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SYSTEMATICS, PHYLOGENY, AND DISTRIBUTION OF *ACER* (MAPLES) IN THE CENOZOIC OF WESTERN NORTH AMERICA

by

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(with 18 Text-figures, 10 Tables and 61 plates)

Contents

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Abstract

The known fossil fruits and leaves of *Acer* from western North America represent 91 species and 28 sections, 12 of which are extinct and are described as new sections of *Acer*. Sixty-four species are described as new, 2 new combinations are proposed, and 6 species are left unnamed; 21 have been previously described. The most diverse sections of *Acer* in the Tertiary of western North America are the extinct *Glabroidea* (at least 13 species), *Negundo* (9 species), *Macrophylla* (8 species), and *Eriocarpa* (8 species). Descriptions of almost all the species are presented, and all species are illustrated.

Although Aceraceae are considered to be derivatives of an early, extinct group of Sapindaceae, Paullinieae (rather than Harpullieae) are considered to be the extant tribe of Sapindaceae most closely related to Aceraceae. A cladistic analysis of Aceraceae and of *Acer* includes Sapindaceae, *Dipteronia*, and the "*Acer*" *arcticum* complex, which is thought to represent an extinct genus of Aceraceae. The cladistic analysis based on extant *Acer* results in the subdivision of *Acer* into 4 informal groups: *Spicata* Group, *Macrantha* Group, *Macrophylla* Group (including section *Acer* and allies), and the *Platanoidea* Group.

Timing of first appearances of the various groups and sections in the fossil record generally parallel the cladistic analysis. The *Spicata* Group is the oldest (latest Paleocene); this group includes three extinct sections in the early middle Eocene, all of which became extinct by the late middle Eocene. First known in the early middle Eocene are extinct sections of the *Macrantha* and *Macrophylla* groups; extant sections of these groups appear by the late middle to early late Eocene. The *Platanoidea* Group appeared in the late middle Eocene, and extant sections appeared by the latest Eocene. A fifth group, the *Orba* Group, is known only as fossil and represents sections that diverged between the divergences of the *Macrantha* and *Macrophylla* groups.

Diversification of *Acer* at the sectional level appears to have taken place in a volcanic upland region in western North America during the Eocene. Although possibly a mesothermal genus during the late Paleocene and early Eocene, *Acer* diversified greatly during the middle and late Eocene as microthermal climates increased in area. During the early middle Eocene, 10 sections (all extinct) and 11 species of *Acer* are known. During the late middle to late Eocene, *Acer* reached maximal diversity in western North America: at least 34 species and 15 sections are known, and occurrences of other species and sections can be inferred. *Acer*, however, was apparently a very minor element in Eocene microthermal vegetation. Sectional diversification of *Acer* was largely completed by the end of the Eocene, although a few derivative sections may be of post-Eocene age. *Acer* reached maximum abundance in western North America during the early and middle Miocene: at least 29 species and 10 sections are known. Following the middle Miocene, *Acer* underwent a major decline in diversity and abundance in western North America; this decline was due primarily to declining summer temperatures at high latitudes and increasing aridity at middle latitudes.

Present distributions of sections and species of *Acer* have resulted from a complex history of dispersals and vicariant events, most of which are related to climate. Probable origin of many extant Asian sections of *Acer* in western North America during the Eocene implies many dispersals from North America to Asia during the Eocene. Many extinct and extant sections of *Acer* became extinct on North America during the late Eocene and early Oligocene; some of these extant sections re-entered North America during the late Oligocene and Miocene but again became extinct during the Miocene.

Cladistic relationships of series Saccharodendron strongly indicate an origin in western Eurasia. Appearance of this section in North America during the early Miocene and absence of a Beringian fossil record indicate long-distance dispersal across the Atlantic Ocean. Absence of a Tertiary record in western North America of *Palmata* indicates a long-distance dispersal from eastern Asia.

Introduction

The genus *Acer*, which has at least 140 extant species (Ogata, 1967), is the largest genus of broad-leaved deciduous trees that today dominate the broad-leaved deciduous forests of the Northern Hemisphere. *Acer* is also found as an accessory to coniferous forests and is a component of broad-leaved evergreen forests in the Northern Hemisphere. In Asia, *Acer* occurs in upland equatorial forests in Java, and, in North America, *Acer* ranges from upland forests in central America north to the southern part of the Taiga in central Canada and southeastern Alaska.

Because of the broad geographic and climatic range and the importance of *Acer* in Northern Hemisphere forests, the genus has occupied a central position in discussions of the historical biogeography of the Northern Hemisphere. *Acer*, moreover, has an extensive representation in Tertiary assemblages and has thus been considered a prime example of an arcto-tertiary genus (Engler, 1883). Understanding the phylogeny and distribution of *Acer* in time and space may reveal patterns that are applicable to other genera of Northern Hemisphere broad-leaved deciduous trees and shrubs.

The North American Tertiary *Acer* fossils are commonly placed in about 20 species. Most paleobotanists have concentrated on finding a "modern equivalent" species for each fossil species. For example, most fossil material that has a similarity to the extant *A. macrophyllum* has been assigned to *A. oregonianum*, which has a supposed range of Eocene through Pliocene. In contrast, our analysis indicates that at least five clearly defined species have been assigned to *A. oregonianum* and that these segregate species have comparatively short stratigraphic ranges. Further, the "modern equivalent" methodology has resulted in a putative modernity of fossil *Acer*, even in the Eocene, and paleobotany has thus contributed little to understanding the phylogeny of the genus.

Not only have paleobotanical studies contributed little, comparative systematic studies of modern *Acer* have not yielded a consensus of phyletic relationships in the genus. Despite the extensive literature on modern *Acer* (for example, Pax, 1890; Pojarkova, 1933; Momotani, 1962; Ogata, 1967), phyletic interpretations have varied widely from one author to another. Part of this variation has resulted from lack of consensus on which floral characters are advanced (specialized) and which are less advanced ("primitive"), as well as from the general uniformity of many character states throughout the genus.

Systematists dealing with modern *Acer* have generally been most concerned with grouping species that are thought to be closely related into sections (and, in some instances, into series). The trend has been to recognize an increasingly large number of sections. Ogata (1967) recognized 33 supraspecific categories, including 26 sections, and de Jong (1976) recognized 26 supraspecific categories, including 14 sections. Intersectional relationships are generally not well understood, although in some instances there is consensus that certain sections are closely related (for example, *Acer, Goniocarpa*, and *Saccharina*).

In our study, because the fossil record of *Acer* is comprised primarily of fruits and leaves, we have concentrated on detailed examinations of the characters of these organs in extant *Acer*. This concentration both adds to the number of characters involved in a phyletic analysis of modern *Acer* and allows valid interpretations of the fossils. The fossil record is particularly significant; we consider that many characters present in early species of *Acer* are in their primitive state for the genus. That the alternative character(s) are advanced is indicated both by their later appearance in the fossil record and their distribution among extant sections. Some fossils may also combine characters of two or more extant sections and thus serve as a basis for inferring a common ancestry of these sections.

If the phylogeny of *Acer* can be inferred, and if fossil material can be validly placed in this phylogenetic framework, then the historical biogeography of the genus can be inferred. Numerous sections of the genus are now disjunct, but relative ages of sections and disjunctions have been unknown. *Acer* has been presumed, because of present great sectional and specific diversity in this area, to have originated and diversified in eastern Asia; documentation for this premise from fossils is lacking. Although we have previously presented some ideas on the biogeography of fossil *Acer* (Tanai and Wolfe, 1981; Wolfe, 1981), since presentation of those ideas we have totally reanalyzed material of fossil *Acer* from western North America; much newly available Eocene material has been included in the current analysis and has formed the basis for extensive revision of some of our earlier concepts regarding the phylogeny of *Acer*.

Because the fruits of *Acer* are winged (samaroid), they have settling velocities approaching those of leaves, and thus fruits and leaves of *Acer* co-occur in many Tertiary beds. Co-occurrence of fruits and leaves of the same genus offers an unusual data base for interpreting systematic position of fossil species, assuming that proper linkage of a particular fruit type with a particular leaf type has been validly inferred. Co-occurrence of different organs also allows an evaluation of one of the most vexing problems in paleobotany: possibility of divergent rates of evolution in different organs.

At least 2,000 specimens of fossil *Acer* have been examined during the present study. These specimens represent collections from at least 170 localities in western North America. The sparse material of *Acer* from the Tertiary of eastern North America was also examined but contributed nothing to understanding the phylogeny and biogeography of the genus.

The present study would have been impossible without the cooperation of many colleagues, who have either sent specimens or have allowed us to examine unpublished collections. Particularly helpful throughout the present study has been Howard E. Schorn. Included in the present study is material from the following collections: Universities of Alberta, British Columbia, California (Berkeley and Davis), Colorado, Idaho, Michigan, Montana, Oregon, and Washington; Harvard, Michigan State, Simon Fraser, and Yale (collections formerly at the New York Botanical Garden) Universities; California Academy of Sciences, Denver Museum of Natural History, Field Museum of Natural History (collections formerly at the University of Chicago Walker Museum), Oregon Museum of Science and Industry, Tyrrell Museum of Palaeontology, and the U.S. National Museum. Colleagues at these and other institutions who have assisted include Melvin Ashwill, D.I. Axelrod, C.B. Beck, P.R. Crane, J.P. Ferrigno, L.V. Hills, F.M. Hueber, A.W. Knoll, Steven Manchester, Rolfe Matthews, C.N. Miller, Jr., G.E. Rouse, H.E. Schorn, C.J. Smiley, R.A. Stockey, R.L. Taggart, and Wesley Wehr. Finally, we wish to thank colleagues who have, through discussions, criticisms, and suggestions, improved the present report: G.R. Upchurch and S.L. Wing. We also thank the various curators of herbaria who have allowed us access to analyze and collect comparative materials for this study. The herbaria are: California Academy of Sciences, Harvard University (Arnold Arboretum and Gray Herbaria), Missouri Botanical Garden, U.S. National Museum, and the Universities of California

(Berkeley) and Colorado.

Previous Classification of *Acer*

The first comprehensive systematic treatment of *Acer* was that of Pax (1890). For over 40 years, Pax' classification was generally followed by other systematists, although the description of new species made necessary some additions to, and other minor modifications of, his classification. In connection with a systematic treatment of *Acer* native to the U.S.S.R., Pojarkova (1933) published a systematic framework for all *Acer*, which considerably differed from Pax' treatment; Pojarkova, moreover, was the first systematist to consider phylogenetic relationships between the sections of *Acer*. Except in the U.S.S.R., however, Pojarkova's system has been generally ignored; Fang (1939), for example, continued to follow Pax in an extensive monograph on Chinese Aceraceae. Momotani (1962) analyzed some aspects of the chemistry of *Acer* and clarified some relationships between sections. Ogata (1967), who added much data on woody anatomy, published a new system of *Acer*, which incorporated many of Pojarkova's and Momotani's concepts. Tanai (1978) followed Ogata's system in analyzing principally areolar venation in *Acer*. The more recent classification of de Jong (1976) failed to consider adequately fruit morphology and vegetative morphology and anatomy and concentrated largely on sexuality; we consider this system less comprehensive than Ogata's (1967). Because Ogata's (1967) system of *Acer* was the most comprehensive when we initiated our study, we have found Ogata's system an excellent working framework. Ogata's (1967) classification of *Acer* into informal groups and formal sections and series is shown in Table 1.

Table 1. Ogata's (1967) classification of *Acer* into informal Groups and formal sections and series. Not assigned to any group was *Pentaphylla*

- Group A
  - *Macrantha*
    - Macrantha
    - Rufinervia
    - Micrantha
  - *Distyla*
  - *Parviflora*
  - *Spicata*
  - *Palmata*
    - Sinensia
    - Palmata
    - Laevigata
  - *Glabra*
  - *Arguta*
  - *Negundo*
    - Cissifolia
  - *Trilobata*
  - *Rubra*
    - Rubra
    - Eriocarpa
- Group B
  - *Platanoidea*
  - *Campestria*
  - *Pubescentia*
- Group C
  - *Acer*
    - Acer
    - Velutina
  - *Goniocarpa*
    - Opulifolia
    - Monspessulana
  - *Saccharina*
- Group D
  - *Integrifolia*
  - *Syriaca*
  - *Trifoliata*
- Group E
  - *Lithocarpa*
  - *Macrophylla*
  - *Laurina*
  - *Decandra*
- Group F
  - *Indivisa*

Cladistic Analysis of *Acer*

Relationships of Aceraceae to other taxa

One method to arrive at an understanding of which character states are plesiomorphic in *Acer* is to analyze relationships of the genus to related taxa. Validity of a cladistic analysis of *Acer* largely depends on the out-groups selected for inclusion in the analysis and on the phyletic relationships between *Acer* and these out-groups. The only other extant genus of Aceraceae is the bitypic *Dipteronia*, which is universally accepted as closely related to *Acer*. Other out-groups must, therefore, be sought.

Aceraceae are generally accepted as most closely related to (and probably directly derived from) Sapindaceae. Sapindaceae are a large family, in which at least 13 tribes are recognized; these tribes have divergent morphological and anatomical trend. Whether Aceraceae are most closely related to (and derived from) Harpullieae, as thought by Radlkofer (1933) and Muller and Leenhouts (1976), is of major importance. Further, also significant is the relative degree of advancement of the various tribes of Sapindaceae; whereas Radlkofer (1934) suggested that Paullinieae have the lowest morphological grade in the family, Muller and Leenhouts (1976) suggested that the lowest grade is in subfamily Dodonaeoidae (including Harpullieae).

The disagreement between Radlkofer (1933) and Muller and Leenhouts (1976) on the relative degree of advancement of Harpullieae and Paullinieae apparently is based on Muller and Leenhout's assumption that the liana habit of Paullinieae is an advanced state, and that a group so advanced in one feature must also be advanced in others. We do not question this basic assumption in the context of the dicotyledons as a whole, but we do question this assumption as it relates to relative advancement within Sapindaceae. Anatomically, the uniseriate to biseriate rays in the wood of the tree-habit members of Sapindaceae (including Harpullieae) is an advanced character, whereas Paullinieae have rays that are three or more cells wide (Metcalfe and Chalk, 1950), which is typically a lower grade. Further, Sapindaceae are almost universally estipulate; the only three genera of the family that have the generally low-grade stipulate condition are members of Paullinieae. The vine habit (and the associated "polystelic" advanced morphology) of Paullinieae is indeed specialized, but mosaic evolution could well yield a group that is specialized in one character and of low advancement in other characters. We suggest that Radlkofer (1933) was probably correct in considering Paullinieae to be the least advanced of tribes of extant Sapindaceae.

More significant is our strong disagreement with Muller and Leenhouts (1976) on which tribe of Sapindaceae is most closely related to Aceraceae. Muller and Leenhouts suggested that Aceraceae have close affinities to, and are probably descended from, Harpullieae; these authors, however, did not list specific criteria that led to this suggestion. From Muller and Leenhout's discussion, we infer that they were influenced by (1) palynological similarities, (2) the tendency in Harpullieae for a reduction in ovules from the three typical for Sapindaceae to the two characteristic of Aceraceae, and (3) the extratropical distribution of some Harpullieae in the Northern Hemisphere, which parallels the generally extratropical distribution of Aceraceae. In regard to palynological similarities, both Harpullieae and Paullinieae have the generalized Type A pollen of Muller and Leenhouts (1976), which is possibly basic to Sapindaceae; neither tribe can thus be regarded to be more closely related to Aceraceae, which are also characterized by this Type A pollen. Reduction in ovules has occurred in many tribes of Sapindaceae, and thus the reduction in Harpullieae can be considered a parallelism to the reductions in other lineages of Sapindaceae and in the lineage leading to Aceraceae. In regard to geographic distribution, we consider this to be a weak (and possibly meaningless) criterion; many now exclusively megathermal groups (for example, Burseraceae and Icacinaceae) had microthermal representatives in the Paleogene (Wolfe and Wehr, 1986).

In contrast to such debatable similarities (none of which are synapomorphies) between Harpullieae and Aceraceae, the dissimilarities are strong. Harpullieae have even-pinnate leaves, whereas *Dipteronia* is odd-pinnate and the three-lobed, actinodromous leaf of *Acer* must be derived from an odd-pinnate leaf. All Harpullieae examined are entire-margined and have intercostal venation that has a strong, dominantly admedially ramified orientation, unlike Aceraceae, which are typically and pronouncedly serrate (except for clearly advanced members of *Acer*) and have compound tertiary veins that dominate the intercostal venation. The wood of Harpullieae has uniseriate to biseriate rays, whereas the mature wood of Aceraceae has uniformly multiseriate rays.

However, Aceraceae and Paullinieae share many characters. Paullinieae, like *Dipteronia* and the hypothetical ancestor of *Acer*, are odd-pinnate. All genera of Paullinieae have conspicuously serrate leaflets. More significantly, some leaves of early fossil *Acer* have a pronounced tendency to have craspedodromous secondary veins alternating with angularly bifurcating secondary veins that brace the dental sinuses; this is the predominant pattern in all Paullinieae. This secondary venation pattern is accompanied in Paullinieae by compound tertiary veins. Fruits of some Paullinieae and all Aceraceae are samaroid, but this is probably homoplasic. In Paullinieae, rays of the wood are typically multiseriate, and septate fibers, which characterize the wood of most sapindaceous taxa, are absent, as in Aceraceae. Of all extant tribes of Sapindaceae, Paullinieae share by far the greatest number of characters with Aceraceae.

Added to the above similarities between Aceraceae and Paullinieae is the morphology of the extinct *Bohlenia* (Wolfe and Wehr, 1986), which combines characters of Aceraceae with those of Paullinieae. The leaves of *Bohlenia* are odd-pinnate, and the leaflets have a serrate margin and alternating craspedodromous and bifurcating secondary veins (here termed bohlenioid pattern). Individual samaras of *Bohlenia* are indistinguishable from those of *Dipteronia*, but the fruit of *Bohlenia* is trilocular. *Bohlenia* strongly links Aceraceae to Paullinieae.

We do not suggest that Aceraceae are directly derived from Paullinieae; we suggest that Aceraceae and Paullinieae are derived from a common ancestor that had the following characters: (1) flower actinomorphic, disk annular, K5/C5 A5+5, (2) fruit trilocular, (3) leaves alternate and odd-pinnate, (4) leaflets that have a serrate margin, bohlenioid pattern of secondary venation, and compound tertiary veins, (5) stipulate, (6) habit a low, possibly scrambling shrub, and (7) wood that had multiseriate rays and no septate fibers. Paullinieae specialized from this hypothetical ancestor by the disk becoming oblique and the habit vine-like (with associated anatomical specializations). Aceraceae specialized by losing stipules and leaves becoming opposite (note that opposite leaves have apparently developed independently in *Valenzuelia*, a member of Thouinieae, the tribe most closely related to Paullinieae), and reducing the locules from three to two.

Bohlenia was originally assigned to Paullinieae on the basis of the trilocular fruit and the bohlenioid secondary veins. A recently discovered specimen of *Bohlenia*, moreover, is odd-pinnate. These characters, however, are common to both Paullinieae and the hypothetical ancestor of this tribe and Aceraceae. Because individual samaras of *Bohlenia* are identical to those of *Dipteronia*, the two genera must be closely related. Because *Bohlenia* has foliage like that of Paullinieae, *Bohlenia* has a lower morphological grade than, and could be ancestral to, *Dipteronia*. If *Bohlenia* is ancestral (although probably not immediately ancestral) to *Dipteronia*, and if the trilocular conditions of *Bohlenia* indicates a placement in Sapindaceae, then most probably *Bohlenia* is a member or a derivative of the extinct tribe that gave rise to both Aceraceae and Paullinieae.

The preceding interpretations also indicate that the common ancestor of Aceraceae and Paullinieae could serve as a common ancestor to other tribes of Sapindaceae, which, as in Aceraceae, developed into shrubs and trees. In these other tribes, rays of the wood were typically reduced to biseriate or even uniseriate. Parallel to Aceraceae, these other tribes also lost stipules. Most of these tribes developed even-pinnate leaves and lost the bohlenioid pattern of secondary venation; note, however, that the bohlenioid pattern has been retained in *Dilodendron* of Cupanieae and *Bridgesia* and *Athyana* of Thouinieae. The extant tribes of Sapindaceae probably share a common ancestor, an ancestor that also gave rise to Aceraceae. If Aceraceae are not included in Sapindaceae, however, Sapindaceae are paraphyletic. From a purely cladistic viewpoint, Aceraceae should be given tribal rank in Sapindaceae.

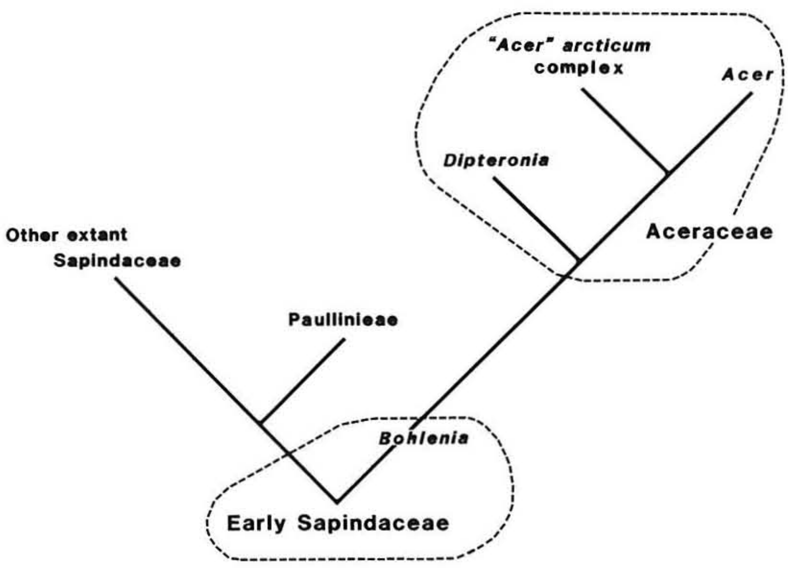
The *"Acer" arcticum* complex

Various Paleocene and Eocene *Acer*-like fruits and leaves have been assigned to *Acer* but lack characters diagnostic of *Acer*. These *Acer*-like fruits have an attachment scar that is on the same side of the samara as are the coalesced veins of the wing; the strongly veined "back" of the samara is thus distal in these fruits, rather than proximal as in *Acer*. Judging by criteria such as attachment angle, venation of the nutlet pericarp, and size, several species of these *Acer*-like samaras were present in the Paleocene and Eocene of western North America.

Associated at some localities with these samaras is foliage typically referred to *"Acer" arcticum* or *"Ampelopsis" acerifolia*. The actinodromous foliage is typically shallowly three-lobed (but varying from deeply lobed to unlobed), the secondary veins are craspedodromous (atypically one bifurcates to brace a dental sinus), the tertiary veins are compound and A-A, and the numerous teeth are of approximately uniform size and are rounded to even emarginate; the polygonal areoles have veinlets that branch two or three times. The bracing of the lobal sinuses in these leaves varies from being formed by an acutely bifurcating medial secondary vein to being formed by a coalescence of two acutely originating external secondary veins, one medial and the other lateral. Although many of these characters are typical of *Acer*, the numerous rounded to emarginate teeth represent a specialization that is not found in extant Aceraceae.

We assume that the associated *Acer*-like fruits and *Acer*-like leaves just described represent the same taxon. This assumption appears reasonable because the fruits and leaves are found in association at several localities in western North America. However, the two fruits illustrated by Heer (1876) from the type locality of *"A." arcticum* in Spitsbergen are indeed valid *Acer* based on our reexamination of them. Whether *Acer*-like fruits (which we think should be associated with *"A." arcticum*) also occur at this locality and the valid *Acer* fruits represent a species other than *"A." arcticum* is unknown. In the instance of *"Ampelopsis" acerifolia*, however, none of the occurrences are accompanied by valid *Acer* fruits, but several occurrences are accompanied by the *Acer*-like fruits. Because the leaves called *"Acer" arcticum* and the leaves called *"Ampelopsis" acerifolia* share several synapomorphies, the two leaf species are considered to be congeneric. The absence of valid *Acer* fruits at *"Ampelopsis" acerifolia* localities but the presence of *Acer*-like fruits at these localities are two facts that suggest that the *Acer*-like fruits that accompany *"Acer" arcticum* leaves at certain localities (for example, at Republic and Princeton/China Creek) are organs of the same entity.

The genus (here termed the *"Acer" arcticum* complex) represented by the *Acer*-like fruits, *"Acer" arcticum* leaves, and *"Ampelopsis" acerifolia* leaves, although not valid *Acer*, may represent an extinct genus of Aceraceae. The relationship of the foliage to *Acer* is indicated by numerous teeth of approximately uniform size, acute dental sinuses, actinodromy, craspedodromous secondary veins, A-A compound tertiary veins, lobal sinal bracing (highly similar, for example, to *Spicata*), and areolar venation, which is Tanai's (1978) first type in *Acer* (here termed Type I). Despite the distal orientation of the strongly veined "back" of the samara, the *Acer*-like samaras also share characters with samaras of *Acer*: the nutlet has a coarse reticulum of veins, the attachment scar is no longer than the nutlet, several veins are coalesced along one margin of the wing, and the veins of the wing anastamose throughout their course. In the several samaroid genera of Malpighiaceae, perianth parts or remnants of abortive locules adhere to the nutlets and the veins of the wing anastomose only close to the wing margin. In samaroid Sapindaceae (primarily Paullinieae), the samaras are typically attached along the length of the wing (as well as along the nutlet) and the veins are not strongly coalesced along one side of the wing; this last character is valid also for sapindaceous samaras that are attached only along the nutlet. However, nutlets of sapindaceous samaras, as in Aceraceae, have a distinct reticulate venation on the pericarp of the nutlet. These *Acer*-like samaras thus appear to have their closest similarity to samaras of Aceraceae. None of the *Acer*-like samaras have been found in attachment, although one early Eocene specimen found by S.L. Wing has two samaras



Text-fig. 1 Suggested cladistic relationships of Aceraceae and allied taxa.

in proximity and that appear to have separated at the point deposition; this apparent two-locular condition would also be indicative of Aceraceae.

Relationships in Aceraceae

The scenario for the evolution within Aceraceae suggested here is (text-fig. 1):

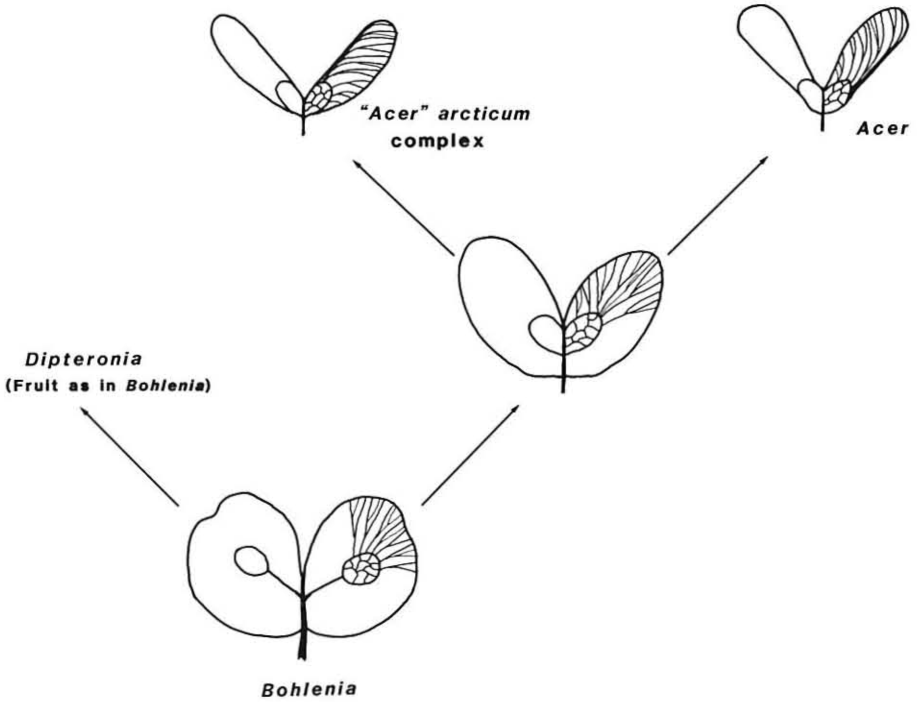
(1) Evolution from a *Bohlenia*-like ancestor of early Aceraceae by loss of stipule, loss of one locule, and change to opposite leaves.

(2) A fundamental divergence into a *Dipteronia* line, which maintained a pinnately compound leaf but largely lost the bohlenioid pattern of secondary venation, and into an *Acer-"Acer" arcticum* complex line, which fused at least three leaflets into an actinodromous leaf. The fruit of this line would still resemble that of *Bohlenia* and *Dipteronia*.

(3) The nutlet becomes basal to the wing (text-fig. 2), so that the wing surrounds the nutlet except along the attachment scar.

(4) A divergence between an *Acer* line, in which veins coalesce along the proximal margin of the wing by condensation of the proximal part of the samara, and an *"Acer" arcticum* complex line, in which the veins coalesce along the distal margin of the wing. In foliage, the *"Acer" arcticum* complex specialized by rounding the teeth and losing the bohlenioid pattern of secondary venation.

The above scenario is the most parsimonious that we can envisage. It involves the origin of the *Bohlenia/Dipteronia* samara once, the origin of the bohlenioid pattern of secondary venation once, and the origin of actinodromy once. A cladistic analysis of



Text-fig. 2 Suggested evolution of fruit morphology in Aceraceae and allied taxa.

Acer will thus involve the following out-groups: Sapindaceae (especially Paullinieae and *Bohlenia*), *Dipteronia*, and the *"Acer" arcticum* complex.

Relationships in *Acer*

Before undertaking an analysis of the various sections of *Acer*, we will analyze each of the major organs in order to determine which character states are probably low grade and which represent higher grades (table 2). Such an analysis will result in a concept of the morphology and anatomy of prototypical *Acer*.

Inflorescence

A many-flowered panicle is basic to both Sapindaceae and *Dipteronia*; this grade is also found in some sections of *Acer*, and the other grades (racemes and umbels) must be considered to be advanced. De Jong (1976) presented a useful analysis of inflorescence structure in *Acer*, in which four basic grades are recognized. Generally, shortening of peduncles and pedicels is considered to be advanced. The significance of pubescence on the inflorescence cannot be evaluated from available data; both conditions are present in Paullinieae and *D. dyeriana* is pubescent and *D. sinensis* is glabrous. The inflorescence in *Dipteronia* is terminal to lateral and is subtended by at least one pair of leaves; the general and probably plesiomorphic condition in *Acer* is a terminal to lateral inflorescence subtended by two to three pairs of leaves; in *Acer* are also found presumably advanced states such as inflorescence only lateral and subtended by no leaves.

Table 2. Characters and character states in *Acer*

Character	Primitive	Advanced
INFLORESCENCE AND FLOWER		
1. Arrangement	A. panicle	B. raceme. C. umbel
2. ditto	A. male & female same	B. male and female different arrangement
3.Flower number	A. many (>50)	B. moderate (20-50). C. Few (>20)
4. Flower difference	A. male & female same number	B. male and female different number
5. Origin	A. terminal & lateral	B. only lateral
6. ditto	A. from many leaves	B. from few leaves. C. from leaves
7. Pubescence	A. present	B. glandular. C. absent
8. Peduncle	A. long	B. short. C. sessile
9. Sepal number	A. 5	B. <5. C. 4—5. D. 4. E. 0
10. Sepals	A. free	B. fused
11. Petal number	A. 5	B. <5. C. 4-5. D. 4. E. 0
12. Petals	A. free	B. fused
13. ditto	A. planar	B. clawed. C. excavate. D. convoluted
14. Petal color	A. greenish-white	B. purplish
15. Stamen number	A. 8	B. 8-10. C. >10. D. 6-8. E. <6.
16. Stamen insertion	A. extrastaminal	B. on disk. C. intrastaminal
17. Stamen shape	A. not apiculate	B. apiculate
18. Disk	A. present	B. absent
19. Disk size	A. large	B. small. C. absent
20. Disk shape	A. mounded	B. flat. C. concave
21. Disk	A. unlobed	B. lobed
22. Vestigial pistil	A. large	B. small. C. absent
23. Vestigial stamens	A. large	B. small. C. absent
24. Sexuality	A. andromonecious	B. androdioecious. C. dioecious
FRUIT		
25. Nutlet	A. symmetrically inflated	B. asymmetrically inflated
26. ditto	A. parallel to wing	B. oblique to wing
27. ditto	A. moderately inflated	B. flattened. C. markedly inflated
28. Nutlet outline	A. circular	B. elliptical. C. spindle-shaped. D. triangular.
29. Nutlet surface	A. smooth	B. with flanges. C. invaginated
30. Nutlet venation	A. reticulate	B. subparallel
31. ditto	A. distinct	B. indistinct
32. ditto	A. passing onto wing	B. coalescing apically. C. coalescing proximally
33. Nutlet veins	A. equal size	B. 1 or more veins larger
34. Nutlet size	A. moderate (0.5-1.0 mm)	B. large (>1 mm). C. small (>0.5 mm)
35. Nutlet exterior	A. glabrous	B. pubescent
36. Nutlet interior	A. glabrous	B. pubescent
37. Nutlet angle	A. small (<20°)	B. large (>20°)
38. Attachment angle	A. moderate (40-50°)	B. large (>50°). C. small (<40°)
39. Attachment scar	A. with proximal & distal keels	B. with proximal keel only C. with distal keel only. D. without keels
40. Nutlet	A. without proximal keel	B. with proximal keel
41. ditto	A. not or slightly proximally expanded	B. markedly proximally expanded

42. Wing	A. along distal side of nutlet	B. along part of distal side. C. apical to nutlet
43. ditto	A. without sulcus	b. with sulcus
44. Coalesced proximal veins	A. <8	B. >7
45. Wing veins	A. not grouped	B. grouped
46. ditto	A. some anastomoses	B. many anastomoses
47. Reticulate veinlets	A. absent	B. present
48. Cotyledon	A. acumbent	B. procumbent
49. ditto	A. eipigeal	B. hypogeal
LEAF		
50. Arrangement	A. simple	B. 3-foliate. C. pinnate. D. 5-foliate
51. Primary veins	A. 3-5	B. >5. C. 3. D. 1
52. Lobal number	A. 3-5	B. >5. C. 3. D. 0
53. Lobal shape	A. oval, elliptic	B. triangular
54. Lobal length	A. approximately equal	B. medial lobe longer
55. Basal part of medial lobe	A. convex	B. straight. C. concave
56. Apices	A. acuminate	B. acute. C. rounded
57. Base	A. broadly rounded, cordate	B. acute. B. deeply cordate
58. Primary veins	A. craspedodromous	B. camptodromous
59. Secondary veins	A. bohlenioid	B. mostly craspedodromous. C. mostly camptodromous. D. entirely camptodromous
60. Intersecondary veins	A. present	B. absent
61. Basal intersecondary veins	A. parallal medial secondary veins	B. higher angle than medial secondary veins
62. Basal laminar bracing	A. A-A	B. A-R. C. R-R. D. A-O
63. ditto	A. compound	B. simple
64. Intercostal venation	A. randomly reticulate	B. admedially ramified
65. Tertiary veins	A. A-A	B. A-R. C. R-R. D. A-O
66. ditto	A. compound	B. simple
67. Fourth order veins	A. irregularly polygonal	b. quadrangular
68. Areoles	A. irregularly polygonal	B. quadrangular
69. ditto	a. isodiametric (±)	b. elongated
70. ditto	A. differ in size	B. uniform size
71. Veinlets	A. branch >once	B. branch 1-2 times. C. unbranched. D. absent
72. Lobal braces	A. by external secondary veins	B. by intersecondary veins. C. by secondary veins
73. ditto	A. acutely originating	B. orthogonally originating
74. ditto	A. acutely bifurcating	B. orthogonally bifurcating
75. External secondary veins	A. acutely originating	B. orthogonally originating
76. ditto	A. craspedodromous	B. camptodromous
77. ditto	A. = number to subsidiary teeth	B. >number subsidiary teeth
78. Axillary braces	A. admedially ramified	B. randomly reticulate
79. Fimbrial vein	A. absent	B. present
80. Teeth	A. many	B. few. C. 0
81. ditto	A. sharp	B. rounded
82. ditto	A. D-1 or D-4	B. other than D-1 or D-4
83. ditto	A. grouped	B. uniform size
84. ditto	A. equally spaced	B. irregularly spaced
85. Lobations	A. absent	B. present

86. Lobal sinuses	A. angular	B. rounded
87. Dental sinuses	A. angular	B. runded
88. Habit	A. deciduous	B. evergreen
WOOD		
89. Ray width	A. 4-5 cells	B. 5-7 cells. C. >8 cells
90. Ray height	A. < 1000 μ	B. > 1000 μ
91. Crystals	A. absent	B. present
MISCELLANEOUS		
92. Latex	A. present	B. absent
93. Haploid number	A. n = 13	n>13
94. Bud scales	A. 2-4 pairs	B. >2-4 pairs

Flower

The flower in Sapindaceae and *Dipteronia* is basically pentamerous. Anthers may be reduced in number from 10, and the formula in *Dipteronia* is K5/C5 A8 (basically, A4 + 4), as is the formula in many Sapindaceae. This formula is also present in many sections of *Acer* and is presumed to be the lowest grade. Tetramery and increases in sepal or petal number above five in *Acer* are thus considered to be advanced. Sepals are free in Sapindaceae, *Dipteronia*, and most *Acer*; fusion into a connate perianth is clearly advanced.

Stamens are inserted at the center of the disk (extrastaminal condition) in Paullinieae, as well as in many sections of *Acer*. Within various sections of *Acer*, the stamens may also be on the disk, inserted between lobes of the disk, or entirely outside the disk, i.e., amphistaminal to intrastaminal; *Dipteronia* has an intrastaminal disk. Position of insertion of the stamens relative to the disk was considered to be of primary significance by Pax (1890) and many later systematists, but clearly the amphistaminal/intrastaminal condition was developed independently in *Acer* versus *Dipteronia* and could thus have developed more than once in *Acer* (or else *Acer* has many times redeveloped an extrastaminal disk). We consider a lobed disk with staminal insertion between the lobes to represent the same manner of insertion as in an amphistaminal disk; in the first instance, the disk is considered to surround incompletely the stamens, and in the second instance the disk surrounds completely the stamens. The most advanced condition is total elimination of the disk.

A vestigial pistil is well developed (large and with distinct stigma) in male flowers of *Dipteronia* and in many *Acer*; reduction in size or elimination of the vestigial pistil in some sections of *Acer* is considered advanced. Sapindaceae and *Dipteronia* have well developed stamens in functionally female flowers. Elimination or reduction of stamens in female flowers is advanced; these reductions typically occur parallel with shifts from andromoneicism to androdioecism to total dioecism.

Other floral features are largely of significance in differentiation of species within sections and series. For example, in *Dipteronia* sepals are larger than petals, whereas in Paullinieae petals are typically larger than sepals; both conditions are present in *Acer*. Some conditions in *Acer* (clawed or convoluted petals) are almost certainly advanced. Some characters in the flower parts (for example, pubescent petals or splitting of the style to its base) are of uncertain significance and, in any case, are probably of minor value.

Pollen

Sapindaceae have primitively tricolporate pollen (Muller and Leenhouts, 1976), a type also found in *Dipteronia* and some *Acer*. A shift to elimination of the pores to a tricolpate condition in *Acer* is almost certainly advanced. Occurrence of striate sculpture in many Sapindaceae, *Dipteronia*, and most *Acer* is probably the primitive condition.

Sexuality

As in Sapindaceae and *Dipteronia*, most *Acer* are andromonoecious: male and female flowers are produced on the same tree and in the same inflorescence. The female of *Acer* typically is morphologically hermaphroditic but always is functionally only female. Of rare occurrence in *Acer* are androdioecism, in which the female/hermaphrodite and male flowers are borne on seperate trees, and true dioecism, in which morphologically female and male flowers are borne on different trees; these conditions are obviously advanced.

Fruit

Although Mai (1983, 1984) extensively described the morphology of a wide range of *Acer* fruits, his study was entirely phenetic and little was inferred relative to primitive or advanced characters. Mai emphasized characterization of individual groups of *Acer* species, although he did suggest some relationships between these groups. However, total reliance was placed on the classification suggested by de Jong (1976), and fruits of *Acer* were not analyzed for their contribution to classification independent of previous concepts.

A moderately inflated nutlet that is equally inflated on both sides is found in both *Dipteronia* and the *"Acer" arcticum* complex, as well as in many extant *Acer*; advanced conditions in *Acer* include nutlets that are asymmetrically inflated, flattened, or markedly inflated. Ogata (1967) noted that markedly inflated nutlets typically have incumbent cotyledons, whereas moderately inflated to flattened nutlets invariably have accumbent cotyledons. The attachment angle in *Bohlenia* is about 50° (means of 32 specimens), which is approximately the same as in *Dipteronia*. In the *"Acer" arcticum* complex, the attachment angle is about 40° (mean of 28 specimens), except that one species has an attachment angle of about 70°. A 40 to 50° attachment angle occurs in many *Acer*, but some have advanced states of very low or very high attachment angles. Elongation of the attachment scar beyond the nutlet to form spurs is inferred to be primitive; these spurs are presumably remnants of reduction of a *Bohlenia*-like samara.

The nutlet of *Bohlenia* and *Dipteronia* is circular in outline. We assume that a circular outline (except for the attachment scar) is the primitive condition in *Acer*. However, the nutlet is elliptical in the *"Acer" arcticum* complex and in many *Acer*. *Acer* nutlets that have very elongated outlines are considered advanced. In the *"Acer" arcticum* complex, the wing extends along the side of the nutlet opposite to the side that has the strongly veined "back"; presumably the low grade in *Acer* is to have the wing extending along the distal side of the nutlet, and advanced grades are those in which the wing is entirely apical to the nutlet. Most *Acer* nutlets, as well as those of *Bohlenia* and most of the *"A." arcticum* complex are about 0.5 to 1.0 cm long. *Dipteronia sinensis* also has a nutlet in this size range, but the nutlet of *D. dyeriana* larger. We assume that nutlets <0.5 cm long and nutlets> 1.0 cm long are advanced.

In *Bohlenia, Dipteronia*, and the *"Acer" arcticum* complex, the nutlets are glabrous. Further the venation of the nutlet pericarp is formed by a few veins that anastomose, and the nutlet veins extend directly onto the wing. The wing veins in these taxa have conspicuous anastomoses, but freely ending veinlets in the areas formed by the anastomoses are typically absent. These characters are also found in some *Acer*. On the other hand, some *Acer* have advanced grades such as nutlet pubescence (exterior and/or interior), nutlet veins that coalesce along the apical margin of the nutlet, or numerous branching veinlets in the wing venation. The nutlets of *Bohlenia, Dipteronia*, and the *"Acer" arcticum* complex are smooth; ridges or invaginations of the nutlets of some *Acer* are thus advanced. Various other nutlet characters occur in specific sections or series that generally have advanced floral characters, e.g., the occurrence of a conspicuous proximal keel or a marked proximal expansion of the nutlet; these characters are assumed to be advanced.

Leaf

As discussed previously, the lobed, actinodromous leaf of *Acer* and the *"A." arcticum* complex is probably basic to *Acer*. De Jong (1976) assumed that the occurrence of trifoliate leaves in *Cissifolia, Negundo*, and *Trifoliata* was retention of a primitive, compound-leaved condition. From the perspective of other characters, however, de Jong's assumption requires the development of a simple leaf a minimum of 12 times. In our cladistic scenario, the simple leaf developed once in Aceraceae but the trifoliate leaf developed 3 times and a pentafoliate leaf once. Further, as discussed later, an Eocene species of section *Macrophylla* has a leaf that is most reasonably interpreted as transitional to a trifoliate leaf. Finally, of the 6 foliar species of the earliest known *Acer*, all are simple-leaved; indeed, of the 24 Paleocene-Eocene foliar species of *Acer* known, 22 are simple-leaved.

The leaves of the *"Acer" arcticum* complex offer points of comparison in character states that are unique to actinodromous leaves (for example, venation connecting medial secondary to lateral primary veins and bracing of lobal sinuses). If the lobes of these actinodromous leaves are homologs of leaflets, then character sets of secondary and higher order venation and of dental morphology can be compared between leaflets and lobes of actinodromous leaves of *Acer*.

The leaf of the *"Acer" arcticum* complex is typically shallowly three-lobed but varies from being unlobed to being deeply five-lobed; five primary veins are, however, typically present. The thickest veins between the most basal medial secondary veins and the lateral primary veins are markedly compound: these veins originate at acute angles from the basal side of the most basal medial secondary veins and from the apical side of the lateral primary veins, extend into the intercostal area, thin, and merge irregularly with the veins extending from the opposite side of the intercostal area. Lobal sinal bracing in the *"Acer" arcticum* complex is somewhat varied: either an external secondary vein extends and bifurcates on approaching the sinus or the external secondary veins merges with a secondary vein that originates on the apical side of a lateral primary vein.

External secondary veins originate acutely in *Bohlenia, Dipteronia dyeriana*, and the *"Acer" arcticum* complex. The orthogonally originating external secondary veins in *D. sinensis* are thus considered to be advanced. Both orthogonally and acutely originating external secondary veins occur in *Acer*, but acuteness is the general condition.

Fourth and fifth order venation are irregularly polygonal and of irregular size in *Bohlenia, Dipteronia*, and the *"Acer" arcticum* complex. In all these taxa, fifth order veins form areoles, and the veinlets typically branch two or three times. This is the Type I venation in *Acer*, as opposed to the Type II venation, in which areoles are quadrangular and veinlets are absent or, if present, are typically unbranched.

Primary teeth are large and of approximately the same size on a given lamina in *Bohlenia, Dipteronia* and the *"Acer" arcticum* complex. Subsidiary teeth are present only in the region of the widest part of the lamina in *Bohlenia* and *Dipteronia* and in the widest part of the lobes in the *"A." arcticum* complex. The teeth of *Bohlenia* and *Dipteronia* are sharply D-1 to D-4 and are separated by angularly acute sinuses, in contrast to the rounded to emarginate teeth and narrowly rounded acute sinuses in the *"Acer" arcticum* complex. As noted previously, the dental and sinal morphology of the *"Acer" arcticum* complex does not occur in any extant *Acer*.

The bohlenioid pattern of secondary venation occurs, of course, in *Bohlenia*, as well as in Paullinieae. This pattern occurs in *Dipteronia* only in the most apical part of the lamina. In the *"Acer" arcticum* complex, a strong intersecondary vein extends half or more the distance from the midrib towards the sinus in many intercostal areas; these intersecondary veins could be the reduced homologs of the bohlenioid bifurcating secondary veins. In some species of early *Acer*, the bohlenioid pattern is conspicuously present, although this pattern is typically highly reduced or typically absent in extant *Acer*; only sections *Negundo* and *Cissifolia* typically have the bohlenioid pattern. Craspedodromy (as opposed to camptodromy) occurs universally in *Bohlenia, Dipteronia*, and the *"Acer" arcticum* complex, as well as in many extant *Acer*; camptodromy is clearly an advanced state in *Acer*.

Braces in the axils of the secondary veins have a dominantly admedially oriented component in Sapindaceae, *Bohlenia*, and *Dipteronia*. This orientation is also present in some *Acer*. However, admedial orientation of third- and fourth-order venation in the entire intercostal area is apparently advanced and occurs only in a small group of *Acer* that are, on other characters, advanced; such orientation is absent in all known Eocene *Acer*.

Wood

As noted previously, the rays in Paullinieae and in *Dipteronia* are four to five cells wide. This ray width also commonly occurs in *Acer; Acer* that depart from this width are considered to be advanced. Width of rays, moreover, appears to be somewhat uncanalized; individual specimens can vary from four to six cells wide (Ogata, 1967). In most other characters, the wood of extant *Acer* is remarkably uniform, although some sections have abundant crystals.

Chemistry

We are not in a position to evaluate the work of Momotani (1962) on seed protein affinities in extant *Acer*; no data are available for Paullinieae or for *Dipteronia*. Pojarkova (1933), however, stressed the occurrence of laticiferous tissues in some sections of *Acer*; such tissue is wide-spread in Sapindaceae and also occurs in *Dipteronia*.

Chromosome Number

Almost all sections of *Acer* are n = 13, and this must be considered basic to the genus. The exceptions are all obvious polyploids. In *Indivisa, Eriocarpa*, and part of section *Acer*, n = 26; in *Rubra*, the number is variable but appears to be either n = 39 or n = 52. However, chromosome numbers are unknown for several extant sections of *Acer*.

The haploid number in *Dipteronia sinensis* is n = 10, whereas in Sapindaceae n = 11 to 16. The number for one genus of Paullinieae is n = 11 and for two other genera n = 12. Apparently the ancestor of Aceraceae could have had n = 11 or 12.

Bud Scales

Bud scales are absent in *Dipteronia*. In extant *Acer*, the sections that generally have low-grade characters have two to four pairs of bud scales, whereas sections that generally have advanced characters have five or more pairs. Ogata (1967), in particular, stressed the significance of numbers of pairs of bud scales in intersectional relationships in *Acer*. However, even if a low number is primitive, sections that have the highest numbers typically share no other synapomorphies, thus suggesting the increases in numbers of bud scales have occurred independently.

We suggest that bud-scale number is somewhat uncanalized and can best be thought of in terms of multiples of a basic number of 4. Reduction from 4 (or a multiple thereof) has typically occurred in an uncanalized manner. The primitive condition is 4 or less pairs (in *Palmata*, the number has been strongly canalized at 4). The more advanced conditions are 2X (5 to 8 pairs), 3X (9 to 12 pairs), and 4X (13 to 16 pairs).

Prototypical *Acer*

To summarize the analysis presented in the preceding section, prototypical *Acer* would have had the following characters:

(1) Inflorescence a many-flowered panicle, terminal to lateral, subtended by two to three pairs of leaves.

(2) Flower with a formula of K5/C5 A8; disk thick, stamens inserted at the inside; vestigial pistil well developed.

(3) Andromonecious.

(4) Fruit samararoid; attachment angle 40° to 50°; nutlet glabrous, moderately and symmetrically inflated, circular in outline; nutlet veins reticulate and extending directly onto wing; all nutlet veins of equal thickness; wing extending along distal margin of nutlet; wing veins with few anastomoses and no (or few) branched veinlets.

(5) Leaf simple and actinodromous; five primary veins; three- to five-lobed; lobal sinuses braced by acutely bifurcating veins that originate as medial external secondary veins or as lateral secondary veins; some secondary veins bifurcate to brace dental sinuses and the other secondary veins craspedodromous (bohlenioid pattern); veins between most basal medial secondary veins compound and A-A; external secondary veins originating acutely; tertiary veins compound and A-A; areoles polygonal and veinlets branching two or three times (Type I areolar venation); primary teeth of uniform size and serrate; teeth sharply D-1 or D-4; subsidiary teeth present only at widest part of lobes; all dental sinuses acute and angular.

(4) Rays of wood four to five cells wide.

(5) Some tissues laticiferous.

(6) Haploid number $n = 13$.

(7) Bud scales two- to four-paired.

Results

From the previous discussion, clearly most advanced characters of *Acer* have been subject to parallel developments. Some characters have been subject to reversals. Parallelisms are particularly apt to occur when many of the derived grades represent reductions or losses; this has particularly occurred in structure of the inflorescence and in floral characters. Such parallelisms and reversals present major obstacles to phylogenetic analyses of extant *Acer* and have resulted in divergent views on intersectional relationships.

Our cladistic analysis of extant *Acer* is given in text-figure 3. Given major weight is the development of tricolpate pollen, which we have assumed occurred but once. The sections of the *Spicata* Group all have tricolporate pollen (except that the pollen of *Distyla* has not been described), the basic number of bud-scale pairs, and venation of the wing of the fruit is uncomplex. The included sections also have a high concentration of plesiomorphic characters in the inflorescence and flower. Specializations in the various sections have occurred primarily in degree of inflation of the fruit or in foliar specializations such as development of camptodromy in *Distyla*.

In the *Macrantha* Group, the major trend in the inflorescence is the reduction to a raceme. A general trend is to androdioecism and ultimately to dioecism. The nutlet tends to become elongated, and the wing veins have a more complicated venation (typically with some veinlets, but the veins diverge acutely) than in the *Spicata* Group. Foliar specialization is particularly pronounced in the development of a trifoliate leaf in the *Negundo-Cissifolia* line.

The umbellate *Rubra-Eriocarpa* line has long been recognized as highly specialized and thus difficult to relate to other sections. The umbel could be developed from any

Text-fig. 3 Suggested cladistic relationships of sections of *Acer*. Classification of extant sections (and series) follows Ogata (1967), but see text for suggested emendation. Extinct sections denoted by asterik.

raceme, such as found in the *Macrantha* Group. The 2X bud scales could indicate a close relationship of the 3X *Trilobata*, but other synapomorphies are lacking. The synapomorphies between *Rubra-Eriocarpa* and the *Macrantha* Group are largely with the latter's more advanced members. A lobed, amphistaminal disk, a reduction in the male pistil, a reduction in the number of leaves subtending the inflorescence, a low fruit-attachment angle, and an elongated nutlet all appear prior to the divergence of the *Glabra-Arguta* and *Cissifolia-Negundo* lines. Trends to an uncanalized 0 to 1 pair of subtending leaves, a laterally borne inflorescence, and tetramery in the flower, occur in the *Cissifolia-Negundo* line.

Alternatively, the Type II areolar venation and 2X bud scale number could indicate a divergence for *Rubra-Eriocarpa* from the line leading to the *Macrophylla* and

Platanoidea Groups, but other synapomorphies are absent. Considering that development of Type II areolar venation is inferred to have occurred independently in the *Spicata* Group and that increase in bud-scale number probably occurred independently in the *Trilobata* line, we suggest that floral and fruit synapomorphies between *Rubra-Eriocarpa* and advanced members of the *Macrantha* Group be given most weight.

The inclusion of the tetraploid *Indivisa* in the *Macrantha* Group is indicated by floral morphology, which has several synapomorphies with both *Cissifolia* and especially *Negundo*. Indeed, the characters by which *Indivisa* differs from *Negundo* are primarily characters that can be derived from character states in *Negundo*. The anomalous simple, pinnately veined leaf of *Indivisa* can be viewed as homologous to the terminal leaflet of *Negundo*. In *Acer* that have eliminated lobes, lateral primary veins are invariably present at the base of the lamina, but no such veins occur in *Indivisa* or leaflets of *Negundo* or *Cissifolia*.

The *Macrophylla* and *Platanoidea* Groups share numerous synapomorphies. The major divergence between the two groups is in fruit morphology. The *Platanoidea* line also primitively became amphistaminal and reduced the flower number.

The inferred relationships between the two series of *Trifoliata* indicate that the section is polyphyletic. Section *Goniocarpa* is, on the other hand, paraphyletic. From a purely cladistic point of view, (1) a series *Monspessulana* could include sections *Pentaphylla* and *Syriaca* and series *Mandshurica* of *Trifoliata* and (2) a series *Opulifolium* could include a series *Saccharodendron*, and a section *Integrifolia* could include series *Grisea* of *Trifoliata*. Indeed, if series *Velutina* of section *Acer* has the placement indicated, section *Acer* should include all taxa in (1) and (2).

Section *Decandra* appears simply as a highly specialized member of section *Platanoidea*. All character states of *Decandra* can be derived from character states in section *Platanoidea*. *Acer decandrum* has particularly strong phenetic similarities to *A. laetum*, a member of *Platanoidea*.

Extinct sections

Douglasa

Known only from foliage, this monotypic section has foliage like that inferred for prototypical *Acer*. Particularly notable is presumed retention of the bohlenioid secondary venation pattern in medial and major lateral lobes. Further, the length/width ratio of lobes approximates the same ratio for leaflets of *Bohlenia* and *Dipteronia*; if isolated lobes of *Douglasa* were found, they could be mistaken for leaflets of these two genera. Foliage of *Douglasa* has the lowest morphologic grade of any section known and could represent prototypical *Acer*.

Alaskana

Alaskana is a monotypic section known only from foliage. Dental morphology is the type that is inferred for prototypical *Acer*. Further, the lamina is three-lobed and areolar venation is Type I. Specializations of *Alaskana* are (1) peculiar lobal sinal bracing (see systematics), (2) only three primary veins, and (3) presence of simple and R-R tertiary veins between the most basal medial secondary veins and lateral primary veins. We cannot negate the possibility that *Alaskana* is an early derivative of *Spicata*, but considering the antiquity of *Alaskana* relative to the earliest known occurence of *Spicata* and the unique specializations of *Alaskana*, we suggest that *Alaskana* represents an early divergence (text-fig. 3) from prototypical *Acer*.

Torada

Most early fruits of *Acer* have a nutlet that has a lateral flange that encloses part of the nutlet. In some taxa, the flange is irregular in degree of development and configuration, while both development and configuration are relatively constant in other taxa. In some taxa, a single flange is present on each side, but other taxa have two flanges on each side. The function of the flanges, which have no analog in extant *Acer*, is unknown. However, many Eocene *Acer* fruits (as well as those of *Bohlenia* and the *"A." arcticum* complex have many insect borings, which may represent borings of a scale insect; the flanges may thus represent outgrowths of the nutlet wall to protect the cotyledon.

The irregularly flanged fruits of *Acer washingtonense* are in nutlet outline and attachment angle like those of *Bohlenia*. Further, the wing veins have low angles of divergence, few veinlets are present, and few veins are coalesced along the proximal margin as in extant members of the *Spicata* Group. The nutlet also has only moderate inflation.

The leaf assigned to *Acer washingtonense* has Type I areolar venation. Dental shape is that of *Douglasa, Alaskana*, and *Spicata*. Bohlenioid venation is absent and teeth are reduced in size.

Fruits of *Acer toradense* are markedly similar to those of *A. washingtonense*, except that *A. toradense* has a pronounced, coarse reticulum of ridges, which are unique in *Acer*. *Acer toradense* is certainly closely related to *A. washingtonense*. Based only on nutlet morphology, these two species could have a common ancestry, or perhaps *A. toradense* is descended from a species that had fruits like *A. washingtonense*. Pending discovery of leaves of *A. toradense*, which would clarify relationships, the two species are assigned to the same section.

Fruits of *Acer stonebergae* are specialized in their large size. The nutlet outline is closely similar to that of *A. toradense*, and the reticulate nutlet venation has the same pattern as the nutlet ridges of *A. toradense* (presumably veins occurred on the ridges). *Acer stonebergae* could be descended from *A. toradense* by reduction of the ridges, or the two species could have a common ancestry.

Most fruit characters of *Torada* could serve as those of prototypical *Acer*. If the nutlet venation of *A. stonebergae* were combined with other aspects of fruit morphology of *A. washingtonense*, the fruit would be like that inferred for prototypical *Acer*. Although none of the known species of *Torada* combine all inferred plesiomorphic fruit characters, this extinct section is closer in fruit morphology to prototypical *Acer* than is any extant section.

Stewarta

Acer stewarti has indistinct nutlet flanges, a circular nutlet outline, and simple wing venation, which are all inferred plesiomorphic characters. The nutlet however, has a small area, indicating that the nutlet was at least moderately (if not markedly) inflated. This type of fruit would characterize the common ancestor of the *Palmata* and *Parviflora-Distyla* lines. *Acer hillsi* also has indistinct flange and is inflated. The deep sulcus is a specialization not present in extant members of the *Spicta* Group.

If the leaves and fruits assigned to *Acer stewarti* are conspecific, a placement of *A. stewarti* between the divergence of *Spicata* and *Palmata* is clear. The leaves of *A. stewarti* are markedly like those of *Spicata* except in bracing of the lobal sinuses. Notable similarities are the Type I areolar venation and strongly acuminate teeth.

Rousea

The single species, *Acer rousei*, has indistinct flanges and wing veins that are simple and diverge at low angles. However, the nutlet is inflated, has a high attachment angle, and is somewhat elongated. The degree of inflation and elongation of the nutlet are less than found in *Palmata*, but the morphological trends evidenced by *A. rousei* could ultimately give rise to the type of fruit found in *Palmata*.

Republica

The fruit on which *Acer republicense* is based has irregular flanges confined to the basal part of the nutlet. The attachment angle is moderate and the nutlet is slightly inflated, both plesiomorphic characters. Wing venation is formed by acutely diverging veins that anastomose several times, enclosing some veinlets; this is the wing venation conspicuous in extant members of the *Macrantha* Group. An elongated nutlet such as found in *A. republicense* would also be expected in an early member of the *Macrantha* Group.

Orba

The fruits of *Orba* have a well defined flange that is consistently placed near the distal margin of the nutlet. The nutlet is small, has a triangular outline, and is apparently well inflated. Wing veins tend to diverge at a high angle, which, although acute, is higher than in the *Macrantha* Group. The wing extends along the distal side of the nutlet. Except for degree of inflation, these fruits have no synapomorphies with any members of the *Spicata* Group and are clearly more advanced. The triangular nutlet, which is basically somewhat elongated, is more advanced than members of the *Macrantha* Group.

The leaf of *Acer orbum* has Type I areolar venation and, especially in the lateral lobes, bohlenioid venation. Teeth are the same shape and size as common in early members of the *Spicata* Group. This type of leaf, however, may have persisted in the line leading to the divergence of the *Macrantha* Group. As discussed below, the fruit morphology of *A. orbum* has synapomorphies with fruits of an early member of the *Macrophylla* Group. Probably *A. orbum* represents a divergence from the line leading to the *Macrophylla* and *Platanoidea* Groups but prior to the development of Type II areolar venation.

Columbiana

The fruit of *Acer stockeyae*, the earliest known species of *Columbiana*, has no trace of flanges. The fruit is specialized in having the nutlet markedly expanded beyond the proximal margin of the wing. The wing venation is more complicated than that of the *Macrantha* Group, and the nutlet veins extend directly onto the nutlet, with no conspicuous convergence near the wing, the wing extends to the attachment scar, and the nutlet is slightly inflated, all plesiomorphic characters. The fruit of *A. stockeyae* is somewhat more advanced than that of the *Macrantha* Group but less specialized than that of the *Macrophylla* Group. Fruits of other species of *Columbiana* do not differ markedly from that of *A. stockeyae.*

The earliest leaves of *Columbiana* are of earliest Eocene age and have a similar morphology to leaves of younger species of the section. Dental morphology of *Columbiana* leaves is similar to that of *Acer orbum* and other early members of *Acer*. Leaves of *Columbiana* are also consistently three-lobed, a characteristic of most sections of the *Spicata* Group and simple-leaved members of the *Macrantha* Group. The areoles of *Columbiana*, however, are quadrangular, as opposed to the irregularly polygonal Type I venation of most member of the *Spicata* and *Macrantha* Groups. Branching of the veinlets in *Columbiana*, however, is typically more than in Type II venation, suggesting that *Columbiana* diverged during the transition from Type I to Type II areolar venation in the line leading to the *Macrophylla* and *Platanoidea* Groups.

Glabroidea

Fruits of *Glabroidea*, which is known from many species, have distinct nutlet flanges. Nutlet outline varies from almost circular to pronouncedly triangular. Wing venation is advanced and typically has numerous reticulate veinlets (except in taxa that have very small wings). The wing extends at least half-way along the distal margin of the nutlet and the nutlet is slightly inflated, both plesiomorphic characters.

Leaves of *Glabroidea* have Type II areolar venation but are otherwise unspecialized. They are almost exclusively three-lobed, axillary venation is admedially ramified in some species, and lobal sinal bracing is unspecialized and acute. In both fruit and leaf morphology, *Glabroidea* is best placed as a divergence following attainment of Type II areolar venation and immediately prior to the divergence of the *Macrophylla* and *Platanoidea* Groups.

The fruit on which *Acer cadaver* is based appears to be highly specialized and would, if still extant, probably be given sectional rank. The strongly ridged nutlet and deep sulcus are advanced features. However, the flanges (although reduced) and the triangular nutlet shape indicate an ancestry within *Glabroidea*.

Although the group is clearly paraphyletic, rather than refer *Orba, Columbiana*, and *Glabroidea* to separate groups, we will refer these intermediate sections to an *Orba* Group.

Princetona

The fruit of *Acer princetonense* has few plesiomorphic characters, such as the extension of the wing along the distal margin of the nutlet. Most of the characters of this taxon are advanced: the nutlet is markedly inflated, the nutlet is elongated along an axis parallel to the attachment scar, the attachment angle is low, a marked distally placed flange is present, the wing venation has veins that diverge at a high angle (preservation does not allow determination of presence or absence of veinlets or presence or absence of pubescence), and 7 or 8 veins coalesced along the proximal margin of the wing. While the marked flange indicates a relationship to the *Orba* Group, the large, markedly inflated nutlet that is elongated along the attachment scar allies *A. princetonense* to the line leading to *Macrophylla-Lithocarpa*.

Spitza

The fruit of *Acer spitzi* has synapomorphies with the *Integrifolia-Acer* line: the nutlet is markedly inflated and circular in outline, a marked sulcus is present, and the wing is markedly thickened at its base. In the basal part of the nutlet, conspicuous but short flanges are present. The prominent proximal keel of the *Integrifolia-Acer* line is absent. Placement of *A. spitzi* near the base of the *Integrifolia-Acer* line is probable.

Manchesteria

Fruits of *Manchesteria* have clear synapomorphies with the *Platanoidea* Group: a markedly flattened nutlet, high attachment angle, a circular nutlet outline, and strongly reticulate wing venation. *Acer axelrodi*, the earliest known species of *Manchesteria*, has a conspicuous medial ridge on the nutlet, which is interpreted as fusion of two flanges.

Leaves of *Manchesteria* are typically three-lobed. Areolar venation is consistently Type II. Teeth are more numerous in *Manchesteria* than in extant members of the *Platanoidea* Group but are fewer than in the *Orba* and *Macrantha* Groups. Teeth are narrowly rounded as is basic for the *Platanoidea* Group, and the lobes are sharply pointed. *Manchesteria* conforms to the predicted morphology of an early member of the *Platanoidea* Group.

Summary and proposed classification of *Acer*

Our proposed classification of *Acer* takes into account both the cladistic analysis (text-fig. 3) and phenetic similarities of fossil taxa that indicate relationships. This dual approach is important because development of homoplasies can be, in many instances, inferred more readily from the fossil record than from comparative studies.

Inflorescences and flowers of extant sections of *Acer* have many character states that our analysis indicates are homoplasies. Thus, the intrastaminal disk has evolved four times: in the *Spicata, Negundo, Rubra*, and *Parviflora* Groups. Reduction from a many-flowered panicle to a fewer-flowered raceme has occurred within extant sections (e.g., *Palmata*); not surprisingly, parallel reductions are inferred to have occurred in other lineages. A nutlet that has a coarse reticulum of pericarp veins occurs today in low-grade *Spicata* and is inferred to have been possessed by prototypical *Acer*; a similar reticulum occurs on the nutlets of *Eriocarpa*, but fossil data indicate that this character state is advanced in this section. Markedly inflated nutlets have evolved separately in the *Palmata* line and in the line leading to the *Macrophylla* Group. Trifoliate leaves have evolved separately in the *Negundo* and *Macrophylla* Groups. Reduction in number of teeth to an entire-margined condition has occurred several times. Such homoplasies have undoubtedly greatly contributed to the absence of consensus on intersectional relationships in *Acer*.

However, some homoplasies appear as parallelisms in sister-groups. For example, reduction of number of teeth (concommitant with increase in size and rounding) is interpreted to have developed separately in closely related groups. Such a homoplasy may result from genetic similarities of closely related groups that, in turn, results in similar phenetic responses to similar environmental pressures. Our proposed classification is shown in table 3.

Table 3. The proposed classification of *Acer* by the authors

- *Spicata* Group
  - *Douglasa*
  - *Alaskana*
  - *Torada*
  - *Spicata*
  - *Stewarta*
  - *Rousea*
  - *Palmata*
  - *Distyla*
  - *Parviflora*
- *Macrantha* Group
  - *Republica*
  - *Trilobata*
  - *Macrantha*
  - *Glabra*
  - *Arguta*
  - *Rubra*
  - *Eriocarpa*
  - *Cissifolia*
  - *Negundo*
  - *Indivisa*
- *Orba* Group
  - *Orba*
  - *Columbiana*
  - *Glabroidea*
- *Macrophylla* Group
  - *Princetona*
  - *Macrophylla*
  - *Lithocarpa*
  - *Laurina*
  - *Spitza*
  - *Integrifolia* (incl. Grisea)
  - *Acer*
    - Acer
    - Monspessulana (incl. *Pentaphylla, Syriaca,* Mandshurica)
    - Saccharodendron (incl. Opulifolia)
- *Platanoidea* Group
  - *Manchesteria*
  - *Campestria*
  - *Platanoidea* (incl. *Decandra*)
  - *Pubescentia*

In several aspects, our classification closely follow that of Ogata (1967): his Group B is equivalent (with inclusion of *Decandra* in *Platanoidea*) to our *Platanoidea* Group, his Groups C and D are equivalent to part of our *Macrophylla* Group, and his Group E (excluding *Decandra*) is equivalent to part of our *Macrophylla* Group. Ogata (1967) was well aware that the largest of his groups, his Group A, is heterogeneous, and it is this group that cladistic analysis and phenetic analysis of the fossils indicate can be subdivided into two distinct groups: our *Spicata* and *Macrantha* Groups. To the latter group we have added Ogata's Group F (*Indivisa*).

Neither Murray (1970) nor de Jong (1976) attempted a phylogenetic classification of *Acer*. However, whereas de Jong considered his sections *Acer* and *Platanoidea* as the most primitive, cladistic analysis (as well as the fossil record) indicates that these sections are the most advanced. Most of de Jong's 14 sections, moreover, represent paraphyletic groups, although in most instances we agree with de Jong that the series he included within a given section are closely related.

Evolution of *Acer* in the Tertiary of Western North America

Comparison of cladistic analysis to apparent ages of sections

Based on our current investigation, fossil *Acer* from the Tertiary of North America is classified into 27 sections and 91 species including 6 taxa indeterminable to specific status (table 4). Of 27 sections 12 are described as new, based either on fossil leaves or fruits. Some workers have assumed that the fossil record is so fragmentary and incomplete that first appearances of taxa have little, if any relation, to the time of evolutionary origin of the taxa. Thus, fossil taxa are given no more weight in evolutionary analyses than are extant taxa, because fossil taxa are not considered to represent forms that gave rise to younger taxa. If fossil occurrences of a given taxon are young in relation to that predicted from a cladistic analysis, many workers will discount the significance of the age of the fossil occurrence rather than re-examining the basic assumptions as to relative advancement of morphological grades on which the cladistic analysis was based. The present study of *Acer,* which includes both (1) cladistic analysis that incorporates fossil and extant taxa and (2) phenetic analysis of fossil taxa, allows evaluation of significance of the fossil record as an independent test of cladistic analyses.

Table 4. Systematic List of Tertiary *Acer* from North America

- *Spicata* Group
  - Section *Douglasa* Wolfe et Tanai
    - *Acer douglasense* Wolfe et Tanai
  - Section *Alaskana* Wolfe et Tanai
    - *Acer alaskense* Wolfe et Tanai
  - Section *Torada* Wolfe et Tanai
    - *Acer stonebergae* Wolfe et Tanai
    - *A. toradense* Wolfe et Tanai
    - *A. washingtonenese* Wolfe et Tanai
  - Section *Spicata* Pax
    - *Acer* sp. 1
  - Section *Stewarta* Wolfe et Tanai
    - *Acer stewarti* Wolfe et Tanai
    - *A. hillsi* Wolfe et Tanai
  - Section *Rousea* Wolfe et Tanai
    - *Acer rousei* Wolfe et Tanai
  - Section *Parviflora* Koidzumi
    - *Acer browni* Wolfe et Tanai
    - *A. smileyi* Wolfe et Tanai
- *Macrantha* Group
  - Section *Republica* Wolfe et Tanai
    - *Acer republicense* Wolfe et Tanai
  - Section *Trilobata* Pojarkova
    - *Acer ashwilli* Wolfe et Tanai
    - *A.* sp. 2
  - Section *Macrantha* Pax
    - *Acer clarnoense* Wolfe et Tanai
    - *A. dettermani* Wolfe et Tanai
    - *A. castorrivularis* Wolfe et Tanai
    - *A. latahense* Wolfe et Tanai
    - *A. palaeorufinerve* Tanai et Onoe

- Section *Glabra* Pax
    - *Acer traini* Wolfe et Tanai
- Section *Arguta* Rehder
    - *Acer ivanofense* Wolfe et Tanai
- Section *Eriocarpa* (Rafinesque) Murray
    - *Acer taurocursum* Wolfe et Tanai
    - *A. kenaicum* Wolfe et Tanai
    - *A. chaneyi* Knowlton
    - *A. ezoanum* Oishi et Huzioka
    - *A. whitebirdene* (Ashlee) Wolfe et Tanai
    - *A. taggarti* Wolfe et Tanai
    - *A. ferrignoi* Wolfe et Tanai
- Section *Rubra* Pax
    - *Acer ovipetrinum* Wolfe et Tanai
    - *A. kluckingi* Wolfe et Tanai
    - *A. tigilense* Chelebaeva
- Section *Cissifolia* Koidzumi
    - *Acer lincolnense* Wolfe et Tanai
- Section *Negundo* (Boehmer) Maximowicz
    - *Acer eonegundo* Wolfe et Tanai
    - *A. sinuofluviatilis* Wolfe et Tanai
    - *A. macginitiei* Wolfe et Tanai
    - *A. cranei* Wolfe et Tanai
    - *A. cascadense* Wolfe et Tanai
    - *A. knolli* Wolfe et Tanai
    - *A. molallense* Wolfe et Tanai
    - *A. heterodentatum* (Chaney) MacGinitie
    - *A. negundoides* MacGinitie

Orba Group

- Section *Orba* Wolfe et Tanai
    - *Acer orbum* LaMotte
- Section *Columbiana* Wolfe et Tanai
    - *Acer stockeyae* Wolfe et Tanai
    - *A. eomedianum* Wolfe et Tanai
    - *A. powellense* Wolfe et Tanai
    - *A. oligomedianum* Wolfe et Tanai
    - *A. medianum* Knowlton
    - *A. niklasi* Wolfe et Tanai
- Section *Glabroidea* Wolfe et Tanai
    - *Acer becki* Wolfe et Tanai
    - *A. bosrivularis* Wolfe et Tanai
    - *A. cadaver* Wolfe et Tanai
    - *A. crokense* Wolfe et Tanai
    - *A. cuprovallis* Wolfe et Tanai
    - *A. elkoanum* Wolfe et Tanai
    - *A. elwyni* (Becker) Wolfe et Tanai
    - *A. florissanti* Kirchner
    - *A. glabroides* R. W. Brown
    - *A. idahoense* Wolfe et Tanai
    - *A. jarbidgianum* Wolfe et Tanai
    - *A. meyeri* Wolfe et Tanai
    - *A. wehri* Wolfe et Tanai
    - ?*A. milleri* Wolfe et Tanai
    - ?*A.* sp. 3
    - ?*A.* sp. 4

- *Macrophylla* Group
  - Section *Princetona* Wolfe et Tanai
    - *Acer princetonese* Wolfe et Tanai
  - Section *Macrophylla* (Pojarkova) Ogata
    - *Acer alvordense* Axelrod
    - *A. salmonense* Wolfe et Tanai
    - *A. osmonti* Knowlton
    - *A. busamarum* Wolfe et Tanai
      - subspecies *busamarum*
      - subspecies *fingerrockense* Wolfe et Tanai
    - *A. oregonianum* Knowlton
    - *A. macrophyllum* Pursh
    - *A. megasamarum* Tanai et Onoe
    - *A.* sp. 5
  - Section *Lithocarpa* Pax
    - *Acer beckeri* Wolfe et Tanai
    - *A. grantense* Wolfe et Tanai
    - *A.* sp. 6
  - Section *Spitza* Wolfe et Tanai
    - *Acer spitzi* Wolfe et Tanai
  - Section *Acer*
    - Series Acer
      - *Acer montanense* Wolfe et Tanai
      - *A. postense* Wolfe et Tanai
    - Series Saccharodendron (Rafinesque) Murray
      - *Acer collawashense* Wolfe et Tanai
      - *A. minutifolium* Chaney
      - *A. schorni* Wolfe et Tanai
      - *A. tyrellense* Smiley
      - *A. bolanderi* Lesquereux
- *Platanoidea* Group
  - Section *Manchesteria* Wolfe et Tanai
    - *Acer axelrodi* Wolfe et Tanai
    - *A. manchesteri* Wolfe et Tanai
  - Section *Campestria* Pax
    - *Acer tiffneyi* Wolfe et Tanai
    - *A. protomiyabi* Endo
    - *A. septilobatum* Oliver
  - Section *Platanoidea* Pax
    - *Acer hueberi* Wolfe et Tanai
    - *A. scottiae* MacGinitie

Cladistic analysis of *Acer* predicts that *Spicata* should be the oldest group. In fact, the oldest foliage of *Acer* is assignable to the *Spicata* Group, and all diagnostic foliage until the late middle Eocene conforms to this group. Fruits of early middle Eocene age are assignable to 11 taxa; 6 are members of the *Spicata* Group, 1 of the *Macrantha* Group, 2 of the *Orba* Group, and 2 of the *Macrophylla* Group. A slightly older fruit taxon represents the *Orba* Group. However, these pre-late middle Eocene taxa generally represent primitive types within their respective groups. Extant advanced sections in the *Macrantha* and *Macrophylla* Groups first appear in the late middle to early late Eocene. A primitive member of the *Platanoidea* Group also appears at about the same time and is followed in the latest Eocene by extant advanced sections. Considering the still incompletely samples Eocene microthermal record, the approximate coincidences of predicted and known first appearances of major groups and individual sections in *Acer* is significant.

Absence of *Palmata* in the North American Tertiary record is considered to be evidence of the evolution of this group (and section) in Asia from an early member of the *Spicata* Group such as *Rousea;* the Eocene plant megafossil record of northeastern Aisa north of Hokkaido is particularly poor. Similarly, other extant sections of the *Spicata* Group may have arisen in Asia from early members of the *Spicata* Group. Tanai (1983) has recorded *Distyla* from the late middle Eocene of Asia.

In the *Macrantha* Group, most extant sections appear in western North America by the late middle to late Eocene. Only *Glabra* might be expected to have a significantly earlier fossil occurrence than now known. However, if *Glabra* early adapted to high altitude environments far removed from basins of deposition (as is the present and probably Neogene habitat of *Acer glabrum*), the apparent absence of *Glabra* in the Paleogene may not be significant. A section such as *Indivisa,* which has a Neogene record in Asia (Tanai, 1983), may have arisen during the post-Eocene in Asia from some early member of the *Negundo* line.

Members of the *Macrophylla* Group appear in the sequence predicted by cladistics. *Laurina* may have arisen in Eurasia from an early member of the *Lithocarpa* line; indeed, *Acer beckeri* could have had floral morphology that could be the type from which both *Lithocarpa* and *Laurina* diverged. In the *Integrifolia-Acer* line, *Integrifolia* may have arisen in Eurasia from *Spitza* or a closely related taxon. Certainly the later diversification of section *Acer* appears to have occurred in Eurasia, and possibly most of this diversification was post-Eocene.

Members of the *Platanoidea* Group also appear in the sequence predicted. However, *Pubescentia* has no known fossil record as yet. *Pubescentia* could have arisen in Eurasia from an early member of the *Platanoidea* line.

The fossil record adds a dimension to the evolution of *Acer* that cannot be obtained from a cladistic analysis. Apparently simultaneous occurrences in the early middle Eocene of species that represent divergences leading to major groups indicate that evolution was proceeding at a very rapid pace. Further, apparently simultaneous appearances in the late middle to early late Eocene of extant sections of these major groups indicate a continuing rapid evolution in each of these groups.

Diversification of *Acer* through the Tertiary

Evaluation of diversity of *Acer* during any given interval of time is dependent on sampling in terms of number of localities, extent of collections from each locality, extent of geographic area sampled, and vegetational types represented by assemblages from various localities. In regard to all four factors, the Miocene has been the most thoroughtly sampled interval in western North America, as well as in other middle and high latitude regions of the Northern Hemisphere. Both the Paleocene and Eocene have been well sampled, but most assemblages of these epochs represent mesothermal or megathermal vegetation, rather than microthermal vegetation in which *Acer* is today best represented. Oligocene assemblages are the least thoroughtly sampled, in regard to geographic coverage and number of extensively collected localities.

Because of generally high temperature levels during the Eocene, microthermal plant assemblages are few in comparison to mesothermal and megathermal assemblages. A far greater number of Eocene microthermal assemblages are, however, known in western North America than in any other Northern Hemisphere region. This comparative abundance of microthermal assemblages is the result of the presence in western North America of an extensive volcanic upland that occupied an area from northern Nevada through the eastern part of the Pacific Northwest and at least as far north as central British Columbia (Wolfe, 1985). This volcanic upland apparently came into existence during the early Eocene, and by the earliest part of the middle Eocene (about 48 to 50 m.y.) highly fossiliferous lacustrine deposits were formed in northeastern Washington and southern and central British Columbia. A few localities in these lacustrine beds have been extensively collected (for example, Republic, Princeton/One Mile Creek, and McAbee), whereas collections of only a few hundred specimens have been made from other localities.

During the latest part of the middle Eocene and the early part of the late Eocene (about 38 to 42 m.y.), lacustrine deposits associated with volcanism were formed in northeastern Nevada (Axelrod, 1966). These lacustrine beds have produced the extensively collected Bull Run and Copper Basin assemblages and the moderately collected Elko assemblage. The Nevada volcanic upland may or may not have been connected to the volcanic upland region of central Idaho (Salmon and Cow Creek assemblages), as well as to the volcanic uplands of central Oregon. In Oregon, the Clarno assemblages (John Day Gulch and Sheep Rock Creek) probably represent vegetation along the western margin or slope of the upland.

Most microthermal assemblages of latest Eocene (about 33 to 38 m.y.) age are concentrated in western Montana; these assemblages are represented by moderate-sized to large collections. The most extensively collected upland flora of this age, however, is the Florissant of central Colorado; the Florissant probably represents cool mesothermal vegetation (MacGinitie, 1953).

The major climatic deterioration at the end of the Eocene resulted in occupation by microthermal vegetation of large areas of the Northern Hemisphere (Wolfe, 1978). Thus, many lowland regions at middle latitudes that had been occupied by mesothermal or megathermal vegetation during the Eocene were occupied by microthermal vegetation. In western North America, however, middle-latitude Oligocene assemblages are largely restricted to central Oregon (Bridge Creek assemblages) and to the volcanic region of the Western Cascade Range in western Oregon and Washington. Many Oligocene assemblages have also been collected in Alaska (Wolfe, 1972), but these typically have a low diversity of woody plants, particularly assemblages of early Oligocene age.

As noted previously, Miocene assemblages have a broad geographic coverage and are represented by many large collections. The known diversity of these assemblages is high, and the known diversity of *Acer* during the Miocene is probably a close reflection of actual diversity.

Our analysis of the diversity of *Acer* through the Tertiary includes taxa that are reasonably inferred to have been present in western North America. For example, during the late middle and late Eocene, *Spicata* is inferred to have been present, because this section is known in both the early middle Eocene and early Oligocene. Further, the cladistic analysis of *Negundo* indicates that the lines leading to both *Acer negundoides* and *A. knolli* had diverged by the latest Eocene; although only one species of *Negundo* is known in the latest Eocene, we infer the presence of two species. Such inferred sections and species are included in our analysis (table 5).

Table 5. Diversity of *Acer* in western North America during the Cenozoic

	Sections			Species		
	Known	Inferred	Total	Known	Inferred	Total
Holocene	5	0	5	5	0	5
Latest Miocene-Pliocene	4	1	5	5	2	7
Late middle-early late Miocene	8	0	8	15	0	15
Late early-early middle Miocene	10	0	10	20	2	22
Earliest Miocene	8	0	8	15	3	18
Late Oligocene	5	2	7	6	6	12
Early Oligocene	10	1	11	11	3	14
Latest Eocene	11	6	17	15	11	26
Late middle-early late Eocene	11	3	4	19	3	22
Early middle Eocene	8	0	8	11	0	11
Pre-middle Eocene	3	0	3	3	0	3

As both sectional and specific levels, *Acer* shows an increasing diversity from the early through the late Eocene. This Eocene diversification of *Acer* is probably related to overall cooler climate of the middle and late Eocene relative to the early Eocene and to possible expansion of the volcanic upland that was previously discussed. Two other major factors were the presence of areas of topographic (and probably edaphic) diversity and the rarity of *Acer,* as indicated by low numerical representation in fossil assemblages. Populations of *Acer* were apparently small and were isolated from one another by the diversity of topography; genetic innovations would thus not be readily swamped.

Certainly diversification of *Acer* appears to have been rapid at the sectional and specific levels during the Eocene. By the end of the middle Eocene, all major groups of *Acer* are known to have been represented. Of the 21 extant sections recognized in this report, 13 are known to have been represented by the end of the Eocene: *Distyla, Trilobata, Macrantha, Arguta, Negundo, Cissifolia, Eriocarpa, Rubra, Macrophylla, Lithocarpa, Acer, Platanoidea,* and *Campestria.* From cladistic relationships, we also infer by the end of the Eocene representation of lines leading to *Spicata, Palmata, Parviflora, Glabra, Indivisa,Laurina, Integrifolia,* and *Pubescentia.* Some advanced sections may be of Oligocene or Neogene origin, but the divergences leading to these sections had already occurred by the end of the Eocene. Sectional diversification in *Acer* appears to have been largely completed by the end of the Eocene.

Following the major climatic deterioration at the end of the Eocene, diversity of *Acer* apparently underwent a significant decline in western North America, both in regard to sections and species. Although in the conterminous United States geographic concentration of early Oligocene assemblages in the Pacific Northwest probably affects known diversity, even inferred diversity is low. Some sections (for example, *Lithocarpa* and *Glabroidea*) persisted into the early Oligocene but are not known in the late Oligocene and certainly not in the extensively collected Neogene flora.

