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PALEOGENE FLORAS FROM THE GULF OF ALASKA REGION

By

Jack A. Wolfe

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Contents

Page

Contents--continued Page

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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 early late 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 narrow region bordering the Tropical Rain forest) based on the physiognomic analysis of foliage; the most diverse families represented are Menispermaceae and Icacinaceae. These are accompanied by palms, Anonaceae, Myristicaceae, Dipterocarpaceae, Barringtoniaceae, and Myrtaceae. A minor element is represented by broad-leaved deciduous plants. The middle Ravenian was somewhat cooler, as indicated by foliar physiognomy, the fewer Tropical Rain forest elements, and the diversity of Lauraceae. The late Ravenian assemblage represents a broad-leaved deciduous forest indicating a temperate climate. The Kummerian assemblages were again dominated by Lauraceae, and the physiognomic characters of the foliage indicate that 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 could probably 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. Strong climatic fluctuations evidenced by foliar physiognomy of Tertiary floras is thought to have been the result of changes in the inclination of the earth's axis.

The history of the development of the Arcto-Tertiary concept is reviewed, and the fundamental lack of evidence for this concept is shown. 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 appear to be of later Neogene origin and have been significant members of the warm temperate forests since that time. Some 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, western North America, and eastern North America.

grows under medium climatic conditions

Introduction

Of all 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 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 are only about 240 km (160 miles) 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, 1905, 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, keeping in mind that the "Arctic Miocene" was considered by Knowlton to be of Eocene age: "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, basing 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 (1913, 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 one of the 12 species that Hollick (1936, p. 23) listed as occurring in the Alaskan Tertiary and to be "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 cool temperate climate.

Mapping of the Gulf of Alaska Tertiary rocks was started by D. J. Miller in the 1940's and 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 and revised the stratigraphy and 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 partially 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 to be of late Eocene age and to be subtropical to tropical based on the physiognomic characters of the leaves. The Tokun-Katalla assemblages were also thought to be warm, although somewhat cooler than the Kushtaka.

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

The help of George Plafker has been invaluable in preparing the stratigraphic discussion. Harry D. MacGinitie and Howard E. Schorn, University of California (Berkeley), have given much time in discussing the floristic and vegetational implications of the Gulf of Alaska floras. D. M. Hopkins, U.S. Geological Survey, and Hugh Iltis, University of Wisconsin, have, through their critical review, assisted in the preparation of this report.

Physical stratigraphy

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. A detailed geologic map of this district is available (Miller, 1961a), from which the map shown here (fig. 2) has been adapted. The structure in this district is complex, but, despite the small scale thrusts and strongly folded beds (Miller, 1961a), 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.

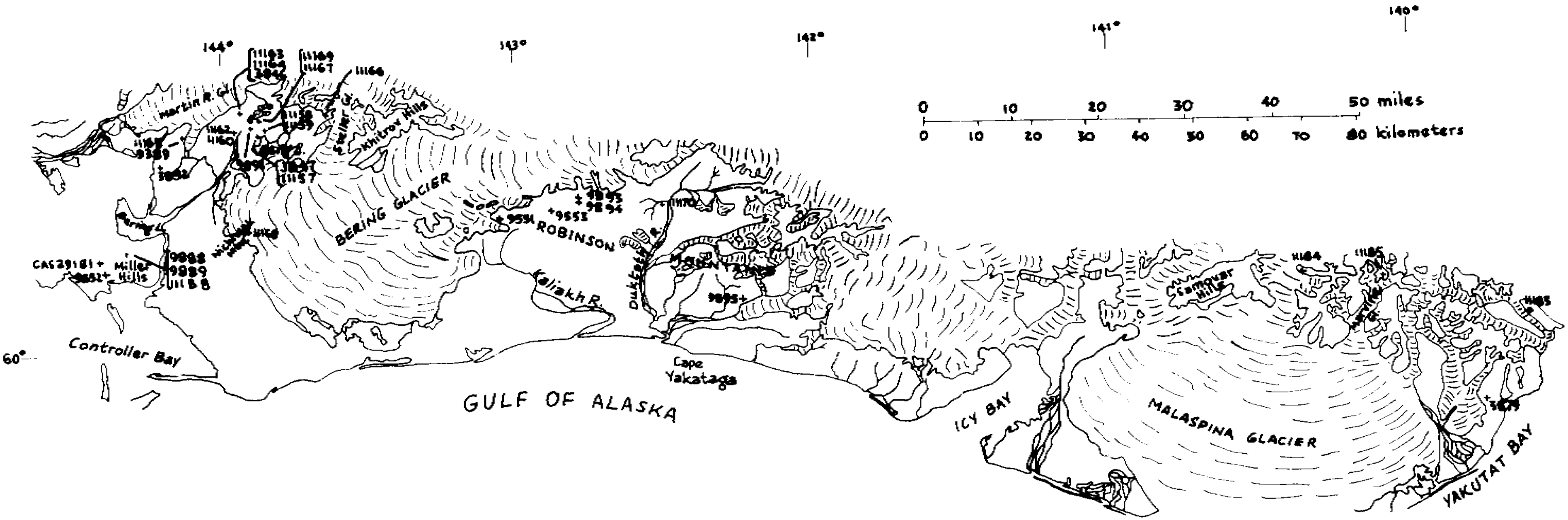

Figure 1.-- Map of the Gulf of Alaska region. Numbers represent plant localities.

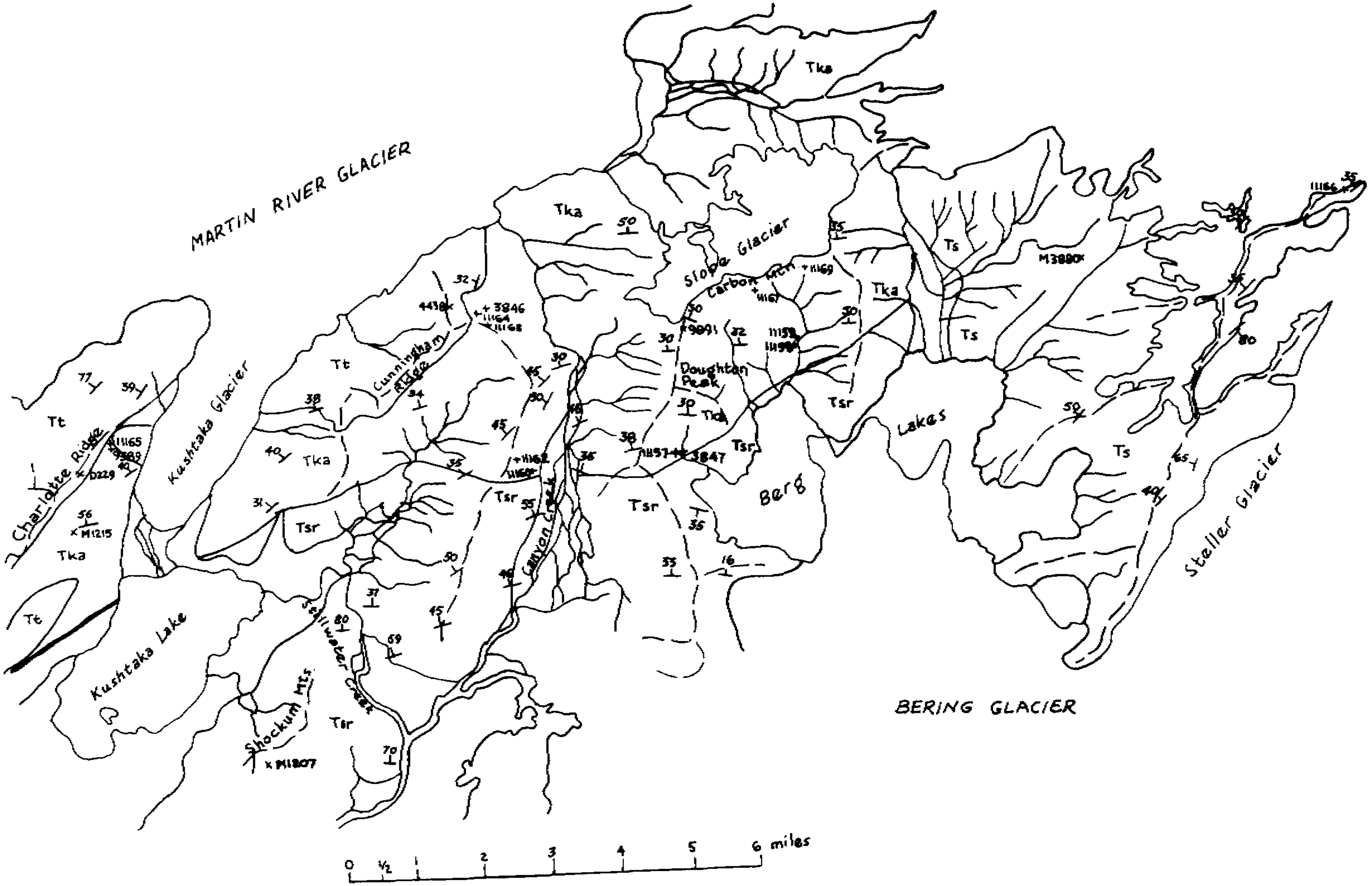

Figure 2.— Generalized geologic map of part of the Katalla district. Geology after Miller (1961a). Dashed lines show position of ridge crests. Ts = Stillwater and Kushtaka Formations undifferentiated, Tsr = Stillwater Formation, Tka = Kushtaka Formation, Tt = Tokun Formation, + = plant locality, x = mollusk locality.

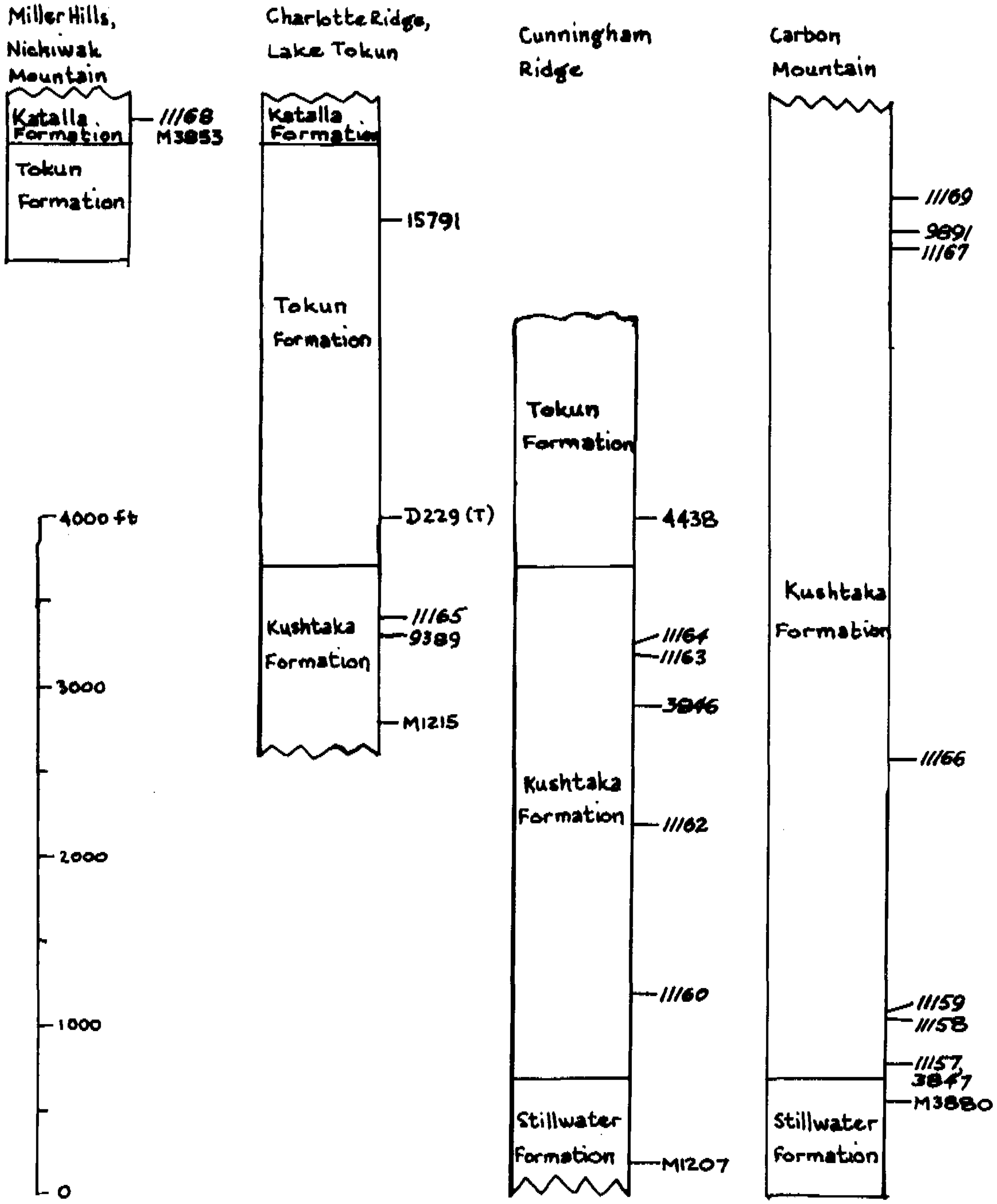

Figure 3.— Stratigraphic position of fossil plant localities in the Katalla district. Italicized numbers represent plant localities, romanized numbers represent mollusk localities.

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.

Katalla district

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 loc. 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 from locality 11166 are approximately 3,000 feet higher. 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 to 2,000 feet stratigraphically higher than localities 3847 and 11157, and about 3,000 feet stratigraphically 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 to 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

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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.

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 (1961, p. 1803) as of middle Eocene age. Thus the Stillwater Formation and possibly the lowest part of the 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, 11162) would also be of middle or late Eocene age.

In the upper part of the Kushtaka Formation 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, which rests conformably on the Kushtaka, marine mollusks have been collected. USGS Cenozoic locality 4438 contains *Perse washingtonensis* (Weaver), which indicates a Tejon (late Eocene) age (W. O. Addicott, oral commun., Sept. 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" 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 grounds 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 grounds. 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). That part of the Tokun 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 as young as Keasey age.

Katalla Formation.--The Katalla Formation appears to be entirely marine, and thus only a few localities have yielded plant megafossils. Most of these localities are in the Split Creek sandstone beds, the basal unit 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 the lower Lincoln index species Bruclarkia fulleri Durham (W. O. Addicott, written commun., Oct. 10, 1968). Elsewhere in the district, the Split Creek sandstone 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 sandstone at localities 3705, 9552, 9988, 9989, and 9990.

The overlying Basin Creek beds of the Katalla has yielded a very few leaves at localities 11181 and California Academy of Sciences locality 29181. The Basin Creek beds are obviously at least in part of Lincoln age, that is, middle Oligocene. This is also attested to by the molluscan fauna, which, according to Vokes (written commun., Jan. 12, 1946) is not younger than the Molopophorus gabbi zone; MacNeil (oral commun., Oct. 1968), however, considers part of the Basin Creek beds 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.

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 given 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 (determined by F. S. MacNeil, written commun., Dec. 20, 1961) Acila shumardi (Dall) and Boreoscala condoni cf. subsp. oregonense Dall. 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 (1957) measured approximately 9,000 feet of Kulthieth in this section, but the plant locality is farther downstream than the base of his 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 (Plafker, oral commun., Oct. 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, which 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 fall 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 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, which flows into Yakutat Bay, has provided a small collection (locality 3879) 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.

Poul Creek Formation.--Only two localities have produced plant megafossils from the Poul Creek. One locality (9895) is apparently in the lower part of the Poul Creek, but no mollusks have been collected in the area of the plant locality. 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.

Another locality (11182) has produced a single fruit of Juglans; the fruit was collected as float, but, according to Miller (written commun., May 25, 1961), the specimen probably came from the Poul Creek Formation.

Yakataga Formation.--Although plants are reported to be abundant at several localities in the Yakataga, only two collections have been made. Locality 11184 from the upper part of the Yakataga in the Pinnacle Hills occurs 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 of lithologic similarities of the plant-bearing sequence to the marine Yakataga elsewhere (Plafker, oral commun., Oct. 1968). This sequence occurs as a sliver along a fault, and cannot be definitely related by field relationships to the Tertiary section elsewhere in the Malaspina district.

Unknown unit.--Plants from locality 11185 came from a sliver along the same fault as locality 11183. No marine fossils occur in this patch 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 rest on the contained plants. The close stratigraphic relationships between some of the mollusk and plant localities also allows a better understanding of the age relationships between the marine megafossil chronology and some of the stages erected 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 appear to contain species definitely indicative of either of these two stages. The two upper stages--the Ravenian and the Kummerian--are represented, however. The Ravenian is probably largely equivalent to the poorly defined Transition "stage" (lower upper Eocene), as well as to the Tejon "stage" (upper Eocene). The Kummerian is probably coeval with the Keasey and lowermost part of the Lincoln "stages."

The unqualified use of terms such as middle and upper Eocene can be misleading because these terms have no universally accepted rigorous definition. On the Pacific coast of North America, the Domengine "stage" and the Transition and Tejon "stages" have generally been equated with the middle and late Eocene, respectively; the lower part of the Keasey "stage" has also generally been placed in the latest Eocene (Weaver and others, 1944). These "stages" are, of course, applicable primarily to beds containing invertebrate megafossils, but to date no type sections have been designated for these "stages" and the faunas have not been studied in sufficient detail to delimit the stratigraphic ranges of many of the species.

Except for some minor departures, the epochal and subepochal boundaries of the marine megafossil geochronology on the Pacific coast will be used in this report. The Ravenian and its probable marine equivalents, the Transition and Tejon "stages," are considered to be of late Eocene age. The Kummerian and its probable marine equivalents, the Keasey and lowermost part of the Lincoln (Molopophorus stephensoni zone) "stages," are considered to be of early Oligocene age; this is a departure from the suggested ages of Weaver and others (1944), because they assign the lower part of the Keasey to the latest Eocene and the M. stephensoni zone to the middle Oligocene. Elsewhere (1968, p. 12) I have discussed the reasons for placing the Keasey "stage" entirely within the Oligocene. The M. stephensoni zone has been considered by some molluscan workers to be of early Oligocene age (H. E. Vokes, written commun., Jan. 12, 1946); because the flora of this zone cannot at this time be distinguished from that of the Keasey, I have adopted Vokes' opinion. The remainder of the Lincoln "stage" of Weaver and others (1944) is considered to be of middle Oligocene age, and the Echinophoria rex zone of the Blakeley "stage" is accepted as upper Oligocene. The Oligocene-Miocene boundary and Oligocene subepochs adopted in this report are probably different from those of the mammalian paleontologists, who would place the boundary about a stage higher.

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 a three-fold 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 Hemitelia pinnata MacG. and of Goweria dilleri at locality 3847 (see table 1). Locality 3846 has also yielded representatives of "Cryptocarya" presamarensis, a species that has previously been found in the middle Ravenian and younger rocks, thus indicating 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 aff. A. longiflorum is apparently restricted to the upper Fultonian in the Puget Group, but thus far it has been found at only a single locality there. Zizyphus aff. Z. fungi, on the other hand, is known at two lower Ravenian localities, and "Laurus" similis is known in the Puget Group from early Ravenian and younger beds. Both Goweria n. sp. and Phytocrene aff. P. blancoi, in addition, 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, 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 (early late Eocene) age.

The age of 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 n. sp. 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 poorly known 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, which 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 occurrence of Celastrus comparabilis and Goweria n. sp. also indicates a probable correlation with the lower Kushtaka, that is, an 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 on an assemblage (Cashman) from what was thought on stratigraphic evidence to be beds equivalent to the lower part of the type section. Although almost all the species known from the type section of the upper Ravenian are also known from the Cashman assemblage, the latter 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 largely 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.

Based largely on an analysis of other late Eocene-early Oligocene assemblages--many whose ages are radiometrically controlled--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 upper 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 upper Ravenian 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" thus implies 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 represent the middle Ravenian. Assemblages from localities 3842, 9389, 11164, and 11165 all come from about the same stratigraphic interval, a short distance beneath the base of the Tokun Formation. Critical elements in these assemblages are Allantodiopsis pugetensis, which has its highest occurrence in the middle Ravenian, and "Artocarpoides" [Dicotylophyllum] kummerensis, which has its lowest occurrence in the middle Ravenian, and Calkinsia n. sp., Carya cashmanensis, Pterocarya pugetensis, and Dryophyllum pugetensis, which indicate either a middle or late Ravenian age. The vegetational analysis indicates a vegetation type more similar to that of the middle than the upper Ravenian. The conclusion that this part of the Kushtaka is of middle Ravenian age is also indicated 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

Table 1.--Checklist of megafossil plants from the Kushtaka, Katalla, and Kulthieth Formations.

