Paleogene Floras From the Gulf of Alaska Region

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By JACK A. WOLFE

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CONTENTS

ILLUSTRATIONS

[Plates follow index]

TABLES

PALEOGENE FLORAS FROM THE GULF OF ALASKA REGION

By Jack A. Wolfe

ABSTRACT

Numerous collections of fossil plants from the Gulf of Alaska region were obtained from rocks that are well dated by marine mollusks. The mollusks indicate that the oldest possible age for the lowest plant assemblage is middle Eocene (Domengine) and that the youngest possible age for the highest Paleogene plant assemblage is middle Oligocene (Lincoln).

Paleobotanical correlations indicate that the lowest plant assemblage is of late middle Eocene (early Ravenian) age, and the highest plant assemblage is of early Oligocene (Kummerian) age. A new provincial stage—the Angoonian— is proposed, based on assemblages from rocks in southeastern Alaska. The Angoonian is thought to be of late Oligocene (early Blakeley) age. Only one stratigraphically isolated assemblage from the Gulf of Alaska region has been recognized as of Angoonian age. The biostratigraphy of the Gulf of Alaska region and of other regions in Alaska indicates that the Seldovian, Homerian, and Clamgulchian Stages are probably entirely of Neogene age.

The early Ravenian assemblages represent Paratropical Rain forest (that is, similar to vegetation of a region bordering the Tropical Rain forest); this conclusion is based on the physiognomic analysis of foliage. The most diverse families represented are Menispermaceae and Icacinaceae, which are accompanied by palms, Annonaceae, Myristicaceae, Dipterocarpaceae, Barringtoniaceae, and Myrtaceae. A minor element is represented by broad-leaved deciduous plants. Middle Ravenian assemblage was somewhat cooler (subtropical), as indicated by foliar physiognomy, the fewer Tropical Rain forest elements, and the diversity of Lauraceae. The late Ravenian assemblage represents a temperate forest. The Kummerian assemblages were again dominated by Lauraceae, and the physiognomic characters of the foliage indicate that a subtropical forest was again represented.

The existence of a broad-leaved evergreen forest in Alaska, such as that of the early Ravenian, indicates that extended periods of darkness may not have existed at that time. The Alaskan Paleogene floras, as well as those from other regions, indicate that the earth's axis of rotation may not have had as great an inclination in the past.

The history of the development of the Arcto-Tertiary concept shows the fundamental lack of evidence for this concept. An alternative, more complex, concept is proposed for the development of the Mixed Mesophytic forest. Paleobotanical evidence indicates that tolerances of many genera have changed during the Tertiary. Many mixed mesophytic genera—particularly those that are today temperate outliers of basically tropical groups—may have had a wide distribution in the Paleogene Paratropical Rain and subtropical forests and have entered the warm temperate forests only during the later Paleogene or Neogene. Some mixed mesophytic groups seem to be of later Neogene origin and have been significant members of the warm temperate forests since that time. Other mixed mesophytic genera apparently were members of the Paratropical Rain forest only in the earliest Paleogene and became adapted to warm temperate climates by the late Eocene or perhaps even earlier. The Mixed Mesophytic forest may have developed independently in Eurasia and western North America.

In the discussion of the systematics of the Gulf of Alaska Ravenian and Kummerian assemblages, at least 160 species are represented, but the fragmentary nature or poor preservation of many does not allow a generic or familial assignment; 126 species are discussed and illustrated. They represent at least 45 families and 83 genera. Systematic revisions of some species in Paleogene floras in conterminous United States are made.

INTRODUCTION

Of all the Tertiary sequences at high northern latitudes, the Gulf of Alaska sequence is unique in having many plant localities in rock units that also contain numerous marine fossils. More significantly, some of the Gulf of Alaska floras of Eocene and early Oligocene age are the most northerly floras that can be definitely stated to be of that age. The significance of these floras, therefore, to floristic and vegetational history is apparent: do all these Eocene and early Oligocene floras represent a temperate, broad-leaved deciduous forest similar to that of the supposed Eocene-Oligocene Kenai Formation? If the concept of an Arcto-Tertiary Geoflora has validity, they must represent this type of vegetation. New collections of fossil plants from the Gulf of Alaska sequence, coupled with a considerable amount of new stratigraphic and molluscan data, allow a far better understanding of floristic and vegetational history in northern latitudes than has been possible before.

The Paleogene floras from the Gulf of Alaska section also have an important bearing on the ages of other Alaskan floras. Some paleontologists, adhering rigorously to the largely unsubstantiated concept of homotaxis, have questioned whether paleobotanical correlations can be made between floras separated by several degrees of latitude. The floras from the Gulf of Alaska section are, however, at approximately the same latitude as the floras from the Kenai Formation in the Cook Inlet basin, and geographically they are only about 240 km (160 mi) distant. Comparisons between the Gulf of Alaska and Kenai assemblages will, therefore, be unaffected by latitudinal zonation of vegetation and climate.

Fossil plants from the Gulf of Alaska sequence were first collected by U.S. Geological Survey field parties in the early 1900's, largely through the efforts of G. C. Martin and R. A. Tarr in the Katalla and Malaspina districts. Early analysis of these collections by F. H. Knowlton yielded conflicting results. Regarding the material from the Malaspina district, Knowlton stated (in Tarr, 1906, p. 63): "***none of the plants is referable to the Kenai, and, if the exigencies of the stratigraphy demand that they should be referred to the Pliocene, there is nothing to contradict it." The material from Berg Lake was considered by Knowlton (in Martin, 1908, p. 35) to be somewhat older: "So far as I am able to determine, this is not Kenai in age, but just what the age is I am uncertain. I should think it ought to be Miocene, but without an extensive comparison with known Miocene floras its exact position is in doubt." Another collection from the same unit as the Berg Lake collection was thought by Knowlton (in Martin, 1908, p. 35) to be considerably older; but we must keep in mind that the "Arctic Miocene" was considered by Knowlton to be of Eocene age. Knowlton stated: "These are well-known forms found in the so-called Arctic Miocene and indicate this age for the beds whence they came." Martin (1908, p. 40), however, who based his conclusions largely on the marine mollusks determined by W. H. Dall, stated: "There is no doubt that the entire sequence is Tertiary and post-Eocene ***."

Shortly after Knowlton's statements were published, Arthur Hollick undertook his studies of Alaskan Tertiary plants. The age of the unit carrying the Berg Lake flora, the Kushtaka Formation, was revised downward by Maddren (1914, p. 130): "The Kushtaka carries fossil plants, which the recent studies of Arthur Hollick have shown to be of Kenai age (Eocene)." In his final description of the Alaskan Tertiary plants, Hollick (1936) did not specifically discuss the age of the Gulf of Alaska plants, but considered that (p. 23) "***the general similarity of the Alaska Tertiary flora to that of the Eocene in the States proper would appear to be demonstrated***." Significantly, however, not 1 of the 12 species that Hollick (1936, p. 23) listed as occurring in the Alaskan Tertiary as being "characteristic of the Fort Union" were listed by Hollick as occurring in any of the Gulf of Alaska assemblages. P. S. Smith (in Hollick, 1936, p. 26) thus remarked concerning the Berg Lake section: "It seems reasonably certain, however, that the entire sequence *** is post-Eocene in age. ***it will be observed that the flora of the coal measures (Kushtaka formation) does not resemble the type Kenai flora, of upper Eocene age, but seems younger."

Chaney (1940) considered the Berg Lake flora to be of Eocene age, although he cited no new evidence in contradicting the age assignment based on the stratigraphic and molluscan evidence that was then available. Chaney's assignment of the Berg Lake flora to his group of "temperate" floras is likewise puzzling. Included in Hollick's determinations were genera such as *Piper, Mohrodendron, Magnolia, Cinnamomum, Persea, Malpoenna, Terminalia,* and *Semecarpus*—none of these genera are indicators of a temperate climate.

Mapping of the Gulf of Alaska Tertiary rocks was started by D. J. Miller in the 1940's and continued by George Plafker in the 1950's. Miller and his associates collected few fossil plants, but the mapping and the many collections of marine mollusks made by Miller and Plafker clarified the stratigraphy and revised the ages of most of the older plant localities. The stratigraphic interpretations adopted in this report are largely those of Miller (1957, 1961a, 1961b, 1961c), Plafker and Miller (1957), and Plafker (1967).

Geologic investigations by the petroleum industry in the 1960's has resulted in several new collections of fossil plants. In particular British Petroleum Company and Shell Oil Company have contributed significant collections.

The collections made by the petroleum industry in the early 1960's and the older collections partly described by Hollick formed the basis for preliminary discussions of the vegetational significance of the Paleogene assemblages from the Gulf of Alaska region (Wolfe, 1964, p. N6; 1966, p. B5). These assemblages were considered to indicate a subtropical climate. Wolfe and Hopkins (1967, p. 70–73) considered the then small mollusk-dated assemblages from the Kushtaka Formation to be of late Eocene age and to be subtropical to tropical because of the physiognomic characters of the leaves. The Tokun and Katalla assemblages were also thought to indicate a warm climate, although somewhat cooler than the Kushtaka.

The present report is based on the old and a few new collections made by U.S. Geological Survey geologists, collections submitted by petroleum companies, and new collections that I obtained in 1968. I particularly wish to thank the Humble Oil Company for providing logistic support during 1968; Drs. Willard Larson and Donald Gunn of Humble

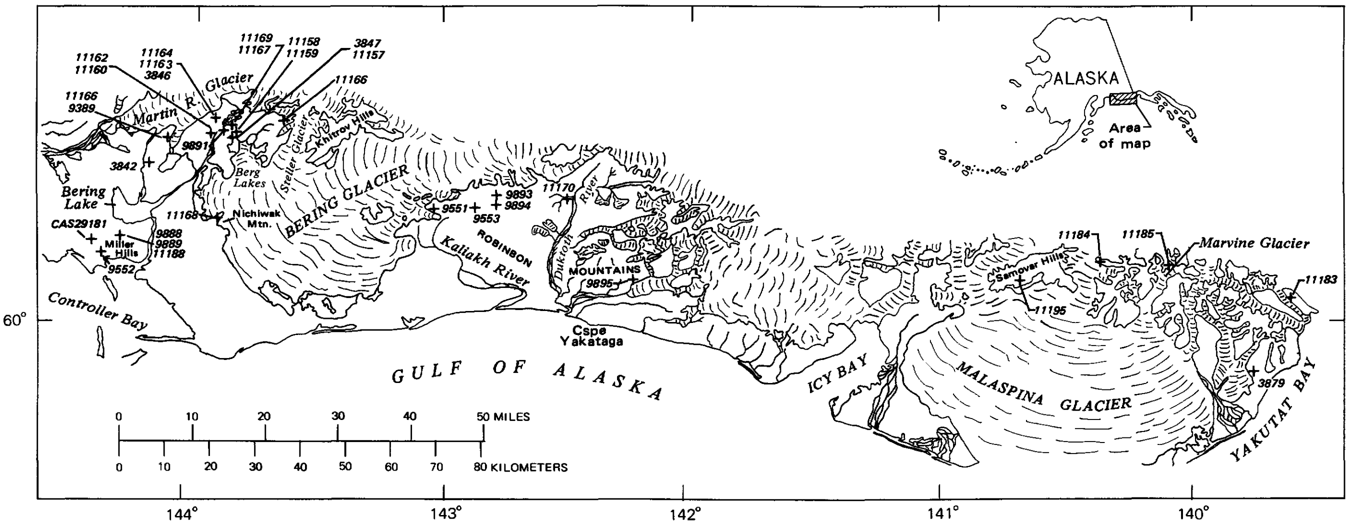

FIGURE 1.—Map of the Gulf of Alaska region. Numbers represent plant localities.

assisted in making most of the new collections.

The help of George Plafker has been invaluable in preparing the stratigraphic discussion. Dr. H. D. MacGinitie and H. E. Schorn, University of California (Berkeley), have given much time in discussing the floristic and vegetational implications of the Gulf of Alaska floras. Dr. Hugh H. Iltis, University of Wisconsin, has also made valuable suggestions about this report.

PHYSICAL STRATIGRAPHY

KATALLA DISTRICT

Most collections from the Gulf of Alaska Paleogene rocks were made north of latitude 60° N. (see fig. 1 and also fig. 6). The most complete sequence of Paleogene plant assemblages was obtained in the western part of the Gulf of Alaska region in the Katalla district. Miller (1961a) made a detailed geologic map of this district, and the map shown here (fig. 2) has been adapted from it. The structure in this district is complex, but, despite the small-scale thrusts and strongly folded beds (see pl. 1), the beds can generally be traced for a considerable distance, and hence a good section can be pieced together (fig. 3). The Paleogene formations in the Katalla district are, in ascending order, the Stillwater, Kushtaka, Tokun, and Katalla Formations.

Most collections from the Yakataga and Malaspina districts, which are east of the Katalla district, are small. The oldest named unit, the Kulthieth Formation, has yielded most of the Paleogene plants; the younger unit, the Poul Creek Formation, has yielded almost no plants. The paucity of material from the Yakataga and Malaspina districts reflects the limited time spent searching for localities and collecting.

STILLWATER AND KUSHTAKA FORMATIONS

The Stillwater Formation is thought to be the oldest of the four units under discussion, although it may in part be a lateral equivalent of the Kushtaka (MacNeil and others, 1961, p. 1803, 1807). In the section exposed northeast of Berg Lakes, in which Miller (1961a) did not differentiate between the two units, a series of sandstones and siltstones grades upward into a sequence of sandstone, siltstone, and coal. Although the lower part of the section contains a minor amount of very thin coal beds, it is lithologically similar to the type section of the Stillwater Formation and this lower part is here considered to be part of the Stillwater. Mollusks from USGS Cenozoic locality M3880 were determined by W. O. Addicott as:

Rimella? aff. *R. macilenta* White
Brachiodontes cowlitzensis (Weaver and Palmer)
Pitar cf. *P. californianus* (Conrad)

Addicott (written commun., Oct. 10, 1968) assigns a middle or late Eocene age to these mollusks. The beds from which the mollusks were obtained grade westward into the coal-bearing Kushtaka Formation and are approximately on strike with plant localities 3847, 11157, 11158, and 11159.[1] Plants from localities 11158 and 11159 are approximately 300 feet stratigraphically above locality M3880, and plants

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[1] All fossil plant localities cited by number in this report are in the U.S. Geological Survey Paleobotany catalog, Washington, D.C. See also p. 93.

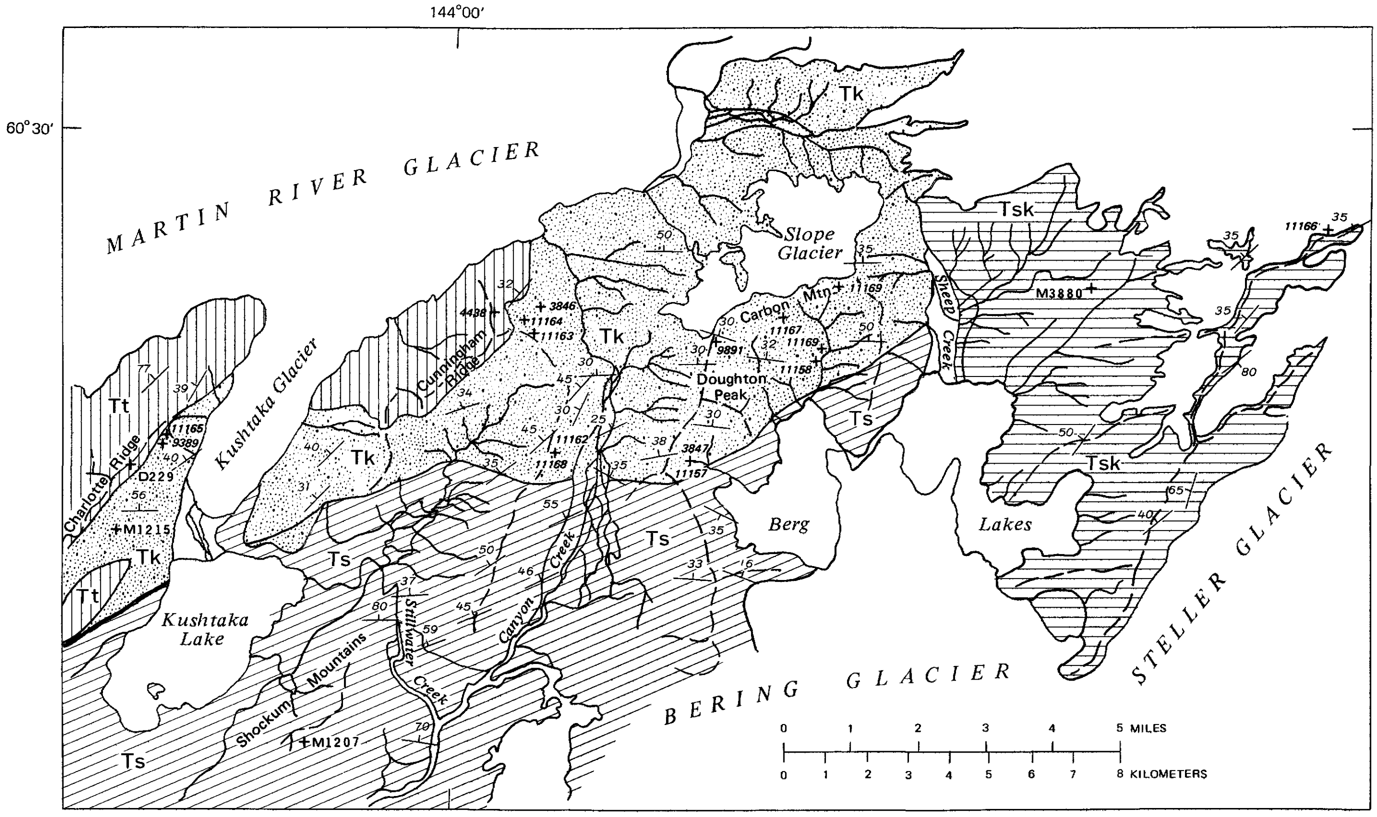

FIGURE 2.—Generalized geologic map of part of the Katalla district. Geology after Miller (1961a). Dashed lines represent ridge crests Ts, Stillwater Formation; Tk, Kushtaka Formation; Tsk, Stillwater and Kushtaka Formations, undivided; Tt, Tokun Formation. Numbers in italic indicate plant localities; numbers in roman type indicate mollusk localities.

from locality 11166 are approximately 2,000 feet higher than locality M3880. The beds at locality 11166 can be traced in a rough manner westward along the flank of Carbon Mountain; these beds appear to crop out on the south nose of Carbon Mountain about 1,500-2,000 feet stratigraphically higher than localities 3847 and 11157, and about 3,000 feet statigraphically lower than plant locality 11167 on Carbon Mountain. Localities 9891 and 11169 are about 50 and 300 feet, respectively, higher than locality 11167.

Assuming that no major structure is concealed by the alluvium in Canyon Creek, plant localities 11160-11162 are estimated to be about 100-1,000 feet higher than locality 11159. Locality 11160, which is in the coal-bearing Kushtaka Formation, is near the base of that unit as mapped by Miller (1961a). Southward the Kushtaka grades stratigraphically downward into the Stillwater Formation. In the Shockum Mountains, mollusks from the Stillwater occur at a locality that is probably more than 1,000 feet below locality 11160, that is, probably a few hundred feet below locality 3847. The mollusks (USGS Cenozoic loc. M1207) include, according to F. S. MacNeil (written commun., Oct. 24, 1961):

Whitneyella cf. *W. sinuata aragoensis* Turner
Tivelina cf. *T. vaderensis* (Dickerson)
Eometrix cf. *E. martini* (Dickerson)

MacNeil assigns a possible middle Eocene age to these mollusks. Collections of mollusks elsewhere in the Stillwater Formation are also regarded by MacNeil and others (1961, p. 1803) as of middle Eocene age. Thus the Stillwater Formation and possibly the lowest part of the overlying Kushtaka Formation exposed in the vicinity of Berg Lakes as well as the Berg Lake fossil plant assemblages (locs. 3847, 11157, 11158, 11159) are, on molluscan and stratigraphic evidence, considered to be of late middle or early late Eocene age. The Canyon Creek assemblages (locs. 11160, 11161, 11162) would also be of middle or late Eocene age.

In the upper part of the Kushtaka Formation that is exposed along Canyon Creek, plants were collected from two localities (locs. 3846 and 11164). These localities are approximately 700 and 1,000 feet, respectively, stratigraphically above locality 11162. A few hundred feet higher than locality 11164 in the basal part of the Tokun Formation that rests conformably on the Kushtaka, marine mollusks have been collected. USGS Cenozoic locality 4438

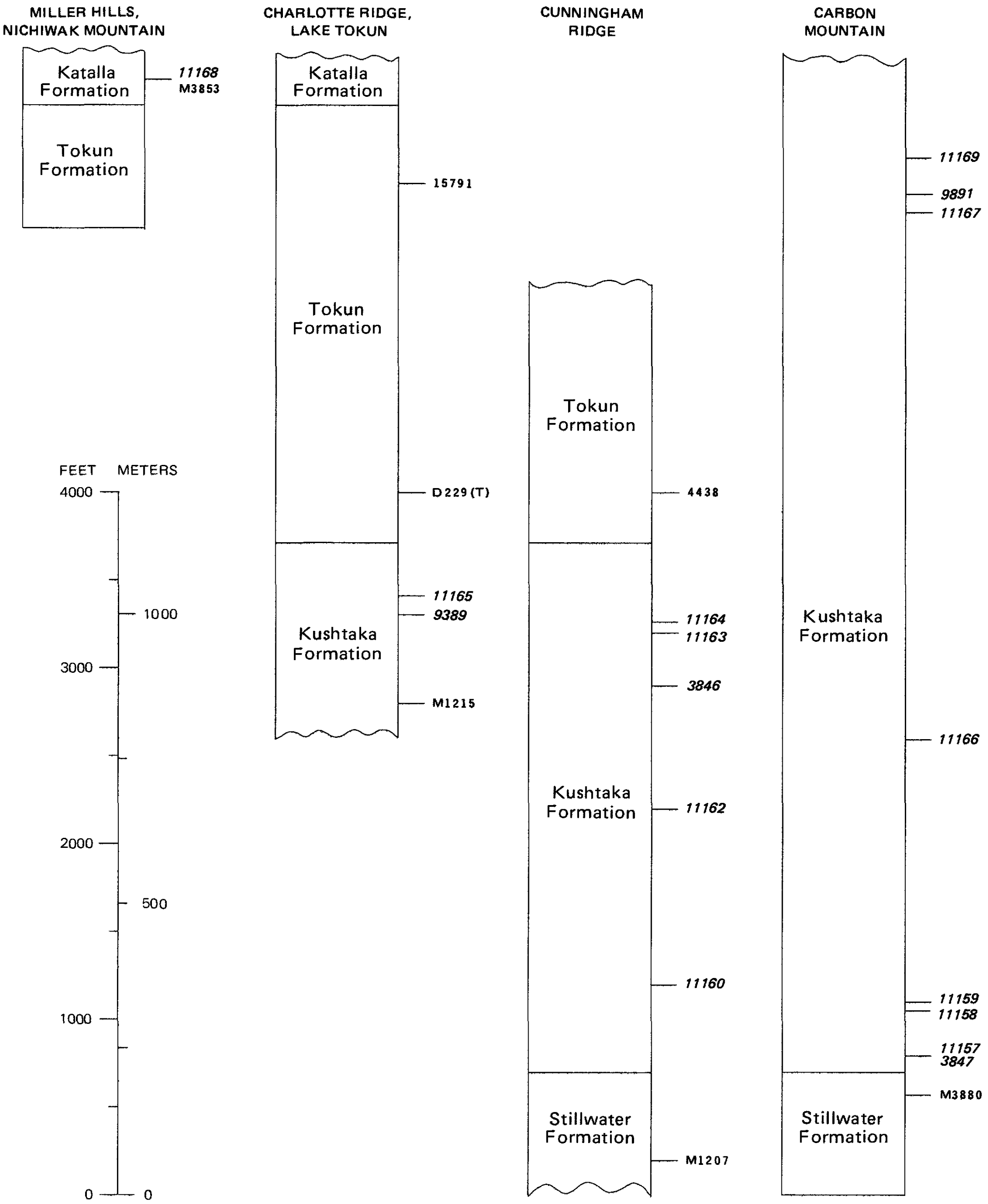

FIGURE 3.—Stratigraphic position of fossil plant localities in the Katalla district. Numbers in italic are plant localities; numbers in roman are mollusk localities.

contains *Perse washingtonensis* (Weaver); this species indicates a Tejon (late Eocene) age (W. O. Addicott, oral commun., September 1968).

To the west on Charlotte Ridge, the basal Tokun has yielded a larger and better preserved fauna. The determinations by L. G. Hertlein (written commun., July 30, 1954) include:

Acila cf. *A. decisa* (Conrad)
Gari cf. *G. columbiana* (Weaver and Palmer)
Pitar cf. *P. californianus* Conrad
Ficopsis cf. *F. cowlitzensis* Weaver
Molopophorus cf. *M. tejonensis* Dickerson
Turritella uvasana Conrad
Whitneyella cf. *W. coosensis* Turner
Whitneyella cf. *W. sinuata* Gabb var.

This fauna, according to Hertlein, is comparable to that of the Tejon "stage" of Weaver and others (1944) and is of late Eocene age. Localities 9389 and 11165 are in the uppermost Kushtaka on Charlotte Ridge; these localities are about 300 feet below the

Kushtaka-Tokun contact. Farther to the southwest on Charlotte Ridge, beds in the Kushtaka that are several hundred feet below the Kushtaka-Tokun contact have yielded mollusks. The mollusks from this locality (USGS Cenozoic loc. M1215, determined by F. S. MacNeil, written commun., Oct. 24, 1961) include:

Whitneyella cf. *W. washingtoniana* (Weaver)
Acila cf. *A. decisa* (Conrad)

MacNeil considers these fossils to be probably late Eocene (Tejon) in age. The upper part of the Kushtaka Formation on Charlotte Ridge and the Charlotte Ridge fossil plant assemblage are thus of probable late Eocene age.

The Tokun Formation is not present on Carbon Mountain, where the Kushtaka Formation attains its greatest thickness. Beds that appear to be equivalent on stratigraphic evidence to the uppermost Kushtaka on Charlotte Ridge are overlain by a few thousand feet of coal-bearing rocks also assignable to the Kushtaka on lithologic evidence. Thus at least part of the Kushtaka on Carbon Mountain is probably equivalent in age to the Tokun Formation. The total age range of the Tokun Formation is thought on molluscan evidence to be late Eocene through earliest Oligocene, that is, of Tejon and Keasey age (MacNeil and others, 1961, p. 1803). The part of the Tokun that is of Keasey age is indicated by the occurrence at USGS Cenozoic locality 15791 of a crushed specimen determined as *Turcicula columbiana* Dall? by H. E. Vokes (written commun., Jan. 12, 1946). The Kushtaka Formation on Carbon Mountain could therefore be at least a young as Keasey age.

KATALLA FORMATION

The Katalla Formation seems to be entirely marine, and thus only a few localities have yielded plant megafossils. Most of these localities are in the Split Creek Sandstone Member, the basal member of the Katalla. The largest assemblage of plants from the Split Creek was obtained at locality 11168 at the base of Nichiwak Mountain. A few mollusks were also collected at this locality, including a gastropod that is closely related to *Bruclarkia fulleri* Durham, an index to the lower part of the "Lincoln Stage" (W. O. Addicott, written commun., Oct. 10, 1968). Elsewhere in the district, the Split Creek Sandstone Member has yielded a large fauna that Vokes (written commun., Jan. 12, 1946) considered to be the same age as the *Molopophorus stephensoni* zone, that is, earliest "Lincoln" (earliest middle Oligocene). Some of the more significant localities are listed at the end of this report. A few specimens of leaves have been obtained from the Split Creek at localities 3705, 9552, 9988, 9989, and 9990.

The overlying Basin Creek Member of the Katalla has yielded a very few leaves at localities 11181 and California Academy of Sciences locality 29181. The Basin Creek is obviously at least in part of "Lincoln" age, that is, middle Oligocene. This age is confirmed by the molluscan fauna, which, according to H. E. Vokes (written commun., Jan. 12, 1946) is not younger than the *Molopophorus gabbi* zone; F. S. MacNeil (oral commun., October 1968), however, considers part of the Basin Creek Member to be as young as early Blakeley (late Oligocene).

A summary of the probable age assignments of the plant-bearing formations of the Katalla district is shown later (p. 21).

YAKATAGA AND MALASPINA DISTRICTS

The geology of these districts has been discussed primarily by Miller (1957, 1961b, 1961c), Plafker and Miller (1957), and Plafker (1967). Three units have yielded plant megafossils: the Kulthieth, Poul Creek, and Yakataga Formations. An unnamed marine siltstone and sandstone sequence in the northwestern part of the Malaspina district is thought to intertongue with, and in part underlie, the Kulthieth Formation (Plafker and Miller, 1957; MacNeil and others, 1961); marine megafossils indicate a probable middle Eocene age for this sequence (MacNeil and others, 1961).

KULTHIETH FORMATION

One of the most extensive sections of the Kulthieth Formation is exposed on a ridge north of a stream that heads near the headwaters of the Kulthieth River in T. 18 S., R. 17 E., and flows southeast into the Duktoth River; the upper part of this section is described in detail by Miller (1957, sec. no. 2). The only determinable marine mollusks thus far collected from this section came from the upper part of the Kulthieth Formation. USGS Cenozoic locality M1368 has yielded a fauna including *Acila shumardi* (Dall) and *Boreoscala condoni* cf. subsp. *oregonense* Dall. (These were determined by F. S. MacNeil, written commun., Dec. 20, 1961.) The *Acila* clearly places this part of the Kulthieth in the Lincoln "stage" (middle Oligocene); the species of *Boreoscala* is restricted to the two lower zones of the Lincoln "stage" and the subspecies to the lowest zone (*Molopophorus stephensoni*) according to Durham (1944). The only determinable plants from this section of the Kulthieth are from locality 11170. The precise stratigraphic separation of this plant locality from the mollusk locality is unknown; Miller and

Plafker measured approximately 9,000 feet of Kulthieth in this section, but the plant locality is farther downstream than the base of Miller and Plafker's measured section. Miller (1957) considered that the rocks in the area of locality 11170 "*** may be largely or entirely represented in the lower part of the section described above." This uncertainty is caused by the complex folding and faulting in this area. In any case it appears highly probable that locality 11170 is at least several thousand feet stratigraphically below the lower middle Oligocene mollusks and is in the lower part of the Kulthieth Formation in this area (George Plafker, oral commun., October 1968). Elsewhere in the Yakataga District the upper part of the Kulthieth has yielded mollusks of late Eocene (Tejon) age (Miller, 1957). The available evidence thus indicates that the flora from locality 11170 is no younger than late Eocene and presumably could be older. The locality, however, that has yielded the most diagnostic mollusks—*Turritella uvasana* Conrad and *Ficopsis cowlitzensis* Weaver—is USGS Cenozoic locality 16859; it is in a complexly folded and faulted area, and the relationship of this locality to the Kulthieth-Poul Creek boundary has not been determined.

Several small collections of plants have been made from the upper part of the Kulthieth Formation in the eastern drainage of the Kulthieth River. Localities 9893 and 9894 are situated at about the Kulthieth-Poul Creek boundary as mapped by Miller (1961b).

One small collection from locality 9551 in the Hanna Lake area is of uncertain stratigraphic position, but D. J. Miller (written commun., May 25, 1961) considered the locality probably to be from the upper part of the Kulthieth.

In the Malaspina district, an isolated outcrop of coal-bearing rocks on Esker Stream (locality 3879), which flows into Yakutat Bay, has provided a small collection of plants. Although assigned with reasonable certainty to the Kulthieth Formation (Plafker and Miller, 1957), the stratigraphic position of this locality within the Kulthieth is unknown.

In the Samovar Hills, the Kulthieth Formation has yielded marine mollusks of Tejon (late Eocene) age (Plafker and Miller, 1957). Stratigraphically well below the mollusk-bearing beds, plants were obtained at locality 11195; these plants are thus no younger than late Eocene and could be of middle Eocene age.

POUL CREEK FORMATION

Plant megafossils from the Poul Creek Formation have been found in only two localities. One locality (9895) is apparently in the lower part of Poul Creek, but no mollusks have been collected from the area. Elsewhere in the region, the Poul Creek contains mollusks of late Lincoln (late middle Oligocene) through late Blakeley (early Miocene) age. Presumably, therefore, the plants from locality 9895 are of late middle or late Oligocene age.

At another locality (11182), a single fruit of *Juglans* was found; the fruit was collected as float, but, according to D. J. Miller (written commun., May 25, 1961), the specimen probably came from the Poul Creek Formation.

YAKATAGA FORMATION

Although plant fossils are reported to be abundant at several localities in the Yakataga Formation, only two collections have been made. Locality 11184 from the upper part of the Yakataga in the Pinnacle Hills is in a sequence that MacNeil (1967) considers to be of late Miocene and Pliocene age, based on the occurrence of certain pectinids. The second assemblage of plants in the Yakataga (loc. 11183) is assigned to the Yakataga Formation because the plant-bearing sequence is similar lithologically to the marine Yakataga elsewhere (George Plafker, oral commun., October 1968). This sequence, which occurs as a sliver along a fault, cannot be definitely related by field relationships to the Tertiary section elsewhere in the Malaspina district.

UNKNOWN UNIT

Plant fossils from locality 11185 and locality 11183 came from slivers along the same fault. No marine fossils occur in this sequence of rocks; although these rocks were considered to be part of the Kulthieth Formation by Stonely (1967), paleozoological or lithologic evidence for the designation is lacking.

BIOSTRATIGRAPHY

INTRODUCTION

The general age assignments of all but one of the Paleogene plant localities are known with reasonable certainty because of their stratigraphic relationships to marine mollusk localities (see preceding section). Some of the localities, however, are not precisely placed stratigraphically relative to mollusk localities, and their age assignments must be based on the contained plant fossils. The close stratigraphic relationships between some of the mollusk and plant localities allows a better understanding of the age relationships between the marine megafossil chronology and some of the Paleogene stages that are based on studies of the plant assemblages of the

Puget Group in Washington (Wolfe, 1968).

Four stages and seven substages were recognized in the Puget Group. The Franklinian—the lowest stage—is thought to be equivalent to at least part of the Capay "stage" (lower Eocene), and the Fultonian is probably equivalent to at least part of the Domengine "stage" (middle Eocene). No assemblages yet known from the Gulf of Alaska section seem to contain species definitely indicative of these two stages. The two upper stages—the Ravenian and the Kummerian—are represented, however.

The time equivalents of the early Ravenian in terms of the Pacific Coast marine megafossil chronology are not certain. The overlying middle Ravenian is almost certainly equivalent in part to the upper Eocene (Tejon "stage"), as indicated by the occurrence of two assemblages. One assemblage—discussed later—on Charlotte Ridge is bracketed stratigraphically by mollusks of Tejon age and is also overlain by several hundred feet of strata that are also of Tejon age. This evidence indicates that the middle Ravenian assemblage falls low in the Tejon "stage." A second assemblage—that from the McIntosh Formation of Washington—is less certainly dated. The foraminifera from the McIntosh indicate that the formation ranges in age from the middle Eocene (later part of the Domengine "stage") to the early part of the late Eocene (Snavely and others, 1958). The assemblage of plants from the McIntosh occurs in strata that cannot be certainly related to the foraminiferal localities, but the plant-bearing beds are in the upper part of the formation and are thus presumably of early late Eocene age. If, therefore, the overlying middle Ravenian is of early late Eocene age, the early Ravenian is most probably of late middle Eocene age, that is, equivalent to part of the Domengine "stage."

In the Puget Group of Washington, early Ravenian assemblages were obtained from the lower part of the Tukwila Formation. Late Fultonian assemblages, however, were obtained from the underlying Tiger Mountain Formation, which, in turn overlies the marine Raging River Formation of middle Eocene age (Wolfe, 1968). The lower Ravenian, therefore, is most probably the time equivalent of the late Domengine and possibly also the "Transition stage;" this stage represents a poorly known interval between the definite middle and definite late Eocene.

Except for some minor departures of no more than zone magnitude, the epochal and subepochal boundaries of the marine megafossil geochronology on the Pacific Coast will be used in this report. The assignments of the various plant stages in terms of epochs is thus: early Ravenian = late middle Eocene, middle Ravenian = early late Eocene, late Ravenian = latest Eocene, and Kummerian = early Oligocene. The two departures from the marine megafossil geochronology are that the lower part of the Keasey "stage" is here considered to be of earliest Oligocene rather than latest Eocene age, and the lowest zone (*Molopophorus stephensoni*) zone of the Lincoln "stage" is here considered to be of latest early rather than earliest middle Oligocene age. Some molluscan workers, in fact, place the *M. stephensoni* zone in the early rather than the middle Oligocene (H. E. Vokes, written commun., Jan. 12, 1946).

The placement of the Eocene-Oligocene boundary in this report is purely arbitrary, but it is in approximate agreement with both mammalian and marine molluscan paleontologists working in western North America (Wolfe, 1968). Foraminiferal workers, however, would probably place this boundary much higher and include all equivalents of the Kummerian Stage and the Keasey and Lincoln "stages" in the late Eocene. At least part of the problem in these differing correlations stems from the lack of agreement on the placement of the Eocene-Oligocene boundary in Europe.

The Oligocene-Miocene boundary adopted in this report is also purely arbitrary, and it is placed between the Angoonian and Seldovian Stages. The Angoonian includes assemblages that are known to be equivalent in age to the uppermost zone of the Lincoln "stage," the lower zone of the Blakeley "stage," and probably to the upper zone of the Blakeley, that is, latest middle Oligocene through earliest Miocene in the marine megafossil geochronology. Foraminiferal workers would place the boundary even higher than I have, whereas mammalian paleontologists would place the boundary lower. As with other epochal boundaries, the varying correlations are in large part a result of lack of agreement in varying paleontological disciplines on the placement of the epochal boundaries in Europe.

RAVENIAN STAGE

LOWER RAVENIAN

In the original definition of the Ravenian Stage (Wolfe, 1968, p. 7), the stage was subdivided into two informal substages, but here (p. 9, 12) a threefold subdivision is proposed. The Kushtaka floras from locality 3846 and stratigraphically lower horizons are no younger than early Ravenian, as indicated by the occurrence at that locality of *Cyathea inequaliteralis* (*Hemitelea pinnata* MacG.) and of *Goweria* *dilleri* at locality 3847 (see table 1). Locality 3846 has also yielded specimens of *Litseaphyllum presamarensis*, a species that has previously been found in the middle Ravenian and younger rocks. Its presence thus indicates that this locality is probably near the border between the lower and middle Ravenian.

Whether some localities low in the Kushtaka near Berg Lake are of late Fultonian or early Ravenian age is not clear. *Alangium bergensis* is apparently restricted to the upper Fultonian in the Puget Group, but thus far it has been found only at a single locality there. *Zizyphus alaskanus*, on the other hand, is known at two lower Ravenian localities, and *Litseaphyllum similis* is known in the Puget Group from early Ravenian and younger beds. In addition, both *Goweria alaskana* and *Phytocrene acutissima* are known from the early Ravenian Steel's Crossing assemblage of the Puget Group. The Alaskan *Illicium* is not sufficiently well preserved to be certain of the identification, but it appears to represent the same species that is known from the Steel's Crossing assemblage. The bulk of the evidence indicates that the lower part of the Kushtaka Formation exposed at Berg Lakes is probably of early Ravenian (late middle Eocene) age.

The lower part of the Kulthieth Formation exposed near Duktoth River is also probably early Ravenian. Several species (see table 1) are common to the assemblage from locality 11170 and the assemblages from the lower part of the Kushtaka. In addition *Anemia gunni* is known to range from the Franklinian through the early Ravenian in the Puget Group (called *A. eocenica* Berr. by Wolfe, 1968, p. 5, 8). *Phytocrene sordida* has been previously recorded from beds of Franklinian age in California (MacGinitie, 1941), but the prior fossil record of leaves of Icacinaceae is so meager that little age significance can be attached to this occurrence in Alaska at this time. The age assignment of the Duktoth River assemblage to the early Ravenian is consistent with the stratigraphic and molluscan evidence (see p. 7); this evidence indicates a late Domengine or early Tejon age for the lower part of the Kulthieth Formation elsewhere in the Yakataga district.

The beds on Esker Stream have yielded only a few species. The occurrence there of *Allantodiopsis pugetensis* indicates an age no younger than middle Ravenian. The occurrences of *Celastrus comparabilis* and *Goweria alaskana* also indicate a probable correlation with the lower Kushtaka, that is, an early Ravenian age.

The lower part of the Kulthieth Formation in the Samovar Hills has yielded a well-preserved although small collection of plants (loc. 11195). The species include *Platycarya pseudobrauni* and *Parashorea pseudogoldiana,* indicating a probable early Ravenian age.

MIDDLE RAVENIAN

The original biostratigraphic definition of the upper Ravenian was based on assemblages from the middle and upper part of the type section and from an assemblage (Cashman) from what was thought, on stratigraphic evidence, to be in beds equivalent to the lower part of the type section. Almost all the species known from the type section of the upper Ravenian are also known from the Cashman assemblage, but the Cashman is much richer than the assemblages from the type section. The situation prevails despite the fact that five localities in the type section were extensively collected. I originally thought that the depauperate nature of the assemblages of the type section might be the result of a peculiar ecology, but that this ecology prevailed during a period in which about 1,000 feet of coal-bearing rocks were deposited appears improbable. Lithologic evidence does not indicate that the environment of deposition during the deposition of that part of the Puget Group was significantly different from the environment during the rest of Puget time.

An analysis of other late Eocene to early Oligocene assemblages—many whose ages are radiometrically dated—shows that the approximate time of deposition of the middle and upper parts of the upper Ravenian represents an interval considerably cooler than somewhat older and younger periods (Wolfe and Obradovich, unpublished data). In the Green River Canyon section of the Puget Group, standard biostratigraphic procedures have not indicated a distinct separation of the lower from the middle and upper parts of the type Ravenian, although many species have their highest occurrence in the middle Ravenian. I nevertheless propose that, because of the strong vegetational difference and because of the informal nature of the substages, the lower part of the type section of the former upper Ravenian (Wolfe, 1960, fig. 2) be considered a distinct substage, the middle Ravenian. The only known assemblage in the Puget Group that represents this interval is the Cashman (loc. 9731). The term "upper Ravenian" as herein used now refers to beds equivalent in age to the beds in the Green River Canyon section from about the Gem-Harris horizon to the base of the Kummer sandstone bed (see Wolfe, 1968, fig. 2).

Four assemblages in the Kushtaka Formation

TABLE 1.—*Checklist of megafossil plants from the Kushtaka. Katalla, Kulthieth, and Poul Creek Formations*

Species	Kushtaka Formation																Katalla Formation						Kulthieth Formation								Poul Creek Formation
	3847	11157	11158	11159	11160	11162	11166	3846	11163	11164	9389	11165	3842	11167	9891	11169	11168	9552	9888	9889	11188	CAS 29181	11170	3879	11195	9551	9553	9893	9894	11189	9895
Anemia gunni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Anemia? sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lygodium larsoni	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyathea inequilateralis	-	-	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Allantodiopsis pugetensis	-	-	-	X	-	-	X	X	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Dryopteris alaskana	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Woodwardia sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glyptostrobus sp	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Phoenicites sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Palmacites sp	-	-	-	-	X	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Palmae, gen. indet	-	-	X	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-
Populus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carya cashmanensis	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Engelhardtia sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juglans sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platycarya pseudobrauni	X	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-
Pterocarya pugetensis	-	-	-	-	-	-	-	-	-	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus cuprovallis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus martini	-	-	X	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Alnus scotti	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Alnus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Betula sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryophyllum pugetensis	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fagus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Girroniera sp	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Girroniera sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Ulmus sp	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetracentron piperoides	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Magnolia reticulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Illicium sp	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anamirta milleri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Calkinsia plafkeri	-	X	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus sp	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diploclisia sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Hypserpa? sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limacia stenophylla	-	-	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paratinomiscium conditionalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-
Pycnarrhena sp	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Knema sp	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myristica sp	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cananga sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Dasymaschalon? sp	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cinnamomophyllum kushtakensis	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cinnamomophyllum latum	X	X	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Litseaphyllum carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
katallaensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	X	-	-	-	-	-
praelingue	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
presamarensis	-	X	-	-	-	-	-	X	-	-	-	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
presanguinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
schorni	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
similis	-	X	-	-	-	-	-	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Litseaphyllum sp	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	X	-	-	-	-	-	-	-	-
sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 1.—*Checklist of megafossil plants from the Kushtaka, Katalla, Kulthieth, and Poul Creek Formations*—Continued

Species	Kushtaka Formation																Katalla Formation						Kulthieth Formation								Poul Creek Formation
	3847	11157	11158	11159	11160	11162	11166	3846	11163	11164	9389	11165	3842	11167	9891	11169	11168	9552	9888	9889	11188	CAS 29181	11170	3879	11195	9551	9553	9893	9894	11189	9895
Litseaphyllum sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corylopsis sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liquidambar? sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eucommia sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platanus comstocki	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X
Prunus nevadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorbus carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caesalpinites sp	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caesalpinites sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Toona sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Euodia alaskana	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Luvunga spatiosa	X	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melanorrhoea alaskana	X	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Rhus cf. *R. mixta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Anacardiaceae, genus?	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ilex carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Celastrus comparabilis	X	-	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
Goweria alaskana	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goweria dilleri	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paleophytocrene elytraeformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Phytocrene acutissima	X	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phytocrene sordida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-
Pyrenacantha sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Stemonurus alaskanus	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhamnus sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sageretia sp	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zizyphus alaskanus	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Allophylus duktothensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Allophylus wilsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	X	-	-	-	-	-	X	X	-	-	-	-
Allophylus sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sapindus? sp	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Meliosma duktothensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-
Meliosma kushtakensis	-	-	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vitis sp	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Tilia carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plafkeria sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saurauia sp	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Theaceae, genus?	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parashorea psuedogoldiana	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Barringtonia sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Kandelia wangi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Alangium bergensis	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alangium sp	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eugenia sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Eugenia? sp	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastixia irregularis	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clethra sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Clerodendrum sp	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helmskioldia speiri?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macclintockia pugetensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	X	-	X	X	X	-	-	-	X	X	X	X	X	X
Macclintockia sp	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicotylophyllum carbonensis	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicotylophyllum kummerensis	-	-	-	-	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

represent the middle Ravenian. Assemblages from localities 3842, 9389, 11164, and 11165 come from about the same stratigraphic interval, a short distance below the base of the Tokun Formation. Critical elements in these assemblages are *Allantodiopsis pugetensis*, which has its latest occurrence in the middle Ravenian, and *Dicotylophyllum kummerensis*, which has its earliest occurrence in the middle Ravenian, and *Calkinsia ravenensis*, *Carya cashmanensis*, *Pterocarya pugetensis*, and *Dryophyllum pugetensis*, which indicate either a middle or late Ravenian age. The vegetational analysis (p. 32) indicates a vegetation type more like that of the middle than the upper Ravenian. The conclusion that this part of the Kushtaka is of middle Ravenian age is also supported by the close stratigraphic superposition of locality 11164 to a lower Ravenian locality (loc. 3846). The fact that several thousand feet of Tejon age rocks (lower part of the Tokun Formation) overlies the part of the Kushtaka containing the middle Ravenian assemblages indicates that the middle Ravenian is probably not of latest Eocene age.

UPPER RAVENIAN

The only Alaskan assemblage thought to be of late Ravenian age is that from locality 11167 in the Kushtaka Formation on Carbon Ridge. The placement of this locality in the Ravenian rather than in the overlying Kummerian is not totally satisfactory. The depauperate flora from this locality has only one species in common with the equally depauperate flora of the type section of the upper Ravenian. Two species, however, from locality 11167 are also known in upland floras in conterminous United States: *Alnus cuprovallis* and *Prunus axelrodi*. These species are known in floras such as the Republic and Copper Basin, whose radiometric ages are about 40 million years (Wolfe and Obradovich, unpublished data), that is, probable latest Eocene. *Pterocarya pugetensis* has a known upper limit in the upper Ravenian of the Puget Group. The striking vegetational and floristic difference between the assemblage from locality 11167 and the overlying Kummerian assemblages from localities 9891 and 11168, moreover, indicates that the assemblage from locality 11167 probably represents a pre-Kummerian stage.

KUMMERIAN STAGE

Macclintockia pugetensis was originally thought to be restricted to the upper part of the Kummerian Stage and was one of the primary reasons for distinguishing an upper from a lower Kummerian substage. Additional collections, for example from the basal part of the Keasey Formation, indicate that this species ranges from the base of the Keasey through the *Molopophorus stephensoni* zone of the Lincoln "stage." The distinction, therefore, between a lower and upper Kummerian substage is of dubious value, and I will here not consider allocation of individual assemblages to substages within the Kummerian.

The rocks in which the Comstock flora of Oregon occurs were assigned by me (1968) to the upper Ravenian. This assignment probably was an error. The occurrence of *Calkinsia dilleri* and *Allantodiopsis pugetensis* was the only basis for placing the Comstock flora in the Ravenian. As now defined, the typical Ravenian species of *Calkinsia* is *C. plafkeri*, which is morphologically intermediate between the Fultonia *C. pugetensis* and *C. dilleri*. The specimen I determined as *Allantodiopsis* is sufficiently fragmentary to question the determination. The Comstock assemblage, therefore, could equally well be referred to the Kummerian, an age indicated by the interpretation of the *C. dilleri* lineage (see p. 63). The base of the Kummerian is thus considered to be approximately equivalent to the base of the Keasey "stage," and the top of the Kummerian is thought to be approximately equivalent to the boundary between the *Molopophorus stephensoni* and *M. gabbi* zones of the Lincoln "stage."

Kummerian assemblages are known from three rock units in the Gulf of Alaska region: the Kushtaka, Katalla, and Kulthieth Formations. In the Kushtaka, Kummerian assemblages are confined to the upper part of the formation exposed on Carbon Ridge. Locality 9891, which is 50 to 100 feet stratigraphically above the late Ravenian locality 11168, contains *Macclintockia pugetensis, Platanus comstocki* (= *Platanus* n. sp. of Wolfe, 1968), and *Dicotylophyllum kummerensis*?; this assemblage is typical of the Kummerian. Presumably the assemblage from locality 11169, which is 300 feet stratigraphically higher than 9891, is also of Kummerian age, although, except for *Tetracentron piperoides*, species diagnostic of a Kummerian as opposed to an immediately post-Kummerian (Goshen) age are lacking.

The largest assemblage from the Katalla Formation was obtained from the basal member—the Split Creek Sandstone Member—at the base of Nichiwak Mountain. Nothing in the assemblage, which includes *Macclintockia pugetensis*, conflicts with the molluscan age assignment to the *Molopophorus stephensoni* zone of the Lincoln "stage." The other plant assemblages from the Split Creek Sandstone Member have also yielded *Macclintockia pugetensis*. The two small collections from an unknown part of the overlying Basin Creek Member also contain *Macclintockia pugetensis*, thus indicating a Kummerian age. As noted previously, MacNeil considers the Basin Creek to range from medial Lincoln to early Blakeley in age, whereas Vokes considered his material from the Basin Creek to be little, if any, younger than the Split Creek. Because *Macclintockia* is elsewhere not known in beds of medial or possibly later Lincoln age, I am inclined to agree with Vokes that the Basin Creek Member—or at least that part that has yielded the plants—is probably no younger than the *Molopophorus gabbi* zone and possibly no younger than the *M. stephensoni* zone.

Several localities in the upper part of the Kulthieth Formation have yielded small collections of plants. Reference to the checklist (table 1) shows that *Macclintockia pugetensis* occurs in most of those collections, and hence the upper part of the Kulthieth is referred to the Kummerian. This age accords with that of the marine megafossils collected from the upper Kulthieth.

POST-KUMMERIAN ROCKS

No Paleogene floras of post-Kummerian age from the Gulf of Alaska section are yet known in association with marine mollusks. Locality 11185 from rocks near Marvine Glacier in the Malaspina district has furnished a small assemblage that is clearly distinct from the floras previously discussed. The three species present in the Marvine Glacier assemblage are: *Metasequoia* cf. *M. glyptostroboides* Hu and Cheng, *Alnus evidens* (Holl.) Wolfe, and *Cercidiphyllum crenatum* (Ung.) R. W. Br. Although the rocks from which this assemblage has been obtained have been assigned to the Kulthieth Formation (Stonely, 1967), they could equally well be the nonmarine equivalent of the Poul Creek Formation (George Plafker, oral commun., October 1968). None of the species and only one genus (*Alnus*) are known in the Alaskan Ravenian and Kummerian floras. The species of *Alnus* is particularly significant because it is characteristic of the pre-Seldovian (lowermost) part of the Kenai Group; this part of the Kenai is here (p. 13) termed Angoonian. The only locality where this species is known in a definite relationship to the marine geochronology is on Sitkinak Island; there *A. evidens* is known from a locality in nonmarine beds that conformably underlie marine beds of late Blakeley (early Miocene) age (Wolfe and others, 1966, p. A17; Moore, 1969). A reasonable assumption is that the plant-bearing beds on Sitkinak Island and at Marvine Glacier are probably of early Blakeley (late Oligocene) age. This age assignment indicates that the beds at Marvine Glacier are nonmarine equivalents of some part of the Poul Creek Formation.

Three localities from the Gulf of Alaska section have yielded leaves of Neogene age. Locality 11183 occurs in nonmarine beds that, on structural and lithologic evidence, may be equivalent to the Yakataga Formation (George Plafker, oral commun., October 1968). The Yakataga Formation ranges in age from early middle Miocene through early Pleistocene (Plafker, 1967). The leaves represent *Osmunda* sp., *Glyptostrobus* sp., *Metasequoia* cf. *M. glyptostroboides* Hu and Cheng, *Alnus cappsi* (Holl.) Wolfe, and *Acer* sp. The species of *Alnus* is characteristic of the Seldovian Stage of the Kenai Group; the species is also known from the Unga Conglomerate, which contains mollusks of middle Miocene age (Burk, 1965, p. 213). The leaves from locality 11183 indicate, therefore, that the enclosing beds are no younger than middle Miocene and hence are probably from the lower part of the Yakataga Formation.

Locality 11184 from the Yakataga Formation in the Pinnacle Hills is close stratigraphically to marine mollusks of late Miocene age (F. S. McCoy, oral commun., April 1968). The one species present is *Carpinus cobbi* Wolfe, a species characteristic of the Homerian Stage of the Kenai Group (Wolfe and others, 1966).

Locality 11186 occurs in marine rocks in Lituya Bay. The age of the mollusks in the same part of the section is considered to be late (but not latest) Miocene (F. S. McCoy, oral commun., April 1968). The single leaf represents a species of *Fagus*; this genus is not known to be present in the Homerian and is thought to have become extinct in Alaska by the end of the Seldovian Stage. The genus is represented, however, in pollen floras from late Miocene rocks on the Queen Charlotte Islands (Martin and Rouse, 1966). The genus, therefore, may have persisted somewhat longer in southeastern Alaska than in other areas of the State, or the Seldovian Stage may include some rocks that in the marine megafossil geochronology are of early late Miocene age.

ANGOONIAN STAGE

Fundamental to understanding Alaskan Tertiary stratigraphy is a knowledge of the type of assemblage represented in the Tsadaka Formation and the lowest part of the Kenai Formation in the

Cook Inlet region. This type of assemblage is widespread in Alaska; for example, such an assemblage is known from St. Lawrence Island, various areas of the Alaska Range, the Copper River basin, the Matanuska Valley, the Cook Inlet Basin, the Alaska Peninsula, the Trinity Islands, the Malaspina district, Admiralty Island, and Kuiu Island. This type of assemblage is typically composed of *Alnus evidens* and *Metasequoia*, although other species, for example, *Cercidiphyllum crenatum*, are represented at many localities. This assemblage was at one time considered to be "lower(?) Seldovian" (Wolfe and others, 1966), but it has since been excluded from the Seldovian Stage (Wahrhaftig and others, 1969).

The only known Alaskan section in which the Tsadaka type of assemblage is represented and in which recognizably older and younger assemblages are also represented is in the Kootznahoo Formation on Admiralty Island near the town of Angoon. Geologic mapping (Lathram and others, 1965) and my own observations made during 10 days of fieldwork in 1961 indicate that the section is continuous, although some repetition is present because of faults of small displacement. This section, therefore, is desirable as a type section for a stage characterized by the Tsadaka type of assemblage.

DEFINITION

The Angoonian Stage is here designated a provincial stage for plant-bearing rocks the same as those in the type area in the Kootznahoo Formation. The type section is designated as that part of the Kootznahoo Formation exposed from the north shore of Long Island (see figs. 4 and 5) south (and stratigraphically upward) to the rocks exposed on the south side of the small island near the west end of Kanalku Bay. Thus the rocks at localities 9826 and 9829 are definitely excluded from the Angoonian.

FLORA

The assemblage in the type section of the Angoonian has not been completely studied; some items remain indetermined. The species thus far determined include:

Gymnospermae
  Ginkgoales
    Ginkgoaceae
      Ginkgo sp.
  Coniferales
    Taxodiaceae
      Metasequoia cf. *M. glyptostroboides* Hu and Cheng
Angiospermae
  Dicotyledonae
    Juglandales
      Juglandaceae
        Juglans magnifica Knowl.
        Pterocarya orientalis (MacG.) Wolfe
    Fagales
      Betulaceae
        Alnus evidens (Holl.) Wolfe
        Alnus carpinoides Lesq.
      Fagaceae
        Fagus sp.
    Rosales
      Hamamelidaceae
        Fothergilla sp.
    Sapindales
      Aceraceae
        Acer aff. *A. glabroides* R. W. Br.
    Rhamnales
      Vitaceae
        Vitis atwoodi Holl.
        Vitis rotundifolia Newb.
    Malvales
      Tiliaceae
        Tilia aspera (Newb.) LaM.
        Plafkeria obliquifolia (Chan.) Wolfe
      Sterculiaceae
        Firmiana alaskana (Newb.) Wolfe

The Angoonian assemblage is floristically and physiognomically temperate. None of the species and only a few of the genera are known in Kummerian assemblages in Alaska or in the Pacific Northwest. Most Angoonian species are related to extant species that live in temperate climates. The percentage of species that have entire-margined leaves is 12.

AGE

Only one Alaskan Angoonian assemblage is known that is definitely stratigraphically related to marine rocks. On Sitkinak Island of the Trinity Islands, *Alnus evidens*, *Cercidiphyllum crenatum*, and *Metasequoia* occur in nonmarine beds a few feet below a conformable contact with overlying marine beds; the marine beds are considered to be of late Blakeley (earliest Miocene) age. Presumably the plants could be as young as earliest Miocene, but I assume that a late Oligocene age is more probable. In conterminous United States, Angoonian assemblages include the Bridge Creek and Willamette floras. Both have radiometric ages of about 31 million years (Evernden and James, 1964); in the mammalian chronology this is presumably very early in the middle Oligocene. The Willamette

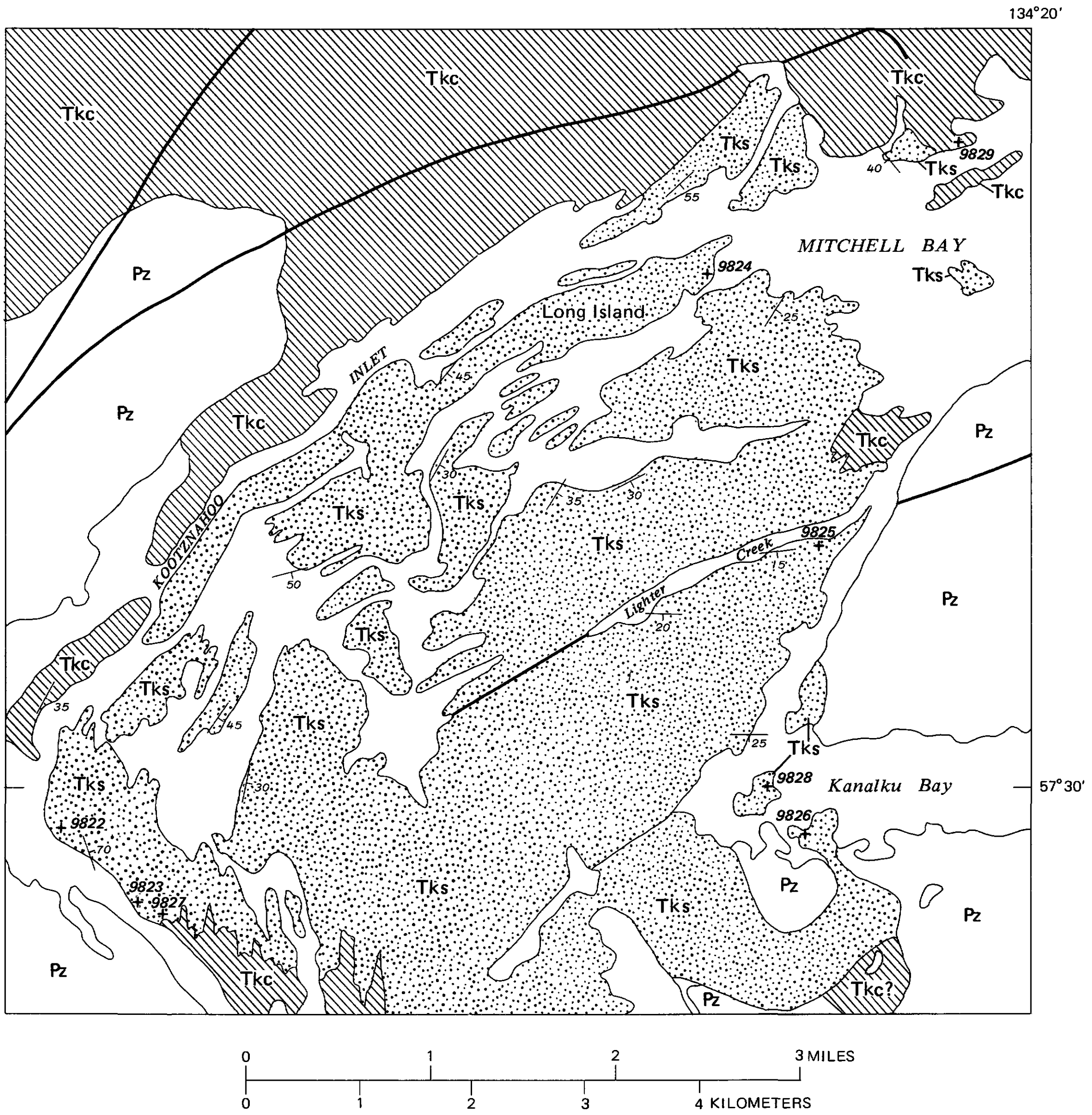

FIGURE 4.—Generalized geologic map of part of Kootznahoo Inlet. Data from Lathram and others (1965). Tks (stippled) is the sandstone and shale part of the Kootznahoo Formation; Tkc (lined) is the conglomeratic part; Pz, undifferentiated Paleozoic rocks. Heavy lines represent faults. Crosses represent plant localities.

flora, however, comes from beds that overlie with an angular unconformity nonmarine beds that have yielded the Goshen flora; in turn, the Goshen beds conformably overlie marine beds containing mollusks of the *Molopophorus gabbi* zone (middle Lincoln) (Vokes and others, 1951). These data indicate that probably the late Oligocene of the marine megafossil workers is equivalent, at least in part, to the middle Oligocene of the vertebrate workers. The Angoonian is considered to be of late Oligocene age.