During the late Oligocene and early Neogene, *Acer* in western North America became progressively more diverse. To some extent, the increasing specific diversity probably reflects actual diversification in sections such as *Negundo* and *Eriocarpa,* but a second major factor was immigration. Thus, *Platanoidea,* which was previously known in the Eocene of western North America but became extinct on this continent at the end of the Eocene, was again a member of the North American flora during the Miocene. A third factor was that of long-distance dispersal and subsequent diversification, as in the instance of the introduction of Saccharodendron to North America in the early Miocene.

Evolutionary patterns

Acer rapidly diversified during the Eocene. Divergences leading to all major groups in the genus had probably occurred by the early middle Eocene (about 47 to 49 m.y.) and possibly occurred sometime during the early Eocene. By the latest middle to early late Eocene (about 38 to 42 m.y.), divergences leading to most extant sections had occurred. Since the end of the Eocene, divergences established in the Eocene have speciated, but few, if any, major divergences have occurred. Sections that may be of post-Eocene origin are probable derivatives of sections known in the Eocene; divergences of advanced series of the *Macrophylla* Group, however, may have occurred during the Oligocene. Certainly during the Neogene, evolution in *Acer* has been almost entirely, if not entirely, on the specific level.

Mosaic evolution has occurred to varying degrees in *Acer.* In *Columbiana, A. niklasi* has a high-grade leaf and a low-grade nutlet, whereas the coeval *A. medianum* has a low-grade leaf and a high-grade nutlet. In *Eriocarpa,* the extant *A. saccharinum* and the Miocene *A. chaneyi* have highly similar foliage that represents a low grade in the section, but the nutlet of *A. saccharinum* is high grade in the section and the nutlet of *A. chaneyi* is low grade. Some taxa (for example, species of *Spicata*) have generally low-grade character states in both foliage and fruit, and other taxa (for example, species of *Saccharina*) have generally high-grade character states in both organs. Mosaic evolution has occurred in *Acer,* but in other instances levels of advancement in foliage parallel levels of advancement in fruit.

Our study of *Acer* has little relevance to the current debate over gradualism versus punctuated equilibrium. Diversification of *Acer* in the Eocene could be interpreted in either conceptual framework, because fossil occurrences of *Acer* are not in closely spaced stratigraphic intervals. Rapidity of diversification in particular the middle Eocene might suggest a punctuated burst (or series of bursts) but could also be the result of rapid (for plants) divergence by gradualism. Interpretation of the post-Eocene record of *Acer* is also equivocal in the same context.

Relation to climate

Occurrences of *Acer* in Alaska in the latest Paleocene and early Eocene are in the southern part of the polar broad-leaved deciduous forest (Wolfe, 1985). This forest was dominated by deciduous plants, both angiospermous and coniferous, although in the southern part of the forest were some broad-leaved evergreens (for example, Palmae). The deciduousness is thought to be a response to low light-levels rather than to temperature; mean annual temperatures in the southern part of the polar broad-leaved deciduous forest are inferred to have been in the mesothermal range (13° to 20°C). The early Eocene occurrence of *Acer* in the Chalk Bluffs flora of northern California must have been in megathermal vegetation; although MacGinitie (1941) suggested a mesothermal temperature regime for the Chalk Bluffs, recent collections from a new Chalk Bluffs locality are indicative of warmer temperatures than suggested by MacGinitie. Apparent absence of microthermal species of *Acer* in the latest Paleocene-early Eocene interval is related to the absence of definite microthermal assemblages; if microthermal climates existed during this interval, they were of exceedingly limited areal extent.

Although the earliest occurrences of *Acer* are in mesothermal to possibly megathermal vegetation, during the middle and late Eocene *Acer* was primarily found in microthermal forests. Middle and late Eocene assemblages from the volcanic upland region of western North America represent evergreen coniferous forest (Axelrod, 1966; Wolfe and Wehr, 1986) which is invariably microthermal (Wolfe, 1979). *Acer* is notably absent in large collections from the Eocen lowland regions such as western Washington, where the vegetation was mesothermal to megathermal (Wolfe, 1978). Although *Acer* is known in cool mesothermal assemblages such as the latest Eocene Florissant (MacGinitie, 1953), the genus is of low diversity in such assemblages. In Alaska, some late Eocene assemblages (for example, Aniakchak Crater) that contain *Acer* appear to represent polar broad-leaved deciduous forest and a cool mesothermal climate. Other late Eocene assemblages (for example, Rex Creek) may represent microthermal vegetation. Certainly the major Eocene diversification of *Acer* was in cool mesothermal to microthermal climates, which are the climates in which *Acer* has great diversity today.

Following the terminal Eocene climatic deterioration, microthermal broad-leaved deciduous forests came into existence (Wolfe, 1978). *Acer* was diversely represented in such vegetation, just as the genus is diversely represented today. The early and middle Miocene Mixed Mesophytic forest of the Pacific Northwest contained at least 17 lineages of *Acer,* and the early and middle Miocene Mixed Northern Hardwood forest in Beringia contained 10. *Acer,* however, continued to be a significant element in coniferous forests, such as those of the middle Miocene in Nevada and the late Miocene of the Columbia Plateaus; *Acer* is represented by 14 lineages in these coniferous forests, although some species (for example, *A. medianum*) appear to occupy early successional habitats rather than to be forest trees.

Acer was largely eliminated from western North America by two major factors: decline in summer temperatures and decline in summer precipitation. In Nevada during the middle Miocene, decline in summer precipitation was probably the major factor, whereas in Alaska during the middle Miocene, decline in summer temperatures was the major factor. During the late Miocene, the Columbia Plateaus region also underwent a decline in summer precipitation, and *Acer* was largely eliminated. *Acer* that have persisted in western North America from the Tertiary are: (1) *A. negundo,* which is of fluviatile habitat, (2) *A. glabrum,* which is a high-altitude species that we assume derives summer moisture from melting snow-packs, (3) *A. macrophyllum,* which is restricted to moist regions west of the Sierra-Cascade axis and is particularly common in coastal regions, and (4) *A. grandidentatum,* which is largely restricted to montane regions that receive some summer precipitation in the form of thunderstorms. Few lineages of *Acer* were able to adapt to decreasing summer precipitation during the Neogene in western North America.

Adaptive strategies

Adaptive significance of phenetic changes in the various organs of *Acer* is, in most instances, obscure or unknown. Changes in morphology of the flower are the most difficult to relate to environmental factors, either physical or biotic. Of what adaptive significance is an extrastaminal versus an intrastaminal disk? Of what value is tetramery versus pentamery? For reasons of economy, it is understandable that the vestigial pistil in the male flower and the non-functional stamens in the female flower are reduced or lost, but such reductions or losses have occurred in only some sections of *Acer.* Sections such as *Palmata* are highly successful today and have both a well developed vestigial pistil in the male flower and non-functional stamens in the female ("hermaphrodite") flower. As emphasized by Cronquist (1968), changes in floral morphology in the angiosperms may, in many instances, have no apparent adaptive significance.

Development of a few-flowered umbel in the *Rubra-Eriocarpa* line is conceivable related to early flowering and fruiting of both sections. The strategy here is to waste little time in growing a large panicle and instead to put available material into many, few-flowered umbels that can produce mature fruit by late spring or early summer. Seedlings are then growing by mid-summer and have considerable growth by the end of the growing season. In this connection, we emphasize that possession of a few-flowered umbel and early flowering and fruiting are syndromes of the same adaptive strategy and thus should not necessarily be considered as two separate character states.

Some changes in the fruit appear to be adaptive. Large size of the nutlets in the Miocene *Acer whitebirdense* and *A. busamarum* could be related to animal dispersal; fruit of the extant *A. macrophyllum,* an extant relative of *A. busamarum,* has a comparatively small nutlet that is known to be collected by rodents. *Acer whitebirdense* must have been largely animal dispersed, because geometry of the fruits indicates that they could not have been autogyrative, whereas fruits of *A. busamarum* were adapted for both animal dispersal and autogyration.

Changes in foliar morphology can perhaps be best explained in terms of adaptation to physical factors. Stenophylly has been suggested as an adaptation to a fluviatile habitat (Richards, 1952). The most stenophyllous *Acer* known is the latest Eocene *A. elwyni*. This species is abundantly represented in the Mormon Creek and Metzel Ranch beds; the irregular orientation of the leaves and the absence of parallel bedding in the matrix bearing *A. elwyni* is indicative of fluviatile deposition, which supports the inferred relation between stenophylly and the fluviatile habitat. Leaflets of *Negundo,* although not strictly stenophyllous, are stenophyllous in relation to the leaves of most other species of *Acer*. Return to the pinnate leaf inferred for the *Negundo* Group may well have been related to pressures of a fluviatile habitat to develop stenophylly.

Total loss of teeth in various lineages of *Acer* is probably related to the general correlation between the entire-margined leaf and high temperatures (Bailey and Sinnott, 1966; Wolfe, 1979). Indeed, *Acer* is a classical example of the relation between margin type and climate. The unlobed and untoothed leaves in *Acer* are concentrated in southeastern Asia and off-shore islands. These *Acer* include series Sinensia of *Palmata, Integrifolia, Laurina, Decandra,* and *Pentaphylla.* These taxa are largely confined to the warm parts of the Notophyllous Broad-leaved Evergreen forest (Wolfe, 1979). Lobed (typically shallowly) but untoothed and unlobed but toothed *Acer* are concentrated in cool parts of the Notophyllous Broad-leaved Evergreen forest in central China and southern Japan; these *Acer* include some *Trilobata,* some *Integrifolia,* and many *Platanoidea.* Deeply lobed and strongly toothed *Acer* are generally in microthermal Mixed Coniferous forest and various types of broad-leaved deciduous forests; such leaves occur in many sections of *Acer.* In subhumid regions of south-central Asia and southern Europe, species of Monspessulana and *Syriaca* show a reduction in lobing and tooth, accompanied by decrease in laminar area. In eastern North America, more northern species of Saccharodendron (for example, *A. saccharum*) are more deeply lobed and have sharper and more numerous teeth than more southern species (for example, *A. floridanum*).

Bracing of lobal sinuses by thick, bifurcating veins can be assumed to be a structural adaptation. Lobal sinuses would be a point of structural weakness in the lamina, and bracing veins offer a defense against tearing. Thus, shallowly lobed leaves in *Acer* typically have thin bracing veins relative to thick bracing veins in moderately to deeply lobed leaves. Further, in deeply lobed leaves, the bracing vein is typically a medial secondary vein rather than an external secondary vein or a secondary vein that originates from the apical side of a lateral primary vein. Structure and economy possibly control this relation: (1) if strong support is needed, a major vein originating from the midrib can supply more support than can a thinner vein that originates as an external secondary vein or as a secondary vein from the apical side of a lateral primary vein, and (2) if less support is needed, the shortest route would be to brace the lobal sinus from the closest secondary or lateral primary vein (that is, a bracing vein that originates from the midrib would be a waste of material).

Loss of the bohlenioid pattern of secondary venation can also be viewed in terms of structure and economy. In most *Acer,* dental sinuses are braced by an external secondary vein of a craspedodromous secondary vein. The secondary vein and its external vein thus perform two functions: supplying vasculature to a primary tooth and bracing a dental sinus. Teeth of *Bohlenia* are larger relative to laminar width (that is, the lamina is more deeply incised) than in most *Acer,* so in *Bohlenia* more support for the dental sinuses is needed than in most *Acer.*

Evolution of Type II areolar venation in *Acer* resulted in a higher venation rank than in Type I areolar venation. That is, fourth and fifth order venation is more rigorously organized in *Acer* that has Type II than in *Acer* that has Type I areolar venation. Possibly more rigorous organization of venation results in greater strength and more economical use of materials than in less rigorous organization. However, *Acer* that have Type I areolar venation (for example, *Macrantha* and *Palmata*) are highly successful in extant vegetation.

That some character states of foliage are adaptive to environmental factors probably indicates that such states are prone to homoplasy more readily than are non-adaptive states. Early systematic work on *Acer,* for example, grouped together species that have unlobed, untoothed leaves into section *Integrifolia;* as emphasized by Ogata (1967), these species are now dispersed among several sections. However, acutely versus orthogonally bifurcating lobal sinal bracing appears to be of no adaptive significance, and the advanced stated of orthogonality should be synapomorphic.

Distribution of *Acer* in the Tertiary of Western North America

Co-occurrences of different organs

Assignment of the same epithet to different organs such as a leaf and a fruit because of association at the same locality can be approached from the standpoint of probability. Most paleobotanists would agree that, in the instances of most Neogene species, the same epithet can be applied to different organs because the organs are closely comparable to respective organs of the same extant species. For example, the common member of *Eriocarpa* in the western American Miocene, *Acer chaneyi*, closely resembles *A. saccharinum* in foliar morphology, and at seven localities fruits comparable in size and shape to those of *A. saccharinum* are also found; the application of the epithet *chaneyi* to these fruits is, we think, warranted.

Analysis of the co-occurrences of Oligocene and Neogene leaves and fruits of *Acer* in western North America provides a probability factor on which older co-occurrences can be evaluated. Each locality of Oligocene and Neogene age that has at least one fruit and at least one leaf of *Acer* has been included in the analysis. A locality that has this minimal requirement has the possibility that the leaf and fruit represent the same species, that is, one match is possible. A locality that has, for example, seven leaf types and three fruit types has only three possible matches, whereas a locality that has five leaf types and four fruit types has four possible matches. Of the 54 Oligocene and Miocene localities analyzed, 66 (73%) of a possible 90 matches occurred. Even at the 30 localities at which only a single match was possible, 21 (70%) matches occurred. This high ratio of actual to possible matches is, in large part, because leaves and fruits of *Acer* probably have low settling velocities and thus both organs are deposited in low-energy environments.

List of localities and occurrences of *Acer*

In the following list, the numbers in parentheses refer either to a particular collector's number cited in publication or, in most instances, to a permanent locality number assigned by the institution that houses the collection. For a list of abbreviations and corresponding institutional names, see the section "Citation of Specimens".

LATEST PALEOCENE:
  ALASKA
    Evan Jones Mine (USGS 9881): *A. alaskense.*
EARLY EOCENE:
  ALASKA
    Cape Douglas (USGS 11361): *A. douglasense.*
  CALIFORNIA
    Chalk Bluffs: *A. orbum.*
EARLIEST MIDDLE EOCENE:
  BRITISH COLUMBIA
    Chu Chua Creek (GSC 4821): *A. wehri.*
    Princeton/Whipsaw Creek (GSC 4573): *A.* sp. 3.
    Princeton/Blue Flame Mine: *A. toradense.*
    Princeton/One Mile Creek (UWBM B-3389): *A. stonebergae, A. stewarti, A. washingtonense, A. rousei, A. stockeyae, A. wehri, A. princetonense.*
    McAbee: *A. rousei.*
    Quilchena: *A. wehri.*
  WASHINGTON
    Republic/Resner Canyon (USGS 11018): *A. washingtonense, A. toradense.*
    Republic: (USGS 7870; UWBM A-0307, A-0308): *A. washingtonense, A. hillsi, A. stonebergae, A. republicense, A. spitzi, A. wehri.*
    Republic/Knob Hill (UWBM B-2737): *A. washingtonense.*
LATE MIDDLE EOCENE TO EARLY LATE EOCENE
  ALASKA
    Aniakchak Crater (USGS 11640): *A. dettermani.*
    Road Island (USGS 11418): *A. ivanofense.*
  OREGON
    Sheep Rock Creek (OMSI 256): *A. becki, A. crookense, A. meyeri, A. sinuofluviatilis, A. ovipetrinum, A. clarnoense, A. postense.*
    John Day Gulch (USGS 9270): *A.* cf. *A. salmonense.*
    Alvord Creek (UCMP N601): *A. alvordense.*
  NEVADA
    Bull Run (UCMP P561, P562): *A. elkoanum, A. eorubrum, A. taurocursum, A. cadaver, A. eomedianum, A. axelrodi.*
    Elko/Catlin (USGS 9175; UCMP P3949, 22261): *A. elkoanum, A.* sp. 6.
    Copper Basin (UCMP P3918): *A. cuprovallis, A. jarbidgianum, A.* sp. 4.
LATEST EOCENE:
  ALASKA
    Rex Creek (USGS 9928): *A.* sp. 2.

- IDAHO
  - Cow Creek (USGS 11341): *A. bosrivularis.*
  - Salmon (USGS 8173): *A. idahoense, A. salmonense.*
- MONTANA
  - Beaver Creek: *A. castorrivularis, A. florissanti, A. milleri, A. salmonense, A. tiffneyi.*
  - Sturgeon Creek: *A. powellense.*
  - Grant (USGS 8513; Becker 69): *A. elwyni, A. grantense, A. tiffneyi.*
  - Christensen Ranch (Becker 32): *A. eomedianum, A. macginitiei, A. alvordense, A. grantense, A. tiffneyi, A. hueberi.*
  - Johnson Creek (Becker 213): *A. florissanti.*
  - Schwartz Creek (Becker 302): *A. hueberi.*
  - "Beaverhead", exact locality unknown: *A. macginitiei, A. alvordense, A. montanense, A. hueberi.*
  - Mormon Creek: *A. elwyni.*
  - Metzel Ranch: *A. elwyni.*
  - York Ranch: *A. elwyni.*
  - Ruby: *A. florissanti, A. elwyni, A. beckeri.*
- WYOMING
  - Gas Hills: *A. elwyni.*
- COLORADO
  - Florissant: *A. florissanti, A. macginitiei.*

EARLY OLIGOCENE:

- ALASKA
  - Redout Point (USGS 11367): *A. kenaicum.*
  - Tsadaka Canyon (USGS 9359): *A.* sp. 1, *A. kenaicum.*
- WASHINGTON
  - Gumboot Mountain (UCMP PA-367): *A. chaneyi, A. osmonti*
- OREGON
  - Lyons (USGS 9351, UCMP PA-487): *A. oligomedianum, A. osmonti.*
  - Willamette (USGS 9086): *A. manchesteri.*
  - Bridge Creek/Allen Ranch (USGS 8641, 11531; UCMP 3741): *A. cranei, A. ashwilli, A. osmonti, A. manchesteri.*
  - Bridge Creek/Clarno NE (UCMP 132): *A. oligomedianum, A. ashwilli, A. osmonti.*
  - Bridge Creek/Dugout Gulch (UCMP P4210; OMSI 241): *A. cranei, A. ashwilli, A. osmonti, A. manchesteri.*
  - Bridge Creek/Fossil (USGS 9420: UCMP P5203, PA-15): *A. cranei, A. ashwilli, A. osmonti, A. manchesteri.*
  - Bridge Creek/Gray Ranch (USGS 8778; UCMP 3748): *A. glabroides, A. oligomedianum, A. cranei.*
  - Bridge Creek/Gray Ranch (UCMP 3750): *A. cranei, A. ashwilli.*
  - Bridge Creek/Gray Ranch (UCMP 3930): *A. kluckingi.*
  - Bridge Creek/Gray Ranch (UCMP 3937): *A. glabroides, A. manchesteri.*
  - Bridge Creek/Kant Ranch (UCMP 3931): *A. ashwilli.*
  - Bridge Creek/Kennedy Ranch (USGS 9422): *A. ashwilli, A. osmonti.*
  - Bridge Creek/Knox Ranch (USGS 9440; UCMP P5405): *A. cranei, A. osmonti, A. manchesteri.*
  - Bridge Creek/Nichol Spring (Ashwill F-5): *A. cranei, A. osmonti.*
  - Bridge Creek/Pentecost Ranch (UCMP PA-2; OMSI 246): *A. cranei, A. kluckingi, A. osmonti.*
  - Bridge Creek/Slanting Leaf Beds (USGS 11528; UCMP PA-421; OMSI 240): *A. kluckingi, A. osmonti, A. manchesteri.*
  - Bridge Creek/Summer Spring (Ashwill F-1, F-10): *A. cranei, A. ashwilli.*
  - Bridge Creek/Twickenham (UCMP P5603): *A. cranei, A. osmonti, A.* sp. 7.
  - Bridge Creek/Woods Hollow (Ashwill F-43): *A. oligomedianum, A. osmonti*

LATE OLIGOCENE:

- ALASKA
  - Kukak Bay (USGS 11812): *A. tigilense, A. chaneyi, A. smileyi, A. megasamarum.*

OREGON
Three Lynx (USGS 9674): *A. oregonianum.*
Cascadia (USGS 9350, UCMP P-388): *A. cascadense, A. smileyi, A. oregonianum.*
Shale City (USGC 9262): *A. oregonianum.*
EARLY PART OF EARLY MIOCENE:
ALASKA
Healy Creek (USGS 9926): *A. tigilense.*
Usibelli Mine (USGS 9925): *A. megasamarum.*
Capps Glacier (USGS 9845): *A. ezoanum.*
Capps Glacier (USGS 9846): *A. smileyi.*
Kanalku Bay (USGS 9826): *A. chaneyi.*
BRITISH COLUMBIA
Chilcotin River (GSC 5786, 6384): *A. traini, A. medianum, A. busamarum fingerrockense, A. minutifolium.*
OREGON
Eagle Creek (USGS 1049; Chaney 4): *A. minutifolium.*
Eagle Creek (Chaney 11): *A. heterodentatum.*
Eagle Creek (USGS 9425): *A. minutifolium.*
Collawash (USGS 9256; UCMP PA-1): *A. heterodentatum, A. negundoides, A. chaneyi, A. browni, A. oregonianum, A. collawashense.*
Little Butte Creek (USGS 8904, 9486): *A. negundoides, A. chaneyi, A. browni, A. medianum, A.* cf. *A. oregonianum.*
NEVADA
'49 Camp (UCMP 97): *A. medianum, A. negundoides, A. tigilense, A. smileyi, A. busamarum fingerrockense, A. collawashense.*
LATE EARLY TO EARLY MIDDLE MIOCENE:
ALASKA
Lignite Creek: *A. tigilense.*
Cache Creek (USGC 9867): *A. tigilense.*
Beluga River (USGS 9849): *A. protomiyabei.*
Bidarki Creek (UMMP ^{1961}): *A. tigilense.*
Seldovia Point (USGS 9856): *A. megasamarum, A. protomiyabei.*
Seldovia Point (USGS 9858): *A. heterodentatum, A. palaeorufinerve, A. megasamarum, A. protomiyabei.*
Coal Bay (USGS 9989): *A. tigilense.*
Skolai Creek (USGS 9927): *A. protomiyabei.*
Skolai Creek (USGS 9933): *A. chaneyi.*
BRITISH COLUMBIA
Skonun (UBCB 60 AB333): *A. browni*
WASHINGTON
Bunker Creek (USGS 9141): *A. browni.*
Kittias Valley (USGS 468): *A. septilobatum.*
Priest Rapids (UWMG A-2508): *A. tyrellense.*
Cottonwood Creek (UOCM 2773): *A. negundoides, A. megasamarum, A. scottiae.*
Grand Coulee (USGS 9078): *A. medianum, A. chaneyi, A. whitebirdense* (the specimens of the last two species are in different matrix and thus represent different horizons).
Latah/Spokane (UCMP 3940): *A. chaneyi.*
Latah/SP & S Cut: *A. whitebirdense.*
Latah/Brickyard: *A. medianum, A. knolli, A. latahense, A. whitebirdense.*
Latah/Deep Creek (USGS 7894): *A. tigilense.*
Latah/Shelley Lake (USGS 7579): *A. chaneyi.*
Latah/Vera: *A. latahense.*
Latah/Vera (USGS 8427): *A. latahense, A. chaneyi, A. browni.*
Latah/Vera (USGS 9756): *A. chaneyi, A. browni.*
OREGON
Cape Blanco (USGS 9743): *A.* sp. indet. (Saccharodendron).

Liberal (USGS 9673): *A. molallense.*

Mascall/Dayville (UCMP P4129): *A. medianum, A. chaneyi, A. negundoides, A. oregonianum, A. schorni.*

Mascall/Meadow (UCMP P4123): *A. medianum, A. negundoides, A. taggarti.*

Mascall/Riverbank (USGS 2699; UCMP P28): *A. medianum, A. negundoides, A. chaneyi, A. oregonianum, A. megasamarum, A. schorni, A. septilobatum.*

Mascall/White Hills (UCMP 3735): *A. medianum, A. traini, A. negundoides, A. tigilense, A. oregonianum, A. scottiae.*

Skull Spring (USGS 11795): *A. busamarum fingerrockense, A. megasamarum, A. septilobatum.*

Sparta (UOCM 2726): *A. busamarum* cf. *fingerrockense, A. tyrellense.*

Baker (USGS 8171): *A. whitebirdense.*

Jamieson (USGS 11241): *A. busamarum* cf. *fingerrockense.*

Succor Creek/"near Oregon-Idaho line" (USGS 1769): *A. medianum.*

Succor Creek/Carter Creek (UMMP PT-11): *A. medianum, A. schorni, A. scottiae.*

Succor Creek/Devils Gate (MSUB 9/22/77 I); *A. medianum, A. negundoides, A. busamarum* cf. *fingerrockense, A. schorni.*

Succor Creek/Fenwick Gulch (UMMP PT-2): *A. medianum, A. negundoides, A. busamarum fingerrockense.*

Succor Creek/McKenzie Ranch (UMMP PT-10): *A. schorni.*

Succor Creek/Quarry (MSUB 7/15/70 II): *A. medianum.*

Succor Creek/Rocky Ford (MSUB 9/16/77 I): *A. chaneyi, A. tyrellense.*

Succor Creek/Sheaville: *A. medianum.*

Succor Creek/Strode Ranch (UMMP PT-4): *A. septilobatum.*

Succor Creek/Upper Type Section (MSUB 9/16/77 II): *A. medianum.*

Succor Creek/Whiskey Creek (MSUB 8/30/62 II, 8/30/69 IV, 7/15/70 II): *A. chaneyi, A. busamarum* cf. *fingerrockense, A. tyrellense, A. scottiae.*

IDAHO

Latah/Couer d'Alene: *A. chaneyi.*

Clarkia (UIB P-33): *A. chaneyi, A. smileyi, A. busamarum fingerrockense.*

Clarkia (UIB P-37): *A. niklasi, A. chaneyi.*

Clarkia (UIB P-40): *A. busamarum fingerrockense.*

Whitebird (USGS 8444; UCMP PA-97): *A. whitebirdense.*

NEVADA

Thurston Ranch (UCMP 5505): *A. traini, A. chaneyi, A. busamarum fingerrockense, A. septilobatum.*

Deadman Creek (USGS 7299): *A. chaneyi.*

Pyramid (UCMP 5202): *A. tigilense, A. chaneyi, A. scottiae, A. septilobatum.*

Purple Mountain (UCMP 6203): *A. chaneyi.*

Purple Mountain (UCMP 6209): *A. traini.*

Buffalo Canyon (UCMP PA-291): *A. negundoides, A. busamarum fingerrockense, A. schorni, A. tyrellense.*

Eastgate (UCMP 6507): *A. chaneyi, A. busamarum fingerrockense, A. tyrellense.*

Middlegate (UCMP P5101): *A. medianum, A. negundoides, A. chaneyi, A. busamarum fingerrockense, A. schorni, A. tyrellense, A. septilobatum.*

Fingerrock (UCMP PA-99): *A. medianum, A. busamarum fingerrockense, A. schorni, A. tyrellense, A. septilobatum.*

Goldyke (UCMP PA-342): *A. busamarum fingerrockense.*

San Antonio (UCMP PA-336): *A. medianum.*

CALIFORNIA

Mint Canyon (UCMP P 40): *A.* sp. indet. (Saccharodendron).

LATE MIDDLE TO EARLY LATE MIOCENE (HOMERIAN)

WASHINGTON:

Toledo (UWBM B-3501): *A. megasamarum.*

Ellensburg/Tyrel (UCMP PA-19); *A. medianum, A. negundoides, A. tyrellense.*

Ellensburg/Sand Pit (UCMP PA-22): *A. medianum.*

Ellensburg/Ahtanum Ridge (UCMP PA-23): *A. medianum.*

OREGON
- Faraday (USGS 9281): *A. oregonianum, A. septilobatum.*
- Weyerhauser (USGS 9997): *A. chaneyi, A. tyrellense.*
- Hidden Lake (USGS 9349): *A. oregonianum.*
- Hidden Lake (USGS 11031): *A. chaneyi.*
- Austin (UCMP P3937): *A. niklasi, A. chaneyi, A. septilobatum.*
- Tipton (UCMP P3936); *A. latahense, A. chaneyi, A. busamarum busamarum, A. septilobatum.*
- Vinegar Creek (UCMP P5404): *A. tigilense.*
- Stinking Water (UCMP P4120): *A. chaneyi, A. whitebirdense, A. busamarum busamarum.*
- Stinking Water (UCMP P4006): *A.* cf. *A. chaneyi, A. schorni.*
- Buelah (USGS 2987): *A. busamarum.*
- Succor Creek/Maple Ridge: *A. medianum, A. negundoides, A. latahense, A. busamarum busamarum, A. scottiae.*
- Trout Creek (USGS 11794; UCMP 275; UMMP PT-A, PT-W): *A. medianum, A. traini, A. negundoides, A. chaneyi, A. busamarum busamarum, A. smileyi, A. schorni, A. scottiae, A. septilobatum.*

IDAHO
- Hog Creek (USGS 8923, UCMP 635): *A. medianum, A. negundoides, A. busamarum busamarum, A. megasamarum, A. schorni, A. tyrellense, A. scottiae, A. septilobatum.*
- Cartwright Ranch (UCMP 3743): *A. chaneyi, A. busamarum busamarum.*
- Horseshoe Bend (USGS 8349): *A. septilobatum.*
- Horseshoe Bend (UCMP 591): *A. chaneyi.*
- Idaho City (USGS 8437): *A. tigilense.*
- Almaden (UCMP P6001): *A. negundoides, A. tyrellense.*
- Alkalai Creek (USGS 8924): *A. tigilense, A. chaneyi.*
- Thorn Creek (UCMP P4600): *A. tigilense, A. macrophyllum, A. septilobatum.*
- Trapper Creek (USGS 9176; UCMP 571): *A. traini, A. negundoides, A. tigilense, A. chaneyi, A. busamarum busamarum, A. tyrellense, A. septilobatum.*

CALIFORNIA
- Table Mountain (UCMP P3715): *A. bolanderi.*

LATEST MIOCENE:

WASHINGTON:
- Hammer Bluff (USGS 9411): *A. oregonianum.*

OREGON
- Lolo Pass (USGS 9737): *A. ferrignoi.*
- The Dalles (UCMP 3941): *A. negundoides.*

NEVADA
- Hazen: *A. schorni.*
- Verdi (UCMP P102): *A.* cf. *A. schorni.*

CALIFORNIA
- Mulholland (UCMP P-386): *Acer* sp. indet. (Saccharodendron).
- Remington Hill (UCMP P3935): *A. negundoides.*
- Denton Creek (UCMP P5602): *A.* sp. indet. (Saccharodendron).

PLIOCENE:

OREGON
- Deschutes (UCMP 3720): *A. negundoides.*

CALIFORNIA
- Niles Canyon (UCMP PA-129): *A. tyrellense.*

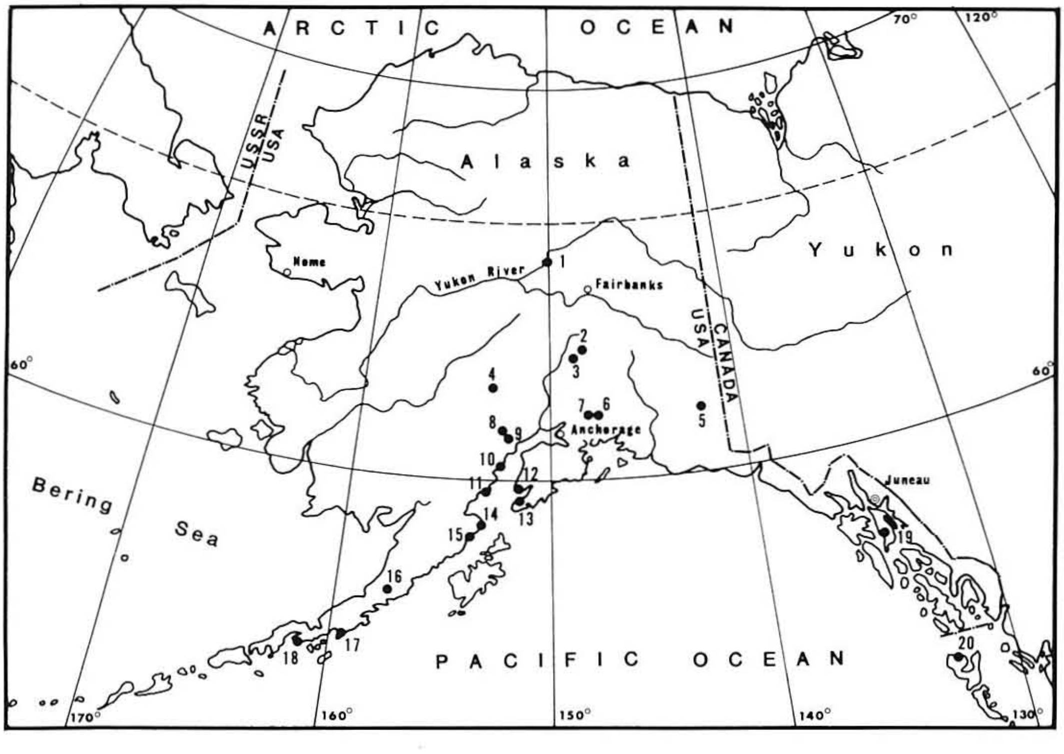
Stratigraphic

Ages of assemblages that contain Acer

Age assignments of assemblages that contain *Acer* in western North America are based on all available data. We have commented on particularly Paleocene and Eocene occurrences because of their significance to dating first appearances of particular sections. To fully document relative ages of many Miocene assemblages that contain *Acer* would be an unnecessary and lengthy digression from the major topics of this report. Note that the age of about 33 to 34 million years that is accepted here for the Eocene-Oligocene boundary is younger than the commonly accepted 37 to 38 Ma. All cited radiometric ages have, if necessary, been corrected for new decay constants.

(a) Paleocene

The oldest known *Acer* is *A. alaskense*, which occurs in beds that have been radiometrically dated (Triplehorn, 1984) at about 54 Ma. If the *"A." arcticum* complex has the relationship to *Acer* that we have proposed (see p. 10), then *Acer* could be older than latest Paleocene. A member of this complex occurs in the latest Maestrichtian (about 65 to 66 Ma) of central Alberta (J.A. Wolfe, unpubl. data). This, however, does not necessarily imply the existence of *Acer* during the latest Maestrichtian; the common ancestor of *Acer* and the *"A." arcticum* compelx could have co-existed with the complex throughout much of the Paleocene before giving rise to *Acer*.



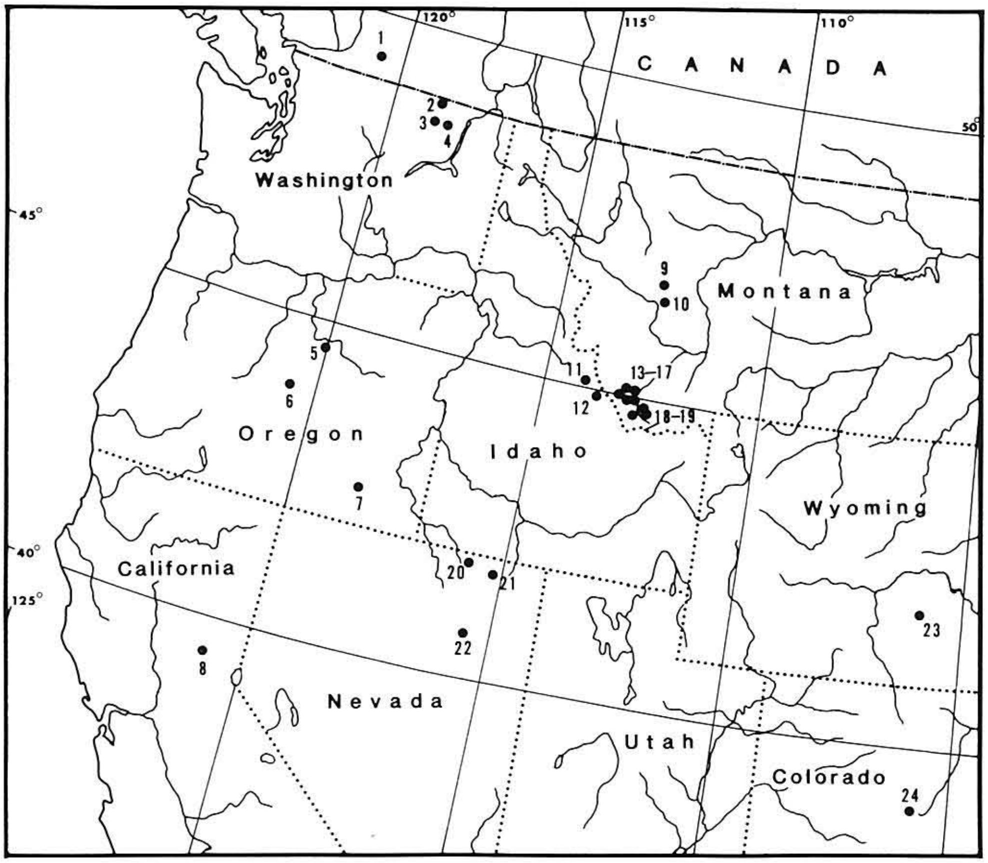
Text-fig. 4 Map of Alaska and adjacent area showing location of floras of Tertiary age in which *Acer* is represented.

1. Rampart 2. California Creek 3. Healy 4. Cache Creek 5. Skolai Creek 6. Evan Jones 7. Tsadaka Canyon 8. Capps Glacier 9. Beluga River 10. Redoubt Point 11. Chinitna Bay 12. Bidarki Creek 13. Seldovia Point 14. Cape Douglas 15. Kukak Bay 16. Aniakchak Crater 17. Road Island 18. Coal Bay 19. Kanalku Bay 20. Skonun

(b) Eocene

Acer douglasense, one of the two early Eocene occurrences of *Acer*, occurs in beds assignable to the West Foreland Formation, a unit that, on other paleobotanical evidence, includes beds of both latest Paleocene and early Eocene age (Magoon and others, 1976). The assemblage that contains *A. douglasense* is thought to be of early Eocene age. The early Eocene occurrence of *Acer* in the conterminous United States, that of *A. orbum* in the Chalk Bluffs flora, has some independent age control. This flora is considered to occur in the Ione Formation, which is about Zone P8 of the planktonic foraminiferal chronology (about 51 Ma; Wolfe, 1981).

The Republic, Knob Hill, Resner Canyon, Princeton, and McAbee occurrences of *Acer* have radiometric ages of about 47 to 49 Ma (Hills and others, 1967; Pearson and Obradovich, 1977), that is, earliest middle Eocene. Probably assignable to the latest



Text-fig. 5 Map showing location of floras of Eocene age in which *Acer* is represented.
1. Princeton 2. Resner Canyon 3,4. Republic 5. John Day Gulch 6. Sheep Rock Creek 7. Alvord Creek 8. Chalk Bluffs 9. Beaver Creek 10. Sturgeon Creek 11. Salmon 12. Cow Creek 13. Beaverhead Grant 14. Christensen Ranch 15. Johnson Creek 16. Schwartz Creek 17. Ruby 18. Mormon Creek 19. Metzel Ranch 20. Bull Run 21. Copper Basin 22. Gass Hill 24. Florissant

middle Eocene is the Bull Run flora. The Bull Run specimens of *Acer* occur in the two lower Bull Run assemblages; the Bull Run plant-bearing beds occur above a radiometric age of 43 Ma and below a radiometric age of 38 Ma (Axelrod, 1966).

Several other floras that contain *Acer* are assigned to the latest middle to early late Eocene (about 38 to 42 Ma) interval. In Oregon, both the John Day Gulch and Sheep Rock Creek assemblages were obtained from the Clarno Formation. The John Day Gulch assemblage occurs in the middle part of the Clarno, an interval that has furnished radiometric ages of about 41 Ma (Wolfe, 1972). On paleobotanical grounds, the Sheep Rock Creek assemblage appears to represent the same interval. The Bull Run assemblage has radiometric ages of about 41 Ma (Axelrod, 1966). The Elko assemblage was obtained from beds that are stratigraphically below a radiometrically dated flow of 38 Ma (McKee and others, 1977). The occurrences of *Acer* in Alaska (Road Island and Aniakchak Crater assemblages) are in the lower part of the Meshik Formation; the lower part of the Meshik has radiometric ages of about 40 to 43 Ma (Detterman and others, 1981).

The Alvord Creek assemblage was once considered of Pliocene age (Axelrod, 1944; Wolfe, 1964), but radiometric ages of overlying basalts are about 16 Ma (Evernden and James, 1964). Indeed, we suggest that the Alvord Creek assemblage is of late Eocene age. This suggestion is based on (1) the occurrence of *Heteromeles cuprovallis* (Axelr.) Wolfe (called *Photinia sonomensis* by Axelrod, 1944), (2) the occurrence of a *Mahonia* that represents a late Eocene stage of evolution in the genus (H.E. Schorn, oral commun., 1984), (3) the occurrence of a fragment of a highly toothed *Platanus* that appears to represent the latest Eocene *P. comstocki* (Sanb.) Wolfe, and (4) absence of *Quercus*, which occurs commonly in microthermal assemblages of post-Eocene age but has yet to be documented in Eocene microthermal assemblages, and (5) the occurrence in the nutlets of *Acer alvordense* of particular insect borings, which have thus far been encountered only in Eocene material.

The age of the Alaskan Rex Creek assemblage was once thought to be late Oligocene (Wahrhaftig and others, 1969), but we now consider this assemblage to be of latest Eocene age. Radiometric ages on underlying intrusive rocks are about 36 Ma (Clyde Wahrhaftig, oral commun., 1985), which establish a lower age limit. The occurrence of broad-leaved evergreens (*Engelhardia* and *Ilex*) indicates an age no younger than Eocene, because broad-leaved evergreens are unknown in any independently dated Alaskan Oligocene or Neogene rocks.

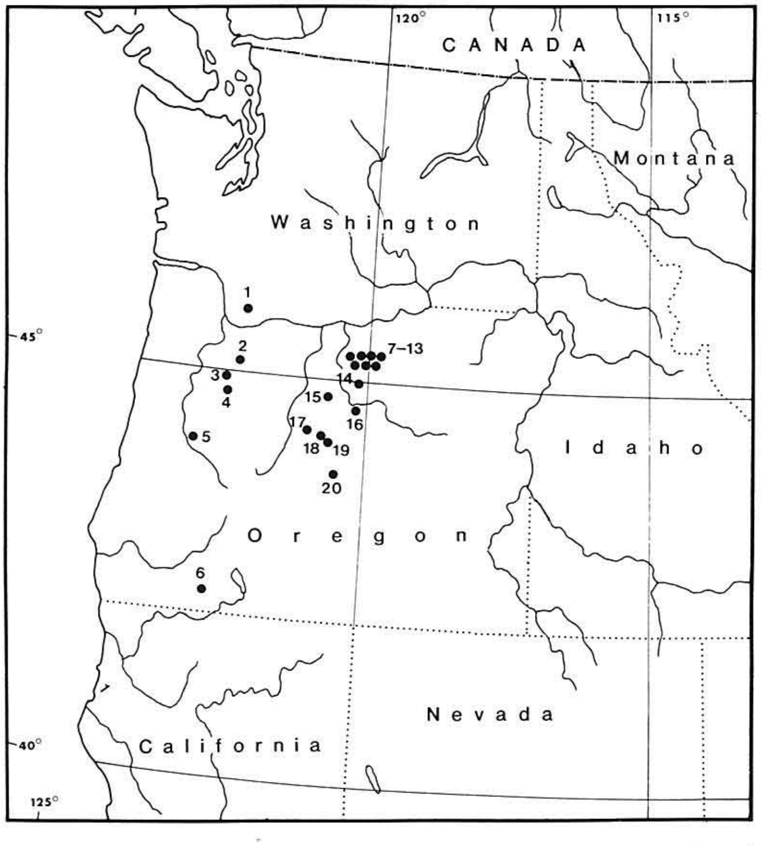
Most latest Eocene (about 33 or 34 to 38 Ma) occurrences of *Acer* are in western Montana and adjacent Idaho. Most of these Montana assemblages are in beds that regional stratigraphy indicates are of Chadronian age in the North American mammalian chronology (Becker, 1972); these assemblages include the Ruby, Mormon Creek, York Ranch, Metzel Ranch, Grant, Christensen Ranch, Johnson Creek, Schwartz Creek, and the "Beaverhead" (an inclusive term used for the last four assemblages if specimens were not labeled as to locality). The Beaver Creek assemblage has many species in common with assemblages such as the Ruby and is thought to be coeval with the Ruby.

The Salmon assemblage in Idaho was originally thought to occur in lake beds of the Challis Volcanics (Axelrod, 1966), but recent mapping indicates that the Salmon lake beds were deposited in a graben whose sides are formed of the Challis; thus, the Salmon assemblage is younger than 41 Ma, which is the youngest radiometric age obtained from the Challis in the Salmon area (M.L. Statz, oral commun., 1983). The Cow Creek assemblage came from lake beds that have a similar relation to the Challis as do the Salmon beds.

The Gas Hills beds that contain *Acer* are in the lower part of the White River Group, which also contains Chadronian mammals. The florissant beds have radiometric ages of about 35 to 36 Ma (Chapin and Eppis, 1976).

(c) Oligocene

In Alaska, the Redoubt Point and Tsadaka Canyon assemblages are, on local



Text-fig. 6 Map of western conterminous United States showing location of floras of Oligocene age in which *Acer* is represented.
1. Gumboot Mountain 2. Three Lynx 3. Lyons 4. Cascadia 5. Wiliamette 6. Shale City 7. Dugout Gulch 8. Cove Creek 9. Pentecost Ranch 10. Fossil 11. Knox Ranch 12. Slanting Leaf Bed 13. Clarno NE 14. Twickenham 15. Kennedy Ranch 16. Allen Ranch 17. Sumner Spring 18. Nicol Spring 19. Woods Hollow 20. Gray Ranch

paleobotanical correlations, assigned an early Oligocene age (Wolfe and Tanai, 1980); the Redoubt Point assemblage occurs in the lower part of the Tyonek Formation and the Tsadaka Canyon assemblage in the Tsadaka Formation (Magoon and others, 1976). Most early Oligocene occurrences of *Acer* in the conterminous United States are in assemblages that were obtained from the lower member of the John Day Formation and that are collectively referred to as the Bridge Creek flora (text-fig. 6); the lower member has radiometric ages of 30 to 33 Ma (Evernden and James, 1964). The Willamette assemblage has a radiometric age of 32 Ma (Evernden and James, 1964). The Lyons and Gumboot Mountain assemblages are not independently dated, although regional stratigraphic relations allow an early Oligocene age, as indicated by the plants.

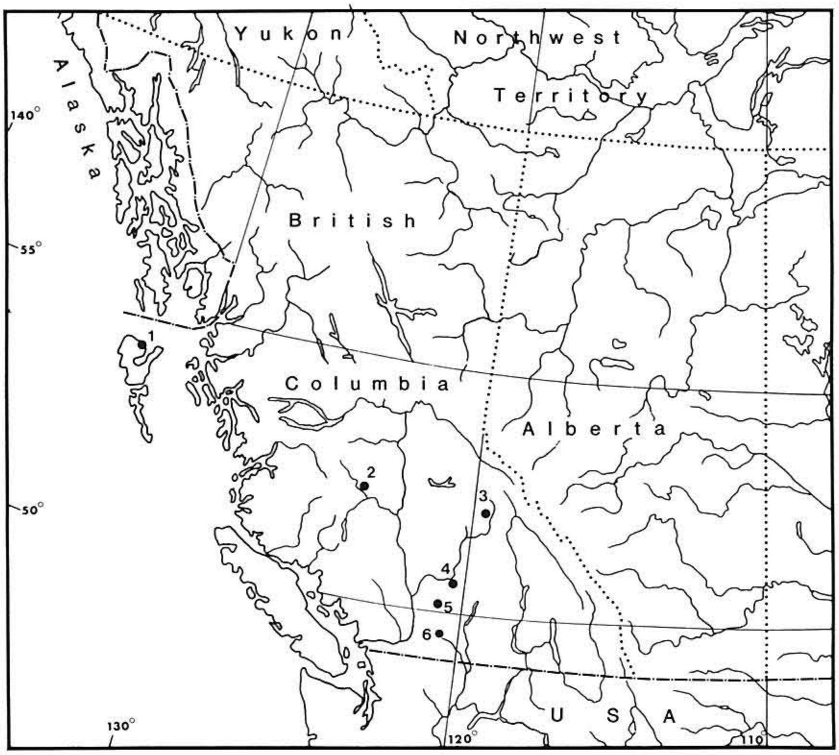
Occurrences of late Oligocene assemblages are few. The Shale City assemblage is from lake beds that are bracketed by radiometric ages of 26 to 28 Ma (J.G. Smith, oral commun., 1982). The Cascadia and Three Lynx assemblages are both in the middle part of the Little Butte Volcanic "Series" and are presumed to be of pre-Miocene age (the Collawash assemblage is in the upper part of this unit and is of early Miocene age) and to be younger than the probable latest Eocene and early Oligocene assemblages (such as the Lyons) in the lower part of the unit. In Alaska, only the Kukak Bay assemblage (Knowlton, 1902; recollected by J.A. Wolfe in 1984) is assigned to the late Oligocene. Absent from the Kukak Bay assemblage are typical Alaskan Miocene taxa such as *Quercus furuhjelmi* and *Alangium mikii*; present, however, are *Salix (Vetrix)* and *Fagus*, which are unknown in assemblages such as the Redoubt Point but are common in the Alaskan early and middle Miocene.

(d) Neogene

The Chilcotin River assemblage from central British Columbia (text-fig. 7) is dated principally by paleobotany. The Skonun assemblage occurs in a unit that contains marine mollusks of early middle Miocene age (Addicott, 1967). The Alaskan Miocene occurrences of *Acer* are in assemblages that are dated by the regional paleobotanical framework (Wolfe and others, 1966; Wolfe and Tanai, 1980). Radiometric data from Alaska are limited but support the Neogene paleobotanical stratigraphy (Turner and others, 1980).

Most Miocene assemblages from the Columbia Plateaus region (text-fig. 8) can be placed stratigraphically by relations of the lake beds to flows of the Columbia River Basalt Group, many of which are radiometrically dated (Swanson and others, 1977). Some of these flows also extend into the Cascade Range and can be used to date assemblages there. For assemblages from the Snake River Plain of Idaho and from adjacent areas of Oregon (principally in the Succor Creek drainage), we have relied on the stratigraphic analysis of fossil plant assemblages and rock units by Fields (1984); his analysis incorporates data on lithostratigraphic correlations, radiometric ages, and mammalian chronology.

The Miocene assemblages from Nevada that contain *Acer* are typically of late early to early middle Miocene age (about 14 to 18 Ma). Assignment to this age interval is based on some radiometric ages (Evernden and James, 1964) and on relations to mammal-bearing beds. Exceptions are the '49 Camp assemblage, which is radiometri-



Text-fig. 7 Map of western Canada showing location of floras of Tertiary age in which *Acer* is represented.
1. Skonun 2. Chilcotin River 3. Chu Chua Creek 4. McAbee 5. Quilchena 6. Princeton

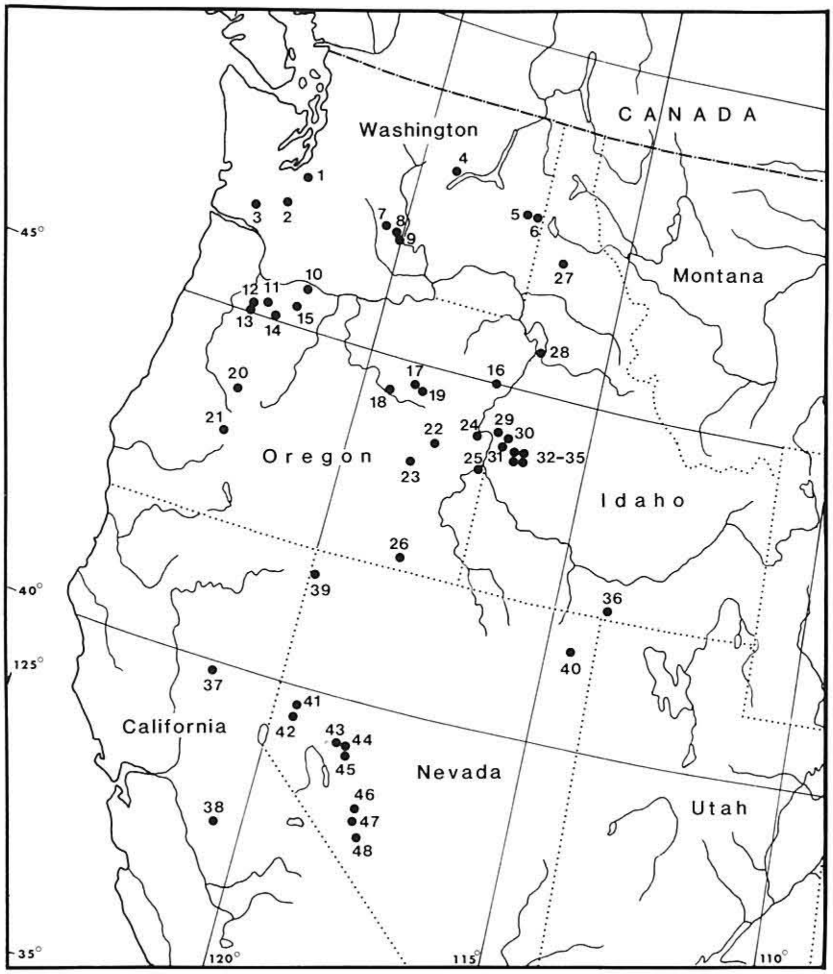
cally dated at about 21 Ma (Evernden and James, 1964) and the Verdi and Hazen, which occur in a unit that also has mammals of latest Miocene age (Axelrod, 1958).

Biostratigraphic significance of stratigraphic ranges

The Eocene species of *Acer* appear to have short stratigraphic ranges. None of the early middle Eocene species, for example, is known in the late middle or late Eocene. This is particularly striking, in view of the fact that more than 30 species are known from the late middle and late Eocene. Almost certainly, the short stratigraphic ranges of Eocone *Acer* are related to rapid evolution. The various Eocene species of *Acer* appear to offer an excellent means of correlating Eocene microthermal assemblages.

Beginning in the Oligocene, however, the species of *Acer* generally have long stratigraphic ranges. The most extreme example is that of *A. chaneyi*, which has an apparent range of about 20 Ma. Other species that have particularly long stratigraphic ranges are *A. oregonianum, A. medianum*, and *A. negundoides*.

However, some post-Eocene species have very short stratigraphic ranges. One category of apparently short-ranging species is comprised of early Oligocene species that are hold-overs of basically Eocene groups in western North America: *A. ashwilli (Trilobata), A. glabroides (Glabroides), A.* sp. 6 *(Lithocarpa)*, and *A. manchesteri (Manchesteria)*. These species may eventually be found in the still poorly known late Oligocene flora, but they are certainly unknown in the well known Miocene flora. A se-



Text-fig. 8 Map of western United States showing location of floras of Miocene age in which *Acer* is represented.

1. Hammer Bluff 2. Toledo 3. Bunker Creek 4. Grand Coulee 5. Brickyard 6. Vera 7. Ellensburg 8. Cottonwood Creek 9. Priest Rapids 10. Eagle Creek 11. Faraday 12. Liberal 13. Weyerhauser 14. Collawash 15. Lolo Pass 16. Sparta 17. Tipton 18. Mascall 19. Austin 20. Hidden Lake 21. Little Butte Creek 22. Buelah 23. Stinking Water 24. Jamieson 25. Succor Creek 26. Trout Creek 27. Clarkia 28. Whitebird 29. Hog Creek 30. Almaden 31. Payette 32. Horseshoe Bend 33. Idaho City 34. Cartwright Ranch 35. Thorn Creek 36. Trapper Creek 37. Remington Hill 38. Table Mountain 39. '49 Camp 40. Thurston Ranch 41. Pyramid 42. Purple Mountain 43. Middlegate 44. Eastgate 45. Buffalo Canyon 46. Fingerrock, Goldyke 47. Monte Cristo 48. San Antonio Mountain

cond category of short-ranging species if comprised of Miocene species that apparently had a localized geographic distribution. Thus, *A. niklasi* and *A. taggarti* are short-ranging and apparently occupied a small geographical area.

The *Acer* flora of the early part of the early Miocene differs from the *Acer* flora of the late early to middle Miocene. Species thus far known in the earliest Miocene are *A. collawashense* and *A. minutifolium*. Characteristic of the early late and younger Miocene are *A. schorni, A. tyrellense, A. septilobatum*, and *A. scottiae*.

In the major part of Alaska, *Acer* became extinct at about 13 to 14 Ma; conceivably some populations may have persisted in southeastern Alaska (where *A. glabrum* is represented today). In the conterminous United States, a less drastic but marked extinction of some *Acer* occurred at about the same time. In central and southern Nevada, all *Acer* (except for Saccharodendron) became regionally extinct. In the region of the Columbia Plateaus, *A. taggarti* became extinct at this time, and *A. niklasi* and *A. smileyi* persisted into the late part of the middle (but not the late) Miocene. Even more marked was extinction of species of *Acer* on the Columbia Plateaus at about 9 to 10 Ma; *A. medianum, A. tigilense, A. scottiae*, and *A. septilobatum* became extinct. *Acer chaneyi* also disappeared from the Columbia Plateaus, but its derivative, *A. ferrignoi*, survived until about 7 Ma in the Cascade Range of Oregon.

At the sectional level, some taxa are obviously good age indicators, although generally of longer range than the constituent species. Extant sections are unknown until the late middle Eocene. The extinct section *Glabroidea* is generally a good index of the Eocene; only one post-Eocene species of this section is known. *Manchesteria* is known in beds as young as early Oligocene, whereas *Columbiana* persists until the early late Miocene. At the end of (or during) the late Eocene, several sections became extinct in North America: *Trilobata, Macrantha, Arguta, Acer, Platanoidea*, and *Campestria*. *Parviflora* appeared in North America in the late Oligocene, Saccharodendron of section *Acer* in the early Miocene, and *Macrantha, Campestria*, and *Platanoidea* reappear in the late early Miocene. During the late Miocene, (aside from *Columbiana*) *Macrantha, Eriocarpa, Rubra, Parviflora, Campestria*, and *Platanoidea* became extinct in western North America. Of the known Tertiary sections of *Acer*, only *Glabra, Negundo, Macrophylla*, and *Saccharina* have survived in western North America.

Abundance

Low abundance of *Acer* in middle Eocene microthermal vegetation is indicated by the collections from One Mile Creek, British Columia, and Republic, Washington. Collections from each of these two localities contain several thousand specimens. *Acer* is represented in the One Mile Creek collections by 3 leaves and 11 fruits and in the Republic collections by 11 fruits; although no actual counts of abundance have been made at either locality, *Acer* is estimated to comprise 0.2 percent (or less) of the fossil plants. In the megathermal (or possibly warm mesothermal) Chalk Bluffs assemblage, *Acer* is represented by four fruits and one leaf (less than 0.1%) of the over 5,000 specimens counted (MacGinitie, 1941; note that almost all the "*A. aequidentatum*" counted represents *Platanus*.

By the early late Eocene, microthermal assemblages such as the Copper Basin contain over 0.4 percent *Acer* (Axelrod, 1966), and latest Eocene cool mesothermal assemblages such as the Florissant contain 0.5 percent (MacGinitie, 1953). Although *Acer* was apparently increasing in abundance during the Eocene, plants of the genus still played a very minor role in the vegetation.

Even with the advent of areally extensive broad-leaved deciduous forests in the early Oligocene, *Acer* was still poorly represented in the vegetation. Chaney (1927), for example, counted only about 0.7 percent *Acer* in the localities at Gray Ranch in central Oregon. Of thousands of early Oligocene specimens examined in the field at Redoubt Point in the Cook Inlet region, Alaska, only one leaf and one fruit of *Acer* were observed (J.A. Wolfe, unpubl. data).

Not until the Miocene was *Acer* a significant element in the vegetation. *Acer* is the second most abundant genus in the late early to early middle Miocene Seldovia Point assemblage in the Cook Inlet region (Wolfe and Tanai, 1980). Although some Miocene assemblages in the Pacific Northwest contain representations of *Acer* as low as 2 and 3 percent (Stinking Water and Austin-Tipton, respectively; Chaney, 1959), other assemblages contain approximately 7 percent *Acer* (Mascall and Trout Creek; Chaney, 1959; Graham, 1965), and the Trapper Creek contains over 10 percent (Axelrod, 1964). Although the relative abundance of a plant in a fossil collection cannot be directly translated to relative abundance in source vegetation (Spicer and Wolfe, *in press*), nevertheless the general trend is clear: *Acer* was not a significant element in western North American microthermal vegetation until the Miocene.

Biogeographic

The classical interpretation of the historical biogeography of *Acer* is that the genus was a member of the "Arcto-Tertiary Geoflora" (the "Turgai flora" of Krystofovich, 1929), which supposedly was a broad-leaved deciduous forest of early Tertiary (or even Late Cretaceous) age that occupied high northern latitudes (Chaney, 1938, 1959). In response to cooling climate, this "geoflora" migrated southward following the Eocene, and numerous constituent taxa became disjunct between North America and Eurasia. Although appealing in simplicity in explaining disjunctions of microthermal, broad-leaved deciduous taxa, such as the disjunctions of (and within) *Acer*, paleobotanical data negate the concept of an "Arcto-Tertiary Geoflora" (Wolfe, 1972, 1977; Wolfe and Tanai, 1980). Indeed, many species of *Acer* occurred in Beringia as late as the Miocene (Chelebaeva, 1978; Wolfe and Tanai, 1980; Tanai, 1983), as well as during the Eocene. The ages of the various disjunctions, both past and present, could well be of different ages and the result of varying factors. We will thus examine each of the disjunctions in *Acer*, in order to determine when various lineages attained a bicontinental distribution and when disjunctions occurred.

The time and place of origin of *Acer* are unknown. *Acer alaskense* (latest Paleocene) is the oldest known member of the genus. In the early Eocene, a low-grade member is also present in Alaska and a somewhat more advanced member in northern California; all the earliest known occurrences of *Acer* represent generally low grades.

Although this could be used as evidence for *Acer* having only recently originated during the late Paleocene, in view of the persistence of low grades to the present day (*Spicata*, for example), such evidence is unreliable. *Acer* may well have originated during the late Maestrichtian and remained low-grade and rare until the burst of diversification at the end of the early Eocene.

Place of origin of *Acer* can, however, be conjectured, at least in a general context. The hypothesized sister-group of Aceraceae, Paullinieae, are today exclusively neotropical, and no fossil members of this tribe are known in Eurasia. *Bohlenia*, which is hypothesized to be a member of the extinct tribe that is ancestral to Aceraceae and Paullinieae, is exclusively North American. No valid fossil record of *Dipteronia* is known (the North American Tertiary *"Dipteronia"* are all referred to *Bohlenia*), but the *"Acer" arcticum* complex is largely, if not entirely, North American during the Maestrichtian and Paleocene. These data suggest that North America was the probable continent of origin of Aceraceae and of *Acer* in particular.

That major diversification at the sectional level of *Acer* occurred in western North America during the Eocene is attested by the fossil record. The oldest records of many extant sections of *Acer* (especially sections of low and medium grade) are in western North America; the oldest species of these sections, moreover, have characters that relate these sections to one another. That is, most North America early middle Eocene species of *Acer* represent a closely interrelated group of species, some of which have characters indicative of membership in, or of being ancestral to, extant sections. In contrast, *Acer* is first known in Eurasia in the late Eocene (Mai, 1981; Tanai, 1983). The late Eocene Eurasian *Acer* are not diverse and do not appear to be closely related to one another.

Spicata

The line leading to *Spicata* is inferred to have been represented in western North America by the early middle Eocene and attained a trans-Beringian distribution during the middle Eocene, as indicated by the occurrence of *Acer oishii* in eastern Asia (Tanai, 1983). The section is found in Beringia as late as the Oligocene but is not present in the Miocene. Perhaps *Spicata* was eliminated from the Beringian region by competition; the late Oligocene and early to middle Miocene in Beringia is characterized by an influx of plants from lower latitudes. The time of disappearance of *Spicata* from Beringia is not marked by any known change in the physical environment. The disjunction of *Spicata* appears to be most probably related to biotic factors.

Palmata

Palmata is interpreted to represent the derivative of an early member of the *Spicata* Group such as *Rousea*. We presume that *Rousea* or a descendant taxon migrated into Eurasia during the Eocene and gradually evolved into *Palmata*. The first valid records of *Palmata* are at middle latitudes of Eurasia during the early Miocene (Mai, 1981; Tanai, 1983).

The present disjunction in *Palmata* is between the western North American *Acer* *circinatum* and Asian members of the section, especially *A. japonicum*. Both species are highly specialized in the section and have thick, purple sepals and cream-colored petals (Ogata, 1967, p. 122). Were the two species in geographic proximity, we suggest that they would be considered as no more than subspecifically distinct. *Palmata* has no fossil record at high latitudes or in western North America. Particularly significant is that the many, extensively collected localities from the late Neogene of the Cook Inlet region in Alaska contain no record of *Palmata*. These data strongly indicate that *A. circinatum* is the product of a late Cenozoic, long-distance dispersal from eastern Asia into western North America.

Parviflora

The probable sister-section *Distyla* is represented in the early late Eocene of eastern Asia (Tanai, 1983), from which we infer that an early member of the *Spicata* Group such as *Stewarta* dispersed into Asia from North America by the early late Eocene. *Parviflora* appears in the late Oligocene of Beringia and of the Pacific Northwest. The section became briefly disjunct during the late middle Miocene but is now extant only in eastern Asia.

Macrantha

Macrantha was present at middle latitudes of western North America, as well as in Beringia, by the late middle Eocene and persisted at middle latitudes until the latest Eocene. Presumably *Macrantha* was also represented at this time in Asian microthermal assemblages. The absence of *Macrantha* in the Beringian Oligocene could indicate that the present eastern Asian-eastern North American disjunction dates from the terminal Eocene climatic deterioration. However, occurrence of *Acer palaeorufinerve* Tanai et Onoe in the Miocene of Beringia (Chelebaeva, 1978; Tanai, 1983) indicates a reentry of *Macrantha* into Beringia. *Acer paleorufinerve* is closely related to the extant *A. pennsylvanicum* and to extant Asian species, as well as to the late early to late Miocene *A. latahense* in the Pacific Northwest. Thus, the present disjunction apparently relates to climatic deterioration of the late middle Miocene.

Arguta-Glabra

The eastern Asian *Arguta* is considered to be a sister-group of the western American *Glabra*. *Arguta* appeared in Beringia in the early late Eocene and possibly also occurred microthermal vegetation of northeastern Asia. Presumably the disjunction between *Arguta* and *Glabra* dates from the terminal Eocene climatic deterioration.

Rubra

Rubra appears at about the same time (late middle to early late Eocene) in both middle latitudes of western North America and eastern Asia (Tanai, 1983). Considering that the *Rubra* Group is of western North American origin, we infer a dispersal of *Rubra* into Asia from North America during the middle Eocene. Following the terminal Eocene climatic deterioration, *Rubra* apparently became disjunct. The section, however, is well represented in the Beringian early and middle Miocene. During this time, the same species (or a group of closely related species) comparable to the extant eastern American *Acer rubrum* occupied a wide region, including middle latitudes of Europe, Asia, western North America, as well as Beringia and Iceland. Disjunction of the section between Eurasia and North America occurred during the late middle Miocene; the *A. rubrum* type survived in eastern Asia into the Pliocene, in western North America into the late Miocene, and into eastern North America into the Holocene. The one extant Asian member of *Rubra, A. pycnanthum*, is a narrow endemic in central Honshu; the foliage of *A. pycnanthum* is more specialized than that of *A. rubrum*, and conceivably *A. pycnanthum* is a late Cenozoic derivative of the *A. rubrum* type.

Eriocarpa

The presence in the Beringian early Oligocene of *Eriocarpa* indicates that this section probably was present in the Beringian late Eocene (cf. Wolfe and Tanai, 1980). The Beringian Oligocene *Acer kenaicum* represents a divergence from the early type of *Eriocarpa* in western North America. This early type of *Eriocarpa* persisted in western north America into the Miocene and is also found in the Beringian late Oligocene; this type entered middle latitudes of eastern Asia during the Miocene and survived into the Pliocene. Thus, this early type of *Eriocarpa* became disjunct between North America and Eurasia during the climatic deterioration of the late middle Miocene.

Negundo-Cissifolia

The common ancestor of the American *Negundo* and the line that led to the Asian *Indivisa* should be of middle Eocene age, and presumably this ancestor entered Asia during this interval; the latest Eocene *A. lincolnense* from Montana indicates that *Cissifolia* probably arose in North America also during the middle Eocene. We assume that disjunction occurred during or at the end of the Eocene. During the early Miocene, *Negundo* established a continuous distribution from middle latitudes of western North America into eastern Asia but became extinct in Asia by the middle Miocene (Tanai, 1983).

Macrophylla

The present disjunction in this group is between the western North American *Macrophylla* and the Asian *Lithocarpa-Laurina*. The common ancestor of *Lithocarpa-Laurina* is inferred to have migrated into Eurasia during the middle Miocene to there give rise to *Laurina* as the same taxon was giving rise to *Lithocarpa* in western North America. A short-lived disjunction occurred at the end of the Eocene, because a *Lithocarpa*-like fruit is known in the early Oligocene of Oregon.

The eastern Asian *Acer fatisiaefolium* (Oligocene to early Miocene) and the western American *A. osmonti* (early Oligocene) appear to represent sister-species, which would indicate a late Eocene, trans-Beringian ancestor that became disjunct at the end of the Eocene. During the Oligocene, *A. osmonti* appears to have spread north from middle latitudes, giving rise to the ancestor of *A. macrophyllum* at high middle latitudes and to *A. megasamarum* in Beringia; the populations of *A. osmonti* at middle latitudes of North America probably gave rise to *A. oregonianum*. During the early Miocene, *A. megasamarum* migrated south into middle latitudes of eastern Asia and, during the middle Miocene, into middle latitudes of western North America. *Acer megasamarum* disappeard from Beringia during the late middle Miocene but persisted during the early late Miocene at middle latitudes of western North America and (as *A. honshuense*) of eastern Asia into the late Miocene.

Acer

Section *Acer* (or a closely related section) was represented in western North America during the late early Eocene, probably descended from a *Spitza*-like ancestor. Section *Acer* presumably spread to Eurasia during the Eocene; the section became extinct in western North America by the end of the Eocene. In Eurasia, we infer that section *Acer* spread westward, giving rise to "Opulifolia" of Saccharodendron during the Oligocene; this series is represented in the Oligocene assemblage from Bois d'Asson in southern France (J.A. Wolfe, unpubl. data). By the early Miocene, the inferred derivative Saccharodendron *(s.s.)* is represented in Europe, western North America, and eastern Asia. Although these data might indicate a dispersal of Saccharodendron across Beringia into North America, fossil data indicate a total absence of this series at high middle and high latitudes of eastern Asia, including the extensively colected assemblages from Primorye, Sakhalin, and Kamchatka. Saccharodendron has also not been found in Beringia. Further, the two eastern Asian Miocene species of Saccharodendron are not closely related to the western Miocene species of the section. Considering that the presence of Saccharodendron in the Miocene of Iceland clearly indicates the occurrence of a long-distance dispersal, we suggest that the North American Saccharodendron from a second long-distance dispersal from Europe to North America near the beginning of the Miocene.

Platanoidea

Although the *Platanoidea* Group originated during the Eocene in western North America, the group disappeared from North America by the end of the Eocene, presumably after *Platanoidea, Campestria*, and the line leading to *Pubescentia* had all dispersed into Eurasia via Beringia. The *Platanoidea* Group is unknown in the Oligocene and earliest Miocene of western North America. In the late part of the early Miocene, however, two lineages of eastern Asian *Campestria* and *Platanoidea* appeared in Beringia, *Acer rotundatum* and *A. protomiyabei* (Chelebaeva, 1978; Wolfe and Tanai, 1980; Tanai, 1983). By the middle Miocene, these lineages had spread into middle latitudes of western North America and were there represented by *A. scottiae* and *A. septilobatum*, respectively. During the late middle Miocene, *Platanoidea* and *Campestria* became extinct in Beringia, and a disjunction of two lineages arose and persisted through the early late Miocene.

Conclusions

The historical biogeography of *Acer* is indeed complex. Many dispersals of lineages of the genus occurred during the Eocene; all the dispersals apparently were from North America into Eurasia via Beringia. Some dispersals might have occurred via the North Atlantic land connection, although this connection was severed by the beginning of the middle Eocene (McKenna, 1984), when the first extant section of *Acer* can be recognized. However, the strait between North America and Europe during the middle and late Eocene might have been narrow and have readily allowed dispersals of plants, particularly *Acer*, whose fruits are readily dispersed by air currents. Certainly the several dispersals of *Acer* between Asia and western North America during the Oligocene and Miocene were via Beringia, as attested by the records in Beringia of the dispersed lineages.

Many of the disjunctions in *Acer* were the result of the climatic deterioration at the end of the Eocene; such old disjunctions, however, are generally between sister-sections or ancestor-descendant sections. Disjunctions between species of a section appear to be of Miocene age in most instances; the cooling during the late middle Miocene appears to be the main causative agent. However, the disjunction in *Palmata* appears to represent a late Cenozoic, long-distance disperal.

Future Work

Gaps in our knowledge of the evolutionary history of *Acer* are primarily in the Paleogene, particularly in the Paleocene and Eocene. Of 50 species of *Acer* that are now known in the Paleocene and Eocene of western North America, only 13 are known from both foliage and fruit, in comparison to 28 of 40 species of Oligocene and Neogene age. Indeed, sections *Douglasa* and *Alaskana* are known only from foliage, and other sections mostly from fruits. Similarly, the Eocene member of *Arguta* is known only from foliage, and Eocene members of *Trilobata, Eriocarpa, Rubra, Acer,* and *Platanoidea* are known only from fruits. Clarification of the phylogenetic position of Eocene fruits resembling those of section *Acer* is needed to determine more accurately the relationships of these Eocene fruits.

Floras of Paleocene and early Eocene age from high middle to high latitudes of western North America (especially British Columbia) should contain members of *Acer* that represent early divergences in the genus. Floras of middle Eocene age from the same region should produce *Acer* that will, in the southern part of the region, elucidate the early diversification of the *Spicata* and *Orba* groups. *Acer* from both middle and late Eocene floras of areas such as Alaska will greatly assist in determining the timing of various dispersals from North America.

Diversity of middle and late Eocene *Acer* in western North America is only partially known. When the pesent study was nearing completion, S.R. Manchester sent the first collection from the Eocene Sheep Rock Creek locality of the Clarno Formation; this collection contained representatives of seven species, six of which were previously unknown. We suspect that additional collecting of Eocene microthermal assemblages in western North America will significantly increase the number of species now known.

The Eocene of northern Asia remains largely unknown in terms of the occurrences of microthermal taxa such as *Acer*. This region could have been part of the same floristic province as northwestern North America and hence the site of diversification in the *Spicata* Group; this region may have been the site of differentiation of *Palmata, Distyla,* and *Parviflora*. Although middle Eocene dispersals into Asia of both an early *Negundo* and *Cissifolia* are inferred, documentation is lacking. Also unknown is whether extinct sections analagous to those of the *Orba* Group evolved in northern Aisa.

Additional knowledge of post-Eocene *Acer* will also be of value, particularly knowledge of Oligocene *Acer*. In western North America, the Oligocene flora is known largely from a geographically limited area of Oregon. Knowledge of the Oligocene flora from areas as Idaho or British Columbia could well increase the number of species of *Acer* and assist in understanding the diversification in sections such as *Negundo, Columbiana, Eriocarpa,* and *Macrophylla*.

Miocene *Acer* are well known in western North America. Additional collecting could lead to the discovery of derived species, such as *A. ferrignoi,* but will not add significantly to understanding phyletic relationships. What is needed most is knowledge of Neogene *Acer* in eastern North America to better understand the historical biogeography of the microthermal flora of that region. For example, presumably the ancestors of *A. spicatum* and of *A. saccharinum* were present during the Neogene in eastern Northe America, but documentation is lacking. Did the western American Neogene species of *Parviflora* and *Platanoidea* extend into eastern North America? Floristic relationship between western North America and eastern Asia are becoming reasonably well understood, but those between eastern North America and other regions are still highly conjectural.

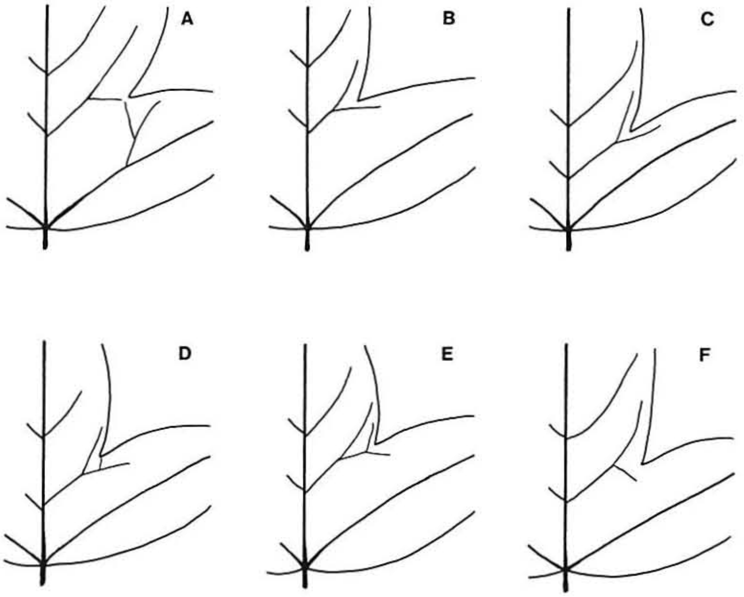
Systematics

Terminology

Foliar

We have generally followed the terminology proposed by Hickey (1973), which is the most comprehensive terminology for foliar morphology proposed to date. Certain character states commonly found in leaves of *Acer,* however, were not considered in detail by Hickey (1973). These character states are thus discussed here.

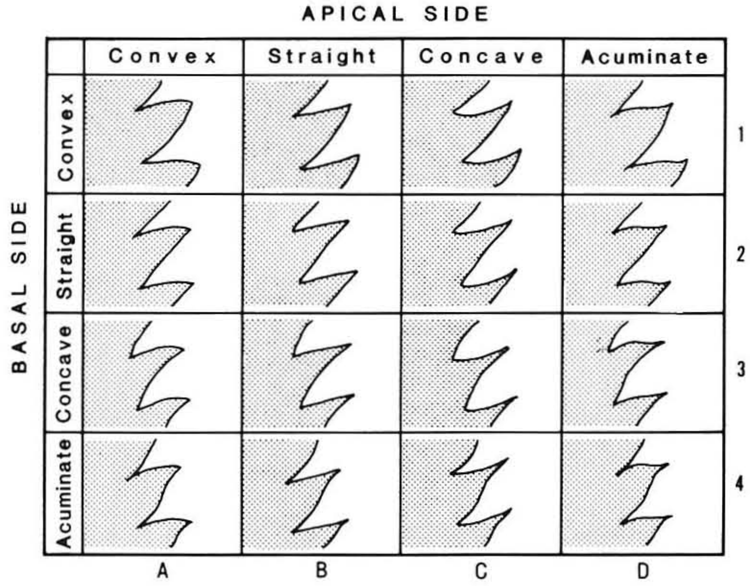
(a) Lobations. — In many instances, the teeth of *Acer* are grouped so as to form a large protuberance from the lamina (for example, in *Columbiana*), or a single primary tooth that has no subsidiary teeth is enlarged to form a large protuberance (for example, in *Macrophylla*); both these character states are considered to be homologous. One of these large protuberances is entered by a secondary vein and the sinuses on either side of the protuberance are braced by either a secondary vein or an external secondary vein; a large protuberance that has these two character states is termed a lobation (text-fig. 9).



Text-fig. 9 Lobal sinal bracing in *Acer*. See text for explanation.

(b) Lobal sinal bracing. — Sinuses between lobes of leaves of *Acer* are braced by veins that can take several different patterns or character states (text-fig. 9); these different patterns are of systematic significance. One pattern (text-fig. 9A) is characterized by the merging of two veins; one of these veins originates as an external secondary vein from a medial secondary vein and the second vein originates as either (1) an external secondary vein from a secondary vein that originates from the apical side of a lateral primary vein, or (2) a secondary vein that originates from the apical side of a lateral primary vein. A second pattern (text-fig. 9B) is characterized by a single vein that originates as an external secondary vein from a medial secondary vein. A third pattern (text-fig. 9C) is characterized by the equal bifurcation of a medial secondary vein or a medial intersecondary vein; a specialized state (text-fig. 9D) of the third pattern is characterized by an additional bifurcation of the major basal branch, with one of the secondary bifurcations extending to the sinus (for example, in *Eriocarpa*). In many *Acer,* the veins that brace the lobal sinuses originate acutely (text-figs. 9, A-D); however, in other *Acer* these veins originate orthogonally (text-fig. 9E). An intermediate morphological state (for example, *Parviflora*) is characterized by an acutely originating external secondary vein that bifurcates orthogonally near the sinus (text-fig. 9F).

(c) Dental sinal bracing. — Bracing of the sinuses between primary teeth and between lobations is, as in lobal sinal bracing, formed by external secondary veins that originate either acutely or orthogonally; the exception is in leaves that have retained the bohlenioid pattern of secondary venation, in which the dental sinuses are braced by acutely



Text-fig. 10 Classification of marginal configuration of dicot leaves (Hickey, 1973).

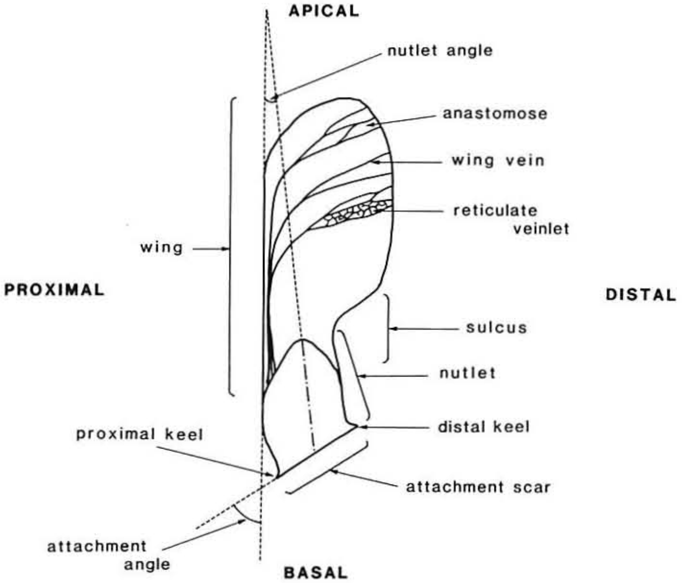
bifurcating secondary veins. A common pattern is characterized by a secondary vein that gives off an external secondary branch that extends along the basal side of a dental sinus, with the secondary vein itself extending along the apical side of the dental sinus and entering a tooth.

(d) Bracing in basal region of lamina. — Veins of tertiary or intersecondary rank originate from the midrib in the basal part of the lamina. In most *Acer,* these tertiary and intersecondary veins originate acutely and generally parallel the medial secondary veins. In other *Acer,* however, these tertiary and intersecondary veins originate orthogonally (or nearly so) and are at a much higher angle than the medial secondary veins (for example, in *Macrophylla*); in such leaves, the veins that brace the lobal sinuses of the medial lobe are also typically at a higher angle than the other medial secondary veins.

(e) Dental shapes. — Hickey (1973) presented a thorough and rigorous classification of dental shapes. Because of the significance of these shapes in *Acer,* Hickey's classification is here reproduced for reference (text-fig. 10).

Fruit

Numerous investigators of extant *Acer* have relied on morphology of fruits to characterize and differentiate various sections. However, as noted by Ogata (1967, p. 101), characterization of the different morphological types is difficult; this difficulty arises from a lack of terminology. Major character sets of fruits of *Acer* are illustrated in text-figure 11.



Text-fig. 11 Terminology of morphologic characters of *Acer* fruit.

(a) Attachment angle. — The attachment angle is the angle formed by the intersection of a line parallel to the attachement scar and a line parallel to the long axis of the samara (also called the extension angle; Tanai, 1983). The attachment angle can vary in a species, but the variation is typically no more than about 20°. The most variable extant species in regard to this character state is *Acer mono,* the different subspecies and varieties of which can have markedly different attachment angles; Ogata (1967), however, noted that probably many of these subspecies should be given specific rank.

(b) Nutlet angle. — The nutlet angle is the angle formed by the intersection of a line parallel to the line connecting the midpoint of the attachment scar to the apex of the nutlet and a line parallel to the long axis of the samara. This character state appears to vary about 10° in a species.

(e) Degree of nutlet inflation. — This character set can take three different states in *Acer.* Markedly inflated nutlets are those in which the expansion of the nutlet along an axis perpendicular to the plane of the samara is more than half the length of the nutlet. Moderately inflated nutlets are those in which the expansion of the nutlet along an axis perpendicular to the plane of the samara is less than half but more than one-tenth the length of the nutlet. Flattened nutlets are those in which the expansion of the nutlet along an axis perpendicular to the plane of the samara is less than one-tenth the length of the nutlet. Most markedly inflated nutlets have, in fact, about a 1:1 ratio between the two measurements, and most flattened nutlets also have the sides of the nutlet parallel.

Citations of specimens

The floral names that have been assigned to various plant megafossil assemblages in western North America can cover collections from many localities. Some of these names can thus have various meanings; for example, "Latah flora" has been used to include all plants from sedimentary rocks that are interbedded with basalts of the Columbia River Group in eastern Washington and adjacent Idaho. We prefer, on the other hand, to restrict the Latah flora to plants from localities of the Latah Formation, which is exposed in the vicinity of Spokane and adjacent Idaho; the Grand Coule, Clarkia, and Whitebird floras are thus excluded from the Latah flora. Further, where possible, we have cited individual assemblages from a given locality; thus, "Latah/Brickyard" indicates that the occurrence of the species is in the flora of the Brickyard locality (in Spokane) of the Latah.