	Kushtaka Formation																	Katalla Formation					Kulthieth Formation							Poul Creek Formation
Species	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	9551	9553	9893	9894	11189	9895
Anemia n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Anemia? sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lygodium n. sp.	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemitelea pinnata	-	-	-	-	x	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Allantodiopsis pugetensis	-	-	-	x	-	-	x	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Dryopteris sp. [Asplenium alaskana]	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Woodwardia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glyptostrobus sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Phoenicites sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabalites spp.	-	-	x	-	x	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Populus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carya cashmanensis	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Engelhardia sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juglans sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platycarya sp. [Planera pseudobrauni]	x	-	-	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Pterocarya pugetensis	-	-	-	-	-	-	-	-	-	-	x	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus cuprovallis	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus n. sp.	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Alnus n. sp.	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Alnus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alnus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Betula sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryophyllum pugetensis	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fagus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x
Girroniera sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Girroniera sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Ulmus sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tetracentron sp. [Cercidiphyllum piperoides]	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Magnolia reticulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Illicium sp.	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anamirta n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Calkinsia n. sp.	-	x	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diploclisia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Hypserpa? sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Limacia n. sp.	-	-	x	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
aff. Tinomiscium sp. [Hampea conditionalis]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Pycnarrhena sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Knema sp.	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myristica sp.	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cananga sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Dasymaschalon sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cinnamomophyllum sp.	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cinnamomophyllum n. sp. [Neolitsea lata]	x	x	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-
Laurophyllum sp. [Persea praelingue]	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp. [Cryptocarya presamarensis]	-	x	-	-	-	-	-	x	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp. [Nectandra presanguinea]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum n. sp.	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp. [Laurus similis]	-	x	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laurophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corylopsis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liquidambar? sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eucommia sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platanus n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Prunus sp. [Euonymus nevadensis]	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorbus n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caesalpinites sp.	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caesalpinites sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euodia n. sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Luvunga sp. [Persea spatiosa]	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melanorrhoea sp. [Semecarpus alaskanus]	x	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Anacardiaceae, genus?	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ilex n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Celastrus comparabilis	x	-	x	x	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-
Goweria n. sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goweria dilleri	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paleophytocrene sp. [Carpolithes elytraeformis]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Phytocrene n. sp.	x	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phytocrene sordida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Pyrenacantha sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Stemonurus n. sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhamnus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sageretia sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zizyphus n. sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Allophylus n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Allophylus wilsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	x	-	-	-	-	x	x	-	-	-	-
Allophylus n. sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sapindus? sp.	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Meliosma n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Meliosma n. sp.	-	-	x	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vitis sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Tilia n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Willisia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saurauia sp.	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Theaceae, genus?	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Parashorea sp. [Rhamnus pseudogoldianus]	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barringtonia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Alangium n. sp.	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alangium sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eugenia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Eugenia? sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrtaceae, genus?	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mastixia sp. [Cornus irregularis]	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clethra sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Clerodendrum sp.	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holmskioldia speiri?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Macclintockia pugetensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x	-	x	x	x	-	-	x	x	x	x	x	-
Macclintockia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicotylophyllum n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicotylophyllum sp. [Artocarpoides kummerensis]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

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 a single species in common to 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 "*Celastrus*" *nevadensis*. 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

Macclintockia pugetensis was originally thought to be restricted to the upper part of the Kummerian and was one of the primary reasons for distinguishing an upper from a lower Kummerian. 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 lower and upper Kummerian 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. It seems probable that this was an erroneous interpretation. "*Hyperbaena*" *dilleri* and *Allantodiopsis pugetensis* were the only basis for placing the Comstock flora in the Ravenian. As now defined, the typical Ravenian species of *Calkinsia* is *C.* n. sp., which is morphologically intermediate between the Fultonian *C. pugetensis* and "*Hyperbaena*" *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 *dilleri* lineage. 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*, "*Mallotus*" [*Platanus*] *comstocki* (= *Platanus* n. sp. of Wolfe, 1968), and "*Artocarpoides*" *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 "*Cercidiphyllum*" *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--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 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 is in accordance with the indications of the marine megafossils that have been collected from the upper Kulthieth.

Post-Kummerian

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 (Plafker, oral commun., Oct. 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 Formation, which is here 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 (Plafker, oral commun., Oct. 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 Formation; 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 Formation (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 may, therefore, 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 an understanding of Alaskan Tertiary stratigraphy is 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 has since been excluded from the Seldovian Stage (Wahrhafting 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 is here proposed as a provincial stage for plant-bearing rocks the same age as those in the type section in the Kootznahoo Formation. The type section is designated as the rocks 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* sp. ["*Juglans*" *orientalis* MacG.]
        - Fagales
            - Betulaceae
                - *Alnus evidens* (Holl.) Wolfe
                - *Alnus carpinoides* Lesq.
            - Fagaceae
                - *Fagus* sp.

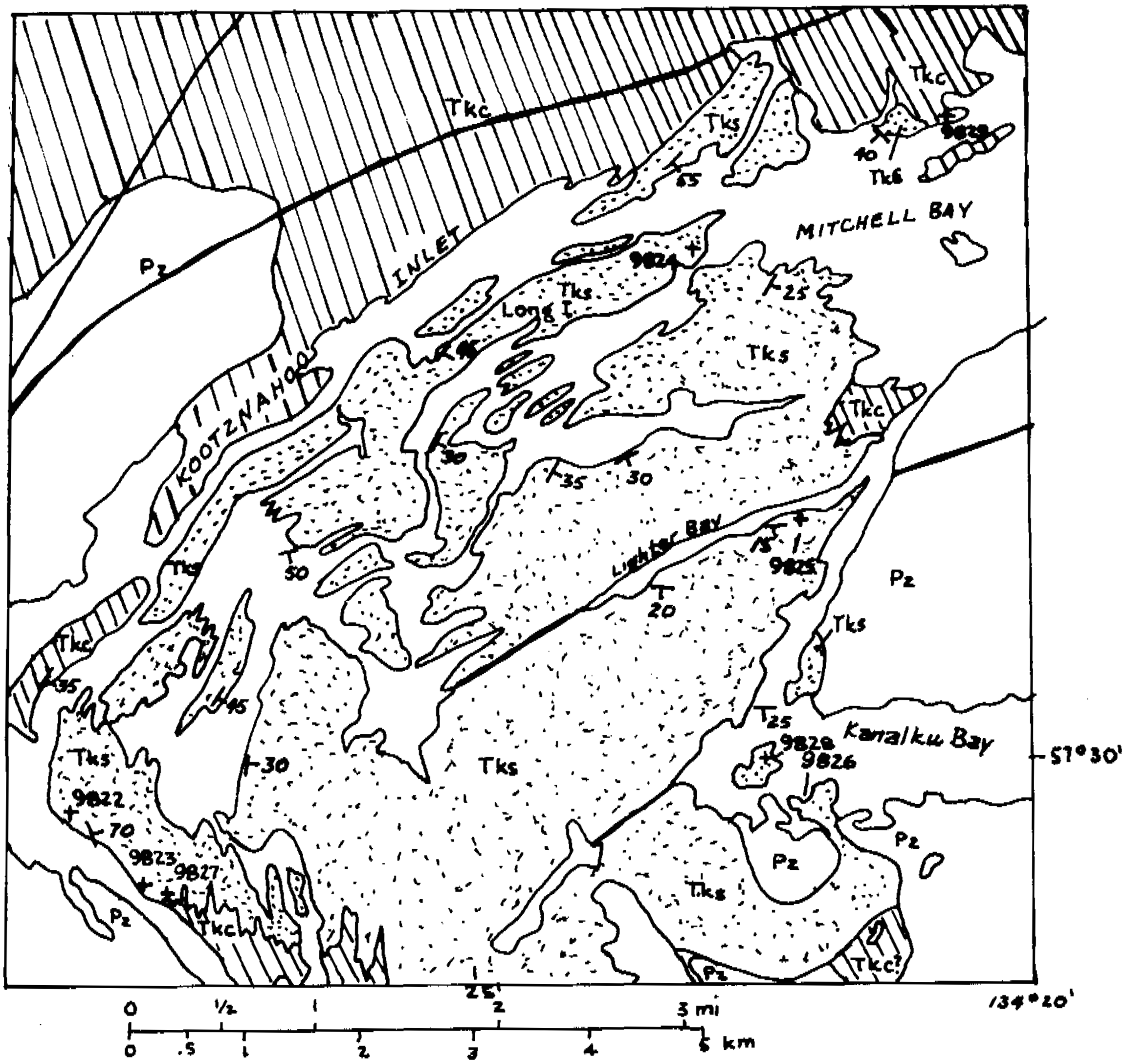

Figure 4.-- Generalized geologic map of part of Kootznahoo Inlet. Data from Lathram and others (1965). Tks (stippled) is the sandy and silty part of the Kootznahoo Formation; Tkc (lined) is the conglomeratic part. Pz represents undifferentiated Paleozoic rocks. Heavy lines represent faults. Crosses represent plant localities.

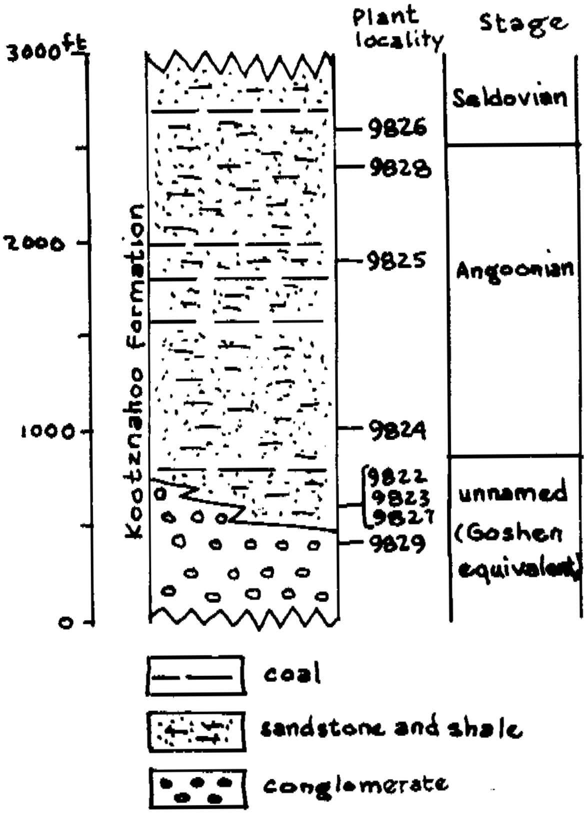

Figure 5.-- Generalized stratigraphic section of the type section of the Angoonian Stage.

Angiospermae (continued)
Dicotyledonae (continued)
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.
Willisia sp. [Celtis obliquifolia Chan.]
Incertae sedis
Ficus alaskana Newb.

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 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, that is, about the same as today in northeastern United States.

Age.--Only one Alaskan Angoonian assemblage is known in definite stratigraphic relationship 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 here 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 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. In this report, 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, "Ocotea" eocernua, Platanus n. sp., "Tetracera" oregona, and Willisia sp. 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 "Ocotea" nor the "Tetracera" are known in conterminous United States in beds younger than middle Oligocene, whereas the Cercidiphyllum and Willisia make their first appearance in beds of middle Oligocene age. The assemblage from locality 9826, which is stratigraphically above the type section of the Angoonian, includes Alnus barnesi, Fagus antipofi, and Quercus furuhjelmi. This assemblage is thus of Seldovian age, which is considered to be of early to middle Miocene age.

The Angoonian Stage is separated from the Kummerian by a 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 (Angoonian) equivalents--of the Kenai Formation are of early Oligocene age; previously they had been referred to the Eocene (Chaney, 1964). This opinion is contrary to that of Wolfe and others (1966) who have referred these floras to the late Oligocene(?) and early to middle Miocene. Chaney's 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 figure 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, in conformity with evidence from the middle Eocene Foraminifera from the overlying beds (Burk, 1965, p. 113). Chaney also included in his correlation, however, plant assemblages that, on marine molluscan evidence, are of middle Miocene age and some that are of late Miocene-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, and I will, therefore, examine the evidence he cites in detail. Chaney (1967, p. 228) lists 12 genera that he thinks are common to the Seldovian and 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,

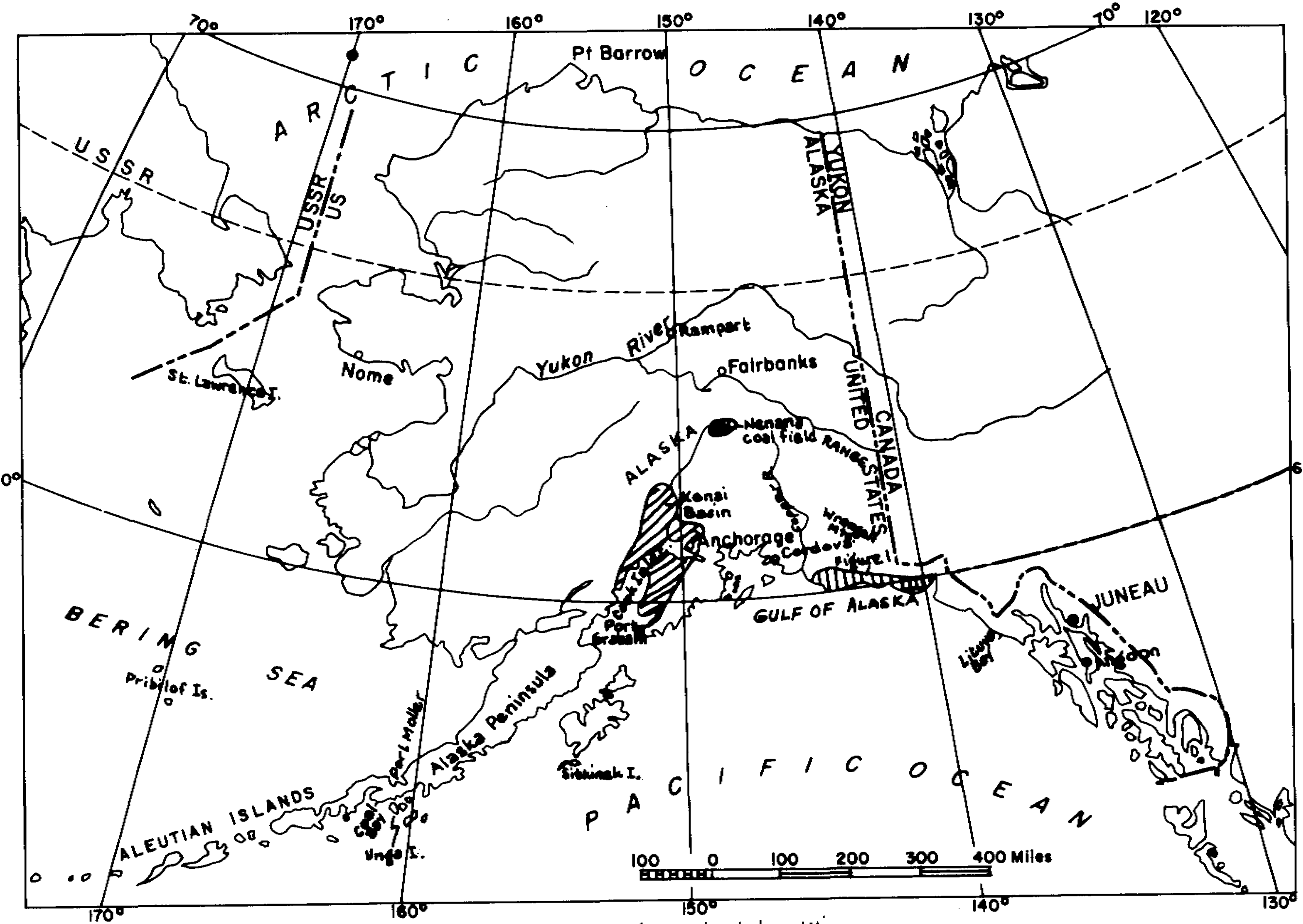

Figure 6. Map of Alaska showing areas of important Tertiary plant localities.

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-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* (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 could be betulaceous, but 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. These specimens have, however, 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 thin conspicuously. 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 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 entire 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 the 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 Mio-Pliocene age based on physical stratigraphy and marine mollusks.

Of the 12 genera supposedly 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 three 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 Mio-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 approximately 3,500 feet altitude. 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). As shown later, the tropical lowland assemblages of early late 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 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 (Steels Crossing)--can be highly misleading in regard to 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 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. Despite the strong vegetational 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.

Vegetational analysis of several assemblages in a given stratigraphic section can probably yield some reliable conclusions as to age. The reliability hinges, however, on the acceptance of the concept of strong climatic fluctuations, particularly during the Paleogene. As Devereux (1967) has pointed out, it is improbable that a major climatic deterioration that can be demonstrated in one region was primarily parochial. In the section on Paleogene climates, I discuss the probability that major climatic fluctuations in the English Eocene approximately match those in western North America if the correlations based on marine megafossil invertebrates are accepted.

The Seldovian and Angoonian 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 is due to a difference in age.

An apparent disagreement exists over the age of fossil plants collected from the Tolstoi Formation at Coal Bay on the Alaska Peninsula. I considered the plants to be of late Oligocene or early to middle Miocene in age, that is, of Seldovian age as this term was used by Wolfe and others (1966). 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 represent broad-leaved deciduous forest. As elsewhere in Alaska, broad-leaved deciduous forests of Oligocene age are in the later part of that epoch.

A flora of the same composition as the Angoonian and Seldovian floraa 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 a Blakeley 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 most 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) that the Seldovian Stage is mostly 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-early Pliocene age (Burk, 1965). A Homerian assemblage from the Alaska Range section has a minimal potassium-argon age of 8 million years, an age not inconsistent with a late Miocene age (Wahrhafting and others, 1969, p. 27-28). 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, in press). 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 iniicate 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), Chelebaeva (1967), and Sinelnikova and others (1967), 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 are I think obligated to present both detailed alternative systematic treatment of the plant megafossils and detailed knowledge of the physical stratigraphy of the plant-bearing beds. Opinions based on a lack of detailed taxonomic work and a lack of knowledge of paleobotanical and stratigraphic literature can not be of service to biostratigraphy or to botany.

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 greater confidence because of our considerable knowledge of Neogene assemblages. The lineage, for example, that has produced the modern *Alnus 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

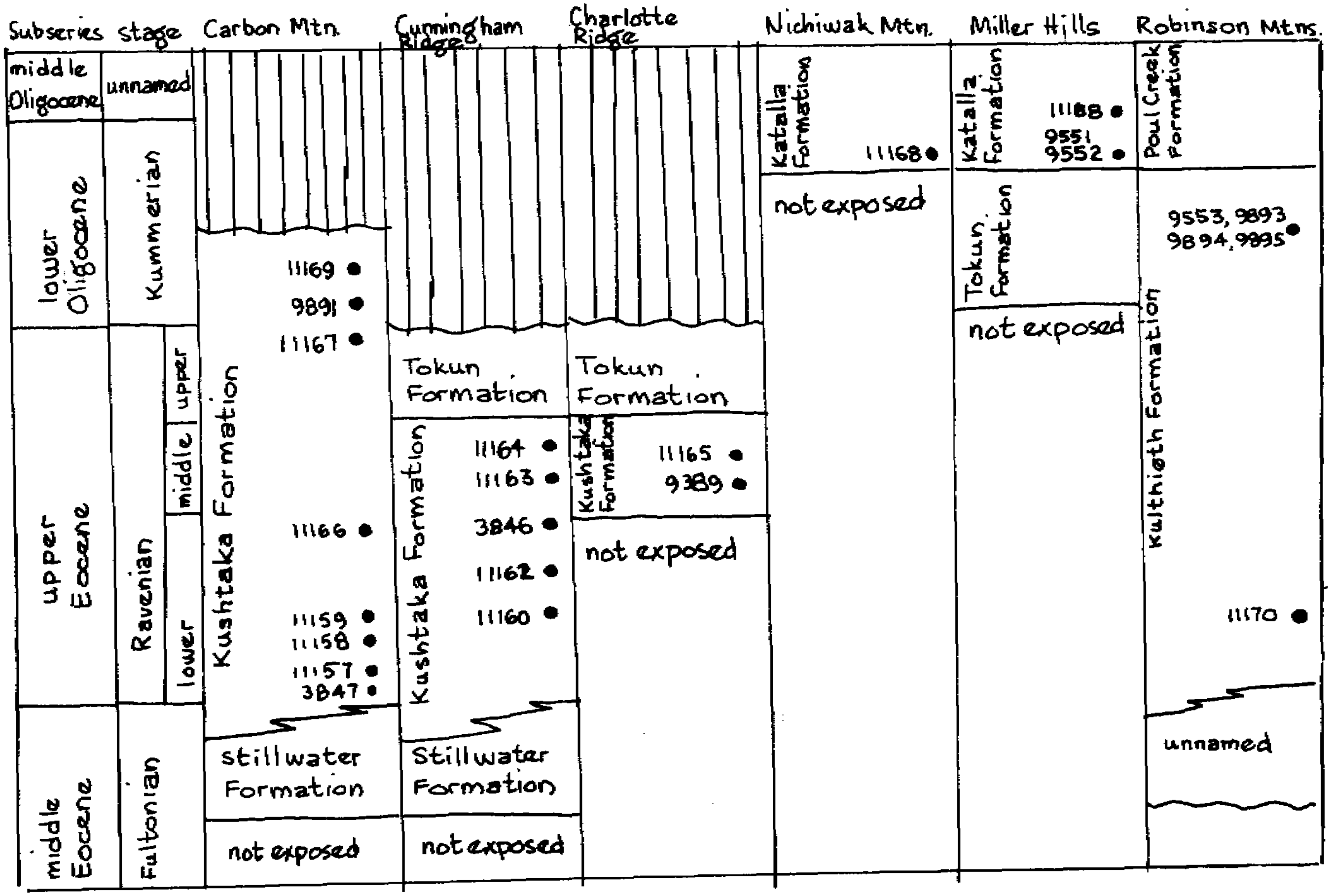

Figure 7.-- Correlation of Paleogene formations in the Katalla and Yakataga districts. Numbers represent plant localities.