The assemblage from locality 9829, which is stratigraphically below the type section of the Angoonian, includes: *Cercidiphyllum crenatum*, *Cinnamomophyllum eocernua*, *Platanus macginitiei*, *Fagus oregona*, and *Plafkeria thomae*. The *Platanus* is the same elaborately toothed species known in the Goshen, Sweet Home, and Scio floras, all of which are of middle Oligocene (middle and upper Lincoln) age. Neither the *Cinnamomophyllum* nor the *Fagus* are known in conterminous United States in beds younger than middle Oligocene, whereas the *Cercidiphyllum* and *Plafkeria* make their first appearance in beds of middle Oligocene age. The assemblage from locality 9826, which is stratigraphically above the type section of the

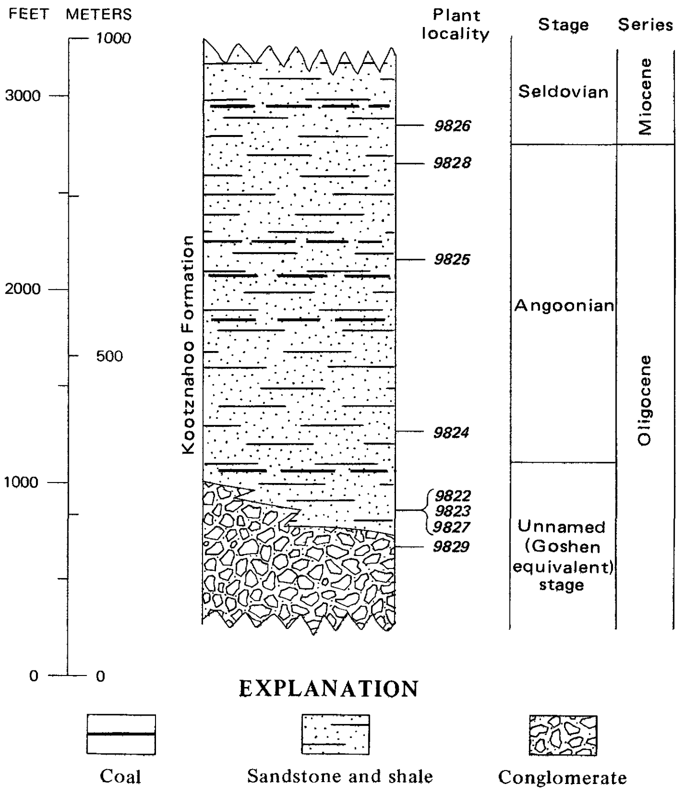

FIGURE 5.—Generalized stratigraphic section of the type area of the Angoonian Stage.

Angoonian, includes *Alnus barnesi*, *Fagus antipofi*, *Quercus furuhjelmi*. This assemblage is thus of Seldovian age, which is considered to early and middle Miocene.

The Angoonian Stage is separated from the older Kummerian by an unnamed stage containing a distinctive assemblage. In Washington, for example, assemblages similar to the Lower Kootznahoo and the Goshen occur in beds demonstrably younger than the Kummerian (Wolfe, 1961, 1968). As yet I know of no section in which assemblages of the Goshen and Lower Kootznahoo type occur above Kummerian and below Angoonian assemblages, and thus no stage is here proposed for the Goshen equivalents.

CORRELATION OF SOME OTHER ALASKAN FLORAS

Chaney (1967, p. 228) has recently expressed the opinion that the lower floras—the Seldovian and the Tsadaka equivalents, here (p. 13) termed Angoonian—of the Kenai Group are of early Oligocene age. His opinion is based on a proposed correlation of the Kenai floras to floras purported to be of early Oligocene age from the Port Moller region of the Alaska Peninsula. Chaney further considers these Port Moller assemblages to be "The nearest occurrence of well-dated marine sediments with associated plant-bearing beds ***" to the Cook Inlet basin. The Port Moller assemblages are, of course, over 300 miles farther from the Cook Inlet basin than are the assemblages from the Katalla district (see fig. 6). Some of the Port Moller assemblages discussed by Chaney, moreover, had been previously shown (Wolfe in Burk, 1965, p. 233-236) to be mostly of Paleocene age, which conforms with evidence from the middle Eocene Foraminifera from the overlying beds (Burk, 1965, p. 113). Chaney also included in his correlation plant assemblages that, on marine molluscan evidence, are of middle Miocene age and some that are of late Miocene or early Pliocene age (Burk, 1965, p. 116-117). The stratigraphic basis for Chaney's proposed correlations is, therefore, invalid.

The paleobotanical basis for Chaney's (1967) correlations, if valid, would be of considerable significance, therefore, I will examine the evidence he cites in detail. Chaney (1967, p. 228) lists 12 genera that he thinks are common to the Seldovian and to his purported early Oligocene assemblages from the Alaska Peninsula. Chaney also states that many of the Seldovian species (although he does not list them) have been recorded by Hollick (1936, p. 18-19) from Chaney's purported early Oligocene of the Alaska Peninsula. The following are the genera listed by Chaney:

Acer.—Hollick (1936) listed two species of *Acer* in three assemblages from the Port Moller region. One of these two species, *Acer arcticum* Heer, is based on specimens (Hollick, 1936, pl. 78, figs. 7, 8) that have the large rounded teeth and venation pattern of *Dicotylophyllum richardsoni* (Heer) Wolfe. The other species listed by Hollick is *Acer trilobatum productum* (A. Br.) Heer. Hollick, however, was following Knowlton (1894) in this listing, and I concur with Hollick (1936, p. 135) that "*** the identification does not appear to be altogether conclusive***." Note that none of the six species of *Acer* listed in the Seldovian (Wolfe and others, 1966, p. A16) was listed in the Port Moller assemblages by Hollick. Also significant is the fact that the Port Moller localities that produced the purported species of *Acer* are now considered to be of Paleocene or early Eocene age (Burk, 1965).

Alnus.—Hollick (1936) listed a single species of *Alnus* as occurring in the Port Moller assemblages. This material of this species, *A. kefersteini* (Goepp.) Heer, has the numerous craspedodrome marginal tertiary veins extending from the basal secondary veins and the rounded to sharp teeth separated by arcuate sinuses of *Grewiopsis ariculaecordatus*

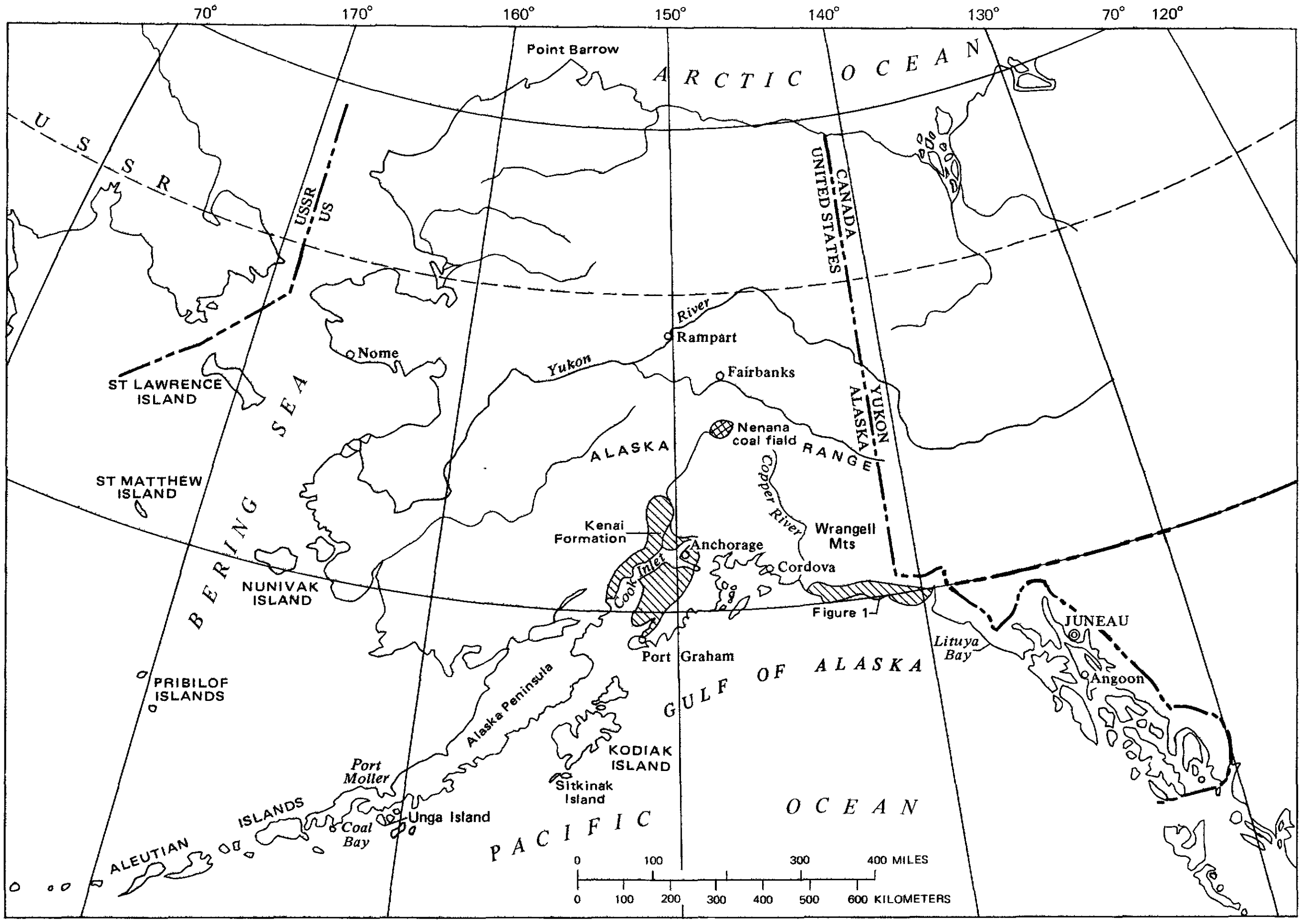

FIGURE 6.—Map of Alaska showing location of some fossil plant assemblages.

(Holl.) Wolfe. Apparently Chaney (1967, p. 225, footnote) thinks that, because I (1966) transferred certain of Hollick's material described as *Corylus* to *Alnus*, all of Hollick's material of *Corylus* was so transferred. However, I specifically stated in the synonymies that only part of Hollick's material was to be considered as *Alnus*. Not one of the six Seldovian species of *Alnus* has ever been listed in the Port Moller assemblages, except for *A. barnesi*, which is thought to occur in the mollusk-dated middle Miocene beds on Unga Island (Burk, 1965, p. 236).

Betula.—Hollick listed two species of *Betula* from the Port Moller assemblages, neither of which was listed (Wolfe and others, 1966, p. A16) in the Seldovian. I am unsure of the familial relationship of the specimens on which the citations are based; at least one of the specimens could be betulaceous, but it is not the Seldovian species *B. sublutea* Tan. and Suz.

Cercidiphyllum.—Hollick did not list any *Cercidiphyllum* from the Port Moller assemblages. Presumably Chaney is accepting Brown's transfer of certain of Hollick's material listed as *Populus arctica* Heer, *P. amblyrnhynca* Ward, and *P. richardsoni* Heer to *Cercidiphyllum arcticum* (Heer) R. W. Br. However, these specimens have since been transferred to *Cocculus flabella* (Newb.) Wolfe and *Dicotylophyllum richardsoni* (Wolfe, 1966, p. B9). None of Hollick's material from the Port Moller region represents *Cercidiphyllum*, and none of it has ever been referred to the Seldovian species *C. crenatum* (Ung.) R. W. Br.

Fraxinus.—A single lamina from the Port Moller region was described as *F. herendeenensis* by Knowlton (1894), a species that has never been recorded from a Seldovian assemblage. The specimen has tertiary veins that are closely spaced, unbranching, oriented at right angles to the secondary veins, and of uniform strength throughout their course; in *Fraxinus*, the tertiary veins are typically widely spaced, branching, oriented obliquely to the secondaries, and conspicuously thin. The Port Moller specimen, therefore, cannot represent *Fraxinus*. The specimen has the same intercostal tertiary venation pattern and sharp (almost spinose) teeth as in *Dicotylophyllum flexuosa* (Newb.) Wolfe, and it probably represents that species.

Ginkgo.—The same species of *Ginkgo* apparently occurs in both the Port Moller and Seldovian assemblages; it also occurs in Paleocene assemblages in the Cook Inlet Region (Wolfe, 1966, p. B2). *Ginkgo* is of almost no stratigraphic value for Tertiary correlations, considering that apparently the same species ranges throughout the Tertiary (Tralau, 1968).

Glyptostrobus.—The material of *Glyptostrobus* from the Port Moller region listed by Hollick is that from Chignik Bay, which I (Wolfe and others, 1966, p. A9) consider to be *G. nordenskioldi* (Heer) R. W. Br.; this species has also been listed (Wolfe and others, 1966, p. A9) from the Paleocene of the Cook Inlet region. The Seldovian *Glyptostrobus* is considered to represent *G. europaeus* (Brong.) Heer (Wolfe, 1966, p. B3). Again, the Port Moller and Seldovian species are distinct and represent a genus that ranges throughout the Cenozoic.

Metasequoia.—The material from the Port Moller assemblages listed by Hollick as *Sequoia langsdorfii* (Brong.) Heer was transferred by Chaney (1951) to *Metasequoia occidentalis* (Newb.) Chaney. Note, however, that, although the Port Moller material is accepted as that species (Wolfe and others, 1966, p. A9), the Seldovian material is thought to represent *M. glyptostroboides* Hu and Cheng (Wolfe, 1966, p. B3).

Nyssa.—The only *Nyssa* from the Port Moller region is based on the unfigured fructifications referred by Lesquereux (1883) to *N. arctica* Heer from middle Miocene marine beds on Unga Island. This material was later transferred by Brown (1939) to *Cercidiphyllum arcticum*. Similar, if not conspecific, fructifications have also been collected at one of the localities near Port Graham; the taxonomic status of this type of fructification is, however, in need of considerable clarification (Chandler, 1961, 1964). In any case, there is no basis for the occurrence of *Nyssa* in the Port Moller assemblages.

Populus.—All species of *Populus* listed by Hollick from the Port Moller region have been transferred to *Cercidiphyllum arcticum* by Brown (1939) and thence to other genera by me (1966). There is no taxonomic basis for Chaney's listing of *Populus* in the Port Moller assemblages.

Pterocarya.—No species of *Pterocarya* was listed by Hollick from the Port Moller assemblages. Chaney is apparently assuming that because I transferred Heer's Port Graham species *Juglans nigella* to *Pterocarya* (a species never recorded in the Port Moller assemblages), all the material listed as *Juglans* by either Hollick or Heer should also be so transferred. This assumption is clearly unfounded. The other species of *Juglans* that Heer described from Port Graham was transferred to *Salix* (Wolfe, 1966, p. B14). Note also that some material attributed to both *Juglans* and *Pterocarya* by Hollick (1936) was transferred to *Dicotylophyllum flexuosa* (Newb.) Wolfe (Wolfe, 1966, p. B11). There is no taxonomic basis for the inclusion of *Pterocarya* in the Port Moller assemblages of Hollick.

Salix.—This genus was recorded from two localities by Hollick (1936) from the Port Moller region. *Salix minuta* Knowlt. from locality 539 is based on a single crudely illustrated specimen; the preservation of the specimen does not warrant generic assignment. The only valid determination of *Salix* made by Hollick (1936) from the Port Moller assemblages is based on the material from locality 5182. This material represents two Homerian species, *S. alaskana* Holl. and *S. kachemakensis* Wolfe, and, as has been previously pointed out (Burk, 1965, p. 235; Wolfe and others, 1966, p. A20), this material is from beds that are of Miocene or Pliocene age based on physical stratigraphy and marine mollusks.

Of the 12 genera considered to be common to the Seldovian and Port Moller assemblages (Chaney, 1967), four either have never been recorded from the Port Moller region—*Pterocarya*—or are based on material that has been formally transferred to other genera—*Populus*, *Cercidiphyllum*, and *Nyssa*. The citations of three other genera—*Acer*, *Alnus*, and *Fraxinus*—are either based on fragmentary material or can be demonstrated to belong to other genera; another genus—*Betula*—may be represented in the Port Moller assemblages, but clearly not by the Seldovian species. At least 3 of the 52 Seldovian genera are represented in Port Moller assemblages, but in two instances by different and distinct species and in the third instance by a stratigraphically insignificant *Ginkgo*. The twelfth genus—*Salix*—is represented in the Port Moller assemblages but at one locality of probable Miocene or Pliocene age. Of Chaney's "many" species in common to both the Seldovian and the Paleogene Port Moller assemblages, only one—the *Ginkgo*—can be demonstrated to be valid. The paleobotanical and stratigraphic basis for Chaney's correlation of the Kenai floras is, therefore, invalid.

Axelrod (1966a, 1966b, 1968) has discussed his interpretations of the altitudinal factor in interpreting ages of Tertiary floras. His conclusion, which is similar to that reached by Chaney (1936, 1940), is that in the Eocene, altitude had a pronounced effect on floristic and vegetational zonation. Thus Axelrod considers the vegetation during the late Eocene of coastal southern Alaska to be temperate; this temperate forest type ascended altitudinally southward, so that in Nevada it was at an approximate altitude of 3,500 feet. Axelrod further considers the lowland and more coastal late Eocene vegetation of the Pacific Northwest to be warm temperate (1966b, p. 42) or subtropical (1966b, p. 25). The Alaskan flora that Axelrod considers to be isochronous to the temperate late Eocene Copper Basin assemblage from Nevada is the Port Graham; the Port Graham assemblage, however, is of early Seldovian (early Miocene) age (MacGinitie, 1962, p. 88; Wolfe and others, 1966; p. 20 of this report). As will be shown later, the marginally tropical lowland assemblages of late middle Eocene age from the Pacific Northwest represent the same fundamental vegetational type as do isochronous assemblages in Alaska. I conclude, therefore, that Axelrod's interpretations are fundamentally invalid; as will be discussed later, during the Eocene there were major climatic fluctuations, and comparisons of two assemblages—one from a cool interval (Copper Basin) and a second from a warm interval (Steel's Crossing)—can be highly misleading in regard to both latitudinal and altitudinal zonation of ancient vegetation.

Altitude can, of course, be a factor in the interpretation of age of a given assemblage of fossil plants, particularly if assemblages are assigned to an age largely or totally on their vegetational aspect rather than on their specific composition. Vegetationally an upland assemblage of latest Eocene age can be similar to a lowland assemblage of Pliocene age, that is, both represent conifer or broad-leaved deciduous forest. The specific composition of these two assemblages—if the fossils are examined in detail—will, however, be totally different (or nearly so). Floristic comparisons, on the other hand, between two assemblages of the same age in the same region typically indicate that some short-ranging species are common to the assemblages irrespective of altitude. This phenomenon stems in part from the fact that some species participate in two or more vegetational types; this is particularly true of fluviatile and lacustrine species that dominate fossil assemblages. During the late Miocene, for example, broad-leaved deciduous forest occupied the lowlands of the Pacific Northwest while conifer forest occupied the uplands (Wolfe, 1969). Despite the strong physiognomic difference between these two vegetational types, species such as *Salix hesperia* (Knowlt.) Cond., *Quercus deflexiloba* H. V. Sm., and *Platanus dissecta* Lesq., are known in both lowland and upland assemblages. The occurrence of these species together in a fossil assemblage—no matter what the altitude—indicates a late Miocene age.

The Angoonian and Seldovian assemblages are not similar to any assemblages from definite Kulthieth, Kushtaka, or Katalla Formations. Families well represented in, and that dominate, the Kenai and Tsadaka assemblages are either poorly represented in the Gulf of Alaska early and middle Ravenian and Kummerian floras—for example, Betulaceae—or are not represented by any taxa—for example, Salicaceae, Rosaceae, and Aceraceae. Conversely, the dominant families of the early and middle Ravenian and Kummerian floras are either sparsely represented—for example, Menispermaceae—or are not represented—for example, Lauraceae and Icacinaceae—in the Kenai and Tsadaka floras. The species of the late Ravenian are distinct from those of the Angoonian and Seldovian. There can be no reasonable doubt that the Kenai and Tsadaka floras are younger than the Kummerian floras. Both depositional areas were at low altitudes, and the fact that the Gulf of Alaska and Cook Inlet basins are at the same latitude (in part, the Kenai localities are south of the Gulf of Alaska sequence) indicates that the differences between the Kenai and Ravenian-Kummerian floras are due to a difference in age.

An apparent disagreement exists over the age of fossil plants collected from the Tolstoi Formation of Burk (1965) at Coal Bay on the Alaska Peninsula. I considered the plants to be of late Oligocene or early to middle Miocene, that is, of Seldovian age as this term was used by Wolfe, Hopkins, and Leopold (1966, p. 1, 17). The marine molluscan fauna is probably of early Blakeley (late Oligocene) or possibly of latest Lincoln (latest middle Oligocene) age (MacNeil in Burk, 1965, p. 222). Rothwell, however, considered the Foraminifera to be mostly of earliest Oligocene age (in Burk, 1965, p. 230). It should be pointed out, however, that Rothwell's usage of early Oligocene is such that he considers part of the Astoria Formation to be of late Oligocene age (this is considered by molluscan workers to be of middle Miocene age; see Moore, 1963) and the lower part of the Blakeley "stage" and the Lincoln "stage" to be of early

Oligocene age (W. T. Rothwell, oral commun., March 27, 1964). The discrepancy, if such exists, between the Foraminifera, on the one hand, and the plants and mollusks, on the other, is not significant. In this report I am accepting the geochronology of the marine mollusks in regard to the placement of epochal boundaries in the western North American Tertiary, and thus the Coal Bay plant assemblages are considered to be most probably of late Oligocene (Angoonian) age. The Coal Bay assemblages include *Salix*, *Fagus*, *Cocculus*, and *Acer*; these assemblages probably represent broad-leaved deciduous forest. As elsewhere in Alaska, broad-leaved deciduous forests of Oligocene age were present only in the later part of that epoch.

A flora of the same composition as the Angoonian and Seldovian floras does indeed occur in the Gulf of Alaska sequence; the Angoonian assemblage occurs in rocks of questionable stratigraphic position that could, on lithologic and structural grounds, be considered the nonmarine equivalent of the Poul Creek Formation. This interpretation would indicate a latest Lincoln or Blakeley age for the Angoonian assemblage. As noted previously (p. 14) a Blakely age is indicated for another Angoonian assemblage on Sitkinak Island. The available evidence indicates that the Angoonian assemblages are of early Blakeley (late Oligocene) age.

The Seldovian assemblages are younger than the Angoonian assemblages. This relationship can be demonstrated both in the Alaska Range section (Wahrhafting and others, 1969) and the Kootznahoo section. If the Angoonian assemblage is of late Oligocene age, as the evidence thus far indicates, then the Seldovian floras are probably early Miocene at the oldest. Only two small assemblages of Seldovian type occur in marine sections in which ages independent of the plants can be obtained. One is the sequence on Unga Island off the Alaska Peninsula. The Unga Conglomerate Member of the Bear Lake Formation of Burk (1965) contains marine mollusks thought to be of middle Miocene age. The plants from this member include *Alnus barnesi* Wolfe, a characteristic Seldovian species. The microfossil flora contains *Carya*, *Pterocarya*, *Fagus*, *Quercus*, *Ulmus*, *Liquidambar*, and *Tilia*; this assemblage is similar to those reported from the type section of the Seldovian (Wolfe and others, 1966). The plant megafossil assemblage from possible Yakataga Formation (locality 11183) includes *Alnus cappsi* (Holl.) Wolfe, a species that is known in Alaska only from the Seldovian. The increasing body of evidence from marine fossils substantiates the conclusion of Wolfe, Hopkins, and Leopold (1966, p. A17) that the Seldovian Stage is of early and middle Miocene age and clearly is not consistent with Chaney's opinion that the Seldovian Stage is of early Oligocene age or Axelrod's opinion that the Seldovian assemblage from Port Graham is of Eocene age.

The provisional age assignment of the Homerian Stage to the upper Miocene was based both on specific composition and the small assemblage from Herendeen Bay on the Alaska Peninsula. The Herendeen Bay assemblage contains characteristic Homerian species of *Salix* and is closely related stratigraphically to mollusks of late Miocene or early Pliocene age (Burk, 1965). A pollen assemblage similar to that of the type section of the Homerian has been obtained from rocks in the Bering Sea that contain marine diatoms referable to the later half of the Miocene (Hopkins and others, 1969). A small collection of leaves from the Yakataga Formation exposed in the Pinnacle Hills contains the characteristic Homerian *Carpinus cobbi* Wolfe, and the marine megafossils from the same section indicate a late Miocene age (F. S. McCoy, oral commun., April 1968). Again, the increasing body of independent evidence indicates a probable late Miocene age for the Homerian and contradicts Chaney's (1967) opinion that the Homerian is of middle Oligocene age. The general epochal assignments of the Seldovian, Homerian, and Clamgulchian types of assemblages has received considerable confirmation from the work of Fotianova (1964, 1967), Sinelnikova, Skiba, and Fotianova (1967), and Chelebaeva (1968), who have noted a similar sequence on Sakhalin and Kamchatka.

Although some revisions based on further collecting and study will undoubtedly be made, I do not think that the tentative correlations presented in figures 7 and 8 will change radically with new information. Critics of the age assignments presented here, I think, are obligated to present both detailed alternative systematic treatment of the plant megafossils and detailed knowledge of the physical stratigraphy of the plant-bearing beds.

FLORISTIC AND VEGETATIONAL ANALYSIS

FLORISTIC ANALYSIS

Interpretations of floristic history, as Mason (1947) has pointed out, must involve "***piecing together genetic lineages." In the Neogene of western North America, this piecing together can be done with confidence because of our considerable knowledge of Neogene assemblages. The lineage, for example, that has produced the modern *Alnus*

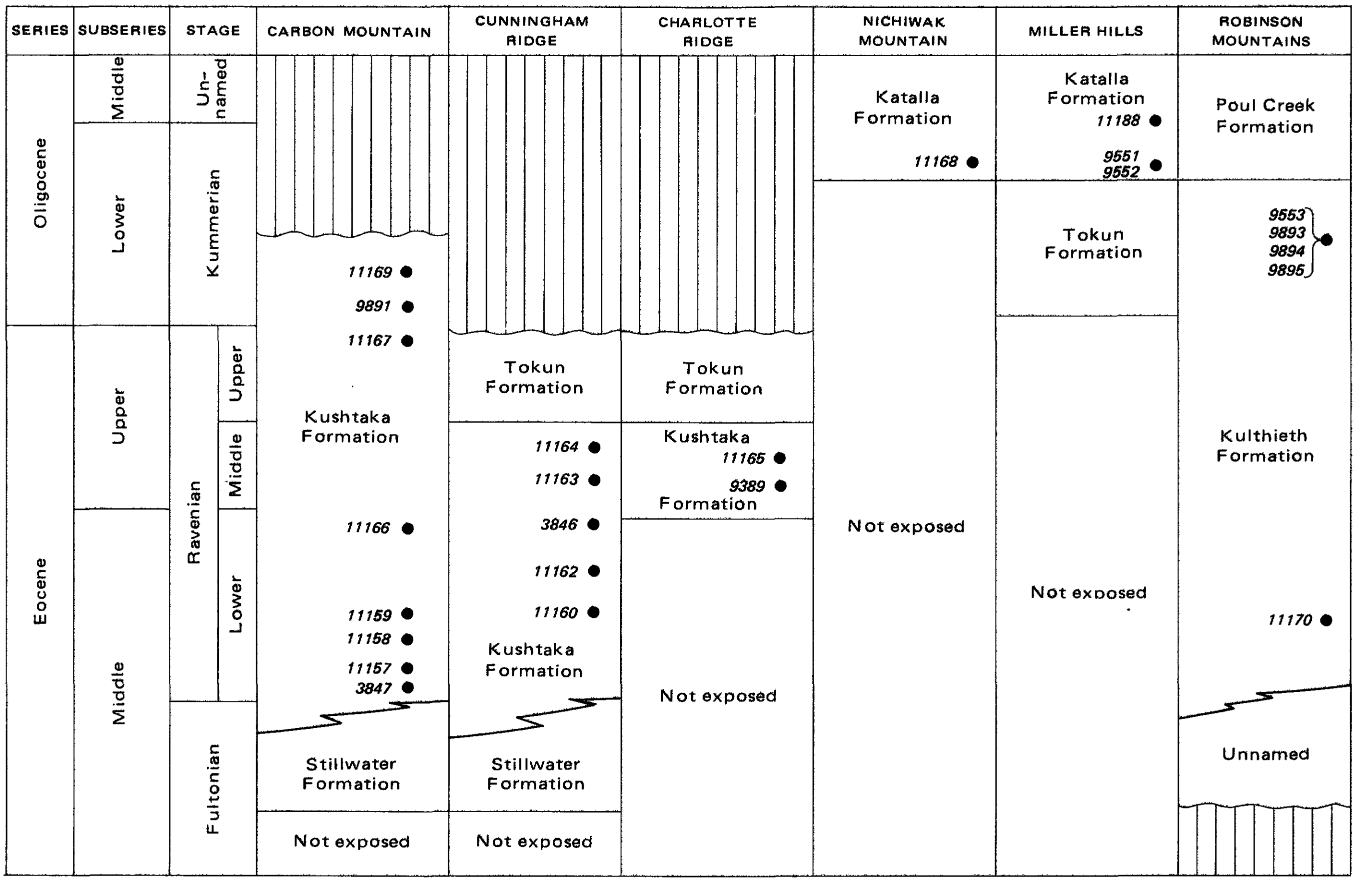

FIGURE 7.—Correlation of Paleogene formations in the Katalla and Yakataga districts. Numbers represent plant localities.

incana can be traced from a rich broad-leaved deciduous forest during the early and middle Miocene, into a rich conifer forest during the late Miocene, and finally into a depauperate boreal conifer forest during the Pliocene (Wolfe, 1966). Similarly an extinct lineage of *Lyonothamnus* was, during the early and middle Miocene, a member of a warm temperate, summer-wet, broad-leaved deciduous forest in the Pacific Northwest, but by the late Miocene the lineage was a member of a conifer-sclerophyllous broad-leaved forest that lived under a summer-dry climate in Nevada (Wolfe, 1964).

Little paleobotanical work has been done on Paleogene—particularly Eocene—assemblages in western North America, therefore, the history of various lineages is obscure. Although the genera and species can be, for the most part, discussed in terms of the most closely related living genera and species, the detailed history of Paleogene lineages is to a great extent speculative. Despite these qualifications, however, the general floristic relationships of some Paleogene assemblages to isochronous assemblages elsewhere and to modern floristic regions can be discerned.

VEGETATIONAL ANALYSIS

INTRODUCTION

The reliance by many Tertiary paleobotanists on the floristic relationships of fossil assemblages in arriving at an understanding of past climates and vegetational types has led to considerable confusion, both in floristic and vegetational history. This approach fundamentally relies upon an extremely strict application of uniformitarianism to tolerances of families, genera, and species. Many workers consider that tolerances of members of a particular taxonomic category have not changed through time. It seems clear, however, that tolerances must have changed in many, if not most, groups during time. For example, the tolerances of extant members of *Platycarya* and *Nipa* are mutually exclusive, and yet both genera are abundant in the early Eocene London Clay (Reid and Chandler, 1933); *Platycarya* has, on Taiwan and mainland China, the opportunity to extend its range downslope into the Paratropical Rain forest but has not. Similarly *Nipa* has the opportunity to extend its range northward into lowland Taiwan but has not. The conclusion

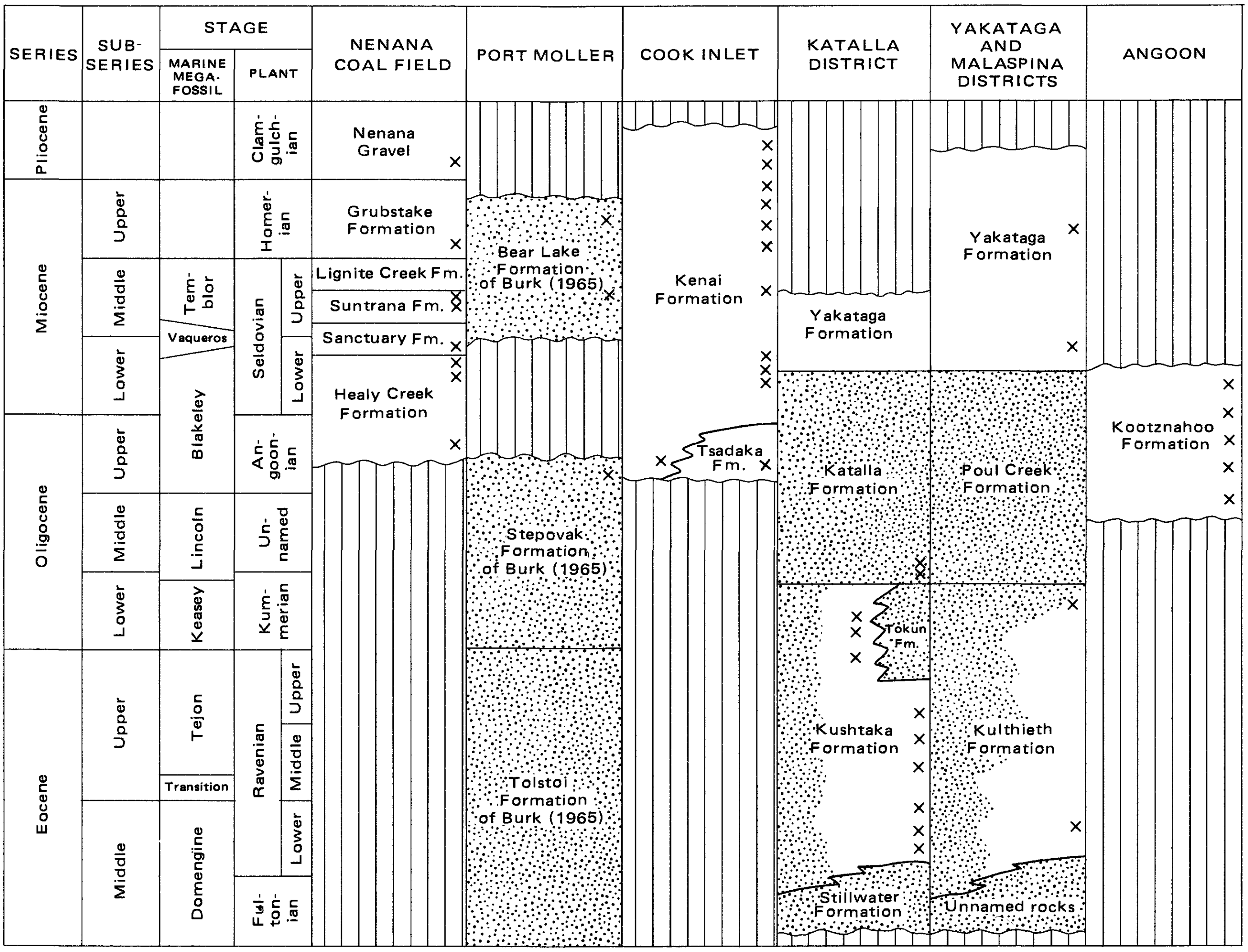

FIGURE 8.—Correlation of some Alaskan Tertiary formations. An (x) denotes approximate stratigraphic position of plant assemblage(s); stippling denotes rocks that are largely or entirely marine.

appears inescapable that the present tolerances of the two genera are mutually exclusive. Some workers (Axelrod, 1966b) have suggested that such mixtures in fossil assemblages are due mostly, if not entirely, to the early Tertiary climates and middle latitudes having been "warm temperate," that is, an essentially frostless climate that had a high equability but a low mean annual temperature. Thus Takhtajan (1957) and Axelrod (1966b) have suggested that the distribution of *Nipa* and certain mangroves is controlled mostly by marine, not land, temperatures, and their presence in the "warm temperate" London Clay flora is a function of marine temperatures. This hypothesis seems unreasonable in that in equable marine areas today *Nipa* and *Platycarya* are not associated and no modern thanatocoenose is known to contain specimens of both genera.

Theoretically it is highly probable that the tolerances of lineages have changed through time: how else could members of a subclass such as Dicotyledones have diversified and occupied widely different habitats? If, as is generally thought, the more primitive members of various families are tropical in distribution, then most, if not all, "temperate" genera must be descended from lineages that were once tropical. The use of floristic relationships to determine vegetational and climatic relationships of fossil assemblages has an inherent tendency to obscure patterns of changing tolerances of given lineages; the fundamental assumption of this method is that tolerances have changed little if at all. A given association is in a constant state of flux when viewed in time; different populations react differently to environmental change. If what is desired is an analysis of the history of a vegetational type such as the Mixed Mesophytic forest or the Paratropical Rain forest, then methods largely independent of floristic composition must be used to identify a fossil assemblage as a particular vegetational type (Wolfe, 1971).

FOLIAR PHYSIOGNOMY AND VEGETATIONAL ANALYSIS

One of the most basic methods of analyzing the climatic and vegetational indications of a fossil leaf flora is by an analysis of the physiognomy of the leaves. In his comprehensive analysis of the Tropical Rain forest Richards (1952, p. 154) states:

> conclusions as to the climates of Tertiary floras are perhaps more firmly based when they are drawn from a statistical study of leaf sizes and similar features *** than when *** they *** rest on the *taxonomic affinities* of the fossil flora rather than its physiognomy, which appears, at least as far as modern vegetation is concerned, to be a very sensitive index of environmental conditions.

The strong relationship between foliar physiognomy and climate has been previously recognized by Bews (1927) and particularly by Bailey and Sinnott (1915, 1916), who were the first to apply this relationship to an analysis of fossil floras. Several paleobotanists (for example, Chaney and Sanborn, 1933, MacGinitie 1941, Wolfe and Hopkins, 1967) have followed the lead of Bailey and Sinnott.

Various physiognomic features of foliage are probably related to climatic conditions. Features such as size can be useful, but the influence of the depositional environment on sorting is a difficult factor to evaluate; larger leaves will tend to be fragmented, and thus the percentages of species in the larger size classes will probably be minimal figures for fossil assemblages. Tropical rain forests have a considerably higher percentage of species that have large leaves than do temperate forests. The presence or absence of drip-tips is also of significance; this adaptation is particularly common in tropical rain forests. The organization (compound vs. simple) and major venation pattern (pinnate vs. palmate) differs somewhat between tropical and temperate vegetation (Bailey and Sinnott, 1916), but the lack of an obvious correlation between environment and these features makes application of such differences very uncertain. One exception is the leaves of lianes; Richards (1952, p. 107) notes:

> The leaves of rain-forest climbers usually fall into the 'mesophyll' size-class and approximate in texture as well as size to those prevailing in the tree stratum which they reach. In shape, however, they tend to be different. Simple elliptical or oblong-lanceolate leaves are relatively uncommon, and there is a marked tendency, as in all climbing plants, towards short leaves broadest at the reniform or cordate base.*** The main veins usually diverge in a palmate manner *** well-defined drip-tips are not uncommon.***The type of leaf described is so strikingly prevalent among climbers, especially twiners, that it is difficult to believe it is due to chance.

The correlation between climbers and climate is striking. Richards (1952, p. 102–103) again notes:

> Climbing plants *** are far more abundant in the Tropical Rain forest than in any other plant formation *** in the West Indies, where Rain forest and similar formations are the predominant vegetation, woody lianes form about 8% of all the flowering plants.*** In Europe climbing plants form less than 2% of the flora.*** The great abundance of lianes in the tropics is hardly surprising in view of the great advantage of the climbing habit in a closed and very tall community such as a rain forest.

Climbers, moreover, are especially abundant in openings in the Tropical Rain forest, particularly along rivers (Richards, 1952, p. 103). Richards also suggests that most lianes are intolerant of high rates of evaporation in the forest undergrowth; the abundance a lianes may, therefore, indicate the lack of a pronounced hot dry season.

Another physiognomic character of leaves that may prove to be useful is the density of venation. Tropical leaves have a pronounced tendency for the lamina to be supplied with many veins and this results in very small areoles; highly branching freely ending veinlets are less common than in temperate plants. There is clearly genetic control of the ultimate venation pattern, because, for example, in Tiliaceae, even the temperate members (such as *Tilia*) have small areoles with few freely ending veinlets, and in Sapindaceae even the tropical members (such as *Euphoria*) have branching freely ending veinlets. In both examples, however, the areoles of the tropical members are typically smaller than the areoles of temperate members of the same family. This relationship of venation to climate is probably also connected to the general xeromorphic nature of tropical leaves; leaves of plants inhabiting xeric regions in the temperate zones also tend to have smaller areoles than related species or genera that inhabit mesic regions of the temperate zones. As yet no quantification of this relationship has been made, involving as it does the clearing of leaves of all or most woody dicotyledonous species of floras in different climatic regimes. The relationship is, however, useful in determining the "tropicality" or "temperateness" of a given extinct species or genus relative to extant related species and genera.

An additional physiognomic character of leaves that is correlated with climate is texture. The texture of some fossils is difficult to evaluate in some specimens because of the type of preservation. In most specimens, however, the texture of a given leaf can be approximately determined. A coriaceous texture is typical of "mesophyllous" tropical plants, as well as the "microphyllous" species of arid and frigid climates. In addition, a coriaceous leaf indicates that the plant was evergreen. Thin leaves are particularly predominant in mesic temperate habitats; such leaves indicate a deciduous habit for the plants.

Perhaps the most striking correlation between climate and foliar physiognomy is the leaf margin. As originally pointed out by Bailey and Sinnott (1915), leaves that have entire margins are overwhelmingly prevalent in tropical regions, and leaves that have nonentire margins are characteristic of mesic temperate regions. The exact relationship between various environmental factors and the leaf margin is unclear; probably physiological aridity is in part responsible, as suggested by Bailey and Sinnott (1916, p. 36). In any case, the correlation of the entire margin on leaves that belong to the "mesophyll" size class with the tropical climates is striking.

The habitat has a significant effect on leaf margins, that is, whether a species is typically a slope or a stream- or lake-side species. Table 2 indicates that vegetation in fluviatile or lacustrine habitats, whether trees or shrubs, has consistently lower percentages of entire-margined species. This fact is particularly significant in the application of leaf-margin analyses to fossil assemblages; MacGinitie (1953, p. 46) has noted that "***fossil floras represent, almost without exception, the specialized streamside or lakeside floras of the time and place***" Fossil assemblages may, therefore, yield lower precentages of entire-margined species than the percentage based on the unknown flora of the entire region. In dealing with temperate Neogene floras, it might be possible to arrive at a better estimate of the regional percentage by, for example, weighting the probable woodland and slope species more than the probable stream- and lakeside species (largely members of Salicaceae and Betulaceae). In dealing with Paleogene tropical and subtropical assemblages, however, the habitats of many, if not most, species are highly conjectural, and habitat data from modern tropical and subtropical vegetation are largely lacking. The tendency for lacustrine and fluviatile species to be more widespread and fewer in number than slope and woodland species is a compensating factor if several assemblages of a given age and from a given region are considered as one. For example, in the late Miocene floras east of the Cascade Range, the same species of Salicaceae and Betulaceae occur regularly in different floras, whereas the greatest floristic difference between individual floras occurs in the probable slope and woodland species. The larger the flora and the more localities represented, therefore, the more valid the leaf-margin analysis becomes.

TABLE 2.—*The effect of habitat on leaf margins*

[Data based on Hitchcock and others (1959, 1961, 1964)]

Habitat	Percentages of species that have entire-margined leaves		
	Trees	Shrubs	Ligneous
West of Cascades, below 500 m;			
Lacustrine of fluviatile	33	25	27
Slope or woodland	40	42	43
All habitats	37	36	36
West of Cascades, above 500 m;			
Lacustrine or fluviatile	29	28	28
Slope or woodland	38	42	42
All habitats	33	36	35

The probable overrepresentation of lacustrine and fluviatile plants in megafossil assemblages also indicates that consideration of leaf-margin percentages should be based on species rather than on specimens. Bailey and Sinnott (1916) note that in tropical forests the individual plants that have nonentire margins are extremely rare, and that a consideration of the percentage of leaves that have entire margins would probably produce an even stronger percentage gradient between the tropical and temperate vegetation than a consideration of the percentage of species; in fossil assemblages, the percentage should, however, be based solely on species.

RELATION OF LEAF MARGINS TO CLIMATE

In order to properly evaluate the climatic significance of a leaf margin or other physiognomic analyses, terms such as "tropical," "subtropical," and "warm temperate," should be related both to climatic conditions and leaf-margin percentages. These terms have been given rigorous definitions by some climatologists and geographers, but there are almost as many definitions as climatologists and geographers. Similarly, botanists apply terms such as "subtropical forest" to widely different vegetational types.

TROPICAL RAIN FOREST

The most commonly accepted definition of tropical climates used by climatologists is that the mean temperature of the coldest month is not below 18°C. If this definition is accepted, the forest of Hong Kong and lowland Taiwan that has been termed Tropical Rain forest by some botanists (Li, 1963, for example) is not truly tropical; these two regions have cold-month means of less than 16°C. Regions that have tropical climates under the meteorological definition and for which leaf-margin percentages have been compiled are (data after Bailey and Sinnott, 1916; Brown, 1919):

	Percent
Brazil, Amazon lowland	89
Malaya	86
Florida Keys	83
Philippine Islands, 200 m	82
Ceylon, lowland	81
Manilla	81
East Indies	79
Philippine Islands, 450 m	76
Hawaii, lowland	75
Philippine Islands, 700 m	72
Philippine Islands, 1,100 m	69

The vegetation in most of these regions has generally been regarded as Tropical Rain forest. Notable exceptions are the oak-laurel forest (termed "Submontane Rain forest" by Richards, 1952, p. 87) at 700 m in the Philippine Islands, lowland Hawaii (presumably Subtropical Rain forest in Richards' terminology), and the montane forest (termed "Montane Rain forest" by Richards, 1952, p. 87) at 1,100 m in the Philippine Islands. In terms of the climatologist, percentages above 68 could be termed "tropical," but to most botanists the Tropical Rain forest is indicated by percentages above 75.

PARATROPICAL RAIN FOREST

There is no universally accepted definition of subtropical, either in regard to climate or vegetation. The use of the term by Richards (1952) includes regions that are frost-free, whereas Wang (1961) and Li (1963) apply the term exclusively to regions that typically receive frost. As used by Richards, the terms "Submontane Rain forest," "Montane Rain forest," and "Subtropical Rain forest," indicate vegetation that is similar to the Tropical Rain forest except that the Tropical Rain forest has more stories and is thus somewhat more complex. Floristically these other vegetational types are closely allied to the Tropical Rain forest but are typically less rich. Wang (1961) has used the term "extratropical rain forest" for the vegetation of lowland southern China (the Subtropical Rain forest of Richards). Wang's term is preferable to Richards' in that, as noted previously, Queensland and Hawaii are truly tropical (not subtropical) in the commonly accepted meteorological definition of tropical. Extratropical, however, has too broad a connotation; the temperate conifer rain forest of the Olympic Peninsula of Washington is an extratropical rain forest.

The term "Paratropical Rain forest" (para, meaning close) is here proposed for the vegetation that Richards (1952) termed "Subtropical Rain forest" and "Submontane Rain forest" and that Wang (1961) termed "extratropical rain forest." This type of forest is vegetationally similar to, but simpler in structure than, the Tropical Rain forest; floristically, the Paratropical Rain forest is closely allied to the Tropical Rain forest. The Paratropical Rain forest is not limited poleward by the mere presence of frost; for example, the Paratropical Rain forest of Taiwan has been subjected to -1° C, and northern Hainan has experienced a temperature of -3° C. The mean annual temperature ranges from about 20°C up to about 25°C. The cold-month temperature has a mean of about 13°C–24°C. Precipitation can be seasonal, but extended dry periods are lacking. These climatic conditions also pertain to the Montane and Submontane Rain forests of Richards (1952), and, except for the precipitation regime, to some monsoonal forests of the tropical region. Leaf margin percentages for the Paratropical Rain forest vary from 57 up to 75 (table 3): Note that the Paratropical Rain forest includes vegetation that is predominately broad-leaved evergreen, although some deciduous plants may be (and typically are) present. Some workers have applied distinct terms such as "Semi-deciduous forest" to vegetation of which a large part is deciduous; such refinements are probably not readily recognizable in relation to fossil assemblages.

TABLE 3.—*Percentages of species that have entire margins in some modern floras*

Flora	Percentage	Vegetation
Brazil, lowland	88	Tropical Rain forest
Malaya	86	Do.
Philippine Islands, 200 m	82	Do.
Ceylon, lowland	81	Do.
Manila	81	Do.
East Indies	79	Do.
Philippine Islands, 450 m	76	Do.
West Indies	76	Do.
Hawaii, lowland	75	Paratropical Rain forest
Ceylon, upland	74	Do.
Philippine Islands, 700 m	72	Do.
Hong Kong	72	Do.
Hainan, lowland	70	Do.
Philippine Islands, 1,100 m	69	Montane Rain forest
Taiwan, 0–500 m	61	Paratropical Rain forest
Ceylon, upland	60	Do.
Hawaii, upland	57	Do.
Hainan, upland	55	Subtropical forest
Taiwan, 500–2,000 m	45	Do.
Mixed Mesophytic forest, China	30	Warm temperate forest

Note that the leaf margin percentages of vegetation of tropical mountains ("Submontane Rain forest," "Montane Rain forest") and of the lowland-part of the Paratropical Rain forest have about the same range. This range indicates some similarity of environmental conditions (for example, mean annual temperature), at least those conditions that affect leaf margins.

Some workers may object to the introduction of the term "paratropical" on the grounds that the concept to which the term is applied is the same concept as subtropical. The term "subtropical," however, covers a much broader range of climates and vegetation types than does paratropical. As noted previously, the term "tropical" is applied to climates in which the mean temperature of the cold month is above 18°C, and subtropical is typically applied to climates that have cold-month means between about 6°C (Landsberg, 1964, p. 924) and 18°C. Within this broad climatic range, the vegetation in mesic regions can be readily classified into two major types. The first, which I call "paratropical," is physiognomically similar to the Tropical Rain forest in that more than one tree story is present, woody lianes are diverse and abundant, and buttressing of the tree trunks is present. The second, to which I prefer to restrict the term "subtropical," is physiognomically dissimilar to the paratropical vegetation and typically has abundant sclerophylls, lacks a diverse and abundant woody liane element, and has no buttressing. Despite the fact that both Paratropical Rain and subtropical forests are dominantly broad leaved evergreen and that both forest types are floristically related, the physiognomy of the two types differs more than does the physiognomy of the Tropical and Paratropical Rain forests.

SUBTROPICAL FOREST

The term "subtropical forest" is reserved here for broad-leaved evergreen vegetation that grows under a climate in which frosts are present, although never severe or of long duration. Some workers might prefer the term "warm temperate," but the Mixed Mesophytic forest of east central Asia, for example, is traditionally considered to be warm temperate, and it exists in a region that receives regular hard frosts (Wang, 1961). The oak-laurel forest of southern China and at moderate altitudes on Taiwan is an example of a subtropical forest. Vegetationally, therefore, the term "subtropical" indicates a broad-leaved evergreen forest (in some instances conifers and broad-leaved deciduous plants are important constituents of this forest) that exists under moderate frost. Mean annual temperature ranges from about 13° to 18°C and the mean of the coldest month ranges from about 0° to 18°C. Leaf-margin percentages vary from about 39 up to 55.

WARM TEMPERATE FOREST

As will be shown, only one Gulf of Alaska Ravenian or Kummerian assemblage has a leaf-margin percentage below 39. The warm temperate vegetation thus needs to be mentioned only briefly. This modern vegetation is broad-leaved deciduous and may have a significant amount of conifers intermixed. Broad-leaved evergreens are present but not dominant. Freezing temperatures can be expected during several months of the year and the temperature regime has a pronounced seasonality. The mean annual temperature ranges from about 11° to 13°C, and the mean of the coldest month ranges from about -3° to 2°C. Leaf-margin percentages range from about 30 to 38. Under less seasonality but the same mean annual temperature, the warm temperate broad-leaved deciduous forests are typically replaced by conifer forests.

LOWER RAVENIAN

FLORISTIC ANALYSIS

Systematic list of the Alaskan lower Ravenian (late middle Eocene) flora

- Filicineae
  - Filicales
    - Schizaeaceae
      - *Anemia gunni* Wolfe
    - Cyatheaceae
      - *Cyathea inequilateralis* (Holl.) Wolfe
    - Aspidaceae
      - *Allantodiopsis pugetensis* Wolfe
      - *Dryopteris alaskana* (Holl.) Wolfe
- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - *Glyptostrobus* sp.
- Angiospermae
  - Monocotyledonae
    - Principes
      - Palmae
        - *Sabalites* sp.
  - Dicotyledonae
    - Juglandales
      - Juglandaceae
        - *Platycarya pseudobrauni* (Holl.) Wolfe

- Angiospermae—Continued
  - Dicotyledonae—Continued
    - Fagales
      - Betulaceae
        - *Alnus martini* Wolfe
        - *Alnus scotti* Wolfe
    - Urticales
      - Ulmaceae
        - *Girroniera* sp.
        - *Girroniera* sp.
    - Ranales
      - Tetracentraceae
        - *Tetracentron piperoides* (Lesq.) Wolfe
      - Menispermaceae
        - *Anamirta milleri* Wolfe
        - *Calkinsia plafkeri* Wolfe
        - *Cocculus* sp.
        - *Diploclisia* sp.
        - *Limacia stenophylla* Wolfe
        - *Paratinomiscium conditionalis* (Holl.) Wolfe
        - *Pycnarrhena* sp.
      - Illiciaceae
        - *Illicium* sp.
      - Annonaceae
        - *Cananga* sp.
        - *Dasymaschalon*? sp.
      - Myristicaceae
        - *Knema* sp.
        - *Myristica* sp.
      - Lauraceae
        - *Cinnamomophyllum latum* (MacG.) Wolfe
        - *Litseaphyllum presamarensis* (Sanb.) Wolfe
        - *Litseaphyllum similis* (Knowlt.) Wolfe
        - *Litseaphyllum* sp.
        - *Litseaphyllum* sp.
    - Rosales
      - Leguminosae
        - *Caesalpinites* sp.
    - Geraniales
      - Meliaceae
        - *Toona* sp.
      - Rutaceae
        - *Euodia alaskana* Wolfe
        - *Luvunga spatiosa* (Holl.) Wolfe
    - Sapindales
      - Anacardiaceae
        - *Melanorrhoea alaskana* (Holl.) Wolfe
        - *Rhus* cf. *R. mixta* (Lesq.) MacG.
      - Celastraceae
        - *Celastrus comparabilis* Holl.
      - Icacinaceae
        - *Goweria alaskana* Wolfe
        - *Goweria dilleri* (Knowlt.) Wolfe
        - *Paleophytocrene elytraeformis* (Holl.) Wolfe

- Angiospermae—Continued
  - Dicotyledonae—Continued
    - Sapindales—Continued
      - Icacinaceae—Continued
        - *Phytocrene acutissima* Wolfe
        - *Phytocrene sordida* (Lesq.) MacG.
        - *Pyrenacantha* sp.
        - *Stemonurus alaskanus* Wolfe
      - Sapindaceae
        - *Allophylus duktothensis* Wolfe
      - Sabiaceae
        - *Meliosma duktothensis* Wolfe
        - *Meliosma kushtakensis* Wolfe
    - Rhamnales
      - Rhamnaceae
        - *Sageretia* sp.
        - *Zizyphus alaskanus* Wolfe
      - Vitaceae
        - *Vitis* sp.
    - Parietales
      - Actinidiaceae
        - *Saurauia* sp.
      - Dipterocarpaceae
        - *Parashorea pseudogoldiana* (Holl.) Wolfe
    - Myrtiflorae
      - Barringtoniaceae
        - *Barringtonia* sp.
      - Rhizophoraceae
        - *Kandelia wangi* Wolfe
      - Alangiaceae
        - *Alangium bergensis* Wolfe
        - *Alangium* sp.
      - Myrtaceae
        - *Eugenia* sp.
    - Umbelliflorae
      - Cornaceae
        - *Mastixia irregularis* (Holl.) Wolfe
    - Ericales
      - Clethraceae
        - *Clethra* sp.
    - Tubiflorae
      - Verbenaceae
        - *Clerodendrum* sp.

The known flora of the lower Ravenian in Alaska is diverse despite the small size of the collections. Altogether at least 71 species are represented, although only 60 show sufficient characters to be determined to family. At least 47 genera and 31 families are represented. The most diverse families represented are Menispermaceae, Lauraceae, and Icacinaceae. The strong floristic relationship of this flora to that of the London Clay is apparent in that 23 families and 10 genera are common to both floras, despite the fact that a leaf flora is being compared to a fruit and seed flora and each have their own organ genera. The floristic similarities are even more pronounced in that the most diverse families of the London Clay are also diverse in the Alaskan lower Ravenian. The majority (27) of the genera and all the families except for Myristicaceae, Barringtoniaceae, and Clethraceae, are also known in early or middle Eocene floras from western conterminous United States. Twenty-one of the lower Ravenian species are represented by the same or closely related species in the Eocene floras from western conterminous United States. Floristically, therefore, the lower Ravenian flora of Alaska is closely related to the early middle Eocene flora of Eurasia and western conterminous United States, as well as to the lower Ravenian flora of Washington.

The relationship of the Alaskan lower Ravenian flora to extant floras is clear: the Alaskan lower Ravenian flora is overwhelmingly paleotropical. Not one of the genera or families determined is exclusively neotropical, whereas four of the families and 23 of the genera are exclusively paleotropical; to the generic figure can be added six additional extinct genera that have their closest living relatives restricted to the paleotropical region. In instances in which a genus is found in both old and new worlds, the fossil most closely resembles the old-world representatives. A few genera are today of warm temperate distribution in Asia; the significance of these genera is discussed in a later section (p. 43).

Several Alaskan lower Ravenian genera are today exclusively members of the Tropical Rain forest, and some species of more wide-ranging genera are most closely related to members of theTropical Rain forest:

Anamirta
Limacia
Pycnarrhena
Knema
Myristica
Euodia
Luvunga
Celastrus comparabilis
Stemonurus
Phytocrene
Pyrenacantha
Parashorea
Barringtonia

The bulk of the genera and species, however, are related to members of the present Paratropical Rain forest or the Submontane Rain forest of the Paleotropical region.

VEGETATIONAL ANALYSIS

In order to eliminate, at least partially, the effect of probable over-representation of stream-side plants, the various Lower Ravenian assemblages have been treated as one for the leaf-margin analysis. This procedure also yields a considerably larger statistical base than if percentages for each assemblage are calculated. It could be argued that, because the assemblages are not from the same precise stratigraphic plane, combining the assemblages eliminates any possibility of recognizing major but brief climatic fluctuations (this indeed happened when I computed the percentage for the type Ravenian—upper Puget—that was published by Wolfe and Hopkins, 1967). If the individual Alaskan assemblages were larger, separate computations should indeed be made, but most assemblages contain such small numbers of species that individual computations are not firmly based statistically. If, for example, the percentage for locality 3847 (80 percent) is compared with that for locality 11166 (57 percent), a considerable deterioration of climate might be construed; such a conclusion should, however, be based on a larger body of data, that is, at least 20 or more specific entities from a given locality.

The percentage of Alaskan lower Ravenian dicotyledonous species that have entire margins is 65; this figure is based on 62 species. In terms of the percentages discussed previously, the lower Ravenian assemblage is neither Tropical Rain forest nor subtropical forest, but the percentage is intermediate between that for the Paratropical Rain forest of Hawaii and that for the Paratropical Rain forest of Taiwan.

