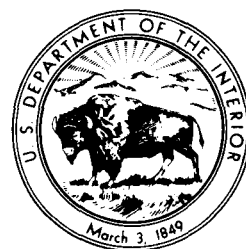


The Miocene Seldovia Point Flora from the Kenai Group, Alaska

By JACK A. WOLFE *and* TOSHIMASA TANAI

GEOLOGICAL SURVEY PROFESSIONAL PAPER 1105



UNITED STATES DEPARTMENT OF THE INTERIOR

CECIL D. ANDRUS, *Secretary*

GEOLOGICAL SURVEY

H. William Menard, *Director*

Library of Congress Cataloging in Publication Data

Wolfe, Jack A. 1936-
The Miocene Seldovia Point flora from the Kenai group, Alaska.

(Geological Survey professional paper ; 1105)

Bibliography: p. 45-47.

Includes index.

1. Paleobotany--Miocene. 2. Paleobotany--Alaska--Cook Inlet region.
I. Tanai, Toshimasa, joint author. II. Title. III. Series: United States.
Geological Survey. Professional paper ; 1105.

QE929.W64

561'.2'097983

79-20550

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402

Stock number 024-001-03282-1

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THE MIOCENE SELDOVIA POINT FLORA FROM THE KENAI GROUP, ALASKA

By JACK A. WOLFE and TOSHIMASA TANAI

ABSTRACT

Approximately 60 species of megafossil plants are illustrated and are assigned to 45 genera. Most of the species are dicotyledonous, although monocotyledons, ginkgo, conifers, and ferns are also represented. Nine species of dicotyledons and one species of monocotyledon are described as new. The flora includes the first described representatives of *Cyclocarya*, *Nymphar*, *Sorbaria*, *Pueraria*, *Decodon*, *Kalopanax*, *Lonicera*, and *Alisma* in the North American Tertiary.

The plant-bearing beds are considered to be part of the Kenai Group. The West Foreland Formation (late Paleocene) is excluded from the Kenai Group, but the following formational units are accepted within the group, in ascending order: Hemlock Conglomerate (early Oligocene), Tyonek Formation (early Oligocene through middle Miocene), Beluga Formation (middle and late Miocene), and Sterling Formation (late Miocene and Pliocene). Paleobotanical evidence indicates that the Seldovia Point beds are equivalent to part of the Tyonek Formation; the geology of these beds indicates that they represent deposits that filled a valley to the south of the main part of the Kenai basin. Paleobotanical correlations also indicate that the Seldovia Point flora is, in provincial terminology, of late Seldovian age and further that the upper part of the Seldovian Stage is of late early and early middle Miocene age.

Analysis of the Seldovia Point assemblage from both floristic and physiognomic standpoints indicates that the assemblage represents Mixed Northern Hardwood forest, although palynological data indicate that coniferous forest was close by. The Seldovia Point assemblage has several genera that no longer participate in Mixed Northern Hardwood forest and that today are restricted to broad-leaved evergreen or Mixed Mesophytic forests. These differences are interpreted in light of the history of Mixed Northern Hardwood and related forest types during the Neogene.

Analysis of the Seldovia Point assemblage in terms of the derivation of component lineages indicates that of those species whose lineages are reasonably well known, about one-third of the species are of east Asian origin, one-third of west American (middle latitude) origin, and one-third of high-latitude origin. The lack of penetration of west American species southward into eastern Asia and the lack of penetration of east Asian species southward into middle latitudes of western North America are suggested to be the result of the loss of genetic plasticity in regard to adaptation to different photoperiodic conditions.

Paleoclimatic conditions inferred from the Seldovia Point assemblage strongly indicate that since the middle Miocene there has been a moderate decline in mean annual temperature and a major decrease in mean annual range of temperature. Analysis of other middle Miocene plant assemblages at middle latitudes in both eastern Asia and western North America indicates that the same basic pattern of temperature shifts occurred, although the changes in mean annual range of temperature were most pronounced in western North America and particularly Alaska. The primary temperature parameter that was altered was warm-month temperatures, which underwent a severe decline; this decline in summer tempera-

tures is probably one of the causes of the initiation of glaciation at high latitudes during the late Cenozoic. The Seldovia Point assemblage, when compared to Alaskan assemblages of early and late Miocene age, is consistent with the concept of a middle Miocene warming, which has been previously documented at middle latitudes.

INTRODUCTION

The floras of the Kenai Group of the Cook Inlet region in Alaska have attracted the interest of paleobotanists for over 100 years. Plants collected by or for Furuhjelm, at one time governor of what was then Russian America, were submitted to the Swiss paleobotanist Oswald Heer; these plants came from two localities—one near the village of Ninilchik on the east shore of Cook Inlet and the second supposedly near English Bay on the southwestern part of the Kenai Peninsula (fig. 1). These plants, along with those from Kuiu Island in southeastern Alaska, were described and illustrated by Heer (1869a) as a part of his monumental *Flora Fossilis Arctica*.

The acquisition of Alaska by the United States in 1867 led ultimately to investigations of the Cook Inlet region by members of the U.S. Geological Survey. These investigations included collection and analysis of the fossil floras of the Kenai Group (for example, Martin and others, 1915), but the only comprehensive taxonomic analysis of these floras prior to the 1960's was by Hollick (1936). It is notable that these earlier collections were small and that none were made by paleobotanists. Hollick's fieldwork in Alaska involved collecting plants from Cretaceous rocks along the Yukon River (Hollick, 1930). Although the late R. W. Chaney discussed the floristic significance of the Kenai floras in numerous papers (for example, Chaney, 1936, 1952, 1967), he never carried out paleobotanical field investigations on the Kenai floras, which occupied a central position in his concept of an "Arcto-Tertiary Geoflora."

The first paleobotanist to undertake collection of the Kenai floras was the late R. W. Brown, who made small collections from five localities in 1955. Brown, however, was nearing retirement and made only tentative, unpublished generic determinations of some of the Kenai material. The need for comprehensive field

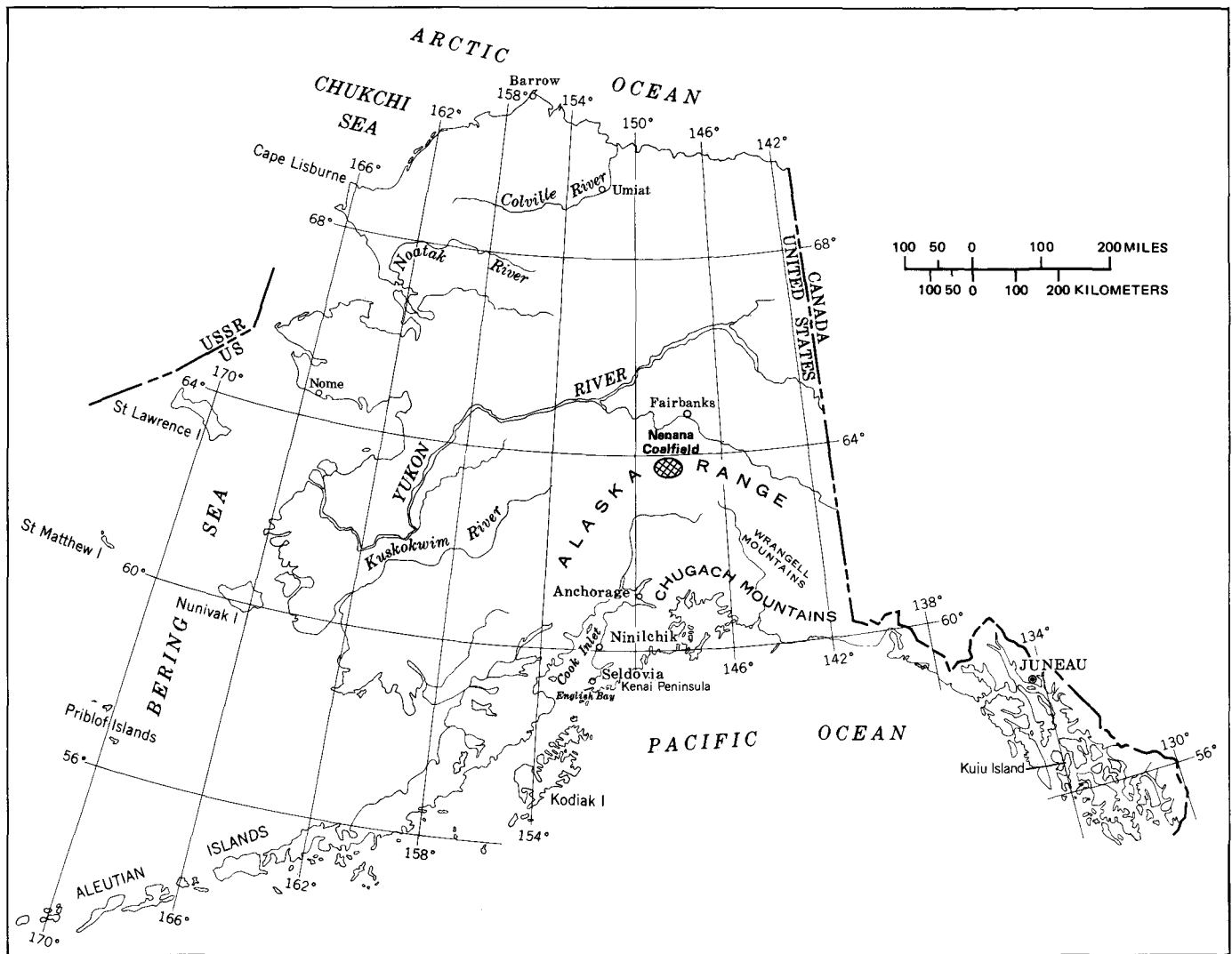


FIGURE 1.—Map of Alaska showing location of Cook Inlet region.

investigations and laboratory studies of not only the Kenai floras but also other Alaskan Tertiary floras was emphasized by many geologists working in Alaska and particularly by D. M. Hopkins. Fieldwork was initiated by Wolfe in southeastern Alaska in 1961 and was extended into the Cook Inlet region in 1962. The decision to concentrate on collection and study of the floras of the Kenai Group was made because of the historical significance of these floras, the discovery of petroleum and natural gas in Kenai rocks, and the considerable thickness of this unit, which indicated the possibility of obtaining numerous assemblages in demonstrable stratigraphic succession. Stratigraphically significant species from the Kenai Formation of former usage were discussed and illustrated by Wolfe (1966), and also incorporating palynological studies by Wolfe and E. B. Leopold, these species formed the

basis for a biostratigraphic framework for the Alaskan Neogene (Wolfe and others, 1966). Wolfe (1966) also gave a tentative list of the Seldovia Point flora.

Collections made in 1962 from localities near Seldovia and extending southwestward to Port Graham (Heer's "English Bay" material was, in fact, obtained from Coal Cove on Port Graham; see also Martin and others, 1915) were the largest obtained from the Kenai, in terms of both specimens and species. Collectively, the material from USGS paleobotanical localities 9856 (Coal Cove), 9857, and 9858 (Seldovia Point) is the basis for the Seldovia Point flora. Additional material was collected by Wolfe in 1967 from Seldovia Point and from new localities along the north shore of Kachemak Bay and elsewhere in the Cook Inlet region. Although the Seldovia Point locality was not visited, we obtained additional material from the

upper part of the Kenai Group in 1973. Added to this material is a modest but nevertheless significant collection made by C. E. Allison in 1971 at Seldovia Point.

The material now in hand from the Kenai Group allows a far better understanding of the floristic, climatic, and stratigraphic significance of the various Kenai floras. Preliminary statements on the significance of these floras have been published elsewhere (Wolfe, 1969a, 1969b, 1972), but this report presents the first thorough study of any of the Kenai floras, a study requisite for the documentation or modification of previous statements. The Seldovia Point flora is particularly significant because it allows an understanding of floristic and climatic relationships around the North Pacific Basin during the middle Miocene; many floras of this time have received detailed attention both in Japan (Tanai, 1972) and in the conterminous United States (Wolfe, 1969a).

We gratefully acknowledge the continuing encouragement of D. M. Hopkins in our studies; the geologic section of the beds at Seldovia Point is based largely on Hopkins' field observations made in 1962. Estella B. Leopold has provided us with valuable data based on her largely unpublished but extensive studies of samples from the Nenana coalfield. For assistance in particular taxonomic problems we are grateful to Professor Huzioka (Akita University) and Dr. H. D. MacGinitie (University of California, Berkeley). Dr. Carol Allison (University of Alaska) allowed us to include her university's collections from Seldovia Point in this study.

GEOLOGIC OCCURRENCE

The bulk of the Tertiary beds of the Cook Inlet region (fig. 2) have been variously referred to as the Kenai Series, Kenai Group, or Kenai Formation. As well, various informal lithologic subdivisions of the Kenai rocks have been proposed (for example, Kelly, 1963), but only recently have formal lithologic subdivisions been proposed (Calderwood and Fackler, 1972).

Three stages have been previously erected for the time interval during which the Kenai Group was deposited (Wolfe and others, 1966); in ascending order, these are the Seldovian, Homerian, and Clamgulchian. The Seldovian Stage was considered to be of Oligocene(?) through approximately middle Miocene age, the Homerian to be probably of later Miocene age, and the Clamgulchian to be largely of Pliocene age. The Seldovian stage was, moreover, informally subdivided into a lower(?) and upper(?) part based on the analysis of certain plant assemblages, some of which appeared to be older than those in the type section of the Seldovian Stage at Capps Glacier and

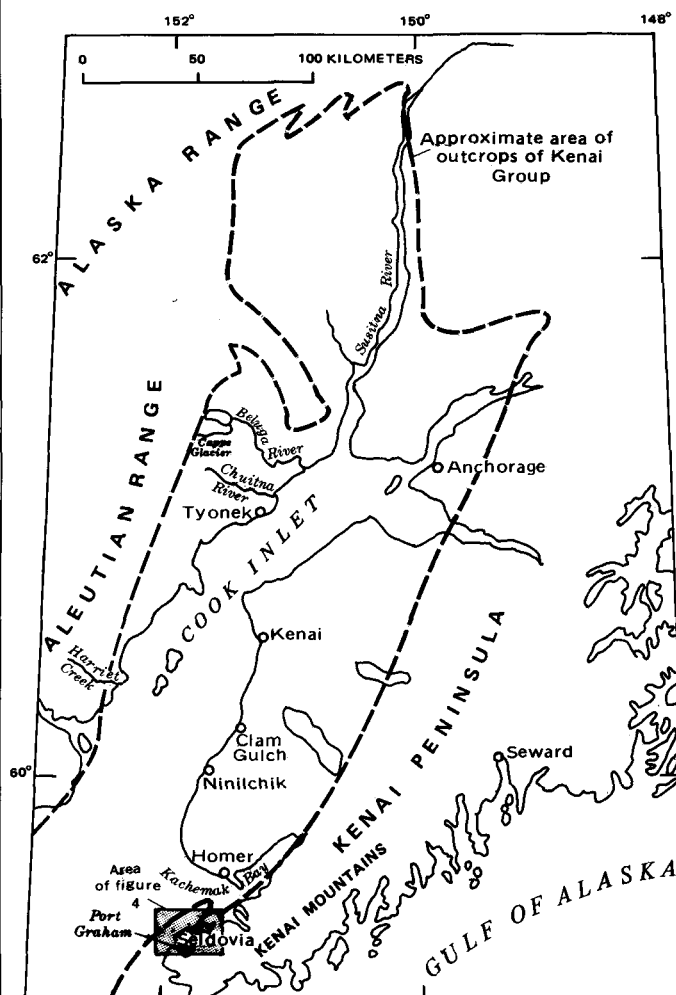


FIGURE 2.—Cook Inlet region, showing approximate extent of outcrops of the Kenai Group.

along Chuitna River and in its reference section of the Seldovian Stage at Seldovia Point. Continued work (Wahrhaftig and others, 1969) indicated that in the Nenana coalfield of the central part of the Alaska Range plant assemblages approximately correlative with the lower(?) Seldovian assemblages in the Cook Inlet region were demonstrably lower stratigraphically than assemblages correlative with those in the type and reference sections of the Seldovian Stage; the rocks containing these lower(?) Seldovian assemblages were consequently excluded from the Seldovian Stage. Wolfe (1969b, 1972, 1977) has applied the term Angoonian Stage to these Oligocene assemblages formerly termed lower(?) Seldovian (fig. 3).

We are here accepting the elevation of the Kenai Formation to the status of Kenai Group as proposed by Calderwood and Fackler (1972), with the exception that we exclude their West Foreland Formation from the Kenai Group, defined as "a tuffaceous siltstone-

Wolfe and others (1966)			Wahrhaftig and others (1969)	Wolfe (1969b, 1972)	This report				
Series	Stage	Formation	Stage	Stage	Stage	Group	Formation	Series	
Pliocene	Clamgulchian Stage	Kenai Formation	Clamgulchian Stage	Clamgulchian Stage	Clamgulchian Stage	Kenai Group	Sterling Formation	Pliocene	
	Homerian Stage		Homerian Stage	Homerian Stage	Homerian Stage		Beluga Formation	Upper	
Upper(?) part of Seldovian Stage	Seldovian Stage (= upper(?) Seldovian)		Seldovian Stage	Seldovian Stage	Seldovian Stage		Tyonek Formation	Middle	Miocene
Lower(?) part of Seldovian Stage								Lower	
Oligocene	?		Pre-Seldovian (= lower(?) Seldovian)	Angoonian Stage	Angoonian Stage		Hemlock Conglomerate	Oligocene	

FIGURE 3.—Changes in usages of stages and ages in the Oligocene through Pliocene series of Alaska.

claystone unit containing a few conglomeratic sandstone and thin coal beds**** (Calderwood and Fackler, 1972, p. 741). Such lithology differs markedly from the overlying Kenai Group, which typically lacks tuffaceous material; indeed, we have observed only one bed of volcanic ash (primarily glass) in the Kenai; this ash bed occurs in the upper part of the Kenai Group south of Clam Gulch. Some coalbeds of the upper part of the Kenai Group also contain ash partings (Triplehorn and others, 1977).

The West Foreland Formation, as noted by Calderwood and Fackler (1972), is probably exposed at the surface along the west side of Cook Inlet. One of the most extensive surface exposures of this unit is south of Capps Glacier and includes rocks mapped as "lower Kenai" by Barnes (1966). These rocks are highly tuffaceous and are angularly unconformable beneath the type section of the Seldovian Stage; elsewhere the West Foreland Formation has a consistent angularly unconformable relationship to overlying units (Calderwood and Fackler, 1972). Although these rocks at Capps Glacier are more conglomeratic than at the

type section of the West Foreland, they are also at the margin of the depositional basin and might be expected to be conglomeratic in part. The age of the West Foreland Formation is not certainly known. If, however, the beds south of Capps Glacier are part of this unit, leaf samples from these beds indicate a latest Paleocene age for the West Foreland (Wolfe, unpub. data). This would indicate that an interval of at least 20 million years is represented by the unconformity between the West Foreland Formation and the Kenai Group, which is probably no older than early Oligocene.

As here recognized, the Hemlock Conglomerate (Calderwood and Fackler, 1972) is the basal formation of the Kenai Group. Surface exposures of the Hemlock Conglomerate are not certainly known, although some of the nonvolcanic conglomerate mapped as "lower Kenai" by Barnes (1966) may represent this unit. Inasmuch as the Hemlock Conglomerate is not separated from the overlying Tyonek Formation by an unconformity and is only about 200 to 250 m thick (Calderwood and Fackler, 1972), the Hemlock is prob-

ably not much older than the Tyonek Formation; the Hemlock Conglomerate is considered to be of early Oligocene age. Indeed, it is possible that the Hemlock is a discontinuous basal conglomerate of the Tyonek Formation and that some typical Tyonek beds may be isochronous with the Hemlock (for example along Harriet Creek).

Calderwood and Fackler (1972) considered that they had only redefined Spurr's (1900) "Tyonek beds." Because they designated the type section in a well, however, it is clear that their Tyonek Formation is a new concept. Additionally, it was previously noted (Wolfe and others, 1966) that fossils from the outcrops of the "Tyonek beds" near Tyonek represent the Homerian Stage, the type section of which (Wolfe and others, 1966), as Calderwood and Fackler pointed out, is part of the next younger Beluga Formation. Calderwood and Fackler (1972) correlated the Kenai Group along the upper part of the Chuitna River with the type section of the Tyonek Formation; this correlation places the type section of the Seldovian Stage within the Tyonek Formation. The Tyonek Formation therefore includes rocks of early and middle Miocene age. That the Tyonek Formation also includes rocks of early and late Oligocene Age (Angoonian) is indicated by Calderwood and Fackler's statement (1972, p. 745) that the Chuitna River section is incomplete and evidenced by basal coalbearing rocks of the Tyonek Formation exposed on Harriet Creek that are of pre-Seldovian age. Elsewhere in Alaska (Wahrhaftig and others, 1969), rocks correlated with the Kenai Group, considered by Wolfe, Hopkins, and Leopold (1966) to be "lower(?) Seldovian," have been excluded from the Seldovian Stage and are now considered to be of early and late Oligocene age. As well, the Tyonek Formation presumably extends into the middle Miocene. This is indicated by the fact that the highest exposures of the Tyonek Formation along Chuitna River are of Homerian age, and no unconformity between the Seldovian and Homerian stages was noted in this section. Thus, the Tyonek Formation is here considered to range in age from early Oligocene through middle Miocene. Considering that the Tyonek Formation has such a great age range and considering the thickness of the unit (over 2,300 m), this unit may be capable of further subdivision. The beds at Seldovia Point are thus probably equivalent in age to the Tyonek Formation.

The Beluga Formation (Calderwood and Fackler, 1972) is the next youngest unit of the Kenai Group. Calderwood and Fackler correlated the Kenai Group exposed near Homer, representing the Homerian Stage, with the Beluga Formation, and hence this part of the Beluga is of middle and late Miocene age. However, the lower part of the reference section of the

Clamgulchian Stage along Kachemak Bay includes calcareous beds, and Calderwood and Fackler (p. 751) indicate that the highest occurrence of calcareous beds in the Kenai Group is in the upper half of the Beluga Formation. Thus, all the Beluga Formation is here considered to be of late middle and late Miocene age. We emphasize, however, that we are accepting the placement of the Miocene-Pliocene boundary generally accepted by European geologists at about 5-6 million years.

The youngest unit of the Kenai Group is the Sterling Formation (Calderwood and Fackler, 1972). The correlation of this unit with surface outcrops from Clam Gulch south beyond Ninilchik (type exposures of the Clamgulchian Stage) appears convincing (Calderwood and Fackler, 1972), and thus the Sterling Formation is considered to be of late Miocene and Pliocene age.

The Seldovia Point flora was collected from beds of the Kenai Group exposed in a discontinuous series of outcrops in the sea cliffs from Barabara Point west and south to Coal Cove on Port Graham (fig. 4). These beds are typically weakly lithified, although the leaf impressions were obtained from limy, indurated lenses. These remnants of the Kenai Group rest un-

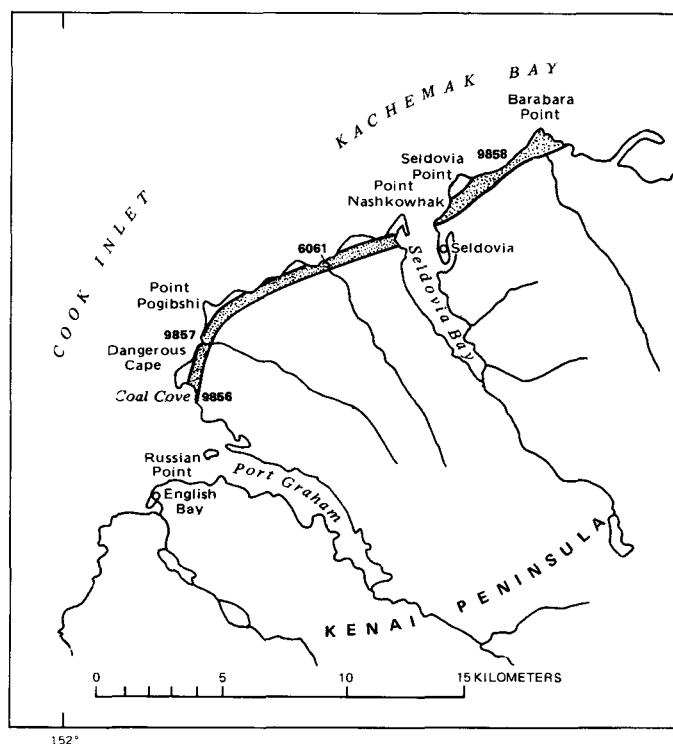


FIGURE 4.—Map of Seldovia area. Outcrops of Kenai Group shown by stippling; numbers refer to U.S. Geological Survey paleobotanical localities.

conformably on altered Mesozoic rocks, which also form the headlands that have protected these remnants from total erosion.

The outcrop of the Kenai Group at Coal Cove probably yielded the collection of plants described by Heer (1869a), and attributed to a locality on English Bay. No Tertiary rocks are exposed on English Bay, and the Coal Cove outcrops were mined for coal for Russian vessels. At the east end of this outcrop, the Kenai dips gently off the Mesozoic basement and contains coarse clasts probably derived from the subjacent Mesozoic rocks; that is, the Kenai rocks resemble a fossilized talus. Indeed, all outcrops of the Kenai Group from the Coal Cove to Barabara Point have taluslike appearances near the contacts with the Mesozoic rocks. In places, coalified logs or casts of logs are abundant in the Kenai. Where observable in fiords, the outcrops of the Kenai Group do not extend far inland but are apparently continuous along a narrow belt that parallels the present coast (fig. 4).

A reasonable interpretation of the lithology and pattern of outcrops of the Kenai Group in this area is that the Kenai here represents the remnants of an ancient drainage system. This system drained from the southwest into the main part of the Kenai basin, as indicated by the greater thickness and areal extent of the Kenai Group at Seldovia Point (fig. 5) in comparison to the outcrops near Point Pogibshi and on Coal Cove. Although most of the rocks represent fluvial deposits, some of the sediments were deposited in slowly moving water; this is indicated not only by the presence of some coals but also by the abundance at locality 9858 of *Potamogeton* and *Nymphar*.

The exact altitude at which the Seldovia Point beds accumulated is not known, but it was probably less than about 100 m. Although no marine beds are known in any part of the Kenai Group, the great thickness of this unit (over 8,000 m), the great areal extent of the basin (about 110 km wide and 330 km long), and the duration of apparently continuous deposition (about 25 m.y.) all indicate deposition near sea level for the main part of the basin. The fact that the Seldovia Point beds (particularly the plant-bearing beds) include fine-grained beds associated with coal also indicates that the drainage had a low gradient. We thus think that the Seldovia Point beds were not deposited at an altitude appreciably higher than the remainder of the Kenai Group.

The nearest marine beds of middle Miocene age to the Seldovia Point localities are on the northeastern part of Kodiak Island, about 170 km to the south (fig. 1). The marine megafossils from the Kodiak beds indicate shallow water (W. O. Addicott, oral commun., Dec. 1973), and this indicates that during the middle Miocene the sea did not extend to the north much be-

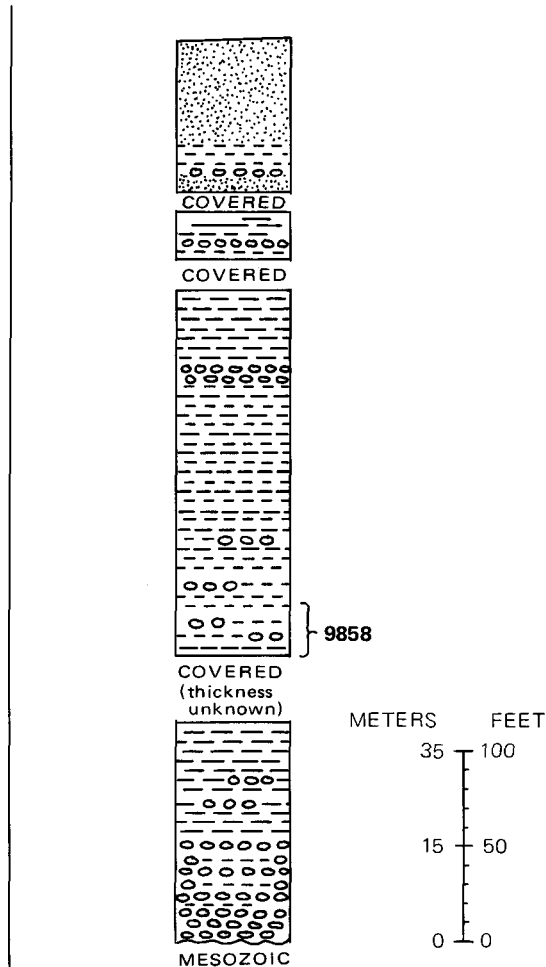


FIGURE 5.—Section of Kenai Group exposed between Seldovia and Barabara Points. Number refers to U.S. Geological Survey paleobotanical locality.

yond northeastern Kodiak Island. To the east of Seldovia, the nearest occurrence of middle Miocene marine beds is in the Yakataga District, about 500 km east and slightly north of Seldovia. Some clastic rocks of the Kenai Group indicate derivation from the area now occupied by the Chugach Mountains, but such rocks are younger than the Beluga Formation, which is probably of Homerian and early Clamgulchian age. There is thus no evidence that the western part of the Chugach Mountains were elevated during the middle Miocene.

Most sediments of the Kenai basin deposited during the early and middle Miocene were apparently derived from the southern part of the Alaska Range (Calderwood and Fackler, 1972, p. 751, 754). Presumably that source area had considerable relief, and these mountains—about 150 km from Seldovia—were the mountains nearest to Seldovia. The central part of the Alaska Range to the north of the Kenai basin was

apparently a low region during the early and middle Miocene, as attested to by the considerable thickness of coals in the Suntrana Formation and the extensive lacustrine deposits of the Sanctuary Formation (Wahrhaftig and others, 1969).

AGE

The Seldovia Point flora has had varied age assignments. Originally dated simply as Miocene by Heer (1869a), the flora from the Port Graham locality (Heer's English Bay locality) was then—without any substantial factual data—assigned to the Eocene Epoch (Knowlton, 1894). The Eocene age was accepted without question by a number of paleobotanists (for example, Hollick, 1936; Chaney, 1936). Reanalysis of illustrations of the material from Port Graham led Wolfe (in MacNeil and others, 1961) to conclude that this flora was no older than late Oligocene; MacGinitie (1962) concurred in this opinion and suggested that the flora might be as young as early Miocene. Basing their conclusions on new material from both Port Graham and Seldovia Point, Wolfe, Hopkins, and Leopold (1966) assigned the Seldovia Point flora (including the Port Graham locality) to the Seldovian Stage, which was thought to be of late Oligocene(?) and earlier Miocene age. Although an attempt was made to reassign this flora to the early Oligocene (Chaney, 1967), the factual basis for this reassignment proved illusory (Wolfe, 1969b). In the most recent summary of Alaskan Tertiary floras, the Seldovia Point assemblage was again assigned to the early Miocene (Wolfe, 1972), but it has also been suggested that the flora is of middle Miocene age (Tanai, 1973). The question of whether the flora is of early Seldovian (earliest Miocene) or late Seldovian (late early and early middle Miocene) age is particularly significant in constructing paleoclimatic models.

The rocks containing the Seldovia Point assemblage were designated as a reference section for the Seldovian Stage (Wolfe and others, 1966). This designation was made primarily because the flora from this reference section was then (and remains) considerably richer than the flora from the type section of the Seldovian Stage at Capps Glacier and along the Chuitna River. Considerable documentation for the early and middle Miocene age of the Seldovian Stage has been presented (Wolfe, 1969b).

The occurrence of the Seldovia Point assemblage in an isolated outcrop of the Kenai Group requires that the placement of these rocks within subdivisions of the Seldovian Stage, however, be based solely on paleobotanical evidence. Only two informal subdivisions—lower and upper—of the Seldovian Stage

are recognized at Capps Glacier and along the Chuitna River; plant megafossils have been found primarily in the lower part of the section (Wolfe and others, 1966), but one small flora (loc. 9848 of Wolfe and others, 1966) is probably in the upper part of the Seldovian Stage, judging from Barnes' (1966) geologic map. Several pollen assemblages, have, however, been studied from both the upper and lower parts of the type section of the Seldovian Stage (Wolfe and others, 1966).

The upper Seldovian has been equated to the middle Miocene, the Homerian to the upper Miocene, and the Clamgulchian to the Pliocene (Wolfe, 1969b, 1972). In terms of the now widely accepted planktonic foraminiferal chronology, however, the upper Seldovian is of late early and early middle Miocene age and the Homerian is of late middle and early late Miocene age (Wolfe, 1980). The Clamgulchian has radiometric ages in its lower part that indicate a latest Miocene age (Triplehorn and others, 1977); the upper Clamgulchian is assumed to be of Pliocene age.

The rocks of the Nenana coalfield of the central Alaska Range (fig. 1) span the entire Seldovian Stage. The lowest megafossil and microfossil assemblages in this conformable sequence are pre-Seldovian, and the highest rocks are of Homerian and Clamgulchian age (Wahrhaftig and others, 1969). This sequence has also been extensively sampled for pollen. Palynologically, some differences are apparent between the pollen assemblages of the lowest part of the Seldovian (the upper part of the Healy Creek Formation) and the remainder of the stage (Sanctuary Formation and the overlying Suntrana Formation).

Upper Seldovian pollen assemblages from the Alaska Range appear to have a greater diversity of broad-leaved trees than do lower Seldovian assemblages. *Ulmus* and *Liquidambar* occur more frequently in upper (table 1) than lower Seldovian assemblages, and *Fagus* and *Tilia*, which are present in

TABLE 1.—Average percentages of samples containing pollen of certain broad-leaved genera in the Seldovian rocks of the Nenana coalfield, Alaska Range

[Based on unpublished data supplied by E. B. Leopold]

	Upper part of Healy Creek Formation (12 samples)	Sanctuary and Suntrana Formations (28 sam- ples)
<i>Fagus</i>	0	29
<i>Quercus</i>	25	29
<i>Liquidambar</i>	17	29
<i>Ulmus</i>	33	89
<i>Tilia</i>	0	21
<i>Carya</i>	42	54
<i>Juglans</i>	8	18
<i>Pterocarya</i>	83	71
<i>Ilex</i>	58	61

about one-fourth the upper Seldovian samples, are absent in lower Seldovian samples. The sample from Seldovia Point has *Ulmus*, *Liquidambar*, *Tilia*, and *Fagus*; the megafossil flora from Seldovia Point also contains representatives of all four genera. Of the four genera, only *Ulmus* is yet known from any lower Seldovian megafossil assemblage. These data indicate that the Seldovia Point flora is of late Seldovian (probably late early and early middle Miocene) age.

Although the megafossil assemblages from the Seldovian rocks of the Nenana coalfield are admittedly small, these can also be interpreted to indicate that the Seldovia Point flora is of late Seldovian age. The flora of the upper part of the Healy Creek Formation (lower Seldovian) is known from moderate-size collections that include:

Metasequoia sp.
Populus kenaiana Wolfe
Populus aff. *P. eotremuloides* Knowlt.
Salix sp.
Carya sp.
Pterocarya nigella (Heer) Wolfe
Alnus cappsi (Holl.) Wolfe
Betula aff. *B. thor* Knowlt.
Quercus furuhjelmi Heer
Ulmus sp.
Cladrastis aff. *C. lutea* Michx.
Acer chaneyi Knowlt.

The flora of the overlying Sanctuary Formation was thought to be very small (Wahrhaftig and others, 1969), but this was due to considering locality 7476 to be in the Healy Creek Formation. Further discussion with Wahrhaftig and reanalysis of Prindle's original field notes indicate that this locality is probably in the Sanctuary Formation. The flora from this locality includes:

Metasequoia sp.
Pterocarya nigella (Heer) Wolfe
Alnus healyensis Wolfe
Fagus antipofi Heer
Quercus furuhjelmi Heer
Cocculus auriculata (Heer) Wolfe

To the above list can be added certain elements of the overlying Suntrana flora:

Populus kenaiana Wolfe
Cyclocarya ezoana (Tanai et Suz.) Wolfe et Tanai
Alangium milii Wolfe et Tanai
Ulmus sp.

Probably significant is that the known Upper Healy Creek flora does not contain certain species that are present in both the Seldovia Point flora and in the flora of the Sanctuary and Suntrana Formations: *Cyclocarya ezoana*, *Fagus antipofi*, *Cocculus auriculata*, and *Alangium mikii*.

The differences between the microfossil assemblages of the upper and those of the lower part of the type section of the Seldovian Stage are not as apparent as in the Alaska Range section, primarily because fewer samples from the type section have been analyzed. In the three lowest samples (locs. D1946, D1953, D1952 of Wolfe and others, 1966), however, *Tilia* is absent, and only one sample contains *Liquidambar* (and the genus is so rare that it did not appear in the pollen counts). In contrast, in the four upper Seldovian pollen samples (locs. D1720, D1718, D1719, D1949) one sample contained rare *Tilia*, and two samples contained significant amounts of *Liquidambar* pollen.

The megafossil assemblages from the lower part of the type section of the Seldovian Stage are based on collections almost as extensive as those from Seldovia Point and were obtained from four horizons. The flora, however, is depauperate in comparison to that at Seldovia Point. Although some species are common to both floras, and in particular *Alangium mikii* also occurs at Capps Glacier, the Capps Glacier assemblage lacks the other three species considered to be significant in correlating the Seldovia Point with the Sanctuary-Suntrana flora. The small collection from the upper part of the Seldovian section along Beluga River (loc. 9848) contains only a few species, but it is perhaps significant that this flora has the only other known occurrence of *Acer ezoanum* in Alaska.

Certainly further collecting in both the type section of the Seldovian Stage and in the Seldovian rocks of the Alaska Range is desirable, but the available data—from both megafossils and microfossils—indicate that the Seldovia Point flora is probably of late Seldovian age. Tentative correlations between the Cook Inlet region and Nenana coalfield are given in figure 6.

The basis for the early and middle Miocene age of the Seldovian Stage has been discussed at some length previously (Wolfe, 1969b). The current systematic treatment of the Seldovia Point flora, however, allows a more definitive basis for correlating this flora with other plant assemblages at lower latitudes on either side of the Pacific Ocean. Most of the gymnospermous species—at least those based on megascopic characters—have such long ranges during the Tertiary as to be of little value in biostratigraphy. It is only certain dicotyledonous species that are of most value in establishing correlations.

Even some of the dicotyledonous species that occur outside of Alaska are of less value than others in biostratigraphy. *Nymphar ebae*, for example, is known both at Seldovia Point and in the early Miocene Aniai flora of Honshu (Huzioka, 1964), but because so little is known of the evolution of Nymphaeaceae during the Tertiary, the stratigraphic value of this species is

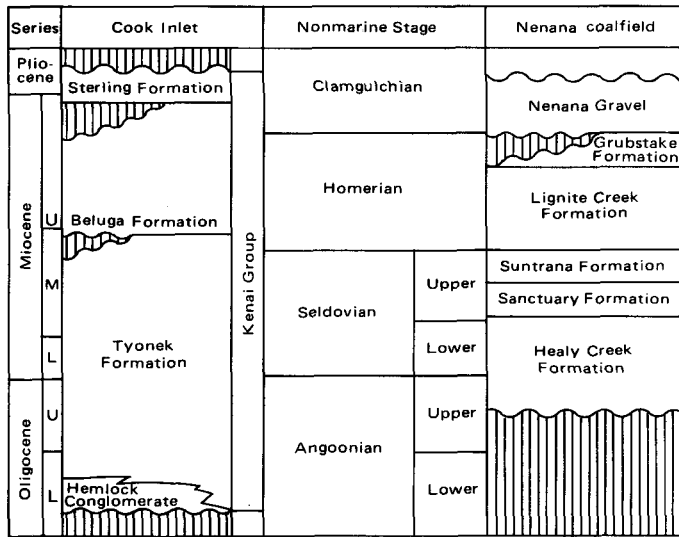


FIGURE 6.—Suggested correlations of the Kenai Group and the coal-bearing group of the Nenana coalfield. Stage nomenclature follows Wolfe, Hopkins, and Leopold (1966) and Wolfe (1968, 1969b).

uncertain. In contrast, the occurrence of *Acer ezoanum* is much more significant in that this species is considered to be a descendant of the Oligocene *S. kushiroanum* (Tanai, 1970, 1972). Similarly, the occurrence in the Seldovia Point flora of species such as *Platanus bendirei* (see p. 29) is also of considerable significance. In table 2 are listed the Seldovia Point species that occur outside Alaska and the known ranges of these species.