Under the side-heading "Typology" is cited only the name-bearing specimen, either a holotype or lectotype. In the instances of new species described in this report, all specimens (other than the holotype) cited in the tables of occurrences are designated paratypes. In the instances of previously named species, all specimens (other than the holotype or lectotype) cited in the tables of occurrences are designated hypotypes, except for those accessory specimens cited by the original author of the species; these accessory specimens are either paratypes, or, if a lectotype has been subsequently designated from among two or more cotypes, the remaining cotypes have paratypical status.

In the tables of occurrences of the various species, the locality number assigned by the collector of the material has been cited. This number may represent the collector's own number but, in most instances, represents a locality number assigned by the institution represented by the collector. In some instances, no locality number was assigned by either the collector or institution. In many instances, more than one number has been assigned to collections from the same locality; this has resulted in large part because collectors of the locality have represented different institutions. For equivalencies of numbers assigned to collections from the same locality, see the appendix "List of localities and occurrences of *Acer*".

At least one specimen has been cited for the occurrence of a given species of *Acer* at a given locality. If both fruits and foliage of a species occur at a given locality, at least one fruit specimen and one foliar specimen are cited. The abbreviations of the various institutions that contain cited specimens or whose locality numbers are cited are:

CAS: California Academy of Sciences (Geology Department), San Francisco.
DMNH: Denver Museum of Natural History (Geology Department), Denver.
GSC: Geological Survey of Canada, Ottawa.
HUBM: Harvard University Botanical Museum, Cambridge.
MSUB: Michigan State University (Botany Department), East Lansing.
NYBG: New York Botanical Garden; material now at Yale University (Peabody Museum of Natural History), New Haven.
OMSI: Oregon Museum of Science and Industry, Portland.
SFUB: Simon Fraser University (Botany Department), Burnaby, British Columbia.

TMP: Tyrrell Museum of Palaeontology, Drumheller, Alberta.
UAPC: University of Alberta Paleobotany Collection, Edmonton.
UBCB: University of British Columbia (Botany Department), Vancouver.
UCMP: University of California Museum of Paleontology, Berkeley.
UCMG: University of Colorado Museum (Geology Department), Boulder.
UIB: University of Idaho (Botany Department), Moscow.
UIG: University of Idaho (Geology Department), Moscow.
UMB: University of Montana (Botany Department), Missoula.
UMMP: University of Michigan Museum of Paleontology, Ann Arbor.
UOCM: University of Oregon Condon Museum, Eugene.
USGS: U.S. Geological Survey, Washington.
USNM: U.S. National Museum (Paleobotany Division), Washington.
UWBM: University of Washington Burke Memorial Museum (Geology Department), Seattle.

Keys to species of *Acer* in the Tertiary of western North America

Foliage

The following key cannot be used to determine all specimens of *Acer* foliage in the Tertiary of western North America. Some specimens that have been assigned by previous investigators to particular species are too poorly preserved or fragmentary for specific determination. The key emphasizes areolar venation, which may be lacking on many specimens; however, if these specimens are keyed out by assuming, in turn, the possession of the three different types of areolar venation, the specimen can probably be at least questionably determined. Further, some species that are readily distinguishable on the basis of associated fruits may be highly similar to one another in foliage, which makes construction and use of a single-organ key difficult. Not included in the key to foliage are species represented by a single specimen and that have not been given a specific epithet.

A. Craspedodromous secondary veins alternate with bifurcating secondary veins
B. Leaf lobed
C. Lobes 5.. *A. douglasense*
C. Lobes 3
A. Secondary veins mostly craspedodromous
B. Areoles irregularly polygonal
C. Leaves simple
D. Major veins between most basal medial secondary veins and lateral primary veins percurrent.. *A. alaskense*
D. Major veins between most basal medial secondary veins and lateral primary veins compound
E. Lobal sinuses angled
F. Lobes markedly attenuate.. *A. ashwilli*
F. Lobes short
G. Lobal sinal braces formed by bifurcating medial secondary veins................. *A. orbum*
G. Lobal sinal braces formed by external secondary veins
H. Teeth attenuate.. *A. stewarti*
H. Teeth acute
I. All external secondary veins craspedodromous

J. Teeth mostly simple........ *A. washingtonense*
J. Teeth mostly compound........ *A. ivanofense*
I. Some external secondary veins camptodromous
K. Teeth not of uniform size
L. Lateral primary veins parallel to medial secondary veins........ *A. clarnoense*
L. Lateral primary veins diverging from medial secondary veins........ *A. latahense*
K. Teeth of uniform size
M. Leaves three-lobed........ *A. dettermani*
M. Leaves unlobed........ *A. castorrivularis*
E. Lobal sinuses arcuate
N. Teeth sharp........ *A. osmonti*
N. Teeth rounded
O. Lobes narrow........ *A. oregonianum*
O. Lobes broad........ *A. megasamarum*
C. Leaves compound
P. Apical sides of teeth point apically
Q. Secondary veins about six pairs........ *A. eonegundo*
Q. Secondary veins >6
R. Leaflets with basal lobations........ *A. heterodentatum*
R. Leaflets without basal lobations........ *A. molallense*
P. Apical sides of teeth perpendicular to midrib........ *A. negundoides*
B. Areoles quadrangular
S. Veinlets branch once or twice
T. Leaves five-lobed
U. Teeth numerous........ *A. niklasi*
U. Teeth few........ *A. busamarum*
T. Leaves three-lobed
V. Most veinlets branch once
W. At least three lobations on medial lobe........ *A. powellense*
W. Typically two lobations on medial lobe........ *A. oligomedianum*
V. Most veinlets branch twice........ *A. medianum*
S. Most veinlets unbranched or absent
X. All external secondary veins originate acutely
Y. Tertiary and intersecondary veins near base originate acutely from midrib and parallel medial secondary veins
Z. Leaves shallowly three-lobed
AA. Teeth A-1........ *A. milleri*
AA. Teeth D-1 or D-4
BB. Lateral lobes same size as medial lobations........ *A. elwyni*
BB. Lateral lobes larger than medial lobations
CC. Teeth on basal sides of lateral lobes of uniform size
DD. Lateral primary veins almost as long as midrib........ *A. glabroides*
DD. Lateral primary veins < half as long as midrib........ *A. idahoense*
CC. Teeth on basal sides of lateral lobes grouped into lobations........ *A. elkoanum*
Z. Leaves three- and five-lobed
EE. Teeth C-3........ *A. ezoanum*
EE. Teeth not C-3
FF. Teeth B-2
GG. Teeth numerous........ *A. whitebirdense*
GG. Teeth few........ *A. taggarti*
FF. Teeth not B-2
HH. Most teeth C-1
II. Medial lobe narrow........ *A. chaneyi*
II. Medial lobe broad........ *A. kenaicum*
HH. Most teeth not C-1
JJ. Teech mixed A-1, B-1, and C-1........ *A. ferrignoi*

JJ. Most teeth D-1
KK. Lobal sinuses concave .... *A. florissanti*
KK. Lobal sinuses convex
LL. Tertiary veins spaced 0.2 to 0.4 cm .... *A. kluckingi*
LL. Tertiary veins spaced 0.4 to 0.7 cm .... *A. tigilense*
Y. Tertiary and intersecondary veins near base originate orthogonally (or almost so) from midrib
MM. Teeth numerous
NN. Lobal sinuses narrowly rounded to acute .... *A. beckeri*
NN. Lobal sinuses broadly rounded .... *A. salmonense*
MM. Teeth few .... *A. alvordense*
X. Most external secondary veins originate orthogonally
OO. Teeth numerous
PP. Four subsidiary teeth on basal flank of some primary teeth .... *A. smileyi*
PP. One or two subsidiary teeth on basal flank of primary teeth .... *A. browni*
OO. Teeth few or absent
QQ. Lobal sinuses arcuate
RR. Teeth typically absent .... *A. scottiae*
RR. Teeth present
SS. Teeth broadly rounded
TT. Leaves five-lobed .... *A. tiffneyi*
TT. Leaves three-lobed .... *A. collawashense*
RR. Teeth sharp to narrowly rounded
UU. Lobes broad .... *A. schorni*
UU. Lobes narrow
VV. One or two teeth per lobal side
WW. Most teeth C-1 .... *A. minutifolium*
WW. Most teeth A-1 or B-1 .... *A. tyrellense*
VV. >two teeth per lobal side
XX. Lobes broad .... *A. protomiyabei*
XX. Lobes narrow .... *A. septilobatum*
QQ. Lobal sinuses narrowly arcuate to acute
YY. Base broadly rounded .... *A. axelrodi*
ZZ. Base cordate .... *A. manchesteri*

Fruit

A. Nutlet with flanges
B. Nutlet with poorly defined flanges
C. Nutlet slightly inflated .... *A. washingtonense*
C. Nutlet markedly inflated
D. Nutlet outline circular
E. Sulcus absent .... *A. stewarti*
E. Sulcus present .... *A. hillsi*
D. Nutlet elongated apically .... *A. rousei*
B. Nutlet with well defined flanges
F. Nutlet triangular to elliptic in outline
G. Nutlet with ridges .... *A. cadaver*
G. Nutlet without ridges
H. Nutlet with flange near distal margin
I. Samara medium-sized (<4 cm long) .... *A. orbum*
I. Samara large (>4 cm long) .... *A. princetonense*
H. Nutlet flange medial
J. Proximal margin of nutlet convex
K. Nutlet flange broad .... *A. elkoanum*
K. Nutlet flange narrow
L. Wing <1.5 cm long .... *A. elwyni*
L. Wing >2.3 cm long

                - M. Nutlet flange extending length of nutlet
                  - N. Wing >4 times length of nutlet
                    - O. Wing veins acute to proximal margin .... *A. wehri*
                    - O. Wing veins perpendicular .... *A. crookense*
                  - N. Wing <3 times length of nutlet .... *A. becki*
                - M. Nutlet flange restricted to basal half of nutlet .... *A. cuprovallis*
          - J. Proximal margin of nutlet concave near base
            - P. Wing extending about half the distal margin of nutlet .... *A. idahoense*
              - Q. Wing extending along entire distal margin of nutlet
                - R. Samara small (about 2 cm long) .... *A. bosrivularis*
                - R. Samara medium-sized (about 3 cm long) .... *A. glabroides*
    - F. Nutlet semicircular to almost circular in outline
      - S. Nutlet slightly inflated
        - T. Nutlet flange extending length of nutlet
          - U. Nutlet flanges forming narrow groove .... *A. florissanti*
          - U. Nutlet flanges forming broad V-shaped area .... *A. meyeri*
        - T. Nutlet flange restricted to basal half of nutlet .... *A. jarbidgianum*
      - S. Nutlet markedly inflated .... *A. spitzi*
- A. Nutlet with no flanges
  - V. Nutlet asymmetrically inflated
    - W. Nutlet with rounded apex
      - X. Nutlet with irregularly bifurcating ridges .... *A. toradense*
      - X. Nutlet with reticulate venation .... *A. stonebergae*
    - W. Nutlet with narrowly rounded to acute apex
      - Y. Nutlet with deep folds .... *A. traini*
      - Y. Nutlet smooth except for veins .... *A. clarnoense*
  - V. Nutlet symmetrically inflated
    - Z. Nutlet slightly inflated
      - AA. Nutlet with several ridges .... *A. ashwilli*
      - AA. Nutlet with one or no ridges
        - BB. Nutlet outline rounded to widely elliptic
          - CC. Nutlet large (>2 cm long) .... *A. whitebirdense*
          - CC. Nutlet moderate-sized (<2 cm long)
            - DD. Nutlet with irregular folds .... *A. taggarti*
            - DD. Nutlet smooth
              - EE. Nutlet proximally expanded
                - FF. Nutlet veins six or seven
                  - GG. Nutlet veins obscure in basal region .... *A. eomedianum*
                  - GG. Nutlet veins conspicuous in basal region
                    - HH. Wing extending along entire distal margin of nutlet
                      - II. Nutlet outline elliptic .... *A. stockeyae*
                      - II. Nutlet outline semicircular .... *A. oligomedianum*
                    - HH. Wing extendng along <half distal margin of nutlet .... *A. niklasi*
                - FF. Nutlet veins 10 to 14 .... *A. medianum*
              - EE. Nutlet not (or only slightly) proximally expanded
                - JJ. Marked sulcus present .... *A. kluckingi*
                - JJ. Marked sulcus absent .... *A. tigilense*
        - BB. Nutlet spindle-shaped
          - KK. Nutlet >0.8 cm wide
            - LL. Nutlet with broad ridge .... *A. taurocursum*
            - LL. Nutlet without ridge
              - MM. Nutlet with 7 veins .... *A. kenaicum*
              - MM. Nutlet with 15 to 20 veins .... *A. chaneyi*
          - KK. Nutlet <0.7 cm wide
            - NN. Subparallel nutlet veins of equal thickness
              - OO. Wing about 2.5 cm long .... *A. macginitiei*

  - OO. Wing >2.7 cm long
    - PP. Wing about 3.0 cm long ...... *A. cascadense*
    - PP. Wing about 3.6 cm long ...... *A. knolli*
- NN. Nutlet with one subparallel vein thicker than others
  - QQ. Major vein near proximal margin ...... *A. heterodentatum*
  - QQ. Major vein medial or near distal margin
    - RR. Major vein curved ...... *A. cranei*
    - RR. Major vein straight
      - SS. Major vein near distal margin ...... *A. sinuofluviatilis*
      - SS. Major vein medial ...... *A. negundoides*
- Z. Nutlet not slightly inflated
  - TT. Nutlet markedly inflated
    - UU. Nutlet veins passing directly onto wing
      - VVv. Nutlet not proximally expanded
        - WW. Nutlet <4.0 cm long ...... *A. salmonense*
        - WW. Nutlet >4.0 cm long
          - XX. Samara without deep sulcus
            - YY. Nutlet with medial ridge
              - ZZ. Attachment scar 0.5 to 0.6 cm long ...... *A. grantense*
              - ZZ. Attachment scar about 1.0 cm long ...... *A.* sp. 6
            - YY. Nutlet without medial ridge
              - AAA. Attachment scar about 0.8 cm long ...... *A. alvordense*
              - AAA. Attachment scar 1.1 to 1.4 cm long ...... *A. busamarum*
          - XX. Samara with deep sulcus
            - BBB. Nutlet veins 16 to 20 ...... *A. osmonti*
            - BBB. Nutlet veins 8 to 12
              - CCC. Nutlet veins all subparallel ...... *A. oregonianum*
              - CCC. Proximal nutlet veins form reticulum ...... *A. macrophyllum*
      - VV. Nutlet proximally expanded
        - DDD. Attachement scar about half the width of nutlet ...... *A. megasamarum*
        - DDD. Attachment scar >half the width of nutlet
          - EEE. Samara <3 cm long ...... *A. smileyi*
          - EEE. Samara >3 cm long ...... *A. browni*
    - UU. Nutlet veine coalescing along apical margin
      - FFF. Nutlet thickest near distal margin
        - GGG. Wing extending along distal margin of nutlet ...... *A. montanense*
        - GGG. Wing entirely apical to nutlet ...... *A. postense*
      - FFF. Nutlet spherical
        - GGG. Nutlet outline U-shaped
          - HHH. Nutlet veins distinct ...... *A. minutifolium*
          - HHH. Nutlet veins obscure ...... *A. tyrellense*
        - GGG. Nutlet outline elliptic ...... *A. schorni*
  - TT. Nutlet flattened
    - III. Nutlet veine obscure
      - JJJ. One nutlet vein thicker than others ...... *A. axelrodi*
      - JJJ. All nutlet veins of equal size
        - KKK. Attachment scar with conspicuous proximal and distal keels ...... *A. manchesteri*
        - KKK. Attachment scar without keels ...... *A. tiffneyi*
    - III. Nutlet veins distinct
      - LLL. Nutlet longer than wide ...... *A. scottiae*
      - LLL. Nutlet about as long as wide
        - MMM. Nutlet angle 35° to 50° ...... *A. hueberi*
        - MMM. Nutlet angle <20°
          - NNN. Nutlet almost as long as wing ...... *A. protomiyabei*
          - NNN. Nutlet <one-third as long as wing ...... *A. septilobatum*

Spicata Group

Section *Douglasa* Wolfe et Tanai, sect. nov.

Diagnosis: Leaves simple, perfectly actinodromous; deeply 4 lobed; medial and lateral secondary veins of 2 alternating types, 1 craspedodromous and the second bifurcating near the sinuses; tertiary veins bracing midrib and lateral primary veins compound and A-A; other tertiary veins simple to typically compound, R-R to R-A; lobal sinal bracing formed by a secondary vein that originates from the midrib and bifurcates acutely near the sinus; teeth numerous and D-1.

Discussion: Leaves of *Acer douglasense* have strong similarity to those of *Spicata:* they are five-lobed and have the same basic type of tertiary veins, lobal sinal bracing, and serrations. Differing from *Spicata* in other than deep lobing, leaves of *Douglasa* have craspedodromous secondary veins alternating with secondary veins that bifurcate near the dental sinuses. Such alternating veins are also found in leaflets of some Sapindaceae (the extinct *Bohlenia* and the extant *Cardiospermum* and *Serjania*). The only other *Acer* to have such alternating secondary veins is *A. orbum* LaM., which, however, is apparently shallowly three-lobed and has alternating secondaries only in the mdeial lobe.

Type species: Acer douglasense Wolfe et Tanai.

Acer douglasense Wolfe et Tanai, sp. nov.

(pl. 1, Figs. 1, 3; text-fig. 12A)

Description: Leaves simple, perfectly actinodromous; deeply and narrowly 5-lobed, with the most basal lobes as deeply incised as the teeth of the lateral lobes; shape oval, 11 cm long and 10 cm wide; base shallowly cordate; medial and lateral lobes about 2-1/2 times long as broad and gradually tapering to acuminate apices; most apical pair of lateral primary veins parallel to medial secondary veins, straight craspedodromous; 6 to 7 secondary veins originating at an angle of 45° from basal side of most apical lateral primary, straight to slightly curving craspedodromous veins alternating with veins that bifurcate near sinuses; 7 to 8 pairs of medial secondary veins, broadly curving, craspedodromous veins alternating with veins that bifurcate near sinuses; tertiary veins between most apical lateral primary veins and midrib compound and A-A; tertiary veins between secondary veins simple to compound, R-R to R-A spaced about 15 mm apart; fourth order venation irregularly polygonal; areolation not preserved; lobal sinal bracing formed by a bifurcating secondary vein that originates from midrib; teeth large, D-1, typically with 1 or 2 subsidiary D-1 teeth on basal flank and none on apical flank.

Nomenclature: Type locality at Cape Douglas, Alaska.

Discussion: See section *Douglasa.*

Distribution: Early Eocene of south-central Alaska.

Typology: Holotype, USNM 396006.

Occurrence: See appendix table.

Section *Alaskana* Wolfe et Tanai, sect. nov.

Diagnosis: Leaves simple, perfectly actinodromous; shallowly 3-lobed (to possibly 2-lobed); medial and lateral secondary veins craspedodromous; tertiary veins between most basal medial secondary veins and lateral primary veins simple and R-R to O-R;

other tertiary veins simple to compound and R-R; lobal sinal bracing formed by an external secondary vein that originates near the midrib from a medial secondary vein and bifurcates acutely near the sinus; areoles small, polygonal, with thick, branching veinlets; teeth numerous and D-1.

Discussion: Although the single leaf of *Acer alaskense* has the numerous D-1 teeth and branching areolar venation of extant *Spicata,* simple tertiary veins that connect the most basal medial secondary veins with lateral primary veins represent a unique specialization in *Acer.* The lobal sinal bracing is also a pattern that we have not seen in any extant *Acer,* although this bracing is found on only one side of the lamina and may be an aberrancy rather than typical for the species.

Type species: Acer alaskense Wolfe et Tanai.

Acer alaskense Wolfe et Tanai, sp. nov.

(pl. 1, fig. 2; text-fig. 12B)

Description: Leaf simple, perfectly actinodromous; shallowly 3-lobed (possibly 2-lobed with a single lateral lobe); shape oval, 10.5 cm long, 8.0 cm wide; base very shallowly cordate (almost truncate); medial lobe about 1-1/2 times long as broad and abruptly tapering to an acuminate apex; lateral primary veins parallel to medial secondary veins, straight, craspedodromous; 8 secondary veins departing at angles of 40° to 50° from basal side of lateral primaries, broadly curving, craspedodromous; 5 pairs of medial secondary veins, broadly curving, craspedodromous; tertiary veins connecting most basal medial secondary veins and lateral primary veins simple and R-R to O-R; other tertiary veins simple to compound and R-R; fourth order venation thick, irregularly polygonal; fifth order venation forming typically pentagonal areoles about 1 mm in diameter that have thick once-or twice-branching veinlets; lobal sinal bracing on 1 side of lamina not preserved and on other side formed by an external secondary vein that originates from a medial secondary vein near the midrib and acutely bifurcates near the sinus; teeth large, D-1, typically with 1 subsidiary D-1 tooth on basal flank and none on apical flank; petiole over 3.8 cm long.

Nomenclature: Type locality in Alaska.

Discussion: See section *Alaskana.*

Distribution: Latest Paleocene of south-central Alaska.

Typology: Holotype, USNM 396009.

Occurrence: See appendix table.

Section *Torada* Wolfe et Tanai, sect. nov.

Diagnosis: Fruits samaroid; wing extending only from apical margin of nutlet; nutlet slightly and asymmetrically inflated, apical margin rounded; attachment scar about 2/3 as long as width of nutlet; attachment angle medium; basal side of attachment scar typically with a pronounced keel; nutlet surface with a few, thin, irregularly bifurcating ridges or with irregular flanges; wing venation formed by angularly diverging veinlets that anastomose a few times; veinlets few or absent.

Discussion: The bifurcating ridges on the nutlet are unique in *Acer.* The outline of the

nutlet is somewhat similar to that of *Spicata,* and both the attachment angle and nutlet angles are similar to those of *A. stewarti* and *A. washingtonense,* which are coeval species; *A. toradense* and *A. washingtonense* also share a marked keel on the proximal side of the attachment scar. Other than ridges, major differences between *A. toradense* and *Spicata* are (1) the wing does not extend along the distal side of the nutlet in *Torada* and (2) the nutlet is slightly inflated in *Torada.*
Type species: Acer washingtonense Wolfe et Tanai.

Acer toradense Wolfe et Tanai, sp. nov.

(pl. 3, figs. 1-4)

Description: Fruits samaroid; nutlet at basal end, 0.6 to 1.0 m wide, 0.7 to 1.3 cm long, apical wing at least 1.4 cm wide, 2.0 cm long; nutlet slightly inflated, outline broadly oval, slightly expanded along proximal margin; attachment angle 45°; attachment scar 0.4 to 0.8 cm long, with a prominent basal keel; nutlet angle about 20°; surface of nutlet with a narrow ridge extending from center of attachment, curving distally about 2/3 length of nutlet, 3 narrow ridges extending proximally from the central ridge at irregular intervals; wing with a broadly convex distal margin and the proximal margin straight for 2/3 the length and then curving convexly to form a rounded apical margin; veins coalesced along proximal margin 7 to 8, wing veins diverging at angles of 20° to 30°, bifurcating 2 or 3 times, no anastamoses..
Nomenclature: Type locality is in the Torada graben.
Discussion: See section *Torada.*
Distribution: Early middle Eocene of northeastern Washington and adjacent British Columbia.
Typology: Holotype, USNM 396010A, B.
Occurrences: See appendix table.

Acer washingtonense Wolfe et Tanai, sp. nov.

(pl. 2, figs. 2, 3; pl. 3, figs. 6, 7, 10, 11, 14, 15, 18; text-fig. 12C)

Description: Leaf simple, perfectly actinodromous; shallowly 3-lobed, with 5 primary veins; lateral lobes 2/3 as long as medial lobe, lobes triangular; shape wide-elliptic, 7.5 cm long, (estimated) 5.0 cm wide; base shallowly cordate, apex acuminate; most apical lateral primary veins parallel to medial secondary veins and markedly convex; 5 secondary veins originating at angles of 40° to 50° from basal side of lateral primary veins, markedly convex, craspedodromous; 7 pairs of medial secondary veins originating at angles of 40° to 70°, markedly convex, craspedodromous; lobal sinal bracing formed by acutely originating medial external secondary vein; tertiary veins A-R, compound, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming polygons 0.7 to 1.5 mm in diameter, veinlets twice-branching; teeth large, D-1 or D-3, simple.

Fruit samaroid, nutlet at basal end; nutlet 0.6 cm long, 0.5 cm wide; outline suborbiculate; nutlet moderately and asymmetrically inflated; a pair of indistinct medial flanges attachment scar 0.4 cm long, with proximal keel; nutlet venation indistinct, but several veins pass onto wing; attachment angle 45°, nutlet angle 20°; proximal margin slightly expanded beyond proximal margin of wing. Wing 2.0 cm long, 0.7 cm wide, extending along distal margin of nutlet; proximal margin straight distal margin broadly convex, forming a broadly U-shaped sulcus with nutlet; proximal margin with 6 prominent veins that extend from apical margin of nutlet; wing veins diverging from proximal margin at angles of 10° to 20°, curving markedly convexly, dichotomizing 5 or 6 times, few anastomoses.

Nomenclature: Type locality is in Washington.

Discussion: Only one leaf and three samaras of *Acer* have been found at the Republic/Knob Hill locality, and presumably all represent the same entity. The leaf has large D-1 (some are D-3) teeth, such as occur in extant *Spicata,* and areolar venation is Type I. Nutlet venation is obscure, but the fruit of *A. washingtonense* resembles in other characters fruits of *A. toradense.*

Distribution: Early middle Eocene of northeastern Washington.

Typology: Holotype, UWBM 56253A, B.

Occurrences: See appendix table.

Acer stonebergae Wolfe et Tanai, sp. nov.

(pl. 3, figs. 5, 8, 9)

Description: Fruits samaroid; nutlet at basal end; nutlet 1.2 cm long, 0.6 to 0.8 cm wide, oval, slightly inflated; nutlet with indistinct flanges and a coarse reticulum of veins: attachment angle 20° to 30°, nutlet angle 10° to 20°; veins on nutlet obscure; proximal margin of nutlet either not or only slightly expanded beyond proximal margin of wing. Wing 4.0 cm long, 1.4 cm wide; proximal margin curved, distal margin broadly convex; proximal margin with 10 prominent veins that originate equally spaced along apical margin of nutlet; wing veins diverging from proximal margin at angles of 30° to 50°, dichotomizing 2 to 4 times, few anastomoses or veinlets.

Nomenclature: Margaret Stoneberg has made available to us the collections of the Princeton District Museum and Archives.

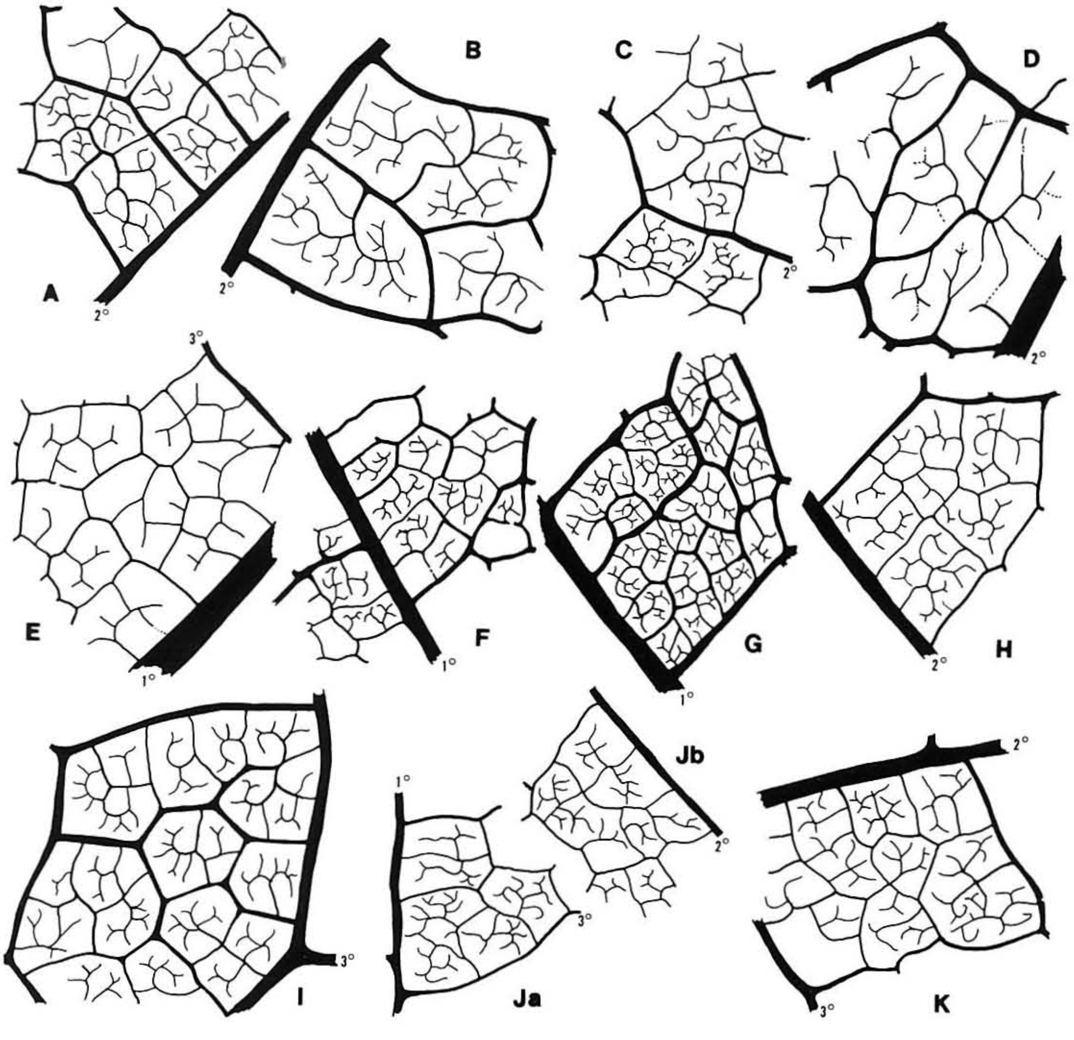
Discussion: The almost circular outline of the nutlet, extension of the wing along the distal margin of the nutlet, indistinct flanges, and poorly organized wing venation ally *Acer stonebergae* to *A. washingtonense.* The former taxon is specialized in its large size and numerous veins coalesced along the proximal margin of the wing.

Two other large-fruited species of *Acer* occur with *A. stonebergae* at the One Mile Creek locality. *Acer princetonense* is clearly distinct from *A. stonebergae* in having a distinct flange in the distal region of the nutlet, a distinct distal spur extending from the attachment scar, and reticulate wing veinlets. *Acer stockeyae* and *A. stonebergae* both have a reticulate nutlet venation, but in *A. stockeyae* only 5 (rather than 20) veins are coalesced along the proximal margin of the wing, the nutlet outline is distinctly elliptical, and the nutlet is expanded beyond the proximal margin of the wing.

Distribution: Early middle Eocene of northeastern Washington and adjacent British Columbia.

Typology: Holotype, PDMA 19840MC 1001.

Occurrences: See appendix table.



Text-fig. 12 Areolar venation characters of fossil *Acer* — (1) Section *Douglasa, Alaskana, Torada, Stewarta, Parviflora, Trilobata, Macrantha* and *Arguta.* (all figures × 12.5)

A. *Acer douglasense* Wolfe et Tanai. Cape Douglas. Holotype USNM 396006B (The counterpart of pl. 1, fig. 3).
B. *Acer alaskense* Wolfe et Tanai. Chikaloon/Evans Jones. Holotype USNM 396009 (pl. 1, fig. 2)
C. *Acer washingtonense* Wolfe et Tanai. Republic/Knob Hill. Holotype UWBM 56253B (pl. 2, fig. 3).
D. *Acer stewarti* Wolfe et Tanai. Princeton/One mile Creek. Holotype UAPC S485 (pl .2, fig. 1).
E. *Acer smileyi* Wolfe et Tanai. Cascadia. Paratype UCMP 9177 (pl. 22, fig. 8).
F. *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Dugout Gulch. Paratype UCMP 9032 (pl. 24, figs. 1, 2).
G. *Acer clarnoense* Wolfe et Tanai. Sheep Rock Creek. Paratype UCMP 9011 (pl. 14, fig. 5).
H. *Acer dettermani* Wolfe et Tanai. Aniakchak Crater. Holotype USNM 396014 (pl. 14, fig. 9).
I. *Acer latahense* Wolfe et Tanai. Latah/Brickyard. Holotype USNM 396136A (pl. 35, fig. 2).
Ja, b. *Acer castorrivularis* Wolfe et Tanai. Beaver Creek. Holotype UCMP 9310A (pl. 14, fig. 1).
K. *Acer iwanofense* Wolfe et Tanai. Road Island. Paratype USNM 396017C (pl. 13, fig. 3).

Section *Spicata* Pax

Acer sp. 1.

(pl. 22, figs. 4)

Discussion: A single laminar fragment of a medial and a partial lateral lobe has very large D-1 teeth. The medial lobe is about as broad as long, as in extant *Spicata,* although the teeth are more attenuated than in any extant species. The teeth are also broader than in *Acer stewarti.*

Distribution: Early Oligocene of south-central Alaska.

Occurrence: See appendix table.

Section *Stewarta* Wolfe et Tanai, sect. nov.

Diagnosis: Leaves simple, actionodromous, shallowly 5-lobed; tertiary veins between lateral and medial primary veins widely spaced, compound, and A-A; secondary veins craspedodromous; areolar venation formed by irregularly polygonal fifth-order veins; veinlets branching more than two times; teeth large and D-1.

Fruits samaroid; nutlets markedly inflated, circular in outline, with indistinct flanges; wing veins acutely diverging, with few anastomoses or veinlets; sulcus present.

Discussion: See below.

Type species: Acer stewarti Wolfe et Tanai.

Acer stewarti Wolfe et Tanai, sp. nov.

(pl. 1, fig. 4; pl. 2, figs. 1, 4; pl. 5, figs. 1-4, 8, 9; text-fig. 12D)

Description: Leaves simple, perfectly actinodromous; shallowly 5-lobed, with the most basal lobes as deeply incised as the teeth of the more apical lateral lobes; leaves oval, over 6.5 cm long (none complete) and 6.0 cm wide; most apical pair of lateral primary veins slightly diverging from medial secondary veins, almost straight, craspedodromous; 4 to 5 secondary veins departing at angles of 30° to 40° from basal side of most apical lateral primary, straight to slightly curving, craspedodromous; at least 4 pairs of medial secondary veins, straight, craspedodromous; tertiary veins between most apical lateral primary veins and midrib widely spaced, compound, and slightly A-A; tertiary veins between secondary veins widely spaced, compound, and R-R; fourth order venation forming areoles, irregularly polygonal, with thin veinlets that branch 1 to 2 times; lobal sinal bracing formed by a compound tertiary vein; teeth large, D-1 and markedly attenuate; petiole more than 0.4 cm long.

Fruits samaroid, nutlet at basal end. Nutlets 0.7 to 0.9 cm long, 0.3 to 0.5 cm wide, outline circular, concave-convex; thin, poorly defined flanges, but otherwise nutlet almost smooth, with 3 to 4 indistinct veins parallel to long axis of nutlet and connected by widely spaced anastomoses; attachment angle about 40°, nutlet angle about 20°; proximal margin of nutlet slightly expanded beyond proximal margin of wing. Wing 1.5 to 2.3 cm long, 0.7 to 1.1 cm wide; proximal margin straight, distal margin broadly convex, forming a broadly V-shaped sulcus with nutlet; proximal margin with 5 or 6 prominent veins that extend from the apical margin of nutlet; wing veins diverging from proximal margin at angles of 10° to 20°, curving markedly convexly, dichotomizing 5 to 6 times, few anastomoses or veinlets.

Nomenclature: We take pleasure in naming this species for Wilson Stewart, who collected the holotype. We particularly wish to recognize, however, his contributions to the teaching of paleobotany.

Discussion: The shallowly five-lobed leaf that has conspicuously attenuated and large D-1 serrations allies *Acer stewarti* to *Spicata.* Lobal sinal bracing formed from a compound tertiary vein is of rare occurrence in extant species of *Spicata,* where typically the bracing is formed by a strong vein originating from either the apical side of a lateral primary vein or from the basal side of a medial secondary vein.

At the One Mile Creek locality, the only leaves of *Acer* are those of *A. stewarti,* but a total of 11 *Acer* fruits have been found. Which fruits are conspecific with *A. stewarti* is thus uncertain. The fruits here referred to *A. stewarti* are the most common fruits of *Acer* (4 specimens) at the One Mile Creek locality; most of the other six species of *Acer* at this locality are represented by a single fruit, and three of the taxa, moreover, are inferred to have had Type II areolar venation. A fourth taxon, *A. washingtonense,* has leaves dissimilar to those of *A. stewarti.* We cannot exclude the possibility that the leaves of *A. stewarti* are conspecific with fruits referred to either *A. stonebergae* or *A. rousei,* but these last two taxa are poorly represented at the One Mile Creek locality.

The fruits referred to *Acer stewarti* have a nutlet outline like that of *A. washingtonense* and other species of *Torada* and also have a conspicuous distal spur extending from the attachment scar. The wing venation is poorly organized as in extant members of the *Spicata* Group and in *Torada.*

Distribution: Early middly Eocene of northeastern Washington and adjacent British Columbia.

Typology: Holotype, UAPC S485.

Occurrences: See appendix table.

Acer hillsi Wolfe et Tanai, sp. nov.

(pl. 5, figs. 6, 7, 12)

Description: Fruit samaroid; nutlet at basal end; nutlet asymmetrically inflated, outline semicircular, 0.5 cm long, 0.5 cm wide; attachment angle 40°, nutlet angle 20°. Wing entirely apical of nutlet, with a pronounce V-shaped sulcus; >2.0 cm long, 1.0 cm wide; distal margin straight basally, expanding and broadly convex apically; 5 veins coalesced along proximal margin; wing veins diverging at angles of 10° to 20°, extending almost straight, bifurcating 2 to 4 times, few anstomoses of veinlets.

Nomenclature: L. V. Hills allowed us to examine his extensive collections from the McAbee locality; we further wish to recognize his extensive contributions to paleobotany and palynology.

Discussion: Although one side of the nutlet of *A. hillsi* is inflated, the other side is concave. Asymmetry is present in extant *Spicata,* but the nutlet is not inflated. In nutlet shape and degree of inflation of one side, *A. hillsi* is similar to *A. stewarti,* but the nutlet in the former is almost circular (rather than semicircular), and a distal spur is present on the attachment scar. Further, the wing veins are convex in *A. stewarti* but are almost straight in *A. hillsi.*

Distribution: Early middle Eocene of northeastern Washington.

Typology: Holotype, UWBM 56260A, B.

Occurrence: See appendix table.

Section *Rousea* Wolfe et Tanai, sect. nov.

Diagnosis: Fruits samaroid; nutlets markedly inflated, outline circular to elliptic, indistinct nutlet flanges, attachment angle high; wing venation formed by acutely diverging veins, anastomoses and veinlets few.

Discussion: The poorly organized wing venation indicates placement in the *Spicata* Group. Specializations are the marked inflation and high attachment angle, which are today found only in *Palmata.* Nutlets of *Palmata,* however, are more elongated, and nutlet flanges are absent.

Type species: A. rousei Wolfe et Tanai.

Acer rousei Wolfe et Tanai, sp. nov.

(pl. 4, figs. 1-6, 15)

Description: Nutlet 0.6 to 0.7 cm long, 0.6 to 0.8 cm wide, apical margin markedly rounded; proximal margin of nutlet expanded beyond proximal margin of wing; nutlet with 2 indistinct flanges placed medially on nutlet and parallel to long axis of fruit; attachment angle 80° to 90°, nutlet angle 0° to 5°; veins on nutlet obscure. Wing 2.3 to 2.5 cm long, 0.7 to 1.1 cm wide, proximal margin approximately straight; distal margin slightly to deeply convex, forming a shallow notch with nutlet proximal margin of nutlet with 6 to 8 prominent veins that appear to originate equally spaced along apical margin of nutlet; wing veins diverging from proximal margin at angles of 20° to 30°, dichotomizing 2 to 4 times, few anastomoses or veinlets.

Nomenclature: Glenn Rouse has supplied us with material of *Acer* from the Eocene of British Columbia.

Discussion: See under *Rousea.*

Distribution: Early middle Eocene of southern British Columbia.

Typology: Holotype, UWBM 39728A, B.

Occurrence: See appendix table.

Section *Parviflora* Koidzumi

Acer browni Wolfe et Tanai, sp. nov.

(pl. 33, figs. 1, 7, 8; pl. 34, figs. 1-8)

Description: Leaves simple, perfectly actinodromous; shallowly 5-lobed; the most apical lateral lobes about 2/3 as long as medial lobe, the most basal lateral lobes small; shape widely elliptic to oblate; 3.7 to 7.2 cm long, 2.9 to 6.0 cm wide; base truncate to cordate, apex acute to attenuate; lobes markedly triangular; most apical lateral primary veins slightly diverging from medial secondary veins; 4 to 6 secondary veins originating at angles of 30° to 50° from basal side of most apical primary veins, straight to broadly convex, craspedodromous; 5 to 7 pairs of medial secondary veins originating at angles of

30° to 50°, straight to broadly convex, craspedodromous; lobal sinal bracing formed by the fusion of 2 external secondary veins, 1 originating from a medial secondary vein and a second originating from a lateral secondary vein, and both acutely to orthogonally originating; tertiary veins compound, A-A, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.3 to 0.5 mm in diameter, veinlets absent or unbranched; teeth small D-1, 1 or 2 subsidiary teeth on basal flank and 1 on apical flank; petiole more than 0.5 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.8 to 1.0 cm long, 0.7 to 0.8 cm wide; outline elliptic to circular, apex broadly rounded; proximal margin expanded beyond proximal margin of wing; attachment scar 0.6 to 0.7 cm long; nutlet markedly inflated and smooth; attachment angle 25° to 30°, nutlet angle 40°. Wing entirely apical to nutlet, forming a shallow U-shaped sulcus with nutlet; 2.5 to 3.0 cm long, 1.0 to 1.2 cm wide; distal margin broadly convex, proximal margin broadly convexed, apex rounded; 5 or 6 veins coalesced along proximal side, wing veins diverging at angles of 10° to 20°, sharply curving and extending straight, bifurcating, few anastomoses.

Nomenclature: For his many contributions to Tertiary paleobotany, we recognize the late Roland W. Brown.

Discussion: Numerous small D-1 teeth, five shallow and triangular lobes, complicated lobal sinal bracing, and quadrangular areoles with no or simple veinlets of *Acer browni* are characters combined in the one extant species of *Parviflora, A. nipponicum.* Strongly inflated nutlets also characterize *A. nipponicum,* although a sulcus is not developed in *A. nipponicum* but is developed in *A. browni.*

Distribution: Early to early middle Miocene of northwestern Oregon, western Washington and Queen Charlotte Islands.

Typology: Holotype, UCMP 9172.

Occurrences: See appendix table.

Acer smileyi Wolfe et Tanai, so. nov.

(pl. 22, figs. 3, 8; pl. 23, fig. 6; figs. 2-6, 9; pl. 34, fig. 9; text-fig. 12E)

Tilia aspera auct. non (Newberry) LaMotte. LaMotte. 1936 (part). 138.

Description: Leaves simple, perfectly actinodromous; shallowly 5-lobed; most apical lobes almost as long as medial lobe; most basal lobes distict; shape orbiculate to suborbiculate; base cordate, apex attenuate; estimated 9 to 12 cm long, 9 to 14 cm wide; lobes triangular; most apical lateral primary veins parallel to or slightly diverging from medial secondary veins; 6 or 7 secondary veins originating at angles of 30° to 55°, broadly convex, craspedodromous; 7 pairs of medial secondary veins originating at angles of 30° to 45°, straight to broadly convex, craspedodromous; lobal sinal bracing formed by a fusion of 2 external secondary veins, 1 originating from a medial secondary vein and a second originating from a lateral secondary vein, and both acutely originating; tertiary veins compound, A-A to A-R, spaced 0.4 to 0.7 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular or pentagonal areoles, 0.4 to 0.7 mm in diameter, veinlets absent or typically, unbranched or once-branching; teeth small, D-1, elongated, typically 4 or more per secondary vein; petiole up to 5.5 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.7 to 1.0 cm long, 0.5 to 0.6 cm wide; outline elliptic, apex narrowly rounded; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.5 to 0.8 cm long; nutlet markedly inflated and smooth; attachment angle 0° to 50°, nutlet angle 30° to 50°. Wing extending along distal margin of nutlet to attachment scar; 1.8 to 2.2 cm long, 0.8 to 0.9 cm wide; distal margin straight to slightly convex, proximal margin slightly convex, apex narrowly rounded; 6 or 7 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, smoothly curving, bifurcating, few anastomoses.

Nomenclature: Charles J. Smiley has devoted much effort to the study of the Clarkia beds and their flora.

Discussion: Leaves of *Acer smileyi* are similar to those of *A. browni* but can be separated by: the stronger development of the most basal lateral lobes, larger areoles, and more numerous and attenuated teeth. In these characters, *A. smileyi* is more closely related to *A. nipponicum* than is *A. browni.*

The fruits of *Acer smileyi* appear to be immature, because they are not strongly inflated and, other than the four fruits illustrated, three pairs of fruits are still attached. Other than the low attachment angle, fruits of *A. smileyi* differ from those of *A. browni* in the extension of the wing along the distal margin of the nutlet and consequent absence of a sulcus. Again, *A. smileyi* appears to be more closely related to *A. nipponicum* than is *A. browni.*

The specializations possessed by *Acer browni* and the close relationship between *A. smileyi* and *A. nipponicum* may indicate that these last two species represent a low grade within *Parviflora.* Further, *A. browni* can be interpreted as a North American derivative of *A. smileyi.*

Distribution: Late Oligocene and early Miocene of central to southern Alaska; late Oligocene through middle Miocene of Oregon and northwestern Nevada.

Typology: Holotype, UCMP 9178.

Occurrences: See appendix table.

Macrantha Group

Section *Republica* Wolfe et Tanai, sect. nov.

Diagnosis: Fruit samaroid, nutlet at basal end; nutlet slightly inflated, outline elongated-elliptic; attachment angle medium; indistinct nutlet flanges, apparently almost fused to form a medial ridge; wing venation formed by acutely diverging veins, some veinlets.

Discussion: The single specimen of *Acer republicense* has wing venation that is more complicated than typical for the *Spicata* Group but like that typical for the *Macrantha* Group. The nutlet inflation and attachment angle are low-grade, but the elongated outline and sinuous proximal margin of the nutlet are specialized features that indicate a relationship to extant members of the *Macrantha* Group. A fruit of *A. sinuofluviatilis* (pl. 15, fig. 2) has particularly strong phenetic resemblance to *A. republicense,* particularly in nutlet and wing shapes.

Type species: Acer republicense Wolfe et Tanai.

Acer republicense Wolfe et Tanai, sp. nov.

(pl. 4, figs. 13, 14, 18)

Description: Fruit samaroid; nutlet at basal end; nutlet 0.7 m long, 0.3 cm wide, outline elliptic, apex narrowly rounded; slightly inflated; two flanges almost fused to form a medial ridge extending the length of nutlet; attachment angle 50°, nutlet angle 10°. Wing extending along half the distal margin of nutlet, 1.7 cm long, 0.7 cm wide; distal margin basally convex and distally straight, proximal margin straight, apex narrowly rounded; 5 veins from nutlet coalescing along proximal margin of wing, then diverging at angles of 10° to 30°, dichotomizing and anastomosing, some veinlets.

Nomenclature: Type locality is at Republic, Washington.

Discussion: See under *Republica.*

Distribution: Early middle Eocene of northeastern Washington.

Typology: Holotype, UAPC S5414A, B.

Occurrence: See appendix table.

Section *Trilobata* Pojarkova

Acer ashwilli Wolfe et Tanai, sp. nov.

(pl. 22, figs. 1, 2, 5-7, 9; pl. 24, figs. 1-4; pl. 25, figs. 13, 14; text-fig. 12F)

Description: Leaves simple, perfectly actionodromous; deeply 3-lobed, lateral lobes about 2/3 as long as medial lobe; shape very wide ovate to ovate; medial lobe broadly triangular, lateral lobes narrowly triangular; 5.0 to 10.5 cm long, 4.0 to 8.0 cm wide; base narrowly to broadly rounded, apex attenuate; lateral primary veins slightly diverging from medial secondary veins; 7 to 9 secondary veins originating at angles of 30° to 60° from basal side of lateral primary vein, broadly convex, craspedodromous; 6 to 9 pairs of medial secondary veins originating at angles of 30° to 50°, broadly convex, craspedodromous, the most basal pair giving off acutely angled external veins to brace the lobal sinuses; tertiary veins compound A-O, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.5 to 0.6 mm in diameter, veinlets thin and branching 2 to 3 times; teeth D-4, 2 to 4 subsidiary teeth on basal flank, 1 or 2 teeth on apical flank; petiole over 0.5 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.5 to 0.9 cm long, 0.3 to 0.6 cm wide; outline elliptic, apex narrowly rounded to triangular; proximal margin tangential to proximal margin of samara; nutlet moderately inflated; 6 to 8 veins of equal size originating along attachment scar, the 3 or 4 most proximal extending to the proximal margin of nutlet and fusing, the others extending to and coalescing at apex of nutlet; attachment angle 20° to 30°, nutlet angle 30° to 45°. Wing extending 1/4 distance along distal side of nutlet, forming a shallow U-shaped sulcus with nutlet; 1.8 to 2.5 cm long, 0.6 to 1.0 cm wide; distal margin broadly convex, proximal margin broadly convex, apex broadly curved; 5 to 7 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, smoothly curving, bifurcating, few anastomoses.

Nomenclature: Melvin Ashwill has assiduously collected from numerous Tertiary localities near Madras, Oregon, and has supplied us with material of *Acer* from these localities.

Discussion: Association of leaves and fruits of *Acer ashwilli* at several Bridge Creek localities leaves little doubt that the two organs are conspecific. At the locality at Fossil, both leaves and fruits are particularly abundant; the only other remains of *Acer* at this locality are rare fruits of *Macrophylla* and *Negundo.*

Leaves of *Acer ashwilli* are conspicuously three-lobed and the lobes are highly attenuate. In combination with Type I areolar venation, the three-lobed condition of *A. ashwilli* indicates a relationship to *Trilobata,* although leaves of *Trilobata* have very short lateral lobes or are unlobed. *Acer ashwilli* has retained bohlenioid secondary venation in most of the lamina, which is also present in leaflets of *Negundo* and *Cissifolia.*

The fruit of *Acer ashwilli* has a nutlet that has several subparallel ridges connected by anastomoses of equal thickness; this is fundamentally like the nutlet of *Trilobata,* which has a pronounced and coarse reticulum of veins and one apically directed vein that is markedly thicker than the others. Note fusion of two or three ridges along the proximal margin of the proximal margin of the nutlet in *A. ashwilli;* in *Trilobata,* some veins have a similar pattern of fusion. Although *A. ashwilli* differs in some characters from extant *Trilobata,* these are characters in *Trilobata* that could be derived from characters in *A. ashwilli.* Thus, *A. ashwilli* could represent a group that gave rise to extant *Trilobata.*
Distribution: Early Oligocene of central Oregon.
Typology: Holotype, UCMP 9036A, B.
Occurrences: See appendix table.

Acer species 2

(pl. 13, fig. 1)

Discussion: A single samara appears to represent *Trilobata.* The specimen has the wing extending along the distal margin of the nutlet to the attachment scar. The nutlet has a convex curvature to basal part of the proximal margin. The venation on the nutlet has several veins originating along the attachment scar and that form a reticulum; the veins in the proximal part of the nutlet appear to coalesce along the proximal margin of the nutlet, and some of the distal veins pass directly onto the wing.
Distribution: Probable latest Eocene of central Alaska.
Occurrence: See appendix table.

Section *Macrantha* Pax

Acer clarnoense Wolfe et Tanai, sp. nov.

(pl. 14, figs. 3-7; text-fig. 12G)

Description: Leaves simple, perfectly actinodromous, with 5 primary veins; shallowly 3-lobed, lateral lobes about 1/2 as long as medial lobe; shape widely ovate, lobes rounded triangular; 3.1 to 5.0 cm long, 2.3 to 3.7 cm wide; base shallowly cordate to truncate, apex acute; lateral lobal apices broadly acute; most apical lateral primary veins diverging from medial secondary veins, most basal lateral primary veins thin; 4 or 5 of secondary veins originating at angles of 40° to 90° (typically close to orthogonal) from the basal side of most apical lateral primary veins, markedly convex, craspedodromous; 4 or 5 pairs of medial secondary veins originating at angles of 30° to 60°, straight to broadly convex, craspedodromous; lobal sinal bracing formed by an acutely bifurcating secondary vein or by an acutely originating medial external secondary vein; tertiary veins compound, R-R, spaced 0.1 to 0.2 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.3 to 0.6 mm in diameter, veinlets branching 2 or 3 times; primary teeth very broadly D-1; subsidiary teeth B-2, 1 or 2 present on basal flank of most basal medial primary teeth; petiole at least 1.6 cm long.

Fruit samaroid, nutlet at basal end. Nutlet 0.8 cm long, 0.3 wide; outline triangular, apex narrowly rounded; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.35 cm long; nutlet flattened, about 6 veins originating along attachment scar, extending apically, reticulate, extending directly onto wing; attachment angle 60°, nutlet angle 5°. Wing barely extending along distal margin of nutlet; 1.3 cm long, over 0.3 cm wide; distal margin and apex not preserved, proximal margin straight; 7 veins loosely coalesced along proximal side, wing veins gradually diverging at angles of 20° to 30°, smoothly curving, bifurcating.

Nomenclature: Type locality is in the Clarno Formation.

Discussion: Leaves of *Acer clarnoense* possess the combination of features characteristic of *Macrantha:* Type I areolar venation, shallow lobing, acutely angled lobal sinal bracing, closely spaced and R-R tertiary veins, and some subsidiary teeth are entered by veins that are branches from external secondary veins (rather than by the external secondary veins).

The single fruit tentatively assigned to *Acer clarnoense* is also assignable to *Macrantha.* The elongated nutlet, high attachment and low nutlet angles and the flattened nutlet that has several veins forming a reticulum are particularly characteristic of *Macrantha.*

Acer dettermani contrasts with *A. clarnoense* in having narrower teeth that are of almost uniform size and in having more widely spaced tertiary veins.

Distribution: Late middle to early late Eocene of central Oregon.

Typology: Holotype, UCMP 9010A, B.

Occurrence: See appendix table.

Acer dettermani Wolfe et Tanai, sp. nov.

(pl. 14, figs. 8, 9: text-fig. 12H)

Description: Leaves simple, perfectly actinodromous; shallowly 3-lobed; lateral lobes about 1/2 as long as medial lobe; shape widely elliptic; estimated 6.5 to 7.0 cm long, 4.5 to 8.0 cm wide; base cordate, apex not preserved; lobes triangular; lateral primary veins parallel to medial secondary veins; 7 or 8 pairs of secondary veins originating at angles of 30° to 50° from basal side of lateral primary veins, broadly convex, craspedodromous; about 5 pairs of medial secondary veins originating at angles of 30° to 60°, broadly convex, craspedodromous; lobal sinal bracing formed by a tertiary vein; tertiary veins compound, R-A, spaced 0.3 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veins quadrangular or pentagonal, forming areoles 0.4 to 0.8 mm in diameter, veinlets typically branching 2 or 3 times; teeth small, A-1 or D-1, 1 or 2 per secondary vein.

Nomenclature: Robert L. Detterman has greatly contributed to understanding the

Tertiary stratigraphy of the Alaska Peninsula.

Discussion: Shallow dissection, three lobes, small teeth of uniform size, and veinlets branching two or three times, place *Acer dettermani* in *Macrantha*. Further, *A. dettermani* has some teeth that are supplied by branches originating from the abmedial side of loops of external secondary veins, a character also found in extant *macrantha* (for example, *A. davidii*).

Distribution: Late middle or early late Eocene of central part of Alaska Peninsula.

Typology: Holotype, USNM 396014.

Occurrence: See appendix table.

Acer castorrivularis Wolfe et Tanai, sp. nov.

(pl. 14, figs. 1, 2; text-fig. 12 Ja,b)

Description: Leaf simple, perfectly actinodromous; unlobed, with 5 primary veins, the most basal pair very weak; shape ovate, (estimated) 7 cm long and 5.1 cm wide; base rounded, apex unknown; most apical lateral primary veins parallel to medial secondary veins, broadly convex; 5 or 6 lateral secondary veins originating at angles of 40° to 60° from basal side of lateral primary veins, broadly convex, craspedodromous or camptodromous; at least 5 pairs of medial secondary veins originating at angles of 40° to 60°, straight to broadly convex, craspedodromous or camptodromous; tertiary veins A-R or R-R, compound, spaced 0.3 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veantion forming irregular polygons, 0.5 to 1.2 mm in diameter, veinlets twice- or thrice-branching; teeth small, A-1, almost of uniform size, about 2 subsidiary teeth per primary tooth.

Nomenclature: Type locality is on Beaver Creek.

Discussion: An unlobed lamina, mixed craspedodromy-camptodromy, and finely serrate margin indicate that *Acer castorrivularis* is a member of *Macrantha*. The other North American Tertiary members of *Macrantha* all have lobes.

Distribution: Latest Eocene of west-central Montana.

Typology: Holotype, UCMP 9310A, B.

Occurrence: See appendix table.

Acer latahense Wolfe et Tanai, sp. nov.

(pl. 35, figs. 2, 4, 5; text-fig. 12I)

Acer glabroides auct. non R. W. Brown. Graham. 1965 (part). 66.

Description: Leaves simple, perfectly actinodromous; shallowly 3-lobed; lateral lobes about 1/3 as long as medial lobe; 3.5 to (estimated) 10 cm long, 2.0 to 8.0 cm wide; base rounded to truncate, lobal apices acute; lobes triangular; 3 or 5 primary veins; most apical lateral primary veins parallel to or diverging from medial secondary veins; 4 to 6 secondary veins originating at angles of 45° to 75° from basal sides of lateral primary veins, broadly curving, craspedodromous; 6 or 7 pairs of medial secondary veins, originating at angles of 30° to 50°, straight to broadly curving, most craspedodromous but some camptodromous; a few intersecondary veins; tertiary veins that connect most basal medial secondary veins to lateral primary veins A-R and compound, spaced 0.3 to

0.5 cm.; fourth order venation irregularly polygonal; fifth order venation forming irregularly polygonal areoles 0.5 to 1.2 mm in diameter, veinlets typically branching 2 or more times; lobal sinal bracing formed by a medial external secondary vein that originates acutely; teeth D-1, typically 1 or 2 subsidiary teeth on basal flank and none (rarely 1) on apical flank; typically 2 or 3 teeth on apical side of lateral lobes; petiole more than 2.2 cm long.

Nomenclature: Type locality is in Latah Formation.

Discussion: Acer latahense has Type I areolar venation, is shallowly three-lobed, and has some camptodromous secondary and external secondary veins; these characters are combined only in *Macrantha.*

Among extant species, *Acer latahense* is most similar to *A. rufinerve* S. et Z., although *A. latahense* has fewer and blunter teeth than this extant species and has A-R (rather than R-R) tertiary veins. The fossil *A. palaeorufinerve* Tanai et Onoe is also similar to *A. latahense; A. latahense* has a narrower medial lobe than *A. palaeorufinerve,* which also has R-R tertiary veins. *Acer latahense,* however, may be derived from *A. palaeorufinerve.*

Distribution: Late early to middle Miocene of northeastern Washington and eastern Oregon.

Typology: Holotype, USNM 3966136A, B.

Occurrence: See appendix table.

Acer palaeorufinerve Tanai et Onoe

(pl. 35, fig. 1)

Acer palaeorufinerve Tanai et Onoe. 1961. 49. pl. 16, f. 2, 3
Tanai. 1983. 306 (see synonymy). pl. 3, f. 11:; pl. 4, 3; pl. 5, f. 10.
Acer glabroides auct. non R. W. Brown. Wolfe & Tanai. 1980 (part). 40.

Nomenclature: Resemblance of the fossils to *Acer rufinerve.*

Discussion: A single samara from Seldovia Point has a high attachment angle and an asymmetrically inflated nutlet. The Seldovia Point specimen is highly similar to the samara illustrated by Huzioka and Uemura (1973, pl. 13, fig. 5) and is, therefore, tentatively assigned to *Acer palaeorufinerve.* No leaves of *A. palaeorufinerve* have been found in Alaska, although Chelebaeva (1978) illustrated foliage of this species from Kamchatka.

Distribution: Late early to early middle Miocene of Beringia; Miocene and Pliocene of North Korea, Hokkaido, and Honshu.

Typology: Holotype, Geological Survey of Japan 4182.

Occurrence: See appendix table.

Section *Glabra* Pax

Acer traini Wolfe et Tanai, sp. nov.

(pl. 37, figs. 16, 20, 21)

Description: Fruits samaroid, nutlet at basal end. Nutlets 0.5 to 0.9 cm long, 0.4 to 0.8 cm wide, triangular, moderately inflated; nutlet with 1 pronounced and 2 smaller ridges; the pronounced ridge approximately medially placed extending from the attachment scar to the apex of the nutlet, the 2 minor ridges irregularly placed; attachment angle 30° to 40°, nutlet angle 40° to 50°; veins on nutlet obscure; proximal margin of nutlet not expanded beyond proximal margin of wing. Wing 1.2 to 2.5 cm long, 0.6 to 1.2 cm wide; proximal margin straight, distal margin broadly convex and basally typically forming a straight line continuous with attachment scar; proximal margin with 6 prominent veins that appear to originate in the apical margin of the nutlet between the proximal margin and the prominent ridge; wing veins diverging from proximal margin at angles of 30° to 50°, dichotomizing 3 to 4 times, few anastamoses or veinlets.

Nomenclature: For the late Percy Train, who made the largest collections from Trout Creek.

Discussion: The fruits illustrated and cited here represent the first valid record of the *Acer glabrum* type in the Tertiary of western North America. Other than typically prominent folds on the nutlet, close relationship to *A. glabrum* is indicated by the proximal and distal margins of the nutlet forming straight lines with respect to margins of the wing.

Indeed, no characters are preserved in fruits of *Acer traini* to separate the fossil fruits from those of *A. glabrum.* Until foliage of *Glabra* is found associated with *A. traini,* we prefer to apply a separate epithet to these fossil fruits. If associated foliage also proves indistinguishable from *A. glabrum,* we suggest that *A. traini* should be considered a junior synonym of *A. glabrum.*

Fruits of *Acer traini* are rare. This rarity, as well as lack of associated foliage of *Glabra,* indicates that plants that produced the fruits grew at considerable distance from, or were rare near, sites of deposition. Considering that today *A. glabrum* typically grows in the upper reaches of mixed Coniferous forest and is poorly represented in vegetation represented by assemblages such as the Trout Creek, *A. traini* appears to have been adapted to the same environments as *A. glabrum.* Apparent similarity in habitat preference between the two species indicates a similar physiology and further indicates that they may well be shown to be conspecific.

Distribution: Early to middle Miocene from central British Columbia south to central Nevada.

Typology: Holotype, UMMP 65138.

Occurrences: See appendix table.

Section *Arguta* Rehder

Acer ivanofense Wolfe et Tanai, sp. nov.

(pl. 13, figs. 2-4; text fig. 12K)

Description: Leaves simple, perfectly actionodromous; medial lobe twice a wide as lateral lobes; 3-lobed shape very wide ovate; base cordate; medial lobe broadly trianglular, lateral lobes narrowly lateral primary veins parallel to medial secondary veins; triangular; 4.5 to 7.8 cm long, 4.0 to 7.5 cm wide; 4 to 7 secondary veins originating at angles of 30° to 60° from basal side of lateral primary veins, broadly convex, craspedodromous, interspersed with intersecondary veins; 5 to 7 pairs of medial secondary veins originating at angles of 40° to 60°, broadly convex, craspedodromous, the most basal pair giving off an external secondary vein to brace the lobal sinus; dental sinal bracing formed by a secondary vein and its external branch; numerous medial intersecondary veins; tertiary veins slightly A-A and compound; fourth order venation irregularly polygonal; fifth order veins forming polygonal aeroles 0.6 to 0.8 mm in-diameter, veinlets branching typically 2 or 3 times; teeth large, D-1, largest teeth typically with 1 or 2 subsidiary teeth on basal flank and 1 tooth on apical flank; petiole 2.2 cm long.

Nomenclature: Type locality is in Ivanof Bay, Alaska.

Discussion: Leaves of section *Arguta* closely resemble those of *Acer rubrum.* Other than areolar venation, however, lobal sinal bracing of *Arguta* differs from that of *Rubra.* In *Rubra,* the most basal medial secondary vein bifurcates about two-thirds the distance from the midrib to the sinus, with the more basal bifurcation extending into the lateral lobe. Typically the basal bifurcation (rarely the apical bifurcation) gives off a weak vein apically that extends to the lobal sinus. In *Arguta,* an external branch of the most basal medial secondary vein extends directly to the sinus, in some instances giving off weak veins both apically and into the lateral lobe. Bracing of dental sinuses in the two sections follws the same basic pattern as bracing of the lobal sinuses. On the basis of lobal and dental sinal bracing, as well as the branching areolar venation, *Acer ivanofense* is considered to represent *Arguta.*

Distribution: Early late Eocene of central part of Alaska Peninsula.

Typology: Holotype, USNM 396017a.

Occurrence: See appendix table.

Section *Rubra* Pax

Acer ovipetrinum Wolfe et Tanai, sp. nov.

(pl. 20, figs. 4, 8)

Description: Fruits samaroid, nutlet at basal end; nutlet 0.7 to 0.8 cm long, 0.35 cm wide; outline elliptic, apex narrowly rounded; apical part of proximal margin straight and tangential to proximal margin of samara, basal part concave from a conspicuous basal beak; attachment scar 0.3 to 0.5 cm long; nutlet moderately inflated; 8 low ridges extending apically from attachment scar, numerous (at least twice as many as ridges) thin veins paralleling ridges; attachment angle 20° to 50°, nutlet angle 20° to 35°. Wing entirely apical to nutlet, forming a deep and broad U-shaped sulcus with nutlet; 2.0 cm long, 0.7 cm wide; distal margin deeply convex, proximal margin shallowly convex, apex narrowly rounded; about 10 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, sharply and smoothly curving, bifurcating, anastomoses numerous, veinlets simple.

Nomenclature: Type locality is on Sheep Rock Creek, Oregon.

Discussion: Fruits of *Acer ovipetrinum* are similar to *A. kluckingi* in having several strong veins with numerous fine veins paralleling the long axis of the nutlet, as well as in the deep sulcus and the presence of a basal beak. In *A. kluckingi,* the number of nutlet veins is reduced and the wing extends slightly along the distal margin of the nutlet.

The several subparallel nutlet veins, elongated nutlet outline, and sinuous proximal margin of the nutlet of *Acer ovipetrinum* are characters that link *Rubra* and *Eriocarpa*. The extant species of these two sections differ markedly in nutlet characters.
Distribution: Probale late middle to early late Eocene of central Oregon.
Typology: Holotype, UCMP 9107.
Occurrence: See appendix table.

Acer kluckingi Wolfe et Tanai, sp. nov.

(pl. 27, figs. 4-11; text-fig. 14E)

Description: Leaves simple, perfectly actinodromous; shallowly to deeply 5-lobed, with the more apical lateral lobes about 2/3 the length of medial lobe and the more basal lateral lobes poorly developed; shape very wide ovate, base cordate, apex acute; medial and more apical lateral lobes elliptic and with lobations; more apical lateral primary veins slightly diverging from medial secondary veins; 4 or 5 secondary veins originating at angles of 35° to 45° from basal side of more apical primary veins, straight to slightly curving, craspedodromous; 3 to 5 pairs of medial secondary veins originating at angles of 40° to 50°, broadly convex, typically craspedodromous; lobal sinal bracing formed by either an acutely originating external secondary vein or by an acutely bifurcating secondary vein; tertiary veins compound, O-A or R-A spaced 0.2 to 0.4 cm; fourth order venation quadrangular; fifth order veins forming quadrangular areoles 0.4 to 0.6 mm in diameter, veinlets absent or unbranched; teeth large, D-1, with 1 to 3 subsidiary teeth on basal flank and no or 1 tooth on apical flank.

Fruits samaroid, nutlet at basal end; nutlets 0.6 to 0.8 cm long, 0.4 to 0.6 cm wide; outline elliptic, apex narrowly rounded; attachment scar 0.4 to 0.6 cm long; nutlet moderately inflated; proximal margin expanding slightly beyond proximal margin of wing; 5 to 7 veins of equal size originating along attachment scar, converging near apex of nutlet; attachment angle 20° to 40°, nutlet angle 30° to 40°. Wing slightly extending along distal margin of nutlet, forming a broadly V-shaped sulcus with nutlet; 2.0 to 2.8 cm long, 0.7 to 0.9 cm wide; distal margin broadly convex, proximal margin broadly convex, apex broadly rounded; 5 to 7 veins coalesced along proximal side, wing veins diverging at angles of 30° to 50°, smoothly curving, bifurcating, few anastomoses.
Nomenclature: Edward P. Klucking made extensive collections from the type locality of this species.
Discussion: At the Bridge Creek/Pentecost Ranch locality, leaves and fruits of *Acer kluckingi* are the most abundant fossils of *Acer* represented. The leaves are most similar to extant *Rubra* in having five lobes, large D-1 teeth (some of which form lobations), and quadrangular areoles with no or unbranched veinlets. The fruits are also similar to those of *Rubra* in their low attachment angle, curved proximal margin, and nutlet veins that coalesce apically.

Fruits of *Acer kluckingi* are similar to those of *A. ashwilli*. *Acer kluckingi* has a more strongly developed sulcus than does *A. ashwilli*, but the major distinction is in the venation of the nutlet: in *A. ashwilli* the most proximal ridges (and the veins on them) coalesce along the proximal margin of the nutlet, whereas in *A. kluckingi* the proximal

veins coalesce with the medial and distal veins near the apex of the nutlet.
Distribution: Early Oligocene of central Oregon.
Typology: Holotype, UCMP 2109.
Occurrences: See appendix table.

Acer tigilense Chelebaeva

(pl. 27, fig. 1; pl. 41, figs. 3, 6-9: text-fig. 14Fa, b)

Acer tigilense Chelebaeva. 1976. 192. pl. 24, f. 3-5; pl. 39, f. B-Q; pl. 40, f. A, B.
  Chelebaeva. 1987. 81. text-f. 32, 1; pl. 20, f. 2; pl. 25, f. 8.
Acer akanthirivus Axelrod (nom. illeg.). 1964. 134.
Acer bendirei auct. non Lesquereux. Knowlton. 1902. 49, pl. 6, f. 4.
  Knowlton. 1926. 45. pl. 27, f. 3.
Acer columbianum Chaney & Axelrod. 1959 (part, non-typic). 192. pl. 40, f. 5.
Acer glabroides auct. non R. W. Brown. Brown. 1937b (part, nontypic). 180 pl. 58, f. 14.
  Smith. 1941. 516. pl. 12, f. 4, 10.
  Chaney & Axelrod. 1959 (part). 193. pl. 40, f. 9-11; pl. 41, F. 1, 2
  Axelrod. 1964 (part). 128. pl. 15, f. 11; 141 (references to Horseshoe Bend and Cartwright Ranch material).
  Wolfe & Tanai. 1980 (part). 40. pl. 17, f. 8.
Acer minor auct. non Knowlton. Berry. 1929. 256. pl. 64, f. 2.
Acer osmonti auct. non Knowlton. LaMotte. 1936 (part). 137. pl. 12, f. 6.
Acer trilobatum productum auct. non (Braun) Heer. Hollick. 1936. 135. pl. 76, f. 2.
Acer sp.? Hollick. 1936. 136. pl. 76, f. 1.

Description: Leaves simple, perfectly actinodromous; 3- or 5-lobed, with degree of dissection variable but never deeply dissected; most apical lateral lobes about 1/3 to typically at least 2/3 as long as medial lobe; shape ovate to typically widely ovate; lobes triangular to elliptic; base acute, truncate, or typically cordate; apex acute; most apical lateral primary veins slightly diverging from medial secondary veins; 4 to 8 secondary veins originating at angles of 35° to 60° from basal side of lateral primary veins, straight to broadly convex, craspedodromous; 5 to 7 pairs of medial secondary veins originating at angles of 30° to 55°, straight to broadly convex, typically craspedodromous; lobal sinal bracing typically formed by an acutely bifurcating secondary vein; intersecondary veins can be present; tertiary veins compound, A-A or A-R, spaced 0.4 to 0.7 cm; fourth order venation quadrangular; fifth order veins forming quadrangular areoles 0.4 to 0.6 mm in diameter, veinlets absent or unbranched; teeth typically large, D-1, with 2 to 4 subsidiary teeth on basal flank and no or 1 on apical flank; petiole at least 2.0 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.5 to 0.7 cm long, 0.3 to 0.5 cm wide; outline elliptic, apex narrowly rounded; distal margin tangential to distal margin of samara; nutlet slightly inflated; attachment scar 0.3 to 0.5 cm long; 4 to 6 veins of equal thickness originating along attachment scar, converging at apex of nutlet, interconnected by a few veins; attachment angle 20° to 30°, nutlet angle 20° to 30°. Wing extending about half the length of distal margin of nutlet; 1.2 to 2.0 cm long, 0.5 to 0.7 cm wide; distal margin straight to broadly convex, proximal margin broadly convex, apex broadly rounded; 4 to 6 coalesced veins along proximal side, wing veins diverging at angles of 10° to 20°, slightly curving, bifurcating, anastomoses few.

Nomenclature: Miocene leaves and fruits similar to those of the extant *Acer rubrum* have traditionally been referred to *A. glabroides.* The lectotype of *A. glabroides,* however, represents the extinct section *Orba.* Axelrod (1964) proposed the epithet *akanthirivus* for *A. rubrum*-like leaves from the Miocene beds on Thorn Creek, Idaho, based entirely on the supposed smaller size of these leaves in comparison to *A. rubrum*-like leaves from beds older than the Thorn Creek beds. Axelrod's basis for such a specific distinction is based largely on his erroneous determination of *A. chaneyi* leaves from these older beds as *A. glabroides.* The Thorn Creek leaves (for example our pl. 29, fig. 6) are clearly as large as any older valid *A. rubrum*-like leaves. Had Axelrod (1964) designated a holotype as required by the International Code of Botanical Nomenclature, his epithet *akanthirivus* would be the oldest valid name for this Miocene species of *Rubra.* Chelebaeva'a (1976) *A. tigilense* thus is the oldest validly published name for this Miocene species. Although Chelebaeva's species is based on material from Kamchatka, the Alaskan specimens are conspecific both with her material and material from conterminous United States.

Discussion: Fruits and leaves of *Acer tigilense* have not been found in association at any locality. The fruits and leaves of *A. tigilense,* however, are closely similar to respective organs of the extant *A. rubrum,* and particularly in Beringian Miocene assemblages, which have a low diversity of *Acer* in comparison to middle latitude assemblages, these fruits and leaves are the only representatives of *Rubra.* We consider conspecifity of the fossil fruits with the fossil leaves highly probable.

Whether *Acer tigilense* is directly descended from *A. kluckingi* is very uncertain. Although leaves of *A. tigilense* could readily be derived from those of *A. kluckingi,* derivation of the fruit of *A. tigilense* from the fruit of *A. kluckingi* requires several modifications. These changes would involve a reduction in the number of nutlet veins, origin of interconnecting nutlet veins (although such could be present but immersed in the pericarp in *A. kluckingi*), and extension of the wing along the distal margin of the nutlet and consequent elimination of the sulcus. No fruits are yet known that have a morphology intermediate between that of *A. tigilense* and that of *A. kluckingi.*

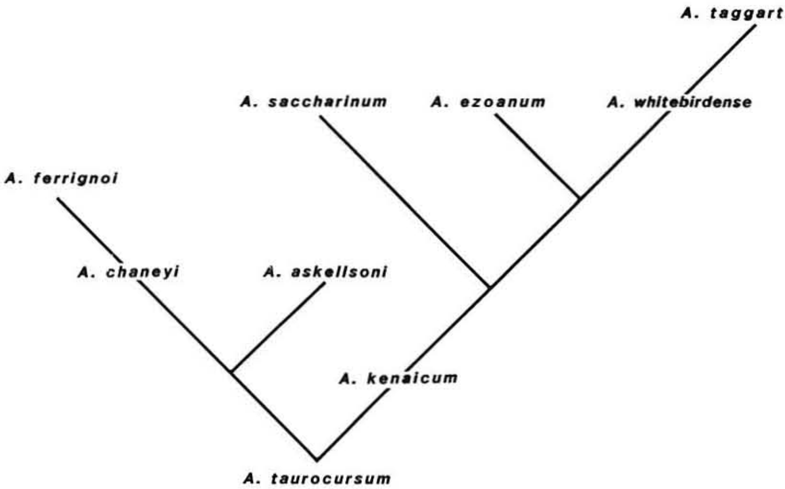
Distribution: Late Oligocene through early middle Miocene of Alaska and adjacent U.S.S.R.; late early through early late Miocene of the Columbia Plateaus, middle Miocene of western Nevada.

Typology: Holotype, Institute of Volcanology, Academy of Science, T60/72 Petropavloskna-Kamchatka (not figured).

Occurrences: See appendix table.

Section *Eriocarpa* (Rafinesque) Murray

Discussion: The one extant species of *Eriocarpa, Acer saccharinum* L., has fruits that have a large wing and an elongated nutlet. The endocarp is moderately thick (about 0.3 mm), and the venation on the nutlet is formed by about 8 to 10 conspicuous nearly parallel veins that are connected by numerous, weaker, acutely angled cross veins. The attachment scar is about one-fifth or less the total length of the nutlet. Leaves are five-lobed, have conspicuous sinal bracing by acutely bifurcating secondary veins, and the margins of the sinuses are typically concave. Areolar venation is composed of thin, irregularly shaped, quadrangular to pentagonal areoles that are 0.3 to 0.5 mm across and



Text-fig. 13 Suggested cladistic relationships of species of Section *Eriocarpa.*

the veinlets are thin, simple or once-branched.

The late middle Eocene *Acer taurocursum* is the earliest known record of definite *Eriocarpa.* The fruit has the large wing and spindle-shaped nutlet characteristic of *Eriocarpa.* The nutlet, however, has at least 20 parallel and somewhat obscure veins and the attachment scar is almost half the length of the nutlet. The distal side of the nutlet is expanded outward and has a vein that forms a broad, low ridge.

Two species of *Eriocarpa* are known in the Oligocene. The early Oligocene Alaskan *A. kenaicum* is known from both fruit and associated foliage. The nutlet has seven veins, the attachment scar is over half the length of the nutlet, and the leaf is five-lobed and has concave-sided dental sinuses. The oldest record of the typically Miocene *Acer chaneyi* is somewhat uncertain. The Kukak Bay occurrence is most probably late Oligocene, but the Gumboot Mountain occurrence, although possible also late Oligocene, probably is early Oligocene. Fruits of *A chaneyi* lack the proximal expansion and ridge of the nutlet but are otherwise highly similar to *A. taurocusum,* particularly in the large number (15 to 20) of obscure veins that parallel the long axis of the nutlet; the length of the attachment scar is about the same in the two species. On the other hand, the leaves of *A. chaneyi* are most similar to those of *A. kenaicum* and to the extant *A. saccharinum.* The probable latest Miocene *A. ferrignoi,* which is represented only by foliage, appears to represent a three-lobed derivative of *A. chaneyi.*

In presence of six to eight nutlet veins that are interconnected, the Miocene *Acer whitebirdense* is clearly distinct from *A. chaneyi* and probably related to *A. kenaicum.* In foliage, *A. whitebirdense* and its probable descendant, *A. taggarti,* have a pronounced tendency to a three-lobed condition and to broaden dental and lobal sinuses.

The relationship of the extant *Acer saccharinum* to the western American Neogene species of *Eriocarpa* appears to be distant. *A. chaneyi,* although having foliage much like that of *A. saccharinum,* has a fruit more similar to that of *A. taurocursum.* The fruit of *A. whitebirdense* is, in nutlet venation, like *A. saccharinum,* but the broad lobes of leaves in *A. whitebirdense* are dissimilar. Only *A. kenaicum* in the early Oligocene appears to offer the appropriate combination of characters to be in the direct ancestry of *A. saccharinum.* Presumably forms linking *A. kenaicum* and *A. saccharinum* occurred in the late Oligocene and Neogene of northeastern North America; the Icelandic Neogene *A. askelssoni* cannot be such a form, because it has the many nutlet veins of *A. taurocursum* (Friedrich and Simonarson, 1976, pl. 1, fig. 1a).

Acer taurocursum Wolfe et Tanai, sp. nov.

(pl. 16, figs. 2, 4)

Description: Fruit samaroid, nutlet at basal end; nutlet 2.5 cm long, 0.8 cm wide; outline narrowly elliptic, apex rounded; nutlet moderately inflated; scar 1.1 cm long, with a proximal keel; about 20 obscure veins originating along attachment scar extending approximately parallel and passing onto wing; prominent broad ridge extending aparallel to and near distal margin of nutlet; attachment angle 20°, nutlet angle 25°. Wing almost entirely apical to nutlet, forming a broad and shallow concave sulcus with nutlet; 4.8 cm long, 1.5 cm wide; distal margin broadly convex and undulatory, proximal margin broadly convex, apex acute; veins from nutlet converging about 1.0 cm apical to nutlet and loosely coalesced, wing veins diverging at angles of 10° to 20°, sharply curving and then extending straight, bifurcating, numerous anastomoses.

Nomenclature: Type locality is in Bull Run, Nevada.

Discussion: The large, spindle-shaped, moderately inflated nutlet indicates a placement in *Eriocarpa* for *Acer taurocursum.* The broad, distally placed ridge on the nutlet may be a remnant of a flange.

Distribution: Late middle Eocene of northeastern Nevada.

Typology: Holotype, UCMP 9089.

Occurrence: See appendix table.

Acer kenaicum Wolfe et Tanai, sp. nov.

(pl. 27, figs. 2, 3)

Description: Leaf simple, perfectly actinodromous; 5-lobed, with most apical lateral lobes probably about 2/3 as long as medial lobe; shape widely ovate; base cordate, lobal apex attenuate; lateral lobes triangular, medial lobe elliptic; most apical lateral primary veins slightly diverging from medial secondary veins; 5 secondary veins originating at angles of 25° to 35° from basal side of most apical lateral primary, straight to broadly convex, craspedodromous; at least 6 pairs of medial secondary veins originating at angles of 35° to 40°, broadly convex, craspedodromous; lobal sinal bracing formed by an acutely bifurcating medial secondary vein; tertiary veins compound, A-R, spaced 0.2 to 0.5 cm; fourth order venation irregularly polygonal; higher order venation not preserved; teeth large, C-1, with 1 or 2 subsidiary teeth on basal flank.

Fruit samaroid, nutlet at basal end; nutlet 1.3 cm long, 0.8 cm wide; outline elliptic, apex rounded; proximal margin tangential to proximal margin of samara; nutlet moderately inflated; attachment scar 1.1 cm long; 7 veins of equal size originating along attachment scar extending apically and passing onto wing; attachment angle 25°, nutlet angle 30°. Wing extending to attachment scar; 3.0 cm long, 1.4 cm wide; distal margin broadly convex, proximal margin straight, apex broadly rounded; veins from nutlet converging immediately apical to nutlet along proximal side, wing veins diverging at angles of 20° to 30°, sharply curving, then extending straight, bifurcating, few anastomoses.

Nomenclature: Type locality is in the Kenai Group.

Discussion: The single leaf of *Acer* from Redoubt Point is not well preserved, although concave-sided sinuses, five lobes, acutely angled lobal sinal braces, and C-1 compound teeth indicate an assignment to *Eriocarpa.* The medial lobe is broader and teeth are smaller in *A. kenaicum* than is typical in *A. chaneyi.* Because the single fruit of *Acer* from Redoubt Point also represents *Eriocarpa,* we suggest that the two organs are conspecific.

The fruit of *Acer kenaicum* is characterized by anattachment scar almost as long as the nutlet and by seven veins crossing the nutlet. Assuming that having many nutlet veins is a low grade in *Eriocarpa, A. kenaicum* is clearly advanced in having the number of nutlet veins reduced.

Distribution: Early Oligocene of Cook Inlet region, Alaska.

Typology: Holotype, USNM 396089.

Occurrences: See appendix table.

Acer chaneyi Knowlton

(pl. 32, figs. 3, 4; pl. 42, figs. 1-4; pl. 43, figs. 1-4; pl. 44, fig. 1; pl. 48, fig. 3; text-fig. 14A, B)

Acer chaneyi Knowlton. 1926. 45. pl. 27, f. 2.
Berry. 1929. 256. pl. 63, f. 13.
MacGinitie. 1933 (part). 61.
Oliver. 1934. 26.
Rhus oregonensis H. V. Smith. 1938b. 561. pl. 29, f. 9.
Urena miocenica Graham. 1963. 934. f. 6, 7.
Acer bendirei auct. non Lesquereux. Chaney & Axelrod. 1959 (part). 191. pl. 38, f. 12; pl. 39, f. 1-3, 5, 6.
Axelrod. 1964. 126. 141 (part). pl. 15, f. 1, 2.
Graham. 1965. 66. pl. 4, f. 1; pl. 6, f. 4.
Axelrod. 1985.
Acer glabroides auct. non R. W. Brown. Chaney & Axelrod. 1959 (part). 193. pl. 40, f. 4. Axelrod. 1964. 141.
Acer merriami auct. non Knowlton. Berry. 1931. 39. pl. 13, f. 13.
Acer middlegatei auct. non Axelrod. Axelrod. 1956 (part, nontypic). 307. pl. 31, f. 7-9.
Axelrod. 1964. 142.
Acer middlegatensis auct. non Axelrod. Axelrod. 1985 (part, nontypic). 171. pl. 14, f. 11.
Acer osmonti auct. non Knowlton. MacGinitie. 1933 (part). 62.
Oliver. 1934. 24.
Brown. 1937a. 513. text-f. 1.
Brown. 1937b (part). 180. pl. 58, f. 16, 17.
Smith. 1939 (part). 116. pl. 3, f. 1; pl. 4, f. 1.
Acer trilobatum auct. non (Sternberg) Heer. Knowlton. 1904. 157. pl. 29, f. 2.
Platanus dissecta auct. non Lesquereux. Axelrod. 1964. 142.
Quercus cf. *Q. pseudo-lyrata* auct. non Lesquereux. Knowlton. 1926. 36, pl. 22, f. 2.