In leaf size and foliar organization (table 4), the Alaskan lower Ravenian assemblage compares well with the Paratropical (Submontane) Rain forest of the Philippine Islands (Brown, 1919), particularly if it is kept in mind that leaves of larger sizes are underrepresented in fossil assemblages. I have also included in table 5 the figures for the early Miocene Collawash flora of Oregon, which is a Mixed Mesophytic, warm temperate forest. Clearly the Alaskan lower Ravenian is unrelated vegetationally to the Mixed Mesophytic forest, although there is some floristic similarity (p. 44).

Comparisons of the leaf-size classes of the Alaskan Early Ravenian assemblage to those of the extant Australian rain forests are informative. In a detailed study, Webb (1959) has shown significant differences in leaf size between the various forest types, ranging from Paratropical Rain forest to temperate rain forest types. Based in part on a study of leaf-size classes, Webb also formally subdivided the three major forest formations of eastern Australia. In table 5 some of Webb's data are summarized. The notophyll-size class is an addition to the Raunkiaer (1934) system of size classes and represents the smaller (2,025–4,500 mm^2) leaves that Raunkiaer included in his mesophyll-size class. (As used

TABLE 4.—*Comparisons between modern and fossil foliar physiognomy*

Flora	Number of species	Percent entire	Percent less than 5 cm in width	Percent less than 10 cm in length
Alaskan early Ravenian	65	65	36	42
Alaskan middle Ravenian	37	54	50	45
Alaskan late Ravenian	20	20	86	91
Alaskan Kummerian	28	55	67	53
Culled dipterocarp forest, Philippines	125	82	32	13
Virgin dipterocarp forest, Philippines	90	76	32	18
Midmountain forest, Philippines	68	72	40	18
Mossy forest, Philippines	16	69	75	69
Collawash, early Miocene, Oregon	119	25	66	66

elsewhere in this report, mesophyllous is used in accordance with Raunkiaer's original definition.) Omitted from table 5 are Webb's data for most of the subformations representing woodland or thicket vegetation; all these have 40 percent or more microphyll species and typically a low percentage of mesophyll species. The Alaskan early Ravenian assemblage in terms of species is: 34 percent mesophyll, 50 percent notophyll, and 16 percent microphyll. Clearly, the early Ravenian does not represent temperate vegetation.

Based on leaf-size classes, the Alaskan early Ravenian assemblage is similar to two Australian vegetation types: the Complex Notophyll Vine forest (Paratropical Rain forest) and the Simple Mesophyll Vine forest (Submontane Rain forest). The Simple Mesophyll Vine forest is in Australia, as elsewhere, tropical in the meteorological definition. The Complex Notophyll Vine forest is subtropical in the meteorological definition; this forest extends from about latitude 21° S. to about 35° S. (Webb, 1959). This area of the Complex Notophyll Vine forest lacks frost. Webb (1959, p. 552–553) notes that "All the Rain forest formations, away from their optimum, have smaller leaf sizes, and undergo other physiognomic and structural changes associated with gradients of temperature (altitude or latitude) soil properties (moisture, drainage, fertility), and exposure." Because the Alaskan early Ravenian assemblage has a somewhat larger percentage (34 compared to 30) of mesophylls than Webb (1959) recorded for any plots in the Complex Notophyll Vine forest, the early Ravenian may represent the optimal development of that forest or may represent simple Mesophyll Vine forest. This suggestion has even more validity if, as suggested previously, the larger size classes are underrepresented in fossil assemblages.

The fragmentary nature of many of the fossils does not allow a complete analysis of the percentage of dicotyledonous species that have drip-tips. Obvious drip-tips are, however, present in many species, for example, *Girroniera* spp., *Limacia stenophylla*, *Luvunga spatiosa*, *Phytocrene* spp., *Parashorea pseudogoldiana*, and *Alangium bergensis*. The climatic conditions that are responsible for the natural selection of drip-tips in tropical lineages were probably present in Alaska during the early Ravenian.

The length of the drip-tip and its absence or presence provide clues as to both the vegetational type, as noted earlier, and the position of the particular species in the vegetation. Richards (1952, p. 84–87) notes that drip-tips are uncommon on leaves from the upper stories in comparison to leaves from the lower stories, including undergrowth. Elongated drip-tips on leaves of *Girroniera* spp., *Alangium bergensis*, and *Phytocrene acutissima*, indicate that these plants were most probably members of the lower stories of the forest. Not so elongated are the drip-tips of *Allophylus duktothensis*, *Luvunga spatiosa*, *Stemonurus alaskanus*, *Phytocrene sordida*, and "*Rhododendron crassum*"; these species could presumably have been members of upper stories. Species such as *Euodia alaskana* would more likely have been members of the upper

TABLE 5.—*Distribution of leaf-size classes in the vegetation of eastern Australia*

[Data from Webb (1959)]

Formation (this report)	Subformation (after Webb)	Percent of species that are:		
		Mesophyll	Notophyll	Microphyll
Paratropical Rain forest	Complex Mesophyll Vine forest	50–70	30–40	0–5
Monsoon forest	Semi-evergreen Mesophyll Vine forest	30	40	30
Submontane Rain forest	Simple Mesophyll Vine forest	30–50	40–50	0–15
Submontane Rain forest	Simple Notophyll Vine forest	0–30	55–70	0–40
Montane Rain forest	Microphyll Mossy thicket	0	0	100
Subtropical forest	Complex Notophyll Vine forest	15–30	50–70	10–20

story, and the emarginate apex of *Caesalpinites* sp. clearly indicates exposure to the hotter conditions of the upper story.

The percentage of probable lianes in the Alaskan lower Ravenian is very high (about 25 percent of the species). Species that have leaves that clearly conform to the morphology of liane leaves mentioned by Richards (1952, p. 107; p. 23 of this report) are *Anamirta milleri*, *Cocculus* sp., *Diploclisia* sp., *Paratinomiscium conditionalis*, *Phytocrene acutissima*, and *P. sordida*. Other species of genera whose extant members are exclusively lianes are *Limacia stenophylla*, *Pycnarrhena* sp., *Luvunga spatiosa*, *Celastrus conditionalis*, *Pyrenacantha* sp., and *Vitis* sp. The tribe Phytocreneae is also today composed exclusively of climbers, and hence *Goweria alaskana*, *G. dilleri*, and *Paleophytocrene elytraeformis* may also be members of the liane element. The diversity of probable lianes is another indication that the Alaskan lower Ravenian vegetation was, in the broad sense, tropical. The coriaceous texture of most of the leaves (see, for example, pl. 5, fig. 7; pl. 6, fig. 8, pl. 8, fig. 4) is a strong indication that the plants that bore them were evergreen.

The Alaskan early Ravenian assemblages contain a probable strand element. *Barringtonia* today grows behind beaches in the South Pacific; the beds from which the Alaskan specimens were obtained are both under- and overlain by beds containing brackish-water mollusks. The mangrove *Kandelia* today extends along shores from southeast Asia north to southern China; I suggest that such a highly specialized habitat as the mangroves of Rhizophoraceae have today is an ancient adaptation and that the Alaskan *Kandelia* was also a mangrove.

Some workers consider that the numerical abundance of plant megafossils closely reflects the relative abundance of organisms of various species in the forest of the area of the site of deposition. For those workers, tables 6 and 7 are presented. The correlation, however, between representation of large organs and representation of species in the forest has yet to be demonstrated; the supposed correlation is an unfounded assumption. Quaternary pollen workers, on the other hand, are of almost unanimous opinion that megafossil assemblages generally represent the vegetation near the immediate site of deposition and thus do not adequately reflect the vegetation of the region (see Faegri and Iversen, 1964, p. 39). This opinion is based on numerous studies of modern pollen rain in a region

TABLE 6.—*Numerical abundance of plant megafossils from the Alaskan lower Ravenian*

Species	11157 3847	11159 11158	11160 11161	11166	3846	11170	3879	11195	Total	Percent
Limacia stenophylla		46		2					48	9.3
Celastrus comparabilis	4	20		5	1	17	1		48	9.3
Allophylus duktothensis				1		39			40	7.5
Alnus martini		22				17			39	7.3
Platycarya pseudobrauni	6					31		1	38	7.1
Meliosma duktothensis						28		1	29	5.6
Sabalites sp		4	14			1		5	24	4.9
Vitis sp				19		1			20	3.8
Phytocrene acutissima	1	13		5					19	3.7
Eugenia sp						19			19	3.7
Dryopteris alaskana	10				1		6		17	3.3
Clethra sp		1		2	1	10			14	2.7
Litseaphyllum similis	4		9						13	2.5
Parashorea pseudogoldiana	9							1	10	1.9
Alnus scotti	8	1							9	1.7
Clerodendrum sp		8							8	1.5
Meliosma kushtakensis		5		3					8	1.5
Allantodiopsis pugetensis		4		1	1		1		7	1.3
Melanorrhoea alaskana	1	3			2	1			7	1.3
Litseaphyllum presamarensis					5				5	1.0
Glyptostrobus sp							4		4	0.8
Alangium bergensis	1			2			1		4	.8
Cyathea inequilateralis			2		1				3	.6
Myristica sp	3								3	.6
Anamirta milleri						3			3	.6
Cinnamomophyllum latum	3								3	.6
Luvunga spatiosa	2			1					3	.6
Euodia alaskana		3							3	.6
Barringtonia sp						3			3	.6
Others	9	21	1	10	2	16	3	7	70	12.6
Totals	61	151	26	51	14	181	16	15	515	99.3

TABLE 7.—*Numerical abundance and diversity of families in the Alaskan lower Ravenian*

Family	Number	Percent	Number of genera	Number of species
Menispermaceae	59	11.6	7	7
Betulaceae	48	9.3	1	2
Celastraceae	48	9.3	1	1
Sapindaceae	40	7.8	1	1
Juglandaceae	37	7.2	1	1
Sabiaceae	37	7.2	1	2
Icacinaceae	26	5.1	5	7
Palmae	25	4.9	2?	2?
Lauraceae	23	4.5	2	5
Vitaceae	20	3.9	1	1
Myrtaceae	19	3.7	1	1
Clethraceae	14	2.7	1	1
Aspidaceae	24	4.7	2	2
Dipterocarpaceae	10	1.9	1	1
Verbenaceae	8	1.6	1	1
Anacardiaceae	7	1.4	1	1
Rutaceae	6	1.2	2	2
Myristicaceae	5	1.0	2	2

as compared to the vegetation, and the application of these data to fossil Quaternary pollen and megafossil assemblages. I agree that the representation of leaves is largely a reflection of the existence of certain species near the site of deposition and that leaf counts are largely meaningless in determining the vegetation of the region of the depositional basin.

The general floristic relationships, the presence of large-leafed ferns (including a genus—*Hemitelia*—whose extant members are tree ferns), palms, diverse probable lianes, a high percentage of species that have entire-margined leaves, many large-leafed species, many species that have drip-tips, and many species that had a coriaceous texture—all these are a strong indication that the Alaskan lower Ravenian vegetation should be considered as Paratropical Rain forest.

MIDDLE RAVENIAN

FLORISTIC ANALYSIS

Systematic list of the Alaskan middle Ravenian (lower upper Eocene) flora

- Filicineae
  - Filicales
    - Schizaeaceae
      - *Lygodium larsoni* Wolfe
    - Aspidaceae
      - *Allantodiopsis pugetensis* Wolfe
- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - *Glyptostrobus* sp.
- Angiospermae
  - Monocotyledones
- Angiospermae—Continued
  - Monocotyledones—Continued
    - Principes
      - Palmae
        - *Phoenicites* sp.
        - *Sabalites* sp.
  - Dicotyledones
    - Juglandales
      - Juglandaceae
        - *Carya cashmanensis* Wolfe
        - *Engelhardtia* sp.
        - *Platycarya pseudobrauni* (Holl.) Wolfe
        - *Pterocarya pugetensis* Wolfe
    - Fagales
      - Fagaceae
        - *Dryophyllum pugetensis* Wolfe
    - Urticales
      - Ulmaceae
        - *Ulmus kushtakensis* Wolfe
    - Ranales
      - Tetracentraceae
        - *Tetracentron piperoides* (Lesq.) Wolfe
      - Menispermaceae
        - *Calkinsia plafkeri* Wolfe
      - Lauraceae
        - *Cinnamomophyllum kushtakensis* Wolfe
        - *Litseaphyllum kushtakensis* Wolfe
        - *Litseaphyllum presamarensis* (Sanb.) Wolfe
        - *Litseaphyllum schorni* Wolfe
        - *Litseaphyllum* sp.
        - *Litseaphyllum* sp.
    - Rosales
      - Hamamelidaceae
        - *Liquidambar*? sp.
      - Eucommiaceae
        - *Eucommia* sp.
      - Leguminosae
        - *Leguminosites* sp.
    - Sapindales
      - Anacardiaceae
        - Genus indet.
      - Sapindaceae
        - *Allophylus* sp.
        - *Sapindus*? sp.
    - Parietales
      - Theaceae
        - *Ternstroemites* sp.
- Incertae sedis
  - *Artocarpoides kummerensis* Wolfe
  - *Macclintockia* sp.

The total number of species known from the Alaskan middle Ravenian is smaller than for the early Ravenian. This apparent lesser diversity may be a function of the fewer localities of middle Ravenian age from which fossils were collected. Locality 11165 has produced representatives of 37 species, although not all could be determined to family because of poor preservation. This assemblage is the richest known from a single Alaskan Eocene locality.

In contrast to the lower Ravenian assemblages, Lauraceae are proportionally better represented; Menispermaceae are poorly represented and Icacinaceae are apparently absent. Juglandaceae are also better represented in the middle than in the lower Ravenian. Most middle Ravenian families and genera are known in the lower Ravenian, either in Alaska or conterminous United States. Many species are also common to the two substages, and it is clear that the bulk of the middle Ravenian flora is closely allied floristically to the lower Ravenian.

The relationships of the middle Ravenian flora to extant floristic regions is Asian, as in the lower Ravenian. The floristic similarities of the middle Ravenian to the Indomalaysian region is, however, much less pronounced. The closest relationship of the middle Ravenian appears to be with the Notophyllous Broad-leaved Evergreen forest. The representation of Juglandaceae (exclusive of *Pterocarya*), Fagaceae, Lauraceae, *Liquidambar*?, and Theaceae, gives the Alaskan middle Ravenian flora a taxonomic aspect that is most similar to that of the notophyllous, subtropical, oak-laurel forest of eastern Asia.

The mixed mesophytic element, although not dominant, is more pronounced in the middle than in the lower Ravenian. The Juglandaceae (exclusive of *Engelhardtia*), *Ulmus*, *Tetracentron*, *Eucommia*, and *Liquidambar*?, are members of this element. Note, however, that five of the seven mixed mesophytic genera in the Alaskan middle Ravenian are known in correlative assemblages in the Puget Group, and a sixth—*Platycarya*—is a common member of early and middle Eocene assemblages in conterminous United States.

VEGETATIONAL ANALYSIS

The percentage of middle Ravenian species that have entire margins is 54, compared to 65 for the lower Ravenian. The middle Ravenian figure is based on 36 dicotyledonous species. Comparisons with modern vegetation (table 4) indicate that the middle Ravenian is only marginally Paratropical Rain forest or more probably in the warmer part of the notophyllous forest. The leaf-margin analysis is corroborated by the proportionately fewer coriaceous and hence probably broad-leaved evergreen species, the sparse representation of probable lianes (the only probable liane is *Calkinsia*), and the almost total lack of leaves that have drip-tips.

The contrast between the lower and middle Ravenian in both vegetation and flora is significant in that both kinds of evidence indicate a cooler climate for the middle Ravenian. In Alaska, light frosts probably characterized the middle Ravenian climate, whereas they were probably lacking in the early Ravenian. In the middle Ravenian of the Puget Group, the physiognomic characters of the foliage indicate the persistence in the conterminous United States of Paratropical Rain forest and hence typically frost-free climate. The middle Ravenian floras of the Puget Group, however, also indicate a climate cooler than that of the lower Ravenian, as shown by a decline in the leaf-margin percentages from 75 to 62 (Wolfe, 1971).

UPPER RAVENIAN

FLORISTIC ANALYSIS

Systematic list of the Alaskan upper Ravenian uppermost Eocene) flora

- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - *Glyptostrobus* sp.
- Angiospermae
  - Dicotyledones
    - Salicales
      - Salicaceae
        - *Populus*? sp.
        - *Salix carbonensis* Wolfe
        - *Salix* sp.
    - Juglandales
      - Juglandaceae
        - *Juglans* (*Cardiocaryon*) sp.
        - *Pterocarya pugetensis* Wolfe
    - Fagales
      - Betulaceae
        - *Alnus cuprovallis* Axelr.
        - *Alnus* sp.
        - *Alnus* sp.
    - Ranales
      - Menispermaceae
        - *Cocculus* sp.
    - Rosales
      - Hamamelidaceae
        - *Corylopsis* sp.
      - Rosaceae
        - *Prunus axelrodi* Wolfe
        - *Sorbus carbonensis* Wolfe

Angiospermae—Continued
  Dicotyledones—Continued
    Sapindales
      Aquifoliaceae
        Ilex carbonensis Wolfe
    Rhamnales
      Rhamnaceae
        Rhamnus? sp.
    Malvales
      Tiliaceae
        Tilia carbonensis Wolfe
        Plafkeria sp.
    Myrtiflorae
      Myrtaceae
        Eugenia? sp.
Incertae sedis
        Dicotylophyllum carbonensis Wolfe

The Alaskan upper Ravenian is, unfortunately, known from only one locality; the preservation of the leaves, however, is the best for any of the Alaskan Eocene localities. At least 21 specific entities are represented, but only 19 were sufficiently complete to determine to family, and one of these (*Dicotylophyllum carbonensis*), although the most abundantly represented species, is thought to represent an extinct genus.

The upper Ravenian assemblage is not closely allied floristically to the lower or middle Ravenian. Only 5 of the 15 genera are known from the earlier Ravenian assemblages. It is also significant that Lauraceae, Rutaceae, and Dipterocarpaceae are unrepresented in the upper Ravenian. Palynologic evidence, however, indicates that some upper Ravenian genera, for example *Salix*, *Juglans*, and *Tilia*, were represented in subtropical or Paratropical Rain forests in conterminous United States during the earlier Eocene and leaves of *Populus* are known in subtropical forests in the middle Eocene (Leopold and MacGinitie, 1972). One element, represented by *Corylopsis* and *Dicotylophyllum carbonensis*, seems to be derived from high-latitude warm temperate and subtropical Paleocene assemblages, although *Corylopsis* was also a member of Paratropical Rain forest during at least the early Eocene (Chandler, 1964). Part of the Alaskan upper Ravenian flora may, therefore, have been derived from elements that were present but rare in the Paratropical Rain and subtropical forests of the early and middle Eocene.

The Alaskan upper Ravenian also has two species that occur in upper Ravenian upland assemblages in conterminous United States. *Alnus cuprovallis* and *Prunus axelrodi* are also known in assemblages such as that from Copper Basin (Axelrod, 1966b). The lowland upper Ravenian assemblages from conterminous United States (Puget Group, John Day Gulch assemblage of the Clarno Formation) has one species, *Pterocarya pugetensis*, that also occurs in the Alaskan upper Ravenian. The Alaskan upper Ravenian rosaceous genera have not been validly recorded from earlier Paleogene assemblages; I suggest that the strong representation of the family in upper Ravenian floras throughout western North America is a reflection of the time of diversification of Rosaceae. Note that Chandler (1964) has only recorded one rosaceous genus, the partially tropical *Rubus*, in the British Eocene.

The relationships of the Alaskan upper Ravenian to modern floristic regions are not clear. The taxa probably derived from the main elements of the Alaskan early and middle Ravenian—*Cinnamomophyllum*, *Plafkeria*, *Eugenia*? sp., and *Glyptostrobus*—are, of course, in a broad sense paleotropical. *Corylopsis* and *Pterocarya* are found today only or primarily in the Mixed Mesophytic forest, and all but four upper Ravenian genera also range into that forest type. In general the Alaskan upper Ravenian flora has its closest relationship to the broad-leaved deciduous forest of eastern Asia.

VEGETATIONAL ANALYSIS

The leaves of the dicotyledonous species represented in the Alaskan upper Ravenian have margins that are overwhelmingly nonentire. Of the 20 dicotyledons known, only 20 percent have entire margins. The leaf margin percentage is about midway between that for mesic temperate forests, such as New England, and that for mesic warm temperate forests, such as the Mixed Mesophytic forest. If, as discussed previously, stream-side types are overrepresented (this is a particularly reasonable assumption for a small assemblage), the upper Ravenian vegetation is more comparable to the Mixed Mesophytic forest. The dicotyledons represented are predominantely deciduous; five species—the *Cinnamomophyllum*, *Plafkeria*, *Eugenia*?, *Dicotylophyllum*, and a fragmentary, generically indetermined species—have a coriaceous texture and thus were probably evergreen.

The small size of the Alaskan upper Ravenian assemblage, however, does not yield a firm statistical base for a precise leaf margin analysis. The fact that 25 percent of the dicotyledons known were broad-leaved evergreen indicates that, if the forest was broad-leaved deciduous, it would have fallen in the highly warm-temperate part, that is, in the warmer part of the Mixed Mesophytic forest where broad-leaved evergreens are significantly represented. Although the assemblage clearly represents vegetation cooler than that of the middle Ravenian, just as clearly more collections are needed to determine beyond reasonable doubt the exact vegetational type represented.

Vegetationally and floristically the Alaskan upper Ravenian assemblage is most similar to the extant Mixed Mesophytic forest of Asia. To consider, however, the forest represented by the Alaskan upper Ravenian as a lineal predecessor floristically or vegetationally of the Mixed Mesophytic forest may not be valid. At least four of the upper Ravenian species—*Pterocarya pugetensis*, *Alnus cuprovallis*, *Alnus* sp., and *Sorbus carbonensis*—appear to represent lineages that survived in Alaska after the late Ravenian; during the early and middle Miocene (Seldovian) these lineages participated in the Alaskan Mixed Northern Hardwood forest, but in the late Miocene (Homerian) the lineages had adapted to a predominately coniferous forest. One lineage has since become extinct, but the lineages of *Alnus* are still represented in the extant Boreal forest. Other genera, as noted previously, are unrepresented in either the Neogene or extant Mixed Mesophytic forest, for example, *Plafkeria*, *Eugenia*?, and the genus represented by *Dicotylophyllum carbonensis*; *Plafkeria*, however, was a member of broad-leaved deciduous forest in the Pacific Northwest during the late Oligocene, but after that the lineage became extinct. In lineages in which the fossil record is even moderately known, it is apparent that vegetational types have undergone much floristic change during the Tertiary.

The particular forest represented by the Alaskan upper Ravenian probably is not the lineal predecessor of the extant Mixed Mesophytic forest. As shown later, the younger (Kummerian) assemblages indicate a return to at least subtropical conditions; what became of the forest zone represented by the upper Ravenian is not clear. This zone was probably restricted to cool upland areas; in conterminous United States, early Oligocene assemblages from the northern Rocky Mountains such as the Ruby (Becker, 1961) are vegetationally similar to upper Ravenian assemblages that apparently grew at moderate elevations in the Pacific Northwest. How extensive these cool upland areas were during the early Oligocene is unknown.

KUMMERIAN STAGE

FLORISTIC ANALYSIS

Systematic list of the Alaskan Kummerian (lower Oligocene) flora

Filicineae
  Filicales
    Schizaeaceae
      Anemia? sp.
    Blechnaceae
      Woodwardia sp.
Angiospermae
  Dicotyledones
    Fagales
      Betulaceae
        Alnus aff. *A. martini* Wolfe
        Betula sp.
      Fagaceae
        Fagus sp.
    Ranales
      Tetracentraceae
        Tetracentron cf. *T. piperoides* (Lesq.) Wolfe
      Magnoliaceae
        Magnolia reticulata Chan. and Sanb.
      Menispermaceae
        Hypserpa? sp.
      Lauraceae
        Litseaphyllum katallensis Wolfe
        Litseaphyllum presanguinea (Chan. and Sanb.) Wolfe
        Litseaphyllum presamarensis (Sanb.) Wolfe
        Litseaphyllum raminervum Potb.
        Litseaphyllum carbonensis Wolfe
        Litseaphyllum sp.
        Litseaphyllum sp.
    Rosales
      Platanaceae
        Platanus comstocki (Sanb.) Wolfe
    Sapindales
      Sapindaceae
        Allophylus wilsoni Chan. and Sanb.
    Tubiflorae
      Verbenaceae
        Holmskioldia speiri (Lesq.) MacG.?
    Incertae sedis
        Macclintockia pugetensis Wolfe
        Artocarpoides kummerensis Wolfe

The Alaskan Kummerian assemblages, although not diverse, give clear evidence of old-world affinities. All the laurels represent foliar types exemplified by the largely paleotropical *Lindera*, *Litsea*, and *Cryptocarya*. Other paleotropical elements include *Hypserpa*? and *Holmskioldia*? The Alaskan Kummerian has stronger relationships to the subtropical forest than to the Paratropical Rain forest; as noted in the discussion of the middle Ravenian assemblages, Lauraceae have their greatest abundance and diversity in the subtropical forests.

The historical floristic relationships of the Alaskan Kummerian assemblages are somewhat obscure; this is largely the result of the high representation of Lauraceae (90 percent of the specimens at loc. 11169 represent Lauraceae)—a family in which foliar taxonomy is difficult to determine—and of the small size of the assemblages. Some Kummerian laurels, for example *Litseaphyllum presamarensis*, and *Tetracentron* appear to represent species known in the lower and middle Ravenian; whether such lineages adapted to the cool late Ravenian climate and were minor elements of the Alaskan vegetation at that time is unknown. It is equally possible that such widespread lineages were totally eliminated from Alaska during the late Ravenian and spread northward again during the Kummerian. Lacking more information, I assume that many Alaskan Kummerian lineages followed this pattern.

Some lineages, for example those represented by the *Betula* and the *Fagus*, are not known in the subtropical and Paratropical Rain forests during the middle Ravenian and earlier times, either in Alaska or the Pacific Northwest. Both genera are represented in the Clarno nut bed assemblage (Scott in Chandler, 1964, p. 58), which represents Paratropical Rain forest. Both genera, however, are also represented in the temperate forest of the upper Ravenian; *Betula* is known in both the John Day Gulch and Republic assemblages, and *Fagus* is known in the presumably upper Ravenian assemblage from Joseph Creek, British Columbia. Both genera could presumably have been represented in the Alaskan upper Ravenian, and the Kummerian representatives could belong to the same lineages.

The floristic relationships of the Alaskan Kummerian to the Kummerian assemblages from the Pacific Northwest are strong; of the 12 specifically determined Alaskan species, 10 are known in the Kummerian of the Pacific Northwest. Alaska again was part of the same floristic province as the lowland Pacific Northwest, as it was in the early and middle Ravenian.

VEGETATIONAL ANALYSIS

The leaf-margin percentage for the Alaskan Kummerian assemblage is 55; this figure is based on the items in the systematic list plus nine fragmentary or poorly preserved, indetermined entities. The Kummerian percentage is the same as that for the middle Ravenian and is indicative of subtropical forest. Most species have coriaceous leaves, thus indicating an evergreen habit. The texture of the leaves in continental deposits (loc. 11169, for example) is predominantly coriaceous as it is at localities in marine rocks (loc. 11168, for example), in which coriaceous leaves would presumably have a higher probability of being preserved. The size of the leaves is small in the collections from marine rocks; the small size is probably a result of destruction of larger leaves in marine currents. Most of the leaves do not have pronounced drip-tips, although such tips are present on at least two species of Lauraceae. The liane element is poorly represented, the *Hypserpa*? sp. being the only probable representative. The vegetational analysis thus corroborates the floristic analysis in indicating that the Kummerian assemblage represents subtropical forest.

The Alaskan Kummerian assemblages, although indicating a strong floristic relationship to the correlative assemblages in the Pacific Northwest, apparently indicate a cooler climate. The Clarno nut bed and the Comstock assemblages of Oregon, and the LaPorte assemblage of northern California contain numerous representatives of Menispermaceae, Annonaceae, Icacinaceae, and Dipterocarpaceae. Leaf-margin percentages range from 64 to 67, indicating definite Paratropical Rain forest.

An interesting aspect of the Alaskan Kummerian assemblages is the presence of a probable strand element. The extinct genus *Macclintockia* seems to have been a strand plant. Although the genus is represented in nonmarine rocks of the Puget Group, the sea was presumably not far distant from the Puget basin of deposition. The common occurrence of *Macclintockia* is, however, in marine rocks or nonmarine rocks that interfinger a short distance laterally with marine rocks. The genus is known in such situations at three localities in the Pacific Northwest and at 13 localities in the Alaskan Kummerian. Koch (1963) has noted a similar situation for the Paleocene species of *Macclintockia*. Whatever family *Macclintockia* represents, it seems to have favored a lowland habitat near the sea. Another possible strand plant is *Allophylus wilsoni*. The occurrence of this species in the post-Kummerian of Oregon (Chaney and Sanborn, 1933) is in rocks that were probably laid down near the margin of a withdrawing embayment (Vokes and Snavely, 1948), and the five Alaskan occurrences—all with *Macclintockia*—are in marine rocks.

CLIMATIC SUMMARY

The early Ravenian (late, middle Eocene) vegetation of Alaska, as interpreted here, indicates that this was the warmest known period in the Alaskan

Tertiary; comparisons cannot be made, however, to the earlier Eocene, because assemblages of that age are not yet known in Alaska. The climate during the early Ravenian is indicated to have been paratropical, that is, it was characterized by a probable lack of frost, a mean annual temperature of 20°–25°C, abundant precipitation throughout the year, and little seasonality of temperature or precipitation. The mean temperature of the coldest month could have been as low as about 13°C, and thus the climate would, in that case, not be considered to be strictly tropical in the sense this term is used by most climatologists (see p. 24).

The middle Ravenian (early late Eocene) assemblages indicate a somewhat cooler climate, probably in the warmer range of subtropical climates. Frosts occurred, although they may have been mild and of short duration. Extant vegetation similar to that of the middle Ravenian lives under climates in which the temperature drops as low as -14°C, the mean annual temperature ranges from 13° to 20°C, and the mean temperature of the coldest month varies from 1° to 18°C. Precipitation would again have been abundant and distributed throughout the year.

The late Ravenian (latest Eocene) assemblage indicates considerably cooler temperatures than either the early or middle Ravenian. The climate was temperate, that is, temperatures probably at least as low as -14°C, a mean annual temperature in the range of 11° to 13°C, and the mean temperature of the coldest month in the range of -3° to 2°C.

By the Kummerian (early Oligocene), climatic conditions were again subtropical. The climate was probably about the same as that of the middle Ravenian. The probable post-Kummerian assemblages from Admiralty Island in southeastern Alaska indicate a subtropical climate which persisted into the middle Oligocene, but at the end of that time another major deterioration occurred that resulted in the cool temperate climate of the Angoonian—cooler than even the late Ravenian. During the warm periods of the early and middle Ravenian and Kummerian, the vegetation and hence the climate showed little latitudinal zonation in comparison to the cool periods of the late Ravenian and the Angoonian, when considerable zonation of vegetation is apparent.

ALASKAN PALEOGENE CLIMATES

The salient feature of the Alaskan lower and middle Ravenian and Kummerian assemblages is that they are broad-leaved evergreen forest; from the standpoint of foliar physiognomy and floristic analysis the lower Ravenian vegetation is similar to the extant Paratropical Rain and Submontane Rain forests. The assumption is here made, that the Alaskan Paratropical Rain forest (the geographic and topographic position demand this appellation) grew under climatic conditions common to these two extant forest types. Such conditions are:

(1) a lack of frost,
(2) a mean annual temperature of 20°–25°C,
(3) abundant precipitation, and
(4) no pronounced dry season.

Compare these conditions with the climatic conditions at Cordova in the Alaska region today:

(1) minimal temperature -28°C,
(2) a mean annual temperature of 5°C,
(3) annual precipitation of 3,700 mm, and
(4) precipitation of driest month 154 mm.

In regard to precipitation, no change is needed; the Paratropical Rain forest exists under less precipitation, both yearly and dry month, than Cordova receives today. Clearly, however, the temperature regime during the early Ravenian in Alaska must have been very different than it is today.

The possibility that the Alaskan Paleogene assemblages described in this report may not be at the latitude at which the enclosing beds were laid down is an important consideration. Some proponents of large-scale continental drift during the Tertiary have in fact suggested that the warm character of the Gulf of Alaska Eocene floras indicates that they lived at more southerly latitudes and the containing rocks have since drifted northward (Hamilton, 1968). The movement to the northwest of the northeastern Pacific plate has been apparently about 2–3 cm per year, but this movement is thought to have started only about 8–10 million years ago (Vine, 1966; Tobin and Sykes, 1968). More significant is that, insofar as present geologic evidence indicates, the Tertiary rocks of the Katalla and Yakataga districts are thought to be part of the upper thrust plate, that is, the rocks were about at their present geographic position 10 million years ago. Whether 35 million years previous to that the rocks were at about their present position is unknown. Grantz (1965), however, suggests that, during the earlier Tertiary, rotation of the active west limb of Carey's (1958) postulated orocline (the Katalla and Yakataga districts are on the east limb) brought western Alaska into a more southerly position relative to the east limb; the east limb of the postulated orocline appears to have been relatively stable during the rotation. What is significant here is that the presently available evidence of large-scale earth movements during the Tertiary indicates that the Eocene rocks of the Gulf of Alaska district are at approximately the same latitude at which they were deposited.

The assumption has generally been made that paleomagnetic data that approximately locate past magnetic poles also indicate the position of the rotational pole. Six Late Cretaceous pole positions have been obtained from North America; these data indicate that the pole was in the Chukchi Sea north of Bering Strait. With one exception, the Paleogene pole positions are located intermediate between the Late Cretaceous pole and the present pole. The pertinent paleomagnetic evidence thus indicates that during the Ravenian, North America was perhaps closer to the magnetic pole than at present. Given the basic assumption previously mentioned, the Alaskan Ravenian vegetation grew at latitude 60° or somewhat closer poleward.

A problem that must be discussed with that of temperature is light. Mason (1947, p. 206) has pointed out that under the present distribution of land masses relative to the poles and the tilted relation of the axis of rotation to the earth's orbit, no broad-leaved evergreen forest could possibly exist at high latitudes:

> To raise the temperature in such an area and not change the long periods of darkness would only aggravate the situation because the increased temperatures would increase the respiration rate to the point that in evergreen species the reserve food supply would soon be depleted***

Dicotyledons have adapted to polar nights in three ways: as low evergreen shrubs that have small leaves, as annual herbaceous forms, and as deciduous trees or shrubs. Evergreen plants have, of course, adapted to long polar nights. The leaves of such plants are, however, of extremely small size in comparison to the probable evergreen species of the early Ravenian. The early Ravenian species almost certainly belong to neither of the first two categories. As mentioned previously, the evergreen nature of most of the species is attested to by the coriaceous texture of their leaves; a deciduous palm, moreover, would be a most curious sight. The idea that broad-leaved evergreen plants in the mesophyll and megaphyll size classes could become dormant during winters in the Arctic is almost certainly invalid; the broad-leaved evergreen species such as palms are limited by the lowest temperature at which photosynthesis can be carried on, that is, the plants must carry on life functions at all times. Also arguing against dormancy is the fact that lineages representing many different orders, families, and genera would have had to adapt to such conditions. Natural selection should yield a forest of deciduous plants at high latitudes if the climate were warmer but the inclination of the earth's axis were the same as at present because these are the plants best able to become dormant for extended periods.

Some tropical plants are capable of attaining dormancy under short days, as shown by the experiments of Peacock and McMillan (1968) on *Prosopis* and *Acacia*. The experimental conditions these investigators used, however, were not comparable to the present light conditions at latitude 60°, because the shortest day period in the experiments was 8 hours (compared to 5 hours at latitude 60°), and the light intensity was considerably higher than the winter light intensity at 60°; note also that the species investigated are deciduous, and dormancy mechanisms are well developed in deciduous plants. Although experimental work on tropical, broad-leaved evergreen plants needs to be done, I think that Mason's (1947) point is well taken: the high temperatures at high latitudes during the Paleogene would, if the light regime was that of today, not have allowed the existence there of a mesophyllous, broad-leaved evergreen forest.

If, as seems probable, the Alaskan early Ravenian assemblages lived approximately at latitude 60° N., if, as has been shown previously, they represent a mesophyllous broad-leved evergreen forest, and if, as what is known of plant physiology indicates, such a forest could not live under the present light conditions at latitude 60° N., then the light conditions during the early Ravenian must have been significantly different from today. This line of reasoning leads me to the conclusion that the axis of rotation of the earth may have had much less—possibly no—inclination.

HISTORY OF THE ARCTO-TERTIARY CONCEPT

The Arcto-Tertiary concept has been the primary contribution of paleobotany to the field of plant geography. The concept fundamentally envisions that a broad-leaved deciduous forest of a particular floristic composition evolved in the Arctic during the Cretaceous, persisted there during the early Tertiary, and, in response to gradually cooling climate, migrated southward during the middle Tertiary into middle latitudes where the forest persists today in east-central Asia and southeastern North America. During its migration, the Arcto-Tertiary flora (or Geoflora) supposedly underwent little change in floristic composition. The fundamental significance of this concept to plant geography is clear; the concept is accepted as fact in standard textbooks on plant geography such as Cain (1944) and Good (1953). Good, in fact, bases one of his six principles of his theory of tolerance on the geofloral concept (1953, p. 361): "Great movements of species and of floras have taken place in the past and are apparently still continuing." As outlined in the present report and elsewhere (Wolfe, 1972), the concept of an Arcto-Tertiary Geoflora is not supported by our current knowledge of the Alaskan Tertiary vegetational and floristic history. I will, therefore, examine in considerable detail the history of the Arcto-Tertiary concept; it is, I think, interesting to consider how such a concept—approximately 100 years old—could gain such wide acceptance as fact.

The concept of homotaxis is the fundamental concept of which the Arcto-Tertiary and other geofloral theories are simply applications. In enunciating his theory of homotaxis, Thomas Huxley stated (1870, p. xlii): "It is possible that similar, or even identical, faunae and florae in two different localities may be of extremely different ages***" This fashionable theory was then adopted by two men—the paleobotanist Gardner and the neobotanist Gray—and the adoption had a profound effect on botanical thinking for the next 90 years.

Gray's adoption of homotaxis was an effort to explain the close floristic relationship between temperate eastern Asia—especially Japan—and temperate eastern North America. Gray (1878, p. 192--193) remarked:

> The [polar] lands***were once the home of those trees, where they flourished in a temperate climate. The cold period which followed, and which doubtless came on by very slow degrees during ages of time, must [have] long before its culmination have brought down to our latitudes, with the similar climate, the forest they possess now, or rather the ancestors of it***Geologists give the same name [Miocene Tertiary] to these beds, in Greenland and Southern Europe, because they contain the remains of identical and very similar species of plants; and they used to regard them as of the same age on account of this identity. But in fact this identity is good evidence that they cannot be synchronous. The beds in the lower latitudes must be later, and were forming when Greenland probably had very nearly the climate which it has now.

Huxley's "possible" was transferred to "good evidence" without any additional data. Note also that Gray's attitude involves little or no evolution of the plant lineages during their supposed migrations.

Gardner's writings have similarly affected paleobotanical thought. Discussing the Tertiary, and especially the Eocene, floras of Europe, Gardner (in Gardner and Ettingshausen, 1879, p. 8) stated:

> There is no great break in passing from one to the other [Eocene to Miocene floras] when we compare them over many latitudes, and but little change beyond that brought about by altered temperature or migration. But if Tertiary floras of different ages are met with in one area, great changes on the contrary are seen, and these are mainly due to progressive modifications in climate, and to altered distribution of land. Imperceptibly, too, the tropical members of the flora disappeared; that is to say, they migrated, for most of their types, I think, actually survive at the present day, many but slightly altered. Then the subtropical members decreased, and the temperate forms, never quite absent even in the Middle Eocenes, preponderated. As decreasing temperature drove the tropical forms south, the more northern must have pushed, from their home in the far north, more and more south as climates chilled, and at last, in the Miocene time, occupied our latitudes. The relative preponderance of these elements, I believe, will assist in determining the age of Tertiary deposits in Europe more than any minute comparison of species. Thus it is useless to seek in the Arctic regions for Eocene floras, as we know them in our latitudes, for during the Tertiary period the climate conditions of the earth did not permit their growth there. Arctic floras of temperate, and therefore Miocene aspect, are in all probability of Eocene age, and what has been recognized in them as newer or Miocene facies is due to their having been first studied in Europe in latitudes which only became fitted for them in Miocene times.

Gardner, as did Gray, thus had a concept of static composition of plant communities and of little morphologic evolution. Gardner's use, however, of "in all probability" indicates that he did not at that time consider the theory proved. Four years later, Gardner (1883, p. 3) still adhered to homotaxis:

> It is obvious***that floras from the south of England, supposed to be of the same age, are too widely separated in latitude from those of Greenland to permit any useful comparison being made directly between their species.

Gardner was also the first paleobotanist to direct himself to the significant problem of what flora or vegetation existed in the north when temperate floras were present at middle latitudes:

> ***the plant-beds below the London Clay [Paleocene of today] are filled with Plane and forms resembling Hazel and Lime, which represent a climate so nearly approximating to that of these latitudes at the present day that no forest of leafy trees could possibly have co-existed with them in the Arctic Circle (Gardner, 1883, p. 7).

Four years later, however, Gardner (1887a, p. 299) made a statement that the proponents of the Arcto-Tertiary Geoflora have curiously neglected:

> These determinations [of Miocene species in the Upper Atanekerdluk flora of Greenland] are for the most part based upon specimens which I regard, under any circumstances, as too fragmentary to be of any value***it would***have been just as easy to have identified them with either Cretaceous, Eocene, or living species as with Miocene. It is not a little significant that none of the finer and most distinctive plants of the Mull, the Antrim, or the Atanekerdluk floras in question were, or could be, identified with Miocene species, but were all admitted to be peculiar. Among these, we have the *Pterospermites****from Atanekerdluk*** recalling the larger leaves of Sezanne [a flora of the type section of the Paleocene]***But the best marked and most thoroughly characteristic leaves of the whole are the *Daphnogene Kanii*, Hr., and the *MacClintockia trinervis*, Hr., forms which are equally represented in the Thanet flora of Gelinden [a Belgian Paleocene flora] and in the Antrim floras***they evidently existed in one definite stage and no other, and afford paleontological evidence that should be conclusive.

This statement clearly contradicts Gardner's previous ideas and by inference brings into question the concept of homotaxis as applied to floras. Gardner was correlating floras because of similar or identical species, that is, he was using the same fundamental basis for correlation as did Oswald Heer, but he disagreed only with Heer's taxonomy. Note that Gardner did not consider any species from the Atanekerdluk to be Miocene species. Gardner had apparently arrived at the conclusion that "minute comparison of species" was, after all, the basis for paleobotany.

Not only had Gardner decided that European Paleogene plant assemblages could be correlated with high-latitude assemblages by means of standard biostratigraphic methods, he also thought that some assemblages described by Heer from the Arctic were—as Heer thought—of Neogene age. "The first acid eruptions were Miocene, as shown by the floras preserved in Iceland." (Gardner, 1887b, p. 91). Not only has Gardner's reversal in his theories been overlooked (or ignored) by the proponents of the Arcto-Tertiary concept, even Friedrich (1966), in his revision of the flora from one of the classic Icelandic Tertiary localities, has apparently been unaware of Gardner's opinion on the Icelandic assemblages.

The term "arcto-tertiary" was first coined by Engler (1882) as the "arcto-tertiäre Element." Engler (1882, p. 327) stated (freely translated) that this element was "***distinguished by numerous conifers and the numerous genera of trees and shrubs that now dominate in North America or in extratropical east Asia and in Europe." Engler (1879, p. 2–3) was aware that Gardner considered at least some of the arctic Tertiary assemblages to be of Eocene age; Engler, however, accepted Heer's age assignment of the "Arctic Miocene" as valid, and noted that the "Arctic Miocene" floras differed sufficiently from the subtropical floras of the southern European Miocene for the "Arctic Miocene" of Heer and the southern European Miocene to be isochronous. Engler's hypothesis has, in large part, been substantiated by the paleobotanical research of this decade.

The American paleobotanist J. S. Newberry, although accepting Gardner's 1879 determination of the Atanekerdluk flora as Eocene, did not accept the original homotaxial basis for that determination. Newberry (1890, p. 8) stated:

> "I called the Fort Union Group Miocene because I identified it with the plant-bearing beds of MacKenzie River, Disco Island, Greenland, etc.***This flora***has since been shown by Mr. J. Starkie Gardner to be Eocene. The Fort Union flora has many species in common with the Eocene beds of the Island of Mull, Bournemouth, etc., and holds undoubtedly the same position."

Newberry's basis for correlation was clearly not any concept of homotaxis but rather was on the community of species between any two floras. The Canadian Sir William Dawson (1888), who had read Gardner's (1887a) paper cited above, clearly concurred with Gardner. Dawson (p. 36) further discussed the several species that were common to various floras of middle and north latitudes that we now, for the most part, call Paleocene. Dawson, however, considered that some of the typical Paleocene species occurred in the Alaskan Tertiary flora described by Heer (1869) and thus he also thought the Alaskan Tertiary flora to be "Lower Eocene" or Paleocene.

Dawson's treatment was followed by that of F. H. Knowlton, who was the next paleobotanist to work on Alaskan Tertiary plants. Knowlton (1894, p. 238) remarked that "***the fossil flora of Alaska is inseparably connected with that of the Disco Island and Atanekerdluk beds of Greenland and the so-called Arctic Miocene of Spitzbergen and Sachalin. Whatever is decided concerning them must apply with equal force to Alaska." Knowlton's basis for considering the Alaskan Tertiary plants to be of Eocene age was thus more the fact that he thought they represented the same species that were also found in other "Eocene" (now Paleocene) floras both at high and middle latitudes. Knowlton (1894, p. 238), however, apparently still considered homotaxis to be probable, because he quoted Gardner (1879, p. 8) and remarked "This change of view as to the age of the so-called Arctic Miocene, as proposed by Gardner, has already received considerable confirmation from American paleobotanists, and while it can hardly be regarded as settled, it may be accepted as extremely probable." Thus, while stating a belief in the significance of homotaxis, Knowlton in practice rejected such a concept for purposes of correlation.

Some substantiating data for the "Eocene" age of the Alaskan Tertiary plants was apparently given by supposed stratigraphic relationships of some of the plant beds to beds containing marine mollusks. On the Alaska Peninsula, plants were collected from beds that were thought by Dall and Harris (1892, p. 251) to underlie conformably Miocene marine beds (the term Oligocene was not then used by Dall). Dall and Knowlton, moreover, based the assignment of the Alaskan Tertiary plants to the Eocene on two assumptions: (1) that all plant-bearing beds in Alaska were essentially synchronous and were part of their Kenai Group, and (2) that the marine lithologic unit on the Alaska Peninsula was the same unit as that found at Astoria, Oregon, some thousands of miles distant. Later Knowlton (in Dall, 1896, p. 842) concluded that these stratigraphic relationships were valid and that "***it would seem that we are justified in referring the Kenai group to the horizon of the Oligocene of European geologists." Still later, however, the Kenai Group (i.e., all plant-bearing beds in Alaska) was assigned to the upper Eocene. This assignment was based on further collections of marine mollusks from the Alaska Peninsula and their supposed stratigraphic relationships to fossil plants. Beds containing the mollusks were assigned by the geologist Atwood (1911) to the "Kenai group," and the mollusks were determined by Dall (1904 and in Atwood, 1911, p. 55) to be of Eocene age. Atwood (1911, p. 58) further stated that the invertebrates occurred "***with typical Kenai plants, in some places on the same slab of rock***" although none of the fossil plant or mollusk localities as given by Atwood were identical.

The next paleobotanist to work on the Alaskan tertiary plants was Arthur Hollick. He (in Martin and others, 1915, p. 88), in discussing the age of the Kenai Formation proper of the Cook Inlet region, considered the Kenai to be of Eocene age because "***the so-called 'Arctic Miocene' of the north circumpolar region*** [is] now generally recognized as Eocene in age." The Kenai in particular was of late Eocene age because some of the species were found in the Fort Union flora and some in Oligocene and Miocene floras, and thus a late Eocene age was a compromise. Later, however, Hollick decided that the closest relationship of the Alaskan Tertiary plants was with the Fort Union flora; he listed 12 Alaskan species that were "***characteristic or index fossils of the Fort Union formation." (Hollick, 1936, p. 22). Moreover, "In view of the facts above set forth the general similarity of the Alaska Tertiary flora to that of the Eocene in the States proper would appear to be demonstrated***" (Hollick, 1936, p. 23). Curiously, Hollick's thinking had the same internal logical schism as did Knowlton, because Hollick went on to quote Gardner's (in Gardner and Ettinghausen, 1879) argument for floral homotaxis. Also curious is the fact that Hollick listed about 30 species from rocks that the geologist P. S. Smith (in Hollick, 1936, p. 26) was "reasonably certain" on geologic and molluscan evidence were of "post-Eocene" age. Hollick (1936, p. 12) did not try to determine whether several different ages were represented in his collections; he considered that the province of the geologists. The failure of Hollick and most other paleobotanists to attempt to differentiate the various fossil plant assemblages from Alaska or elsewhere in the Arctic is puzzling. Perhaps the most astute observation was that of Chaney (1927, p. 98): "The Arctic floras of Greenland and Spitzbergen have been called Miocene in age, but it seems probable that***several horizons are represented, of which the oldest may be Eocene or Oligocene."

After publication of Hollick's work, there was no futher research on Alaskan Tertiary floras until the present decade. Most Arctic Tertiary floras, indeed, were neglected until about 1955. In the meantime, the Arcto-Tertiary concept of homotaxis was almost unchallenged. Published originally as a theory, it became increasingly accepted as a fact by almost all paleobotanists (Krystofovich, 1929; Berry, 1930b; Chaney, 1936). The most thorough discussion of the Arcto-Tertiary theory was by Chaney (1936; 1938; 1940), who remarked (1940, p. 474): "Only the evidence of their stratigraphic occurrence has subsequently demonstrated that the 'Arctic Miocene' flora of Heer comes from lower levels than the Bridge Creek and other Middle Tertiary floras from temperate latitudes." What, in fact, was the "evidence"? From the preceding discussion, in 1940 only two floras in Alaska were known to have some independent evidence as to age. One of these floras, from the Alaska Peninsula, was considered to be Eocene, but the other, from the Bering River coal field (Berg Lake flora of Chaney), was considered to be Oligocene or Miocene. Each of these two floras contained about 30 species. These data indicate that the "evidence of their stratigraphic occurrence" was, in fact, contradictory.

Chaney's concept of the Arcto-Tertiary Geoflora clearly has its roots in Clementsian ecology: "The differentiation of Tertiary vegetation into a series of climaxes, or a clisere, in response to differences in latitude and altitude was suggested by Clements almost twenty years ago" (Chaney, 1936, p. 62). The Clementsian ecology was coupled with Huxley's homotaxis: "It might even be said that if a flora from Oregon was closely similar in composition to one from Alaska, the age of the two must be different" (Chaney, 1936, p. 319). The confusion of vegetation and flora is clearly apparent in the more sophisticated Arcto-Tertiary concept of Chaney: "A separation in latitude of 20 degrees may be expected to have involved, in the past as at the present time, the development of plant assemblages of wholly distinctive composition" (Chaney, 1936, p. 319). It is, of course, true that there is some vegetational difference between the coastal conifer forest of, for example, Cordova, and the lowland forest of the Pacific Northwest today; floristically, however, the difference is much less. Approximately 70 percent of the species of woody plants near Cordova extend southward into the Pacific Northwest and about 40 percent are found at low altitudes. The present strong latitudinal zonation of vegetation has not only been extended back in time by the proponents of the Arcto-Tertiary concept, but they have also equated—erroneously I think—vegetational zonation with floristic zonation.

One of the main points of Chaney's (1940) paper was that the Arctic Tertiary floras showed clear evidence of climatic zonation and that no subtropical floras had been discovered there. A curious aspect of the development of the theory of an Arcto-Tertiary Geoflora is the vegetational treatment by the proponents of this theory of the so-called Berg Lake flora. This assemblage (loc. 3847) was originally published by Hollick, who listed 18 species (Hollick, 1936, p. 15). Although temperate genera were listed (*Populus*, *Juglans*, *Planera*, *Ulmus*, *Rhamnus*, *Cornus*, *Rhododendron*, and *Fraxinus*), an equal number of tropical elements were listed (*Artocarpidium*, *Mohrodendron*, *Magnolia*, *Cinnamomum*, *Persea*, *Malpoenna*, *Terminalia*, and *Semecarpus*). Without any revision of Hollick's taxonomy, Chaney (1940) considered the Berg Lake flora to be temperate, and he reiterated the same opinion later (Chaney, 1964). The simple utilization of leaf margin percentages (71 percent of Hollick's "species" have entire margins) would have indicated that this assemblage could not be temperate. Note that the systematic revision of Hollick's illustrated Berg Lake material indicates the presence of: *Dryopteris*, *Platycarya*, *Alnus*, *Knema*, *Myristica*, *Cinnamomophyllum*, *Luvunga*, *Melanorrhoea*, *Celastrus*, *Parashorea*, and *Alangium*. Even without additional collections, it should have been apparent that the Berg Lake assemblage floristically was closely allied to the modern tropical flora. Further, the "climatic zonation" was based on "Eocene" floras that were either small or of other ages. Three examples will illustrate this point: (1) The "temperate" Kobuk River flora was known to contain only one species, a *Ginkgo* (Knowlton in Mendenhall, 1902)—one species is hardly sufficient to determine climate or age; (2) the "temperate Eocene" Norton Sound assemblage had been shown to be of medial Cretaceous age (Martin in Hollick, 1930, p. 21); (3) the "Eocene" Simonova flora was thought to be of Late Cretaceous age (Krystofovich, 1929, p. 304). The supposed climatic zonation thus loses its validity, at least in regard to high latitude floras as they were then known.

The supposed strong resemblance mentioned by Chaney (1936) between middle Tertiary floras such as the Bridge Creek and the "Kenai flora" has never been documented. Only five species have ever been listed (Chaney, 1952, p. 107) as conspecific between Alaskan "Eocene" and the Bridge Creek; this number of species is not impressive in view of the fact that Hollick listed over 300 species from the Alaskan Tertiary.

Opposition to the Arcto-Tertiary concept began on the theoretical level in 1947. Mason (1947, p. 205) argued:

> It is difficult***to envisage such floristics as an Arcto-Tertiary flora (Chaney, 1936) in contrast to a Madro-Tertiary flora (Axelrod, Mss.) as accounting for floristic sources and centers of origin during Tertiary time. Such concepts of floristic organization and development demand unity and stability of communities in time and space beyond what is possible in the light of the nature of floristic dynamics such as are bound up with the genetics of the population, the physiology of the individual, and the diversity and fluctuation of the environment.

Mason's reasoning was apparently ignored by proponents of the Arcto-Tertiary concept. Preliminary studies of the Alaskan Tertiary floras indicated that the Arcto-Tertiary concept was invalid. We (MacNeil and others, 1961, p. 1801) stated that:

> "***evaluation by Wolfe of new and old plant collections from Alaskan rocks whose age is determined by marine invertebrates clearly shows that floras of the same age in Alaska and in Oregon or Washington are similar on the specific level."

MacGinitie (1962, p. 87) "***questioned whether any flora, as a unit, migrated during the Tertiary*** The terms 'Arcto-tertiary,' 'Madro-Tertiary,' and the like imply extremely useful concepts if we do not think of these terms as representing areas or centers from which mass migrations occurred. They picture to us in a general way the vegetation occupying an area***." MacGinitie (1962, p. 88), moreover, concurred that the Port Graham assemblage (early Seldovian of present usage) was of earlier Miocene age.

Preliminary evaluation of the earlier Paleogene floras of Alaska (Wolfe, 1964, p. N6) indicated that they contained "***abundant cycads, palms, Lauraceae, Menispermaceae, *Alangium*, and other taxa indicative of subtropical if not tropical climates." In connection with a discussion of the Kenai assemblages, it was noted (Wolfe, 1966, p. B4):

> The general aspect of the Chickaloon flora is so greatly dissimilar to the overlying Seldovian flora that it is evident that, as a floristic type, the Seldovian flora did not exist in the Kenai region during the Paleocene. The nearest well-dated Eocene floras are those of middle and late Eocene age at the head of the Gulf of Alaska***these Eocene floras look very much like those in the Eocene at middle latitudes.

At about the same time that revision of Alaskan floras was undertaken, advances were also being made in Siberia. Most of the Siberian work has been on Neogene assemblages. The classic Upper Dui flora of Sakhalin, for example, had been described by Heer (1878) as part of his "Arctic Miocene." Chaney (1940, 1964) had considered the Upper Dui as an Eocene flora, but marine mollusks indicate a middle

Miocene age for this assemblage (Krystofovich, 1960, 1964). Fotianova (1964) described a late Miocene assemblage from mollusk-dated rocks on Sakhalin, and she (1967) has also discussed the significant aspects of the Upper Dui assemblage. The Pliocene plants from the predominantly marine Enemtensky Formation on Kamchatka were described by Fotianova (in Sinelnikova and others, 1967); she remarked on the vegetational similarity of the Enemtensky and Clamgulchian assemblages and the general similarity of Neogene vegetational history at northern latitudes.

In 1967 Chaney attempted to defend the Arcto-Tertiary concept; he claimed that Neogene assemblages were unknown north of Hokkaido and Washington. Chaney was apparently unaware of the Siberian paleobotanical work (his most recent citation concerning Siberian paleobotany is a 1934 paper) and the stratigraphic work in Alaska published by Burk (1965), which included lists of plants from Neogene, mollusk-dated rocks.

Some workers might argue that the probable lack of Arctic waters pouring into the North Pacific in combination with a warmer Japan Current would lead to warmer conditions along the Alaskan coast. Paratropical Rain or subtropical forest could then extend along a narrow coastal strip, but in areas of interior Alaska, interior northern North America, and interior northern Siberia, an Arcto-Tertiary Geoflora could have persisted during the Paleogene. Such an hypothesis has no more factual foundation than the previously discussed "evidence" for the Arcto-Tertiary concept. As noted elsewhere (p. 54), a fan palm is known from interior Alaska (lat 65½° N.); the age of this palm is unknown, but its occurrence indicates that warm conditions extended at times into central Alaska. Insofar as I am aware, no definite Eocene or Oligocene assemblages are known from the Canadian shield area; analysis of the little known Tertiary plant assemblages from the Arctic Islands north of Canada may shed considerable light on the floristic and vegetational history of that region, but neither stratigraphic nor paleobotanical evidence is sufficient at present.

The existence of Paratropical Rain forest at latitude 60° N. in fact probably indicates that temperate broad-leaved deciduous forest was not present in Alaska during the early Ravenian. Because the known early Ravenian assemblages are not marginally Paratropical Rain forest, they indicate that more of this vegetation extended north from the Gulf of Alaska region. North from the northern limit of the Paratropical Rain forest, it is reasonable to expect the development of subtropical vegetation. Considering the generally slight zonation of climate during warm periods of the Paleogene, it is possible that all Alaska was occupied by Paratropical Rain and subtropical forests during the early Ravenian. Conceivably montane areas could have supported temperate vegetation, but on Taiwan today the Paratropical Rain forest is separated altitudinally from the temperate forest by 1,500 m. Mountains of that height are not known to have existed in Alaska during the Paleogene. Large mountain masses, such as the central part of the Alaska Range and the Wrangell Mountains, are largely or entirely of later Neogene origin. The deposition of the Nenana Gravel marks the beginning of the uplift of the central part of the Alaska Range, and this gravel is probably of Pliocene age (Wahrhaftig and others, 1969). The Wrangell Lava, which forms the bulk of the high country of the Wrangell Mountains, overlies the Frederika Formation of Miocene age (MacKevett, 1970). If, therefore, temperate broad-leaved deciduous forest existed during warm periods such as the early Ravenian, the forest would probably have grown as isolated pockets in montane areas of the northern and interior parts of the northern continents.

In Siberia, much the same overall vegetational development occurred as in Alaska. In the Paleogene: "The Eocene was the warmest epoch to occur during this time span. In places, the temperate forest zone moved northward, beyond latitude 50°–60° N. Proof of this shift is the fact that in the south Urals and in West Kazakhstan Late Cretaceous Platanaceae forests were succeeded by narrow-leaf, subtropical vegetation, including palms." (Vakhrameyev, 1966, p. 16). The important point is that Vakhrameyev infers that temperate vegetation must have been present north of latitude 50°–60° N., although, insofar as I am aware, no temperate Eocene assemblages are known from Siberia. The presence in western Siberia of the extensive embayment that lasted until the early Oligocene would also have favored the development in Siberia of tropical or subtropical vegetation. The forests of Siberia during the Eocene and Oligocene represent, insofar as known, dominately broad-leaved evergreen vegetation (Iljinskaja, 1963).