Data presented in table 2 indicate that the Seldovia Point flora is probably of late early or early middle Miocene age. This age is consistent with the occurrence of some Seldovian species elsewhere in Alaska in beds independently dated from marine invertebrates (Wolfe, 1969a). We emphasize that, as discussed in the section on vegetation, the Seldovia Point assemblage represents a vegetational type cooler than that found in the late early to early middle Miocene of Japan and the conterminous United States. The occurrence of some species both at Seldovia Point and farther to the south is analogous to the present distribution of certain woody species that (1) occur from Japan to Alaska and at low altitudes to the conterminous United States (for example *Oplopanax horridum* (J.E. Sm.) Miq. and *Myrica gale* L.), (2) occur from Alaska to the conterminous United States at low altitudes (for example *Malus fusca* (Raf.) Sarg. and *Populus trichocarpa* Torr. et Gray), and (3) occur from Alaska to Japan (for example, *Rhododendron camtschaticum* Pall. and *Phyllodoce aleutica* (Spreng.) Heller). We suggest that the geologic ranges of many dicotyledonous species during the Tertiary are sufficiently restricted to allow correlations to be made

TABLE 2.—Known stratigraphic ranges of *Seldovia Point* dicotyledonous species in Japan and conterminous United States

[....., Japan; — U.S.]

Species	Oligocene	Miocene			Pliocene
		L	M	U	
<i>Nymphar ebae</i>			---		
<i>Cocculus auriculata</i>			-----		
<i>Liquidambar pachyphylla</i>			-----		
<i>Platanus bendirei</i>			-----		
<i>Eucommia montana</i> (cf.)	---				
<i>Ulmus knowltoni</i>			-----		
<i>Ulmus ovyheensis</i>			-----		
<i>Ulmus speciosa</i>			-----		
<i>Zelkova browni</i>			-----		
<i>Zelkova ungeri</i>			-----		
<i>Alnus cappsi</i>			-----		
<i>Alnus fairi</i>			-----		
<i>Alnus healyensis</i>			-----		
<i>Betula sublutea</i> (cf.)			-----		
<i>Ostrya oregoniana</i> (cf.)			-----		
<i>Fagya antipofi</i>			-----		
<i>Carya bendirei</i>			-----		
<i>Cyclocarya ezoana</i>			-----		
<i>Pterocarya nigella</i>			-----		
<i>Populus kenaiana</i>			-----		
<i>Tilia subnobilis</i>			-----		
<i>Cladrastis aniensis</i> (cf.)			-----		
<i>Pueraria mothunbergiana</i>			-----		
<i>Hemitrapa borealis</i>			-----		
<i>Acer glabroides</i>			-----		
<i>Acer heterodontatum</i>			-----		
<i>Acer ezoanum</i>			-----		
<i>Nyssa knowltoni</i> (cf.)			-----		
<i>Alangium mikii</i>			-----		
<i>Kalopanax n-suzuki</i>			-----		
Total	6	21	29	13	3

irrespective of the latitudes at which the species are found.

FLORISTIC COMPOSITION

In the following list, the classification of the dicotyledons is that of Takhtajan (1969):

- Pterophyta
 - Filicinae
 - Filicidae
 - Aspidiales
 - Aspidiaceae
 - Dryopteris* sp.
 - Onoclea sensibilis* Linnaeus
- Coniferophyta
 - Coniferae
 - Coniferidae
 - Coniferales
 - Taxodiaceae
 - Glyptostrobus europaeus* (Brongniart) Heer
 - Metasequoia* cf. *M. glyptostroboides* Hu et Cheng
 - Ginkgoidae
 - Ginkgoales
 - Ginkgoaceae
 - Ginkgo biloba* Linnaeus

- Magnoliophyta (Angiospermae)
 Magnoliatae (Dicotyledones)
 Magnoliidae
 Magnolianae
 Nymphaeales
 Nymphaeaceae
Nymphar ebae (Huzioka) Ozaki
 Ranunculidae
 Ranunculanae
 Ranunculales
 Menispermaceae
Cocculus auriculata (Heer) Wolfe
 Hamamelididae
 Hamamelidanae
 Cercidiphyllales
 Cercidiphyllaceae
Cercidiphyllum alaskanum Wolfe et Tanai
 Hamamelidales
 Hamamelidaceae
Liquidambar pachyphylla Knowlton
 Platanaceae
Platanus bendirei (Lesquereux) Wolfe
 Eucommiales
 Eucommiaceae
Eucommia cf. *E. montana* R. W. Brown
 Urticales
 Ulmaceae
Celtis sp.
Ulmus knowltoni Tanai et Wolfe
Ulmus ovyheensis H. V. Smith
Ulmus speciosa Newberry
Ulmus sp.
Zelkova browni Tanai et Wolfe
Zelkova ungeri Kovats
 Fagales
 Fagaceae
Fagus antipoffi Heer
Fagus aff. *F. crenata* Blume
Quercus furuhjelmi Heer
 Betulales
 Betulaceae
Alnus cappsi (Hollick) Wolfe
Alnus fairi (Knowlton) Wolfe
Alnus healyensis Wolfe
Betula cf. *B. sublutea* Tanai et Suzuki
Carpinus seldoviana Wolfe
Corylus sp.
Ostrya cf. *O. oregoniana* Chaney
 Juglandales
 Juglandaceae
Carya bendirei (Lesquereux) Chaney et Axelrod
Cyclocarya ezoana (Tanai et Suzuki) Wolfe et Tanai
Pterocarya nigella (Heer) Wolfe
 Dilleniidae
 Dillenianaes
 Salicales
 Salicaceae
Populus kenaiana Wolfe
Populus sp.
Salix cappsensis Wolfe
Salix hopkinsi Wolfe et Tanai
Salix picroides (Heer) Wolfe
Salix seldoviana Wolfe et Tanai
 Malvanae
 Malvales
 Tiliaceae
Tilia subnobilis Huzioka
 Rosidae
 Rosanae
 Saxifragales
 Hydrangeaceae
Hydrangea sp.
 Rosales
 Rosaceae
Crataegus chamisonii (Heer) Wolfe et Tanai
Prunus kenaica Wolfe et Tanai
Prunus aff. *P. padus* Linnaeus
Sorbaria hopkinsi (Wolfe) Wolfe et Tanai
 Fabales
 Leguminosae
Cladrastis cf. *C. aniensis* Huzioka
Pueraria miothunbergiana Hu et Chaney
 Myrtanae
 Myrtales
 Lythraceae
Decodon alaskana Wolfe et Tanai
 Trapaceae
Hemitrapa borealiis (Heer) Miki
 Rutanae
 Sapindales
 Aceraceae
Acer ezoanum Oishi et Huzioka
Acer glabroides R. W. Brown
Acer grahamensis Knowlton et Cockerell
Acer heterodontatum (Chaney) MacGinitie
 Araliansae
 Cornales
 Nyssaceae
Nyssa cf. *N. knowltoni* Berry
 Alangiaceae
Alangium mikii Wolfe et Tanai

Araliaceae	
<i>Kalopanax n-suzuki</i> Wolfe et Tanai	
Celastranae	
Rhamnales	
Vitidaceae	
<i>Vitis seldoviana</i> Wolfe et Tanai	
Oleales	
Oleaceae	
<i>Fraxinus kenaica</i> Wolfe et Tanai	
Asteridae	
Lamianae	
Dipsacales	
Caprifoliaceae	
<i>Lonicera</i> sp.	
Liliatae (Monocotyledones)	
Alismidae	
Alismanae	
Alismatales	
Alismataceae	
<i>Alisma seldoviana</i> Wolfe et Tanai	
Najadales	
Potamogetonaceae	
<i>Potamogeton alaskanus</i> Wolfe et Tanai	
Incertae Sedis	
<i>Monocotylphyllum alaskanum</i> (Heer) Wolfe et Tanai	
<i>Monocotylphyllum</i> spp.	

The Seldovia Point flora is composed primarily of members of subclass Hamamelididae (23 species), and particularly the evolutionarily more advanced families such as Ulmaceae and Betulaceae. Except for the specialized aquatic *Nymphaea*, Magnoliidae are absent. Also absent or poorly represented are orders considered to be primitive in the Dilleniidae (for example, Theales and Dilleniales) and the Rosidae (Saxifragales). Within the orders of Dilleniidae and Rosidae, the Seldovia Point species typically belong to the more advanced families in the respective orders, for example Tiliaceae, Trapaceae, Aceraceae, Alangiaceae, Araliaceae. Evolutionarily, therefore, the Seldovia Point flora is highly advanced.

A comparison with the Eocene Copper Basin flora of northern Nevada (Axelrod, 1966) is informative. Although the Copper Basin assemblage grew under more equable conditions than did the Seldovia Point assemblage (see section on "Paleoclimatology"), both assemblages represent cool temperate (microthermal) vegetation. In regard to the dicotyledonous flora at the specific level, the representation of most subclasses is distinctly different in the two assemblages:

Subclass	Copper Basin (percent)	Seldovia Point (percent)
Magnoliidae -----	4	2
Ranunculidae -----	11	2
Hamamelididae -----	14	43
Dilleniidae -----	14	15
Rosidae -----	57	36
Asteridae -----	0	2

Despite having a number of families in common, the Copper Basin flora is less advanced than the Seldovia Point flora. One of the most notable differences is in the low diversity of Hamamelididae in the Copper Basin flora, a diversity that is just as low at the generic level as at the specific. Although generic diversification in the Hamamelididae had been largely completed during the Eocene Epoch (Wolfe, 1973), it is apparent that (1) many of the genera that now include microthermal members had not yet invaded microthermal climates in the Eocene and (2) specific diversity within the genera that had entered microthermal climates was low. It is thus evident that microthermal forests have undergone major changes in floristic composition.

VEGETATION

MEGAFOSSILS

All the species in the Seldovia Point flora that are thought to represent trees, shrubs, or vines were probably deciduous. Of the vegetational types described by Wang (1961) for eastern Asia, only one type—the Mixed Northern Hardwood forest—combines the exclusively broad-leaved deciduous habit with a diversity similar to that of the Seldovia Point assemblage. From the standpoint of foliar physiognomy the Seldovia Point assemblage also compares well with the Mixed Northern Hardwood forest. Only 16 percent of the Seldovia Point species have entire-margined leaves, and in Mixed Northern Hardwood forest the percentage ranges from 9 to 24 (Wolfe, 1979a). Of the various species listed by Wang (1961) as occurring in this forest, almost 20 percent have palmately lobed leaves in comparison with 16 percent for the Seldovia Point assemblage.

In floristic composition as well the Seldovia Point assemblage resembles Mixed Northern Hardwood forest, although there are some notable differences. Of the 18 genera listed by Wang (1961, p. 76) as composing the tree stratum of the Mixed Northern Hardwood forest in the northeastern provinces of China, 13 are represented in the Seldovia Point flora. Other Seldovia Point tree genera (table 3; *Cercidiphyllum*, *Pterocarya*, *Fagus*) occur in the Mixed Northern Hardwood forest (*Fagus* zone of many Japanese

TABLE 3.—Assumed growth habits of Seldovia Point species

Trees	
<i>Cercidiphyllum alaskanum</i>	<i>Fraxinus kenaica</i>
<i>Liquidambar pachyphylla</i>	<i>Glyptostrobus europaeus</i>
<i>Platanus bendirei</i>	<i>Metasequoia cf. M. glyptostroboides</i>
<i>Eucommia montana</i>	<i>Ginkgo biloba</i>
<i>Ulmus knowltoni</i>	Shrubs
<i>Ulmus ovyheensis</i>	<i>Celtis</i> sp.
<i>Ulmus speciosa</i>	<i>Alnus cappsensis</i>
<i>Zelkova browni</i>	<i>Corylus</i> sp.
<i>Zelkova ungeri</i>	<i>Salix cappsensis</i>
<i>Carya bendirei</i>	<i>Salix hopkinsi</i>
<i>Cyclocarya ezoana</i>	<i>Salix picroides</i>
<i>Pterocarya nigella</i>	<i>Salix seldoviana</i>
<i>Alnus fairi</i>	<i>Hydrangea</i> sp.
<i>Alnus healyensis</i>	<i>Crataegus chamissonii</i>
<i>Betula cf. B. sublutea</i>	<i>Sorbaria hopkinsi</i>
<i>Carpinus seldoviana</i>	<i>Decodon alaskana</i>
<i>Ostrya cf. O. oregoniana</i>	<i>Alangium mikii</i>
<i>Fagus antipofi</i>	<i>Lonicera</i> sp.
<i>Fagus aff. F. crenata</i>	Vines
<i>Quercus furuhjelmi</i>	<i>Cocculus auriculata</i>
<i>Populus kenaiana</i>	<i>Pueraria miothunbergiana</i>
<i>Populus</i> sp.	<i>Vitis seldoviana</i>
<i>Tilia subnobilis</i>	Terrestrial herbs
<i>Prunus kenaica</i>	<i>Dryopteris?</i> sp.
<i>Cladrastis cf. alimensis</i>	<i>Onoclea sensibilis</i>
<i>Acer ezoanum</i>	<i>Monocotylphyllum</i> spp.
<i>Acer glabroides</i>	Aquatic herbs
<i>Acer grahamensis</i>	<i>Alisma seldoviana</i>
<i>Acer heterodontatum</i>	<i>Potamogeton alaskana</i>
<i>Nyssa cf. N. knowltoni</i>	<i>Nymphaea ebae</i>
<i>Kalopanax n-suzukii</i>	<i>Hemitrapa borealis</i>

botanists) in Japan (Hara, 1959). Further, Wang (1961, p. 77) notes that the shrubs in the Mixed Northern Hardwood forest belong to genera such as *Corylus*, *Crataegus*, *Sorbaria*, and *Lonicera*, and vines (including *Vitis*) are present.

If only floristic associations were relied upon to determine vegetational (and hence climatic) type, the Seldovia Point assemblage would be considered as most probably representing Mixed Mesophytic forest, a conclusion arrived at previously (Wolfe, 1966; Wolfe and Leopold, 1967). The majority of the most closely related extant species are found in this vegetational type (table 4), and several Seldovia Point genera occur only in Mixed Mesophytic forest or in broad-leaved evergreen forests in eastern Asia: *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Cocculus*, *Liquidambar*, *Carya*, *Cyclocarya*, *Cladrastis*, and *Nyssa*. In contrast, of all the Seldovia Point genera, only *Sorbaria* is presently restricted to cool temperate forests such as the Mixed Northern Hardwood. The physiognomic data, however, clearly indicate that the Seldovia Point assemblage represents Mixed Northern Hardwood forest. The lack of a closer floristic resemblance between the Seldovia Point assemblage and the extant

TABLE 4.—Distribution of most closely related extant species in vegetational types in eastern Asia

[Occurrence enclosed in parentheses indicate that the extant Asian species may only be distantly related to Seldovia Point species]

	Broad-leaved Evergreen	Mixed Mesophytic	Broad-leaved Deciduous	Mixed Northern Hardwood
<i>Ginkgo biloba</i>	x			
<i>Metasequoia glyptostroboides</i>		x?		
<i>Glyptostrobus pensilis</i>	x			
<i>Cocculus trilobus</i>		x		x
<i>Cercidiphyllum japonicum</i>	x		x	x
<i>Liquidambar formosana</i>	x			
<i>Ulmus</i> spp.	(x)	(x)	(x)	(x)
<i>Zelkova serrata</i>	x	x		
<i>Carya tonkinensis</i>	x			
<i>Cyclocarya paliurus</i>	x	x		
<i>Pterocarya rhoifolia</i>		x	x	x
<i>Alnus hirsuta</i>				x
<i>Carpinus cordata</i>	x	x	x	x
<i>Corylus</i> spp.	(x)	(x)	(x)	(x)
<i>Betula</i> spp.	(x)	(x)	(x)	(x)
<i>Ostrya</i> spp.	(x)	(x)	(x)	(x)
<i>Fagus crenata</i>		x	x	x
<i>Populus</i> spp.	(x)	(x)	(x)	x
<i>Salix</i> spp.	(x)	(x)	(x)	(x)
<i>Tilia nobilis</i>	x			
<i>Hydrangea</i> spp.	(x)	(x)	(x)	(x)
<i>Crataegus</i> spp.		(x)	(x)	(x)
<i>Prunus vanioti</i>	x			
<i>Prunus padus</i>				x
<i>Sorbaria lindleyana</i>				x
<i>Cladrastis wilsonii/platycarpa</i>		x		
<i>Pueraria thunbergiana</i>	x	x	x	
<i>Acer henryi</i>		x		
<i>Acer miyabei</i>				x
<i>Nyssa</i> spp.	(x)	(x)		
<i>Alangium chinensis</i>	x	x	x	
<i>Kalopanax pictus</i>	x	x		x
<i>Vitis</i> spp.	(x)	(x)	(x)	(x)
<i>Fraxinus hopeiensis</i>		x	x	x
<i>Lonicera</i> spp.	(x)	(x)	(x)	(x)
Total	13 (10)	13 (11)	8 (10)	12 (9)

Mixed Northern Hardwood forest of eastern Asia can be explained in terms of the historical development of this forest and the related Mixed Mesophytic forest. As well, the assumptions commonly made concerning present distribution of taxa relative to climate (and hence vegetational type) may not be valid.

The inclusion in the Seldovia Point flora of *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Cocculus*, *Liquidambar*, *Platanus*, *Carya*, *Cyclocarya*, *Cladrastis*, *Nyssa*, and *Alangium* indicates a deceptively warm climate if the present distributions of these genera are considered. The resistance to freezing of extant species of many of these genera has, however, been analyzed (Sakai, 1971, 1972; Sakai and Weiser, 1973). Following are listed the results of these investigations in regard to some of the Seldovia Point genera (the temperatures are the highest of the freezing resistances of bud, leaf, or twig):

<i>Ginkgo biloba</i>	-30°C
<i>Glyptostrobus pensilis</i>	-18°
<i>Metasequoia glyptostroboides</i>	-30°
<i>Platanus occidentalis</i>	-20°
<i>Liquidambar styraciflua</i>	-25°
<i>Liquidambar formosana</i>	-17°
<i>Pterocarya rhoifolia</i>	-30°
<i>Nyssa sylvatica</i>	-30°

Sakai's data also illustrate the wide variation of freezing resistance from one species to another con-

generic species. Again the highest of the three temperatures are selected:

<i>Acer macrophyllum</i>	-20°C
<i>A. mono</i>	-25°
<i>A. rubrum</i>	-30°
<i>A. saccharum</i>	-40°
<i>Quercus garryana</i>	-15°
<i>Q. lyrata</i>	-20°
<i>Q. mongolica</i>	-30°
<i>Q. macrocarpa</i>	-40°

Even within the same species, different geographic races may exhibit considerably different tolerances to freezing (Sakai and Weiser, 1973). We emphasize that the present geographic area occupied by a species may have little or no bearing on the paleoecologic significance of that species, its ancestors, or other extinct congeneric lineages.

Wang (1961, p. 239-246) has noted that today the Mixed Northern Hardwood forest of eastern Asia, although containing many genera in common with the Mixed Mesophytic forest, has few species in common with that forest. Despite this specific differentiation, Wang hypothesized that most species now in Mixed Northern Hardwood forest were derived from Mixed Mesophytic lineages during the Tertiary and that, prior to glaciation, Mixed Northern Hardwood forest had more genera and species than now.

That the Mixed Northern Hardwood forest was considerably richer in the past is fully attested to by the Seldovia Point flora, as well as by assemblages representing the same vegetational type in eastern Asia. Numerous genera are present in these assemblages that no longer participate in Mixed Northern Hardwood forest. This is valid in regard to the east Asian Miocene Mixed Northern Hardwood forest (for example, *Alangium*, *Cyclocarya*, *Liquidambar*), which is the lineal ancestor of the present Mixed Northern Hardwood forest.

Wang's (1961) hypothesis concerning the origin of Mixed Northern Hardwood lineages is, however, valid only in regard to the lineages of the West American element (see p. 17) in the Seldovia Point flora—lineages that typically did not become part of the Mixed Northern Hardwood forest in eastern Asia. In the Pacific Northwest, several early and middle Miocene assemblages represent Mixed Mesophytic forest (for example, Latah and equivalents in Washington and adjacent parts of British Columbia and Idaho, Collawash in Oregon), and these assemblages have several species in common with the Seldovia Point assemblage (table 5).

In eastern Asia, however, Mixed Mesophytic forest is probably of a more recent origin than Mixed Northern Hardwood forest. The early Miocene Aniai-type

TABLE 5.—*Seldovia dicotyledonous species also occurring in Mixed Mesophytic forest in the early and middle Miocene of the Pacific Northwest*

<i>Seldovia Point</i>	
<i>Cocculus auriculata</i>	
<i>Liquidambar pachyphylla</i>	
<i>Platanus bendirei</i>	
<i>Ulmus knowltoni</i>	
<i>Ulmus owyheensis</i>	
<i>Ulmus speciosa</i>	
<i>Zelkova browni</i>	
<i>Alnus fairi</i>	
<i>Alnus healyensis</i>	
<i>Ostrya oregoniana</i>	
<i>Carya bendirei</i>	
<i>Pterocarya nigella</i>	
<i>Populus kenaiana</i>	
<i>Acer glabroides</i>	
<i>Acer macrophyllum</i> type	
<i>Acer heterodentatum</i>	
<i>Nyssa knowltoni</i>	
<i>Other Seldovia localities</i>	
<i>Acer</i> aff. <i>A. pennsylvanicum</i>	
<i>Acer</i> aff. <i>A. saccharinum</i>	

floras (Tanai, 1961) all represent broad-leaved deciduous forest without broad-leaved evergreens; that is, this type of forest is Mixed Northern Hardwood. This is true of assemblages from Kyushu and western Honshu, although admittedly these assemblages are small and poorly known. As discussed in the section on paleoclimatology, the vegetational zonation during the early and middle Miocene excluded Mixed Mesophytic forest, but Mixed Northern Hardwood forest occupied a broad area north of latitude 44° N. The first evidence in eastern Asia of Mixed Mesophytic forest is in the late Miocene. The Mitoku flora from western Honshu (Tanai and Onoe, 1961) is dominantly broad-leaved deciduous but also contains some notophyllous broad-leaved evergreens; this assemblage thus probably represents Mixed Mesophytic forest. As noted by Tanai and Onoe (1961, p. 15), some of the Mitoku species are also found in the Aniai-type assemblages, which would indicate the reverse of what Wang (1961) suggested, that is, that some Mixed Mesophytic lineages were derived from Mixed Northern Hardwood lineages.

Some of the Mitoku species also occur in Japanese middle Miocene assemblages that we interpret as representing Wang's (1961) Deciduous Broad-leaved forest. Such a pattern of derivation of some Mixed Mesophytic lineages is to be expected as the climate in eastern Asia changed from one favorable to the development of this forest to one favorable to the development of Mixed Mesophytic forest (see p. 19). The third major source for Mixed Mesophytic lineages has been from Wang's Sclerophyllous Broad-leaved Evergreen forest, and these lineages include both broad-leaved evergreen and deciduous plants (as well as conifers such as *Cunninghamia*). Indeed, today the Mixed Mesophytic and Sclerophyllous Broad-leaved

Evergreen forests of China share many species.

Assuming the validity of our paleoclimatological suggestions (p. 19), most species in the Mixed Northern Hardwood forest of eastern Asia were derived primarily from lineages of Deciduous Broad-leaved forest, although the ultimate origin of the lineages must be in broad-leaved evergreen vegetation; that is, in an area such as Japan, the probable sequence during the Oligocene climatic deterioration would have been from broad-leaved evergreen forest into Wang's (1961) lower oak forest, then into Deciduous Broad-leaved forest, and finally into Mixed Northern Hardwood forest. At least part of such a sequence has been demonstrated in the Oligocene of Hokkaido (Tanai, 1970). Lineages that have followed such a pattern are exemplified by *Acer kushiroanum*-*A. ezouanum*-*A. miyabei* (Tanai, 1972). This pattern is also indicated by the large number of species common to the Yoshioka flora (Deciduous Broad-leaved forest) and the isochronous Mixed Northern Hardwood assemblages such as the Abura (Tanai and Suzuki, 1963) and Upper Dui (Fotianova, 1967).

POLLEN

Only three samples from the Seldovia Point localities have been analyzed for pollen. The samples from localities 9856 and 9858 are poor, and only 67 and 100 grains, respectively, were counted in these two samples. Locality 9857, however, produced an abundant and well-preserved pollen assemblage, and the percentages (table 6) are based on 300 grains.

The pollen assemblage from locality 9858 at Seldovia Point is dominated by broad-leaved plants. It is unknown whether the pollen of *Alnus* came from trees or shrubs or both, but the probable broad-leaved tree pollen (Juglandaceae, Betulaceae other than *Alnus*, Fagaceae, *Liquidambar*) in sample 9858 represents 20 percent of the total in contrast to only 6 percent pollen of Pinaceae.

The samples from 9856 and 9857, however, have a very small broad-leaved element. Members of Pinaceae account for over half the pollen in both samples. The abundance of *Picea* and *Tsuga* is particularly significant and gives strong evidence that the forest in this area was dominantly coniferous. Assuming that the assemblages from the three localities are approximately isochronous, the data indicate that the area around Seldovia was forested primarily by broad-leaved trees but that in the area of Port Graham the forest was primarily needle leaved, with broad-leaved vegetation confined only to the small valleys. This, in turn, indicates that in the more equable coastal area of southern Alaska, the vegeta-

TABLE 6.—Percentages of pollen types in samples from the Seldovia Point beds

[×, present but not included in counts]

Pollen type	9858	Locality 9857	9856
Aff. <i>Cedrus</i>	?	×	--
<i>Picea</i>	21	34	33
<i>Pinus</i>	4	1	3
<i>Pseudotsuga/Larix</i>	--	1	4
<i>Tsuga</i>	1	16	22
Taxodiaceae/Cupressaceae	1	8	1
<i>Salix</i>	--	×	4
<i>Carya</i>	×	1	1
<i>Juglans</i>	--	×	--
<i>Pterocarya/Cyclocarya</i>	×	1	6
<i>Alnus</i>	45	30	6
<i>Betula</i>	--	1	--
<i>Ostrya/Carpinus</i>	2	3	--
<i>Fagus</i>	×	2	--
<i>Ulmus/Zelkova</i>	4	1	3
<i>Liquidambar</i>	14	--	1
<i>Ilex</i>	1	--	3
<i>Tilia</i>	--	×	×
Ericales	--	×	--
<i>Lonicera</i>	--	--	1
Indet. dicotyledons	12	1	9
<i>Typha</i>	--	×	--
Indet. monocotyledons	15	--	--
<i>Osmunda</i>	×	×	--
Polypodiaceae	--	×	×

tion was probably dominantly coniferous.

The lack of Pinaceae in our megafossil collections is apparently somewhat contradictory. The largest collections, however, were made at locality 9858, and the pollen data indicate that Pinaceae were far distant from this locality. In some instances, however, we think that megafossil assemblages can yield a highly distorted picture of the actual vegetation. One example is the assemblages from the Homeric (late Miocene) part of the Kenai Group. Large collections made in 1962 from the Homeric contained no megafossils of Pinaceae (Wolfe and others, 1966), but the pollen assemblages are dominated by Pinaceae (Wolfe, 1969b) and were interpreted as indicating the presence of a coniferous forest throughout the Cook Inlet area during the late Miocene (Wolfe and Leopold, 1967). Two new localities, first collected in 1967, did produce a diverse and abundant pinaceous flora, thus substantiating the earlier interpretation. A second example is the late Miocene Hidden Lake assemblage from Oregon (Wolfe, 1969b). Although pollen of *Picea* accounts for almost half the pollen, megafossils of *Picea* represent less than one percent of over 2,000 specimens counted; the association of some 18 species of conifers, however, leaves no reasonable doubt that the vegetation was dominantly coniferous despite the low representation of conifers in the megafossil count. We conclude, therefore, that the pollen data indicate the dominance of conifers in the Port Graham area during the early and middle Miocene.

DISTRIBUTION

As discussed previously, the coastal area of southern Alaska was probably occupied by coniferous forest. The early and middle Miocene megafossil assemblages of that area are unknown, so a comparison with the Seldovia Point flora is impossible. In the Wrangell Mountains (fig. 7), however, the late Seldovian assemblage represents coniferous forest, attested to by both the dominance of Pinaceae in the pollen assemblage and the diversity of this family in the megafossil assemblage (Wolfe, 1972). The broad-leaved adjuncts to this coniferous forest included *Populus*, *Salix*, *Pterocarya*, *Alnus*, *Betula*, *Fagus*, *Ulmus*, *Acer* (both *macrophyllum* and *saccharinum* types), and *Lonicera*. Presumably the composition of the coastal coniferous forest was similar.

A small assemblage at the northern margin of the Kenai basin was collected from beds of the Kenai Group. Because these thin beds on Cache Creek include both Seldovian as well as Homeric floras (Wolfe and others, 1966), the Seldovian beds there are most probably of late Seldovian age. The Cache creek assemblage includes:

Metasequoia cf. *M. glyptostroboides*
Cocculus auriculata
Cercidiphyllum alaskanum
Fagus antipofi

Quercus furuhjelmi
Alnus cappsii
Populus kenaiana
Salix spp.
Acer aff. *A. rubrum*

This assemblage is consistent with the occurrence of Mixed Northern Hardwood forest both to the south (Seldovia Point) and north (Sanctuary and Suntrana) of Cache Creek during the late Seldovian.

The Mixed Northern Hardwood forest extended north at least to the central Alaska Range. In the Sanctuary and Suntrana Formations, the following have been found:

Metasequoia sp.
Cocculus auriculata
Ulmus sp.
Alnus sp.
Fagus antipofi
Quercus furuhjelmi
Carya bendirei
Cyclocarya ezoana
Pterocarya nigella
Populus kenaiana
Populus spp.
Salix spp.
Alangium mikii

Additional broad-leaved genera from E. B. Leopold's (1969, unpub. data) pollen work include *Liquidambar*, *Platanus*, *Juglans*, *Eucommia?*, *Betula*, *Corylus*, *Ostrya/Carpinus*, *Ericales*, *Malvaceae*, *Tilia*, *Rosaceae*, *Acer*, *Ilex*, *Eleagnus*, *Nyssa*, *Compositae*, and *Caprifoliaceae* (*Lonicera* type). The Sanctuary-Suntrana assemblage is similar to the Seldovia Point assemblage from the standpoint of both megafossils and microfossils. We emphasize, however, that warmer elements are fewer in number than in the Seldovia Point assemblage, and in all probability the Sanctuary-Suntrana climate had a lower mean annual temperature and a higher mean annual range of temperature.

The northern limit of Mixed Northern Hardwood forest in Alaska during the late Seldovian is not known with certainty. A few of the Sanctuary-Suntrana pollen samples are dominated by *Picea*, thus indicating that the coniferous forest was probably not far to the north. This would place the boundary between the two vegetational types at about lat 64° N. This placement is consistent with the pollen assemblage from the Noxapaga Formation of Sainsbury (1974) on Seward Peninsula (lat 65° N). The two samples examined are dominated by Pinaceae (*Picea*, *Pinus*, *Tsuga*, *Abies*, and *Larix/Pseudotsuga*, in order of decreasing abundance). Except for Betulaceae, none of the broad-leaved genera exceeds one percent; this

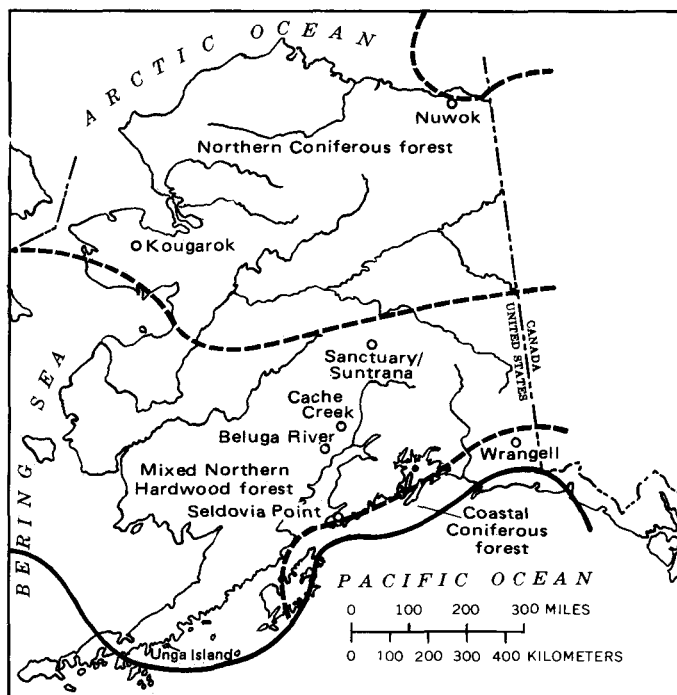


FIGURE 7.—Suggested distribution of vegetational types in Alaska during the late early and early middle Miocene. Approximate extent of land shown by heavy solid line.

element is, however, moderately diverse and includes *Fagus*, *Quercus*, *Carya*, *Pterocarya/Cyclocarya*, *Ulmus*, *Populus*, *Salix*, and *Symphoricarpos*. Farther north, the Nuwok pollen assemblage of middle Miocene age (lat 70° N) is almost totally coniferous but has minor amounts of *Pterocarya/Cyclocarya* and *Ulmus*.

The coastal coniferous forest during the early Miocene was isolated from other coniferous forest. To the southeast, the coniferous forest theoretically gave way to Mixed Northern Hardwood or Mixed Mesophytic forest. To the southwest, coniferous forest was clearly bounded by Mixed Northern Hardwood forest, which has been recorded from Kamchatka (Chelebaeva, 1968). The northern area of coniferous forest probably had a great longitudinal extent. Neogene pollen assemblages from northeastern Siberia (Baranova and others, 1968) are dominated by Pinaceae; it should be noted, however, that all these assemblages have not been independently dated, and their exact placements within the Neogene sequence are not certainly known.

COMMUNITIES

Counts of the leaf impressions in terms of abundance of individual species were not made; such counts have not yet been proved reliable in indicating the actual abundance of plants in the original vegetation. The most abundant dicotyledonous tree species in our collections from the Seldovia Point locality are:

Fagus antipofi
Acer ezoanum
Zelkova spp.
Alnus spp.
Salix spp.
Platanus bendirei
Quercus furuhjelmi
Carpinus seldoviana

The above species may well represent the dominant forest species in the vicinity of Seldovia during the early and middle Miocene. We thus envisage the main forest community to have been an association of *Fagus-Acer-Zelkova-Quercus-Carpinus-Ulmus*. Near Port Graham, the forest association was somewhat different; there, *Fagus* and *Ulmus* are the most common megafossils, *Carpinus* is absent, and apparently *Acer ezoanum* was replaced by *A. grahamensis*.

Some of the Seldovia Point species can very clearly be relegated to a streamside element. This assignment is supported not only by the habitats of extant relatives but also—and perhaps most significantly—by the abundance of leaves of these species in association on the same slabs. Such species include *Salix hopkinsi*, *S. cappensis*, *S. picroides*, *S. seldoviana*, *Platanus bendirei*, *Decodon alaskana*, and *Alnus cappsi*.

The Seldovia Point flora has a strong aquatic element at locality 9858. Leaves of the extinct *Nymphaea* are particularly common, as are seeds and, to a lesser degree, leaves of *Potamogeton*. *Nuphar* (a genus related to *Nymphaea*) and *Potamogeton* today typically inhabit quiet water, and *Nuphar* typically lives in lakes.

FLORISTICS

Traditionally the species composing a fossil flora have been placed into elements, each of which either represents the geographic region where the most closely related extant species are found (for example, East Asian element, East American element) or represents the region where the lineage to which the species belongs putatively originated (for example, Arcto-Tertiary element, Madro-Tertiary element). Both of these approaches to floristic analysis have some validity, despite the fact that particular concepts such as that of the Arcto-Tertiary element have probably been invalidly applied (Wolfe, 1969b, 1972; Tanai, 1971). The areas of origin of the floristic element in the Seldovia Point flora are particularly significant to concepts of floristic history because the flora from the Port Graham locality has been one of the fundamental bases for the concept of an Arcto-Tertiary Geoflora, which, in turn, has served as the "type" geoflora for the geofloral concept.

We emphasize that the assignment to elements such as East Asian or West American by Chaney (for example, 1959) and his followers was done primarily for paleoclimatic purposes. That is, in west American Tertiary floras, a dominant East American-East Asian element indicated abundant summer precipitation, whereas a dominant West American element indicated little summer precipitation. This usage of "element" has little floristic value and should be abandoned.

To place species such as *Liquidambar pachyphylla* in an "East American" element is, in view of the history of this lineage, unwarranted. There is no direct relationship between *L. pachyphylla* and the extant east American *L. styraciflua*, although the two species may belong to lineages that were derived from a common stock in the Paleogene. *L. pachyphylla* is a distinctive member of a middle latitude, West American element. Similarly, to the same element belongs the type of *Cyclocarya* found in the Tertiary of the Pacific Northwest, a type that is only distantly related to the extant Asian *C. paliurus*. Despite the fact that the lineages to which *L. pachyphylla* and the west American *Cyclocarya* belong are now extinct, these lineages have the same floristic significance as the *Platanus bendirei* lineage, which has survived in

western North America as *P. racemosa*. Indeed, as pointed out previously (Wolfe, 1969b), several "Madro-Tertiary" lineages are in fact members of this same element.

Prior to the Oligocene deterioration of climate (Wolfe and Hopkins, 1967; Wolfe, 1971, 1978), the climates of the Paleogene were characterized by high equability (that is, a low mean annual range of temperature). Just as temperate broad-leaved deciduous forests are today absent in the highly equable Southern Hemisphere temperate regions, it is highly probable that temperate broad-leaved deciduous forests were absent in the Northern Hemisphere during the Eocene and the Oligocene prior to the deterioration (Wolfe, 1978). The Oligocene deterioration was thus characterized not only by a dramatic decline in mean annual temperature but also by a major increase in mean annual range of temperature (Wolfe, 1971). Broad-leaved deciduous forests appeared in a geologically short period of time throughout middle and high latitudes of the Northern Hemisphere. The lineages that composed these forests were derived from two major sources (Wolfe, 1972): (1) lineages that were present in broad-leaved evergreen forest prior to the deterioration and that were preadapted (or had the genetic capability to adapt rapidly) to climates characterizing broad-leaved deciduous forest and (2) lineages that were present in temperate coniferous forests and that moved downslope during the Oligocene deterioration. During the later Oligocene and Miocene some lineages from broad-leaved evergreen forest also adapted gradually and moved into the broad-leaved deciduous forests (Wolfe, 1972).

Terms such as East Asian Element can thus be defined relative to the geographic region in which it is thought a given lineage entered broad-leaved deciduous forest for the first time. Species such as *Liquidambar pachyphylla* and *Carya bendirei*, although belonging to genera that are no longer native to western North America, are consequently considered to belong to the West American Element, because the lineages to which these species belong were present in western North America at middle latitudes prior to the Oligocene deterioration.

The significance of the concept of this west American, mid-latitude element is considerable to paleoecological reconstructions. Just as the tolerances of *Carya* in eastern Asia are, at least in part, different from the tolerances of *Carya* in eastern North America, so it can be expected that the tolerances of the now extinct west American *Carya* were also different. This, we think, is at least partly the explanation for the presence of *Liquidambar* in the Seldovia Point assemblage; it is also notable that *Liquidambar* was a conspicuous member of fluvial vegetation in the

late Miocene upland coniferous forest in the Pacific Northwest, but today none of the surviving members of the genus are associated with Temperate Coniferous forest.

The Seldovia Point flora has three known floristic elements: East Asian, West American, and Beringian. The Beringian element is composed of those lineages that are thought to have entered into the temperate forests in Alaska and adjacent high-latitude regions. The basis for the assignment to the various floristic elements (table 7) is given in the discussions of the systematic treatments of the various species.

Assignment to the various floristic elements is well documented in instances such as *Platanus bendirei* and less well documented in other instances. It is assumed that if a particular lineage appears in a given area immediately following the Oligocene deterioration, that lineage is assigned to that area's element.