Description: Leaves simple, perfectly actinodromous; 3- to typically 5-lobed; typically deeply dissected with the most apical lateral lobes about 2/3 as long as medial lobe;

shape widely ovate to orbiculate; base rounded to cordate, apex attenuate; lobes typically elliptic; most apical lateral primary veins slightly diverging from medial secondary veins; 5 to 11 secondary veins originating at angles 25° to 50° from basal sides of most apical primary vein, straight to broadly concave or broadly convex, craspedodromous; 6 to 10 pairs of medial secondary veins originating at angles of 30° to 60°, straight to broadly convex, craspedodromous; lobal sinal bracing typically formed by an acutely bifurcating medial secondary vein; intersecondary veins common; tertiary veins compound, A-A to A-O, spaced 0.2 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.2 to 0.4 cm in diameter, veinlets absent or unbranched; teeth large, C-1, with 1 to 3 subsidiary teeth on basal flank and none or 1 on apical flank.

Fruits samaroid, nutlet at basal end; nutlets 1.0 to 3.2 cm long, 0.5 to 1.2 cm wide; outline narrowly elliptic, apex acute and indistinct; proximal margin tangential to proximal margin of samara; nutlet moderately inflated; attachment scar 0.5 to 1.4 cm long, with proximal keel; 15 to 20 equal-sized veins originating along attachment scar, extending apically and passing onto wing; attachment angle 10° to 40°, nutlet angle 20° to 30°. Wing extending along one-fourth the distal margin of nutlet, forming a shallow concave sulcus with nutlet; 2.0 to 5.7 cm long, 1.5 to 2.2 cm wide; distal margin broadly convex, proximal margin straight to slightly convex, apex broadly to narrowly rounded; veinlets from nutlet loosely coalesced along proximal side apical to nutlet, wing veins diverging at angles of 10° to 20°, sharply curving, then extending straight, bifurcating, few anastomoses.

Nomenclature: Chaney and Axelrod (1959) proposed that the species of *Eriocarpa* commonly found in the Miocene of western North America be referred to *Acer bendirei,* and restricted the species to one of Lesquereux' original cotypes. This restriction is, as pointed out by Wolfe (1964), contrary to the recommendations of the International Code of Botanical Nomenclature; Lesquereux' (1883) description of *A. bendirei* clearly applies primarily to the three specimens of *Platanus* excluded by Chaney and Axelrod (1959) from *A. bendirei.* Wolfe (1964) thus proposed the new combination *Platanus bendirei* (Lesq.) Wolfe. Even if Chaney and Axelrod's (1959) restriction were acceptable, we would argue that Lesquereux' (1883) description would not validate an *Acer bendirei,* that is, no validating description for *Acer bendirei sensu* Chaney and Axelrod (1959) has yet been published.

The next available name for the common western North American *Eriocarpa* might be considered as Knowlton's (1902) *Acer gigas.* Although Knowlton's type probably does represent a fruit of *A. chaneyi,* the specimen was broken prior to deposition and the attachment scar is not preserved; as well, the quality of preservation of the specimen is very poor.

The next oldest epithet that probably applies to this Miocene *Eriocarpa* is *grahamensis.* Heer (1869) described *A. macropterum* from Port Graham, Alaska, although the name was a junior homonym. Knowlton and Cockerell (1919) substituted *grahamensis* for Heer's epithet. The fruits have numerous veins passing from the apical region of the nutlet onto the wing, as in *A. chaneyi.* The base of the nutlet (including the attachment scar) is, however, lacking, and we prefer to reject *A. grahamensis* as being based on material lacking specifically diagnostic characters. We suggest that Knowlton's (1926) *A. chaneyi* is the oldest epithet for this *Eriocarpa* that is based on a specimen that has sufficient defining characters preserved.

Discussion: Although the leaves of *Acer chaneyi* compare well with those of the extant *A. saccharinum,* fruits of the two species are only grossly similar. The attachment scar is about twice as long in *A. chaneyi* as in *A. saccharinum,* and the nutlet of *A. chaneyi* has over twice as many veins as does the nutlet of *A. saccharinum.*

Fruits of *Acer chaneyi* are most similar to the fruit of *A. taurocursum.* The single specimen of *A. taurocursum* has a strongly convex proximal margin and a broad, distally placed ridge on the nutlet; the proximal margin of *A. chaneyi* samaras may be slightly convex but is typically straight, and no ridges are present on the nutlet.

Distribution: Early Oligocene of the Cascade Range of southern Washington; late Oligocene of northern part of the Alaska Peninsula; early to early middle Miocene of central to southeastern Alaska and south into the Columbia Plateaus and western Nevada; late middle to early late Miocene of Columbia Plateaus and Cascade Range of Oregon.

Typology: Holotype, UCMP 22862

Occurrences: See appendix table.

Acer ezoanum Oishi et Huzioka

(pl. 44, fig. 2; text-fig. 14C)

Acer ezoanum Oishi et Huzioka. 1943. 89. pl. 10, f. 1-3; pl. 11, f. 1-4; pl. 12, f. 1, 2.
Tanai. 1983. 320. pl. 4, f. 1; pl. 6, f. 1, 4-6; pl. 7, f. 1-3, 5-8.

Discussion: Because of the single occurrence of this typically east Asian species in Alaska and because of the recently published emended description and discussion by Tanai (1983), we will not present a complete synonymy or description of *Acer ezoanum* here.

The single Alaskan specimen of *Acer ezoanum* compares well to some of the east Asian specimens illustrated by Tanai (1983). Particularly significant are: broad medial lobe, short most-basal lateral lobes, and presence of large, C-3 teeth. *Acer whitebirdense* has longer most-basal lateral lobes than *A. ezoanum* and teeth are dominantly B-2.

Distribution: Early to middle Miocene of south-central Alaska; west to Kamchatka and south to the maritime provinces of the U.S.S.R., Sakhalin, Hokkaido, and northern Honshu.

Typology: Holotype, Hokkaido University Museum of Paleontology 9360 (Tanai, 1983, pl. 6, fig. 5).

Occurrence: See appendix table.

Acer whitebirdense (Ashlee) Wolfe et Tanai, comb. nov.

(pl. 45, figs. 1-3; pl. 46, figs. 1-7; pl. 47, fig. 1; pl. 48, fig. 2; text-fig. 14D)

Viburnum whitebirdense Ashlee. 1932. 82. pl. 2, f. 17.
Acer florissanti auct. non Kirchner. Berry. 1934. 118, pl. 24, f. 5-7.
Acer oregonianum auct. non Knowlton. Berry. 1934. 118. pl. 24, f. 1.
Acer osmonti auct. non Knowlton. Brown. 1937b (part). 180. pl. 58, f. 18.
Platanus dissecta auct. non Lesquereux. Berry. 1934. 111. pl. 21, f. 2.

Description: Leaves simple, perfectly actinodromous; 5-lobed; most apical lateral lobes about 3/4 as long as medial lobe, most basal lateral lobes about 1/2 as long as most apical lateral lobes; shape orbiculate; base cordate, apex acute; 7.0 to (estimated) 20 cm long, 7.0 to 29 cm wide; lobes orbiculate to broadly triangular; most apical lateral primary veins parallel to or slightly diverging from medial secondary veins; 5 to 7 secondary veins originating at angles of 30° to 60° from basal sides of most apical primary veins, straight to broadly convex, craspedodromous; 6 to 8 pairs of medial secondary veins originating at angles of 35° to 70°, broadly convex, craspedodromous; lobal sinal bracing formed either by a secondary vein that angularly bifurcates or by an angularly originating external secondary vein; tertiary veins compound, R-A or A-A, spaced 0.2 to 1 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.2 to 0.4 mm in diameter, veinlets absent or unbranched; teeth B-2, large, typically without subsidiary teeth, but medial lobations can have 1 to 3 subsidiary teeth on basal flank and 1 on apical flank; petiole 2.5 to 6.0 cm long.

Fruits samaroid, nutlet at basal end; nutlets 1.0 to 2.7 cm long, 0.5 to1.6 cm wide; outline widely elliptic, apex broadly rounded; proximal margin expanded beyond proximal margin of wing; attachment scar 0.2 to 0.7 cm long; nutlet moderately inflated; 5 to 7 veins of equal size originating along attachment scar, spreading apically over nutlet, slightly converging in apical region of nutlet and passing onto wing, connected by irregularly placed minor veins; attachment angle 20° to 55°, nutlet angle 10° to 40°. Wing extending about half the length of distal margin of nutlet; 1.5 to 4.0 cm long, 0.6 to 1.5 cm wide; distal margin broadly convex, proximal margin broadly convex, apex broadly curved; 4 to 6 poorly coalesced veins along proximal side, wing veins diverging at angles of 5° to 10°, smoothly curving, bifurcating, some anastomoses.

Nomenclature: Brown (1937b) correctly interpreted the Whitebird leaves and fruits of *Acer* as representing *Eriocarpa;* Chaney and Axelrod (1959), in contrast, decided that some of the Whitebird leaves represented *Rubra.* Further, Ashlee's (1934) *Viburnum whitebirdensis* has been totally ignored by all subsequent workers. Only one species of *Acer* is present in the collections from Whitebird, and this species is the same as Ashlee's (1934) *"Viburnum".*

Discussion: Leaves of *Acer whitebirdense* are unique in *Eriocarpa* in having consistently broad medial lobes and large B-2 teeth. Even more unique in *Eriocarpa* are the fruits of *A. whitebirdense.* Although venation of the nutlet is the basic pattern found in the extant *A. saccharinum,* the nutlets are over one-third as long as the wing and the nutlets are widely elliptic in outline. A similar relation of length of nutlet to length of wing is found in *A. askelssoni* Fried. et Simon. from the Neogene of Iceland, but this species has a spindle-shaped nutlet that has many closely spaced veins.

Large size of the nutlet in relation to the wing could create an aerodynamic problem for an autogyrative samara, because the center of gravity of the samara could shift too far toward the base for autogyration. On the other hand, the pericarp of the nutlet of *Acer whitebirdense* could have been very thin (as in *A. saccharinum*), which would decrease the mass of the nutlet and place the center of gravity farther towards the apex. Still, the total wing area to nutlet area in *A. saccharinum* is about 1:3, whereas this ratio in *A. whitebirdense* is about 1:2. These data indicate that the samara of *A. whitebirdense* probably was not autogyrative but rapidly fell to the ground. Possibly *A. whitebirdense* was adapted for animal rather than wind dispersal.

Distribution: Early to middle Miocene of the Columbia Plateaus.

Typology: Holotype, UIB (not figured).

Occurrences: See appendix table.

Acer taggarti Wolfe et Tanai, sp. nov.

(pl. 47, figs. 2-8; pl. 48, figs. 1, 4)

Acer bendirei auct. non Lesquereux. Lesquereux. 1884 (part, nontypic). 14, pl. 8, f. 1. Chaney & Axelrod. 1959 (part). 191. pl. 39, f. 4.

Acer bolanderi auct. non Lesquereux. Chaney & Axelrod. 1959. 192. pl. 39, f. 7-12.

Acer glabroides auct. non R. W. Brown. Chaney & Axelrod. 1959 (part). 193. pl. 40, f. 6.

Description: Leaves simple, perfectly actinodromous; 3- to 5-lobed; the most apical lateral lobes at least 2/3 as long as medial lobe, the most basal lateral lobes (if present) small; shape asymmetrically ovate to very widely ovate; base rounded to cordate, apex acute; 2.5 to (estimated) 6 cm long, 3.2 to 7.5 cm wide; most apical lateral primary veins diverging from medial secondary veins; 3 to 5 secondary veins originating at angles of 40° to 90° from most apical lateral primary vein, straight to broadly convex, craspedodromous to typically brochidodromous; 3 to 5 pairs of medial secondary veins originating at angles of 40° to 65°, straight to broadly convex, craspedodromous or typically brochidodromous; lobal sinal bracing formed by an acutely bifurcating secondary vein; tertiary veins compound, A-A, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; higher order venation not preserved; teeth large, B-2, typically 1 or 2 on basal sides of most apical lobes and no more than 1 on apical sides; typically 1 or 2 teeth on each side of medial lobe; no subsidiary teeth; petiole 0.9 to 1.4 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.6 to 1.2 cm long, 0.4 to 0.7 cm wide; outline elliptic, apex rounded; proximal margin typically expanded beyond proximal margin of wing; attachment scar 0.4 to 0.7 cm long, some with a proximal keel; nutlet moderately inflated; some nutlets with irregularly placed creases; 8 to 12 veins of equal size originating along attachment scar, extending apically and passing onto wing; attachment angle 20° to 45°, nutlet angle 20° to 50°. Wing extending about 1/2 the length of distal margin of nutlet, forming a broadly V-sharped sulcus with nutlet; 2.2 to 3.5 cm long, 0.8 to 1.2 cm wide; distal margin broadly convex, proximal margin straight to broadly convex, apex rounded; 6 to 8 veins loosely coalesced along proximal side, wing veins diverging at angles of 10° to 30°, sharply curving and extending straight, bifurcating, few anastomoses.

Nomenclature: Ralph E. Taggart has contributed to understanding successional aspects fo Neogene assemblages and, as well, has provided us access to the numerous, unpublished Succor Creek collections.

Discussion: Acutely bifurcating lobal sinal braces and B-2 teeth exclude the leaves of *Acer taggarti* from *Saccharina,* a sectional assignment suggested by Chaney and Axelrod (1959). Similarly, the fruits thought to represent *Saccharina* (and from the same beds as the leaves) lack the strongly inflated nutlet with a strongly developed reticulate venation characteristic of *Saccharina;* these fruits have numerous veins that cross the nutlet and extend onto the wing and, like the leaves, represent *Eriocarpa.*

Leaves of *Acer taggarti* have few teeth and are strongly asymmetrical. These characters are not found in the one extant species of *Eriocarpa,* but they represent a continuation of the trends seen in *A whitebirdense.* The fruit of *A. taggarti* could also be derived from that of *A. whitebirdense* by reduction. The irregular folds in most fruits of *A. taggarti* may represent folding of a thin endocarp.

Distribution: Early middle Miocene of central Oregon.

Typology: Holotype, UCMP 9104.

Occurrences: See appendix table.

Acer ferrignoi Wolfe et Tanai, sp. nov.

(pl. 41, figs. 1, 2, 4, 5)

Description: Leaves simple, perfectly actinodromous; 3-lobed, the lateral lobes about 1/2 to 3/4 as long as medial lobe; shape ovate to very widely ovate; base rounded, apex attenuate; 3 to (estimated) 7 cm long, 2.8 to 9 cm wide; medial lobe triangular, lateral lobes typically narrowly triangular; 3 to 10 secondary veins originating at angles of 30° to 60° from basal sides of lateral primary veins, straight to broadly convex, craspedodromous or some brochidodromous with craspedodromous external veins; 4 to 10 medial secondary veins originating at angles of 40° to 70°, straight to broadly convex, craspedodromous or brochidodromous with craspedodromous external veins; lobal sinal bracing formed by an acutely bifurcating secondary vein; tertiary veins compound, O-A to R-, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; higher order venation not preserved; teeth small, A-1, B-1, or C-1, lobations typically not formed, teeth 2 to 4 per secondary vein; petiole more than 0.5 cm long.

Nomenclature: James P. Ferrigno has been of invaluable assistance in locating and sending us type material from the U.S.N.M. collections.

Discussion: Small, irregularly shaped teeth and tendency towards camptodromous secondary veins are the most notable characters of *Acer ferrignoi.* Highly attenuate lateral lobes and concave-sided lobal sinuses are found in *A. chaneyi,* and we suggest that *A. ferrignoi* is a latest Miocene derivative of *A. chaneyi.*

Distribution: Latest Miocene of the Cascade Range of northern Oregon.

Typology: Holotype, USNM 396125.

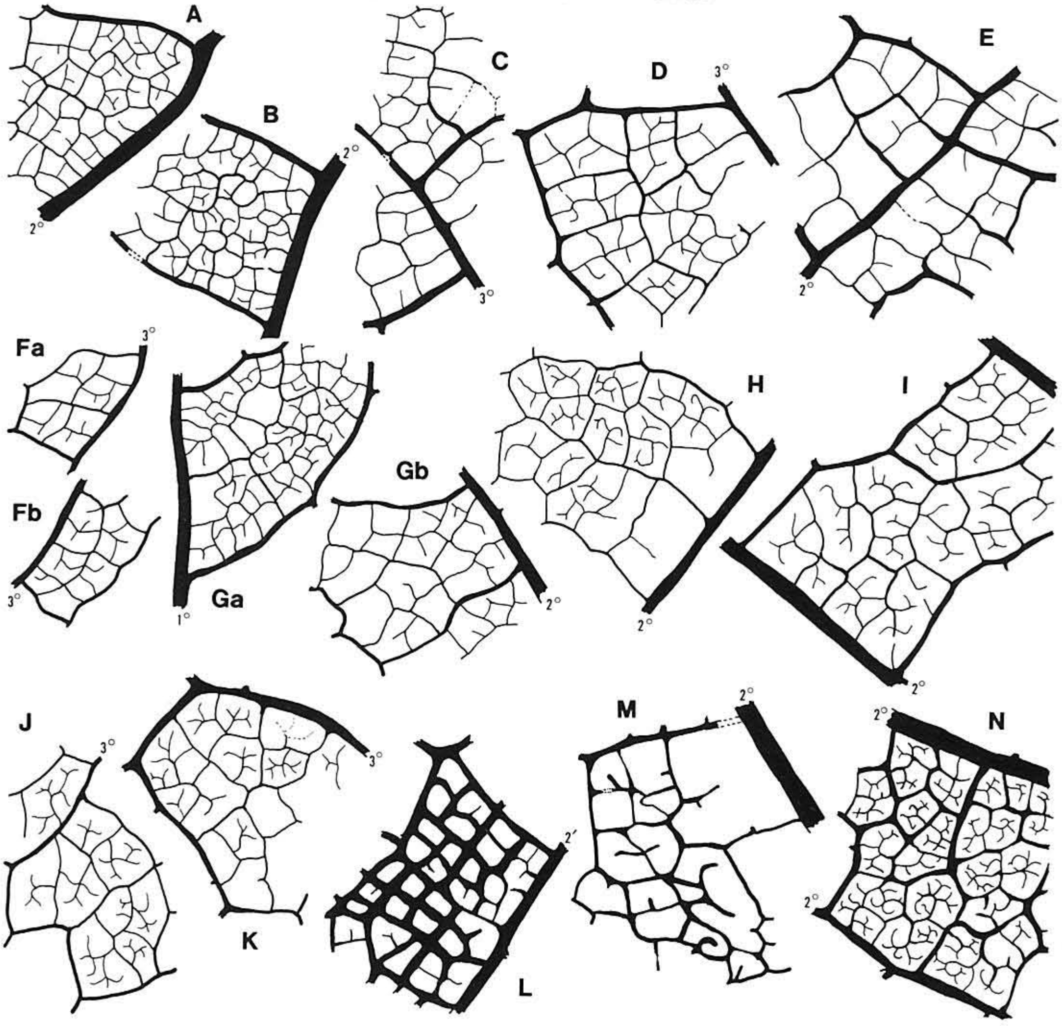
Occurrence: See appendix table.

Section *Cissifolia* Koidzumi

Acer lincolnense Wolfe et Tanai, sp. nov.

(pl. 15, figs. 1, 2, 3, 5; text-fig. 14Ga, b)

Description: Leaf trifoliate; leaflets sessile; leaflets pinnately veined; terminal leaflet incomplete, but base symmetrical with acute base; lateral leaflets elliptic, 1.5 to 4.8 cm long, 0.8 to 2.0 cm wide; base asymmetrically acute, apex acute; 5 to 7 pairs of secondary veins, craspedodromous pairs alternating with pairs that bifurcate acutely to brace dental sinuses; tertiary veins A-R or R-R, compound, spaced 0.7 to 1.3 cm; fourth order



Text-fig. 14 Areolar venation charactrs of fossil *Acer* — (2) Section *Eriocarpa, Rubra, Cissifolia, Negundo, Orba* and *Columbia*. (all figures × 12.5)

A. *Acer chaneyi* Knowlton. Latah/Vera. Hypotype USNM 396095 (pl. 42, fig. 2).
B. *Acer chaneyi* Knowlton. Latah/Spokane, Holotype UCMP 22862 (pl. 42, fig. 4)
C. *Acer ezoanum* Oishi et Huzioka. Capps Glacier. Hypotype USNM 396108 (pl. 44, fig. 2).
D. *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Whitebird. Hypotype USNM 396115 (pl 46, fig. 7).
E. *Acer kluckingi* Wolfe et Tanai. Bridge Creek/Pentecost. Paratype UCMP 9110 (pl. 27, fig. 8).
Fa, b. *Acer tigilense* Chelebaeva. Thorn Creek. Hypotype UCMP 3207 (Chaney & Axelrod, 1959; pl. 40, fig. 9).
Ga, b. *Acer lincolnense* Wolfe et Tanai. Beaver Creek. (a) Paratype UCMP 9312 (pl. 15, fig. 1), (b) Holotype UCMP 9311 (pl. 15, fig. 5).
H. *Acer molallense* Wolfe et Tanai. Liberal. Holotype USNM 396062 (pl. 36, fig. 2).
I. *Acer heterodentatum* (Chaney) MacGinitie. Eagle Creek. Lectotype UCWM 22348 (pl. 35, fig. 8).
J. *Acer heterodentatum* (Chaney) MagGinitie. Collawash. Hypotype UCMP 9173 (pl. 35, fig. 8).
K. *Acer orbum* LaMotte. Chalk Bluff. Lectotype UCMP 2283 (pl. 2, fig. 6).
L. *Acer oligomedianum* Wolfe et Tanai. Bridge Creek/Slanting. Bridge Creek/Dugout Gulch. Paratype UCMP 9031 (not illustrated in plates).
M. *Acer powellense* Wolfe et Tanai. Sturgeon Creek. Holotype UCMP 9314 (pl. 16, fig. 6b).
N. *Acer medianum* Knowlton. Succor Creek/Devils Gate. Hypotype MSUB 9/22/771-88 (pl. 39, fig. 9).

veins forming irregularly polygonal areoles 0.7 to 1.3 mm in diameter, veinlets typically lacking or single and thin; teeth large, mostly simple, but largest with 2 subsidiary teeth, B-1; rachis >1.4 cm long.

Fruit samaroid; nutlet at basal end; nutlet 1.0 cm long, 0.4 cm wide; outline lanceolate, apex narrowly rounded; attachment scar 0.4 cm long; nutlet with a markedly convex proximal margin; nutlet venation obscure, but with a thick vein extending parallel to, and near, distal margin; nutlet somewhat flattened; attachment angle 30°, nutlet angle 40°. Wing apical to nutlet; 1.2 cm long, 0.7 cm wide; distal margin broadly convex, proximal margin broadly convex, apex rounded; proximal side with 7 weakly coalesced veins, wing veins diverging at angles of 5° to 10°, slightly curving and undulatory, bifurcating, few anastomoses.

Nomenclature: Type locality is in Lincoln County, Montana.

Discussion: Bohlenioid secondary venation combined with a trifoliate condition are confined to *Negundo* and *Cissifolia.* Extant *Cissifolia* has larger areoles and typically fewer secondary veins and a more acute base than extant *Negundo; Cissifolia* also typically has B-1 rather D-1 teeth. In these charcters, the fossil leaves resemble *Cissifolia.* However, the leaflets are sessile, whereas in both *Negundo* and *Cissifolia* terminal leaflets typically have a short petiolule.

Some associated fruits are also of the *Negundo-Cissifolia* type. The markedly convex proximal margin of the nutlet of the fossils indicates a closer relationship to *Cissifolia* than to *Negundo.* Undulatory wing veins are not typical of either *Negundo* or *Cissifolia* but typically occur in *Indivisa.*

Whether *Acer lincolnense* is validly assigned to *Cissifolia* is questionable. We have inferred the presence in the North American Eocene of an *Acer* that gave rise to both *Cissifolia* and *Indivisa,* and conceivablly *A. lincolnense* represents such an ancestor. In both foliage and fruit, this ancestor would closely resemble *Cissifolia* and would be distinguishable only in inflorescence from the two derived extant sections.

Distribution: Latest Eocene of west-central Montana.

Typology: Holotype, UCMP 9311A, B.

Occurrence: See appendix table.

Section *Negundo* (Boehm.) Maxim.

Discussion: Negundo has been elevated to generic rank by several systematists, although they consider the genus to be very closely related to *Acer.* Although characters such as the lack of a disk, the total dioecism, and three- to five-foliate leaves indeed set sect. *Negundo* apart from most other species of *Acer,* as pointed out by Ogata (1967), complete dioecism is normal in *Cissifolia,* as is the the three-foliate leaf. Absence of a disk seems insufficient grounds to separate *Negundo* at the generic level.

Most systematists recognize a single extant species of *Negundo, Acer negundo* L. Within this species, however, a number of subspecies and varieties have been recognized, some of which have been given specific rank by various systematists. Among the more distinctive subspecific categories in *A. negundo* are subspecies *californicum* (Tor. et Gray) Wesm. (*Negundo californicum* Torr. et Gray) and subspecies *mexicanum* (DC.)

Wesm. (*A. mexicanum* DC.), both of which are geographically very isolated from the main distributional area of *A. negundo* in eastern North America. Also distinct is subsp. *interior* (Britt.) Wesm. (=*A. interior* Britt.), which is largely isolated in the Rocky Mountains, but intergrades with subsp. *negundo* on the High Plains.

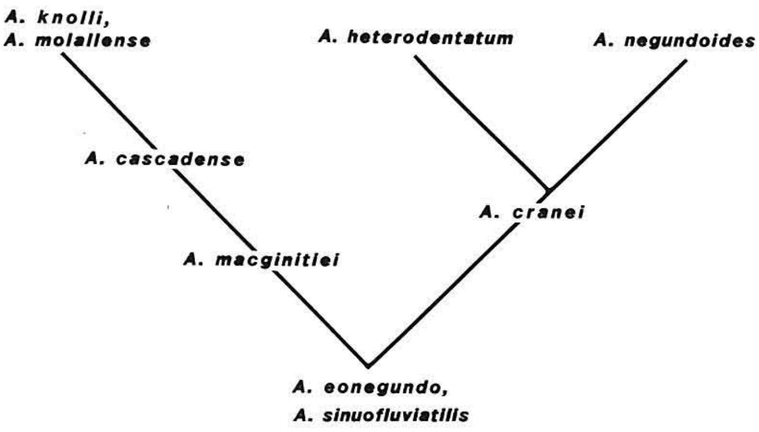
California and Central American subspecies of *Negundo* can be separated from Rocky Mountain and eastern American subspecies on the basis of nutlet morphology. Subspecies *californicum* and *mexicanum* have a few subparallel veins that are of almost equal strength; cross veins are few or absent. In subspecies *interior* and *negundo,* the nutlet has one vein much more prominent than the other subparallel veins, and the veins are interconnected by conspicuous cross veins. In subspecies *negundo,* the nutlet is typically much more elongated than in subspecies *interior.*

The earliest known foliar record of *Negundo, Acer eonegundo,* is represented by a partial terminal leaflet and a nearly complete lateral leaflet that appear to be part of the same leaf. Comparison of number and degree of curvature of secondary veins and of size and shape of teeth of the lateral leaflet indicate a marked similarity to a lateral lobe of *A. orbum,* inferered to be closely allied to the ancestor of *Negundo.*

Relationships of *Acer eonegundo* to later species of *Negundo* is unclear. The apical sides of the teeth in *A. eonegundo* are apically pointing, as in *A. heterodentatum* and *A. molallense.* The few, widely spaced secondary veins of *A. eonegundo* is a character shared with *A. negundoides.* Absence of a major lobation in the basal part of the lamina is also found in *A. molallense. Acer eonegundo* could be ancestral to all these later taxa.

If the pinnately compound leaf of *Negundo* is derived from a simple leaf such as that of *A. orbum,* then the few secondary veins of *A. eonegundo* represent a primitive character in *Negundo.* This character has been maintained in the group comprised of *A. negundoides* and *A. negundo sensu stricto.*

The Florissant fruits of *Negundo, Acer macginitiei,* have several equal-sized veins crossing the nutlet. These veins are connected by fine cross-veins. The large number of veins and cross-veins represent a specialization, and this may indicate that *A. macginitiei*



Text-fig. 15 Suggested cladistic relationships of species of section *Negundo.*

is an off-shoot of an early *Negundo* (text-fig. 16). The major vein parallels the distal margin of the nutlet until nearing the apex of the nutlet, where the vein curves distally to apex of the nutlet and then parallels the proximal margin of the wing. In the Miocene *A. negundoides,* the major vein extends straighht from the attachment scar to the apex of the nutlet. The nutlet of *A. negundoides* is also both larger and proportionately more elongated than the nutlet of *A. cranei* (table 6); the length of the samara also averages greater in the Miocene species. The proximal side of the nutlet in *A. cranei* is slightly convex, except near the base, where the margin is shallowly concave and forms a basal beak.

The samaras of *A. heterodentatum* and *A. knolli* are dissimilar from those of the *A. cranei-A. negundoides* type. The samara of *A. heterodentatum* is particularly divergent: the distal side of the samara is typically strongly convex, the attachment scar angle is 70° or greater, and the nutlet is small. The position of the major vein and its ridge indicate that *A. heterodentatum* may have a common ancestry with *A. negundoides;* some samaras of *A. cranei* have a strongly convex distal margin. The samaras of *A. knolli* have 3 to 4 major veins of approximately equal thickness on the nutlet; the general shape of both nutlet and samara is similar to *A. negundoides,* indicating a probably common ancestry.

On foliage, three distinct types of *negundo* are present in the Miocene of western North America. *Acer heterodentatum* has leaflets that have at least 10 secondary veins, and the secondaries are typically straight. Apical margins of the teeth and the basal lobations are at about a 45° angle to the midrib. Areoles are 0.5 to 0.7 mm in diameter, are formed by thin veins, and veinlets are thin and branch two or more times. *Acer negundoides* has leaflets that have about seven secondary veins, and the secondaries typically curve. Apical margins of the teeth and the basal lobations are at about a 90° angle to the midrib; areolar venation of this species is currently unknown. *Acer molallense* is known from a single leaflet; this has 11 pairs of secondary veins, and the secondaries are straight to slightly curving. Apical margins of the teeth and basal lobations are at about a 90° angle to the midrib. Areoles are about 0.8 to 0.9 mm in diameter and the veinlets appear to branch at least 3 times. This leaflet also has about twice as many subsidiary teeth as in *A. negundoides.*

Table 6. Statistical comparisons of fruits of section *Negundo.*

Ln = length of nutlet, Wn-width of nutlet, Lw = length of wing. All measurements are in centimetres.

Species	Average					Variation		
	No.	Ln	Wn	Ln	Lw	Ln	Wn	Lw
Acer heterodentatum	8	0.7	0.3	2.3	2.1	0.5-0.8	0.2-0.3	1.5-2.7
A. cranei	32	0.9	0.4	2.3	2.2	0.6-1.2	0.2-0.6	1.6-2.7
A. negundoides	50	1.2	0.4	3.0	2.8	0.8-1.7	0.3-0.5	2.0-3.5
A. knolli	11	1.3	0.5	2.6	3.6	1.0-1.7	0.3-0.7	3.0-4.3
A. cascadense	3	1.0	0.4	2.5	3.0	1.0-1.1	0.4	2.8-3.2
A. macginitiei	9	1.2	0.4	3.0	2.5	0.9-1.4	0.4-0.5	2.2-3.0
A. sinuofluviatilis	9	1.0	0.4	2.5	1.6	0.7-1.2	0.3-0.5	1.2-2.8

Fruits of three of the Miocene species of *Negundo* are known. The fruit of *A. heterodentatum* is small and typically has a strongly convex proximal margin. The attachment angle is about 0° to 20°, and the major ridge and vein start in the middle of the attachment scar and curve apically toward the proximal side of the nutlet. The fruit of *A. negundoides* is of moderate size and typically has a straight proximal margin. The attachment angle is about 30° to 40°, and the major ridge and vein start in the middle of the attachment scar and extend straight to the apex of the nutlet. The fruit of *A. knolli* is large and has a straight proximal margin. The attachment angle is about 35°, and there are four of five ridges and veins that are subparallel and of equal strength.

Relationships of the four Miocene species of *Negundo* are suggested in text-figure 16. In foliar morphology, *Acer heterodentatum* and *A. negundoides* appear to be closely related and probably share a common ancestry; presence of a single major ridge and vein in the nutlet also points to a close relationship. *Acer knolli* is highly distinct from other Miocene *Negundo* in nutlet morphology. Indeed, nutlet morphology of *A. knolli* more closely resembles that of the Eocene *A. macginitiei* than does any other post-Eocene species; nutlet morphology of *A. macginitiei* has, in fact, more resemblance to that of the *A. heterodentatum-A. negundoides* group, indicating that the common ancestry of *A. knolli* and this group preceded *A. macginitiei.*

Nutlet morphology of *Acer knolli* is represented in extant *Negundo* by subspecies *mexicanum*. This subspecies also has the numerous equal-sized teeth of *A. molallense.* These similarities indicate that the type of *Negundo* represented by *A. knolli, A. molallense,* and subspecies *mexicanum* is an ancient type that diverged from the *A. negundoides* type during the late Eocene.

Fruits ascribed to *Acer heterodentatum* by MacGinitie (1962) from the middle Miocene of Nebraska have the elongated nutlet that has the prominent ridge of subspecies *negundo.* This type of *negundo,* as does the *negundoides* type (that is, the subspecies *interior* and subspecies *californicum* type), appears to be derived from a common ancestor such as *A. macginitiei.* We thus have the situation where subspecies *mexicanum* appears to have diverged during the early part of the late Eocene, subspecies *negundo* appears to have diverged at about the Eocene-Oligocene transition, and subspecies *interior* and *californicum* to have diverged following the late Miocene. These data should make systematists dealing with extant *Negundo* reconsider the rank of the various subspecies. We suggest that the various subspecies of *A. negundo* probably are valid species.

Acer eonegundo Wolfe et Tanai, sp. nov.

(pl. 15, figs. 15, 17)

Description: Leaf compound, with a terminal and at least 1 pair of lateral leaflets; leaflets pinnate; lateral leaflet asymmetrical, elliptic; base narrowly rounded, apex acute; 4.8 cm long, 2.4 cm wide; 7 pairs of secondary veins, broadly curving, craspedodromous; external secondary branches extending to sinuses; intersecondary veins about 1 per secondary; tertiary veins R-A and compound; fourth order venation irregularly polygonal; fifth order veins thick, forming irregularly polygonal areoles 0.7 to

0.9 mm in diameter, veinlets branching 1 to 3 times; teeth D-1, typically with 1 or 2 subsidiary teeth on basal flank and none on apical flank; slightly petiolulate.
Nomenclature: An Eocene species of *Negundo.*
Discussion: See discussion under *Negundo.*
Distribution: Late middle Eocene of northeastern Nevada.
Typology: Holotype, UCMP 9043.
Occurrence: See appendix table.

Acer sinuofluviatilis Wolfe et Tanai, sp. nov.

(pl. 15, figs. 4, 7, 10-12)

Description: Fruits samaroid, nutlet at basal end. Nutlet 0.6 to 1.2 cm long, 0.3 to 0.5 cm wide; shape narrowly ovate, apex triangular to narrowly rounded; apical part of proximal margin straight and tangential to proximal margin of samara, basal part convex; attachment scar 0.3 to 0.7 cm long; nutlet moderately inflated; 3 to 5 veins originating along attachment scar, extending apically, reticulate, extending directly onto wing; 1 vein placed distally can extend apically and then curve or can be straight (in some specimens this vein is thicker than other nutlet veins and forming a ridge or narrow flange); attachment angle 15° to 50°, nutlet angle 25° to 35°. Wing extending about half the length of distal margin of nutlet forming a shallowly U-shaped sulcus with nutlets; 1.3 to 2.1 cm long, 0.5 to 0.8 cm wide; distal margin broadly to deeply convex, proximal margin straight, apex narrowly to broadly rounded; 5 to 7 veins coalesced along proximal side, wing veins diverging at angles of 20° to 30°, curving smoothly bifurcating and closely spaced, several anastomoses.
Nomenclature: Type locality is in the Crooked River Valley, Oregon
Discussion: Fruits of *Acer sinuofluviatilis* have similarities to fruits of both *A. macginitiei* and *A. cranei.* In *A. macginitiei,* major nutlet veins are invariably of equal size and the attachment scar has a proximal beak. Further, *A. macginitiei* has no vestige of a nutlet flange, which is present on some specimens of *A. sinuofluviatilis.* In *A. cranei,* a major nutlet vein is invariably present and has a characteristic curve in the apical part of the nutlet; as well, a proximal beak is typically present on the attachment scar.
Distribution: Probable early late Eocene of central Oregon.
Typology: Holotype, UCMP 9044.
Occurrence: See appendix table.

Acer macginitiei Wolfe et Tanai, sp. nov.

(pl. 15, figs. 6, 8, 9, 13, 14, 16)

Acer heterodentatum auct. non (Chaney) MacGinitie. MacGinitie. 1953 (part, nontypic). 140. pl. 57, f. 3.
Acer minor auct. non Knowlton. Becker. 1969 (part). 113. pl. 35, F. 9-12.

Description: Fruits samaroid, nutlet at basal end; nutlet 0.9 to 1.4 cm long, 0.4 to 0.5 cm wide; outline narrowly elliptic, apex narrowly rounded; attachment scar 0.3 to 0.5 cm long; nutlet moderately inflated; 4 to 5 veins originating along attachment scar, of equal strength, extending almost parallel to apex of nutlet, connected by minor cross veins; attachment angle 15° to 40°, nutlet angle 20° to 40°. Wing extending about 1/2 the distance along distal margin of nutlet; 1.3 to 1.7 cm long, 0.7 to 0.8 cm wide; distal margin broadly convex, proximal margin concave to straight, apex narrowly to broadly rounded; 4 or 5 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, smoothly and sharply curving, bifurcating, numerous anastomoses.

Nomenclature: In recognition of Harry D. MacGinitie's major contributions (including his work on the Florissant flora) to the Tertiary paleobotany of western North America.

Discussion: See discussion under *Negundo.*

Distribution: Latest Eocene of western Montana south to central Colorado.

Typology: Holotype, UCMP 3828.

Occurrences: See appendix table.

Acer cranei Wolfe et Tanai, sp. nov.

(pl. 25, figs. 2, 3, 7, 8, 10-12)

Acer negundoides auct. non MacGinitie. Brown. 1935 (part). 580. pl. 69, f. 9, 10.

Acer osmonti auct. non Knowlton. Chaney. 1927 (part). 126. pl. 18, f. 7.

Description: Fruits samaroid, nutlet at basal end; nutlet 0.6 to 1.2 cm long, 0.2 to 0.3 cm wide; outline elliptic to narrowly elliptic, apex narrowly rounded to acute; attachment scar 0.4 to 0.5 cm long: nutlet moderately inflated and expanded beyond proximal margin of wing; a major vein extending from middle of attachment scar parallel to distal margin, curving sharply proximally in apical part of nutlet to apex; attachment angle 25° to 60°, nutlet angle 10° to 30°. Wing extending 1/3 to 1/2 along distal margin of nutlet, 2.2 to 3.8 cm long, 0.6 to 0.9 cm wide; distal margin broadly convex, proximal margin slightly concave to broadly convex, apex narrowly to broadly rounded; 4 or 5 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, smoothly curving, bifurcating, numerous anastomoses.

Nomenclature: In recognition of Peter R. Crane's contibutions to Tertiary paleobotany and for his assistance in sending us material of fossil *Acer* from the collections of the Field Museum of Natural History.

Discussion: Although found at eight Bridge Creek localities, as yet no foliage of *Negundo* has been collected from these extensively collected localities.

Distribution: Early Oligocene of central Oregon.

Typology: Holotype, USNM 396053.

Occurrences: See appendix table.

Acer cascadense Wolfe et Tanai, sp. nov.

(pl. 25, figs. 1, 4-6)

Description: Fruits samaroid, nutlet at basal end; nutlets 1.0 to 1.1 cm long, 0.4 cm wide; outline narrowly elliptic, proximal margin tangential to proximal margin of samara, apex acute; attchment scar 0.3 to 0.4 cm long; nutlet moderately inflated; 5 or 6 veins of equal strength originating along attachment scar, extending approximately parallel towards apical part of nutlet; attachment angle 35° to 50°, nutlet angle 15° to 20°. Wing restricted apical to nutlet; 1.7 to 2.1 cm long, 0.8 to 0.9 cm wide; distal margin broadly convex, proximal margin straight, apex narrowly rounded; 4 or 5 coalesced veins along proximal side, wing veins diverging at angles of 10° to 30°, smoothly convex, bifurcating, numerous anastomoses.

Nomenclature: Type locality is in the northern part of the Cascade Range of Oregon.

Discussion: Fruits of *Acer cascadense* are characterized by their elongated nutlet that has several parallel veins of about equal strength. *Acer macginitiei* has a broader nutlet than *A. cascadense,* although the nutlet venation is similar between the two species. *Acer cranei* has a vein that dominates the nutlet surface and that curves in the apical part of the nutlet.

Distribution: Oligocene (possibly late) of the northern part of the Cascade Range in Oregon.

Typology: Holotype, UCMP 9055.

Occurrence: See appendix table.

Acer knolli Wolfe et Tanai, sp. nov.

(pl. 37, figs. 1-5, 17)

Acer negundoides auct. non MacGinitie. Brown. 1935 (part). 580. pl. 69, f. 11.
Brown. 1937b. 180. pl. 58, f. 1.
Acer oregonianum auct. non Knowlton. Berry. 1929 (part). 255. pl. 57, f. 2.

Description: Fruits samaroid, nutlet at basal end; nutlet 1.0 to 1.7 cm long, 0.3 to 0.7 cm wide; outline narrowly ovate, proximal margin tangential to proximal margin of samara, apex acute; attachment scar 0.4 to 0.8 cm long; 4 to 6 veins originating along attachment scar, extending almost parallel towards apex of nutlet; nutlet moderately inflated; attachment angle 40° to 45°, nutlet angle 10° to 15°. Wing extending about 1/3 along distal margin of nutlet; 1.8 to 2.5 cm long, 0.6 to 1.2 cm wide; distal margin broadly convex, proximal margin straight, apex broadly rounded; 4 or 5 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, sharply curving and becoming almost straight, bifurcating, numerous anastomoses.

Nomenclature: We are grateful to Andrew Knoll for sending us material of fossil *Acer* from the Latah Formation.

Discussion: Fourteen *Negundo* fruits are known from the Latah Formation at Spokane, Washington. All these fruits are large (for the section), have a broad, somewhat flattened nutlet, and veins crossing the nutlet are several (4 to 6) with no single vein dominating the others. These characters of *Acer knolli* ally the taxon most closely to the extant *A. negundo* subspecies *mexicanum* DC. The largest fruit of this extant subspecies is 3.5 cm, whereas in *A. knolli* fruits are typically about 3.5 cm in length, and one fruit is 4.7 cm.

Acer knolli has nutlet venation characteristic of *A. cascadense.* Although these two species are probably related, they can be differentiated on the basis of larger size and more pronounced nutlet veins of *A. knolli.*

Distribution: Early middle Miocene of northeastern Washington.

Typology: Holotype, USNM 396061.

Occurrence: See appendix table.

Acer molallense Wolfe et Tanai, sp. nov.

(pl. 36, fig. 2; text-fig. 14H)

Description: Leaflet pinnately veined; shape elliptic; base asymmetrically rounded, apex attenuate; 11.2 cm long, 4.0 cm wide; 11 pairs of secondary veins originating at angles of 40° to 55°, straight to broadly convex, craspedodromous; 1 to 3 craspedodromous external secondary veins per secondary vein, the most basal of a set bifurcating, with basal branch extending to sinus; tertiary veins compound, A-A, spaced about 0.2 to 0.3 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.6 to 0.8 mm in diameter, veinlets apparently branching 1 to 3 times; teeth D-1, 1 or 2 subsidiary teeth on basal flank and none on apical flank; apical flanks of teeth almost perpendicular to midrib; petiolule 0.5 cm long.

Nomenclature: Type locality is near the town of Molalla, Oregon.

Discussion: Many D-1 teeth that are of approximately uniform size and numerous secondary veins indicate that *Acer molallense* is related to the extant *A. negundo* ssp. *mexicanum. Acer knolli* has a similar relationship, but fruits of *A. knolli* have not been found in association with *A. molallense* foliage.

Distribution: Middle (?) Miocene of northwestern Oregon.

Typology: Holotype, USNM 396062.

Occurrence: See appendix table.

Acer heterodentatum (Chaney) MacGinitie

(pl. 35, figs. 3, 6-8; pl. 36, figs. 1, 5; pl. 37, figs. 8—10, 19; text-fig. 14I, J)

Acer heterodentatum (Chaney)MacGinitie. 1953 (part, new combination only). 140.
Wolfe & Tanai. 1980. 41. pl. 16, f. 6; pl. 17, f. 4; pl. 18, f. 2-4; pl. 19, f. 3.
Crataegus heterodentata Chaney. 1920. 175. pl. 16, f. 1, 2.

Description: Leaflets pinnately veined; shape ovate to narrowly ovate; base acute, apex attenuate; 5.4 to 8.5 (incomplete) cm long, 3.0 to 5.5 cm wide; 8 or 9 pairs of secondary veins originating at angles of 40° to 50°, straight to broadly convex, craspedodromous; pairs of secondary veins that enter primary teeth alternate with pairs that unequally bifurcate, the strong apical bifurcation entering a subsidiary tooth and the weak basal bifurcation extending along basal side of sinus; tertiary veins compound, R-A to A-A spaced about 0.2 to 0.3 cm; fourth order venation irregularly polygonal; fifth order veins forming irregular polygons about 0.3 to 1.0 mm in diameter, veinlets typically branching 1 to 3 times; 5 or 6 major A-1 teeth per side of lamina, pointing apically; the most basal on 1 side strongly developed as a lobation; typically with 4 to 6 subsidiary teeth on basal flank and 1 or 2 on apical flank; other major teeth typically with 1 or 2 subsidiary teeth on basal flank and no or 1 tooth on apical flank; petiolule 0.3 to 0.5 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.5 to 0.8 cm long, 0.2 to 0.3 cm wide; outline elliptic, apex acute, proximal side of nutlet tangential to proximal margin of samara; attachment scar 0.3 to 0.4 cm long; nutlet slightly inflated; nutlet with 3 minor and 1 major vein, which originates at midpoint of attachment scar and curves apically; attachment angle 60° to 90°, nutlet angle 10° to 20°. Wing almost entirely apical to nutlet; 0.9 to 1.6 cm long, 0.4 to 0.9 cm wide; distal margin broadly convex, proximal margin straight to broadly convex, apex narrowly to broadly rounded; proximal side with 4 to 5 coalesced veins, wing veins diverging at angles of 10° to 30°, irregularly and sharply curving, bifurcating, anastomoses few.

Nomenclature: As first pointed out by MacGinitie (1953), Chaney's *Crataegus heterodentata* from Eagle Creek represents a member of *Negundo.* Other material from the Eagle Creek flora assigned to *Acer heterodentatum* by MacGinitie, however, represents other taxa.

Discussion: Leaflets of *Acer heterodentatum* differ from those of *A. negundoides* and *A. negundo* in several characters:

(1) secondary veins in *A. heterodentatum* are closely spaced, averaging about 0.6 cm apart (the average in *A. negundo* is about 1.0 cm),

(2) secondary veins in *A. heterodentatum* are straight or slightly curving, whereas in *A. negundo* they are markedly curving,

(3) the vein that braces the most basal major sinus does not result from an equal bifurcation of a secondary vein in *A. heterodentatum,*

(4) sinuses in *A. heterodentatum* are acute as opposed to orthogonal in *A. negundo,* and thus teeth are apically directed in *A. heterodentatum;* in *A. negundo* the apical side of the tooth is orthogonal to the midrib.

Distinctive leaflets of *Acer heterodentatum* occur at the Collawash locality with highly distinctive fruits of a new type of *Negundo.* Other than their typically high attachment angle, these fruits have a small nutlet that is approximately bisected by a major, curving vein.

Distribution: Early Miocene of the Cascade Range in northern Oregon and late early to early middle Miocene of south-central Alaska.

Typology: Lectotype here designated, UCWM (FMNH) 22348.

Occurrences: See appendix table.

Acer negundoides MacGinitie

(pl. 36, figs. 3, 4, 6: pl. 37, figs. 6, 7, 11-15, 18)

Acer negundoides MacGinitie. 1933. 62. pl. 11, f. 2, 3.
Dorf. 1936. 121. pl. 3, f. 2.
LaMotte. 1936 (part). 136. pl. 12, f. 3.
Chaney. 1938. 216. pl. 6, f. 2; pl. 7, f. 1a, 1b.
Smith. 1938b. 562. pl. 29, f. 5.
Smith. 1939. 228. pl. 1, f. 13.
Condit. 1944a. 50.
Axelrod. 1985. 172 (part). pl. 14, f. 8, 9.
Acer minor auct. non Knowlton. Axelrod. 1956 (part). 308. pl. 32, f. 5-7.
Chaney and Axelrod. 1959. 194. pl. 41, f. 3-5.
Smiley. 1963. 227. pl. 13, f. 4, 6; pl. 14, f. 1, 6.
Axelrod. 1964. 128. pl. 15, f. 13-17.
Graham. 1965. 67. pl. 5, f. 2.
Acer, fruits of. Lesquereux. 1888 (part). 15. pl. 7, f. 2.
Acer sp., cf. *A. negundoides* MacGinitie. Brooks. 1935. 298, pl. 21, f. 2.

Description: Leaflets pinnately veined; shape ovate; base acute to rounded, apex acute; 5.5 to 8.5 cm long, 3.3 to 7.5 cm wide; 5 to 8 pairs of secondary veins originating at angles of 30° to 40°, straight to typically broadly convex, most craspedodromous; some secondary veins bifurcating, the apical bifurcation entering a subsidiary tooth or camptodromous, the basal bifurcation extending along the basal side of a sinus; some sinuses braced by an external secondary vein; tertiary veins compound, R-A to A-A, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins thin, forming irregular polygons 0.6 to 1.0 cm in diameter, veinlets branching 1 to 3 times; major teeth broadly A-1, 3 to 5 per side of lamina, the most basal on 1 side strongly developed as a lobation, typically with no to 2 subsidiary teeth on basal flank, no or 1 on apical flank; other major teeth typically with no or 1 subsidiary tooth on basal flank and none on apical flank; apical flank of teeth approximately perpendicular to midrib; petiolule 0.2 to 0.8 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.8 to 1.7 cm long, 0.3 to 0.5 cm wide; outline lanceolate, apex acute to narrowly rounded proximal side of nutlet typically tangential to proximal margin of samara; nutlet slightly inflated; nutlet with 4 minor veins and 1 major vein, which originates in distal 1/3 of attachment scar and extends straight to apex; attachment angle 35° to 45°, nutlet angle about 10°. Wing extending about 1/2 the length of distal margin of nutlet; 1.2 to 2.2 cm long, 0.8 to 1.0 cm wide; distal margin broadly convex, proximal margin typically straight, apex broadly to narrowly rounded; proximal side with 5 or 6 coalesced veins, wing veins diverging at angles of 10° to 30°, irregularly and sharply curving, bifurcating, some anastomoses.

Nomenclature: Chaney and Axelrod (1959) selected as lectotype for *Acer minor* the specimen illustrated by Knowlton (1902, pl. 14, fig. 3); this specimen is poorly preserved and lacks the basal part of the nutlet, and consequently the identity of *A. monor* will always be speculative. The next available name based on specifically diagnostic material is MacGinitie's (1933) aptly named *A. negundoides.*

Discussion: Leaflets of *Acer negundoides* are typically rare, in contrast to abundant occurrences of fruits of this species. Only a few localities are known at which both foliage and fruits of this species are known. Both foliage and fruits are closely similar to (if not specifically inseparable from) respective organs of *A. negundo* ssp. *californicum* and ssp. *interius.*

Fruits of *Acer negundoides* are abundantly represented at three localities (table 7). Statistical comparisons of these presumed three populations show no significant variation, either geographic or stratigraphic.

Distribution: Early to latest Miocene, Pacific Coast States and Great Basin.

Typology: Holotype, UCMP 617.

Occurrences: See appendix table.

Table 7. Statistical comparisons of fruits of different populations of *Acer negundoides.*

Ln = length of nutlet, Wn = width of nutlet, Lw = length of wing. All measurements are in centimetres.

FLORA	Average					Variation		
	No.	Ln	Wn	Ln/Wn	Lw	Ln	Wn	Lw
Hog Creek	16	1.2	0.4	3.0	2.6	0.9-1.7	0.3-0.5	2.1-3.2
Trout Creek	21	1.1	0.4	2.8	2.7	0.8-1.4	0.3-0.5	2.0-3.3
Middlegate	13	1.2	0.4	3.0	2.9	1.0-1.5	0.4-0.5	2.2-3.5

Orba Group

Section *Orba* Wolfe et Tanai, sect. nov.

Diagnosis: Leaf simple, actinodromous, 3-lobed; some secondary veins craspedodromous and some secondary veins bifurcating to brace dental sinuses; lobal sinal braces acutely bifurcating and originating from midrib; areolar venation formed by polygonal areoles, veinlets more than twice branching; primary teeth large, D-1; subsidiary teeth present.

Fruits samaroid, nutlet at basal end; nutlet small, inflated; attachment angle medium; single distinct flange in distal part of nutlet; nutlet outline triangular; wing extending along distal side of nutlet to attachment scar; wing venation formed by veins that bifurcate at moderately high (but acute) angles, with numerous anastomoses.

Discussion: The single leaf of *Acer orbum* has Type I areolar venation and large, D-1 teeth, both low-grade characters. Bohlenioid secondary veins are present, particularly on the lateral lobes. The only significant specialization of the leaf is reduction in size of subsidiary teeth relative to primary teeth.

The presumed fruits of *Acer orbum* have a distinct, distally placed flange and are strongly inflated. These fruits are thus more specialized than any known in either the *Spicata* or *Macrantha* groups. Wind venation is not well preserved, and we cannot determine whether veinlets are present; however, the wing veins diverge at higher angles than typical for the *Macrantha* Group.

Type species: Acer orbum LaMotte.

Acer orbum LaMotte

(pl. 2, fig. 6; pl. 3, figs. 12, 13, 16, 17; text-fig. 14K)

Acer orbum LaMotte. 1952. 55.

Acer aequidentatum auct. non Lesquereux. MacGinitie. 1941. 143. pl. 37, f. 1-4.

Description: Leaf simple, apparently actinodromous (base lacking), apparently 3-lobed; medial lobe about twice as large as lateral lobes; shape ovate, (estimated) 8 to 9 cm long, 7.0 cm wide; medial lobe expanding at its midpoint and then tapering to an acute apex; lobations well developed on medial lobe; lateral primary veins parallel to medial secondary veins broadly convex; at least 8 secondary veins originating at angles of 40° to 50° from basal side of lateral primary veins, broadly convex, craspedodromous; craspedrodromous medial secondary veins 4, alternating with secondary veins that bifurcate near sinuses, broadly convex, originating at angles of 40° to 45°; tertiary veins connecting most basal medial secondary veins to lateral primary veins compound, R-A, spaced about 0.4 cm apart; other tertiary veins compound, R-A to R-R; fourth order veins thinning, forming irregularly polygonal areoles about 0.4 to 0.6 mm in diameter; veinlets orthogonally branching 1 to 3 times; lobal sinal bracing formed by a medial secondary vein that acutely bifurcates near sinus; external secondary veins originating acutely; teeth D-1, typically 1 to 3 D-1 subsidiary teeth on the basal flank, some with 1 or 2 small teeth on apical flank.

Fruit samaroid; nutlet at basal end; nutlets 0.4 to 0.7 cm long, 0.3 to 0.5 cm wide, broadly triangular in outline, narrowly rounded apex, expanded slightly proximally attachment scar 0.3 to 0.6 cm long, nutlet moderately inflated, smooth except for a narrow flange that is near and parallel to distal margin; attachment angle about 50°, nutlet angle 20° to 30°. Wing extending along distal margin of nutlet; 2.1 to 3.0 cm long, 1.2 to 1.3 cm wide, distal margin straight to broadly convex, proximal margin straight for at least 2/3 the length, apex broadly rounded; proximal margin with at least 5 coalesced veins, wing veins diverging from proximal margin at angles of 20° to 50°, dichotomizing at angles of 30° to 40°, irregularly anastomosing 2 to 4 times.

Nomenclature: LaMotte (1952) pointed out that Lesquereux' types of *"Acer" aequidentatum* represent Platanaceae and, therefore, proposed the epithet *orbum*, based on MacGinitie's (1941) description and illustrations. Becker (1960) ignored this epithet and invalidly referred some leaves (referred to *A. elwyni* in the current report) to *A. aequidentatum*.

LaMotte's reason for using the epithet *orbum* is unknown to us. The primary meaning for *orbum* is disk, but neither leaf nor fruit of *Acer orbum* is disk-shaped. Perhaps LaMotte was referring to the archaic use of "orb" as earth, that is, *A. orbum* was a fossil of, or from, the earth (in which case *orbense* would be appropriate).

Discussion: See previously under section *Orba*.

Distribution: Late early Eocene of northern California.

Typology: Lectotype here designated, UCMP 2283.

Occurrence: See appendix table.

Section *Columbiana* Wolfe et Tanai, sect. nov.

Diagnosis: Leaves simple, perfectly actinodromous; typically deeply 3-lobed (but 1 5-lobed species known), with large lobations on medial lobe and basal sides of lateral lobes; lateral lobes almost equal in length to medial lobe; typically an external primary branch originates on the basal side of a lateral primary vein and enters a lobation; lobal sinuses typically braced by an acutely bifurcating intersecondary vein or by an acutely bifurcating external vein of a medial secondary vein; tertiary veins A-A and compound; areolar venation quadrangular, veinlets absent or typically once-branching.

Fruit samaroid; nutlet at basal end; nutlet moderately inflated, smooth except numerous approximately parallel veins that cross the nutlet wide elliptic to round; attachment angle about 25° to 30°; nutlet proximally expanded; wing extending along at least 1/2 along distal margin of nutlet.

Discussion: Foliage that is here referred to *Columbiana* has a strong resemblance to foliage of *Acer glabrum*, and indeed *A. columbianum* Chan. et Axler. (= *A. tuckeri* of the present report) was considered to be the "fossil equivalent" of that extant species. Leaves of *A. medianum* are now known at 19 localities, but at only 2 of these localities do the characteristic fruits of *Glabra* also occur. Instead, at 8 of the 19 localities occur fruits assigned to *Columbiana*. Further, the same basic type of foliage and fruit (but representing species other than *A. medianum*) co-occur at Clarkia and 3 Bridge Creek localities.

Resemblance of foliage of *Columbiana* to foliage of *Glabra* is particularly pronounced in overall shape and the presence in many leaves of *Columbiana* of a strong lateral secondary vein (which can also be termed an external primary vein) that enters a major lobation on the basal side of a lateral lobe. In *Glabra*, however, the sinus between the lateral and medial lobes is braced by a strong secondary vein that bifurcates before reaching the sinus; in *Columbiana*, sinal bracing is accomplished by a bifurcating vein of intersecondary order or by an external secondary vein. In *Glabra*, the sinuses between the medial lobations and the superadjacent teeth are also braced by bifurcating secondary veins, whereas in *Columbiana* the homologous veins are intersecondaries or external secondary veins. Also significant is that areolar venation in *Columbiana* is formed by small, quadrangular areoles that typically have once-branched veinlets, whereas in *Glabra* areolar venation is formed by large irregularly polygonal areoles that have profusely branching veinlets.

Sinal bracing, although weak in *Columbiana* in comparison to *Glabra*, is of about the same strength and specialization as found in some species of *Glabroidea* (for example, *Acer elkoanum* and some specimens of *A. florissanti*). Areolar venation of *Columbiana* could readily be derived from the pattern in *A. orbum*. Acutely angled external secondary veins and basically three-lobed leaf of *Columbiana* also indicate a close relationship between *Columbiana, Glabroidea*, and *Orba*; the earliest species of *Columbiana* for which foliage is known is exclusively three-lobed. Overall, foliage of *Columbiana* indicates a close relationship to *Orba* and to *Glabroidea*.

Fruits of *Columbiana* have numerous subparallel veins that pass directly onto the wing (although somewhat convergent apically) and a typically elliptic shape and low attachment angle. These general characters are also found in *Glabroidea* and in extant species such as *A. saccharinum* of *Eriocarpa*. As with foliage, fruits of *Columbiana* indicate an origin near *Orba* and *Glabroidea*.

Type species: Acer medianum Knowlton (=*A. columbianum* Chaney and Axelrod).

Acer stockeyae Wolfe et Tanai, sp. nov.

(pl. 5, figs. 10, 11, 14)

Description: Fruit samaroid; nutlet at basal end; nutlet slightly inflated, outline elliptic, 0.8 cm long, 0.6 cm wide, apex rounded, distal margin expanded proximally; obscure, coarsely reticulate veins; attachment angle 20°, nutlet angle 0°. Wing extending completely along distal margin of nutlet; 3.3 cm long, 1.1 cm wide; distal margin convex, proximal margin straight, apex narrowly rounded; 5 veins coalesced along proximal margin; wing veins diverging at angles of 10° to 30°, bifurcating acutely and anastomosing several times, some veinlets.

Nomenclature: Ruth A. Stockey has been of invaluable assistance in supplying us with material of Eocene *Acer*.

Discussion: The reticulate nutlet venation that extends directly onto the nutlet and proximally expanded nutlet ally *Acer stockeyae* to the later species of *Columbiana*. The elliptic nutlet is atypical for these later species, but this character suggests a relationship for *A. stockeyae* with other members of the *Orba* Group.

Distribution: Early middle Eocene of south-central British Columbia.

Typology: Holotype, UAPC S13273A, B.
Occurrence: See appendix table.

Acer eomedianum Wolfe et Tanai, sp. nov.

(pl. 16, figs. 3, 5)

Description: Fruits samaroid, nutlet at basal end; nutlets 0.7 cm long, 0.5 to 0.6 cm wide, outline elliptic, apex broadly rounded; attachment scar 0.6 cm long; nutlet moderately inflated; nutlet proximally expanded; 7 subparallel veins, passing onto wing, veins extending from attachment scar and somewhat converging near apex; attachment angle 20° to 35°, nutlet angle 15° to 20°; wing extending along distal margin of nutlet to attachment scar; 2.5 cm long, 0.8 to 0.9 cm wide; distal side broadly convex, proximal side straight for 1/2 the length and then curving convexly, apex narrowly convex; proximal side with 7 coalesced veins, wing veins diverging at angles of 10° to 20°, curving sharply and smoothly convexly, bifurcating.
Nomenclature: An Eocene species possibly in the lineage leading to *Acer medianum*.
Discussion: In the Bull Run specimen, which is the holotype, a poorly defined depression occurs in the medial part of the nutlet; this feature may represent a reduced nutlet flange. Nutlet veins are also obscure in the basal part of the nutlet in the holotype.
Distribution: Late middle Eocene of northeastern Nevada and latest Eocene of southwestern Montana.
Typology: Holotype, UCMP 9065.
Occurrence: See appendix table.

Acer powellense Wolfe et Tanai, sp. nov.

(pl. 16, figs. 1, 6: text-fig. 14M)

Description: Leaves simple, perfectly actinodromous; deeply 3-lobed, lateral lobes as long as medial lobe; shape very wide ovate, about 7 cm long and 7 cm wide; base rounded, apex acuminate; 3 primary veins, the lateral primary veins diverging from medial secondary veins, straight; 4 or 5 secondary veins originating at angles of 30° to 40° from basal side of lateral primary veins, straight, craspedodromous; about 5 pairs of medial secondary veins originating at angles of 30° to 40°, straight, craspedodromous; lobal sinal bracing formed by an acutely bifurcating intersecondary vein; tertiary veins R-R, compound, spaced 0.4 to 0.6 cm; fourth order venation irregularly quadrangular; fifth order venation thick, forming mostly quadrangular areoles 0.4 to 0.6 mm in diameter, veinlets thick, once-branching; primary teeth forming marked lobations, about 3 or 4 per lobe, D-1; subsidiary teeth about 2 per basal flank and none or 1 per apical flank.
Nomenclature: Type locality is on Sturgeon Creek, Powell County, Montana.
Discussion: Acer powellense represents the oldest known leaves assignable to *Columbiana*. Like leaves of later species of the section, *A. powellense* has marked lobations, although in *A. powellense* lobations are three or four on the medial lobe in contrast to typically two in later species. Leaves of *Columbiana* show a decrease in areolar size,

which is 0.4 to 0.6 mm in *A. powellense*, 0.3 to 0.5 mm in *A. oligomedianum*, and 0.3 to 0.4 in *A. medianum*.
Distribution: Latest Eocene of west-central Montana.
Typology: Holotype, UCMP 9314A, B.
Occurrence: See appendix table.

Acer oligomedianum Wolfe et Tanai, sp. nov.

(pl. 26, figs. 1-10; text-fig. 14L)

Acer osmonti auct. non Knowlton. Chaney. 1927 (part). 126, pl. 17, f. 6.
Acer sp. Knowlton, 1902, pl. 13, f. 1, 2.
Acer sp. Meyer. 1973. pl. 4, f. 5.

Description: Leaves simple, perfectly actinodromous; 3-lobed, lateral lobes almost as long as medial lobe; shape elliptic to orbiculate; base broadly rounded to shallowly cordate; lobes elliptic, lateral lobes strongly asymmetrical; medial lobe with 2 pairs of large lobations, lateral lobes with 1 or 2 large lobations on basal side; lateral primary veins parallel to medial secondary veins; 4 to 7 secondary veins originating at angles of 30° to 40° from basal side of lateral primary vein, broadly convex, craspedodromous; 5 to 7 pairs of bradly convex medial secondary veins originating at angles of 30° to 50°, craspedodromous; lobal sinal bracing typically formed by an acutely bifurcating intersecondary vein; tertiary veins A-A to A-R and compound; fourth order venation quadrangular; fifth order venation thick forming quadrangular areoles 0.3 to 0.5 mm in diameter, veinlets typically once-branching; teeth typically D-1, with 1 or 2 subsidiary teeth on basal flank and no or 1 tooth on apical flank; petiole over 1.2 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.7 to 1.0 cm long; 0.5 to 0.7 cm wide; outline elliptic, apex broadly rounded; attachment scar 0.5 to 0.7 cm long; nutlet expanded beyond proximal side of wing; 6 or 7 veins originating along attachment scar, subparallel, somewhat converging near apex of nutlet; attachment angle 25° to 40°, nutlet angle 10° to 30°. Wing typically extending along distal margin of nutlet to attachment scar; 1.4 to 2.7 cm long, 0.5 to 0.9 cm wide; distal margin convex to concave in basal part and convex in apical part, proximal margin straight to broadly convex, apex broadly rounded; proximal side with 6 or 7 coalesced veins, wing veins diverging at angles of 10° to 30°, sharply and smoothly curving, bifurcating, few anastomoses.
Nomenclature: An Oligocene species possibly in the lineage leading to *Acer medianum*.
Discussion: At two Bridge Creek localities at which leaves of *Acer oligomedianum* are found, one has also produced the fruits just described. Because the same basic type of leaf and fruit are also associated at many Miocene localities, we consider highly probably the conspecifity of these Oligocene leaves and fruits.

The fruit of *Acer oligomedianum* has no trace of a possible flange, which is present in *A. eomedianum*. Further, the venation is well expressed in the basal region of the nutlet.
Distribution: Early Oligocene of central and western Oregon.
Typology: Holotype, USNM 396076.
Occurrences: See appendix table.

Acer medianum Knowlton

(pl. 38, figs. 1-6; pl. 39, figs. 1-9; pl. 40, figs. 1-5, 7, 8, 11; text-fig. 14N)

Acer medianum Knowlton. 1902. 76. pl. 14, f. 4, 5
Acer tuckeri (H.V. Smith) LaMotte. 1952. 57.
Engelhardtia tuckeri H.V. Smith. 1938a. 226. pl. 1, f. 4.
Quercus malheurensis H.V. Smith. 1938b. 560. pl. 29, f. 1.
Acer middlegatei Axelrod. 1956 (part, typic). 307. pl. 31, f. 10, 11.
Acer middlegatensis Axelrod. 1985 (part). 171. pl. 14, f. 10, 12.
Acer columbianum Chaney et Axelrod (non Penhallow, 1908). 1959 (part, typic), 192. pl. 40, f. 103.
    Smiley. 1963. 227. pl. 13, f. 7, 8.
    Graham. 1965. 66. pl. 6, f. 1.
Acer nevadensis Axelrod. 1985 (part, typic). 173. pl. 13, f. 5.
Acer bolanderi auct. non Lesquereux. Smith. 1938b. 562. pl. 28, f. 5; pl. 29, f. 8.
    Smith. 1939. 116. pl. 3, f. 3.
    Chaney & Axelrod. 1959 (part). 192. pl. 40, f. 7.
    Wolfe. 1964. N29. pl. 5, f. 7.
Acer chaneyi auct. non Knowlton. MacGinitie. 1933 (part). 61.
    Brooks. 1935 (part). 297. pl. 19, f. 5.
    Dorf. 1936 (part). 120.
    Smith. 1938a. 228.
Acer merriami auct. non Knowlton. Dorf. 1936. 120. pl. 3, f. 8.
Acer oregonianum auct. non Knowlton. Smith. 1938a. 228.
Acer osmonti auct. non Knowlton. MacGinitie. 1933 (part). 62.
    Brooks. 1935. 298. pl. 20, f. 2.
    LaMotte. 1936 (part). 137.
    Smith. 1939 (part). 116. pl. 3, f. 6.

Description: Leaves simple, perfectly actinodromous; 3-lobed, lateral lobes typically almost as long as medial lobe; shape elliptic to orbiculate; 2.4 to 6.7 cm long, 2.0 to 7.0 cm wide; base acute to broadly rounded to narrowly or broadly cordate; lobes elliptic, lateral lobes strongly asymmetrical; medial lobe with 1 or 2 pairs of large lobations on basal side; lateral primary veins parallel to or typically diverging from medial secondary veins; 3 to 5 secondary veins originating at angles of 30° to 60° from basal side of lateral primary vein, broadly convex to concave (especially the external primary branch), craspedodromous; 3 to 5 pairs of broadly convex medial secondary veins, craspedodromous; lobal sinal bracing typically formed by an acutely bifurcating intersecondary vein; tertiary veins A-A to A-R and compound; fourth order venation quadrangular; fifth order venation quadrangular, forming areoles 0.3 to 0.4 mm in diameter, veinlets branching 1 to 3 times; teeth D-1, typically with 1 or 2 subsidiary teeth on basal flank and no or 1 tooth on apical flank; petiole 1.2 to 3.4 cm long.

Fruits samaroid, nutlet at basal end; nutlets 1.2 to 1.5 cm long, 0.7 to 1.2 cm wide; outline elliptic, apex broadly rounded; attachment scar 0.7 to 1.0 cm long; nutlet expanded beyond proximal side of wing; 10 to 14 veins originating along attachment scar, subparallel, passing onto wing, somewhat converging near apex of nutlet; nutlet moderately inflated; attachment angle 25° to 30°, nutlet angle to 10° to 35°. Wing extending 1/2 or more the distance along distal margin of nutlet; 3.5 to 3.8 cm long, 0.9 to 1.6 cm wide; distal margin broadly convex, proximal margin straight to typically broadly convex, apex broadly rounded; proximal side with 6 to 9 coalesced veins, wing veins diverging at angles of 10° to 20°, sharply and smoothly curving, bifurcating, some anastomoses.

Nomenclature: As indicated in the synonymy, *Acer medianum* is the oldest valid name for this species. The epithet *medianum* is based on two fruits, which have typically been referred to *Macrophylla*. Although typical fruits of *Macrophylla* have been collected from the Riverbank locality (the types of *A. oregonianum*), these are readily distinguishable from the fruits of *A. medianum* in having the proximal side of the nutlet tangential to the proximal side of the samara and in having a high nutlet angle and a semicircular nutlet outline. Fruits that compare well with the types of *A. medianum* are of common occurrence in the Miocene of western North America and have been found at 13 localities other than the Riverbank.

At 8 of the 14 localities at which *Acer medianum* fruits occur, leaves of *Acer columbianum* of Chaney and Axelrod also occur, including the Riverbank locality, which is the type locality for both *A. medianum* and *A. columbianum*. Despite the wide occurrence of *A. columbianum* foliage and its supposed membership in *Glabra*, only at the White Hills and Trout Creek localities have both this foliar type and fruits of *Glabra* been collected. In contrast, *A. medianum* fruits and *A. columbianum* leaves are of common occurrence at localities such as Fingerrock, Devils Gate, and Hog Creek. As noted in the discussion under *Columbiana*, leaves of *A. columbianum* are only convergent with leaves of *Glabra*. *Acer medianum* and *A. columbianum* are here considered to represent the same species.

Other than the fact that the epithet *columbianum* is a junior homonym, this epithet is also a junior synonym of several other epithets, including four based on foliage (*diluvialis, tuckeri, malheurensis*, and *middlegatei*).

Knowlton (1902) used the criterion of size to distinguish his *Acer medianum* from the larger *A. gigas* and the smaller *A. minor*, hence the epithet *medianum* for these middle-sized fruits.

Discussion: Foliage of *Acer medianum* is highly variable in degree of incision and prominence of lobations. At localities such as Devils Gate, the leaf assemblage occurs in beds that palynologically represent an early successional stage following a volcanic eruption (Cross and Taggart, 1983). Abundance and variability of foliage of *A. medianum* at such localities may reflect an immature stage of growth of parent plants; such plants typically display a high degree of foliar variability.

Fruits of *Acer medianum* are readily distinguishable from those of *A. oligomedianum*. Other than their larger size, fruits of *A. medianum* have about twice as many veins crossing the nutlet than in *A. oligomedianum*.

Distribution: Early to early late Miocene from central British Columbia south to southwestern Nevada and from south central Idaho west to the eastern margin of the Cascade Range. By the late Miocene, *Acer medianum* was restricted to the Columbia Plateaus.

Typology: Lectotype here designated, USNM 8498.

Occurrences: See appendix table.

Acer niklasi Wolfe et Tanai, sp. nov.

(pl. 40, figs. 6, 9, 10)

Acer glabroides auct. non R.W. Brown. Chaney and Axelrod. 1959 (part). 193. pl. 40, f. 8.

Description: Leaf simple, perfectly actinodromous; deeply 5-lobed, most basal lateral lobes as large as lateral lobations, most apical lateral lobes about as long as medial lobe; most apical lateral and medial lobes with 2 pairs of large lobations; shape orbiculate, 4.0 cm long, 5.7 cm wide; base cordate; lobes elliptic; most apical lateral primary veins slightly diverging from medial secondary veins; 4 secondary veins originating at angles of 30° to 60° from basal side of most apical primary veins, broadly convex, craspedodromous; intersecondary veins about 1 per secondary vein, bifurcating near the lobal and dental sinuses; tertiary veins A-R and compound; fourth order venation polygonal; fifth order venation not preserved; teeth D-1, typically with 1 or 2 subsidiary teeth on basal flank and none of apical flank; petiole more than 0.5 cm long.

Fruits samaroid, nutlet at basal end; netlets 0.7 to 1.0 cm long, 0.5 to 0.7 cm wide; outline elliptic, apex broadly rounded; attachment scar 0.3 to 0.4 cm long; nutlet expanded proximally; 5 to 7 veins originating along attachment scar, subparallel, passing onto wing, somewhat converging near apex of nutlet; nutlet moderately inflated; attachment angle 35° to 40°, nutlet angle about 10°. Wing extending about half the length along distal margin of nutlet; 2.3 to 2.6 cm long, 1.0 to 1.3 cm wide; distal margin broadly convex, proximal margin broadly convex, apex broadly rounded; proximal side with 5 or 6 coalesced veins; wing veins diverging at angles of 10° to 30°, smoothly curving, bifurcating, numerous anastomoses.

Nomenclature: In recognition of Karl J. Niklas' contributions to paleobiochemistry in general and to his work on Clarkia leaves in particular.

Discussion: The single leaf of *Acer niklasi* is clearly five-lobed, a character that is totally absent in other species of *Columbiana*, even in the highly variable populations of *A. medianum*. In outline and all aspects of secondary and terriary venation (including the characteristic sinal bracing by bifurcating intersecondary veins), *A. niklasi* compares well with *A. medianum*. Development of a five-lobed condition is thus considered to be a specialization that characterizes *A. niklasi.*

Fruits os *Acer niklasi* are distinguishable from fruits of *A. medianum.* In both size and number of veins on the nutlet, *A. niklasi* is much more similar to *A. oligomedianum* than to *A. medianum*. Like some fruits of *A. medianum*, however, *A. niklasi* has the wing restricted to the apical margin of the nutlet, rather than extending completely to the attachment scar. If *A. oligomedianum* is indeed ancestral to both Miocene species of *Columbiana*, then a clear instance of mosaic evolution is presented: *A. medianum* has a specialized fruit but an ancestral type of leaf, whereas *A. niklasi* has a specialized leaf but an ancestral type of fruit.

Distribution: Early middle Miocene of north central Idaho and northeastern Washington; late middle Miocene of northeastern Oregon.

Typology: Holotype, UCMP 9085.

Occurrences: See appendix table.

Section *Glabroidea* Wolfe et Tanai, sect. nov.

Diagnosis: Leaves simple, perfectly actinodromous; 3-lobed (some individual leaves in *Acer florissanti* are 5-lobed), with medial lobe larger than lateral lobes; lobations typically present on medial lobes; tertiary veins connecting most basal medial secondary veins to lateral primary veins compound and A-A; external secondary veins acute to secondary veins; lobal sinal bracing typically formed by medial secondary vein that bifurcates acutely near the sinus or by a secondary vein and its acutely branched external vein; areoles typically quadrangular and with no veinlets or 1 simple veinlet.

Fruits samaroid; nutlet at basal end. Veinlets on nutlet parallel to long axis of nutlet, coalescing apically to form thickening along proximal side of wing; nutlet symmetrically and typically slightly inflated; flanges that parallel long axis of nutlet projecting from nutlet; endocarp typically thick.

Discussion: The flanged nutlets are one of the most characteristic features of many Eocene fruits of *Acer* in western North America. Placement of the flange varies from proximal *(A. cadaver)* to distal *(A. elwyni)* although most are approximately medial. The flange is narrow *(A. elwyni)* to broad *(A. wehri)*, and extends the full length of the nutlet in some species *(A. wehri)* and is restricted to the basal region in other species *(A. cuprovallis)*. The wing typically extends along the distal margin of the nutlet.

No extant species of *Acer* has such nutlet flanges as do the various species of *Glabroidea*. In *A. pentapomicum* Stew., both sides of the nutlet expand distally to form lobes, but these are not the narrow flanges of *Glabroidea*. In *A. glabrum* Torr. and the various species of *Arguta*, folds form outwardly extending ridges, but these are irregularly palced in a given species; in *Glabroidea*, the flanges are consistently placed within a species. In many species of extant *Acer*, one nutlet vein can be more pronounced and project farther away from the nutlet than other veins; such pronounced veins may be homologs of the nutlet flanges of *Glabroidea* but are in no sense flanges.

At numerous localities (text-figs. 5, 6), *Acer* foliage occurs with *Acer* fruits that have flanged nutlets. Such associations include:

(1) Copper Basin: 2 fruits of *A. cuprovallis*, 8 fruits of *A. jarbidgianum*, and 1 leaf.
(2) Elko: 10 fruits of *A. elkoanum* and 5 leaves.
(3) Salmon: 5 fruits of *A. idahoense* and 4 leaves (except for fruits and leaves of *Macrophylla*).
(4) Mormon Creek: 1 fruit and 7 leaves of *A. elwyni*.
(5) York Ranch: 15 fruits (same species) and 14 leaves of *A. elwyni*.
(6) Florissant: over 20 fruits (same species) and over 40 leaves of *A. florissanti* except for 3 fruits of *Negundo*.
(7) Gray Ranch: 2 fruits and 3 leaves of *A. glabroides*.

Indeed, at 3 different localities, foliage of *Acer elwyni* is associated with the same species of fruit, strong evidence that the fruits represent *A. elwyni*. At a total of 10 localities, the same basic type of *Glabroidea* foliage is associated with flanged *Acer* fruits. The leaves associated with the flanged fruits have a morphological unity as diagnosed previously. The numerous associations indicate to us that the flanged fruits and the *Glabroidea* leaves represent the same taxon.

Leaves of *Glabroidea* have an areolar venation similar to that of extant *Rubra*: quadrangular areoles without veinlets or with a single, unbranched veinlet. Some bohlenioid secondary veins occur in the medial lobes of *A. florissanti* and *A. elkoanum*. *Type species: Acer glabroides* R.W. Brown.

Acer becki Wolfe et Tanai, sp. nov.

(pl. 10, figs. 10, 11)

Description: Fruits samaroid; nutlets at basal end; nutlet slightly inflated, triangular, 0.4 to 0.5 cm long, 0.3 cm long, apex narrowly rounded, strongly convex proximal margin; 2 distinct flanges; attachment angle 30°, nutlet angle 30°. Wing extending entire length of distal margin of nutlet; 1.2 to 1.4 cm long, 0.4 cm wide; distal margin convex, proximal margin convex, apex rounded; 5 veins coalesced along proximal margin; wing veins diverging at angles of 20° to 30°, sharply curving until perpendicular to proximal margin, diverging acutely, anastomosing several times, some veinlets.
Nomenclature: C.B. Beck has been of great assistance in supplying us with material from the collections of the University of Michigan.
Discussion: As in *Acer crookense, A. becki* has pronounced nutlet flanges and wing veins that are oriented perpendicular to the proximal margin. However, in *A. becki*, the nutlet flanges (when viewed from the interior) form a broad, V-shaped region, as opposed to the narrow groove in *A. crookense*. Further, the nutlet shape is more triangular and narrower in *A. crookense*, which also has a long, narrow wing.
Distribution: Late middle to early late Eocene of central Oregon.
Typology: Holotype, UCMP 9304.
Occurrence: See appendix table.

Acer bosrivularis Wolfe et Tanai, sp. nov.

(pl. 10, figs. 3, 4, 9)

Description: Fruit samaroid, nutlet at basal end; nutlet 0.5 cm long, 0.3 cm wide, triangular in outline, narrowly rounded apex; attachment scar 0.3 cm long, with a rounded keel at junction with proximal margin; nutlet moderately inflated, smooth except for a medially placed flange; attachment angle 50°, nutlet angle 20°. Wing extending almost entire length of distal margin of nutlet; 1.7 cm long, 0.8 cm wide, distal margin broadly convex, proximal margin straight, apex broadly rounded; proximal side with 7 coalesced veins, wing veins diverging at angles of 10° to 30°, irregular in course, irregularly bifurcating, some anastomoses.
Nomenclature: Type locality is on Cow Creek.
Discussion: The single *Acer* samara from the Cow Creek locality has nutlet and wing shapes similar to those of *A. rousei* and many veins converge apical to the nutlet, also as in *A. rousei*. In *A. bosrivularis*, however, the wing extends farther along the distal margin of the nutlet, the wing veins are markedly more irregular in course, and the fruit is smaller than in *A. rousei*.

Distribution: Late Eocene of west-central Idaho.
Typology: Holotype, USNM 396021A, B.
Occurrence: See appendix table.

Acer cadaver Wolfe et Tanai, sp. nov.