Also significant is the work of Dorofeyev (1963), who has described large fruit and seed assemblages from localities that are at latitudes 55°–60° N. in western Siberia. The localities are in rocks that rest on earlier Oligocene marine rocks, and Dorofeyev assigns some assemblages to the Oligocene and some to the Neogene. The assemblages are floristically allied to the broad-leaved deciduous forests. The lack of leaf assemblages makes it necessary to rely on the floristic relationships to determine the vegetation; the occurrence of genera such as *Magnolia*, *Sinomenium*, and *Leitneria* indicates a warm temperate forest. The floristic relationships of the various assemblages indicate that Mixed Mesophytic forest persisted in central Eurasia at northern latitudes well into the Miocene, just as this vegetational type did in Alaska. Some genera, for example *Magnolia*, that persisted into the Miocene in central Eurasia are not known in the Alaskan Miocene; this may indicate that the warmer summers of an interior location allowed some genera that are sensitive to this parameter of tolerance to persist longer in the interior of continental regions. Dorofeyev (1963) notes that continentality increased from the Oligocene into the Miocene.

Also significant is the recognition by Russian workers of what is probably the same Oligocene climatic deterioration as detected in western North America. Zhilin (1966, p. 2 of English translation) remarked that the floristic data from Kazakhstan "***indicate a considerable difference of climate between the early Oligocene and the second half of the Oligocene in West Kazakhstan. The Early Oligocene climate was transitional from subtropical to warm temperate***The climate at the end of the Late Oligocene can be described as warm temperate." Zhilin, of course, did not have the radiometric data available that indicate that this climatic shift was rapid (Wolfe and Hopkins, 1967).

The large late Oligocene leaf assemblage described by Krystofovich (1956) and his colleagues from latitude 48° N. in Kazakhstan also indicates that the interior vegetation was not significantly different from the Alaskan vegetation at that time. The leaf-margin percentage for this Eurasian assemblage is 18 as compared to 6–22 for the Alaskan late Oligocene assemblages. If, during the late Oligocene and most of the Miocene, continentality did not play a significant role in the differentiation of vegetation, I do not think continentality was a significant factor during the early Paleogene. During the Paleogene neither latitude nor continentality seem to have been as significant in the differentiation of vegetation as they are today.

The conclusion is, I think, inescapable that the Arcto-Tertiary concept has never had a satisfactory stratigraphic foundation. The older theories of the relationships between plants and their environments allowed, if not demanded, the acceptance of a Arcto-Tertiary Geoflora. As knowledge of genetics and physiology increased, it should have been apparent, as Mason (1947) pointed out, that the Arcto-Tertiary concept was invalid. The discarding of this concept, which is indicated by the Alaskan and Siberian assemblages of fossil plants, is fundamental to an understanding of floristic and vegetational history.

A THEORY OF THE ORIGINS OF THE MIXED MESOPHYTIC FOREST

The Mixed Mesophytic forest is a complex floristic and vegetational type (Wang, 1961). The vegetation, which is characteristic of a warm temperate climate, is floristically diverse, notably in families such as Salicaceae, Juglandaceae, Betulaceae, Fagaceae (including the "lobed" oaks), Ulmaceae, Hamamelidaceae, Rosaceae, Aceraceae, Rhamnaceae, and Ericaceae. Notable also is the presence of numerous monotypic and oligotypic genera, for example, the woody ranalean *Cercidiphyllum*, *Euptelea*, *Trochodendron*, and *Tetracentron*. No single genus or family dominates the canopy of the forest; next to the tropical forest types, the Mixed Mesophytic forest is the most complex and most diverse vegetational type extant.

The origins of this forest have attracted the attentions of both botanists and paleobotanists for over a century. As noted in the preceding section of this report, the widely accepted explanation of the origin of this forest—the concept of an Arcto-Tertiary Geoflora—is contradicted by what is known of the Tertiary stratigraphy at high northern latitudes (see previous sections). The vegetational and floristic history of the Northern Hemisphere has been confused in large part because of the apparent confusion by many paleobotanists of vegetation and flora (see also p. 40). This confusion is inherent in such a concept as a "Geoflora," which includes both taxonomic composition and vegetational type. Similarly it must be emphasized that the Mixed Mesophytic forest is recognized by both taxonomic composition and vegetational type. Only by keeping distinct the history of warm temperate vegetation from the history of lineages can the origins of the Mixed Mesophytic forest be understood. Warm temperate vegetation has probably always been present on the earth since the time of origin of land plants. Clearly, however, the composition of warm temperate vegetation prior to the origin of the angiosperms and their assumption of dominance in the Late Cretaceous is of little value to this discussion. Although some workers have stated that the "Arcto-Tertiary Geoflora" should be called the "Arcto-Cretaceo-Tertiary Geoflora," the evidence for the presence of most mixed mesophytic genera in the

Cretaceous has never been documented. Considering the nature of Late Cretaceous pollen floras (see, for example, Góczán and others, 1967), in which almost no extant dicotyledonous genera have been detected, it is clear that Late Cretaceous vegetation could not have represented a Mixed Mesophytic forest. Similarly, Paleocene floras, although somewhat more modern in taxonomic composition, contain numerous extinct genera. Some mixed mesophytic genera can be recognized, for example, *Alnus*, *Corylopsis*, and *Sinowilsonia*, but the inclusion in the same assemblages of genera such as *Fagopsis*, *Pterospermites*, *Grewiopsis*, *Macclintockia*, and numerous species of *Dicotylophyllum* that cannot be relegated to any extant family indicates that none of the Paleocene forests can properly be classed as Mixed Mesophytic. Indeed the fact that a few species, notably *Cocculus flabella*, *Fagopsis groenlandica*, *Dicotylophyllum flexuosa*, and *D. richardsoni*, appear to have dominated the warm temperate vegetation over very broad areas and that the Paleocene assemblages are not particularly diverse indicates also that vegetation resembling the Mixed Mesophytic forest was not in existence during the Paleocene. Not until the Eocene did significant numbers of mixed mesophytic genera become recognizable.

In the following discussion I have used in many instances only generic records. My reason for this in part stems from the fact that the occurrences of many mixed mesophytic genera are documented by diverse organs—fructifications, leaves, and pollen—and it cannot, of course, be determined in most instances whether a particular seed belongs to the same lineage as a particular leaf species. The assumption is made, for example, that, if a particular mixed mesophytic genus is known from non-foliar organs only from tropical types of vegetation in the Eocene, an Oligocene leaf species from temperate vegetation was probably derived from a tropical lineage. The record of lineages known from leaf species is more complete from the late Eocene and younger horizons that in pre-late Eocene time. Note that in the following discussion the unqualified use of the word tropical in reference to vegetation denotes both Tropical and Paratropical Rain forest.

The Alaskan early and middle Ravenian (late middle and early late Eocene) and Kummerian (early Oligocene) assemblages represent, respectively, Paratropical Rain forest and the last two subtropical forest (p. 35). These assemblages contain a significant number of mixed mesophytic genera and lineages, including:

Carya (*bendirei* type)
Platycarya
Pterocarya
Alnus
Betula sp.
Fagus sp.
Ulmus (*newberryi* type)
Tetracentron piperoides
Cocculus
Eucommia
Liquidambar?
Platanus (*bendirei* type)
Toona
Euodia
Rhus
Celastrus
Sageretia
Zizyphus
Vitis
Alangium
Clethra

Most of these genera and many others have been recorded from tropical Eocene and early Oligocene floras in the Pacific Northwest (Wolfe, 1968, and unpublished data; Scott in Chandler, 1964):

Carya
Juglans
Alnus
Betula
Fagus
Quercus
Calycocarpum
Euptelea
Cercidiphyllum
Tetracentron
Liriodendron
Magnolia
Hydrangea
Fothergilla
Hamamelis
Liquidambar (*pachyphylla* type)
Platanus
Cladrastis (*japonica* type)
Sageretia
Vitis
Alangium
Nyssa

Additional mixed mesophytic genera have been recorded from various subtropical or tropical Paleogene assemblages in Eurasia and North America:

Populus
Salix
Comptonia
Myrica
Carpinus
Celtis
Zelkova
Cinnamomum
Exbucklandia
Fortunearia
Sinowilsonia
Rubus
Pachysandra
Ailanthus
Cedrela
Ilex
Rhus
Toxicodendron
Acer
Ampelopsis
Paliurus
Tilia
Actinidia
Eurya
Gordonia
Cornus
Diospyros
Symplocos
Halesia
Styrax
Ehretia
Catalpa
Sambucus

The significant fact is that these genera occur with regularity in fossil assemblages that on physiognomic criteria and overall floristic composition represent tropical or subtropical vegetation. Significant also is the fact that some of these genera (*Platycarya, Tetracentron, Trochodendron, Euptelea, Calycocarpum, Fortunearia*), although apparently widespread in the Paleogene tropical forests, have not been recorded from the Mixed Mesophytic forest as represented in the Neogene of western North America. The evidence thus indicates that some of the most characteristic genera now endemic to the Mixed Mesophytic forest attained their widest distribution in the Paleogene tropical forests and not in the Neogene Mixed Mesophytic forest. The modern distribution of many mixed mesophytic genera and alliances, in fact, indicates that many are fundamentally tropical or subtropical today, the mixed mesophytic representatives being only warm temperate outliers; the following genera exemplify this distribution:

Quercus
Akebia
Cocculus
Calycocarpum
Euodia
Vitis
Liriodendron
Magnolia
Liquidambar
Celastrus
Sageretia
Zizyphus
Alangium
Clethra

It is, therefore, not surprising that paleobotanical evidence also indicates that many mixed mesophytic genera adapted to warm temperate conditions after attaining a wide distribution in tropical forests during the Paleogene.

The late Ravenian (latest Eocene) assemblages from Alaska, British Columbia, and conterminous United States record a pronounced interval during which most of the region was occupied by broad-leaved deciduous or at least subtropical forest that had a diverse deciduous element (p. 33). By the latest Eocene, some taxa that, earlier in the Tertiary, were distributed in the Paratropical Rain and subtropical forests had adapted to more temperate climates. The Alaskan late Ravenian assemblage includes:

Populus?
Salix
Juglans (*Cardiocaryon*)
Pterocarya pugetensis
Alnus (*cappsi* type)
Corylopsis
Rhamnus
Tilia

To this list can be added genera known from late Ravenian floras farther south that display a similar distribution pattern:

Fagus
Betula (*papyrifera* type)
Comptonia
Carya (*bendirei* type)
Ulmus
Zelkova
Tetracentron (*piperoides* type)
Acer (*rubrum* type)
Vitis

These warm temperate forests were apparently taxonomically depauperate in comparison with the Mixed Mesophytic forest of the Neogene. Note that Hamamelidaceae are almost absent, in contrast to the widespread occurrences of *Liquidambar* and *Exbucklandia* in the middle Miocene of the Pacific Northwest. *Cercidiphyllum*, *Euptelea*, *Liriodendron*, *Magnolia*, and *Platycarya* are also absent from these late Ravenian temperate assemblages, although these genera are present in the early Oligocene tropical assemblages in the Pacific Northwest. Some genera had apparently not achieved a distribution outside the tropical vegetation during the latest Eocene and probably extended into the temperate regions only at a later time. Also of significance is that genera such as *Acer* are represented by only a few species in the late Ravenian but are well represented in later temperate vegetation, and, of course, "lobed" oaks are totally lacking in the later Ravenian assemblages. Although vegetationally the late Ravenian temperate forest is probably somewhat similar to the extant Mixed Mesophytic forest and although some floristic similarities exist, in general the late Ravenian temperate forest is not a Mixed Mesophytic forest.

During the early to middle Oligocene, temperate vegetation was apparently restricted to upland regions in the interior of the continent. Such assemblages as the Ruby of Montana (Becker, 1961) and, in part, the Florissant of Colorado (MacGinitie, 1953) represent this type of vegetation. Various lineages and genera are represented in these two assemblages that indicate a floristic relationship to late Ravenian vegetation. Species of *Acer*, *Dipteronia*, *Fagopsis*, *Alnus*, Rosaceae, and Ulmaceae were represented in the early and middle Oligocene upland and late Ravenian assemblages by identical or closely related species. Note, however, that most characteristic mixed mesophytic genera lacking in the late Ravenian are also lacking in the early and middle Oligocene temperate vegetation but are present at that time in tropical vegetation. Some groups, for example, the "lobed" oaks and most Ericaceae, are not known in any early and middle Oligocene assemblages. As with the late Ravenian assemblages, the upland early and middle Oligocene assemblages represent warm temperate vegetation but not the mixed mesophytic forest.

The rapid climatic deterioration of the late Oligocene (the deterioration is probably of latest middle Oligocene age in the marine megafossil chronology but is apparently of early middle Oligocene age in the vertebrate chronology, that is, about 32 million years ago) led to wide lowland areas of warm to cool temperate climate. Assemblages such as those of Angoonian age in Alaska (Tsadaka) and Oregon (Bridge Creek, Willamette) represent broad-leaved deciduous forest; in Oregon broad-leaved evergreens such as *Cinnamomum*, *Paleophytocrene*, and *Willisia* were a minor element in the vegetation (Wolfe, in Peck and others, 1964), but this element is represented only by *Willisia* in southeastern Alaska and is lacking in the Cook Inlet and other regions of Alaska. Floristically this vegetation is closely related to that of the uplands of the early and middle Oligocene, as shown by numerous closely related species of *Alnus*, *Betula*, Rosaceae, *Acer*, and *Dipteronia*. Added to the Angoonian assemblages in Oregon, however, are the following genera or lineages that have not been recorded from older upland assemblages but were found in the lowland early and middle Oligocene:

Engelhardtia	*Liquidambar*
Cercidiphyllum	*Platanus* (*dissecta* type)
Cinnamomum	*Toxicodendron*
Exbucklandia	

This element appears to have been added to the temperate vegetation during, or shortly after, the major climatic deterioration. In Alaska, but not in Oregon, Salicaceae played a major role in the vegetation. Some mixed mesophytic genera that had been members of the temperate or the tropical forest of the early and middle Oligocene apparently became extinct in western North America at about the time of the deterioration; these include *Platycarya*, *Tetracentron*, *Trochodendron*, *Euptelea*, and *Calycocarpum*. Renewed warming in the latest Oligocene resulted in marginally subtropical (leaf margin percentages are about 40) assemblages in at least coastal Oregon, and marginally warm temperate assemblages in Alaska. In Oregon, Lauraceae were represented by several species, but broad-leaved deciduous species were still apparently dominant members of the vegetation; most of these species are either conspecific with, or closely related to, species of the older late Oligocene temperate assemblages. In Alaska, the flora was more diverse during late Oligocene than during the earlier and cooler part of the Angoonian; broad-leaved evergreens are represented by *Engelhardtia* (characteristic involucres have been found in late Angoonian rocks in the central Alaska Range), *Ilex*, and *Alangium*. Pollen records include *Cedrela/Melia*. Rosaceae also were apparently more diverse in Alaska than previously and include *Duchesnea* or *Fragraria*, *Rubus*, *Sorbus*, and *Spiraea*. The temperate vegetation seems to have been enriched, partly through the adaptation of tropical lineages to temperate climates and partly through the diversification of lineages previously present in temperate vegetation.

The early Miocene (early Seldovian) seems to have been cooler than the latest Oligocene. Leaf-margin percentages in Oregon for early Miocene assemblages are about 25 and in Alaska are about 12. Despite the cooling, the broad-leaved deciduous forest seems to have been taxonomically more diverse than anytime in the Angoonian. In Oregon, the Collawash assemblage contains representatives of 140 megafossil and about an additional 20 microfossil entities; this assemblage is the richest Neogene assemblage known in North America, although the middle Miocene Latah flora of Washington approaches the Collawash in diversity. The inclusion in the Collawash of diverse Salicaceae, Juglandaceae, Betulaceae, Fagaceae (including "lobed" oaks), Ulmaceae, Hamamelidaceae, Rosaceae, Aceraceae, and Ericaceae, along with some broad-leaved evergreens such as Lauraceae, indicates that floristically the warm temperate vegetation was a Mixed Mesophytic forest for the first time. This vegetation in Oregon, however, lacked some genera that were present earlier in the Tertiary in North America and today are members of the Asian or east American Mixed Mesophytic forest, such as, *Platycarya*, *Euptelea*, *Trochodendron*, *Tetracentron*, *Calycocarpum*, *Corylopsis*, *Sinowilsonia*, *Fortunearia*, *Eucommia*, and *Dipteronia*. Some of these genera apparently did not adapt to temperate conditions in western North America, although some, for example, *Dipteronia*, have a record in the temperate vegetation of this region from at least the late Eocene through the late Oligocene. These genera were following a different pattern in western North America than in Eurasia.

Families such as Betulaceae, Salicaceae, Rosaceae, and Aceraceae, and genera such as *Fagus* and *Castanea*, that were taxonomically depauperate in the Paleocene and Eocene floras, although present in the Paleogene subtropical and tropical forests, were able to adapt readily to the new temperate climates and diversified. From both described and undescribed material from the Tertiary of western North America, table 8 has been compiled. Although the table may reflect in part the lesser knowledge of Eocene and Pliocene floras as compared to other epochs, the table probably reflects primarily the relative diversity of the families. Ericalean pollen is known from earlier Paleogene rocks but is rare. Lineages of some Rosaceae and Aceraceae can be traced to the upland floras of the early middle Oligocene, but in the instances of Salicaceae and Betulaceae, new morphologic types appeared, apparently suddenly, and diversified rapidly. The diversification of *Populus*, Betulaceae, Rosaceae (at least in part), and Aceraceae, seems to have reached its maximum in the early and middle Miocene in the Mixed Mesophytic forest as far as the west American record is concerned. Note that the diversity of Betulaceae and Aceraceae was greater in the Mixed Mesophytic forest of the Miocene of Asia (Tanai, 1961), as it is today in Asia, than in North America. Both *Salix* and Ericaceae, although present in considerable diversify in the Miocene Mixed Mesophytic forest, continued to diversity in western North America after the decline of the Mixed Mesophytic forest here; Ericaceae continued to diversify also in the Mixed Mesophytic forest of Asia, as evidenced by the richness of genera such as *Rhododendron*. Such diversification is unparalleled in North America. Note that warm temperate rosaceous and ericaceous genera display the greatest degree of endemism in the extant Mixed Mesophytic forest. This endemism probably indicates that many of these genera are of more recent origin; by the time they had evolved, the Alaskan forest definitely indicates a cooler climate than was present in conterminous United States (Wolfe and Leopold, 1967) and would thus inhibit the interchange between Asia and North America of more newly evolved warm temperate genera. An additional barrier to the dispersal of some taxa during the Miocene may have been precipitation: the Mixed Mesophytic forest of the Pacific Northwest includes numerous genera that have, at least during the later Tertiary, displayed a proclivity for summer dry climates. Included are:

Umbellularia
Cercocarpus
Holodiscus
Heteromeles
Lyonothamnus
Peraphyllum
Ceanothus
Colubrina
Karwinskia
Xylonagra
Garrya
Arbutus
Arctostaphylos

The mechanics of the atmospheric circulation of the earth demand that the west coasts of major land masses be winter wet; although the Miocene Mixed Mesophytic forest in the Pacific Northwest probably had much more summer precipitation than at present, the climate probably could not have been as summer-wet as in the regions where the Mixed

TABLE 8.—*Specific diversity through time of some families represented in the west American Tertiary*

[The term "many" indicates numerous species, but the taxonomic status is not satisfactory]

Family or genus	Paleocene	Eocene		Oligocene			Miocene		Pliocene
				early	early	late	early and middle	late	
		tropical	temperate	tropical	upland				
Taxodiaceae	4	3	3	3	3	5	5	2	2
Pinaceae	?	2	7	0	9	13	13	21	23
Salicaceae	1	3	3	0	8	10	25	35	many
Juglandaceae (excluding *Englehardtia*)	3	13	1	5	3	8	10	6	3
Betulaceae	2	4	4	3	2	15	12	12	4
Ulmaceae	4?	11	2	3	3	8	6	3	1
Trochodendraceae (s.l.)	5	5	1	4	1	1	1	1	0
Magnoliaceae	?	4	0	4	0	2	2	1	0
Lauraceae	many	many	3	many	2	7	7	1	1
Menispermaceae	many	many	0	many	0	2	1	0	0
Hamamelidaceae	6	6	1	3	0	4	4	1	0
Rosaceae	2?	2	8	1	17	12	20	28	28
Aceraceae	2	2?	3	0	5	6	11	6	4
Ericaceae	0	0	1	0	0	2	4	12	14

Mesophytic forest still survives. Alaska receives more summer precipitation today than the Pacific Northwest, and the same relationship probably prevailed in the Miocene. Thus, the cooler climate in combination with the wetter summers may have acted as an effective barrier to the exchange of many genera between Eurasia and western North America.

The Mixed mesophytic forest of the Miocene of western North America thus seems to have had three major sources:

1. Genera derived directly from the Paleogene tropical and subtropical forests,
2. genera that had adapted by the late Eocene or early to middle Oligocene to interior warm temperate uplands, and
3. genera that evolved during the Oligocene and Miocene from lineages that were associated with either group 1 or group 2.

The history of the Mixed Mesophytic forest has involved little if any significant amount of migration of the association on a major scale. As a recognizable floristic and vegetational unit, the Mixed Mesophytic forest developed in the early and middle Miocene from the depauperate temperate vegetation that resulted from the middle late Oligocene climatic deterioration. The progressive enrichment of the Mixed Mesophytic forest in Asia continued during the Neogene, probably both by diversification of lineages already part of the forest and by extensions into the forest of subtropical and tropical lineages. In western North America, the Mixed Mesophytic forest was eliminated by increasingly pronounced summer-dry conditions by the end of the middle Miocene, although individual lineages of the Mixed Mesophytic forest persist to this day in western North America.

In eastern North America, the Mixed Mesophytic forest does not seem to have been as rich at any point in time as the Mixed Mesophytic forests of either eastern Asia or western North America. Almost all woody genera now present in the eastern Mixed Mesophytic forest were also present in the west American forest. Although the Neogene fossil record in eastern North America is scanty, megafossil and microfossil assemblages from the middle and late Miocene of the central Atlantic coast states indicate that numerous Mixed Mesophytic genera were apparently not present there that were in western North America:

Gingko
Keteleeria
Pseudolarix
Metasequoia
Zelkova
Schoepfia
Mahonia
Litsea
Lindera
Umbellularia
Cinnamomum
Cercidiphyllum
Exbucklandia
Cercocarpus
Holodiscus
Lyonothamnus
Peraphyllum
Cedrela
Euodia
Pistacia
Colubrina
Ceanothus
Karwinskia
Zizyphus
Xylonagra
Garrya
Arbutus
Clerodendrum
Idesia

Although many of these genera are apparently less tolerant of summer moisture, others are typical of regions of summer-wet climate today. Certain of the genera would be expected in eastern North America if there had been an Arcto-Tertiary Geoflora that gradually migrated southward. The apparent depauperateness of the eastern Mixed Mesophytic forest may be the result of four major factors:

1. The middle to late Oligocene climatic deterioration that probably would have left—as it did in northwestern North America—a depauperate flora,
2. the elimination at the same time of the tropical forest entirely or in large part from southeastern United States, thus making it more difficult for a progressive enrichment of the temperate forest from the tropical forest,
3. the essential isolation of eastern North America both from Europe and western North America, and
4. the little topographic diversity of eastern North America.

The first two factors may account for the poor development of fundamentally tropical families in the eastern Mixed Mesophytic forest. At present, only two genera of Lauraceae—*Persea* and *Sassafras*—are represented in the eastern forest, as compared to the Miocene of western North America where six genera (*Cinnamomum*, *Lindera*, *Litsea*, *Persea*, *Sassafras*, and *Umbellularia*) were represented, and to the forest of eastern Asia where six genera have been, and are now, represented (*Cinnamomum*, *Lindera*, *Litsea*, *Neolitsea*, *Persea*, and *Sassafras*). In western north America, the Miocene forest, in addition to Lauraceae, contained many genera of fundamentally subtropical or tropical relationships: *Cedrela*, *Clerodendrum*, *Cocculus*, *Colubrina*, *Diospyros*, *Exbucklandia*, *Gordonia*, *Idesia*, *Karwinskia*, *Magnolia*, *Nyssa*, *Oreamunoa*, *Oreopanax*, *Pistacia*, *Schoepfia*, *Vitis*, *Zizyphus*; many of these same genera plus many other genera were and are well represented in the Asian Mixed Mesophytic forest. In eastern North America, the comparatively few genera of this type are: *Berchemia*, *Calycocarpum*, *Cocculus*, *Gordonia*, *Magnolia*, *Nyssa*, *Symplocos*, and *Vitis*. Genera of Lauraceae, Leguminosae, and Sapotaceae that were abundant in the tropical Paleogene forest of eastern North America are, for the most part, unrepresented by species in the Mixed Mesophytic forest—Tertiary or extant—of the same region.

The fourth factor may account for the little generic diversification that took place in families such as Rosaceae and Ericaceae, and the third factor—isolation—prevented any great amount of floristic interchange with regions that had topographic diversity. It should be noted that the Paleogene tropical forest of eastern North America apparently had few genera in common with the Paleogene forest of western North America and Eurasia; the floristic isolation of eastern North America seems to have been ancient (MacGinitie, 1969). Most of the vicarious species between eastern North America and eastern Asia today belong to genera that are found in Paleogene tropical forests and that have—in western North America and Eurasia—shown a definite tendency to become readily adapted to temperate conditions; these same genera have in some instances been recorded from the Paleogene tropical forest of eastern North America (Gray, 1960). Historical factors have, therefore, probably been responsible for the independent development of the Mixed Mesophytic forest in Eurasia, western North America, and eastern North America, as well as for the greater similarity between the forest in the Miocene of western North America and Eurasia.

As has been emphasized previously (Wolfe, 1972), the lineages that are represented in the Mixed Mesophytic forest—whether that extant in eastern Asia and eastern North America or that of the Neogene of western North America—are in this forest coincidentally. The lineages have, in some instances, followed similar patterns of distribution, but as the history of the lineages has become clearer through paleobotanical work, several different patterns have emerged. I think that as more work is done, many more patterns will become apparent. Some lineages have followed a general pattern for a longer period than have other lineages, for example, some lineages have been adapted to temperate climates for a longer period. Some lineages have participated in the temperate vegetation of North America but became extinct before the optimal development of the Mixed Mesophytic forest. The warm temperate forest of the Northern Hemisphere has been and will continue to be in a continual state of flux.

> Lineages have entered and departed from this vegetation at different times in different places in response to different and changing parameters of the tolerances of the individual members of the lineages. Various lineages have diversified in the warm temperate vegetation at different times and in different regions. The history of the Mixed Mesophytic forest is complex and can be understood best by reconstructing the patterns of distribution in time and space of the component lineages (Wolfe, 1972, p. 231).

PALEOGENE TROPICAL MIGRATION ROUTES

The existence in Alaska during parts of the Paleogene of Paratropical Rain forest has an important bearing on the times and routes of migration of tropical lineages (Wolfe, 1975). In a significant paper, van Steenis (1962) has discussed in detail the significance of trans-Pacific angiospermous genera and families, and he concludes that the only means of attaining such a bicontinental distribution for a tropical group is by means of former trans-Pacific land bridges that were within present tropical latitudes.

The disjunctions of northern warm temperate or subtropical genera between North America and Eurasia are, as van Steenis (1962, p. 243) points out, in many instances involved with the disjunctions of tropical groups. The probable phytogeographic history of many warm temperate or subtropical disjunct groups has been discussed in the preceding section of this report; such disjunctions have, in many instances, the same basic historical pattern as the disjunct tropical groups.

Van Steenis (1962) is primarily concerned with the "Amphi-transpacific" genera and families that are megatherms (that is, "adapted to tropical climate"; van Steenis, 1962, p. 239). He logically concludes (p. 290) "****that there is no reason to assume significant changes during the geological past in the thermo-ecology of the majority of the tropical genera concerned.*" Tropical lineages could not, therefore, have adapted to cool conditions to cross, for example Beringia, and then become readapted to tropical conditions. Van Steenis (p. 271–322) also discusses seven other explanations for the present distribution of tropical groups, some of which, for example, polyphyletic origins, are almost certainly improbable. The only explanation that van Steenis considers credible is that of transoceanic land bridges at tropical latitudes.

The data presented here indicate that van Steenis' conclusion is, at least in regard to some tropical disjunctions, not necessary. He was led to disregard the significance of the Beringian route for tropical genera for two major reasons. First, he assumed (1962, p. 271) a "steady state" framework for the earth, that is, there has been little or no continental drift, the inclination of the axis of rotation has been unchanged, and latitudinal climatic zonation has changed little. From these assumptions he concludes (p. 271) that the areas between latitudes 50°–70° N. "***might have been warm-temperate to subtropical and the majority of the trees must have been deciduous." Second, van Steenis (p. 271–281) accepts without question the concept of the Arcto-Tertiary Geoflora and as well considers the London Clay flora to be atypical of Eocene vegetation at latitude 50° N. Chandler (1964, p. 86–89) has adequately invalidated van Steenis' conclusions regarding the London Clay; that assemblage almost certainly represents warm Paratropical to marginally Tropical Rain forest (Richards, 1952, p. 154).

Van Steenis (1962, p. 273) recognizes the physiological problems encountered if tropical plants had grown at high northern latitudes: "Though at present low temperature is more important than light, increase of the world's temperature will, at arctic latitudes, very soon find its bottleneck in the form of this same light." He thus considers reasonable the existence during the Paleogene of broad-leaved deciduous and conifer forests at high northern latitudes. Discounting the occurrence of palms in the Greenland Tertiary, van Steenis (p. 272) states:

> ***palms have never been found beyond about 50° latitude. Their distribution forms a most important argument for the conservative view of only slight climatic changes in zonation at medium latitudes and a full confirmation of the steady state principle.

No mention is made of the well-documented occurrences of fan palms at latitudes 57° and 61.5° N. in Alaska (Hollick, 1936).

The data given in the present report clearly indicate that tropical forests (in van Steenis' concept of tropical vegetation, the Paratropical Rain forest is included) indeed existed in Alaska. The Alaskan early Ravenian (late middle Eocene) assemblages include some of van Steenis' "Amphi-transpacific" genera: *Sageretia*, *Meliosma*, and *Saurauia*. Van Steenis (1962, p. 268), moreover, considers that more significant than genera are the various exclusively "pantropical larger megatherm families" and the "tropical *pro majore parte*" pantropical families. In the first category are the early Ravenian Annonaceae, Myristicaceae, and Lecythidaceae (including Barringtoniaceae), and in the second category are the early Ravenian Palmae, Menispermaceae, Lauraceae, Rutaceae, Anarcadiaceae, Icacinaceae, Sapindaceae, Vitaceae, Theaceae, Myrtaceae, and Verbenaceae. Added to these are the early Ravenian groups that are exclusively paleotropical (p. 28). Considering the small size of the known Alaskan early Ravenian flora, the families listed above are impressive evidence that many pantropical or "Amphi-transpacific" genera and families could have attained such a distribution by way of Beringia. By analogy, some tropical groups may have been distributed by way of a high latitude Southern Hemisphere migration route, although paleobotanical documentation for such a route is lacking.

Considering that many fundamentally tropical groups were distributed through Beringia and into middle latitudes of western North America during the Tertiary, it is significant that the present tropical floras of the Americas and southeastern Asia do not have more genera in common today. The known Paratropical Rain forest of the Paleogene of western United States contains the following now exclusively paleotropical groups:

Menispermaceae: *Anamirta*, *Diploclisia*, *Hypserpa*, *Limacia*, *Pycnarrhena*, *Tinomiscium*, *Tinospora*
Myristicaceae: *Knema*, *Myristica*
Annonaceae: *Cananga*
Olacaceae: *Erythropalum*, *Olax*
Hamamelidaceae: *Altingia*
Rutaceae: *Euodia*, *Luvunga*
Anacardiaceae: *Dracontomelon*, *Poupartia*
Icacinaceae: *Iodes*, *Miquelia*, *Phytocrene*, *Pyrenacantha*, *Stemonurus*
Vitaceae: *Tetrastigma*
Barringtoniaceae: *Barringtonia*
Dipterocarpaceae: *Parashorea*
Alangiaceae: *Alangium*
Cornaceae: *Mastixia*

The fact that these genera have not survived in the American tropics may be the result of the major climatic change during the Oligocene coupled with the small land area of humid tropical and paratropical climates in North America (Wolfe, 1975).

Disjunction of tropical genera and families, therefore, may not be the result of migrations of lineages across tropical latitude land bridges that have subsequently disappeared. Some of the migrations were probably by way of Beringia. The times of such migrations could have been during the Paleocene because *Eohypserpa*, *Macaranga*, *Melanolepis*, and *Sabalites* are known from the Alaskan Paleocene (Wolfe, 1966; Burk, 1965), during early Eocene when warming in Alaska is assumed to have occurred simultaneous with that known in middle latitudes, or during early late Eocene or the early Oligocene when the very warm subtropical forest indicates that locally warmer areas might have allowed some tropical lineages to have migrated through Alaska. Chance dispersal through tropical or middle latitudes across various islands should also not be overlooked as a means of attaining pantropical or "Amphi-transpacific" distribution; such migrations are "land-bridge dispersals" of van Steenis (1962). It is doubtful if each tropical disjunction can be explained in terms of precisely the same pattern in regard to both time and space. I think that various patterns, as discussed in reference to the Mixed Mesophytic forest, will be found to be valid in explaining tropical disjunctions.

SYSTEMATICS

The preservation of many specimens is not so good as could be desired. In most, venation below the fourth order is not preserved. Sufficient characters are preserved, however, to allocate most of the material to genera. If the specimen is fragmentary but well preserved, no specific epithet is assigned in most instances. I emphasize that the apparently modern aspects of the floras at the generic level may be a reflection of the lack of preservation of fifth and sixth order venation.

Uncleared herbarium specimens of foliage of tropical plants are typically difficult to compare to fossil leaves. The thick texture of most tropical leaves obscures the venation pattern so that in most instances venation below the level of secondaries or tertiaries cannot be clearly seen. The use of cleared material is almost mandatory for the study of assemblages such as that of the early Ravenian in Alaska. To a certain extent, therefore, the determinations made here are a reflection of the extent of the U.S. Geological Survey's reference collection of cleared leaves. At this time (May 1971) this collection comprises about 2,000 species representing about 1,200 genera; over 1,000 of these species are of tropical distribution.

The systematic lists of Eocene assemblages such as the early Ravenian differ markedly in one important aspect from modern floras. Members of Sympetalae are notably scarce or lacking in Eocene and older assemblages. Families of Sympetalae that are diverse in the tropical regions today—Rubiaceae, Boraginaceae, and Bignoniaceae, for example—are proportionately underrepresented in most Eocene assemblages in comparison with their present diversity; this observation applies to both leaf and seed floras. I suggest that the diversification of many families of Sympetalae was largely post-Eocene.

With the exception of a few specimens in the collections of the California Academy of Sciences (here abbreviated CAS) and some comparative material from the collections of the University of California Museum of Paleontology (UCMP), all figured or cited specimens are deposited in the United States National Museum (USNM). Rather than retouch photographs, which can be highly misleading, I have included camera lucida drawings of most critical features.

The material from the Gulf of Alaska Coastal Province illustrated by Hollick (1936) includes some specimens that, although determined to species by Hollick, are inadequate for either generic or specific assignment. Species that are here relegated to *nomina dubia* are:

Piper disputabilis Hollick. Although the specimen matches well the specimen of *Cornus irregularis* Holl. from the same locality, the type of *P. disputabilis* is extremely fragmentary and is not a satisfactory name-bearing type.

Mohrodendron inopinum Hollick. Hollick's specimen lacks both base and apex, and is, therefore, not a satisfactory name-bearing specimen.

Rhododendron crassum Hollick. the venation below the level of secondaries is lacking.

Hollick (1936) also based citations of previously described species on poor material. The following citations should not be considered valid and cannot be satisfactorily synonymized to other species:

Canavalia eocenica Berry
Rhamnus decheni Weber

Hollick (1936, p. 130, pl. 93, fig. 3) cited *Tetrapteris harpyiarum* Ung. as occurring at locality 3879; in fact, the specimen came from locality 5892 in the Chickaloon Formation of the Matanuska Valley. This specimen belongs to *Dicotylophyllum flexuosa* (Newb.) Wolfe (1966, p. B11). Name-bearing specimens of Hollick (1936) from the Gulf of Alaska region not discussed above are:

Asplenium alaskanum Holl. = *Dryopteris alaskanum* (Holl.) Wolfe
Pteris inaequilateralis Holl. = *Cyathea inaequilateralis* (Holl.) Wolfe
Celastrus comparabilis Holl., determination valid
Piper concavum Holl. = *Cryptocarya presamarensis* Sanb.
Ulmus pseudobraunii Holl. = *Platycarya pseudobraunii* (Holl.) Wolfe
Planera aquaticiformis Holl. = *Platycarya pseudobraunii* (Holl.) Wolfe
Hampea conditionalis Holl. = *Paratinomiscium conditionalis* (Holl.) Wolfe

Persea spatiosa Holl. = *Luvunga spatiosa* (Holl.) Wolfe
Semecarpus alaskana Holl. = *Melanorrhoea alaskana* (Holl.) Wolfe
Rhamnus pseudogoldianus Holl. = *Parashorea pseudogoldiana* (Holl.) Wolfe
Carpolithes elytraeformis Holl. = *Paleophytocrene elytraeformis* (Holl.) Wolfe
Cornus irregularis Holl. = *Mastixia irregularis* (Holl.) Wolfe

Transfers of citations by Hollick of previously described species are:

Cinnamomum cinnamomeum of Hollick (non *Phyllites cinnamomeus* Rossm., 1840) = *Cinnamomophyllum latum* (MacG.) Wolfe
Malpoenna magnifica of Hollick (pl. 66, fig. 5 only) = *Alangium bergensis* Wolfe
Glyptostrobus europaeus (Brongn.) Heer = *Glyptostrobus* sp.
Magnolia wormskioldi Heer = *Cananga* sp.
Daphnogene kanii Heer = *Macclintockia pugetensis* Wolfe
Dryophyllum stanleyanum Daws. = *Melanorrhoea alaskana* (Holl.) Wolfe
Cornus buchii Heer = *Laurophyllum presamarensis* (Sanb.) Wolfe
Cornus hyperborea Heer? = *Parashorea pseudogoldiana* (Holl.) Wolfe
Populus balsamoides Goepp. = *Celastrus comparabilis* Holl.
Juglans thermalis Lesq. = *Goweria dilleri* (Knowl.) Wolfe
Artocarpidium alaskanum Holl. (nontypic) = *Alnus scotti* Wolfe
Magnolia ovalis Lesq. = indet. leaf
Rhamnus marginatus Lesq. = *Parashorea pseudogoldiana* (Holl.) Wolfe
Terminalia? sp. of Holl. = *Myristica* sp.
Fraxinus lateralis Holl. (pl. 105, fig. 6) = *Platycarya pseudobraunii* (Holl.) Wolfe

Order FILICALES

Family SCHIZAEACEAE

Genus Anemia Swartz

Anemia gunni Wolfe, new species

Plate 2, figure 3

Diagnosis.—Pinna pinnatifid, apparently ovate, at least 25 cm long and 26 cm wide; at least 8 pinnules, decurrent along midrib, reflexed basally, decidedly slender and acuminate; secondary veins thinning towards apices of pinnules; tertiary veins simple to twice-branching, typically basal dichotomy dichotomizing again and apical dichotomy unbranching, craspedodrome; margin finely serrate; texture coriaceous.

Discussion.—The single specimen is an incomplete pinna, because the fertile pinnules are lacking; in *Anemia*, the basal pinnules are typically fertile. Among described species, the Kulthieth specimen most closely resembles *A. occidentalis* Knowlt. in the shape of the pinna and pinnules, but Knowlton's species is described as having once-dichotomizing tertiary veins (Knowlton, 1917, p. 285). Both *A. eocenica* Berr. and *A. elongata* (Newb.) Knowlt. have pinnules that are deeply incised or "lobed." The tertiary venation pattern, as well as texture, however, of *A. gunni* are similar to *A. eocenica*. *A. gunni* also occurs in the Puget Group; I (1968) had included the fragmentary Puget material in *A. eocenica*.

This species is named for Dr. Donald Gunn, Humble Oil and Refining Corporation, who assisted in collecting the material.

Holotype.—USNM 43246.

Occurrence.—Kulthieth Formation, loc. 11170.

Anemia? sp.

Plate 28, figure 5

Discussion.—A fragment, apparently representing the apex of a pinnule of *Anemia*, has a serrate margin and once- or twice-dichotomizing veins.

Specimen.—USNM 43247.

Occurrence.—Kushtaka Formation, loc. 9891.

Genus Lygodium Swartz

Lygodium larsoni Wolfe, new species

Plate 20, figures 1, 2

Diagnosis.—Sterile pinnules palmately two-lobed; one lobe larger and more elongated than the other; short lobe up to 5 cm in length, long lobe up to 7 cm in length; lobes about 1.2–1.5 cm in width; base broadly rounded to shallowly cordate; apex narrowly rounded; primary veins strong basally but thinning apically and about two-thirds the distance to the apex becoming the same strength as the secondary veins; secondary veins departing at low angles, dichotomizing two to three times; margin entire.

Discussion.—All 16 nearly complete specimens are bilobed, although one fragment apparently has a weakly developed third lobe. The widespread Eocene species *Lygodium kaulfussi* includes material that is bilobed, but the leaves of that species typically have three lobes. *L. binervatum* (Lesq.) Berr. has bilobed leaves, but the lobes are very blunt and short.

This species is named for Dr. Willard Larson, Humble Oil and Refining Corporation, who assisted in collecting the material.

Holotype.—USNM 43248.

Paratype.—USNM 43249.

Occurrence.—Kushtaka Formation, locs. 9389, 11165.

Family Cyatheaceae

Genus Cyathea Smith

Cyathea inequilateralis (Hollick) Wolfe, new combination

Plate 3, figure 3

Pteris inequilateralis Hollic, 1936, U.S. Geol. Survey Prof. Paper 182, p. 38, pl. 5, fig. 1.

Hemitelea pinnata MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, p. 97, pl. 10, fig. 1.

Cyathea pinnata (MacGinitie) LaMotte, 1951, Geol. Soc. America Mem. 51, p. 140.

Pabst, 1968, California Univ. Pubs. Geol. Sci., v. 76, p. 36, pl. 2, fig. 1c; pl. 3, fig. 2; pl. 4, fig. 2; pl. 5.

Discussion.—The asymmetry displayed by Hollick's specimen can also be seen in the material figured by MacGinitie (1941) and Pabst (1968). The epithet proposed by Hollick is clearly the senior synonym. The material of *Asplenium magnum* Knowl. from Eocene beds in Yellowstone Park is, as MacGinitie (1941, p. 98, stated, not so deeply dissected as in *Cyathea inequilateralis.*

Holotype.—USNM 38665.

Hypotype.—USNM 43250.

Occurrence.—Kushtaka Formation, locs. 3846, 11160, 11162.

Family ASPIDACEAE

Genus Allantodiopsis Knowlton and Maxon

Allantodiopsis pugetensis Wolfe

Plate 2, figures 1, 2; plate 20, figure 4

Allantodiopsis pugetensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 14, pl. 1, fig. 6.

Discussion.—The Alaskan specimens have the same linear shape, serrate margin, and simple or once-branching veins as in the types of *Allantodiopsis pugetensis.*

Hypotypes.—USNM 38957, 43251, 43252.

Occurrence.—Kushtaka Formation, locs. 3846, 11159, 11165, 11166; Kulthieth Formation, loc. 3879.

Genus Dryopteris Adanson

Dryopteris alaskana (Hollick) Wolfe, new combination

Plate 3, figures 1, 4

Asplenium alaskanum Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 38, pl. 3, figs. 1, 1a, lax; pl. 4, figs. 1a, lax, 1b, 1bx, 2-6, 6a; pl. 5, fig. 5 only.

Discussion.—The diagnostic characters of sterile specimens of *Dryopteris gibbsi* listed by Pabst (1968, p. 39-40), namely the arched, falcate pinnules and alternate venation, are also present in Hollick's material of *Asplenium alaskanum.* The sori of *D. gibbsi* are, however, round, whereas the sori of *D. alaskana* are decidedly oval.

Lectotype.—USNM 38664.

Syntypes.—USNM 38662, 245724.

Occurrence.—Kushtaka Formation, loc. 3847; Kulthieth Formation, loc. 3879.

Family BLECHNACEAE

Genus Woodwardia J. E. Smith

Woodwardia sp.

Plate 28, figure 1

Discussion.—The specimen is a fertile frond and has kidney-shaped sori next to the rachillae; the pinnae are confluent along the rachis. These characters indicate that the specimen represents *Woodwardia*, although the assignment should be considered tentative because of the poor preservation of the venation.

Specimen.—USNM 43253.

Occurrence.—Kushtaka Formation, loc. 9891.

Order CONIFERALES

Family TAXODIACEAE

Genus Glyptostrobus Endlicher

Glyptostrobus sp.

Plate 3, figure 2; plate 20, figures 3, 6; plate 21, figure 2a

Discussion.—Lacking fertile material I cannot determine which species is represented or indeed if more than one species is represented. The strongly dimorphic character of the foliage at the Charlotte Ridge locality (pl. 21, fig. 2a) indicates that this species probably does not represent *Glyptostrobus nordenskioldi* (Heer) R. W. Br.

Glyptostrobus is today the member of Taxodiaceae that consistently inhabits a paratropical climate. Despite this modern tolerance, it is certain that the genus contained members of widely differing tolerances. The genus was still represented in the Clamgulchian, for example, when Alaska had a paratemperate climate (Wolfe, 1966). *Glyptostrobus* is the only genus of its family known to be represented in every epoch of the Tertiary in Alaska. Although much has been made of the former wide distribution of *Metasequoia*—particularly at high latitudes—it seems that *Glyptostrobus* is even more characteristic of high latitude Tertiary assemblages.

Specimens.—USNM 38724, 43254-43256.

Occurrence.—Kushtaka Formation. locs. 11165, 11167; Kulthieth Formation, loc. 3879.

Order PRINCIPES

Family PALMAE

Genus Phoenicites Brongnairt

Phoenicites sp.

Plate 20, figure 5

Discussion—The specimens represent a species of feather palm. The rachis does not appear to have been spinose, and no spines can be detected on the margins of the pinnules. Both specimens have the pinnules arranged alternately. The midrib of the pinnules is very thick; several lateral veins are present, and some are thicker than others. In method of attachment of the pinnules, which narrow and are not folded at the point of attachment, and in venation, the fossils resemble the sago palm, *Metroxylon.* This genus, however, typically has widely spaced spines on the margins of the pinnules, although spines are lacking on some pinnules. *Ptycoraphis* is also similar to the fossils. Considering the fragmentary nature of the specimens, however, no generic assignment other than to the organ genus *Phoenicites* is warranted.

Specimen.—USNM 43257.

Occurrence.—Kushtaka Formation, loc. 11165.

Genus Palmacites Brongniart
Palmacites sp.

Plate 4, figure 5

Discussion.—The generic determination of leaves of fan palms is highly problematic; some probably can be determined, but the type known in the Kushtaka Formation is too generalized to determine to genus. Palms are especially abundant at locality 11160 and can be seen on numerous blocks in this slumped area. A large palm leaf that has an elongated hastula (and would thus represent *Sabalites*) was seen on a large block near locality 11158 but was not collected.

The Ravenian occurrences of palms are not the most northerly known. Hollick (1936, pl. 21) illustrated an obvious fan palm from Paleocene rocks in the Matanuska Valley at about lat 61.5° N., and new collections from Paleocene rocks at about lat 62° N. contain a species different from Hollick's. A collection of specimens of apparent Eocene age from lat 65.5° N. along the Yukon River also contains a fan palm. Koch (1963) considers some seeds from the Paleocene of Greenland at about lat 70°N. to represent palm; Chaney (1967, p. 221) considers these seeds to be "***Of rather doubtful status," but inasmuch as Chaney has not stated the morphologic basis for his conclusion, I think Koch's determination should be accepted.

Specimen.—USNM 43258.

Occurrence.—Kushtaka Formation, locs. 9389, 11160.

Genus and species indetermined

Discussion.—Numerous fragments of palm leaves occur at several localities. None of these fragments are attached to a leaf-base, and thus are generically indeterminable.

Specimen.—USNM 43279.

Occurrence.—Kushtaka Formation, locs. 11158, 11165; Kulthieth Formation, locs. 11170, 11195.

Order SALICALES
Family SALICACEAE

Members of this family are lacking in the Ravenian and Kummerian except for the occurrence of *Populus* and *Salix* in the one late Ravenian assemblage. Whether the Paleocene occurrences of *Salix* are valid is highly questionable. In describing the Paleocene *S. aquilina*, Brown (1962, p. 55) stated: "These fragmentary leaves are referred to *Salix* with some hesitation." The fragmentary leaves are neither sufficiently well described nor illustrated to substantiate the generic assignment. Insofar as I am aware, the oldest valid species of either *Populus* or *Salix* is in the subtropical assemblages from the Wind River Formation (latest early Eocene) of Wyoming (MacGinitie, in press); MacGinitie (oral commun., February 1968) also reports that the extant *P. dimorpha* Brandg. is common along streams in the lowland tropical area near Mazatlan, Mexico. In western North America, the members of the family appear to have diversified primarily in the upland areas of the Eocene and Oligocene ancestral Rocky mountains and later in the late Oligocene and Neogene of Alaska. Few members of the family apparently ever adapted to the Paratropical or Tropical Rain forests; I suspect that the group that gave rise to Salicaceae—presumably in the Paleocene or early Eocene—had an extended history in temperate vegetation. The entry of members of the family into temperate vegetation in any diversity appears to have occurred in the early Miocene; Salicaceae are notably rare or lacking in the various assemblages of the late Oligocene Bridge Creek flora and coeval assemblages in the Pacific Northwest. In Alaska, however, several species are known in the type Angoonian, Tsadaka, and Rex Creek assemblages. Similarly the family is more diverse in Seldovian assemblages from Alaska than in the assemblages from the Pacific Northwest. Salicaceae seem to be one of the few families of woody plants that can be considered truly boreal.

Genus Populus Linnaeus
Populus sp.

Plate 26, figure 1

Discussion.—The single fragmentary specimen has palmate venation, medial secondary veins parallel to the lateral primaries, camptodrome lateral secondary veins, closely spaced and sinuous intercostal tertiary veins, irregularly shaped areoles intruded by branching freely ending veinlets, and a nonentire margin. The combination of these features indicates that the specimen represents *Populus*, although the determination should be considered tentative until more complete material is found.

Specimen.—USNM 43259.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Salix Linnaeus

Salix carbonensis Wolfe, new species

Plate 26, figures 11, 13

Diagnosis.—Leaves simple; venation pinnate; shape broadly oval; base rounded, apex acute; six or seven pairs of secondary veins, broadly curving, camptodrome; marginal tertiary veins craspedodrome; intercostal tertiary veins numerous, closely spaced, slightly oblique to secondaries, typically branching; many closely spaced, small, narrowly rounded teeth; sinuses angular.

Discussion.—The fossils resemble the leaves of the extant *Salix wilsoni* Seem. in having a broad shape and numerous small teeth. *S. wilsoni*, however, has more widely spaced secondary veins and numerous intersecondary veins. The fossils also resemble in venation leaves of *S. richardsoni* Hook., but the extant species has sharp sickle-shaped teeth.

Holotype.—USNM 43260.

Paratype.—USNM 43261.

Occurrence.—Kushtaka Formation, loc. 11167.

Salix sp.

Plate 26, figure 2

Discussion.—The single fragmentary specimen has numerous, sharp, glandular teeth; secondary veins that depart at a low angle and are camptodrome; marginal tertiary veins that are craspedodrome and enter the teeth centrally; intercostal tertiary veins that are numerous and oriented almost perpendicular to the midrib; and fourth-order venation that is highly irregular. These features—particularly those of the margin and the intercostal venation—are characteristic of *Salix*. Considering, however, the fragmentary nature of the specimen, the generic determination should be considered tentative.

Specimen.—USNM 43262.

Occurrence.—Kushtaka Formation, loc. 11167.

Order JUGLANDALES

Family JUGLANDACEAE

Genus Carya Nuttall

Carya cashmanensis Wolfe

Plate 20, figure 8

Carya cashmanensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 15, pl. 1, figure 2; text figure 5.

Discussion.—The Kushtaka leaflet compares well with the type material from the Puget Group. Particularly significant are the conspicuously forking secondary veins and the numerous, sharp teeth.

Hypotype.—USNM 43263.

Occurrence.—Kushtaka Formation, loc. 11165.

Genus Engelhardtia Leschenault

Engelhardtia sp.

Plate 20, figure 7

Discussion.—Although the base is missing, the specimen is thought to represent a leaflet; the angle of divergence of the secondary veins is considerably different on the two lateral halves of the lamina, particularly in the more basal part of the specimen. The counterpart of the figured specimen, moreover, appears to have an asymmetric shape in the more basal part. Leaflets that have similar numerous, closely spaced, and rounded teeth occur in both Juglandaceae (*Engelhardtia*) and Burseraceae (*Canarium*). In the latter genus, however, the leaflets have smoothly curving secondary veins that do not fork and that have small loops apical to the juncture of any two secondary veins; the secondary veins forming the basal part of such a loop would, if extended to the margin, form about a 45° angle with the margin. in both *Engelhardtia* and the fossil, the secondary veins fork conspicuously and form comparatively large loops; the vein forming the basal side would intersect the margin at about an 80° angle. In addition, the toothed leaves of *Canarium* have apical secondary veins that do not extend far along the margin, in contrast to the apical secondary veins of *Engelhardtia* and the fossil, which extend for a considerable distance. Among extant species of *Engelhardtia*, the fossil most closely resembles the leaflets of *E. apoensis* Elm., particularly in having numerous teeth. Most species of *Engelhardtia* (*Engelhardtia*) and all species of *E.* (*Oreamunoa*) have entire-margined leaflets.

The fossil is the only foilage of *Engelhardtia* from North America to be validly referred to the genus. The fossil record of the genus in North America is comprised, except for the Kushtaka specimen, of the characteristic involucres. Most of the involucres have venation that is palmate and characteristic of *Oreamunoa*, that is, in the lobes of the involucre are typically two veins that flank the midrib and extend at least half way to the apex without looping. In the subgenus *Engelhardtia*, the lobes lack the flanking veins. Despite having the venation of *Oreamunoa*, most west American Tertiary involucres lack the large posterior lobe characteristic of *Oreamunoa* and in this respect are similar to *Engelhardtia*. These

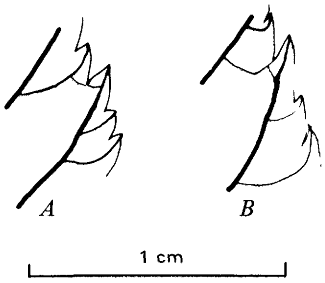

FIGURE 9.—Marginal venation of *Platycarya*. *A*, *P. pseudobrauni*, hypotype, USNM 43267, loc. 11170. *B*, *P. strobilacea*, USGS Ref. Colln. 253.

involucres may represent an extinct subgenus (or genus if *Oreamunoa* is considered generically distinct from *Engelhardtia*). That *Engelhardtia* (*Engelhardtia*) was present in the American Tertiary is indicated, however, both by the Kushtaka leaflet and some involucres from the West Branch Creek locality of the Clarno Formation. During the Angoonian, the genus *Engelhardtia* is represented in western North America by the probably extinct subgenus mentioned previously; the genus had almost certainly adapted to temperate climates, as indicated by the presence of characteristic involucres in the Angoonian rocks of the central Alaska Range.

Specimen.—USNM 43264.

Occurrence.—Kushtaka Formation, loc. 11165.

Genus Juglans Linnaeus

Juglans sp.

Plate 26, figure 3

Discussion.—Although fragmentary, the specimen is well preserved. The reference to Juglandaceae is certain because of the intercostal tertiary veins, which are uniformly spaced perpendicular to the secondary veins, and the forking craspedodrome secondary veins. The broad mucronate teeth that are elongated basally and the craspedodrome secondary veins that enter the teeth centrally indicate that the specimen represents a species of the section *Cardiocaryon* of *Juglans*.

Specimen.—USNM 43265.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Platycarya Siebold and Zuccarrini

Platycarya pseudobrauni (Hollick) Wolfe, new combination

Plate 4, figure 4; plate 5, figures 1, 2; plate 21, figure 2b; text figure 9

Ulmus pseudobraunii Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 105, pl. 58, figs. 1-3.

Planera aquaticiformis Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 107, pl. 57, fig. 7.

Fraxinus lateralis Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 164, pl. 105, fig. 6 only.

Discussion.—Pollen of *Platycarya* is of wide occurrence in the Eocene of North America (Leopold and MacGinitie, 1972), although no North American fossil leaflets have been previously referred to the genus. Hollick's material listed in the synonymy has considerably broader teeth than is typical of the one extant species of the genus, but specimens from one locality (11170) show an intergradation from broad teeth to the sharp teeth as in *P. strobilacea* Sieb. and Zucc. Considering the variation displayed by the Alaskan material, it is possible that the leaflets referred to a new genus, *Vinea* (Wolfe, 1968), may eventually prove to belong to *Platycarya*. *Platycarya* was almost certainly adapted to much warmer conditions during the Tertiary; the fruits of the genus are abundant in the London Clay assemblage (Reid and Chandler, 1933) in association with abundant *Nipa*, Menispermaceae, and Icacinaceae. Although predominately a member of the Mixed Mesophytic forest today, *Platycarya* also forms a minor element in the subtropical broad-leaved evergreen forest of China (Wang, 1961, p. 145). I do not think that the present tolerance, however, of the species of a monotypic genus such as *Platycarya* can be extended to include extinct species; it would in fact be remarkable if an extinct species had the same tolerances as an extant species of the same genus. The numerous occurrences of *Platycarya* pollen in Eocene assemblages that represent subtropical to Paratropical Rain forest is a clear indication that some extinct species of the genus tolerated considerably warmer climates than does the extant species.

Lectotype.—USNM 38895 (Hollick's pl. 58, figs. 1, 2).

Hypotypes.—USNM 38893, 39063, 43266, 43267, 245726.

Occurrence.—Kushtaka Formation, locs. 3847, 11165, 11166; Kulthieth Formation, locs. 11170, 11195.

Genus Pterocarya Kunth

Pterocarya pugetensis Wolfe

Plate 21, figure 4; text figure 10

Pterocarya pugetensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 16, pl. 1, figs. 3-5; text fig. 8.

Discussion.—The specimen figured in this report has the smoothly looping secondary veins and the numerous, closely spaced, and sharp teeth of *Pterocarya pugetensis*. The lineage to which this species is thought to belong is well represented in the Mixed Mesophytic forest of the Neogene of both the Pacific Northwest and Alaska (Wolfe, 1966, p. B15; 1968, p. 17).

A single incomplete specimen from locality 11167 has many small, rounded, broad teeth, tertiary veins

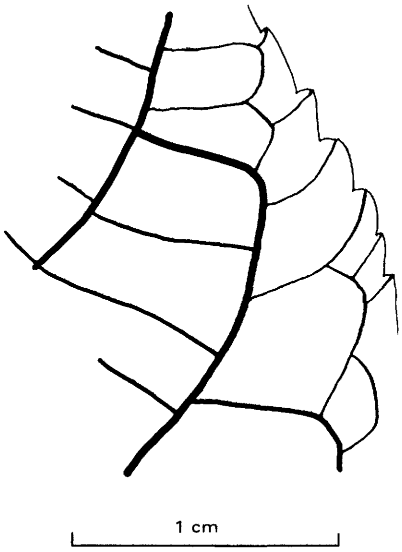

FIGURE 10.—Marginal venation of *Pterocarya pugetensis*. Hypotype, USNM 43269, loc. 11167.

that are craspedodrome, secondary veins that fork and are camptodrome, and uniformly intercostal tertiary veins that are oriented perpendicular to the secondary veins. These features indicate that the specimen represents *Pterocarya* and the spacing and shape of the teeth is the same as in *P. pugetensis.*

Hypotype.—USNM 43268, 43269.

Occurrence.—Kushtaka Formation, locs. 9389, 11165, 11167.

Order FAGALES

Family BETULACEAE

This family is typically thought of as a boreal temperate family. The fossil occurrences of the family, however, indicate that the family has a long history in the Paratropical and subtropical rain forests. From palynologic data, the earliest definite record of the family is the occurrence of *Alnus* in Maestrichtian rocks of the Rocky Mountain region (R. Tschudy, written commun., January 1969). *Alnus* is also known in the Paleocene, but the pollen is scarce in the material described from basal Paleocene rocks on Greenland; Manum (1962, p. 119) suggests that *Alnus* was not a significant part of the vegetation in that area at that time. Leaves of certain betulaceous character that have been referred to *Corylus* or *Corylites* and *Betula* have been recorded from a number of localities in Paleocene rocks in Alaska (Wolfe, 1966) and the high plains region of Canada and conterminous United States (Brown, 1962), as well as from Paleocene rocks of Greenland (Koch, 1963) and Great Britain. The diversity of the family during the Paleocene does not appear to have been great. The Paleocene occurrences are in assemblages that, on physiognomic characters of the foliage, represent warm temperate to subtropical forests. The Eocene occurrences of the family are primarily those of *Alnus*; leaves of this genus have been recorded from a number of assemblages in western North America that represent subtropical or Paratropical Rain forests (MacGinitie, 1941; Wolfe, 1968). Chandler (1964) similarly records *Alnus* from British Eocene assemblages that represent Paratropical or Tropical Rain forests. The leaves are the types that have simple teeth, that is, the teeth are not grouped into conspicuous "lobes." The secondary veins of many of the leaves tend to be camptodrome. These types of alder leaves are today more southern in distribution than the "lobed" types. Note, however, that *Alnus* does not appear to have been diverse in the Paratropical Rain forest; a few lineages apparently were represented. Distinctive types, such as the latest Eocene *A. cuprovallis* Axelr., have a pronounced tendency towards the grouping of the teeth into "lobes." The dominant types of alders, however, in the late Eocene and early to middle Oligocene cool assemblages are related to the alders of the Paratropical Rain forest. The genus persisted in the Paratropical Rain forest in western North America through at least the Kummerian. The Angoonian assemblages—both in the Pacific Northwest and Alaska—display a diversity of Betulaceae, particularly *Alnus*, that is unmatched in the earlier Paleogene. The groups that have "lobed" types of leaves became increasingly diverse. The genus reached its acme in western North America during the early and middle Miocene.