TABLE 7.—Analysis of the Seldovia Point assemblage in terms of floristic elements

Species	East Asian	West American	Beringian	Unknown
<i>Dryopteris?</i> sp				x
<i>Onoclea sensibilis</i>				x
<i>Glyptostrobus europaeus</i>			x	
<i>Metasequoia</i> cf. <i>M. glyptostroboidea</i>			x	
<i>Ginkgo biloba</i>				x
<i>Nymphar ebeae</i>				x
<i>Cocculus auriculata</i>		x		
<i>Cercidiphyllum alaskanum</i>	x			
<i>Liquidambar pachyphylla</i>		x		
<i>Platanus bendirei</i>		x		
<i>Eucornia</i> cf. <i>E. montana</i>		x?		
<i>Celtis</i> sp				x
<i>Ulmus knoultoni</i>		x		
<i>Ulmus ovyheensis</i>		x		
<i>Ulmus speciosa</i>		x		
<i>Zelkova browni</i>		x		
<i>Zelkova ungeri</i>	x			
<i>Fagus antipofi</i>			x	
<i>Fagus</i> aff. <i>F. crenata</i>			x	
<i>Quercus furuhjelmi</i>	x?			
<i>Alnus cappsii</i>			x	
<i>Alnus fairi</i>		x		
<i>Alnus healyensis</i>		x		
<i>Betula</i> cf. <i>B. sublutea</i>			x?	
<i>Carpinus seldoviana</i>	x			
<i>Corylus</i> sp				x
<i>Ostrya</i> cf. <i>O. oregoniana</i>		x		
<i>Carya bendirei</i>		x		
<i>Cyclocarya ezoana</i>	x			
<i>Pterocarya nigella</i>		x		
<i>Populus kenaiana</i>			x	
<i>Populus</i> sp				x
<i>Salix cappsensis</i>			x	
<i>Salix hopkinsi</i>			x	
<i>Salix picroides</i>			x	
<i>Salix seldoviana</i>			x	
<i>Tilia subnobilis</i>	x			
<i>Hydrangea</i> sp				x
<i>Crataegus chamisonii</i>				x
<i>Prunus kenaica</i>				x
<i>Prunus</i> sp				x
<i>Sorbaria hopkinsi</i>			x	
<i>Cladrastis</i> cf. <i>C. anienensis</i>	x			
<i>Pueraria mothunbergiana</i>	x			
<i>Decodon alaskana</i>	x			
<i>Hemitrapa borealis</i>	x			
<i>Acer ezoanum</i>	x			
<i>Acer grahamensis</i>		x		
<i>Acer heterodontatum</i>		x		
<i>Nyssa</i> cf. <i>N. knoultoni</i>		x		
<i>Alangium mikii</i>	x			
<i>Kalopanax n-suzukii</i>	x			
<i>Vitis seldoviana</i>	x			
<i>Fraxinus kenaica</i>				x
<i>Lonicera</i> sp				x
<i>Potamogeton alaskana</i>				x
<i>Monocotylaphyllum alaskanum</i>				x
<i>Monocotylaphyllum tenuistriatus</i>				x
Total	14	16	12	16

For example, *Metasequoia* is not known in the Alaskan Eocene, but the early Angoonian assemblages immediately following the deterioration contain abundant *Metasequoia*, which therefore is assigned to the Beringian element; this genus could equally well be assigned to the other two elements, but there is no need to invoke immigration from another region.

The West American element has suffered far more extinction than the remaining two elements. Only three West American lineages in the Seldovia Point flora still survive: *Platanus bendirei* (*P. racemosa*), *Acer heterodentatum* (*A. negundo*), and *A. grahamensis* (*A. macrophyllum*). Of the East Asian element, only *Cercidiphyllum alaskanum* and *Decodon alaskana* have definitely become extinct. Of the Beringian element, possibly many lineages yet survive, particularly in *Alnus* and *Salix*.

Today, many boreal species extend southward, particularly in North America, along mountain chains. Similarly, during the late Miocene many species are known from lowland Alaska to the uplands of the Pacific Northwest to the south (Wolfe, 1969b). None of these species are, however, members of the East Asian element as defined in this report; although not yet known in Alaska, *Acer scottiae* must have had such a distribution and would clearly have been East Asian. Such data emphasize the difficulty of floristic interchange between midlatitude forests on either side of the Pacific during the Neogene, at least in regard to woody plants.

The few West American lineages that probably migrated into eastern Asia during the Miocene are:

Pterocarya rhoifolia type.—Earliest records of this type are in the middle and late Oligocene of Alaska (Tsadaka Formation). This type appears in the early Miocene of Japan and Oregon and persisted in the Pacific Northwest through at least the late Miocene. The type of foliage with which the seeds are most frequently associated is that assigned to *P. nigella*, which is thought to be descended from the west American *P. pugetensis*.

Acer negundo type.—This type extends in North America back to at least the early Oligocene (MacGinitie, 1953) and occurs in many younger assemblages. The first record in Alaska is in the Seldovia Point flora, but the occurrence of this group in Japan in the early to middle Miocene (Tanai, 1961) indicates that the lineage probably migrated through Alaska no later than the early Miocene. The lineage became extinct in Japan but probably survived on the Asian mainland as *A. henryi* Pax.

Cocculus auriculata.—This extinct lineage is thought to be descended from an undescribed species in the Puget Group and is hence West American. The lineage has a Miocene distribution similar to that of

A. negundo type but became extinct in North America by the late Miocene.

The only East Asian species that probably migrated into middle latitudes of western North America during the Neogene are:

Acer mono type (*A. scottiae* MacG.).—This type has not yet been found in the Alaskan Tertiary sequence, but the common occurrence of this type in the middle and late Miocene assemblages from the Pacific Northwest indicates that the lineage probably passed through Alaska during the Seldovian.

Acer miyabei type.—This type has not been previously recorded from the conterminous United States, but seeds from Skull Springs, Oreg., (middle Miocene) and south-central Idaho (middle or late Miocene) probably represent *Acer ezoanum*. This lineage has a long history in eastern Asia (Tanai, 1972).

Excluded from this listing is *Acer circinnatum*, a species closely allied to *A. japonicum*, which has an Asian record extending back at least into the early Miocene (Tanai, 1972). No fossil record of this type is known in North America, which is curious in view of the current abundance and widespread occurrence of *A. circinnatum* in the forests of the Pacific Northwest. We suggest that this is a rare example of long-distance dispersal from Japan to the Pacific Northwest during the Pliocene or Quarternary.

Neither the West American nor the East Asian element apparently penetrated significantly southward in Asia or North America, respectively. Few species are found in the Neogene of both Japan and the Pacific Northwest. We suggest that the northern populations of these two elements were unable to compete successfully with endemic, more southerly populations; that is, while it was apparently easy for many species to spread northward, producing populations better adapted to the more rigorous conditions at higher latitudes, the reverse process was not easy. Possibly these northern populations were genetically less plastic than the southern populations of the same species. Another explanation is the possibility that the midlatitudes of western North America, although clearly having more summer precipitation in the Neogene than now, had an insufficient amount for most East Asian species; the lack of penetration of most West American species into Asia, however, would remain unexplained. We think that the available data support van Steenis' (1962) suggestion that it is improbable that many species could adapt first to rigorous conditions and then readapt to conditions similar to those of the early member populations of the species.

Van Steenis (1962) was particularly referring to the problem of day length (particularly the lack of winter light) relative to floristic interchange over high-

latitude land bridges such as Beringia. We are, however, discussing deciduous species, which are leafless during winter, and thus the relative darkness of the winter is irrelevant. Temperature is not likely to be significant as a barrier to migration, because high-altitude areas at middle latitudes can have the same mean annual and mean annual range of temperature as low-altitude areas at high latitudes. The only major environmental factor that remains is that of day length as related to the phenomenon of photoperiodism. Although we have noted probable exceptions, we think that the data in this report suggest that generally it is impossible to reverse the trend of photoperiodic specialization in woody deciduous plants.

PALEOCLIMATOLOGY

Figure 8 shows the distribution of major temperature parameters relative to vegetational types at higher middle to high latitudes of eastern Asia (Wolfe,

1979a). The placement of each climatic station in a given vegetational type follows the maps of Wang (1961), Honda (1928), Hara (1959), and Suslov (1961). That the Seldovia Point assemblage is Mixed Northern Hardwood forest has been discussed above, in terms of both foliar physiognomy and general floristic affinities.

The climatic region now occupied by Mixed Northern Hardwood forest in eastern Asia is broad. The Seldovia Point assemblage is, we think, assignable to the warmer and more equable part of that vegetational type; that is, the Seldovia Point assemblage probably lived at temperatures similar to those of southwestern Hokkaido. In this area, some broad-leaved deciduous plants of a typically more southerly distribution occur: for example, *Lindera*, *Cercidiphyllum*, *Berchemia*, *Pterocarya*, *Schisandra*, and *Cocculus* (Hara, 1959). Analogous genera in the Seldovia Point assemblage are: *Cocculus*, *Cercidiphyllum*, *Pueraria*, *Alangium*, *Platanus*, and *Liquidambar*.

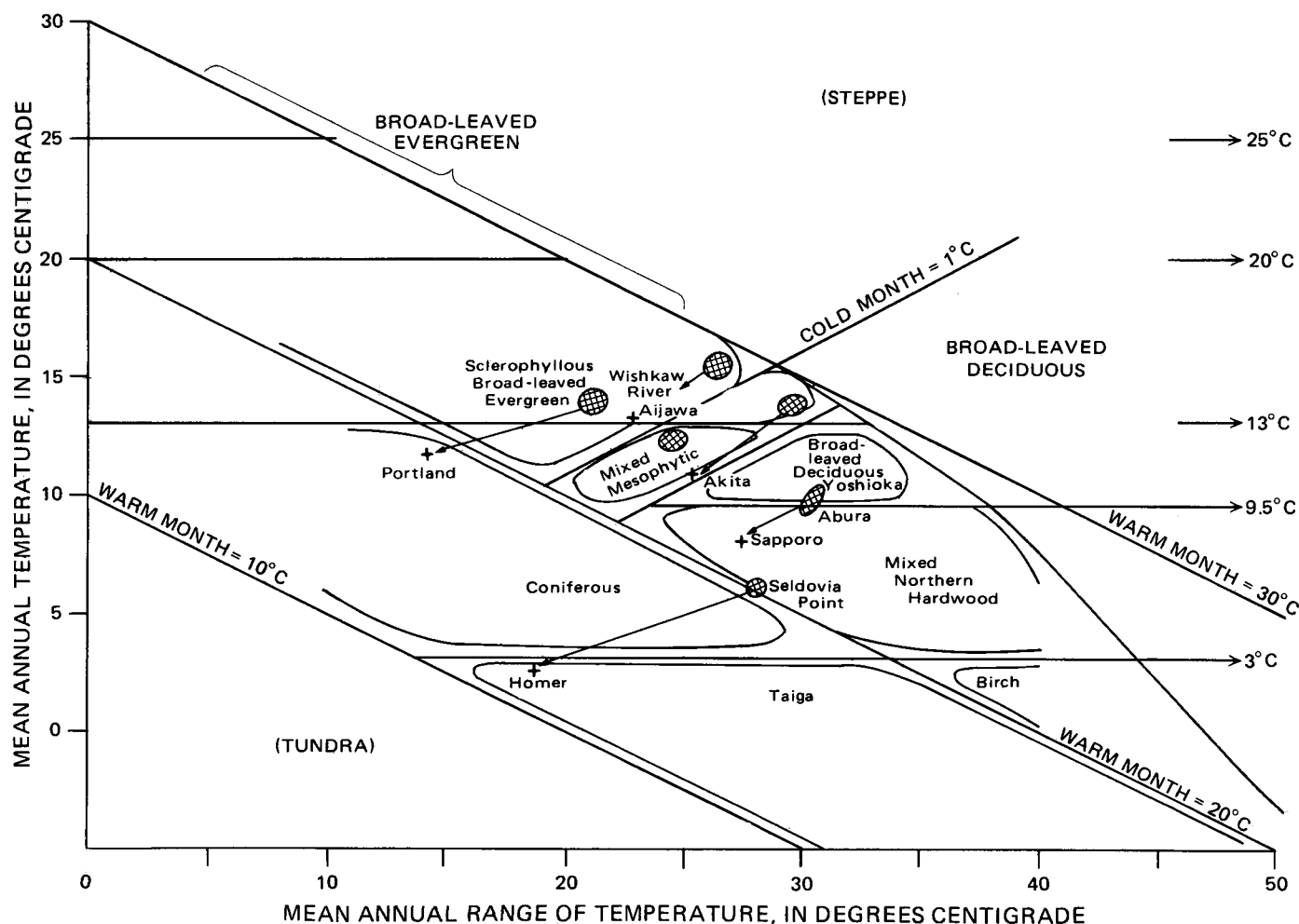


FIGURE 8. Temperature parameters of modern vegetational types in eastern Asia and the probable temperature parameters of certain early and middle Miocene assemblages.

That the Seldovia Point assemblage had a climate that at least was along the more equable margin of Mixed Northern Hardwood forest is also shown by the fact that coniferous forest was not far distant. Although megafossils of Pinaceae have not been collected at any of the Seldovia Point localities, the microfossil assemblages contain up to 34 percent *Picea* pollen, accompanied by a diversity of other pinaceous genera (aff. *Cedrus*, *Picea*, *Pinus*, *Tsuga*). The samples that have the numerically and taxonomically most abundant representation of Pinaceae are the more southerly localities, indicating that probably the coastal area was occupied by coniferous forest.

The temperature regime thus indicated for the Seldovia Point assemblage is 6–7°C mean annual temperature (see fig. 8); if coniferous forest were not far distant, then a mean annual range of temperature of 26–27°C is indicated. These estimates in turn indicate that mean annual temperature has declined since the middle Miocene by about 3–5°C. As noted previously (Wolfe, 1971), however, the Seldovia Point mean annual range of temperature was 9–11°C greater than now; that is, the present climate at Seldovia is considerably milder than the middle Miocene climate. There has been almost no change (if anything, perhaps a slight increase) in winter temperatures, but there has been a drastic change in warm month temperatures; the mean temperature of the warmest month has declined by about 7–8°C. We suggest that it is this strong decline in summer temperatures during the Neogene that was a major factor in the initiation of widespread glaciation during the later Cenozoic.

Today areas such as southern Alaska have a considerably lower mean annual range of temperature (that is, have a milder climate) than do areas to the southwest. The same situation appears to have prevailed during the middle Miocene, judging from paleobotanical data from Sakhalin and particularly Japan. In Sakhalin, Fotianova's (1967) analysis of the Upper Dui flora (fig. 9) indicated the total absence of members of Pinaceae; that is, the assemblage represents a broad-leaved deciduous forest that was geographically not close to coniferous forest. That the Upper Dui assemblage represents Mixed Northern Hardwood forest is clear from the diversity of lobed leaves (primarily *Acer*); another similarity to the Seldovia Point assemblage is in the abundance and diversity of Ulmaceae. Although Fotianova (1967) does not list *Fagus* as a member of the Upper Dui flora, Heer (1978) illustrated many examples of *F. antipofi*.

Floras from other areas of Sakhalin are generally similar to the Upper Dui. The Esutoru, Odasu, Naihoro, and Kashihi floras (Huzioka, 1949) lack Pinaceae but have a diversity of Ulmaceae, Betulaceae, Aceraceae, and Salicaceae. Among probable trees,

Populus, *Alnus*, *Ulmus*, and *Acer* are particularly common; *Alangium* is also well represented.

Overall the Upper Dui and other floras from Sakhalin do not appear to differ vegetationally from the Seldovia Point assemblage, except for the apparent absence of members of Pinaceae. The warmer elements present in the Sakhalin middle Miocene flora—*Alangium*, Leguminosae—are also represented in the Seldovia Point assemblage. What is known of the middle Miocene flora of Kamchatka (Chelebaeva, 1968) supports the suggestion that mean annual temperature during the middle Miocene was almost constant from Sakhalin through Kamchatka and into southern Alaska; the same situation prevails today. This interpretation of the paleobotanical data would also indicate—at least for Kamchatka—a decrease in mean annual range of temperature since the middle Miocene.

The middle Miocene Yoshioka flora of southwestern Hokkaido was interpreted by Tanai (Tanai and Suzuki, 1963) to be Mixed Mesophytic forest (*Castanea* zone of many Japanese botanists). Although many of the Yoshioka species occur primarily in this vegetational type in both Japan and central China, it is significant that broad-leaved evergreen plants—typically shrubs but some also scattered trees—occur in Mixed Mesophytic forest (Wang, 1961, p. 98, 100). In the Yoshioka assemblage, in contrast, the broad-leaved evergreen element is represented only by two microphyllous species, *Quercus elliptica* and *Camellia protojaponica*.

In several respects the Yoshioka assemblage resembles what Wang (1961) termed Deciduous Broad-leaved forest; this type of vegetation has been greatly disturbed, and in fact eliminated, in most areas of the Great Plain of North China. In this vegetation, broad-leaved deciduous trees and shrubs predominate, and broad-leaved evergreens are rare. Notable, however, is the occurrence in the vegetation of broad-leaved deciduous plants that are typical of more southern vegetational types: *Castanea*, *Gleditschia*, *Cedrela*, *Pistacia*, for example.

The mean annual temperatures under which this Deciduous Broad-leaved forest lives, however, are approximately the same as those under which Mixed Mesophytic forest lives, and thus the mean annual temperature suggested for the Yoshioka assemblage by Tanai (10–14°C; Tanai and Suzuki, 1963) is probably valid. Judging, however, from the diversity of lobed leaves in the Yoshioka (most representing *Acer*), Mixed Northern Hardwood forest, in which lobed species are common, was not far distant. Indeed, the slightly altitudinally higher Abura flora probably represents this vegetational type (Tanai in Tanai and Suzuki, 1963), and we thus suggest that the mean an-

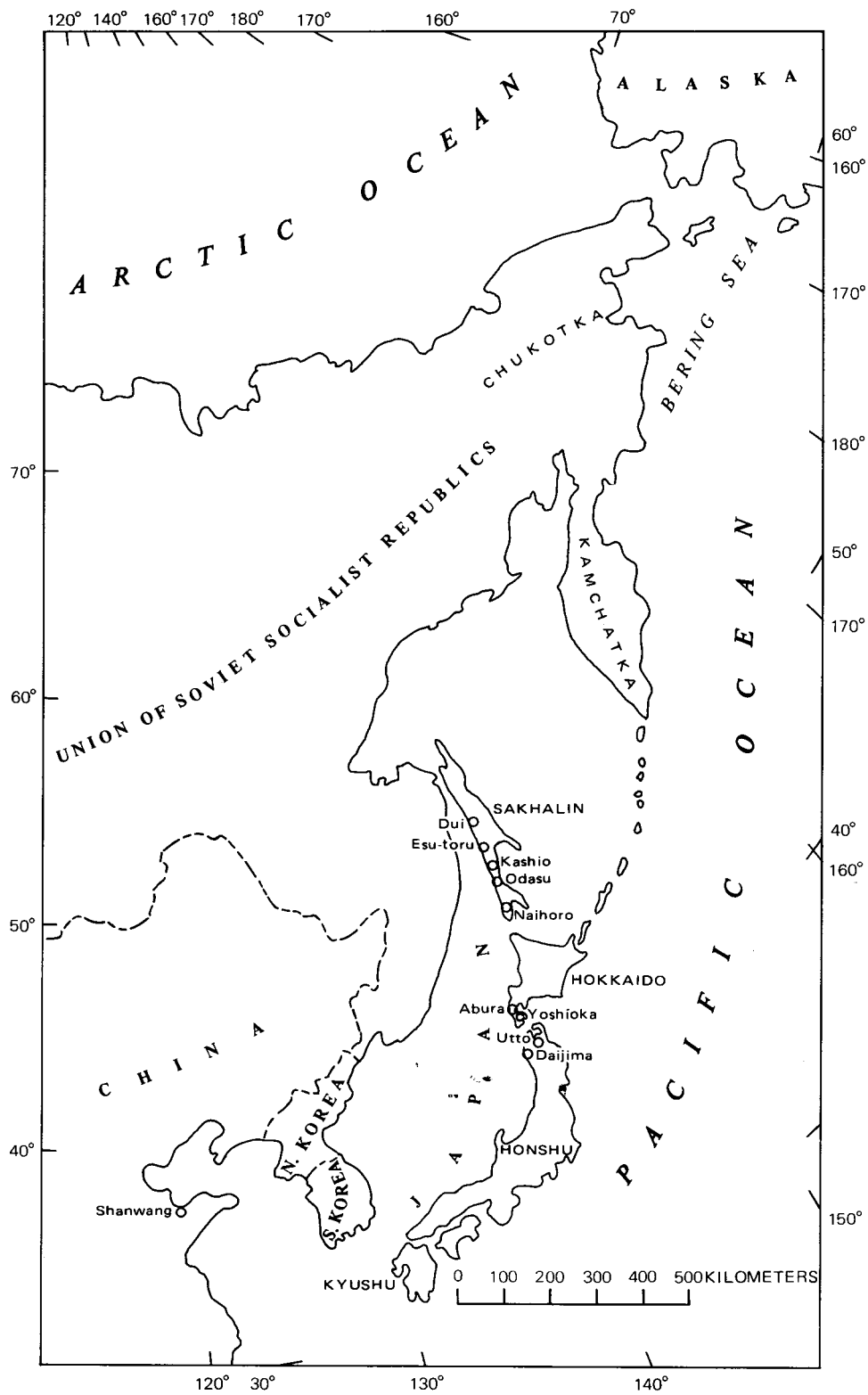


FIGURE 9.—Map of northeastern Asia showing location of some middle Miocene assemblages.

nual temperature for the Yoshioka assemblage was probably 10–12°C.

The Utto flora of northwestern Honshu was interpreted to have lived under a mean annual temperature of 15°C but at the same time to have represented broad-leaved deciduous forest (Huzioka, 1963). As analyzed by Huzioka, the forest also included broad-leaved evergreen trees, and the shrub component included both broad-leaved evergreen and deciduous plants. The evergreen element includes members of Lauraceae and Fagaceae, which account for almost half this element. Comparisons were made with vegetation in southern Honshu, but in that area the vegetation—except for secondary vegetation—is dominantly broad-leaved evergreen. Broad-leaved deciduous forests that have a floristic composition highly similar to the Utto assemblage do, however, exist in mainland China. In the southern parts of Shensi and Kansu and adjacent parts of Honan provinces, the forest (lower oak forest of Wang, 1961) is primarily broad-leaved deciduous, but the trees, as well as the shrubs, include both broad-leaved evergreen and deciduous types. Evergreen Lauraceae and Fagaceae are particularly notable (Wang, 1961, p. 89–90).

The mean annual temperature suggested for the Utto Flora by Huzioka (15°C) is present in the area occupied by the lower oak forest, and this would indicate a decline of mean annual temperature of about 4°C since the middle Miocene. The significant point to be made in the above comparison is that in the area occupied by this lower oak forest the mean annual range of temperature is typically higher than the present range at the Utto localities. The change in mean annual range of temperature since the middle Miocene need not have been great (perhaps only 2–3°C), but such a change is consistent with the change indicated by high-latitude floras.

Fossil assemblages farther south in Japan have been uniformly compared to the modern Evergreen Sclerophyllous Broad-leaved forest (Tanai, 1961, 1967a, 1972; Matsuo, 1963; Ishida, 1970). These assemblages typically contain elements indicating somewhat warmer mean annual temperatures during the middle Miocene than now, but estimates of mean annual range of temperature are almost impossible to arrive at. It is clearly possible that this vegetational type lived under a higher mean annual and mean annual range of temperature than now exists at the fossil localities. Data from these more southerly floras neither contradict nor substantiate the changes in mean annual range of temperature indicated by the more northerly floras. The middle Miocene latitudinal vegetational zonation indicated for eastern Asia indicates, however, that there has been a decrease in

mean annual range of temperature since that time.

In western North America at middle latitudes (fig. 10), most of the known middle Miocene assemblages grew in uplands. These uplands, moreover, are east of the Sierra-Cascade axis, and interpretations of changes in climate since the middle Miocene are greatly complicated by tectonic and altitudinal factors. In the Pacific Northwest, comparisons are best made to climatic data from the region west of the Cascade Range.

Middle Miocene floras such as the Latah (Knowlton, 1926; Chaney, 1959), Grand Coulee (Berry, 1931), St. Eugene (Hollick, 1927), and Fish Creek (Wolfe, in Peck and others, 1964) represent Mixed Mesophytic forest. These assemblages are dominantly broad-leaved deciduous but contain some notophyllous broad-leaved evergreens (*Magnolia*, Lauraceae, *Ex-bucklandia*, *Arbutus*). These assemblages, however, grew at an altitude perhaps over 500–600 m (Wolfe, 1969a, p. 93). The Latah and similar assemblages lived in a mean annual temperature of 10–13°C and a mean annual range of temperature of 19–27°C. Comparisons with data for Cedar Lake (a station on the west side of the Cascades at an altitude of almost 500 m) indicate that since the middle Miocene mean annual temperature has declined by at least 1–3°C and that mean annual range of temperature has decreased by 4–12°C.

Lowland assemblages of middle Miocene age are still poorly known in the Pacific Northwest. The undescribed Wishkaw River assemblage from western Washington and particularly the undescribed Cape Blanco assemblage from southwestern Oregon probably represent Sclerophyllous Broad-leaved Evergreen forest. Notophyllous members of evergreen Fagaceae and Lauraceae are conspicuous elements in these assemblages. If this vegetation type is represented, then there has probably been a moderate (at least 2–3°C) decline in mean annual temperature since the middle Miocene. In areas lacking major mountains parallel to the coast (such as the middle Miocene Pacific Northwest), mean annual range of temperature increases only a few degrees a few hundred kilometers from the coast. It is improbable that mean annual range of temperature in the lowlands during the middle Miocene was more than a few degrees less than that indicated for upland assemblages such as the Latah (19–27°C). If a minimal mean annual range of temperature of 15°C is assumed for the Cape Blanco and Wishkaw River climates, then mean annual range of temperature in the coastal areas has lessened since the middle Miocene; mean annual range is today almost 7°C at Port Orford near Cape Blanco and almost 12°C near Wishkaw River. On Cape Blanco itself mean annual range of temperature is less than 5°C.

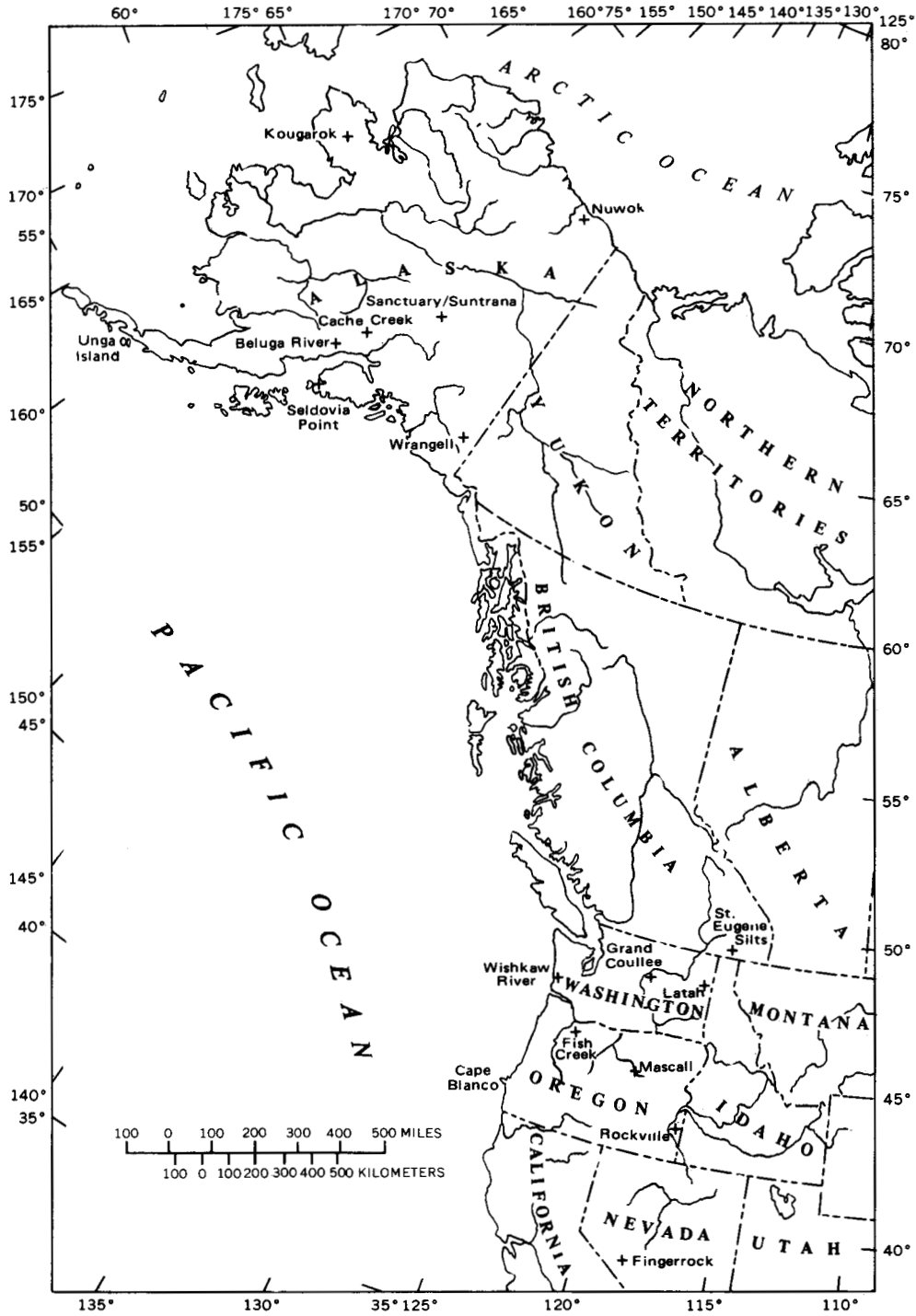


FIGURE 10.—Northwestern North America showing location of some middle Miocene assemblages.

The paleobotanical evidence is thus consistent around the North Pacific Basin: mean annual temperature has declined since the middle Miocene, although the decline has been greatest at high latitudes. Similarly, mean annual range of temperature has declined, and the decline has been greatest at high latitudes. Concomitant with the decline in mean annual range of temperature, the decline in mean annual temperature primarily results in a lowering of summer temperatures; we emphasize again that such a decline in summer temperatures was a major factor in the initiation of late Cenozoic glaciation.

Previous analysis of paleoclimates from western North America (Wolfe and Hopkins, 1967; Wolfe, 1971) has indicated that the middle Miocene was warmer than either the earliest or late Miocene, and paleobotanical analyses based on eastern Asian materials are in basic agreement (Tanai and Huzioka, 1967; Tanai, 1967a, 1967b, 1971). The Alaskan data clearly are also in agreement in comparing the earliest with the late early to early middle Miocene climates.

The vegetation represented by the assemblages from the lower Seldovian of the Cook Inlet region was also probably Mixed Northern Hardwood forest but more depauperate than that of the upper Seldovian. The assemblages of probable early Seldovian age in the Cook Inlet region are Capps Glacier (locs. 9845, 9846, 9937 of Wolfe and others, 1966) and Houston (loc. 9365 of Wolfe and others, 1966). Preliminary determinations of the flora from the localities indicate that the following are represented:

Glyptostrobus europaeus
Metasequoia cf. *M. glyptostroboides*
Keteleeria sp.
Chamaecyparis sp.
Cercidiphyllum alaskanum
Ulmus sp.
Quercus furuhjelmi
Alnus barnesi
Alnus cappsii
Alnus fairi
Alnus healyensis
Carpinus cappsensis
Comptonia naumannii
Myrica sp.
Pterocarya nigella
Populus kenaiana
Populus spp.
Salix cappsensis
Salix picroides
Salix spp.

Hydrangea sp.
Crataegus sp.
Sorbaria sp.
Spiraea weaveri
Cladrastis aff. *C. lutea*
Acer aff. *A. pennsylvanicum*
Acer aff. *A. saccharinum*
Aesculus cf. *A. majus*
Alangium mikii

Notable in these assemblages is the diversity of both Betulaceae and Salicaceae, which are also the most abundant megafossils. Just as significant is the lesser diversity in the lower as compared to the upper Seldovian flora of Fagaceae, Ulmaceae, Juglandaceae, and Aceraceae. Genera such as *Cocculus*, *Liquidambar*, *Platanus*, and *Cyclocarya* are absent from the lower Seldovian megafossil assemblages.

The most reasonable interpretation of such floristic differences is that the middle Miocene warming documented at middle latitudes allowed the northward expansion of some species into southern Alaska. Because the physiognomy of the early Seldovian assemblages also indicates broad-leaved deciduous forest, it appears that mean annual range of temperature also decreased from the early into the middle Miocene; this suggestion accords with the trend after the middle Miocene.

The Homeric (late middle to early late Miocene) assemblages from Alaska, although representing coniferous forest, do not necessarily indicate that mean annual temperature declined. From figure 8 it can be seen that a change from broad-leaved deciduous to coniferous forest can be the result of a decrease in mean annual range of temperature alone. The rich broad-leaved deciduous tree element that is conspicuous even in coniferous assemblages of Seldovian age (for example, Wrangell and Noxapaga assemblages) is absent in the early Homeric megafossil assemblages, and only sparse amounts of *Pterocarya/Cyclocarya* and *Ulmus/Zelkova* occur in some microfossil assemblages. If, as seems probable, broad-leaved trees are better adapted to higher summer heat than are most coniferous trees, and if diversity of broad-leaved trees increases with overall warmth, then the simplest way to eliminate broad-leaved trees from Alaska following the Seldovian would be to drastically lower summer temperatures and overall heat. Such a lowering is accomplished by lowering both mean annual and mean annual range of temperature.

SYSTEMATICS

The preliminary list of the Seldovia Point flora pre-

viously published (Wolfe, 1966) differs in several respects from that reported here. In order to clarify any differences, the following is presented:

Wolfe, 1966	This report
<i>Equisetum</i> sp	Not recognized; specimen lost?
<i>Dryopteris</i> sp	<i>Dryopteris</i> sp.
<i>Onoclea sensibilis</i>	<i>Onoclea sensibilis</i> .
<i>Ginkgo biloba</i>	<i>Ginkgo biloba</i> .
<i>Glyptostrobus europaeus</i>	<i>Glyptostrobus europaeus</i> .
<i>Metasequoia glyptostroboides</i>	<i>Metasequoia</i> cf. <i>M. glyptostroboides</i> .
<i>Taxodium distichum</i>	Not recognized; probably aberrant shoots of <i>Glyptostrobus</i> or <i>Metasequoia</i> .
<i>Potamogeton</i> sp.	<i>Potamogeton alaskanus</i> .
<i>Smilax</i> sp	<i>Alisma seldoviana</i> .
<i>Poa</i> <i>tenuistriatus</i>	<i>Monocotylphyllum</i> spp.
<i>Cyperacites</i> sp	<i>Monocotylphyllum</i> sp.
<i>Populus kenaiana</i>	<i>Populus kenaiana</i> .
<i>Populus reniformis</i>	<i>Populus</i> sp.
<i>Populus</i> sp. aff. <i>P. ciliata</i>	<i>Populus kenaiana</i> .
<i>Salix inquirenda</i>	<i>Salix picroides</i> .
<i>Salix picroides</i>	<i>Salix picroides</i> .
<i>Salix</i> sp	<i>Salix cappsensis</i> .
<i>Carya bendirei</i>	<i>Carya bendirei</i> .
<i>Carya</i> sp. aff. <i>C. sessilis</i>	<i>Carya bendirei</i> .
<i>Pterocarya mixta</i>	<i>Pterocarya nigella</i> .
<i>Pterocarya nigella</i>	<i>Pterocarya nigella</i> .
<i>Pterocarya</i> (<i>Cycloptera</i>) sp	<i>Cyclocarya ezoana</i> .
<i>Alnus cappsii</i>	<i>Alnus cappsii</i> .
<i>Alnus healyensis</i>	<i>Alnus healyensis</i> .
<i>Alnus fairi</i>	<i>Alnus fairi</i> .
<i>Carpinus seldoviana</i>	<i>Carpinus seldoviana</i> .
<i>Fagus antipofi</i>	<i>Fagus antipofi</i> .
<i>Fagus</i> sp. cf. <i>F. paleocrenata</i>	<i>Fagus</i> aff. <i>F. crenata</i> .
<i>Quercus bretzi</i>	<i>Quercus furuhjelmi</i> .
<i>Quercus furuhjelmi</i>	<i>Quercus furuhjelmi</i> .
<i>Ulmus longifolia</i>	<i>Ulmus owyheensis</i> .
<i>Ulmus newberryi</i>	<i>Ulmus knowltoni</i> .
<i>Zelkova oregoniana</i>	<i>Zelkova browni</i> , <i>Z. ungeri</i> .
<i>Nuphar</i> sp	<i>Nymphar ebae</i> .
<i>Cercidiphyllum crenatum</i>	<i>Cercidiphyllum alaskanum</i> .
<i>Cocculus auriculata</i>	<i>Cocculus auriculata</i> .
<i>Hydrangea</i> sp	<i>Hydrangea</i> sp.
<i>Liquidambar mioformosana</i>	<i>Liquidambar pachyphylla</i> .
<i>Platanus bendirei</i>	<i>Platanus bendirei</i> .
<i>Crataegus</i> sp	<i>Crataegus chamisonii</i> .
<i>Prunus</i> sp	<i>Prunus kenaica</i> .
<i>Spiraea? andersoni</i>	Not considered; based only on Heer's illustration.
<i>Alchornea? sp</i>	Indeterminate leaf.
<i>Mallotus</i> sp	<i>Pueraria miothunbergiana</i> .
<i>Acer ezoanum</i>	<i>Acer ezoanum</i> .
<i>Acer fatisiaefolia</i>	<i>Acer ezoanum</i> .
<i>Acer macropterum</i>	<i>Acer grahamensis</i> .
<i>Acer</i> sp. aff. <i>A. crataegifolium</i>	<i>Acer heterodontatum</i> .
<i>Acer</i> sp. cf. <i>A. subpictum</i>	<i>Acer ezoanum</i> fruits.
<i>Vitis</i> sp	<i>Vitis seldoviana</i> .
<i>Tilia</i> sp	<i>Tilia subnobilis</i> .
<i>Nyssa</i> sp. cf. <i>N. knowltoni</i>	<i>Nyssa</i> cf. <i>N. knowltoni</i> .
<i>Hemitrapa borealis</i>	<i>Hemitrapa borealis</i> .
<i>Kalopanax</i> sp	<i>Kalopanax acerifolius</i> .
<i>Fraxinus</i> sp	<i>Fraxinus kenaica</i> .
<i>Symphoricarpos</i> sp	<i>Decodon alaskana</i> .

Family *Aspidiaceae*
Genus *Dryopteris* Adanson
Dryopteris sp.

Plate 1, figures 5, 9

Description.—A portion of a pinna 3.5 cm long and 1.7 cm wide at the lower part, lanceolate; pinnules ovate, suboppositely pinnatifid by shallow but narrow sinus, nearly entire or having a few teeth on margin; midvein of each pinnule leaving pinna axis at angles of 40 to 50 degrees, somewhat zigzag, forking at the apical part, having 3 or 4 pairs of lateral veins that fade out near the margin without any bifurcation.

Discussion.—A single pinna and its counterpart are fragmentary and sterile, and the generic assignment is uncertain. But these specimens show close resemblance to the pinnae of some extant *Dryopteris* in shape of pinnae and venation, such as *D. decipiens* O. Kuntze and *D. tokyoensis* (Mats.) C. Chr. living in East Asia. Our Alaskan specimens are quite different in venation from *D. guyotti* (Lesq.) MacG. and *D. idahoensis* Knowlt., which were described from the middle Tertiary of the conterminous United States.

Occurrence.—9858

Specimen.—USNM 208348A, B.

Genus *Onoclea* L.
Onoclea sensibilis L.
Plate 1, figures 3, 4

Discussion.—Several fragmentary pinnae from Seldovia Point are undoubtedly referable to the genus *Onoclea* by their characteristic venation, which is quite well preserved. Except for the wavy margin of the apical part, they are regularly lobed (each lobe having a rounded apex) but are otherwise entire margined. The pinnae axis bears a single series of low and long areoles on each side. The midvein of each pinnule is thin but distinct and gives off thin secondaries that frequently branch, forming a prolonged reticulation nearly parallel to or at acute angles to the midvein. These characters show that our Alaskan specimens are identical with the modern monotypic species, *Onoclea sensibilis* L., distributed in northeastern Asia and eastern North America and may represent the pinnae of the middle or proximal parts of the frond.

The sterile foliage of *Onoclea* has frequently been recorded from the Upper Cretaceous and Paleogene of North America, and Brown (1962) gave a new specific name of *O. hesperia* to them. As stated previously (Wolfe, 1966), the original specimens of *O. hesperia* include both finely serrate and entire margins and are thus separable from the Seldovian specimens.

Hypotypes.—USNM 208349, 208350.

Occurrence.—9858.

Family Taxodiaceae

Genus *Glyptostrobus* Endl.*Glyptostrobus europaeus* (Brongniart) Heer

Plate 1, figure 8

Glyptostrobus europaeus (Brongniart) Heer, 1855, Flora Tertiaria Helvetia, v. 1, p. 51, pl. 19; pl. 20, fig. 1.

Discussion.—This species is represented only by fragmentary foliage shoots, which have slender leaves. No fossil cone of *Glyptostrobus* has been collected from the Seldovia Point localities. This Eurasian species was widely distributed during the Tertiary, and it is difficult to separate from *G. oregonensis* Brown of the North American Tertiary only by foliar characters. Cones collected from other Seldovian localities, however, are typical for *G. europaeus*.

Hypotype.—USNM 208351.

Occurrence.—9858.

Genus *Metasequoia* Miki*Metasequoia* cf. *M. glyptostroboides* Hu et Cheng

Plate 1, figures 2, 6, 7, 10

Metasequoia glyptostroboides Hu et Cheng, 1948, Fan Memorial Inst. Botany Bull., new ser., v. 1, p. 154.