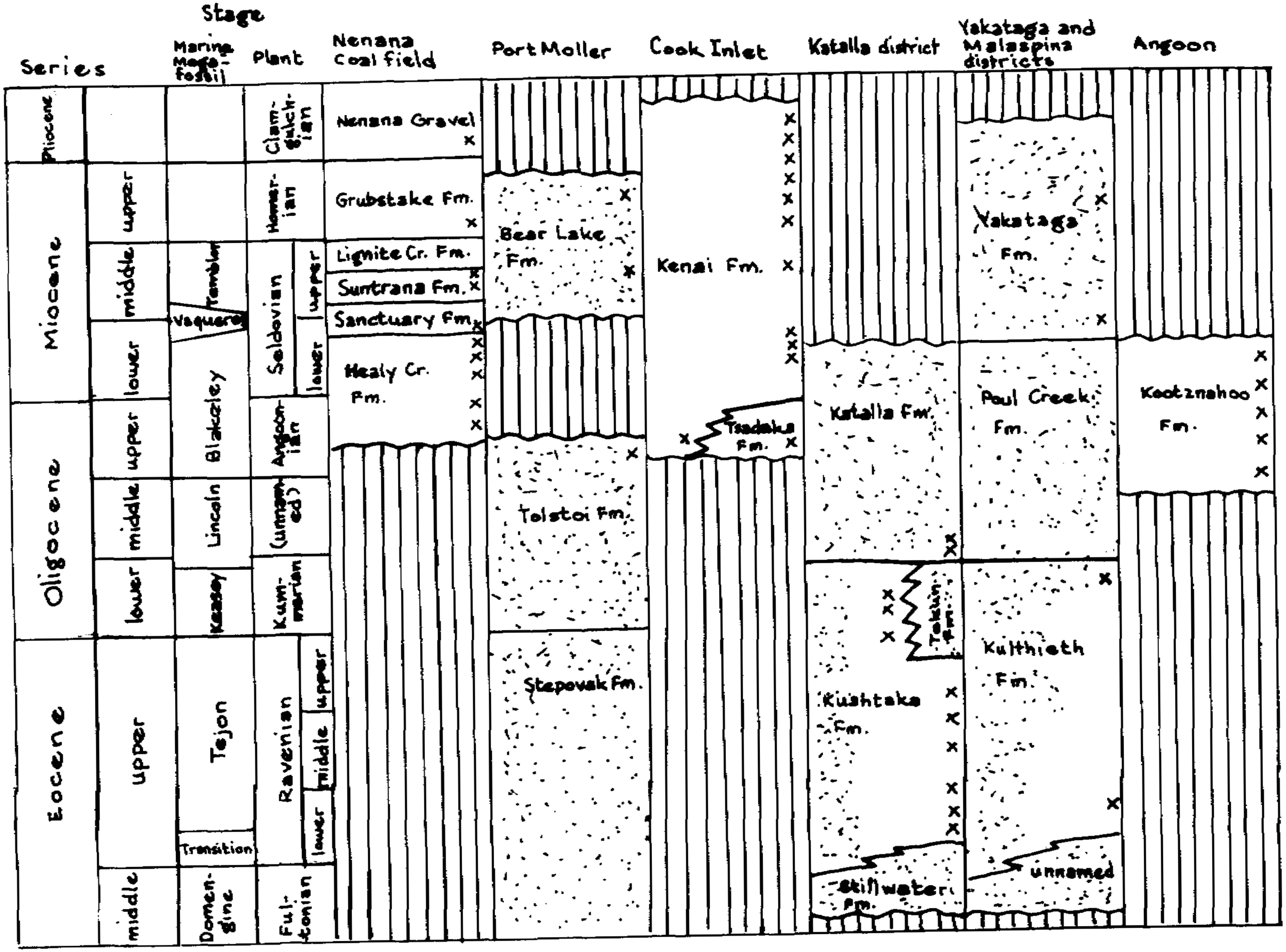

Figure 8.— Correlation of some Alaskan Tertiary formations. An "x" denotes approximate stratigraphic position of plant assemblage(s); stippling denotes rocks that are largely or entirely marine.

(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. The history of various lineages is, therefore, 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 speculatory. 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 have an inherent dislike for any ideas that indicate that tolerances of members of a particular taxonomic category have 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 abundantly represented in the early Eocene London Clay (Reid and Chandler, 1933); Platycarya has, on Taiwan and mainland China, an opportunity to extend its range downslope into the Paratropical Rain forest. Similarly Nipa has an opportunity to extend its range northward into lowland Taiwan. The conclusion 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 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 explanation hardly seems appropriate inasmuch as Nipa fruits are widely dispersed today in warm marine waters; it seems clear that today it is the environmental tolerance of the adult sporophyte on land that limits the distribution of Nipa.

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 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.

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 predominant 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 twinners, 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 of 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. This is difficult to evaluate in some instances because of the type of preservation. In most instances, 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 habitates and 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.

Within a given vegetational type in a limited region, the leaf margin percentage does not appear to vary greatly, even at different altitudes. Two examples are cited in support of this contention. Data compiled on the vegetation of Taiwan are given in table 2. Percentages of entire-margined species were compiled for each 200 m interval for species whose altitudinal limits are given by Li (1963). The interval from 400 to 600 m represents the ecotonal region between the lowland Paratropical Rain forest, which generally extends up to 500 m, and the Subtropical oak-laurel forest. The percentage for the 600 to 800 m interval is greatly influenced by the Sun-Moon Lake area; this upland lake (750 m) is connected with the lowlands by a broad valley, up which extend many fundamentally tropical species to their highest altitude in Taiwan. The Subtropical forest, once the ecotonal region is passed, has a very uniform percentage through an interval of 1,200 m (about 3,700 feet). A second example is taken from the vegetation of Oregon, based on altitudinal ranges given by Hitchcock and others (1959, 1961, 1964). The percentage for species that occur below 500 m and the percentage for those that occur above 500 m are almost identical (table 3).

A more significant effect on leaf margin percentages is the habitat, that is, whether a species is typically a slope or a stream- or lake-side species. Table 3 indicates that vegetation in fluviatile or lacustrine habitats, whether trees or shrubs, has consistently lower percentages of entire-margined species. This is particularly significant in the application of leaf margin analyses to fossil assemblages: MacGinitie

Table 2.--Relationship between leaf margins and altitude in the modern tropical and subtropical vegetation of Taiwan. Data compiled from Li (1963).

Altitudinal interval (m)	Vegetation	Percent entire-margined species
1,800 - 2,000	subtropical	40.5
1,600 - 1,800	subtropical	41.2
1,400 - 1,600	subtropical	39.8
1,200 - 1,400	subtropical	40.5
1,000 - 1,200	subtropical	41.8
800 - 1,000	subtropical	44.8
600 - 800	subtropical	48.0
400 - 600	subtropical-paratropical	47.0
200 - 400	subtropical-paratropical	47.5
0 - 200	paratropical	63.5

Table 3.--The effect of habitat on leaf margins. Data based on Hitchcock and others (1959, 1961, 1964).

	Percentages of species that have entire-margined leaves		
Habitat	Trees	Shrubs	Ligneous
West of Cascades, below 500 m			
Lacustrine or fluviatile	33%	25%	27%
Slope or woodland	40	43	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

(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 percentages 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 lake-side 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.

The probable over-representation 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 analysis, terms such as "tropical", "subtropical", "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 use terms such as "subtropical forest" in widely differing manners.

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 months means of less than 16°C. Regions that have tropical climates under the meteorological definition and for which leaf margin percentages have been compiled (data after Bailey and Sinnott, 1916 and Brown, 1919):

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. 86) 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 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 appears to be limited poleward by the presence of frost; for example, the Paratropical Rain forest of Taiwan has been subjected to -1°C only once as far as the records are known (Li, 1963, p. 6) and it is unknown how wide spread this frost was in Taiwan. The mean annual temperature ranges from about 22°C up to about 25°C. The mean cold month temperature has a mean of about 15°C to 25°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 fot the precipitation regime, to some of the monsoonal forests of the tropical region. Leaf margin percentages for the Paratropical Rain forest vary from 57 up to 75 (table 4). 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" in instances in which a large part of the vegetation is deciduous; such refinements are probably not readily recognizable in relation to fossil assemblages.

Note that the leaf margin percentages of vegetation of tropical mountains (Submontane Rain forest, Montane Rain forest) and of the Paratropical Rain forest have about the same range. This indicates some similarity of environmental conditions, at least those that affect leaf margins. Most Tertiary leaf assemblages, however, come from rocks that are thought to have been deposited at low elevations, and thus the term Paratropical Rain forest is appropriate for those lowland, broad-leaved evergreen assemblages that have leaf margin percentages in the range of 57 to 75.

Some workers may object to the introduction of 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, 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 a single tree level, lacks a diverse and abundant woody liane element, and buttressing is absent. Despite the fact that both Paratropical Rain and Subtropical forests are dominately 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.

(Page 43 follows)

Table 4.--Percentages of species that have entire margins in some modern floras.

Flora	Percentage	Vegetation
Brazil, lowland	88	Tropical Rain forest
Malaya	86	Tropical Rain forest
Philippine Islands, 200 m	82	Tropical Rain forest
Ceylon, lowland	81	Tropical Rain forest
Manilla	81	Tropical Rain forest
East Indies	77	Tropical Rain forest
Philippine Islands, 450 m	76	Tropical Rain forest
West Indies	76	Tropical Rain forest
Hawaii, lowland	75	Paratropical Rain forest
Ceylon, upland	73	Submontane Rain forest
Philippine Islands, 700 m	72	Submontane Rain forest
Hong Kong	72	Paratropical Rain forest
Hainan, lowland	70	Paratropical Rain forest
Philippine Islands, 1,100 m	69	Montane Rain forest
Taiwan, 0-500 m	61	Paratropical Rain forest
Hawaii, upland	57	Montane Rain forest
Hainan, upland	55	Subtropical forest
Taiwan, 500-2,000 m	45	Subtropical forest
Mixed Mesophytic forest, China	30	Warm temperate forest

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 planta are important constituents of this forest) that exists under moderate frost. Mean annual temperature ranges from about 15°C to 19°C and the mean of the coldest month ranges from about 6°C to 10°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°C to 16°C and the mean of the coldest month ranges from about -3° C to 5°C. Leaf margin percentages vary from about 20 up to 35. 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 (lower upper Eocene) flora.

- Filicineae
  - Filicales
    - Schizaeaceae
      - *Anemia* n. sp.
    - Cyatheaceae
      - *Hemitelia pinnata* MacG.
    - Aspidaceae
      - *Allantodiopsis pugetensis* Wolfe
      - *Dryopteris* sp. [*Asplenium alaskanum* Holl.]
- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - *Glyptostrobus* sp.
- Angiospermae
  - Monocotyledonae
    - Principes
      - Palmae
        - *Sabalites* sp.
  - Dicotyledonae
    - Juglandales
      - Juglandaceae
        - *Platycarya* sp. [Ulmus pseudobrauni Holl.]
    - Fagales
      - Betulaceae
        - *Alnus* n. sp. A
        - *Alnus* n. sp. B
    - Urticales
      - Ulmaceae
        - *Girroniera* sp.
        - *Girroniera* sp.

- Angiospermae (continued)
  - Dicotyledonae (continued)
    - Ranales
      - Tetracentraceae
        - *Tetracentron* sp. [*Cercidiphyllum piperoides* (Lesq.) LaM.]
      - Menispermaceae
        - *Anamirta* aff. *A. cocculus* Wight and Arn.
        - *Calkinsia* n. sp.
        - *Cocculus* sp.
        - *Diploclisia* sp.
        - *Limacia* aff. *L. oblonga* Miers
        - aff. *Tinomiscium* sp. [*Hampea conditionalis* Holl.]
        - *Pycnarrhena* sp.
      - Illiciaceae
        - *Illicium* sp.
      - Anonaceae
        - *Cananga* sp.
        - *Dasymaschalon*? sp.
      - Myristicaceae
        - *Knema* sp.
        - *Myristica* sp.
      - Lauraceae
        - *Cinnamomophyllum* sp. [*Neolitsea lata* MacG.]
        - *Laurophyllum* sp. [*Cryptocarya presamarensis* Sanb.]
        - *Laurophyllum* sp. [*Laurus similis* Knowlt.]
        - *Laurophyllum* sp.
        - *Laurophyllum* sp.
    - Rosales
      - Leguminosae
        - *Caesalpinites* sp.
    - Geraniales
      - Rutaceae
        - *Euodia* aff. *E. crassifolia* Merr.
        - *Luvunga* sp. [*Persea spatiosa* Holl.]
    - Sapindales
      - Anacardiaceae
        - *Melanorrhoea* sp. [*Semecarpus alaskana* Holl.]
      - Celastraceae
        - *Celastrus comparabilis* Holl.
      - Icacinaceae
        - *Goweria* n. sp.
        - *Goweria dilleri* (Knowlt.) Wolfe
        - *Paleophytocrene* sp. [*Carpolithes elytraeformis* Holl.]
        - *Phytocrene* aff. *P. blancoi* (Aza.) Merr.
        - *Phytocrene sordida* (Lesq.) MacG.
        - *Pyrenacantha* sp.
        - *Stemonurus* aff. *S. scorpiodes* Becc.
      - Sapindaceae
        - *Allophylus* n. sp.

- Angiospermae (continued)
  - Dicotyledonae (continued)
    - Sapindales (continued)
      - Sabiaceae
        - *Meliosma* aff. *M. pungens* Walp.
        - *Meliosma* sp.
    - Rhamnales
      - Rhamnaceae
        - *Sageretia* sp.
        - *Zizyphus* aff. *Z. fungi* Merr.
      - Vitaceae
        - *Vitis* sp.
    - Parietales
      - Actinidiaceae
        - *Saurauia* sp.
      - Dipterocarpaceae
        - *Parashorea* sp. [*Rhamnus pseudogoldianus* Holl.]
    - Myrtiflorae
      - Barringtoniaceae
        - *Barringtonia* sp.
      - Alangiaceae
        - *Alangium* aff. *A. longiflorum* Merr.
        - *Alangium* sp.
      - Myrtaceae
        - *Eugenia* sp.
    - Umbelliflorae
      - Cornaceae
        - *Mastixia* sp. [*Cornus irregularis* Holl.]
    - Ericales
      - Clethraceae
        - *Clethra* sp.
    - Tubiflorae
      - Verbenaceae
        - *Clerodendrum* sp.

The known flora of this substage in Alaska is diverse despite the small size of the collections. Altogether at least 68 species are represented, although only 57 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 and represented 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.

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 the Tropical Rain forest:

Anamirta
Limacia
Pycnarrhena
Knema
Myristica
Euodia
Luvunga
Celastrus
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 (indeed, this 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 Hong Kong and that for the Paratropical Rain forest of Taiwan.

In leaf size and foliar organization (table 5), the Alaskan lower Ravenian assemblage compares well with the Submontane Rain forest of the Philippine Islands (Brown, 1919), particularly if it is kept in mind that leaves of larger size-classes are under-represented 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.

Comparisons of the leaf size-classes of the Alaskan early Ravenian assemblage to 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 Tropical 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 6 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 sq mm) leaves that Raunkiaer included in his mesophyll size-class (as used elsewhere in this report, mesophyllous is used in accordance with Raunkiaer's original definition). Omitted from table 6 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 both tropical and 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 and, as elsewhere in the paratropical regions, the mean annual temperature ranges from about 22°C to 25°C. 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

Table 5.--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	62	65	36	42
Alaskan middle Ravenian	37	54	50	45
Alaskan late Ravenian	20	20	86	91
Alaskan Kummerian	26	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

Table 6.--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
Tropical 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	5-15
Submontane Rain forest	Simple Notophyll Vine forest	0-30	55-70	0-40
Montane Rain forest	Microphyll Mossy thicket	0	0	100
Paratropical Rain forest	Complex Notophyll Vine forest	15-30	50-70	10-20

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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, which development today occurs in the meteorological tropics. This suggestion has even more validity if, as suggested previously, the larger size-classes are under-represented 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* sp., *Luvunga* sp., *Phytocrene* spp., *Parashorea* sp., and *Alangium* sp. 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* sp., and *Phytocrene* sp., indicate that these plants were most probably members of the lower stories of the forest. Not as elongated are the drip-tips of *Allophylus* sp., *Luvunga* sp., *Stemonurus* sp., *Phytocrene sordida*, and "*Rhododendron*" *crassum*; these species could presumably have been members of more upper stories. Species such as *Euodia* sp. would more probably have been members of the upper 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) are *Anamirta* sp., *Cocculus* sp., *Diploclisia* sp., aff. *Tinomiscium* sp., *Phytocrene* sp., and *P. sordida*. Other species of genera whose extant members are exclusively lianes are *Limacia* sp., *Pycnarrhena* sp., *Luvunga* sp., *Celastrus conditionalis*, *Pyrenacantha* sp., and *Vitis* sp. The tribe Phytocreneae is also today composed exclusively of climbers, and hence *Goweria* sp., *G. dilleri*, and *Paleophytocrene* sp. 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 is a strong indication that the plants that bore them were evergreen.

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 7 and 8 are presented. The correlation, however, between representation of large organs and representation of species in the forest

Table 7.--Numerical abundance of plant megafossils from Alaskan lower Ravenian.

Species	11157 3847	11159 11158	11160 11161	11166	3846	11170	3879	Total	Percent
Limacia sp.	--	46	--	2	--	--	--	48	9.6
Celastrus comparabilis	4	20	--	5	1	17	1	48	9.6
Allophylus sp.	--	--	--	1	--	39	--	40	8.0
Alnus n. sp. A.	--	22	--	--	--	17	--	39	7.8
Platycarya sp.	6	--	--	--	--	31	--	37	7.4
Meliosma aff. M. pungens	--	--	--	--	--	28	--	28	5.6
Vitis sp.	--	--	--	19	--	1	--	20	4.0
Sabalites sp.	--	4	14	--	--	1	--	19	3.8
Phytocrene sp.	1	13	--	5	--	--	--	19	3.8
Eugenia sp.	--	--	--	--	--	19	--	19	3.8
Dryopteris sp.	10	--	--	--	1	--	6	17	3.4
Clethra sp.	--	1	--	2	1	10	--	14	2.8
"Laurus" similis	4	--	9	--	--	--	--	13	2.6
Alnus n. sp. B.	8	1	--	--	--	--	--	9	1.8
Parashorea sp.	9	--	--	--	--	--	--	9	1.8
Clerodendrum sp.	--	8	--	--	--	--	--	8	1.6
Meliosma aff. M. pendens	--	5	--	3	--	--	--	8	1.6
Allantodiopsis pugetensis	--	4	--	1	1	--	1	7	1.4
Melanorrhoea sp.	1	3	--	--	2	1	--	7	1.4
"Cryptocarya" presamarensis	--	--	--	--	5	--	--	5	1.0
Glyptostrobus sp.	--	--	--	--	--	--	4	4	0.8
Alangium aff. A. longiflorum	1	--	--	2	--	--	1	4	0.8
Hemitelea pinnata	--	--	2	--	1	--	--	3	0.6
Myristica sp.	3	--	--	--	--	--	--	3	0.6
Anamirta sp.	--	--	--	--	--	3	--	3	0.6
"Neolitsea" latum	3	--	--	--	--	--	--	3	0.6
Luvunga sp.	2	--	--	1	--	--	--	3	0.6
Euodia sp.	--	3	--	--	--	--	--	3	0.6
Barringtonia sp.	--	--	--	--	--	3	--	3	0.6
Others	9	21	1	10	2	16	3	62	12.4
Totals	61	151	26	51	14	181	16	500	100.6

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 as compared to the vegetation, and the extension to fossil Quaternary pollen and megafossil assemblages of these data. I am in agreement 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.