The other genera of Betulaceae have a poorly documented record. *Betula stevensoni* Lesq. represents, at least in part, a species of *Ostrya* or *Carpinus*, as indicated both by the lack of branching freely ending veinlets and the sharp apical bend of the secondary veins within the teeth. *Carpinus* has been recorded from the British Eocene tropical assemblages. *Betula* has been described from the Claiborne flora, but, without knowing the ultimate venation pattern, it is not possible to determine whether *Betula* or *Ostrya-Carpinus* is represented. In the later Eocene, *Betula* is known both from the upland Republic assemblage of Washington and the lowland John Day Gulch assemblage of Oregon. In the early Oligocene, *Betula* wood is known from the Clarno nut bed assemblage (Chandler, 1964); although it is possible that the wood was derived from more upland vegetation, I think that it is improbable that the upland vegetation bordering the Clarno basin was any cooler than subtropical. By the late Oligocene, *Betula* was apparently more diverse than previously, but the diversity attained was not of as great a magnitude as that of *Alnus*. *Ostrya* and *Carpinus* were apparently of little diversity in the Mixed Mesophytic forest of western North America, in contrast to their considerable diversity in the Mixed Mesophytic forest of the Japanese Cenozoic.

Corylus has an extremely poor record. Some Paleocene leaves of *Corylites* may represent *Corylus* or a closely allied genus, but Eocene and younger records of the genus are generally poor. Material from the late Oligocene and late Miocene of Alaska referred to *Corylus harrimani* Knowlt. and *C. chuitensis* Wolfe, respectively, have small areoles intruded by typically unbranching veinlets; the lineage represented probably represents *Ostryopsis*, which today is a monotypic genus inhabiting the northern, more temperate regions of China.

The Betulaceae, therefore, display several distribution patterns. The best documented pattern is that of *Alnus*, which during the Paleogene—particularly the Eocene—was a little diversified genus of the Paratropical and subtropical Rain forests. The cooling of the middle late Oligocene opened wide areas of temperate climate into which *Alnus* apparently extended and diversified rapidly. Some of the other genera were also represented in the Paratropical Rain forest of the Paleogene but poorly in comparison to alders. These genera also apparently diversified from the late Oligocene through the later Cenozoic, but a genus such as *Carpinus* never attained the diversity in western North America that it did in Asia. *Ostryopsis*, however, from its first appearance in the late Oligocene of Alaska, did not have any tendency to diversify and, at least from the late Oligocene, has been a member of temperate vegetation.

Genus Alnus Linnaeus

Alnus cuprovallis Axelrod

Plate 26, figure 7; text figure 11

Alnus cuprovallis Axelrod, 1966, California Univ. Pubs. Geol. Sci., v. 59, p. 66, pl. 11, figs. 1-13.

Discussion.—Axelrod (1966b, p. 66) states that the leaves of *Alnus cuprovallis* and *A. crispa* differ "***only slightly in that the secondaries in the fossils tend to be more curved distally." Note, however, that in *A. cuprovallis* the teeth are broad, the maximum number of teeth per secondary vein is seven, the intercostal tertiary veins are spaced about 1.5 mm apart, and the areoles are formed by fourth-order venation and are about 1 mm across. In *A. crispa* the teeth are elongated and sharp, any given leaf typically has a secondary vein that feeds at least 9-10 teeth, the intercostal tertiary veins are spaced about 0.5 mm apart, and the areoles are formed by fifth-order venation and are about 0.2-0.3 mm across. Any relationship between *A. crispa* and *A. cuprovallis* is distant. The leaves of *A. incana*, however, are more closely related to *A. cuprovallis*. This is indicated by the following characters of the extant species: broad teeth that can be mucronate; typically 3-6 teeth per secondary vein; the intercostal tertiary veins that are spaced about 1 mm apart; and the areoles that are formed by fourth-order venation and are about 0.5 mm across. *A. cuprovallis* appears to be the oldest known member of the *A. incana* lineage, which is well represented in Alaska in the late Oligocene and Neogene.

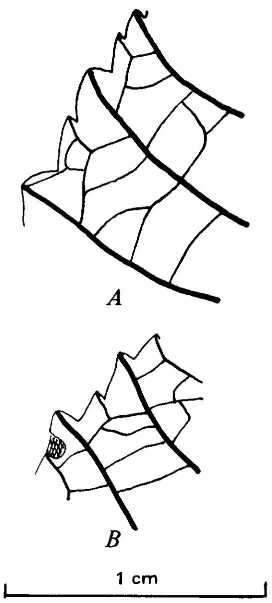

FIGURE 11.—Marginal venation of *Alnus cuprovallis*. *A*, hypotype, USNM 43270, loc. 11167. *B*, paratype, UCMP 20003, Copper Basin flora.

Hypotype.—USNM 43270.

Occurrence.—Kushtaka Formation, loc. 11167.

Alnus martini Wolfe, new species

Plate 5, figures 3, 5: plate 21, figure 3; text figure 12

Diagnosis.—Leaves simple; venation pinnate; base acute to typically broadly rounded; apex acute; shape oval; 7-11 pairs of broadly curving secondary veins; camptodrome or craspedodrome and entering the teeth centrally; intercostal tertiary veins uniformly spaced, approximately perpendicular to secondary veins; marginal tertiary veins craspedodrome; typically entering teeth along apical sides; typically 3 to 4 sharp to narrowly rounded and small teeth per secondary vein.

Discussion.—These leaves are related to the Asian alders, such as *Alnus japonica* Sieb. and Zucc. and its allies, in having some camptodrome secondary

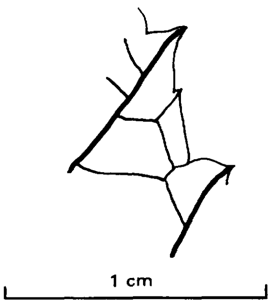

FIGURE 12.—Marginal venation of *Alnus martini.* Holotype, USNM 43271, loc. 11158.

veins and some marginal tertiary veins that enter the teeth along the apical side. In *A. japonica* and its allies, however, the craspedodrome secondary veins typically enter the teeth along the apical sides; an exception to this is *A. fauriei* Lev., but the cuneate base, obovate shape, and irregular spacing of the intercostal tertiary veins readily distinguish *A. fauriei* from *A. martini.* Neither *A. martini* nor *A. scotti* appear to be closely related to any extant species.

Alnus martini is named in recognition of G. C. Martin's work in the Katalla district.

Holotype.—USNM 43271.

Paratypes.—43272, 43279.

Occurrence.—Kushtaka Formation, locs. 11158, 11163; Kulthieth Formation, loc. 11170.

Alnus scotti Wolfe, new species

Plate 4, figures 1-3

Artocarpidium alaskanum Hollick, 1936 (part, nontypic), U.S. Geol. Survey Prof. Paper 182, p. 108, pl. 59, figs. 1-4.

Diagnosis.—Leaves simple; pinnately veined; base rounded, typically slightly asymmetric; apex acuminate; 6-9 pairs of craspedodrome secondary veins; intercostal tertiary veins oriented obliquely to secondary veins; marginal tertiary veins craspedodrome; teeth large, 2-3 per secondary vein, typically separated by arcuate sinuses.

Discussion.—Most alders, unlike *Alnus scotti,* have leaves that have intercostal tertiary veins oriented perpendicular to the secondary veins, although the tertiaries of *A. sinuata* Rydb. are also oblique to the secondary veins. Also unusual are the arcuate sinuses, but a few species, for example *A. nitida* Endl., have arcuate sinuses. The combination, however, of large teeth, oblique tertiary veins, and arcuate sinuses is unique.

This species is named in recognition of the work of R. A. Scott on the Paleogene floras of western North America.

Holotype.—USNM 38899.

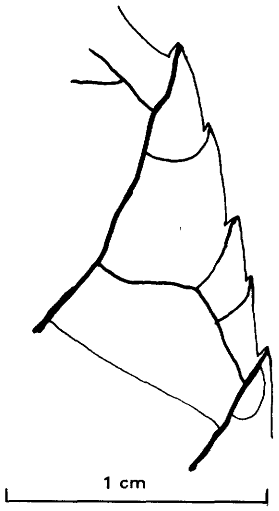

FIGURE 13.—Marginal venation of *Alnus* sp. USNM 43277, loc. 11167.

Paratypes.—USNM 43273, 43274.

Occurrence.—Kushtaka Formation, locs. 3847, 11158; Kulthieth Formation, loc. 11170.

Alnus sp.

Plate 26, figures 4, 10

Discussion.—Fragmentary specimens from the late Ravenian locality represent a species of *Alnus* that has a cordate base and slight indications of "lobing." The rounded teeth, as well as these other features, indicate a relationship to the strongly "lobed" *A. barnesi* Wolfe.

Specimens.—USNM 43275, 43276a.

Occurrence.—Kushtaka Formation, loc. 11167.

Alnus sp.

Text figure 13

Discussion.—One specimen of an alder leaf has very sharp teeth reflexed basally; although insufficient for specific determination, it does not belong to either of the other two species of *Alnus* represented in the same collection. The cuneate base and tertiary veins oriented obliquely to the secondary veins indicate a possible relationship to *A. healyensis* Wolfe; the Seldovian species, however, has considerably more teeth per secondary vein.

Specimen.—USNM 43277.

Occurrence.—Kushtaka Formation, loc. 11167.

Alnus sp.

Plate 28, figure 3

Discussion.—Two specimens from the Kummerian have small, rounded to sharp teeth and marginal tertiary veins that enter the teeth along the apical sides. These leaves thus resemble *A. martini,* but the

Kummerian species has a base apparently decurrent along the petiole and fewer (5-6) secondary veins.

Specimen.—USNM 43278.

Occurrence.—Kushtaka Formation, loc. 9891.

Genus Betula Linnaeus

Betula sp.

Plate 28, figure 4

Discussion.—A single battered specimen has a sharply serrate margin and craspedodrome secondary veins that bend sharply apically within the teeth. The ultimate venation is poorly preserved, but the areoles appear to be intruded by branching veinlets, and thus the specimen probably represents *Betula*.

Specimen.—USNM 43280.

Occurrence.—Katalla Formation, Split Creek Sandstone Member, loc. 11168.

Family FAGACEAE

Genus Dryophyllum Debey

Dryophyllum pugetensis Wolfe

Plate 21, figures 1, 5, 6

Dryophyllum pugetensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 18, pl. 3, figs. 4, 8.

Discussion.—Two fundamental types of leaves have been assigned to *Dryophyllum*. One type, as represented by *D. pugetensis*, has marginal venation that is typical of genera such as *Castanopsis*, *Lithocarpus*, and *Quercus*; in this type, the apical tertiary branch that is nearest the margin is aparallel to the intercostal tertiary veins and approximately parallels the margin. In the second type, as represented by *D. tennesseensis* Berr., the marginal venation is similar to *Fagus*, that is, the apical tertiary branch nearest the margin typically is parallel to the intercostal tertiary veins. This is a fundamental difference in Fagaceae and indicates to me that two different genera are represented. I have, however, not seen material of the type species of *Dryophyllum* and thus cannot determine whether *D. pugetensis* is validly assigned to that genus. Whether *Dryophyllum* contains ancestors of other fagaceous genera is unknown. The extremely thick texture of the leaves of *D. pugetensis* indicates a probable evergreen habit.

Hypotypes.—USNM 43281-43283.

Occurrence.—Kushtaka Formation, locs. 3842, 9389, 11165.

Genus Fagus Linnaeus

Fagus sp.

Plate 28, figure 2

Discussion.—A fragmentary leaf has numerous straight secondary veins that end in small teeth. What may represent the same species also occurs in rocks assigned to the basal part of the Poul Creek Formation.

Specimen.—USNM 43284.

Occurrence.—Katalla Formation, Split Creek Sandstone Member, loc. 9552.

Order URTICALES

Family ULMACEAE

Genus Girroniera Gaudich

Girroniera sp.

Plate 5, figure 7

Discussion.—The specimen has an entire margin except for a few rounded small teeth a short distance from the apex. The secondary veins are camptodrome and the teeth are entered by tertiary veins. The leaf also has a pronounced drip-tip. Similar leaves are present in extant species of *Girroniera*; these leaves can have an entire margin or a few rounded teeth near the apex.

Specimen.—USNM 43285.

Occurrence.—Kushtaka Formation, loc. 11158.

Girroniera sp.

Plate 5, figure 8

Discussion.—The leaf is similar to the specimen of *Girroniera* from the Kushtaka Formation, but differs in having sharper teeth and almost twice as many secondary veins. The secondaries also loop closer to the margin in the Kulthieth specimen.

Specimen.—USNM 43286.

Occurrence.—Kulthieth Formation, loc. 11170.

Genus Ulmus Linnaeus

Ulmus sp.

Plate 23, figure 1

Discussion.—Four specimens have an asymmetric base, numerous and almost straight secondary veins that are craspedodrome, craspedodrome marginal tertiary veins that depart from the basal sides of the secondaries, and a finely compound serrate margin. These features indicate that the specimens represent *Ulmus*, although the lack of preservation of the intercostal venation does not allow application of a specific epithet. In characters that are preserved, the specimens are similar to leaves of *U. newberryi* Knowlt., except that the latter has considerably larger teeth.

Ulmus has a long history in the subtropical forest; ulmaceous pollen grains (these could represent *Ulmus*, *Zelkova*, or possibly an ancestral genus) are first known in Paleocene rocks in warm temperate and subtropical forests. In the Eocene, representatives of the genus are found in both Paratropical

Rain and subtropical forests; in the Eocene the genus is also known in temperate forests such as represented by the Republic assemblage. In the early to middle Oligocene, the genus is represented primarily in the upland forests, and from the late Oligocene on it has been a significant element of the warm temperate forests.

Specimen.—USNM 43287.

Occurrence.—Kushtaka Formation, locs. 9389, 11165.

Order RANALES

Family TETRACENTRACEAE

Genus Tetracentron Oliver

Tetracentron piperoides (Lesquereux) Wolfe, new combination

Plate 5, figure 4; plate 22, figure 3; plate 28, figure 7

Zizyphus piperoides Lesquereux, 1878, Harvard Coll. Mus. Comp. Zoology Mem., v. 6, no. 2, p. 28, pl. 8, figs. 10, 11.
Zizyphus microphyllus Lesquereux, 1878, Harvand Coll. Mus. Comp. Zoology Mem., v. 6, no. 2, p. 28, pl. 8, fig. 9.
Zizyphus californica Knowlton and Cockerell, 1919, U.S. Geol. Survey Bull. 696, p. 659.
Ceanothus idahoensis Brown, 1935, Journ. Paleontology, v. 9, p. 581, pl. 69, fig. 8.
Cercidiphyllum elongatum Brown, 1939 (part), Jour. Paleontology, v. 13, p. 494, pl. 55, figs. 1, 2, 7 only; 56, fig. 9 only.
MacGinitie, 1941 (part), Carnegie Inst. Washington Pub. 534, p. 112, pl. 12, fig. 4; pl. 13, fig. 4 only; pl. 14, figs. 1, 2 only.
Becker, 1961 (part), Geol. Soc. America Mem. 82, p. 66, pl. 10, fig. 8; pl. 19, figs. 1-5 only.
Cercidiphyllum piperoides (Lesquereux) LaMotte, 1952, Geol. Soc. America Mem. 51, p. 120.
Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 19.
Trochodendroides zaddachi Sanborn non *Populus zaddachi* Heer. Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 16, pl. 3, fig. 2.
Populus smilacifolia auct. non Newberry. Jennings, 1920, Carnegie Mus. Mem., v. 8, p. 409, pl. 26, fig. 4.
Populus glandulifera auct. non Heer. Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 694, pl. 84, fig. 1.
Populus daphnogenoides auct. non Ward. Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 695, pl. 84, fig. 2.
Populus speciosa auct. non Ward. Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 694, pl. 84, fig. 3.
Populus xantholithensis Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 695, pl. 85, figs. 1, 2.
Zizyphus serrulata auct. non Ward. Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 740, pl. 101, figs. 4, 5.
Cercidiphyllum crenatum Brown non *Grewia crenata* Unger. Brown, 1935 (part), Journ. Paleontology, v. 9, p. 575, pl. 68, figs. 1, 6, only.
Brown, 1939 (part), Jour. Paleontology, v. 13, p. 494, pl. 56, fig. 7.
Trochodendroides arctica Berry non *Populus arctica* Heer. Berry, 1926, Canada Geol. Survey Bull. 42, p. 109, pl. 13, figs. 1–4.
Populus richardsoni auct. non Heer. Lesquereux, 1878, U.S. Geol. Survey Terr. Rept., v. 7, p. 177, pl. 22, figs. 10-12.
Populus rotundifolia auct. non Newberry. Dawson, 1895, Royal Soc. Canada Trans., 2nd ser., v. 1, sec. 4, p. 147, text fig. 10.

Discussion.—Few previous citations of the occurrence of *Cercidiphyllum* in the Tertiary of North America have proved to be valid. The Paleocene specimens assigned to this genus represent several different genera and species, primarily *Cocculus flabella* (Newb.) Wolfe, *Trochodendroides serrulata* (Ward) Wolfe, and *Dicotylophyllum richardsoni* (Heer) Wolfe (Wolfe, 1966, p. B9-B10). A few unfigured specimens from the Fort Union Formation do, however, represent *Cercidiphyllum.* Similarly the citations of *Cercidiphyllum* in the Eocene have proved to be invalid, although unfigured material from probable early Eocene rocks in north-central Washington does represent *Cercidiphyllum,* and Scott (in Chandler, 1964, p. 58) reported wood of the genus from the Clarno nut bed (latest Eocene). The late Oligocene and Miocene occurrences of *Cercidiphyllum crenatum* (Ung.) R. W. Br. also are valid citations of the genus.

The leaves of extant *Tetracentron* and *Cercidiphyllum* are indeed difficult to distinguish. Leaves of *Tetracentron* are, of course, typically more elongated than those of *Cercidiphyllum*; on this basis alone, the Eocene and early Oligocene specimens synonymized here are assignable to *Tetracentron.* In addition, the teeth of *Tetracentron* are typically larger and more equal sided than those of *Cercidiphyllum*; the items in the synonymy are again closer to *Tetracentron.* Perhaps most significant, however, is that in *Tetracentron* veins connect the glandular region of the tooth to the adjacent sinuses, but in *Cercidiphyllum* such veins are absent; well-preserved fossil material, including topotypic material from Chalk bluffs, indicates that "*Zizyphus*" *piperoides* is *Tetracentron.* Sanborn (1935) also compared her specimens of "*Trochodendroides zaddachi*" to *Tetracentron.*

The various seeds and fruits associated at some localities with these fossil leaves were thought to represent *Cercidiphyllum.* Chandler (1961, p. 84), however, has demonstrated that the English material thought by Brown (1962) to be *Cercidiphyllum* is of unknown affinities.

MacGinitie (1941, p. 112) noted that the early Eocene specimens of this taxon are more elongated than the late Eocene specimens, and that the early Eocene material has a regularly and more finely crenate margin whereas the late Eocene material has an irregularly and more coarsely crenate margin. Two species may indeed be represented, but the almost complete transition of suites of these leaves in the Puget Group from the early Eocene through the early Oligocene makes it difficult to delineate more than one taxon. The Alaskan material collected thus far is closer to the Puget material from the Fultonian and Ravenian than to Franklinian leaves of the species.

Hypotypes.—USNM 43288-43290.

Occurrence.—Kushtaka Formation, locs. 9389, 11165, 11169; Kulthieth Formation, loc. 11170.

Family MAGNOLIACEAE

Genus Magnolia Linnaeus

Magnolia reticulata Chaney and Sanborn

Plate 30, figure 7

Magnolia reticulata Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 70, pl. 13, figs. 1, 2, 4.

Discussion.—The fossil has numerous secondary and intersecondary veins that depart from the midrib at a high angle; the secondaries extend with little or no curvature towards the margin, and loop sharply. The intercostal venation, which is considerably weaker than the secondaries, forms a uniform quadrangular mesh. In shape and venation, therefore, the fossil falls within the range of variation of the Goshen species.

An undescribed species of *Magnolia* from the early Miocene Collawash assemblage of Oregon has venation that is similar to the Goshen and Katalla species. The Collawash species has fewer intersecondary veins and tends toward an obovate shape, but otherwise it is similar to *M. reticulata.*

Hypotype.—USNM 43291.

Occurrence.—Katalla Formation, Split Creek Sandstone Member, loc. 11168.

Family ILLICIACEAE

Genus Illicium Linnaeus

Illicium sp.

Plate 15, figure 3

Discussion.—The single specimen, which lacks the basal part of the lamina, has several features that indicate an assignment to *Illicium*: (1) widely spaced secondary veins that loop sharply at the margin to form a trapezoidal intercostal area, (2) an extensive series of loops of marginal tertiary veins that are elongated parallel to the midrib, (3) widely and irregularly spaced, rounded, small teeth, and (4) an attenuated apex. The fossil is particularly similar to the extant *I. lanceolatum* A. C. Sm. from southern China.

Specimen.—USNM 43292.

Occurrence.—Kushtaka Formation, loc. 11159.

Family MENISPERMACEAE

Genus Anamirta Colebrooke

Anamirta milleri Wolfe, new species

Plate 6, figure 6; text figure 14

Diagnosis.—Leaves simple; venation palmate; base cordate, apex acuminate; seven primary veins, first lateral pair extending about half the distance to apex; second pair parallel to lateral secondaries of first lateral primaries, forming a series of 5-7 loops; lateral primaries and all secondary and marginal tertiary veins camptodrome; intercostal tertiary veins spaced about 0.4 cm apart, irregularly branching, oriented approximately perpendicular to midrib; marginal vein present.

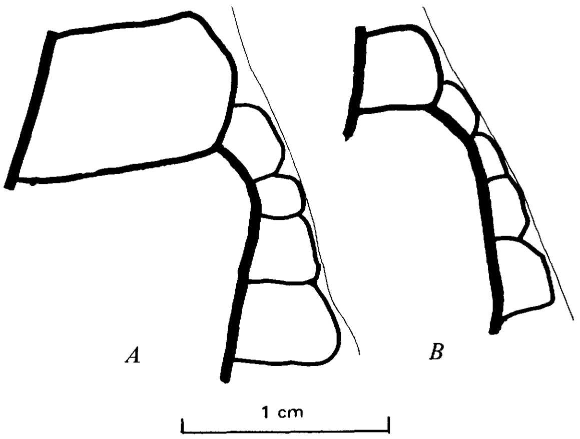

FIGURE 14.—Marginal venation of *Anamirta*. *A*, *A. milleri*, holotype, USNM 43293, loc. 11170. *B*, *A. cocculus*, USGS Ref. Colln. 491.

Discussion.—The prominent marginal vein, irregularly branching intercostal tertiaries, palmate venation, and cordate base, ally these fossils to Menispermaceae. The lack of craspedodrome secondary or tertiary veins, as well as the cordate base, indicates that the most closely allied genera are *Anamirta*, *Tinomiscium*, and *Tinospora*. In both *Tinomiscium* and *Tinospora* the intercostal tertiary veins are widely spaced; the spacing of these veins is, however, similar in the fossils and in *Anamirta*. *A. cocculus* Wight and Arn. has leaves very similar to the fossils, but the fossils are widest at the base whereas the leaves of *A. cocculus* are widest above the base.

Holotype.—USNM 43293.

Occurrence.—Kulthieth Formation, loc. 11170.

Genus Calkinsia Wolfe

Calkinsia plafkeri Wolfe, new species

Plate 6, figure 8; plate 23, figures 3, 4, 6, 7b

Hyperbaena dilleri (Knowlton) Wolfe, 1968 (part, nontypic), U.S. Geol. Survey Prof. Paper 571, p. 21, specimens listed from locs. 8640, 9680, 9731, 9738.

Diagnosis.—Leaves simple; venation palmate; shape oval; base acute, apex acuminate; length 2-12 cm, width 1.5-7 cm; three or four pairs of broadly convex medial secondary veins, departing at an angle of 20°-30°; lateral secondaries departing at an angle of 40°-80°; tertiary veins departing from midrib at an angle of 70°-80°.

Discussion.—As noted previously (Wolfe, 1968, p. 21), the fossils have conspicuously branched intercostal tertiary veins; the spacing of these veins, however, is much wider in extant species of *Hyperbaena* than in the fossils. Leaves of *Hyperbaena,* moreover, typically do not have such a broad oval shape. In the spacing of the nervilles and broad shape, the fossils can be matched most closely by *Calkinsia franklinensis* Wolfe, the type species of the genus. *C. franklinensis,* however, typically has a broader and obovate shape and the apex is narrowly rounded. The tertiaries, moreover, typically depart from the midrib at an angle of 90° in *C. franklinensis.*

Morphologically, therefore, *Calkinsia franklinensis* and *C. plafkeri* are closely related and probably represent the same phylad. *C. franklinensis* is known in the Franklinian and lower Fultonian and *C. plafkeri* is known in the lower through upper Ravenian. The tendency towards a narrower shape is continued in this lineage by *C. dilleri,* which is known in the Comstock and Upper Clarno assemblages of Oregon.

Calkinsia has been likened to the extant genus *Hypserpa*; this resemblance is enhanced by the configuration of the tertiary veins between the first lateral primaries and the most basal medial secondaries. Material of *Hypserpa* studied at the time the original diagnosis of *Calkinsia* was written did not have lateral primaries extending into the apical half of the lamina. A specimen of *Hypserpa nitida* Miers, since added to the University of California Herbarium (sheet no. 1011338), bears leaves that have the first lateral primaries extending slightly more than half way to the apex. *Calkinsia,* therefore, is probably most closely related to *Hypserpa.* Seeds of *Eohypserpa* have been found in the late Eocene Clarno nut bed (Scott in Chandler, 1964, p. 58), where I have collected leaves of *C. dilleri. Calkinsia* and *Eohypserpa* may possibly represent organs of the same genus.

This species is named in recognition of George Plafker's invaluable help in the preparation of this report.

Holotype.—USNM 43296.

Paratypes.—USNM 43294-43295, 43297, 43298, 43312.

Occurrence.—Kushtaka Formation, locs. 11157, 11164, 11165.

Genus Cocculus Miers

Cocculus sp.

Plate 6, figure 5

Discussion.—The seven primary veins, camptodrome lateral secondary veins that form angular loops, the craspedodrome lateral tertiary veins that fuse with the marginal vein, the widely spaced and branching intercostal tertiaries, the cordate base, and the rotund shape of the fossil can be matched by an undescribed species from the early Ravenian of the Puget Group. The upper margin of the Alaskan specimen appears to have been untoothed, but the Puget Group specimens vary from having an entire to a toothed margin. In shape and overall venation pattern, the early Ravenian species is similar to the Paleocene *Cocculus flabella* (Newb.) Wolfe and to the Neogene or extant species such as *C. auriculata* (Heer) Wolfe and *C. trilobus* DC. The early Ravenian species, however, has areoles that are about 1 mm or slightly more in width, but the areoles of *C. auriculata* average about 2 mm or slightly more in width. The early Ravenian species, which inhabited Paratropical Rain forest, is probably in the ancestry of the Neogene and Quaternary species of the Mixed Mesophytic forest.

Specimen.—USNM 43299.

Occurrence.—Kushtaka Formation, loc. 11166.

Cocculus sp.

Plate 26, figure 5

Discussion.—The fragmentary specimen has palmate venation, lateral secondary veins that are camptodrome, lateral tertiary veins that are craspedodrome into the marginal vein, and areoles intruded by veinlets that branch two or three times. The species represented probably does not belong to the group that produced the toothed, deeply cordate species of *Cocculus* that were or are members of the Mixed Mesophytic forest. The mixed mesophytic group is represented in the early Ravenian Steel's Crossing assemblage of Washington and in the Alaskan early Ravenian by a species that has areoles about twice as large as the species under discussion. It is more probable that the late Ravenian species was separately derived from another tropical group of the genus.

Specimen.—USNM 43300.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Diploclisia Miers

Diploclisia sp.

Plate 6, figure 7; text figure 15

Discussion.—The conspicuously forking lateral primary veins and forking, craspedodrome lateral secondary veins indicate that this fossil is a member of *Diploclisia.* The incompleteness of the specimen, however, does not allow a satisfactory specific diagnosis or description.

Specimen.—USNM 43301.

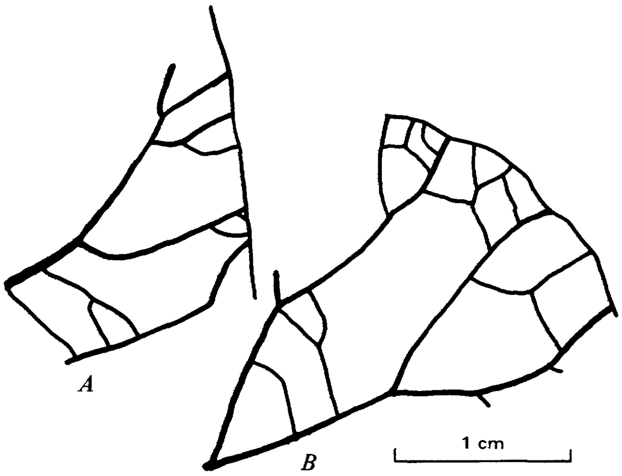

FIGURE 15.—Marginal venation of *Diploclisia*. *A*, *D.* sp., USNM 43301, loc. 11170. *B*, *D. chinensis*, USGS Ref. Colln. 242.

Occurrence.—Kulthieth Formation, loc. 11170.

Genus Hypserpa Miers

Hypserpa? sp.

Text figure 16

Discussion.—A fragmentary leaf has a marginal vein, apparently palmate venation (the base is missing), only one pair of conspicuous presumed lateral primaries, craspedodrome marginal tertiary veins, and a linear shape. Although clearly a member of Menispermaceae, the generic reference is questionable because of the incompleteness of the specimen.

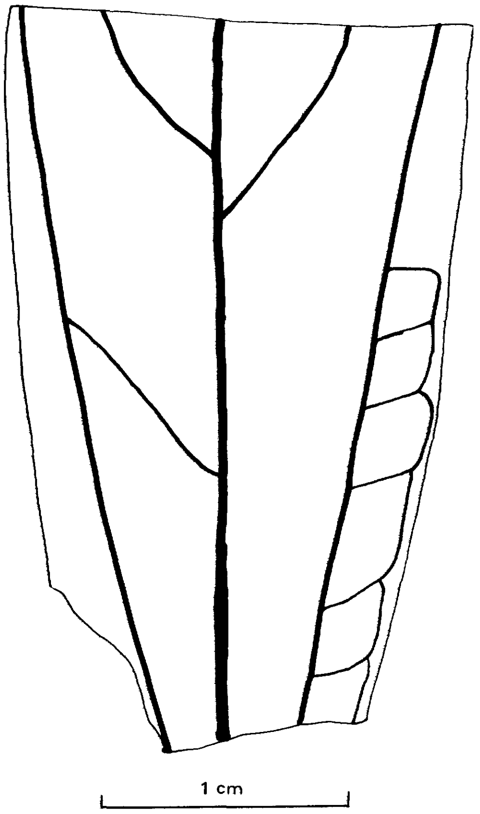

FIGURE 16.—*Hypserpa*? sp. USNM 43302, loc. 11168.

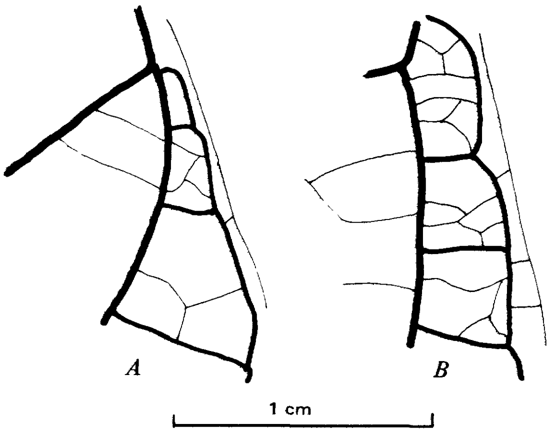

FIGURE 17.—Marginal venation of *Limacia*. *A*, *L. stenophylla*, paratype, USNM 43305, loc. 11159. *B*, *L. oblonga*, USGS Ref. Colln. 1803.

Specimen.—USNM 43302.

Occurrence.—Katalla Formation, Split Creek Sandstone Member, loc. 11168.

Genus Limacia

Limacia stenophylla Wolfe, new species

Plate 6, figures 1-3; plate 7, figures 4, 7; text figure 17

Diagnosis.—Leaves simple; venation palmate; shape ovate, linear; base narrowly rounded, apex acute; length 6-12 cm, width 2-4 cm; a single pair of conspicuous lateral primaries extending less than a third the distance to the apex; secondaries and lateral primaries camptodrome; inconspicuous lateral secondaries; 7-10 pairs of medial secondaries, departing at an angle of 40°-70°, straight to broadly curving, looping sharply near margin; numerous intersecondaries; intercostal tertiary veins branching, approximately perpendicular to secondary veins, widely spaced.

Discussion.—The fossils show the following points of resemblance to leaves of Menispermaceae: palmate venation, a strong marginal vein, and craspedodrome lateral secondary veins near the apex that join the marginal vein. Among extant Menispermaceae, the fossils most closely resemble *Limacia*. This resemblance is particularly strong in (1) several widely spaced medial secondary veins, as in *L. velutina* Miers and *L. oblonga* Miers; (2) craspedodrome lateral secondary veins near the apex, as in *L. velutina* and *L. scandens* Lour.; (3) camptodrome medial secondary veins, as in *L. velutina* and *L. oblonga*; (4) widely spaced and

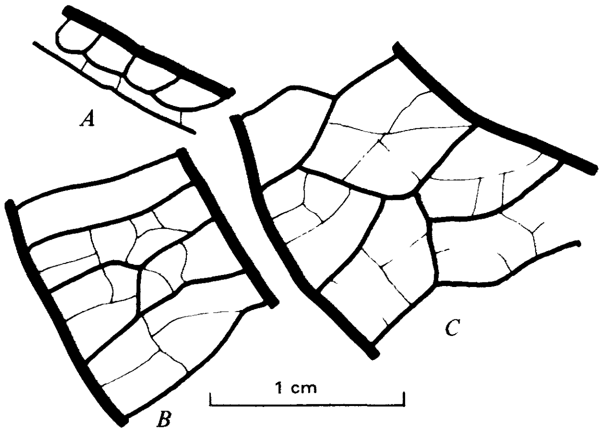

FIGURE 18.—Marginal and intercostal venation of *Paratinomiscium* and *Tinomiscium*. *A*, *P. conditionalis*, holotype, USNM 39117, loc. 3879 (*A*, marginal; *B*, intercostal venation). *C*, *T. petiolare*, USGS Ref. Colln. 1808.

branching tertiary veins connecting the lateral primaries to the midrib, as in all extant species examined; (5) only one pair of lateral primaries, as in all extant species examined; and (6) a narrowly rounded base, as in *L. oblonga.* The major features of the fossil can, therefore, be found in *Limacia*, although no single species of *Limacia* combines all these features. *L. stenophylla*, in addition, has a more elongated shape than in the extant species examined.

Holotype.—USNM 43303.

Paratypes.—USNM 43304-43307.

Occurrence.—Kushtaka Formation, locs. 11158, 11159, 11166.

Genus Paratinomiscium Wolfe, new organ genus

Diagnosis.—Leaves simple; venation palmate; base broadly rounded; five primary veins, first pair extending into apical half of lamina, camptodrome; lateral secondary veins camptodrome, forming loops; a few pairs of medial secondary veins, camptodrome, forming loops; marginal tertiary veins craspedodrome, joining conspicuous marginal vein; intercostal tertiary veins approximately perpendicular to secondary veins, branching or unbranching, closely spaced; quartary mesh irregularly polygonal; petiole long.

Type species.—*P. conditionalis* (Hollick) Wolfe [*Hampea*].

Discussion.—The fossils apparently represent a new genus of Menispermaceae. Among extant genera, the fossils are most similar to *Tinomiscium* in the broadly rounded base, lateral primary veins extending about two-thirds the distance to the apex, conspicuous marginal vein, and long petiole. In *Tinomiscium*, however, the intercostal tertiary veins are spaced about twice the distance apart as in *Paratinomiscium* and the marginal tertiary veins form a series of loops.

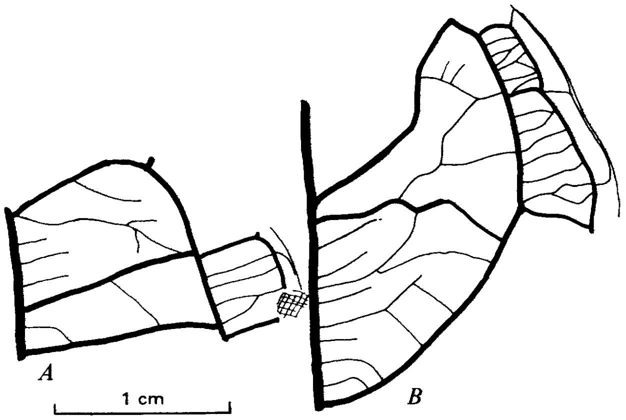

FIGURE 19.—Venation of *Pycnarrhena*. *A*, *P.* sp., USNM 43308, loc. 11166. *B*, *P. celebica*, USGS Ref. Colln. 1806.

Paratinomiscium conditionalis (Hollick) Wolfe

Plate 7, figure 5; text figure 18

Hampea conditionalis Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 150, pl. 118, fig. 1.

Holotype.—USNM 39117.

Occurrence.—Kulthieth Formation, locs. 3879, 11195.

Genus Pycnarrhena Miers

Pycnarrhena sp.

Plate 6, figure 4; text figure 19

Discussion.—The fossil leaf is palmately veined, although the lateral primaries extend a short distance above the top of the petiole parallel to the midrib. The first pair of lateral primaries is prominent, and extend about half the distance to the apex. The area formed by the midrib and the looping secondary veins are almost square. The tertiary venation has a strong tendency to extend in an abmedial direction and disappear, presumably thinning into fourth order venation, which is not preserved. Although the leaves of the two extant species of *Pycnarrhena* examined both have more trapezoidal areas formed by the secondary veins, the thinning tertiary venation, closely spaced tertiary veins within the marginal loops, and the presence of a series of tertiary loops; these characteristics indicate a close relationship to the fossil.

Specimen.—USNM 43308.

Occurrence.—Kushtaka Formation, loc. 11166.

Family MYRISTICACEAE

Genus Knema Loure

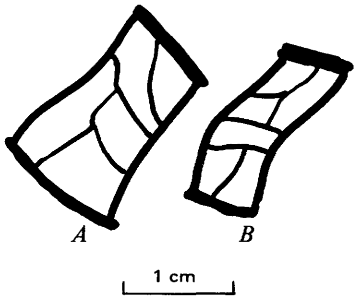

FIGURE 20.—Intercostal venation of *Knema*. *A*, *K*. sp., USNM 43309, loc. 3847. *B*, *K. glauca*, USGS Ref. Colln. 1827.

Knema sp.

Plate 8, figures 3, 4; text figure 20.

Rhamnus marginatus auct. non Lesquereux. Hollick, 1936, U.S. Geol. Survey Prof. paper 182, p. 140, pl. 78, figs. 1, 2.

Discussion.—The numerous secondary veins that loop close to the margin, unequally spaced intercostal tertiary veins, and fourth-order venation that is irregularly branching and typically set at oblique angles to the intercostal tertiary veins are features that ally these fossils to *Knema*. Although some extant species of the genus have thick veins, I have not seen any quite so thick as in the fossil leaves. Among extant species, the fossil most closely resembles *K. glauca* (Blanco) Merr. in shape and extensive secondary looping and *K. korthalsii* Warb. in the spacing of the intercostal tertiary veins.

Specimens.—USNM 38915, 43309.

Occurrence.—Kushtaka Formation, loc. 3847.

Genus Myristica Gronov

Myristica sp.

Plate 5, figure 6; plate 8, figure 1; text figure 21

Terminalia sp.? Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p.155, pl. 93 fig. 6.

Magnolia ovalis auct. non Lesquereux. Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 114, pl. 63, fig. 1 only.

Discussion.—The extensive and irregular secondary and tertiary loops, closely spaced and undulatory intercostal tertiary veins, and branching fourth-order venation indicate that the fossil represents a species of *Myristica*. The secondary loops are more elongated perpendicular to the midrib than in any extant species examined.

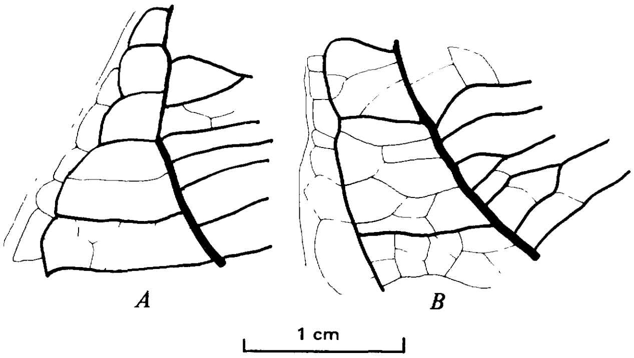

FIGURE 21.—Marginal venation of *Myristica*. *A*, *M*. sp., USNM 38667, loc. 3847. *B*, *M. guaterrifolia*, USGS Ref. Colln. 1833.

Specimens.—USNM 38667, 39019.

Occurrence.—Kushtaka Formation, loc. 3847.

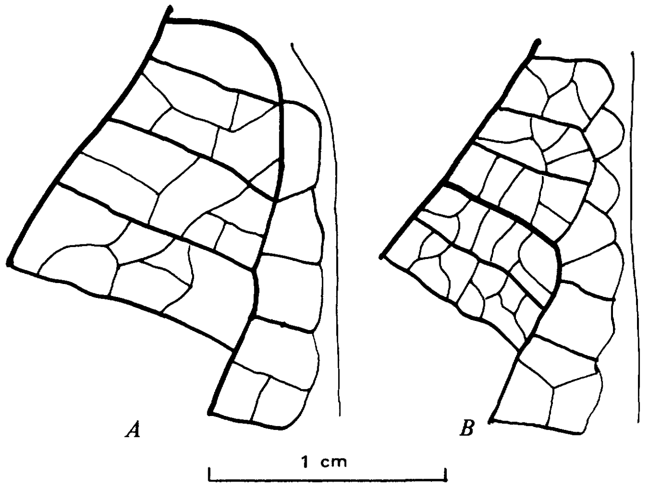

FIGURE 22.—Marginal venation of *Cananga*. *A*, *C*. sp., USNM 38911, loc. 3879. *B*, *C. odorata*, USGS Ref. Colln. 1632a.

Family ANNONACEAE

Genus Cananga (DeCandolle) Hooker f. and Thomas

Cananga sp.

Plate 8, figure 6; text figure 22

Magnolia wormskioldi auct. non Heer. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 115, pl. 63, fig. 3.

Discussion.—The fossil appears to represent Annonaceae and in particular resembles *Cananga odorata* Hook. f. This resemblance is in the very broadly rounded base, curvature of the secondary veins, thick midrib but thin secondary veins, angular looping of the secondary veins and orientation of the apical side of the loop, slightly irregular looping of the marginal tertiary veins, orientation and spacing of the intercostal tertiary veins, irregularly branching quartary veins, and entire margin lacking a marginal vein.

Specimen.—USNM 38911.

Occurrence.—Kulthieth Formation, loc. 3879.

Genus Dasymaschalon (Hooker f. and Thomas) Dalla Torre and Harms

Dasymaschalon? sp.

Plate 8, figure 5

Discussion.—The combination of a broadly rounded cordate base, pinnate venation, and entire margin, is unusual. Some Annonaceae, however, display such a combination of features. Broadly arching and thin secondary veins that extend a considerable distance towards the apex are found in *Dasymaschalon trichophorum* Merr., as is a broadly cordate base. Because the tertiary venation of the fossil is obscured by the coriaceous texture, the generic reference should not be considered certain.

Specimen.—USNM 43310.

Occurrence.—Kushtaka Formation, loc. 11158.

Family LAURACEAE

Foliage of Lauraceae is difficult to determine as to genus under the best of circumstances. Many species in the western Tertiary—particularly the Paleogene—have been assigned to extant genera simply on the basis that a particular fossil species most closely resembles a particular species; that is, the generic assignment has no morphologic basis in that the fossil species is not stated to display the characters diagnostic of the particular genus. In fact few extant genera of Lauraceae can be diagnosed on the features of the leaves—particularly noncuticular features. This circumstance should not be surprising in view of the fact that Reid and Chandler (1933) were unable to clearly delimit the genera of Lauraceae despite having well-preserved fruits. An approach to lauraceous leaves that has morphologic validity is to use organ genera that represent morphologic types except in the few instances (for example, *Sassafras*) that assignments to extant genera can be confidently made.

One grouping that can be made of lauraceous leaves, as pointed out by Krausel and Weyland (1951), is of those leaves that have secondary veins that are approximately parallel and of approximately the same strength; the name *Litseaphyllum* is applicable to such leaves. This organ genus, in addition, should be emended so as to include leaves that have few or no freely ending veinlets; if freely ending veinlets are present, they are unbranching. An additional character of the genus is the presence of a continuous marginal vein. *Litseaphyllum* thus includes leaves of *Laurus*, *Machilus*, *Persea*, *Lindera* (part), and *Litsea*; definitely excluded because of the presence of branching veinlets are *Endiandra*, *Ocotea*, *Nectandra*, *Licaria*, *Phoebe*, and *Umbellularia*. The various species from the west American Tertiary that have been attributed to *Nectandra* are all *Litseaphyllum* on the basis of ultimate venation.

A second grouping of lauraceous leaves are those that have a pseudo-palmate venation, that is, one pair of secondary veins—typically departing a short distance above the top of the petiole—are aparallel to, and typically thicker than, the other secondary veins. Additionally, a continuous marginal vein is present and the areoles have few or no freely ending veinlets; if present, the veinlets are unbranching. Leaves of this type are referred to *Cinnamomophyllum* (Kräusel and Weyland, 1951). Included in *Cinnamomophyllum* are leaves of *Cinnamomum*, *Cryptocarya*, *Lindera* (part), and *Neolitsea*; excluded because of the presence of branching veinlets are *Ocotea* and *Sassafras*. Note that *Cinnamomophyllum* only includes leaves of genera that are today old world in distribution. Significantly, none of the species from the west American Tertiary that have been attributed to *Ocotea* represent that genus; without exception they have the ultimate venation of *Cinnamomophyllum*.

Genus Cinnamomophyllum Krausel and Weyland

Cinnamomophyllum kushtakensis Wolfe, new species

Plate 23, figures 5, 7a

Diagnosis.—Leaves simple; venation pinnate; shape ovate, linear; base acute; five or six pairs of conspicuous secondary veins, the lowest pair more pronounced, extending about half the distance to apex, aparallel to other secondary veins; other secondary veins departing at an angle of about 40°-60°, curving apically, looping; intercostal tertiary veins widely spaced, branching; areoles intruded by unbranching or typically no veinlets; margin entire, with marginal vein.

Discussion.—The description of the ultimate venation is based on a specimen from locality 9731 in the Puget Group; this specimen in other respects matches well the Katalla specimens. *Cinnamomophyllum kushtakensis* can be separated from other described species of the genus primarily by the linear shape. *C. kushtakensis* may be closely related to *C. latum*.

Holotype.—USNM 43311.

Paratypes.—USNM 43312-43313 (loc. 9732, Puget Group).

Occurrence.—Kushtaka Formation, locs. 9389, 11165.

Cinnamomophyllum latum (MacGinitie) Wolfe, new combination

Plate 8, figure 2; plate 9, figures 3, 10

Neolitsea lata MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, p. 118, pl. 20, figs. 2, 3.

Cinnamomum cinnamomeum auct. non *Phyllites cinnamomeus* Rossmaessler. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 115, pl. 64, fig. 2.

Discussion.—MacGinitie's holotype has a distinct marginal vein and almost no freely ending veinlets and is thus transferred to *Cinnamomophyllum*.

Hypotypes.—USNM 38914, 43314-43315.

Occurrence.—Kushtaka Formation, locs. 3847, 11157, 11160, 11166.

Genus Litseaphyllum Wolfe, new name

Laurophyllum Goeppert, 1853, Neues Jahrb., p. 434.

Discussion.—The name "*Laurophyllum*" is an orthographic variant of the anacard *Laurophyllus* Thunb., and this extant genus has clear priority. A new name for the organ genus is thus needed.

Litseaphyllum carbonensis Wolfe, new species

Plate 28, figures 6, 9

Diagnosis.—Leaves simple; venation pinnate; shape oval; base acute to narrowly rounded, apex acute; three or four pairs of conspicuous secondary veins, departing at low angles, curving sharply apically, looping; second pair of secondary veins extending about three-fourths distance to apex, third pair extending to apex; intercostal tertiaries oriented approximately perpendicular to midrib, closely and uniformly spaced; areoles intruded by unbranching or typically no veinlets; margin entire.

Discussion.—This species closely resembles *Laurophyllum presamarensis* in general aspect, but in *L. carbonensis* the secondary veins curve more sharply and extend farther towards the apex.

Holotype.—USNM 43317.

Paratype.—USNM 43316.

Occurrence.—Kushtaka Formation, loc. 11169.

Litseaphyllum katallaensis Wolfe, new species

Plate 29, figures 1, 3

Diagnosis.—Leaves simple, venation pinnate; shape oval to ovate; base acute, apex acute; seven to nine pairs of secondary veins, curving apically, extending almost to margin and looping weakly; weak basal secondary veins, intercostal tertiary veins spaced uniformly about 0.5 cm apart, branching, approximately at right angles to secondary veins; areoles with unbranching veinlets; margin entire.

Discussion.—This species resembles in shape and secondary venation "*Laurophyllum*" *raminervum* Potb., but that species has areoles intruded by branching veinlets (Potbury, 1935, p. 67) and cannot represent *Litseaphyllum* as this genus is conceptualized in this report.

Holotype.—USNM 43319.

Paratype.—USNM 43318.

Occurrence.—Katalla Formation, Split Creek beds, loc. 11168; Kulthieth Formation, loc. 9551.

Litseaphyllum praelingue (Sanborn) Wolfe, new combination

Plate 22, figure 6

Persea praelingue Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 20, pl. 6, fig. 1.

Magnolia californica auct. non Lesquereux. Sanborn, 1935 (in part), Carnegie Inst. Washington Pub. 465, p. 17, pl. 2, figs. 3–5.

Discussion.—Sanborn's holotype of *Persea praelingue* appears to be an aberrant leaf of the species she also called *Magnolia californica.* In *Litseaphyllum praelingue*, the intercostal tertiary veins are oblique to the secondary veins, the intramarginal loops have a pronounced trapezoidal shape, the midrib is thick, and the petiole is thick.

Hypotype.—USNM 43324.

Occurrence.—Kushtaka Formation, loc. 11165.

Litseaphyllum presamarensis (Sanborn) Wolfe, new combination

Plate 9, figure 2; plate 22, figures 1, 2; plate 28, figures 8b, 10a, b

Cryptocarya presamarensis Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 19, pl. 5, figs. 4, 6.

Discussion.—Although these leaves could presumably represent *Cryptocarya*, they cannot be satisfactorily distinguished from leaves of several other genera of Lauraceae. Ultimate venation of leaves from locality 9731 in the Puget Group provide the basis for referring this species to *Litseaphyllum.*

Hypotypes.—USNM 43325-43330.

Occurrence.—Kushtaka Formation, locs. 3842, 3846, 11157, 11165, 11169.

Litseaphyllum presanguinea (Chaney and Sanborn) Wolfe, new combination

Plate 29, figure 9

Nectandra presanguinea Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 73, pl. 18, figs. 1, 2, 5, 7.

Discussion.—The ultimate venation of the type of this species indicates that the specimen cannot represent *Nectandra* but is related to various Asian laurels (see p. 67). The undulatory secondary veins that loop well within the margin, numerous intersecondary veins, and linear shape characterize this species.

Hypotype.—USNM 43331.

Occurrence.—Kushtaka Formation, loc. 9891.

Litseaphyllum schorni Wolfe, new species

Plate 25, figures 1, 2, 6

Diagnosis.—Leaves simple; venation pinnate; shape oval to obovate; base cuneate, apex acuminate; weak pair of basal secondary veins that extend a short distance along margin; 11–13 pairs of secondary veins, uniformly spaced, broadly curving towards margin, curving sharply and looping near margin; short series of small, angular loops extending apically to about where next most apical secondary loops; intercostal tertiary veins numerous, straight or branching, perpendicular to secondaries; margin entire; petiole thick and long.

Discussion.—Well-preserved leaves from the middle Ravenian of the Puget Group appear to have the diagnostic features of *Litseaphyllum schorni*; the Puget leaves have small areoles, most of which lack freely ending veinlets. The fossils closely resemble *Cryptocarya infectoria* (Bl.) Miq. of the Philippine Islands. The resemblance is particularly strong in the secondary veins, which are strongly, smoothly, and gradually curving and sharply looping near the margin, and in the spacing and strength of the intercostal tertiary veins. The fossils, however, have more numerous and closely spaced secondary veins and a longer petiole than does *C. infectoria*.

This species is named for H. E. Schorn in recognition of his assistance in discussing the vegetational and floristic aspects of this report.

Holotype.—USNM 43333.

Paratypes.—USNM 43332, 43334.

Occurrence.—Kushtaka Formation, locs. 9389, 11165.

Litseaphyllum similis (Knowlton) Wolfe, new combination

Plate 9, figures 1, 4; plate 23, figure 2; plate 29, figure 2

Laurus similis Knowlton, 1900, U.S. Geol. Survey 20th Ann. Rept., pt. 3, p. 48, pl. 5, figs. 1-4.

Persea pseudocarolinensis auct. non Lesquereux. Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 20, pl. 5, fig. 3.

Discussion.—*Laurus similis* was synonymized to *Persea pseudocarolinensis* by Sanborn (1935). In *Persea*, however, the veins that depart from the midrib basal to the first pair of conspicuous secondaries are stronger than the tertiary veins and typically are perpendicular to the midrib. *Laurus similis* does not represent a *Persea-Machilus* type of leaf, but appears to be related to laurels such as *Laurus*, *Lindera*, and *Litsea*.

Hypotypes.—USNM 43320-43323.

Occurrence.—Kushtaka Formation, locs. 11157, 11165, 11169.

Litseaphyllum spp.

The species of *Litseaphyllum* discussed on the following pages do not, in most instances, have the ultimate venation preserved. Most of the species, although having the weak basal secondary veins characteristic of Lauraceae, are therefore only tentatively referred to *Litseaphyllum*; I am thus using *Litseaphyllum* in a broader sense than for the named species previously discussed.

Litseaphyllum sp.

Plate 9, figure 7

Discussion.—The specimen has an entire margin and a highly coriaceous texture. Weak, basal secondary veins are present. The few secondary veins give off strong branches near the margin, unlike the secondaries of *Litseaphyllum presamarensis* and *L. similis*. The quartary mesh is formed of almost quadrangular areoles, and thus the fossil resembles leaves of some species of *Lindera* and *Litsea*.

Specimen.—USNM 43335.

Occurrence.—Kushtaka Formation, loc. 11159.

Litseaphyllum sp.

Plate 29, figure 5

Discussion.—These small leaves have a coriaceous texture. The secondary veins in the basal part of the lamina depart from the midrib almost at a right angle; this feature is also found in leaves of *Machilus* and *Persea*.

*Specimen.*USNM 43336.

Occurrence.—Kulthieth Formation, loc. 11170; Katalla Formation, Split Creek beds, loc. 11168.

Litseaphyllum sp.

Plate 22, figure 5

Discussion.—The specimen has weak secondary veins departing from the midrib at an angle of about 90° in the basal part of the lamina; as the preceding species, this species is apparently allied to *Machilus* or *Persea* (considered by some neobotanists to be the same genus). The more numerous secondary veins that do not curve as sharply indicate that the specimen from the Kushtaka does not represent the same species as the preceding form.

Specimen.—USNM 43337.

Occurrence.—Kushtaka Formation, loc. 11165.

Litseaphyllum sp.

Plate 22, figure 4

Discussion.—This leaf has a pronounced asymmetric, ovate shape and broadly arching secondary veins; these features distinguish the species from *Litseaphyllum praelingue*. The secondary veins give off strong branches that loop with the next most basal secondary vein; the loops thus formed are angular. The intercostal tertiary venation is obscure, but the tertiaries appear to be evenly and widely spaced and approximately perpendicular to the secondary veins.

Specimen.—USNM 43338.

Occurrence.—Kushtaka Formation, loc. 11165.

Litseaphyllum sp.

Plate 28, figure 8a

Discussion.—This leaf is distinguished from the other laurels discussed in this report by the linear, ovate shape and the numerous secondary veins.

Specimen.—USNM 43339.

Occurrence.—Kushtaka Formation, loc. 11169.

Litseaphyllum sp.

Plate 29, figure 8

Discussion.—This linear leaf has fewer and more widely spaced secondary veins that the preceding form. The shape, in addition, is oval rather than ovate.

Specimen.—USNM 43340.

Occurrence.—Kushtaka Formation, loc. 9891.

Order ROSALES

Family HAMAMELIDACEAE

Genus Corylopsis Siebold and Zuccarrini

Corylopsis sp.

Plate 26, figure 6

Discussion.—The asymmetric shape, palmate-appearing venation, and nonentire margin are characters indicative of the subfamily Hamamelioideae. The specimen has numerous, sharp—almost spinose—teeth, smoothly curving secondary venation, and a cordate base; a species of *Corylopsis* is, therefore, represented. The only other almost spinose leaves in the subfamily belong to *Fortunearia* and *Sinowilsonia*; in both these genera, however, the secondary venation is undulatory and conspicuously forking.

Koch (1963) has described leaves from Greenland as *Corylopsiphyllum*; I can see no morphologic basis for referring these leaves to any genus other than *Corylopsis*. Various species of *Hamamelis* and *Hamamelites* have been described from Paleocene and Eocene assemblages throughout the northern hemisphere. Most of these leaves have the diagnostic features of the subfamily, although some of the species do not appear to be clearly referrable to any extant genus. Together with the occurrence of *Corylopsis* in the tropical London Clay assemblage (Chandler, 1964), *Fothergilla* in the tropical middle Eocene assemblages of the Puget Group (Wolfe, 1968), and of *Fortunearia* in the subtropical early basic breccia assemblage (see p. 89), the Paleogene occurrences of the subfamily indicate an adaptation in the early Tertiary to the tropical vegetation types. The fact that some extant members of the subfamily are winter-flowering—a peculiar adaptation for a temperate, deciduous plant—could be explained in terms of a former wide distribution in tropical vegetation types, in which the time of flowering would not have been significant. the winter-flowering may thus be an anachronism.

Specimen.—USNM 43341A, B.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Liquidambar Linnaeus

Liquidambar? sp.

Plate 24, figure 1

Discussion.—The margin and venation of this specimen is not well preserved, but the deeply cut lobes and apparently finely serrate margin combined with the camptodrome secondary veins, indicate that the specimen is *Liquidambar.* In species of *Acer* that have nonentire margins, the secondary veins are typically craspedodrome.

Specimen.—USNM 43342.

Occurrence.—Kushtaka Formation, loc. 11165.

Family EUCOMMIACEAE

Genus Eucommia Oliver

Eucommia sp.

Plate 24, figure 7

Discussion.—The specimen has widely and irregularly spaced secondary veins, the apical ones curving more sharply than the more basal ones. The secondaries are camptodrome; two sets of inframarginal loops are present, and thus the quartary veins are craspedodrome. The teeth are numerous and are separated by either arcuate or angular sinuses. The intracostal tertiary veins are obscure, but they appear to be widely spaced and slightly oblique to the secondaries. In the features preserved, the specimen is assignable to *Eucommia.*

Brown (1962) has assigned some Paleocene leaves to *Eucommia.* These leaves, however, have both craspedodrome and camptodrome secondary veins, craspedodrome tertiary veins, and apical secondary veins that are typically approximately parallel to the more basal secondaries; these leaves do not represent *Eucommia.* The seeds from the Claiborne assemblage that Brown (1940) referred to *Eucommia* also do not appear to represent that genus. In *Eucommia*, a conspicuous vascular strand extends from the base of the samara alongside the seed, splits at the apical cleft and extends to the apex of the samara along either side of the cleft. It is clear from Berry's illustration (1930a, pl. 44, figs. 15, 16) that such a vein and an apical cleft are not present. The other Claiborne specimen assigned to *Eucommia* by Brown (1940) similarly is not *Eucommia*; Berry's illustrations (1930a, pl. 33, figs. 5, 6) indicate that the seed was basal and an expanded samara extended apically.

Eucommia montana R. W. Br. and *E. browni* Beck. both appear to be valid representatives of the genus. The three known North American representatives of *Eucommia* indicate that the genus was present in both lowland subtropical forest in the late Eocene and upland temperate forest in the early to middle Oligocene. The genus, however, apparently did not survive in North America to become a member of the Neogene Mixed Mesophytic forest.

Specimen.—USNM 43343.

Occurrence.—Kushtaka Formation, loc. 11165.

Family PLATANACEAE

Genus Platanus Linnaeus

Platanus comstocki (Sanborn) Wolfe, new combination

Plate 29, figure 7

Mallotus comstocki Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 23, pl. 6, fig. 9.