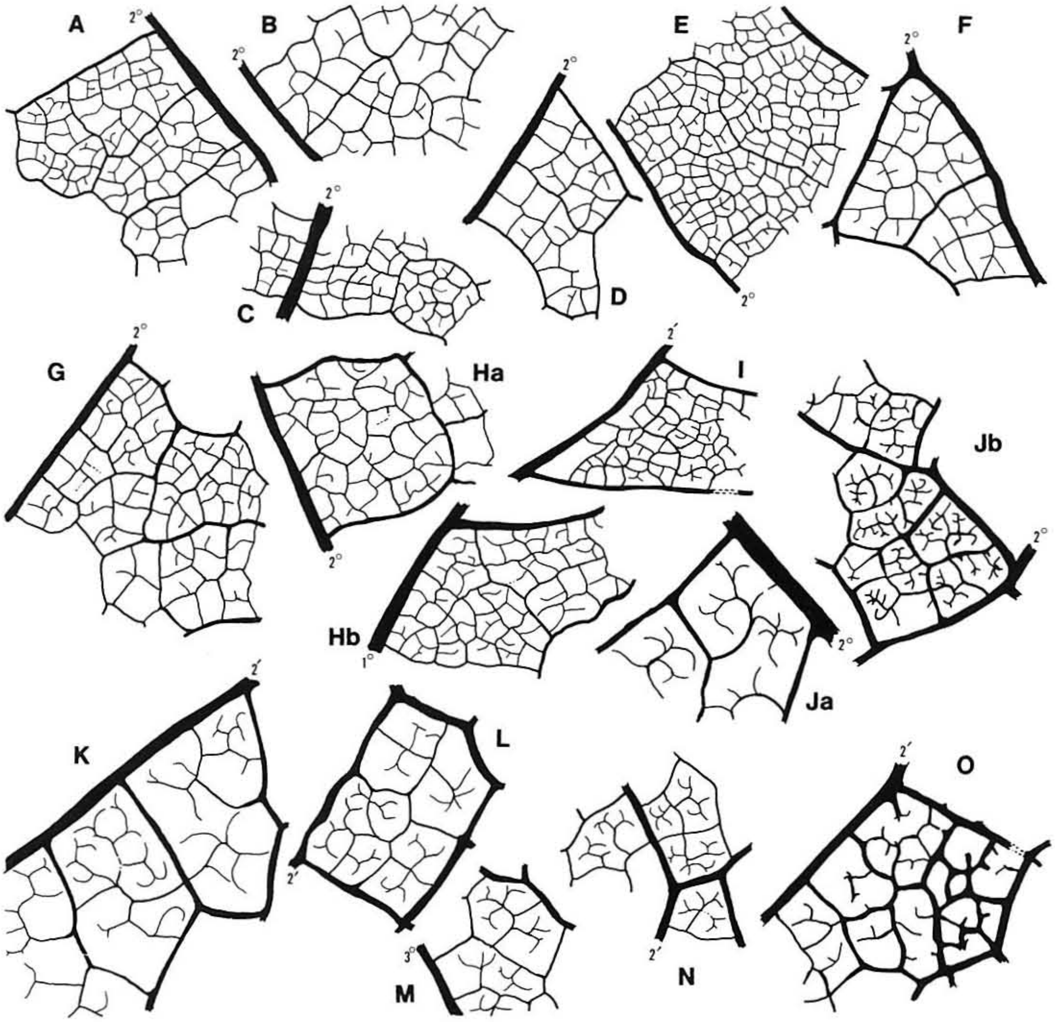
(pl. 12, figs. 10, 11)

Description: Fruit samaroid, nutlet at basal end; nutlet 0.6 cm long, 0.4 cm wide, narrowly triangular in outline, narrowly rounded apex; attachment scar 0.4 cm long; nutlet moderately inflated; 7 prominent ridges parallel to long axis of nutlet and a small flange near the proximal margin of the basal part of the nutlet; attachment angle 35°, nutlet angle 30°. Wing entirely apical to nutlet, forming a U-shaped sulcus with nutlet; 1.3 cm long, 0.7 cm wide; distal margin convex, proximal margin slightly convex, apex broadly rounded; proximal side with 7 veins that pass from apical margin of nutlet and coalesce apical to nutlet; wing veins diverging at angles of 10° to 30°, smoothly curving, bifurcating, few anastomoses.
Nomenclature: Type locality is in the Dead Horse Tuff of Axelrod (1966).
Discussion: The single fruit on which *Acer cadaver* is based has a small, although definite, flange on the nutlet, a character definitive of *Glabroidea.* The presence of many parallel ridges in *Acer cadaver* is unique in *Glabroidea.*
Distribution: Late Middle Eocene of northeastern Nevada.
Typology: Holotype, UCMP 9019.
Occurrence: See appendix table.

Acer crookense Wolfe et Tanai, sp. nov.

(pl. 10, figs. 1, 2, 5, 6)

Description: Fruit samaroid, nutlet at basal end; nutlet 0.5 cm long, 0.35 cm wide; nutlet outline triangular, apex narrowly rounded; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.45 cm long, forming a proximal beak with proximal margin; nutlet moderately inflated, numerous (probably 8 to 10) veins originating along attachment scar, extending apically directly onto wing; distinct, medially placed flange extending length of nutlet, broad at base and narrow in apical 2/3 of nutlet; attachment angle 40°, nutlet angle 20°. Wing extending almost to attachment scar, forming a shallow U-shaped sulcus with nutlet; 2.3 cm long, 0.6 cm wide; distal margin broadly and shallowly convex, proximal margin straight, apex narrowly rounded; 7 coalesced along proximal side, wing veins diverging at angles of 10° to 30°, sharply curving, irregularly bifurcating at high (60° to 70°) angles, numerous anastomoses, veinlets branching.
Nomenclature: Type locality is in Crook County, Oregon.
Discussion: The nutlet flange characteristic of *Glabroidea* is pronounced in the samaras of *Acer crookense*. Shapes of the nutlet and wing are similar to *A. cuprovallis*. In *A. cuprovallis*, however, the wing extends only a short distance along the distal margin of the nutlet, the nutlet flange is poorly developed, and the wing veins bifurcate at low (about 30°) angles. As discussed previously, *A. crookense* has strong similarities to *A.*



Text-fig. 16 Areolar venation characters of fossil *Acer* — (3) Section *Glabroidea* and *Macrophylla*. (all figures × 12.5 unless otherwise stated)

A. *Acer elkoanum* Wolfe et Tanai. Elko. Paratype UCMP 9021B (the counterpart of pl. 6, fig. 5).

B. *Acer elkoanum* Wolfe et Tanai. Elko. Holotype USNM 396022A (pl. 6, fig. 2)

C. *Acer elwyni* Wolfe et Tanai. Mormon Creek. Holotype UMNP 36249 (pl. 7, fig. 7).

D, F. *Acer florissanti* Kirchner. Florissant. (D) Hypotype UCMP 3827 (pl. 8, fig. 7), (F) Hypotype USNM 39040 (pl. 9, fig. 7).

E. *Acer florissanti* Kirchner. Beaverhead. Hypotype NYBG 830b (Becker, 1969; pl. 36, fig. 3).

G. *Acer idahoense* Wolfe et Tanai. Salmon. Holotype USNM 396033B (the counterpart of pl. 7, fig. 6).

Ha, b. *Acer milleri* Wolfe et Tanai. Beaver Creek. Paratype UCMP 9303 (pl. 13, fig. 7).

I. *Acer salmonense* Wolfe et Tanai. Salmon. Paratype USNM 396144 (pl. 17, fig. 4)

Ja, b. *Acer alvordense* Axelrod. Alvord Creek. (a) Paratype UCMP 2137B (the counterpart of pl. 18, fig. 1) × 25, (b) UCMP 9123 (not illustrated in plates).

K. *Acer osmonti* Knowlton. Lyons. Hypotype USNM 396157 (pl. 30, fig. 3).

L. *Acer oregonianum* Knowlton. Cascadia. Hypotype USNM 39169 (pl. 30, fig. 5).

M. *Acer oregonianum* Knowlton. Collawash. Hypotype UCMP 9347 (pl. 49, fig. 3).

N. *Acer megasamarum* Tanai et N. Suzuki. Seldovia Point. Hypotype USNM 208475 (Wolfe et Tanai, 1980; pl. 19, fig. 2).

O. *Acer busamarum* Wolfe et Tanai subsp. *busamarum*. Trout Creek. Holotype UCMP604 (pl. 51, fig. 6).

becki.

Distribution: Late middle to early late Eocene of central Oregon.

Typology: Holotype, UCMP 9020A, B.

Occurrence: See appendix table.

Acer cuprovallis Wolfe et Tanai, sp. nov.

(pl. 11, figs. 1-3, 5-8)

Acer minor auct. non Knowlton. Axelrod. 1966 (part). 76, pl. 18, f. 9, 10.

Description: Fruits samaroid, nutlet at basal end; nutlet 0.5 to 0.5 cm wide, narrowly oval in outline, rounded apex; attachment scar 0.4 to 0.5 cm long; nutlet moderately inflated; about 6 parallel veins on apical part of nutlet; a short flange near distal margin and basal part of nutlet; attachment angle 40°, nutlet angle 25°. Wing with a narrow extension along apical 1/3 of distal margin of nutlet, forming a shallow U-shaped sulcus; 2.3 cm long, 0.8 cm wide; distal margin convex, proximal margin straight, apex narrowly rounded; proximal side with 5 coalesced veins diverging at angles of 30° to 50°, smoothly curving, bifurcating, few anastomoses.

Nomenclature: Type locality is in Copper Basin, Nevada.

Discussion: In shape of nutlet and wing, *Acer cuprovallis* resembles *A. wehri*. The nutlet flange of *A. cuprovallis* is short but is placed in about the same position as in *A. wehri*. Other than smaller size and length of flange of *A. cuprovallis*, the two taxa are similar.

Distribution: Early late Eocene of northeastern Nevada.

Typology: Holotype, UCMP 20127A, B (note: 20127B = 20128 of Axelrod, 1966).

Occurrences: See appendix table.

Acer elkoanum Wolfe et Tanai, sp. nov.

(pl. 6, figs. 1-3, 5-7; pl. 10, figs. 7, 8, 12-14; text-fig. 16A, B)

Description: Leaves simple, perfectly actinodromous; shallowly to deeply 3-lobed, with the medial lobe largest; shape oval, about 2.0 to 6.0 cm long, 1.8 to 4.5 cm wide; base broadly rounded to shallowly cordate; medial lobe expanding apically from lobal sinuses, then gradually narrowing to an acuminate apex; lateral lobes typically triangular; lateral primary veins slightly diverging from medial secondary veins, almost straight, craspedodromous; 5 to 6 secondary veins originating at angles of 30° to 50° from basal sides of lateral primary veins, broadly curving, craspedodromous; 6 to 8 pairs of broadly curving medial secondary veins, 1/2 totally craspedodromous and 1/2 bifurcating near dental sinuses, the apical branch craspedodromous, tertiary veins that connect most basal medial secondary veins to lateral primary veins A-A and compound; other tertiary veins A-A to R-A and compound; fourth order venation transitional with fifth order venation forming quadrangular areoles about 0.2 to 0.4 mm in diameter, veinlets typically absent or, if present, unbranched; lobal sinal bracing formed by a bifurcating medial secondary vein or an external branch and its secondary vein of origin; teeth D-1, typically with subsidiary teeth on basal flank; 2 to 4 teeth on apical side of lateral lobes; petiole 1.3 to 3.6 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.5 to 0.6 cm long, 0.3 to 0.4 cm wide, oval to triangular in outline, rounded apex, attachment scar 0.3 to 0.4 cm long; nutlet moderately inflated, smooth except for a shallow medially placed flange; attachment angle 25° to 45°, nutlet angle 30° to 50°; wing extending about 1/2 length of distal margin of nutlet; 1.0 to 1.5 cm long, 0.5 to 0.8 cm long, distal margin broadly convex, proximal margin straight, apex narrowly to broadly rounded; proximal side with 4 to 5 coalesced veins, wing veins diverging at angles of 20° to 40°, irregular in course, irregularly bifurcating, few anastomoses.

Nomenclature: Type locality is in the Elko Oil shale near Elko, Nevada.

Discussion: Leaves and fruits of *Acer elkoanum* represent the only material of *Acer* collected from USGS locality 9175. The leaves are represented by several specimens, as are the fruits, and we assume leaves and fruits represent the same species. The same leaf type and fruit type are also present in the Bull Run beds, where, however, other leaf and fruit types of *Acer* are present. Foliage of *Acer elkoanum* is similar to that of *A. orbum* in shape, degree of lobal incision, presence of conspicuous (although somewhat smaller) lobations. Other than areolar venation, leaves of the two species differ in the higher angle of divergence of the lateral lobes from the medial lobe and closer spacing of tertiary veins in *A. elkoanum*. Fruits of the two species are markedly different. Leaves of *Acer idahoense* are distinct from those of *A. elkoanum* in (1) *A. idahoense* has a triangular medial lobe, (2) apical flanks of the teeth in *A. idahoense* do not have teeth, and (3) lateral lobes in *A. idahoense* are shorter and broader.

Fruits of *Acer elkoanum*, although notably smaller, are similar to fruits of *A. wehri* in nutlet shape. *Acer wehri*, however, has wing veins of uniform course, numerous veins on the apical part of the nutlet, and a higher attachment angle.

Distribution: Late middle to early late Eocene of northeastern Nevada.

Typology: Holotype, USNM 396022A, B.

Occurrences: See appendix table.

Acer elwyni (Becker) Wolfe et Tanai, comb. nov.

(pl. 7, figs. 1-4, 7, 8; pl. 11, figs. 12-15, 17; text-fig. 16C)

Quercus elwyni Becker. 1960. 103. pl. 19, f. 5-7; pl. 28, f. 1-7.
Crataegus elwyni (Becker) Becker. 1972 (part). 39. pl. 9, f. 1-11.
Acer aequidentatum auct. non Lesquereux. Becker. 1960. 113. pl. 23, f. 3; pl. 32, f. 5.
Acer florissanti auct. non Kirchner. Becker. 1961 (part). 79, pl. 25, f. 9.
Acer glabroides auct. non R.W. Brown. Becker. 1961 (part). 80, pl. 25, f. 9.
    Becker. 1966. 109. pl. 4, f. 2-4.
    Becker. 1969. 113. pl. 36, f. 1.
    Becker. 1972. 44. pl. 11, f. 17-26.
Acer minor auct. non Knowlton. Becker. 1972. 45, pl. 11, f. 15-16.
Acer, samaras. Becker. 1960. pl. 32, f. 6; pl. 33, f. 6, 7.

Description: Leaves simple, perfectly to slightly suprabasally actinodromous; 3-lobed, but lateral lobes typically same size as medial lobation; shape oval to narrowly oval, 3.3 to 10.6 cm long, 1.6 to 3.7 cm wide; base narrowly rounded, medial lobe narrowly triangular and narrowing to an acuminate apex; 1 to 7 lobations well developed on medial lobe; lateral primary veins parallel to medial secondary veins, straight, craspedodromous; medial secondary veins typically straight, craspedodromous, except for most basal pair which are weak and bifurcate to brace the lobal sinuses; tertiary veins that connect most basal medial secondary veins and other tertiary veins A-R and compound fourth order venation much thinner than third order venation, polygonal; fifth order venation forming quadrangular areoles 0.2 to 0.3 mm in diameter; areoles typically without veinlets but a few with a single unbranched veinlet; teeth (lobations) D-1, typically with several subsidiary teeth on basal flank and none on apical flank, which is almost orthogonal to midrib; external secondary veins originating acutely; petiole short, but up to 1.3 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.3 to 0.4 cm long, 0.2 to 0.3 cm wide, outline narrowly triangular, apex narrowly rounded; attachment scar 0.3 to 0.4 cm long, with a slight distal beak; nutlet slightly inflated; nutlet smooth except for narrow flange that extends from distal end of attachment scar to apex of nutlet; attachment angle 50° to 65°, nutlet angle 40° to 50°. Wing extending along apical 1/2 of distal margin of nutlet and forming a distinct V-shaped sulcus; 1.1 to 1.5 cm long, 0.5 to 0.8 cm wide; distal margin broadly convex, proximal margin straight, apex broadly rounded; proximal side with 4 or 5 coalesced veins, wing veins diverging at angles of 20° to 40°, smoothly curving, bifurcating, anastomoses almost absent.

Nomenclature: The specimens that are cited in the synonymy all intergrade. Becker's (1960, 1972) assignment of leaves of this species to *Quercus* or *Crataegus*, both of which have uniformly pinnately veined leaves, is untenable.

Discussion: Association of leaves and fruits here referred to *Acer elwyni* at three localities (Ruby, Mormon Creek, and York Ranch) strongly indicates that the two organs represent the same species. At Ruby, the only other *Acer* represented is foliage of *Campestria* and *Lithocarpa*, and at the other two localities no other material of *Acer* is present.

Shorter leaves of *Acer elwyni* are invariably basally actinodromous, whereas the primary veins are somewhat suprabasal in elongated leaves (that is, the suprabasal condition is probably related to elongation of the lamina). Less elongated leaves of *A. elwyni* closely resemble leaves of *A. orbum*, although all leaves of *A. elwyni* appear to have highly elongated apices. The high degree of stenophylly (particularly for *Acer*) in *A. elwyni*, concomitant with abundant representation of both fruits and leaves in the Mormon Creek and York Ranch localities, may well indicate a fluviatile habitat for this species.

Samaras of *A. elwyni* have a pronounced flange extending apically and parallel to the distal margin of the nutlet, a feature also found in *A. orbum*. Other than their con-

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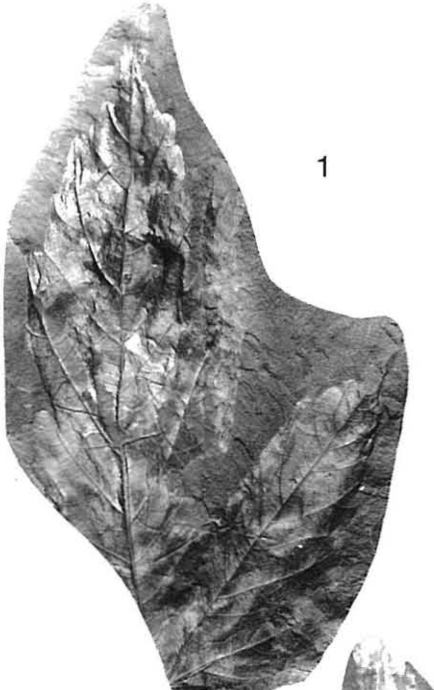
Explanation of Plate 1.

(all figures natural size)

Figs. 1, 3 *Acer douglasense* Wolfe et Tanai. Cape Douglas. Paratype USNM 396007A (Fig. 1). Holotype USNM 396006A (Fig. 3).

Fig. 2 *Acer alaskense* Wolfe et Tanai. Chickaloon/Evan Jones Mine. Holotype USNM 396009.

Fig. 4 *Acer stewarti* Wolfe et Tanai. Princeton/One Mile Creek. Paratype UAPC S6946.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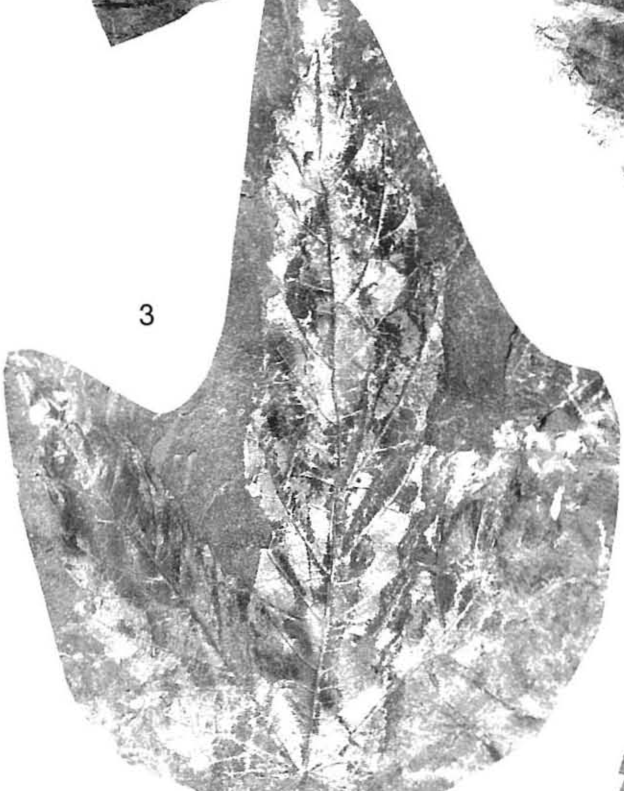
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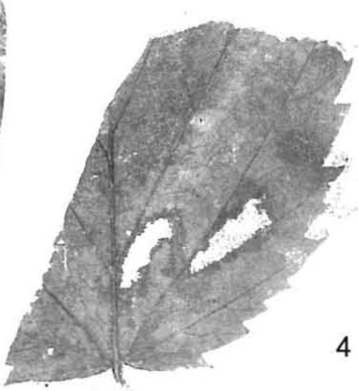
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siderably smaller size, samaras of *A. elwyni* differ from those of *A. orbum* in pronouncedly triangular shape of the nutlet, higher nutlet angle, and sharper expansion of the wing apical to the nutlet.

Distribution: Latest Eocene of southwestern Montana and south central Wyoming.

Typology: Holotype, UMMP 36429.

Occurrences: See appendix table.

Acer glabroides R.W. Brown, emend. Wolfe et Tanai

(pl. 23, figs. 1-5)

Acer glabroides R.W. Brown. 1937b (part, name only). 180.

Acer osmonti auct. non Knowlton. Chaney. 1927 (part). 126. pl. 18, f. 1, 5.

Description: Leaves simple, perfectly actinodromous, shallowly 3-lobed; shape wide elliptic; medial lobe over twice as broad as lateral lobes; base rounded to shallowly cordate; lobes triangular, apices acute, with 2 or 3 small lobations; lateral primary veins approximately parallel to medial secondary veins; 6 to 9 secondary veins originating at angles of 40° to 60° from basal sides of lateral primary veins, broadly convex, craspedodromous; 5 or 6 pairs of broadly convex medial secondary veins originating at angles of 30° to 40°, the most basal pair acutely bifurcating to brace lobal sinus, the other pairs craspedodromous; tertiary veins A-A and compound; fourth order venation thin, quadrangular; areolar venation indistinct; teeth small, A-1 or D-1, with 2 or 3 small teeth on basal flank and none on apical flank; petiole 2.4 cm long.

Fruit samaroid, nutlet at basal end; nutlet 0.7 cm long, 0.6 cm wide, outline triangular, apex narrowly rounded; attachment scar 0.6 cm long, with a rounded proximal keel; nutlet moderately inflated, smooth except for a narrow medially placed flange; attachment angle 40°, nutlet angle 20°. Wing extending along almost entire distal margin of nutlet, forming a shallow V-shaped sulcus; 2.7 cm long (not quite complete), 1.0 cm wide; distal margin broadly convex, proximal margin straight, apex not preserved; proximal margin with 6 coalesced veins, wing veins diverging at angles of 20° to 30°, sharply convex, irregular in course, bifurcating, some anastomoses.

Nomenclature: Brown (1937b) proposed *Acer glabroides* as a "new name," and he furnished no description. In fact, *A. glabroides* was a new species, which was validated only by Brown's citation of the previously published description by Chaney (1927). Of four leaves (three from Gray Ranch) on which Chaney based his description, one (from near Clarno; his pl. 18, f. 3) is very poorly preserved and a second fragment (his pl. 17, f. 6) is referred by us to *A. oligomedianum*. A third leaf (Chaney's pl. 18, f. 5) and its

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Explanation of Plate 2.

(all figures natural size)

Figs. 1, 4 *Acer stewarti* Wolfe et Tanai. Princeton/One Mile Creek. Holotype UAPC S485 (Fig. 1). Paratype UAPC S13271 (Fig. 4).

Figs. 2, 3 *Acer washingtonense* Wolfe et Tanai. Republic/Knob Hill. Holotype UMBM 56253A (Fig. 2), UWBM 56253B (Fig. 3).

Fig. 5 *Acer* sp. 3 (sect. *Orba*). Princeton/Whipsaw Creek. GSC 82969.

Fig. 6 *Acer orbum* LaMotte. Chalk Bluffs. Lectotype UCMP 2283.

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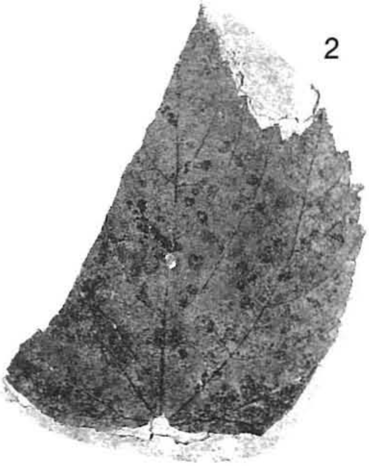

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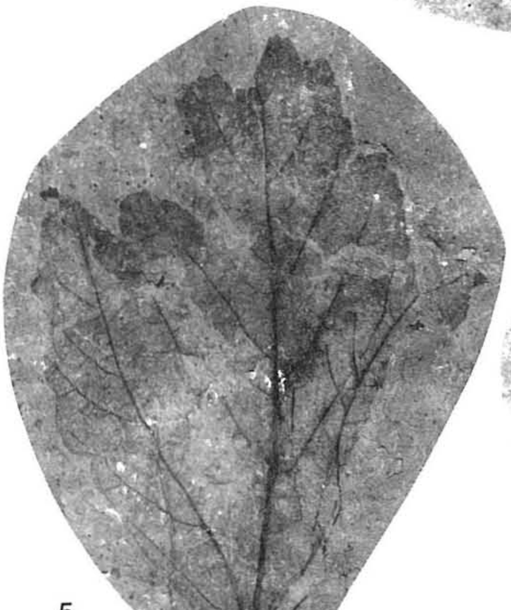

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counterpart is almost complete and, except for areolar venation, is well preserved; this leaf is designated as the lectotype. The fourth specimen (Chaney's pl. 18, f. 1) represents two-thirds of a leaf that belongs to the same species as the third specimen.

Both Chaney (1927) and Brown (1937b) thought the Gray Ranch species to be related to the extant *Acer glabrum* Torr.

Discussion: Other than two leaves and two fruits here placed in *Acer glabroides*, UCMP locality 3748 (=USGS loc. 8778) has produced fruits of *A. cranei (Negundo)* and leaves and fruits of *A. oligomedianum (Columbiana)*. Because the leaves of *A. glabroides* are highly dissimilar to foliage of *Negundo,* and because the leaves of *A. glabroides* and the remaining single samara both represent *Orba,* we consider these leaves and samara to represent the same species.

In shape and shallow lobing, leaves of *Acer glabroides* are most similar to those of *A. idahoense. Acer glabroides*, however, has more numerous subsidiary teeth than *A. idahoense* and subsidiary teeth are A-1 rather than D-1. Additionally, the medial lobe is more attenuated in *A. idahoense* than D-1. Additionally, the medial lobe is more attenuated in *A. idahoense* than in *A. glabroides.*

The fruit of *Acer glabroides* is, in nutlet outline and wing venation, similar to *A. bosrivularis*. In *A. glabroides*, however, the attachment angle is lower and the wing veins are thinner than in *A. bosrivularis*. Fruits of *A. idahoense* are also similar to the fruit of *A. glabroides*, although the wing of *A. glabroides* extends along almost the entire distal margin of the nutlet in contrast to *A. idahoense*, in which the wing is restricted to the apical third of the distal margin.

Distribution: Early Oligocene of central Oregon.

Typology: Lectotype here designated, UCMP 108A, B.

Occurrences: See appendix table.

Acer idahoense Wolfe et Tanai, sp. nov.

(pl. 7, figs. 5, 6, 9; pl. 10, figs. 15-20; text-fig. 16G)

Acer glabroides auct, non R.W. Brown. Brown. 1937b (part, non-typic). 180. pl. 58, f. 13.

Description: Leaves simple, perfectly actinodromous; shallowly 3-lobed, with medial

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Explanation of Plate 3.

(all figures natural size unless otherwise stated)

Figs. 1-3 *Acer toradense* Wolfe et Tanai. Republic/Resner Canyon. Holotype USNM 396010A, 396010B (Figs. 1, 2, ×7.5).

Fig. 4 *Acer toradense* Wolfe et Tanai. Princeton/Blue Flame Mine. Paratype UBCB 2400.

Fig. 5 *Acer stonebergae* Wolfe et Tanai. Princeton/One Mile Creek. Creek. Holotype PDMA 19840MC 1001.

Figs. 6, 7, 10,14 *Acer washingtonense* Wolfe et Tanai. Republic/Knob Hill. Paratypes UWBM 71135A (Figs. 6, 10), UWBM 71135B (Fig. 7), UWBM 56255 (Fig. 14).

Figs. 8, 9 *Acer stonebergae* Wolfe et Tanai. Republic. paratype UWBM 56254A (Fig. 8), UWBM 56254B (Fig. 9).

Fig. 11 *Acer washingtonense* Wolfe et Tanai. Republic/Resner Canyon. USNM 396011.

Figs. 12, 13, 16, 17 *Acer orbum* La Motte. Chalk Bluffs. Paratypes UCMP 2284 (Fig. 12), UCMP 2285 (Fig. 13), UCMP 2286 (Figs. 16, ×5; 17).

Figs. 15, 18 *Acer washingtonense* Wolfe et Tanai. Republic. Paratype UWBM 54308 (Fig. 18, ×5).


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lobe markedly larger than lateral lobes; shape oval, about 5 to 10 cm long, 4 to 7 cm wide; base rounded; medial lobe rounded-triangular, narrowing to an apparently acuminate apex; lateral primary veins parallel to medial secondary veins, broadly curved, craspedodromous; 5 to 8 secondary veins originating at angles of 30° to 50° from basal sides of lateral primary veins, broadly curving craspedodromous; 5 to at least 7 pairs of medial secondary veins, originating at angles of 30° to 60°, broadly curving, craspedodromous; a few intersecondary veins; tertiary veins that connect most basal medial secondary veins to lateral primary veins R-A and compound; other tertiary veins R-A and compound; fourth order venation typically quadrangular; fifth order venation forming quadrangular areoles 0.2 to 0.4 mm in diameter, veinlets absent or, if present, typically unbranched; lobal sinal bracing formed by a medial or lateral secondary vein that bifurcates near sinus; teeth D-1, typically 1 subsidiary tooth on basal flank and none on apical flank; 1 or more teeth on apical side of lateral lobes.

Fruits samaroid, nutlet at basal end; nutlets 0.5 to 0.8 cm long, 0.4 to 0.6 cm wide, triangular in outline, narrowly rounded apex, attachment scar 0.4 to 0.6 cm long; nutlet moderately inflated, smooth except for a medially placed flange; attachment angle 40°, nutlet angle 30° to 40°. Wing extending about 1/3 length of the distal margin of the nutlet, forming a distinct V-shaped sulcus; 1.1 to 1.7 cm long, 0.8 to 1.0 cm wide, distal margin broadly convex, proximal margin straight, apex rounded; proximal side with 5 to 7 coalesced veins, wing veins diverging at angles of 10° to 30°, irregular in course, irregularly bifurcating, few anastomoses.

Nomenclature: Although USNM 39428 (from Salmon, Idaho, here re-illustrated on pl. 7, fig. 9) was the only leaf of *Acer glabroides* illustrated by Brown (1937b) when he erected the species, the validating description for the species (Chaney, 1927) is based on leaves from the Gray Ranch locality, and one of the Gray Ranch specimens must serve as lectotype. The Gray Ranch *A. glabroides* is distinct from the Salmon material, and thus a new species is here proposed for the Salmon material.

Discussion: Leaves of *Acer idahoense* are characterized, in part, by typically having a single subsidiary tooth on the basal flank of a primary tooth. As well, intersecondary veins are present; these may have resulted from reduction of secondary veins. One

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Explanation of Plate 4.

(all figures natural size unless otherwise stated)

Figs. 1-4, 15 *Acer rousei* Wolfe et Tanai. McAbee. Paratypes TMP P83.39.586A (Fig. 1), TMP P83.39.586B (Figs. 2; 15, ×5), TMP P83.39.585A (Fig. 3), UBCB 2401 (Fig. 4).

Figs. 5, 6 *Acer rousei* Wolfe et Tanai. Princteon/One Mile Creek. Paratype UWBM 54107A (Fig. 5). Holotype UWBM 56256A (Fig. 6).

Figs. 7-9, 12, 16, 17 *Acer wehri* Wolfe et Tanai. Republic. Holotype UWBM 39728A (Figs. 7; 16, ×7.5), UWBM 39728B (Fig. 17, ×7.5). Paratypes UWBM 56257 (Fig. 8), USNM 396039 (Fig. 9), UWBM 56260 (Fig. 12).

Fig. 10 *Acer wehri* Wolfe et Tanai. Chu Chua Creek. Paratype GSC 82970A.

Fig. 11 *Acer wehri* Wolfe et Tanai. Princeton/One Mile Creek. Paratype UWBM 564108.

Figs. 13, 14, 18 *Acer republicense* Wolfe et Tanai. Republic. Holotype UAPC S5414A (Figs. 13; 18, ×7.5), UAPC S5414B (Fig. 14).


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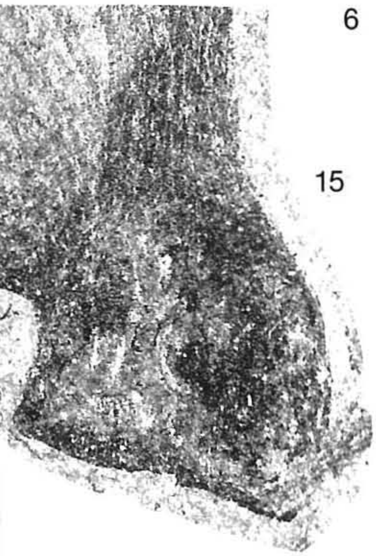
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specimen has lobal sinal bracing originating from lateral primary veins, a feature unique in *Glabroidea*.

Fruits of *Acer idahoense* are similar to the fruit of *A. bosrivularis* in size and in shape of the nutlet. The wing in *A. idahoense*, however, is restricted to the apical third of the distal margin of the nutlet.

Distribution: Late Eocene of west-central Idaho.

Typology: Holotype, USNM 396033A, B.

Occurrence: See appendix table.

Acer wehri Wolfe et Tanai, sp. nov.

(pl. 4, figs. 7-9, 10-12, 16, 17)

Acer negundoides auct. non MacGinitie. Brown. 1935 (part: reference to Republic material). 580.
Acer oregonianum auct. non Knowlton. Berry. 1929 (part: reference to Republic material). 255.

Description: Fruits samaroid; nutlet at basal end; nutlets 0.5 to 0.7 cm long, 0.5 to 0.7 cm wide, outline broadly triangular, apex rounded, attachment scar 0.5 to 0.7 cm long with conspicuous distal keel, nutlet slightly inflated; about 10 approximately parallel and obscure veins in apical 1/2 of nutlet, extending onto wing; broad flange over 1/2 width of nutlet basally and narrowing apically; attachment angle 50° to 55°, nutlet angle 30° to 40°. Wing extending along apical 1/3 to 1/2 of distal side of nutlet, forming a broadly U-shaped sulcus, 2.0 to 2.5 cm long, 0.8 to 1.0 cm wide, widest in apical 1/3; distal margin broadly convex, proximal margin straight apex narrowly rounded; veins from nutlet coalescing after passing onto wing along proximal side, then diverging at angles of 10° to 30°, dichotomizing 3 to 5 times, numerous anastomoses.

Nomenclature: Wesley Wehr has been of immeasurable assistance and encouragement. He has supplied most material of Republic *Acer*, as well as other material from the Tertiary of the Pacific Northwest.

Discussion: As noted above, *Acer wehri* appears to be closely related to several later species of *Glabroidea*.

Distribution: Early middle Eocene of northeastern Washington and adjacent British Columbia.

Typology: Holotype, UWBM 39728A, B.

Occurrences: See appendix table.

Explanation of Plate 5.

(all figures natural size unless otherwise stated)

Figs. 1-4, 8, 9 *Acer stewarti* Wolfe et Tanai. Princeton/One Mile Creek. Paratypes UWBM 56258 (Fig. 1), UWBM 54106A (Fig. 2), UWBM 54106B (Fig. 3), UMBM 56259A (Fig. 4), UAPC S6946A (Fig. 8), UAPC S6946B (Fig. 9).

Figs. 5, 13 *Acer spitzi* Wolfe et Tanai. Republic. Holotype UWBM 31272 (Fig. 13, ×7.5)

Figs. 6, 7, 12 *Acer hillsi* Wolfe et Tanai. Republic. Holotype UWBM 56260A, (Figs. 6; 12, ×7.5), UWBM 56260B (Fig. 7).

Figs. 10, 11, 14 *Acer stockeyae* Wolfe et Tanai. Princeton/One Mile Creek. Holotype UAPC S13273B, S13273A (Fig. 14, ×5)

Figs. 15, 16 *Acer princetonense* Wolfe et Tanai. Princeton/One Mile Creek. Holotype UAPC S5543 (Fig. 16, ×5)


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Acer florissanti Kirchner

(pl. 8, figs. 1-7; pl. 9, figs. 1-8; pl. 12, figs. 1-9; text-fig. 16D-A)

Acer florissanti Kirchner. 1898. 181. pl. 11, f. 1.
  MacGinitie. 1953. 139. pl, 57, f. 1; pl. 58, f. 2, 4, 7, 9; pl. 59, f. 1c; pl. 73, f. 8.
  Becker. 1961 (part). 79. pl, 25, f. 5.
Acer mystichum Kirchner. 1898. 181. pl. 11, f. 2.
Acer kirchnerianum Knowlton. 1916. 282.
Acer glabroides auct. non R.W. Brown. Becker. 1969 (part). 113, pl. 35, f. 15; pl. 36, f. 3.
Acer indivisum Lesquereux (part, non-typic; non Weber, 1852). 1883. 18. pl. 36, f. 9.

Description: Leaves simple, perfectly actinodromous; typically deeply (87%) 3-lobed, but some (13%) 5-lobed; shape typically ovate, but some wide ovate to very wide ovate, length 1.6 to 6.4 cm, width 2.0 to 8.1 cm; base rounded to truncate; medial and lateral lobes typically elliptic and acute to attenuate apices; medial lobe at least 1-1/2 as long as lateral lobes medial lobe with 1 to 4 lobations; lateral (or most apical lateral primary veins in 5-lobed leaves) primary veins slightly diverging from medial secondary veins; 4 to 6 secondary veins originating from apical side, broadly convex, typically craspedodromous (or rarely bifurcating); 3 to 9 pairs of broadly convex medial secondary veins, the most basal pair bifurcating near lobal sinus, the more apical pairs alternating between craspedodromous and bifurcating veins; tertiary veins typically A-A and compound; fourth order venation quadrangular; fifth order venation quadrangular, forming areoles 0.2 to 0.4 mm in diameter, without veinlets or, if present, veinlets unbranched; teeth D-1, typically with 1 to 3 subsidiary teeth on basal flank and 1 to 3 subsidiary teeth on apical flank; petiole 1.0 to 2.8 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.5 to 0.8 cm long, 0.3 to 0.6 cm wide, elliptic in outline, broadly rounded apex; attachment scar 0.3 to 0.6 cm long; nutlet moderately inflated; smooth, except for a large, medially placed flange; attachment angle 30° to 45°, nutlet angle 40° to 50°. Wing extending almost entire lenth of distal margin of nutlet; 1.0 to 2.2 cm long, 0.5 to 1.0 cm wide, distal margin shallowly convex, proximal margin straight, apex broadly rounded; proximal side with 5 to 7 coalesced veins, wing veins diverging at angles of 30° to 50°, smoothly curving, bifurcating, numerous anastomoses.

Nomenclature: Supposedly named for the town of, or fossiliferous beds near, Florissant, Colorado, the proper epithet should have been *florissantense, florissantensis*, or *florissantum*.

Discussion: Except for three fruits of *Negundo (Acer macginitiei)*, the only fruits of *Acer* at Florissant are those described as *A. mystichum*; 20 of these fruits are present in the collections examined. Leaves of *Acer* at Florissant represent only *A. florissanti*;

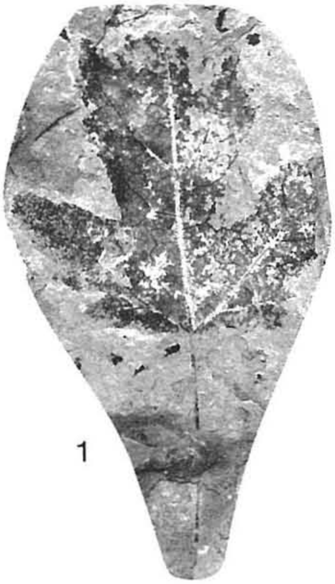
Explanation of Plate 6.

(all figures natural size unless otherwise stated)

Figs. 1, 2, 5 *Acer elkoanum* Wolfe et Tanai. Elko. Paratypes UCMP 9021A (Fig. 1), USNM 396023A (Fig. 5). Holotype USNM 396022A (Fig. 2).

Figs. 3, 6, 7 *Acer elkoanum* Wolfe et Tanai. Bull Run. Paratypes UCMP 9023 (Fig. 3), UCMP 9024 (Fig. 6), UCMP 9025 (Fig. 7, ×2.5)

Fig. 4 *Acer* sp. 4. Copper Basin. UCMP 20113.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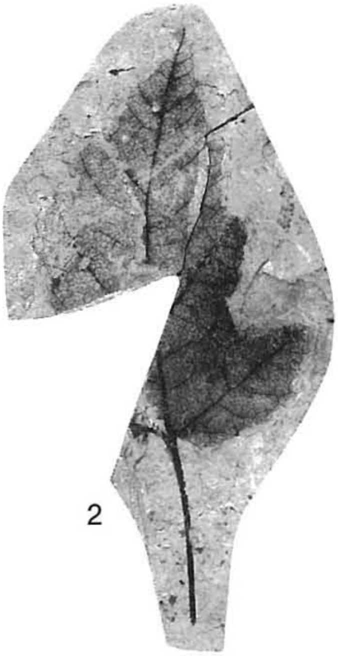
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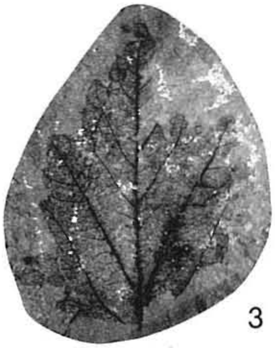
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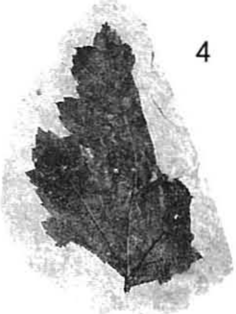
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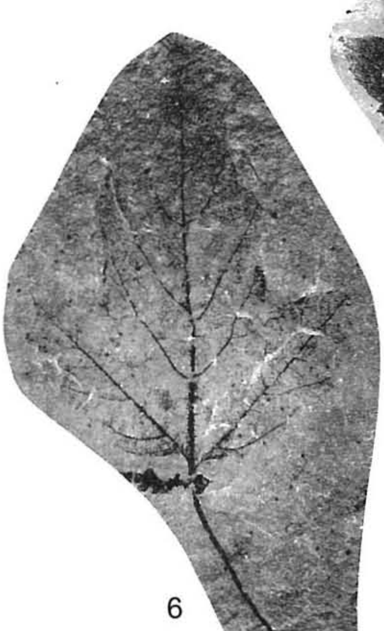
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about 40 of these leaves have been examined. Leaves of *A. florissanti* are certainly unrelated to *Negundo*, and we assume that *A. florissanti* and *A. mystichum* represent the same species. *Acer florissanti* is unique in *Glabroidea* in having some five-lobed leaves, although these are uncommon. Lobations are also particularly well developed on both sides of all lobes in *A. florissanti*. As well, teeth of *A. florissanti* are typically sharper than in other species of *Glabroidea* except in *A. elwyni*.

Distribution: Latest Eocene of central Colorado and possibly latest Eocene of southwestern Montana. The specimen from the Ruby flora of Montana (Becker, 1969) is in matrix more similar to that containing the Florissant leaves than to other Ruby matrix. The citation of *Acer indivisum* Lesquereux (1883) is based on a specimen from Florissant and not from the Green River Formation.

Typology: Holotype, USNM 33673; not illustrated here because the specimen, although comparing well in outline and major venation to our pl. 9, fig. 1, is very poorly preserved.

Occurrences: See appendix table.

Acer jarbidgianum Wolfe et Tanai, sp. nov.

(pl. 11, figs. 4, 9, 10, 18-20)

Acer bolanderi auct. non. Lesquereux. Axelrod. 1966. 75. pl. 18, f. 13.
Acer columbianum auct. non Chaney et Axelrod. Axelrod. 1966 (part). 76. pl. 18, f. 2-5.
Acer minor auct. non Knowlton. Axelrod. 1966. 76.

Description: Fruits samaroid, nutlets at basal end; nutlets 0.4 to 0.5 cm long, 0.4 to 0.5 cm long; oval to round in outline, broadly rounded apex; attachment scar 0.4 to 0.5 cm long, with a distal keel; nutlet moderately inflated; several obscure parallel veins on apical part of nutlet; a broadly triangular short flange on medial part of nutlet; attachment angle 35°, nutlet angle 20° to 40°. Wing entirely apical to nutlet; 2.0 cm long, 0.5 cm wide; distal margin broadly convex, proximal margin straight, apex narrowly rounded; proximal side with 6 coalesced veins wing veins diverging at angles of 20° to 40°, smoothly curving, bifurcating, few anastomoses.

Nomenclature: Type locality is near Jarbidge, Nevada.

Discussion: The attachment scar of *Acer jarbidgianum* has a distal keel as in *A. wehri*; the shape of the nutlet flange is also similar, although the flange is smaller in *A. jarbidgianum* than in *A. wehri*. Other than their smaller size, fruits of *A. jarbidgianum* differ from *A. wehri* in having a round nutlet outline.

Explanation of Plate 7.
(all figures natural size)

Figs. 1, 4, 7 *Acer elwyni* (Becker) Wolfe et Tanai. Mormon Creek. Paratypes UMMP 36487 (Fig. 1), UMMP 36431 (Fig. 4). Holotype UMMP 36429 (Fig. 7).

Figs. 2, 8 *Acer elwyni* (Becker) Wolfe et Tanai. Ruby. Hypotypes UMMP 36931 (Fig. 2), UMMP 51456 (Fig. 8).

Fig. 3 *Acer elwyni* (Becker) Wolfe et Tanai. Metzel Ranch. Hypotype NYBG 2072B (Fig. 3).

Figs. 5, 6, 9 *Acer idahoense* Wolfe et Tanai. Salmon. Paratype USNM 396033A (Fig. 5), USNM 39428 (Fig. 9). Holotype USNM 396033A (Fig. 6).


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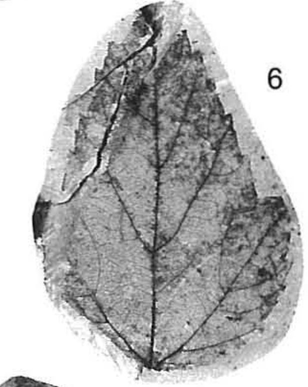
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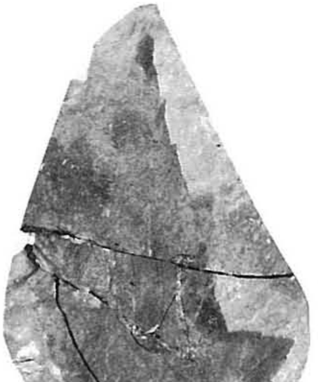
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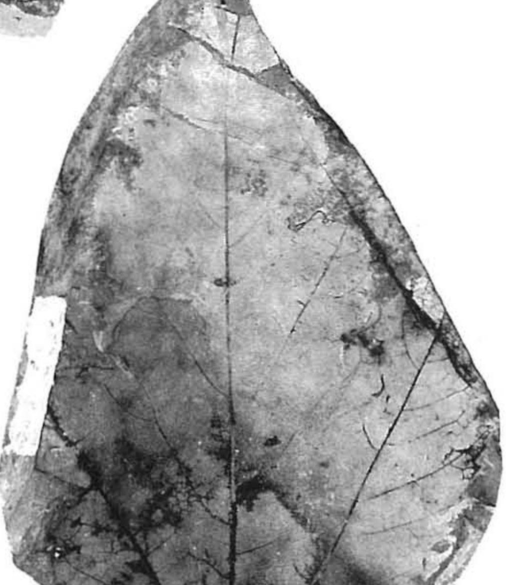
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Distribution: Early late Eocene of northeastern Nevada.
Typology: Holotype, UCMP 20120.
Occurrence: See appendix table.

Acer meyeri Wolfe et Tanai, sp. nov.

(pl. 11, figs. 11, 16)

Description: Fruit samaroid; nutlet at basal end; nutlet slightly inflated, broadly triangular, 0.6 cm long, 0.5 cm wide, apex broadly rounded; 2 distinct flanges forming a broad, V-shaped area; proximal margin markedly convex; attachment angle 20°, nutlet angle 40°. Wing extending to attachment scar; distal margin convex, proximal margin convex, apex broadly rounded; 6 veins coalesced along proximal margin; wing veins diverging at angles of 10° to 30°, anastomosing several times, some veinlets.
Nomenclature: H.W. Meyer has made major collections from particularly the Gumboot Mountain and Lyons localities.
Discussion: Acer meyeri has the nutlet shape of some specimens of *A. florissanti* but has flanges that form a broad, V-shaped area and has a pronouncedly convex margin.
Distribution: Late middle to early late Eocene of central Oregon.
Typology: Holotype, UCMP 9028.
Occurrence: See appendix table.

Acer milleri Wolfe et Tanai, sp. nov.

(pl. 13, figs. 5, 7; text-fig. 16Ha, b)

Description: Leaves simple, perfectly actinodromous; shallowly to deeply 3-lobed; medial lobe about twice as large as lateral lobes; shape wide elliptic to ovate; base broadly rounded; medial lobe elliptic, apex acute to rounded with 1 pair of lobations; lateral lobes tapering to acute to rounded apices; lateral primary veins parallel to, or slightly diverging from, medial secondary veins; 5 or 6 secondary veins originating from basal sides of lateral primary veins at angles of 30° to 60°, straight to broadly convex, craspedodromous; 1 to 3 secondary veins originating from apical sides of lateral primary veins, broadly convex, craspedodromous, 4 or 5 pairs of medial secondary veins originating at angles of 30° to 40°, straight to broadly convex, the most basal pair acutely bifurcating to brace the lobal sinus, the others craspedodromous; tertiary veins A-A and compound; fourth order venation irregularly polygonal; fifth order veins thin, forming quadrangular areoles 0.2 to 0.5 mm in diameter, veinlets typically absent, or, if present, unbranched; teeth A-1, with no or 1 subsidiary tooth on basal flank and none on apical flank; petiole over 2.2 cm long.
Nomenclature: Charles A. Miller generously furnished us with undescribed material

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Explanation of Plate 8.
(all figures natural size)

Figs. 1-7 *Acer florissanti* Kirchner. Florissant. Hypotypes UCM-PB 34052 (Fig. 1), UCM-PB 34051 (Fig. 2), UCM-PB 34053 (Fig. 3), USNM 396042 (Fig. 4), DMNH 804 (Fig. 5), DMNH 802 (Fig. 6), UCMP 3827 (Fig. 7).

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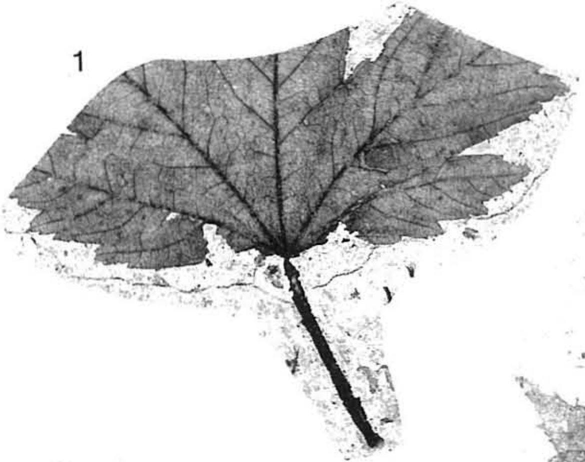

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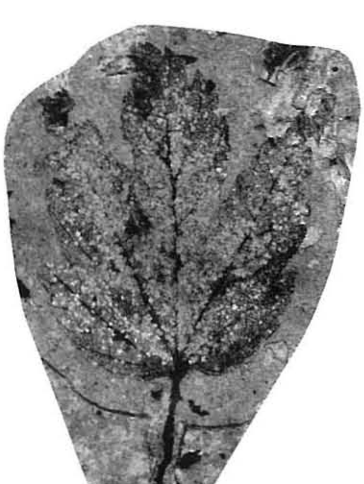

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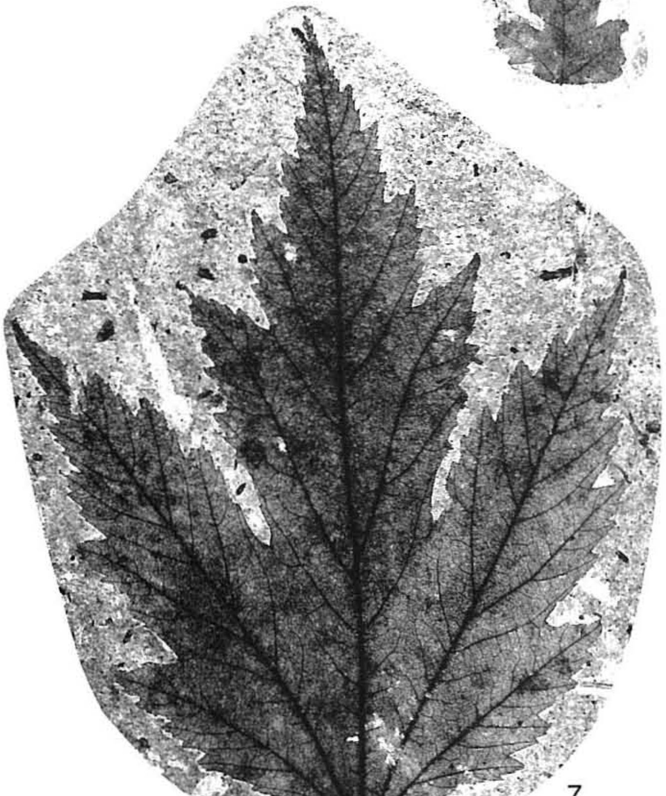

from the Beaver Creek locality.
Discussion: The three-lobed condition, acutely braced lobal sinuses, and areolar venation suggest that *Acer milleri* is a member of *Glabroidea*. Within *Glabroidea, A. milleri* is unique in having a single pair of large lobations on the medial lobe combined with A-1 teeth. As noted following, *A. milleri* is similar to the unnamed *A.* sp. 3 from Whipsaw Creek.
Distribution: Latest Eocene of western Montana.
Typology: Holotype, UCMP 9307A, B.
Occurrence: See appendix table.

Acer sp. 3

(pl. 2, fig. 5)

Discussion: A single leaf from the Whipsaw Creek locality lacks venation above the third order. That the leaf possibly represents *Glabroidea* is indicated by the trilobed condition with the medial lobe dominant, tertiary veins that connect the most basal medial secondary veins to the lateral primary veins and that are A-A and compound, lobal sinal bracing that is accomplished by medial secondary veins that bifurcate near the sinuses, presence of lobations on the medial lobe, and large D-1 teeth.

The Whipsaw Creek species of *Acer* has a narrowly rounded base, weakly incised lateral lobes that extend halfway to the apex, a broadly triangular medial lobe, and lobations that have a rounded-triangular outline. This last specialized character indicates a relationship to *A. milleri*, which, however, has more deeply incised lobes; in *A. milleri* the distance between the apices of medial lobations is equal to, or typically greater than, the distance between lobal sinuses.
Distribution: Early middle Eocene of southern British Columbia.
Occurrence: See appendix table.

Acer sp. 4

(pl. 6, fig. 4)

Discussion: The only leaf of *Acer* from Copper Basin apparently represents *Glabroidea*. This sectional assignment is indicated by the trilobed condition, small size of the lateral lobes relative to the medial lobes, presence of distinct lobations on the medial lobe, lobal sinal bracing formed by a bifurcating medial secondary vein, D-1 teeth, and quadrangular areoles about 0.2 to 0.3 mm in diameter. Most areoles lack veinlets; a few areoles have a single, unbranched veinlet.

The lateral lobes of *Acer* sp. 4 are shallowly incised and are about the same size as the medial lobations; this last character sets this species apart from other species of *Glabroidea*.

Explanation of Plate 9.
(all figures natural size)
Figs. 1-8 *Acer florissanti* Kirchner. Florissant. Hypotypes USNM 396040 (Fig. 1), USNM 396043 (Fig. 2), UCM-PB 34054 (Fig. 3), UCM-PB 34055 (Fig. 4), DMNH (Fig. 5), USNM 306044 (Fig. 6), USNM 396040 (Fig. 7), UCM-PB 34056 (Fig. 8).

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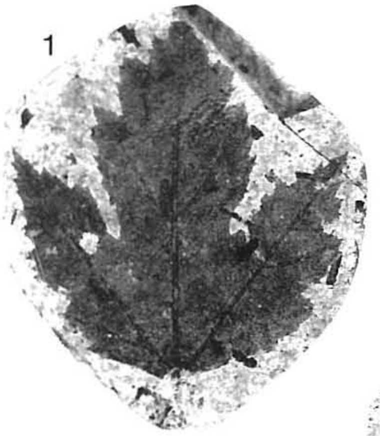

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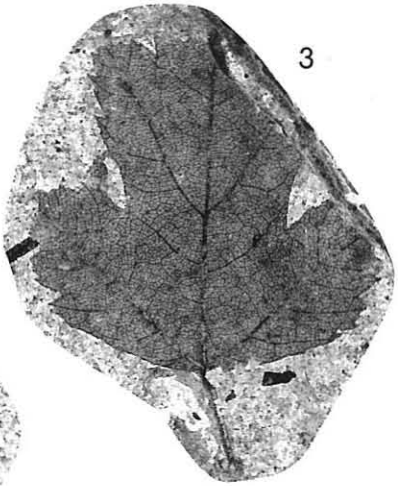

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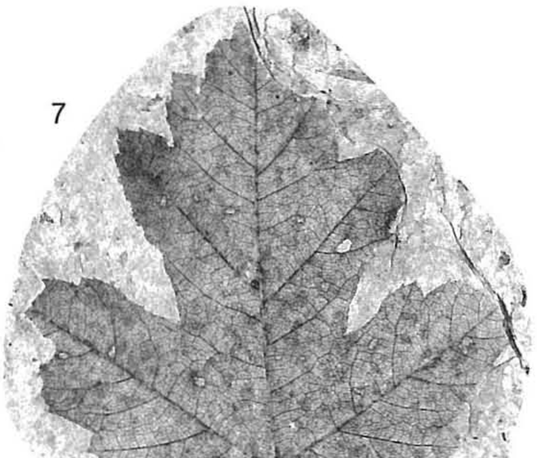

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Distribution: Early late Eocene of northeastern Nevada.
Occurrence: See appendix table.

Macrophylla Group

Section *Princetona* Wolfe et Tanai, sect. nov.

Diagnosis: Fruit samaroid; nutlet at basal end; fruit large; nutlet markedly inflated, shape elliptic, elongated along attachment scar, proximal margin markedly convex; attachment angle low; two flanges almost fused in distal 1/3 of nutlet; attachment scar with marked distal spur; wing mostly apical to nutlet; numerous wing veins coalesced along proximal margin; wing veins with numerous anastmoses; veinlets reticulate.
Discussion: See below.
Type species: Acer princetonense Wolfe et Tanai.

Acer princetonense Wolfe et Tanai, sp. nov.

(pl. 5, figs. 15, 16)

Description: Fruit samaroid; nutlet at basal end; nutlet 1.2 cm long, 0.8 cm wide, elliptic, markedly inflated; nutlet with 2 flanges placed in distal 1/3 of the nutlet and curving approximately parallel to the distal margin of nutlet; attachment angle 30°, nutlet angle 20°; veins on nutlet obscure; proximal margin of nutlet markedly convex. Wing 3.0 to 4.0 cm long, 1.1 to 1.4 cm wide; proximal margin straight, distal margin broadly convex, forming a shallow notch with nutlet; proximal margin with 9 prominent veins that appear to originate equally spaced along apicl margin of nutlet; wing veins diverging from proximal margin at angles of 30° to 50°, dichotomizing >4 times, numerous anastomoses, veinlets reticulate.
Nomenclature: Type locality furnished part of the Princeton flora.
Discussion: Marked nutlet inflation, elongated oval shape of the nutlet, low attachment angle, and large wing are characters that indicate a relationship to *Macrophylla;* preservation does not allow a determination as to presence or absence of nutlet pubescence. The two flanges on the nutlet, however, indicate a relationship to the *Orba* Group.
Distribution: Early middle Eocene of southern British Columbia.

Explanation of Plate 10.

(all figures natural size unless otherwise stated)

Figs. 1, 2, 5 *Acer crookense* Wolfe et Tanai. Sheep Rock Creek. Holotype UCMP 9020A, (Figs. 1, ×7.5; 5), UCMP 9020B (Fig. 2, ×7.5).

Fig. 6 *Acer crookense* Wolfe et Tanai. Elko. Paratype USNM 396029.

Figs. 3, 4, 9 *Acer bosrivularis* Wolfe et Tanai. Cow Creek. Holotype USNM 396021A (Figs. 3, ×7.5; 9), USNM 396021B (Fig. 4, ×7.5).

Figs. 7, 8, 12-14 *Acer elkoanum* Wolfe et Tanai. Cow Creek. Paratypes USNM 396025A (Fig. 7, ×7.5), USNM 396025B (Fig. 8, ×7.5), USNM 396026 (Fig. 12), USNM 39027 (Fig. 13), USNM 39028 (Fig. 14).

Figs. 10, 11 *Acer becki* Wolfe et Tanai. Sheep Rock Creek. Paratype UCMP 9305 (Fig. 10). Holotype UCMP 9304 (Fig. 11).

Figs. 15-20 *Acer idahoense* Wolfe et Tanai. Salmon. Paratypes USNM 396036 (Fig. 15), USNM 396037A (Figs. 16; 19, ×7.5), USNM 396037B (Figs. 17; 20, ×7.5), USNM 396038 (Fig. 18).


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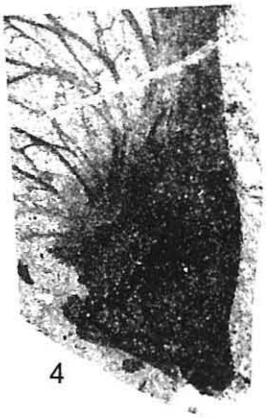
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Typology: Holotype, UAPC S5543.
Occurrence: See appendix table.

Section *Macrophylla* (Pojarkova) Ogata

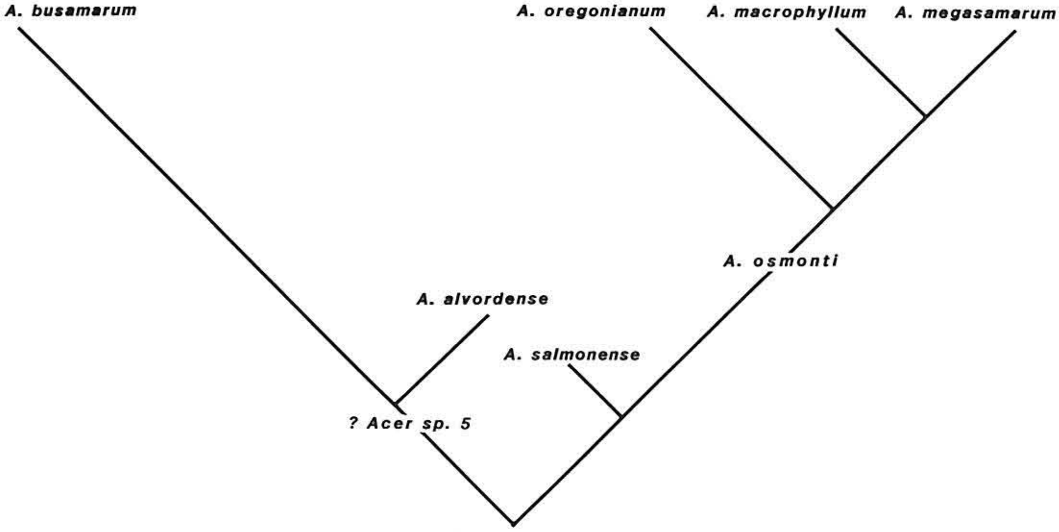
Discussion: The name *Acer oregonianum* Knowlton has been applied to western American Tertiary fossils of *Macrophylla* of late Eocene through Neogene age, with the exception of the Beringian *A. megasamarum* (= *A. grahamensis* of Wolfe & Tanai, 1980). Within the material previously referred to *A. oregonianum,* we recognize seven species, which, with *A. megasamarum,* make *Macrophylla* the most second-most diverse section (after *Negundo*) in the late Eocene and post-Eocene of western North America.

The oldest known record of *Macrophylla* is the late (probably early late) Eocene *Acer alvordense.* The fruits of this species have several similarities to the 47-49 Ma. *A. princetonense,* which has a markedly inflated nutlet. The leaves of *A. alvordense* also have quadrangular areoles, but have branching veinlets (Type I), a character common to most species of the *Orba* Group. Leaves of the late Eocene *A. salmonense* have Type II areolar venation and have more numerous and sharper teeth than later species of *Macrophylla;* such dental characters might be expected in early *Macrophylla* if the section were derived from the *Orba* Group.

Possibly coeval with *A. alvordense* is *A.* sp. 5, represented only by a leaf fragment. This fragment has numerous, sharp teeth as in *A. salmonense,* but has one character that is well developed in the Miocene *A. busamarum.* By the early late Eocene, *Macrophylla* possessed a diversity that suggests that *Macrophylla* is at least as old as late middle Eocene.

The early Oligocene *Acer osmonti* appears to be derived from a form such as *A. salmonense.* The areolar venation possessed by *A. osmonti* is a pattern possessed by later species, such as *A. oregonianum, A. macrophyllum,* and *A. megasamarum;* this pattern has large, irregularly polygonal areoles that have veinlets that branch two or three times. Of these three later species, *A. megasamarum* first appears in the late Oligocene of Beringia and is highly specialized in characters of the fruit. *Acer oregonianum,* which is the most similar to *A. osmonti,* first appears in the late Oligocene of western Oregon. The single fossil record of *A. macrophyllum* is early late Miocene in the mountains of west central Idaho. The indicated morphologic relations of the post-*osmonti* species suggests that, despite the poor fossil record of *A. macrophyllum,* we are basically dealing with a northward migrating evolutionary sequence of *A. oregonianum-A. macrophyllum* (or its immediate ancestor)-*A. megasamarum* during the Oligocene. *Acer oregonianum* evolved first in the southern area from *A. osmonti, A. macropohyllum* (or its immediate ancestor) evolved in British Columbia, and *A. megasamarum* evolved in Beringia. By the early middle Miocene, *A. megasamarum* had migrated southward into the Pacific Northwest. *Acer macrophyllum* may not have expanded its early range into the Pacific Northwest until the late Miocene, where it was apparently rare until all other species of *Macrophylla* had become extinct.

The Miocene *Acer busamarum* has areolar venation somewhat intermediate between that of *A. salmonense* (and *A. alvordense*) and that of *A. osmonti.* The *busamarum*



Text-fig. 17 Suggested cladistic relationships of species of section *Macrophylla.*

lineage diverged from the *osmonti-macrophylla* line from an ancestor that had *salmonense-alvordense* type areolar venation. As noted previously, a species coeval with *A. salmonense* had some characters of *A. busamarum.* Whereas *A. osmonti* and its derivatives were largely coastal, *A. busamarum* appears largely in the interior; if floras of Oligocene age were known in the interior, we suggest that representatives of *Macrophylla* would represent the *busamarum* type.

The earliest fruits assigned to *Macrophylla,* those of *Acer salmonense,* are small in comparison to later species of the section (table 8). The fruits of *A. alvordense* and *A.*

Table 8. Statistical comparisons of fruits of section *Macrophylla.*

La = length of attachment scar, Ln = width of nutlet (measured from midpoint of attachment scar to apex), Ls = length of samara (including nutlet).
All measurements are in centimetres. Measurements of extant *Acer macrophyllum* are based on material at CAS.

SPECIES	Average				Variation		
	No.	La	Ln	Ls	La	Ln	Ls
Acer megasamarum	7	0.9	1.2	5.7	0.6-1.0	1.0-1.5	5.0-6.8
A. macrophyllum							
extant	100	0.9	0.8	4.7	0.7-1.3	0.6-1.2	3.4-6.3
Thorn Creek	1	0.8	0.8	4.6			
A. oregonianum	9	1.0	0.8	4.9	0.7-1.4	0.6-1.1	3.8-5.6
A. busamarum ssp.							
busamarum	41	1.4	1.0	7.5	0.8-2.0	0.7-1.5	5.4-9.7
fingerrockense	36	1.1	0.8	6.3	0.7-1.4	0.6-1.1	4.6-8.1
A. osmonti	20	1.1	0.7	4.9	0.7-1.4	0.6-0.8	4.0-6.5
A. alvordense	6	0.8	0.6	4.7	0.8-0.9	0.5-0.7	4.0-6.3
A. salmonense	7	0.5	0.5	3.4	0.4-1.0	0.4-0.7	3.0-4.0

osmonti are about as large as those of the extant *A. macrophyllum* but are markedly smaller than those of *A. busamarum.* During the Miocene, the samaras of *Acer busamarum* underwent a significant increase in size. By the late middle to early late Miocene, the samaras are up to 9.7 cm long, which makes them the largest *Acer* samaras known. The nutlets of *A. busamarum* also increase significantly in size (up to 2 cm across). The relation between nutlet and samara size indicates that *A. busamarum* was still capable of autogyration (and hence wind dispersal), but the increase in nutlet size may indicate an adaptation also for animal dispersal; today, squirrels and other rodents collect the comparatively small fruits of *A. macrophyllum.*

Acer alvordense Axelrod

(pl. 17, figs. 16, 19; pl. 18, figs. 1-7; text-fig. 16Ja, b)

Acer alvordense Axelrod. 1944. 261. pl. 45, f. 6, 7; pl. 46, f. 1, 2.
Acer oregonianum auct. non Knowlton. Becker. 1969 (part). 113, pl. 35, f. 16.

Description: Leaves simple, perfectly actionodromous; deeply 5-lobed (some dissected almost to base); most apical lateral lobes almost as long as medial lobe, most basal lateral lobes up to 1/2 as long as most apical lateral lobes; shape orbiculate to oblate; 2 to (estimated) 15 cm long, 3 to 20 cm wide; base cordate, apex acute; most apical lateral primary veins slightly diverging from medial secondary veins; 6 to 8 secondary veins originating at angles of 30° to 60° from basal side of most apical primary veins, broadly convex, most brochidodromous; 7 or 8 pairs of medial secondary veins originating at angles of 30° to 70°, broadly curving, most brochidodromous; lobal sinal bracing formed by an angularly bifurcating medial secondary vein or by a fusion of a medial with a lateral secondary vein; intersecondary veins numerous, those basal to the lobal sinal bracing and originating from the midrib almost orthogonal to midrib; tertiary veins compound, R-A, A-A, or R-R, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.4 to 0.6 mm in diameter, veinlets 1 to 3 times branching; teeth large, narrowly rounded, C-1, or poorly defined, rounded bumps; typically 2 or 3 teeth on basal side of most apical lateral lobes and on medial lobe, no subsidiary teeth; petiole 3.0 to 6.5 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.8 to 0.9 cm long; 0.5 to 0.7 cm wide; outline very widely ovate, apex broadly rounded; proximal margin tangential to proximal margin of samara; attachment scar 0.7 to 0.9 cm long, with distal keel; nutlet

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Explanation of Plate 11.

(all figures natural size unless otherwise stated)

Figs. 1-3, 5-8 *Acer cuprovallis* Wolfe et Tanai. Copper Basin. Paratype UCMP 20126A (Figs. 1, ×7.5; 5), UCMP 20126B (Figs. 2, ×7.5; 6). Holotype UCMP 20127A (Figs. 3, ×7.5; 7), UCMP 20127B (Fig. 8).

Figs. 4, 9, 10, 18-20 *Acer jarbidgianum* Wolfe et Tanai. Copper Basin. Paratypes UCMP 20120, (Figs. 4; 9, ×7.5), UCMP 20115A (Fig. 10), UCMP 20130 (Fig. 19). Holotype UCMP 20114A (Fig. 18, ×7.5) UCMP 20114B (Fig. 20, ×7.5).

Figs. 11, 16 *Acer meyeri* Wolfe et Tanai. Sheep Rock Creek. Holotype UCMP 9028 (Fig. 11, ×7.5).

Figs. 12-15; 17 *Acer elwyni* (Beck) Tanai et Wolfe. Metzel Ranch. Paratypes NYBG2093A (Fig. 12), NYBG 2093B (Fig. 13), NYBG 2097A (Fig. 14), NYBG 2097B (Fig. 15), NYBG 2091A (Fig. 17, ×5).


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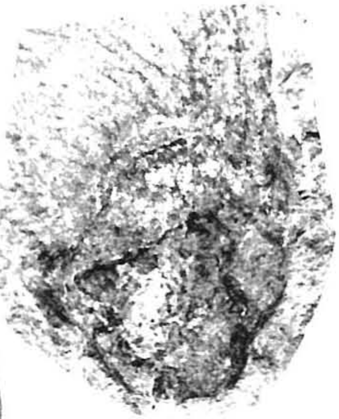
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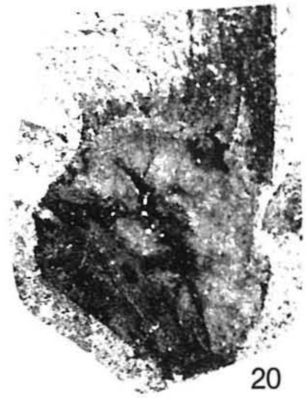
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markedly inflated, with 12 to 16 poorly defined veins of equal strength originating along attachment scar and converging apical to nutlet; attachment angle 20° to 30°, nutlet angle 40° to 50°; nutlet with simple hairs. Wing entirely (or almost so) apical to nutlet, forming a shallow U-shaped sulcus with nutlet; 3.3 to 5.5 cm long, 1.0 to 1.8 cm wide; distal margin broadly and deeply convex, proximal margin straight, apex narrowly to broadly rounded; 12 to 14 strongly coalesced veins along proximal side, wing veins diverging at angles of 10° to 30°, sharply curving then extending straight to shallowly convex, bifurcating, numerous anastomoses.

Nomenclature: Type locality is in the Alvord Creek Formation.

Discussion: Although Axelrod (1944) considered leaves of *Acer alvordense* to be separable from those of the "fossil equivalent" of *A. macrophyllum* only on degree of dissection, the leaves (as well as samaras) of *A. alvordense* differ from *A. oregonianum* and *A. macrophyllum* in several respects. Areoles in *A. alvordense* are smaller. If leaves of *A. macrophyllum* are deeply dissected (although they are never as deeply dissected as some leaves of *A. alvordense*), teeth are also very large (that is, the dental, as well as lobal, sinuses are deeply dissected), whereas in *A. alvordense* the most deeply dissected leaves have the most reduced teeth. Lobes of *A. alvordense* have a far greater length/width ratio than in *A. macrophyllum* or *A. oregonianum.* The nutlet of *A. alvordense* is smaller and has far fewer veins and the sulcus is shallower than in *A. macrophyllum* or *A. oregonianum.*

Some leaves of *Acer alvordense* have the major sinus between medial and most apical lateral lobes extending almost to the laminar base. If continued, such deep dissection could result in a trifoliate leaf. Considering that in *A. alvordense* deep dissection is accompanied by reduction in teeth, a resulting trifoliate leaf would have small teeth (or even be entire-margined); such a leaf would be similar the trifoliate leaf of *Trifoliata,* although no relationship to *Trifoliata* is suggested.

Distribution: Late Eocene of southeastern Oregon and southwestern Montana.

Typology: Holotype, UCMP 2137, A, B.

Occurrences: See appendix table.

Acer salmonense Wolfe et Tanai, sp. nov.

(pl. 17, figs. 1-6, 8-11; text-fig. 16I)

Acer bendirei auct. non Lesquereux. Brown. 1937b (part). 179. pl. 58, f. 21.

Description: Leaves simple, perfectly actionodromous; 5-lobed; the most apical lateral lobes about 2/3 as long as medial lobe, most basal lateral lobes distinct; shape ovate to very widely ovate; 2.5 to 5.0 cm long, 1.7 to 6.0 cm wide; base cordate, apex acute; lobes

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Explanation of Plate 12.

(all figures natural size unless otherwise stated)

Figs. 1-9 *Acer florissanti* Kirch. Florissant. Hypotypes UCMG 18702 (Fig. 1), UCMP 3834 (Fig. 2), USNM 396045 (Fig. 3), USNM 333296 (Fig. 4, ×7.5), USNM 333401 (Fig. 5, ×7.5), UCMP 20819 (Fig. 6, ×7.5; 7), USNM 33674 (Fig. 8; holotype of *A. mystichum* Kirchner), UCMG 5188(D) (Fig. 9).

Figs. 10, 11 *Acer cadaver* Wolfe et Tanai. Bull Run. Holotype UCMP 9019 (Fig. 11, ×5).

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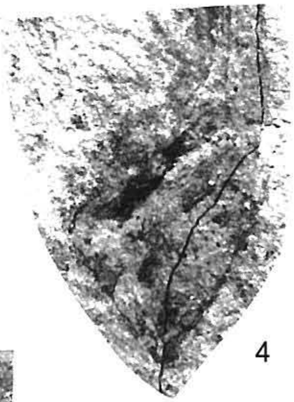

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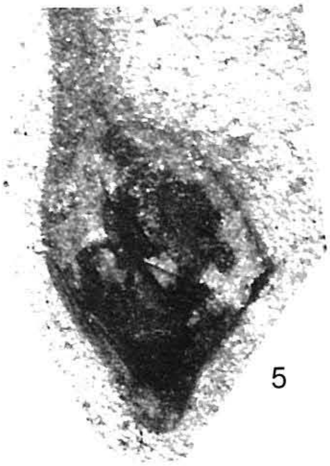

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triangular to ovate; most apical lateral primary veins diverging from medial secondary veins; 5 or 6 secondary veins originating at angles of 30° to 60°, broadly convex, craspedodromous; 4 or 5 pairs of medial secondary veins originating at angles of 40° to 60°, straight to broadly convex, craspedodromous; lobal sinal bracing formed by an acutely bifurcating secondary vein; tertiary veins compound, R-A, spaced about 0.2 mm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.1 to 0.3 mm in diameter, veinlets absent or unbranched; teeth large, sharp, C-1, C-2, or C-3, 3 on basal side and 1 or 2 on apical side of most apical lateral lobes, 5 or 6 on each side of medial lobe, the subsidiary tooth on basal flank of basal tooth of medial lobe; petiole at least 1.6 cm long.

Fruits samaroid, nutlet at basal end; nutlets 0.4 to 1.0 cm long, 0.4 to 0.7 cm wide, outline ovate, apex broadly rounded; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.3 to 0.7 cm long; nutlet markedly inflated, smooth; attachment angle 0° to 30°, nutlet angle 40° to 50°. Wing entirely apical to nutlet, forming a broadly U-shaped sulcus with nutlet; 2.0 to 3.1 cm long, 0.7 to 1.3 cm wide; distal margin broadly convex, proximal margin straight, apex narrowly to broadly rounded; 8 to 10 veins coalesced along proximal side, wing veins diverging at angles of 10° to 20°, sharply curving and extending straight, bifurcating, anastomoses numerous.

Nomenclature: Type locality is near Salmon, Idaho.

Discussion: Brown (1937b) correctly placed the fruits of *Acer salmonense* in *Macrophylla.* They are strongly inflated, the nutlets have an ovate outline, the attachment angle is low, and a pronounced sulcus is present.

Foliage of *Acer salmonense* has Type II areolar venation rather than the Type I of extant *Macrophylla,* although rounded sinuses, few C-1 to C-3 teeth, and spreading five lobes relate the fossil leaves to *Macrophylla.* Sharpness of teeth of *A. salmonense* is also atypical for extant *Macrophylla.*

Distribution: Late Eocene of east central Idaho and latest Eocene of western Montana.

Typology: Holotype, USNM 396141.

Occurrence: See appendix table.

Acer osmonti Knowlton

(pl. 28, figs. 1, 2, 4; pl. 29, figs. 1-3; pl. 30, figs. 1, 3, 5; pl. 31, figs. 1-6; text-fig. 16K)

Acer osmonti Knowlton. 1902. 72. pl. 13, f. 3
Chaney. 1927 (part). 126. pl. 18, f. 8, 9.

Description: Leaves simple, perfectly actinodromous; 5- to 7-lobed; the most apical lateral lobes as long (or almost so) as medial lobe, the next more basal lobes about 1/2 as

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Explanation of Plate 13.
(all figures natural size)

Fig. 1 *Acer* sp. 2. Rex Creek. USNM 396013.

Figs. 2-4 *Acer ivanofense* Wolfe et Tanai. Road Island. Paratypes USNM 396017B (Fig. 2), USNM 396017C (Fig. 3). Holotype USNM 396012A (Fig. 4).

Figs. 5-7 *Acer milleri* Wolfe et Tanai. Beaver Creek. Paratypes UCMP 9308 (Fig. 5), UCMP 9309 (Fig. 7). Holotype UCMP 9307A (Fig. 6).


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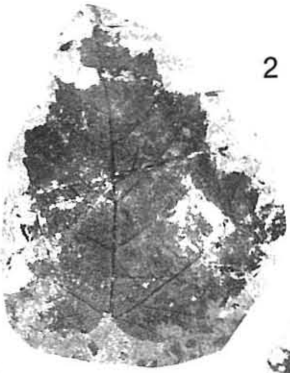
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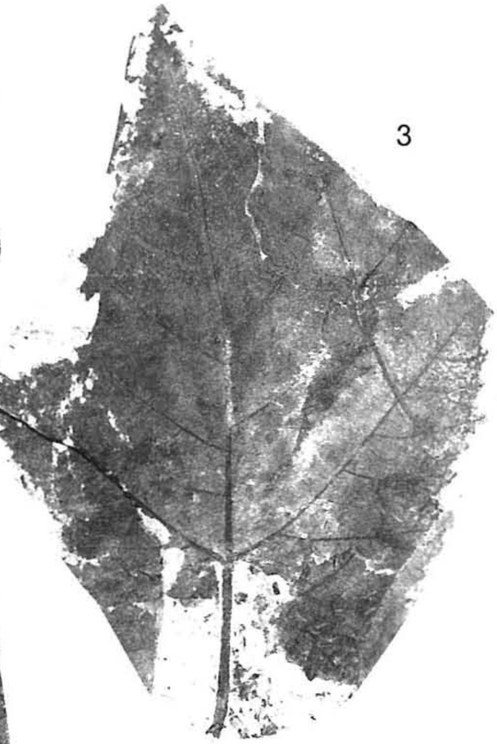
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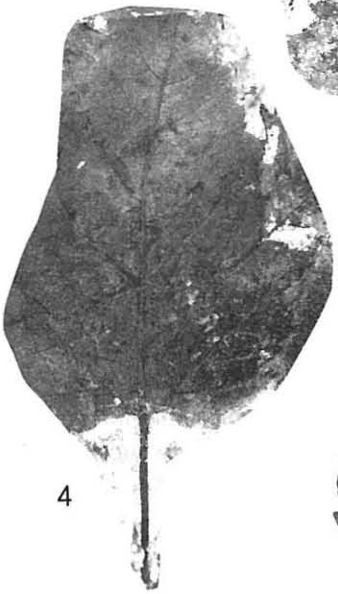
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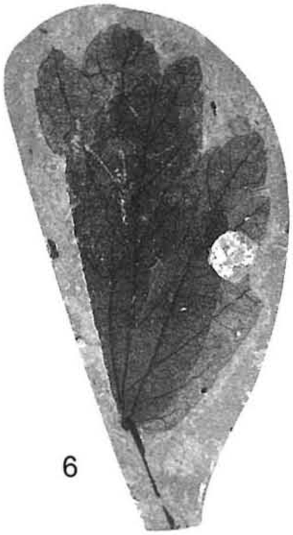
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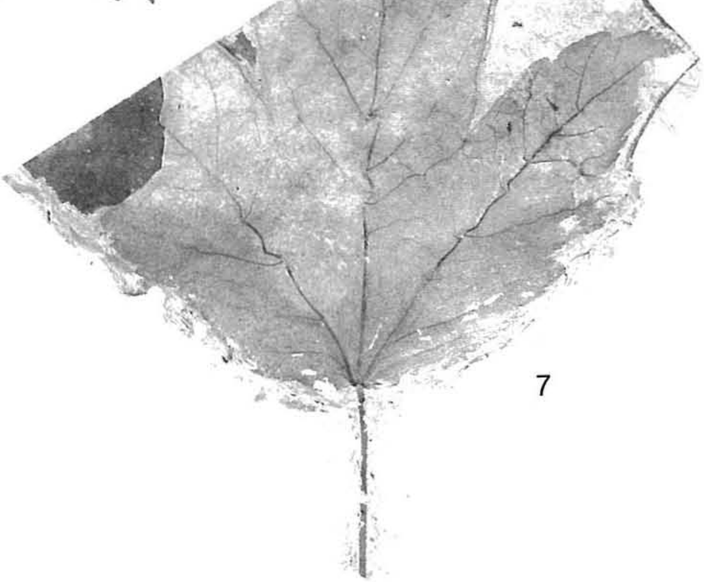
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long as most apical lateral lobes; shape orbiculate; base cordate, apex acute; 4.5 to 22 cm long, 5.5 to 24 cm wide; lobes elliptic; most apical lateral primary veins slightly diverging from medial secondary veins; 5 to 9 secondary veins originating at angles of 30° to 70° from basal side of most apical lateral primary veins, straight to broadly convex, 1/2 craspedodromous and 1/2 brochidodromous; 8 or 9 medial secondary veins originating at angles of 40° to 50°, straight to broadly convex, half craspedodromous and half brochidodromous; lobal sinal bracing formed by an angularly bifurcating medial secondary vein; intersecondary veins numerous, those basal to the lobal sinal bracing and originating from midrib almost orthogonal to midrib; tertiary veins compound, A-A, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.7 to 1.2 mm in diameter, veinlets branching 2 or 3 times; teeth large, sharp, C-1 or C-2, typically 5 on each side of medial and basal side of most apical lateral and basal side of most basal lateral lobes; 1 or 2 small subsidiary teeth on basal flank of largest teeth.

Fruit samaroid, nutlet at basal end; nutlet 0.7 to 1.4 cm long, 0.6 to 0.8 cm wide; outline ovate, apex broadly rounded; proximal margin tangential to proximal margin of samara; attachment scar 0.8 to 1.2 cm long, with distal keel; nutlet markedly inflated, 16 to 20 veins of equal size originating along attachment scar and coalescing beyond apex of nutlet; attachment angle 15° to 35°, nutlet angle 30° to 40°; nutlet with many, simple hairs. Wing entirely apical to nutlet, forming a U-shaped or V-shaped sulcus with nutlet; 3.5 to 5.2 cm long, 1.1 to 1.8 cm wide; distal margin deeply convex, proximal margin straight, apex broadly rounded 12 to 16 veins coalesced along proximal side, wing veins diverging at angles of 10° to 20°, sharply curving, extending straight, bifurcating, numerous anastomoses.

Nomenclature: Although Knowlton (1902) suggested a relationship between *Acer osmonti* and *A. macrophyllum,* subsequent workers thought *A. osmonti* to be a member of *Eriocarpa.* Knowlton named *A. osmonti* for the original collector, V. C. Osmont.