Table 8.--Numerical abundance and diversity of families in the Alaskan lower Ravenian

Family	Number	Percent	Number of genera	Number of species
Menispermaceae	58	11.6	7	7
Betulaceae	48	9.6	1	2
Celastraceae	48	9.6	1	1
Sapindaceae	40	8.0	1	1
Juglandaceae	37	7.4	1	1
Sabiaceae	36	7.2	1	2
Icacinaceae	26	5.2	5	7
Lauraceae	23	4.6	2	5
Palmae	20	4.0	2?	2?
Vitaceae	20	4.0	1	1
Myrtaceae	19	3.8	1	1
Clethraceae	14	2.8	1	1
Aspidaceae	24	4.8	2	2
Dipterocarpaceae	9	1.8	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

The general floristic relationships, the presence of large-leafed ferns (including a genus--Hemitelia--whose extant members are tree ferns), of 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 (middle upper Eocene) flora.

- Filicineae
  - Filicales
    - Schizaeaceae
      - Lygodium n. sp.
    - Aspidaceae
      - Allantodiopsis pugetensis Wolfe
- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - Glyptostrobus sp.
- Angiospermae
  - Monocotyledones
    - Principes
      - Palmae
        - Phoenicites sp.
        - Sabalites sp.
  - Dicotyledones
    - Juglandales
      - Juglandaceae
        - Carya cashmanensis Wolfe
        - Engelhardia sp.
        - Platycarya sp. [Ulmus pseudobrauni Holl.]
        - Pterocarya pugetensis Wolfe
    - Fagales
      - Fagaceae
        - Dryophyllum pugetensis Wolfe
    - Urticales
      - Ulmaceae
        - Ulmus sp.
    - Ranales
      - Tetracentraceae
        - Tetracentron sp. [Cercidiphyllum piperoides (Lesq.) LaM.]
      - Menispermaceae
        - Calkinsia n. sp.
      - Lauraceae
        - Cinnamomophyllum n. sp.
        - Laurophyllum sp. [Cryptocarya presamarensis Sanb.]
        - Laurophyllum n. sp. A
        - Laurophyllum n. sp. B
        - Laurophyllum sp.
        - Laurophyllum sp.

- Angiospermae (continued)
  - Dicotyledones (continued)
    - 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 that 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 thus 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, as in the lower Ravenian, Asian. The floristic similarities of the middle Ravenian to the Indomalaysian region is, however, much less pronounced. The strongest relationship of the middle Ravenian appears to be with the Subtropical forest. The representation of Juglandaceae (exclusive of Pterocarya), Fagaceae, Lauraceae, Liquidambar?, and Theaceae, gives the Alaskan middle Ravenian a taxonomic aspect that is more similar to that of the 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 *Engelhardia*), *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 37 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 Subtropical 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 regard to both vegetation and flora is significant in that both lines of reasoning indicate a cooler climate for the middle Ravenian. In Alaska, light frosts probably characterized the middle Ravenian climate, whereas they were lacking in the early Ravenian. In the middle Ravenian of the Puget Group, the physiognomic characters of the foliage indicate the persistence in conterminous United States of Paratropical Rain forest and hence 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 72 to 62.

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* n. sp.
        - *Salix* sp.

- Angiospermae (continued)
  - Dicotyledones (continued)
    - Juglandales
      - Juglandaceae
        - *Juglans* (*Cardiocaryon*) sp.
        - *Pterocarya pugetensis* Wolfe
    - Fagales
      - Betulaceae
        - *Alnus cuprovallis* Axelrod
        - *Alnus* sp.
        - *Alnus* sp.
    - Ranales
      - Menispermaceae
        - *Cocculus* sp.
    - Rosales
      - Hamamelidaceae
        - *Corylopsis* sp.
      - Rosaceae
        - *Prunus* sp. [*Euonymus nevadensis* Axelr.]
        - *Sorbus* n. sp.
    - Sapindales
      - Aquifoliaceae
        - *Ilex* n. sp.
    - Rhamnales
      - Rhamnaceae
        - *Rhamnus*? sp.
    - Malvales
      - Tiliaceae
        - *Tilia* n. sp.
        - *Willisia* sp.
    - Myrtiflorae
      - Myrtaceae
        - *Eugenia*? sp.
    - Incertae sedis
      - *Dicotylophyllum* sp.

The Alaskan upper Ravenian is, unfortunately, known from but a single 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* sp.), 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. Significant also is that Lauraceae, Rutaceae, and Dipterocarpaceae are unrepresented in the upper Ravenian. Palynologic evidence, however, indicates that some of the upper Ravenian genera, for example *Salix*, *Juglans*, and *Tilia*, were represented in Subtropical or Paratropical Rain forest in conterminous United States during the earlier Eocene (E. B. Leopold, oral commun., Jan. 1969; Wolfe, unpublished data) and leaves of Populus are known in Subtropical forest in the middle Eocene (MacGinitie, in press). One element, represented by Corylopsis and Dicotylophyllum sp., appears 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 sp. 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) also 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 is not clear. The taxa probably derived from the main elements of the Alaskan early and middle Ravenian--Cocculus, Willisia, 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 of the 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 dicotyledonous species represented in the Alaskan upper Ravenian have leaves 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 probably 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 predominately deciduous; only four species --the Cocculus, Willisia, Eugenia?, and a fragmentary, generically indetermined species--have a coriaceous texture and thus were probably evergreen.

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 sp.--appear to represent lineages that survived in Alaska after the late Ravenian; during the early and middle Miocene (Seldovian) these lineages participated in the cool Alaskan facies of the Mixed Mesophytic forest, but in the late Miocene (Homerian) the lineages had adapted to a predominately conifer forest. One lineage has since become extinct, but some of 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, Willisia, Eugenia?, and the genus represented by Dicotylophyllum sp.; Willisia, however, was a member of broad-leaved deciduous forest in the Pacific Northwest during the late Oligocene, but after that the lineage then 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

Floristic analysis

Systematic list of the Alaskan Kummerian (lower Oligocene) flora.

- Filicineae
  - Filicales
    - Schizaeaceae
      - Anemia? sp.
    - Blechnaceae
      - Woodwardia sp.
- Angiospermae
  - Dicotyledones
    - Fagales
      - Betulaceae
        - Alnus sp.
        - Betula sp.

- Angiospermae (continued)
  - Dicotyledones (continued)
    - Fagales (continued)
      - Fagaceae
        - Fagus sp.
    - Ranales
      - Tetracentraceae
        - Tetracentron sp.
      - Magnoliaceae
        - Magnolia reticulata Chan. and Sanb.
      - Menispermaceae
        - Hypserpa? sp.
      - Lauraceae
        - Laurophyllum sp. [Nectandra presanguinea Chan. and Sanb.]
        - Laurophyllum sp. [Cryptocarya presamarensis Sanb.]
        - Laurophyllum raminervum Potb.
        - Laurophyllum n. sp. C
        - Laurophyllum n. sp. D
        - Laurophyllum sp.
        - Laurophyllum sp.
    - Rosales
      - Platanaceae
        - Platanus sp. [Mallotus comstocki Sanb.]
    - 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 dominately 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 diversity in the Subtropical forest.

The historical floristic relationships of the Alaskan Kummerian assemblages is 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 of the laurels, for example "Cryptocarya" 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 broad-leaved deciduous 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 Kummerian 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 is 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 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 predominately 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 represent a cooler vegetation. The Clarno nut bed and the Comstock assemblages of Oregon, and the LaPorte assemblage of northern California contain numerous representatives of Menispermaceae, Anonaceae, 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 appears 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 representation 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 appears 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 (early late 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 early and middle 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 lack of frost, a mean annual temperature of 22°C to 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 15°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.

The middle Ravenian (middle late Eocene) assemblages indicate a somewhat cooler climate, probably in the warmer range of subtropical climates. Frosts probably occurred, although they would 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 -7°C, the mean annual temperature ranges from 15°C to 19°C, and the mean temperature of the coldest month varies from 5°C to 10°C (Wang, 1961, p. 131). Precipitation would again have been abundant and distributed throughout the year.

The late Ravenian (latest Eocene) assemblages indicate 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°C to 16°C, and the mean temperature of the coldest month in the range of -3°C to 5°C. These data are based on the climatic conditions of similar extant vegetation (Wang, 1961, p. 97).

By the Kummerian (early Oligocene), climatic conditions were again subtropical. The climate was probably about the same as that of the middle Ravenian. Based on probable post-Kummerian assemblages from Admiralty Island in southeastern Alaska, the subtropical conditions 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-middle Ravenian and Kummerian, the vegetation and hence the climate showed little zonation in comparison to the cool periods of the late Ravenian and the Angoonian, when considerable zonation of vegetation is apparent.

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 Kummerian 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 22°C to 25°C,
3) abundant precipitation, and
4) no pronounced dry season.

Compare these conditions with the climatic conditions at Cordova today:

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

In regard to precipitation, no drastic 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 greatly different than that 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 to 3 cm per year, but this movement is thought to have started only about 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.

Paleomagnetic evidence, moreover, does not indicate that the magnetic poles were at much different positions during the Paleogene than today.

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: 1) as low evergreen shrubs that have small leaves, 2) as herbaceous forms, and 3) 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; palms, of course, are never remotely deciduous. The idea that broad-leaved evergreen plants in the "mesophyllous" and "megaphyllous" 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 were, however, 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 their 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-leaved 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 must have had much less--possibly no--inclination. If this hypothesis is accepted, several paleoclimatological problems can be solved and placed in a coherent framework. The hypothesis is, of course, not new; it was debated in the last century (see, for example, Waring, 1884).

1. _Rapidity of climatic changes_. Only one climatic deterioration has excellent radiometric control. The LaPorte flora of northern California has been dated at 32.2 to 32.5 million years (Evernden and James, 1964); based on some of the revisions included in this report, percentage of species that have entire-margined leaves is 68. The Bridge Creek flora of Oregon has been dated at 31.5 million years (Evernden and James, 1964); the leaf margin percentage for this assemblage is 25. The LaPorte and Bridge Creek radiometric ages are virtually identical; within the limits of potassium-argon analysis they are indistinguishable (G. B. Dalrymple, oral commun., Jan. 1969). The change from temperate to Subtropical forest (in leaf margin percentages, from 20 to 55) in the Carbon Mountain section occurred while less than 100 feet of sediments were being deposited, indicating that the climatic change was apparently rapid.

The probable rapidity of the climatic changes probably accounts for the relative depauperateness of the cool period floras in comparison to the warm period floras. Climatic changes of the magnitude suggested in this report and occurring within a period of a million years--perhaps within a period of thousands of years--probably would not allow sufficient time for extensive adaptations of all the lineages; the flora following a major deterioration would probably be composed primarily of lineages that were preadapted to a cool climate. These lineages would in part have been members during the warm periods of the tropical forests and in part have been members of cooler upland forests. Because North America was, compared to today, relatively low-lying during most if not all of the early Tertiary, the upland sources for temperate lineages would have been limited. The depauperateness of temperate vegetation following the deterioration 32 million years ago is apparent both in Oregon and Alaska. The Bridge Creek assemblage has been extensively collected over a period of about 90 years and from many localities in an area of several hundred square miles; the total number of species known is about 75, in comparison to the vegetationally comparable Miocene Collawash assemblage, which includes at least 140 megafossil entities from a single locality. Similarly, the Alaskan assemblages coeval with the Bridge Creek are known from at least 30 localities in an area of about 250,000 square miles; less than 50 species are known from all these assemblages in comparison to the vegetationally comparable Seldovia Point assemblage (approximately coeval with the Collawash), which includes at least 50 megafossil entities from a single locality.

2. Latitudinal differences in the effect of fluctuations. The effect of the climatic fluctuations is more pronounced at high latitudes than at middle latitudes, and apparently more pronounced at middle latitudes than at low latitudes. In Alaska, the differences between the leaf margin percentages for the warm late Eocene and cool latest Eocene assemblages is about 45, whereas in the Pacific Northwest the difference is about 30. The differences between the Alaskan warm earlier Oligocene and cool later Oligocene assemblages at the same latitude (60° N.) is about 50, whereas the equivalent difference in the Pacific Northwest is about 42. So far as known, low latitude climates did not fluctuate significantly during the Tertiary. Note also that during warmer periods, the difference between the percentages of entire leaf margins for Alaska and the Pacific Northwest are only about 5 to 12, whereas in the (cooler) latest Eocene the difference is about 34 and in the later Oligocene it is about 19 to 22 (the lesser difference in the later Oligocene as compared with the latest Eocene is probably a function of the leaf margin analysis, that is, 34 subtracted from the Bridge Creek percentage of 25 yields an obviously impossible percentage of -9).

The differences suggested above indicate that a cause of climatic change is needed that has a significantly greater effect the higher the latitude. If the cause is a change in the inclination of the axis of rotation, the effect would be greater on the vegetation of higher than on that of middle latitudes, and low latitudes would have little, if any, vegetational change.

3. Apparently less seasonality during the Tertiary. The seasonality of present temperatures is, of course, primarily the result of the inclination of the axis of rotation. A number of workers (see, for example, MacGinitie, 1962, in press) have argued from vegetational analysis of Tertiary plants that seasonality was not as pronounced in the Tertiary as now. Seasonality, of course, probably was never totally absent during any part of the Tertiary. The eccentricity of the earth's orbit results, for example, in the earth receiving about seven percent more solar radiation during perihelion. If at any time the earth had almost no inclination, this would result at times in the reversal of the northern hemisphere's seasons; perihelion now occurs, of course, during January.

The western edges of continents must always receive less precipitation during what is now the summer than during the winter because of the Coreolis effect. Nevertheless, assemblages such as the Clarno nut bed do not represent savanna vegetation, which grows under extended dry periods such as now prevail in Oregon, but represents Paratropical Rain forest, which has ample precipitation throughout the year (the precipitation is, as of most vegetational types, greater during some parts of the year than during others). Similarly, the Mixed Mesophytic forest of the Oregon Neogene contains many genera, the extant species of which will not grow under a climate that has extended dry periods during the growing season. The Mixed Mesophytic forest survives today only in areas that have no extended dry period during the growing season.

The probable effect of less inclination of the axis of rotation would be to lessen seasonality of temperature and thus of precipitation. During periods of weak zonal circulation (caused largely by weaker latitudinal differences in temperature), the low pressure system in the northeastern Pacific tends to split up into two weaker lows, one of which extends far southward and in turn depresses the eastern Pacific high pressure system southward; during such periods, precipitation commonly occurs in California and the Pacific Northwest (Fletcher, 1966).

4. Northward extension of Tropical Rain forest during the Tertiary. Most Claiborne (Eocene) assemblages from as far north as latitude 36° represent Tropical--not Paratropical--Rain forest. The leaf margin percentages for most of these assemblages ranges from 76 to 83; this is a clear indication of Tropical Rain forest. The other physiognomic features of the foliage, for example, the numerous drip-tips, also indicate Tropical Rain forest. Today Tropical Rain forest extend to areas that are about 45° from the caloric equator during periods of the year. Under a no-tilt condition, Tropical Rain forest could presumably extend to about 45° N. latitude; local conditions, of course, might not allow such a northward extension in every region.

5. Apparent periodicity of climatic fluctuations. In an earlier discussion of Tertiary climatic change, it was suggested that the climate warmed gradually from the late Paleocene to the Eo-Oligocene, but it was

also recognized that the data were too incomplete to determine whether or not this trend was interrupted by fluctuations. Increasing evidence (Wolfe and Schorn, unpublished data) indicates that the cool period of the late Paleocene was followed by a pronounced warm period in the earliest Eocene; this would correspond, for example, to the London Clay flora (Chandler, 1964) of late Ypresian age. This period was followed by another cool period and then by the warm period of the early late Eocene. Chandler (1964) has interpreted all the British Eocene assemblages to represent the same vegetational type, but, as Richards (1952, p. 154) has pointed out, the floristic approach used by Miss Chandler may not be completely reliable. If the British Eocene vegetation fluctuated between marginally Tropical and Paratropical Rain forest or between the extremes of Paratropical Rain forest, there would be little recognizable floristic difference between the various assemblages. I have computed leaf margin percentages for the British Eocene fruit and seed assemblages, using the assumptions of Edwards (1936); that is, a seed of Lauraceae almost certainly was borne by a plant that had entire-margined leaves. The British Eocene assemblages show striking climatic changes. For example, the London Clay has an assumed percentage of about 76, whereas the succeeding Lower Bagshot assemblage has a percentage of 50 and the even younger Bartonian has a percentage of 80. Using the European-west American correlations suggested by Clark and Vokes (1936) for the Eocene, the fluctuations in the British Eocene match those in the west American Eocene.

One significant problem in the discussion of Paleogene climates is the probable latest Eocene (late Ravenian) cool period. The Alaskan assemblage of late Ravenian age clearly represents a considerably cooler climate than either the middle Ravenian or the Kummerian. In conterminous United States, the upper Ravenian assemblages in the type section of the stage similarly represent cooler vegetation than either the middle Ravenian or Kummerian assemblages from the Puget Group. In the Eocene to Oligocene Clarno Formation of Oregon, the cool period can also be detected: the Clarno nut bed assemblage, which is of Kummerian age and a correlative of the Comstock assemblage, on floristic grounds, probably represents the Paratropical Rain forest. The West Branch Creek assemblage of the Clarno is the Clarno flora of most authors; this assemblage is in the basal part of the Clarno Formation (Hay, oral commun., Feb. 1969) stratigraphically well below the nut bed and is probably of early or middle Ravenian age. No leaf margin percentage has been computed for the West Branch Creek assemblage, but it is estimated to be in excess of 60. Stratigraphically between the two well-known Clarno assemblages is the John Day Gulch assemblage; based on 38 species of dicotyledons, the leaf margin percentage for this assemblage is 36, and the dicotyledons include genera such as Betula, Mahonia, and Rubus. The John Day Gulch assemblage again indicates a late Eocene cool period.

Axelrod (1966b) has obtained a number of potassium-argon ages for various assemblages from Washington, Idaho, and Nevada. The age obtained on the Republic assemblage (55 million years) is not in agreement with new data, which indicate a considerably younger age (Obradovich, written commun., Aug. 29, 1966). The complex stratigraphy in the Challis volcanics

indicates that the ages obtained for the Thunder Mountain and the Salmon assemblages cannot be accepted as reliable at this time (B. F. Leonard, oral commun., Jan. 1969). Only three of the ages on Eocene assemblages published by Axelrod (1966b) can be accepted as probably reliable: Copper Basin (39 ± 1, 40 ± 1 million years), Bull Run (35 to 42 million years; the average would be 38.5 million years), and Lower Cedarville (40 million years). I think that the available radiometric data support the concept that the cool "upland" assemblages represent a period very late in the Eocene (that is, centering approximately around 38 to 40 million years ago).

The fluctuations of the late Eocene and Oligocene and Miocene have been documented either in this report or by Wolfe and Hopkins (1967). The Oligocene climatic deterioration has been recognized not only in western North America, but also in western Europe (Nemejč, 1964) and in central Asia (Zhilin, 1966). Vlasov (1964) notes that, based on studies of the Tertiary molluscan faunas of eastern Siberia, the Tertiary climates certainly displayed considerable fluctuations. Where radiometric control is good or inferred by correlations to assemblages that are radiometrically dated, the fluctuations appear to fit a pattern that has a periodicity of about 9.5 million years, that is, a given warm or cool period apparently lasted about 4.5 to 5.0 million years. Much more radiometric control is needed to determine if this suggested periodicity is valid, but the available data strongly indicate that the climatic fluctuations are periodic. Some other factor than the 9.5 million-year periodicity is involved in climatic change because the peaks and troughs of the leaf margin curves decline from sometime in the Eocene as the Quaternary is approached.