Platanus aceroides auct. non Goeppert. Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 21, pl. 6, fig. 10.

Discussion.—*Mallotus,* as do many Euphorbiaceae, has leaves in which the quartary veins are perpendicular to the tertiary veins; this situation is clearly not present in Sanborn's *Mallotus comstocki.* Her interpretation of the leaf as being subpeltate is due to the fusion of the acropetiolar stipule to the lamina, which is typical of *Platanus. P. aceroides* is a strongly toothed and "lobed" species, unlike *P. comstocki.*

Hypotype.—USNM 43344.

Occurrence.—Kushtaka Formation, loc. 9891; Kulthieth Formation, loc. 11189.

Family ROSACEAE

The geologic history of Rosaceae is largely confined to the latest Eocene, Oligocene, and Neogene. In contrast to the diversity of the family in the warm temperate assemblages of the Neogene, the family is apparently lacking in warm temperate Paleocene assemblages. Brown (1962) has attributed some leaves from the Rocky Mountain Paleocene to *Prunus*, but none of these leaves has the acropetiolar glands or glandular teeth characteristic of *Prunus.* The fructifications assigned by Brown (1962) to *Prunus* should be reinvestigated; they have obvious similarities to the fruits of Icacinaceae. Chandler (1964) recorded seeds of *Rubus* from the early Eocene, and MacGinitie (1941) has recorded *Vauquelinia* in the early Eocene. The family does not appear to have been well represented in subtropical or Paratropical Rain forest during the Paleogene—a situation that still obtains today in these vegetational types. In the cool period of the latest Eocene, Rosaceae appear for the first time in diversity. Genera that appear to be validly recorded from beds of this age are: *Amelanchier, Crataegus, Chamaebatiaria, Potentilla, Prunus, Pyrus, Rubus,* and *Sorbus.* Note that all four subfamilies were represented. Most of these genera occur in the more temperate vegetation in lowland Alaska and upland Pacific Northwest, but one genus—*Rubus*—is known in the John Day Gulch assemblage, which is warm temperate to subtropical.

The upland floras of the early to middle Oligocene (Ruby, Florissant) display a considerable diversity of Rosaceae. In addition to the genera that first appeared in the latest Eocene, several other genera, such as *Cercocarpus,* are represented; more significantly, the specific diversity within each genus appears to have been greater during the early to middle Oligocene than during the latest Eocene. From the later Oligocene on, the family appears to have increased in both generic and specific diversity. The early Miocene Collawash assemblage from Oregon—representing the Mixed Mesophytic forest—contains numerous Rosaceae: *Amelanchier, Cercocarpus, Crataegus* (three species), *Holodiscus, Lyonothamnus, Peraphyllum* (or a closely related genus), *Prunus* (three species), *Pyrus, Rosa,* and *Rubus.* By the Miocene, almost all woody genera of Rosaceae now native to western North America had appeared, and several of the lineages represented appear to be the same as those that have survived to the present time.

Genus Prunus Linnaeus

Prunus axelrodi Wolfe, new name

Plate 26, figure 9; text figure 23

Euonymus nevadensis Axelrod, 1966b, California Univ. Pubs. Geol. Sci., v. 59, p. 75, pl. 18, figs. 7, 8.

Prunus chaneyi auct. non Condit. Axelrod, 1966b (part), California Univ. Pubs. Geol. Sci., v. 59, p. 72, pl. 17, fig. 1 only.

Prunus harneyensis auct. non Axelrod 1944. Axelrod, 1966b, California Univ. Pubs. Geol. Sci., v. 59, p. 72, pl. 17, figs. 4-7.

Discussion.—The holotype of *Euonymus nevadensis* has large glandular teeth just apical from the top of the petiole and is thus clearly *Prunus.* The flowing intercostal venation indicates a relationship to *P. serotina* Ehren. The Alaskan fossil tentatively referred to *P. axelrodi* is fragmentary, but it has about the same spacing and type of teeth and the same tertiary venation as does *P. axelrodi*; in addition, the spacing of the secondary veins, their angle of departure, and their curvature in the Alaskan fossil is the same as in *P. axelrodi.*

The epithet "*nevadensis*" has been previously applied to a species of *Prunus,* and thus a new name is required. This species is named for the original describer, D. I. Axelrod.

Hypotype.—USNM 43345A, B.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Sorbus Linnaeus

Sorbus carbonensis Wolfe, new species

Plate 27, figures 3, 4; text figure 24

Diagnosis.—Leaf compound; venation of leaflet

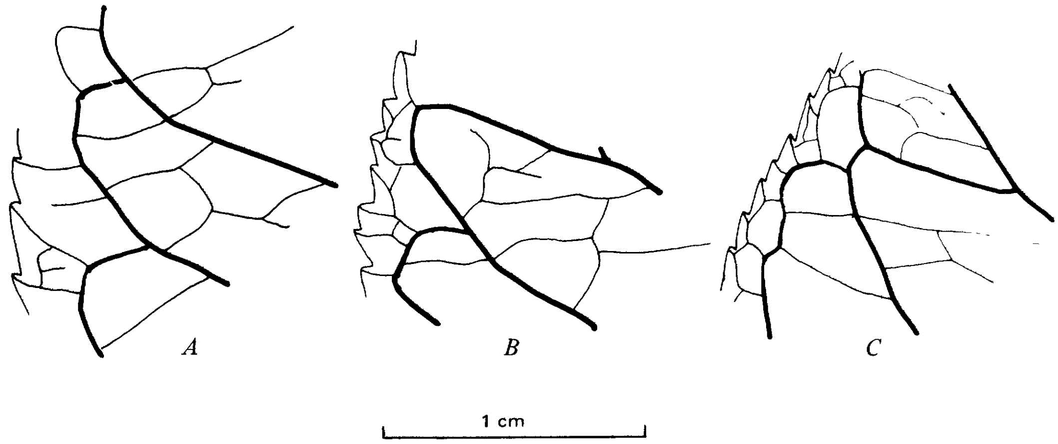

FIGURE 23.—Marginal venation of *Prunus*. *A*, *P. axelrodi*, hypotype, USNM 43345B, loc. 11167. *B*, *P. axelrodi*, holotype, UCMP 20111A, Copper Basin flora. *C*, *P. serotina*, USGS Ref. Colln. 1202.

pinnate; shape linear, oval; base asymmetric; at least 13 pairs of secondary veins, straight to slightly curving, craspedodrome; marginal tertiary veins craspedodrome; intercostal tertiary veins oriented perpendicular to secondaries, branching; quartary venation forming irregularly polygonal areoles intruded by profusely branching veinlets; teeth very sharp, about two per secondary vein.

Discussion.—The single leaflet has the finely and compoundly serrate margin of leaflets of *Sorbus*. The most closely related species to *S. carbonensis* is an undescribed species from the type section of the Seldovian Stage; this undescribed species typically has three or four teeth per secondary vein, but it has the same intercostal venation as does *S. carbonensis*.

Holotype.—USNM 43346A, B.

Occurrence.—Kushtaka Formation, loc. 11167.

Family LEGUMINOSAE

Genus Caesalpinites Saporta

Caesalpinites sp.

Plate 9, figure 6; text figure 25

Discussion.—The single leaflet has features of a number of genera of legumes. In my opinion, however, most isolated leaflets of legumes cannot be satisfactorily assigned to a genus because of the overlap of characters between genera.

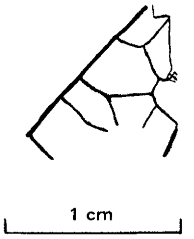

FIGURE 24.—Marginal venation of *Sorbus carbonensis*. Holotype, USNM 43346B, loc. 11167.

Specimen.—USNM 43347.

Occurrence.—Kushtaka Formation, loc. 3847.

Caesalpinites sp.

Plate 25, figure 5

Discussion.—The leaflet has secondary veins that extend directly to the margin; as with the preceding species, assignment to other than an organ genus is not warranted.

Specimen.—USNM 43348.

Occurrence.—Kushtaka Formation, loc. 11165.

Order GERANIALES

Family MELIACEAE

Genus Toona Roemer

Toona sp.

Plate 19, figure 4

Discussion.—A single leaflet resembles the leaflets of some species of *Toona*. The fossil is petiolulate, linear. Camptodrome secondary veins curve close to the margin. Widely spaced, branching tertiary veins are perpendicular to the secondary veins. A revolute margin has two irregularly spaced notches. These features are also found in some leaflets of *Toona*, particularly *T. sureni* (Blume) Merr.; this species

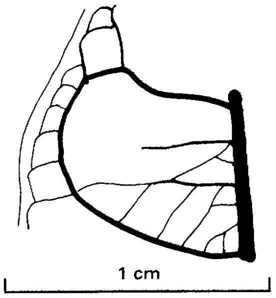

FIGURE 25.—Venation of *Caesalpinites* sp. USNM 43347, loc. 3847.

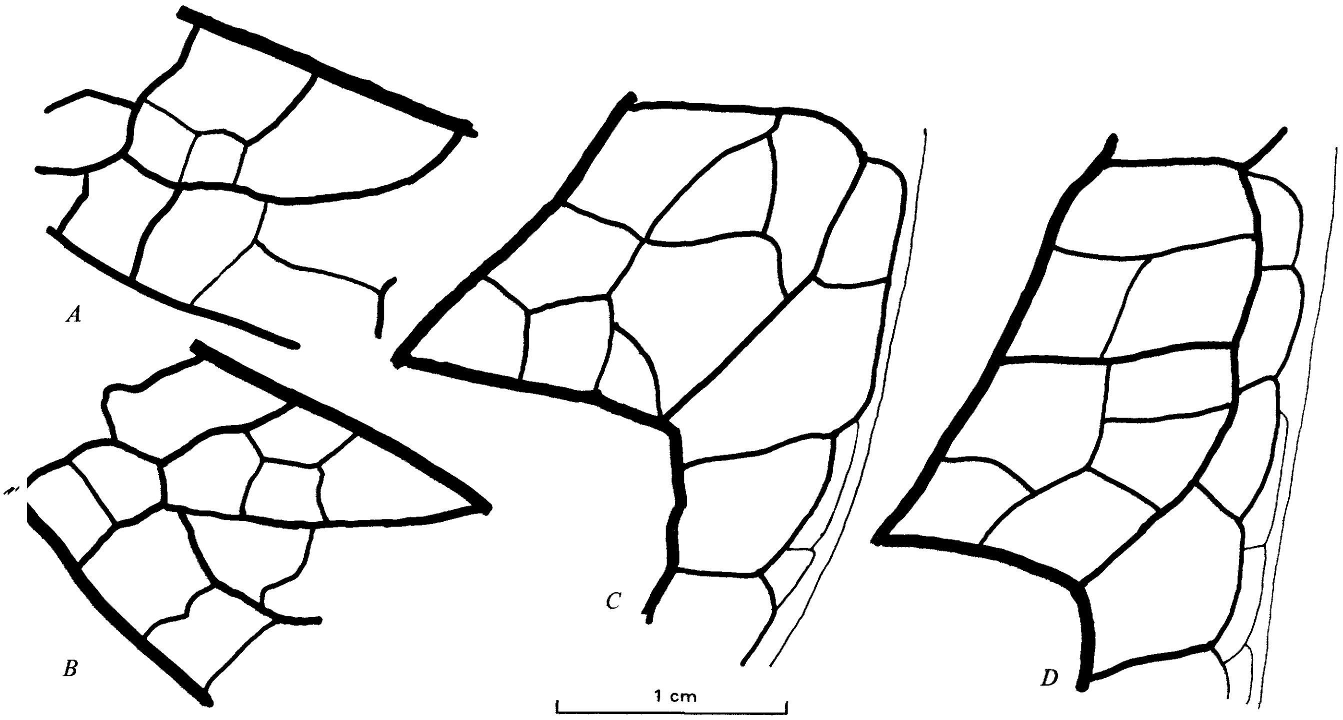

FIGURE 26.—Marginal and intercostal venation of *Luvunga*. *A*, *L. spatiosa*, hypotype, USNM 43352, loc. 3847. *B*, *D*, *L. latifolia*, USGS Ref. Colln. 1696. *C*, *L. spatiosa*, holotype, USNM 38920, loc. 3847.

inhabits the Paratropical Rain forest of southern China.

Specimen.—USNM 222842.

Occurrence.—Kulthieth Formation, loc. 11195.

Family RUTACEAE

Genus Euodia J. R. and G. Forster

Euodia alaskana Wolfe, new species

Plate 9, figures 5, 8, 9

Diagnosis.—Leaf compound; venation of leaflets pinnate; shape oval to ovate; base cuneate, slightly asymmetric; apex narrowly rounded; 12–15 pairs of secondary veins, extending at high angles straight or undulatory, thick, camptodrome, forking conspicuously, some loops extending to margin; intercostal tertiary veins uniformly spaced, forking; intersecondary veins absent or no more than one per secondary vein; margin entire, undulatory; texture coriaceous.

Discussion.—The fossil leaflets have conspicuously forking secondary veins, highly irregular "flowing" intercostal venation (which tends to extend abmedially, recurve, and extend admedially), and a highly undulate, almost crenulate margin; these characters are those of leaflets of *Euodia*. Among extant species, *E. crassifolia* Merr. from the Philippine Islands has leaflets most similar to the fossil. This similarity is particularly displayed in the marginal venation; some of the secondary veins fork and extend straight to the margin. *E. alaskana* has but one or no intersecondary vein per intercostal area, whereas *E. crassifolia* has two or more, one of which typically extends abmedially almost to the margin.

Holotype.—USNM 43349.

Paratypes.—USNM 43350, 43351.

Occurrence.—Kushtaka Formation, loc. 11158.

Genus Luvunga

Luvunga spatiosa (Hollick) Wolfe, new combination

Plate 10, figures 1, 4; text figure 26

Persea spatiosa Holick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 116, pl. 65, fig. 1.

Discussion.—The pronounced asymmetry of Hollick's specimen and of the additional specimen referred here to this species indicate that they were leaflets, not leaves as in Lauraceae. The widely spaced and irregularly branching intercostal tertiary veins are also not lauraceous. The leaflets of Rutaceae, particularly those of *Luvunga*, are very similar to the fossils. These similarities are: (1) an entire margin, (2) broadly curving secondary veins, (3) extensive and large loops, some of which are elongated parallel to the midrib, (4) numerous intersecondary veins that parallel the secondary veins and that extend at least half way to the margin, (5) widely spaced and irregularly branching intercostal tertiary veins some of which join to form

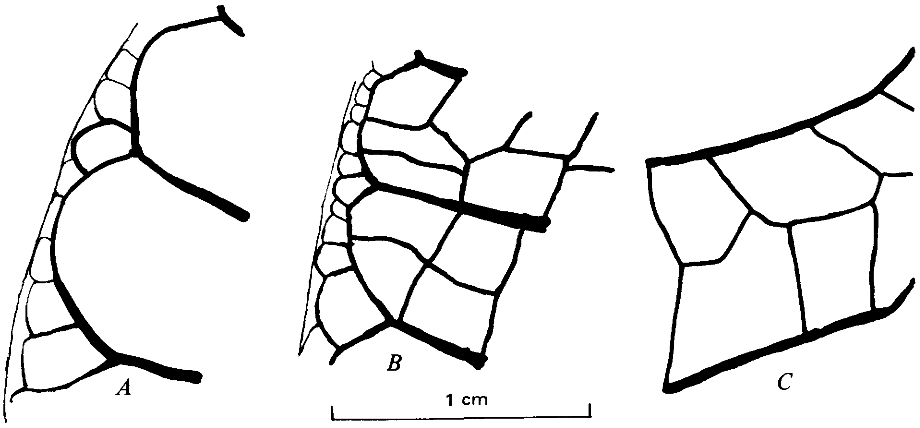

FIGURE 27.—Marginal and intercostal venation of *Melanorrhoea*. *A*, *M. alaskana*, holotype, USNM 39020, loc. 3847. *B*, *M. macrocarpa*, USGS Ref. Colln. 1769. *C*, *M. alaskana*, hypotype, USNM 43353, loc. 11158.

a chevron pointing abmedially, and (6) an abruptly acute apex forming a drip-tip. *L. spatiosa* particularly resembles *L. latifolia* Tan. and *L. crassifolia* Tan., both of which are scandent vines of Melanesia.

Holotype.—USNM 38920.

Hypotype.—USNM 43352.

Occurrence.—Kushtaka Formation, locs. 3847, 11166.

Order SAPINDALES

Family ANACARDIACEAE

Genus Melanorrhoea Wallich

Melanorrhoea alaskana (Hollick) Wolfe, new combination

Plate 10, figures 2, 3, 5; text figure 27

Semecarpus alaskana Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 130, pl. 93, fig. 7.

Dryophyllum stanleyanum auct. non Dawson. Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 103, pl. 56, fig. 4 only.

Discussion.—Hollick's assignment of this species to Anacardiaceae is considered valid. The significant characteristics of this species are the forking and change in orientation of the intercostal tertiary veins midway between the secondaries and the conspicuous thinning of the secondary veins near the margin. The fossils have about the same shape as the leaflets of some species of *Toxicodendron*, but in that genus the intercostal tertiaries thin to become fourth order veins. In *Semecarpus* the leaflets have a pronounced obovate shape, the tertiary veins do not change direction, and the intramarginal loops are strong. The fossils most closely resemble the leaflets of *Melanorrhoea*, particularly in regard to shape of the intercostal area, pattern and size of the third order mesh, and the presence of a series of loops formed by the marginal tertiary veins.

Holotype.—USNM 39020.

Hypotypes.—USNM 38885, 43353.

Occurrence.—Kushtaka Formation, locs. 3846, 3847, 11158; Kulthieth Formation, loc. 11170.

Genus Rhus Linnaeus

Rhus cf. R. mixta (Lesq.) MacGinitie

Plate 19, figure 3

Discussion.—The single specimen is fragmentary, but it displays the diagnostic features of leaflets of *Rhus*, that is, it has broad teeth that have elongated basal flanks, craspedodrome secondary veins that may or may not fork, numerous intersecondary veins that may or may not extend to the sinuses, and intercostal tertiary veins that are oblique to the secondary veins and that thin conspicuously midway between secondary veins. MacGinitie (1941) has illustrated many leaflets from the early Eocene of California that are similar to the Alaskan fossil, but its fragmentary nature does not allow specific assignment.

Specimen.—USNM 222840.

Occurrence.—Kulthieth Formation, loc. 11195.

Genus and species indetermined

Plate 25, figure 4

Discussion.—The specimen has secondary veins that thin conspicuously as they approach the margin. Although this feature indicates an assignment to Anacardiaceae, the preservation of the venation below the level of secondaries is too poor for generic assignment.

Specimen.—USNM 43354.

Occurrence.—Kushtaka Formation, loc. 11165.

Family AQUIFOLIACEAE

Genus Ilex Linnaeus

Ilex carbonensis Wolfe, new species

Plate 26, figure 12; text figure 28

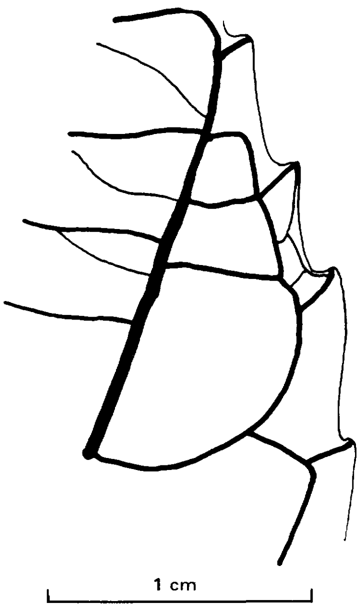

FIGURE 28.—Marginal venation of *Ilex carbonensis*. Holotype, USNM 43355M, loc. 11167.

Diagnosis.—Leaf apparently pinnate (base missing); venation pinnate; shape oval; at least six pairs of secondary veins, widely spaced, curving broadly, forking to form angular loops; marginal tertiary veins camptodrome; marginal quartary veins craspedodrome, entering along apical side of teeth; intercostal tertiary veins few, widely and irregularly spaced, irregularly branching; fourth order mesh irregularly polygonal, forming areoles intruded by profusely branching veinlets; margin with three to four teeth per secondary vein; teeth small, separated by arcuate sinuses; margin thickened.

Discussion.—The arcuate sinuses, the irregular intercostal tertiary pattern, and the profusely branching veinlets indicate an assignment to *Ilex*. In size of areoles, *I. carbonensis* is most similar to *I. geniculata* Maxim. of Japan; in marginal venation and size of the teeth, the fossil is more similar to *I. micrococca* Maxim. from the temperate upland region of southern China.

Holotype.—USNM 43355A, B.

Occurrence.—Kushtaka Formation, loc. 11167.

Family CELASTRACEAE

Genus Celastrus Linnaeus

Celastrus comparabilis Hollick

Plate 11, figures 1, 4-6; plate 18, figure 4

Celastrus comparabilis Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 132, pl. 75, fig. 1a only.

Populus balsamoides auct. non Goeppert. Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 65, pl. 23, fig. 4 only.

Discussion.—Hollick's (1936) determination of this species as a member of *Celastrus* is valid. The characters of the fossils that indicate such a relationship are: a uniformly, closely serrate margin; several widely spaced, camptodrome secondary veins; two series of loops near the margin; intercostal tertiary veins that bifurcate and that are typically almost perpendicular in orientation to the midrib; branches from the tertiary veins that tend to thin and form a highly irregular pattern of fourth order venation; some tertiary veins that depart from the midrib and fork more than once, each fork joining the next most basal secondary vein. These characteristics also indicate a close relationship to extant members of the subgenus *Celastrus*, which is distributed in Madagascar, southeast Asia, Melanesia, and eastern United States; the subgenus, however, has its current center in the tropical and subtropical region of southeastern Asia (Hou, 1955, p. 223). The fossils appear to be most closely related to *C. monospermoides* Loes., which is widely distributed from New Guinea to the Philippine Islands and Malaya.

Lectotype.—USNM 38956.

Hypotypes.—USNM 38744, 43356, 43357, 245728.

Occurrence.—Kushtaka Formation, locs. 3846, 3847, 11158, 11159, 11166; Kulthieth Formations locs. 3879, 11170.

Family ICACINACEAE

Genus Goweria Wolfe, emended

Goweria Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 20.

Discussion.—Leaves of this organ genus were stated to have a marginal vein and were placed in Menispermaceae. Reexamination of the type species, *Goweria dilleri*, from the Puget Group, indicates that I had misinterpreted a thickened margin as a vein. One specimen from the early Ravenian of the Puget clearly displays the small marginal protuberances typical of *Phytocrene*. *Goweria*, however, differs from *Phytocrene* in a few important characteristics: *Goweria* has only five primary veins, and the fourth order mesh is composed of polygons elongated parallel to the tertiary veins. In *Phytocrene*, there are seven primary veins and the fourth order mesh is approximately quadrangular. Four species of *Goweria* are now known: *Goweria linearis*, an undescribed species related to *G. alaskana* from the early Fultonian of the Puget Group, *G. alaskana*, and *G. dilleri*. *Goweria* may represent the same genus as *Paleophytocrene*; both organ genera are represented in a very small assemblage from the Kulthieth formation (loc. 3879).

Goweria alaskana Wolfe, new species

Plate 13, figure 3; text figure 29

Diagnosis.—Leaves simple, pinnately veined; five

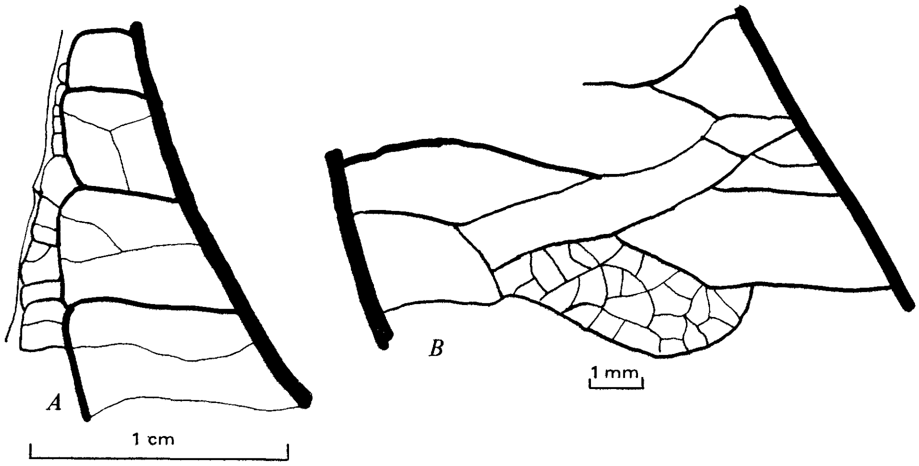

FIGURE 29.—Marginal and intercostal venation of *Goweria alaskana*. *A*, *B*, Holotype, USNM 43358A, loc. 11158.

primary veins; first lateral pair of primaries extending apparently about half the distance to the apex, subparallel to medial secondary veins, camptodrome, apical sides of loops approximately perpendicular to midrib; second pair of lateral primaries weak; at least two pairs of medial secondary veins; intercostal tertiary veins closely spaced, extending perpendicular to midrib or slightly apically, forking or unforking, about half the thickness of the secondary veins; marginal tertiary veins camptodrome or craspedodrome and ending in irregularly spaced marginal bumps.

Discussion.—The apparently few pairs of medial secondary veins and the extension of the first lateral primaries into the apical half of the lamina distinguish this species from other described species of *Goweria*. An undescribed species from the early Fultonian of the Puget Group closely resembles *G. alaskana*, but the Fultonian species is considerably more rotund and the medial secondaries are more closely spaced than in *G. alaskana*.

Holotype.—USNM 43358A.

Occurrence.—Kushtaka Formation, loc. 11158.

Goweria dilleri (Knowlton) Wolfe

Plate 11, figure 3

Goweria dilleri (Knowlton) Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 20, pl. 7, figs. 1, 2; text fig. 13.

Benzoin dilleri Knowlton, 1900, U.S. Geol Survey 20th Ann. Rept., pt. 3, p. 46, pl. 4, fig. 3.

Juglans thermalis auct. non Lesquereux. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 79, pl. 60, fig. la.

Discussion.—The single fragmentary specimen was probably palmately veined; this is inferred from the strong difference in orientation between the two lowest major veins on the left side of the specimen. The specimen has the marginal protuberances, broad shape, and slightly sinuous intercostal venation of *G. dilleri*.

Hypotype.—USNM 38901.

Occurrence.—Kushtaka formation, loc. 3847.

Genus Paleophytocrene Reid and Chandler

Paleophytocrene elytraeformis (Hollick) Wolfe, new combination

Plate 13, figure 2

Carpolithes elytraeformis Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 171, pl. 120, figs. 3, 4.

Discussion.—The specimen illustrated by Hollick does not have the pits arranged as precisely in rows as Hollick or his illustrator show. The pits actually are in irregular rows. The specimen was broken before fossilization, but it is an almost complete impression. The pits are circular or slightly oval in cross section; together with their somewhat irregular arrangement, these kinds of pits indicate that the specimen represents *Paleophytocrene*. *P. elytraeformis* resembles some specimens of *P. foveolata* Reid and Chandl., but the Alaskan species has about sixteen pits lengthwise and the British species typically has only 12. R. A. Scott of the U.S. Geological Survey first suggested to me that Hollick's species represented *Paleophytocrene*.

Holotype.—USNM 39127A, B.

Occurrence.—Kulthieth Formation, loc. 3879.

Genus Phytocrene Wallich

Phytocrene acutissima Wolfe, new species

Plate 12, figures 1-6; plate 13, figure 1; text figure 30

Diagnosis.—Leaves simple; palmately veined; shape ovate; base broadly rounded to cordate; apex pronouncedly acuminate, forming a drip-tip; seven primary veins, the most basal pair weak; lateral and medial secondary veins camptodrome, widely spaced;

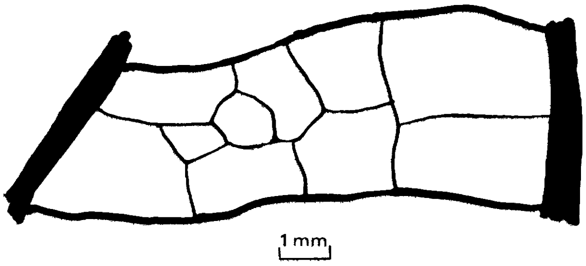

FIGURE 30.—Intercostal venation of *Phytocrene acutissima.* Holotype, USNM 43362B, loc. 11158.

intercostal tertiary veins sinuous; fourth order mesh quadrangular; marginal tertiary veins camptodrome or craspedodrome and ending in small, irregularly spaced marginal protuberances.

Discussion.—The extremely elongated apex distinguishes this species from other species of *Phytocrene* that have been examined. Other species have, in addition, a consistently cordate base. The characters of the fossils that indicate that they are *Phytocrene* are, except for the base, the same as listed under *P. sordida.*

Holotype.—USNM 43362A, B (figs. 4 and 6 on pl. 13 are counterparts).

Paratypes.—USNM 43359-43361, 43363, 43364.

Occurrence.—Kushtaka Formation, locs. 3847, 11158, 11166.

Phytocrene sordida (Lesquereux) MacGinitie

Plate 13, figure 4

Phytocrene sordida (Lesquereux) MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, p. 140, pl. 35, fig. 2; pl. 36, fig. 3.
Ficus sordida Lesquereux, 1878, Harvard Mus. Comp. Zoology Mem., v. 6, no. 2, p. 17, pl. 4, figs. 6, 7.

Discussion.—The seven primary veins, cordate base, and few craspedodrome marginal tertiary veins that end as small protuberances at the margin, place these leaves in *Phytocrene.* The spacing of the intercostal tertiary veins and the angle of departure of the medial secondary veins in the fossils are similar to that of *P. blancoi* (Aza.) Merr., but this species does not have craspedodrome tertiary veins. The marginal characteristics of the fossils are similar to those of *P. bracteata* Wall., but the intercostal tertiary veins are more widely spaced and the medial secondaries in the apical region depart almost perpendicularly from the midrib.

Hypotype.—USNM 43365.

Occurrence.—Kulthieth Formation, locs. 11170, 11195.

Genus Pyrenacantha Wight

Pyrenacantha sp.

Plate 11, figure 2; text figure 31A

Discussion.—The fossil leaf has several characteristics that indicate a close relationship of *Pyrenacantha*: pinnate venation, a weak pair of basal secondaries that form marginal loops whose apical sides are oriented basally, the next more apical secondaries are stronger than the basal pair, some tertiary veins that depart and extend basally from the midrib, widely spaced and irregularly branching intercostal tertiary veins, and marginal tertiary veins that extend from loops of the secondary veins

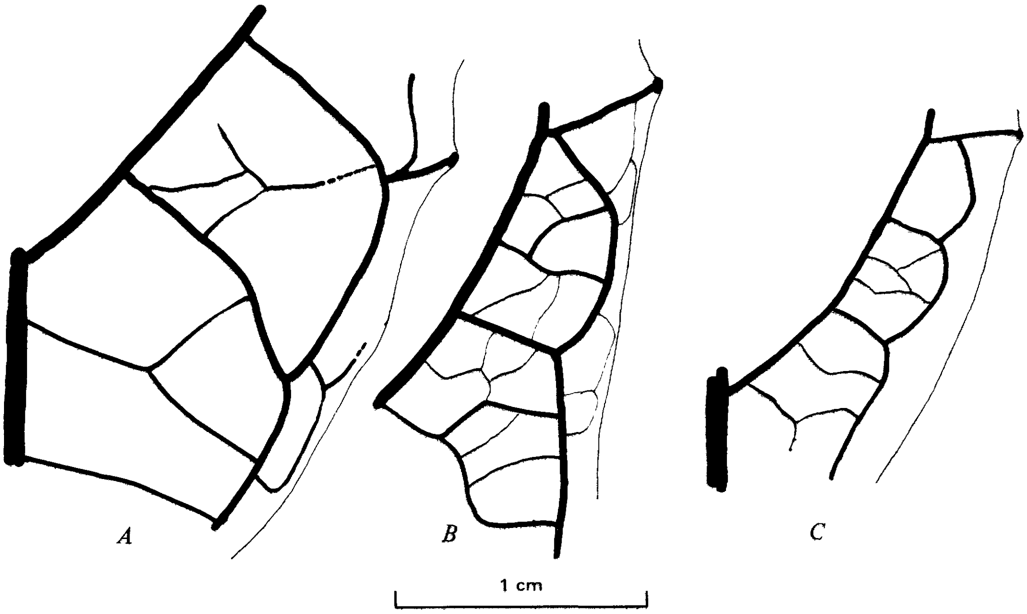

FIGURE 31.—Marginal venation of *Pyrenacantha. A, Pyrenacantha* sp., USNM 43366, loc. 11170. *B, P. repanda,* USGS Ref. Colln. 1873. *C, P. volubilis,* USGS Ref. Colln. 1052a.

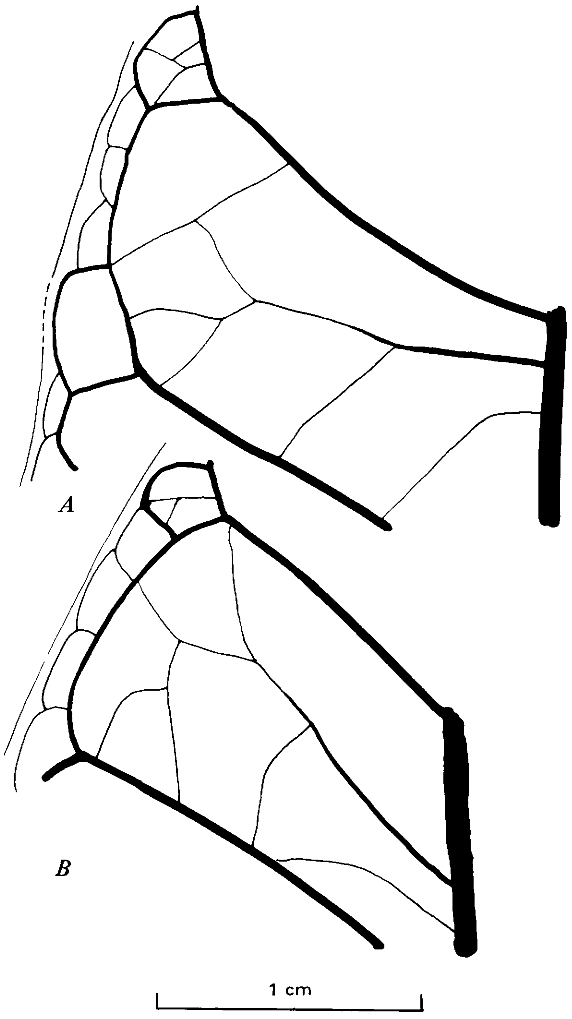

FIGURE 32.—Marginal venation of *Stemonurus*. *A*, *S. alaskanus*, holotype, USNM 43368, loc. 11158. *B*, *S. scorpiodes*, USGS Ref. Colln. 1874.

to a few widely spaced glands on the margin. The Kulthieth species is particularly close to *P. volubilis* Wight from Hainan; the fossil differs from leaves of this extant species in having the loops of the secondary veins placed much closer to the margin.

Specimen.—USNM 43366.

Occurrence.—Kulthieth Formation, loc. 11170.

Genus Stemonurus Blume

Stemonurus alaskanus Wolfe, new species

Plate 13, figures 5, 6; text figure 32A

Diagnosis.—Leaves simple; venation pinnate; shape oval; base acute, apex abruptly acute with drip-tip; 9–12 pairs of secondaries broadly curving or straight, the most basal pair aparallel to the others, looping sharply near the margin; marginal tertiary veins forming a series of small, angular loops; intersecondaries numerous, extending almost to major loops, forking; intercostal tertiary veins irregularly spaced, few, irregularly forking; margin entire; texture coriaceous; petiole thick.

Discussion.—The difference in orientation between the most basal pair of secondaries and the remaining secondaries, the numerous intersecondaries, the irregular tertiary venation, and the angular looping of the fossils indicates a close relationship to *Stemonurus*, and particularly to *S. scorpiodes* Becc. The fossils differ from leaves of this extant Indonesian species in the broader shape and slight curvature of the secondary veins of the fossils.

Holotype.—USNM 43368.

Paratype.—USNM 43367.

Occurrence.—Kushtaka Formation, loc. 11158.

Family SAPINDACEAE

Genus Allophylus Linnaeus

Allophylus duktothensis Wolfe, new species

Plate 14, figures 3, 4

Diagnosis.—Leaf compound; venation of leaflets pinnate; shape oval to ovate, broad; base acute, apex acuminate; six to eight pairs of secondary veins, straight to slightly curving, craspedodrome, entering teeth along apical sides or ending in sinuses or forking, with one fork extending apically and the other entering the teeth or sinus; some marginal tertiary veins craspedodrome; intercostal tertiary veins forming a thin, irregularly forking, large mesh; teeth typically one or two per secondary vein; sinuses arcuate.

Discussion.—Toothed leaves of most Sapindaceae have secondary veins that tend to enter teeth along apical sides or to end in the sinuses. This feature, in combination with the irregular intercostal tertiary venation pattern, indicates that the fossils represent *Allophylus*. Among extant species, *A. duktothensis* most closely resembles *A. peduncularis* Radlk. in shape and intercostal venation; this extant Philippine species, however, has but one tooth per secondary vein and the sinusus are arcuate or angular.

Holotype.—USNM 43372.

Paratype.—USNM 43367.

Occurrence.—Kulthieth Formation, loc. 11170.

Allophylus wilsoni Chaney and Sanborn

Plate 29, figures 4, 6

Allophylus wilsoni Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 81, pl. 24, figs. 1-4, 6.

Discussion.—Some Alaskan specimens are narrower than the Goshen specimens of this species, but other Alaskan specimens are just as broad.

Hypotypes.—USNM 43374A, B, 43375.

Occurrence.—Katalla Formation, Split Creek beds,

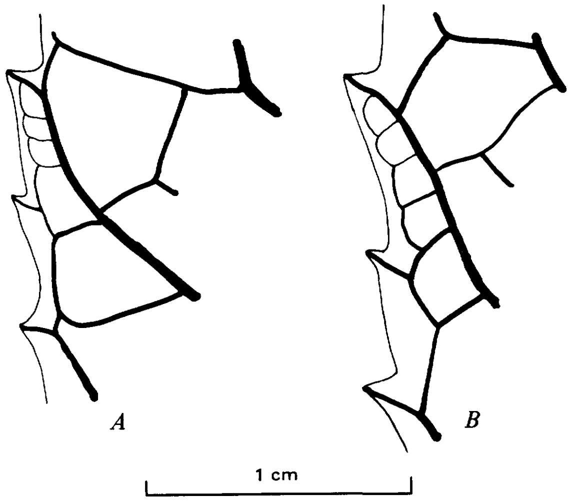

FIGURE 33.—Marginal venation of *Meliosma*. *A*, *M. duktothensis*, holotype, USNM 43378, loc. 11170. *B*, *M. pungens*, USGS Ref. Colln. 100.

locs. 9552, 9889, 11168; Kulthieth Formation, locs. 9551, 9553.

Allophylus sp.

Plate 24, figure 3

Discussion.—The asymmetry of the basal part of the lamina indicates that this specimen represents a leaflet. The marginal venation is typically sapindaceous, and the teeth—about one per secondary vein—also resemble the teeth of *Allophylus*. The poor preservation of the tertiary venation, however, makes the generic reference tentative.

Specimen.—USNM 43376.

Occurrence.—Kushtaka Formation, loc. 11165.

Genus Sapindus Linnaeus

Sapindus? sp.

Plate 24, figure 9

Discussion.—The strongly falcate shape, thick primary vein, entire margin, and camptodrome secondary venation indicate a relationship to *Sapindus*. The thick texture of the specimen has obscured the tertiary venation pattern, and thus the generic reference is not secure.

Specimen.—USNM 43377.

Occurrence.—Kushtaka Formation, loc. 11165.

Family SABIACEAE

Genus Meliosma Blume

Meliosma duktothensis Wolfe, new species

Plate 14, figures 6–8; text figure 33

Diagnosis.—Leaves simple; venation pinnate; shape narrowly oval to obovate; base cuneate; 8–12 pairs of broadly curving secondary veins, departing at an angle of about 45°, forking near margin, apical fork extending apically and the basal entering tooth; intercostal tertiary veins widely spaced, branching, approximately perpendicular to secondaries; margin typically with one or two teeth per secondary vein; teeth small, almost spinose, separated by arcuate sinuses; petiole long.

Discussion.—The fossil leaves have the arcuate sinuses and sharp teeth characteristic of *Meliosma*; the forking of the secondary veins near the margin is characteristic of some species of *Meliosma*, for example *M. simplicifolia* (Roxb.) Walp. (van Beusekom, 1971, p. 407). This extant subtropical Asian species also resembles *M. duktothensis* in having one or two teeth per secondary vein. *M. simplicifolia*, however, has a short petiole and the secondary veins fork farther from the margin than in *M. duktothensis*.

Holotype.—USNM 43378.

Paratypes.—USNM 43379, 43380.

Occurrence.—Kulthieth Formation, locs 11170, 11195.

Meliosma kushtakensis Wolfe, new species

Plate 14, figures 1, 2

Diagnosis.—Leaves simple; venation pinnate; shape oval; base cuneate; 13 or 14 pairs of secondary veins, broadly curving, departing at an angle of approximately 60°, typically craspedodrome and branching; intercostal tertiary and quartary veins approximately perpendicular to secondaries and alternating, closely spaced; typically two teeth per secondary vein; teeth small, almost spinose, separated by arcuate sinuses; petiole long.

Discussion.—The character of the intercostal venation indicates a relationship to the extant *Meliosma simplicifolia*. The intercostal venation, tendency towards craspedodromy, and higher angle of departure of the secondary veins distinguishes *M. kushtakensis* from *M. duktothensis*. Although both fossil species are related to the same extant species, van Beusekom (1971) considered them to resemble different subspecies, which some systematists considered to be of specific rank.

Holotype.—USNM 43382.

Paratype.—USNM 43381.

Occurrence.—Kushtaka Formation, locs. 11158, 11159, 11166.

Order RHAMNALES

Family RHAMNACEAE

Genus Rhamnus Linnaeus

Rhamnus sp.

Plate 27, figure 2

Discussion.—The fossil has a finely serrate margin, smoothly curving and parallel secondary veins that extend along the margin, and branching tertiary veins that are oriented obliquely to the secondaries. The specimen appears, therefore, to represent a species of *Rhamnus*.

Specimen.—USNM 43369.

Occurrence.—Kushtaka Formation, loc. 11167.

Genus Sageretia Brongnairt

Sageretia sp.

Plate 15, figure 1

Discussion.—Leaves of *Sageretia* typically have: many small and closely spaced, rounded teeth; smoothly curving, camptodrome secondary veins; a pair of secondary veins that depart at or near the base, giving the leaf an almost palmate venation; a broadly rounded base; and numerous, closely spaced, and anastomosing intercostal tertiary veins that are oriented perpendicular (or nearly so) to the midrib. In all these features, a few fragmentary specimens from the Kushtaka Formation qualify as *Sageretia.*

Sageretia is also known in the early Eocene Chalk Bluffs assemblage from California (see p. 91) and the middle Miocene Latah assemblage from Washington.

Specimen.—USNM 43370.

Occurrence.—Kushtaka Formation, loc. 11166.

Genus Zizyphus Linnaeus

Zizyphus alaskanus Wolfe, new species

Plate 14, figures 5, 9

Diagnosis.—Leaf simple; venation palmate, with five primary veins; shape pronouncedly ovate; base broadly rounded, apex acuminate; first pair of lateral primaries extending about three-quarters distance to apex and looping; second pair confined to basal quarter of lamina; lateral secondary veins numerous, camptodrome; lateral tertiary veins craspedodrome; two pairs of medial secondary veins, camptodrome; numerous, closely spaced intercostal tertiary veins, oriented perpendicular to midrib; numerous small teeth, rounded.

Discussion.—The fossil leaf superficially resembles the leaves of *Tetracentron piperoides* (Lesq.) Wolfe, but the closely spaced tertiary veins that connect the lateral primaries to the midrib and the smaller teeth of the fossil indicate that it is distinct from Trochodendraceae and Cercidiphyllaceae. The following characteristics of the fossil, however, indicate that it is assignable to *Zizyphus*: (1) palmate venation, (2) a steeply ascending pair of first lateral primaries and a weak pair of second lateral primaries, (3) closely spaced tertiary veins that connect the first lateral primaries to the midrib, (4) medial secondary veins that are aparallel to the first lateral primaries that depart from the midrib more than half way to the apex, (5) camptodrome marginal tertiary veins and craspedodrome marginal quartary veins, (6) closely and regularly spaced and glandular teeth, (7) a broadly rounded base, and (8) a highly attenuated apex. In lacking acrodrome first lateral primary veins, *Z. alaskana* most closely resembles the leaves of the extant *Z. fungi* Merr. of Hainan; the latter species, however, has numerous intersecondary veins that are lacking in *Z. alaskana* and smaller and fewer teeth. Intercostal venation similar to that of the fossil is found in *Z. inermis* Merr. from the Philippine Islands, but this species has smaller teeth and acrodrome first lateral primaries. In size and spacing of the teeth, *Z. alaskana* is similar to *Z. yunnanensis* from the Paratropical Rain forest of southern China, but this living species has acrodrome first lateral primaries. Although all characters of the fossil can be found in leaves of extant members of *Zizyphus*, no living species has leaves that have all the characters of *Z. alaskana*. It should be noted that the modern leaves morphologically most similar to the fossil are found in species of the Paleotropical rain forest; the warm temperate and neotropical species of *Zizyphus* do not have leaves closely similar to *Z. alaskana*.

Holotype.—USNM 43371A, B.

Occurrence.—Kushtaka Formation, loc. 11158.

Family VITACEAE

Genus Vitis Linnaeus

Vitis sp.

Plate 15, figures 2, 4, 5

Discussion.—This species is represented by abundant material, but I have not examined a sufficient amount of cleared material of extant members of *Vitis* to diagnose the species. The lack of lobes, narrow leaf shape (for *Vitis*), and shallowly cordate base, make this species readily recognizable. What appears to represent the same species is also known in an early Ravenian assemblage from the Puget Group.

Specimens.—USNM 43383-43385.

Occurrence.—Kushtaka Formation, loc. 11166; Kulthieth Formation, loc. 11170.

Order MALVALES

Genus Tilia Linnaeus

Tilia carbonensis Wolfe, new species

Plate 27, figures 1, 5

Diagnosis.—Leaves simple; venation palmate; shape ovate; base broadly rounded, apex acute; first lateral pair of primary veins extending about one-

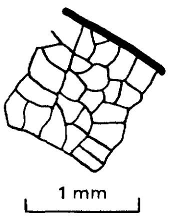

FIGURE 34.—Ultimate venation of *Plafkeria* sp. USNM 43388A, loc. 11167.

third distance to apex, craspedodrome, giving off about four or five craspedodrome lateral secondary veins; six to eight pairs of medial secondary veins, straight to slightly curving, craspedodrome, giving off no or up to two (greater basally) craspedodrome branches on basal sides; intercostal tertiary veins closely and uniformly spaced, perpendicular to secondaries, branching to form a quartary vein perpendicular to tertiary; quartary branch of tertiary extending midway to adjacent tertiary, bending sharply to parallel tertiary and extending to join secondary; teeth large, uniformly spaced, aristate shaped, separated by angular sinuses.

Discussion.—The palmate venation, closely and uniformly spaced tertiary veins, and the aristate teeth indicate that the fossils represent *Tilia*. No extant species of *Tilia* that I have examined appears to be closely related to *T. carbonensis*. Most species have either a cordate base or more numerous teeth or both.

Holotype.—USNM 43386A.

Paratype.—USNM 43387.

Occurrence.—Kushtaka Formation, loc. 11167.

Family TILIACEAE

Genus Plafkeria Wolfe, new name

Willisia Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 24.

The name *Willisia* was originally proposed by Warming in 1901 for a genus of Podostemaceae. The name that I proposed in 1968 for a genus of tiliaceous leaves is thus clearly a junior homonym. This genus is here renamed *Plafkeria*, in recognition of George Plafker's extensive contributions to our knowledge of the geology of the Gulf of Alaska region.

Type species.—Plafkeria rentonensis (Wolfe) Wolfe, new combination: *Willisia rentonensis* Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 24, pl. 7, figs. 3, 5; text figure 19A.

Plafkeria sp.

Plate 27, figure 6; text figure 34

Discussion.—The incompleteness of the specimen unfortunately does not allow it to become a name-bearing specimen, although it has features that distinguish it from the other two known species of *Plafkeria*. The Kushtaka species differs from the genotype *P. rentonensis* in having broader, more widely spaced intercostal tertiary veins, a more strongly developed pair of second lateral primary veins, and areoles that are slightly larger. The Kushtaka species differs from *P. obliquifolia* in having a less broad base, the inframarginal loops closer to the margin, and the second pair of lateral primaries less strongly developed. The morphologic gradation indicates that these three species of *Plafkeria* may represent a lineage; no Kummerian representative of the lineage is yet known.

Specimen.—USNM 43388A.

Occurrence.—Kushtaka Formation, loc. 11167.

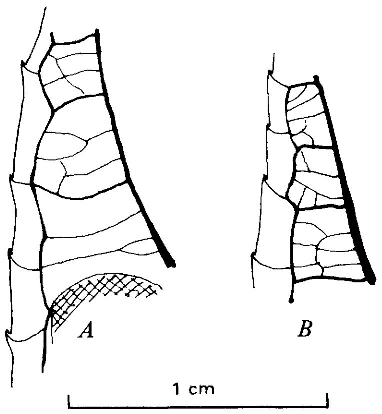

FIGURE 35.—Marginal venation of *Saurauia*. *A*, *S.* sp., USNM 43389, loc. 3846. *B*, *S. reinwardtiana*, USGS Ref. Colln. 505.

Order PARIETALES

Family ACTINIDIACEAE

Genus Saurauia Wildonow

Saurauia sp.

Plate 18, figure 1; text figure 35

Discussion.—Several features of the specimen indicate that it represents *Saurauia*: widely spaced, sharp, small teeth; numerous, closely spaced, branching intercostal tertiary veins that tend to be oriented perpendicular to the midrib; broadly curving secondary veins that curve sharply towards the apex as they approach the margin and form an extensive series of loops; and craspedodrome marginal tertiary veins. The Kushtaka leaf resembles most closely *S. reinwardtiana* Miq. of Indonesia. The only significant differences noted are in the slightly wider spacing of both teeth and intercostal tertiary veins in the Kushtaka leaf.

Specimen.—USNM 43389.

Occurrence.—Kushtaka Formation, loc. 3846.

Family THEACEAE

Genus and species indetermined

Plate 25, figure 3

Discussion.—Several leaves have (1) a short, thick petiole, (2) a margin that is entire in the basal part and that has a few, irregularly spaced, rounded teeth in the apical part, (3) secondary veins that are straight to slightly curving and that loop angularly near the margin, and (4) a coriaceous texture. Therefore, these leaves probably represent Theaceae, but the poor preservation of the venation does not allow a generic assignment.

Specimen.—USNM 43390.

Occurrence.—Kushtaka Formation, loc. 11165.

Family DIPTEROCARPACEAE

The published fossil record of dipterocarps is meager, particularly in regard to Paleogene occurrences. Rasky (1956) has recorded a flower of the family from the late Eocene of central Europe, but the family is notably lacking in the extremely diverse early Eocene London Clay flora. Because of the apparent scarcity of the family in the Paleogene, I concluded several years ago that the members of the family either had leaves that did not preserve well or that the family had not yet achieved a significant place in tropical forests; I had, therefore, not examined closely the extant foliage. Today, of course, the family is one of the dominant families of the Paleotropical rain forest and extends into the Paratropical Rain forest. Regarding the preservation factor, the leaves hold together extremely well in the clearing process, and it thus seems probable that the leaves should preserve well.

Leaves of most genera of Dipterocarpaceae are characterized by having tertiary veins that are considerably thinner than the secondary veins and that are closely spaced and undulatory or anastomosing. The secondary veins, moreover, either extend to, or almost to, the margin without looping; the secondaries thin conspicuously near the margin, and the loops are typically not conspicuous. Leaves of some members of Rhamnaceae—particularly *Berchemia*, *Karwinskia*, and *Rhamnidium*—are similar in venation, but they can be distinguished from Dipterocarpaceae of the type just discussed. *Karwinskia* and *Rhamnidium* both have pellucid dots, which can be discerned on well-preserved fossils. Even in poorly preserved material, however, dipterocarps can be distinguished from Rhamnaceae by the character of the tertiary venation that extends from the midrib to the secondary veins. In the rhamnaceous genera mentioned, the tertiary veins typically are perpendicular to the midrib and extend in an approximately straight line to intersect the secondary veins obliquely. In Dipterocarpaceae the tertiary veins are also typically perpendicular to the midrib, but they curve basally and intersect the secondary veins at approximately a right angle. On this basis, the leaves described as *Rhamnidium chaneyi* Potbury (1935), *Rhamnites cashmanensis* Wolfe, and *R. franklinensis* Wolfe (1968) are members of Dipterocarpaceae. The preservation of the specimens on which these species are based is such that pellucid dots would have been preserved.

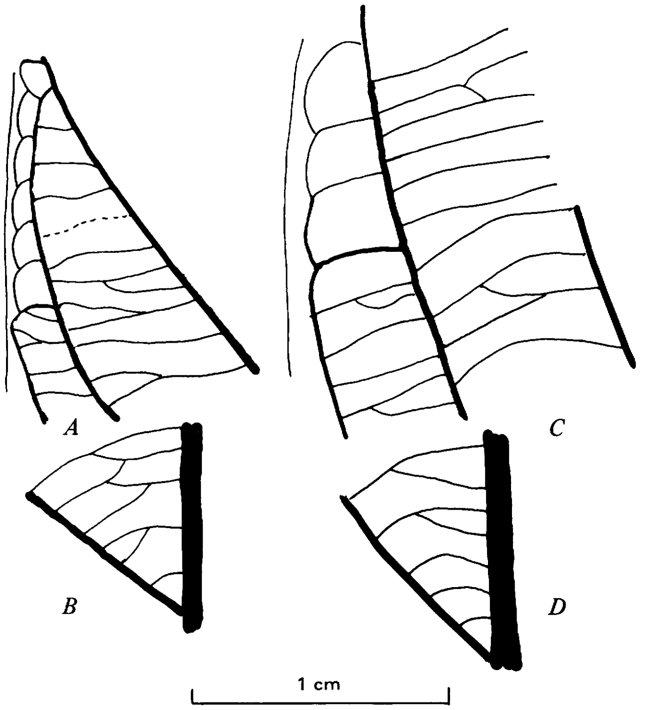

FIGURE 36.—Venation of *Parashorea*. *A*, *B*, *P. pseudogoldiana*, lectotype, USNM 38978, loc. 3847. *C*, *P. pseudogoldiana*, hypotype, USNM 222841, loc. 11195, *D*, *P. malaanon*, USGS Ref. Colln. 1663.

Genus Parashorea Kurz

Parashorea pseudogoldiana (Hollick) Wolfe, new combination

Plate 16, figures 6–8; plate 19, figure 6, text figure 36A, B

Rhamnus pseudogoldianus Hollick, 1936 (part), U.S. Geol. Survey Prof. Paper 182, p. 139, pl. 79, figs. 1, 2 only.
Rhamnus marginatus auct. non Lesquereux. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 140, pl. 78, figs. 1, 2.
Cornus hyperborea auct. non Heer. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 158, pl. 99, figs. 2, 3.

Discussion.—The fossils display the marginal and intercostal venation of Dipterocarpaceae noted previously. In their broadly rounded to slightly cordate base and numerous steeply ascending secondary veins, the fossils are most similar to leaves of the extant *Parashorea*.

A fragmentary specimen from the Kulthieth Formation has well-preserved ultimate venation.

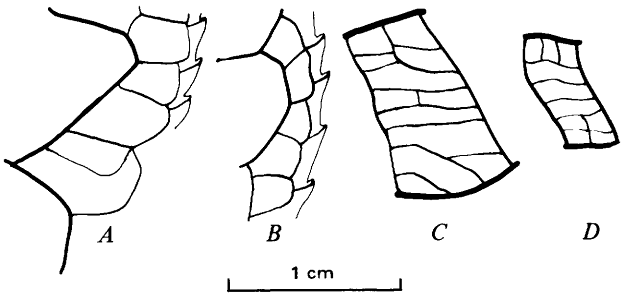

FIGURE 37.—Marginal and intercostal venation of *Barringtonia*. *A, C, B.* sp., USNM 43392B, loc. 11170. *B, D, B. acutangula*, USGS Ref. Colln. 1986.

The pattern is strikingly similar to the extant *Parashorea* in having small, quadrangular areoles that lack freely ending veinlets and in having the next coarser order of venation forming a quadrangular mesh. The areoles of the fossil, however, are somewhat larger than the areoles of *P. malaanonan* collected from British North Borneo. The larger areoles probably indicate that the Alaskan climate was somewhat cooler than that of the Melanesian region today (p. 23).

Lectotype.—USNM 38978, which is the specimen figured on Hollick's (1936) plate 79, figure 2, lower left leaf.

Syntype.—USNM 43391.

Hypotopes.—USNM 39034, 39035, 222841.

Occurrence.—Kushtaka Formation, loc. 3847; Kulthieth Formation, loc. 11195.

Order MYRTIFLORAE

Family BARRINGTONIACEAE

Genus Barringtonia Forster

Barringtonia sp.

Plate 17, figures 3, 4; text figure 37

Discussion.—The fossils superficially resemble some leaflets of Juglandaceae. In that family the fourth order intercostal venation forms a quadrangular or polygonal mesh, but in the fossils the fourth order intercostal veins are perpendicular to and directly connect the tertiary veins. This unusual fourth order venation, the closely serrate margin, and the two series of marginal loops (the marginal quartary veins are craspedodrome) represent a highly characteristic combination of characters that among extant plants I have seen only in leaves of *Barringtonia.* Except for the wider spacing and higher degree of percurrency of the intercostal tertiary veins of *B. duktothensis*, the fossils are very similar to *B. speciosa* Bl.

Specimen.—USNM 43392A, B.

Occurrence.—Kulthieth Formation, loc. 11170.

Family RHIZOPHORACEAE

Genus Kandelia Wight and Arn.

Kandelia wangi Wolfe, sp. nov.

Plate 19, figs. 1, 5a, b.

Diagnosis.—Leaves pinnately veined, simple; oval apex broadly rounded, base decurrent along petiole; midrib thick; about six pairs of secondary veins; pronouncedly decurrent along the midrib in the basal half of the lamina, departing at angles of about 30° in the basal half and about 45° in the upper half, extending straight towards the margin, curving apically about three-fourths the distance to the margin, camptodrome, with the loops almost paralleling the margin; between two adjacent secondary veins one or two strong veins extend admedially, branch irregularly about one-half the distance to the margin; tertiary veins widely and irregularly spaced, branching irregularly to form a coarse, irregular mesh; fourth order veins extending into the mesh, thinning conspicuously, branching irregularly to form areoles; areoles intruded by irregularly and profusely branching veinlets; margin entire, without marginal vein; petiole thick and short.

Discussion.—Leaves of several genera of Rhizophoraceae are closely similar in having secondary veins that extend straight towards the margin and loop approximately parallel to the margin and an irregular intercostal venation. In *Rhizophora, Bruguiera*, and *Ceriops*, however, there are typically two or more strong veins between and parallel to the secondary veins. In *Carallia* there are large, irregular loops between the secondary loops and the margin. In *Cassipourea* the margin has a few, irregularly spaced teeth. In *Blepharistemma* the secondary and intercostal venation is formed by conspicuously weak veins.

In *Kandelia candel* (L.) Druce, all significant features of the fossils can be matched although the secondary veins are more closely spaced in the fossils than in this extant species. Notable similarities, other than those common to the several genera of Rhizophoraceae previously mentioned, occur in the marginal and ultimate venation. The marginal venation has a single series of small, angular loops of irregular shape between the secondary loops and the margin. The areoles are composed of irregularly shaped fourth order veins and are intruded by thick, profusely branching veinlets.

Holotype.—USNM 222843.

Paratype.—USNM 222844.

Occurrence.—Kulthieth Formation, loc. 11195.

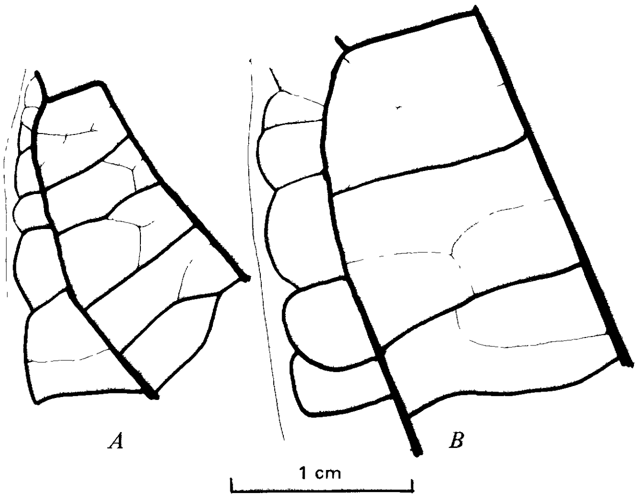

FIGURE 38.—Marginal venation of *Alangium*. *A*, *A. bergensis*, holotype, USNM 38926, loc. 3847. *B*, *A. longiflorum*, USGS Ref. Colln. 1931.