Discussion: Sinuses, which are typically arcuate, teeth, which are few, large, and C-1 or C-2, and the most basal intersecondary veins, which are almost orthogonal to the midrib, all indicate that the type of *Acer osmonti* is a member of *Macrophylla.* Leaves that have these characters and that also have areolar venation preserved have large, irregularly polygonal areoles and branched veinlets characteristic of *A. macrophyllum* and highly dissimilar to the areolar pattern of *Eriocarpa.* Further, at the eight localities (including the type locality) at which leaves of *A. osmonti* occur, seven have produced fruits of *Macrophylla* and only one locality (Gumboot Mountain) has produced a fruit of *Eriocarpa* (as well as a fruit of *Macrophylla*).

Explanation of Plate 14.

(all figures natural size unless otherwise stated)

Figs. 1, 2 *Acer castorrivularis* Wolfe et Tanai. Beaver Creek. Holotype UCMP 9310A, 9310B.

Figs. 3-7 *Acer clarnoense* Wolfe et Tanai. Sheep Rock Creek. Paratypes UCMP 9014 (Figs. 3; 4, ×5), UCMP 9011 (Fig. 5), UCMP 9012 (Fig. 6). Holotype UCMP 9010A (Fig. 7).

Figs. 8, 9 *Acer dettermani* Wolfe et Tanai. Aniakchak Crater. Paratype USNM 396015 (Fig. 8). Holotype USNM 396014 (Fig. 9).

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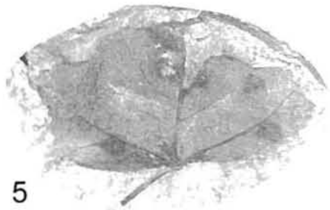

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Leaves of *Acer osmonti* clearly differ from those of both *A. salmonense* and *A. alvordense* in areolar venation. The number and degree of sharpness of the teeth is, however, similar between *A. osmonti* and *A. salmonense,* although comparisons are hampered by the unusually small size of known *A. salmonense* leaves.

Fruits of *Acer osmonti* are considerably larger than those of *A. salmonense* and have distinct veins on the nutlet. More comparable to *A. osmonti* are fruits of *A. alvordense,* which are somewhat smaller and have fewer veins on the nutlet.

Distribution: Early Oligocene of central Oregon, Cascade Range of Oregon and southern Washington.

Typology: Holotype, UCMP 2505.

Occurrences: See appendix table.

Acer busamarum Wolfe et Tanai, sp. nov.

(pl. 50, figs. 1-6; pl. 51, figs. 1-6; pl. 52, fig. 8; pl. 53, figs. 3, 4, 6; text-fig. 160)

[for synonymy, see under subspecies *busamarum* and subspecies *fingerrockense*].

Description: Leaves simple, perfectly actionodromous; deeply 5-lobed; most apical lateral lobes almost as long as medial lobe, most basal lateral lobes at least 1/2 as long as most apical lateral lobes; shape orbiculate; 9 to 15 cm long, 11 to 17 cm wide; base cordate, apex acute; lobes ovate; most apical lateral primary veins diverging from medial secondary veins; 6 to 8 secondary veins originating at angles of 30° to 50° from basal sides of most apical lateral primary veins, broadly convex, most brochidodromous; 5 or 6 pairs of medial secondary veins originating at angles of 30° to 45°, straight to broadly convex, most brochidodromous; lobal sinal bracing formed by an angularly bifurcating secondary vein; intersecondary veins numerous and intergrading with secondary veins; tertiary veins compound, A-A or R-A, spaced 0.3 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.3 to 0.5 mm in diameter, veinlets simple to once-branching; teeth large, B-1, B-2, or A-1, typically 2 per side of medial lobe (the most basal very elongated), 1 per apical side and 1 or 2 per basal side of most apical lateral lobes, none or 1 per basal side of most basal lateral lobes; petiole 2.5 to 5.0 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.7 to 2.0 cm long, 0.6 to 1.5 cm wide; outline ovate, apex broadly rounded; proximal margin tangential to proximal margin of samara; attachment scar 0.9 to 2.2 cm long, with distal keel; nutlet markedly inflated,

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Explanation of Plate 15.

(all figures natural size unless otherwise stated)

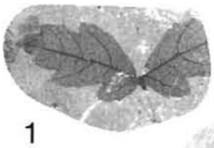
Figs. 1, 2, 3, 5 *Acer lincolnense* Wolfe et Tanai. Beaver Creek. Paratypes UCMP 9312 (Fig. 1), UCMP 9313A (Fig. 2), 9313B (Fig. 3). Holotype UCMP 9311 (Fig. 5).

Figs. 4, 7, 10-12 *Acer sinuofluviatilis* Wolfe et Tanai. Sheep Rock Creek. Paratypes UCMP 9045 (Fig. 4), UCMP 9046 (Fig. 11), UCMP 9047 (Fig. 12). Holotype UCMP 9044 (Figs. 7, ×5; 10).

Figs. 6, 9, 13, 16 *Acer macginitiei* Wolfe et Tanai. Florissant. Holotype UCMP 3828, (Figs. 6; 13, ×5). Paratypes UCMG 5188(1) (Fig. 9), 5188(4) (Fig. 16).

Figs. 8, 14 *Acer macginitiei* Wolfe et Tanai. Beaverhead/Christensen Ranch. Paratypes NYBG 506 (Fig. 8), NYBG 508 (Fig. 14).

Figs. 15, 17 *Acer eonegundo* Wolfe et Tanai. Bull Run. Holotype UCMP 9019 (Fig. 11, ×5).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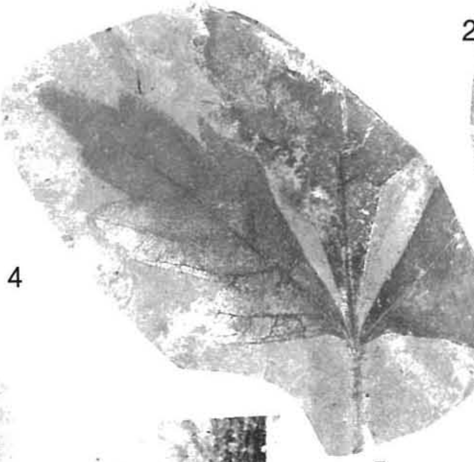
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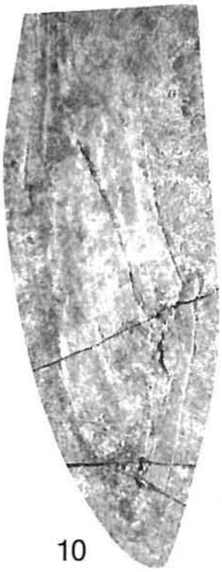
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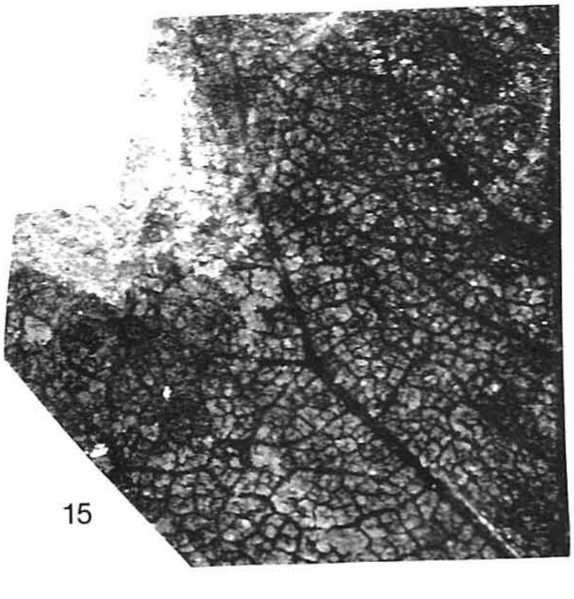
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with 20 to 26 veins of equal size originating along attachment scar and converging apical to nutlet; attachment angle 20° to 40°, nutlet angle 45° to 60°. Wing typically extending along distal margin of nutlet to attachment scar, sulcus absent or very broadly concave; 4.0 to 8.0 cm long, 1.1 to 2.8 cm wide; distal margin deeply convex, proximal margin straight, apex rounded; 15 to 20 veins coalesced along proximal side, wing veins diverging at angles of 20° to 40°, sharply curving, extending straight, bifurcating, anastomoses numerous.

Nomenclature: In reference to large size of samara.

Table 9. Statistical comparisons of fruits of different populations of *Acer busamarum* subspecies *busamarum.*

La = length of attachment scar, Ln = width of nutlet (measured from midpoint of attachment scar to apex), Ls = length of samara (including nutlet). All measurements are in centimetres.

FLORA	Average				Variation		
	No.	La	Ln	Ls	La	Ln	Ls
Trapper Creek	25	1.4	1.0	7.5	1.1-2.0	0.8-1.1	6.2-8.7
Hog Creek	1	2.0	1.5				
Trout Creek	6	1.2	1.0	8.0	0.8-1.8	0.7-1.5	5.4-9.7
Succor Creek (part)	5	1.4	1.0	8.0	1.0-1.7	0.8-1.2	6.5-9.5
Stinking Water	2	1.5	1.1	8.7	1.0-1.9	0.9-1.3	8.7
Buelah	1	2.0	1.3	9.3			
Tipton	1	1.5	1.0	8.4			

Acer busamarum subspecies *busamarum*

(pl. 51, figs. 3-6; pl. 52, fig. 8; pl. 53, figs. 3, 6; text-fig. 160)

Acer bendirei auct. non Lesquereux. Brown. 1937b (part). 179. pl. 58, f. 20, 22.
Smith. 1938b. 561. pl. 29, f. 4.
Acer merriami auct. non Knowlton. Macginitie. 1933 (part). 61, pl. 10, f. 1.
Acer oregonianum auct. non Knowlton. Oliver. 1934 (part). 24.
Chaney & Axelrod. 1959 (part). 195. pl. 41, f. 12.
Axelrod. 1964 (part). 128, 141, 142. pl. 16, F. 1, 2.
Graham. 1965. 67, pl. 5, f. 1.
Acer tyrelli auct. non Smiley. Axelrod, 1985 (part). 176. pl. 33, f. 3.

Description: Nutlets 0.8 to 2.0 cm long (typically about 1.4 cm), 0.7 to 1.5 cm wide (typically about 1.0 cm); overall length of samara 5.4 to 9.7 cm (typically about 7.5 cm; table 9).

Discussion: See following subspecies.

Typology: Holotype, UCMP 275.

Occurrences: See appendix table.

Explanation of Plate 16.

(all figures natural size unless otherwise stated)

Figs. 1, 6 *Acer powellense* Wolfe et Tanai. Sturgeon Creek. Paratypes UCMP 9316 (Fig. 1a), UCMP 9317 (Fig. 1b), UCMP 9316 (Fig. 6a). Holotype UCMP 9314 (Fig. 6b).

Figs. 2, 4 *Acer taurocursum* Wolfe et Tanai. Bull Run. Holotype UCMP 9089 (Fig. 4, ×5).

Figs. 3, 5 *Acer eomedianum* Wolfe et Tanai. Bull Run. Holotype UCMP 9065 (Fig. 5, ×5).


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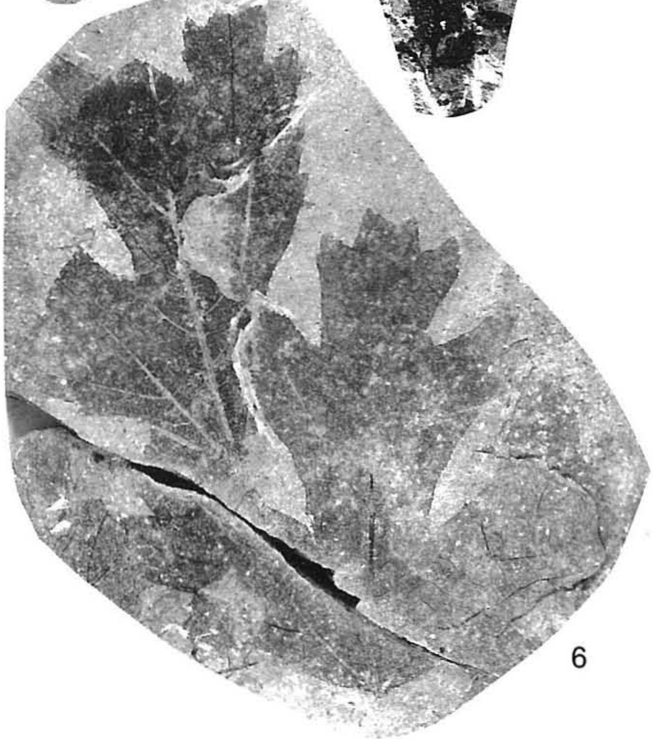
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Acer busamarum subspecies *fingerrockense* Wolfe et Tanai, subsp. nov.

(pl. 50, figs. 1-6; pl. 51, figs. 1, 2; pl. 53, fig. 4)

Acer alvordense auct. non Axelrod. Axelrod. 1956 (part). 306. pl. 30, f. 9, 10.
Acer macrophyllum auct. non Pursh. Wolfe. 1964. N29. pl. 5, f. 4-6.
Acer merriami auct. non Knowlton. LaMotte. 1936. 135. pl. 12, f. 7.
Acer oregonianum auct. non Knowlton. Axelrod. 1985. 175. pl. 13, f. 8-9; pl. 15, f. 4, 5; pl. 34, f. 1, 2.

Description: Nutlets 0.7 to 1.4 cm long (typically 1.1 cm), 0.6-1.1 cm wide (typically about 0.8 cm); overall length of samara 4.6 to 8.1 cm (typically about 6.3 cm).

Nomenclature: Type specimen is from Fingerrock flora.

Discussion: The samara of *Acer busamarum* is the largest known for any species of *Acer*. The largest samara of *A. macrophyllum* that we have seen is 6.3 cm long, which is the average length for *A. busamarum fingerrockense* (table 10); almost all samaras of *A. busamarum busamarum* are longer than 6.3 cm. In addition to their large size, samaras of *A. busamarum* are distinguished by nutlets having many veins of equal size and by the typical absence of a sulcus.

Table 10. Statistical comparisons of fruits of different populations of *Acer busamarum* subspecies *fingerrockense*.

La = length of attachment scar, Ln = length of nutlet (measured from midpoint of attachment scar to apex), Ls = length of samara (including nutlet). All measurements are in centimetres.

FLORA	Average				Variation		
	No.	La	Ln	Ls	La	Ln	Ls
Fingerrock	9	1.0	0.7	6.2	0.7-1.2	0.6-0.8	5.4-7.2
Goldyke	1	1.0	0.6	7.0			
Eastgate	2	1.1	0.9	5.9	0.9-1.3	0.7-1.1	4.6-7.2
Middlegate	18	1.2	0.8	6.0	0.9-1.4	0.7-1.0	4.6-8.1
Buffalo Canyon	1			7.0			
Skull Spring	2	1.0	0.7		0.7-1.3	0.7	
Clarkia	2	1.3	1.0	6.7	1.2-1.4	0.9-1.0	5.5-7.9
Chilcotin River	1	0.9	0.6	5.0			

Explanation of Plate 17.
(all figures natural size unless otherwise stated)

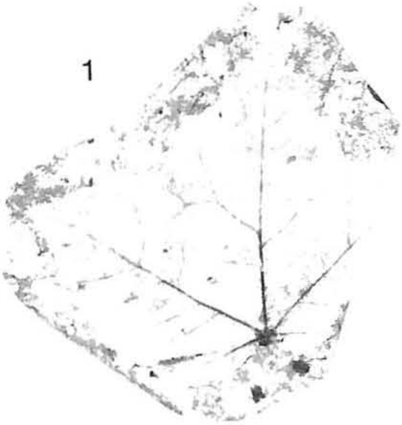
Figs. 1-6, 8, 9, 11 *Acer salmonense* Wolfe et Tanai. Salmon. Paratypes USNM 396142 (Fig. 1), USNM 396143 (Fig. 2). Holotype USNM 396141 (Fig. 3). Paratypes USNM 396144 (Fig. 4), USNM 396145 (Fig. 5), USNM 396146 (Fig. 6), USNM 396147 (Fig. 8), USNM 396148 (Fig. 9), USNM 396143 (Fig. 11, ×7.5).

Fig. 10 *Acer salmonense* Wolfe et Tanai. Beaver Creek. Paratype UCMP 9319.

Figs. 7, 12-14, 17, 18 *Acer postense* Wolfe et Tanai. Sheep Rock Creek. Paratypes UCMP 9185 (Fig. 7), UCMP 9186 (Fig. 12), UCMP 9230 (Fig. 13), UCMP 9187 (Fig. 14), UCMP 9188 (Fig. 17). Holotype UCMP 9184 (Fig. 18).

Fig. 15 *Acer montanense* Wolfe et Tanai. "Beaverhead". Holotype NYBG 461A.

Figs. 16, 19 *Acer alvordense* Axelrod. Alvord Creek. Paratype UCMP 9122 (Fig. 16). Lectotype UCMP 2136 (Fig. 19).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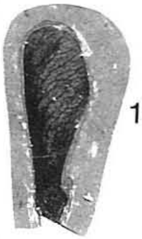
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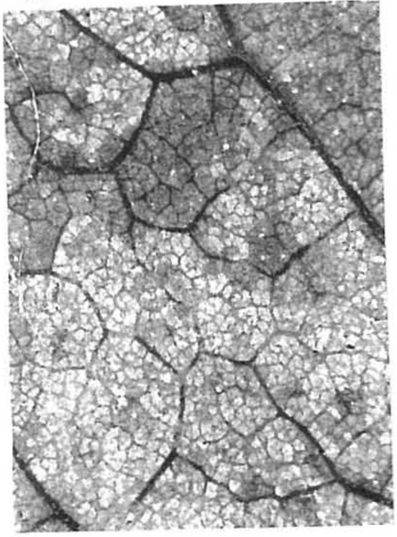
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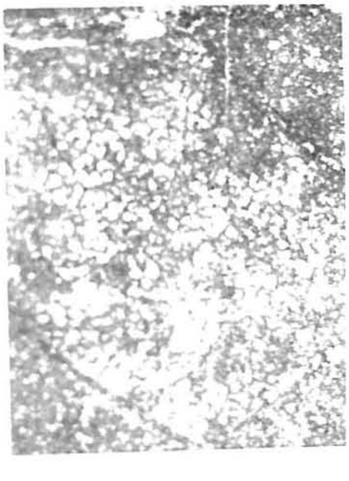
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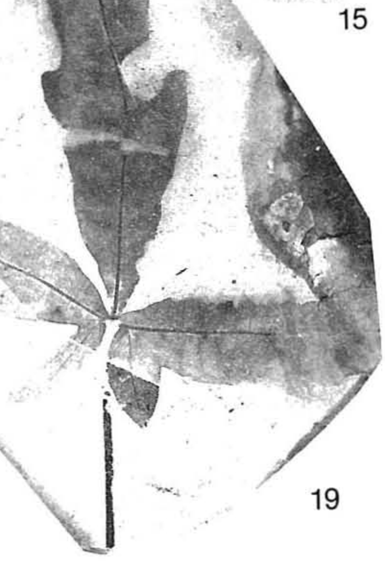
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Areolar venation of *Acer busamarum* is somewhat similar to that of *A. alvordense*. Samaras of *A. alvordense* are also similar to those of *A. busamarum* in having a reduced sulcus, although *A. busamarum* has more numerous veins on the nutlet than any other species of *Macrophylla*. Distincition between the two subspecies of *A. busamarum* is strictly on size of nutlets and wing. Some occurrences of *A. busamarum* could, on size, represent either subspecies. The large size of *A. busamarum* fruits in the late middle to early late Miocene has not been observed in earlier floras.

Distribution: Early to early late Miocene, from central British Columbia south to the Columbia Plateaus and Great Basin.

Typology: Holotype, UCMP 9161.

Occurrences: See appendix table.

Acer oregonianum Knowlton

(pl. 28, figs. 3; pl. 30, figs. 1, 5; pl. 31, fig. 7; pl. 49, figs. 1-8, 10; pl. 53, fig. 5; text-fig. 16L, M)

Acer oregonianum Knowlton. 1902. 75. pl. 13, f. 5-8.
Chaney & Axelrod. 1959 (part). 195. pl. 41, f. 11, 13.

Description: Leaves simple, perfectly actionodromous; typically deeply 5-, but up to 7-lobed; most apical lateral lobes about 2/3 as long as medial lobe, next most apical lateral lobes small or up to 1/2 as long as most apical lateral lobes; shape orbiculate to oblate; 2.5 to (estimated) 15 cm long, 3.0 to (estimated) 14 cm wide; base cordate, apex acute to attenuate; lobes elliptic to ovate; most apical lateral primary veins diverging from medial secondary veins; 6 to 8 secondary veins originating at angles of 30° to 60° from basal side of most apical lateral primary veins, broadly convex, most camptodromous but some craspedodromous; 6 or 7 pairs of medial secondary veins originating at angles of 30° to 50°, broadly convex, most brochidodromous, but some craspedodromous; lobal sinal bracing formed by an acutely bifurcating secondary vein; intersecondary vein numerous, those basal to the lobal sinal bracing and originating from midrib almost orthogonal to midrib; tertiary veins compound, A-A, spaced 0.1 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.4 to 0.8 mm in diameter, veinlets branching 2 or 3 times; teeth typically large, sharp or rounded, A-1, B-1, or C-1, typically 2 on either side of medial lobe, none or 1 on apical side and 2 or 3 on basal side of most apical lateral lobes; petiole more than 6.8 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.7 to 1.4 cm long, 0.6 to 1.1 cm wide; outline very widely ovate, apex broadly rounded; proximal margin tangential to proximal margin of samara; attachment scar 0.7 to 1.4 cm long; nutlet markedly inflated, with 8 to 12 veins of equal size originating along attachment scar and coalescing beyond

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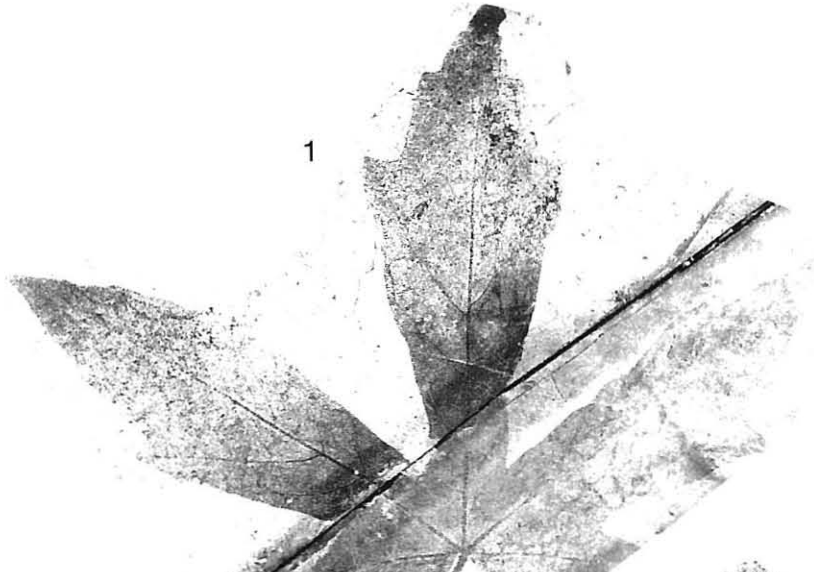
Explanation of Plate 18.
(all figures natural size unless otherwise stated)

Figs. 1, 2, 4-7 *Acer alvordense* Axelrod. Alvord Creek. Paratypes UCMP 2140 (Fig. 1), UCMP 2137A (Fig. 2; one of cotypes), UCMP 2139 (Fig. 7). Hypotypes UCMP 9125 (Fig. 4), UCMP 9126 (Figs. 5; 6, ×5).

Fig. 3 *Acer alvordense* Axelrod. Christensen Ranch. Hypotype NYBG 510.

Fig. 8 *Acer* sp. 5. Elko. UCMP 9170.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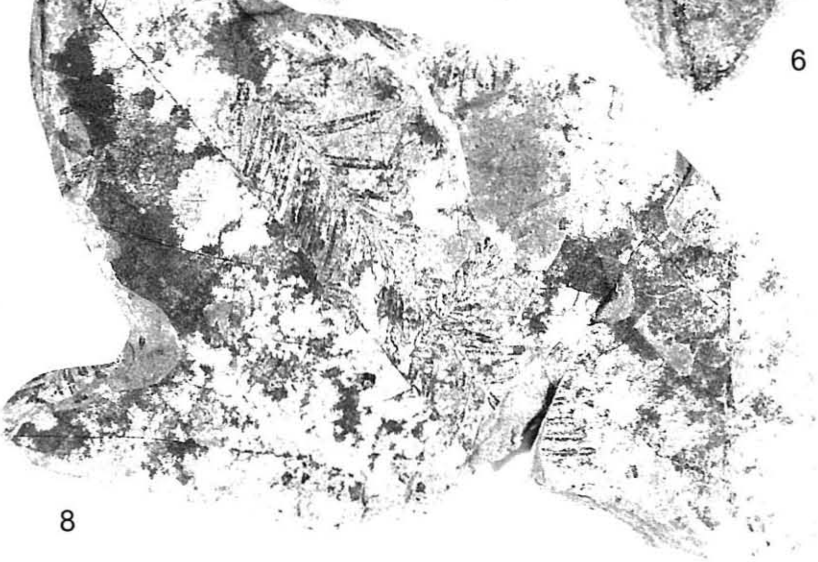
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apex of nutlet; attachment angle 10° to 40°, nutlet angle 35° to 70°. Wing entirely apical to nutlet, forming a deep V-shaped sulcus with nutlet; 3.1 to 4.3 cm long, 1.0 to 1.7 cm wide; distal margin deeply convex, proximal margin straight, apex narrowly to broadly rounded; 7 to 12 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, sharply curving, extending straight, bifurcating, numerous anastomoses.

Nomenclature: Although *Acer oregonianum* has been widely applied to Tertiary fruits and leaves of *Macrophylla,* fruits that have the morphology of Knowlton's types are actually few, and no foliage associated with such fruits has been previously described.

Discussion: Fruits of *Acer oregonianum* are characterized by their deep, V-shaped sulcus and 7 to 12 veins of equal size that are equally spaced in their course across the nutlet. In size and possession of a deep sulcus, these fossil fruits are comparable to those of *A. macrophyllum.* Fruits of *A. osmonti* are similar to those of *A. oregonianum,* except the sulcus is deeper and the nutlet has fewer veines in *A. oregonianum.*

Foliage of *Acer oregonianum* cannot be separated from that of *A. macrophyllum,* although the known fossil leaves of *A. oregonianum* are either small (as those from the Collawash locality) or fragmentary. Were large, complete leave of *A. oregonianum* known, they might prove to be specifically separable from leaves of *A. macrophyllum. Acer osmonti* has consistently sharp and more numerous teeth than does *A. oregonianum,* as well as larger areoles.

Distribution: Late Oligocene to early late Miocene of western Washington, Oregon, and westernmost Idaho.

Typology: Lectotype here designated, USNM 8497.

Occurrences: See appendix table.

Acer macrophyllum Pursh

(pl. 49, figs. 9; pl. 53, fig. 1)

Acer macrophyllum Pursh. 1814. 267.
Acer sp. H. V. Smith. 1941. 518. pl. 12, f. 6.

Discussion: Fruits of *Acer macrophyllum* have nutlets that have a few thick veins that originate along the distal half of the attachment scar and extend and bifurcate towards the apical region of the nutlet, producing a total of about seven veins that are coalesced along the proximal side of the wing. The area on the proximal side of the nutlet is occupied by a reticulum of obscure veins, which contribute only one or two thin veins to the proximal coalescence of veins. An additional large vein, which is a continuation of the keel of the proximal margin of the nutlet, lays along the proximal margin of the wing. Thus, the proximal coalescence of veins in *A. macrophyllum* contains a maximum of eight veins, most of which are derived from the distal half of the nutlet. Of all the fruits

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Explanation of Plate 19.

(all figures natural size unless otherwise stated)

Figs. 1, 3, 5, 6 *Acer grantense* Wolfe et Tanai. Beaverhead/Christensen Ranch. Holotype NYGB 502 (Fig. 1, ×5; 6). Paratypes NYGB 503 (Fig. 3), NYBG 504 (Fig. 5).

Fig. 2 *Acer grantense* Wolfe et Tanai. Beaverhead/Grant. Paratype NYBG 600.

Figs. 4, 7, 8 *Acer beckeri* Wolfe et Tanai. Ruby. Holotype UMMP 38272 (Figs. 7, ×2; 8, ×7.5).

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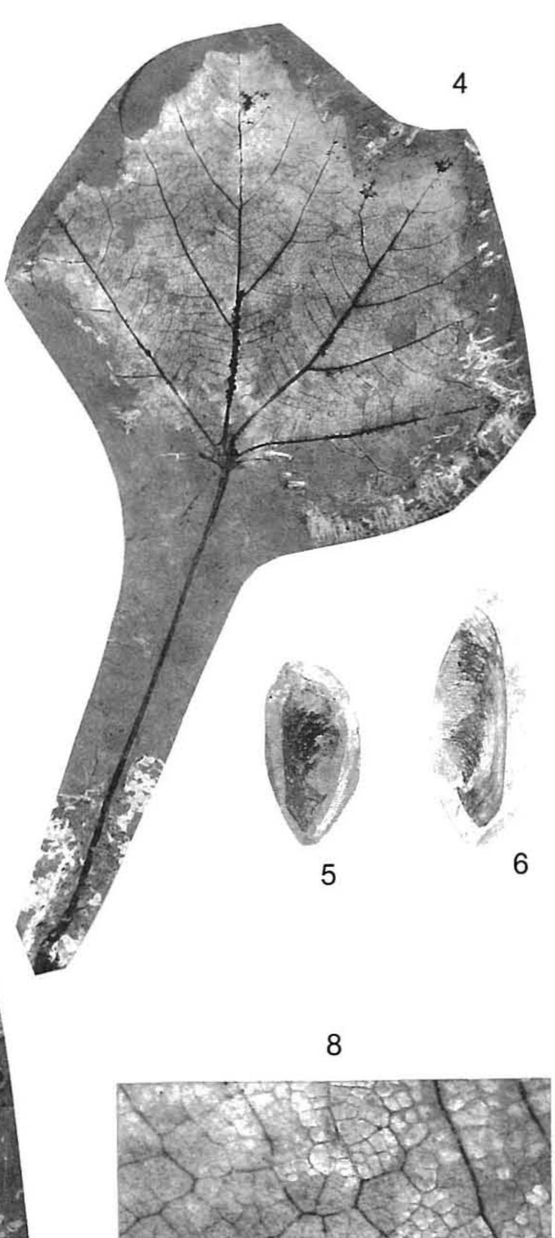

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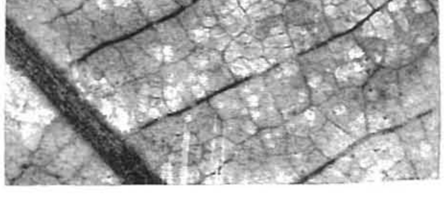

of *Macrophylla* known from the Tertiary of western North America, only one has the morphology just described: the specimen from Thorn Creek.
Distribution: Late Miocene of west-central Idaho.
Occurrence: See appendix table.

Acer megasamarum Tanai et Suzuki

(pl. 52, figs. 1-7; pl. 53, fig. 2; text-fig. 16N)

Acer megasamarum Tanai et Suzuki. 1960. 560. pl. 5, f. 1.
Acer oknensis Chelebaeva. 1978. 82. text-f. 30-1; pl. 19, f. 5.
Acer grahamensis auct. non Knowlton and Cockerell. Wolfe & Tanai. 1980. 40. pl. 17, F. 6; pl. 18, f. 5; pl. 19, f. 1, 4.

Description: Leaves simple, perfectly actinodromous; deeply 7-lobed; most apical lateral lobes at least 2/3 as long as medial lobe, next most apical lateral lobes about 1/2 as long as most apical lateral lobes, most basal lateral lobes small; shape orbiculate; about 10 to 13 cm long, 12 to 14 cm wide; base cordate, apex of lobes acute; lobes elliptic; most apical lateral primary veins diverging from medial secondary veins; 6 to 9 pairs of secondary veins originating at angles of 30° to 50° from basal side of most apical lateral primary vein, straight to broadly convex, most brochidodromous but a few craspedodromous; 5 secondary veins originating at angles of 30° to 50° from basal side of next most apical lateral lobes, straight to broadly convex, 2 or 3 brochidodromous and the others craspedodromous; 6 to 8 pairs of medial secondary veins originating at angles of 30° to 60°, broadly convex, most brochidodromous, but 2 craspedodromous; lobal sinal bracing formed by an acutely bifurcating medial secondary vein; intersecondary veins numerous, those basal to lobal sinal bracing and originating from midrib almost orthogonal to midrib; tertiary veins compound, A-A, spaced 0.2 to 0.4 cm; fourth order venation irregularly polygonal; fifth order veins forming irregularly polygonal areoles 0.4 to 0.7 mm in diameter, veinlets branching 2 or 3 times; teeth large, narrowly rounded, A-1 or B-1, typically 2 on each side of medial lobe, 1 on apical side and 2 on basal side of most apical lateral lobes, none on apical side and 2 on basal side of next most apical lateral lobes.

Fruits samaroid, nutlet at basal end; nutlet 1.3 to 1.6 cm long, 0.7 to 1.1 cm wide; outline elliptic, apex broadly rounded; proximal margin of nutlet markedly convex and expanded beyond proximal margin of wing; attachment scar 0.6 to 0.7 cm long; nutlet markedly inflated, 8 to 12 veins originating along attachment scar, extending across nutlet and interconnected to form a reticulum, coalescing apical to nutlet; attachment angle 30° to 70°, nutlet angle 20° to 50°. Wing extending along about one-third of distal margin of nutlet, forming a shallow U-shaped sinus with nutlet; 2.5 to 4.2 cm long, 1.0

Explanation of Plate 20.
(all figures natural size unless otherwise stated)
Fig. 1 *Acer hueberi* Wolfe et Tanai. "Beaverhead". Holotype NYBG 964.
Fig. 2 *Acer hueberi* Wolfe et Tanai. Schwartz Creek. Paratype NYBG 963.
Figs. 3, 5-7, 9, 10 *Acer axelrodi* Wolfe et Tanai. Bull Run. Holotype UCMP 9203 (Figs. 3; 9, ×7.5). Paratypes UCMP 9204 (Figs. 5, ×5; 6), UCMP 9205 (Figs. 7; 10, ×5).
Figs. 4, 8 *Acer ovipetrinum* Wolfe et Tanai. Sheep Rock Creek. Holotype UCMP 9107 (Fig. 8, ×5).


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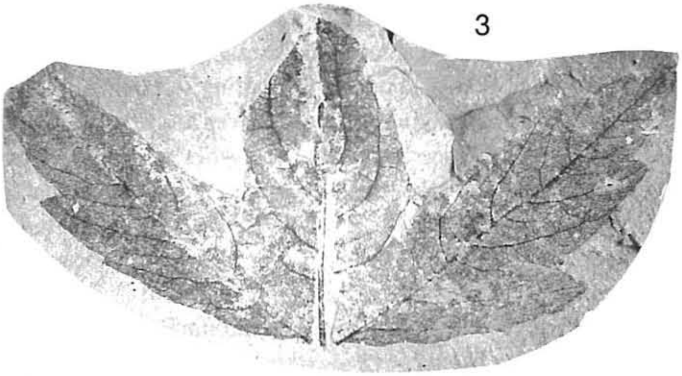
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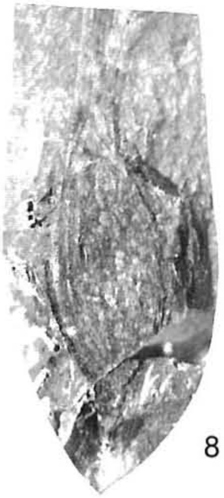
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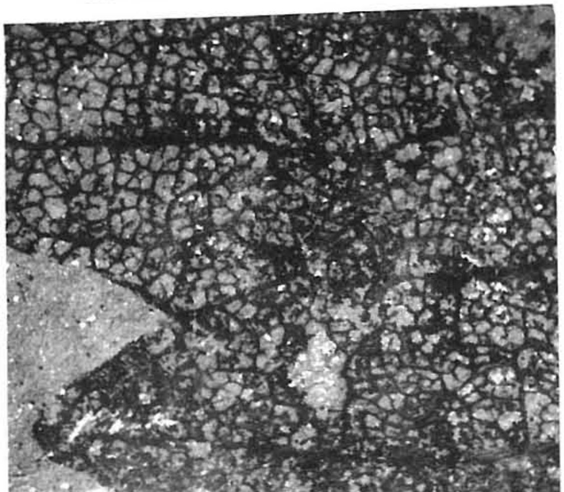
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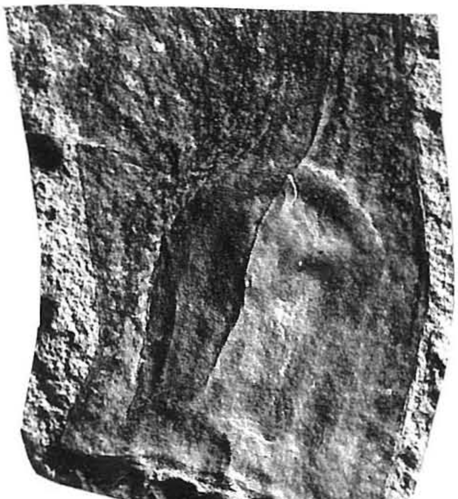
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to 1.2 cm wide; distal margin broadly convex, proximal margin slightly convex, apex broadly rounded; 7 to 10 veins coalesced along proximal side, wing veins diverging at angles of 10° to 20°, broadly convex, bifurcating, anastomoses numerous.

Nomenclature: We (1980) originally placed leaves and fruits of the type just described in *Acer grahamensis.* We now conclude that the types of *A. grahamensis* are too fragmentary to be satisfactory name-bearing specimens, and that these specimens may well represent *Eriocarpa.* Chelebaeva's (1978) *A. oknensis,* on the other hand, is based on an almost complete leaf and the epithet *megasamarum* proposed by Tanai and Suzuki (1960) is based on a complete samara.

Discussion: Characteristic fruits of *Acer megasamarum* are found with foliage that compares well with Chelebaeva's type of *A. oknensis* only at the Toledo, Washington, locality, where, however, these are the only fossils of *Acer.* Note that at Seldovia Point the fruits occur at one locality and the leaves at a second. Fruits and leaves assigned to *A. megasamarum* are the only fossils of *Macrophylla* found in the Alaskan late Oligocene through early middle Miocene.

Leaves of *Acer megasamarum* have, for *Macrophylla,* shallowly incised lobations. These leaves also appear to be consistently seven-lobed, which is atypical for other species of *Macrophylla.* In areolar venation, however, *A. megasamarum* is similar to *A. oregonianum* and *A. macrophyllum.*

Fruits of *Acer megasamarum* have reticulate venation on the nutlet, which is, in *Macrophylla,* only known in *A. macrophyllum.* The proximally expanded nutlet of *A. megasamarum* sets this species apart from all other *Macrophylla.*

Distribution: Late Oligocene through early middle Miocene of central and southern Alaska and Kamchatka; early middle to early late Miocene of western Washington and Columbia Plateaus.

Typology: Holotype, Hokkaido University Museum of Paleontology 2517 (not illustrated).

Occurrences: See appendix table.

Acer species 5

(pl. 18, figs. 8)

Discussion: This single, fragmentary leaf from Elko represents part of a medial and most of a lateral lobe. The lateral lobe has a large lobation on the basal side and the medial lobe also appears to be expanding into a large lobation. At least two other teeth are present on the basal side of the lateral lobe and two on the apical side. Areolar venation is not preserved.

Of other Eocene species of *Macrophylla, Acer salmonense* is not known to have large lobations, and the medial lobations have subsidiary teeth on the basal flank (absent in

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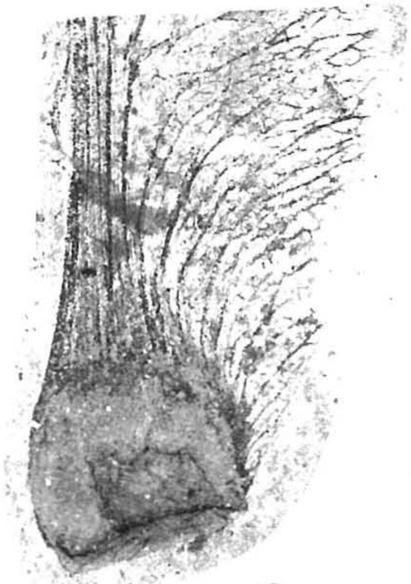
Explanation of Plate 21.

(all figures natural size unless otherwise stated)

Figs. 1, 2, 4-6 *Acer tiffneyi* Wolfe et Tanai. Beaverhead/Christensen Ranch. Paratype NYBG 513 (Figs. 1, ×5; 2). Holotype NYBG 599B (Fig. 4), NYBG 599A (Figs. 5; 6, ×7.5).

Fig. 3 *Acer tiffneyi* Wolfe et Tanai. Beaver Creek. Paratype UCMP 9320.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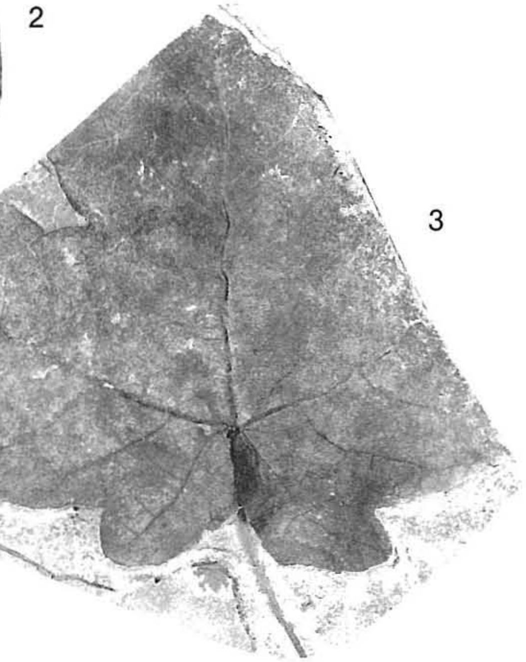
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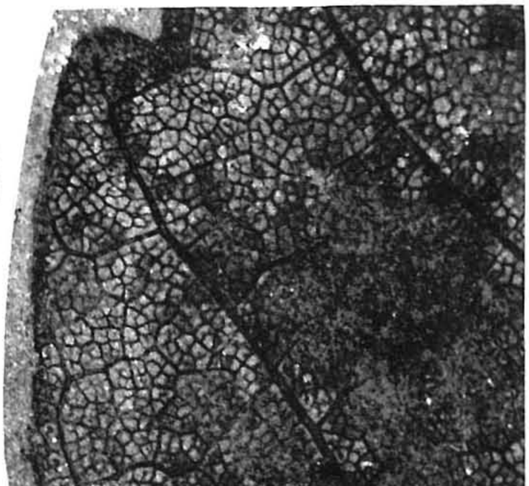
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Acer sp. 5). *Acer alvordense* also lacks such large lobations on lateral lobes and the other teeth are more reduced than in *Acer* sp. 5. Large, attenuated lobations characterize the Miocene *A. busamarum,* which, however, has fewer and more rounded teeth than in *Acer* sp. 5.

Distribution: Early late Eocene of northeastern Nevada.

Occurrence: See appendix table.

Section *Lithocarpa* Pax

Discussion: Because of their characteristic morphology, *Acer beckeri, A. grantense,* and *A.* sp. 6 have been assigned to *Lithocarpa.* We emphasize, however, that the cladistic analysis infers the presence of a type of *Acer* that has foliage and fruits characteristic of *Lithocarpa* but that also has an inflorescence and floral morphology lower in grade than *Lithocarpa* and approaching *Macrophylla.* These fossils probably represent such a low grade taxon, because we also infer from the apparent absence of *Laurina* in the western American Tertiary that the North American Paleogene representatives of the *Lithocarpa* alliance first dispersed into Asia prior to giving rise to *Lithocarpa* and *Laurina.*

Acer beckeri Wolfe et Tanai, sp. nov.

(pl. 19, figs. 4, 7, 8; text-fig. 18A)

Acer glabroides auct. non R. W. Brown. Becker. 1961 (part). 80, pl. 26, f. 1.

Description: Leaf simple, perfectly actinodromous; shallowly 5-lobed; most apical lateral lobes almost as long as medial lobe, most basal lateral lobe about 2/3 as long as most apical lateral lobes; shape orbiculate; (estimated) 6 cm long, 7 cm wide; base cordate, lobal apices acute and narrowly rounded; lobes broadly triangular; most apical lateral primary veins slightly diverging from medial secondary veins; 5 secondary veins originating at angles of 45° to 50°, broadly convex, craspedodromous; 4 pairs of medial secondary veins originating at angles of 30° to 60°, broadly convex, craspedodromous; lobal sinal bracing formed by an acutely originating external secondary vein; tertiary veins compound, A-A; spaced about 0.2 cm, many veins of tertiary thickness originating almost orthogonally from basal part of midrib; fourth order venation quadrangular; fifth order veins forming quadrangular areoles 0.2 to 0.4 mm in diameter, areoles unbranched or typically absent; teeth rounded, broad, A-1, typically 1 per secondary vein; petiole 6.7 cm long.

Nomenclature: In recognition of the late Herman F. Becker's contributions to the Ter-

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Explanation of Plate 22.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Summer Spring. Paratype UOCM F-33531.

Figs. 2, 5, 6 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Fossil. Paratypes USNM 396050 (Fig. 2), UCMP 9039 (Fig. 5), UCMP 9040 (Fig. 6).

Figs. 7, 9 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Dugout Gulch. Paratypes UCMP 9034 (Fig. 7), UCMP 9033 (Fig. 9).

Fig. 3 *Acer smileyi* Wolfe et Tanai. Kukak Bay. Paratype USNM 30138.

Fig. 4 *Acer* sp. 1. Tsadaka Canyon. USNM 396012A.

Fig. 8 *Acer smileyi* Wolfe et Tanai. Cascadia. Paratype UCMP 9177.


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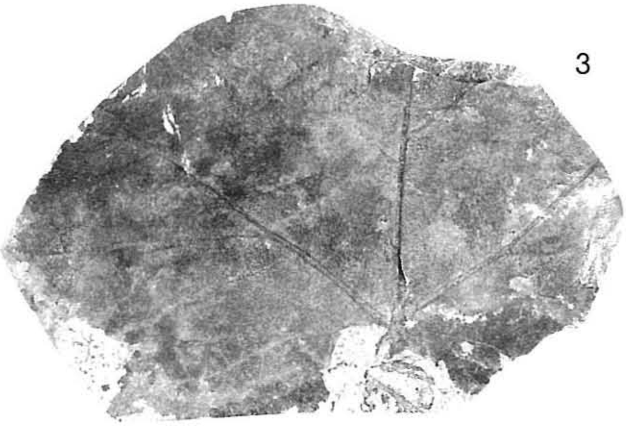
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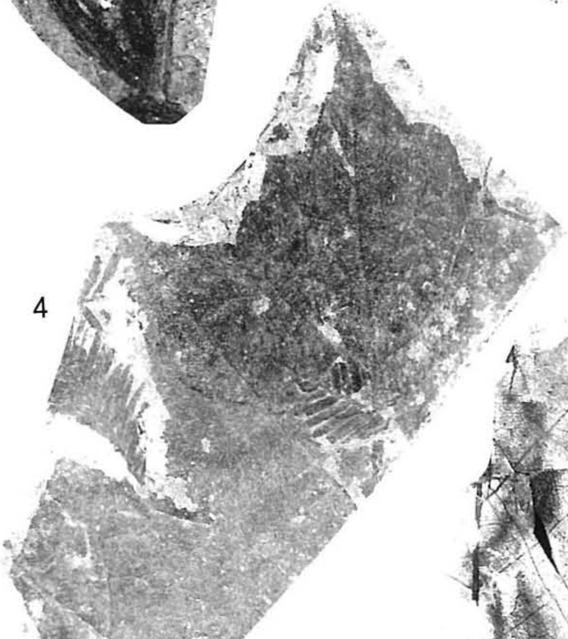
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tiary paleobotany of southwestern Montana.

Discussion: Acer beckeri is most similar to leaves of extant *Lithocarpa*. Critical similarities include: (1) broad, narrowly rounded teeth, (2) narrowly rounded V-shaped sinuses, (3) lobal sinal bracing formed by an acutely originating external secondary vein, (4) closely spaced tertiary veins, (5) numerous tertiary veins originating almost orthogonally from the basal part of the midrib. The triangular lobes of *A. beckeri,* however, differ from *Lithocarpa,* which has lobes narrowest at the lobal sinuses (and are hence elliptic). Further, veinlets of extant *Lithocarpa* are typically present and unbranched or once-branching, whereas in *A. beckeri* veinlets are typically absent and, if present, are unbranched. Characters in which *A. beckeri* differs from extant *Lithocarpa* are, however, shared with *A. salmonense.*

Distribution: Latest Eocene of southwestern Montana.

Typology: Holotype, UMMP 38272.

Occurrence: See appendix table.

Acer grantense Wolfe et Tanai, sp. nov.

(pl. 19, figs. 1-3, 5, 6)

Acer glabroides auct. non R. W. Brown. Becker. 1969 (part). 113. pl. 36, f. 9, 11, 12, 15, 16, 18.

Description: Fruits samaroid, nutlet at basal end; nutlet 0.6 to 0.7 cm long, 0.4 to 0.7 cm wide; outline very widely ovate, apex broadly rounded proximal margin tangential to proximal margin of samara and then convexly curving; attachment scar 0.5 to 0.6 cm long, with pronounced distal keel; nutlet markedly inflated, a large ridge extending apically from medial part of attachment scar, veins not visible except near apical margin; attachment angle 30° to 40°, nutlet angle 40° to 50°; apparently with many simple hairs. Wing extending along distal margin of nutlet to attachment scar; 1.5 to 2.5 cm long, 0.7 to 1.4 cm wide; distal margin deeply convex, proximal margin broadly convex, apex narrowly to broadly rounded; 7 to 9 veins coalesced along proximal side, wing veins gradually diverging and convexly curving, bifurcating, numerous anastomoses and reticulate veinlets.

Nomenclature: The occurrences of *Acer grantense* are in the general vicinity of Grant, Montana.

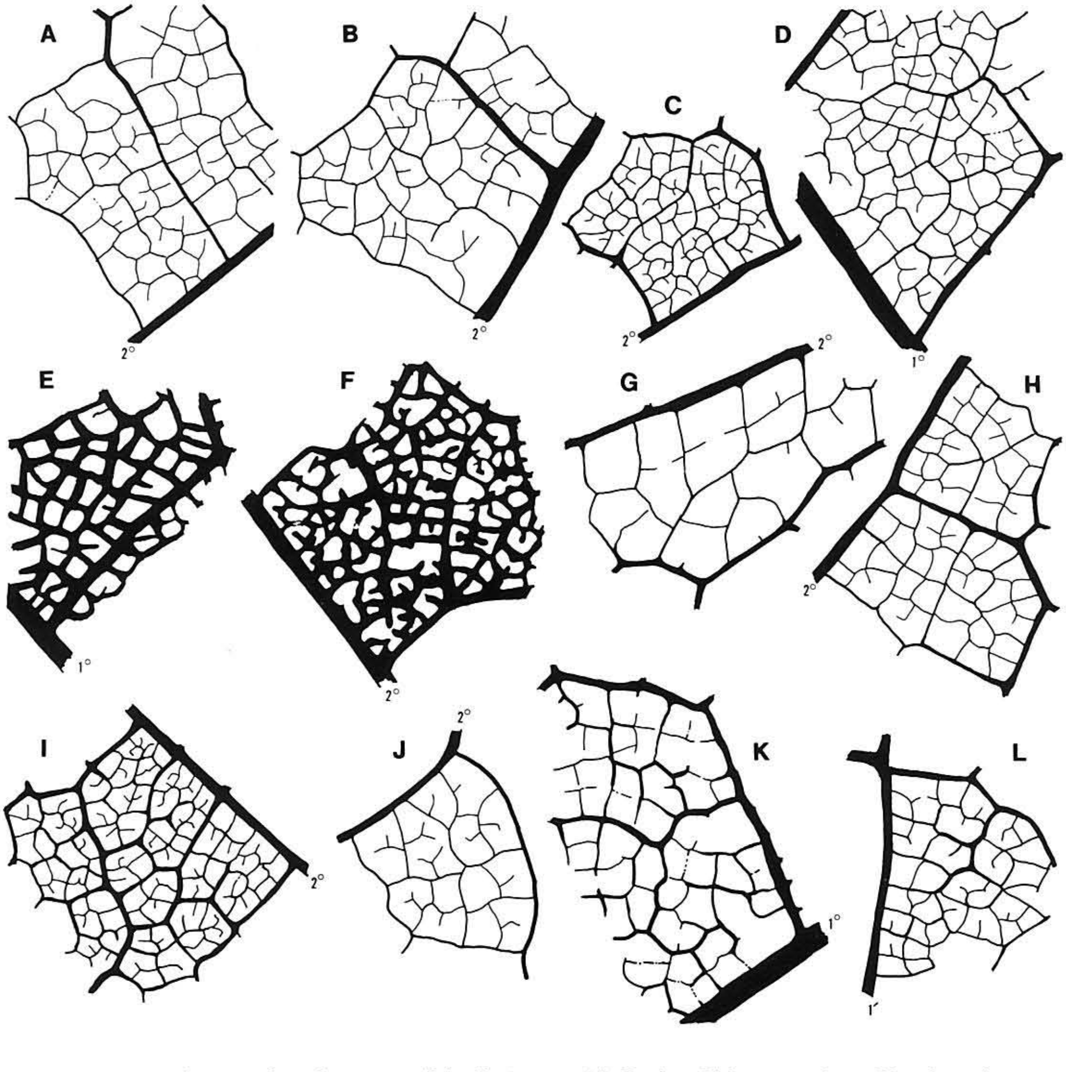
Discussion: A markedly inflated nutlet, large medial ridge, convex curvature of the basal part of the proximal margin of the nutlet, low attachment angle, marked distal keel to the attachment scar, broadly convex proximal margin of the wing, gradually diverging wing veins, and presence of reticulate veinlets all ally *Acer grantense* to *Lithocarpa.* Structures that appear to represent impressions of simple hairs are present on, and immediately apical to, the nutlet.

Considering that both *Acer beckeri* and *A. grantense* are found in coeval beds in southwestern Montana, we suspect that both represent the same species. Until found in association at the same locality, however, we prefer to maintain them as separate taxa.

Distribution: Latest Eocene of southwestern Montana.

Typology: Holotype, NYBG (YUPM) 502.

Occurrences: See appendix table.



Text-fig. 18 Areolar venation characters of fossil *Acer* — (4) Section *Lithocarpa, Acer, Manchesteria, Campestria* and *Platanoidea* (all figures × 12.5)

A. *Acer beckeri* Wolfe et Tanai. Ruby. Holotype UMMP 38272 (pl. 19, fig. 4)
B. *Acer collawashense* Wolfe et Tanai. Collawash. Holotype UCMP 9351 A (pl. 54, fig. 2).
C. *Acer bolanderi* Lesquereux. Table Mountain. Lectotype UCMP 1825 (pl. 57, fig. 4).
D. *Acer minutifolium* Chaney. Eagle Creek. Hypotype UCMP 9190 (PL. 54, fig. 4).
E. *Acer schorni* Wolfe et Tanai. Fingerrock. Paratype UCMP 9192B (the counterpart of pl. 55, fig. 7).
F. *Acer tyrellense* Smiley. Middlegate. Hypotype UCMP 6669 (pl. 56, fig. 1).
G. *Acer manchesteri* Wolfe et Tanai. Bridge Creek/Dugout Gulch. Holotype UCMP 9203 (pl. 32, fig. 2).
H. *Acer manchesteri* Wolfe et Tanai. Bridge Creek/Gray Ranch. paratype UCMP 9209A (pl. 32, fig. 1).
I. *Acer tiffneyi* Wolfe et Tanai. Beaverhead/Christensen. Holotype NYBG 599A (pl. 21, fig. 5).
J. *Acer protomiyabei* Endo. Seldovia Point. Hypotype USNM 208468 (pl. 63, fig. 2).
K. *Acer scottiae* MacGinitie. Succor Creek/Maple Ridge. Hypotype UMMP 21460 (pl. 58, fig. 5).
L. *Acer septilobatum* Oliver. Trout Creek. Hypotype VOCM F-33532 (pl. 62, fig. 4).

Acer species 6

(pl. 30, figs. 2, 4)

Discussion: This single fruit has a low attachment angle and the markedly inflated nutlet has a strong, medial ridge that extends apically from the middle of the attachment scar, which has a distal keel. The wing extends along the distal side of the nutlet to the attachment scar. Wing veins gradually diverge and anastomose profusely with many reticulate veinlets. The nutlet has many simple hairs. These charactes place *Acer* sp. 6 in *Lithocarpa.*

Acer sp. 6 probably is specifically distinct from *A. grantense.* The attachment scar is about 1.0 cm long in *A.* sp. 6, as opposed to 0.5 to 0.6 cm in *A. grantense.* Additionally, *A.* sp. 6 is larger and has a lower (20° vs. 30° to 40°) attachment angle than *A. grantense.*

Distribution: Early Oligocene of central Oregon.

Occurrence: See appendix table.

Section *Spitza* Wolfe et Tanai, sect. nov.

Diagnosis: Fruit samaroid; nutlet at basal end; nutlet markedly inflated, outline circular; distinct nutlet flanges, almost fused; attachment angle medium; sulcus absent; wing entirely apical to nutlet; wing thickened basally; at least 8 wing veins coalesced proximally; wing veins with numerous anastomoses, reticulate veinlets present.

Discussion: See below.

Type species: Acer spitzi Wolfe et Tanai.

Acer spitzi Wolfe et Tanai, sp. nov.

(pl. 5, figs. 5, 13)

Description: Fruits samaroid; nutlets at basal end; nutlets 0.7 to 0.8 cm long, 0.5 cm wide, outline broadly oval, expanded slightly proximally, attachment scar 0.4 to 0.6 cm long; nutlet strongly inflated; about 8 obscure, approximately parallel veins on apical half on nutlet; flanges paralleling distal margin of nutlet, placed in distal 1/3 of nutlet, almost fused; attachment angle about 40°, nutlet angle about 30°. Wing entirely apical to nutlet; 1.8 to 2.2 cm long, 0.8 to 1.0 cm wide, widest in apical 1/3; thickened basally; distal margin broadly convex, proximal margin straight for about 2/3 of length, apex broadly rounded; about 6 coalesced veins along proximal side, wing veins diverging at angles of 10° to 30°, irregular in course, irregularly bifurcating, anastomoses common, reticulate veinlets present.

Nomenclature: Mark Spitz has assiduously collected and sent to us material of *Acer* from the Republic flora.

Discussion: The nutlet of *Acer spitzi* is markedly inflated. The attachment scar is wide (extending at least 0.2 cm into the matrix), as in extant inflated nutlets. Veins on the

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Explanation of Plate 23.

(all figures natural size unless otherwise stated)

Figs. 1-5 *Acer glabroides* Brown, emend. Wolfe et Tanai. Bridge Creek/Gray Ranch. Lectotype UCMP 108A (Fig. 1). Hypotypes UCMP 106 (Fig. 2), UCMP 9321 (Fig. 3), UCMP 9027 (Figs. 4; 5, ×7.5).

Fig. 6 *Acer smileyi* Wolfe et Tanai. Kukak Bay. Paratype USNM 396197A.

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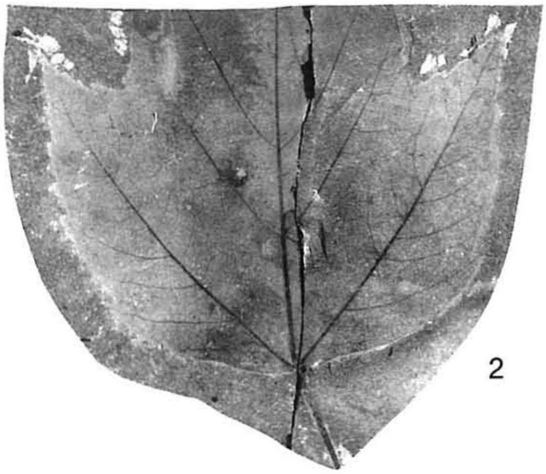

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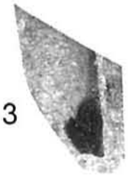

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distal third of the nutlet do not coalesce with the other nutlet veins, and these distal veins appear to extend directly into the distal part of the wing. The marked thickening of the basal region of the wing is an uncanalized character that appears in many extant members of section *Acer.* This, combined with the marked nutlet inflation and complicated wing venation, suggests that *A. spitzi* is an early member of the line leading to section *Acer* and perhaps also to *Integrifolia.* No nutlet pubescence, however, is present on *A. spitzi.*

Distribution: Early middle Eocene of northeastern Washington.

Typology: Holotype, UWMG 31272A.

Occurrence: See appendix table.

Section *Acer*

Series Acer

Acer montanense Wolfe et Tanai, sp. nov.

(pl. 17, figs. 15)

Acer glabroides auct. non R. W. Brown. Becker. 1969 (part). 113. pl. 36, f. 14.

Description: Fruit samaroid; nutlet at basal end. Nutlet 0.8 cm long, 0.8 cm wide; outline circular; proximal margin with a keel and expanded beyond proximal margin of wing; attachment scar 0.4 cm long, with a distal keel; nutlet markedly inflated, surface irregular, veins coalescing at apex of nutlet; attachment angle 25°, nutlet angle 40°. Wing extending along distal side of nutlet to attachment scar, and forming a small V-shaped sulcus; 2.5 cm long, 1.0 cm wide; distal margin deeply convex proximal margin broadly convex, apex broadly rounded; 8 veins coalesced along proximal side, wing veins gradually diverging and straight, then sharply curving, irregularly bifurcating, anastomoses numerous, veinlets reticulate.

Nomenclature: Type specimen is from Beaverhead flora of Montana.

Discussion: In observable charcters, *Acer montanense* compares well with section *Acer.* A strongly inflated nutlet that is circular in outline, keeled and expanded proximal margin of the nutlet, keeled and short attachment scar, coalescence of all nutlet veins at the apex of the nutlet, and irregularly bifurcating and reticulate wing venation are characters found in section *Acer.* The fossil, however, does not show reticulate venation on the nutlet; this absence could perhaps be due to the fossil displaying the interior rather than the exterior surface of the nutlet. We prefer, therefore, to consider the sectional assignment tentative.

Distribution: Latest Eocene of southwestern Montana.

Typology: Holotype, NYBG (YUPM) 461A, B.

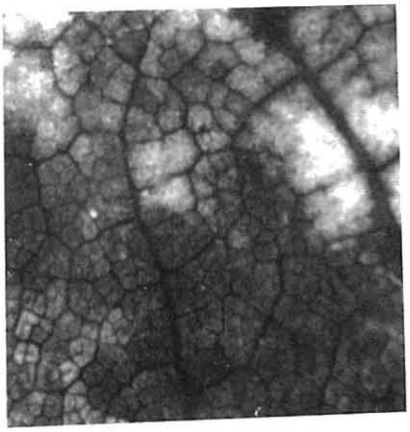
Occurrence: See appendix table.

Explanation of Plate 24.

(all figures natural size unless otherwise stated)

Figs. 1, 2 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Dugout Gulch. Paratype UCMP 9032 (Fig. 1, ×7.5).

Figs. 3, 4 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Fossil. Paratypes UCMP 9036A (Fig. 3), USNM 396048 (Fig. 4).



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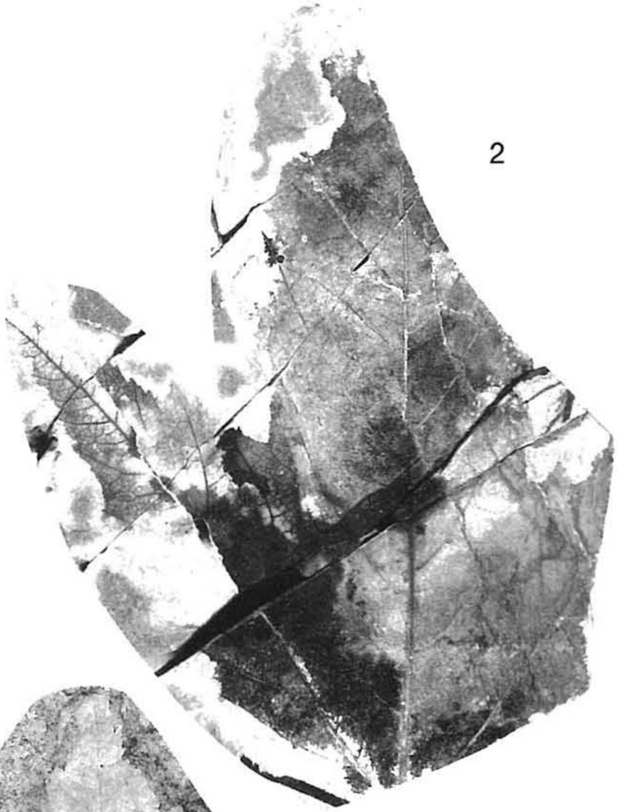

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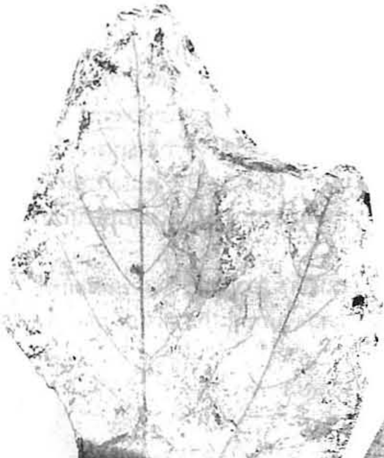

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Acer postense Wolfe et Tanai, sp. nov.

(pl. 17, figs. 7, 12-14, 17, 18)

Description: Fruits samaroid, nutlet at basal end. Nutlet 0.5 to 0.6 cm long, 0.3 to 0.45 cm wide; outline elliptic to narrowly ovate, apex broadly rounded; proximal margin typically slightly expanded beyond proximal margin of wing; attachment scar 0.2 to 0.4 cm long; nutlet markedly inflated, thickest in distal part; nutlet venation an obscure reticulum; attachment angle 50° to 60°, nutlet angle 25° to 35°. Wing entirely apical to nutlet, forming a broadly to narrowly V-shaped sulcus with nutlet; 1.4 to 2.3 cm long, 0.5 to 0.8 cm wide; distal margin deeply convex, proximal margin straight to shallowly convex, apex broadly to narrowly rounded; 7 or 8 veins coalesced (in some specimens veins are not individually separable) along proximal side, wing veins diverging at angles of 10° to 30°, sharply and irregularly curving, irregularly bifurcating, numerous anastomoses, veinlets reticulate.

Nomenclature: Post, Oregon, is the settlement nearest to the type locality.

Discussion: A strongly inflated nutlet that has obscurely reticulate venation indicates that *Acer postense* is a member of section *Acer,* as do irregularly bifurcating wing veins and reticulate veinlets. Nutlets of Goniocarpa and Saccharodendron tend to be spherical, even more inflated than the fossils, and have a proximal keel. In having the nutlet more inflated distally than proximally, in degree of inflation, and in absence of a conspicuous proximal keel, *A. postense* is assigned to series Acer.

Although both are assigned to section *Acer, A. postense* differs from *A. montanense,* which has a more circular nutlet outline and a wing that extends along the distal margin of the nutlet.

Distribution: Late middle to early late Eocene of central Oregon.

Typology: Holotype, UCMP 9184.

Occurrence: See appendix table.

Series Saccharodendron (Rafinesque) Murray

Acer collawashense Wolfe et Tanai, sp. nov.

(pl. 54,, figs. 8, 9; text-fig. 18B)

Description: Leaves simple, perfectly actinodromous, with 5 primary veins; 3-lobed, lateral lobes about as long as medial lobe; shape orbiculate to oblate; 3.5 to 4.0 cm long,

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Explanation of Plate 25.

(all figures natural size unless otherwise stated)

Figs. 1, 4-6 *Acer cascadense* Wolfe et Tanai. Cascadia. Holotype UCMP 9055 (Figs. 1, ×5; 6). Paratypes USMN 396059 (Fig. 4), USNM 396060 (Fig. 5).

Figs. 2, 10-12 *Acer cranei* Wolfe et Tanai. Bridge Creek/Allen Ranch. Holotype UCMP 9322 (Figs. 2, ×5; 11). Paratypes UCMP 9323 (Fig. 10), UCMP 9224, (Fig. 12).

Fig. 3 *Acer cranei* Wolfe et Tanai. Bridge Creek/Twickenham. Paratype UCMP 9054.

Fig. 7 *Acer cranei* Wolfe et Tanai. Bridge Creek/Gray Ranch. Paratype USNM 396056.

Fig. 8 *Acer cranei* Wolfe et Tanai. Bridge Creek/Fossil. Paratype UCMP 9050.

Figs. 9, 13 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Fossil. Holotype UCMP 9036A (Fig. 9). Paratype USNM 396048 (Fig. 14).

Fig. 14 *Acer ashwilli* Wolfe et Tanai. Bridge Creek/Clarno NE. Paratype UCMP 9029.


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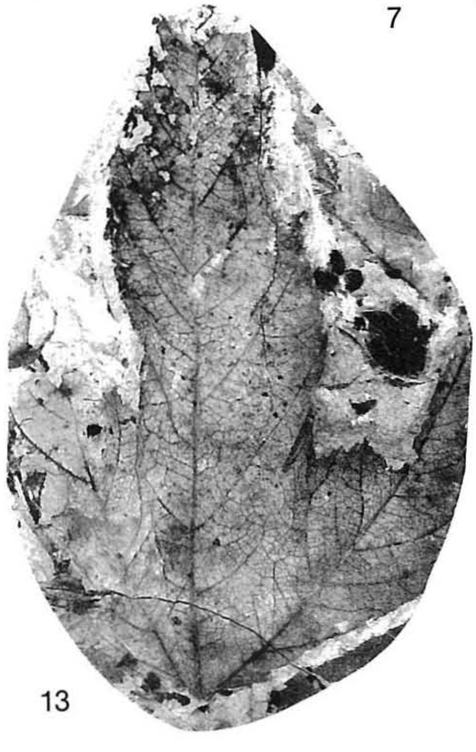
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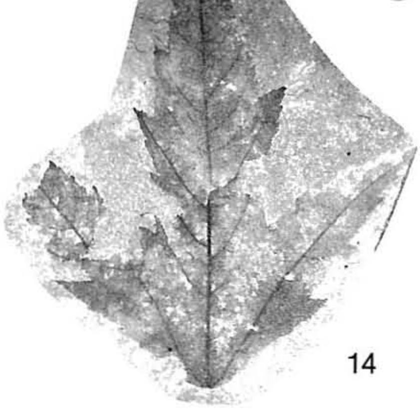
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4.4 to 5.0 cm wide; base narrowly cordate, apex attenuate; lobes elliptic; lateral primary veins slightly diverging from medial secondary veins; 5 or 6 secondary veins originating at angles of 50° to 80° from basal side of lateral primary veins, broadly convex, brochidodromous; 5 or 6 pairs of medial secondary veins originating at angles of 45° to 60°, broadly convex, brochidodromous; lobal sinal bracing formed by an orthogonally bifurcating secondary vein; intersecondary veins numerous; tertiary veins compound, R-R forming a quadrangular reticulum in intercostal area; fourth order venation irregularly polygonal; fifth order veins forming quadrangular areoles 0.3 to 0.6 mm in diameter, veinlets absent or unbranching; teeth broadly rounded protuberances, 1 or 2 on each side of medial lobe, 1 on basal side of lateral lobe; petiole more than 1.0 cm.
Nomenclature: Type locality is in the drainage of the Collawash River, Oregon.
Discussion: In *Acer collawashense,* secondary veins that enter the highly reduced teeth are brochidodromous; the vein entering a tooth is an external branch of a secondary loop. This character is also pronounced in the extant *A. barbatum, A. leucoderme,* and *A. nigrum.* Of these, *A. leucoderme* is typically three-lobed, although *A. nigrum* also produces some three-lobed leaves. In areolar size, however, *A. collawashense* is most similar to *A. saccharum.*
Distribution: Early Miocene of northwestern Oregon and northwestern Nevada.
Typology: UCMP 9351A, B.
Occurrences: See appendix table.

Acer minutifolium Chaney

(pl. 54, figs. 1-7; text-fig. 18D)

Acer minutifolia Chaney. 1920. 179. pl. 19, f.2.
Liriodendron trilobata Chaney. 1920. 173. pl. 14, f. 4.

Description: Leaves simple, perfectly actinodromos with 5 primary veins; 3- or 5-lobed; most apical lateral lobes 1/2 to 2/3 as long as medial lobes, most basal lateral lobes small; shape orbiculate or very widely ovate; base narrowly cordate, apex attenuate: lobes ovate; most apical lateral primary veins slightly diverging from medial secondary veins; 4 or 5 secondary veins originating at angles of 40° to 60°, straight or broadly convex, some brochidodromous, some craspedodromous; 5 or 6 medial secondary veins originating at angles of 35° to 65°, straight to broadly convex, some brochidodromous, some craspedodromous; lobal sinal bracing formed by an orthogonally bifurcating secondary vein; intersecondary veins numerous, intergrading with secondary veins; tertiary veins compound, R-R or A-R forming a large reticulum in intercostal area with intersecondary veins; fourth order venation irregularly polygonal; fifth order veins for-

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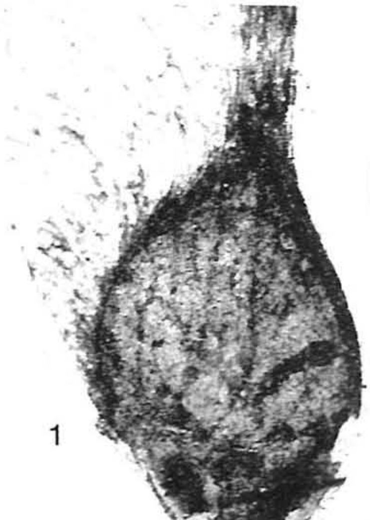
Explanation of Plate 26.
(all figures natural size unless otherwise stated)

Figs. 1-4, 7, 10 *Acer oligomedianum* Wolfe et Tanai. Bridge Creek/Allen Ranch. Holotype USNM 396076 (Figs. 1, ×5.2; 2). Paratypes UCMP 105 (Fig. 3), USNM 396075 (fig. 4), UCMP 9067 (Fig. 7), USNM 396076 (Fig. 10).

Figs. 5, 6, 8 *Acer oligomedianum* Wolfe et Tanai. Lyons. Paratypes UCMP 9071 (Fig. 5), UCMP 9072 (Fig. 6), UCMP 9326 (Fig. 8).

Fig. 9 *Acer oligomedianum* Wolfe et Tanai. Bridge Creek/Clarno NE. Paratype UCMP 9070.



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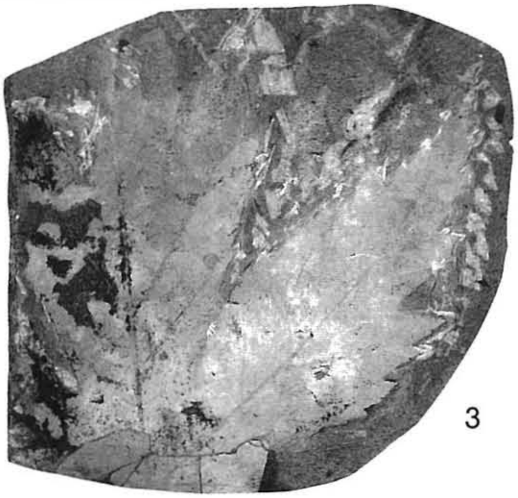

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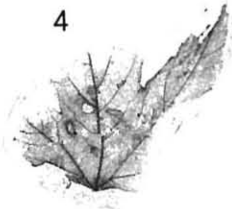

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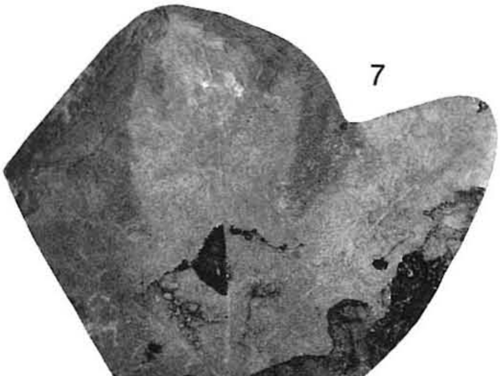

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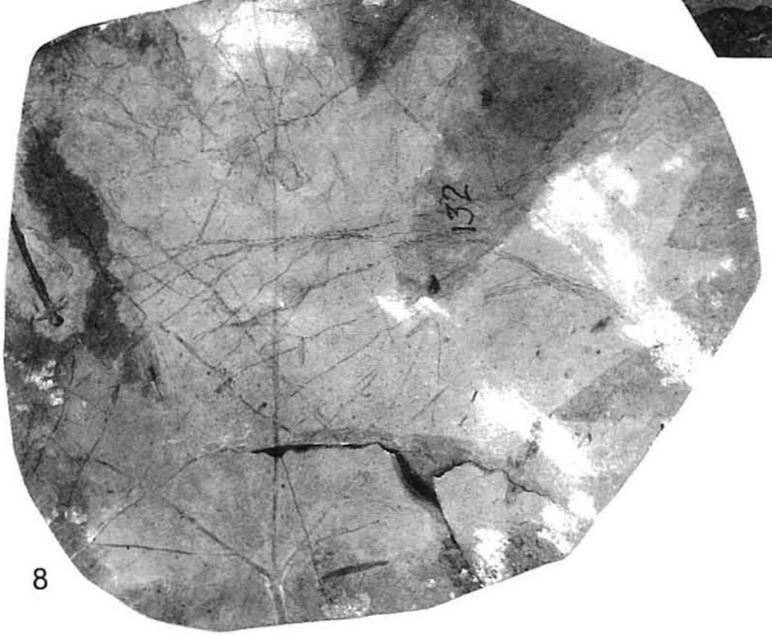

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ming quadrangular areoles 0.2 to 0.4 mm in diameter, veinlets unbranched or typically absent; teeth sharp, typically C-1, typically 2 or 3 on each side of medial and basal side of lateral lobes, none or 1 on apical side of lateral lobes; petiole up to 2.1 cm long.

Fruit samaroid, nutlet at basal end. Nutlet 0.6 cm long, 0.5 cm wide; outline suborbiculate, apex broadly rounded; proximal margin expanded beyond proximal margin of samara; attachment scar 0.4 cm long; nutlet markedly inflated, 9 veins originating along attachment scar, extending apically and forming a reticulum converging at apex of nutlet; attachment angle 65°, nutlet angle 30°. Wing extending about one-third the length of distal margin of nutlet, forming a broadly V-shaped sulcus with nutlet; 1.9 cm long, 0.8 cm wide; distal margin deeply convex, proximal margin straight, apex broadly rounded; wing thickened basally; 7 veins coalesced along proximal side, wing veins diverging at angles of 20° to 40°, curving sharply, extending at angles of about 80° to proximal margin, bifurcating, anastomoses numerous, veinlets reticulate.

Nomenclature: Chaney's (1920) *Acer minutifolia* has been ignored by subsequent workers. *Liriodendron trilobata,* on the other hand, was considered to represent *Negundo* by MacGinitie (1953) and Chaney and Axelrod (1959); the type is actinodromous and has areolar venation typical of *Saccharodendron.*

Discussion: The sharply toothed *Acer minutifolium* is readily separable from other early Miocene species of *Saccharodendron, A. collawashense. Acer minutifolium* also has smaller areoles than *A. collawashense.*

Among extant species, leaves of *Acer minutifolium* most closely resemble those of *A. saccharum* in having sharp and, for *Saccharodendron,* numerous teeth. Leaves of *A. saccharum* however, are typically five-lobed (some are seven-lobed), typically have seven primary veins, and the areoles are about 0.4 to 0.6 mm in diameter.

At the Chilcotin River locality, a single leaf of *Acer minutifolium* is associated with a single samara of *Saccharodendron;* this samara is provisionally assigned to *A. minutifolium.* This fruit has greatest similarities to fruits of *A. grandidentatum* in: (1) a straight proximal margin of the wing, (2) attachment and nutlet angles, (3) shape and size of nutlet, including the expanded proximal margin. Veins on the nutlet form a well defined, fine reticulum in *A. minutifolium* in contrast to the poorly defined, coarse reticulum in *A. grandidentatum.*

Distribution: Early Miocene of central British Columbia and northwestern Oregon.

Typology: Holotype, UCWM (FMNH) 22392.

Occurrences: See appendix table.

Explanation of Plate 27.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer tigilense* Chelebaeva. Kukak Bay. Hypotype USNM 396131.

Figs. 2, 3 *Acer kenaicum* Wolfe et Tanai. Redoubt point. Paratype USNM 396088 (Fig. 2). Holotype USNM 396089 (Fig. 3).

Figs. 4-11 *Acer kluckingi* Wolfe et Tanai. Bridge Creek/Pentecost Ranch. Paratypes UCMP 9114 (Fig. 4), UCMP 9115 (Figs. 5, ×5; 10), UCMP 9116 (Fig. 6), UCMP 9117 (Fig. 7), UCMP 9110 (Fig. 8), UCMP 9111 (Fig. 9). Holotype UCMP 9109 (Fig. 11).

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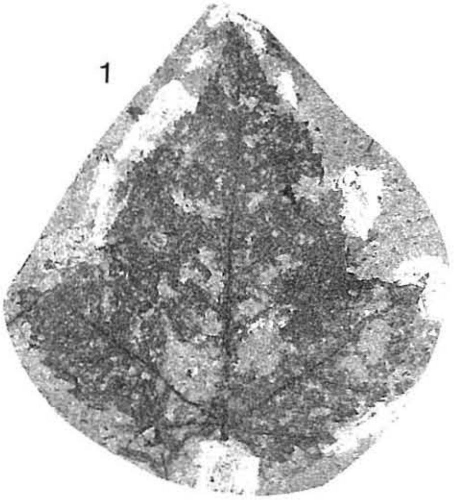

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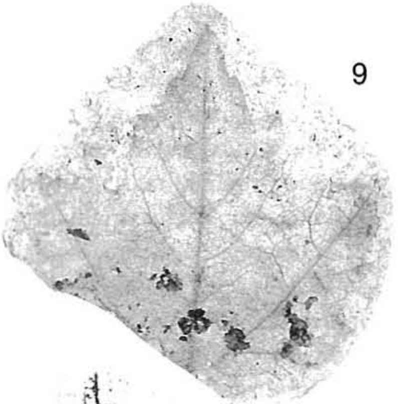

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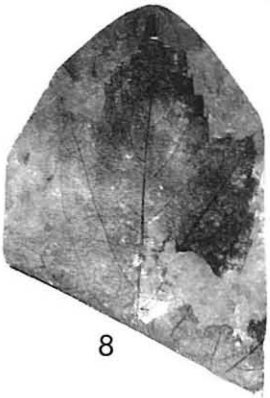

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Acer schorni Wolfe et Tanai, sp. nov.

(pl. 54, figs. 10; pl. 55, figs. 1-6; text-fig. 18E)

Acer arida auct. non Axelrod. Axelrod. 1956 (part). 307. pl. 31, F. 1-4.
Acer bolanderi auct. non Lesquereux. Axelrod. 1944. 142.
    Chaney & Axelrod. 1959 (part). 192. pl. 39, f. 7-9.
    Graham. 1965. 66. pl. 5, f. 5.
Acer columbianum auct. non Chaney et Axelrod. Chaney & Axelrod. 1959 (part, nontypic). 192. pl. 40, f. 5.
Acer minor auct. non Knowlton. Knowlton. 1902 (part, nontypic). 76. pl. 14, f. 2.
Quercus prelobata auct. non Condit. Axelrod. 1958. 129. pl. 23, f. 10.
Acer tyrelli auct. non Smiley. Axelrod. 1985 (part). 176. pl. 14, f. 4.

Description: Leaves simple, perfectly actinodromous, with 7 primary veins; 3- or typically 5-lobed, the most apical lateral lobes about as long as medial lobe, most basal lobes (if present) small; shape typically oblate; 3.2 to estimated 7 cm long, 3.5 to 10 cm wide; base cordate, apex acute; lobes triangular; most apical lateral primary veins diverging from medial secondary veins; 4 to 6 secondary veins originating at angles of 30° to 60°, straight or broadly convex, 1 or 2 craspedodromous, the others brochidodromous; 4 to 6 pairs of medial secondary veins originating at angles of 35° to 50°, straight or broadly convex, typically 2 craspedodromous and the others brochidodromous; lobal sinal bracing formed by an orthogonally to typically obtusely bifurcating secondary vein; intersecondary veins numerous, intergrading with secondary veins; tertiary veins compound, R-R, forming a coarse reticulum with intersecondary veins; fourth order venation irregularly polygonal; fifth order veins thick, forming quadrangular areoles 0.2 to 0.3 mm in diameter, veinlets unbranched or typically absent; teeth typically large, A-1 or B-1, 1 or 2 on each side of medial lobe, 1 on apical side and 2 on basal side of most apical lateral lobes; petiole at least 2.5 cm long.

Fruits samaroid, nutlet at basal end. Nutlet 0.6 to 0.8 cm long, 0.4 to 0.7 cm wide; outline suborbiculate, apex narrowly rounded; proximal margin typically expanded beyond proximal margin of wing; attachment scar 0.2 to 0.5 cm long; nutlet markedly inflated, 6 or 7 veins originating along attachment scar forming a reticulum, coalescing at apex of nutlet; attachment angle 10° to 30°, nutlet angle 25° to 80°. Wing extending 1/3 to 1/2 the length along distal margin of nutlet forming a broadly U-shaped sulcus with nutlet; 1.0 to 2.0 cm long, 0.5 to 1.0 cm wide; distal margin deeply convex, proximal margin straight to broadly convex, apex broadly rounded; 6 or 7 veins coalesced along proximal side, wing veins diverging at angles of 10° to 20°, sharply curving, extending slightly concavely at about a 45° angle to proximal margin, bifurcating, anastomoses numerous, veinlets reticulate.