The proposed periodicity of climatic change has obvious significance to the interpretation of past vegetation. During various cool and warm periods, various climates would be more widespread than at other times and these climates would favor the extensive development of particular vegetation types. For example, today the Paratropical Rain forest is, compared to both the Subtropical and Tropical Rain forests, of limited distribution and could even be thought of as an ecotone between these two other vegetational types. During the warm periods of the Eocene, however, the climate that favors Paratropical Rain forest was widespread. Chaney (1949) has interpreted some Paleogene assemblages as ecotonal, but the fact that these "ecotonal" assemblages are geographically widespread indicates that they represent a vegetational type and not the transition vegetation between two other vegetational types. A second example is that of the warm temperate climate that favors the development of the Mixed Mesophytic forest. During the Miocene, the climate favoring this vegetation was apparently more widespread than at any other time in the Tertiary; in western North America assemblages representing this vegetation occur over a latitude of 30°, and in eastern Asia a similar latitudinal range during the Miocene appears probable. This long period of extensive warm temperate climate (from about 14 to about 32 million years), during which the periodic fluctuations were minor in comparison to the older fluctuations, allowed the development of a rich warm temperate forest that is called the Mixed Mesophytic forest.

also recognized that the data were too incomplete to determine whether or not this trend was interrupted by fluctuations. Increasing evidence (Wolfe and Schorn, unpublished data) indicates that the cool period of the late Paleocene was followed by a pronounced warm period in the earliest Eocene; this would correspond, for example, to the London Clay flora (Chandler, 1964) of late Ypresian age. This period was followed by another cool period and then by the warm period of the early late Eocene. Chandler (1964) has interpreted all the British Eocene assemblages to represent the same vegetational type, but, as Richards (1952, p. 154) has pointed out, the floristic approach used by Miss Chandler may not be completely reliable. If the British Eocene vegetation fluctuated between marginally Tropical and Paratropical Rain forest or between the extremes of Paratropical Rain forest, there would be little recognizable floristic difference between the various assemblages. I have computed leaf margin percentages for the British Eocene fruit and seed assemblages, using the assumptions of Edwards (1936); that is, a seed of Lauraceae almost certainly was borne by a plant that had entire-margined leaves. The British Eocene assemblages show striking climatic changes. For example, the London Clay has an assumed percentage of about 76, whereas the succeeding Lower Bagshot assemblage has a percentage of 50 and the even younger Bartonian has a percentage of 80. Using the European-west American correlations suggested by Clark and Vokes (1936) for the Eocene, the fluctuations in the British Eocene match those in the west American Eocene.

One significant problem in the discussion of Paleogene climates is the probable latest Eocene (late Ravenian) cool period. The Alaskan assemblage of late Ravenian age clearly represents a considerably cooler climate than either the middle Ravenian or the Kummerian. In conterminous United States, the upper Ravenian assemblages in the type section of the stage similarly represent cooler vegetation than either the middle Ravenian or Kummerian assemblages from the Puget Group. In the Eocene to Oligocene Clarno Formation of Oregon, the cool period can also be detected: the Clarno nut bed assemblage, which is of Kummerian age and a correlative of the Comstock assemblage, on floristic grounds, probably represents the Paratropical Rain forest. The West Branch Creek assemblage of the Clarno is the Clarno flora of most authors; this assemblage is in the basal part of the Clarno Formation (Hay, oral commun., Feb. 1969) stratigraphically well below the nut bed and is probably of early or middle Ravenian age. No leaf margin percentage has been computed for the West Branch Creek assemblage, but it is estimated to be in excess of 60. Stratigraphically between the two well-known Clarno assemblages is the John Day Gulch assemblage; based on 38 species of dicotyledons, the leaf margin percentage for this assemblage is 36, and the dicotyledons include genera such as *Betula*, *Mahonia*, and *Rubus*. The John Day Gulch assemblage again indicates a late Eocene cool period.

Axelrod (1966b) has obtained a number of potassium-argon ages for various assemblages from Washington, Idaho, and Nevada. The age obtained on the Republic assemblage (55 million years) is not in agreement with new data, which indicate a considerably younger age (Obradovich, written commun., Aug. 29, 1966). The complex stratigraphy in the Challis volcanics indicates that the ages obtained for the Thunder Mountain and the Salmon assemblages cannot be accepted as reliable at this time (B. F. Leonard, oral commun., Jan. 1969). Only three of the ages on Eocene assemblages published by Axelrod (1966b) can be accepted as probably reliable: Copper Basin (39 ± 1, 40 ± 1 million years), Bull Run (35 to 42 million years; the average would be 38.5 million years), and Lower Cedarville (40 million years). I think that the available radiometric data support the concept that the cool "upland" assemblages represent a period very late in the Eocene (that is, centering approximately around 38 to 40 million years ago).

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The concept of major climatic fluctuations has an important bearing on concepts of past zonation of vegetation and hence climate. Chaney (1940, 1964), for example, has attempted to indicate the zonation of certain vegetational types in the Paleogene, through the use of "isoflors." As Good (1954, p. 266-267) has remarked:

> "These conclusions as to the former distribution of certain climatic values may in fact be entirely justifiable but it is clear enough that the proof of this by the use of isoflors can have validity only when there can be no room for doubt as to the exact contemporaneity of the fossil floras involved, and the paper [Chaney, 1940] makes it clear that this fundamental basis does not exist."

As is discussed in this report, Good's doubt is well substantiated, because the "isoflors" were based on assemblages that range from Late Cretaceous to Pliocene. Axelrod's (1966a) attempt to determine both latitudinal and altitudinal zonation of vegetation is similarly deficient in comparing floras of widely different ages, ranging from late Eocene (Steels Crossing--early Ravenian) to early Miocene (Port Graham assemblage of the Kenai--early Seldovian); that is, assemblages differing in age by approximately 20 million years have been considered isochronous.

The suggested hypothesis of periodicity of climatic change has a considerable amount of data that appear to fit the model well. I would, however, emphasize the word "appear." That major climatic fluctuations occurred during the Tertiary is, I think, well documented in diverse areas (Nemejč, 1964; Zhilin, 1964; Vlasov, 1964; Wolfe and Hopkins, 1967; Devereux, 1967), including central Europe, central Asia, the Far East, Alaska, the Pacific Northwest, and New Zealand. The periodicity (or lack of) of these fluctuations can only be tested by radiometric ages and those available indeed appear to fit a periodic model. More radiometric ages, coupled with studies of plant assemblages in sequences, are clearly needed.

If the periodicity proves to be valid, I think that it is clear that the climatic changes most probably result from a factor outside the earth. Conceivably the earth might have a nutation longer than the known 26,000-year nutation, but probably astronomical observations would have detected longer nutations. The cycles suggested by Malankovitch (1939) are far too short (in terms of hundreds of thousands of years) to be involved in the periodicity suggested here. Assuming that the 9.5 million-year periodicity results from changes in the earth's inclination, it is unlikely that a long period nutation is involved, because the changes appear to have been sudden, not gradual as in a nutation.

History of the Arcto-Tertiary concept

This concept has been the primary contribution of paleobotany to the field of historical 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, however, 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 wide acceptance as fact.

The concept of homotaxis is the fundamental concept on which the Arcto-Tertiary and other geofloral theories are based. 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 pressed closely upon them. The Northern Eocene, or the temperate floras of that period, 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 rather 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 mid 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 own 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 (loosely 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 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) had read Gardner's (1887a) paper cited above, and 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 also occurred in the Alaskan Tertiary flora described by Heer (1869) and thus the Alaskan Tertiary flora was also thought to be "Lower Eocene" or Paleocene.

Dawson's treatment was followed by F. H. Knowlton, who was the next 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 that 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 giving lip service to 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) all plant-bearing beds in Alaska were essentially synchronous and were part of the 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 (<u>in</u> 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 <u>in</u> 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 (<u>in</u> 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, listing 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 had the same internal logical schism as did Knowlton, because Hollick went on to quote Gardner's (1879) argument for floral homotaxis. Also curious is the fact that Hollick listed about 30 species from rocks that the geologist P. S. Smith (<u>in</u> 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, considering 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 further 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. This, then, was the in fact contradictory "evidence of their stratigraphic occurrence."

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 to subtropical 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 the same opinion was reiterated 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 but one species, a *Ginkgo* (Knowlton *in* Mendenhall, 1902), which 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 considerable 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 the Alaskan "Eocene" and the Bridge Creek, which 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 a theoretical basis 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 but found support in subsequent work on high latitude Tertiary floras. Preliminary studies of the Alaskan Tertiary floras indicated that the Arcto-Tertiary concept was invalid. We (MacNeil and others, 1961, p. 1802) 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) has 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), who 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, claiming 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 1935 paper) and the stratigraphic work in Alaska published by Burk (1965), which included lists of plants from Neogene, mollusk-dated rocks. Chaney also relied heavily on the pollen floras described by Manum (1963) from mollusk-bearing units on Spitzbergen to establish the presence of the Arcto-Tertiary Geoflora at high latitudes during the Paleogene. These mollusks were at one time thought to be of Paleocene-Eocene age, but recent work (MacNeil, 1965; Durham and MacNeil, 1967) indicates that the mollusks are probably no older than middle Miocene.

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 had no more factual foundation than the previously discussed "evidence" for the Arcto-Tertiary concept. As noted elsewhere, a fan palm is known from interior Alaska (lat 65½° N.); the age of this palm is unknown, but the 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 poorly 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 knowledge 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. The known early Ravenian assemblages are not marginally Paratropical Rain forest; they indicate that north from the Gulf of Alaska region more of this vegetation extended. 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 forest 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 mostly of Pliocene age (Wahrhaftig and others, 1969). The Wrangell lavas, which form the bulk of the high country of the Wrangell Mountains, overlay the Frederika Formation of middle Miocene age (MacKevett,in press). If, therefore, temperate broad-leaved deciduous forest existed during warm periods such as the early Ravenian, the forest would most probably have been 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 Eo-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° to 60° N. 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 necessarily makes reliance on the floristic relationships to determine 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) remarks 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 to 22 for the Alaskan late Oligocene assemblages. If, during the later 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 earlier Paleogene. During the Paleogene neither latitude nor continentality appear 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 concepts of the relationships between plants and their environments allowed, if not demanded, the acceptance of an 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 as currently used is indicated by the Alaskan and Siberian assemblages of fossil plants and 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 floristically and vegetationally complex type (Wang, 1961). It is a warm temperate type of vegetation that 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. 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 later 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*, *Quercophyllum 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. 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 than 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 (early and middle parts of the late Eocene) and Kummerian (early Oligocene) assemblages represent, respectively, Paratropical Rain forest and the last two Subtropical forest. These assemblages contain a significant number of Mixed Mesophytic genera and lineages, including:

Carya (*bendirei* type)
Platycarya
Pterocarya
Alnus
Betula
Fagus
Ulmus (*newberryi* type)
Tetracentron
Cocculus
Eucommia

Liquidambar?
Platanus (*bendirei* type)
Euodia
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
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 forest. By the latest Eocene, some taxa that, earlier in the Tertiary, were distributed in the Paratropical Rain or Subtropical forests, had become 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 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 genera or lineages that have not been recorded from older upland assemblages but were found in the lowland early and middle Oligocene:

Engelhardia
Cercidiphyllum
Cinnamomum
Exbucklandia

Liquidambar
Platanus (*dissecta* type)
Toxicodendron

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 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 than during the earlier and cooler part of the Angoonian; broad-leaved evergreens are represented by Engelhardia (characteristic involucres have been found in late Angoonian rocks in the central Alaska Range), Ilex, and Alangium. Pollen records include Cedrela/Melia. Rosaceae were apparently more diverse in Alaska than previously and include Duchesnea or Fragraria, Rubus, Sorbus, and Spiraea. The temperate vegetation appears to have been enriched, partly through the adaptation of tropical lineages to temperate climates and partly through the diversification of lineages previously present in the temperate vegetation.

The early Miocene (early Seldovian) appears to have been cooler than the late 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 appears 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 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: 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, although present in the Paleogene subtropical and tropical forests, were taxonomically depauperate in the Paleocene and Eocene floras 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 9 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, appears 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. Both Salix and Ericaceae, although present in considerable diversity in the Miocene Mixed Mesophytic forest, continued to diversify 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, which 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 probably indicates that many of these genera are of more recent origin; by the time they had evolved, the Alaskan forest, although of Mixed Mesophytic type, 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 highly 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 Mesophytic forest still survives. Alaska receives more summer precipitation today

Table 9.--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 tropical	Eocene temperate	Oligocene tropical	Oligocene upland	late Oligocene	early-mid Miocene	late Miocene	Pliocene
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 Engelhardia)	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

than in 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 between Eurasia and western North America of many genera.

The Mixed Mesophytic forest of the Miocene of western North America thus appears 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-middle Oligocene to interior warm temperate uplands.

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 appear 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
Umbellularia

Lyonothamnus
Peraphyllum
Cedrela
Euodia
Pistacia
Colubrina
Karwinskia
Zizyphus
Xylonagra

Cinnamomum
Cercidiphyllum
Exbucklandia
Cercocarpus
Holodiscus
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-late Oligocene climatic deterioration that probably would leave--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,

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 three genera of Lauraceae--*Lindera*, *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*, *Diospyros*, *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 had few genera in common with the Paleogene forest of western North America and Eurasia; the isolation of eastern North America appears to have been ancient (MacGinitie, in press). 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.

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 only by reconstructing the patterns of distribution in space and time of the component lineages.

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. In a significant paper, van Steenis (1962) has discussed in detail the significance of trans-Pacific angiospermous genera and families and 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 is, 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 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 re-adapted 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 trans-oceanic land bridges at tropical latitudes.

The data presented here indicate that van Steenis' explanation 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 (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° to 70° N. "...might have been warm-temperate to subtropical and the majority of the trees must have been deciduous." Second, van Steenis accepts (p. 271-281) 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 presented 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 (earliest late Eocene) assemblages include some of van Steenis' "Amphi-transpacific" genera: *Sageretia*, *Meliosma*, and *Saurauia*. Van Steenis (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 Anonaceae, Myristicaceae, and Lecythidaceae (including Barringtoniaceae), and in the second category are the early Ravenian Palmae, Menispermaceae, Lauraceae, Rutaceae, Anacardiaceae, Icacinaceae, Sapindaceae, Vitaceae, Theaceae, Myrtaceae, and Verbenaceae. Added to these are the early Ravenian groups that are exclusively paleotropical. 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*

Anonaceae: *Cananga*

Olacaceae: *Erythropalum*, *Olax*

Hamamelidaceae: *Altingia*

Rutaceae: *Euodia*, *Luvunga*

Anacardiaceae: *Dracontomelon*, *Poupartia*

Icacinaceae: *Iodes*, *Miquelia*, *Phytocrene*, *Pyrenacantha*, *Stemonurus*

Vitaceae: *Tetrastigma*

Barringtoniaceae: *Barringtonia*

Dipterocarpaceae: *Doona*, *Parashorea*

Alangiaceae: *Alangium*

Cornaceae: *Mastixia*

The fact that these genera have not survived in the American tropics may indicate that the major barrier to floristic interchange was in southwestern North America. As noted previously, there was apparently little floristic interchange during the Paleogene between the tropical vegetation of western United States and the Gulf Coastal Plain; the latter, which had a great diversity of "mesophyllous" legumes, was apparently floristically and vegetationally allied to the Caribbean and South American region, whereas the western American tropical forests were dominately paleotropical. What the barrier(s) was (were) is unknown; the tropical lineages of the western North American Paleogene were, for the most part, not incorporated into the extant tropical vegetation of North America. I suspect that the barrier must have been largely climatic, such as a wide region of highly seasonal precipitation that would have led to savanna vegetation largely impassable for lineages of the Paratropical Rain forest.

Disjunctions 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 (*Eohypserpa*, *Macaranga*, *Melanolepis*, and *Sabalites*, are known from the Alaskan Paleocene; Wolfe, 1966; Burk, 1965), early Eocene (assuming a warming in Alaska simultaneous with that known in middle latitudes), early late Eocene, or the early Oligocene (in Alaska the very warm Subtropical forest indicates that locally warmer areas might have allowed some tropical lineages to have migrated through). 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.

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 Borls 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 commun., 1948). Vokes regards 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.

11157. 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' W. From west wall of canyon. Kushtaka Formation. Collectors: Wolfe and Larson, 1968. Lower Ravenian.

11159. Lat 60°25.2' N., long 143°48.8' W. 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' N., 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, Katalla Formation. Collectors: Wolfe, Larson, and Gunn, 1968.

11169. Lat 60°27.5' N., long 143°48.8' W. 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 later Miocene age. Collector: Miller, 58AMr 333. Seldovian or Homerian.

11188. Unknown position in Basin Creek Member, 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 square miles 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*, 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.

Faunal data

Mollusks from the Stillwater, Kushtaka, and Tokun Formations have been listed in the section on physical stratigraphy, and a few mollusks were listed from the Katalla Formation. Other important localities in the Split Creek and Basin Creek beds of the Katalla are:

USGS Cenozoic locality 15796. 3.47 miles S. 55° E. of junction of principal tributaries of Burls Creek, Miller Hills. Split Creek beds. Fossils include (H. E. Vokes, written commun., Jan. 12, 1956):

Spisula cf. *S. packardi* Dickinson
Spisula aff. *S. pittsburgensis* Clark *frustrata* Tegland
Molopophorus aff. *M. stephensoni* Dickerson
Molopophorus cf. *M. dalli* Anderson and Hanna
Perse sp. cf. *P. gabbi* (Dickerson)

USGS Cenozoic loc. 15815. 8.18 miles N. 69° E. of junction of two main tributaries of Burls Creek, Miller Hills. Basin Creek beds. Fossils include (H. E. Vokes, written commun., Jan. 12, 1946):

Nemocardium weaveri (Anderson and Martin)

In his report on the above collections, Vokes was concerned because the *Nemocardium*, which was collected stratigraphically above locality 15796, is only known from beds stratigraphically lower than Split Creek equivalents in the Pacific Northwest. The *Nemocardium* indicated a correlation to the Keasey Formation, but the fauna of the Split Creek is correlative to the fauna of the younger *Molopophorus stephensoni* zone. Part of the problem may be that *N. weaveri* has a somewhat longer range in Alaska than in the Pacific Northwest, and Vokes (written commun., Jan. 12, 1946) noted that Durham (1944) reported a *Nemocardium* from middle Oligocene beds in Washington that Vokes considered to be at least subspecifically distinct from *N. weaveri s.s.* In any case, the correlation of the Split Creek and Basin Creek to the upper part of the lower half of the Oligocene (marine megafossil terminology) is reasonably well established.

References

Atwood, W. W., 1911, Geology and mineral resources of parts of the Alaska Peninsula: U.S. Geol. Survey Bull. 467, 137 p., 14 pls.

Axelrod, D. I., 1966a, A method for determining the altitudes of Tertiary floras: Palaeobotanist, v. 14, p. 144-171.

——— 1966b, The Eocene Copper Basin flora of northeastern Nevada: California Univ., Pubs. Geol. Sci., v. 59, 125 p.

——— 1967, Quaternary extinctions of large mammals: California Univ., Pubs. Geol. Sci., v. 74, 42 p.

——— 1968, Tertiary floras and topographic history of the Snake River basin, Idaho: Geol. Soc. America Bull., v. 79, p. 713-734.

Bailey, I. W., and Sinnott, E. W., 1915, A botanical index of Cretaceous and Tertiary climates: Science, v. 41, p. 831-834.

——— 1916, The climatic distribution of certain types of Angiosperm leaves: Am. Jour. Botany, v. 3, p. 24-39.

Becker, H. F., 1961, Oligocene plants from the upper Ruby River basin, southwestern Montana: Geol. Soc. America Mem. 82, 127 p., 32 pls.

Berry, E. W., 1930a, Revision of the lower Eocene Wilcox flora of the Southeastern States: U.S. Geol. Survey Prof. Paper 156, 196 p., 50 pls.

Berry, E. W., 1930b, The past climate of the north polar region: Smithsonian Misc. Coll., v. 82, no. 6, 29 p.

Bews, J. W., 1927, Studies in the ecological evolution of the Angiosperms: New Phytologist, v. 26, p. 1-21.

Brown, W. H., 1919, Vegetation of Philippine mountains: Dept. of Agriculture and Natural Resources, Manila, Pub. 1, 434 p., 41 pls.

Brown, R. W., 1939, Fossil leaves, fruits, and seeds of *Cercidiphyllum*: Jour. Paleontology, v. 13, p. 485-499.

——— 1962, Paleocene flora of the Rocky Mountains and Great Plains: U.S. Geol. Survey Prof. Paper 375, 119 p., 69 pls.

Burk, C. A., 1965, Geology of the Alaska Peninsula - Island Arc and continental margin (Part I): Geol. Soc. America Mem. 99, pt. 1, 250 p.

Cain, S. A., 1944, Foundations of Plant Geography: New York, N. Y., Harper and Brothers, 556 p.

Carey, S. W., 1958, A tectonic approach to continental drift, *in* Carey, S. W., ed., Continental drift, a symposium: Tasmania Univ. Geol. Dept., Symposium no. 2, p. 177-355.

Chandler, M. E. J., 1961, The lower Tertiary floras of southern England, I: London, British Mus. (Nat. History), 354 p., 34 pls.

——— 1964, The lower Tertiary floras of southern England, IV: London, British Mus. (Nat. History), 151 p., 4 pls.