Family ALANGIACEAE

Genus Alangium Lamarck

Alangium bergensis Wolfe, new species

Plate 16, figure 2; text figure 38

Malpoenna magnifica (Saporta) Hollick, 1936 (part, nontypic), U.S.. Geol. Survey Prof. Paper 182, p. 118, pl. 66, fig. 5, only.

Diagnosis.—Leaves simple, venation palmate; shape slightly obovate; base asymmetric and rounded, apex acuminate with drip-tip; five primary veins, the first lateral pair extending about half distance to apex; second lateral primary veins weak; eight or nine lateral secondary veins per first lateral primary, extending almost straight and looping sharply close to margin; four or five pairs of medial secondary veins, gradually curving, looping sharply near margin and forming a series of small angular loops adjacent to margin; intercostal tertiary veins widely spaced, branching in a Y pattern; quartary venation forming an irregularly polygonal, large, mesh; margin entire.

Discussion.—The fossil leaf is somewhat similar to leaves of certain Tiliaceae (*Microcos*, for example) and Sterculiaceae (*Pterospermum*). In Tiliaceae, however, the branches of the intercostal tertiary veins are approximately perpendicular to the tertiary veins. In Sterculiaceae, the intercostal tertiary veins are closely spaced and somewhat sinuous. In features of primary and intercostal venation, the fossil is similar to *Alangium*. Among extant species the fossil shows similarities to both *A. chinense* (Lour.) Rehd. and *A. longiflorum* Merr. The few medial secondary veins, extension of the first lateral primary veins about half way to the apex, and the narrow, slightly obovate shape, are features that ally *A. bergensis* to *A. longiflorum*. The main feature that distinguishes leaves of these two species is that the looping of the secondary and tertiary veins is considerably closer to the margin in the fossil than in *A. longiflorum*; marginal looping similar to the fossil is found in *A. chinense*, which, however, has numerous medial secondary veins, first lateral primary veins extending only about one third the distance to the apex, and a broad, ovate shape. *A. bergensis* is considered to be most closely related to *A. longiflorum*.

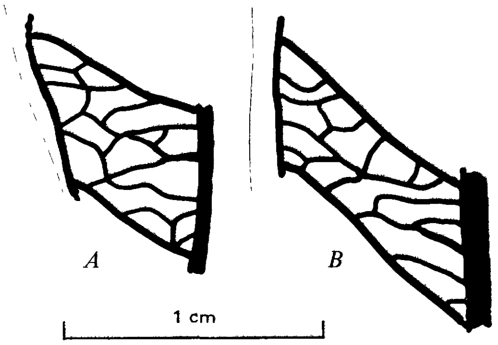

FIGURE 39.—Intercostal venation of *Eugenia*. *A*, *E.* sp., USNM 43395, loc. 11170. *B*, *E. jambos*, USGS Ref. Colln. 1709.

Hollick's material from the Paleocene Hamilton Bay assemblage was also referred to *Malpoenna magnifica*; this material represents a species that has pinnate venation, weak basal secondary veins, and a pair of strong secondary veins departing from the midrib apically from the base, that is, the species has the diagnostic features of a member of Lauraceae.

Holotype.—USNM 38926.

Occurrence.—Kushtaka Formation, loc. 3847.

Alangium sp.

Plate 16, figure 1

Discussion.—The specimen has tertiary veins branching in a Y pattern and the irregular fourth order mesh of *Alangium*. *A. bergensis* cannot be represented, however, because of the highly asymmetric base, the presence of seven primary veins, and the more closely spaced intercostal tertiary veins.

Specimen.—USNM 43393.

Occurrence.—Kushtaka Formation, loc. 11166.

Family MYRTACEAE

Genus Eugenia Linnaeus

Eugenia sp.

Plate 16, figures 3-5; text figure 39A

Discussion.—The continuous inframarginal vein (formed by looping of the secondary veins), the closely spaced and numerous secondary veins, and the numerous intersecondary veins paralleling the secondaries indicate that these fossils are referable to Myrtaceae. Among extant species the fossils appear to be closest to members of *Eugenia*. In the highly linear shape, the fossils resemble the extant *E. jambos* L.; leaves of this species differ from the fossils in having the submarginal vein spaced farther from the margin, and the intervening space has an additional series of loops. The leaves of *E. multiflora* Hance are similar to the fossils in marginal venation, but the former are ovate.

Specimens.—USNM 43394-43396.

Occurrence.—Kulthieth Formation, loc. 11170.

Eugenia? sp.

Plate 27, figure 7.

Discussion.—The continuous inframarginal vein places this fragment in Myrtaceae. The anastomosing intercostal tertiary veins indicate an assignment to *Eugenia*, but considering the fragmentary nature of the specimen the determination is questioned. The leaf is wider and the intercostal areas more elongated than in the early Ravenian *Eugenia* that was previously discussed.

Specimen.—USNM 43397.

Occurrence.—Kushtaka Formation, loc. 11167.

Order UMBELLIFLORAE

Family CORNACEAE

Genus Mastixia Blume

Mastixia irregularis (Hollick) Wolfe, new combination

Plate 15, figure 6

Cornus irregularis Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 158, pl. 99, fig. 1.

Discussion.—The close spacing and anastamosing of the intercostal tertiary veins and the thickened margin (probably a marginal vein) indicate that this leaf is referable to *Mastixia* rather than to *Cornus*. Among extant species, the fossil resembles leaves of *M. philippinensis* Merr., but in that extant species the leaves have more closely spaced intercostal tertiary veins and the more basal secondary veins do not extend as far towards the apex.

Holotype.—USNM 39033.

Occurrence.—Kushtaka Formation, loc. 3846.

Order ERICALES

Family CLETHRACEAE

Genus Clethra Gronov

Clethra sp.

Plate 18, figure 2

Discussion.—Although the fossils superficially resemble some leaflets of Juglandaceae, all the fossils are symmetric and have a petiole, indicating that they are simple leaves. The finely and uniformly serrate margin, camptodrome secondary veins, craspedodrome tertiary veins, and intercostal tertiary veins that are numerous and regularly spaced and that are not perpendicular to the secondary veins are characters that indicate that the fossils are a species of *Clethra*. Among extant species of the genus, *C. alaskana* appears most similar to *C. delavayi* Franch. from Yunnan. The fossils differ chiefly in having the secondary veins extending closer to the margin before looping.

Specimen.—USNM 43398.

Occurrence.—Kulthieth Formation, loc. 11170.

Order TUBIFLORAE

Family VERBENACEAE

Genus Clerodendrum Linnaeus

Clerodendrum sp.

Plate 7, figures 1-3, 6; plate 17, figure 1

Discussion.—This species is represented by five incomplete specimens in proximity on one slab and its counterpart. The most complete specimen is the one figured on plate 7, figure 3 and its counterpart on plate 17. The following features of the fossils indicate an assignment to *Clerodendrum*: extremely thick and short petiole, extremely thick midrib that thins conspicuously in an apical direction, broadly curving and widely spaced secondary veins, that are camptodrome and form a series of almost quadrangular loops, intercostal tertiary veins that are thin and branch to form quartary veins that thin conspicuously, a thickened margin, and extremely small teeth. Whether the small teeth should be considered teeth is questionable; as in the leaves of some extant species of the genus, the "teeth" of the fossils appear to be only slight bumps. The fossils particularly resemble the extant *C. nutans* Wall. of Burma, differing primarily in the pronounced rounding of the base.

Specimens.—USNM 43399, 43400, 43401A, B, 43402.

Occurrence.—Kushtaka Formation, loc. 11158.

Genus Holmskioldia Retzius

Holmskioldia speiri (Lesquereux) MacGinitie?

Plate 30, figure 4

Holmskioldia speirii (Lesquereux) MacGinitie, 1953, Carnegie Inst. Washington Pub. 599, p. 156, pl. 74, figs. 1, 2 (see synonymy).

Porana speirii Lesquereux, 1883, U.S. Geol. Survey Terr. Rept., v. 8, p. 172, pl. 28, fig. 15.

Discussion.—This determination is queried because of the fragmentary nature of the specimen. In details of venation, however, the Alaskan specimen matches material from conterminous United States assigned to this species.

Specimen.—USNM 43403.

Occurrence.—Katalla Formation, Split Creek Sandstone Member, loc. 11168.

INCERTAE SEDIS

Genus Macclintockia Heer

Macclintockia pugetensis Wolfe

Plate 30, figures 5, 6, 8-10

Macclintockia pugetensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 26, pl. 7, figs. 8, 9.

Discussion.—Fragments of this characteristic species are present in almost every plant collection that has been made by geologists from marine rocks of Keasey and earliest Lincoln age in the Gulf of Alaska province. The leaves must have been very coriaceous to be so widely dispersed in the sea.

Hypotypes.—USNM 43404-43408.

Occurrence.—Kushtaka Formation, loc. 9891; Katalla Formation, Split Creek Sandstone Member, locs. 9552, 9889, 11168, Basin Creek beds locs. 11188?, CAS 29181; Kulthieth Formation, locs. 9551, 9553, 9893, 9894, 11189.

Macclintockia sp.

Plate 25, figure 8

Discussion.—The basal parts of two leaves have the characteristic venation of *Macclintockia*. Both specimens are broader than *M. pugetensis*, and they have strong lateral veins that depart from the top of the petiole. Although possibly related to the Kummerian species, the middle Ravenian species appears to be a distinct entity.

Specimen.—USNM 43409.

Occurrence.—Kushtaka Formation, loc. 11164.

Genus Dicotylophyllum Saporta

Dicotylophyllum carbonensis Wolfe, new species

Plate 27, figures 8, 10

Diagnosis.—Leaves simple; venation pinnate; shape linear, oval; base acute, apex acute; 7-10 pairs of secondary veins straight to typically broadly curving, craspedodrome or camptodrome; if camptodrome, branching to send more basal branch into tooth centrally and more apical branch to parallel margin and join next more apical secondary vein; intercostal tertiary veins approximately perpendicular to secondaries, forking, widely spaced; margin with widely and uniformly spaced almost spinose teeth separated by arcuate sinuses.

Discussion.—I am unable to suggest what extant group these fossils might represent. They are similar to *Dicotylophyllum flexuosa* (Newb.) Wolfe, a widespread Paleocene species. This older species, however, has more closely spaced teeth and the secondary veins are typically camptodrome.

Holotype.—USNM 43410.

Paratype.—USNM 43411.

Occurrence.—Kushtaka Formation, loc. 11167.

Dicotylophyllum kummerensis (Wolfe) Wolfe, new combination

Plate 25, figure 7; plate 30, figure 11

Artocarpoides kummerensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 19, pl. 4, figs. 1, 7.

Discussion.—I agree with MacGinitie (in press) that the leaves he described as *Laurophyllum litseafolia* and that I transferred to *Artocarpoides* represent neither Lauraceae nor Moraceae, but what family these leaves represent is unknown. The close relationship between MacGinitie's species and the species described from the upper part of the Puget Group is apparent, and I thus transfer *A. kummerensis* to *Dicotylophyllum.*

Specimens.—USNM 43412, 43413.

Occurrence.—Kushtaka Formation, locs. 9891, 11164.

Dicotylophyllum spp.

Plate 17, figure 2.—The specimen is an entire margined leaf that has steeply ascending secondary veins and numerous intersecondaries. It may represent Lauraceae, but is is too fragmentary for determination. USNM 43414, locality 11170, Kulthieth Formation.

Plate 18, figure 3.—This is the holotype of *Rhododendron crassum* Hollick. Almost nothing remains of the secondary venation pattern, it is obscured by the extremely coriaceous texture. I therefore propose that *Rhododendron crassum* Hollick, 1936, p. 160, pl. 99, fig. 4, be declared a nomen nudum because of insufficient characters. USNM 39036, locality 3847, Kushtaka Formation.

Plate 18, figure 5.—The margin has widely spaced, small, and sharp teeth. The character of the margin and the widely spaced, branching intercostal tertiary veins are features also found in *Pterostyrax*; leaves of this genus, however, have straight secondary veins. USNM 43415, locality 11159, Kushtaka Formation.

Plate 18, figure 6.—This leaf may be an aberrant leaf of *Alnus scotti*; the intercostal venation is particularly similar to that alder. None of the specimens attributed to *A. scotti*, however, have the pronouncedly angular sinuses. USNM 43416, locality 11158, Kushtaka Formation.

Plate 24, figure 2.—The difference in angle of departure of the secondary veins on one half the lamina as compared to the other indicate that this may represent a leaflet. The secondary veins fork before entering the teeth, and one branch enters a tooth along the apical side. The specimen may represent Sapindaceae. USNM 43417, locality 11165, Kushtaka Formation.

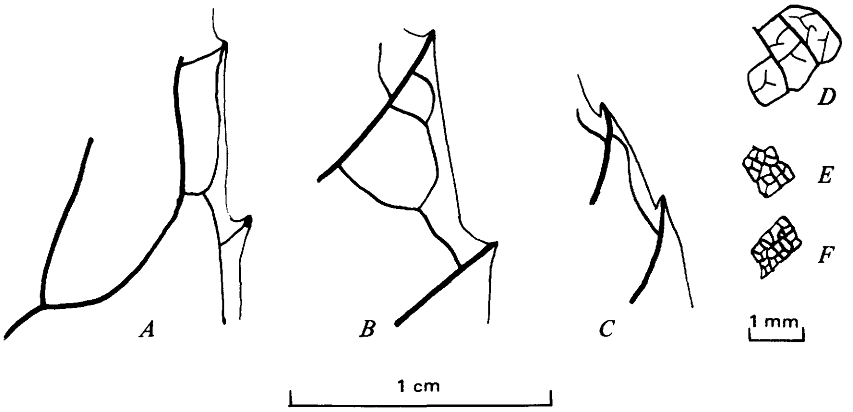

FIGURE 40.—Venation of *Salix* and *Lithocarpus*. *A, D, S. coatsi*, paratype, UCMP 8910. *B, E, L. densiflora*, USGS Ref. Colln. 45. *C, F, L. glabra*, USGS Ref. Colln. 192.

Plate 24, figure 4.—The specimen has an entire margin and a mucronate apex. A pair of weak basal secondary veins appears to be present; the specimen could represent a species of Lauraceae. USNM 43418, locality 11165, Kushtaka Formation.

Plate 24, figure 6.—The linear shape, coriaceous texture, and entire margin occur in a wide range of plants. The venation is too poorly preserved for determination. USNM 43419, locality 9389, Kushtaka Formation.

Plate 24, figure 5.—The margin appears to have irregularly spaced, rounded teeth. In combination with the straight, sharply looping secondary veins, this could indicate an affinity to Rutaceae. USNM 43420, locality 11165, Kushtaka Formation.

Plate 24, figure 8.—The falcate shape indicates that the specimen represents a leaflet. A sapindaceous alliance is indicated by the broadly curving secondary veins and the few teeth that appear to be entered by veins along the apical sides. USNM 43421, locality 11165, Kushtaka Formation.

Plate 26, figure 8.—The specimen has camptodrome secondary veins, percurrent tertiary veins, and widely spaced, small teeth. It may represent a rosaceous genus, such as *Prunus*, but characters for generic assignment are too few. USNM 43430, loc. 11167, Kushtaka Formation.

Plate 27, figure 9.—Two fragments of a lamina have an entire margin and broadly curving secondary veins. The material is too fragmentary to even suggest possible affinities. USNM 43422, locality 11167, Kushtaka Formation.

Plate 30, figure 1.—The secondary venation, which is poorly preserved, appears to have been pinnate and camptodrome. The entire margin, rotund shape, and thick petiole separate this leaf from other members of the Alaskan Kummerian flora. USNM 43423, locality 11168, Katalla Formation, Split Creek Sandstone Member.

Plate 30, figure 2.—The asymmetry indicates that the specimen is a leaflet. The margin is nonentire, but the preservation is too poor to determine the manner of entry of the veins into the teeth. USNM 43424, locality 11169, Kushtaka Formation.

Plate 30, figure 3.—This poorly preserved leaf was apparently coriaceous. The teeth are few and widely spaced; the sinuses appear to have been arcuate. The secondary veins fork and send a branch into the teeth. USNM 43425, locality 11168, Katalla Formation, Split Creek Sandstone Member.

SYSTEMATIC REVISIONS OF OTHER PALEOGENE SPECIES

The late Roland Brown of the U.S. Geological Survey performed a service to Tertiary paleobotany in publishing, from time to time, short papers in which he described new species and revised previously published species. Any paleobotanist who deals with an entire assemblage of Tertiary plants has an inherent difficulty in attempting to be familiar with a wide array of foliar types; some of us are more familiar with certain taxonomic groups than with others, and hence errors of specific, generic, and even familial assignments are made. Some of the previously published determinations that I consider to be invalid are thus revised here; particular attention has been directed to systematic revisions that document some of the distributions mentioned in previous sections of this report.

Salix coatsi (Axelrod) Wolfe, new combination

Text figure 40

Lithocarpus coatsi Axelrod, 1966b (part, typic), California Univ. Pubs. Geol. Sci., v. 59, 67, pl. 10, figs, 12–14; pl. 12, figs. 1–8 only.

Discussion.—Leaves of *Lithocarpus* (including the Asian species that many authors refer to *Pasania*) have a characteristic venation: the areoles are small (less than 0.5 mm in diameter) and typically lack freely ending veinlets, the secondary veins (on toothed leaves) are typically craspedodrome or fork once to send a strong branch into the tooth, and the loops are approximately square. The teeth, in addition, lack glands. The specimens of *Lithocarpus coatsi*, however, have large (over 1 mm in diameter) areoles that are intruded by once- or twice-branching veinlets, and the secondary veins (on toothed leaves) are camptodrome, typically fork well within the margin, and the fork in turn gives off a weak branch into a glandular tooth; the marginal loops are irregular in shape and elongated perpendicular to the midrib. The fossils do not, therefore, represent *Lithocarpus*. A much closer comparison can be made with leaves of some willows, such as *Salix exigua* Nutt., in venation and the presence of glandular teeth.

Pterocarya orientalis (MacGinitie) Wolfe, new combination

Juglans orientalis MacGinitie, 1937, Carnegie Inst. Washington Pub. 465, p. 135, pl. 3, fig. 6; pl. 4.

Discussion.—The Weaverville specimens and material from late Oligocene assemblages in Oregon represent *Pterocarya* rather than *Juglans*. Members of the section *Cardiocaryon*, to which MacGinitie (1937) likened this species, have leaflets that have rounded, broad, abmedially pointing teeth. In members of the section *Platyptera* of *Pterocarya*, the leaflets have teeth that are sharp and apically pointing, and the secondary veins are camptodrome and form only a single series of marginal loops; on this basis MacGinitie's species is transferred to *Pterocarya*.

Fagopsis groenlandica (Heer) Wolfe, new combination

Quercus groenlandica Heer, 1968 (part), Flora Fossilis Arctica, v. 1, pt. 1, p. 108, pl. 8, fig. 8; pl. 10, fig. 1 only; pl. 11, fig. 4; pl. 47, fig. 1.
1880, Flora Fossilis Arctica, v. 6, no. 2, p. 10, pl. 4, fig. 5.
1883 (part), Flora Fossilis Arctica, v. 7, no. 2 p. 89, pl. 69, fig. 4.
Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 99, pl. 57, fig. 6.
Brown, 1962 (part), U.S. Geol. Survey Prof. Paper 375, p. 58, pl. 19, figs. 3, 6, 12; pl. 40, figs. 1, 2.
Quercophyllum groenlandicus (Heer) Koch, 1963, Medd. om Grønland, v. 172, no. 5, p. 34, pl. 5, figs. 1-4; pl. 6, figs. 1-3.

Discussion.—Koch (1963, p. 36) noted the similarity between *Quercophyllum groenlandicus* and the Oligocene *Fagopsis longifolia* (Lesq.) Holl. The similarities between these two species are in the typically asymmetric base, uniformly spaced teeth that are one per secondary vein, overall shape of the teeth, and numerous, uniformly spaced secondary veins. The Paleocene *Q. groenlandicus* thus falls within the limits of *Fagopsis*.

Fagopsis groenlandica typically has more numerous secondary veins and rounder teeth than *F. longifolia*. An undescribed species of the genus from the Eocene Republic assemblage of Washington has the round teeth of *F. groenlandica* and the fewer secondary veins of *F. longifolia*, indicating that the three species may constitute a phylad.

Fagopsis was transferred to Betulaceae by MacGinitie (1953), largely based on his interpretation of the associated and attached aments; any interpretation based on such impressions, however, is difficult. Leaves of all species of *Fagopsis* have a distinct marginal vein; this vein eliminates them from Betulaceae and allies the genus to Fagaceae. If *Fagopsis* is Fagaceae, it is clearly not extant; the marginal venation is that of *Fagus* (see following discussion of *F. oregona*), but the aments (some are also associated with leaves of *Fagopsis* near Republic) clearly indicate that the two genera can only be distantly related. It is possible that *Fagopsis* represents an extinct family of Fagales in which the aments are betulaceous and the leaves fagaceous. E. B. Leopold (oral commun., February 1969) reports that pollen extracted from the aments from Florissant is tricolpate; this kind of pollen is a feature of Fagaceae but not of Betulaceae.

Fagopsis groenlandica is one of the most characteristic and widespread species in the Paleocene. The species is known from many localities in conterminous United States, Alaska, and Greenland.

Fagus oregona (Chaney and Sanborn) Wolfe, new combination

Tetracera oregona Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 87, pl. 31, figs. 5-7; pl. 32, fig. 1.

Discussion.—Leaves of *Tetracera* have irregularly polygonal areoles intruded by profusely branching veinlets that thin conspicuously; leaves of *Fagus*, as well as the fossils under discussion, have almost quadrangular areoles intruded by simple or once-branching veinlets that do not thin conspicuously. That the fossils are not some other fagaceous genus is indicated by the character of the marginal venation: in other Fagaceae, the most abmedial tertiary vein that departs apically from a secondary vein is parallel to the margin and aparallel to the intercostal tertiary veins. In both extant *Fagus* and the fossils the most abmedial tertiary vein typically departs from the secondary vein in a course parallel to the intercostal tertiary veins. Sanborn's (1947) citation of *Tetracera oregona* is based on leaves that have widely spaced intercostal tertiary veins and a doubly serrate margin; they are, therefore, not conspecific with *F. oregona*.

Fagus oregona resembles *F. pacifica* Chan., which is known in the late Oligocene of Oregon. Similarities between these two species are in the sharp teeth, consistently craspedodrome secondary veins, and closely spaced intercostal tertiary veins. Dissimilarities include the more numerous secondary veins and oval shape of *F. oregona*.

The occurrence of *Fagus* in a subtropical assemblage such as the Goshen should not be surprising. Wang (1961, p. 145) notes that *Fagus* is abundant in the subtropical evergreen oak forest of China.

Calkinsia dilleri (Knowlton) Wolfe, new combination

Cinnamomum dilleri Knowlton, 1900, U.S. Geol. Survey 20th Ann. Rept., pt. 3, p. 47, pl. 4, fig. 1.
Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 59.
Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 18, pl. 4, figs. 1, 3, 4, 6-8.
Hyperbaena dilleri (Knowlton) Wolfe, 1968 (part), U.S. Geol. Survey Prof. Paper 571, p. 21, text fig. 15A only.

Discussion.—As noted previously (p. 00), this species represents the genus *Calkinsia.* In the illustration of this species and modern comparative material (Wolfe, 1968, text fig. 15), the captions for 15B and 15C were inadvertently reversed, that is 15B is *Cinnamomum trichophylla* and 15C is *Hyperbaena mexicana.*

Calkinsia franklinensis Wolfe

Calkinsia franklinensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 20, pl. 4, figs. 4, 8.
Hyperbaena dilleri (Knowlton) Wolfe, 1968 (part, nontypic), U.S. Geol. Survey Prof. Paper 571, p. 21, references to locs. 1027, 9678.

Discussion.—The early Fultonian specimens referred to *Hyperbaena dilleri* are merely slightly narrower leaves of *Calkinsia franklinensis* (see also p. 63).

Cinnamomophyllum bendirei (Knowlton) Wolfe, new combination

Cinnamomum bendirei Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 57, pl. 10, fig. 4.
Philadelphus bendirei (Knowlton) Chaney, 1927 (part), Carnegie Inst. Washington Pub. 346, p. 118, pl. 17, figs. 1, 2 only.
Sassafras bendirei (Knowlton) Brown, 1940, Washington Acad. Sci. Jour., v. 30, p. 350.
Sassafras columbiana Chaney and Axelrod (nontypic), 1959, Carnegie Inst. Washington Pub. 617, p. 179, pl. 34, fig. 2 only.
Persea pseudocarolinensis auct. non Lesquereux. Chaney and Axelrod, 1959 (part), Carnegie Inst. Washington Pub. 617, p. 177, pl. 34, fig. 3 only.

Discussion.—The generic determination of this species has almost come full circle. The validity of the reference of the species to Lauraceae was demonstrated by Brown (1940), but he considered that the species represented *Sassafras.* Leaves of *Cinnamomum* and *Sassafras* are, however, readily separable, even if "unlobed" leaves of *Sassafras* are compared with leaves of *Cinnamomum.* In *Cinnamomum*, as in the fossils cited in the synonymy, a distinct marginal vein is present and the areoles are small, quadrangular, and typically lack freely ending veinlets. *Sassafras*, in contrast, lacks a marginal vein and the areoles are large, irregularly polygonal, and intruded by profusely branching veinlets. The fossils may represent *Cinnamomum*, but the leaves of genera such as *Neolitsea* are equally similar.

Cinnamomophyllum eocernua (Chaney and Sanborn) Wolfe, new combination

Octoea eocernua Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 74, pl. 19, figs. 1-3, 5.
Potbury, 1935, Carnegie Inst. Washington Pub. 465, p. 68, pl. 6, fig. 1.

Discussion.—These fossils have small, quadrangular areoles, most of which lack freely ending veinlets. If veinlets are present, they are unbranching. The areoles of *Octoea* are considerably larger, irregularly polygonal, and are intruded by branching veinlets. The fossils are, therefore, referable to *Cinnamomophyllum.*

Euptelea orientalis (Sanborn) Wolfe, new combination

Diospyros orientalis Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 26, pl. 10, fig. 3.
Aralia taurinensis auct. non *Celastrus taurinensis* Ward. Sanborn, 1935, Carnegie Inst. Washington Pub. 465, p. 27, pl. 10, figs. 1, 2, 4.

Discussion.—The sharp teeth separated by arcuate sinuses, closely spaced and branching intercostal tertiary veins that are perpendicular to the secondary veins, and the mixed condition of camptodrome or craspedodrome secondary and marginal tertiary veins are features that indicate that these leaves represent *Euptelea. E. orientalis* resembles most closely the extant *E. pleiosperma* Hook. f. and Thoms. Scott and Barghoorn (1955) have recorded the wood of this genus from the Clarno nut bed assemblage.

Fortunearia weedi (Knowlton) Wolfe, new combination

Quercus weedii Knowlton, 1899, U.S. Geol. Survey Mon. 32, p. 705, pl. 87, fig. 4.
Corylus macquarryi auct. non Heer. Knowlton, 1899, U.S. Geol. Survey Mon. 32, pl. 86, fig. 3.

Discussion.—These leaves, which are from the Yellowstone National Park Eocene, represent *Fortunearia.* This generic assignment is substantiated by the: basal pair of secondary veins, widely spaced and branching intercostal tertiary veins, craspedodrome (typically) or camptodrome secondary veins, and widely spaced and spinose teeth. The Yellowstone leaves are the first North American record of this extant monotypic genus of the Mixed Mesophytic forest; the genus is not known to be represented in the Neogene Mixed Mesophytic forest of western North America. Note that the Eocene occurrence is in subtropical forest; the extant species is also found in the evergreen oak-laurel forest of China (Wang, 1961, p. 143) although the species is more common in the Mixed Mesophytic forest.

Platanus macginitiei Wolfe, new species

Platanus aceroides auct. non Goeppert. Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 78, pl. 25, fig. 6. Sanborn, 1937, Oregon State Mon., Studies in Geology, no. 4, p. 22, pl. 7, fig. 1.

Diagnosis.—Leaves simple; venation pseudopalmate, that is, veins equal in strength to midrib depart above base of lamina; shape oval to ovate, three (typically) or five "lobes" that are separated by shallow sinuses; 8–12 pairs of secondary veins, typically straight, craspedodrome; numerous craspedodrome marginal tertiary veins; intercostal tertiary veins branching, slightly arcuate, numerous, areoles formed by fifth order veins, about 1 mm in diameter, approximately square, intruded by once- to thrice-branching veinlets; margin conspicuously toothed; teeth large (those entered by secondary veins) or small (those entered by tertiary veins), separated by arcuate sinuses; small teeth typically at least five per large tooth at widest part of leaf.

Discussion.—This species of *Platanus* is one of the most characteristic in the North American Tertiary because of the many small teeth between the large teeth. The late Oligocene and earlier Miocene *P. bendirei* (Lesq.) Wolfe is probably related; this younger species typically has one or two (rarely as many as four or five) small teeth per large tooth. Thus far *P. macginitiei* is known only from assemblages of middle Oligocene age: Scio (including the Bilyeu Creek assemblage), Sweet Home, Goshen, Ohanapecosh, and the pre-Angoonian assemblages from the Kootznahoo Formation.

This species is named for Dr. H. D. MacGinitie, in recognition of his many contributions to the Tertiary paleobotany of North America.

Holotype.—USNM 245723 (Sweet Home, Oregon, loc. 9107).

Paratypes.—UCMP 203; Oregon State College Paleobotanical collection No. 500.

Crataegus cuprovallis Axelrod

Crataegus cuprovallis Axelrod, 1966b, California Univ. Pubs. Geol. Sci., v. 59, p. 71, pl. 16, figs. 1-5.

Holodiscus harneyensis auct. non (Arnold) Axelrod, 1950. Axelrod, 1966b, California Univ. Pubs. Geol. Sci., v. 59, p. 72, pl. 16, fig. 10.

Discussion.—I can see no morphologic basis for separating the specimen relegated to *Holodiscus* from those of *Crataegus cuprovallis.* Extant species of *Holodiscus* have very thin veins forming the areoles, whereas leaves of *Crataegus* have thick veins forming the areoles. In this respect, the Copper Basin *Holodiscus* should be attributed to *Crataegus.*

Heteromeles cuprovallis (Axelrod) Wolfe, new combination

Text figure 41

Salix cuprovallis Axelrod, 1966b, California Univ. Pubs. Geol. Sci., v. 59, p. 65, pl. 9, figs. 1-3.

Discussion.—Axelrod (1966b) compared the fossils to extant willows such as *Salix barclayi* Anders. and *S. bebbiana* Sarg. As the accompanying drawings show (see fig. 41), these modern willows have leaves that have numerous, uniformly spaced intercostal tertiary veins, and smoothly curving secondary veins that form an extensive series of loops. *S. cuprovallis*, on the other hand, has irregularly and widely spaced intercostal tertiaries that are typically oblique to the secondary veins, and almost straight secondary veins that fork conspicuously and do not form an extensive series of loops. The fossils are similar, however, to the leaves of the extant *Heteromeles arbutifolia* M. Roem.

Dracontomelon sanbornae Wolfe, new species

Allophylus wilsoni auct. non Chaney and Sanborn. Sanborn, 1935, Carnegie Inst. Wash. Pub. 465, p. 25, pl. 9, fig. 5.

Diagnosis.—Leaf compound; venation of leaflet pinnate; shape ovate; base asymmetric; apex acuminate with drip-tip; 14 or 15 pairs of secondary veins, uniformly spaced, broadly curving, curving sharply at margin, forming extensive series of small loops; intercostal tertiary veins approximately perpendicular to secondaries, closely spaced, typically branching midway between secondaries, one branch extending admedially and branching profusely; margin entire.

Discussion.—The entire margin of the leaflet removes it from *Allophylus wilsoni.* In the intercostal tertiary venation—particularly in the profusely branching veins that extend admedially—the fossil is similar to the leaflets of *Dracontomelon.* The fossil particularly resembles *D. mangiferum* Bl., but leaflets of that extant species typically have fewer secondary veins that extend farther along the margin, slightly more closely spaced intercostal tertiary veins, and an oval shape. Scott (in Chandler, 1964) has recorded fruits of this genus from the Clarno nut-bed assemblage, which is approximately coeval with the Comstock.

This species is named for the late Dr. Ethel I. Sanborn, in recognition of her contributions to the paleobotany of Oregon.

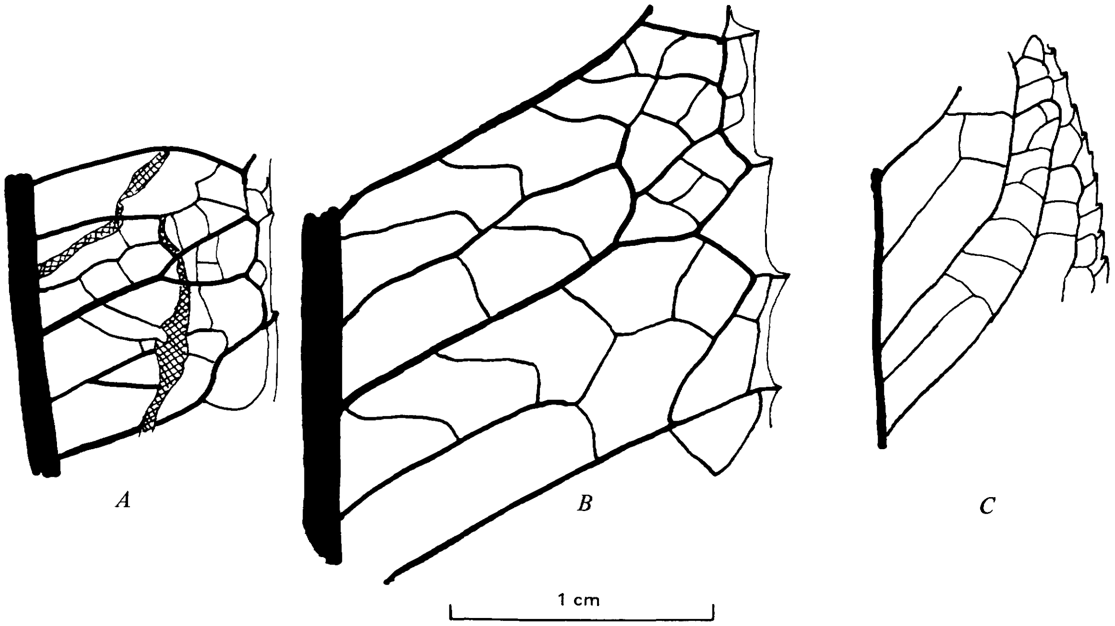

FIGURE 41.—Venation of *Heteromeles* and *Salix*. *A*, *H. cuprovallis*, holotype, UCMP 8963. *B*, *H. arbutifolia*, USGS Ref. Colln. 785. *C*, *S. barclayi*, USGS Ref. Colln. 904.

Holotype.—UCMP 760.

Miquelia californica Wolfe, new species

Ficus densifolia auct. non Knowlton. MacGinitie, 1941, Carnegie Inst. Washington Pub. 543, p. 110, pl. 16, figs. 3-5.

Diagnosis.—Leaves simple; venation pinnate; shape asymmetric, oval; base rounded, apex acute; five to seven pairs of secondary veins, departing at angles of 45°-80° (greater apically), looping sharply; intercostal tertiary mesh large, veins forking at right angles and thinning conspicuously into profusely branching fourth order mesh; margin entire.

Discussion.—The characteristic third and fourth order mesh of the fossils allies them to *Miquelia*, a member of the tribe Phytocreneae of the Icacinaceae. *M. californica* is particularly similar to *M. reticulata* Merr. from the Philippine Islands. The most conspicuous difference between the two species is that all the secondary veins of this extant species depart at about an 80° angle and form an intercostal area that is approximately trapezoidal.

Holotype.—UCMP 2180.

Paratypes.—UCMP 2179, 2181.

Sageretia laurinea (Lesquereux) Wolfe, new combination

Juglans laurinea Lesquereux, 1878, Harvard Museum Comp. Zoology Mem., v. 6, no. 2, p. 35, pl. 9, fig. 11.

Phyllites laurinea (Lesquereux) MacGinitie, 1941, Carnegie Inst. Washington Pub. 543, p. 162, pl. 45, fig. 8.

Discussion.—MacGinitie (1941) noted that the basal secondaries of these leaves were "pseudoprimaries," that is, they arose from the base of the leaf. This feature together with the finely serrate margin and the intercostal tertiary veins being oriented obliquely to the secondary veins indicate that the fossils represent *Sageretia*. Comparisons can be made to species such as *S. elegans* (H.B.K.) Brongn.

Plafkeria obliquifolia (Chaney) Wolfe, new combination

Text figure 42

Celtis obliquifolia Chaney, 1925, Carnegie Inst. Washington Pub. 349, p. 52, pl. 1, figs. 1, 3, 5.

Viburnum thomae Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 98, pl. 40, figs. 5, 6.

Tilia williamsi Sanborn, 1947, Oregon State Monographs, Studies in Geology, no. 4, p. 23, pl. 6, figs. 1-3.

Alangium thomae (Chaney and Sanborn) Lakhanpal, 1958, California Univ. Pubs. Geol. Sci., v. 35, p. 34, pl. 10, figs. 1, 2.

Discussion.—The ultimate venation of these specimens indicates that they are not *Alangium*, because that genus has large areoles intruded by profusely branching veinlets. The leaves resemble *Byttneriophyllum tiliaefolium* (A. Br.) Knobl. and Kvac., particularly in shape and intercostal tertiary venation. The fourth order venation of *Byttneria*, however, is highly characteristic: the tertiary veins typically branch about halfway between the secondaries and send a fourth order branch almost perpendicularly but the branch curves rapidly to parallel the tertiary vein. This feature is well illustrated by Knobloch and Kvacek (1964, pl. 3, fig. 2). In *Plafkeria*, the fourth order veins are numerous, branching, and extend between two adjacent

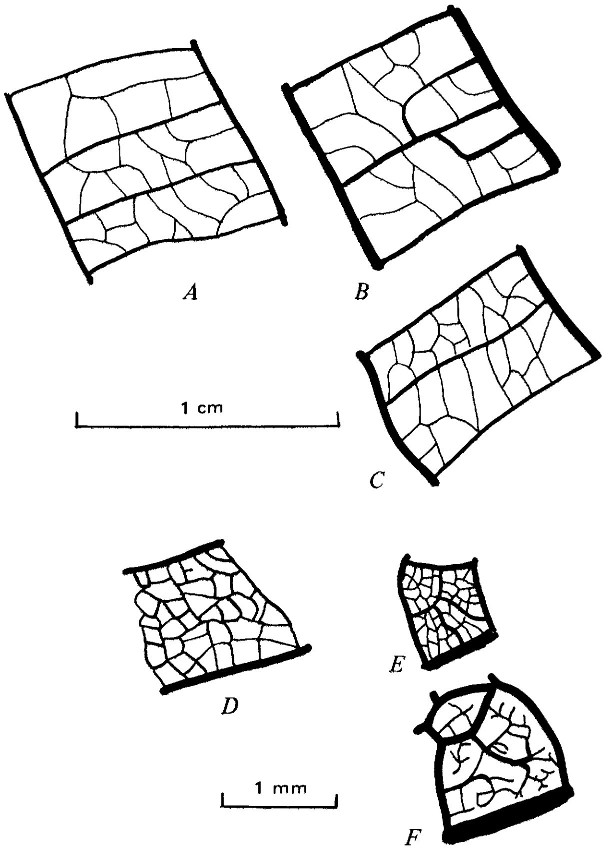

FIGURE 42.—Venation of *Plafkeria*, *Byttneria*, and *Alangium*, *A*, *D*, *W. obliquifolia*, hypotype, USNM 43431. *B*, *E*, *B. aspera*, USGS Ref. Colln. 560. *C*, *F*, *A. chinense*, USGS Ref. Colln. 1225.

secondaries (fig. 42). Sanborn's (1947) reference of her material to Tiliaceae, was, therefore, justified.

Camelia oregona (Chaney and Sanborn) Wolfe, new combination

Ilex oregona Chaney and Sanborn, 1933, Carnegie Inst. Washington Pub. 439, p. 80, pl. 22, figs. 2, 5, 6.

Discussion.—Dr. Copeland McClintock of Yale University first pointed out to me that the Goshen material assigned to *Ilex* represented *Camellia*. This assignment is indicated by the irregularly shaped marginal areoles that are intruded admedially by profusely branching veinlets and by the rounded teeth that are separated by angular sinuses.

Doona? chaneyi (Potbury) Wolfe, new combination

Text figure 43

Rhamnidium chaneyi Potbury, 1935 (part), Carnegie Inst. Washington Pub. 465, p. 75, pl. 11, figs. 1, 4, 5 only.

Discussion.—These leaves have the intercostal venation typical of Dipterocarpaceae (p. 82). The similarity of *Doona* is in the almost ladder-like fifth order venation and the closely spaced intercostal tertiary veins (fig. 43). The reference to *Doona* is questioned because this genus is generally thought to have evolved on Ceylon and to have never reached mainland Asia. If so, *D.? chaneyi* presumably evolved from a common ancestor. One of Potbury's types is excluded from this species because it has more widely spaced intercostal tertiary veins and the areoles are almost twice as large as those of the three remaining elements.

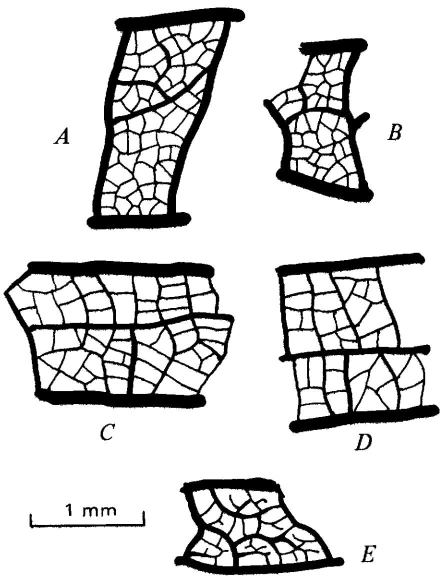

FIGURE 43.—Venation of Dipterocarpaceae and Rhamnaceae. *A*, *Parashorea cashmanensis*, paratype, USNM 42130. *B*, *P. malaanon*, USGS Ref. Colln. 1663. *C*, *Doona? chaneyi*, syntype, UCMP 933. *D*, *D. ovalifolia*, USGS Ref. Colln. 1656. *E*, *Rhamnidium elaeocarpa*, USGS Ref. Colln. 1528.

Lectotype.—UCMP 935.

Syntypes.—UCMP 933, 934.

Parashorea chasmanensis (Wolfe) Wolfe, new combination

Text figure 43

Rhamnites cashmanensis Wolfe, 1968, U.S. Geol. Survey Prof. Paper 571, p. 23, pl. 6, fig. 2; text fig. 18.

Discussion.—As noted previously (p. 82), this species has venation features characteristic of Dipterocarpaceae. In spacing of the intercostal tertiary veins, the fossils are most similar to *Parashorea*. Note (in fig. 43) that the ultimate venation pattern is clearly not rhamnaceous but is dipterocarpaceous. When I first described this species, I stated (Wolfe, 1968, p. 23): "I am not absolutely convinced that *Rhamnites cashmanensis* is a member of Rhamnaceae, but this familial reference is the best one that I can make at this time."

Alangium oregonensis Wolfe, new species

Celtis obliquifolia Chaney (non typic), 1927, Carnegie Inst. Washington Pub. 346, p. 115, pl. 13, fig. 12.

Diagnosis.—Leaves simple; venation palmate; shape asymmetrical, ovate; base oblique and broadly rounded, apex acuminate; six primary veins, first lateral pair extending about one third to about half way towards apex, camptodrome; five to six pairs of medial secondary veins, looping sharply near margin; intercostal tertiary veins; intercostal tertiary veins spaced about 0.4 cm apart, perpendicular to secondary veins.

Discussion.—These leaves have the ultimate venation of *Alangium* (see discussion of *Willisia obliquifolia*). Among extant species, the fossils most closely resemble in shape the leaves of *A. chinense* (Lour.) Rehd., but leaves of that species typically have fewer primary veins and more widely spaced intercostal tertiary veins.

Holotype.—UCMP 73.

LOCALITY DATA

3842. Grade Trail cabin, opening along west contact of coal with shale. Kushtaka Formation. Collector: Maddren, 1905. Middle Ravenian.

3846. From creek flowing into head of Canyon Creek from Mt. Chezum at elevation of 2,000 feet. Kushtaka Formation. Collector: Maddren, 1905. Lower Ravenian. (Reference to the topographic map published by Martin, 1908, indicates that the 2,000-foot contour on his map is well below the conspicuous break in slope, and this collection is thus from beds stratigraphically below localities 11163 and 11164.

3847. From gulch on creek emptying into Berg Lake where Happy Hollow trail passes around shore. Kushtaka Formation. Collectors: Martin, Paige, and Maddren, 1905. Lower Ravenian.

3879. Yakutat Bay, west shore at Dalton's coal outcrop on Esker Stream. Kulthieth Formation. Collector: Tarr, 1905. Lower Ravenian.

9389. East slope Charlotte Ridge, 0.4 mile NE of NE cor. sec. 10, T. 17 S., R. 7 E., at approximate altitude of 1,000 feet. About 200 feet below base of Tokun Formation. Kushtaka Formation. Collector: F. F. Barnes, 1955. Middle Ravenian.

9551. Small stream 3.0 mile N. 45° E. of north end of Hanna Lake, near edge of moraine. Kulthieth Formation, probably upper part. Collector: Miller, 46AMr 43. Kummerian?

9552. Near top of Split Creek Sandstone Member, 6.11 miles S. 76½° W. from the point of intersection of the two principal tributaries of Burls Creek; lat 60°13′38″ N., long 144°17′ 14″ W. Katalla Formation. Collector: Rossman, 44ARm 1. Kummerian.

9553. Near USGS Cenozoic loc. 17831 (see Miller, 1961b); lat 60° 18.5′ N., long 142°47.0′ W. Mollusks from this locality include *Volsella* aff. *V. eugenensis* (Clark), *Tellina* cf. *lincolnensis* Weaver, and *Solena* cf. *clarki* (Weaver and Palmer), as determined by H. E. Vokes (written communication, 1948). Vokes believes the mollusks to be of middle Oligocene, i.e., Lincoln age. Upper part Kulthieth Formation. Collector: Miller, 47AMr 60. Kummerian.

9888. Sec. 10, T. 19 S., R. 6 E., lower part Katalla Formation. Collector: Shell Oil Co., 62H4 30. Kummerian.

9889. Sec. 10, T. 19 S., R. 6 E., lower part Katalla Formation. Collector: Shell Oil Co., 62H4 35. Kummerian.

9891. Sec. 30, T. 16 S., R. 9 E., in saddle just north of Doughton Peak. Kushtaka Formation. Collector: Shell Oil Co., 62H 603 200. Kummerian.

9893. Sec. 19, T. 18 S., R. 16 E. Upper part Kulthieth Formation. Collector: Shell Oil Co., 62H 1609 40. Kummerian.

9894. Sec. 19, T. 18 S., R. 16 E. Upper part Kulthieth Formation. Collector: Shell Oil Co., 62H 1609 367. Kummerian.

9895. Sec. 25, T. 20 S., R. 18 E., Poul Creek Formation. Collector: Shell Oil Co., 62J 266. Kummerian.

1157. Lat 60°24.8′ N., long 143°51.8′ W. From bed of creek. Kushtaka Formation. Collector: Wolfe, 1968. Lower Ravenian.

11158. Lat 60°25.2′ N., long 143°48.8′ N. From west wall of canyon. Kushtaka Formation. Collectors: Wolfe and Larson, 1968. Lower Ravenian.

11159. Lat 60°25.2′ N., long 143°48.8′ N. From west wall of canyon, about 200 feet north of loc. 11158. Kushtaka Formation. Collector: Gunn, 1968. Lower Ravenian.

11160. Lat 60°24.0′ N., long 143°57.5′ W. From slump area just south of creek. Kushtaka Formation. Collector: Wolfe, 1968. Lower Ravenian.

11162. Lat 60°23.9′ N., long 143°57′ W. From sandstone bed just beneath crest of ridge and about 800 feet higher than loc. 11160. Kushtaka Formation. Collector: Wolfe, 1968. Lower Ravenian.

11163. Lat 60°26.,5′ N., long 143°57.4′ W. From west side of small gully. Kushtaka Formation. Collectors: Wolfe, Larson, and Gunn, 1968. Middle Ravenian.

11164. Lat 60°26.7′ N., long 143°57.5′ W. Along east side of small gully. Kushtaka Formation. Collectors: Wolfe, Larson, and Gunn, 1968. Middle Ravenian.

11165. Lat 60°25.5′ N., long 144°7.7′ W. Cliff face about 300 feet below contact with Tokun Formation. Kushtaka Formation. Collectors: Wolfe, Larson, and Gunn, August, 1968. Middle Ravenian.

11166. Lat 60°28.5′ N., long 143°37′ W. At base of prominent cliff. Kushtaka Formation. Collectors: Wolfe, Larson, and Gunn, 1968. Lower Ravenian.

11167. Lat 60°27.1′ N., long 143°51′ W. Just above prominent break in slope, from concretionary bed. Kushtaka Formation. Collectors: Wolfe and Larson, 1968. Upper Ravenian.

11168. Lat 60°16.7′ No., long 143°51.8′ W. From southeast side of northeast tip of Nichiwak Mountain, about same altitude as top of Bering Glacier. Split Creek Sandstone member of the Katalla Formation. Collectors: Wolfe, Larson, and Gunn, 1968. Kummerian.

11169. Lat 60°27.5′ N., long 143°48.8′ N. On south side Carbon Ridge, about 50 feet below crest. Kushtaka Formation Collectors: Wolfe, Larson, and Gunn, 1968. Kummerian.

11170. Lat 60°19.5′ N., long 142°29.9′ W. On south side of valley of creek. Kulthieth Formation. Collectors: Wolfe, Larson, and Gunn, 1968. Lower Ravenian.

11183. Lat 60°6.1′ N., long 139°11.5′ W. North side of Haenke Glacier. Yakataga? Formation Collector: Plafker, 1968. Seldovian.

11184. Lat 60°9.3′ N., long 140°20.5′W. Yakataga Formation. Collector: Phillips Petroleum Co., 1967. Homerian.

11185. Lat 60°8.8′ N., long 140°8.25′ W. Poul Creek? Formation Collector: British Petroleum Co., GB 1215. Angoonian.

11186. Southwest shore of Cenotaph Island in Lituya Bay; along strike of beds from a point 0.85 mile N. 84° W. of easternmost cape on the island to a point 0.68 mile S. 70° W. of the same cape. Unnamed beds of late Miocene age. Collector: Miller, 58AMr 333. Seldovian or Homerian.

11188. Unknown position in the Basin Creek Member of the Katalla Formation; 1.60 miles N. 11° W. from the point of intersection of the two principal tributaries of Burls Creek, lat 60°13′38″ N., long 144°17′14″ W. Collector: Rossman, 44ARm 27. Kummerian.

11189. The map furnished by British Petroleum has an area west of Hope Creek of about 10 mi^2 circled and the notation that their locality GA3024 is "in this area." This area only has rocks that belong well up in the Katalla Formation. Because this locality produced both *Macclintockia pugetensis* and *Platanus comstocki*, the locality data are probably erroneous.

CAS 29181. Headwaters of Redwood Creek, 2,000 feet north of junction with east fork. Lower part Katalla Formation. Collector: Hanna, 1938. Kummerian.

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INDEX

[Italic page numbers indicate both major references and descriptions]

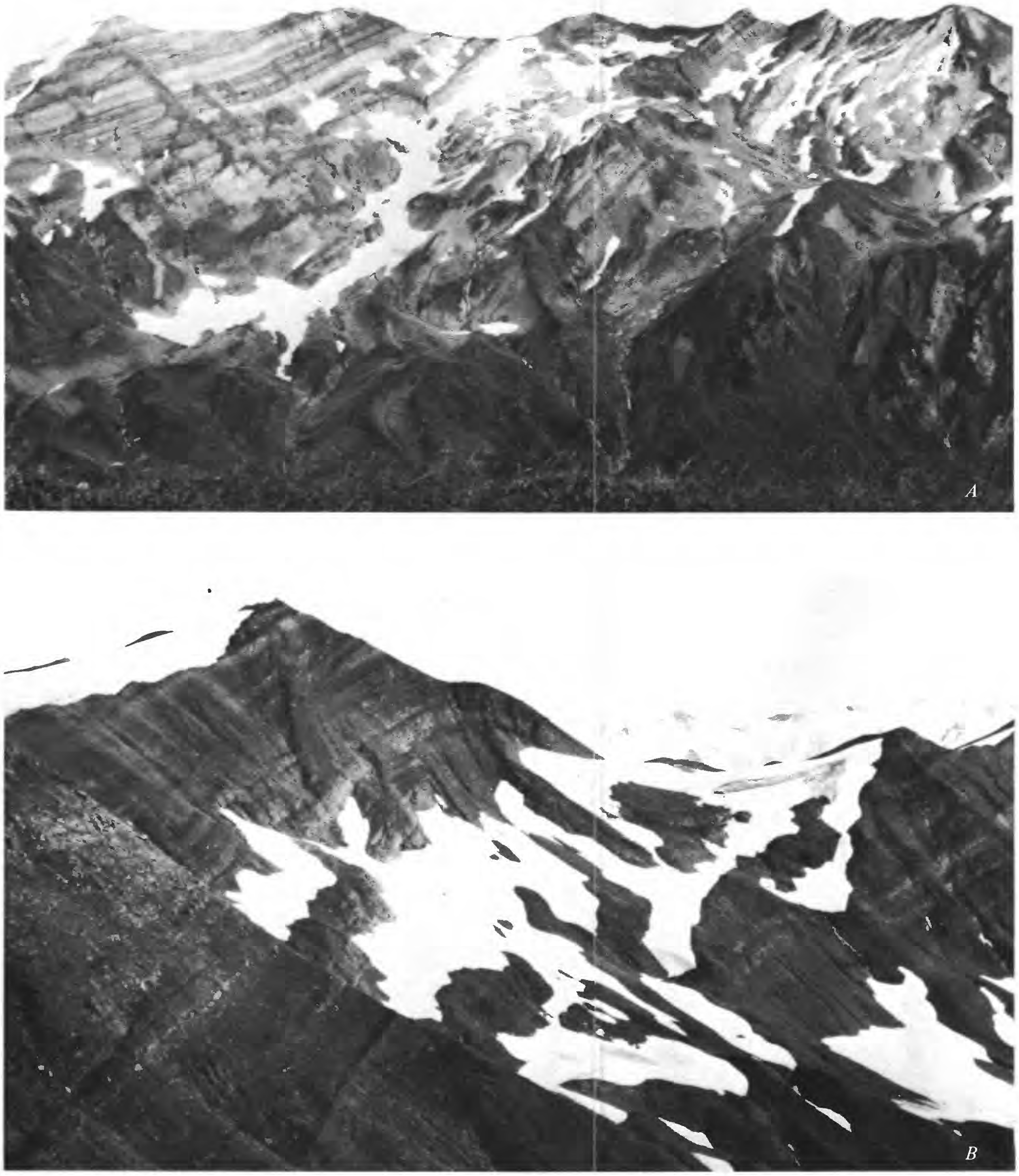
PLATES 1—30

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

A, West side of Carbon Mountain; photograph taken from the lower slopes of Cunningham Ridge above locality 11162. Doughton Peak is to the left; locality 9891 is to the left of this peak. Most of the rocks shown are probably of middle and late Ravenian age.

B, Looking east along the crest of Carbon Mountain from locality 11169. Note the strong folding in the Kushtaka Formation.



THE KUSHTAKA FORMATION ON CARBON MOUNTAIN

PLATE 2

[All figures natural size]

FIGURES 1, 2. *Allantodiopsis pugetensis* Wolfe. (p. 53.).
  1. Hypotype, USNM 43251; loc. 11159.
  2. Hypotype, USNM 38957; loc. 3879.

3. *Anemia gunni* Wolfe. (p. 52).
  Holotype, USNM 43246; loc. 11170.

1

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3

LOWER RAVENIAN FLORA

PLATE 3

[All figures natural size]

FIGURES 1, 4. *Dryopteris alaskana* (Holl.) Wolfe. (p. 53).
  1. Lectotype, USNM 38664; loc. 3879.
  4. Syntype, USNM 245724; loc. 3879.
2. *Glyptostrobus* sp. (p. 53).
  USNM 38724; loc. 3879.
3. *Cyathea inequilateralis* (Holl.) Wolfe. (p. 53).
  Holotype, USNM 38665; loc. 3846.

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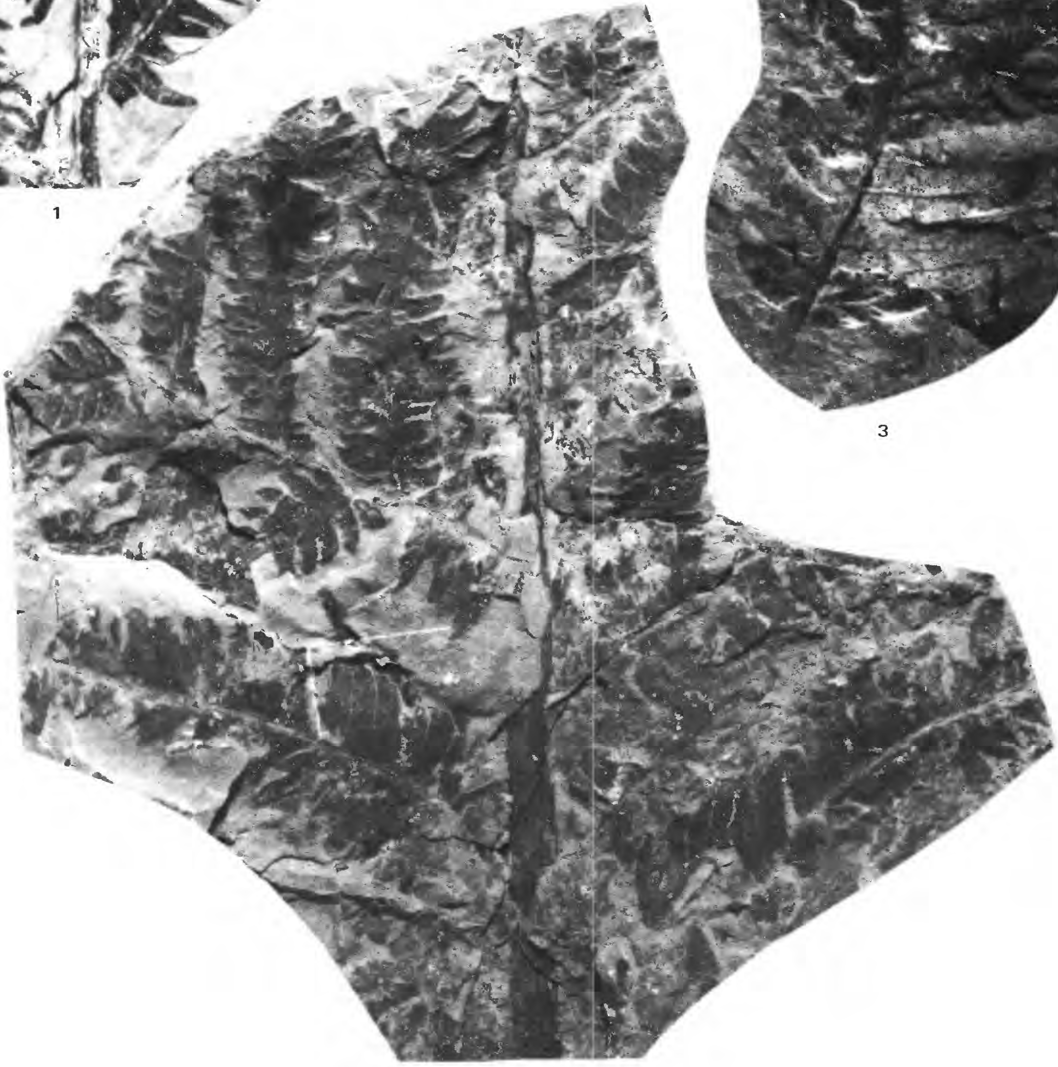

4

LOWER RAVENIAN FLORA

PLATE 4

FIGURES 1–3. *Alnus scotti* Wolfe. (p. 59).

1. Paratype, USNM 43273; loc. 11170, X 1.
2. Paratype, USNM 43274; loc. 3847, X 1.
3. Holotype, USNM 38899; loc. 3847, X 1.

4. *Platycarya pseudobrauni* (Holl.) Wolfe. (p. 56).
Hypotype, USNM 43266; loc. 11170, X 1.

5. *Palmacites* sp. (p. 54).
USNM 43258; loc. 11160, X ½.

1

2

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4

5

LOWER RAVENIAN FLORA

PLATE 5

[All figures natural size]

FIGURES 1, 2. *Platycarya pseudobrauni* (Holl.) Wolfe. (p. 56).
  1. Hypotype, USNM 43267; loc. 11170.
  2. Hypotype, USNM 38893; loc. 3847.
3, 5. *Alnus martini* Wolfe. (p. 58).
  1. Holotype, USNM 43271; loc. 11158.
  2. Paratype, USNM 43272; loc. 11170.
4. *Tetracentron piperoides* (Lesq.) Wolfe. (p. 61).
  Hypotype, USNM 43288; loc. 11170.
6. *Myristica* sp. (p. 66).
  USNM 39019; loc. 3847.
7. *Girroniera* sp. (p. 60).
  USNM 43285; loc. 11158.
8. *Girroniera* sp. (p. 60).
  USNM 43286; loc. 11170.