Discussion.—Numerous short shoots and pistillate cones of *Metasequoia* from the Seldovia Point localities are indistinguishable from homologous parts of the extant species. Lacking preservation of epidermal features, however, we hesitate to place the fossil material in the extant species. The material should not be assigned to *M. occidentalis* (Newb.) Chan. because the types, as well as other Paleocene shoots of *Metasequoia*, typically have shorter and blunter needles than in middle to late Tertiary specimens of *Metasequoia*.

Specimens.—USNM 208352–208355.

Occurrence.—9856–9858.

Family Ginkgoaceae

Genus *Ginkgo* Linnaeus*Ginkgo biloba* Linnaeus

Plate 1, figure 1

Ginkgo biloba Linnaeus, 1771, Linn. Mant., v. 2, p. 313.

Discussion.—In his extensive review of the geologic history of *Ginkgo*, Tralau (1968) noted that later Tertiary specimens for which epidermal details were known did not differ specifically from the extant species. We think that there is no reasonable basis for excluding later Tertiary material of this genus from the extant species.

Hypotype.—USNM 208356.

Occurrence.—9857.

Family Nymphaeaceae

Genus *Nymphar* Ozaki*Nymphar ebae* (Huzioka) Ozaki

Plate 1, figures 11–14

Nymphar ebae (Huzioka) Ozaki, 1978, Yokohama Natl. Univ. Sci. Repts., sec. 2, no. 25, p. 17, pl. 1, figs. 1, 3–5; text-figs. 4B–D, 5A, B.

Nymphar ebae Huzioka, 1964, Akita Univ. Mining Coll. Jour., ser. A, v. 3, no. 4, p. 82, pl. 11, fig. 6; pl. 12, figs. 1–3.

Supplementary description.—Floating leaves ovate to oval in shape, 2.1 to 5.2 cm long and 1.3 to 3.2 cm wide; apex obtuse to rounded; base auriculate with deep sinus; midvein distinct, nearly straight to apex; secondary veins slender, 9 to 15 pairs, irregularly spaced, leaving the midrib at angles of 50 to 70 degrees, a basal pair more spreading, dichotomizing 3 or 4 times toward the margin and forming series of loops, camptodrome; the intersecondary veins sometimes developing but weak; the tertiary veins thin, forming irregularly large networks which enclose small polygonal areoles formed by the fourth order veins; margin entire; petiole rather slender, more than 2 cm long.

Discussion.—These are the most abundant leaves in our collection, and they are identical in shape and venation to *Nymphar ebae*, which was described from a lower Miocene flora of Honshu.

Hypotypes.—USNM 208357–208360.

Occurrence.—9858.

Family Menispermaceae

Genus *Cocculus* DeCandolle*Cocculus auriculata* (Heer) Wolfe

Plate 2, figure 7

Cocculus auriculata (Heer) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398–B, p. B24, pl. 7, fig. 1.

Hedera auriculata Heer, 1869, Flora Foss. Arctica, v. 2, pt. 2, p. 36, pl. 9, fig. 6.

Populus heteromorpha Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140–A, p. 30, pl. 12, figs. 8–10; pl. 13, figs. 1–7; pl. 14, figs. 1–3; pl. 15, figs. 3–5.

Berry, 1929, U.S. Geol. Survey Prof. Paper 154, p. 242.

Hoffman, 1932, Jour. Geology, v. 40, p. 735.

Populus fairii Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 30, pl. 15, fig. 2; pl. 16, figs. 1–3.

Cebatha multiformis Hollick, 1927, New York Bot. Garden Mem., v. 7, p. 406, pl. 38, figs. 1–6; pl. 39, figs. 1–3.

Cissampelos dubiosa Hollick, 1927, New York Bot. Garden Mem., v. 7, p. 408, pl. 37, figs. 4–7; pl. 39, fig. 4.

Cebatha heteromorpha (Knowlton) Berry, 1931, U.S. Geol. Survey Prof. Paper 170, p. 37.

Berry, 1934, U.S. Geol. Survey Prof. Paper 185, p. 112.

LaMotte, 1936 [part], Carnegie Inst. Washington Pub. 455, p. 126 [unfigured specimen 839 only].

Cocculus heteromorpha (Knowlton) Brown, 1946, Washington Acad. Sci. Jour., v. 36, p. 352.

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., ser. IV, p. 324, pl. 21, fig. 7.

Discussion.—This species is one of the most widespread plants in the Miocene of the areas bordering the North Pacific, occurring from Honshu north to Alaska and south to northern California. In Alaska, *Cocculus auriculata* is known only from the Seldovia Point flora and from the Seldovian rocks at Cache Creek and in the Nenana coalfield (Wahrhaftig and others, 1969).

The specimen assigned by Becker (1969, pl. 26, figs. 12, 13) to *Cocculus heteromorpha* is certainly *Populus*, as indicated by the numerous small teeth and the closely spaced sinuous tertiary veins that are oriented at an acute angle to the secondary veins. In *Cocculus auriculata* (including the junior synonym *C. heteromorpha*), the teeth are few and large, and the tertiary veins are widely spaced and perpendicular to the secondary veins.

Cocculus auriculata is clearly related to Paleogene species of the genus such as *C. ezoensis* Tanai from the Oligocene of Japan. Undescribed material of the same group of *Cocculus* also occurs commonly in the Eocene Ishikari floras of Hokkaido. *C. ezoensis* is, however, typically entire margined, although some toothed specimens are known (Tanai, 1970), in contrast to *C. auriculata*, which in illustrated specimens and material we have observed always has some teeth. Undescribed material from the lower Ravenian of the Puget Group of Washington (loc. 8640 and 9694 of Wolfe, 1968) has numerous teeth, but the areoles are smaller than in *C. auriculata* and the leaves have small mounds of apparently cutinized material. The small mounds, which are also present in the Paleocene *C. flabella* (Newb.) Wolfe, indicate a thick leaf and probable evergreen habit (Wolfe, 1966), in contrast to the thin leaf and probably deciduous habit of *C. auriculata*.

Hypotype.—USNM 208369.

Occurrence.—9856, 9858.

Family Cercidiphyllaceae

Genus *Cercidiphyllum* Sieb. et Zucc.

Cercidiphyllum alaskanum Wolfe et Tanai, sp. nov.

Plate 2, figures 1, 3, 4; plate 11, figures 3, 5

Cercidiphyllum crenatum auct. non (Unger) Brown.

Chelebaeva, 1968, Bot. Zhurn., v. 53, p. 744, pl. 4, figs. 1, 2; text-fig. 4a–b.

Description.—Leaves simple; lamina symmetrical,

wide ovate to very wide ovate; apex obtuse to acute; base cordate; margin simply to doubly crenate, teeth glandular; venation actinodromous; midrib and first two lateral pairs of primary veins of moderate size, two additional pairs of lateral primary veins weak; lateral primary veins markedly curved, irregularly brochidodromous, first lateral pair acrodromous; secondary veins irregularly brochidodromous, diverging at a widely acute angle, uniformly to abruptly curved, branched; intercostal areas between midrib and first lateral pair of primary veins braced by widely and irregularly spaced tertiary veins that are approximately perpendicular to primary veins, typically with a composite intersecondary vein; composite intersecondary veins typically present in area between first and second pairs of lateral primary veins; fourth order venation irregularly spaced, tending to be orthogonal; fifth order venation forming irregularly polygonal and randomly oriented areoles intruded by irregularly branching freely ending veinlets.

Discussion.—Typically orbicular leaves of the *Cercidiphyllum* type were assigned to the European species *C. crenata* (Unger) R. W. Br. (Brown, 1935, 1939), and most workers have typically followed this practice. Comparison of the Seldovia Point material with topotypic material from the Swiss Tertiary indicates a marked difference in ultimate venation, particularly in regard to the size of the areoles. Additionally, in the Swiss material the marginal glands are incorporated in the foliar tissue, whereas in the Seldovia Point material and the extant *C. japonicum* Siev. et Zucc. the glands are situated abmedial to the teeth. The Seldovia Point species also has larger areoles than in *C. japonicum*.

Cercidiphyllum alaskanum also has a characteristic pattern in the lateral tertiary venation. The intercostal area between the first (from the midrib) lateral primary and the second lateral primary typically is braced by an intersecondary vein extending abmedially and giving off tertiary braces that extend to the second lateral primary and the most basal secondary of the first lateral primary. In *Cercidiphyllum japonicum* and in most other fossil material of *Cercidiphyllum* that we have examined, an intersecondary is lacking and the bracing is accomplished only by tertiary veins. The only other species of *Cercidiphyllum* that has the type of bracing seen in *C. alaskanum* is *C. eojaponicum* Endo ex Tanai, which was originally described from the early Oligocene Fushun beds of Manchuria and later found in approximately isochronous beds on Hokkaido (Tanai, 1970). An additional similarity between *C. alaskanum* and *C. eojaponicum* is the presence of some doubly crenate teeth (see, for example, Endo, 1968, pl. 15, figs. 3, 4).

We have not investigated the areolar size in *C. eo-japonicum*, but this species differs from *C. alaskanum* in that the lateral primary and the secondary veins loop well within the margin. The strong similarities between these two species, however, indicate that they may be phyletically related.

Other material assigned to *Cercidiphyllum crenatum* by Brown (1935, 1939) should also be excluded from that species. Material from the Eocene beds at Republic, Wash., for example, has an areolar size comparable to that of the Swiss material, but the leaf base is never deeply cordate (typically it is broadly rounded) and the teeth are sharp with glands abmedial to the teeth. We suggest that there is great need for a comprehensive examination and analysis of other material assigned to *C. crenatum*.

Holotype.—USNM 208361A, B.

Paratypes.—USNM 208362, 208363A, B.

Occurrence.—9856, 9858.

Family Hamamelidaceae

Genus *Liquidambar* L.

Liquidambar pachyphylla Knowlton

Plate 2, figures 5, 6; plate 3, figures 1–3

Liquidambar pachyphylla Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 63, pl. 9, fig. 1.

Chaney, 1920, Walker Mus. Contr., v. 2, p. 174, pl. 15, figs. 2, 3.

Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 42, pl. 22, fig. 7; pl. 29, fig. 1.

Brown, 1946, Washington Acad. Sci. Jour., v. 36, p. 352.

Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 181, pl. 35, fig. 5 only.

Liquidambar europaeum patulum Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 62, pl. 10, fig. 5.

Liquidambar acutilobum Chaney, 1920, Walker Mus. Contr., v. 2, p. 175, pl. 15, fig. 4.

Arisaema hesperia Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 29, pl. 10, fig. 1.

Liquidambar europaeum auct. non Al. Braun. Heer, 1869, Flora Fossilis Arctica, v. 2, no. 2, p. 25, pl. 2, fig. 7.

Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 14.

Chaney, 1920, Walker Mus. Contr., v. 2, p. 174.

Liquidambar californicum auct. non Lesquereux. Chaney, 1920, Walker Mus. Contr., v. 2, p. 174.

Berry, 1929, U.S. Geol. Survey Prof. Paper 154, p. 250.

Berry, 1934, U.S. Geol. Survey Prof. Paper 185, p. 113.

Berry, 1938, Torrey Bot. Club Bull., v. 65, p. 96, text-fig. 3.

Liquidambar protensum auct. non Unger. Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 13, pl. 8, fig. 3.

Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 62.

Discussion.—Early collections from the Seldovia Point locality contained one poorly preserved specimen of *Liquidambar* that was three lobed; the specimen was thus assigned to the typically three-lobed *L. mioformosana* Tanai et Onoe. Additional specimens obtained in 1967, however, indicated that the Seldovia Point *Liquidambar* varied from three to five lobed, a condition that is typical for *L. pachyphylla* (Chaney and Axelrod, 1959, p. 182).

Analysis of available specimens of *Liquidambar* from early and middle Miocene localities in the western United States (Collawash, Latah, Eagle Creek, Mascall) indicates that this species is about evenly divided between three- and five-lobed leaves, in contrast to late Miocene leaves of *Liquidambar* (Faraday, Hidden Lake, Blue Mountains, Molalla, Weyerhauser), which are almost invariably five lobed (only one three-lobed specimen has been found in late Miocene beds). Additionally, the typical (early and middle Miocene) *L. pachyphylla* has sharp teeth that have a basal side about three times as long as the apical side, and the areoles are about 0.6–0.75 mm in diameter. The late Miocene material has rounded teeth that have a basal side about twice as long or less as the apical side and the areoles are about 1.5–2.1 mm in diameter. These differences are sufficient to exclude the late Miocene material from *L. pachyphylla*.

The present distribution of *Liquidambar* makes this genus an unlikely member of the Alaskan Neogene flora (see p. 17). The genus, however, was apparently not common. In most pollen samples from the Capps Glacier Seldovian and the Seldovian of the Alaska Range the genus is absent, although the genus is more persistent in the samples from the Suntrana Formation, which is late Seldovian and presumably middle Miocene. The high (14 percent) representation of *Liquidambar* in the sample from Seldovia Point is the highest we know of in the Alaskan Neogene sequence.

Hypotypes.—USNM 208364–208368.

Occurrence.—9856, 9858.

Family Platanaceae

Genus *Platanus* Linnaeus

Platanus bendirei (Lesquereux) Wolfe

Plate 3, figure 4; plate 4, figures 1, 2, 4

Platanus bendirei (Lesquereux) Wolfe, 1964, U.S. Geol. Survey Prof. Paper 454–N, p. N24, pl. 4, figs. 1, 2, 4.

- Acer bendirei* Lesquereux, 1888 [part], U.S. Natl. Mus. Proc., v. 11, pl. 5, fig. 5; pl. 6, fig. 1; pl. 7, fig. 1.
- Acer merriami* Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 74, pl. 14, fig. 7.
- Platanus youngii* Graham, 1963, Am. Jour. Botany, v. 50, p. 925, fig. 12.
Graham, 1965, Kent State Univ. Bull., Research Ser. 9, p. 89.
- Magnolia ingelfieldi* auct. non Heer. Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 13.
- Platanus aceroides* auct. non (Goepfert) Heer. Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 19, pl. 5, fig. 7.
Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 65.
Arnold, 1937, Michigan Univ. Mus. Paleontology Contr., v. 5, p. 88, pl. 3, fig. 1.
- Platanus nobilis* auct. non Newberry. Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 19.
Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 65.
- Platanus raynoldsii* auct. non Newberry. Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 19.
- Platanus aspera* auct. non Newberry. Berry, 1931, U.S. Geol. Survey Prof. Paper 170, p. 34.
- Platanus dissecta* auct. non Lesquereux. Berry, 1929, U.S. Geol. Survey Prof. Paper 154, p. 248, pl. 53, figs. 1, 2; pl. 61.
Berry, 1931, U.S. Geol. Survey Prof. Paper 170, p. 34.
Berry, 1934, U.S. Geol. Survey Prof. Paper 185, p. 111, pl. 21, fig. 2.
Arnold, 1937, Michigan Univ. Mus. Paleontology Contr., v. 5, p. 88, pl. 9, figs. 1-3.
Brown, 1937 [part], U.S. Geol. Survey Prof. Paper 186, p. 174, pl. 52, fig. 2 only.
Brown, 1937, Washington Acad. Sci. Jour., v. 27, p. 515.
Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 182, pl. 36, fig. 3.
Graham, 1965 [part], Kent State Univ. Bull., Research Ser. 9, p. 88, pl. 13, fig. 1; pl. 14, figs. 1, 5 ["Sucker Creek" occurrences only].

Discussion.—Some workers (for example, Becker, 1969) have applied the epithet *dissecta* to any three- to five-lobed leaves of *Platanus* that also have numerous teeth. Such a morphological concept for *P. dissecta* results in the inclusion in this species of several distinctive (and probably in part unrelated) groupings of *Platanus*. As pointed out previously (Wolfe, 1964, p. N24), the late Miocene *P. dissecta* has leaves that are typically five lobed and typically without subsidiary teeth between the major teeth, in contrast to the early

to middle Miocene *P. bendirei*, which has typically three-lobed leaves (although five-lobed leaves are also present) that have subsidiary teeth. Moreover, in contrast to an undescribed species from the later Oligocene of the Pacific Northwest that has several subsidiary teeth between any two adjacent major teeth, *P. bendirei* typically has only one or two subsidiary teeth. On this basis, the Seldovia Point material is referable to *P. bendirei*.

The reduction in marginal serrations suggested for the *Platanus bendirei* lineage led to the Pliocene *P. paucidentata* Dorf (differing from the next species in having larger areoles) and culminated in the extant *P. racemosa* Nutt. Thus far this lineage has been found only in North America; the few occurrences of *Platanus* in the Neogene of Japan represent the *P. aceroides* complex.

Hypotypes.—USNM 208370-208373.

Occurrence.—9858.

Family Eucommiaceae

Genus *Eucommia* Oliv.

Eucommia cf. *E. montana* Brown

Plate 4, figure 6

Eucommia montana Brown, 1940, Washington Acad.

Sci. Jour., v. 30, no. 8, p. 349, fig. 3.

Discussion.—This specimen, although incomplete, is probably separable from *E. montana* in size and wing shape. Unfortunately this Alaskan material is carbonized, and the reticulate venation pattern over the seed part, as is characteristic of *Eucommia*, is not visible. In preserved features, our specimen is closely similar to the samara of the modern monotypic *E. ulmoides* Oliver of central China. No fossil leaves referable to *Eucommia* have been found in the Seldovia Point flora.

Specimen.—USNM 208374.

Occurrence.—9858.

Family Ulmaceae

Genus *Celtis* Linn

Celtis sp.

Plate 4, figure 7

Discussion.—A single, small leaf is, although lacking the basal part, referred to the genus *Celtis* partly on the basis of the pronounced subprimary veins and camptodromous venation. The leaf is similar in general features to *C. kansana* Chaney et Elias from the Miocene and Pliocene of the conterminous United States but appears to differ in having apiculate teeth.

Specimen.—USNM 208375.

Occurrence.—9858.

Genus *Ulmus* Linnaeus
Ulmus knowltoni Tanai et Wolfe
 Plate 5, figures 1, 2

Ulmus knowltoni Tanai and Wolfe, 1977, U.S. Geol. Survey Prof. Paper 1026, p. 5, pl. 1C, F, G; pl. 2A, C, H, I, J [see synonymy and discussion].

Discussion.—Two incomplete specimens are referred to *U. knowltoni* on the basis of a strongly asymmetric cordate base and nearly single blunt teeth. This species is somewhat similar to *U. paucidentata* H. V. Smith and *U. owyheensis* H. V. Smith in marginal serrations but differs in shape of the base and in the tertiary branches of the basal secondary vein, which develop only on one side of the base.

Hypotypes.—USNM 208376, 208377.

Occurrence.—9856.

Ulmus owyheensis H. V. Smith
 Plate 4, figure 8; plate 6, figures 7a, 7b

Ulmus owyheensis Smith, 1939, Michigan Acad. Sci., Arts and Letters Papers, v. 24, p. 113, pl. 6, fig. 4.

Tanai and Wolfe, 1977, U.S. Geol. Survey Prof. Paper 1026 p. 6, pl. 2B, D, E, F; pl. 3A [see synonymy and discussion].

Ulmus plurinervis Unger. Heer, 1869, Kongl. Svenska Vet.-Akad. Handl., bd. 8, no. 4, p. 34, pl. 5, fig. 1.

Discussion.—Our Alaskan specimens are quite identical in shape, venation, and marginal serrations with *Ulmus owyheensis* H. V. Sm., which was originally described from the Miocene Sucker Creek flora. As discussed elsewhere (Tanai and Wolfe, 1977), the leaves of this species vary in laminar shape from ovate to oval and in basal shape from rounded to broadly rounded. This species, however, is distinguishable from other Tertiary elms by the following characters: single, apiculate teeth having in many instances a minute subsidiary tooth, less unequal and slightly cordate base, irregularly percurrent tertiary veins, and three or four prominent tertiary branches that depart from a basal pair of secondaries and end in the teeth. A single specimen figured as *U. plurinervis* from English Bay (Heer, 1869a) is included in *U. owyheensis*.

Hypotypes.—USNM 208376, 208377.

Occurrence.—9856, 9858.

Ulmus speciosa Newberry
 Plate 4, figures 3, 5

Ulmus speciosa Newberry, 1898, U.S. Geol. Survey Mon. 35, p. 80, pl. 45, figs. 3, 4 (excluding figs. 2, 5–8).

Tanai and Wolfe, 1977, U.S. Geol. Survey Prof. Paper 1026, p. 8, pl. 3C, F [see synonymy and discussion].

Discussion.—Two leaves, although lacking about half the base, match well in their venation and marginal characters *Ulmus speciosa*, which was recently reinstated (Tanai and Wolfe, 1977). The primary teeth of our Alaskan specimens typically have two subsidiary teeth of nearly equal size, fed by tertiary branches from the secondaries. The intercostal tertiary veins are mostly percurrent, crossing to the secondaries, and enclose irregularly polygonal nets formed by fourth order veins.

Hypotypes.—USNM 208381, 208382.

Occurrence.—9858.

Genus *Zelkova* Spach
Zelkova browni Tanai et Wolfe
 Plate 5, figures 3, 6, 8a, 8c; plate 6, figure 8

Zelkova browni Tanai and Wolfe, 1977, U.S. Geol. Survey Prof. Paper 1026, p. 8, pl. 4A, C–G [see synonymy and discussion].

Planera ungeri auct. non Ettingshausen. Heer, 1869, Kongl. Svens. Vet.-Akad. Handl., bd. 8, no. 4, p. 34, pl. 5, fig. 2.

Discussion.—This species was recently established on the basis of well-preserved material from the Miocene Collawash flora of Oregon, because the type specimen of *Z. oregoniana* was ascertained to belong to *Ulmus* (Tanai and Wolfe, 1977). *Zelkova browni* is distinguishable from *Z. ungeri* in marginal characters: larger and rather bluntly deltoid teeth, sometimes with a minute subsidiary tooth. Leaves of this species are highly variable in shape; some have a slightly cordate base and a minute subsidiary tooth on the primary teeth and superficially resemble some leaves of *Ulmus owyheensis* H. V. Smith. *Ulmus owyheensis*, however, differs from *Z. browni* in the serration of basal part of the lamina, the tertiaries branching outward from the basal pair of secondary veins, and the irregularly percurrent intercostal tertiary veins. *Zelkova browni* is similar to the modern *Z. carpinifolia* Spach of the Caucasus region in foliar shape and marginal serration.

A single specimen figured as *Planera ungeri* from "English Bay" (Heer, 1869a) has the margin of *Z. browni*, although the lower half of the blade is lacking. It is significant in the past distribution of *Zelkova* that all specimens from the conterminous United States are of the *Z. browni* type and that this species lived together with the Eurasian species *Z. ungeri* in Alaska during the Miocene.

Hypotypes.—USNM 208384–208388.

Occurrence.—9856, 9858.

Zelkova ungeri Kovats

Plate 5, figures 4, 7; plate 6, figures 1, 2, 6

Zelkova ungeri Kovats in Unger, 1852, Iconogr., p. 42, pl. 20, fig. 19.

Kovats, 1856, Fossile Flora von Erdöbenye, p. 27, pl. 5, figs. 6, 7.

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 10, no. 2, p. 322, pl. 18, figs. 1-4, 6-9, 11.

Discussion.—A number of our Alaskan specimens are identical with *Zelkova ungeri*, which is common in the Neogene of Eurasia. These leaves are characterized by apiculate, usually single-serrate teeth with somewhat incurved pointing tip. The tertiary veins in the intercostal areas are mostly wavy and typically appear to form irregularly quadrangular or pentagonal meshes due to thick connecting fourth order veins. These marginal and venation characters show that this species is closely related to the modern *Z. serrata* Mak. from Japan and *Z. sinica* Schn. from mainland China.

As far as we know, *Z. ungeri* has not been found in the Tertiary of the conterminous United States. Becker (1969) reported a leaf of *Z. ungeri* from the Beaverhead basin of southern Montana, but his specimens appear to be referable to *Z. browni* in characters of the serrations.

Hypotypes.—USNM 208389-208393.*Occurrence.*—9856, 9858.

Family Fagaceae

Genus *Fagus* Linn.*Fagus antipofi* Heer

Plate 5, figure 8b; plate 6, figures 3, 4; plate 7, figures 1, 5, 6

Fagus antipofi Heer, in Abich, 1858, Acad. Sci. St. Petersburg Mem., ser. 6, v. 7, p. 572, pl. 8, fig. 2.

Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 30, pl. 5, fig. 4a; pl. 7, figs. 4-8; pl. 8, fig. 1.

Hollick, 1936, U.S. Geol. Survey Prof. Paper 186, p. 95, pl. 53, figs. 1, 2.

Castanea ungeri Heer 1869, Flora Fossilis Arctica, p. 32, pl. 7, figs. 1-3.*Fagus macrophylla* auct. non Unger. Heer, 1869, Flora Fossilis Arctica, p. 31, pl. 8, fig. 2.

Discussion.—Leaves referred to *Fagus* are very common in the Seldovia Point localities; these leaves are generally elliptical to oblong in shape, typically serrate with minute teeth, and have 14 to 26 pairs of secondary veins. Although highly variable in gross shape and size, these Alaskan leaves match well those of *Fagus antipofi* in venation and marginal characters. The specimen figured as *F. macrophylla* from the "English Bay" locality by Heer (1869a) represents a large leaf of *F. antipofi*. Heer also described three large-

toothed leaves as *Castanea ungeri* from the same locality; these are included in *F. antipofi*, because we also collected several leaves having a similar margin. Our material lacks the secondary vein termination near the teeth characteristic of *Castanea*. In measurements of many of the Seldovia Point specimens, including Heer's material, the foliar characters of the Alaskan beech such as leaf indices (length to width ratio) is well consistent with measurements of *F. antipofi* from East Asia, as discussed elsewhere (Tanai, 1973).

Hypotypes.—USNM 208394-298399.*Occurrence.*—9856, 9858.*Fagus* aff. *F. crenata* Blume

Plate 6, figure 5

Discussion.—A single elliptical leaf has, though incomplete, features characteristic of *Fagus* in venation and margin: the midvein is somewhat zigzag in its upper portion, the secondaries abruptly arise up along the margin, and the margin is sinuately undulate. Judging from the restoration, this leaf probably has less than 13 pairs of secondary veins. All these characters show that this specimen is closely similar to leaves of the extant *F. crenata* Blume in Japan. While *F. crenata* has been known to have appeared since the late Pliocene in Japan (Tanai, 1973), this Alaskan fossil beech is, though fragmentary, noteworthy for the evolutionary history of beech.

An undescribed leaf from the Oligocene part of the Kenai Group (loc. 9884) has a margin of the *Fagus crenata* type. The number of secondary veins is, however, well over 13, and in this feature the leaf is more similar to leaves of *F. antipofi*. We tentatively suggest that the lineage to which *F. crenata* belongs diverged from the *F. antipofi* line at high latitudes and has since migrated southward.

Specimen.—USNM 208400.*Occurrence.*—9856.Genus *Quercus* Linnaeus*Quercus furuhjelmi* Heer

Plate 7, figures 2-4; plate 8, figures 1-3

Quercus furuhjelmi Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 32, pl. 5, fig. 10; pl. 6, figs. 1, 2.

?Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 98, pl. 55.

Quercus pandurata Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 33, pl. 6, fig. 6.*Populus leucophylla* auct. non Unger. Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 26, pl. 2, fig. 6.*Quercus etymodrys* auct. non Unger. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 98, pl. 54, figs. 6, 7.

Quercus pseudocastanea auct. non Goeppert. Heer, 1869, *Flora Fossilis Arctica*, v. 2, pt. 2, p. 32, pl. 6, figs. 3-5.

Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 98, pl. 54, figs. 4, 5.

Discussion.—The specimen assigned to this species by Hollick (1936, p. 55) is fragmentary but does have several points of similarity to *Quercus furuhjelmi*. Hollick's specimen, however, appears to have considerably more secondary veins than in any specimen of *Q. furuhjelmi*; this apparent difference, as well as the fragmentary nature of the specimen, makes specific assignment to *Q. furuhjelmi* questionable.

The numerous large serrations of these leaves allies *Quercus furuhjelmi* to the so-called chestnut oaks. The chestnut oaks are, however, an apparently polyphyletic group. The chestnut oaks of eastern Asia (for example, *Q. crispula* Blume) have been placed in the subgenus *Heterobalanus* in contrast to the chestnut oaks of eastern North America (for example, *Q. prinoides* Willd.), which are placed in subgenus *Leucobalanus* (Trelease, 1924); the one chestnut oak of western North America—*Q. sadleriana* R. Br.—has been allied to *Leucobalanus* by some authorities and to *Heterobalanus* by others. Examination of cleared leaves of almost all species of chestnut oaks does not indicate any fundamental distinction between foliage of these groups, although some species of *Heterobalanus* have some aristate teeth, which are absent in *Leucobalanus*. Some specimens of *Q. furuhjelmi* also possess some aristate teeth (pl. 8, fig. 3), which indicates that this species is probably allied to *Heterobalanus*.

Quercus furuhjelmi is similar to the Korean and Japanese *Q. microcrispula* Huz., which has been compared to both *Q. crispula* Blume (Huzioka, 1954) and to *Q. mongolica* Fisch. var. *grosseserrata* (Blume) R. et W. (Tanai, 1961). In having teeth that are narrowly rounded in the basal part of the lamina and that grade into acute to acute-aristate teeth near the apex, *Q. furuhjelmi* is distinct from these fossil and extant species.

Hypotypes.—USNM 208401-208406.

Occurrence.—9856, 9858.

Family Betulaceae
Genus *Alnus* Linnaeus
Alnus cappsi (Hollick) Wolfe
Plate 8, figure 5

Alnus cappsi (Hollick) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B19, pl. 6, figs. 1, 4; pl. 7, figs. 2, 6; text-fig. 6 [see synonymy].

Crataegus cappsi Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 86, pl. 49, fig. 3.

Discussion.—The close relationship of *Alnus cappsi* to the Alaskan Oligocene *A. evidens* indicates that this lineage is of Beringian origin.

Hypotype.—USNM 208407.

Occurrence.—9858.

Alnus fairi (Knowlton) Wolfe
Plate 8, figure 4; plate 9, figure 2

Alnus fairi (Knowlton) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B17, pl. 7, fig. 3; text-fig. 3 [see synonymy].

Betula fairii Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 33, pl. 17, fig. 4.

Discussion.—Although Becker (1973) ignored the transfer of the Latah "*Betula*" *fairii* to *Alnus*, the type of ultimate venation possessed by both the Alaskan and Latah material (see Wolfe, 1966, text-fig. 3) of this species does not occur in *Betula*.

Hypotypes.—USNM 208408, 208409.

Occurrence.—9856 (Heer's material), 9858.

Alnus healyensis Wolfe
Plate 8, figure 6; plate 9, figure 1

Alnus healyensis Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B17, pl. 7, fig. 4, text-fig. 4.

Artocarpidium alaskanum Hollick, 1936 [part], U.S. Geol. Survey Prof. Paper 182, p. 108, pl. 59, fig. 5.

Quercus oregoniana auct. non Knowlton. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 103, pl. 50, fig. 5.

Alnus relatus auct. non (Knowlton) Brown. Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 159, pl. 22, fig. 6 only.

Discussion.—*Alnus healyensis* occurs in both the early (Collawash flora) and middle (Latah, Mascall) Miocene in the conterminous United States. In Alaska, this species occurs in the lower (Capps Glacier, Houston, Upper Healy Creek) and upper (Seldovia Point, Sanctuary/Suntrana) Seldovian. A species having, as in *A. healyensis*, sharp and basally reflexed secondary teeth is represented in the Oligocene Bridge Creek flora of Oregon (Klucking, 1959), and thus *A. healyensis* is thought to be of West American derivation. The Eocene *A. kluckingi* Wolfe also has similar but fewer teeth.

Hypotypes.—USNM 208410, 208411.

Occurrence.—9856 (Hollick's material from Coal Cove), 9858.

Genus *Betula* Linnaeus
Betula cf. *B. sublutea* Tanai et N. Suzuki
Plate 9, figure 8

Betula sublutea Tanai and N. Suzuki, 1963, Tertiary floras of Japan, Miocene floras, p. 114, pl. 8, fig. 8; pl. 10, figs. 7-9.

Discussion.—A single leaf is referred to *Betula* on the basis of its shape and marginal serration, particularly on the basis of the apically pointing teeth and secondary veins. It is nearly identical with *B. sublutea* in having rather obtuse teeth and a cordate base, though the detailed venation is not visible. Our Alaskan leaf is different from the finely and sharply serrate *B. vera* R. W. Br., which was described from the Miocene of Washington.

Specimen.—USNM 208413.

Occurrence.—9858.

Genus *Carpinus* Linnaeus

***Carpinus seldoviana* Wolfe**

Plate 9, figure 7; plate 10, figures 1–3

Carpinus seldoviana Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398–B, p. B23, pl. 6, fig. 6; text-fig. 11D.

Supplementary description.—Involucre obovate in shape, asymmetrically cuneate at base, rounded but abruptly pointed apex, 19 mm long and 9.6 mm wide; palmately three veined, the principal veins leaving the base, entering large teeth; secondary veins thin, diverging at nearly right angles or obliquely from the principal veins, forming irregular networks with thinner tertiary veins; margin compoundly serrate in the upper half, sparse, minute teeth, excepting the principal three lobes; nutlet not preserved.

Discussion.—This species is characterized by leaves having a strongly cordate base and apiculate marginal teeth with aristate tips, thus closely resembling the modern *Carpinus cordata* Blume living in north-eastern Asia. The intercostal tertiary veins are nearly perpendicular to the secondaries, and typically bifurcate halfway between the secondaries. The fourth and fifth order veins form quadrangular or pentagonal networks, which are rarely intruded by single branched veinlets. These venation characters also resemble well those of the extant species. An incomplete involucre is closely similar to those of the extant *C. cordata* in shape and venation and is included in *C. seldoviana*.

C. seldoviana occurs abundantly at the Seldovia Point locality and rarely at the Port Graham locality. This Alaskan species is probably related to *C. subcordata* Nathorst, which is common in the Miocene of Japan.

Hypotypes.—USNM 208414–208417.

Occurrence.—9856, 9858.

Genus *Corylus* Linnaeus

***Corylus* sp.**

Plate 9, figure 3

Discussion.—In shape of the teeth, these fragmentary leaves are similar to the extant *Corylus chinensis*

Franch. The fossils, however, have areoles about half the size of the areoles of this extant species; in this feature, the fossils are more similar to species such as *C. rostrata* (Ait.) Pursh. These fossils thus represent a new species, but we consider the present material to be too fragmentary for the basis of a specific concept. One of the two specimens on which Heer (1869a, pl. 10, fig. 2) based his *Tilia alaskana* represents the same species, but that specimen (as well as the second fragment that is not *Corylus*) represents less than half a leaf; we, therefore, reject *Tilia alaskana* Heer (1869, p. 36, pl. 10, figs. 2, 3) under Article 70 of the International Code of Botanical Nomenclature.

Specimens.—USNM 208418, 208419.

Occurrence.—9856, 9858.

Genus *Ostrya* Scop.

***Ostrya* cf. *O. oregoniana* Chaney**

Plate 9, figures 4–6

Ostrya oregoniana Chaney, 1927, Carnegie Inst. Washington Pub. 346, p. 106, pl. 9, fig. 12; pl. 10, figs. 1, 4.

Discussion.—Our involucre specimens of *Ostrya* vary from elliptical to oval in shape and 7 to 11 in number of primary veins; these are nearly identical with the involucres of *O. oregoniana*, which was defined by both leaves and involucres. Unfortunately we did not collect any leaves of *Ostrya* at the Seldovia Point localities. These Alaskan specimens are, therefore, only tentatively assigned to *O. oregoniana*, because of the difficulty of making specific separations in *Ostrya* on the basis of involucres alone.

Specimens.—USNM 208420–208422.

Occurrence.—9858.

Family Juglandaceae

Genus *Carya* Nuttall

***Carya bendirei* (Lesquereux) Chaney et Axelrod**

Plate 10, figure 7; plate 11, figures 1, 2

Carya bendirei (Lesquereux) Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 155, pl. 19, figs. 1–5 [not many items synonymized.]

Wolfe, 1964, U.S. Geol. Survey Prof. Paper 454–N, p. N20, pl. 1, fig. 7.

Graham, 1965, Kent State Univ. Bull., Research Ser., 9, p. 81, pl. 12, fig. 8.

Rhus bendirei Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 15, pl. 9, fig. 2.

Salix engelhardti Lesquereux, 1888, U.S. Natl. Mus. Proc., v. 11, p. 17, pl. 8, fig. 2.

Hicoria dentata Chaney, 1920, Walker Mus. Contr., v. 2, p. 163, pl. 8, fig. 1.

Hicoria orientalis Chaney, 1920, Walker Mus. Contr., v. 2, p. 163, pl. 8, fig. 2.

Hicoria pecanoides Chaney, 1920, Walker Mus. Contr., v. 2, p. 164, pl. 8, fig. 3.

Carya egregia auct. non *Juglans egregia* Lesquereux. LaMotte, 1936, p. 116, pl. 4, figs. 5, 6; pl. 6, figs. 1, 2.

Brown, 1937, U.S. Geol. Survey Prof. Paper 186, p. 169, pl. 57, fig. 4.

Beck, 1938, Mineralogist, v. 6, no. 8, p. 22, text-fig. 3.

Smith, 1939, Michigan Acad. Sci. Papers, v. 24, p. 111, pl. 7, fig. 1.

Smith, 1941, Am. Midland Naturalist, v. 25, p. 500, pl. 5, fig. 3.

Juglans egregia auct. non Lesquereux. Berry, 1931, U.S. Geol. Survey Prof. Paper 170, p. 35, pl. 11, fig. 3.

Ptelea miocenica auct. non Berry. LaMotte, 1936 [part], Carnegie Inst. Washington Pub. 455, p. 133, pl. 11, fig. 4 only.

Arbutus matthesii auct. non Chaney. LaMotte, 1936 [part], Carnegie Inst. Washington Pub. 455, p. 140, pl. 14, fig. 3 only.

Discussion—Many of the items synonymized under *Carya bendirei* are rejected by us. For example, the types of *Prunus? merriami* Knowlton (1902, p. 67) represent *Cyclocarya*. Additionally, *Carya simulata* (Knowlton) R. W. Brown (1937, p. 169) is considered to represent a valid species distinct from *C. bendirei*. In *C. simulata*, (1) the secondary veins fork conspicuously to give a ladderlike appearance to the secondary external veins and (2) the apical and basal sides of the teeth are equal in length.

The Seldovia Point leaflets are assigned to *Carya* on the basis of (1) finely serrate margin with uniformly spaced and sized teeth, (2) mixed craspedodromous and camptodromous secondary venation, (3) central entry of the teeth by secondary or external secondary veins, (4) fourth rank venation, and (5) typically quadrangular areoles formed by fifth order veins and either lacking veinlets or intruded by simple veinlets. *Carya* is also known from the Neogene of eastern Asia (Hu and Chaney, 1940; Tanai and Suzuki, 1963), but the Asian *C. miocathayensis* Hu et Chan. is consistently camptodromous, has about 25 pairs of secondary veins, and typically has a narrowly rounded base. In contrast, the Seldovian material—as in material of *C. bendirei* from the conterminous United States—has some camptodromous and some craspedodromous secondary veins, has fewer (about 12–18) pairs of secondary veins, and has some leaflets with a broadly rounded base. No extant species of *Carya* closely resembles *C. bendirei*. In members of

section *Carya*, which is exclusively North American, the teeth have a pronouncedly elongated basal side and tend to be pointed apically. In members of section *Apocarya*, which is disjunct between North America (Mexico and eastern United States) and east Asia (Vietnam and China), the teeth have apical and basal sides of almost equal length and many of the teeth are pointed abmedially. On this basis, *C. bendirei* is referable to *Apocarya*.

Hypotypes.—USNM 208423, 208424.

Occurrence.—9856, 9858.

Genus *Cyclocarya* Iljinskaja

Cyclocarya ezoana (Tanai et N. Suzuki) Wolfe et Tanai, comb. nov.

Plate 10, figures 4–6, 8, 9

Pterocarya ezoana Tanai and N. Suzuki, 1963, Tertiary Floras Japan, v. 1, p. 110, pl. 6, figs. 2–5, 8, 9, 11; pl. 19, fig. 1; pl. 21, fig. 10.

Ishida, 1970 [part], Kyoto Univ. Fac. Sci. Mem., Ser. Geology and Mineralogy, v. 37, no. 1, p. 70, pl. 5, fig. 2 only.

Discussion.—In establishing this species, Tanai and Suzuki (1963, p. 110) noted the close resemblance to leaflets of the extant *Pterocarya paliurus* Skan. This extant species, however, is now generally accorded monotypic status as *Cyclocarya paliurus* (Skan.) Ilj., and we consequently transfer the fossil material to *Cyclocarya*.

As noted by Tanai and Suzuki (1963, p. 110), *Cyclocarya ezoana* is readily distinguished from *Pterocarya asymmetrosa* in that the secondary veins bend sharply towards the apex about two-thirds of the distance from the midrib to the margin and in having sharper and more widely spaced teeth. The same criteria also distinguish *C. ezoana* from *P. nigella*. Additionally, the areoles of *Cyclocarya* (including *C. ezoana*) are about one-half the size of the areoles in *Pterocarya*.