Chaney, R. W., 1927, Geology and palaeontology of the Crooked River basin with special reference to the Bridge Creek flora: Carnegie Inst. Washington Pub. 346, p. 45-138, 20 pls.

——— 1936, The succession and distribution of Cenozoic floras around the northern Pacific basin, *in* Goodspeed, T. H., ed., Essays in Geobotany in honor of William Albert Setchell: Berkeley, Calif., California Univ. Press, p. 55-85.

——— 1938, Paleoecological interpretations of Cenozoic plants in western North America: Bot. Rev., v. 9, p. 371-396.

——— 1940, Tertiary forests and continental history: Geol. Soc. America Bull., v. 51, p. 469-488.

——— 1949, Early Tertiary ecotones in western North America: Natl. Acad. Sci. Proc., v. 35, p. 356-359.

Chaney, R. W., 1951, A revision of fossil Sequoia and Taxodium in western North America based on the recent discovery of Metasequoia: Am. Philos. Soc. Trans., n.s., v. 40, p. 171-263.

_____1952, Conifer dominants in the middle Tertiary of the John Day basin, Oregon: Palaeobotanist, v. 1, p. 105-113.

_____1964, Some observations on climatic relations of Tertiary floras bordering the North Pacific Basin, in Nairn, A. E. M., ed., Problems in Climatology: London, John Wiley and Sons, p. 40-43.

_____1967, Miocene forests of the Pacific Basin; their ancestors and their descendants: Jubilee Pub. commemorating Prof. Sasa, 60th Birthday, p. 209-239.

Chaney, R. W., and Sanborn, E. I., 1933, The Goshen flora of west-central Oregon: Carnegie Inst. Washington Pub. 439, 103 p., 40 pls.

Chelebaeva, A. I., 1968, Neogenovaya flora reki Levoi Pirozhnikovoi na Kamchatke [The Neogene flora of the River Pirozhnikovoi in Kamchatka]: Akad. Nauk SSSR, Bot. Zhurnal, v. 53, p. 737-748, 4 pls.

Clark, B. L., and Vokes, H. E., 1936, Summary of marine Eocene sequence of western North America: Geol. Soc. America Bull., v. 47, p. 851-878.

Dall, W. H., 1896, Report on coal and lignite of Alaska: U.S. Geol. Survey 17th Ann. Rept., pt. 1, p. 763-908.

_____1904, Neozoic invertebrate fossils: Harriman Alaska Expedition, v. 4, p. 99-122, 2 pls.

Dall, W. H., and Harris, G. D., 1892, Correlation papers--Neocene: U.S. Geol. Survey Bull. 84, 349 p.

Dawson, J. W., 1888, Note on fossil woods and other plant remains from the Cretaceous and Laramie formations of the western territories of Canada: Royal Soc. Canada Trans., v. 5, sec. IV, p. 31-37.

Devereux, Ian, 1967, Oxygen isotope paleotemperature measurements on New Zealand Tertiary fossils: New Zealand Jour. Sci., v. 10, p. 988-1011.

Dorofeyev, P. I., 1963, Tretichnyye flory Zapadnoy Sibiri [Tertiary floras of western Siberia]: Izd-vo Akad. Nauk SSSR, 346 p.

Durham, J. W., 1944, Megafaunal zones of the Oligocene of northwestern Washington: California Univ., Pubs. Geol. Sci., v. 27, p. 101-212.

Durham, J. W., and MacNeil, F. S., 1967, Cenozoic migrations of marine invertebrates through the Bering Strait region, in Hopkins, D. M., ed., The Bering Land Bridge: Stanford, Calif., Stanford Univ. Press, p. 326-349.

Edwards, W. N., 1936, The flora of the London Clay: Geol. Assoc. London Proc., v. 47, p. 22-31.

Engler, Adolf, 1879, Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der nördlichen Hemisphäre: Leipzig, Wilhelm Engelmann, 202 p.

_____1882, Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der südlichen Hemisphäre und der tropischen Gebiete: Leipzig, Wilhelm Engelmann, 386 p.

Evernden, J. F., and James, G. T., 1964, Potassium-argon dates and the Tertiary floras of North America: Am. Jour. Sci., v. 262, p. 945-974.

Feagri, Knut, and Iversen, Johannes, 1964, Textbook of Pollen Analysis: New York, N. Y., Hafner Publ. Co., 237 p.

Fletcher, J. O., 1966, The Arctic heat budget and atmospheric circulation, in Fletcher, J. O., ed., Proceedings of the symposium on the Arctic heat budget and atmospheric circulation: Santa Monica, Calif., Rand Corp., p. 23-43.

Fotianova, L. I., 1964, Upper Miocene flora of the west coast of Sakhalin: Akad. Nauk SSSR, Bot. Zhurnal, v. 49, no. 5, p. 649-651 (in Russian). English translation by Lydia A. Hutchison, 1968.

_____1967, Special features of the mid-Miocene flora of Sakhalin: Moscow Univ. Vestnik, no. 3, p. 78-81 (in Russian). English translation by Lydia A. Hutchison, 1968.

Friedrich, Walter, 1966, Zur Geologie von Brjánslaekur (nordwest-Island) unter besonderer Berücksichtigung der fossilen Flora: Köln Univ. Geol. Inst. Sonderveröffentlichungen 10, 108 p., 7 pls.

Gardner, J. S., 1883-86, A monograph of the British Eocene flora, II, Gymnospermae: London, Palaeontographical Soc., 159 p.

_____1887a, On the leaf-beds and gravels of Ardtun, Carsaig, etc., in Mull: Geol. Soc. London Quart. Jour., v. 43, p. 270-300, pls. 43-48.

_____1887b, The Ardtun leaf-beds: Geol. Mag., v. 24, p. 91-92.

Gardner, J. S., and Ettingshausen, Constantin von, 1879, A monograph of the British Eocene flora: London, Palaeontographical Soc., 159 p.

Góczán, Ferenc, Groot, J. J., Krutsch, Wilfried, and Pacltová, Blanka, 1967, Die Gattungen des "Stemma Normapolles Pflug 1953b" (Angiospermae): Paläontologische Abhand., Abt. B, Paläobotanik, v. 2, no. 3, p. 429-539, 19 pls.

Good, Ronald, 1953, The Geography of the Flowering Plants: London, Longmans Green and Co., 452 p.

Grantz, Arthur, 1965, Strike-slip faults in Alaska: U.S. Geol. Survey Open-file Rept., 82 p.

Gray, Asa, 1878, Forest geography and archaeology: Am. Jour. Sci., v. 16, p. 85-94, 183-196.

Gray, Jane, 1960, Temperate pollen genera in the Eocene (Claiborne) flora: Science, v. 132, p. 808-810.

Hamilton, Warren, 1968, Cenozoic climatic change and its cause: Meteorol. Mon., v. 8, no. 30, p. 128-133.

Heer, Oswald, 1869, Flora fossilis Alaskana: Kgl. svenska vetensk. akad. Handl., v. 8, no. 4, 41 p., 10 pls.

________1878, Miocene Flora der Insel Sachalin: St. Petersbourg Acad. Imp. Sci., v. 25, no. 7, 61 p., 15 pls.

Hitchcock, C. L., Cronquist, Arthur, Owenbey, Marion, and Thompson, J. W., 1959, Vascular plants of the Pacific Northwest; Pt. 4, Hitchcock, C. L., Cronquist, Arthur, and Owenbey, Marion, Ericaceae through Campanulaceae: Washington Univ., Pubs. in Biology, v. 17, 510 p.

________1961, Vascular plants of the Pacific Northwest; Pt. 3, Hitchcock, C. L., and Cronquist, Arthur, Saxifragaceae to Ericaceae: Washington Univ., Pubs. in Biology, v. 17, 614 p.

________1964, Vascular plants of the Pacific Northwest; Pt. 2, Hitchcock, C. L., and Cronquist, Arthur, Salicaceae to Saxifragaceae: Washington Univ., Pubs. in Biology, v. 17, 597 p.

Hollick, Arthur, 1911, Results of a preliminary study of the so-called Kenai flora of Alaska: Am. Jour. Sci., v. 31, p. 327-330.

________1930, The Upper Cretaceous flora of Alaska: U.S. Geol. Survey Prof. Paper 159, 123 p., 87 pls.

________1936, The Tertiary floras of Alaska: U.S. Geol. Survey Prof. Paper 182, 185 p., 122 pls.

Hopkins, D. M., Scholl, D. W., Addicott, W. O., Pierce, R. L., Smith, P. J., Wolfe, J. A., Gershanovich, David, Kotonev, Boris, Lohman, K. E., and Obradovich, John, 196_, Cretaceous, Tertiary, and early Pleistocene rocks from the continental margin in the Bering Sea: Geol. Soc. America Bull., in press.

Huxley, T. H., 1870, The anniversary address of the President: Geol. Soc. London Quart. Jour., v. 26, p. xlii-xliv.

Iljinskaja, I. A., 1963, Iskolaemaya flora Gorshchi Kiin-Kerish Eaysanskogo basseyna [The fossil flora of the Mountain Kiin-Kerish Zaisan basin]: Akad. Nauk SSSR Inst. Botanicheskii Komarova Trudy, ser. 8, Palaeobotanica, v. 4, p. 141-187, 12 pls.

Knoblock, Ervín, and Kvaček, Zlatko, 1964, Byttneriophyllum tiliaefolium (Al. Braun) Knoblock et Kvaček in der tertiären Floren der Nordhalbkugel: Sborník Geol. Věd., řada P, sv. 5, p. 123-166, 12 pls.

Knowlton, F. H., 1894, A review of the fossil flora of Alaska: U.S. Natl. Mus. Proc., v. 17, p. 207-240, pl. 9.

Koch, B. E., 1963, Fossil plants from the lower Paleocene of the Agatdalen (Angmartussut) area, central Nugssuaq Peninsula, northwest Greenland: Medd. om Grønland, v. 172, no. 5, 120 p., 55 pls.

Krystofovich, A. N., 1929, Evolution of the Tertiary flora in Asia: New Phytologist, v. 28, p. 303-312.

______, ed., 1956, Oligotsenovalaia flora Gory Ashutas v Kazahstane [Oligocene flora of Mount Ashutas in Kazakhstan]: Akad. Nauk SSSR Inst. Botanicheskii Komarova Trudy, ser. 8, Palaeobotanica, v. 1, 179 p., 61 pls.

Krystofovich, A. V., 1960, Obosnovanie vydeleniya yarusov v Tretichn'ikh otlozheniy Sakhalina [The basis for separating out the stages of the Tertiary deposits of Sakhalin]: Akad. Nauk SSSR, Tr. Geol. Inst., vyp. 154, Paleont. sb. no. 2, p. 84-141.

______1964, Mollyuski Tretichn'ikh otlozheniy Sakhalina [Mollusks of the Tertiary deposits of Sakhalin]: Akad. Nauk SSSR, Tr. Geol. Inst., vyp. 232, 342 p., 55 pls.

Landsberg, H. E., 1964, Climate and climatology, in Dodge, J. V., ed., Encyclopedia Britannica: Chicago, William Benton, v. 5, p. 914-926.

Lathram, E. H., Pomeroy, J. S., Berg, H. C., and Loney, R. A., 1965, Reconnaissance geology of Admiralty Island, Alaska: U.S. Geol. Survey Bull. 1181-R, p. R1-R48, 2 pls.

Lesquereux, Leo, 1883, Contributions to the Miocene flora of Alaska: U.S. Geol. Survey Terr. Rept., v. 8, p. 257-263.

Li, H. L., 1963, Woody Flora of Taiwan: Narbeth, Pa., Livingston Publ. Co. and Morris Arboretum, 974 p.

MacGinitie, H. D., 1941, A middle Eocene flora from the central Sierra Nevada: Carnegie Inst. Washington Pub. 543, 178 p., 47 pls.

_____1953, Fossil plants of the Florissant beds, Colorado: Carnegie Inst. Washington Pub. 599, 198 p., 75 pls.

_____1962, The Kilgore flora: California Univ., Pubs. Geol. Sci., v. 35, no. 2, p. 67-158.

_____196_, The fossil flora of the Green River beds in northwestern Colorado and northeastern Utah: California Univ., Pubs. Geol. Sci. (In press).

MacKevett, E. M., 196_, Geologic map and sections of the McCarthy C-5 quadrangle, Alaska: U.S. Geol. Survey Geol. Quad. Map GQ-___. (In press).

MacNeil, F. S., 1965, Evolution and distribution of the genus *Mya*, and Tertiary migrations of Mollusca: U.S. Geol. Survey Prof. Paper 483-G, p. G1-G51, 11 pls.

MacNeil, F. S., Wolfe, J. A., Miller, D. J., and Hopkins, D. M., 1961, Correlation of Tertiary formations of Alaska: Am. Assoc. Petroleum Geologists Bull., v. 45, p. 1801-1809.

Manum, Sven, 1962, Studies in the Tertiary flora of Spitzbergen: Norsk Polarinst., Skr., no. 125, p. 7-124.

Martin, G. C., 1908, Geology and mineral resources of the Controller Bay region, Alaska: U.S. Geol. Survey Bull. 335, 141 p., 10 pls.

Martin, G. C., Johnson, B. L., and Grant, U. S., 1915, Geology and mineral resources of Kenai Peninsula: U.S. Geol. Survey Bull. 587, 243 p.

Martin, H. A., and Rouse, G. E., 1966, Palynology of late Tertiary sediments from the Queen Charlotte Islands, British Columbia: Canadian Jour. Botany, v. 44, p. 171-208.

Mason, H. L., 1947, Evolution of certain floristic associations in western North America: Ecol. Mon., v. 17, p. 201-210.

Mendenhall, W. C., 1902, Reconnaissance from Fort Hamlin to Kotzebue Sound, Alaska, by way of Dall, Kanuti, Allen, and Kowak rivers: U.S. Geol. Survey Prof. Paper 10, 68 p.

Milankovitch, M., 1938, Astronomische Mittel zur Erforschung der erdgeschichtlichen Klimate: Handbuch der Geophysik, bd. 9, pt. 3, p. 593-698.

Miller, D. J., 1957, Geology of the southeastern part of the Robinson Mountains, Yakataga district, Alaska: U.S. Geol. Survey Oil and Gas Inv. Map OM-187.

_____1961a, Geology of the Katalla district, Gulf of Alaska Tertiary province, Alaska: U.S. Geol. Survey Open-file map, June 2, 1961.

_____1961b, Geology of the Yakataga district, Gulf of Alaska Tertiary province, Alaska: U.S. Geol. Survey Open-file map, June 2, 1961.

_____1961c, Geology of the Lituya district, Gulf of Alaska Tertiary province, Alaska: U.S. Geol. Survey Open-file map, June 2, 1961.

Moore, E. J., 1963, Miocene marine mollusks from the Astoria formation in Oregon: U.S. Geol. Survey Prof. Paper 419, 109 p., 32 pls.

Moore, G. W., 1969, New formations on Kodiak and adjacent islands, Alaska, *in* Cohee, G. V., and others, Contributions to stratigraphy 1969: U.S. Geol. Survey Bull. 1274-A, p. A27-A35.

Nemejč, F., 1964, Biostratigraphic sequence of floras in the Tertiary of Czechoslovakia: Časopis pro mineralogii a geologii, Rōcnik, v. 9, p. 107-109

Newberry, J. S., 1890, The Laramie group - its geological relations, its economic importance, and its fauna and flora: New York Acad. Sci. Trans., v. 9, p. 27-32.

Peacock, J. T., and McMillan, Calvin, 1968, The photoperiodic response of American Prosopis and Acacia from a broad latitudinal distribution: Am. Jour. Botany, v. 55, p. 153-158.

Peck, D. L., Griggs, A. G., Schlicker, H. G., Wells, F. G., and Dole, H. M., 1964, Geology of the central and northern parts of the Western Cascade Range in Oregon: U.S. Geol. Survey Prof. Paper 449, 56 p.

Plafker, George, 1967, Geologic map of the Gulf of Alaska Tertiary province, Alaska: U.S. Geol. Survey Misc. Geol. Inv. Map I-484.

Plafker, George, and Miller, D. J., 1957, Reconnaissance geology of the Malaspina district, Alaska: U.S. Geol. Survey Oil and Gas Inv. Map OM-189.

Potbury, S. S., 1935, The La Porte flora of Plumas County, California: Carnegie Inst. Washington Pub. 465, p. 29-82, 19 pls.

Raunkiaer, C., 1934, The life forms of plants and statistical plant geography: Oxford, Clarendon Press, 632 p.

Reid, M. E., and Chandler, M. E. J., 1933, The London Clay flora: London, British Mus. (Nat. History), 561 p., 33 pls.

Richards, P. W., 1952, The Tropical Rain Forest: Cambridge, Cambridge Univ. Press, 450 p., 15 pls.

Sanborn, E. I., 1935, The Comstock flora of west central Oregon: Carnegie Inst. Washington Pub. 465, p. 1-28, 10 pls.

Scott, R. A., and Barghoorn, E. S., 1955, The occurrence of Euptelea in the Cenozoic of western North America: Jour. Arnold Arbor., v. 36, p. 259-265, 3 pls.

Sinelnikova, V. N., Skiba, L. A., and Fotianova, L. I., 1967, On the Pliocene (Enemtensky) flora of western Kamchatka: Akad. Nauk SSSR Izvestiia, Geol. Ser., no. 8, p. 114-124 (in Russian). English translation by Lydia A. Hutchison, 1968.

Steenis, C. G. G. J., van, 1962, The land-bridge theory in botany: Blumea, v. 11, p. 235-372.

Stoneley, Robert, 1967, The structural development of the Gulf of Alaska sedimentary province in southern Alaska: Geol. Soc. London Quart. Jour., v. 123, p. 25-57.

Takhtajan, A. L., 1957, Kvolrosu o lroiskhozhdenii umerennoi flory Evraeii [On the origin of the temperate flora of Eurasia]: Akad. Nauk SSSR, Bot. Zhurnal, v. 42, p. 1635-1653.

Tanai, Toshimasa, 1961, Neogene flora change in Japan: Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 2, p. 119-298, 32 pls.

Tarr, R. S., 1906, The Yakutat Bay region, *in* Brooks, A. H., and others, Report on progress of investigations of mineral resources of Alaska in 1905: U.S. Geol. Survey Bull. 284, p. 61-64.

Tobin, D. G., and Sykes, L. R., 1968, Seismicity and tectonics of the northeast Pacific Ocean: Jour. Geophys. Res., v. 73, no. 12, p. 3821-3845.

Tralau, Hans, 1968, Evolutionary trends in the genus *Ginkgo*: Lethaea, v. 1, p. 63-101.

Vakhrameyev, V. A., 1966, Botanic-geographic zonality in the geologic past and the evolution of the plant kingdom: Paleont. Zhur., no. 1, p. 6-18 (in Russian). English translation available from Telberg Book Co., New York, N. Y.

Vine, F. J., 1966, Spreading of the ocean floor: new evidence: Science, v. 154, p. 1405-1415.

Vlasov, G. M., 1964, Paleogene and Neogene climatic fluctuations in the Far East: Doklady Akad. Nauk SSSR, v. 157, p. 589-592. English translation published by Am. Geol. Inst., 1965, p. 17-20.

Vokes, H. E., and Snavely, P. D., 1948, The age and relationships of the Eugene and Fisher formations: Geol. Soc. Oregon Country News Letter, v. 14, p. 39-41.

Vokes, H. E., Snavely, P. D., and Myers, D. A., 1951, Geology of the southern and southwestern border areas of the Willamette Valley, Oregon: U.S. Geol. Survey Oil and Gas Inv. Map OM-110.

Wahrhaftig, Clyde, Wolfe, J. A., Leopold, E. B., and Lanphere, M. A., 1969, The coal-bearing group in the Nenana coal field, Alaska: U.S. Geol. Survey Bull. 1274-D, p. D1-D30.

Wang, Chi-Wu, 1961, The forests of China: Harvard Univ., Maria Moors Cabot Found., Pub. 5, 313 p.

Waring, C. B., 1884, The uniformity of geological climate in high latitudes: New York Acad. Sci. Trans., v. 3, p. 84-94.

Weaver, C. E., and others, 1944, Correlation of the marine Cenozoic formations of western North America: Geol. Soc. America Bull., v. 55, p. 569-598.

Webb, L. J., 1959, Physiognomic classification of Australian Rain forests: Jour. Ecology, v. 47, p. 551-570, pls. 14-17.

Wolfe, J. A., 1961, Age of the Keechelus andesitic series of the Cascade Range, Washington: U.S. Geol. Survey Prof. Paper 424-C, art. 232, p. C228-C230.

_____1964, Miocene floras from Fingerrock Wash, southwestern Nevada: U.S. Geol. Survey Prof. Paper 454-N, p. N1-N36, 12 pls.