Nomenclature: More than any other curator, Howard E. Schorn has contributed to the present study of *Acer*.

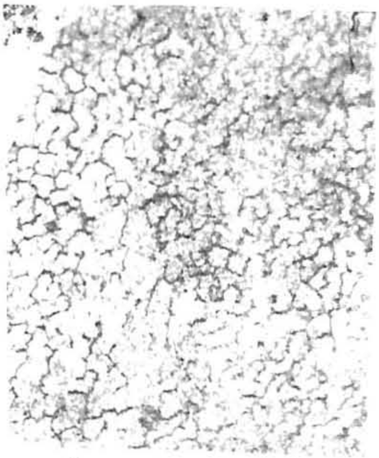
Explanation of Plate 28.

(all figures natural size unless otherwise stated)

Figs. 1, 4 *Acer osmonti* Knowlton. Bridge Creek/Knox Ranch. Hypotypes USNM 396154 (Fig. 1, ×7.5), USNM 396155 (Fig. 4).

Fig. 2 *Acer osmonti* Knowlton. Bridge Creek/Clarno NE. Hypotype UCMP 9129.

Fig. 3 *Acer oregonianum* Knowlton. Cascadia. Hypotype UCMP 9163.



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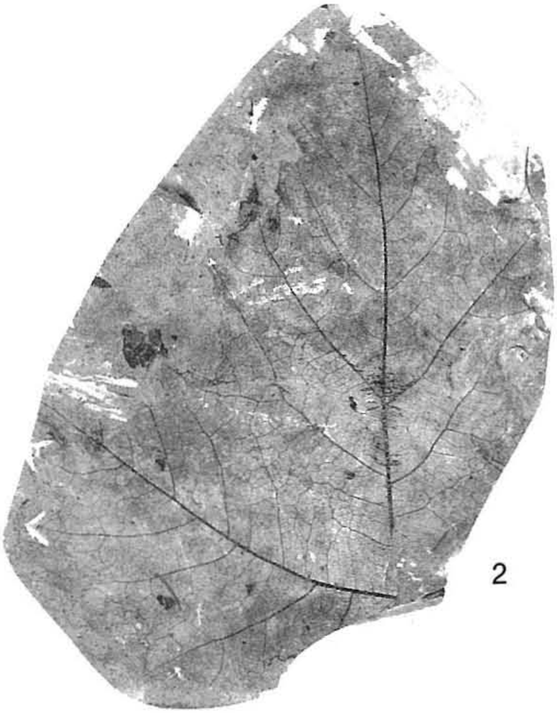

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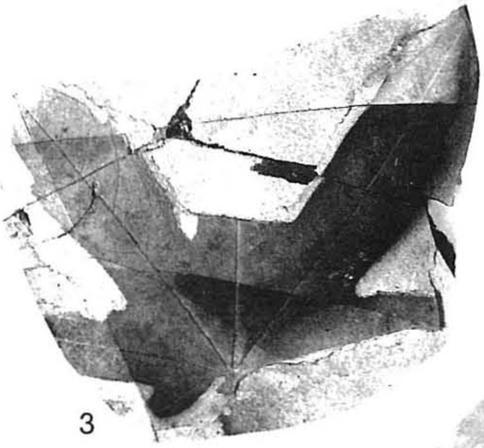

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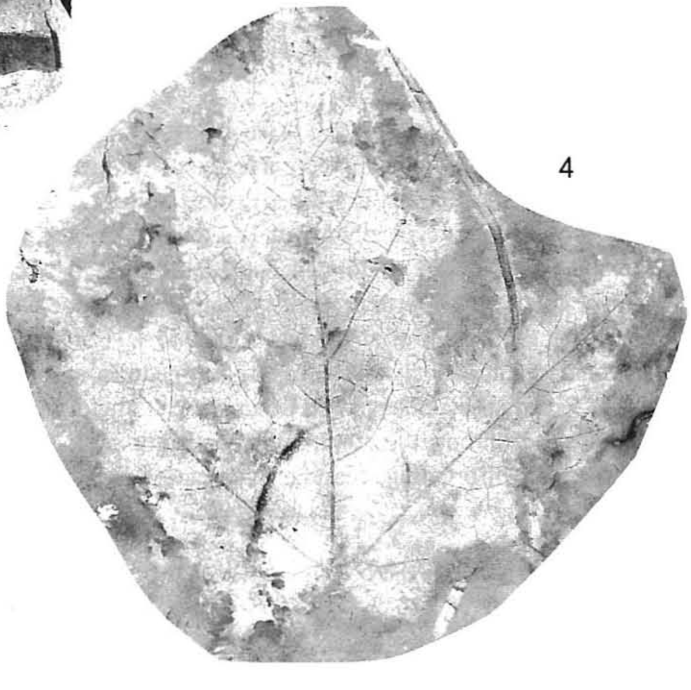

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Discussion: Leaves of *Acer schorni* are most like those of the extant *A. brachypterum,* which some systematists consider a southern variation of *A. grandidentatum* and other systematists consider a southern vartiation of *A. saccharum.* Other than greater degree of incision and narrower lobes in *A. grandidentatum* than in *A. brachypterum,* fourth order venation grades into the tertiary venation and veinlets are typically present and many are branched in *A. grandidentatum,* whereas in *A. brachypterum* third and fourth order venation systems are markedly differentiated and veinlets are unbranched or typically absent. *Acer saccharum* has areoles over twice as large as those of *A. brachypterum.* We consider *A. brachypterum* to be a valid species.

Fruits that we think represent *Acer schorni* are associated with *A. schorni* leaves at two of the three localities that have produced *A. schorni* leaves (the third locality produced no *Acer* fruits). These fruits are characterized by elliptical outline of the nutlet, low attachment angle, and low angle of the wing veins relative to the proximal margin.

One leaf (pl. 55, fig. 6) of *Acer schorni* has the teeth on the medial lobe entered, as in *A. collawashense,* by external vein that originate from a secondary loop. On the other hand, *A. schorni* has more teeth, more lobes, and smaller areoles than *A. collawashense.*

Distribution: Early middle Miocene through late Miocene from central and eastern Oregon east to westernmost Idaho and south to southwestern Nevada.

Typology: Holotype, UMMP 44835.

Occurrences: See appendix table.

Acer tyrellense Smiley

(pl. 55, figs. 7-11; pl. 56, figs. 1-4; text-fig. 18F)

Acer tyrellense Smiley. 1963. 227. pl. 13, f. 3, 5.
 Axelrod. 1985 (part). 176. pl. 14, f. 1-3, 5, 6; pl. 33, f. 6, 7, 9-12; pl. 34, f. 3, 4.
Acer arida auct. non Axelrod. Axelrod. 1956. (part). 307. pl. 31, f. 5, 6.
Acer bendirei auct. non Lesquereux. Hoxie. 1965 (part). 30.
Acer bolanderi auct. non Lesquereux. Axelrod. 1964. 127. pl. 16, f. 10-12.
Acer columbianum auct. non Chaney et Axelrod. Axelrod. 1964 (part). 127. pl. 15, f. 6, 7, 9.
Acer nevadensis auct. non Axelrod. Axelrod. 1985 (part, nontypic). pl. 13, f. 6.

Description: Leaves simple, perfectly actinodromous, with 5 primary veins; deeply 5-lobed (one specimen is 3-lobed); most apical lateral lobes 3/4 as long as medial lobe, most basal lobes typically about 1/2 as long as most apical lateral lobes; shape oblate; 2.6 to estimated 4.5 cm long, 4.3 to 7.0 cm wide; base cordate, apex acute; lobes elliptic; most apical lateral primary veins diverging from medial secondary veins; 4 or 5 secondary veins originating at angles of 30° to 60° from basal side of most apical lateral primary vein, broadly convex, 1 to 3 craspedodromous and the others borchidodromous; 4 or 5 medial secondary veins originating at angles of 35° to 60°, broadly convex, 1 or 2 craspedodromous, the others brochidodromous; lobal sinal branching formed by an orthogonally bifurcating secondary vein; intersecondary veins numerous; tertiary venation

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Explanation of Plate 29.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer osmonti* Knowlton. Gumboot Mountain. Hypotype UCMP 9147.

Fig. 2 *Acer osmonti* Knowlton. Bridge Creek/Pentecost Ranch. Hypotype UCMP 9135 (×5).

Fig. 3 *Acer osmonti* Knowlton. Lyons. Hypotype UCMP 9144.

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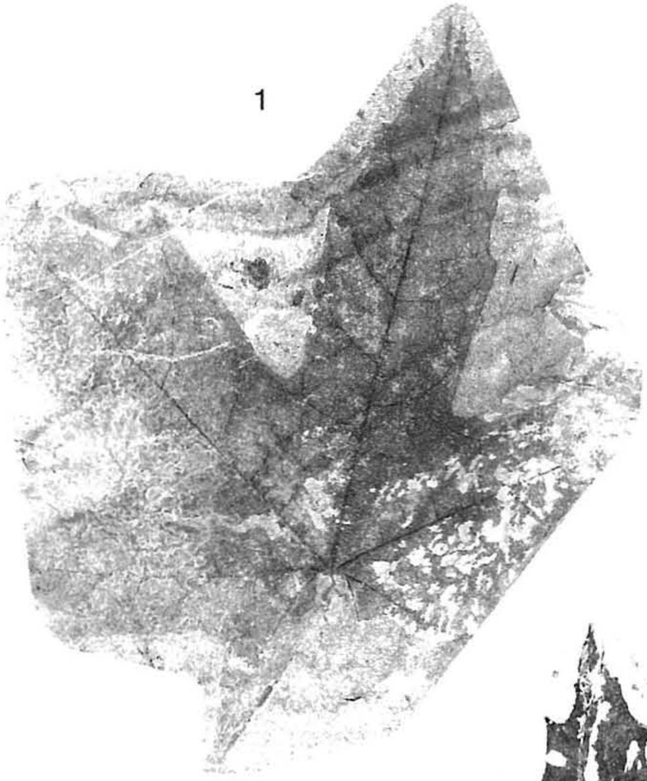

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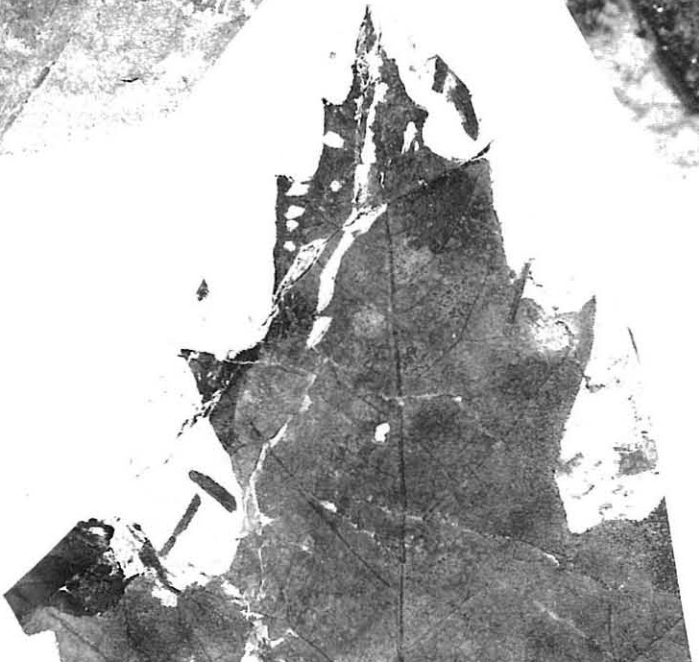

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compound, R-R, grading into fourth order venation; fifth order veins forming thick quadrangular areoles 0.2 to 0.4 mm in diameter; teeth large, A-1 or B-1, typically 1 or 2 on each side of medial lobation, 1 on apical and 1 or 2 on basal side of most apical lateral lobes; petiole 1.5 to 3.2 cm long.

Fruits samaroid; nutlet at basal end. Nutlets 0.8 to 1.0 cm long, 0.5 to 0.7 cm wide; outline U-shaped, apex broadly rounded; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.4 to 0.6 cm long; nutlet markedly inflated, with about 9 veins originating along attachment scar and forming an indistinct reticulum; attachment angle 20° to 50°, nutlet angle 30° to 60°. Wing extending no more than 1/3 along the distal margin of nutlet, forming a broadly V-shaped sulcus with nutlet; wing thickened basally; 2.7 to 3.0 cm long, 1.0 to 1.2 cm wide; distal margin deeply convex, proximal margin straight, apex narrowly to broadly rounded; 8 or 9 veins coalesced along proximal side, wing veins diverging at angles of 10 to 30°, curving sharply, extending almost straight at about a 60° to 80° angle to proximal margin, bifurcating, anastomoses numerous, veinlets reticulate.

Nomenclature: The Tyrell locality furnished Smiley's (1963) holotype of this species; the epithet should have been *Tyrellense.*

Discussion: Leaves of *Acer tyrellense* are typically small, five-lobed, deeply incised, lobes widest at about their midpoint, and teeth large relative to lobal size. As pointed out by Smiley, these leaves are comparable to those of *A. grandidentatum.*

Leaves of *Acer tyrellense* are known at eight localities, but only two of these have produced fruits of *Saccharodendron.* At the Middlegate locality, two types of *Saccharodendron* samaras occur, one of which is the type we have assigned to *A. schorni.* The second type of *Saccharodendron* samara from Middlegate is also the only type of *Sacchrodendron* samara that occurs with leaves of *A. tyrellense* at Eastgate.

Fruits that we think are those of *Acer tyrellense* are, like the foliage, also similar to *A. grandidentatum;* these similarities are straight proximal margin of the wing, U-shaped nutlet, thickened basal part of the wing, and wing veins at a high angle with respect to the proximal margin. Differences between fruits of the two species are: fruits of *A. tyrellense* are larger and have more numerous nutlet and proximally coalesced veins than *A. grandidentatum.*

Acer tyrellense has similarities to *A. minutifolium* in both leaf and fruit. In foliage, both species are primarily five-lobed, lobes are elliptical, and areolar venation is basically the same; teeth in *A. minutifolium* are typically smaller and sharper than in *A. tyrellense* and lobes are attenuated. In fruit, both species have a U-shaped nutlet, straight proximal margin of the wing, thickened basal part of the wing, and high angles of wing veins relative to the proximal margin; however, the reticulum on the nutlet of *A. minutifolium*

Explanation of Plate 30.

(all figures natural size unless otherwise stated)

Figs. 1, 5 *Acer oregonianum* Knowlton. Cascadia. Hypotypes USNM 396169 (Fig. 1), USNM 396170 (Fig. 5).

Figs. 2, 4 *Acer* sp. 6. Bridge Creek/Twickennham. UCMP 9171A (Fig. 2, ×5), 9171B (Fig. 4).

Fig. 3 *Acer osmonti* Knowlton. Lyons. Hypotype USNM 396157.

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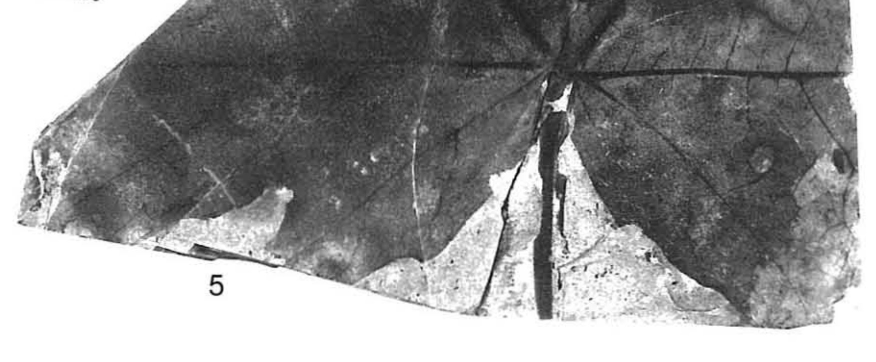

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is distinct, where the reticulum in *A. tyrellense* is very obscure, and the single samara of *A. minutifolium* is smaller than any known of *A. tyrellense. Acer tyrellense,* however, may be descended from *A. minutifolium.*

Distribution: Early middle Miocene of eastern Washington, eastern Oregon and western Nevada; late middle to early late Miocene of Columbia Plateaus and western Oregon; Pliocene or early Pleistocene of central California.

Typology: Holotype, UCMP 5472.

Occurrences: See appendix table.

Acer bolanderi Lesquereux

(pl. 56, figs. 5-11; text-fig. 18C)

Acer bolanderi Lesquereux. 1878. 27. pl. 7, f. 7-11.
Condit. 1944b. 85. pl. 19, f. 5, 6.

Description: Leaves simple, perfectly actinodromous; 3-lobed, the lateral lobes about 3/4 as long as medial lobe; shape suborbiculate; base rounded to narrowly cordate, apex acute; 2 to (estimated) 6 cm long, 2.5 to 6 cm wide; lobes elliptic; lateral primary veins parallel to or slightly diverging from medial secondary veings; 5 to 8 secondary veins originating at angles of 60° to 90° from basal side of lateral primary veins, straight to broadly convex, most brochidodromous; 3 or 4 pairs of medial secondary veins originating at angles of 30° to 60°, straight to broadly convex, most brochidodromous; lobal sinal bracing formed by an acutely to orthogonally bifurcating medial secondary vein; tertiary veins compound, A-A, spaced 0.2 to 0.4 cm; fourth order venation polygonal; fifth order veins forming quadrangular areoles 0.3 to 0.7 cm in diameter, veinlets absent or thin and unbranched; teeth large, B-1, typically 1 each on each side of medial lobe and on basal sides of lateral lobes; petiole up to 1.7 cm long.

Nomenclature: Lesquereux named this species for the collector of the material on which the species is based.

Discussion: Acer bolanderi, which is known only from leaves, has strong similarities to leaves of *A. schorni* in number and distribution of teeth. However, *A. schorni* is typically five-lobed and has small areoles, in contrast to *A. bolanderi,* which is only three-lobed and has large areoles.

Distribution: Early late Miocene of central California.

Typology: Lectotype here designated, UCMP 1825.

Occurrence: See appendix table.

Explanation of Plate 31.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer osmonti* Knowlton. Bridge Creek/Allen Ranch. Holotype UCMP 2505.

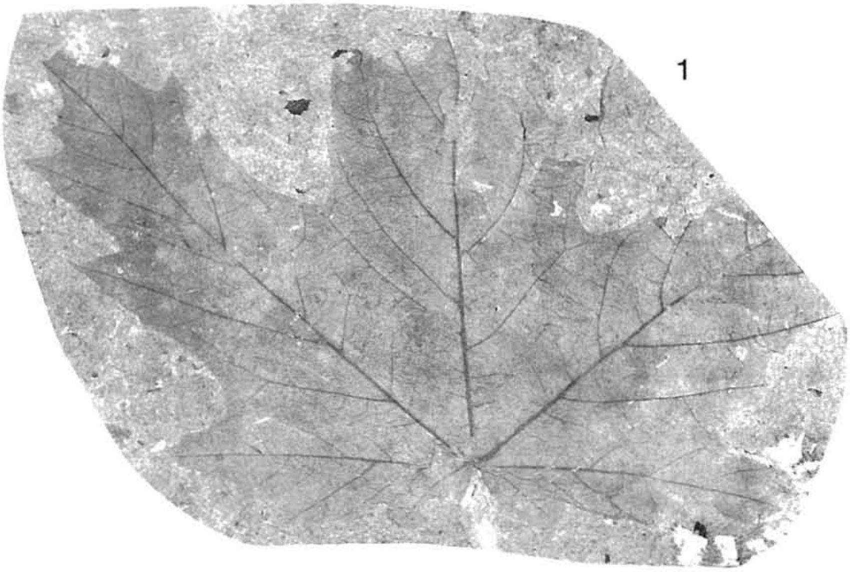
Figs. 2, 4 *Acer osmonti* Knowlton. Bridge Creek/Twickenham. Hypotypes UCMP 9141 (Fig. 2), UCMP 9142 (Fig. 4).

Fig. 3 *Acer osmonti* Knowlton. Lyons. Hypotype UCMP 9146.

Fig. 5 *Acer osmonti* Knowlton. Bridge Creek/Knox Ranch. Hypotype USNM 396154.

Fig. 6 *Acer osmonti* Knowlton. Bridge Creek/Pentecost Ranch. Hypotype UCMP 9135.

Fig. 7 *Acer* cf. *A. oregonianum* Knowlton. Shale City. USNM 396171.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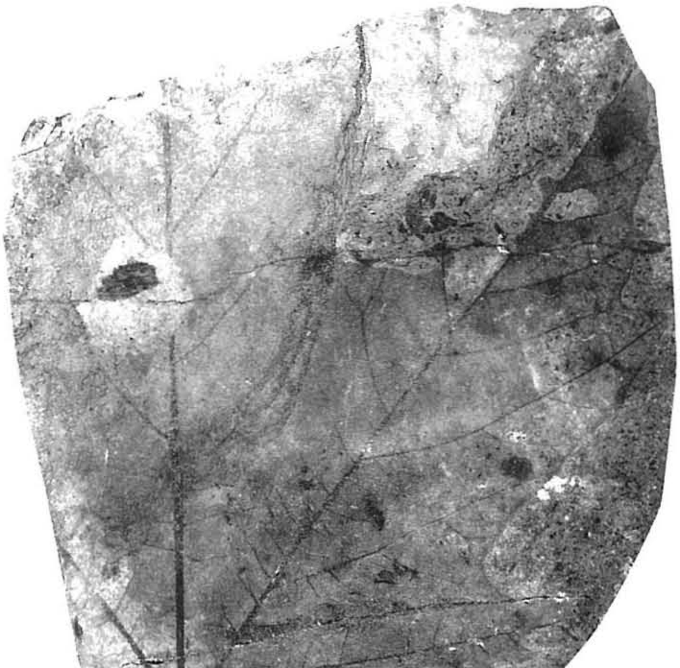
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Acer species indetermined

Quercus prelobata auct. non Condit. Axelrod. 1958. 129. pl. 23, f. 10.

Discussion: Several leaves have characters indicative of *Saccharodendron* but are too fragmentary or poorly preserved for specific determination.

Occurrences: See appendix table.

Platanoidea Group

Section *Manchesteria* Wolfe et Tanai, sect. nov.

Diagnosis: Leave simple, perfectly actinodromous; deeply 3-lobed, with lateral lobes from 2/3 the length of, to almost as long as, medial lobe; 3 primary veins; lobal sinal bracing typically formed by an orthogonally bifurcating secondary vein; tertiary veins compound, A-A to A-R; areoles formed by quadrangular, thick fifth order veins, veinlets typically simple; teeth A-1, mostly simple.

Fruits samaroid, nutlet at basal end; nutlet flattened; numerous veins originating along attachment scar, extending parallel across nutlet and passing onto wing; attachment angle 40° or higher.

Discussion: The three-lobed condition and quadrangular areoles with simple veinlets indicate that *Manchesteria* is related to *Orba.* Long lateral lobes and orthogonally braced sinuses are, however, characters not found in *Orba.* The tendency to have simple A-1 teeth is also atypical for *Orba.*

The flattened nutlets of *Manchesteria* are similar to those of the extant *Campestria* and *Platanoidea.* The somewhat distally placed major vein on the nutlet of *A. axelrodi* may be a relict of a pair of flanges.

Type species: Acer manchesteri Wolfe et Tanai.

Acer axelrodi Wolfe et Tanai, sp. nov.

(pl. 20, figs. 3, 5-7, 9, 10)

Description: Leaf simple, perfectly actinodromous; deeply 3-lobed; shape very wide ovate; base very broadly rounded; lobal apex acute; over 4.5 cm long (incomplete), about 9 cm wide; lateral primary veins diverging from medial secondary veins; about 7 lateral secondary veins originating at angles of 30° to 40° from basal side of lateral primary vein, broadly convex, craspedodromous, interspersed with intersecondary veins; at least 3 pairs of medial secondary veins, the most basal pair orthogonally or obtusely

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Explanation of Plate 32.

(all figures natural size)

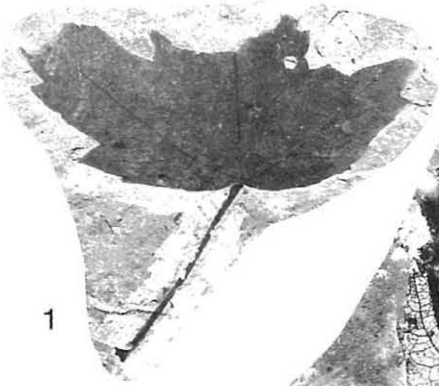
Figs. 1, 5 *Acer manchesteri* Wolfe et Tanai. Bridge Creek/Gray Ranch. Paratypes UCMP 9209A (Fig. 1), UCMP 9210 (Fig. 5).

Figs. 2, 6-10 *Acer manchesteri* Wolfe et Tanai. Bridge Creek/Dugout Gulch. Paratypes UCMP 9204 (Fig. 6), UCMP 9105 (Fig. 7), UCMP 9206 (Fig. 8), UCMP 9207 (Fig. 9), UCMP 9208 (Fig. 10). Holotype UCMP 9203 (Fig. 2).

Fig. 3 *Acer chaneyi* Knowlton. Gumboot Mountain. Hypotype UCMP 9090.

Fig. 4 *Acer chaneyi* Knowlton. Kukak Bay. Hypotype USNM 30230.

Figs. 11, 12 *Acer manchesteri* Wolfe et Tanai. Bridge Creek/Allen Ranch. Paratypes USNM 396211 (Fig. 11), USNM 396212 (Fig. 12).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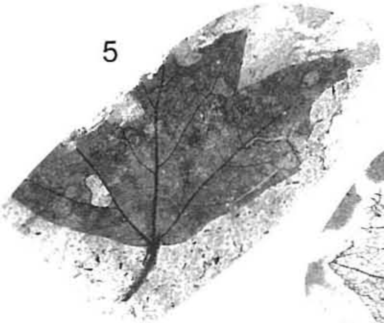
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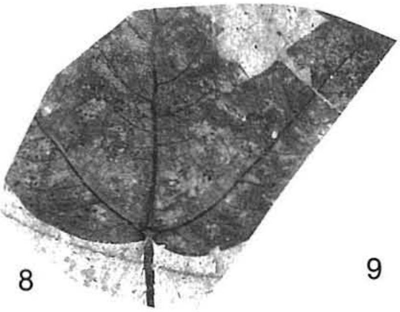
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bifurcating to brace lobal sinuses; tertiary veins compound, R-A, spaced 0.2 to 0.4 cm; fourth order venation quadrangular; fifth order veins thick, forming quadrangular areoles 0.3 to 0.5 mm in diameter, veinlets absent or unbranched; 3 large A-1, narrowly rounded teeth on basal sides of lateral lobes.

Fruits samaroid, nutlet at basal end; nutlets 0.5 to 0.7 cm long, 0.6 cm wide; outline inverse U-shaped, apex broadly rounded; attachment scar 0.5 to 0.6 cm long, with a distal keel; nutlet flattened, with 6 or 7 obscure and 1 major vein originating along attachment scar and extending parallel across nutlet, extending onto wing; major vein about 2/3 the distance from proximal to distal margin; attachment angle 75° to 80°, nutlet angle 10° to 20°. Wing extending about 1/2 the length along distal side of nutlet; 1.3 to 1.8 cm long, 0.8 to 1.0 cm wide; distal margin broadly convex, proximal margin straight, apex broadly rounded; 6 or 7 poorly coalesced veins on proximal side, wing veins diverging at angles of 10° to 20°, sharply and irregularly curving, bifurcating, few anastomoses.

Nomenclature: In recognition of his many works in Tertiary paleobotany and for allowing us access to unpublished collections, we name this species for Daniel I. Axelrod.

Discussion: The single leaf and two fruits from Bull Run that are described here as *Acer axelrodi* show characters that link the respective organs both to the *Orba* Group and to the extant *Campestria* and *Platanoidea.* Further, similar fruits and leaves are associated at Oligocene localities. On both the intermediate relationships and associations of similar organs, we suggest that the Bull Run leaf and fruits represent the same species; more associations would, however, be desirable to increase the probability of conspecificity.

Distribution: Late middle Eocene of northeastern Nevada.

Typology: Holotype, UCMP 9203.

Occurrence: See appendix table.

Acer manchesteri Wolfe et Tanai, sp. nov.

(pl. 32, figs. 1, 2, 5-12; text-fig. 18G, H)

Acer glabroides auct. non R. W. Brown. Brown. 1937b (part, nontypic). 180. pl. 58, f. 15.

Description: Leaves simple, perfectly actinodromous; 3-lobed, lateral lobes almost as long as medial lobe; shape elliptic to orbiculate; base rounded to shallowly cordate; apex attenuate to acute; lobes elliptic; strong lobations may be present on medial or lateral lobes; lateral primary veins slightly diverging from medial secondary veins; 4 to 8 secondary veins originating at angles of 30° to 40° from basal side of lateral primary vein, broadly convex, craspedodromous; 5 to 7 medial secondary veins originating at angles of 30° to 50°, broadly convex, craspedodromous; lobal sinal bracing typically

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Explanation of Plate 33.

(all figures natural size)

Figs. 1, 7, 8 *Acer browni* Wolfe et Tanai. Collawash. Paratypes UCMP 9328 (Fig. 1a), UCMP 9329 (Fig. 1b), UCMP 9330 (Fig. 7), UCMP 9331 (Fig. 8).

Figs. 2-6 *Acer smileyi* Wolfe et Tanai. Clarkia. Paratypes UCMP 9179 (Fig. 2), UCMP 9180 (Fig. 3), UCMP 9181 (Fig. 4), UCMP 9182 (Fig. 5), UCMP 9183 (Fig. 6).

Fig. 9 *Acer smileyi* Wolfe et Tanai. Trout Creek. Paratype UMMP 69154.


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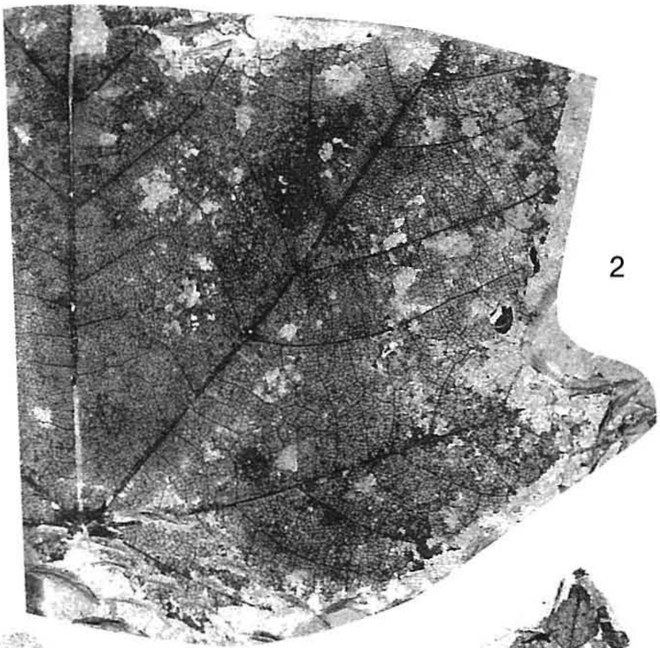
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formed by an orthogonally bifurcating secondary vein; external secondary veins originating orthogonally or acutely; tertiary veins compound, A-A to A-R spaced 2 to 3 cm; fourth order venation quadrangular; fifth order veins thick, forming quadrangular areoles 0.3 to 0.5 mm in diameter, veinlets thick and typically simple; teeth typically A-1, sharp, typically no or 1 subsidiary tooth on basal flank and none on apical flank; petiole up to 2.7 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.6 to 1.0 cm long, 0.5 to 0.8 cm wide; outline widely ovate to elliptic, apex broadly rounded; attachment scar 0.5 to 0.8 cm long, with pronounced proximal and distal keels; nutlet flattened, with 8 to 10 veins of equal thickness originating along attachment scar and parallel across nutlet, passing onto wing; attachment angle 40° to 60°, nutlet angle 20° to 30°. Wing extending about 1/2 the length along distal margin of nutlet; 1.5 to 3.2 cm long, 0.6 to 1.0 cm wide; distal margin broadly convex, proximal margin straight to broadly concave, apex broadly rounded; proximal side with 5 or 6 coalesced veins, wing veins diverging at angles of 10° to 20°, smoothly curving, bifurcating, some anastomoses.

Nomenclature: Steven R. Manchester has assisted us in supplying new material from various localities in central Oregon.

Discussion: Fruits of *Acer manchesteri* are similar in size and general shape to those of *A. oligomedianum,* and, because both species occur in the Bridge Creek flora, might be confused with one another. The attachment scar of *A. manchesteri,* however, has pronounced proximal and distal keels, which are absent in *A. oligomedianum,* and the attachment angle is typically high in *A. manchesteri.* Relation of nutlet veins to wing veins also provides a separation of fruits of the two species: in *A. manchesteri,* nutlet veins do not coalesce and maintain their identity in passing onto the wing, whereas in *A. oligomedianum,* nutlet veins tend to coalesce near the apical margin of the nutlet and then pass onto the wing. This character difference is particularly noticeable in the distal part of the nutlet and adjacent wing. Yet another distinction is that in *A. manchesteri* the wing extends along the distal margin of the nutlet to the attachment scar, whereas in *A. oligomedianum* the wing extends about half the length of the distal margin of the nutlet.

Leaves of *Acer manchesteri* are similar in gross appearance to the leaves of both *A. oligomedianum* and *A. ashwilli.* The main character that separates *A. manchesteri* from these two other foliar types is in bracing of the lobal sinuses: in *A. manchesteri,* bracing is accomplished by a secondary vein (or in some instances a vein of intersecondary thickness) that bifurcates orthogonally, whereas in the other two species bracing is accomplished either by an external secondary vein that originates acutely or by an acutely bifurcating secondary (or intersecondary) vein. Other distinguishing features include

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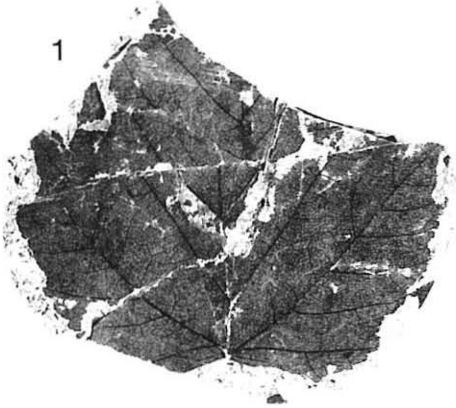
Explanation of Plate 34.

(all figures natural size)

Figs. 1, 2, 4-8 *Acer browni* Wolfe et Tanai. Collawash. Paratypes UCMP 9332 (Fig. 1), UCMP 9335 (Fig. 2), UCMP 9333 (Fig. 4), UCMP 9336 (Fig. 6), UCMP 9337 (Fig. 7), UCMP 9334 (Fig. 8). Holotype UCMP 9172 (Fig. 5).

Fig. 3 *Acer browni* Wolfe et Tanai. Latah/Vera. Paratype USNM 396189.

Fig. 9 *Acer smileyi* Wolfe et Tanai. Clarkia. Holotype UCMP 9178.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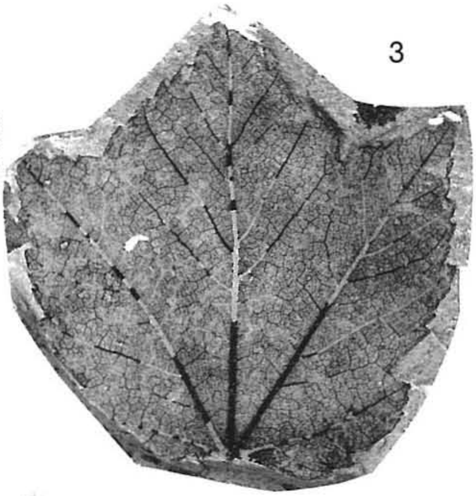
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fewer and larger, A-1 teeth of *A. manchesteri* in contrast to more numerous and smaller D-1 teeth in the other two species. Areolar venation is typically not preserved in Bridge Creek specimens, but, if present, areoles of *A. manchesteri* are quadrangular and small, are formed by thick veins, and have veinlets that are thick, simple and few. In *A. oligomedianum,* areoles are larger, are formed by thinner veins, and veinlets are thin, and in *A. ashwilli* areoles are very large, irregularly polygonal, and thin veinlets branch two or three times.

Characters of both foliage and fruit ally *Acer manchesteri* to *A. axelrodi.* Unfortunately, foliage of *A. axelrodi* is known from a single specimen, but in areolar venation and few and large D-1 teeth the two species are highly similar. Teeth of *A. axelrodi* are however, rounded, in contrast to narrowly rounded to sharp teeth of *A. manchesteri.* Similarities in fruits include high attachment angle, flattened nutlets, extension of the wing half way along the distal margin of the nutlet, and continuity of the veins from the nutlet passing onto the wing. In *A. manchesteri,* however, fruits are larger, the attachment scar has prominent proximal and distal keels, and the nutlet lacks the remnant of a flange.

Distribution: Early Oligocene of central and western Oregon.

Typology: Holotype, UCMP 9216A, B.

Occurrences: See appendix table.

Section *Campestria* Pax

Acer tiffneyi Wolfe et Tanai, sp. nov.

(pl. 21, figs. 1-6; text-fig. 18I)

Acer glabroides auct. non R. W. Brown. Becker. 1969 (part). 113. pl. 36, f. 22.
Acer oregonianum auct. non Knowlton. Becker. 1969 (part). 113. pl. 35, f. 17.
Acer scottiae auct. non MacGinitie. Becker. 1969 (part). 114. pl. 35, f. 5, 7.
Acer? sp. Becker. 1961. 81. pl. 25, f. 10, 11.

Description: Leaves simple, perfectly actinodromous, with 7 primary veins; deeply 5-lobed; most apical lateral lobes almost as long as medial lobe, most basal lateral lobes small; shape orbiculate; estimated 5 to 10 cm long, estimated 4 to 11 cm wide; base cordate, apex narrowly rounded and acute; lobes elliptic, except most basal lateral lobes broadly rounded-triangular; most apical lateral primary veins diverging from medial secondary veins; 5 or 6 secondary veins originating at angles of 45° to 65° from basal side of most apical lateral primary veins, broadly convex, most brochidodromous, 2 or 3 craspedodromous; about 6 pairs of medial secondary veins originating at angles of 45° to

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Explanation of Plate 35.
(all figures natural size)

Fig. 1 *Acer palaeorufinerve* Tanai et Onoe. Seldovia Point. Hypotype USNM 208471.
Fig. 2 *Acer latahense* Wolfe et Tanai. Latah/Brickyard. Holotype USNM 396136A.
Figs. 3, 6, 7 *Acer heterodentatum* (Chaney) MacGinitie. Collawash. Hypotypes UCMP 9173, (Fig. 3), UCMP 9174 (Fig. 6), UCMP 9056 (Fig. 7).
Fig. 4 *Acer latahense* Wolfe et Tanai. Succor Creek/Maple Ridge. Paratype UMMP 44840.
Fig. 5 *Acer latahense* Wolfe et Tanai. Latah/Vera. Paratype USNM 396137.
Fig. 8 *Acer heterodentatum* (Chaney) MacGinitie. Eagle Creek. Lectotype UCWM 22348.

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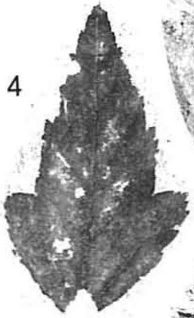

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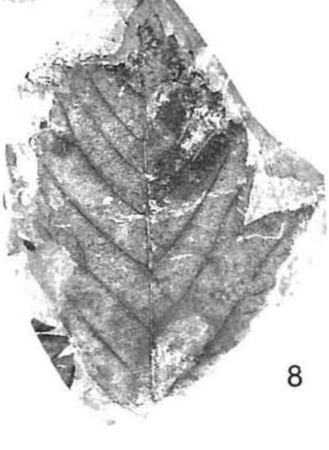

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50°, broadly convex, most brochidodromous, 2 or 3 craspedodromous; lobal sinal bracing formed by an orthogonally bifurcating medial secondary vein; bracing of minor sinus between 2 lateral lobes formed by a tertiary vein; intersecondary veins numerous; tertiary veins compound, A-A or A-R, spaced 0.2 to 0.3 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular or pentagonal areoles 0.2 to 0.4 mm in diameter, veinlets absent or typically unbranching; teeth rounded, A-1 or B-1, 2 or 3 on each side of medial lobe, none to 2 on apical side, and 2 on basal side of most apical lateral lobe; petiole 3.0 cm long.

Fruit samaroid, nutlet at basal end; nutlet 0.4 cm long, 0.5 cm wide; outline almost semicircular; proximal margin slightly expanded beyond proximal margin of wing; attachment scar 0.45 cm long; nutlet flattened, with some obscure veins passing onto wing; attachment angle 70°, nutlet angle 30°. Wing extending along distal side of nutlet to attachment scar; over 1.3 cm long, 0.8 cm wide; distal margin broadly convex, proximal margin broadly concave, apex not preserved; 7 veins loosely coalesced along proximal side, wing veins diverging gradually, then sharply curving, bifurcating, anastomoses numerous.

Nomenclature: In recognition of Bruce H. Tiffney's contributions to the biogeography of Tertiary plants.

Discussion: The combination of characters in leaves of *Acer tiffneyi* strongly indicate an assignment to *Campestria.* In particular, these characters include (1) five lobes, (2) orthogonally angled lobal sinal bracing of major lobes, (3) weak bracing by tertiary veins between lateral lobes, (4) few and irregularly spaced teeth, (5) rounded teeth and lobal apices. Rounding of the teeth and lobal apices differentiates *Platanoidea* from *Campestria,* which otherwise have similar foliage. The second and third characters eliminate *Macrophylla,* which has some acutely bifurcating major veins bracing dental sinuses.

The fruit assigned to *Acer tiffneyi* also has characters of *Campestria* samaras: high attachment angle, flattened nutlet, nutlet almost semicircular in outline, and veins passing from nutlet directly onto wing. Fruits of *Platanoidea* are also similar to *A. tiffneyi,* except veins on the nutlet are distinct in *Platanoidea.*

Distribution: Latest Eocene of western Montana.

Typology: Holotype, NYBG (YUPM) 599A, B, 511; the base (511) of th holotype was assigned to *Acer oregonianum* and the apex (599A, B) to *A. scottiae* by Becker (1968).

Occurrences: See appendix table.

Explanation of Plate 36.

(all figures natural size)

Fig. 1 *Acer heterodentatum* (Chaney) MagGinitie. Eagle Creek. Second of Chaney's cotypes. UCWM 22347.

Fig. 2 *Acer molallense* Wolfe et Tanai. Liberal. Holotype USNM 396062.

Fig. 3 *Acer negundoides* MacGinitie. Buffalo Canyon. Hypotype UCMP 9061A.

Fig. 4 *Acer negundoides* MacGinitie. Collawash. Hypotype UCMP 9338.

Fig. 5 *Acer heterodentatum* (Chaney) MacGinitie. Seldovia Point. Hypotype USNM 208480.

Fig. 6 *Acer negundoides* MacGinitie. Succor Creek/Maple Ridge. Hypotype UMMP 21457.


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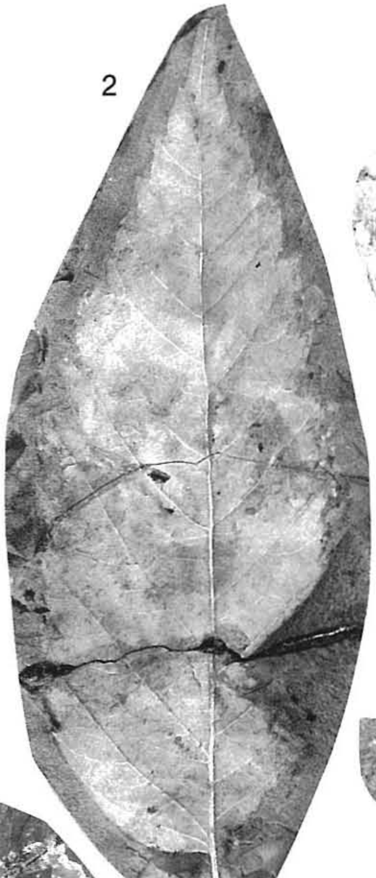
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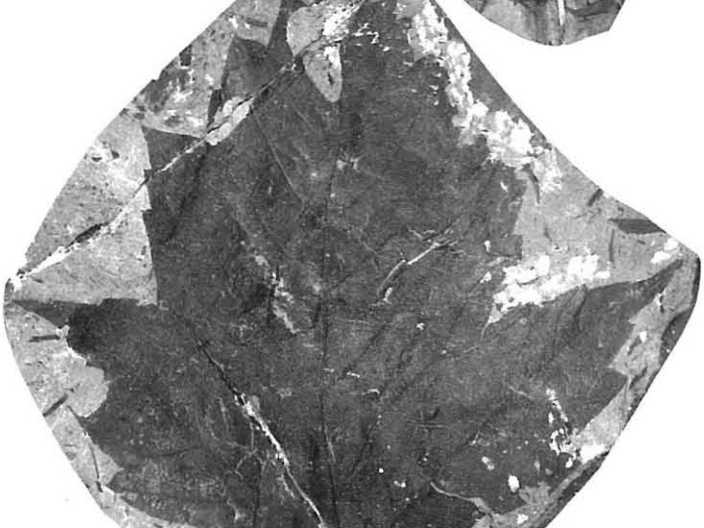
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Acer protomiyabei Endo

(pl. 61, figs. 1-4; text-fig. 18J)

Acer protomiyabei Endo. 1950. 15. pl. 3, f. 11.
  Tanai. 1983. 334. pl. 6, f. 2. 3; pl. 7, f. 4; pl. 8, f. 1-3, 6.
Acer ezoanum auct. non Oishi et Huzioka. Wolfe. 1966. B25. pl. 8, f. 6.
  Wolfe. 1972. pl. 10, f. 4.
  Wolfe & Tanai. 1980. 40. pl. 17, f. 1-3, 5; pl. 19, f. 2, 5.

Description: See Tanai (1983, p. 334).

Nomenclature: As demonstrated by Tanai (1983), the type of *Acer ezoanum* represents *Eriocarpa,* and most fossils previously assigned to *A. ezoanum* he reassigned to *A. protomiyabei.*

Discussion: Although *Acer protomiyabei* has been compared to the extant *A. miyabei* of *Campestria,* Tanai (1983) noted that in the fossils both teeth and lobal apices are sharper than typical for *Campestria,* but not as sharp as typical for *Platanoidea.* Whereas the 2 extant species of *Campestria* both have rounded teeth and lobal apices, of the 12 of 16 species of *Platanoidea* we have examined, all have sharp teeth (if present) and lobal apices. On this basis, *A. protomiyabei* could belong to either *Platanoidea* or *Campestria.*

Several of the Alaskan leaves of *Acer protomiyabei* have seven lobes (some even have nine). These leaves cannot be distinguished on any other character, other than number of lobes, from the five-lobed leaves typical of *A. protomiyabei.* In having some leaves that have more than five lobes, *A. protomiyabei* is more typical of *Platanoidea* than of *Campestria.* Perhaps both *A. protomiyabei* and *A. septilobatum* represent an extinct section that has characters intermediate between these two extant sections.

Distribution: Early to early middle Miocene of southern Alaska and Kamchatka; early to late Miocene of the maritime provinces of U.S.S.R., Korea, northeastern China, Hokkaido, and Honshu.

Typology: Holotype, Institute of Geology and Paleontology, Tohoku Univ. 60994 (not illustrated).

Occurrences: See appendix table.

Explanation of Plate 37.

(all figures natural size unless otherwise stated)

Figs. 1-5, 17 *Acer knolli* Wolfe et Tanai. Latah/Brickyard. Paratypes UCMG 17047 (Fig. 1), USNM 39325 (Fig. 2), USNM 396061 (Fig. 4), USNM 36444 (Fig. 5). Holotype USNM 39666 (Figs. 3, ×5; 17).

Fig. 6 *Acer negundoides* MacGinitie. Collawash. Hypotype UCMP 9339.

Fig. 7 *Acer negundoides* MacGinitie. Trout Creek. Hypotype UCMP 617.

Figs. 8-10, 19 *Acer heterodentatum* (Chaney) MacGinitie. Collawash. Hypotypes UCMP 9340 (Fig. 8), UCMP 9341 (Fig. 9), UCMP 9342 (Figs. 10, 19, ×5).

Fig. 11 *Acer negundoides* MacGinitie. Buffalo Canyon, Hypotype UCMP 9062A.

Figs. 12-15, 18 *Acer negundoides* MacGinitie. Hog Creek. Hypotypes USNM 396070 (Fig. 12), USNM 396071 (Fig. 13), USNM 396072 (Fig. 14), 396073 (Fig. 15), 396074 (Fig. 18, ×5).

Fig. 16 *Acer cranei* Wolfe et Tanai. Bridge Creek/Allen Ranch. Paratype UCMP 9225.

Figs. 20, 21 *Acer traini* Wolfe et Tanai. Trout Creek. Holotype UMMP 65138 (Fig. 20). Paratype UMMP 65139 (Fig. 21).

Fig. 21 *Acer traini* Wolfe et Tanai. Trapper Creek. Paratype UCMP 9343.

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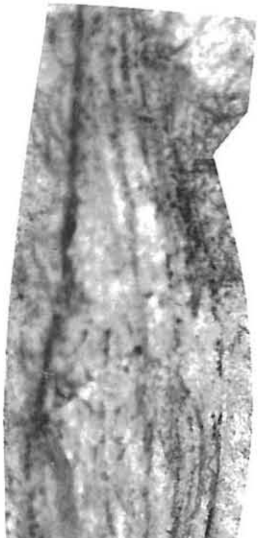

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Acer septilobatum Oliver

(pl. 58, figs. 1-4; pl. 59, figs. 1-7; pl. 60, figs. 1-4; text-fig. 18L)

Acer septilobatum Oliver. 1934. 15. pl. 4, f. 1, 2.
Dorf. 1936. 122. pl. 3, f. 5.
Acer alvordensis auct. non Axelrod. Axelrod. 1956 (part). 306. pl. 30, f. 11.
Acer oregonianum auct. non Knowlton. Chaney & Axelrod. 1959 (part). 195. pl. 41, f. 14.
Axelrod. 1964 (part). 128.
Acer scottiae auct. non MacGinitie. MacGinitie. 1933 (part, nontypic). 62, pl. 11, f. 4.
Brown. 1937a. 514. text-f. 2.
Smith. 1941 (part). 516. pl. 12, f. 8.
Chaney & Axelrod. 1959 (part). 196. pl. 41, f. 8, 9.
Axelrod. 1964 (part). 129. pl. 15, f. 3-5.
Axelrod. 1985. 176. pl.15, f. 10, 11.
Acer nevadensis auct. non Axelrod. Axelrod. 1985 (part, nontypic). 13. pl. 13, f. 7.

Description: Leaves simple, perfectly actinodromous, with 5 to 9 primary veins; deeply 5- or 7-lobed; most apical lateral lobes almost as long as medial lobe, more basal lobes of variable relative lengths; shape typically orbiculate; 3.0 to estimated 12 cm long, 4.0 to estimated 15 cm wide; base cordate, apex acute; lobes elliptic, except for small, triangular most basal lobes; most apical lateral primary veins parallel to or slightly diverging from medial secondary veins; 4 to 6 pairs of secondary veins originating at angles of 30° to 60° from basal side of most apical lateral primary veins, straight to broadly convex, brochidodromous or craspedodromous; 4 to 6 pairs of medial secondary veins originating at angles of 30° to 60°, straight to broadly convex, brochidodromous or craspedodromous; major lobal sinal bracing formed by a medial secondary vein that bifurcates orthogonally or by a medial external secondary vein that originates orthogonally; minor lobal sinal bracing typically formed by a tertiary vein; intersecondary veins numerous; tertiary veins compound, A-A to A-R, spaced 0.3 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veins forming quadrangular or pentagonal areoles 0.2 to 0.4 mm in diameter, veinlets unbranched or typically absent; teeth sharp, typically B-1 or C-1, typically 2 on either side of medial lobe, 1 or 2 on apical side and 2 on basal side of most apical lateral lobe, and a low but variable number on most basal lobes; petiole over 2.5 cm long.

Fruits samaroid; nutlet at basal end; nutlet 0.7 to 1.1 cm long, 0.7 to 1.1 cm wide; outline typically broadly U-sharped; proximal margin expanded beyond proximal margin of wings; attachment scar 0.7 to 1.1 cm long, with prominent distal keel; nutlet flattened, with many (8 to 15?) veins originating along attachment scar and extending apically onto wing; attachment angle 65° to 110°, nutlet angle 0° to 20°. Wing extending about half the length of distal margin of nutlet, forming a shallow U-shaped sulcus with

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Explanation of Plate 38.
(all figures natural size)

Figs. 1, 5 *Acer medianum* Knowlton. Succor Creek/Fenwick Gulch. Hypotypes UMMP 69143 (Fig. 1), UMMP 69144 (Fig. 5).

Fig. 2 *Acer medianum* Knowlton. Succor Creek/Devils Gate. Hypotype MSUB 9/22/77-I-126A.

Figs. 3, 6 *Acer medianum* Knowlton. Fingerrock. Hypotypes UCMP 9073 (Fig. 3), UCMP 9074 (Fig. 6).

Fig. 4 *Acer medianum* Knowlton. Middlegate. Hypotype (holotype of *A middlegatei* Axelrod) UCMP 4388.

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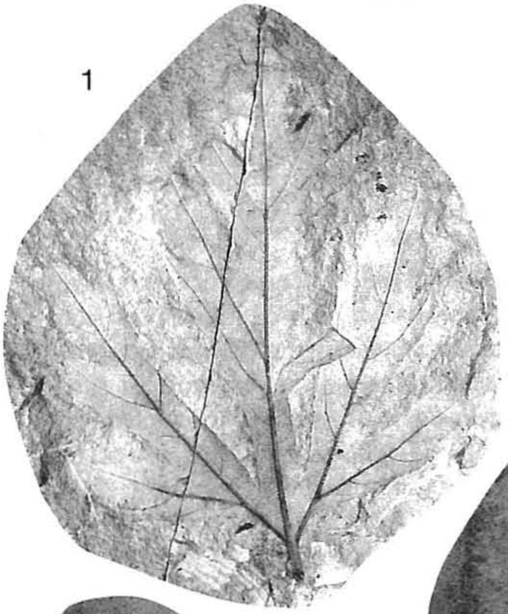

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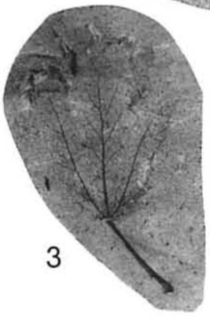

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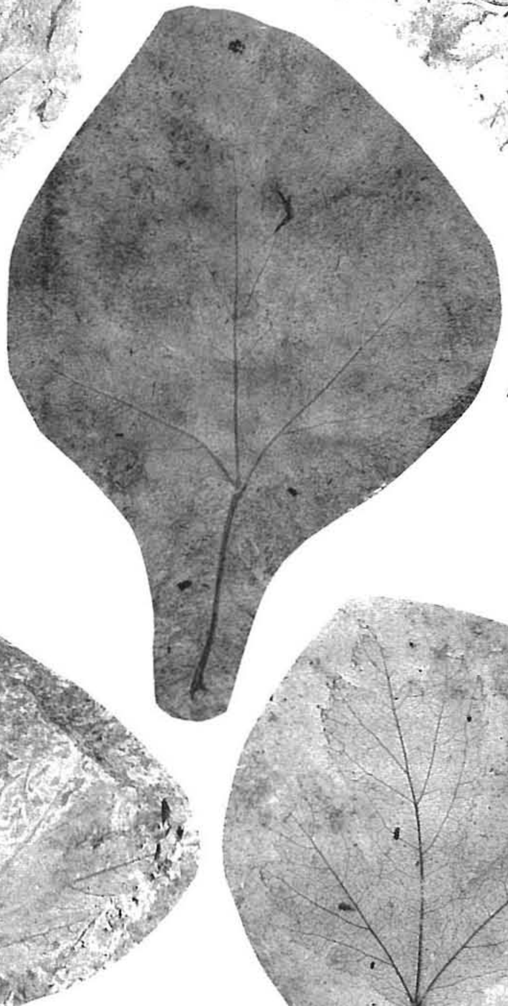

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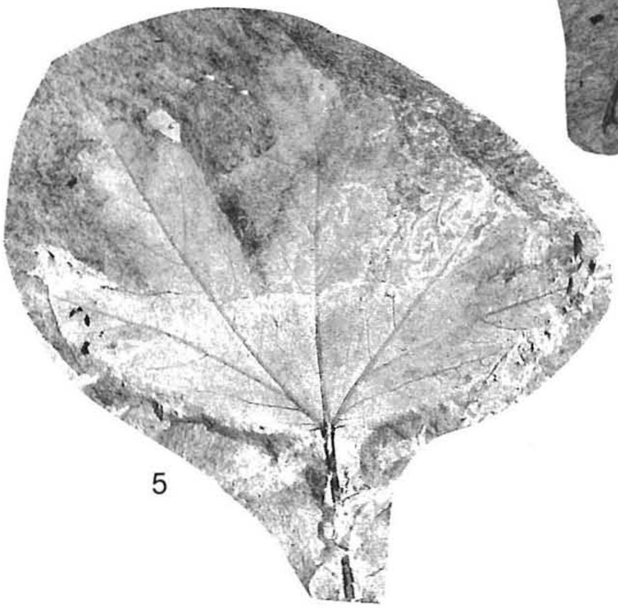

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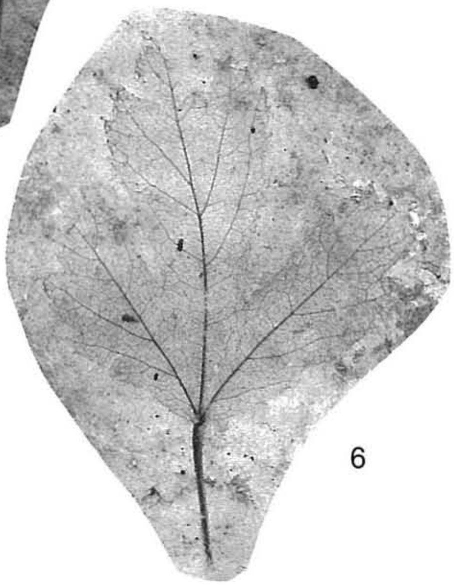

nutlet; 2.1 to estimated 4 cm long, 0.9 to 1.8 cm wide; distal margin shllowly to deeply convex, proximal margin straight to shallowly concave, apex narrowly rounded; 6 to 9 veins loosely coalesced along proximal margin, wing veins diverging gradually, smoothly curving, bifurcating, anastomoses numerous.

Nomenclature: All leaves included in the synonymy have been previously placed in *Macrophylla,* whereas the samaras were referred to *Platanoidea.* Oliver's types of *A. septilobatum* are seven-lobed, and hence the epithet.

Discussion: Leaves of *Acer septilobatum* have a high degree of convergence with leaves of Neogene *Macrophylla.* Areolar venation of *A. septilobatum* is clearly distinct from that of Neogene *Macrophylla,* but in many specimens areolar venation is not preserved. Leaves of *A. septilobatum,* however, have characters of secondary venation that allow these leaves to be separated from Neogene *Macrophylla.* In *Macrophlla,* most lobal sinal bracing is formed by acutely bifurcating secondary veins; this acute bracing also occurs in the dental braces and all external secondary veins also originate acutely. In *A. septilobatum,* on the other hand, braces are orthogonal (except in some seven-to nine-lobed leaves) and most external secondary veins originate orthogonally; as well, bracing between the lateral lobes is weak and is formed by a tertiary vein. Orthogonal bracing and orthogonally originating external secondary veins are typical of *Platanoidea* and *Campestria.*

Oliver (1934) considered *A. septilobatum* to be allied to *A. circinnatum* and therefore a member of *Palmata.* On the basis of this supposed relationship, Dorf (1936) assigned a fruit to *A. septilobatum.* Dorf's fruit, however, is decidedly unlike *Palmata* samaras, but this specimen was placed by Brown (1937a) in *A. scottiae.* We think that Dorf (1936) was correct in assigning this fruit to *A. septilobatum,* although his reasoning and observations were invalid.

Samaras that we assign to *Acer septilobatum* are characteristic of *Platanoidea,* as noted by MacGinitie (1933); these samaras can also be compared to those of *Campestria,* particularly in having obscure nutlet venation. At four localities, *A. septilobatum* leaves are associated with such samaras; this is half the localities at which *A. septilobatum* leaves have been noted. Further, *Acer septilobatum* leaves have strong similarities to those of *A. protomiyabei.* A strong similarity is also present between the samaras we assign to *A. septilobatum* and those assigned to *A. protomiyabei.* Indeed, *A. septilobatum* may have speciated from *A. protomiyabei.*

Distribution: Early middle Miocene of the Columbia Plateaus and northern and

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Explanation of Plate 39.

(all figures natural size)

Fig. 1 *Acer medianum* Knowlton. Succor Creek. Hypotype (holotype of *Quercus malheurensis* Smith) UMMP 20010.

Fig. 2 *Acer medianum* Knowlton. Trout Creek. Hypotype UMMP 69145.

Figs. 3, 5, 6 *Acer medianum* Knowlton. Fingerrock. Hypotypes UCMP 9075 (Fig. 3), UCMP 9076 (Fig. 5), UCMP 9077 (Fig. 6).

Figs. 4, 8 *Acer medianum* Knowlton. Hog Creek. Hypotypes UCMG (Fig. 4), USNM 396087 (Fig. 8).

Fig. 7 *Acer medianum* Knowlton. Succor Creek/Upper Type Section. Hypotype MSUB9-16-77-117A.

Fig. 9 *Acer medianum* Knowlton. Succor Creek/Devils Gate. Hypotype MSUB 9/22/77-126A.


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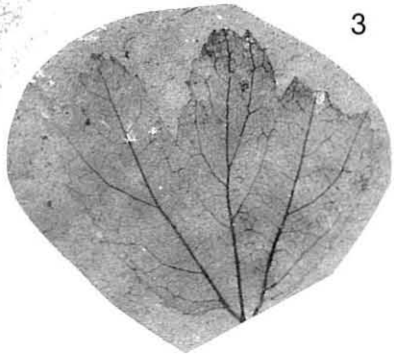
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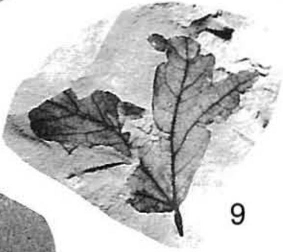
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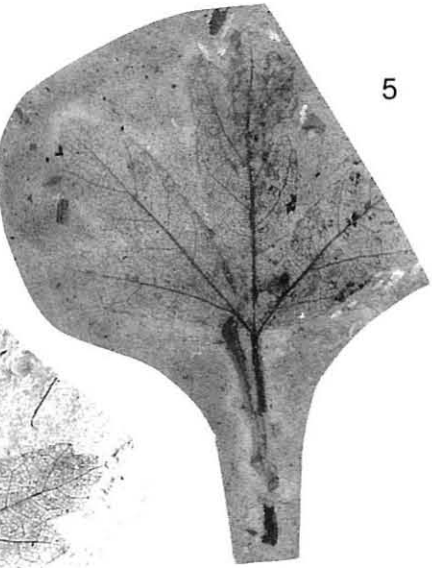
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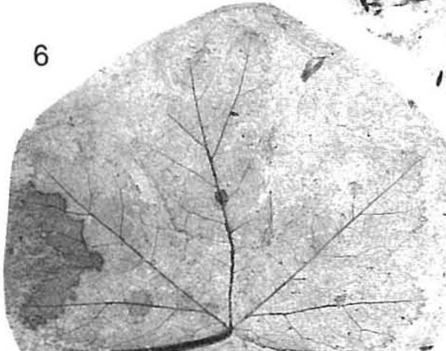
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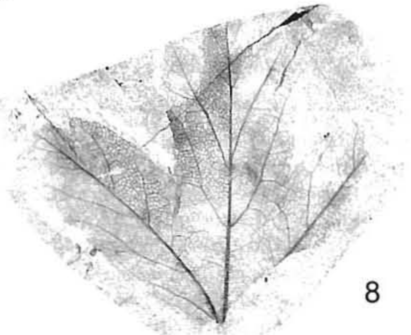
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southwestern Nevada; late middle to early late Miocene of the Columbia Plateaus and western Oregon.

Typology: Lectotype here designated, UCMP 699.

Occurrences: See appendix table.

Section *Platanoidea* Pax

Acer hueberi Wolfe et Tanai, sp. nov.

(pl. 20, figs. 1, 2)

Acer glabroides auct. non R. W. Brown. Becker. 1969 (part). 113. pl. 36, f. 13, 17.

Acer scottiae auct. non MacGinitie. Becker. 1969 (part). 114. pl. 35, f. 6.

Description: Fruits samaroid; nutlet at basal end. Nutlet 0.6 to 0.7 cm long, 0.6 to 0.7 cm wide; outline semicircular; proximal margin expanded beyond proximal margin of wing; attachment scar 0.4 to 0.5 cm long; nutlet flattened, veins indistinct but several passing from distal 1/2 of apical part of nutlet directly onto wing; attachment angle 35° to 70°, nutlet angle 35° to 50°. Wing extending along distal margin of nutlet to attachment scar; 1.7 to 2.0 cm long; distal margin shallowly convex, proximal margin shallowly convex, apex broadly rounded; about 10 veins coalesced along proximal side, wing veins diverging at angles of 10° to 30°, smoothly curving concavely, bifurcating, anastomoses numerous, veinlets reticulate.

Nomenclature: In recognition of Francis M. Hueber's contributions to paleobotany and for his assistance in providing material of fossil *Acer.*

Discussion: Flattened nutlets that are semicircular in outline have a relationship to three extant sections: *Campestria, Platanoidea,* and *Pubescentia.* Of these, *Platanoidea* has, as in *Acer hueberi,* a distal keel on the attachment scar.

Distribution: Latest Eocene of southwestern Montana.

Typology: Holotype, NYBG (YUPM) 963.

Occurrences: See appendix table.

Acer scottiae MacGinitie

(pl. 57, figs. 1-8; pl. 58, figs. 5-7; pl. 59, fig. 8; text-fig. 18K)

Acer scottiae MacGinitie. 1933 (part, typic). 62. pl. 11, f. 8; pl. 12, f. 4.
Smith. 1939. 116.
Smith. 1941 (part). 516. pl. 12, f. 9.
Chaney & Axelrod. 1959 (part). 196. pl. 41, f. 6, 10; pl. 42, f. 1.
Graham. 1965. 67. pl. 4, f. 3.
Acer sp. H. V. Smith. 1941. 518. pl. 12, f. 5.

Description: Leaves simple, perfectly actionodromous, with 5 to 9 primary veins; leaves

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Explanation of Plate 40.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer medianum* Knowlton. Succor Creek/Devils Gate. Hypotype MSUB 9/22/77-I-9-91A.

Figs. 2-4, 7 *Acer medianum* Knowlton. Fingerrock. Hypotypes UCMP 9078 (Fig. 2), UCMP 9079 (Fig. 3), UCMP 9080 (Fig. 4), UCMP 9081 (Fig. 7).

Fig. 5 *Acer medianum* Knowlton. Mascall/Riverbank. Lectotype USNM 8498.

Figs. 6, 9, 10 *Acer niklasi* Wolfe et Tanai. Clarkia. Holotype UCMP 9085 (Fig. 6). Paratypes UCMP 9086 (Fig. 9), UCMP 9087 (Fig. 10, ×5).

Figs. 8, 11 *Acer medianum* Knowlton. Latah/Brickyard. Hypotype USNM 396084 (Fig. 11, ×5).


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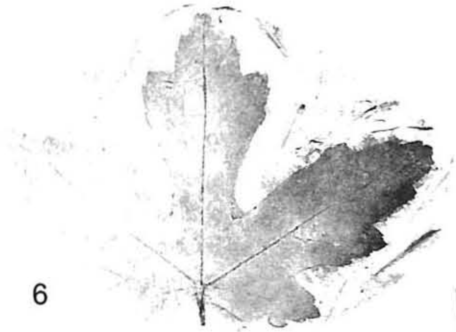
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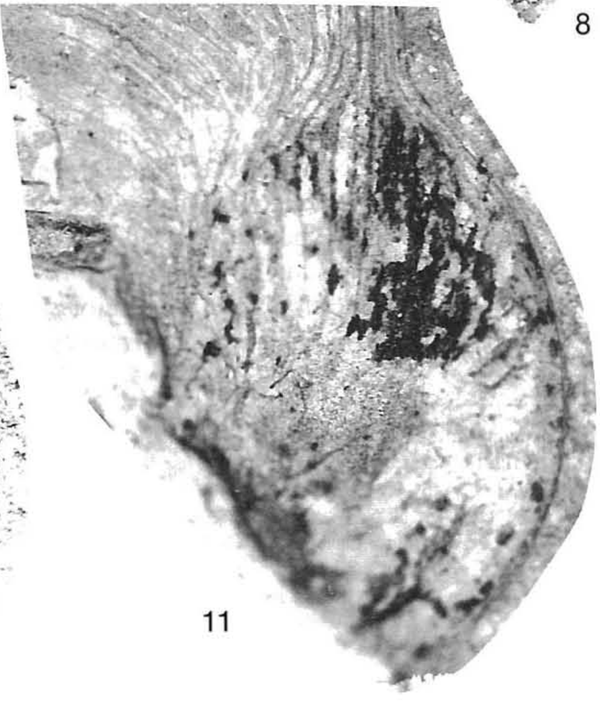
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shallowly 3- to 7-lobed; most apical lateral lobes at least 3/4 as long as medial lobe, other lateral lobes variable in relative lengths; shape orbiculate; 4.5 to (estimated) 15 cm long, 5.0 to (estimated) 14 cm wide; base rounded to cordate, lobal apices acute to attenuate; lobes triangular; most apical lateral primary veins diverging from medial secondary veins; 5 to 7 secondary veins originating at angles of 30° to 80° from basal side of most apical lateral primary veins, straight to broadly convex, brochidodromous (rarely craspedodromous); 5 to 7 medial secondary veins originating at angles of 35° to 60°, straight to broadly convex brochidodromous; major lobal sinal bracing formed by orthogonally bifurcating secondary veins; bracing of other lobal sinuses typically formed by a tertiary vein; intersecondary veins numerous; tertiary veins compound, A-A or A-R, spaced 0.3 to 0.5 cm; fourth order venation irregularly polygonal; fifth order veins forming areoles, 0.3 to 0.5 cm in diameter, veinlets unbranched or typically absent; teeth typically absent, on 2 specimens a single C-2 tooth occurs on the basal side of 1 of most apical lateral lobes; petiole 2.5 to more than 3.5 cm long.

Fruits samaroid, nutlet at basal end; nutlet 0.7 to 1.0 cm long, 0.5 to 0.7 cm wide; outline inverse U-shaped to broadly V-shaped, apex broadly rounded; proximal margin can expand beyond proximal margin of wing or not; attachment scar 0.5 to 0.7 cm, with prominent distal keel; nutlet flattened, typically with 1 or 2 apically directed folds, and with 5 to 7 veins originating along attachment scar and extending apically onto wing; attachment angle 70° to 90°, nutlet angle 5° to 20°. Wing extending 1/2 to all the length of the distal side of nutlet, in some instances forming a shallow U-shaped or V-shaped sulcus; 2.3 to 2.7 cm long, 0.8 to 1.2 cm wide; distal margin deeply to shallowly convex, proximal margin broadly convex to broadly concave, apex narrowly to broadly rounded; 4 to 5 loosely coalesced veins along proximal side, wing veins diverging at angles of 10° to 40°, rapidly curving, bifurcating, numerous anastomoses.

Nomenclature: MacGinitie (1933) named this species for Agnes Scott Train, the wife of Percy Train, who was the major collector at Trout Creek.

Discussion: Leaves of *Acer scottiae* almost invariably have no teeth, and, as MacGinitie (1933) noted, are comparable to the species now known as *A. mono.*

Fruits here assigned to *Acer scottiae* are unusual in *Platanoidea* in having apically directed folds on the nutlet, although some fruits of *A. mono* have weakly developed folds. In size of the nutlet and possession of a low number of nutlet veins, *A. scottiae* is most comparable to the extant *A. fulvescens.*

Fruits and leaves assigned to *Acer scottiae* are associated only at the Trout Creek

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Explanation of Plate 41.

(all figures natural size)

Figs. 1, 2, 4, 5 *Acer ferrignoi* Wolfe et Tanai. Lolo Pass. Paratypes USNM 396126 (Fig. 1), USNM 396127 (Fig. 2), USNM 396128 (Fig. 5). Holotype USNM 396125 (Fig. 4).

Fig. 3 *Acer tigilense* Chelebaeva. Cache Creek. Hypotype USNM 396134a.

Fig. 6 *Acer tigilense* Chelebaeva. Bidarki Creek. Hypotype UMMP 69147.

Fig. 7 *Acer tigilense* Chelebaeva. Thorn Creek. Hypotype UCMP 9122.

Fig. 8 *Acer tigilense* Chelebaeva. Latah/Brickyard. Hypotype USNM 39664.

Fig. 9 *Acer tigilense* Chelebaeva. Healy Creek. Hypotype USNM 396132.


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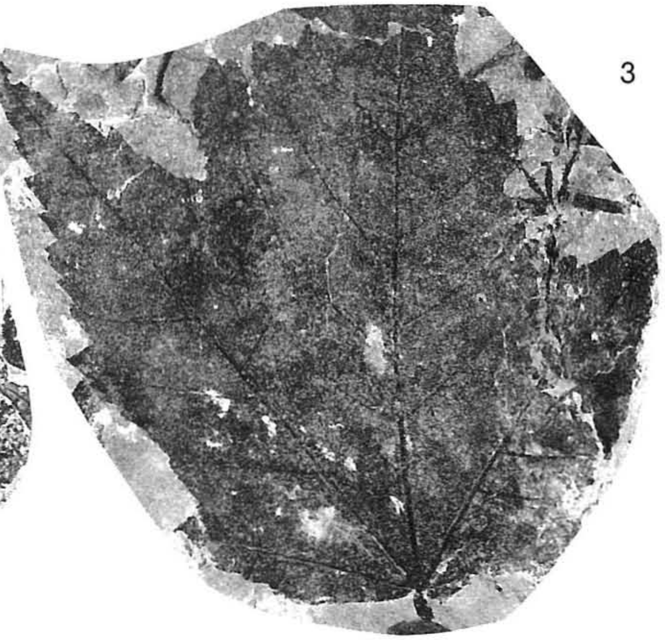
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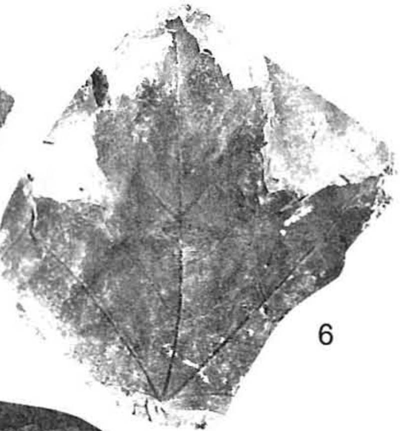
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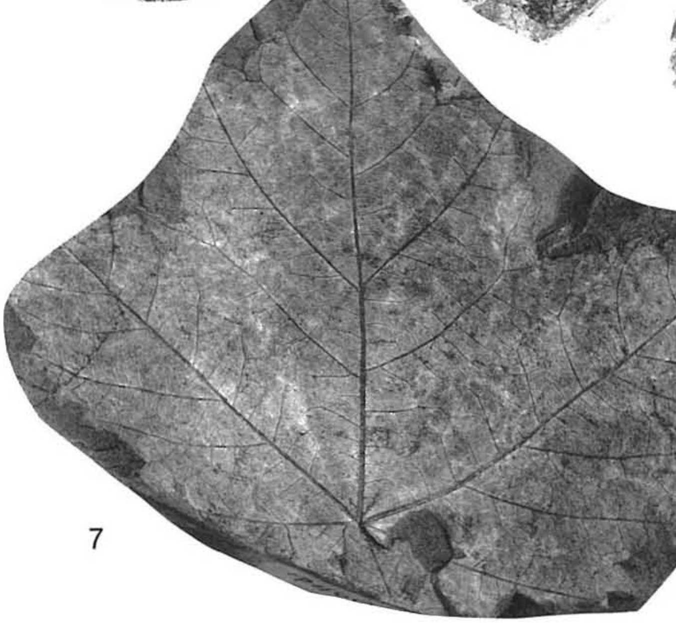
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locality, where leaves of *A. septilobatum* occur, as well as fruits of a second type of the *Platanoidea* Group. As noted in the discussion of *A. septilobatum,* the second type of *Platanoidea* fruits and leaves are associated at three other localities. Thus, by the process of elimination, we suggest that the fruits just described represent *A. scottiae.* Further, the leaves of *A. scottiae* have very sharp pointed lobes and teeth, as typical of *Platanoidea,* and in the *Platanoidea* Group, only *Platanoidea* can have somewhat elongated nutlets.

Distribution: Middle to early late Miocene of the Columbia Plateaus and early middle Miocene of western Nevada.

Typology: Holotype, UCMP 613.

Occurrences: See appendix table.

Epithets rejected as *nomina dubia*

Some epithets are based on specimens that are almost certainly *Acer* but are specifically indeterminate; these epithets should be considered of dubious validity and should not be used:

Acer completum Chaney, 1920
Acer crataegifolium (Knowlton) LaMotte, 1952
Acer dimorphum Lesquereux, 1888
Acer gigas Knowlton, 1902
Acer grahamensis Knowlton et Cockerell, 1919
Acer minor Knowlton, 1902

Species rejected from *Acer*

We have attempted to examine all fossil material from western North America that has been referred to *Acer.* Of particular concern are name-bearing specimens. In the course of the study, some material that was examined proved to have characters indicative of assignment to families other than Aceraceae. In some instances, the proper familial reference of a name-bearing specimen is apparent, but, in other instances, the material is referred to *Dicotylophyllum:*

Acer aequidentatum Lesquereux, 1878, = *Platanus appendiculata* Lesquereux
Acer aquilum Chaney, 1920, = *Vitis aquila* (Chaney) Wolfe et Tanai
Acer arida (Axelrod) Axelrod, 1950, = *Dicotylophyllum lobata* (Axelrod) Wolfe et Tanai
Acer bendirei Lesquereux, 1888, = *Platanus bendirei* (Lesquereux) Wolfe
Acer collieri Hollick, 1930, = *Cissus marginata* (Lesquereux) R. W. Brown (see Brown, 1962, p. 79)

Explanation of Plate 42.
(all figures natural size)
Figs. 1, 3 *Acer chaneyi* Knowlton. Collawash. Hypotypes UCMP 9091 (Fig. 1), UCMP 9092 (Fig. 3).
Fig. 2 *Acer chaneyi* Knowlton. Latah/Vera. Hypotype USNM 396095.
Fig. 4 *Acer chaneyi* Knowlton. Latah/Spokane. Holotype UCMP 22862.

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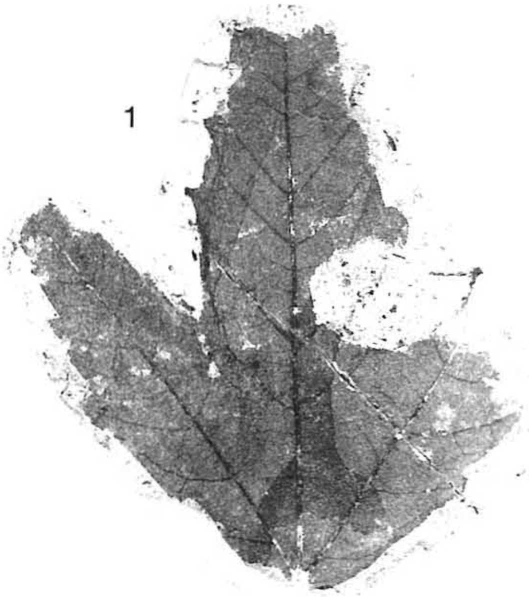

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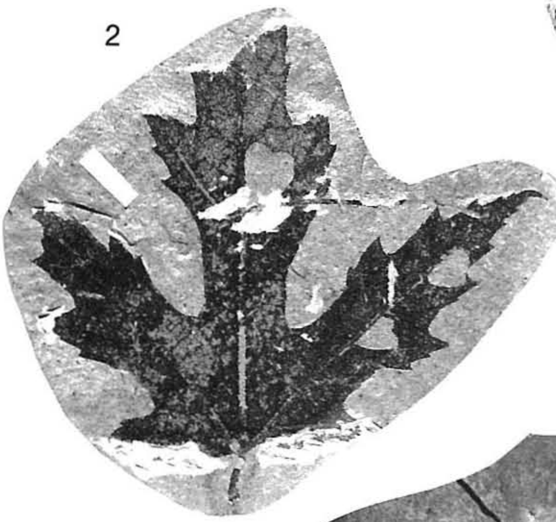

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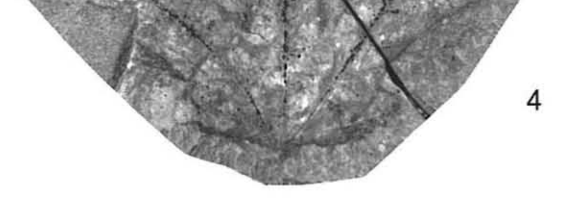

Acer coloradense MacGinitie, 1953, = *Rubus coloradensis* (MacGinitie) Wolfe et Tanai

Acer decurrens (Lesquereux) LaMotte, 1952, = *Cissus marginata* (Lesquereux) R. W. Brown (see Brown, 1962, p. 79)

Acer disputabilis Hollick, 1936, = *Dicotylophyllum disputabilis* (Hollick) Wolfe et Tanai

Acer florigerum Cockerell, 1908, = indetermined flower

Acer fragilis Knowlton, 1917 = *Cissites panduratus* Knowlton

Acer fremontensis Berry, 1930 = *Aleurites fremontensis* (Berry) MacGinitie (see MacGinitie, 1974, p. 69)

Acer gracilescens Lesquereux, 1883, = *Platanus raynoldsi* Newberry (see Brown, 1962, p. 65)

Acer lesquereuxii Knowlton, 1898, = *Dicotylophyllum lesquereuxii* (Knowlton) Wolfe et Tanai

Acer merriami Knowlton, 1902, = *Platanus bendirei* (Lesquereux) Wolfe

Acer negundifolium (Dawson) LaMotte, 1952, = unknown leaf; the original illustration (Dawson, 1891) is poor and we have been unable to locate the specimen.

Acer newberryi R. W. Brown, 1962, = *Dicotylophyllum triloba* (Newberry) Wolfe et Tanai

Acer silberlingi R. W. Brown, 1962, = *Dicotylophyllum silberlingi* (R. W. Brown) Wolfe et Tanai

Acer triloba (Newberry) LaMotte, 1952, = *Dicotylophyllum triloba* (Newberry) Wolfe et Tanai

Acer visibilis Hollick, 1936, = *Dicotylophyllum visibilis* (Hollick) Wolfe et Tanai

Acer vivarium Knowlton, 1898, = *Platanus vivarium* (Knowlton) Wolfe et Tanai

Platanus L.

Platanus vivarium (Knowlton) Wolfe et Tanai, comb. nov.

Acer vivarium Knowlton. 1898. 735. pl. 98, f. 4.

Discussion: This leaf is palinactinodromous, and, in combination with the strongly arcuate dental sinuses, an assignment to *Platanus* is indicated.

Rubus L.

Rubus coloradense (MacGinitie) Wolfe et Tanai, comb. nov.

Acer coloradense MacGinitie. 1953. 139. pl. 58, f. 8.

Discussion: Although high order venation is not preserved, this leaf of supposed *Acer* has thorns on midrib and petiole. The presence of thorns, as well as the trifoliate condition, conform well to *Rubus*.

Explanation of Plate 43.

(all figures natural size)

Fig. 1 *Acer chaneyi* Knowlton. Trapper Creek. Hypotype USNM 396107.

Fig. 2 *Acer chaneyi* Knowlton. Clarkia. Hypotype UCMP 9097.

Figs. 3, 4 *Acer chaneyi* Knowlton. Collawash. Hypotypes UCMP 9344, 9345.

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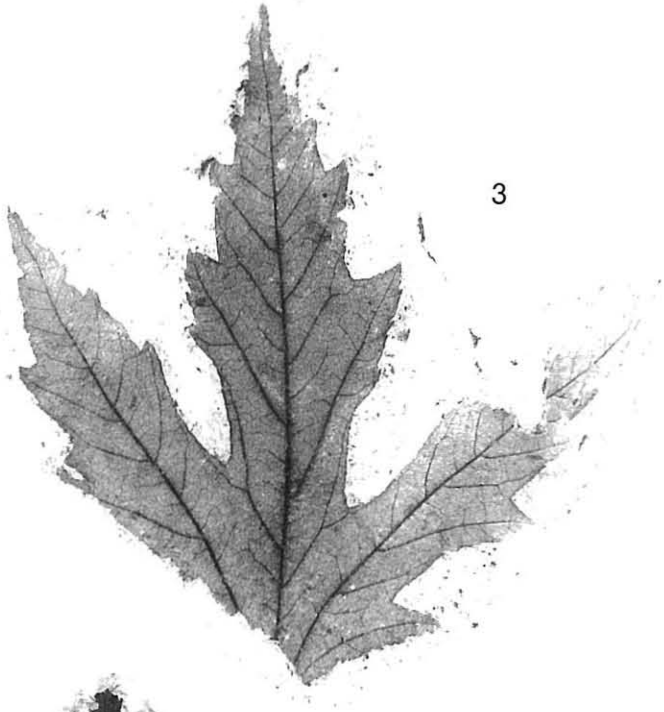

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Vitis L.

Vitis aquila (Chaney) Wolfe et Tanai, comb. nov.

Acer aquilum Chaney. 1920. 178. pl. 17, f. 4, 5; pl. 18, f. 1; pl. 19, f. 1.