Leaflets similar to the extant *Cyclocarya* also occur in the Neogene of the conterminous United States (Wolfe, 1959), but the material from the Pacific Northwest is specifically distinct from the Alaskan and Japanese material. In particular, the teeth of the material from the Pacific Northwest are broader, and the areoles are large as in *Pterocarya*, although in secondary venation and overall shape of the teeth the material is most similar to *Cyclocarya*. We suggest that the species from the Pacific Northwest represents an extinct lineage of *Cyclocarya*; the leaflets in the Collawash flora are associated with a fruit of *Cyclocarya*.

Hypotypes.—USNM 208425–208429.

Occurrence.—9856, 9858.

Genus *Pterocarya* Kunth
Pterocarya nigella (Heer) Wolfe
 Plate 11, figures 4, 6

Pterocarya nigella (Heer) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B15, pl. 3, fig. 3.

Juglans nigella Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 38, pl. 9, figs. 2-4.

Juglans oregoniana Lesquereux, 1878, Harvard Coll. Mus. Comp. Zoology, Mem., v. 6, no. 2, p. 35, pl. 9, fig. 10.

Salix varians auct. non Goeppert. Heer, 1869 [part], Flora Fossilis Arctica, v. 2, pt. 2, p. 27, pl. 2, fig. 8 only.

Pterocarya mixta auct. non (Knowlton) Brown. Chaney and Axelrod, 1959, Carnegie Inst. Washington Pub. 617, p. 157, pl. 21, figs. 1, 2. Axelrod, 1964, California Univ. Pubs. Geol. Sci., v. 51, p. 115, pl. 10, figs. 8, 9.

Discussion.—As noted previously (Wolfe, 1966, p. B15), these leaflets have features that ally them to the extant members of section *Platyptera*. In particular, leaflets of *P. rhoifolia* Sieb. et Zucc. are similar to the fossils. The Japanese Neogene *P. asymmetrosa* Kon'no is also closely similar to *P. rhoifolia* (Tanai and Suzuki, 1963, p. 110), and probably some material now referred to *P. asymmetrosa* is conspecific with *P. nigella*. Other material referred to *P. asymmetrosa* may, however, be referable to other species, and we consequently defer a formal synonymy until such time as the Japanese Neogene material of this species is thoroughly reviewed. *P. nigella* was probably one of the most geographically wide ranging species, occurring from Oregon to Alaska and to Honshu.

Hypotypes.—USNM 208430, 208431.

Occurrence.—9856 (Heer's material), 9858.

Pterocarya sp.
 Plate 11, figure 7

Description.—Fruit representing nut with two wings, incomplete in preservation, more than 17 mm wide and 8 mm high; wings linear-oblong in shape, rather thin in texture; alate veins thin, more than 10 in each wing, leaving the nut part, then branching once or twice toward the apical part of wing; nut ovoid, 6 mm high and 3.5 mm wide, pointed at apex; axis of nut parallel to the wing plane.

Discussion.—A two-winged nut, though poorly preserved, is certainly referable to *Pterocarya*; this specimen is closely similar to the extant *P. fraxinifolia* Skan. of the Middle East by its shape and the direction of nut axis. This fossil fruit may represent *P. nigella*, but leaflets of that species are more similar to *P. rhoifolia* than to *P. fraxinifolia*.

Specimen.—USNM 208432.

Occurrence.—9856.

Family Salicaceae
 Genus *Populus* Linnaeus
Populus kenaiana Wolfe

Plate 11, figure 9; plate 12, figure 1

Populus kenaiana Wolfe, 1966, U.S. Geol. Survey Prof. Paper, 398-B, p. B12, pl. 3, fig. 1.

Vitis crenata Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 36, pl. 8, fig. 6.

Populus lindgreni Knowlton, U.S. Geol. Survey 18th Ann. Rept., pt. 3, p. 725, pl. 100, fig. 3.

Chaney and Axelrod, 1959, Carnegie Inst. Washington Pub. 617, p. 151, pl. 17, figs. 1-3.

Vitis heeriana Knowlton and Cockerell, 1919, U.S. Geol. Survey Bull. 696, p. 648.

Discussion.—Although a member of the aspen group of *Populus*, relationships to extant species appear distant. This or a closely related species occurs in the middle and late Oligocene Alaskan flora; the youngest occurrence of the species in both Alaska and the conterminous United States is late Miocene.

Hypotypes.—USNM 42264B, 208433.

Occurrence.—9856 (Heer's material), 9858.

Populus sp.
 Plate 11, figure 8

Discussion.—This fragmentary specimen has lateral primary veins that extend more admedially than apically (as is typical in *Populus kenaiana*). Although representing a separate species, the material is inadequate for specific determination.

Specimen.—USNM 208434.

Occurrence.—9858.

Genus *Salix* Linnaeus

Four morphologic types can be differentiated in the Seldovia Point material of *Salix*. The previously described *S. picroides* is characterized by the small, apically pointing teeth that may be appressed to the lamina; the tertiary venation is irregular but tends to be percurrent, and the lamina tends to be narrowly oblanceolate. In shape, *S. cappsensis* is similar to *S. picroides*, but the former species has large, widely spaced, and basally reflexed teeth and the tertiary venation is more uniformly percurrent. *Salix seldoviana* has an elliptical shape, but most characteristic are the small, closely spaced, and irregularly shaped teeth. *Salix hopkinsi* is almost entire margined, has a narrowly elliptic shape, and has closely spaced tertiary veins.

None of the Seldovia Point species of *Salix* are known outside of Alaska; the material listed as *S. inquirenda* Knowlt. by Wolfe (1966) is now considered to represent *S. picroides*. *Salix seldoviana* is similar to

some leaves attributed to *S. varians* Goepf., but leaves of the *variens* type from the German Miocene do not have a margin as finely serrate as *S. seldoviana*. The relationships of the Seldovia Point species of *Salix* to extant species are not clear. *Salix cappensis* is thought to be in the same lineage that gave rise to the extant Alaskan *S. richardsonii* Hook., and *S. picroides* has some similarities to the extant *S. pseudomonticola* Ball (Wolfe, 1966); these suggested relationships, as well as the relationships of *S. seldoviana* and *S. hopkinsi*, require further study, particularly considering the large amount of as yet specifically undetermined material of *Salix* in the collections from the Homeric and Clamgulchian. This material should provide much information on the relationships of the Seldovia Point willows to extant species.

Salix cappensis Wolfe

Plate 12, figure 8; plate 13, figures 1, 2, 4; plate 14, figures 3, 4
Salix cappensis Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B12, pl. 4, fig. 6.

Discussion.—A closely related but undescribed species occurs in Oligocene beds at Kukak Bay; this older species has fewer teeth than *Salix cappensis*. As noted previously (Wolfe, 1966), *S. cappensis* appears to be ancestral to the Homeric *S. chuitensis* Wolfe and, in turn, to the extant *S. richardsonii* Hook.

Hypotypes.—USNM 208435–208439.

Occurrence.—9858.

Salix hopkinsi Wolfe et Tanai, sp. nov.

Plate 12, figure 4; plate 13, figures 5, 6

Description.—Leaves simple, venation pinnate; shape narrowly elliptic, apex acute, base acuminate; length 4.5 to 7.0 cm, width 2.0 to 2.8 cm; about seven pairs of secondary veins, irregularly spaced, departing at an angle of 60 to 80 degrees, some slightly decurrent, bending sharply towards apex, eucamptodromous, approaching margin closely; intersecondaries numerous, gradational with tertiary veins; tertiary veins irregularly spaced, oblique to secondary veins, branching, sinuous; fourth order venation forming a highly irregular reticulum of thinning veins and apparently forming areoles; margin entire except for a few irregularly spaced small teeth; petiole incomplete, at least 0.5 cm long.

Discussion.—Leaves of *Salix* from the Homeric appear similar to *Salix hopkinsi*; whether these younger specimens are conspecific with *S. hopkinsi* requires further study.

We take pleasure in naming this species for David M. Hopkins, who has aided this study in numerous ways.

Holotype.—USNM 208440.

Paratype.—USNM 208441.

Occurrence.—9858.

Salix picroides (Heer) Wolfe

Plate 12, figures 5–7; plate 13, figures 3, 7

Salix picroides (Heer) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B p. B14.

Juglans picroides Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 39, pl. 9, fig. 5.

Discussion.—*Salix picroides* is also represented in collections from the lower Seldovian at Capps Glacier and Houston. In the Nenana coalfield, *S. picroides* also occurs in both the lower and upper Seldovian.

Hypotypes.—USNM 208442–208445.

Occurrence.—9856 (Heer's material), 9858.

Salix seldoviana Wolfe et Tanai, sp. nov.

Plate 12, figures 2, 3; plate 14, figure 2

Description.—Leaves simple, pinnately veined; shape elliptical, apex not known, base cuneate; length 8.5 to more than 10 cm, width 5 to 6 cm; about nine pairs of secondary veins, irregularly spaced, departing at an angle of 50 to 70 degrees, eucamptodromous, approaching margin closely; a few short intersecondary veins; tertiary veins oblique to secondary veins, tending to be oriented perpendicular to midrib in outer part of intercostal area, percurrent to branching, somewhat sinuous; fourth order venation forming a reticulation of irregular shape and size; fifth order and ultimate venation indistinct; margin finely serrate, basal side of tooth convex, about twice as long as apical side, which is slightly convex to straight; teeth entered centrally by branches of secondary veins; petiole incomplete, at least 0.5 cm long.

Discussion.—The finely serrate margin combined with the few secondary veins and few short intersecondary veins separate this species from others found at Seldovia Point. *Salix seldoviana* does not closely resemble any other known Alaskan Tertiary *Salix*.

Holotype.—USNM 208446.

Paratype.—USNM 208447.

Occurrence.—9858.

Family Tiliaceae

Genus *Tilia* Linnaeus

Tilia subnobilis Huzioka

Plate 15, figure 1

Tilia subnobilis Huzioka, 1943, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 7, no. 1, p. 125, pl. 22, figs. 2, 3.

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., v. 11, no. 2, p. 370, pl. 29, fig. 1.

Discussion.—A single leaf is referred to the genus *Tilia* on the basis of its venation and marginal serrations with glandular teeth. The tertiary veins are nearly straight or slightly convex and percurrent; the fourth order veins are thin, forming quadrangular or pentagonal meshes that are penetrated by once- or twice-branched veinlets. This Alaskan specimen is referred to *T. subnobilis* in the oval shape, deeply cordate base and venation, although the marginal teeth are smaller in the Alaskan leaf. *T. subnobilis* has been reported from a few localities in the lower and middle Miocene of Hokkaido and Korea. Our specimen shows a slight resemblance in general outline to *T. oregona* LaMotte from the Bridge Creek flora of Oregon (LaMotte, 1935) but differs in venation characters.

Hypotype.—USNM 208448.

Occurrence.—9856.

Family *Hydrangeaceae*
Genus *Hydrangea* Linnaeus
Hydrangea sp.
Plate 14, figure 1

Discussion.—A single leaf and its counterpart, although fragmentary, show characters of the genus *Hydrangea* in having finely and closely serrate margin and the secondary veins loop well within the margin. Superficially these specimens resemble *Prunus elliptica* but differ in the sharply rising secondary veins and marginal looping. This Alaskan specimen is closely similar in venation to an incomplete leaf described as *Ilex insignis* Heer from the "English Bay" (Heer, 1869a) locality but differs in the marginal teeth, if his specimen was accurately illustrated.

Specimen.—USNM 208449A, B.

Occurrence.—9858.

Family *Rosaceae*
Genus *Crataegus* Linnaeus
Crataegus chamissoni (Heer) Wolfe et Tanai, comb. nov.
Plate 14, figures 5, 6

Quercus chamissoni Heer, 1869, Kongl. Svenska Vet.-Akad. Handl., v. 8, p. 33, pl. 6, figs. 7, 8.

Discussion.—The type specimens of *Quercus chamissoni* have a cuneate base, irregularly duplicate-dentate teeth, and irregularly spaced secondary veins that enter the teeth that are mixed craspedodromous-camptodromous. The camptodromous secondaries join with the next secondary above or with the intersecondaries. These characters show that Heer's specimens are not leaves of *Quercus* but are those of *Crataegus*.

Two incomplete specimens in our collections are referred to *Crataegus chamissoni*; one specimen is

ovate-lanceolate in shape, quite similar to one of the type specimens (Heer, 1869a), pl. 6, fig. 8), while another is obliquely ovate, having well-preserved fine venation. In venation and marginal characters *C. chamissoni* is similar to the extant *C. douglasii* Lindl. of western North America, which includes ovate-lanceolate to oval leaves.

Hypotypes.—USNM 208450, 208451.

Occurrence.—9856 (Heer's material), 9858.

Genus *Prunus* Linnaeus
Prunus kenaica Wolfe et Tanai, sp. nov.
Plate 15, figures 2, 5

Description.—Leaves elliptic to elliptic-oblong in shape, 10.7 to 17 cm long (estimated) and 4.2 to 5.3 cm wide; base gradually narrowed, broadly cuneate, apex unknown; midrib stout, nearly straight or slightly arcuate; secondary veins somewhat slender but distinct, more than 11 pairs, subopposite, somewhat irregularly spaced, diverging from the midvein at angles of 40 to 50 degrees in the lower half of blade, at wider angles in the upper, nearly straight and then turning up near the margin, camptodromous, looping distinctly with the next secondary above; tertiaries branching outward from the secondaries also looping well within the margin; fourth order veins branching from the looping tertiaries entering teeth or irregularly looping; intercostal tertiaries forming large, irregularly polygonal networks that enclose small fourth order nets; veinlets once or twice branching; margin finely serrate with inward-pointed, acute teeth; texture rather thin; petiole missing.

Discussion.—Three leaves and their counterparts are referred to the genus *Prunus* on the basis of their marginal loops and serrations. The fourth and fifth order veinlets show a close similarity to those of many modern cherry leaves. In the conterminous United States no cherry leaves are comparable to this new species. Several fragmentary leaves were described under the name of *P. scotti* Heer from Paleocene of Greenland (Heer, 1868, 1869b, 1880, 1883) and some show close resemblance in secondary venation and shape, although the finer venation was not figured. Two leaves described as *P. scotti* from the Mormon Creek flora of southwestern Montana (Becker, 1960) are different in venation from *P. kenaica*, although somewhat similar in shape.

Among extant species our specimens are similar to leaves of *P. bicolor* Koehne and especially *P. vaniotti* Levl., which live in Szechuan.

Holotype.—USNM 208452.

Paratype.—USNM 208453.

Occurrence.—9856.

Prunus aff. *P. padus* Linnaeus
Plate 14, figure 7

Description.—Leaf incomplete, almost half missing, broadly ovate in general shape, acute or probably acuminate at apex, base unknown; midrib stout, slightly arcuate; secondary veins distinct, about 10 subopposite pairs, irregularly spaced, diverging from the midrib at angles of 40 to 50 degrees in the middle and upper parts of the lamina, higher angles in the lower part, slightly curving upward, then forming distinct, large loops with the next secondary above; some slender intersecondary veins leaving the midvein, nearly parallel to the secondaries, halfway to the margin connecting with the tertiaries; tertiary veins branching from the secondaries near the margin, forming small marginal loops; fourth order veins branching from tertiary vein loops, entering marginal teeth; intercostal tertiaries irregularly percurrent or branching, enclosing quadrangular or pentagonal areoles; areoles intruded by once or twice branching veinlets; margin coarsely duplicate serrate with acute teeth; texture probably thin; petiole missing.

Discussion.—A single leaf and its counterpart, although incomplete, shows venation typical of *Prunus* and is distinguishable from the *P. elliptica* in having an ovate shape and coarser marginal serrations. Among the fossil cherry leaves of North America, our specimens are somewhat similar to some leaves of *Prunus? merriami* Knowlton from the Miocene sequence of Oregon (Knowlton, 1902, pl. 11, figs. 6, 7 (not figs. 2, 3)) but are different in the marginal looping of the secondaries. Except for this species, no fossil cherry leaves are comparable to our specimens; these Alaskan specimens are, however, too incomplete to form the basis for a new species.

Among extant *Prunus*, our leaves are most similar to *P. padus* L. of northeastern Asia.

Specimen.—USNM 208454A, B.

Occurrence.—9858.

Genus *Sorbaria* A. Braun
Sorbaria hopkinsi (Wolfe) Wolfe et Tanai, comb. nov.
Plate 16, figures 1-2

Spiraea hopkinsi Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B24, pl. 8, fig. 2.

Discussion.—The generic determination of this species was based on comparisons to the extant "*Spiraea*" *lindleyana*. This modern species, however, is properly placed in *Sorbaria*, a small genus of northeast Asian shrubs.

Sorbaria has been previously found as fossil in the Eocene of Sakhalin (Borsuk, 1956); an undescribed species has also been found in the late Oligocene rocks of the Alaska Range (loc. 9749 of Wahrhaftig and

others, 1969), and an additional species is known in the early Seldovian Capps Glacier flora. The stratigraphic range of *S. hopkinsi* is now known to be longer than indicated by Wolfe, Hopkins, and Leopold (1966). This report extends the range downward into the upper Seldovian Stage, and collections made in 1967 from the lower part of the Clamgulchian along Kachemak Bay also includes this species. *S. hopkinsi* is, however, much more common and widespread in rocks of Homerian age.

Hypotypes.—USNM 208455-208458.

Occurrence.—9858.

Family Leguminosae
Genus *Cladrastis* Rafinesque
Cladrastis cf. *C. aniensis* Huzioka
Plate 15, figure 4; plate 16, figures 3, 4

Cladrastis aniensis Huzioka, 1963, Tertiary floras of Japan, Miocene floras, p. 205, pl. 35, figs. 5, 6.

Discussion.—Two leaflets, although incomplete, are referred to the genus *Cladrastis* on the basis of venation characters and are closely similar to *C. aniensis* Huzioka from the middle Miocene of Japan. Our leaflets have a lower angle of departure of the secondary veins and have two more secondary veins than the type specimens. These differences are not thought to be specifically significant, but we hesitate to refer them to *C. aniensis* because our specimens are incomplete. The Alaskan specimens have the fine venation preserved and are closely similar to the modern *C. platycarpa* (Maxim.) Mak. living in central and western Honshu and Shikoku, Japan. An incomplete flattened pod including three seeds is linear in shape and has irregular networks between the dorsal and ventral ridges. This pod of *Cladrastis* is additional evidence of the presence of this genus in the Seldovia Point flora.

On the basis of well-preserved leaflets, Wolfe (1966) reported *Cladrastis* from the Homerian flora (loc. 9844 and 9361) and the Capps Glacier flora (loc. 9845). These leaves were described as *C. japonica* by emending *Nyssa japonica* Tanai and N. Suzuki from the Miocene Yoshioka flora of Hokkaido (Tanai and Suzuki, 1963) and further by including *C. aniensis*. However, our further investigations reveal that the type specimens of "*Nyssa japonica*" are not *Cladrastis* (although they are also not *Nyssa*) but that all Alaskan leaflets described as "*C. japonica*" are rather similar to the modern *C. lutea*. This second Alaskan species of *Cladrastis* is distinguishable from *C. aniensis* in shape, number of the secondary veins, and irregular, well-developed, percurrent tertiary veins. Accordingly, these *Cladrastis* leaflets from the Homerian

and the Capps Glacier locality should be described as a new species.

Specimens.—USNM 208459, 208460.

Occurrence.—9858.

Genus *Pueraria* DeCandolle
Pueraria miothunbergiana Hu et Chaney
Plate 15, figure 3

Pueraria miothunbergiana Hu and Chaney, 1938, *Palaeont. Sinica*, New Ser. A, no. 1, p. 52, pl. 28, fig. 1.

Discussion.—A single leaflet and its counterpart compare well with terminal leaflets of the *Pueraria* in shape and venation characters: both the secondary and tertiary veins branch outward from the secondaries, gently curve up along the margin, but do not form distinct marginal loops; the intercostal tertiaries are irregularly percurrent and frequently fork once. Our specimens are, although small in size, identical to *P. miothunbergiana*, which has been reported from the lower and middle Miocene of east Asia. This Alaskan fossil is the first record of the genus *Pueraria* in North America.

Hypotype.—USNM 208461.

Occurrence.—9858.

Family Lythraceae
Genus *Decodon* J. F. Gmelin
Decodon alaskana Wolfe et Tanai, *sp. nov.*
Plate 15, figure 6; plate 16, figures 5, 7, 8.

Description.—Leaves simple; shape oval to linear oval, base acute, apex acute to acuminate; length 5 to more than 10 cm, width 3 to 6 cm; pinnately veined; 12 to 15 pairs of irregularly spaced secondary veins departing from midrib at 80 to 90 degrees, slightly curving, sharply brochidodromous; one or two intersecondary veins per intercostal area; tertiary venation forming a large, irregular mesh, the veins at a variable angle relative to the secondaries; fourth order veins of irregular pattern; a series of marginal loops by branches of the secondary veins irregular in size and tending to be elongated perpendicular to the midrib; margin entire.

Discussion.—The pronounced series of brochidodromous loops that form an intramarginal vein readily differentiate *Decodon alaskana* from other members of the Seldovia Point flora. Such major venation is characteristic of members of Myrtales and allied orders (Hickey and Wolfe, 1975). Within most myrtalean families, the intramarginal vein is a continuous arc, but in the Seldovia Point leaves—as in leaves of the extant *D. verticillatus* (L.) E11.—the intramarginal vein is formed by a series of arcs. Further re-

semblances between the fossils and modern leaves of *Decodon* are in the presence of weak loops abmedial to the intramarginal vein, the presence in some intercostal areas of a tertiary vein system that (1) extends directly to the intramarginal vein (intersecondary veins) and giving off right-angle branches to the secondary veins, or (2) extends only a short distance from the midrib, and the presence of a weak fourth order vein system. The fossils differ slightly from modern leaves of *Decodon* in having a higher proportion of intersecondary veins that extend to the intramarginal vein and in having the loops at the margin elongated perpendicular to the midrib (in *D. verticillatus* the loops are approximately square or are elongated parallel to the midrib).

The Seldovia Point specimens of *Decodon* occur on the same slabs as leaves of *Salix*. Such an association is to be expected in view of the marsh to swamp habitat of *D. verticillatus* and many extant species of *Salix*.

Decodon was particularly widespread in the Neogene of Eurasia (Dorofeyev, 1963; Eyde, 1972), but the Seldovia Point material represents the first occurrence of the genus as a fossil in North America. The leaf described as *Myrtus oregonensis* Lesq., however, probably represents *Decodon*; despite the specific epithet proposed by Lesquereux (1883), the leaf actually came from the late Miocene of California (Condit, 1938). The same or a closely allied species also occurs in the Miocene Collawash flora of Oregon (Wolfe, unpub. data).

Holotype.—USNM 208462.

Paratypes.—USNM 208463, 208464.

Occurrence.—9858.

Family Trapellaceae
Genus *Hemitrapa* Miki
Hemitrapa borealis (Heer) Miki

Hemitrapa borealis (Heer) Miki, 1953, *Palaeobotanist*, v. 1, p. 349, text-fig. 2 A.

Trapa borealis Heer, 1869, *Kongl. Svenska Vet.-Akad. Handl.*, bd. 8, no. 4, p. 38, pl. 8, figs. 9–14.

Discussion.—This species was transferred from the genus *Trapa* by Miki (1953) and is characterized by having two spindle-shape appendages and a well-developed brushy haired apical part. Heer (1869a) figured several specimens from the "English Bay" locality, but later collections from this and other Seldovian localities have failed to produce additional specimens. *Hemitrapa* has been described from numerous lower and middle Miocene localities of Japan and Sakhalien; the only putative occurrence from the conterminous United States (MacGinitie, 1937) is

based on material properly referable to *Trapa*.

Occurrence.—9856 (Heer's material).

Family Aceraceae
Genus *Acer* Linnaeus

Five species of *Acer* were originally thought to be represented in the Seldovia Point flora (Wolfe, 1966), but our studies indicate the presence of only four. Other Seldovian localities, however, have produced representatives of two additional species related to the extant *A. saccharinum* and *A. pennsylvanicum* (or *A. rufinerve*). Presumably a species of *Acer* related to the extant Asian *A. mono* was also a member of the Seldovian flora, because a closely related species (*A. scottiae*) is known from the middle and late Miocene of the Pacific Northwest. Clearly *Acer* was an important element in the early and middle Miocene flora of Alaska.

***Acer ezoanum* Oishi et Huzioka**

Plate 17, figures 1–3, 5; plate 19, figures 2, 5

Acer ezoanum Oishi and Huzioka, 1943, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 7, p. 89, pl. 10, figs. 1–4; pl. 11, figs. 1–4; pl. 12, fig. 2.

Tanai and N. Suzuki, 1969, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 10, p. 556, pl. 1, figs. 1, 2; pl. 2, figs. 1, 2; pl. 3, figs. 1–4; pl. 9, figs. 20–25 [see synonymy for references through 1960].

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, p. 356, pl. 26, figs. 1, 2, 5.

Tanai and N. Suzuki, 1963, Tertiary Floras Japan, v. 1, p. 137.

Huzioka, 1964, Akita Univ. Mining Coll. Jour., ser. A, v. 3, no. 4, p. 89, pl. 14, figs. 6–9.

Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398–B, p. B25, pl. 8, fig. 6.

Ishida, 1970, Kyoto Univ. Fac. Sci. Mem., Geology and Mineralogy Ser., v. 37, p. 95.

Huzioka, 1972, Akita Univ. Mining Coll. Jour., ser. A, v. 5, no. 1, p. 63, pl. 8, fig. 2.

Tanai and N. Suzuki, 1972, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 15, p. 335, pl. 7, figs. 1–5.

Discussion.—A number of leaves are referred to *A. ezoanum*, which was originally described from the lower Miocene of Hokkaido and Sakhalin. Several winged fruits with expanded seeds are also found from the same locality and are also referred to *A. ezoanum*. Our Alaskan leaves are more closely related to those of the modern Japanese maple, *A. miyabei* Maxim., than to any of the North American maples. Leaves of *A. ezoanum* closely resemble in general appearance those of the modern *A. macrophyllum* Pursh. but dis-

tinctly differ in fine venation. The quadrangular or pentagonal areoles are intruded by simple or once branched veinlets in *A. ezoanum* as well as in *A. miyabei*, but the irregularly four-sided areoles are intruded by twice or more branched veinlets in *A. macrophyllum*.

The only other known Alaskan occurrence of *Acer ezoanum* is a leaf from locality 9848 along Beluga River (Wolfe, 1966). This locality is apparently also of middle Miocene age (see p. 8).

Hypotypes.—USNM 208465–208470.

Occurrence.—9856 (fruits), 9858 (fruits and leaves).

***Acer glabroides* R. W. Brown**

Plate 17, figures 7, 8

Acer glabroides Brown, 1937, U.S. Geol. Survey Prof. Paper 186–J, p. 180, pl. 58, figs. 13–15.

Discussion.—Two samaras are similar to both Brown's type material and to the extant *Acer rubrum*. No leaves of the *rubrum* type have yet been collected from Seldovia Point, but such leaves occur at other Seldovian localities (for example, loc. 9867 on Cache Creek).

Hypotypes.—USNM 208471, 208472.

Occurrence.—9858.

***Acer grahamensis* Knowlton et Cockerell**

Plate 17, figure 6; plate 18, figure 5; plate 19, figures 1, 4

Acer grahamensis Knowlton and Cockerell, 1919, U.S. Geol. Survey Bull. 696, p. 50.

Acer macropterum Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 37, pl. 9, figs. 8, 9 (excluding fig. 7).

Discussion.—Two samaras are identical to *Acer macropterum* in their large size and venation of the wing; this species was originally described from the "English Bay" locality by Heer (1869a). The epithet instituted by Heer is, however, a junior homonym, and Knowlton and Cockerell (in Knowlton, 1919) proposed the name *A. grahamensis* for this material. Although our samaras are also incomplete as in the case of Heer's specimens, one of ours has an elliptical seed and suggests that this species may be related to the extant *A. macrophyllum* Pursh. living in the western United States. A fragmentary leaf was included in *A. macropterum* by Heer, but that leaf does not appear to be similar to *A. macrophyllum*. Two deeply lobed leaves of *Acer* from Seldovia Point are, although fragmentary, distinctly different in the secondary venation looping and the pattern of fine veinlets from foliage of *A. ezoanum*; especially the veinlets usually branch more than twice and are closely similar to those of *A. macrophyllum*. Accordingly, these two incomplete specimens may represent leaves of *A.*

grahamensis. This species is closely similar to *A. oregonianum* Knowlton from the Miocene of the conterminous western United States. Chelebaeva (1968) assigned samaras from the middle Miocene of Kamchatka to *Acer* cf. *grahamensis*. Although in features preserved her specimens are similar to *A. grahamensis*, we concur with Chelebaeva that the lack of seeds attached to the samaras makes the specific determination uncertain.

Hypotypes.—USNM 208473–208475.

Occurrence.—9856, 9858.

Acer heterodontatum (Chaney) MacGinitie

Plate 16, figure 6; plate 17, figure 4;
plate 18, figures 2–4; plate 19, figure 3

Acer heterodontatum (Chaney) MacGinitie, 1953, Carnegie Inst. Washington Pub. 599, p. 140, pl. 57, fig. 3 [see synonymy and discussion].

Discussion.—This species is represented by two terminal and several lateral leaflets that show a close resemblance to the modern *Acer negundo* L. and *A. henryi* Pax. Leaflets of this type are uncommon in the Tertiary of the conterminous western United States, but fruits of the *negundo* type have been commonly reported. Our Alaskan leaflets are generally larger than the type specimens: the terminals are 9 to 12 cm (estimated) long and 8 to 9.5 cm wide, and the laterals are 9 to 18 cm long and 3 to 8 cm wide. These leaflets are more closely related in venation to *A. negundo* than to the East Asiatic *A. henryi* or *A. cissifolium* (Sieb. and Zucc.) K. Koch.: the fourth order veins form irregularly quadrangular or pentagonal meshes, which are intruded by unbranched or once branched veinlets. However, two samaras from the same locality closely resemble those of *A. cissifolium* in their shape and size of seeds.

There have been several different opinions regarding the specific name for this Tertiary boxelder. As already noted by MacGinitie (1953, p. 141), two types of *Rulac crataegifolium* and *Phyllites bifurcies* are too poorly preserved to serve as type specimens, though they resemble the modern boxelder leaflets. Although *Rulac crataegifolium* was transferred to *Acer* by LaMotte (1952, p. 53), the new combination in any case is homonymous for the extant *A. crataegifolium* Sieb. et Zucc. Chaney and Axelrod (1959) nominated "*Acer minor*," but the type specimen figured by Knowlton (1902) lacks the seed and is not an adequate name-bearing specimen. Thus we concur with MacGinitie (1953) and accept *A. heterodontatum* as the oldest valid combination for this species.

Hypotypes.—USNM 208476–208481.

Occurrence.—9858.

Family Nyssaceae
Genus *Nyssa* Linnaeus
Nyssa cf. *N. knowltoni* Berry
Plate 18, figure, 1

Nyssa knowltoni Berry, 1929, U.S. Geol. Survey Prof. Paper 154–H, p. 261, pl. 59, fig. 7.

Discussion.—One leaf, although fragmentary, is assigned firmly to *Nyssa* on the basis of its venation characters and irregularly large teeth. It closely resembles the leaves described as *N. knowltoni* from the Miocene Latah flora of Oregon (Berry, 1929; Brown, 1937) but is too fragmentary for specific determination. Brown (1937) and Chaney and Axelrod (1959) transferred many Tertiary fossil leaves from the western United States resembling the modern *N. aquatica* to *N. hesperia*, which was originally defined on the basis of seeds (Berry, 1931). However, as already pointed out by Eyde (1963), it can be difficult to distinguish the modern *N. aquatica* and *N. sylvatica* by only external features of the seeds. Furthermore, some leaves of *N. sylvatica* have large irregularly spaced teeth, similar to those of *N. aquatica*. Until, therefore, venation characters are thoroughly investigated in west American leaves of *Nyssa*, the synonymy of *N. hesperia* and *N. knowltoni* cannot be accepted without scepticism.

Specimen.—USNM 208482.

Occurrence.—9858.

Family Alangiaceae
Genus *Alangium* Lamarek
Alangium mikii Wolfe et Tanai, sp. nov.
Plate 20, figures 1, 2; plate 21

Marlea aequalifolia (Goepfert) Oishi, 1950, Illust. Catalogue of East Asiatic Fossil Plants, p. 171, pl. 50, fig. 1.

Tanai, 1952, Japanese Jour. Geology and Geography, v. 22, p. 132, pl. 5, fig. 3.

Huzioka, 1955, Illust. Fossil Catalogue in Fukui Pref., no. 6, p. 8, pl. 3, figs. 6–8.

Alangium aequalifolium (Goepfert) Kryshtfovich and Borsuk, 1939, Problems Palaeont., no. 5, p. 390, pl. 5, figs. 1–8; pl. 6, fig. 12.

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 2, p. 371, pl. 30, fig. 1; pl. 31, fig. 9.

Huzioka, 1963, Tertiary Floras of Japan, Miocene Floras, p. 212, pl. 38, fig. 9.

Matsuo, 1963, Tertiary Floras of Japan, Miocene Floras, p. 242, pl. 52, fig. 6; pl. 53, figs. 3–5 (excluding pl. 53, fig. 1).

Huzioka, 1964, Akita Univ. Mining Coll. Jour., ser. A, v. 3, no. 4, p. 96, pl. 17, fig. 1.

Huzioka, 1972, Akita Univ. Mining Coll. Jour., ser. A, v. 5, no. 1, p. 70, pl. 14, fig. 4.

?*Marlea iragawaense* Tanai, 1952, Japanese Jour.

Geology and Geography, v. 22, p. 133, pl. 5, fig. 5.

Description.—Leaves simple, actinodromous; shape symmetrical to asymmetrical and broadly oval, apex acute, base cordate and typically asymmetrical; length 10 to more than 22 cm, width 10 to more than 22 cm; four or five pairs of lateral primaries, the first pair (from the midrib) paralleling the medial secondary veins and extending into the apical half of the lamina, five to seven lateral secondaries on basal side; second lateral pair of primaries paralleling secondaries of first lateral primary, also with five to seven pairs of lateral secondaries on basal side (these are absent or reduced on smaller side of highly asymmetrical laminae); third lateral primary veins conspicuous only on enlarged side of highly asymmetrical laminae, with three or four lateral secondary veins; medial secondary veins five to seven pairs, departing at an angle of 60 to 70 degrees, straight to broadly curving, brochidodromous, looping close to margin; intersecondary veins typically absent; tertiary veins regularly and closely spaced, perpendicular to secondaries, branched or percurrent, slightly arched abmedially; fourth order veins numerous, closely spaced, perpendicular to tertiaries, branching acutely; fifth order veins forming a polygonal areolation that is intruded by profusely branching freely ending veinlets; margin entire; petiole thick, incomplete but more than 3 cm long.

Discussion.—Considerable uncertainty and confusion exist concerning the nomenclatural and systematic position of *Alangium*-like foliage from the Tertiary of Eurasia. Many *Alangium*-like leaves have previously been referred to either *A. aequifolium* (Goepf.) Krysh. et Bors. or *A. tiliaefolium* (Ung.) Krysh.; both species are based on material from the European Tertiary record. Knobloch and Kvacek (1964), however, synonymized these two species and further considered them to represent a sterculiaceae plant, *Byttneriophyllum tiliaefolium* (A. Braun) Knobl. et Kvac. This reassignment is based on examination of nontype material from Tertiary rocks of Czechoslovakia, which showed that this material possessed compound trichomes in contrast to the uniformly simple trichomes in extant *Alangium*.

We emphasize that the megascopic characters of the leaves from which Knobloch and Kvacek obtained cuticular material have not been illustrated (Knobloch and Kvacek, 1964, p. 162). In *Byttneria*, as in most woody Malvales, the fourth and higher order venation is organized into pronouncedly orthogonal patterns (that is, the branching of any particular order is at approximately right angles), and the various orders of venation are well differentiated in size from one another (see Knobloch and Kvacek, 1964, pl. IV). In

Alangium, the fourth and higher order venation branches at definite acute angles (a Y-shaped pattern predominates in the fourth order venation), and the veins thin so gradually that the fourth and higher order veins are not clearly differentiated in size.

Examination of topotypic material of *Byttneriophyllum tiliaefolium* (= *Cordia tiliaefolia* A. Braun) from Oeningen (material in the U.S. Geol. Survey collections) substantiates Knobloch and Kvacek's (1964) opinion. This material has an orthogonal pattern in the fourth and higher order venation. Material from Sotzka, on which Goepfert based *Dombeyopsis aequifolia*, has not been examined; Goepfert's (1852) illustrations of this species are inadequate for determination, but, if accurately drawn, the specimen on the same slab assigned to *Dombeyopsis grandifolia* would also be malvacean because of the predominately orthogonal fourth order venation.

The east Asian Neogene leaves reassigned by Knobloch and Kvacek (1964) to *Byttneriophyllum tiliaefolium*, however, have intercostal venation of *Alangium*. These leaves represent the same species as that found at Seldovia Point and the Capps Glacier Seldovian. The Capps Glacier material, moreover, shows that the trichomes are all simple (pl. 20, fig. 2), leaving no reasonable doubt that *Alangium* is represented. The epithet *iragawaense* is rejected for these leaves because it is based on poorly preserved material. We have, therefore, established a new species, *A. mikii*, to include the Alaskan and east Asian Neogene leaves previously assigned to *A. aequifolium*.

Although *Alangium* was a conspicuous element in some Paleogene floras in North America (MacGinitie, 1969; Eyde and others, 1969), this is the first validated occurrence for the genus in the Neogene of North America. Pollen of the *A. barghoornianum* type (Traverse, 1955) has, however, been found in the middle Miocene part of the Kirkwood Formation of New Jersey (Wolfe, unpub. data). *A. barghoornianum*, *A. riparius* (MacG.) MacG., and *A. mikii* all represent the section *Marlea*. The species of *Alangium* from the Eocene of Alaska (Wolfe, 1977), however, is a member of the section *Alangium*.

We take pleasure in naming this species in recognition of the contributions of the late Professor Shiguru Miki to the fossil history of the Cornales.

Holotype.—USNM 208483.

Paratypes.—USNM 208485 (loc. 11091), 208484 (loc. 9858).

Occurrence.—9858, 11091 (Capps Glacier).

Family Araliaceae

Genus *Kalopanax* Miguel

Kalopanax n-suzukii Wolfe et Tanai, sp. nov.

Plate 22, figure 4

Kalopanax acerifolium auct. non (Nathorst) Hu and

Chaney. Hu and Chaney (nontypic), 1940, Carnegie Inst. Washington Pub. 507, p. 70, pl. 47, figs. 3, 5.

Okutsu, 1955, Tohoku Univ. Sci. Repts., ser. 2, v. 26, p. 110, pl. 5, fig. 1.

Tanai and Onoe, 1960, Japan Geol. Survey Rept. 187, p. 285, pl. 7, fig. 4.

Tanai, 1961, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, p. 377.

Tanai and Suzuki, 1965, Palaeont. Soc. Japan Spec. Paper 10, p. 43, pl. 20, fig. 2.

Huzioka and Uemura, 1973, [Tokyo] Natl. Sci. Mus. Bull., v. 16, p. 723, pl. 18, fig. 1.

Description.—See Hu and Chaney (1940, p. 70–71).

Discussion.—Examination of Nathorst's type of *Acanthopanax acerifolium* indicates that these represent *Acer* and not any genus of Araliaceae. Hu and Chaney's (1940) Shanwang material, however, does represent *Kalopanax* and the same species that occurs in the Seldovia Point flora. We accept Hu and Chaney's (1940) description, but the unavailability of the specimens on which that description was based make it desirable to designate as types specimens that are in existence. We thus designate as holotype University of Hokkaido Museum of Paleontology 25727 (figured by Tanai and Suzuki, 1965, pl. 20, fig. 2) and as paratypes 25726 and 25729; all these specimens are from the Shanabuchi locality.

Kalopanax is known from several localities in eastern Asia and is known to range from the early Miocene through the Holocene (Tanai, 1972). The Seldovia Point occurrence is the first known in North America.

We take pleasure in naming this species for Mr. Nobuo Suzuki, in recognition of his contributions to the Tertiary floras of Japan.

Hypotype.—USNM 208486.

Occurrence.—9856, 9858.

Family Vitaceae
Genus *Vitis* Linnaeus

Vitis seldoviana Wolfe et Tanai, sp. nov.