_____1966, Tertiary plants from the Cook Inlet region, Alaska: U.S. Geol. Survey Prof. Paper 398-B, p. B1-B32, 8 pls.

_____1968, Paleogene biostratigraphy of nonmarine rocks in King County, Washington: U.S. Geol. Survey Prof. Paper 571, 33 p., 7 pls.

Wolfe, J. A., and Hopkins, D. M., 1967, Climatic changes recorded by Tertiary land floras in northwestern North America, *in* Hatai, Kotora, ed., Tertiary Correlation and Climatic Change in the Pacific: Pacific Sci. Cong., 11th, Tokyo, Aug.-Sept., 1966, Symposium 25, p. 67-76.

Wolfe, J. A., Hopkins, D. M., and Leopold, E. B., 1966, Tertiary stratigraphy and biostratigraphy from the Cook Inlet region, Alaska: U.S. Geol. Survey Prof. Paper 398-A, p. A1-A29, 2 pls.

Wolfe, J. A., and Leopold, E. B., 1967, Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia, in Hopkins, D. M., ed., The Bering Land Bridge: Stanford, Calif., Stanford Univ. Press, p. 193-206.

Zhilin, S. G., 1966, A new species of Carya from the late Oligocene: Paleont. Zhur., no. 4, p. 104-108 (in Russian). English translation available from Telberg Book Co., New York, N. Y.

Illustrations of some critical fossils

Open-file reports such as the present one could be considered as valid publication under Article 29 of the International Rules of Botanical Nomenclature; the reports are produced by offset and are available to the general public. Consequently no new names or combinations are here introduced and the morphologic basis for the systematic position of the plants is not discussed in this report. Following, however, are some illustrations of fossils critical to the floristic, vegetational, and stratigraphic interpretations presented previously. Hollick (1936) illustrated many fossils from the lower Ravenian (early late Eocene) from localities 3846, 3847, and 3879; these specimens have been determined as follows:

Hollick, 1936	Present determination
Pl. 3, fig. 1	Dryopteris sp.
Pl. 4, figs. 1, 2, 5, 6	Dryopteris sp.
Pl. 5, fig. 1	Hemitelia pinnata MacG.
Pl. 5, fig. 5	Dryopteris sp.
Pl. 18, figs. 2, 3	Glyptostrobus sp.
Pl. 23, fig. 4	Celastrus comparabilis Holl.
Pl. 56, fig. 4	Melanorrhoea sp.
Pl. 58, figs. 1-3	Platycarya sp.
Pl. 59, figs. 1-4	Alnus sp.
Pl. 60, fig. 1a	Goweria dilleri Wolfe
Pl. 60, fig. 1b	indet. leaf
Pl. 63, fig. 1	Myristica sp.
Pl. 63, fig. 2	indet. leaf
Pl. 63, fig. 3	Cananga sp.
Pl. 64, fig. 2	Cinnamomophyllum sp. [Neolitsea lata MacG.]
Pl. 65, fig. 1	Luvunga sp.
Pl. 66, fig. 5	Alangium sp.
Pl. 75, fig. 1a	Celastrus comparabilis Holl. (holotype)
Pl. 75, fig. 1b	Allantodiopsis pugetensis Wolfe
Pl. 78, figs. 1, 2	Knema sp.
Pl. 79, figs. 1, 2	Parashorea sp.
Pl. 93, fig. 3	from loc. 5892, Chickaloon Formation, Paleocene
Pl. 93, fig. 6	Myristica sp.
Pl. 93, fig. 7	Melanorrhoea sp.
Pl. 98, fig. 7	Laurophyllum sp. [Cryptocarya presamarensis Sanb.]
Pl. 99, fig. 1	Mastixia
Pl. 99, figs. 2, 3	Parashorea sp.
Pl. 99, fig. 4	indet. leaf
Pl. 114, fig. 10	Laurophyllum sp.
Pl. 115, fig. 1	Laurophyllum sp. [Cryptocarya presamarensis Sanb.]
Pl. 118, fig. 1	aff. Tinomiscium sp.
Pl. 120, figs. 3, 4	Paleophytocrene sp.

Between Hollick (1936) and this report, 55 species from the Gulf of Alaska Ravenian and Kummerian have been illustrated.

Plate 1

[All figures natural size except for 9]

Figure 1. Hemitelia pinnata MacG. Loc. 3846, Kushtaka Formation.
2. Laurophyllum sp. [Laurus similis Knowlt.]. Loc. 11157, Kushtaka Formation.
3. Platycarya sp. [Ulmus pseudobrauni Holl.]. Loc. 11170, Kulthieth Formation.
4. Girroniera sp. Loc. 11158, Kushtaka Formation.
5. Allantodiopsis pugetensis Wolfe. Loc. 11159, Kushtaka Formation.
6. Limacia sp. Loc. 11159, Kushtaka Formation.
7. Anamirta sp. Loc. 11170, Kulthieth Formation.
8. Alnus sp. Loc. 11170, Kulthieth Formation.
9. Sabalites sp. Loc. 11160, Kushtaka Formation.

Plate 2

[All figures natural size]

Figure 1. Stemonurus sp. Loc. 11158, Kushtaka Formation.
2. Meliosma sp. Loc. 11170, Kulthieth Formation.
3. Euodia sp. Loc. 11158, Kushtaka Formation.
4. Clerodendrum sp. Loc. 11158, Kushtaka Formation.
5. Parashorea sp. [Rhamnus pseudogoldianus Holl.]. Loc. 3847, Kushtaka Formation.
6. Phytocrene sordida (Lesq.) MacG. Loc. 11170, Kushtaka Formation.
7. Phytocrene sp. Loc. 11158, Kushtaka Formation.

Plate 3

[All figures natural size]

Figure 1. *Dicotylophyllum* sp. [*Artocarpoides kummerensis* Wolfe]. Loc. 11164, Kushtaka Formation.
2. *Phoenicites* sp. Loc. 11165, Kushtaka Formation.
3. *Laurophyllum* sp. [*Laurus similis* Knowlt.]. Loc. 11165, Kushtaka Formation.
4. *Pterocarya pugetensis* Wolfe. Loc. 11165, Kushtaka Formation.
5. *Laurophyllum* sp. Loc. 11165, Kushtaka Formation.
6. *Lygodium* sp. Loc. 9389, Kushtaka Formation.
7. *Calkinsia* sp. Loc. 11165, Kushtaka Formation.
8. *Sapindus*? sp. Loc. 11165, Kushtaka Formation.
9. *Carya cashmanensis* Wolfe. Loc. 11165, Kushtaka Formation.
10. *Dryophyllum pugetensis* Wolfe. Loc. 11165, Kushtaka Formation.

Plate 4

[All figures natural size]

Figure 1. *Tilia* sp. Loc. 11167, Kushtaka Formation.
2. *Juglans* sp. Loc. 11167, Kushtaka Formation.
3. *Ilex* sp. Loc. 11167, Kushtaka Formation.
4. *Alnus cuprovallis* Axelr. Loc. 11167, Kushtaka Formation.
5. *Willisia* sp. Loc. 11167, Kushtaka Formation.
6. *Corylopsis* sp. Loc. 11167, Kushtaka Formation.
7. *Salix* sp. Loc. 11167, Kushtaka Formation.
8. *Magnolia reticulata* Chan. and Sanb. Loc. 11168, Katalla Formation.
9. *Macclintockia pugetensis* Wolfe. Loc. 9891, Kushtaka Formation.
10. *Laurophyllum* sp. Loc. 11169, Kushtaka Formation.
11. *Laurophyllum* sp. Loc. 9551, Kulthieth Formation.
12. *Laurophyllum* sp. [*Cryptocarya presamarensis* Sanb.]. Loc. 11169, Kushtaka Formation.

Plate 5

Figure 1. *Pterocarya pugetensis* Wolfe. Loc. 11167 (Upper Ravenian), Kushtaka Formation.
2. *Sorbus* sp. Loc. 11167 (Upper Ravenian), Kushtaka Formation.
3. A. *Myristica* sp. [*Magnolia ovalis* of Holl.]. Loc. 3847 (Lower Ravenian), Kushtaka Formation.
   B. *Myristica ceylanica* DC. Modern leaf from Mindoro, Philippine Islands.
4. A, C. *Barringtonia* sp. Loc. 11170 (Lower Ravenian), Kulthieth Formation.

Plate 5--continued

Figure 4. B, D. *Barringtonia acutangula* (L.) Gaertn. Modern leaf from Luzon, Philippine Islands.
5. A. *Cananga* sp. [*Magnolia wormskioldi* of Holl.]. Loc. 3879 (Lower Ravenian), Kulthieth Formation.
   B. *Cananga odorata* Baill. Modern leaf from Luzon, Philippine Islands.
6. A. *Saurauia* sp. Loc. 3846 (Lower Ravenian), Kushtaka Formation.
   B. *Saurauia reinwardtiana* Miq. Modern leaf from Java, Indonesia.
7. A. *Eugenia* sp. Loc. 11170 (Lower Ravenian), Kulthieth Formation.
   B. *Eugenia jambos* L. Modern leaf from Luzon, Philippine Islands.
8. A. *Knema* sp. [*Rhamnus marginatus* of Holl.]. Loc. 3847 (Lower Ravenian), Kushtaka Formation.
   B. *Knema glauca* (Blanco) Merr. Modern leaf from Mindanao, Philippine Islands.
9. A. *Alnus cuprovallis* Axelr. Copper Basin assemblage (Late Ravenian), Nevada.
   B. *Alnus cuprovallis* Axelr. Loc. 11167 (Upper Ravenian), Kushtaka Formation.
10. A. *Parashorea* sp. [*Rhamnites cashmanensis* Wolfe]. Loc. 9731 (Middle Ravenian), Puget Group, Washington.
   B. *Parashorea malaanonan* (Blanco) Merr. Modern leaf from British North Borneo.
   C. *Doona* sp. [*Rhamnidium chaneyi* Potb.]. LaPorte assemblage (Kummerian), California.
   D. *Doona ovalifolia* Shw. Modern leaf from Ceylon.
   E. *Rhamnidium elaeocarpa* Reiss. Modern leaf from Paraguay.
11. A, C. *Parashorea* sp. [*Rhamnus pseudogoldianus* Holl.]. Loc. 3847 (Lower Ravenian), Kushtaka Formation.
   B, D. *Parashorea melaanonan* (Blanco) Merr. Modern leaf from British North Borneo.

Plate 6

Figure 1. A, C. *Luvunga* sp. [*Persea spatiosa* Holl.]. Loc. 3847 (Lower Ravenian), Kushtaka Formation.
   B, D. *Luvunga latifolia* Tan. Modern leaf from British North Borneo.
2. A. *Meliosma* sp. Loc. 11170 (Lower Ravenian), Kulthieth Formation.
   B. *Meliosma pungens* Walp. Modern leaf from Salween watershed, southern China.
3. A. *Platycarya* sp. [*Ulmus pseudobrauni* Holl.]. Loc. 11170 (Lower Ravenian), Kulthieth Formation.
   B. *Platycarya strobilacea* Sieb. and Zucc. Modern leaf from central China.

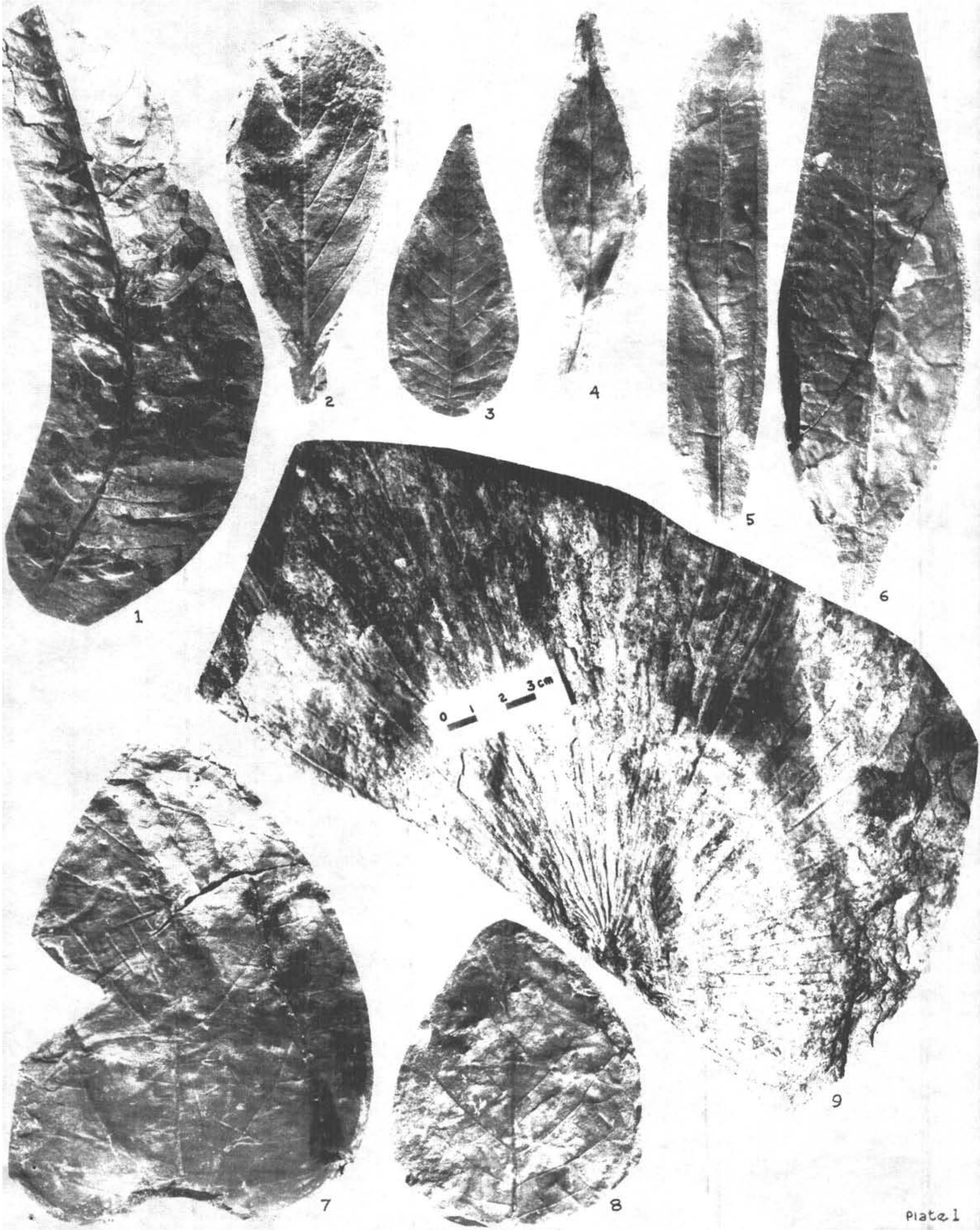
Plate 6--continued

Figure 4. A, C. Melanorrhoea sp. [Semecarpus alaskana Holl.]. Locs. 3847, 11158 (Lower Ravenian), Kushtaka Formation.

B. Melanorrhoea macrocarpa Engl. Modern leaf from British North Borneo.

5. A. Stemonurus sp. Loc. 11158 (Lower Ravenian), Kushtaka Formation.

B. Stemonurus scorpioides Becc. Modern leaf from Sumatra, Indonesia.



LOWER RAVENIAN

Plate 1

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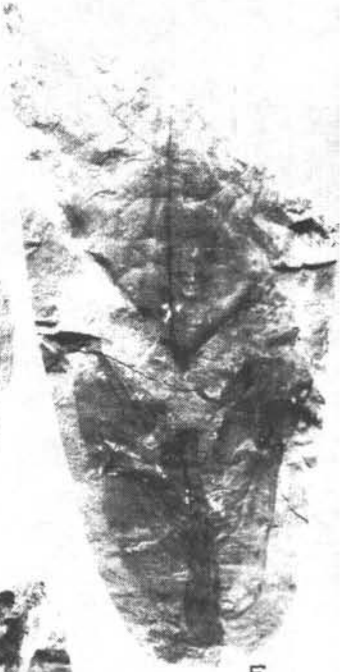

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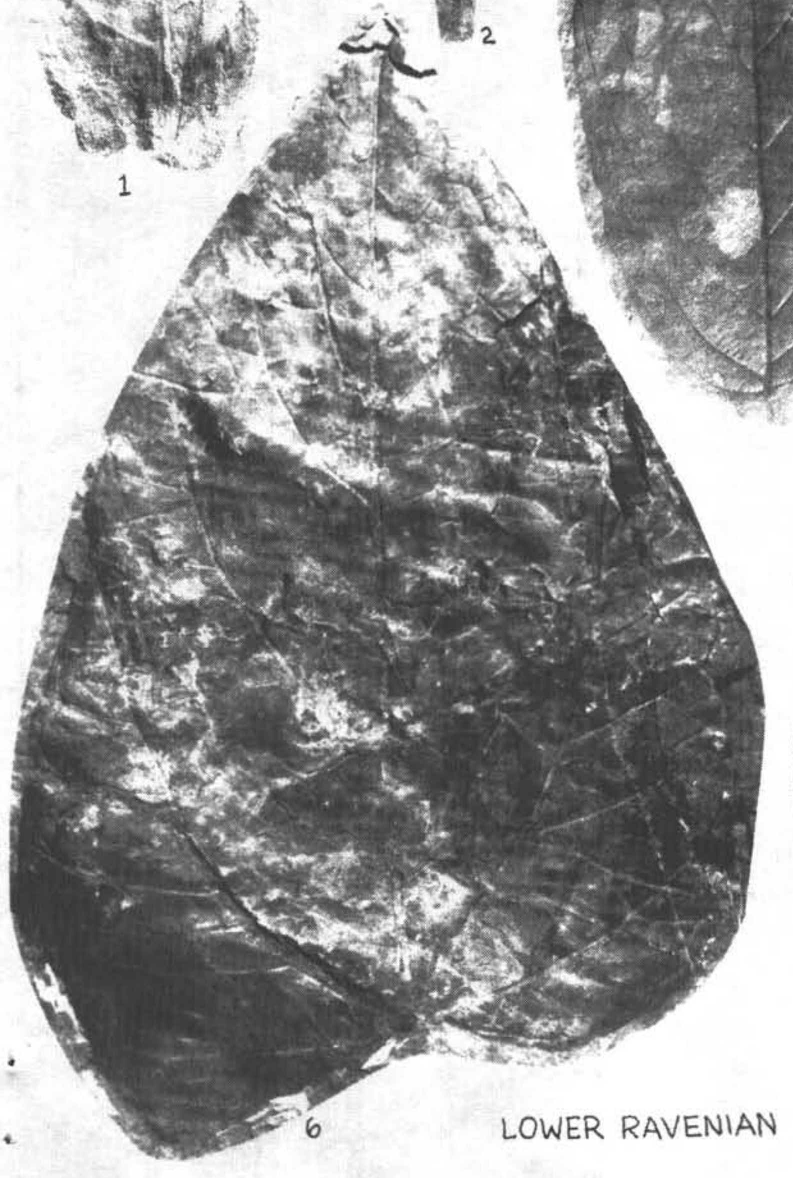

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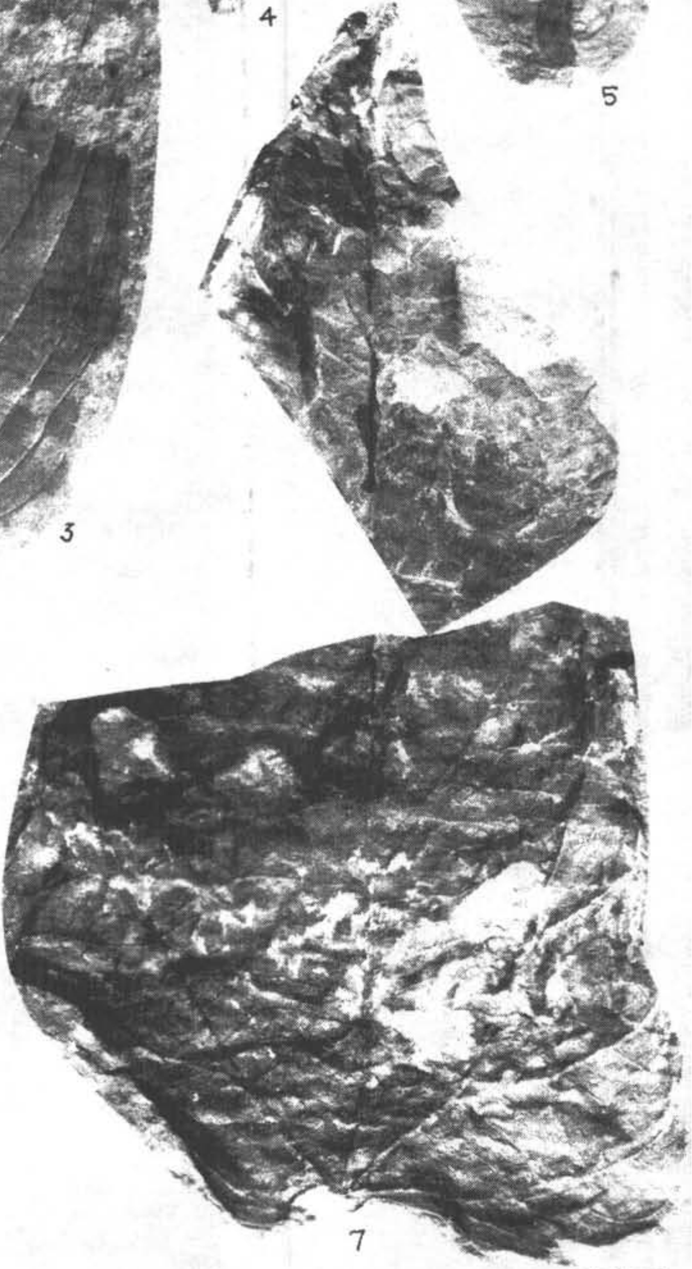