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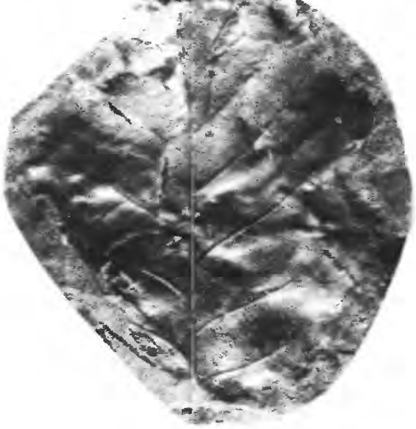
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LOWER RAVENIAN FLORA

PLATE 6

[All figures natural size]

FIGURES 1-3. *Limacia stenophylla* Wolfe. (p. 64).
  1. Holotype, USNM 43303; loc. 11159.
  2, 3. Paratypes, USNM 43304, 43305; loc. 11159.
4. *Pycnarrhena* sp. (p. 65).
  USNM 43308; loc. 11166.
5. *Cocculus* sp. (p. 63).
  USNM 43299; loc. 11166.
6. *Anamirta milleri* Wolfe (p. 62).
  Holotype, USNM 43293; loc. 11170.
7. *Diploclisia* sp. (p. 63).
  USNM 43301; loc. 11170.
8. *Calkinsia plafkeri* Wolfe. (p. 62).
  Paratype, USNM 43294; loc. 11157.

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LOWER RAVENIAN FLORA

PLATE 7

[All figures natural size]

FIGURES 1-3, 6. *Clerodendrum* sp. (p. 85).
USNM 43399, 43400, 43401A, 43402; loc. 11158.
4, 7. *Limacia stenophylla* Wolfe. (p. 64).
4. Paratype, USNM 43306; loc. 11159.
7. Paratype, USNM 43307; loc. 11166.
5. *Paratinomiscium conditionalis* (Holl.) Wolfe. (p. 65).
Holotype, USNM 39117; loc. 3879.

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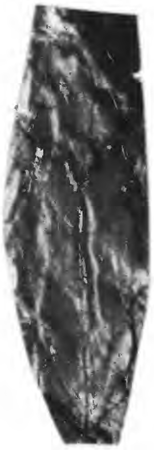

7

LOWER RAVENIAN FLORA

PLATE 8

[All figures natural size]

FIGURE 1. *Myristica* sp. (p. 66).
USNM 38667; loc. 3847.
2. *Cinnamomophyllum latum* (MacG.) Wolfe. (p. 67).
Hypotype, USNM 38914; loc. 3847.
3, 4. *Knema* sp. (p. 66).
USNM 38915, 43309; loc. 3847.
5. *Dasymaschalon*? sp. (p. 66).
USNM 43310; loc. 11158.
6. *Cananga* sp. (p. 66).
USNM 38911; loc. 3879.


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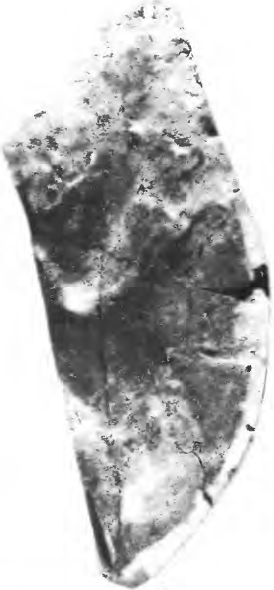
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LOWER RAVENIAN FLORA

PLATE 9

[All figures natural size]

FIGURES 1, 4. *Litseaphyllum similis* (Knowlt.) Wolfe. (p. 69).
Hypotypes, USNM 43320, 43321; loc. 11157.
2. *Litseaphyllum presamarensis* (Sanb.) Wolfe. (p. 68).
Hypotype, USNM 43325; loc. 3846.
3, 10. *Cinnamomophyllum latum* (MacG.) Wolfe. (p. 67).
  3. Hypotype, USNM 43314; loc. 11166.
  10. Hypotype, USNM 43315; loc. 11157.
5, 8, 9. *Euodia alaskana* Wolfe. (p. 73).
  5. Holotype, USNM 43349; loc. 11158.
  8, 9. Paratypes, USNM 43350, 43351; loc. 11158.
6. *Caesalpinites* sp. (p. 72).
USNM 43347; loc. 3847.
7. *Litseaphyllum* sp. (p. 69).
USNM 43335; loc. 11159.


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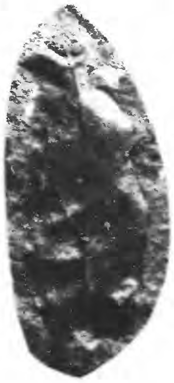
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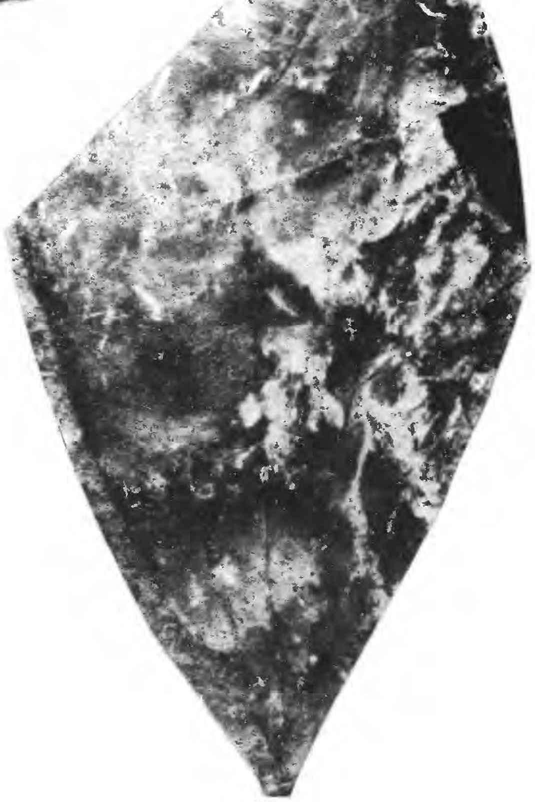
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LOWER RAVENIAN FLORA

PLATE 10

[All figures natural size]

FIGURES 1, 4. *Luvunga spatiosa* (Holl.) Wolfe. (p. 73).
  1. Hypotype, USNM 43352; loc. 3847.
  4. Holotype, USNM 38920; loc. 3847.

2, 3, 5. *Melanorrhoea alaskana* (Holl.) Wolfe. (p. 74).
  2. Hypotype, USNM 38885; loc. 3846.
  3. Hypotype, USNM 43353; loc. 11158.
  5. Holotype, USNM 39020; loc. 3847.

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LOWER RAVENIAN FLORA

PLATE 11

[All figures natural size]

FIGURES 1, 4-6. *Celastrus comparabilis* Holl. (p. 75).
  1. Hypotype, USNM 43356; loc. 11158.
  4. Hypotype, USNM 43357; loc. 11170.
  5. Hypotype, USNM 38744; loc. 3847.
  6. Holotype, USNM 38956; loc. 3879.

2. *Pyrenacantha* sp. (p. 77).
  USNM 43366; loc. 11170.

3. *Goweria dilleri* (Knowlt.) Wolfe. (p. 76).
  Hypotype, USNM 38901; loc. 3847.


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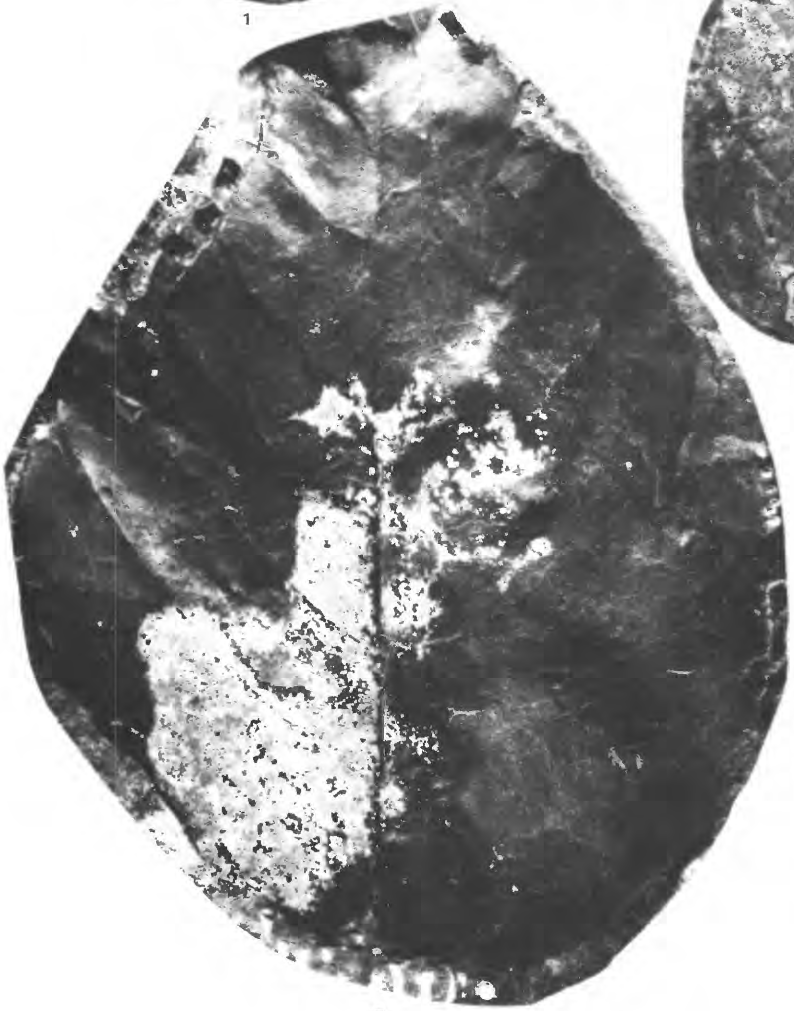
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LOWER RAVENIAN FLORA

PLATE 12

[All figures natural size]

FIGURES 1-6. *Phytocrene acutissima* Wolfe. (p. 76).

1-3, 5. Paratypes, USNM 43359-43361, 43363; loc. 11158.
4, 6. Holotype, USNM 43362A, B; loc. 11158.

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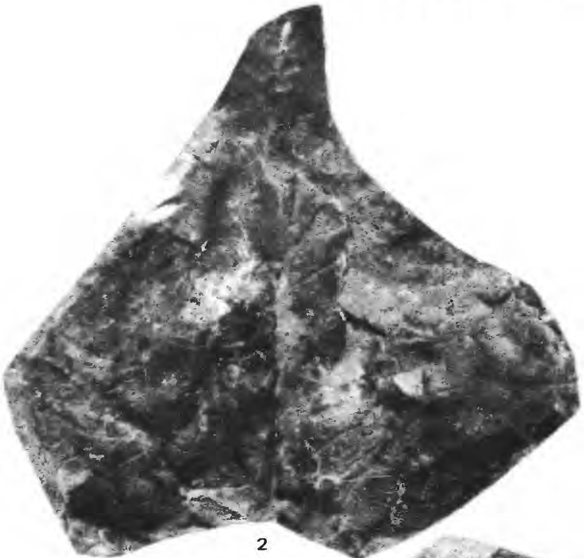

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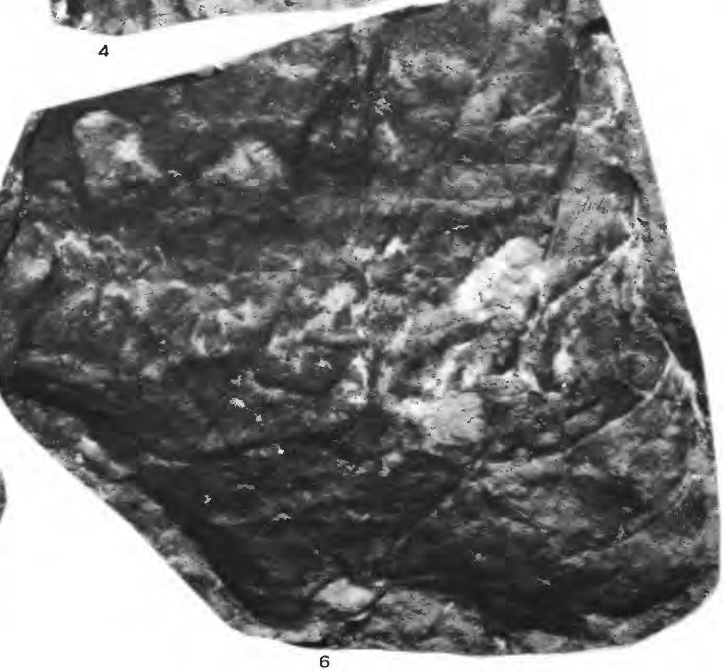

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LOWER RAVENIAN FLORA

PLATE 13

[All figures natural size]

FIGURE 1. *Phytocrene acutissima* Wolfe. (p. 76).
Paratype, USNM 43364; loc. 11166.
2. *Paleophytocrene elytraeformis* (Holl.) Wolfe. (p. 76).
Holotype, USNM 39127A; loc. 3879.
3. *Goweria alaskana* Wolfe. (p. 75).
Holotype, USNM 43358A; loc. 11158.
4. *Phytocrene sordida* (Lesq.) MacG. (p. 77).
Hypotype, USNM 43365; loc. 11170.
5, 6. *Stemonurus alaskanus* Wolfe. (p. 78).
5. Paratype, USNM 43367; loc. 11158.
6. Holotype, USNM 43368; loc. 11158.

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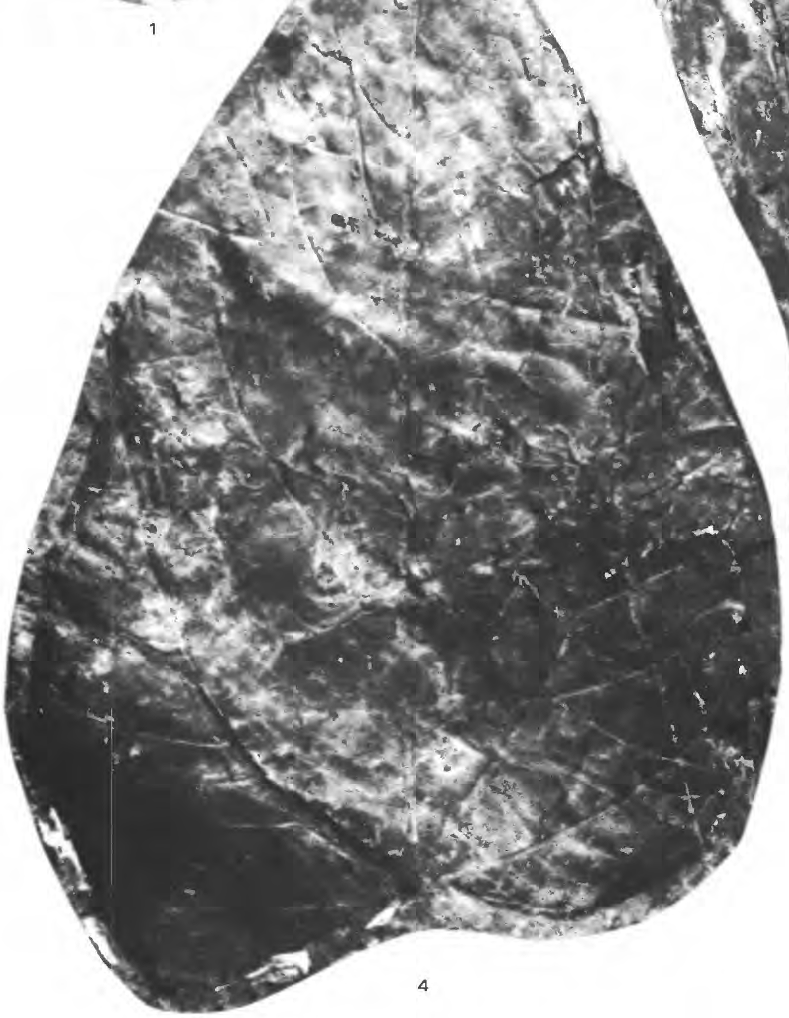

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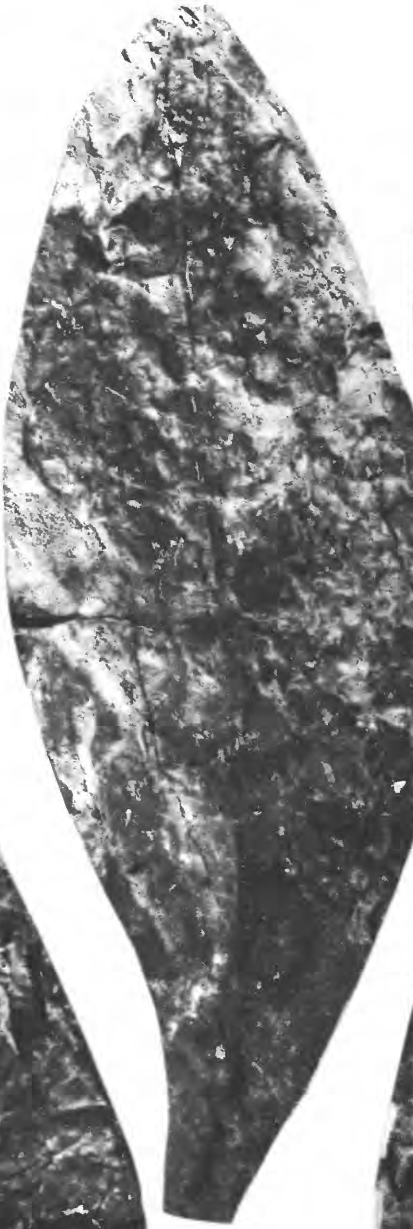

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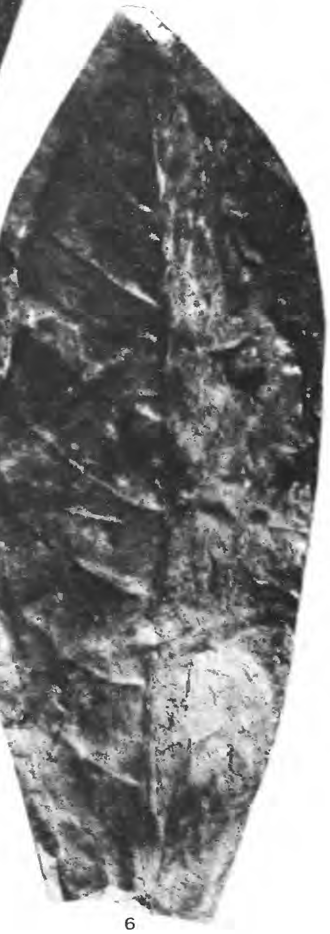

6

LOWER RAVENIAN FLORA

PLATE 14

[All figures natural size]

FIGURES 1, 2. *Meliosma kushtakensis* Wolfe. (p. 79).
  1. Paratype, USNM 43381; loc. 11158.
  2. Holotype, USNM 43382; loc. 11166.
3, 4. *Allophylus duktothensis* Wolfe. (p. 78).
  3. Holotype, USNM 43372; loc. 11170.
  4. Paratype, USNM 43373; loc. 11170.
5, 9. *Zizyphus alaskanus* Wolfe. (p. 80).
  Holotype, USNM 43371A, B; loc. 11158.
6-8. *Meliosma duktothensis* Wolfe. (p. 79).
  6. Holotype, USNM 43378; loc. 11170.
  7, 8. Paratypes, USNM 43379, 43380; loc. 11170.


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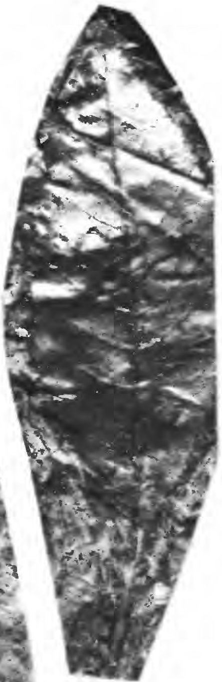
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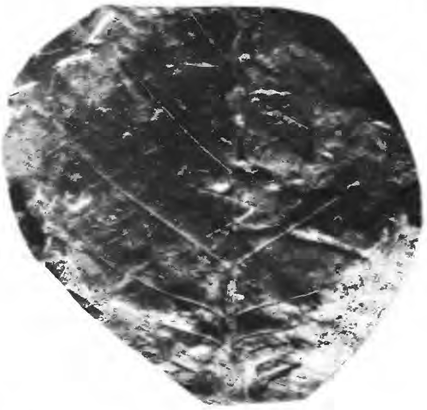
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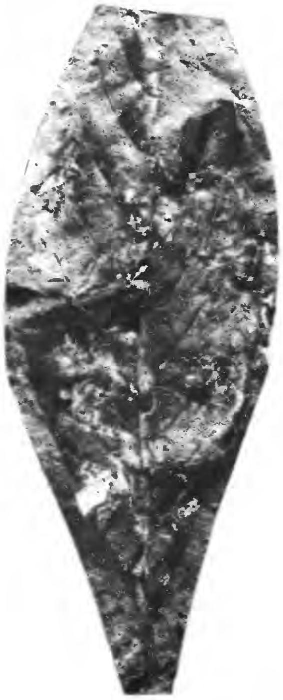
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9

LOWER RAVENIAN FLORA

PLATE 15

[All figures natural size]

FIGURE 1. *Sageretia* sp. (p. 80).
USNM 43370; loc. 11166.
2, 4, 5. *Vitis* sp (p. 80).
USNM 43383-43385; loc. 11166.
3. *Illicium* sp. (p. 62).
USNM 43292; loc. 11159.
6. *Mastixia irregularis* (Holl.) Wolfe. (p. 85).
Holotype, USNM 39033; loc. 3846.

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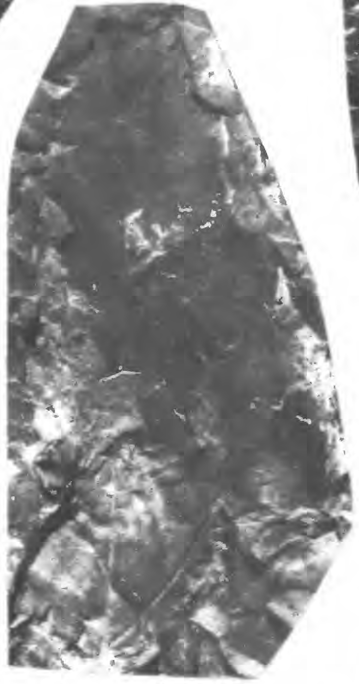

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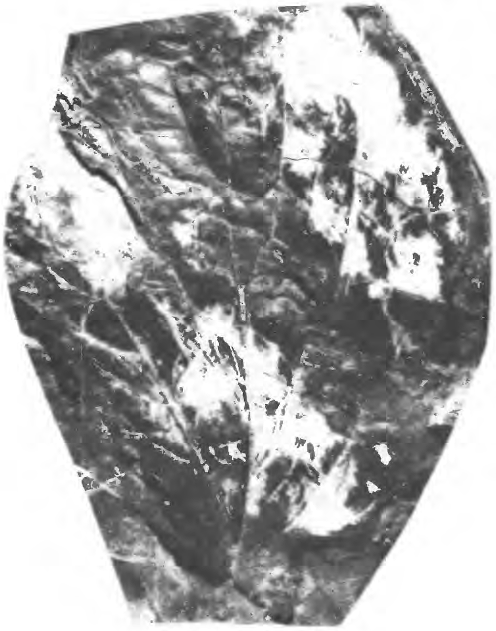

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LOWER RAVENIAN FLORA

PLATE 16

[All figures natural size]

FIGURE 1. *Alangium* sp. (p. 84).
USNM 43393; loc. 11166.
2. *Alangium bergensis* Wolfe. (p. 84).
Holotype, USNM 38926; loc. 3847.
3-5. *Eugenia* sp. (p. 84).
USNM 43394-43396; loc. 11170.
6-8. *Parashorea pseudogoldiana* (Holl.) Wolfe. (p. 82).
6. Hypotype, USNM 39035; loc. 3847.
7. Lectotype, USNM 38978; loc. 3847.
8. Syntype, USNM 43391; loc. 3847.

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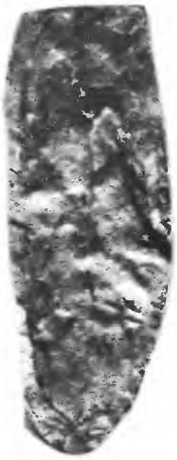

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LOWER RAVENIAN FLORA

PLATE 17

[All figures natural size]

FIGURE 1. *Clerodendrum* sp. (p. 85).
USNM 43401B; loc. 11158.
2. *Dicotylophyllum* sp. (p. 86).
USNM 43414; loc. 11170.
3, 4. *Barringtonia* sp. (p. 83).
USNM 43392A, B; loc. 11170.

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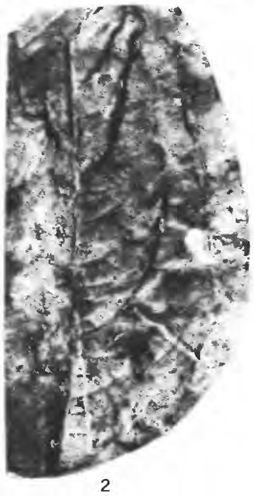

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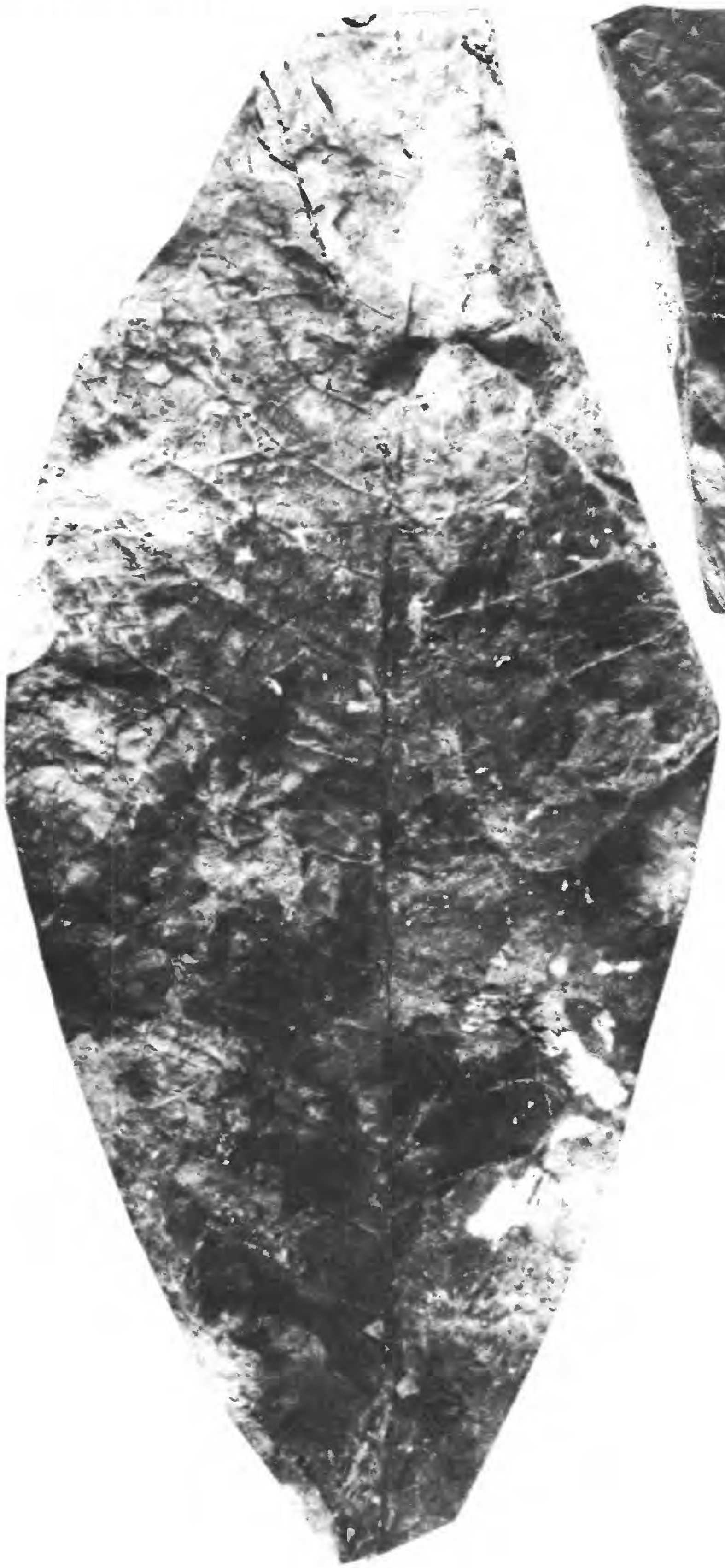

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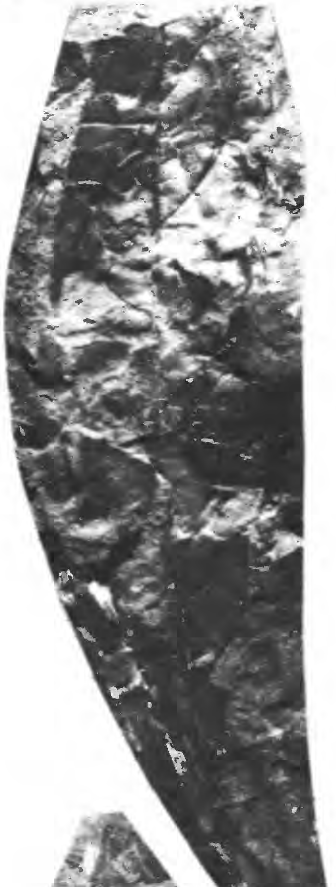
LOWER RAVENIAN FLORA

PLATE 18

[All figures natural size]

FIGURE 1. *Saurauia* sp. (p. 81).
USNM 43389; loc. 3846.
2. *Clethra* sp. (p. 85).
USNM 43398; loc. 11170.
3. *Dicotylophyllum* sp. (p. 86).
USNM 39036; loc. 3847.
4. *Celastrus comparabilis* Holl. (p. 75).
Hypotype, USNM 245725; loc. 11170.
5. *Dicotylophyllum* sp. (p. 86).
USNM 43415; loc. 11159.
6. *Dicotylophyllum* sp. (p. 86).
USNM 43416; loc. 11158.



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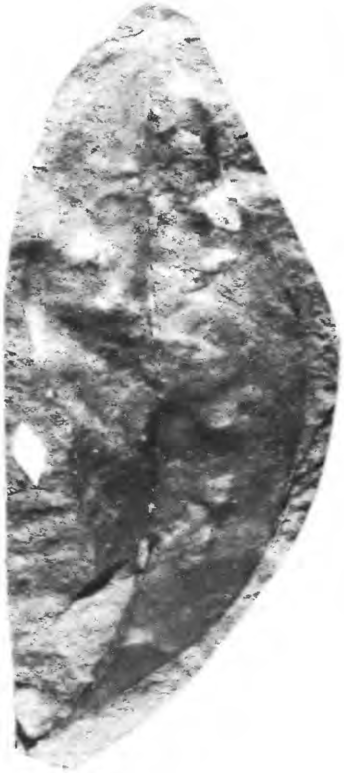

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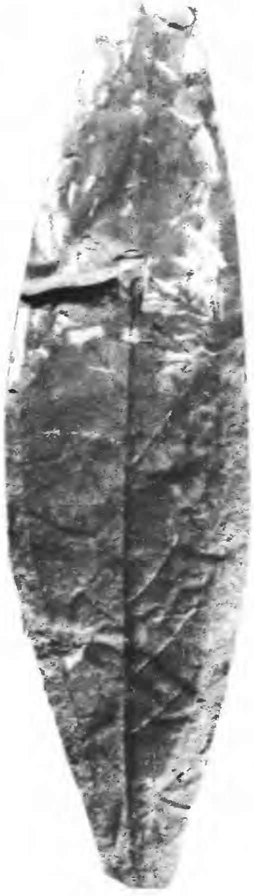

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LOWER RAVENIAN FLORA

PLATE 19

[All figures natural size]

FIGURES 1, 5a,b. *Kandelia wangi* Wolfe. (p. 83).
  1. Holotype, USNM 222843; loc. 11195, X 5.
  5a. Paratype, USNM 222844; loc. 11195, X 1.
  5b. Holotype, USNM 222843; loc. 11195, X 1.
2. *Kandelia candel* (L.) Druce. Extant species for comparison.
  USGS Ref. Colln. 1752. X 5.
3. *Rhus* cf. *R. mixta* (Lesq.) MacG. (p. 74).
  USNM 222840; loc. 11195, X 1.
4. *Toona* sp. (p. 72).
  USNM 222842; loc. 11195, X 1.
6. *Parashorea pseudogoldiana* (Holl.) Wolfe. (p. 82).
  Hypotype, USNM 222841; loc. 11195, X 5.
7. *Parashorea malaanonan* (Blanco) Vid. Extant species for comparison.
  USGS Ref. Colln. 1663, X 5.

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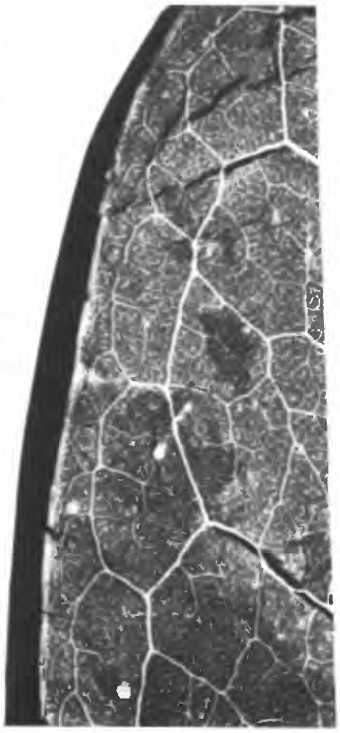

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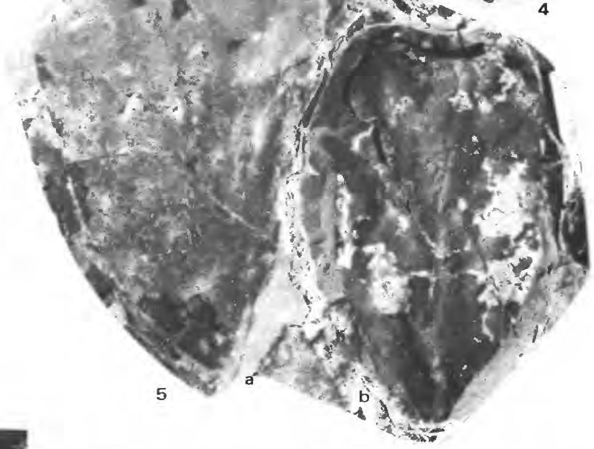

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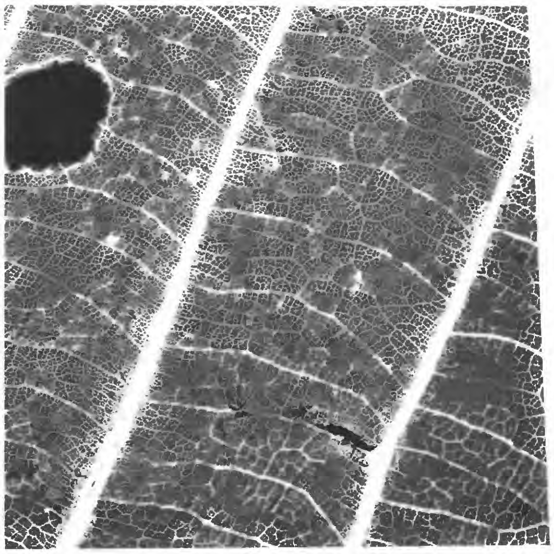

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LOWER RAVENIAN FLORA

PLATE 20

[All figures natural size]

FIGURES 1, 2. *Lygodium larsoni* Wolfe. (p. 52).
  1. Holotype, USNM 43248; loc. 9389.
  2. Paratype, USNM 43249; loc. 11165.
3, 6. *Glyptostrobus* sp. (p. 53).
  USNM 43254, 43255; loc, 11165.
4. *Allantodiopsis pugetensis* Wolfe. (p. 53).
  Hypotype, USNM 43252; loc. 11165.
5. *Phoenicites* sp. (p. 53).
  USNM 43257; loc. 11165.
7. *Engelhardtia* sp. (p. 55).
  USNM 43264; loc. 11165.
8. *Carya cashmanensis* Wolfe. (p. 55).
  Hypotype, USNM 43263; loc. 11165.


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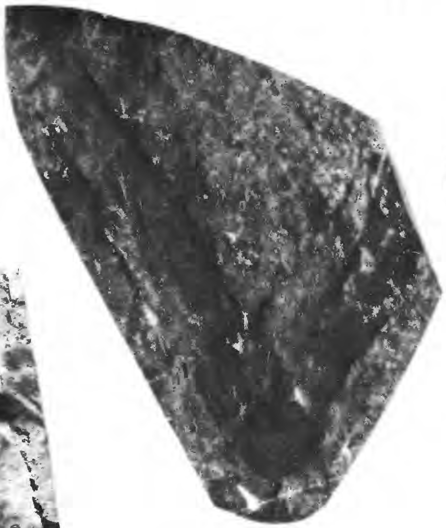
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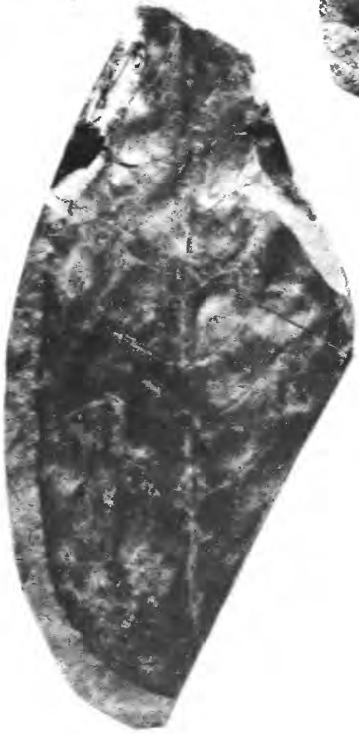
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MIDDLE RAVENIAN FLORA

PLATE 21

[All figures natural size]

FIGURES 1, 5, 6. *Dryophyllum pugetensis* Wolfe. (p. 60).
1, 6. Hypotypes, USNM 43281, 43283; loc. 11165.
5. Hypotype, USNM 43282; loc. 3842.

2a. *Glyptostrobus* sp. (p. 53).
USNM 43256; loc. 11165.

2b. *Platycarya pseudobrauni* (Holl.) Wolfe. (p. 56).
Hypotype, USNM 245726; loc. 11165.

3. *Alnus martini* Wolfe. (p. 58).
Paratype, USNM 43279; loc. 11163.

4. *Pterocarya pugetensis* Wolfe. (p. 56).
Hypotype, USNM 43268; loc. 11165.


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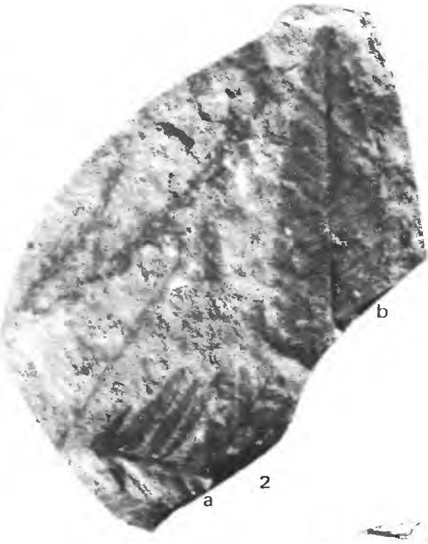

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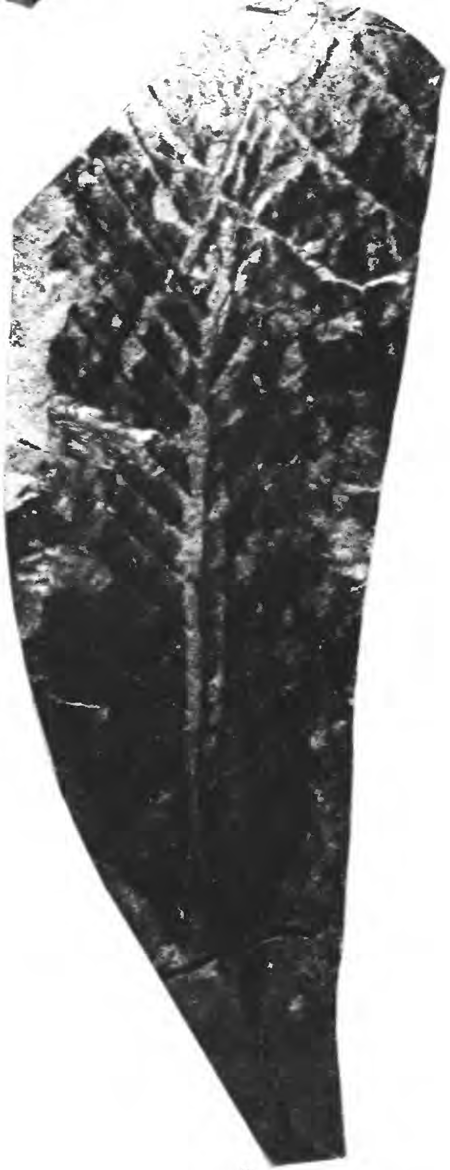
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MIDDLE RAVENIAN FLORA

PLATE 22

[All figures natural size]

FIGURES 1, 2. *Litseaphyllum presamarensis* (Sanb.) Wolfe. (p. 68).
Hypotypes, USNM 43326, 43327; loc. 3842.
3. *Tetracentron piperoides* (Lesq.) Wolfe. (p. 61).
Hypotype, USNM 43289; loc. 11165.
4. *Litseaphyllum* sp. (p. 69).
USNM 43338; loc. 11165.
5. *Litseaphyllum* sp. (p. 69).
USNM 43337; loc. 11165.
6. *Litseaphyllum praelingue* (Sanb.) Wolfe. (p. 68).
USNM 43324; loc. 11165.

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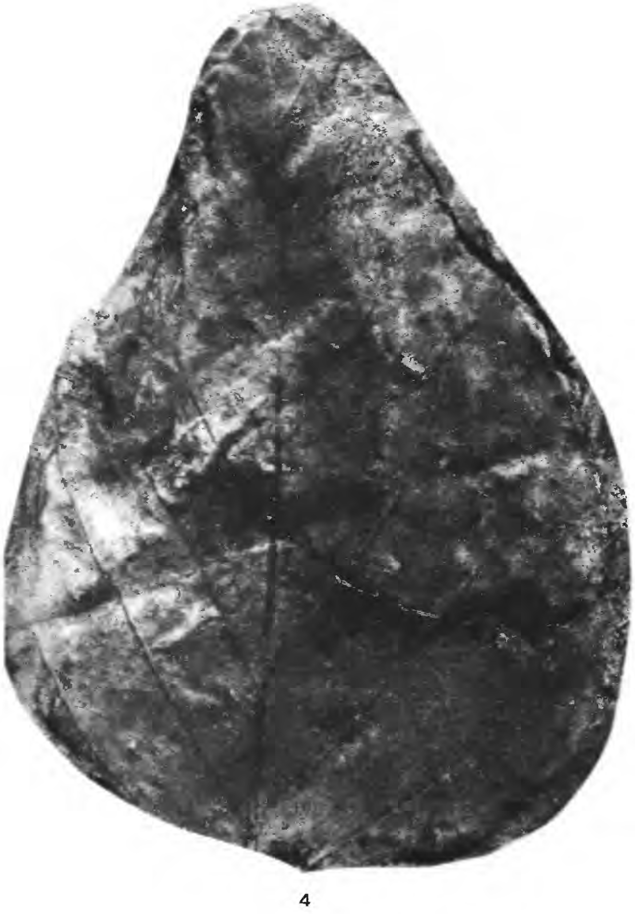

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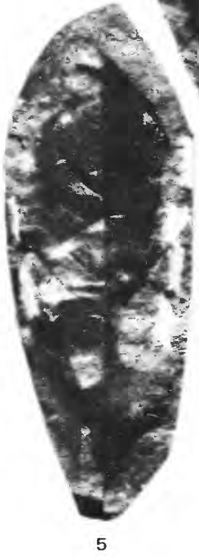

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MIDDLE RAVENIAN FLORA

PLATE 23

[All figures natural size]

FIGURE 1. *Ulmus* sp (p. 60).
USNM 43287; loc. 11165.
2. *Litseaphyllum similis* (Knowlt.) Wolfe. (p. 69).
Hypotype, USNM 43322; loc. 11165.
3, 4, 6, 7b. *Calkinsia plafkeri* Wolfe. (p. 62).
3, 6, 7b. Paratypes, USNM 43295, 43297, 43298; loc. 11165.
4. Paratype, USNM 43312; loc. 11165.
5, 7a. *Cinnamomophyllum kushtakensis* Wolfe. (p. 67).
5. Holotype, USNM 43311; loc. 9389.
7a. Paratype, USNM 43312; loc. 11165.


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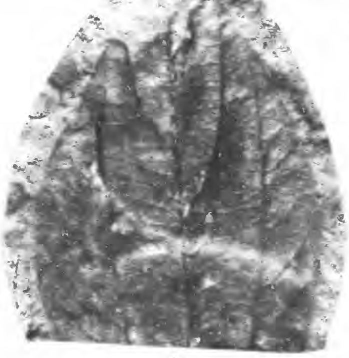
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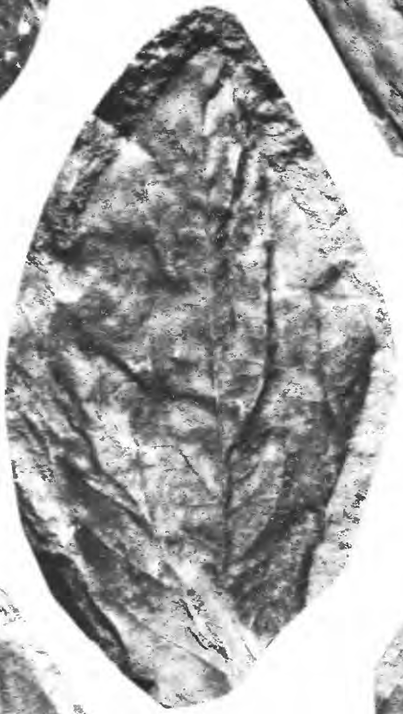
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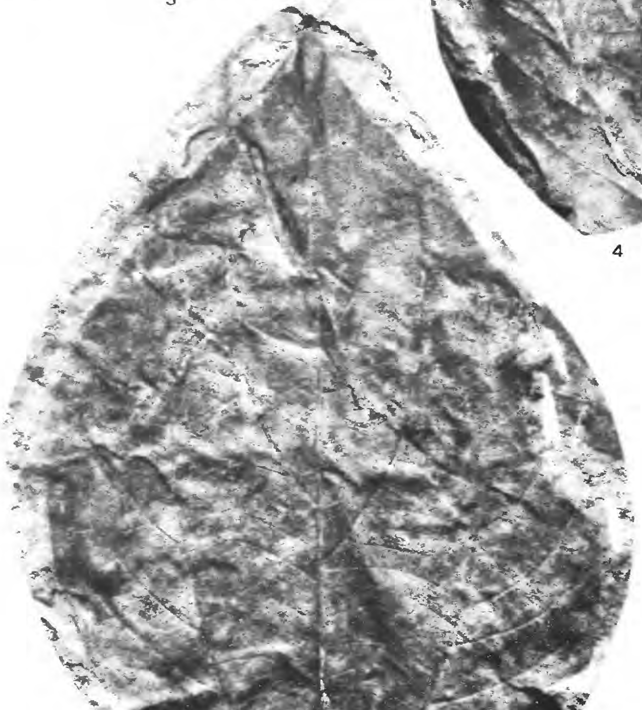
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MIDDLE RAVENIAN FLORA

PLATE 24

[All figures natural size]

FIGURE 1. *Liquidambar*? sp. (p. 70).
USNM 43342; loc. 11165.
2. *Dicotylophyllum* sp. (p. 86).
USNM 43417; loc. 11165.
3. *Allophylus* sp. (p. 79).
USNM 43376; loc. 11165.
4. *Dicotylophyllum* sp. (p. 87).
USNM 43418; loc. 11165.
5. *Dicotylophyllum* sp. (p. 87).
USNM 43420; loc. 11165.
6. *Dicotylophyllum* sp. (p. 87).
USNM 43419; loc. 9389.
7. *Eucommia* sp. (p. 70).
USNM 43343; loc. 11165.
8. *Dicotylophyllum* sp. (p. 87).
USNM 43421; loc. 11165.
9. *Sapindus*? sp. (p. 79).
USNM 43377; loc. 11165.


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MIDDLE RAVENIAN FLORA

PLATE 25

[All figures natural size]

FIGURES 1, 2, 6. *Litseaphyllum schorni* Wolfe. (p. 68).
    1, 6. Paratypes, USNM 43332, 43334; loc. 11165.
    2. Holotype, USNM 43333; loc. 11165.
3. Theaceae, gen. and sp. indetermined. (p. 82).
    USNM 43390; loc. 11165.
4. Anacardiaceae, gen. and sp. indetermined. (p. 74).
    USNM 43354; loc. 11165.
5. *Caesalpinites* sp. (p. 72).
    USNM 43348; loc. 11165.
7. *Dicotylophyllum kummerensis* (Wolfe) Wolfe. (p. 86).
    Hypotype, USNM 43412; loc. 11164.
8. *Macclintockia* sp. (p. 86).
    USNM 43409; loc. 11164.


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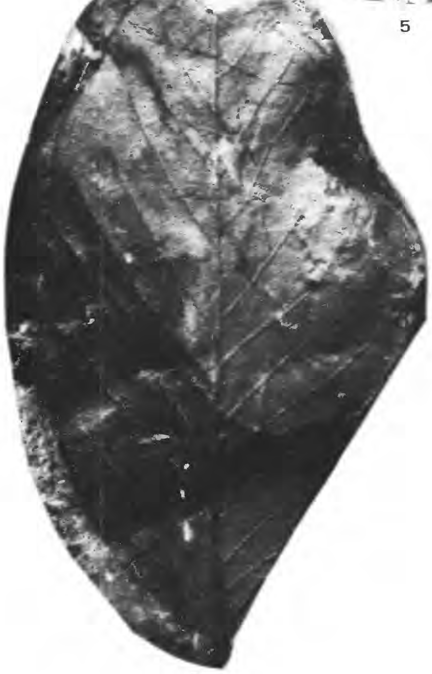
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MIDDLE RAVENIAN FLORA

PLATE 26

[All figures natural size]

FIGURE 1. *Populus* sp. (p. 54).
USNM 43259; loc. 11167.
2. *Salix* sp. (p. 55).
USNM 43262; loc. 11167.
3. *Juglans* sp. (p. 56).
USNM 43265; loc. 11167.
4, 10. *Alnus* sp. (p. 59).
USNM 43275; 43276a; loc. 11167.
5. *Cocculus* sp. (p. 63).
USNM 43300; loc. 11167.
6. *Corylopsis* sp. (p. 70).
USNM 43341A; loc. 11167.
7. *Alnus cuprovallis* Axelr. (p. 58).
Hypotype, USNM 43270; loc. 11167.
8. *Dicotylophyllum* sp. (p. 87).
USNM 43430; loc. 11167.
9. *Prunus axelrodi* Wolfe. (p. 71).
Holotype, USNM 43345A; loc. 11167.
11, 13. *Salix carbonensis* Wolfe. (p. 55).
11. Paratype, USNM 43261; loc. 11167.
13. Holotype, USNM 43260; loc. 11167.
12. *Ilex carbonensis* Wolfe. (p. 74).
Holotype, USNM 43355A; loc. 11167.


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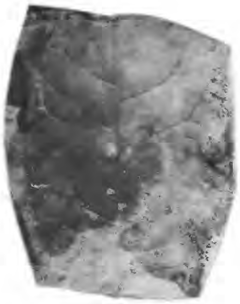
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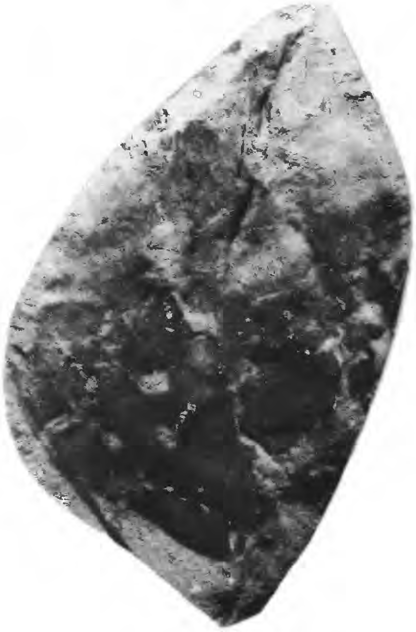
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UPPER RAVENIAN FLORA

PLATE 27

[All figures natural size]

FIGURES 1, 5. *Tilia carbonensis* Wolfe. (p. 80).
    1. Holotype, USNM 43386A; loc. 11167.
    5. Paratype, USNM 43387; loc. 11167.
2. *Rhamnus* sp. (p. 79).
    USNM 43369; loc. 11167.
3, 4. *Sorbus carbonensis* Wolfe. (p. 71).
    Holotype, USNM 43346A, B; loc. 11167.
6. *Plafkeria* sp. (p. 81).
    USNM 43388A; loc. 11167.
7. *Eugenia*? sp. (p. 85).
    USNM 43397; loc. 11167.
8, 10. *Dicotylophyllum carbonensis* Wolfe. (p. 86).
    8. Holotype, USNM 43410; loc. 11167.
    10. Paratype, USNM 43411; loc. 11167.
9. *Dicotylophyllum* sp. (p. 87).
    USNM 43422; loc. 11167.


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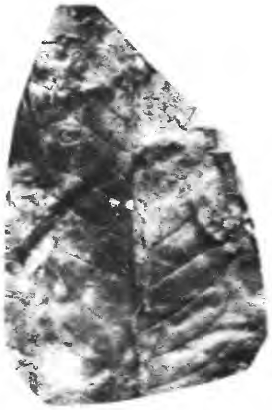
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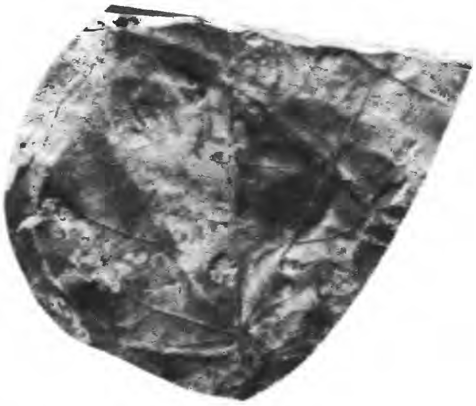
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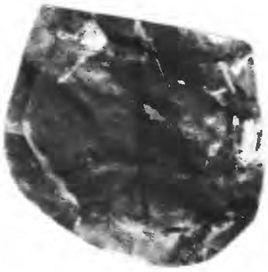
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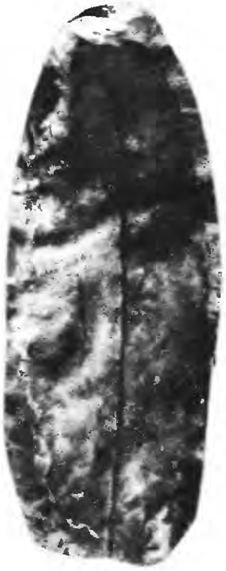
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UPPER RAVENIAN FLORA

PLATE 28

[All figures natural size]

FIGURE 1. *Woodwardia* sp. (p. 53).
USNM 43253; loc. 9891.
2. *Fagus* sp. (p. 60).
USNM 43284; loc. 9552.
3. *Alnus* sp. (p. 59).
USNM 43278; loc. 9891.
4. *Betula* sp. (p. 60).
USNM 43280; loc. 11168.
5. *Anemia*? sp. (p. 52).
USNM 43247; loc. 9891.
6, 9. *Litseaphyllum carbonensis* Wolfe. (p. 68).
6. Paratype, USNM 43316; loc. 11169.
9. Holotype, USNM 43317; loc. 11169.
7. *Tetracentron piperoides* (Lesq.) Wolfe. (p. 61).
Hypotype, USNM 43290; loc. 11169.
8a. *Litseaphyllum* sp. (p. 69).
USNM 43339; loc. 11169.
8b, 10a,b. *Litseaphyllum presamarensis* (Sanb.) Wolfe. (p. 68).
Hypotypes, USNM 43328–43330; loc. 11169.

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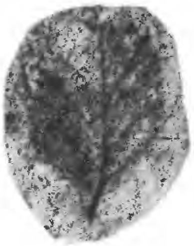

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KUMMERIAN FLORA

PLATE 29

[All figures natural size]

FIGURES 1, 3. *Litseaphyllum katallaensis* Wolfe. (p. 68).
    1. Paratype, USNM 43318; loc. 9551.
    3. Holotype, USNM 43319; loc. 11168.
2. *Litseaphyllum similis* (Knowlt.) Wolfe. (p. 69).
    Hypotype, USNM 43323; loc. 11169.
4, 6. *Allophylus wilsoni* Chan. and Sanb. (p. 78).
    4. Hypotype, USNM 43374A; loc. 11168.
    6. Hypotype, USNM 43375; loc. 9553.
5. *Litseaphyllum* sp. (p. 69).
    USNM 43336; loc. 11168.
7. *Platanus comstocki* (Sanb.) Wolfe. (p. 71).
    Hypotype, USNM 43344; loc. 9891.
8. *Litseaphyllum* sp. (p. 70).
    USNM 43340; loc. 9891.
9. *Litseaphyllum presanguinea* (Chan. and Sanb.) Wolfe. (p. 68).
    Hypotype, USNM 43331; loc. 9891.


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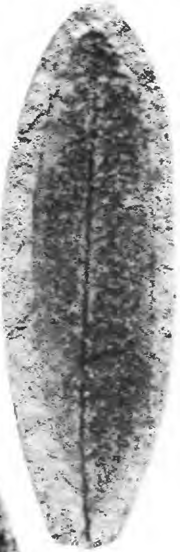
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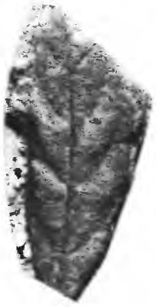
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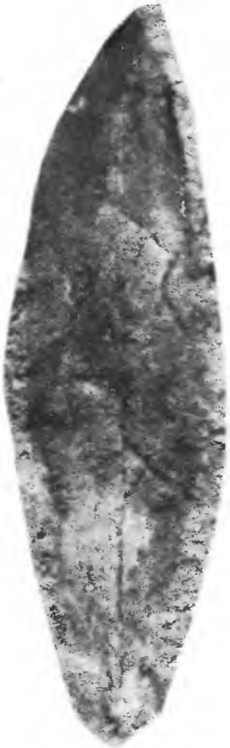
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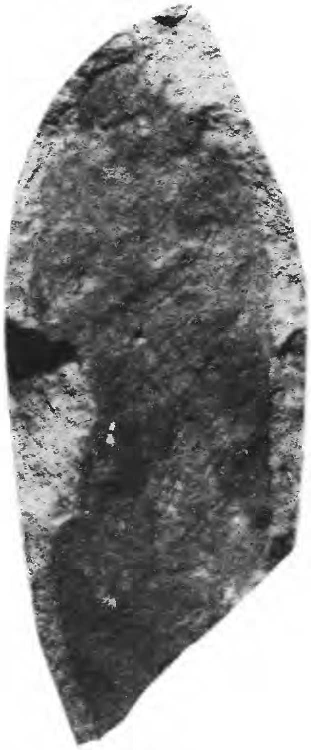
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KUMMERIAN FLORA

PLATE 30

[All figures natural size]

FIGURE 1. *Dicotylophyllum* sp. (p. 87).
USNM 43423; loc. 11168.
2. *Dicotylophyllum* sp. (p. 87).
USNM 43424; loc. 11169.
3. *Dicotylophyllum* sp. (p. 87).
USNM 43425; loc. 11168.
4. *Holmskioldia speiri* (Lesq.) MacG.? (p. 85).
USNM 43403; loc. 11168.
5, 6, 8–10. *Macclintockia pugetensis* Wolfe. (p. 86).
5. Hypotype, USNM 43404; loc. 9891.
6, 10. Hypotypes, USNM 43405, 43408; loc. 11168.
8, 9. Hypotypes, USNM 43406, 43407; loc. 11189.
7. *Magnolia reticulata* Chan. and Sanb. (p. 62).
Hypotype, USNM 43291; loc. 11168.
11. *Dicotylophyllum kummerensis* Wolfe?. (p. 86).
USNM 43413; loc. 9891.


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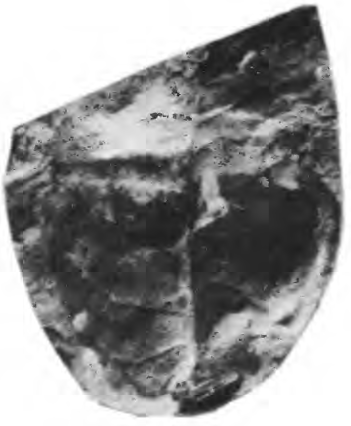
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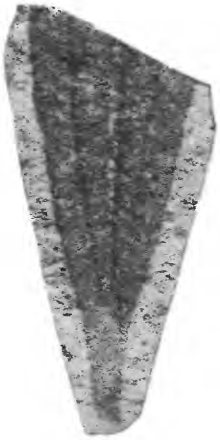
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KUMMERIAN FLORA