Plate 22, figure 1; plate 23, figures, 1, 3

Description.—Leaves incomplete, pentagonal in general outline, palmately five lobed, broadly cordate at base; midvein thick, nearly straight, giving off more than four pairs of secondaries, which are nearly parallel to the inner primaries; the inner pair of the primaries well defined, making angles of 40 to 60 degrees with the midvein, giving off about six pairs of secondaries which end in large teeth, the intersecondary veins leaving midrib, nearly parallel to the secondaries, camptodromous; the lowest pair of the

primaries somewhat slender, nearly at right angles to the midvein, with five or more secondaries; the intercostal tertiary veins thin but distinct, irregularly percurrent, nearly perpendicular to the secondaries; the tertiaries near the margin branching from the secondaries, forming loops with the intersecondaries; fourth and fifth order veins forming quadrangular or pentagonal areoles which are penetrated by once or twice branching veinlets; margin coarsely dentate, with large deltoid teeth; petiole thick, more than 2.2 cm long.

Discussion.—Several incomplete specimens represent leaves of *Vitis* on the basis of their marginal dentation and vein characters. No fossil leaves of *Vitis* from North America are comparable to our Alaskan materials. Although all the specimens are fragmentary the general character of the foliage can be reconstructed. These leaves superficially resemble *V. naumannii* (Nathorst) Tanai, which was reported from the lower to upper Miocene of Japan, but differ distinctly in having larger teeth and well-defined intercostal tertiary veins.

Vitis seldoviana also superficially resembles *V. alia* Holl. from the Miocene of British Columbia (Hollick, 1936). The latter species, however, has narrower and more pronounced teeth, and the tertiary veins extend perpendicularly from the midrib; in *V. seldoviana*, homologous tertiary veins are oriented at an acute angle to the midrib.

Holotype.—USNM 208487.

Paratypes.—USNM 208488, 208489.

Occurrence.—9856.

Family Oleaceae
Genus *Fraxinus* Linnaeus
Fraxinus kenaica Wolfe et Tanai, sp. nov.
Plate 24, figures 1–3

Description.—Presumably a leaflet; venation pinnate; shape oval; apex not preserved, base acute; length at least 17 cm, width 9 cm; about 13 pairs of secondary veins, irregularly spaced, departing at angles of 70 to 80 degrees (higher on one side of lamina), slightly curving, irregularly brochidodromous; intersecondaries numerous, strong; tertiary veins thin, irregularly spaced, oblique to more apical secondary veins and orthogonal to more basal secondary veins, branching irregularly; fourth order veins forming a thin reticulum of irregular shape and size; loops abmedial to secondary loops of irregular shape and size, one side formed by veins that extend toward sinuses, these veins either ending in sinuses or extending along apical side of teeth; margin coarsely and irregularly serrate; teeth tending to have convex basal and apical sides; petiolule(?) about 2 cm long.

Discussion.—The specimen gives no certain indica-

tion whether it is a leaf or leaflet, although—assuming the validity of the generic assignment—the lack of an inflated area at the base of the petiolule is consistent with the morphology of terminal leaflets of *Fraxinus*, which typically are conspicuously stalked and lack an inflated area. Lateral leaflets may also be stalked in *Fraxinus* but not as elongated as in the fossil.

The assignment to *Fraxinus* is based on characters of intercostal and marginal venation. In extant *Fraxinus* the intercostal areas are typically highly irregular in size (that is, the secondaries are very irregularly spaced), the tertiary and higher order veins are also inconsistent in spacing, and the areoles, which are formed by sixth order venation, are intruded by profusely branching veinlets. The secondary veins are consistently camptodromous but give off external branches that either bifurcate, sending one branch into the sinus or apically along the margin, or rarely enter the teeth centrally.

Fraxinus kenaica appears to be most closely related to the extant *F. hopeinsis* Tang from northern China. Particularly notable similarities are in the sharpness and large size (for *Fraxinus*) of the teeth. In this extant species, however, the secondary veins are considerably more apically directed, and there are fewer centrally entered teeth.

Holotype.—USNM 208490A, B.

Occurrence.—9858.

Family Caprifoliaceae
Genus *Lonicera* Linnaeus
Lonicera sp.
 Plate 25, figure 2

Discussion.—This single specimen has an entire margin except for a single small tooth along the lower left-hand side. The secondary venation forms irregularly shaped intercostal areas that contain irregularly spaced branching tertiary veins. Abmedial to the secondary loops is a single series of loops that are also irregular in size and shape. Such features indicate a relationship to certain genera of Caprifoliaceae, but the Seldovia Point specimen is too incomplete and poorly preserved to make generic determination. In characters preserved, this specimen appears conspecific with undescribed leaves from the overlying Homerian assemblages; these younger leaves have the morphology of *Lonicera*.

Specimen.—USNM 208491.

Occurrence.—9858.

Family Alismataceae
Genus *Alisma* Linnaeus
Alisma seldoviana Wolfe et Tanai, sp. nov.
 Plate 25, figures 3, 6

Description.—Leaves elliptic-lanceolate in shape,

7.2 to 15 cm (estimated) long and 2.2 to 5.5 cm wide; apex gradually narrowed, somewhat acuminate; base rounded to slightly cordate, sometimes slightly twisted; nine principal veins leaving the very base, acrodromous; midvein stout and thick, nearly straight; two pairs of lateral primaries rather thick, but more slender than the midvein, making initial angles of about 20 to 50 degrees with the midvein, then gently arched, nearly parallel to the margin; outer two pairs of the lateral primaries thinner and more slender than the inner primaries, running along the margin; the tertiaries thin, obliquely transverse to the primaries with the angles of about 40 to 70 degrees, irregularly spaced; fourth order veins very fine, crossing with the tertiary veins, nearly parallel to the primaries, once or twice bifurcating to form elongate reticulation; margin entire; texture thin; petiole missing.

Discussion.—These fossils superficially resemble leaves of *Smilax*, but in that genus the fourth order venation is randomly reticulate. In *Alisma*, however, the fourth order veins are, as in the fossils, consistently perpendicular to the tertiary veins. *Alisma seldoviana* closely resembles the extant *A. plantago-aquatica* L., a species (or species complex) of wide distribution throughout the Northern Hemisphere.

Holotype.—USNM 208492.

Paratype.—USNM 208493.

Occurrence.—9858.

Family Najadaceae
Genus *Potamogeton* Linnaeus
Potamogeton alaskanus Wolfe et Tanai, sp. nov.
 Plate 22, figures 2, 3; plate 25, figures 1, 7

Description.—Floating leaves variable in size and shape, 0.5 to 3.5 cm wide and 1.4 to 6.5 cm (estimated) long, elliptic to broadly elliptic in shape; base cuneate or rounded; apex incomplete but probably obtuse; petiole rather thick; midvein thick, nearly straight; lateral primary veins, three or four on both sides of midvein, acrodromous; thin and slender lateral subprimaries running nearly parallel to lateral primaries, one or two among each interlateral space; numerous secondary veins very thin, crossing somewhat irregularly to the primaries; margin entire. Submerged leaves narrowly linear, 2 or 3 mm wide, more than 5 cm long; base sessile; apex unknown; veins three, lateral veins inconspicuous.

Fruits obliquely suborbicular or obovoid, 1.5 to 2 cm long and 1.2 to 2 cm wide; the side flat; dorsal keel prominent, alate, undulate and with sutures; lateral keel low but evident, slightly detate; beak prominent, straight or slightly incurved, 0.8 mm long; apex of seeds pointing slightly above basal end; embryo coiled.

Discussion.—A number of leaves and fruits referred to *Potamogeton* occur at the Seldovia Point locality, and it is reasonably supposed that the plant-bearing rocks were mainly deposited in fresh, slowly moving water. Many leaves of *Potamogeton* have been reported from the Tertiary of the conterminous United States, but our Alaskan specimens are not identical with any species described before. *P. alaskanus* somewhat resembles *P. hetrophylloides* Berry from the Latah flora of eastern Washington (Brown, 1940) but differs in having the lateral subprimary veins. Dorofeyev (1963) described many species of *Potamogeton* on the basis of fruits from the Miocene of western Siberia, of which species *P. alaskanus* is most similar to *P. tertiaris* Dorof. in characters of the dorsal and lateral keels.

Holotype.—USNM 208494.

Paratypes.—USNM 208495–208497.

Occurrence.—9856, 9858.

Mocotyledonae Incertae sedis
Genus *Monocotylophyllum* Chandler

Monocotylophyllum alaskanum (Heer) Wolfe et Tanai, comb. nov.
Plate 23, figure 2; plate 25, figure 8

Phragmites alaskana Heer, 1869, Kongl. Svenska Vet.-Akad. Handl., v. 8, no. 4, p. 24, pl. 1, fig. 12.

Discussion.—A number of fragmentary linear leaves with many parallel veins are similar to *Phragmites alaskana*, which are originally described from the "English Bay" locality. This generic reference may, however, not be valid, because the monocot leaves of Gramineae and other monocotyledonous families are too simply nerved to determine their generic status. Our specimens are from 1.2 to 4 cm in width, but their length is unknown.

Hypotypes.—USNM 208498, 208499.

Occurrence.—9856, 9858.

***Monocotylophyllum* spp.**
Plate 25, figures 4, 5

Poacites tenuistriatus Heer, 1869, Kongl. Svenska Vet.-Akad. Handl., v. 8, no. 4, p. 24, pl. 1, fig. 12.

Discussion.—These species are represented by several fragmentary leaves which are linear with about 17 to 30 mm width and contain numerous indistinct, parallel veins. The genus *Poacites* has been used for the grass leaves, and it is uncertain whether or not our specimens belong to the Gramineae. *Poacites* was originally proposed by Schlotheim for the Carboniferous grasslike specimens, but, as pointed out by Andrews (1970), the original specimens are not grass but are lycopod.

Specimens.—USNM 208500–208503.

Occurrence.—9856, 9858.

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PLATES 1–25

[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 figures natural size unless otherwise stated]

- FIGURE 1. *Ginkgo biloba* Linnaeus. (p. 26).
Hypotype, USNM 208356; loc. 9857.
- 2, 6, 7, 10. *Metasequoia* sp. cf. *M. glyptostrobooides* Hu et Cheng. (p. 26).
2, 10. USNM 208352, 208355; loc. 9858.
6, 7. USNM 208353, 208354; loc. 9857.
- 3, 4. *Onoclea sensibilis* Linnaeus. (p. 25).
3, 4. Hypotypes USNM 208349, 208350; loc. 9858.
- 5, 9. *Dryopteris* sp. (p. 25).
USNM 208348A, B; loc. 9858.
8. *Glyptostrobus europaeus* (Brongniart) Heer. (p. 26).
×2. Hypotype, USNM 208351; loc. 9858.
- 11-14. *Nymphar ebae* (Huzioka) Ozaki (p. 26).
Hypotypes, USNM 208357-208360; loc. 9858. Fig. 13, ×2.

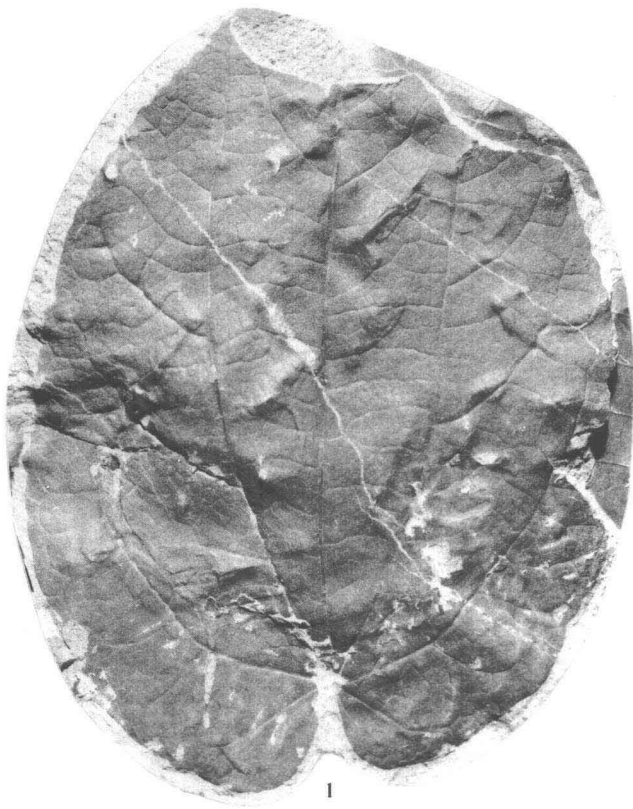


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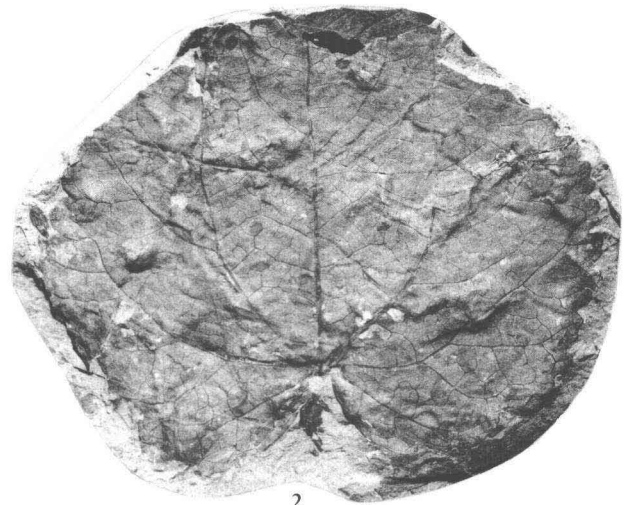
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[All figures natural size unless otherwise stated]

- FIGURES 1-4. *Cercidiphyllum alaskanum* Wolfe et Tanai. (p. 27).
1, 4. Holotype, USNM 208361A, B; loc. 9856.
2. Paratype, USNM 208362; loc. 9858.
3. Showing fine veinlets (enlargement of holotype specimen).
5, 6. *Liquidambar pachyphylla* Knowlton. (p. 28).
5, 6. Hypotypes USNM 208364, 208365; loc. 9858.
7. *Cocculus auriculata* (Heer) Wolfe. (p. 26).
Hypotype USNM 208369; loc. 9858.



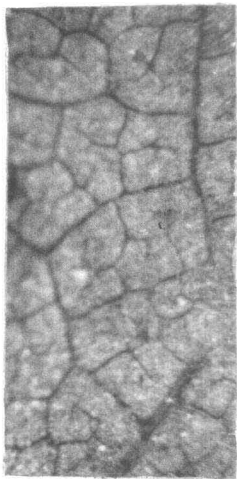
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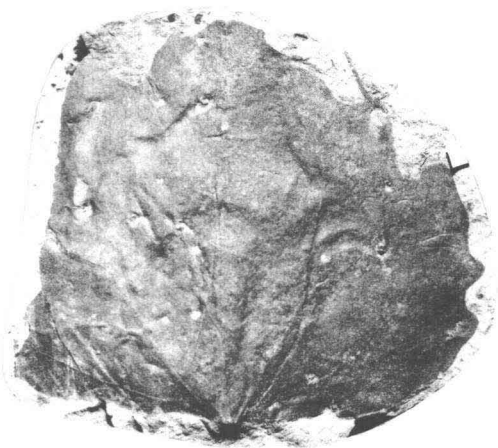
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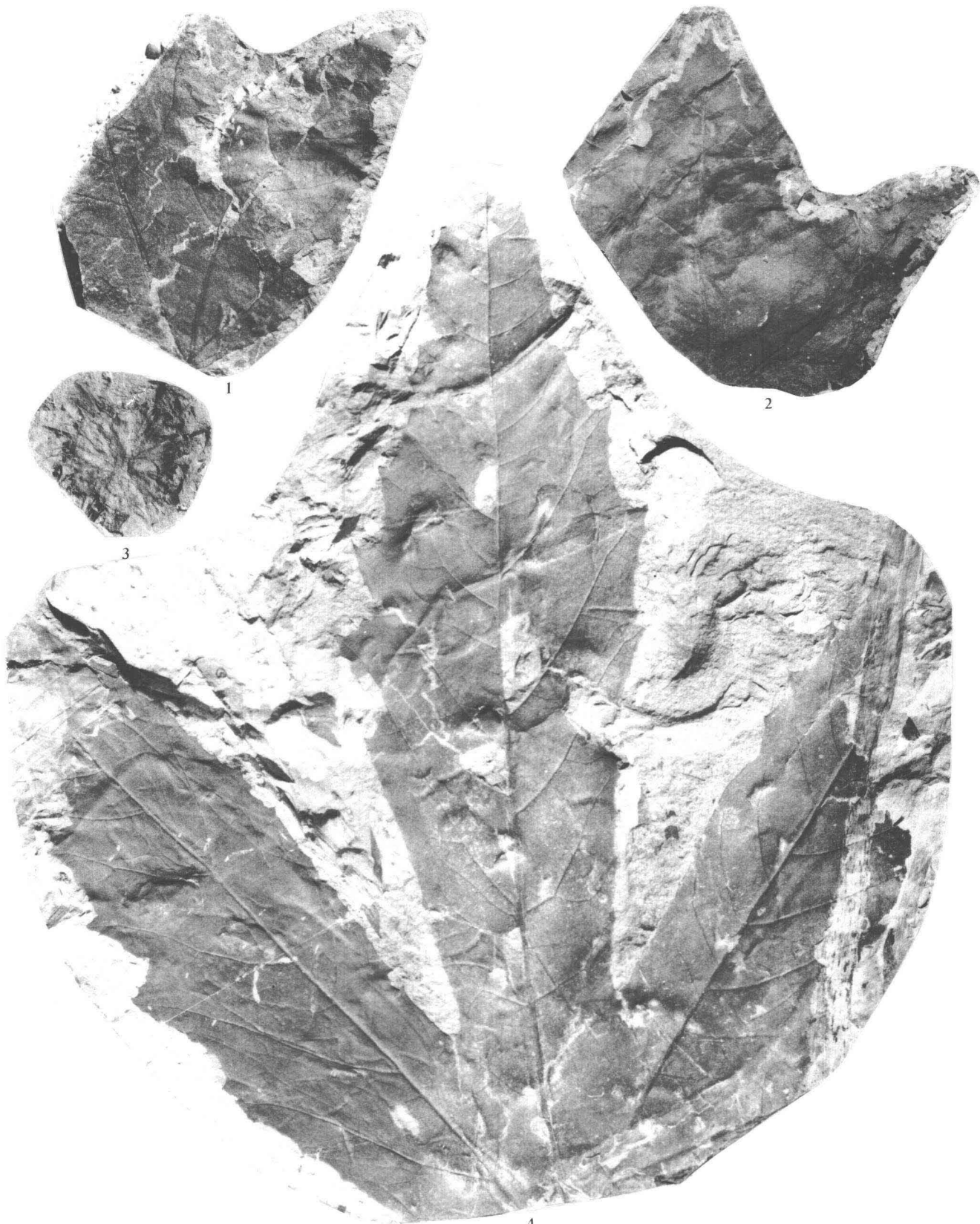
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HAMAMELIDIDAE, RANUNCULIDAE

PLATE 3

[All natural size]

- FIGURE 1-3. *Liquidambar pachyphylla* Knowlton. (p. 28).
Hypotypes USNM 208366-208368; loc. 9858.
4. *Platanus bendirei* (Lesquereux) Wolfe. (p. 28).
Hypotype USNM 208370; loc. 9858.

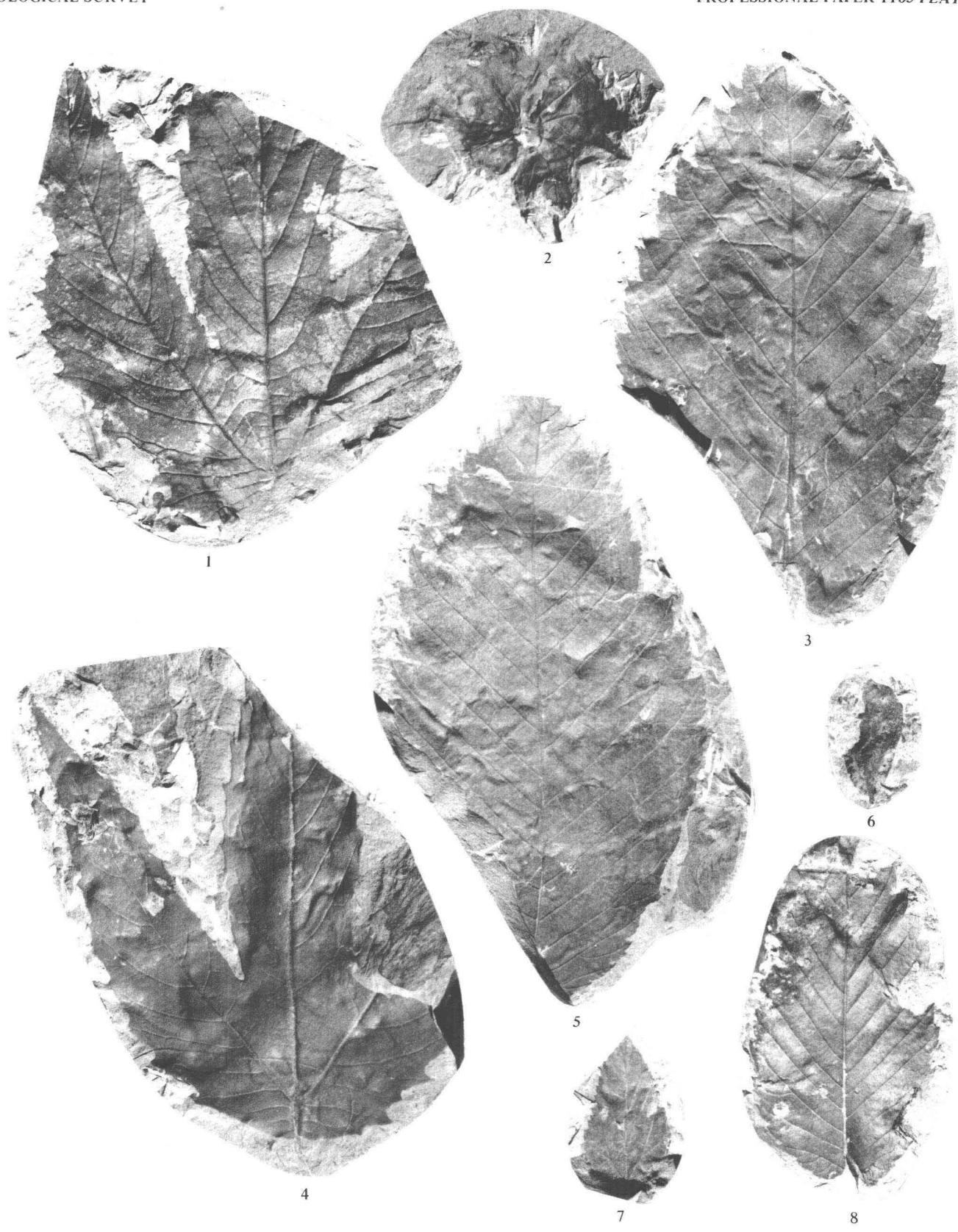


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HAMAMELIDIDAE

PLATE 4

[All natural size]

- FIGURES 1, 2, 4. *Platanus bendirei* (Lesquereux) Wolfe. (p. 28).
Hypotypes USNM 208371–208373; loc. 9858.
- 3, 5. *Ulmus speciosa* Newberry. (p. 30).
Hypotypes USNM 208381, 208382; loc. 9858.
6. *Eucommia* cf. *E. montana* R. W. Brown. (p. 29).
USNM 208374; loc. 9858.
7. *Celtis* sp. (p. 29).
USNM 208375; loc. 9858.
8. *Ulmus owyheensis* H. V. Smith. (p. 30).
Hypotype USNM 208376; loc. 9858.

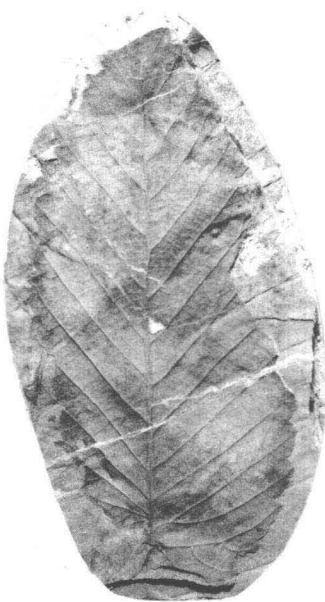


HAMAMELIDIDAE

PLATE 5

[All figures natural size unless otherwise stated]

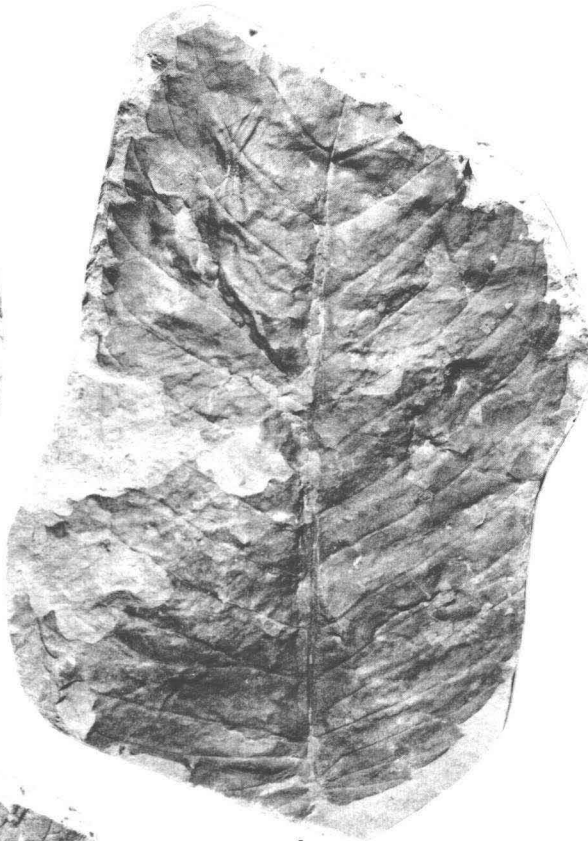
- FIGURES 1, 2. *Ulmus knowltoni* Tanai et Wolfe. (p. 30).
Hypotypes USNM 208376, 208377; loc. 9856.
- 3, 6, 8a, 8c. *Zelkova browni* Tanai et Wolfe. (p. 30).
3, 6. Hypotypes USNM 208384–208385; loc. 9858.
8a, 8c. Hypotypes USNM 208386–208388; loc. 9856.
- 4, 7. *Zelkova ungeri* Kovats. (p. 31).
Hypotypes USNM 208389, 208390; loc. 9858.
5. *Ulmus* sp.
USNM 208383; loc. 9856.
- 8b. *Fagus antipofi* Heer. (p. 31).
Hypotype, USNM 208394; loc. 9856.



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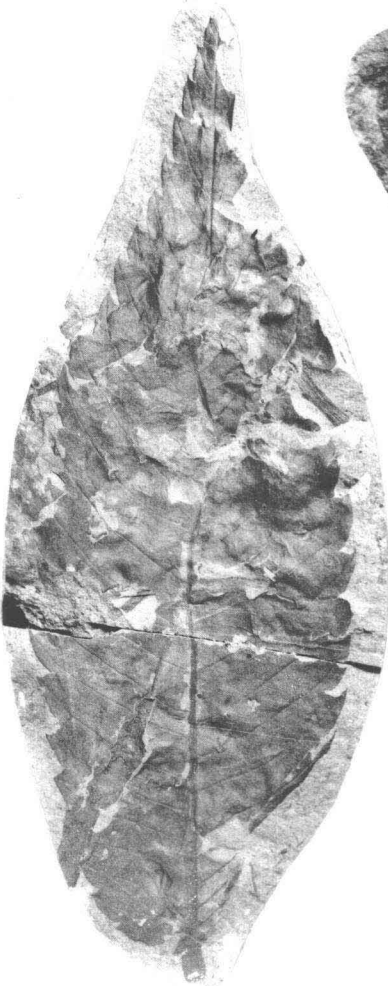
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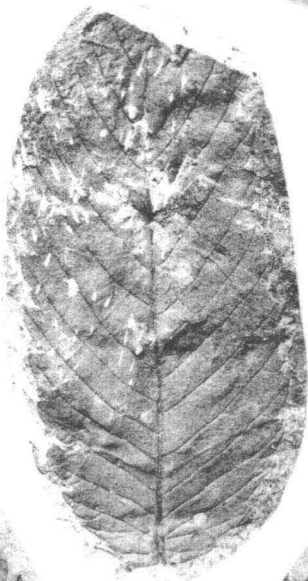
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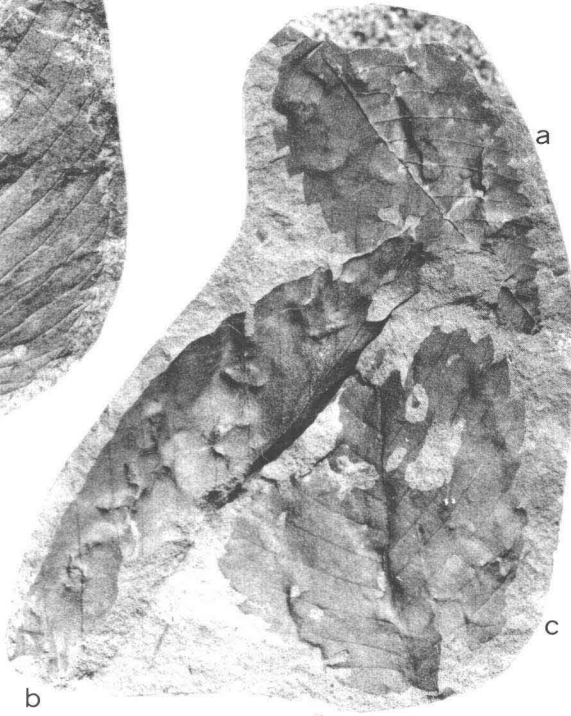
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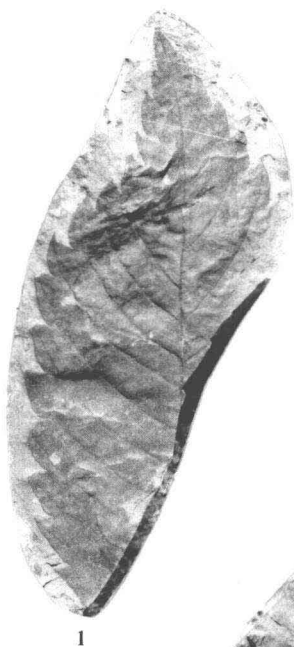
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HAMAMELIDIDAE

PLATE 6

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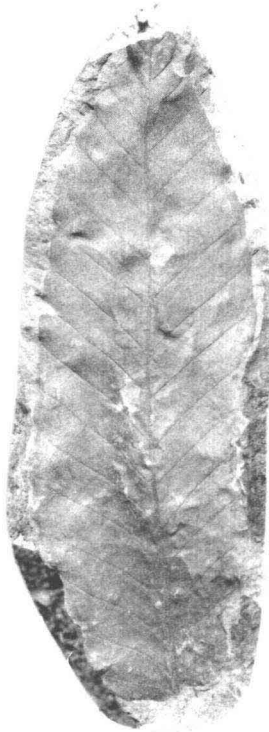
- FIGURES 1, 2, 6. *Zelkova ungeri* Kovats. (p. 31).
Hypotypes, USNM 208391, 208392, 208393; loc. 9858.
- 3, 4. *Fagus antipofi* Heer. (p. 31).
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5. *Fagus* sp. aff. *F. crenata* Blume. (p. 31).
Hypotype USNM 208400; loc. 9856.
- 7a, 7b. *Ulmus ovyheensis* H. V. Smith. (p. 30).
Hypotypes USNM 208377A, 208377B; loc. 9856.
8. *Zelkova browni* Tanai et Wolfe. (p. 30).
Hypotype USNM 208388; loc. 9858.



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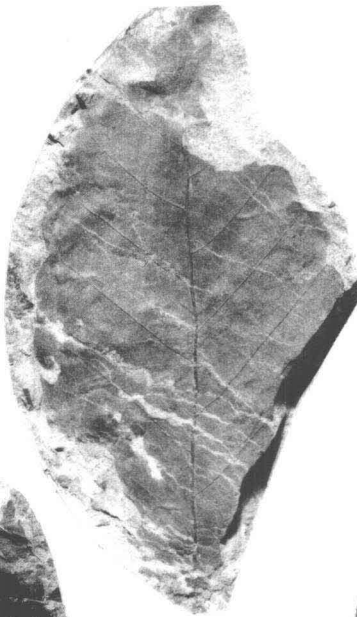
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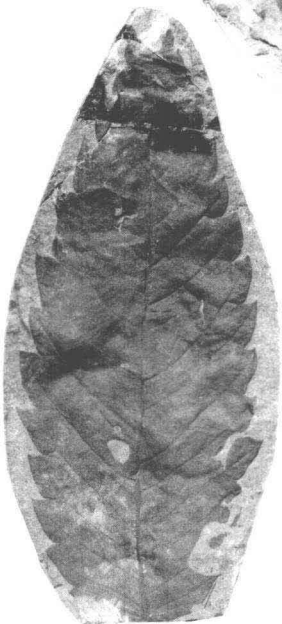
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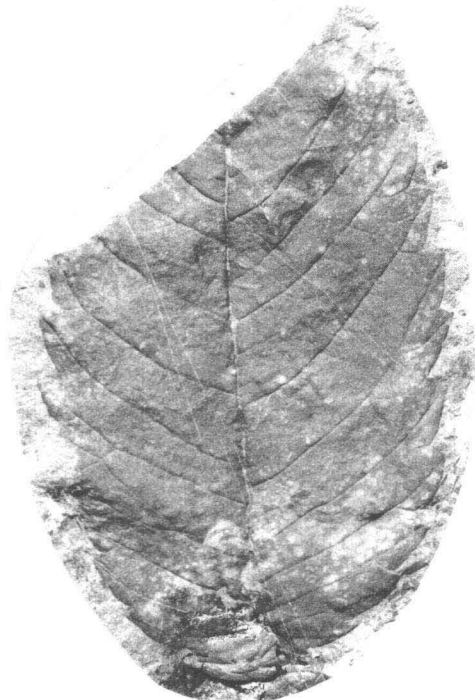
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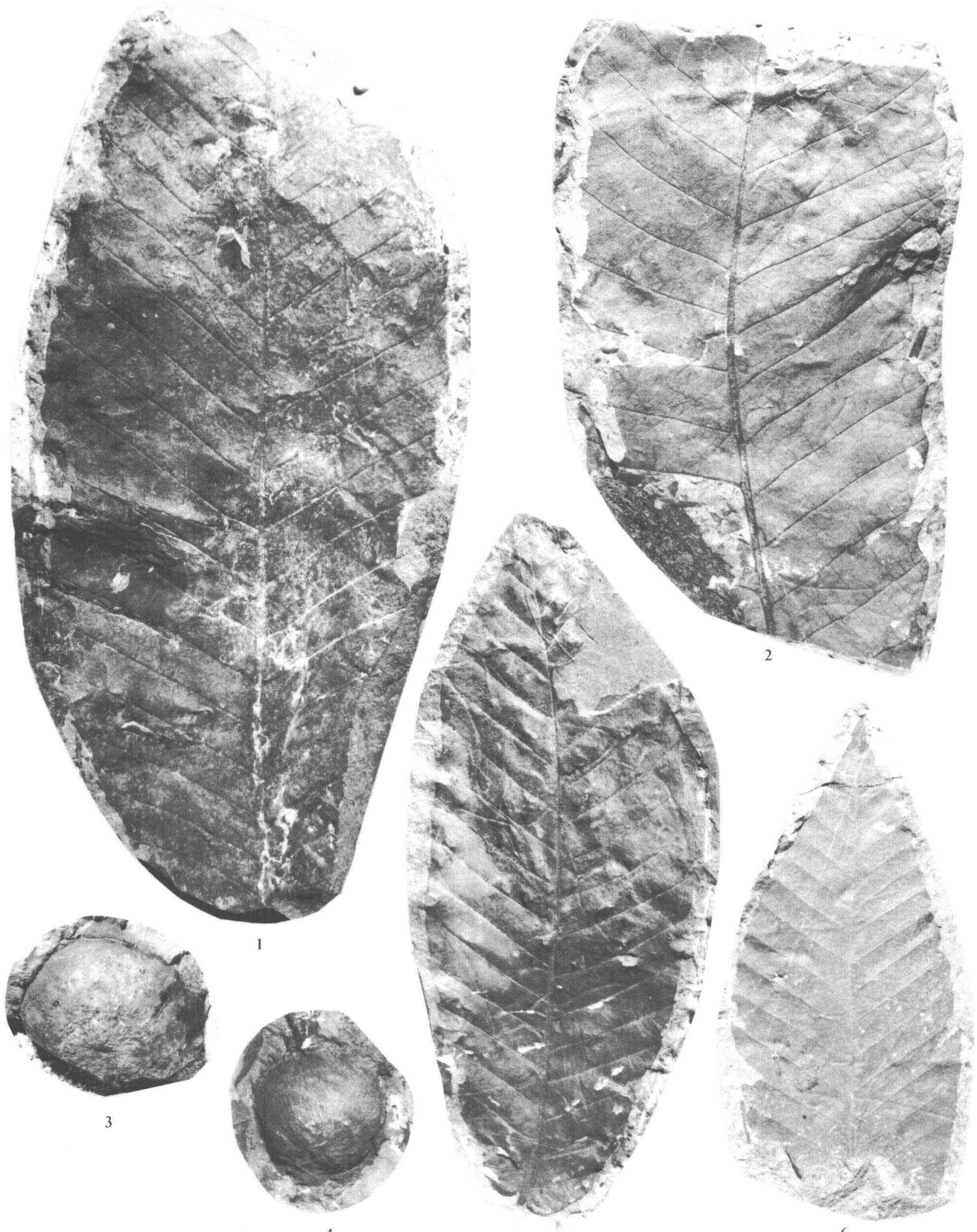
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HAMAMELIDIDAE

PLATE 7

(All figures natural size)

- FIGURES 1, 5, 6. *Fagus antipofi* Heer. (p. 31).
Hypotypes USNM 208397, 208398, 208399; loc. 9858.
2-4. *Quercus furuhjelmi* Heer. (p. 31).
Hypotypes USNM 208401, 208402, 208403 loc. 9858.



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HAMAMELIDIDAE

PLATE 8

[All figures natural size]

- Figures 1-3. *Quercus furuhjelmi* Heer. (p. 31).
Hypotypes USNM 208404, 208405, 208406; loc. 9858.
4. *Alnus fairi* (Knowlton) Wolfe. (p. 32).
Hypotype USNM 208408; loc. 9858.
5. *Alnus cappsii* (Hollick) Wolfe. (p. 32).
Hypotype USNM 208407; loc. 9858.
6. *Alnus healyensis* Wolfe. (p. 32).
Hypotype USNM 208410; loc. 9858.

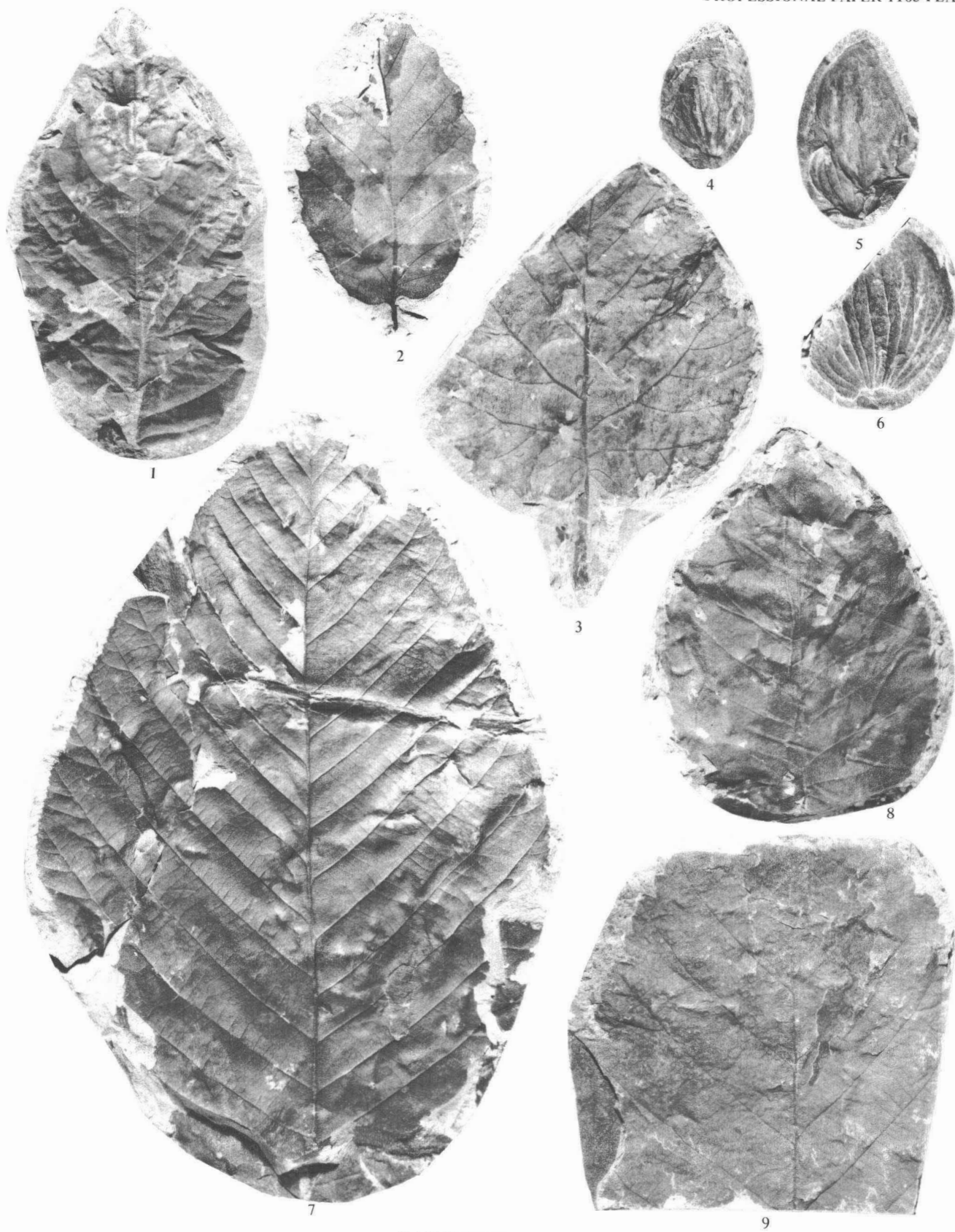


HAMAMELIDIDAE

PLATE 9

[All figures natural size unless otherwise stated]

- FIGURE
1. *Alnus healyensis* Wolfe. (p. 32).
Hypotype USNM 208411; loc. 9858.
 2. *Alnus fairi* (Knowlton) Wolfe. (p. 32).
Hypotype USNM 208409; loc. 9858.
 3. *Corylus* sp. (p. 33).
USNM 208419; loc. 9858.
 - 4-6. *Ostrya* sp. cf. *O. oregoniana* Chaney. (p. 33).
USNM 208420-208422; loc. 9858. ×2.
 7. *Carpinus seldoviana* Wolfe. (p. 33).
Hypotype USNM 208414; loc. 9858.
 8. *Betula* sp. cf. *B. sublutea* Tanai et N. Suzuki. (p. 32). USNM 208413; loc. 9858.
 9. *Alnus* sp.
USNM 208412; loc. 9858.