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LOWER RAVENIAN

Plate 2


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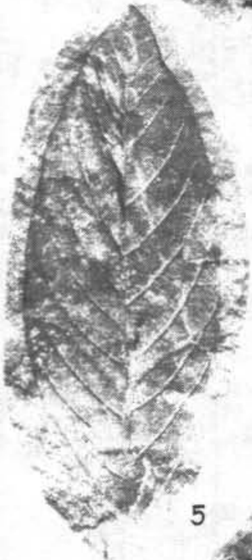
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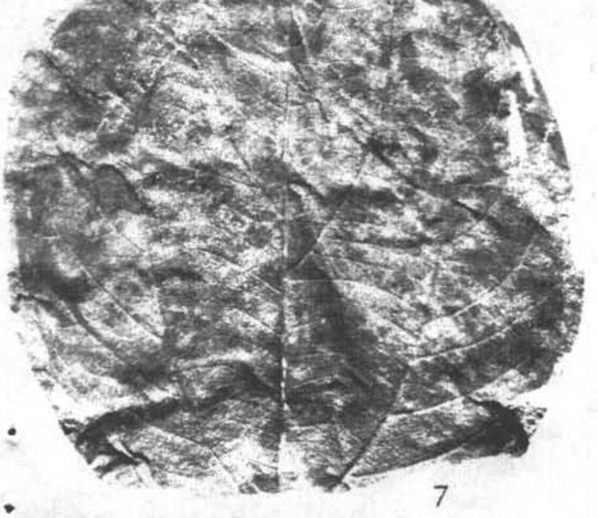
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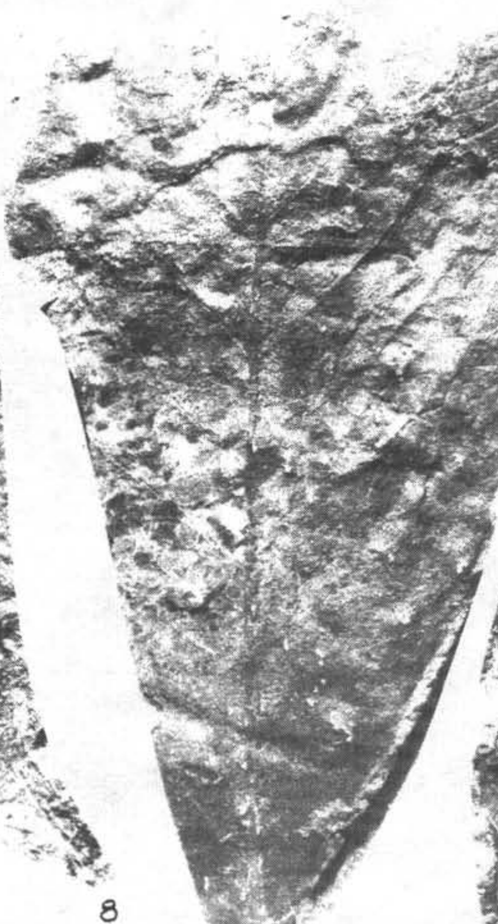
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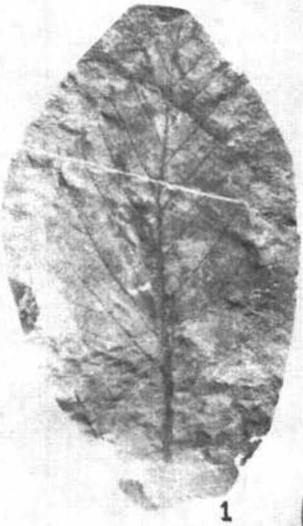
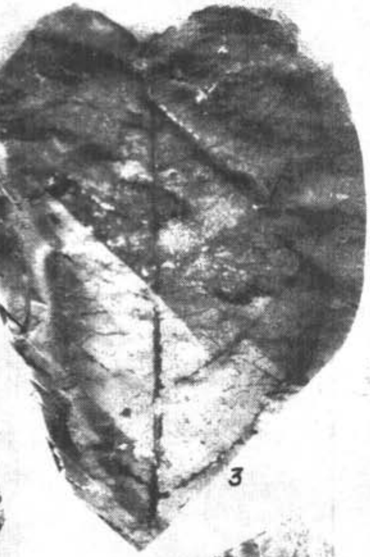
MIDDLE RAVENIAN

Plate 3


1


2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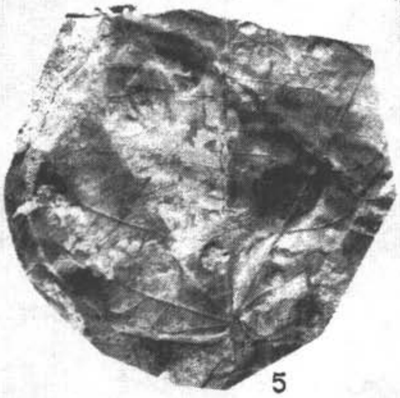
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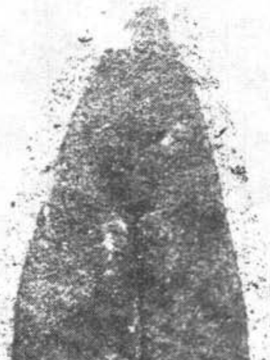
6


7

UPPER RAVENIAN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9

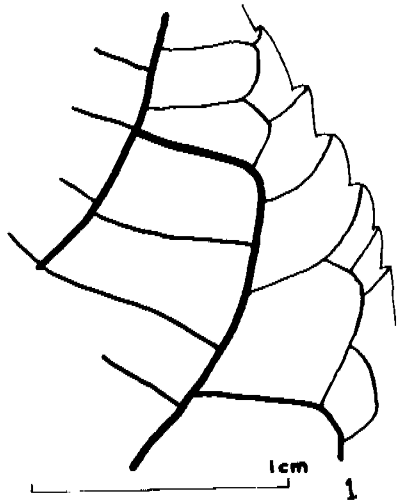

10


11


12

KUMMERIAN

Plate 4



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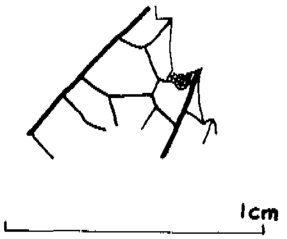

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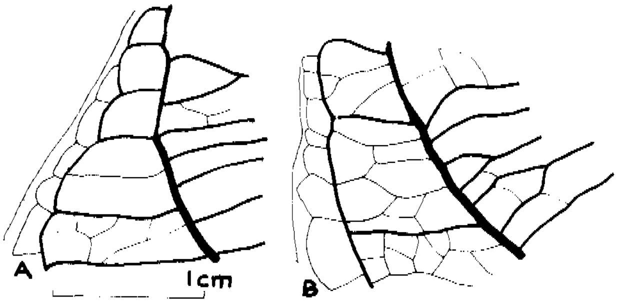

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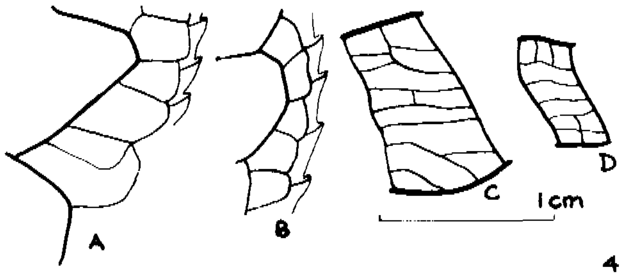

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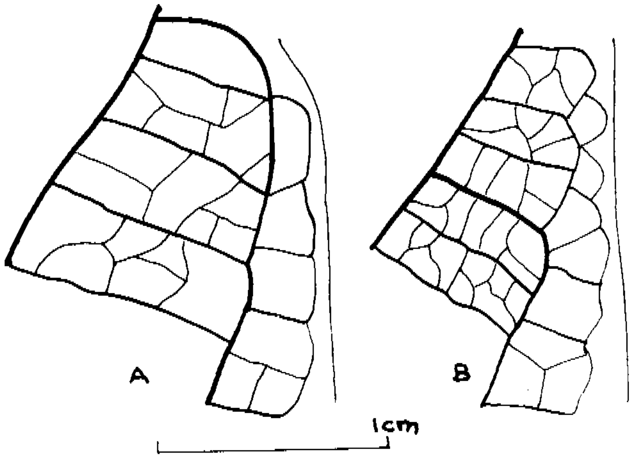

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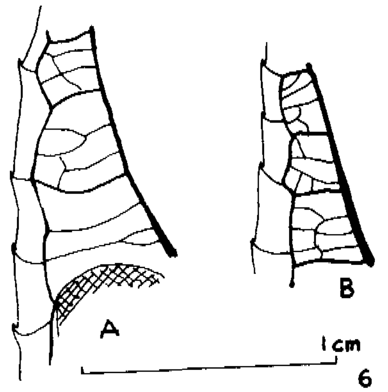

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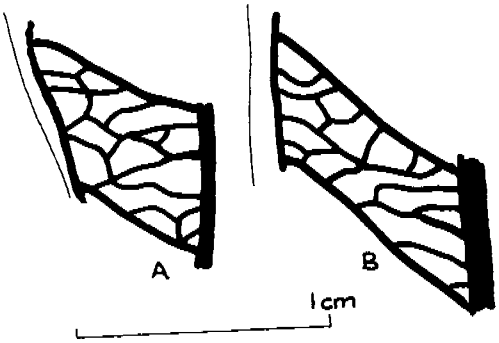

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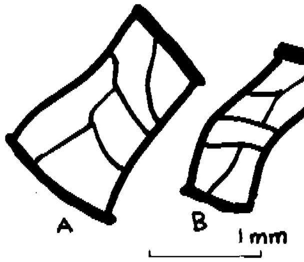

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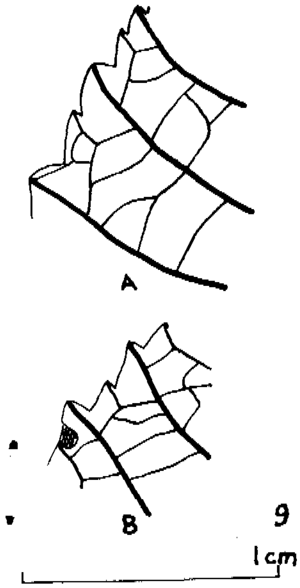

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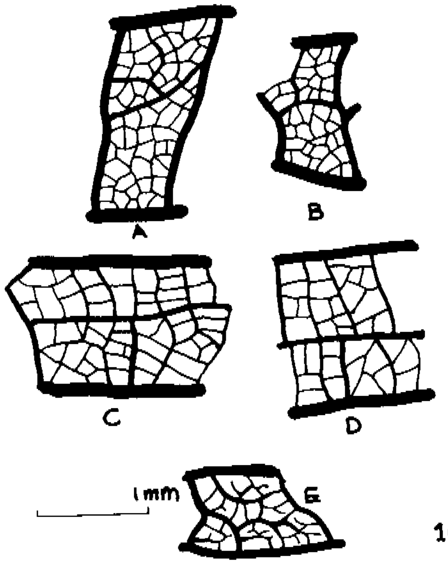

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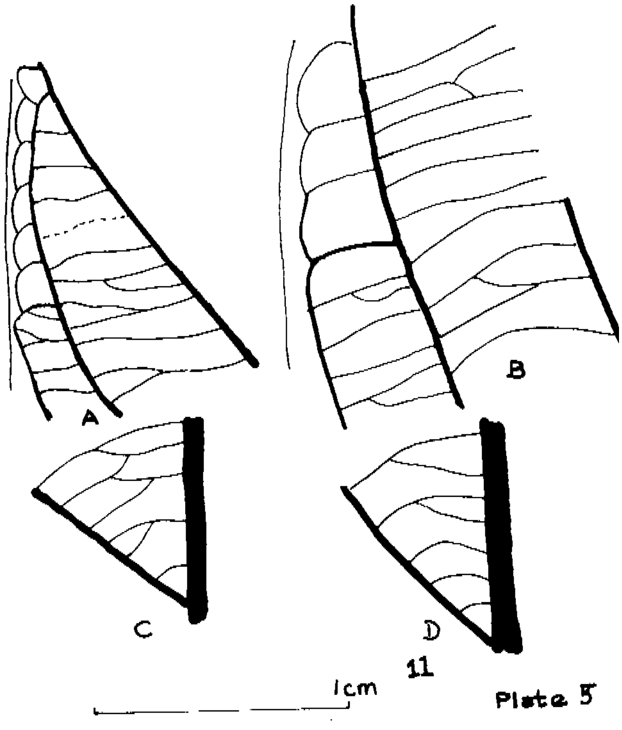

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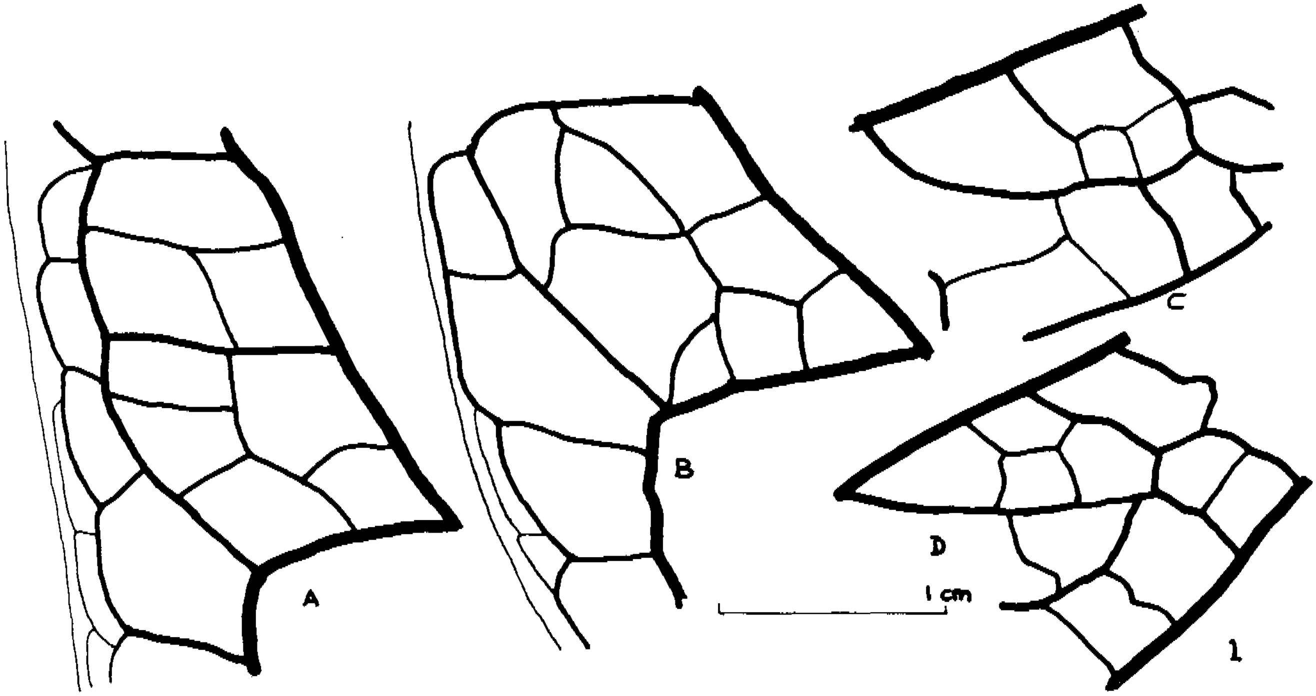
Plate 5



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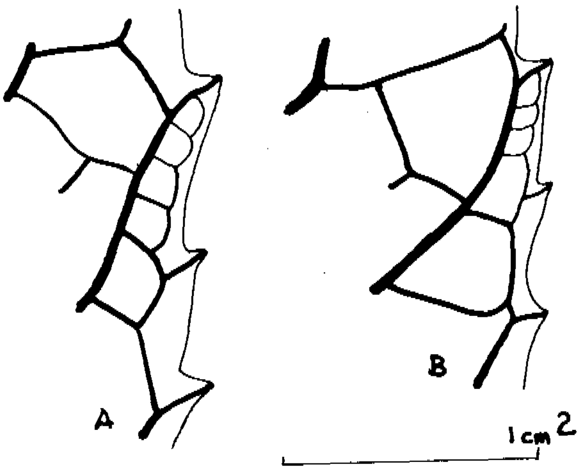

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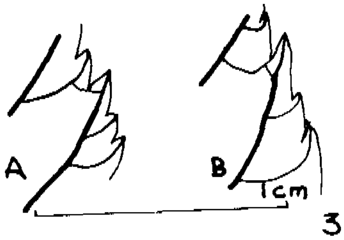

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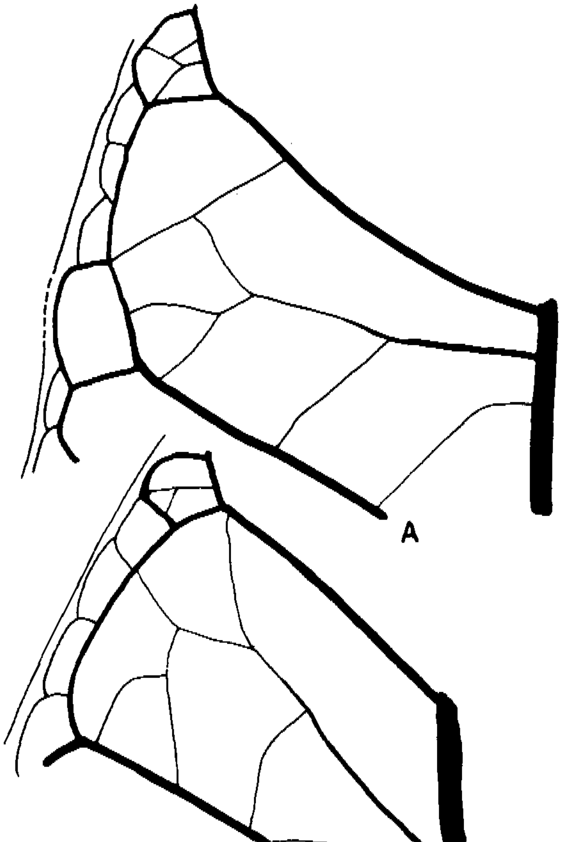

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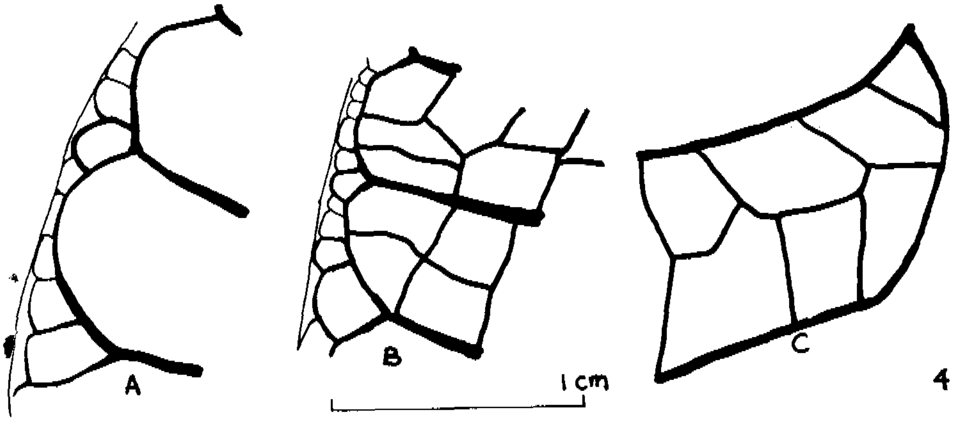

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Plate 6