolfe et Wehr (p. 22)
Hypotypes USNM 32683, UW 39194. Fig. 2, × 4 (enlargement of fig. 3). Loc. 8428.

4, 5. *Republica hickeyi* Wolfe et Wehr (p. 22)
Hypotypes USNM 32697A, B. Fig. 5, × 4. Loc. 8428.

1



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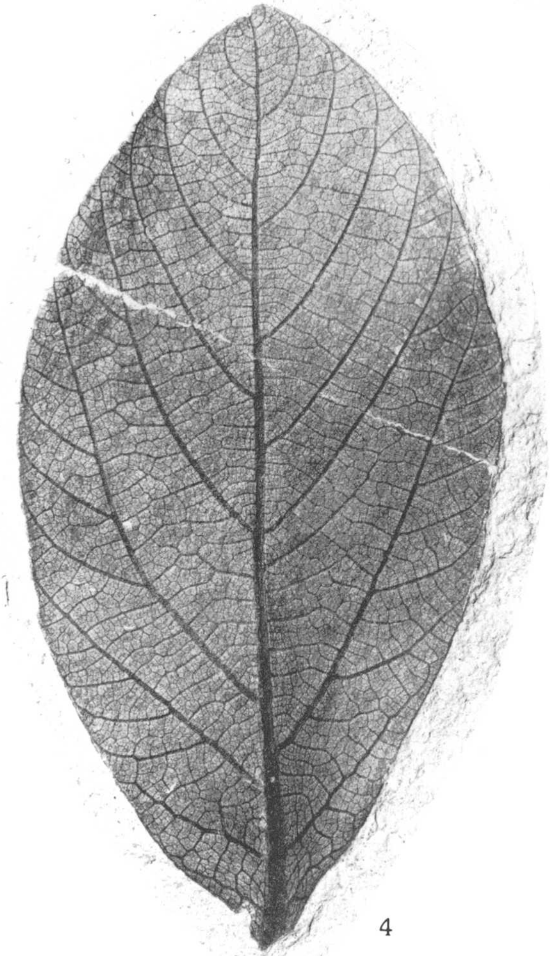

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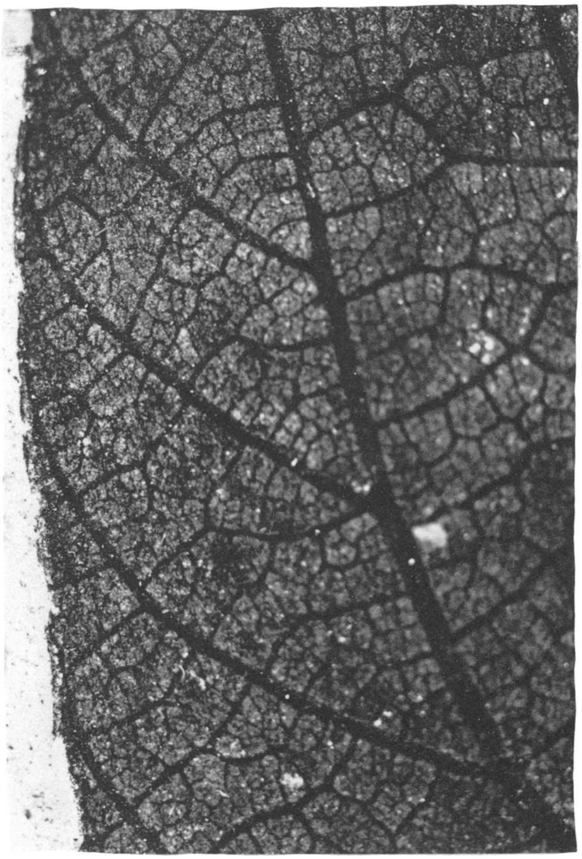

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SCHOEPFIA AND *REPUBLICA*