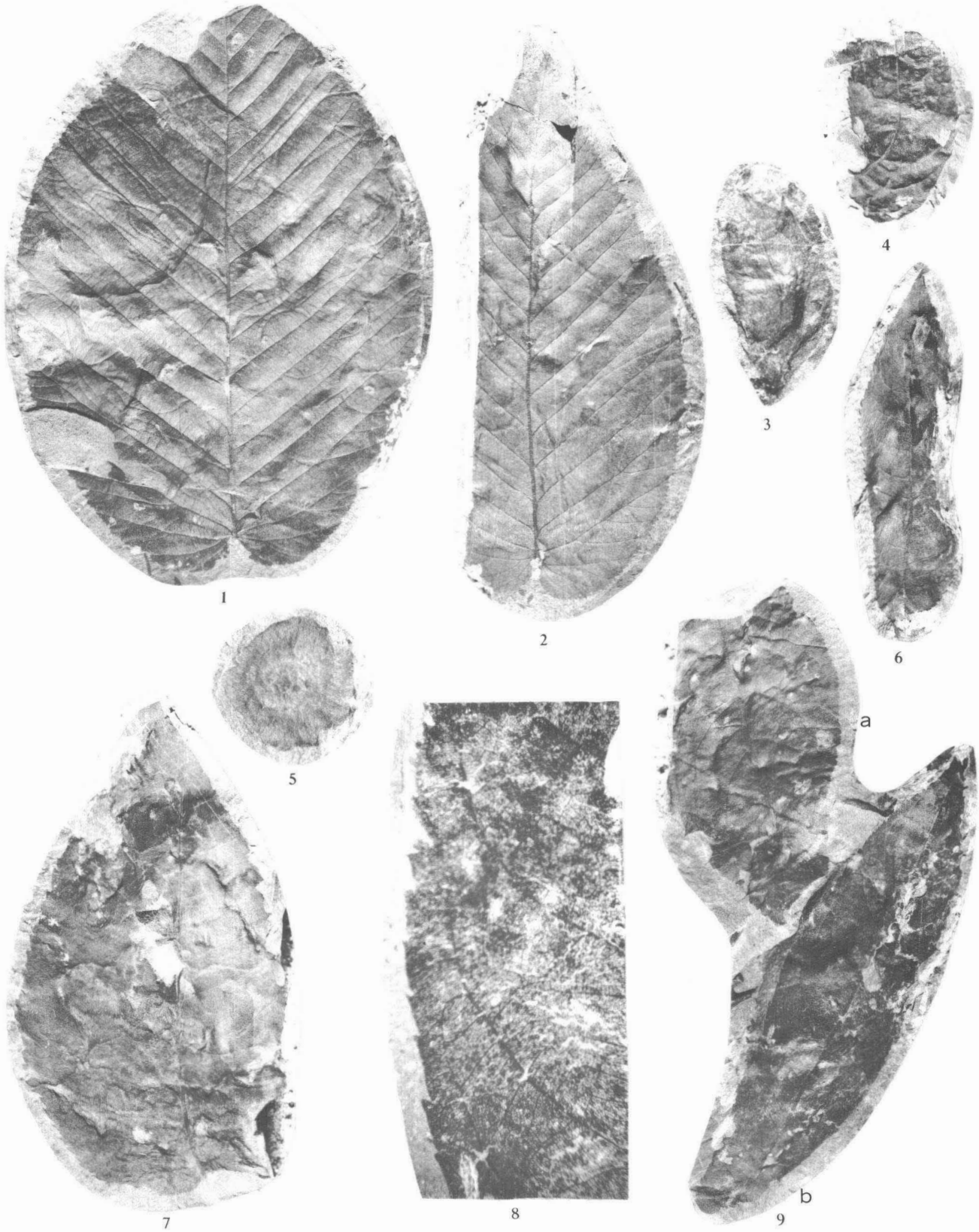


HAMAMELIDIDAE

PLATE 10

[All figures natural size unless otherwise stated]

- FIGURE 1-3. *Carpinus seldoviana* Wolfe. (p. 33).
Hypotypes USNM 208415, 208416, 208417; loc. 9858.
(fig. 3, $\times 2$).
- 4-6, 8, 9a, 9b. *Cyclocarya ezoana* (Tanai et N. Suzuki) Wolfe et Tanai. (p. 34).
4, 5, 8, 9a, 9b. Hypotypes USNM 208425, 208426, 208427, 208428, 208429;
loc. 9858.
(fig. 5, $\times 2$; fig. 9, $\times 3$).
6. Hypotype USNM 208426; loc. 9856.
7. *Carya bendirei* (Lesquereux) Chaney and Axelrod. (p. 33).
Hypotype USNM 208424; loc. 9858.

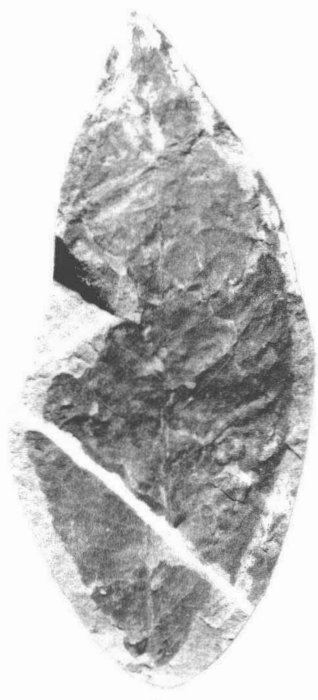


HAMAMELIDIDAE

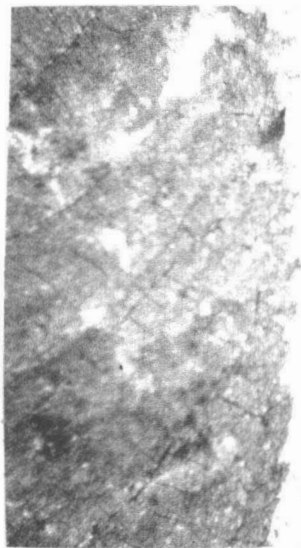
PLATE 11

[All figures natural size unless otherwise stated]

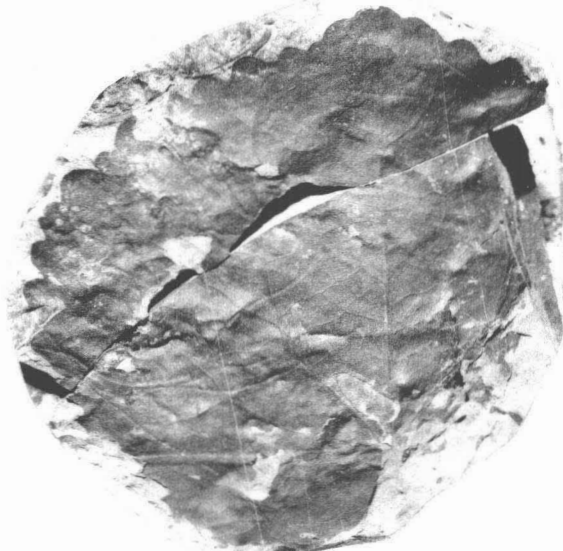
- FIGURES 1, 2. *Carya bendirei* (Lesquereux) Chaney et Axelrod. (p. 33).
1, 2. Hypotype USNM 208423; loc. 9856 (fig. 2, ×3).
- 3, 5. *Cercidiphyllum alaskanum* Wolfe et Tanai. (p. 27).
Paratypes USNM 208363A, B; loc. 9858.
- 4, 6, 7. *Pterocarya nigella* (Heer) Wolfe. (p. 35).
4, 6. Hypotypes USNM 208430, 208431; loc. 9858.
7. Hypotype USNM 208432; loc. 9856. ×2.
8. *Populus* sp. (p. 35).
USNM 208434; loc. 9858.
9. *Populus kenaiana* Wolfe. (p. 35).
Hypotype USNM 208433; loc. 9858.



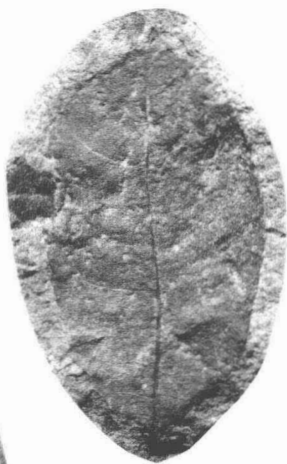
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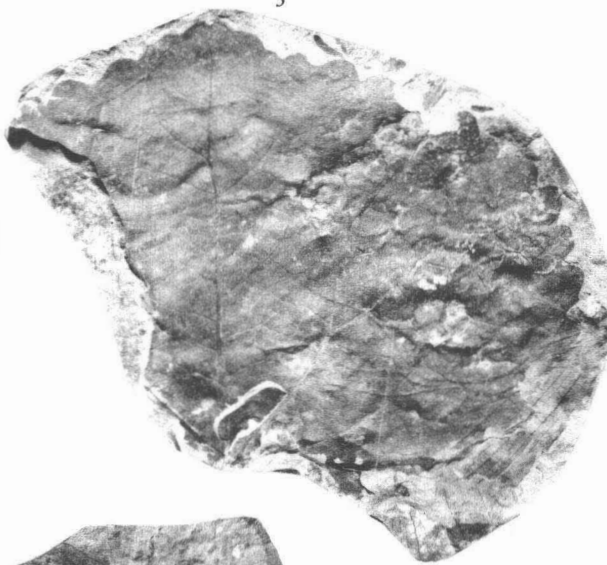
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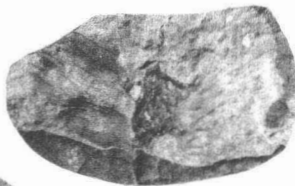
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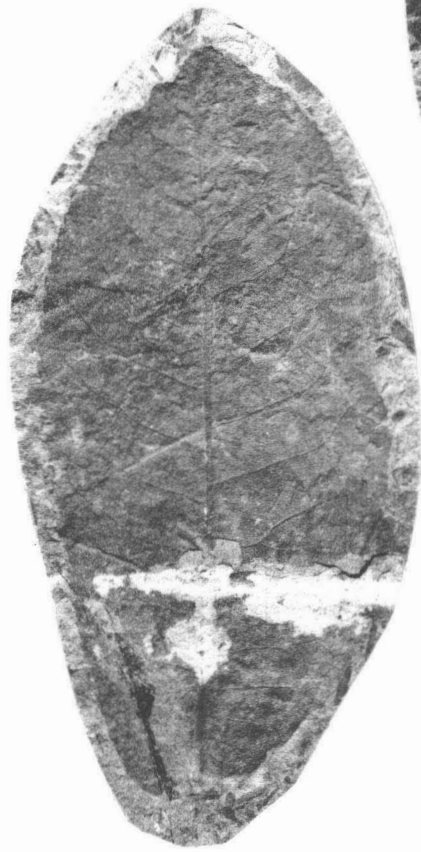
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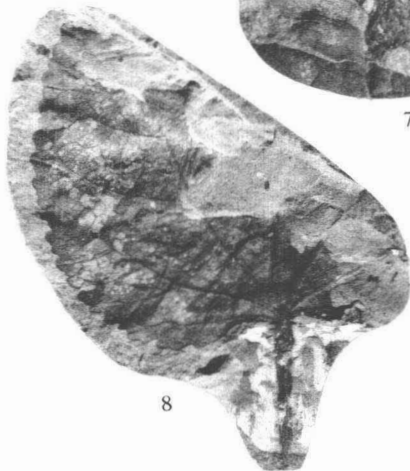
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HAMAMELIDIDAE, DILLENIIDAE

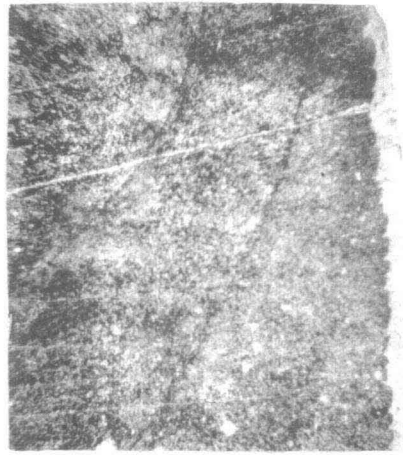
PLATE 12

[All figures natural size unless otherwise stated]

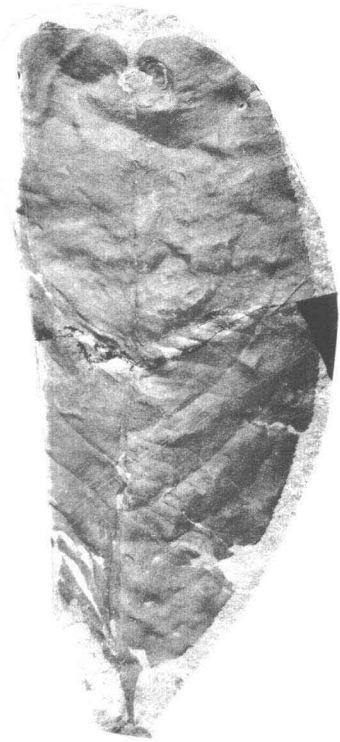
- FIGURES
1. *Populus kenaiana* Wolfe. (p. 35).
Hypotype USNM 42264B; loc. 9858.
 - 2, 3. *Salix seldoviana* Wolfe et Tanai. (p. 36).
2, 3. Holotype USNM 208446; loc. 9858. Fig. 2, $\times 3$.
 4. *Salix hopkinsi* Wolfe et Tanai. (p. 36).
Holotype USNM 208440; loc. 9858.
 - 5-7. *Salix picroides* (Heer) Wolfe. (p. 36).
5, 7. Hypotypes USNM 208442, 208443; loc. 9858.
6. Showing fine venation and margin of USNM 208442 (fig. 5). Ca. $\times 3$.
 8. *Salix cappsensis* Wolfe. (p. 36).
Hypotype USNM 208435; loc. 9858.



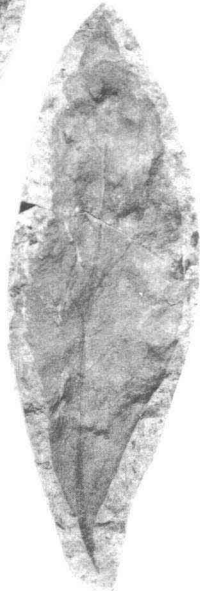
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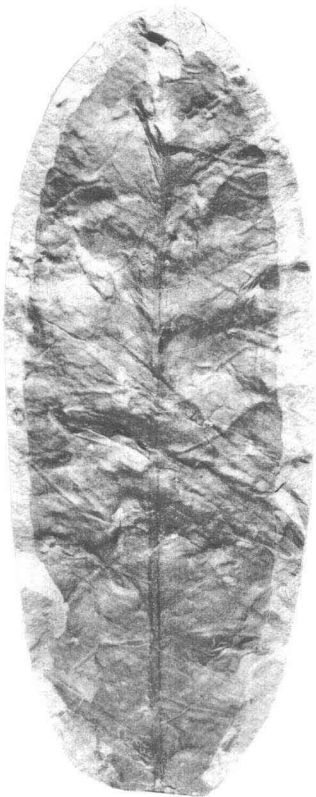
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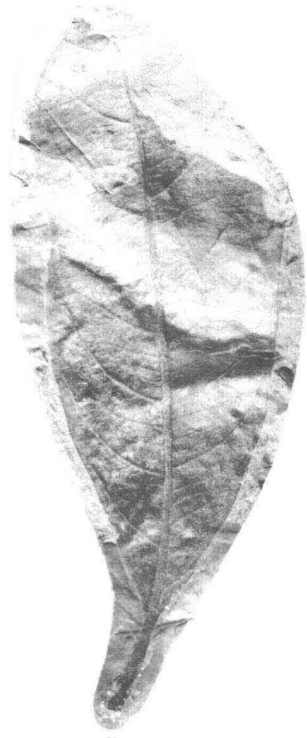
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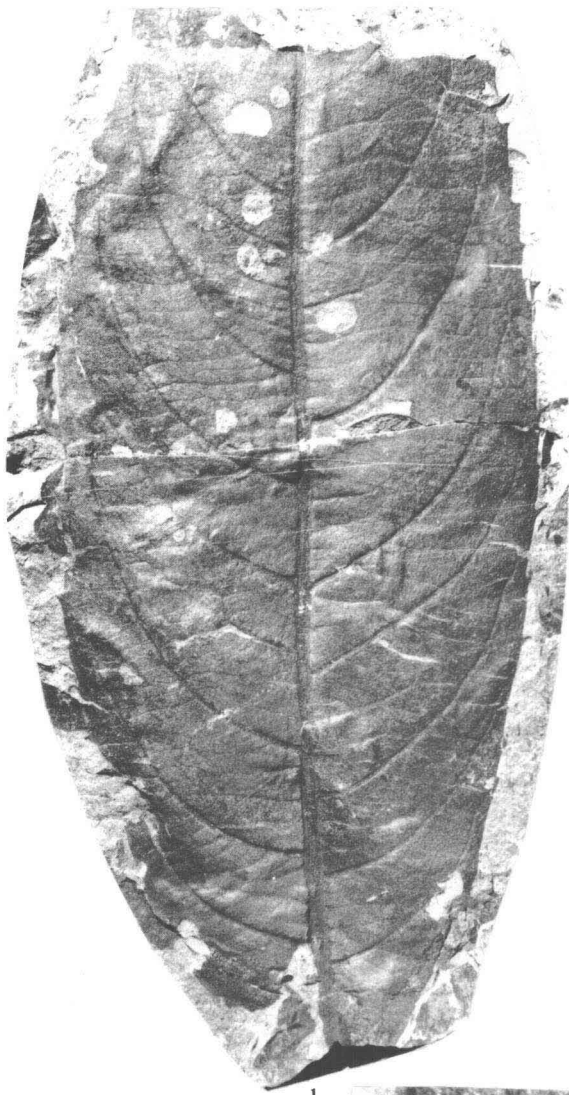
8

DILLENIIDAE

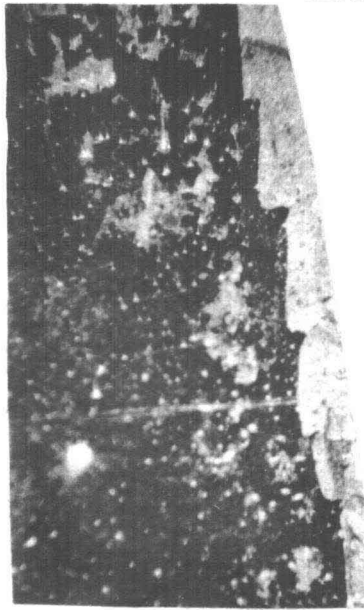
PLATE 13

[All figures natural size unless otherwise stated]

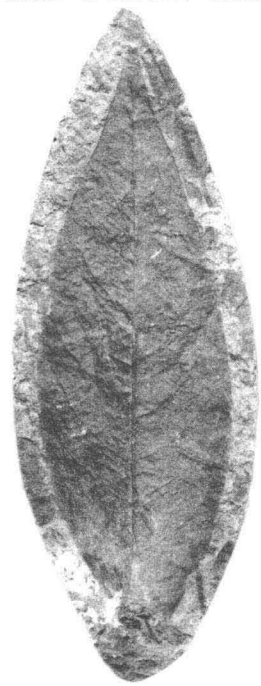
- FIGURES 1, 2, 4. *Salix cappsensis* Wolfe. (p. 36).
1, 2, 4. Hypotypes USNM 208436, 208437, 208438;
loc. 9858. Fig. 2, $\times 3$.
- 3, 7. *Salix picroides* (Heer) Wolfe. (p. 36).
Hypotypes USNM 208444, 208445; loc. 9858.
- 5, 6. *Salix hopkinsi* Wolfe et Tanai. (p. 36).
5, 6. Paratypes USNM 208441A, 208441B; loc. 9858.
Fig. 6, $\times 3$.



1



2



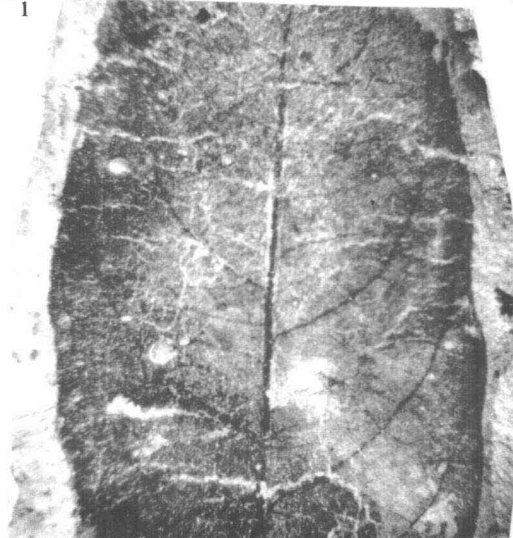
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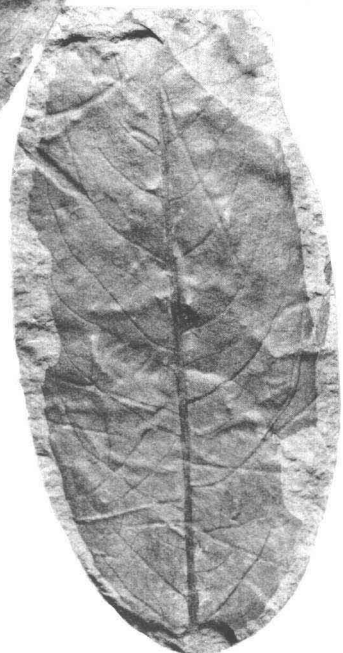
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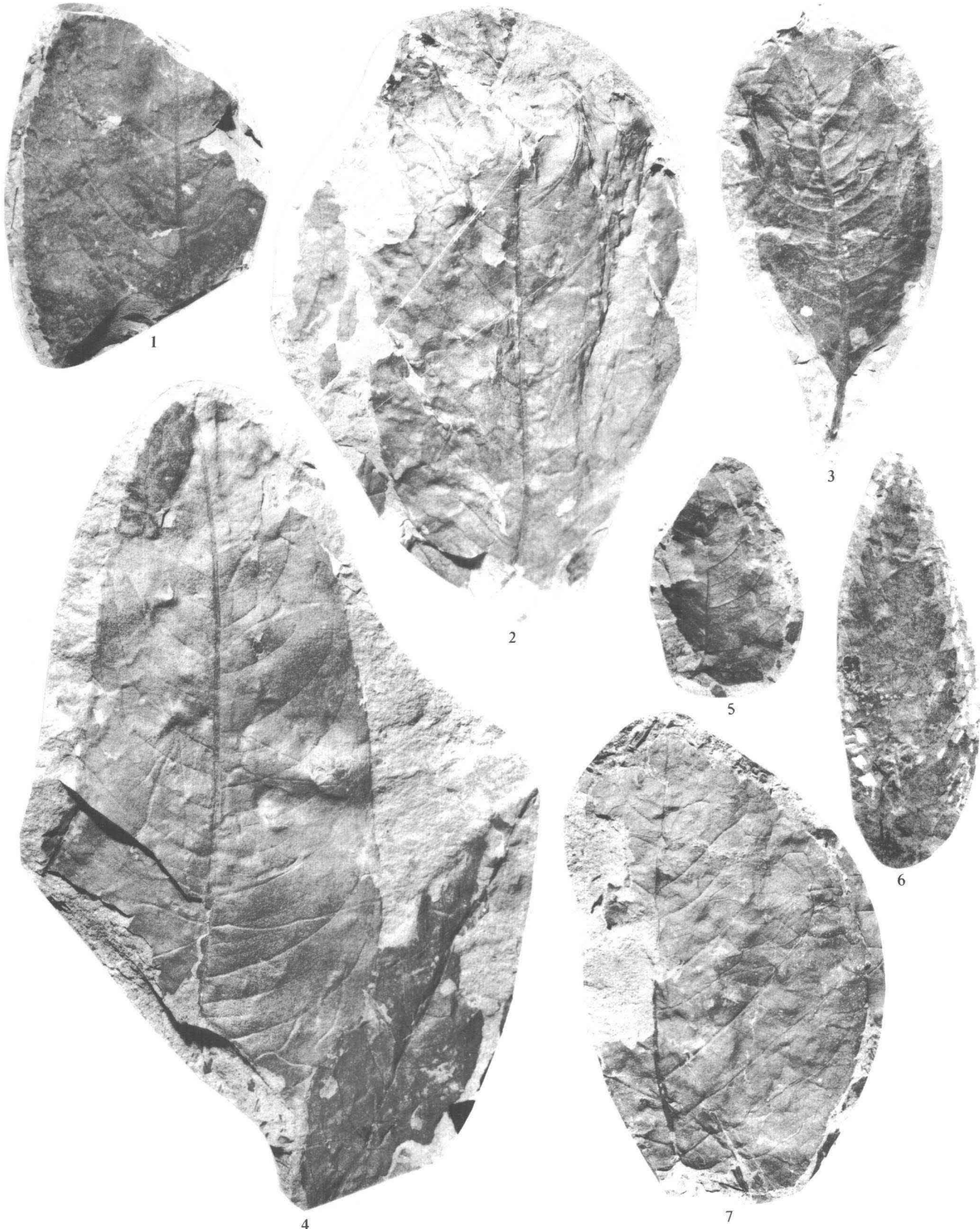
7

DILLENIDAE

PLATE 14

[All figures natural size]

- FIGURES
1. *Hydrangea* sp. (p. 37).
USNM 208449A; loc. 9858.
 2. *Salix seldoviana* Wolfe et Tanai. (p. 36).
Paratype USNM 208447; loc. 9858.
 - 3, 4. *Salix cappsensis* Wolfe. (p. 36).
Hypotypes USNM 208439A, 208439B; loc. 9858.
 - 5, 6. *Crataegus chamissoni* (Heer) Wolfe et Tanai. (p. 37).
Hypotypes USNM 208450, 208451; loc. 9858.
 7. *Prunus* sp. (p. 38).
USNM 208454A, B; loc. 9858.

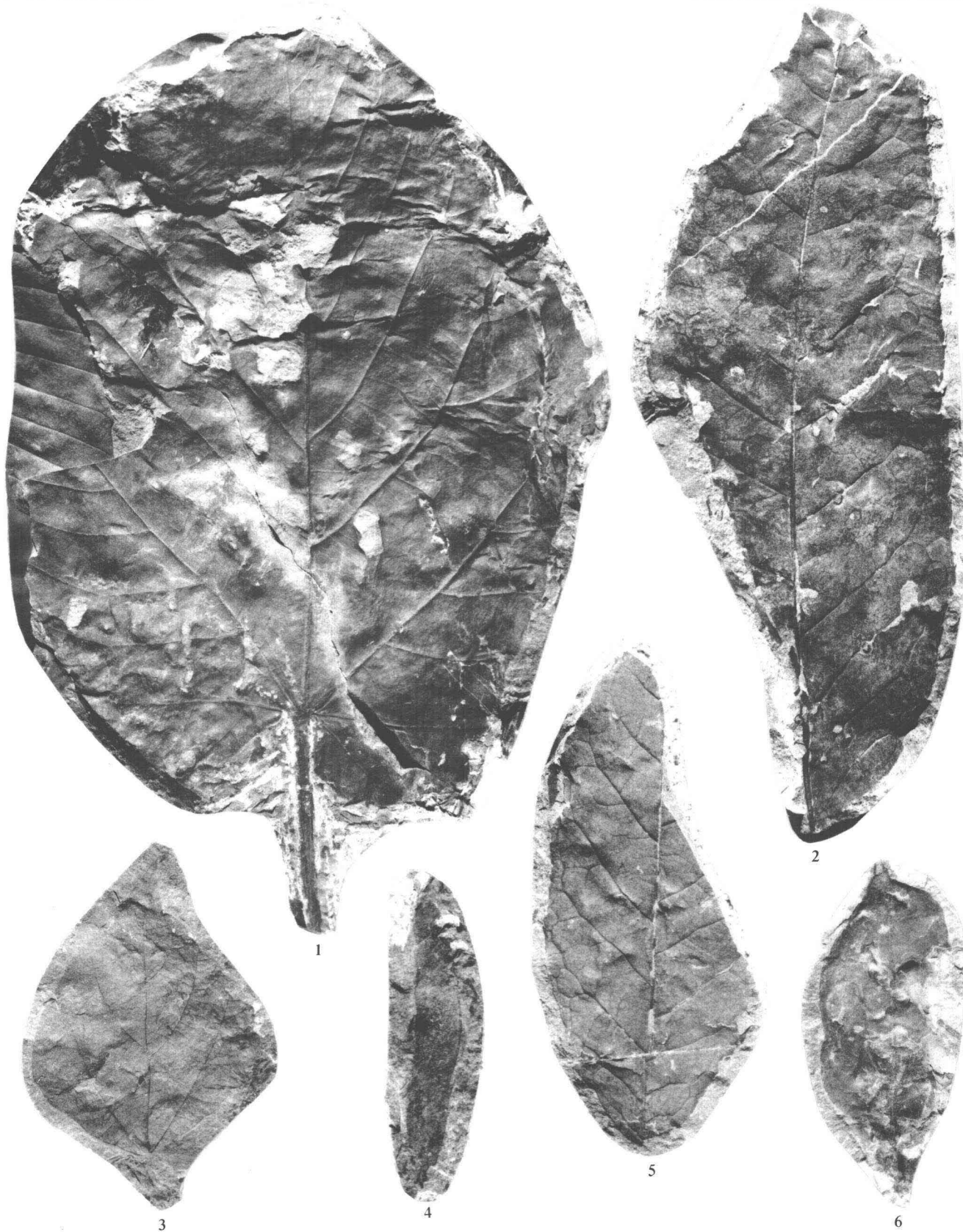


DILLENIIDAE, ROSIDAE

PLATE 15

[All figures natural size unless otherwise stated]

- FIGURES
1. *Tilia subnobilis* Huzioka. (p. 36).
Hypotype USNM 208448; loc. 9856.
 - 2, 5. *Prunus kenaica* Wolfe et Tanai. (p. 37).
2. Holotype USNM 208452; loc. 9856.
5. Paratype USNM 208453; loc. 9856.
 3. *Pueraria miothunbergiana* Hu et Chaney. (p. 39).
Hypotype USNM 208461; loc. 9858.
 4. *Cladrastis* sp. cf. *C. aniensis* Huzioka. (p. 38).
Hypotype USNM 208459; loc. 9858. ×2.
 6. *Decodon alaskana* Wolfe et Tanai. (p. 39).
Paratype USNM 208464; loc. 9858.

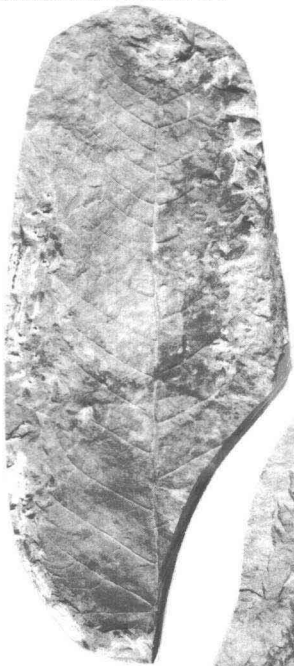


DILLENIIDAE, ROSIDAE

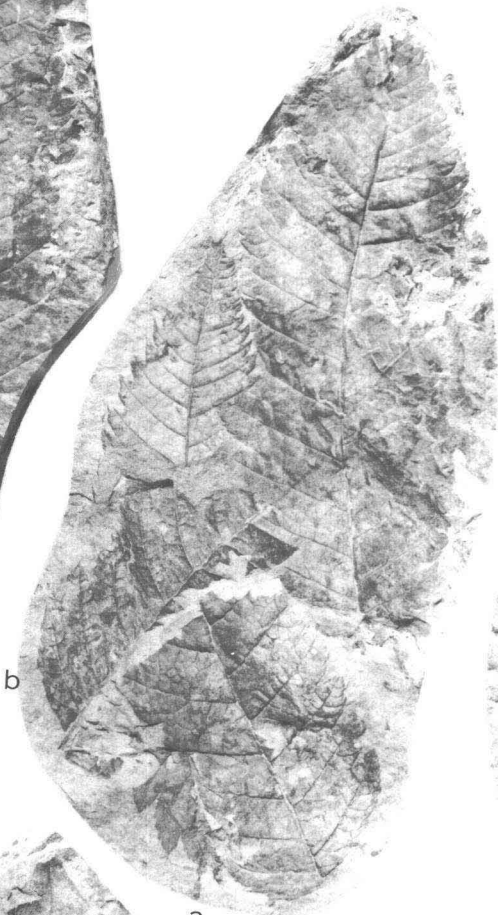
PLATE 16

[All figures natural size unless otherwise stated]

- FIGURES 1, 2a, b, c. *Sorbaria hopkinsi* (Wolfe) Wolfe et Tanai. (p. 38).
Hypotypes USNM 208455–208458; loc. 9858.
- 3, 4. *Cladrastis* sp. cf. *C. aniensis* Huzioka. (p. 38).
3, 4. USNM 208460; loc. 9858. Fig. 4, ×3.
- 5, 7, 8. *Decodon alaskana* Wolfe et Tanai. (p. 39).
5. Paratype USNM 208463; loc. 9858.
7, 8. Holotype USNM 208462; loc. 9858. Fig. 8, ×3.
6. *Acer heterodentatum* (Chaney) MacGinitie. (p. 41).
Hypotype USNM 208476; loc. 9858.



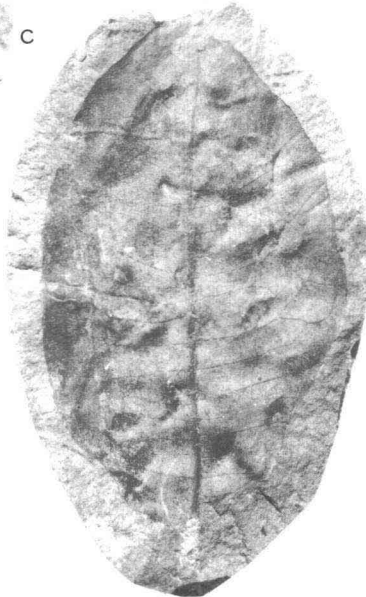
1



b

a

2

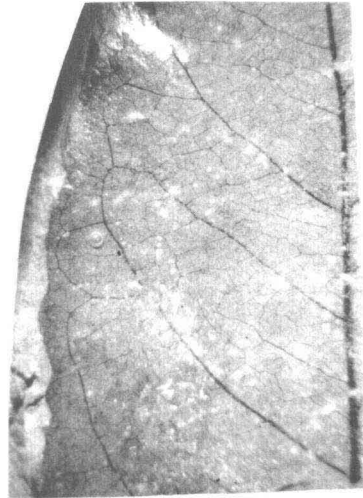


c

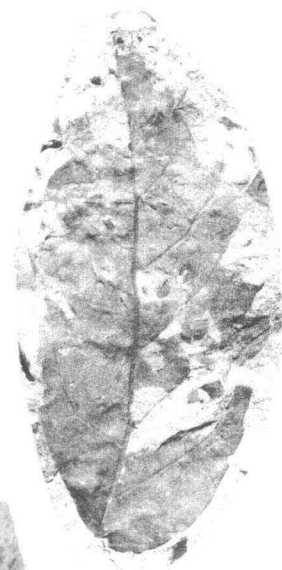
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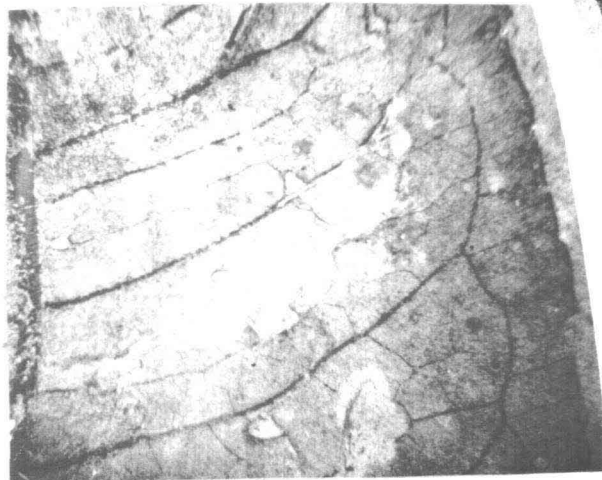
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ROSIDAE

PLATE 17

[All figures natural size]

- FIGURES 1-3, 5. *Acer ezoanum* Oishi et Huzioka. (p. 40).
Hypotypes USNM 208466, 208467, 208468; loc. 9858.
4. *Acer heterodentatum* (Chaney) MacGinitie. (p. 41).
Hypotype USNM 208477; loc. 9858.
6. *Acer grahamensis* Knowlton et Cockerell. (p. 40).
Hypotype USNM 208473; loc. 9858.
- 7, 8. *Acer glabroides* Brown. (p. 40).
Hypotypes USNM 208471, 208472; loc. 9858.



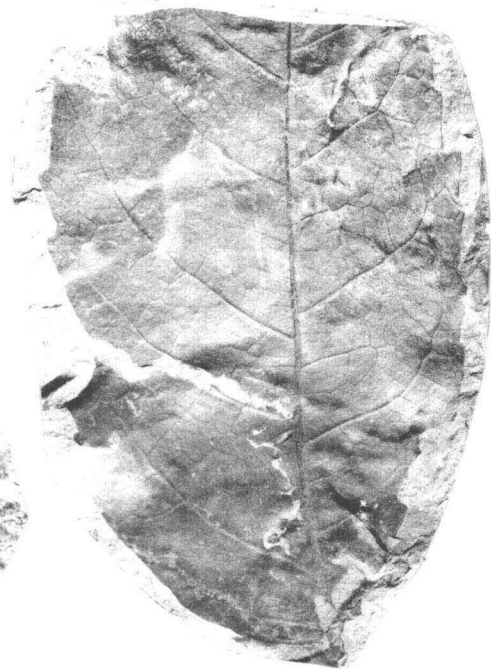
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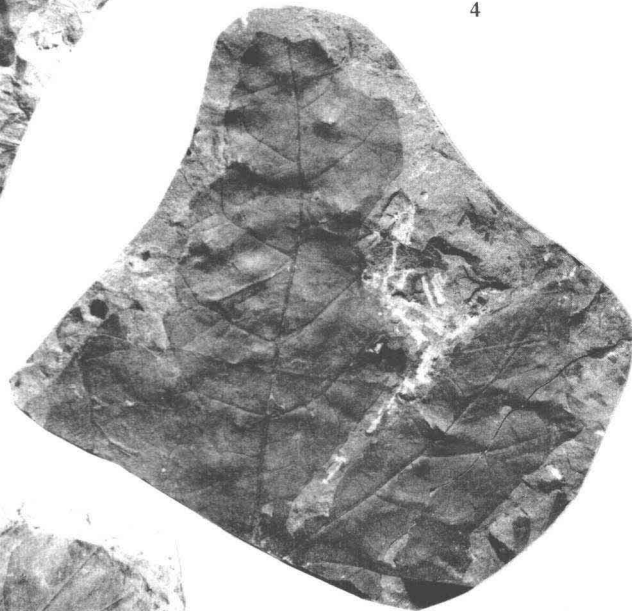
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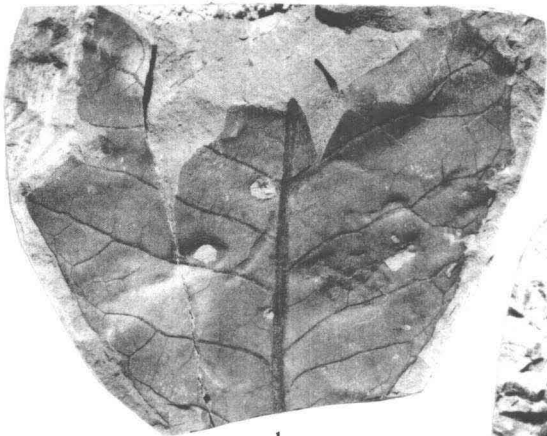
8

ROSIDAE

PLATE 18

[All figures natural size]

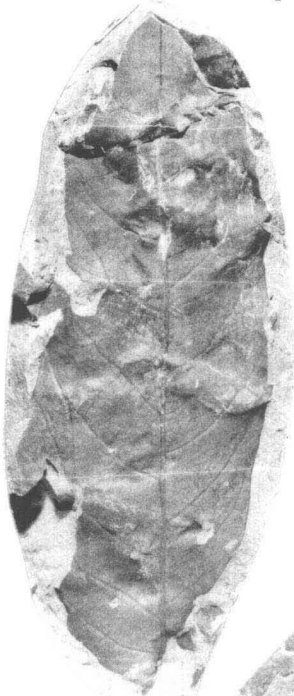
- FIGURE 1. *Nyssa* sp. cf. *N. knowltoni* Berry. (p. 41).
USNM 208482; loc. 9858.
- 2-4. *Acer heterodentatum* (Chaney) MacGinitie. (p. 41).
Hypotypes USNM 208478, 208479, 208480; loc. 9858.
5. *Acer grahamensis* Knowlton et Cockerell. (p. 40).
Hypotype USNM 208474; loc. 9856.



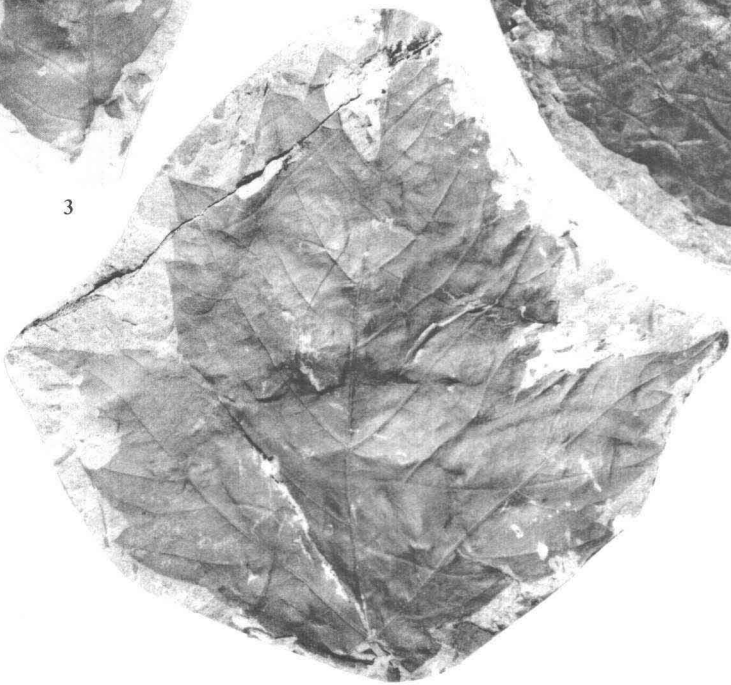
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ROSIDAE

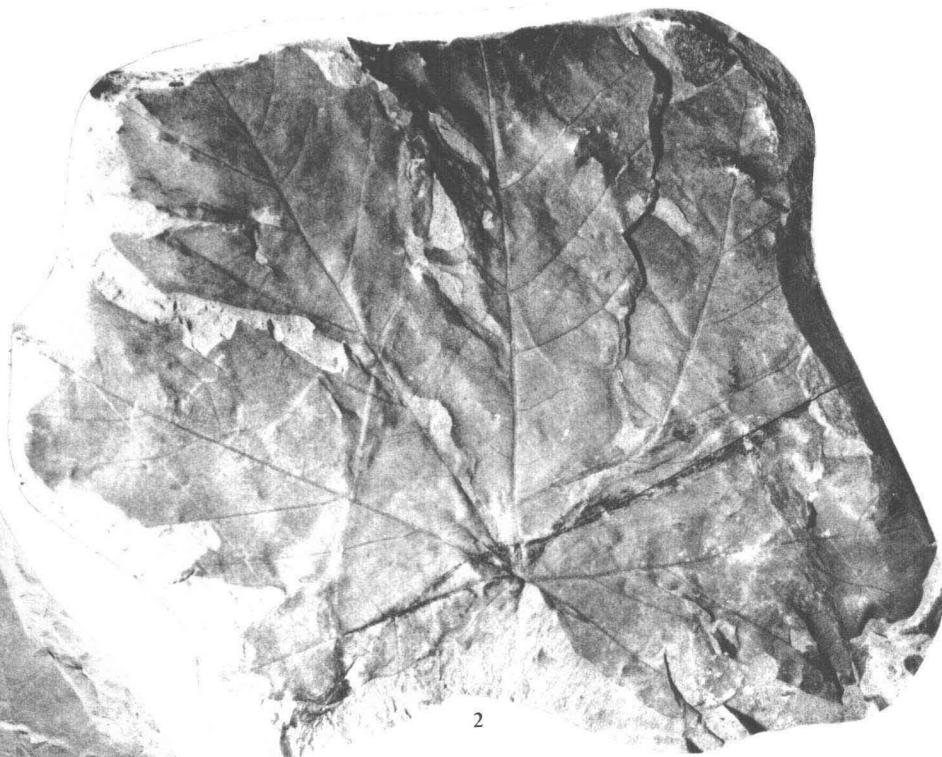
PLATE 19

[All figures natural size]

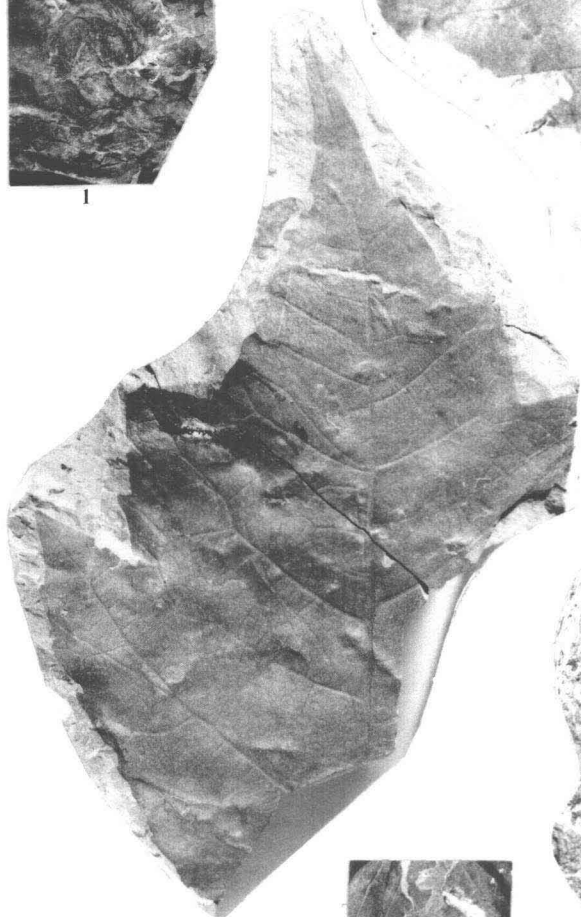
- FIGURES 1, 4. *Acer grahamensis* Knowlton et Cockerell. (p. 40).
Hypotype USNM 208475; loc. 9856.
- 2, 5. *Acer ezoanum* Oishi et Huzioka. (p. 40).
Hypotypes USNM 208469, 208470; loc. 9858.
3. *Acer heterodontatum* (Chaney) McGinitie. (p. 41).
Hypotype USNM 208481; loc. 9858.



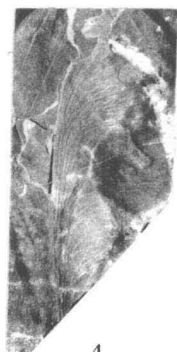
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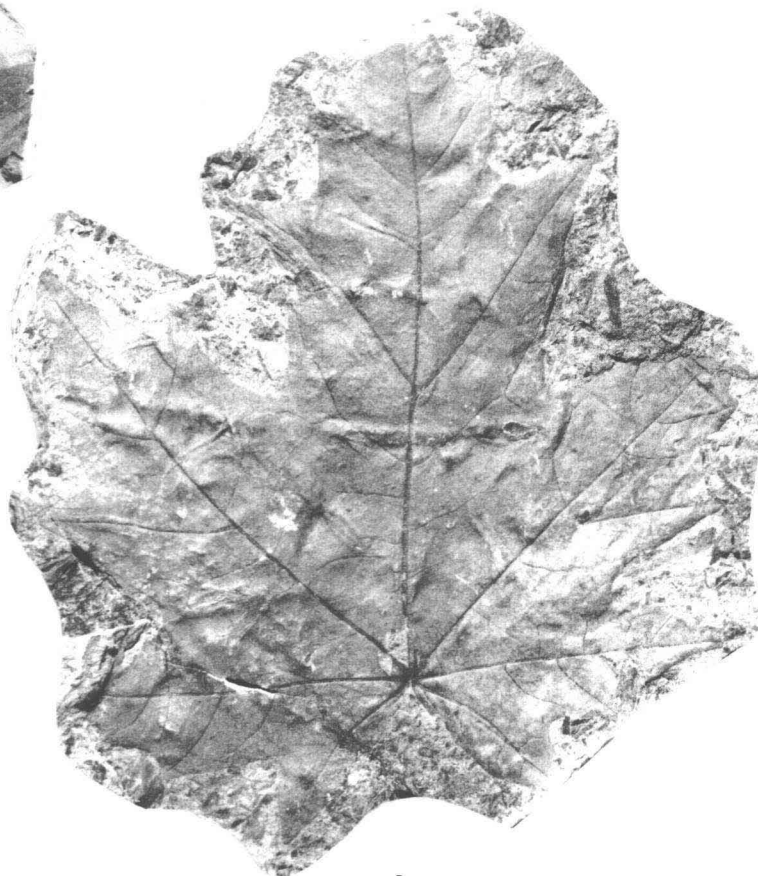
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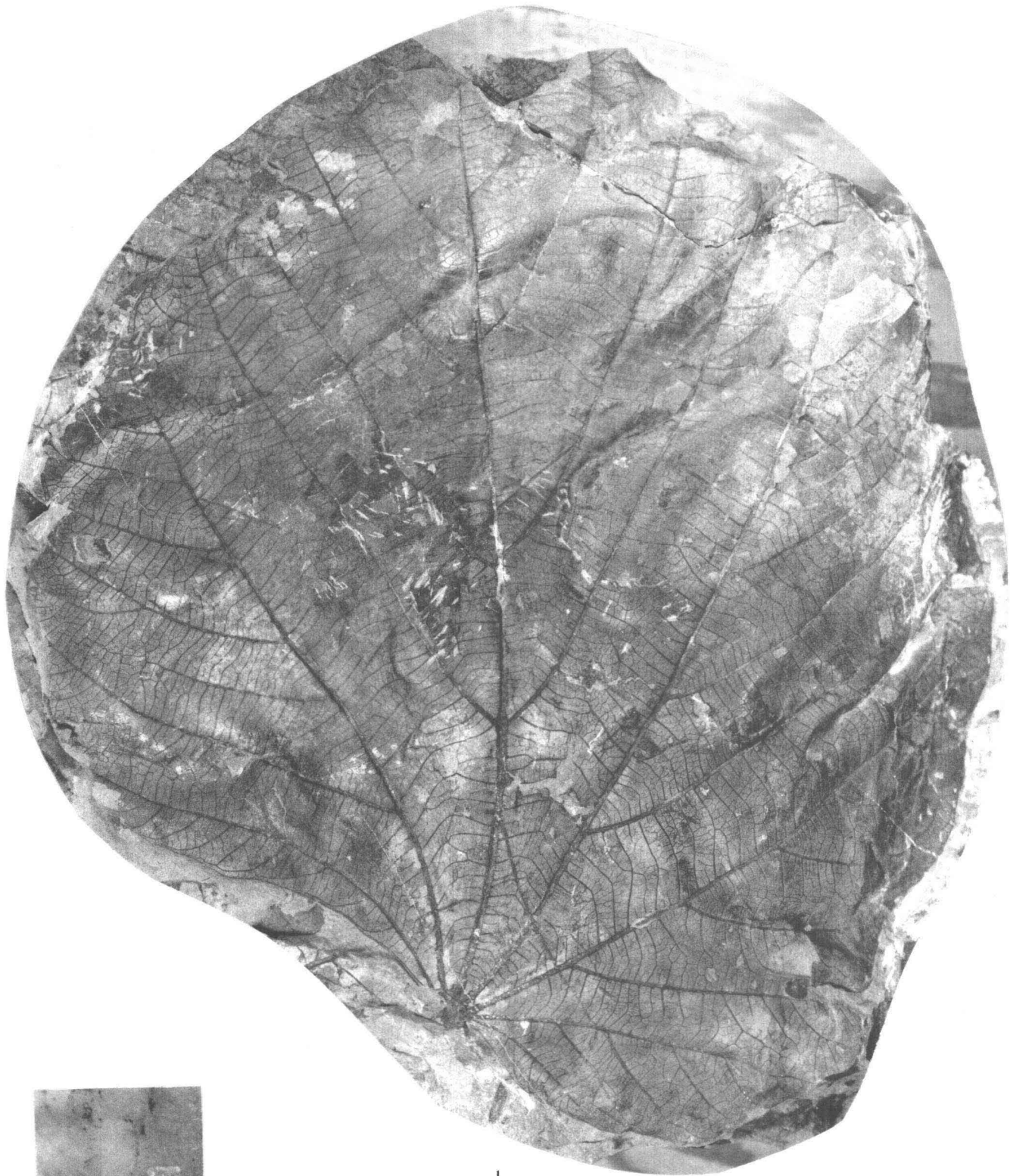


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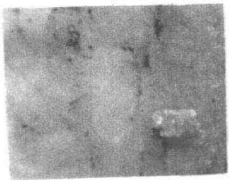
ROSIDAE

PLATE 20

- FIGURE 1, 2. *Alangium mikii* Wolfe et Tanai. (p. 41).
1. Holotype, USNM 208483; loc. 9858. ×1.
2. Paratype USNM 208485; loc. 11091 (Capps Glacier), ca. ×.



1



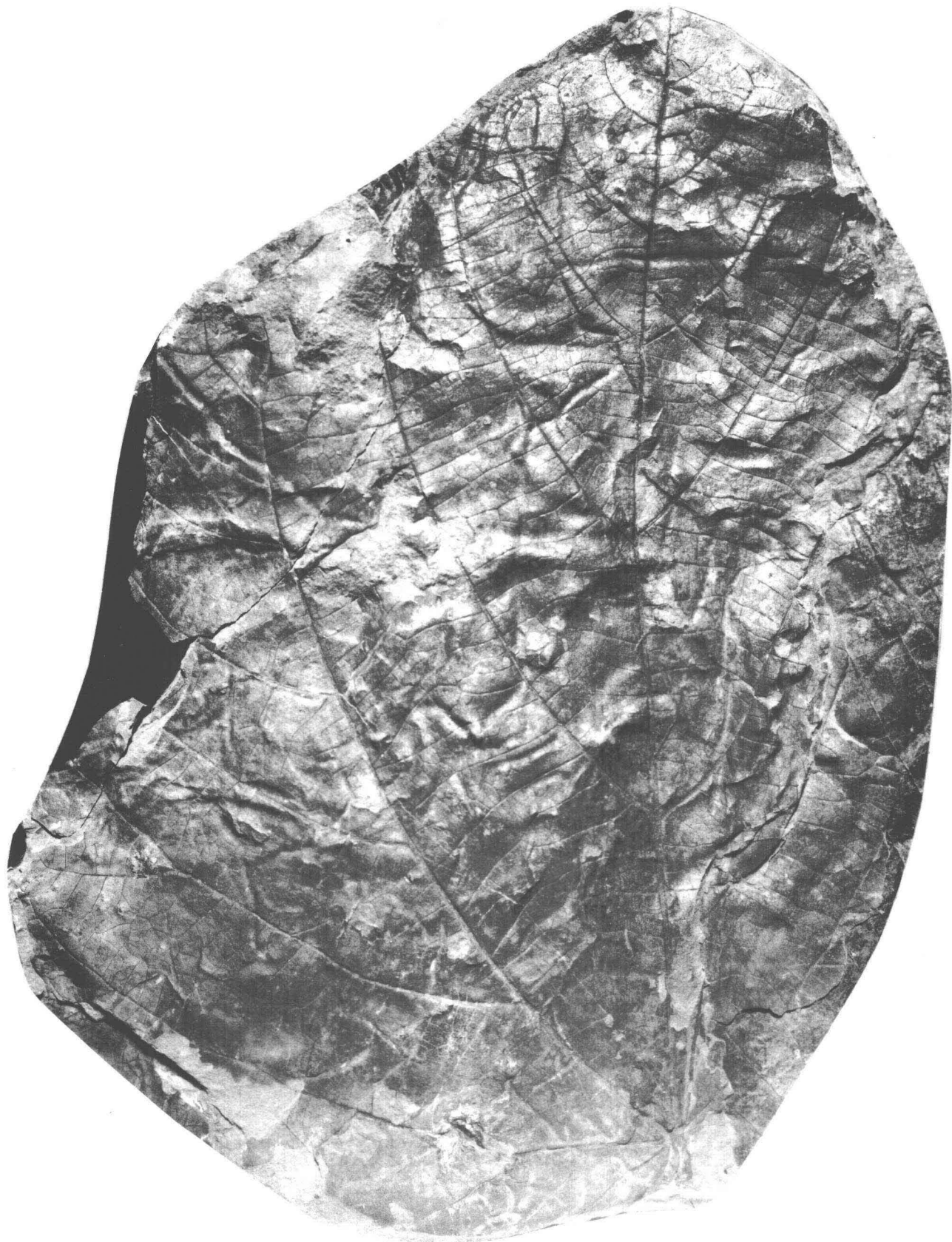
2

ROSIDAE

PLATE 21

[Natural size]

Alangium mikii Wolfe et Tanai. (p. 41).
Paratype USNM 208484; loc. 9858.

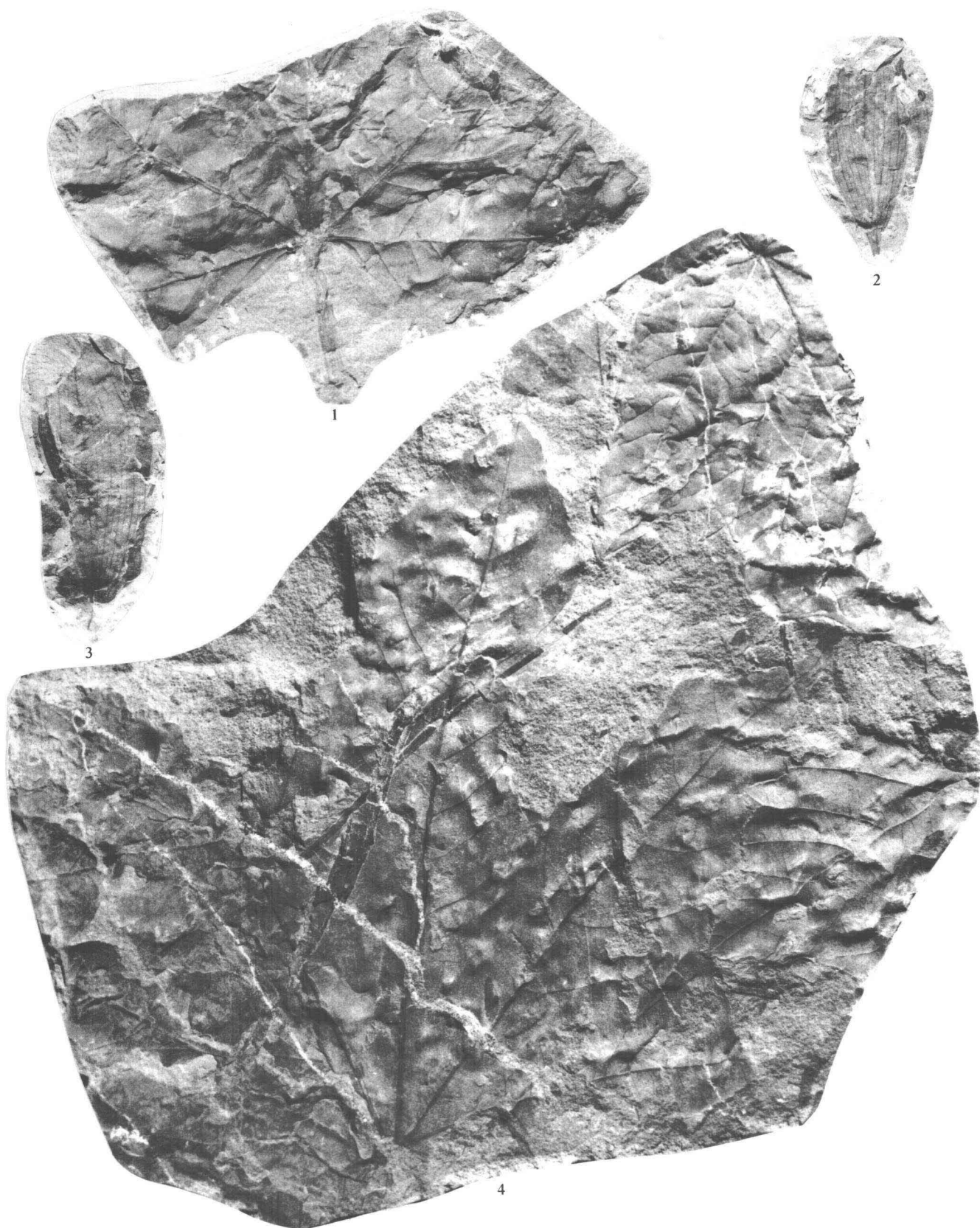


ROSIDAE

PLATE 22

[All figures natural size]

- FIGURES
1. *Vitis seldoviana* Wolfe et Tanai. (p. 43).
Paratype USNM 208488; loc. 9856.
 - 2, 3. *Potamogeton alaskanus* Wolfe et Tanai. (p. 44).
 2. Paratype USNM 208495; loc. 9858
 3. Holotype USNM 208494; loc. 9858.
 4. *Kalopanax n-suzikii* Wolfe et Tanai (p. 42).
Hypotype USNM 208486; loc. 9856.

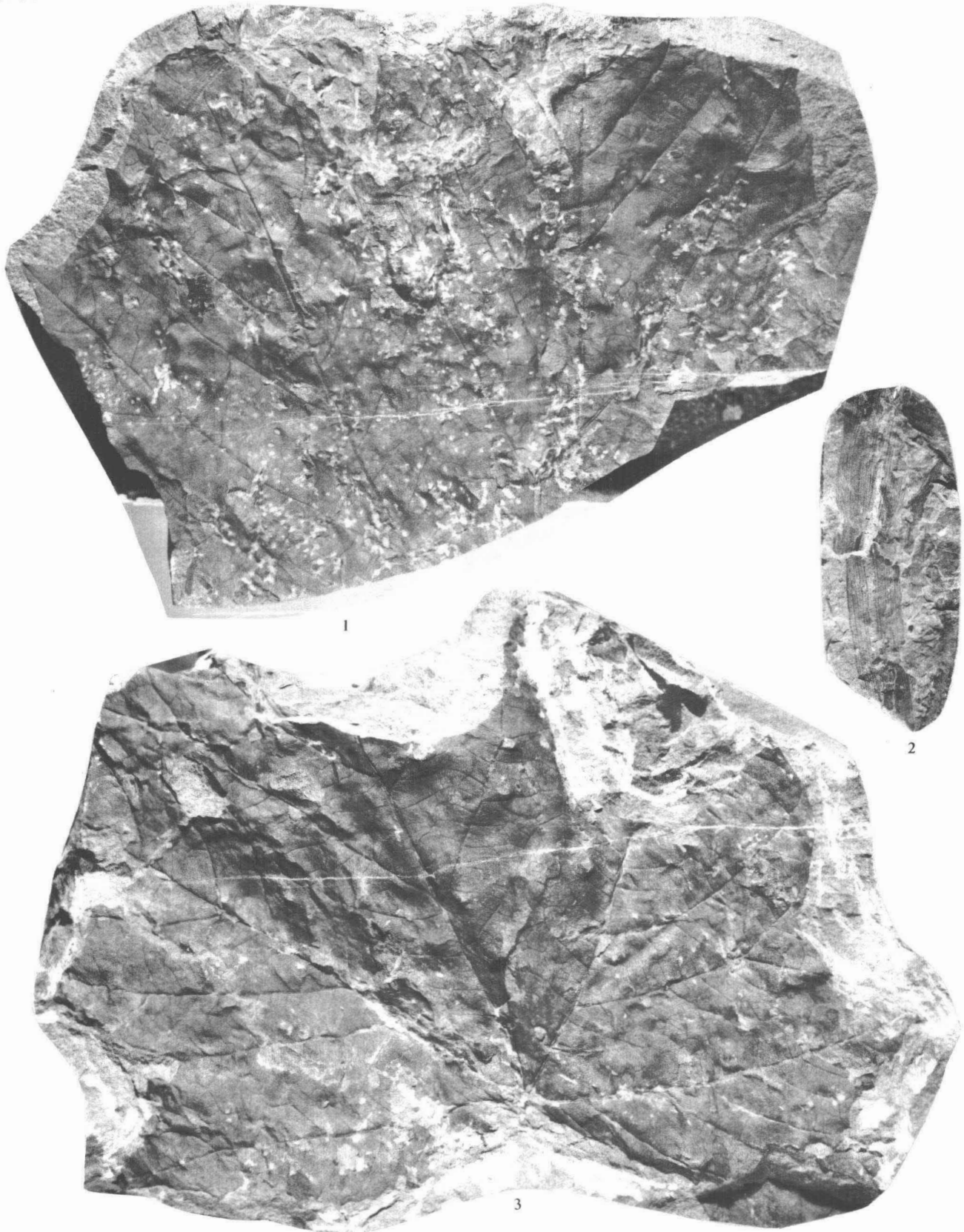


ROSIDAE, MONOCOTYLEDONES

PLATE 23

[All figures natural size]

- FIGURES** 1, 3. *Vitis seldoviana* Wolfe et Tanai. (p. 43).
1. Paratype USNM 208489; loc. 9856.
3. Holotype USNM 208487; loc. 9856.
2. *Monocotylophyllum alaskanum* (Heer) Wolfe et Tanai. (p. 45).
Hypotype USNM 208498; loc. 9858.

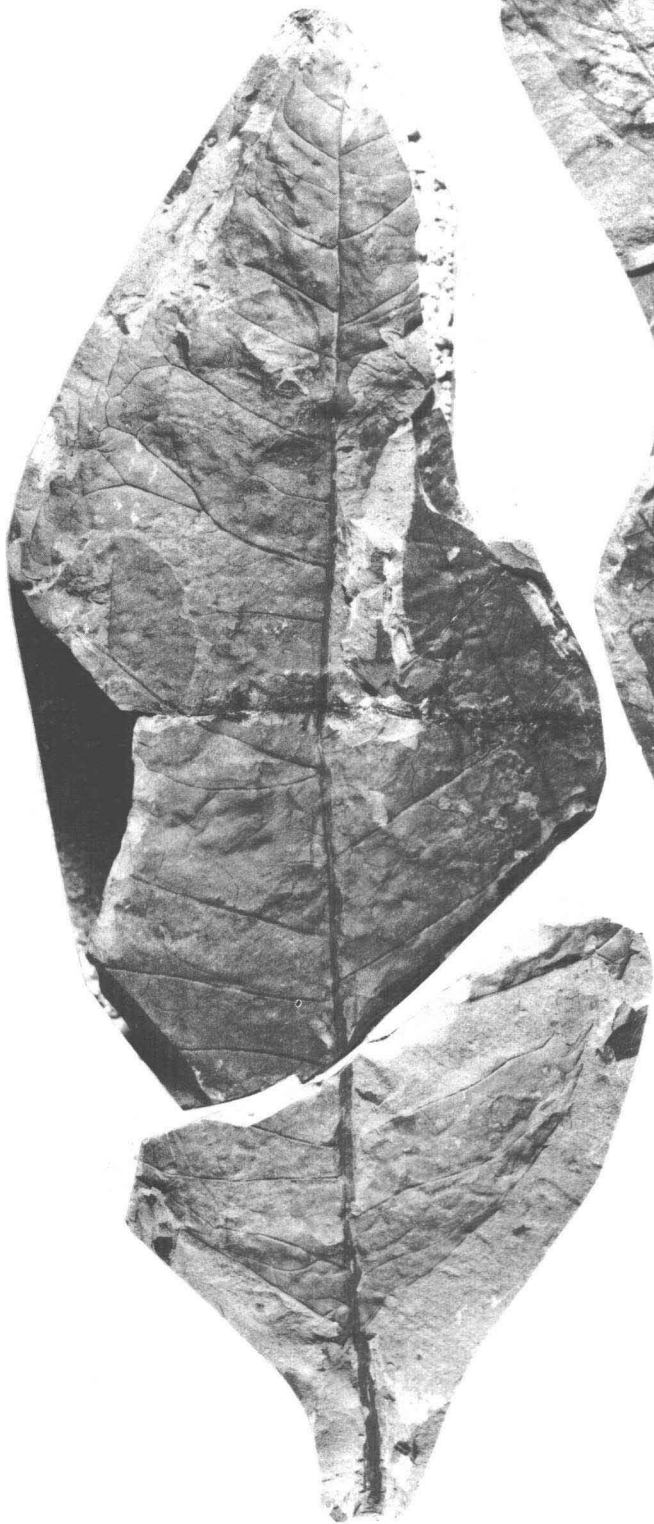


ROSIDAE, MONOCOTYLEDONES

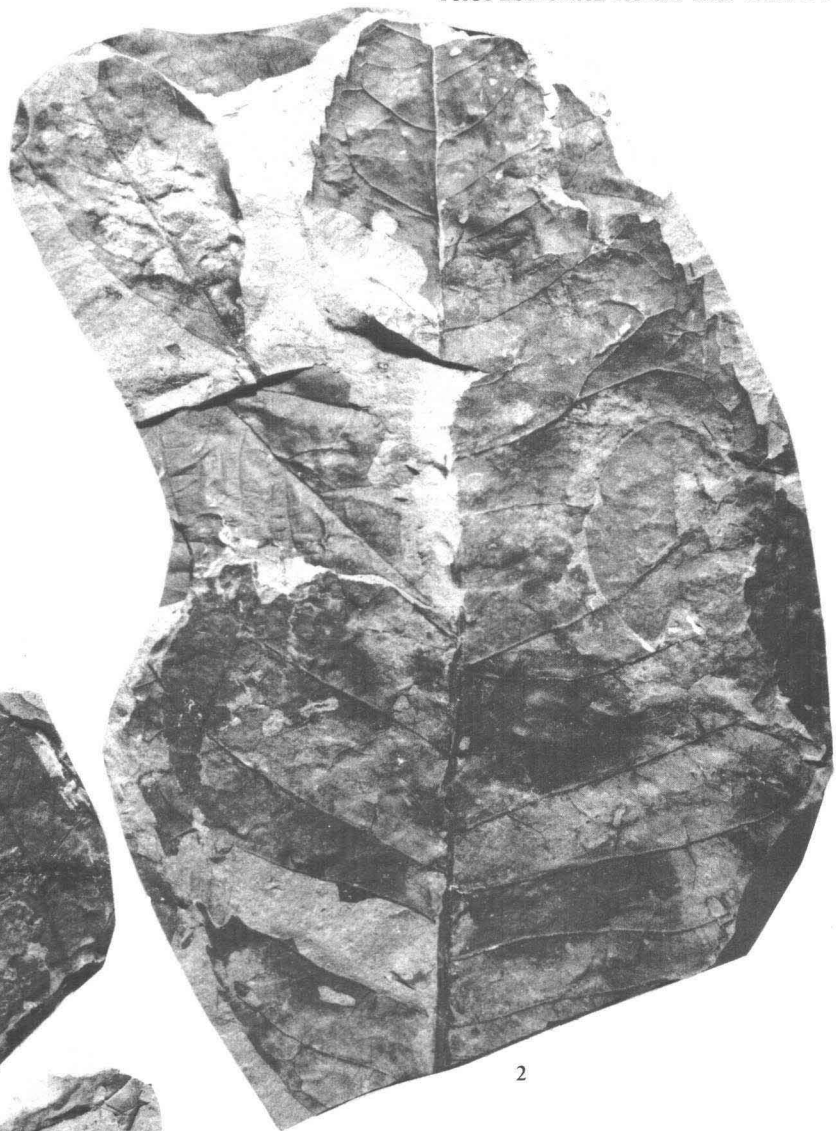
PLATE 24

[All figures natural size unless otherwise stated]

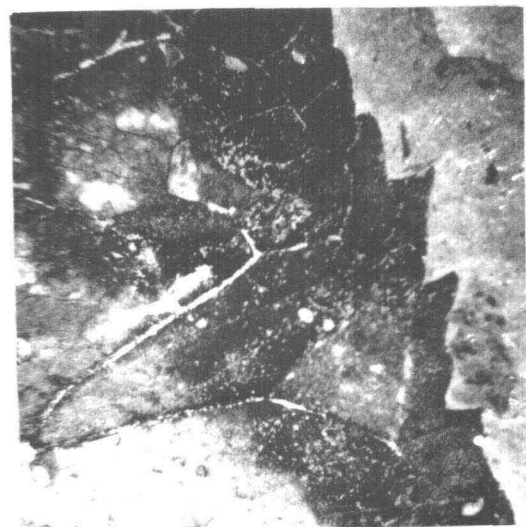
FIGURES 1-3. *Fraxinus kenaica* Wolfe et Tanai. (p. 43).
Holotype USNM 208490 A, B; loc. 9858. Fig. 3, $\times 3$.



1



2



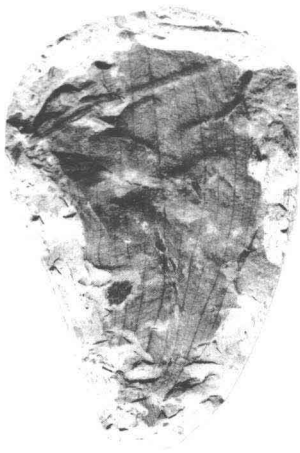
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ROSIDAE

Plate 25

[All figures natural size unless otherwise stated]

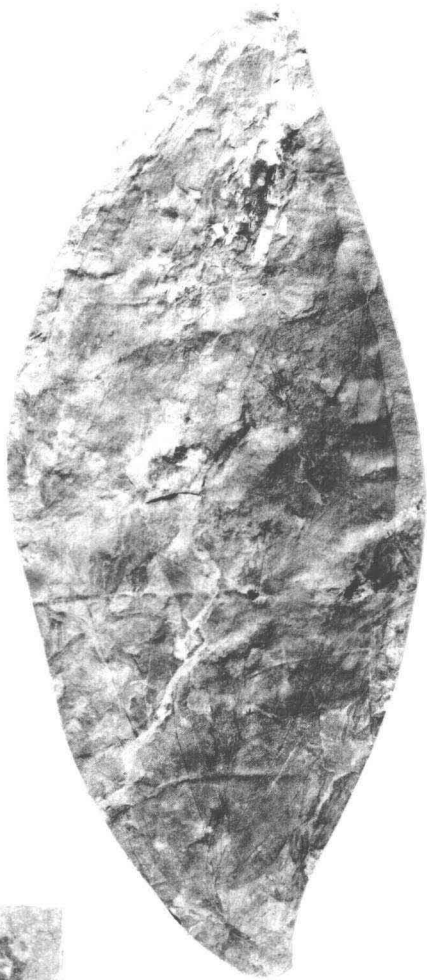
- FIGURES 1, 7. *Potamogeton alaskanus* Wolfe et Tanai. (p. 44).
1. Paratype USNM 208496; loc. 9858.
7. Paratype USNM 208497; loc. 9858. ×5.
2. *Lonicera* sp. (p. 44).
USNM 208491; loc. 9858.
- 3, 6. *Alisma seldoviana* Wolfe et Tanai. (p. 44).
3. Paratype USNM 208493; loc. 9858.
6. Holotype USNM 208492; loc. 9858.
4. *Monocotylophyllum* sp. a. (p. 45).
USNM 208500, loc. 9858.
5. *Monocotylophyllum* sp. a. (p. 45).
USNM 208503, loc. 9858.
8. *Monocotylophyllum alaskanum* (Heer) Wolfe et Tanai. (p. 45).
Hypotype USNM 208499; loc. 9858.



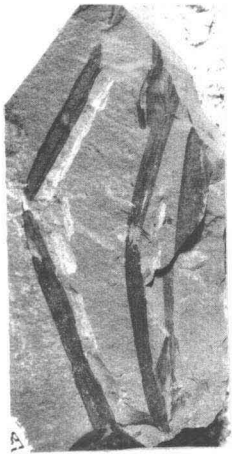
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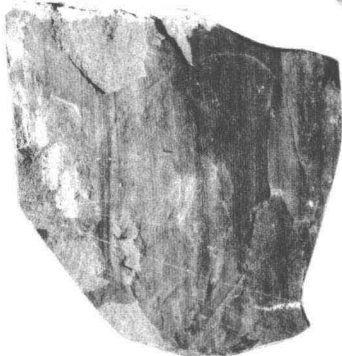
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3



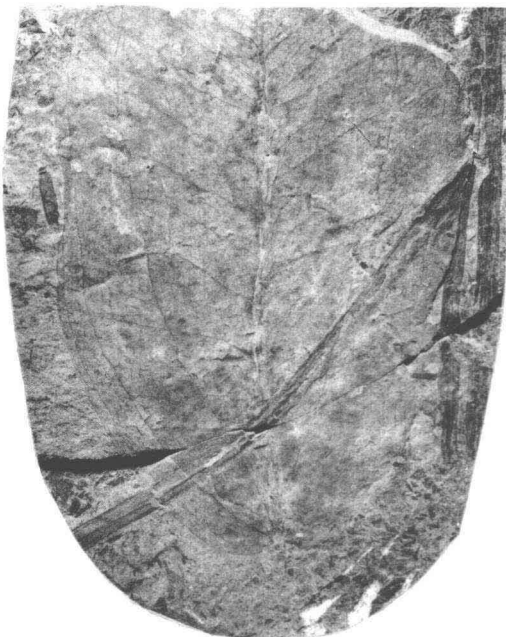
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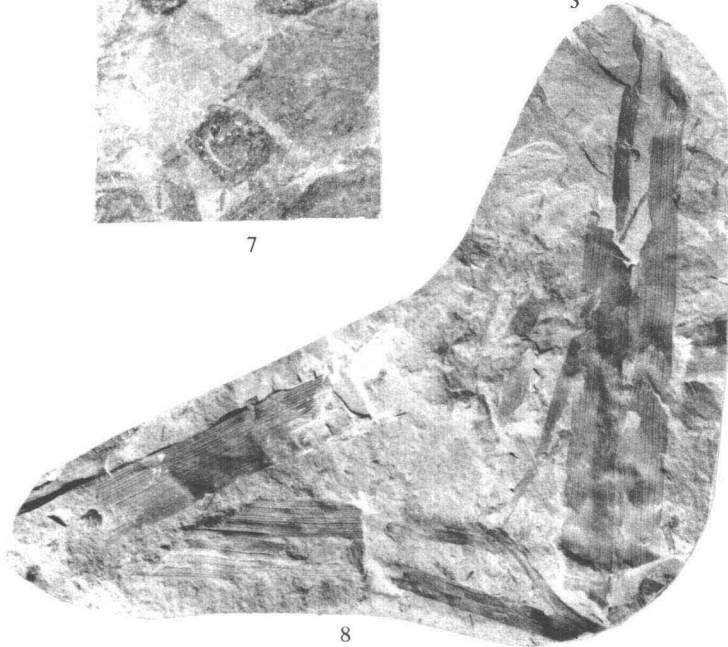
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ASTERIDAE, MONOCOTYLEDONES