Discussion: These perfectly actinodromous leaves cannot be assigned to section *Negundo,* as was done by Lamotte (1952), MacGinitie (1953), and Chaney and Axelrod (1959). Seven primary veins are typically present. The laminae are strongly asymmetrical, and the teeth are broadly triangular, are separated by boradly V-shaped sinuses, and are distinctly rosoid. This combination of character states is unique to *Vitis.* Chaney's plate 18, figure 1 (UCWM 22418) is here designated as lectotype.

Dicotylophyllum Saporta

Dicotylophyllum lobata (Axelrod) Wolfe et Tanai, comb. nov.

Fremontia lobata Axelrod. 1939. 123. pl. 11, f. 8, 10.
Acer arida Axelrod. 1950. 209. pl. 6, f. 6.

Discussion: Although the specimens are poorly preserved, the teeth appear to be malvoid. Axelrod (1939) was possibly correct in referring this species to Sterculiaceae, although a reference to Malvaceae might also be valid. The Nevada specimens referred by Axelrod (1956) to *Acer arida* represent Saccharodendron.

Dicotylophyllum disputabilis (Hollick) Wolfe et Tanai, comb. nov.

Acer disputabilis Hollick. 1936. 134. pl. 74, f. 4.

Discussion: Recent collections from the early Eocene part of the Tolstoi Formation on the Alaska Peninsula contain an abundance of this species. The teeth are small and almost spinose, and the tertiary veins in the basal part of the lamina have a spider-web appearance; these leaves are probably referable to Euphorbiaceae. *Euphorbiophyllum* is based on leaves that are pinnately veined and should not be applied to leaves such as *Dicotylophyllum disputabilis,* which are actinodromous.

Dicotylophyllum lesquereuxii (Knowlton) Wolfe et Tanai, comb. nov.

Acer lesquereuxii Knowlton. 1898. 26.

Discussion: The small, glandular teeth appear to be violoid. This removes these leaves from *Acer* and may indicate, in combination with actinodromy, a placement in Euphorbiaceae.

Dicotylophyllum silberlingi (R. W. Brown) Wolfe et Tanai, comb. nov.

Acer silberlingi R. W. Brown. 1962. 76. pl. 46, f. 7.

Discussion: The single specimen of *"Acer" silberlingi* has intercostal venation comprised of many, admedially oriented tertiary veins, some camptodromous secondary veins,

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Explanation of Plate 44.
(all figures natural size)
Fig. 1 *Acer chaneyi* Knowlton. Collawash. Hypotype UCMP 9346.
Fig. 2 *Acer ezoanum* Oishi et Huzioka. Capps Glacier. Hypotype USNM 396108.

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narrowly arcuate dental sinuses, and veins that enter teeth have strong lateral bracing veins. The specimen is clearly not *Acer,* but we are unable to suggest a valid familial assignment.

Dicotylophyllum trilobum (Newberry) Wolfe et Tanai, comb. nov.

Negundo triloba Newberry. 1868. 57.
Acer triloba (Newberry) LaMotte. 1952. 57.
Acer newberryi R. W. Brown. 1962. 75. pl. 46, f. 2, 3, 6, 8.

Discussion: The only criterion on which the foliage just cited has been placed in *Acer* is a trifoliate condition. The leaflets lack bifurcating secondary veins that brace dental sinuses (as are present in *Negundo*); the dental sinuses are braced by an apically directed external secondary vein that originates from a secondary vein subjacent to the sinus, a morphology unknown in *Acer.* Although the tertiary veins are A-A, they are more closely spaced than in *Acer* and have a "stringy" appearance. No extant family combines such characters.

Dicotylophyllum visibilis (Hollick) Wolfe et Tanai, comb. nov.

Acer visibilis Hollick. 1936. 135. pl. 76, f. 3, 4.

Discussion: Hollick (1936) interpreted this leaf to be lobed, but the "lobe" appears to be a tear in the lamina. The secondary veins are camptodromous to craspedodromous, and the teeth are salicoid. The specimen possibly represents *Populus.*

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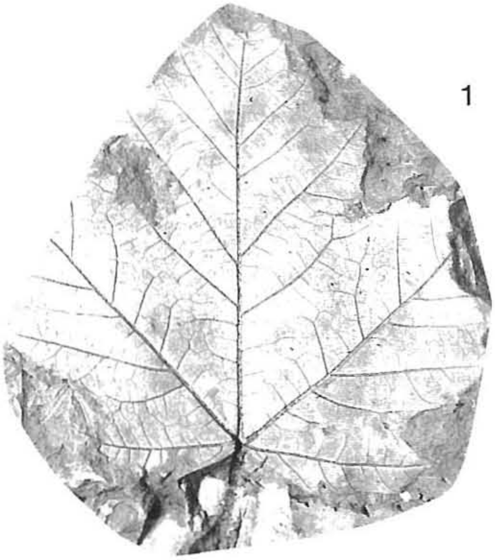
Explanation of Plate 45.

(all figures natural size unless otherwise stated)

Figs. 1-3 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Whitebird. Hypotypes (topotypic) USNM 396113 (Fig. 1), UCMP 9100 (Fig. 2), USNM 396114 (Fig. 3, ×0.6).



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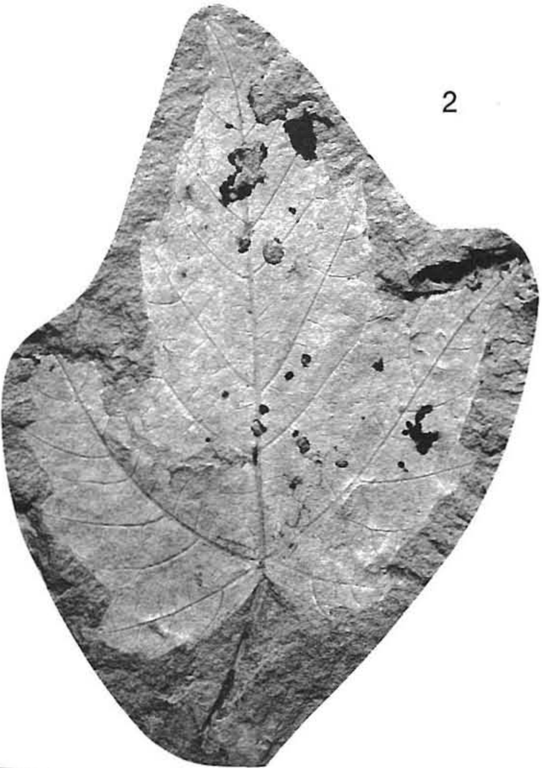

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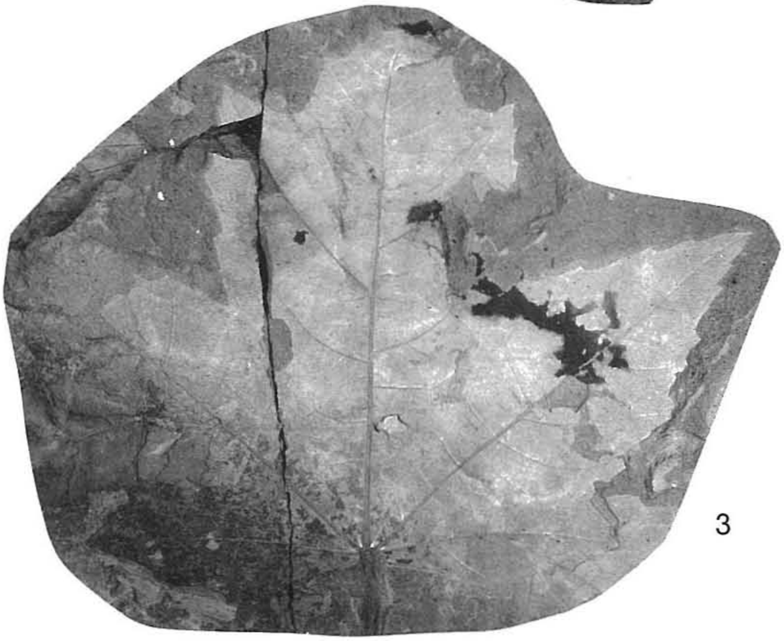

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Explanation of Plate 46.

(all figures natural size unless otherwise stated)

Fig. 1 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Stinking Water. Hypotype UCMP 9101.

Figs. 2, 3, 4, 6, 7 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Whitebird. Hypotypes (topotypic) USNM 39669 (Fig. 2), UWBM 18484 (Fig. 3), UWBM 56258 (Fig. 4, ×0.7), USNM 396118 (Fig. 6), USNM 396115 (Fig. 7, ×0.5).

Fig. 5 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Latah/Brickyard. Hypotype USNM 396109.

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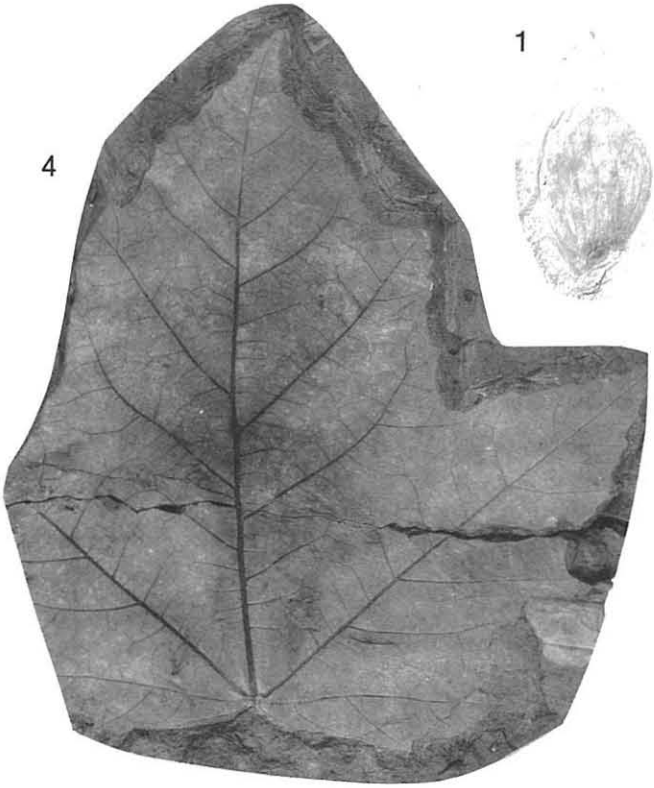

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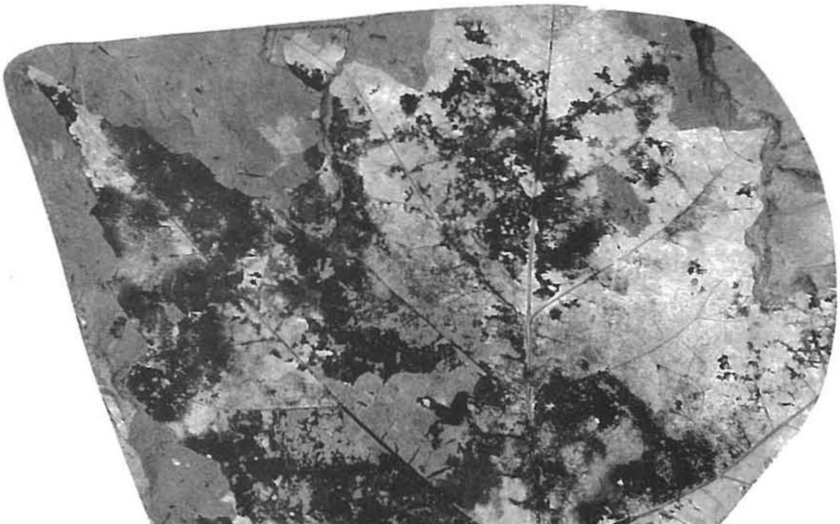

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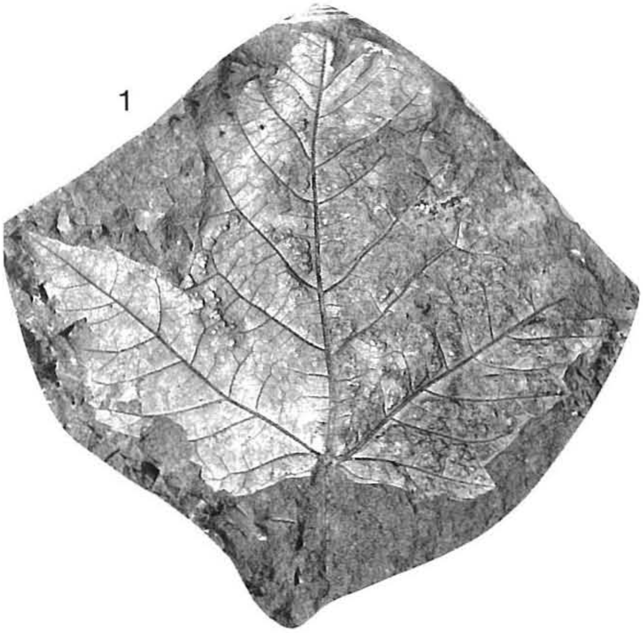
Explanation of Plate 47.

(all figures natural size)

Fig. 1 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Whitebird. Hypotype (topotypic) USNM 396116.

Figs. 2-8 *Acer taggarti* Wolfe et Tanai. Mascall/White Hills. Paratypes UCMP 3189 (Fig. 2), UCMP 3187 (Fig. 3), UCMP 3184 (Fig. 4), UCMP 3185 (Fig. 5), UCMP 3186B (Fig. 6), UCMP9104 (Fig. 8). Holotype UCMP 9103 (Fig. 7).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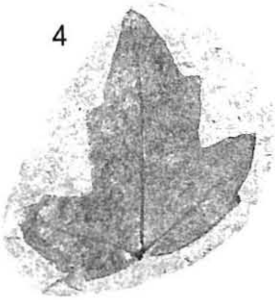
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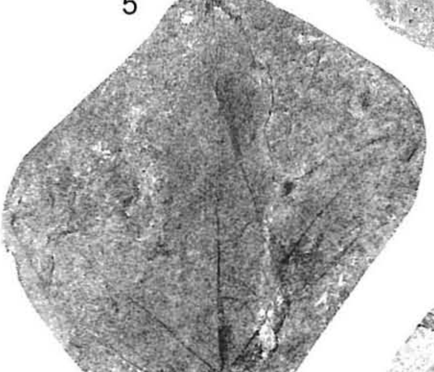
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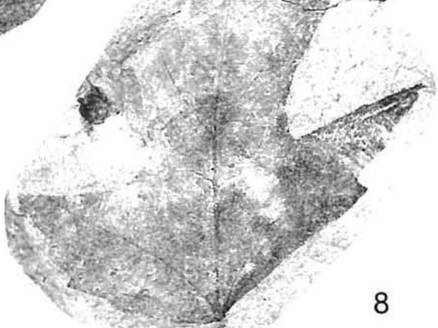
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Explanation of Plate 48.

(all figures ×5)

Figs. 1, 4 *Acer taggarti* Wolfe et Tanai. Mascall/White Hills. Paratypes UCMP 9105 (Fig. 1), UCMP 9106 (Fig. 4).

Fig. 2 *Acer whitebirdense* (Ashlee) Wolfe et Tanai. Stinking Water. Hypotype UCMP 9101.

Fig. 3 *Acer chaneyi* Knowlton. Tipton. Hypotype UCMP 22563.

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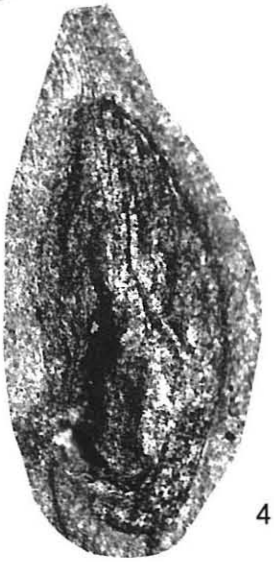

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Explanation of Plate 49.

(all figures natural size)

Fig. 1 *Acer oregonianum* Knowlton. Mascall/Riverbank. Lectotype USNM 8497.

Figs. 2, 3, 7, 8 *Acer oregonianum* Knowlton. Collawash. Hypotypes UCMP 9350 (Fig. 2), UCMP 9347 (Fig. 3), UCMP 9348 (Fig. 7), UCMP 9349 (Fig. 8).

Fig. 4 *Acer oregonianum* Knowlton. Hog Creek. Hypotype USNM 396181.

Fig. 5 *Acer oregonianum* Knowlton. Hidden Lake. Hypotype USNM 396179.

Figs. 6, 10 *Acer oregonianum* Knowlton. Hammer Bluff. Hypotypes USNM 396019 (Fig. 6), USNM 396018 (Fig. 10).

Fig. 9 *Acer macropyhllum* Pursh. Thorn Creek. Hypotype UMMP 21512.


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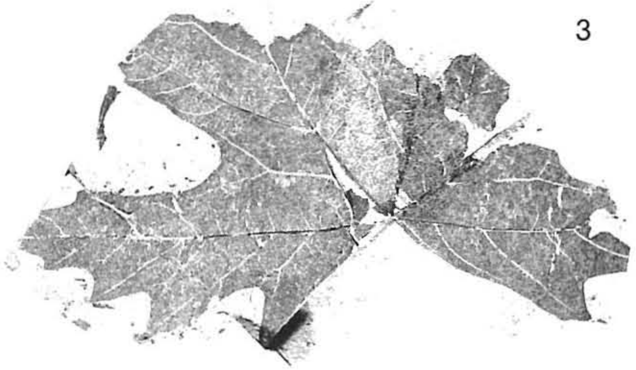
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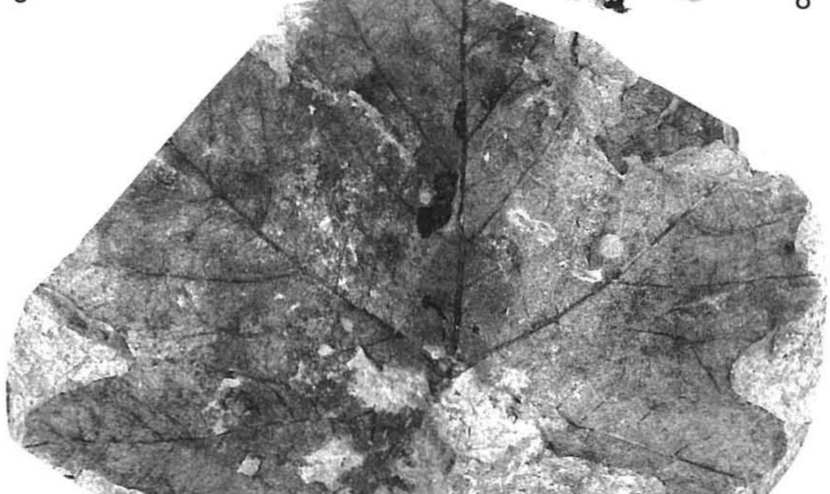
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Appendix Table: Occurrences and cited specimens of fossil *Acer* in North America

Species	Flora	Locality	Organ	Specimen
Acer alaskense	Evan Jones Mine	USGS9881	leaf	USNM396009
Acer alvordense	Alvord Creek	UCMP N601	leaf	UCMP 2136, 2137A, B, 2138, 9122-9124
			fruit	UCMP 2139, 2140, 9125, 9126
	Christensen Ranch	Becker 32	fruit	NYBG 510
	"Beaverhead"		fruit	NYBG 504
Acer ashwilli	Bridge Creek/Allen Ranch	USGS 11531	fruit	USNM 396047
	Bridge Creek/Clarno NE	UCMP 132	leaf	UCMP 9029
	Bridge Creek/Dugout Gulch	UCMP P4210	leaf	UMCP 9030, 9031
		OMSI 241	leaf	UCMP 9032
		UCMP P4210	fruit	UCMP 9033
		OMSI 241	fruit	UCMP 9034, 9035
	Bridge Creek/Fossil	USGS 9420	leaf	USNM 396048, 396049
		UCMP PA-15	leaf	UCMP 9036A, B; 9037A, B
		UCMP P5203	leaf	UCMP 9038
		USGS 9420	fruit	USNM 396050
		UCMP P5203	fruit	UCMP 9039, 9040
	Bridge Creek/Gray Ranch	UCMP P3750	fruit	UCMP 9041
	Bridge Creek/Kant Ranch	UCMP 3931	leaf	USNM 39182
			fruit	UCMP 9042
	Bridge Creek/Kennedy Ranch	USGS 9422	leaf	USNM 396051
			fruit	USNM 396052
	Bridge Creek/Sumner Spring	Ashwill F-1	fruit	UOCM
Acer axelrodi	Bull Run	UCMP P62	leaf	UCMP 9203
			fruit	UCMP 9204, 9205
Acer beckeri	Ruby	——	leaf	UMMP 38272
Acer becki	Sheep Rock Creek	OMSI 256	fruit	UCMP 9304, 9305
Acer bolanderi	Table Mountain	——	leaf	UCMP 1825-18290, 2765-2768, 9199
Acer bosrivularis	Cow Creek	USGS 11341	fruit	USNM 396021A, B

Explanation of Plate 50.

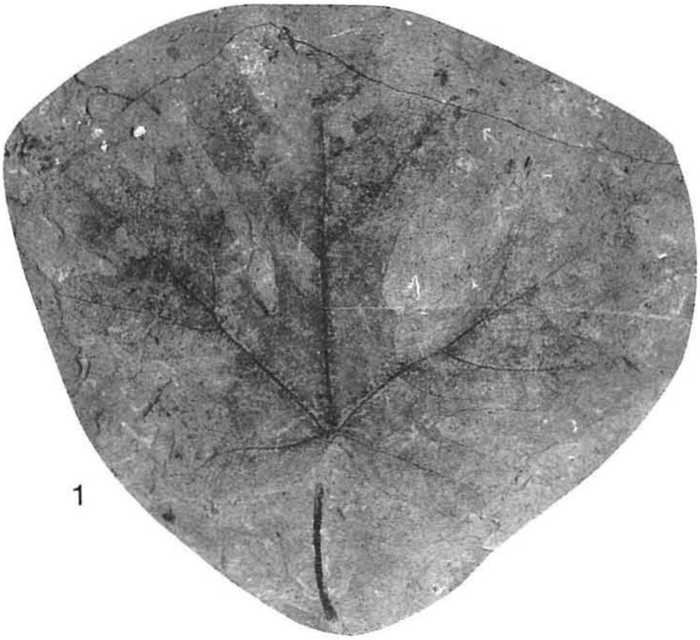
(all figures natural size)

Figs. 1, 4 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Eastgate. Holotype UCMP 7089 (Fig. 1). Paratype UCMP 7088 (Fig. 4).

Fig. 2 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Chilcotin River. Paratype GSC 82966.

Figs. 3, 6 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Clarkia. Paratypes UCMP 9152 (Fig. 3), UCMP 9153 (Fig. 6).

Fig. 5 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Fingerrock. Paratype UCMP 9159.



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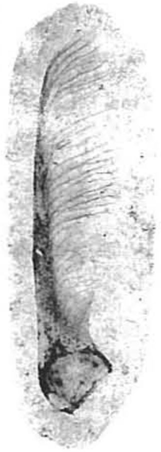

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Acer browni	Skonun	UBCB 60 AB 333	leaf	UBCB
	Latah/Vera	USGS 8427	leaf	USNM 396188
		USGS 9756	leaf	USNM 396189
	Bunker Creek	USGS 9141	leaf	USNM 396190
	Collawash	UCMP PA-1	leaf	UCMP 9328-9334
			fruit	UCMP 9335-9337, 9175, 9176
	Little Butte Creek	USGS 8904	fruit	USNM 396196
Acer busamarum subsp. *busamarum*	Tipton	USGS 8169	leaf	USNM 315300
			fruit	USNM 205241
	Buelah	USGS 2987	fruit	USNM 396160
	Stinking Water	UCMP P4120	fruit	UCMP 3195, 9151
	Succor Creek/Maple Ridge	——	fruit	USNM 396161
		UCMP 3744	fruit	UCMP 9152
	Trout Creek	UCMP 275	leaf	UCMP 604
		UMMP PT-W-19-20	leaf	UMMP 69150
		UMMP PT-W-32	fruit	UMMP 44837
		UMMP PT-W-6	fruit	UMMP 69151
		UMMP PT-W-33	fruit	UMMP 69152
	Hog Creek	——	fruit	UCMG
	Cartwright Ranch	UCMP 3743	fruit	UCMP 8743
	Trapper Creek	USGS 9176	fruit	USNM 396162-39164
		UCMP P571	fruit	UCMP 8483-8486, 8498-8508
Acer busamarum subsp. *fingerrockense*	Chilcotin River	GSC 6384	fruit	GSC 82966A, B
	Clarkia	UIB P-40	fruit	UCMP 9152, 9153
		UIB P-33	fruit	UCMP 9154
	Skull Spring	USGS 11795	fruit	USNM 396165
	Sparta	UOCM 2726	fruit	UOCM F25044 (cf.)
	Jamieson	USGS 11241	fruit	USNM 396166 (cf.)
	Succor Creek/Devils Gate	MSUB 9/22/77 I	fruit	MSUB 81 (cf.)
	Succor Creek/Fenwick Gulch	UMMP PT-2	fruit	UMMP 69153
	Succor Creek/Whiskey Creek	MSUB 8/30/69 IV	fruit	MSUB 3 (cf.)
	'49 Camp	UCMP 97	leaf	UCMP 856
			fruit	UCMP 821
	Thurston Ranch	UCMP 5505	fruit	UCMP 9155
	Buffalo Canyon	UCMP 6101	fruit	UCMP 9156
	Middlegate	UCMP P5101	leaf	UCMP 6659, 6662
			fruit	UCMP 4373-4379, 6652-6658, 6660-6663
	Eastgate	UCMP P5607	leaf	UCMP 708-7090, 7099, 7085-7087
	Goldyke	UCMP PA-342	fruit	UCMP 9157
	Fingerrock	UCMP PA-99	leaf	UCMP 9158
			fruit	UCMP 9159-9162
Acer cadaver	Bull Run	UCMP P562	fruit	UCMP 9019, 9020
Acer cascadense	Cascadia	USGS 9350	fruit	USNM 396059, 396060
		UCMP P-388	fruit	UCMP 9055
Acer castorrivularis	Beaver Creek	——	leaf	UCMP 9310A, B

Explanation of Plate 51.

(all figures natural size)

Figs. 1, 2 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Fingerrock. Paratypes UCMP 9160 (Fig. 1), UCMP 9161 (Fig. 2).

Figs. 3, 5 *Acer busamarum* Wolfe et Tanai ssp. *busamarum.* Trapper Creek. Paratypes USNM 396162 (Fig. 3), USNM 396163 (Fig. 5).

Figs. 4, 6 *Acer busamarum* Wolfe et Tanai ssp. *busamarum.* Trout Creek. Paratype UMMP 44837 (Fig. 4). Holotype UCMP 604.


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Acer chaneyi	Kukaka Bay	USGS 11812	leaf	USNM 396091
			fruit	USNM 30230
	Gumboot Mountain	UCMP PA-393	fruit	UCMP 9090
	Skolai Creek	USGS 9933	fruit	USNM 396092
	Kanalku Bay	USGS 9826	fruit	USNM 396093
	Latah/Spokane	UCMP 3940	leaf	UCMP 22862
	Latah/Vera	USGS 8427	leaf	USNM 396094
		USGS 9756	leaf	USNM 396095
		—	leaf	HUBM 24077
	Latah/Shelly Lake	USGS 7579	leaf	USNM 396096
	Latah/Five Mile Canyon	—	leaf	HUBM 24112
	Latah/Couer d'Alene	—	leaf	USNM 41807A, B
	Grand Coulee	USGS 9078	leaf	USNM 396097
	Collawash	UCMP PA-1	leaf	UCMP 9344, 9345, 9091, 9092
		USGS 9256	fruit	USNM 396101A, B
	Little Butte Creek	USGS 9486	fruit	USNM 396102
	Mascall/Dayville	UCMP P4129	leaf	UCMP 3179
			fruit	UCMP 3177
	Mascall/Riverbank	UCMP P28	leaf	UCMP 3176
	Succor Creek/Whiskey Creek	MSUB 8/30/62 II	leaf	MSUB 16A
	Succor Creek/Rocky Ford	MSUB 9/16/77 I	leaf	MSUB 66, 91, 126
	Clarkia	UIB P-33	leaf	UCMP 9093, 9094
		UIB P-37	leaf	UCMP 9095, 9096
			fruit	UCMP 9097
	Cartwright Ranch	UCMP 3743	leaf	UCMP 3183, 8789, 8790, 8729-8742
	Horseshoe Bend	UCMP P591	leaf	UCMP 8724-8728
	Middlegate	UCMP P5101	fruit	UCMP 4393, 6644
	Eastgate	UCMP 65078	leaf	UCMP 7082
	Purple Mountain	UCMP 6203	fruit	UCMP 9098
	Pyramid	UCMP P5202	fruit	UCMP 9099
	Weyerhauser	USGS 9997	fruit	USNM 396103
	Hidden Lake	USGS 11031	fruit	USNM 396104
	Stinking Water	UCMP P4120	fruit	UCMP 3180, 3181
		UCMP P4006	fruit	UCMP 5133 (cf.)
	Austin	UCMP P3937	leaf	UCMP 695, 701, 3173, 3174, 3203
			fruit	UCMP 702
	Tipton	UCMP P3936	leaf	UCMP 694
			fruit	UCMP 3172, 3175, 22563
	Trout Creek	UMMP PT-W-20	leaf	UMMP 69146
		UCMP 275	leaf	UCMP 610
			fruit	UCMP 3182
	Alkalai Creek	USGS 8924	fruit	USNM 396105
	Deadman Creek	USGS 7299	fruit	USNM 396106
	Trapper Creek	USGS 9176	fruit	USNM 396107
		UCMP 275	fruit	UCMP 8466-8472

Explanation of Plate 52.

(all figures natural size)

Fig. 1 *Acer magasamarum* Tanai et Suzuki. Cottonwood Creek. Hypotype UOCM F-31578.

Fig. 2 *Acer magasamarum* Tanai et Suzuki. Skull Spring. Hypotype USNM 396185.

Fig. 3, 6 *Acer magasamarum* Tanai et Suzuki. Toledo. Hypotypes UWBM 56258 (Fig. 3), UWBM 56259 (Fig. 6).

Fig. 4 *Acer magasamarum* Tanai et Suzuki. Hog Creek. Hypotype USNM 396186A.

Fig. 5 *Acer magasamarum* Tanai et Suzuki. Kukak Bay. Hypotype USNM 396182A.

Fig. 7 *Acer busamarum* Wolfe et Tanai ssp. *busamarum*. Buelah. Paratype USNM 396160.

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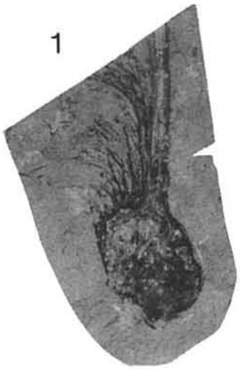

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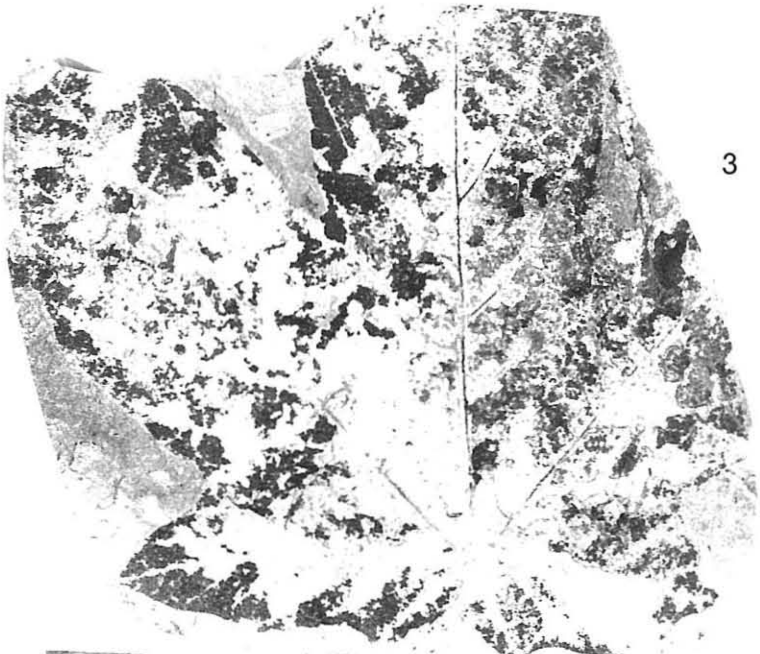

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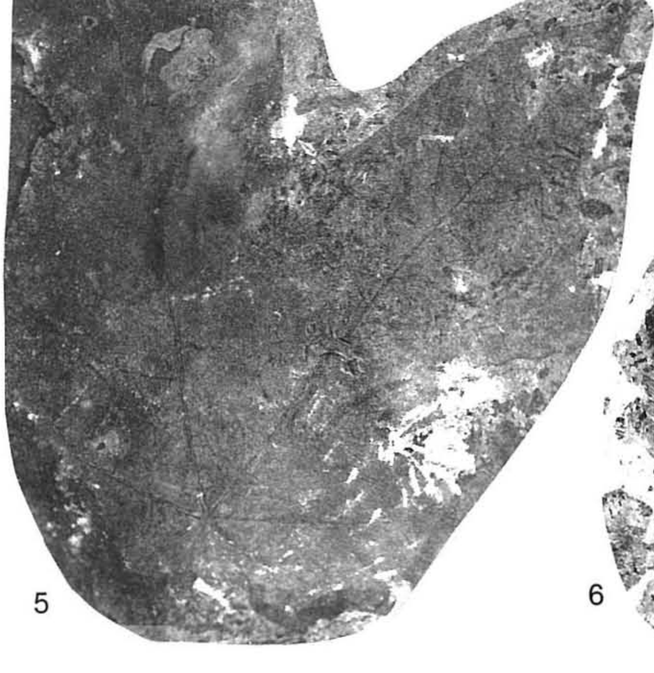

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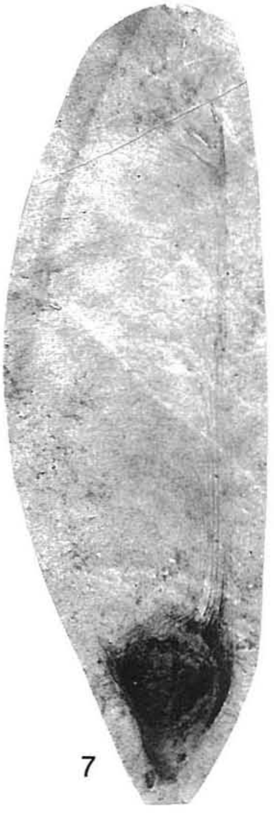

Acer clarnoense	Sheep Rock Creek	OMSI 256	leaf	UCMP 9010A, B; 9011-9014
Acer collawashense	Collawash	UCMP PA-1	leaf	UCMP 9351A, B
	'49 Camp	UCMP 97	leaf	UCMP 9189
Acer cranei	Bridge Creek/Allen Ranch	USGS 8641	fruit	USNM 396053-396055, 396058
	Bridge Creek/Dugout Gulch	UCMP P4210	fruit	UCMP 9049
	Bridge Creek/Fossil	UCMP P5203	fruit	UCMP 9050
	Bridge Creek/Gray Ranch	USGS 8778	fruit	USNM 396056, 396057
		UCMP 3748	fruit	UCMP 9051
		UCMP 3750	fruit	UCMP 9052
	Bridge Creek/Nichol Spring	Ashwill F-5	fruit	UOCM
	Bridge Creek/Pentecost Ranch	UCMP PA-2	fruit	UCMP 9053
	Bridge Creek/Sumner Spring	Ashwill F-1	fruit	UOCM
	Bridge Creek/Twickenham	UCMP P5603	fruit	UCMP 9054
Acer crookense	Sheep Rock Creek	OMSI 256	fruit	UCMP 9020A, B
	Elko/Catlin Plant	USGS 9175	fruit	USNM 396028
Acer cuprovallis	Copper Basin	UCMP P3918	fruit	UCMP 20126A, B*
			fruit	UCMP 20127A, B*
	* UCMP 20126B and 20127B were assigned UCMP 20131 and 20128, respectively			
Acer dettermani	Aniakchak Crater	USGS 11640	leaf	USNM 396014, 396015
Acer douglasense	Cape Douglas	USGS11361	leaf	USNM 39600A, B; 396007A, B; 396008
Acer elkoanum	Elko/Catlin Plant	USGS 9175	leaf	USNM 396022A, B; 396023A, B; 396024
			fruit	USNM 396025-396027
		UCMP P3949	leaf	UCMP 9021A, B; 9022
		UCMP P562	leaf	UCMP 9023-9025
Acer elwyni	Mormon Creek	——	leaf	UMMP 36429-36435, 36487
		——	fruit	UMMP 36488
	York Ranch		leaf	NYBG 1642-1647, 1649, 1650, 1954-1956
	Metzel Ranch	——	leaf	NYBG 2033, 2072, 2075, 2076
			fruit	NYBG 2081-2087, 2090, 2091A, B; 2092, 2093A, B; 2094, 2097, 2099, 2193
	Ruby	——	leaf	UMMP 36937, 51456A, B
			fruit	UMMP 51457
	Grant	Becker 69	leaf	NYBG 828
		USGS 8513	fruit	USNM 396029
	Gas Hills	USGS	leaf	USNM 396030, 396031
Acer eomedianum	Bull Run	UCMP P562	fruit	UCMP 9065
		UCMP P561	leaf	UCMP 9066
Acer eonegundo	Bull Run	UCMP P562	leaf	UCMP 9043

Explanation of Plate 53.

(all figures ×5)

Fig. 1 *Acer macrophyllum* Pursh. Thorn Creek. Hypotype UMMP 21512.

Fig. 2 *Acer megasamarum* Tanai et Suzuki. Hog Creek. Hypotype USNM 396186A.

Fig. 3 *Acer busamarum* Wolfe et Tanai ssp. *busamarum*. Stinking Water. Paratype UCMP 9151.

Fig. 4 *Acer busamarum* Wolfe et Tanai ssp. *fingerrockense* Wolfe et Tanai. Fingerrock. Paratype UCMP 9161.

Fig. 5 *Acer oregonianum* Knowlton. Mascall Riverbank. Lectotype USNM 8497.

Fig. 6 *Acer busamarum* Wolfe et Tanai ssp. *busamarum*. Trapper Creek. Paratype USNM 396164.


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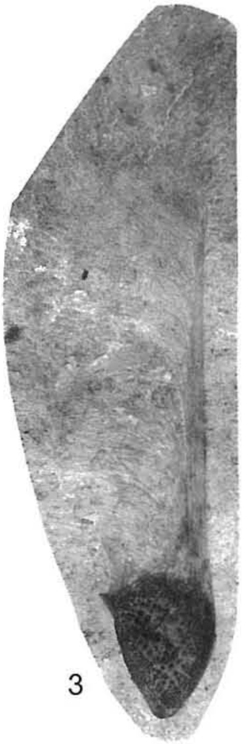
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Acer ezoanum	Capps Glacier	USGS 9845	leaf	USNM 396108
Acer ferrignoi	Lolo Pass	USGS 9737	leaf	USNM 396125-396128, 396130
Acer florissanti	Florissant	——	leaf	USNM 33673, 33761, (holotype of *Acer kircherianum*)
		USGS 8511	leaf	USNM 396040-396044
		——	leaf	UCMG (6 specimens)
		——	leaf	DMNH 802, 804, and 3 specimens
		——	leaf	UCMP 3827
		——	fruit	USNM 1833 (cotype of *Acer indivisum*); 33674 (holotype of Acer mystichum); 33296, 333297, 333401, 396045, 396046
		——	fruit	UCMG 5188(D), 18702
		——	fruit	UCMP 3834, 20819
	Ruby	——	leaf	UMMP 33618
	Johnson Creek	Becker 213	leaf	NYBG 828, 830A, B
	Beaver Creek	——	fruit	UCMP 9324
Acer glabroides	Bridge Creek/Gray Ranch	UCMP 3748	leaf	UCMP 108A, B
			fruit	UCMP 9027
		USGS 8778	leaf	USNM 396032
		UCMP 3937	leaf	UCMP 106
Acer grantense	Christensen Ranch	Becker 32	fruit	NYBG 502, 504
	Grant	USGS 8513	fruit	USNM 396187
		Becker 69	fruit	NYBG 503, 597, 600
Acer heterodentatum	Collawash	UCMP PA-1	leaf	UCMP 9173, 9174, 9056
			fruit	UCMP 9340, 9341, 9057, 9058
	Eagle Creek	Chaney II	leaf	UCWM 22347, 22348
	Seldovia Point	USGS 9858	leaf	USNM 208477, 20847A, B, 208469-208481
Acer hillsi	Republic	UWBM A-0308	fruit	UWBM 56260A, B
Acer hueberi	Christensen Ranch	Becker 32	fruit	NYBG 512
	Schwartz Creek	Becker 302	fruit	NYBG 963
	"Beaverhead"	——	fruit	NYBG 964
Acer idahoense	Salmon	USGS 8173	leaf	USNM 39428, 396033A, B; 396034A, B; 396035
			fruit	USNM 396036, 396037A, B; 396038
Acer ivanofense	Road Island	USGS 11418	leaf	USNM 396017a-d
Acer jarbidgianum	Copper Basin	UMP P3918	fruit	UCMP 20114-20117, 20119-20121, 20123, 20129, 20130
Acer hillsi	Republic	UWBM A-0308	fruit	UWBM 56260A, B

Explanation of Plate 54.

(all figures natural size)

Figs. 1, 2, 5, 6, 7 *Acer minutifolium* Chaney. Eagle Creek. Holotype UCWM 22392 (Fig. 7), Hypotypes USNM 396200A (Fig. 1), USNM 396201 (Fig. 2), UCMP 9190 (Fig. 5), USNM 396202 (Fig. 6).

Figs. 3, 4 *Acer minutifolium* Chaney. Chilcotin River. Hypotypes GSC 82967 (Fig. 3), GSC 82968 (Fig. 4).

Fig. 8 *Acer collawashense* Wolfe et Tanai. Collawash. Holotype UCMP 9351A.

Fig. 9 *Acer collawashense* Wolfe et Tanai. '49 Camp. Paratype UCMP 9189.

Fig. 10 *Acer schorni* Wolfe et Tanai. Hazen. Holotype CAS 61357.

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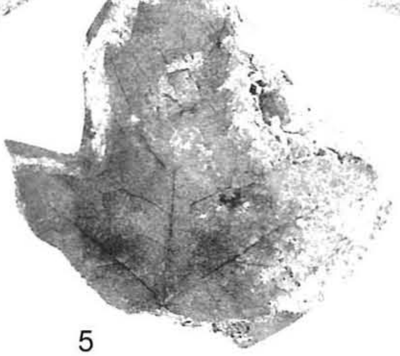

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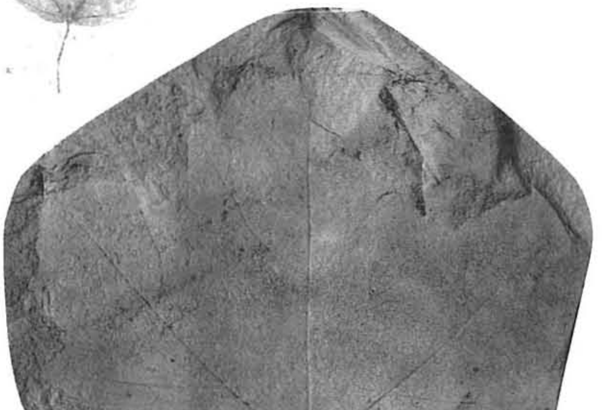

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Acer hueberi	Christensen Ranch	Becker 32	fruit	NYBG 512
	Schwartz Creek	Becker 302	fruit	NYBG 963
	"Beaverhead"	—	fruit	NYBG 964
Acer idahoense	Salmon	USGS 8173	leaf	USNM 39428, 396033A, B; 396034A, B; 396035
			fruit	USNM 396036, 396037A, B; 396038
Acer ivanofense	Road Island	USGS 11418	leaf	USNM 396017a-d
Acer jarbidgianum	Copper Basin	UMP P3918	fruit	UCMP 20114-20117, 20119-20121, 20123, 20129, 20130
Acer kenaicum	Redoubt Point	USGS 11367	leaf	USNM 396088
			fruit	USNM 396089
	Tsadaka Canyon	USGS 9359	leaf	USNM 396090
Acer kluckingi	Bridge Creek/Gray Ranch	UCMP 3930	leaf	UCMP 9108
	Bridge Creek/Pentecost Ranch	UCMP PA-2	leaf	FUCMP 9109-9113
			fruit	UCMP 9114-9117
	Bridge Creek/Slanting Leaf Beds	OMSI 240	leaf	UCMP 9118
			fruit	UCMP 9119
Acer knolli	Latah/Brickyard	USGS 7884	fruit	USNM 38157, 39325, 39666, 36444, 396061
		—	fruit	UCMG 17047, 17080
		—	fruit	HUBM 23479, 23481, 24254
Acer latahense	Latah/Vera	USGS 8427	leag	USNM 396032A, B
	Latah/Vera	—	leaf	USNM 396137
	Latah/Brickyard	USGS 7884	leaf	USNM 396136A, B
	Succor Creek/Maple Ridge	UMMP PT-5A	leaf	UMMP 44840
	Tipton	UCMP 3936	leaf	UCMP 9323
Acer lincolnense	Beaver Creek	—	leaf	UCMP 9311A, B; 9312
			fruit	UCMP 9313A, B
Acer macginitiei	Florissant	—	fruit	UCMG 5188(1), 5188(4)
		—	fruit	UCMP 3828
	Christensen Ranch	Becker 32	fruit	NYBG 506-509
	"Beaverhead"	unknown	fruit	NYBG 777
Acer macrophyllum	Thorn Creek	—	fruit	UMMP 21512
Acer manchesteri	Bridge Creek/Allen Ranch	USGS 8641	fruit	USNM 396211, 396212
	Bridge Creek/Dugout Gulch	OMSI 241	leaf	UCMP 9206-9208
		UCMP P4210	leaf	UCMP 9202, 9210
		OMSI 241	fruit	UCMP 9211, 9212
		UCMP P4210	fruit	UCMP 9213, 9214
	Bridge Creek/Fossil	USGS 9420	fruit	USNM 396213

Explanation of Plate 55.

(all figures natural size)

Figs. 1, 6 *Acer schorni* Wolfe et Tanai. Trout Creek. Paratypes UMMP 44835 (Fig. 1), UMMP 69159 (Fig. 6).

Fig. 2 *Acer schorni* Wolfe et Tanai. Fingerrock. Paratype UCMP 9192A.

Fig. 3 *Acer schorni* Wolfe et Tanai. Succor Creek/Devils Gate. Paratype MSUB 9/22/77-I-94-A.

Figs. 4, 5 *Acer schorni* Wolfe et Tanai. Hog Creek. Paratypes USNM 396204 (Fig. 5), USNM 396203 (Fig. 4).

Fig. 7 *Acer tyrellense* Smiley. Priest Rapids. Hypotype UWBM 56259.

Fig. 8 *Acer tyrellense* Smiley. Almaden. Hypotype UCMP 9197.

Figs. 9, 10 *Acer tyrellense* Smiley. Middlegate. Hypotypes 6669 (Fig. 9), UCMP 6667 (Fig. 10).

Fig. 11 *Acer tyrellense* Smiley. Eastgate. Hypotype UCMP 7090.

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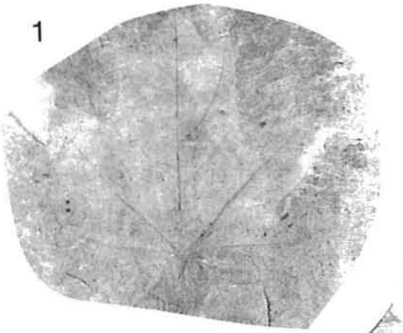

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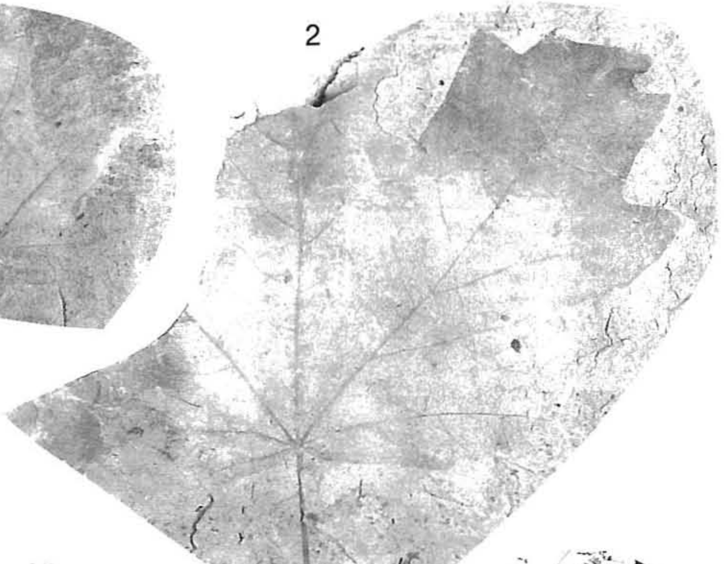

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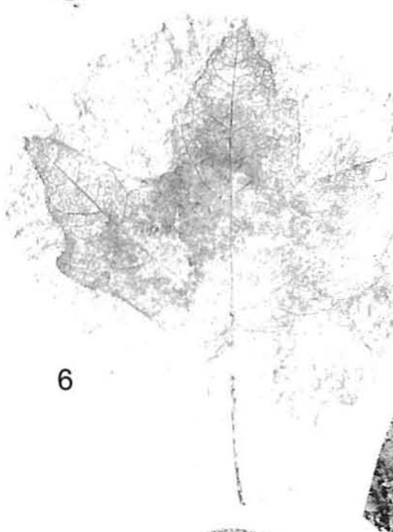

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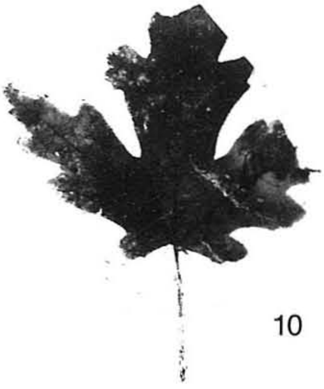

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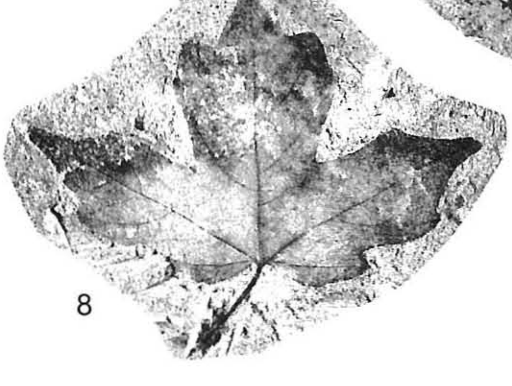

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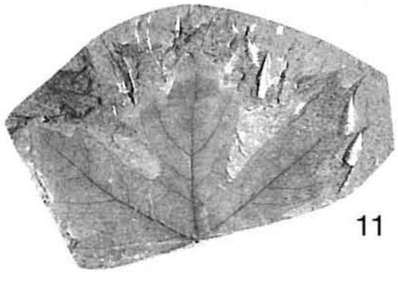

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Acer manchesteri	Bridge Creek/Gray Ranch	UCMP 3930	leaf	UCMP 9215
			leaf	USNM 39183 (UCMP 9215 and USNM 39183 are counterparts)
		UCMP 3937	leaf	UCMP 9216A, B
	Bridge Creek/Knox Ranch	UCMP P5405	fruit	UCMP 9217, 9218
	Bridge Creek/Slanting Leaf Beds	UCMP PA-421	leaf	UCMP 9219, 9220
			fruit	UCMP 9221
	Willamette	USGS 9086	fruit	USNM 396214
Acer medianum	Little Butte Creek	USGS 9486	fruit	USNM 396082
	Grand Coulee	USGS 9068	fruit	USNM 396083
	Chilcotin River	GSC 6384	fruit	GSC 82972
	'49 Camp	UCMP 97	leaf	UCMP 858-860, 5128
	Fingerrock	UCMP PA-99	leaf	UCMP 9073-9077
			fruit	UCMP 9078-9081
	San Antonio	UCMP PA-336	leaf	UCMP 9082
	Middlegate	UCMP P5101	leaf	UCMP 4382, 4388-4390, 6643, 6645-6649
	Latah/Brickyard	USGS 7884	fruit	USNM 396084
	Succor Creek/Maple Ridge	—	leaf	UMMP 20010, 21458
	Succor Creek	USGS 1769	leaf	USNM 396085
			fruit	USNM 396086
	Succor Creek/Sheaville	—	fruit	USNM 372311
	Succor Creek/Devils Gate	MSUB 9/22/77I	leaf	MSUB 126A, B
			fruit	MSUB 91A
	Succor Creek/Fenwick Gulch	UMMP PT-2	leaf	UMMP 69143, 69144
	Succor Creek/Upper Type Section	MSUB 9/16/77 II	leaf	MSUB 27, 109, 115, 117A, B
	Succor Creek/Carter Creek	UMMP PT-11	leaf	UMMP 18385
	Succor Creek/Quarry	MSUB 9/16/77 II	leaf	MSUB 12A, B
	Mascall/Riverbank	UCMP P28	leaf	UCMP 5129, 5131, 5132
		—	fruit	USNM 8498, 8499
	Mascall/Roadcut	UCMP P4129	fruit	UCMP 9083
	Mascall/White Hills	UCMP P3735	leaf	UCMP 5130
	Mascall/Meadow	UCMP P4123	leaf	UCMP 9084
	Trout Creek	UMMP Pt-32-33	leaf	UMMP 69145
	Hog Creek	USGS 8923	leaf	USNM 396087
			leaf	UCMG
		UCMP 635	leaf	UCMP 1221-1222
			fruit	UCMP 1224
			fruit	UCMG
	Ellensburg/Ahtanum Ridge	UCMP PA-23	leaf	UCMP 5411
	Ellensburg/Sand Pit	UCMP PA-22	leaf	UCMP 5410
	Ellensburg/Tyrell	UCMP PA-19	leaf	UCMP 5406-09
Acer megasamarum	Kukak Bay	USGS 11812	leaf	USNM 396182A, B
	Usibelli Mine	USGS 9925	fruit	USNM 396184
	Seldovia Point	USGS 9856	leaf	USNM 20874, 20875
		USGS 9858	fruit	USNM 208473
	Toledo	UWBM B3501	leaf	UWBM 56258
			fruit	UWBM 56259

Explanation of Plate 56.

(all figures natural size)

Fig. 1 *Acer tyrellense* Smiley. Ellensburg/Tyrell. Holotype UCMP 5472.

Fig. 2 *Acer tyrellense* Smiley. Niles Canyon. Hypotype UCMP 9198.

Fig. 3 *Acer tyrellense* Smiley. Hog Creek. Hypotype USNM 396207A.

Fig. 4 *Acer tyrellense* Smiley. Middlegate. Hypotype UCMP 6671.

Figs. 5-11 *Acer bolanderi* Lesquereux. Table Mountain. Part of Lesquereux' cotypes UCMP 1827 (Fig. 5), UCMP 1826 (Fig. 8), UCMP 1829 (Fig. 10), UCMP 1828 (Fig. 11). Lectotype UCMP 1825 (Fig. 7). Hypotypes UCMP 2767 (Fig. 6), UCMP 9322 (Fig. 9).

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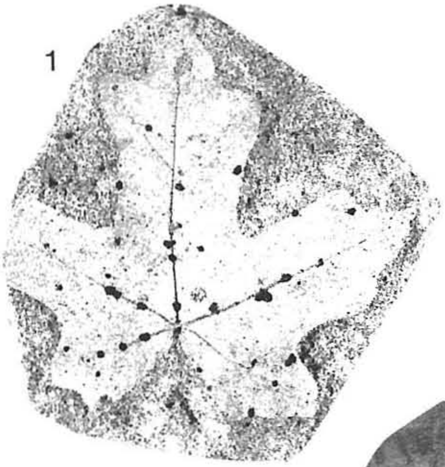

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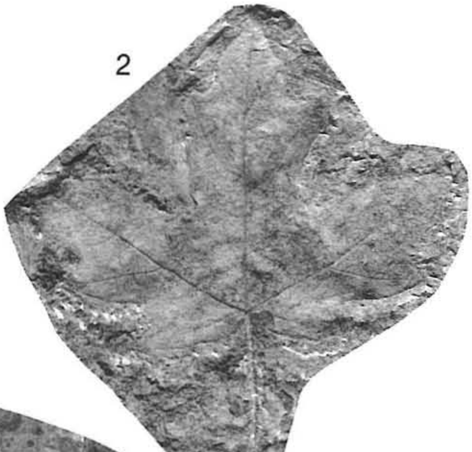

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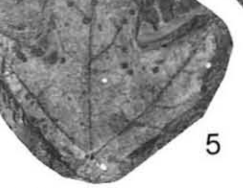

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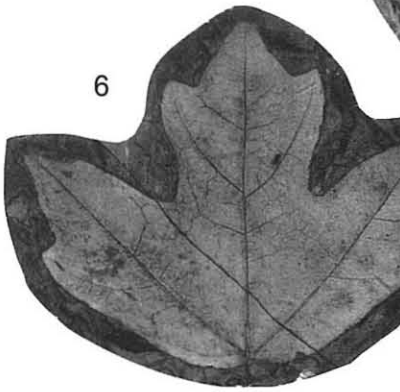

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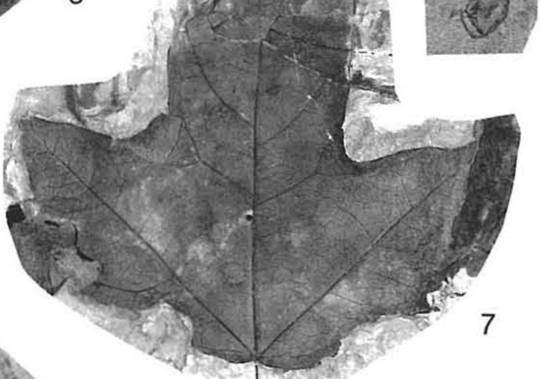

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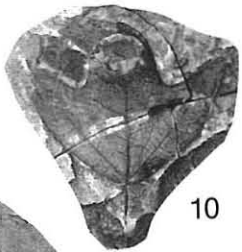

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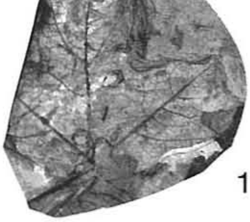

Acer megasamarum	Cottonwood Creek	UOCM 2773	fruit	UOCM F-31578A, B
	Skull Spring	USGS 11795	fruit	USNM 396185
	Mascall/Riverbank	UCMP P4126	fruit	UCMP 9169
	Hog Creek	USGS 8923	fruit	USNM 396186A, B
Acer meyeri	Sheep Rock Creek	OMSI 256	fruit	UCMP 9028
Acer milleri	Beaver Creek	——	leaf	UCMP 9307A, B; 9308, 9309
Acer minutifolium	Chilcotin River	GSC 5786	leaf	GSC 82967
			fruit	GSC 82968
	Eagle Creek	Chaney 4	leaf	UCWM 22392, 22358 (hototype of *Liriodendron trilobata*)
		USGS 1049	leaf	USNM 396020A, B
		USGS 9425	leaf	USNM 396200, 396201
		——	leaf	UCMP 9190
Acer molallense	Liberal	USGS 9673	leaf	USNM 396062
Acer montanense	"Beaverhead"	——	fruit	NYBG 461A, B
Acer negundoides	Collawash	USGS 9256	leaf	UCMP 9338
			fruit	UCMP 9339
	Little Butte Creek	USGS 9486	fruit	USNM 396069
	'49 Camp	UCMP 97	fruit	UCMP 535-538, 815, 857
	Cottonwood Creek	UOCM 2773	fruit	UOCM 33533
	Mascall/Dayville	UCMP 4129	fruit	UCMP 9059
	Mascall/Meadow	UCMP P4123	fruit	UCMP 9060
	Mascall/Riverbank	UCMP 28	fruit	UCMP 3199
	Mascall/White Hills	UCMP 3735	fruit	UCMP 3196, 3198
	Succor Creek/Fenwick Gulch	UMMP PT-2	fruit	UMMP 65141
	Succor Creek/Maple Ridge	——	leaf	UMMP 21457
	Succor Creek, Devils Gate	MSUB 9/22/77 I	fruit	MSUB 347A, B
	Buffalo Canyon	UCMP PA-291	leaf	UCMP 9061A, B
			fruit	UCMP 9062A, B; 9063
	Middlegate	UCMP P5101	fruit	UCMP 4396-4401, 6638-6641
	Trout Creek	UCMP 275	fruit	UCMP 617
		UMMP-PT-D-3-5	fruit	UMMP 65142
	Almaden	UCMP P6001	leaf	UCMP 9064
	Trapper Creek	UCMP P571	fruit	UCMP 8490-8497
	Hog Creek	USGS 8923	fruit	USNM 396070A, B; 396071A, B; 396072A, B; 396073, 396074
		UCMP 635	fruit	UCMP 1225-1227
	Ellensburg/Tyrell	UCMP PA-19	leaf	UCMP 2795-2798
	The Dalles	UCMP 3941	leaf	UCMP 5415-5420
	Deschutes	UCMP P3720	leaf	UCMP 1132-1134
	Remington Hill	UCMP P3935	fruit	UCMP 2424, 2425
Acer niklasi	Clarkia	UIB P-37	leaf	UCMP 9085
			fruit	UCMP 9086
		UIB P-33	fruit	UCMP 9087, 9088
	Latah/Brickyard	——	fruit	HUBM 24153
	Austin	UCMP 3937	fruit	UCMP 3937

Explanation of Plate 57.

(all figures natural size)

Fig. 1 *Acer scottiae* MacGinitie. Succker Creek/Maple Ridge. Hypotype UMMP 21460.

Figs. 2, 3, 6, 8 *Acer scottiae* MacGinitie. Trout Creek. Hypotypes (topotypic) UCMP 9222 (Fig. 2), UOCM F-33531 (Fig. 3), UMMP 69162 (Fig. 8). Holotype UCMP 613 (Fig. 6).

Fig. 4 *Acer scottiae* MacGinitie. Succor Creek/Whiskey Creek. Hypotype UCMP 9352.

Fig. 5 *Acer scottiae* MacGinitie. Succor Creek/Maple Ridge. Hypotype UMMP 21460.

Fig. 7 *Acer scottiae* MacGinitie. Hog Creek. Hypotype UCMP 9321.

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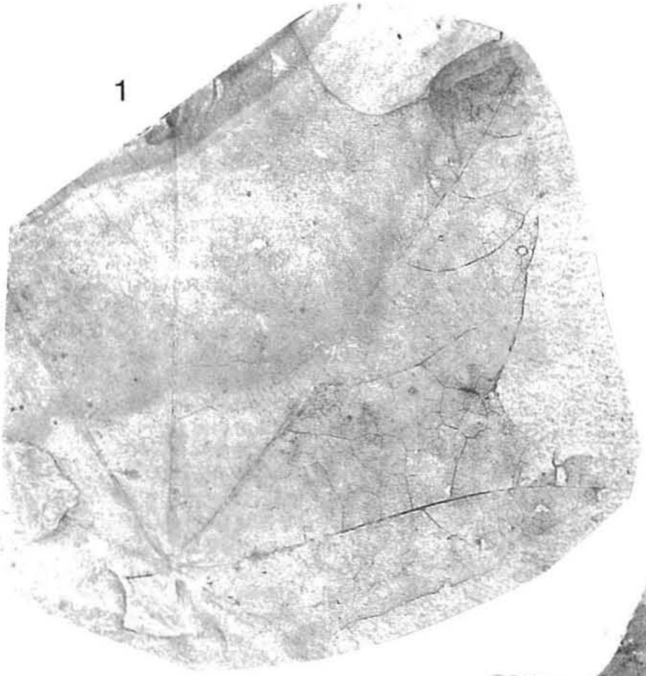

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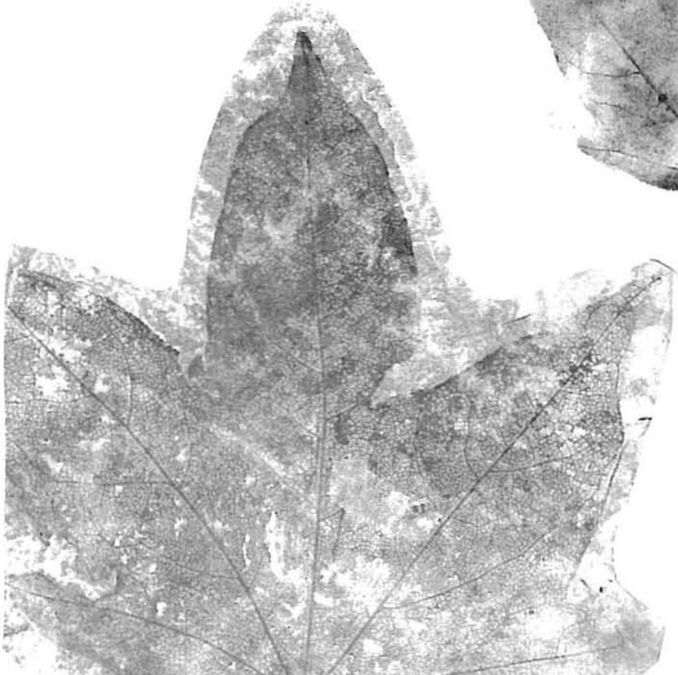

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Acer oligomedianum	Bridge Creek/Gray Ranch	USGS 8778	leaf	USNM 396075
		UCMP 3748	leaf	UCMP 105, 9067-9069
		USGS 8778	fruit	USNM 396076-396079
	Bridge Creek/Clarno NE	UCMP 132	leaf	UCMP 9070
	Lyons	USGS 9351	fruit	USNM 396080, 396081
		UCMP PA-487	fruit	UCMP 9071, 9072, 9326
Acer orbum	Chalk Bluffs	—	leaf	UCMP 2283
			fruit	UCMP 2284-2286, 9018
Acer oregonianum	Three Lynx	USGS 9674	leaf	USNM 396167, 396168
	Cascadia	USGS 9350	leaf	USNM 396169, 396170
		UCMP P-388	leaf	UCMP 9163-9166
	Shale City	USGS	fruit	USNM 396171 (cf.)
	Collawash	UCMP PA-1	leaf	UCMP 9167, 9347-9349
			fruit	UCMP 9350
	Little Butte Creek	USGS 9486	fruit	USNM 396176 (cf.)
	Mascall/Dayville	UCMP P4129	fruit	UCMP 9168
	Mascall/Riverbank	USGS 2699	fruit	USNM 8494-8497
	Mascall/White Hills	UCMP 3735	fruit	UCMP 3192, 3193
	Faraday	USGS 9349	leaf	USNM 396177
	Hidden Lake	USGS 9349	leaf	USNM 396178
			fruit	USNM 396179, 396180
	Hog Creek	USGS 8923	fruit	USNM 396181
	Hammer Bluff	USGS 9411	leaf	USNM 396018
			fruit	USNM 396019
Acer osmonti	Bridge Creek/Allen Ranch		leaf	UCMP 2505
		USGS 8641	leaf	USNM 396152
		UCMP 3741	fruit	UCMP 9127, 9128
	Bridge Creek/Clarno NE	UCMP 132	leaf	UCMP 9129
	Bridge Creek/Dugout Gulch	UCMP P4210	fruit	UCMO 9130
		OMSI 241	fruit	UCMP 9131
	Bridge Creek/Fossil	UCMP P5203	fruit	UCMP 9132, 9133
	Bridge Creek/Kennedy Ranch	USGS 9422	fruit	USNM 396153
	Bridge Creek/Knox Ranch	USGS 9440	leaf	USNM 396154, 396155
			fruit	USNM 396156
	Bridge Creek/Nichol Spring	Ashwill F-5	fruit	UOCM
	Bridge Creek/Pentecost Ranch	OMSI 246	leaf	UCMP 9134
		UCMP PA-2	fruit	UCMP 9135, 9136
	Bridge Creek/Slanting Leaf Beds	OMSI 240	leaf	UCMP 9137
			fruit	UCMP 9138, 9139
	Bridge Creek/Twickenham	UCMP P5603	leaf	UCMP 9140
			fruit	UCMP 9141-9143
	Bridge Creek/Wood Hollow	Ashwill F-43	fruit	UOCM
	Lyons	USGS 9351	leaf	USNM 396157-396159
		UMP PA-487	leaf	UCMP 9144, 9145
			fruit	UCMP 9146
	Gumboot Mountain	UCMP PA-393	leaf	UCMP 9147-9149
			fruit	UCMP 9150

Explanation of Plate 58.

(all figures natural size)

Fig. 1 *Acer septilobatum* Oliver. Trout Creek. Hypotype USNM 396223.

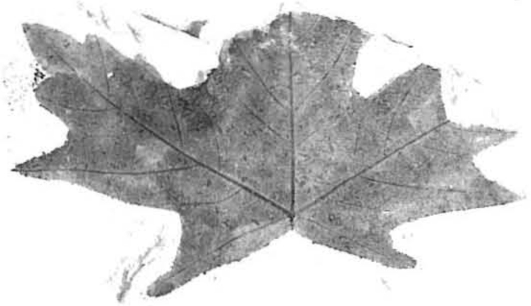
Fig. 2 *Acer scottiae* MacGinitie. Trout Creek. Paratype UCMP 614.

Fig. 3 *Acer septilobatum* Oliver. Austin. Hypotype (topotypic) UCMP 9223.

Fig. 4 *Acer septilobatum* Oliver. Pyramid. Hypotype UCMP 9225.

Fig. 5 *Acer scottiae* MacGinitie. Hog Creek. Hypotype USNM 396129.

Figs. 6, 7 *Acer scottiae* MacGinitie. Succor Creek/Carter Creek. Hypotypes UMMP 69160 (Fig. 6), UMMP 69161 (Fig. 7).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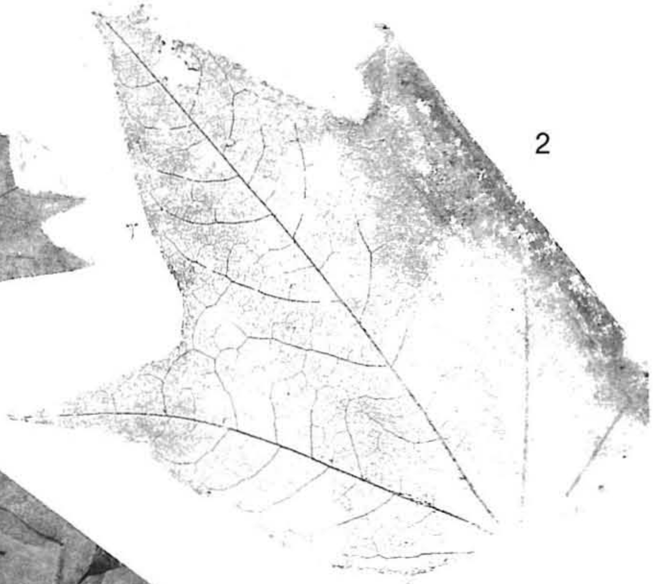
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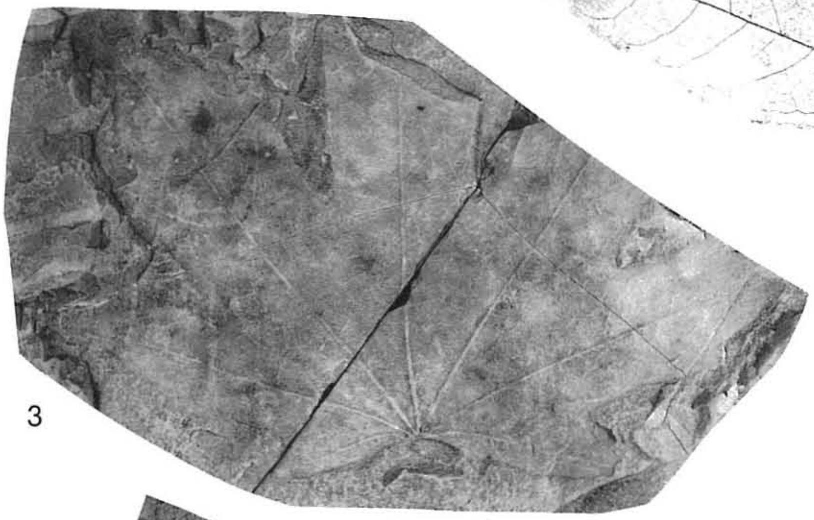
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Acer ovipetrinum	Sheep Rock Creek	OMSI 256	fruit	UCMP 9107
Acer palaeorufinerve	Seldovia Point	USGS 9858	fruit	USNM 208471
Acer postense	Sheep Rock Creek	OMSI 256	fruit	UCMP 9184-9188, 9230
Acer powellense	Sturgeon Creek		leaf	UCMP 9314A, B; 9315A, B; 9316, 9317
Acer princetonense	Princeton/One Mile Creek	—	fruit	UAPC S5543
Acer protomiyabei	Beluga River	USGS 9849	leaf	USNM 396215A, B
	Seldovia Point	USGS 9859	leaf	USNM 208467-208470, 396216
			fruit	USNM 208465, 208466
	Skolai Creek	USGS 9927	leaf	USNM 396217, 396218
Acer rousei	McAbee	—	fruit	TMP P83.39.586A, B; P83.39.585A, B
		—	fruit	UBCB 2401
	Princeton/One Mile Creek	UWBM B-3389	fruit	UWBM 56256A, B; 54107A, B
Acer salmonense	Salmon	USGS 8173	leaf	USNM 39614-396145
			fruit	USNM 39662A, B; 396146A, B; 396147, 396148, 396149A, B; 396150
	Beaver Creek		fruit	UCMP
	John Day Gulch	USGS 9270	fruit	USNM 396151 (cf.)
Acer schorni	Mascall/Dayville	Ashwill F-27	fruit	UOCM F—33534
	Mascall/Riverbank	USGS 2699	fruit	USNM 8501A, B
	Succor Creek/Carter Creek	UMMP PT-11	fruit	UMMP 69155, 69156
	Succor Creek/Devils Gate	MSUB 9/22/77 I	fruit	MSUB 94, 95, 99, 107
	Succor Creek/Mckenzie Ranch	UMMP PT-10	fruit	UMMP 69157
	Buffalo Canyon	UCMP 6101	fruit	UCMP 9191
	Middlegate	UCMP P5101	fruit	UCMP 4383-4387, 4392, 4395, 6670
	Fingerrock	UCMP PA-99	leaf	UCMP 9192A, B
			fruit	UCMP 9193, 9194
	Trout Creek	UMMP PT-A-6-7	leaf	UMMP 69158
		UMMP PT-W-9	leaf	UMMP 44835
		UMMP PT-W-11-12	leaf	UMMP 69159
		USGS 11794	fruit	USNM 396202
	Stinking Water	UCMP P4006	fruit	UCMP 3191
	Hog Creek	USGS 8923	fruit	USNM 396203-396205
	Hazen	—	leaf	CAS 61357
	Verdi	UCMP P102	leaf	USNM 42462 (cf.)
Acer scottiae	Cottonwood Creek	UOCM 2773	fruit	UOCM F-33535
	Mascall/White Hills	UCMP 3735	leaf	UCMP 3212-3216
	Succor Creek/Carter Creek	UMMP PT-11	fruit	UMMP 69160, 69161
	Succor Creek/Maple Ridge	—	leaf	UMMP 21460
	Succor Creek/Whiskey Creek	—	fruit	UCMP 9352
	Trout Creek	UCMP 275	leaf	UCMP 613
		UMMP PT-W-1-2	leaf	UMMP 69162

Explanation of Plate 59.

(all figures natural size)

Fig. 1 *Acer septilobatum* Oliver. Trout Creek. Hypotype UMMP 69118.

Fig. 2 *Acer septilobatum* Oliver. Faraday. Hypotype USMN 396222.

Figs. 3, 5 *Acer septilobatum* Oliver. Trout Creek. Hypotypes UMMP 69118 (Fig. 3), UCMP 615 (Fig. 5; paratype of *A. scottiae*).

Fig. 4 *Acer septilobatum* Oliver. Trapper Creek. Hypotype UCMP 8510.

Fig. 6 *Acer septilobatum* Oliver. Middlegate. Hypotype UCMP 6664.

Fig. 7 *Acer septilobatum* Oliver. Skull Spring. Hypotype USNM 396221.

Fig. 8 *Acer scottiae* MacGinitie. Trout Creek. Hypotype UMMP 69163.

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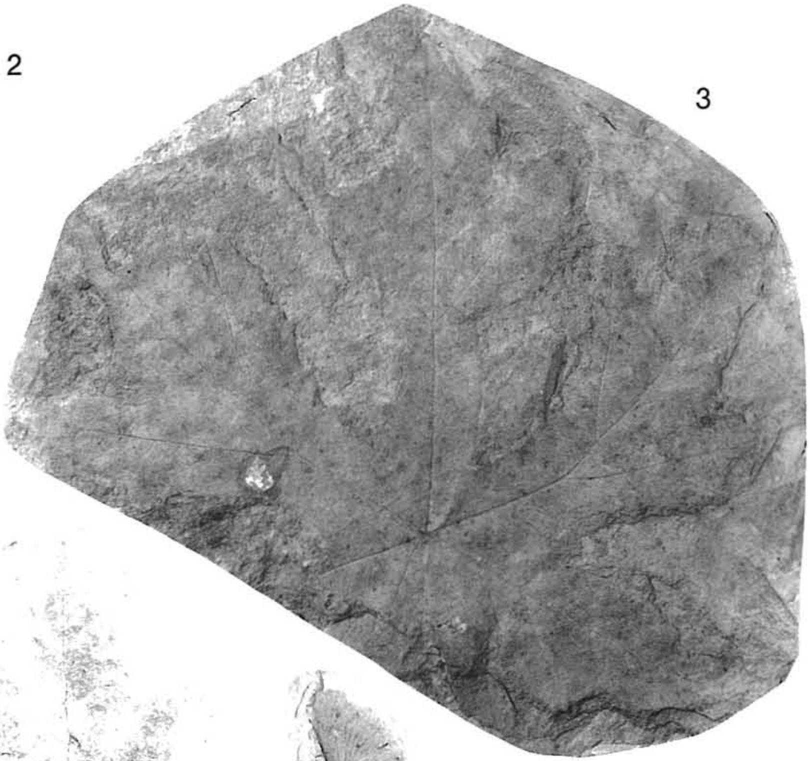

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Acer scottiae		UMMP PT-W-8-9	leaf	UMMP 69163
		UCMP 275	fruit	UCMP 9222
		UOCM 2590	fruit	UOCM F-33531
		UMMP PT-AAT-2	fruit	UMMP 69164
	Pyramid	UCMP P5202	leaf	UCMP 9223
	Hog Creek	USGS 8923	fruit	USNM 396219
		——	fruit	UCMG
Acer septilobatum	Kittias Valley	USGS 468	fruit	USNM 396220
	Mascall/Riverbank	UCMP P28	fruit	UCMP 3217
	Skull Spring	USGS 11795	fruit	USNM 396221
	Succor Creek/Strode Ranch	UMMP PT-4	leaf	UMMP 69165
	Thurston Ranch	UCMP 5505	fruit	UCMP 9224
Acer septilobatum	Pyramid	UCMP P5202	leaf	UCMP 9225
	Middlegate	UCMP P5101	leaf	UCMP 4368-4372, 6665
			fruit	UCMP 6651, 6664
	Fingerrock	UCMP PA-99	fruit	UCMP 9226
	Faraday	USGS 9281	fruit	USNM 396222
	Austin	UCMP 3937	leaf	UCMP 699, 700, 9227
	Tipton	UCMP 3936	leaf	UCMP 698, 3194
	Trout Creek	USGS 11794	leaf	USNM 396223, 396224
		UCMP 275	leaf	UCMP 606
		UMMP PT-A-6-7	leaf	UMMP 17222, 69166
		UMMP PT-W-10-11	leaf	UMMP 69167
		UOCM 2590	leaf	UOCM F-33532
		UCMP 275	fruit	UCMP 615
		UMMP PT-W-1	fruit	UMMP 69140
		UMMP PT-W-7-8-9	fruit	UMMP 69149
	Hog Creek	USGS 8923	fruit	USNM 396225
	Horseshoe Bend	USGS 8349	fruit	USNM 39714
	Thorn Creek	UCMP P4600	leaf	UCMP 9228, 9229
			fruit	UMMP 21513
	Trapper Creek	UCMP P571	leaf	UCMP 8509-8511
			fruit	UCMP 8477, 8512-8519
Acer sinuofluviatilis	Sheep Rock Creek	OMSI 256	fruit	UCMP 9044-9048
Acer smileyi	Kukak Bay	USGS 11812	leaf	USNM 30138, 396197A, B
	Cascadia	UCMP P388	leaf	UCMP 9177
	Capps Glacier	USGS 9846	leaf	USNM 396198a, b
	'49 Camp	UCMP 97	leaf	UCMP 861
			fruit	UCMP 816
	Clarkia	UIB P-33	leaf	UCMP 9178, 9197
			fruit	UCMP 9180-9183
	Trout Creek	UMMP PT-W-10	leaf	UMMP 69154
Acer spitzi	Republic	UWBM A-0307	fruit	UWBM 31272
Acer stewarti	Princeton/One Mile Creek	——	leaf	UAPC S485, S6946, S13271
			fruit	UAPC S6946A, B
		UWBM B-3389	fruit	UWBM 54106A, B; 56258, 56259A, B
Acer stockeyae	Princeton/One Mile Creek	——	fruit	UAPC S13273A, B
Acer stonebergae	Princeton/One Mile Creek	——	fruit	PDMA 1984 OMC 1001
	Republic	UWBM A-0307	fruit	UWBM 56254A, B

Explanation of Plate 60.
(all figures natural size)
Fig. 1 *Acer septilobatum* Oliver. Middlegate. Hypotype UCMP 4369.
Fig. 2 *Acer septilobatum* Oliver. Thorn Creek. Hypotype UCMP 9228.
Figs. 3, 4 *Acer septilobatum* Oliver. Trout Creek. Hypotypes UCMP 606 (Fig. 3), UOCM F-33532 (Fig. 4).

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Acer taggarti	Mascall/Meadow	UCMP P4123	leaf	UCMP 9102
	Mascall/White Hills	UCMP 3735	leaf	UCMP 318A, B; 3185, 3186A, B; 3202, 9103, 9104
			fruit	UCMP 3178, 3187-3189, 9105, 9106
Acer tauroucursum	Bull Run	UCMP P562	fruit	UCMP 9089
Acer tiffneyi	Christensen Ranch	Becker 32	leaf	NYBG 511A, B (NYBG 511 and 599 are parts of same specimen)
			fruit	NYBG 513
	Grant	Becker 69	leaf	NYBG 594
	Beaver Creek	——	leaf	UCMP 9320
Acer tigilense	Kukak Bay	USGS 11812	leaf	USNM 396131
	Healy Creek	USGS 9926	fruit	USNM 396132
	Lignite Creek	——	leaf	USNM 396133
	Cache Creek	USGS 9867	leaf	USNM 396134a, b
	Bidarki Creek	UMMP 1961	leaf	UMMP 69147, 69148
	Seldovia Point	USGS 9858	fruit	USNM 208471, 208472
	Coal Bay	USGS 9989	leaf	USNM 396135
	Latah/Brickyard	USGS 7884	fruit	USNM 39664
	Latah/Deep Creek	YSGS 7894	fruit	USNM 38166
	Mascall/White Hills	USGS 2699	fruit	USNM 396138
	'49 Camp	UCMP 97	fruit	UCMP 816
	Pyramid	UCMP P5202	leaf	UCMP 9120
	Vinegar Creek	UCMP P5404	leaf	UCMP 9121
	Stinking Water	UCMP P4006	fruit	UCMP 5133
	Alkalai Creek	USGS 8924	leaf	USNM 396139
	Idaho City	USGS 8437	leaf	USNM 396140
	Thorn Creek	UCMP 4600	leaf	UCMP 3206-3210, 9122
	Trapper Creek	UCMP P571	leaf	UCMP 8487, 8488
Acer toradense	Resner Canyon	USGS 11018	fruit	USNM 396010A, B
	Princeton/Blue Flame Mine	——	fruit	UBCB 2400
Acer traini	Chilcotin River	GSC 5786	fruit	GSC 82971
	Purple Mountain	UCMP 6209	fruit	UCMP 9015
	Thurston Ranch	UCMP 5505	fruit	UCMP 9016
	Mascall/White Hills	UCMP 3735	fruit	UCMP 9017
	Trout Creek	UMMP PT-W-39	fruit	UMMP 65138, 65139
	Trapper Creek	USGS 9176	fruit	USNM 396016
Acer tyrellense	Priest Rapids	UWBM A2508	lead	UWBM 56259
	Mascall/White Hills	——	fruit	USNM 8501 (cotype of *Acer minor*)
	Sparta	UOCM 2726	fruit	UOCM F25044
	Succor Creek/Rocky Ford	MSUB 9/16/77 I	leaf	MSUB 70
	Succor Creek/Whisky Creek	MSUB 7/15/70 II	fruit	MSUB
	Buffalo Canyon	UCMP 6101	fruit	UCMP 9195
	Eastgate	UCMP 6507	leaf	UCMP 7092-7096
			fruit	UCMP 7084A, B; 7091, 7097, 7098
	Middlegate	UCMP P5101	leaf	UCMP 4380, 4381, 6667-6669, 6674
			fruit	UCMP 6671-6673, 6675
	Fingerrock	UCMP PA-99	fruit	UCMP 9196
	Ellensburg/Tyrell	UCMP PA-19	leaf	UCMP 5472

Explanation of Plate 61.

(all figures natural size)

Figs. 1, 2, 4 *Acer protomiyabei* Endo. Seldovia Point. Hypotypes USNM 208468 (Fig. 1), USNM 396216 (Fig. 2), USNM 208466 (Fig. 4).

Fig. 3 *Acer protomiyabei* Endo. Beluga River. Hypotype USNM 396215A.

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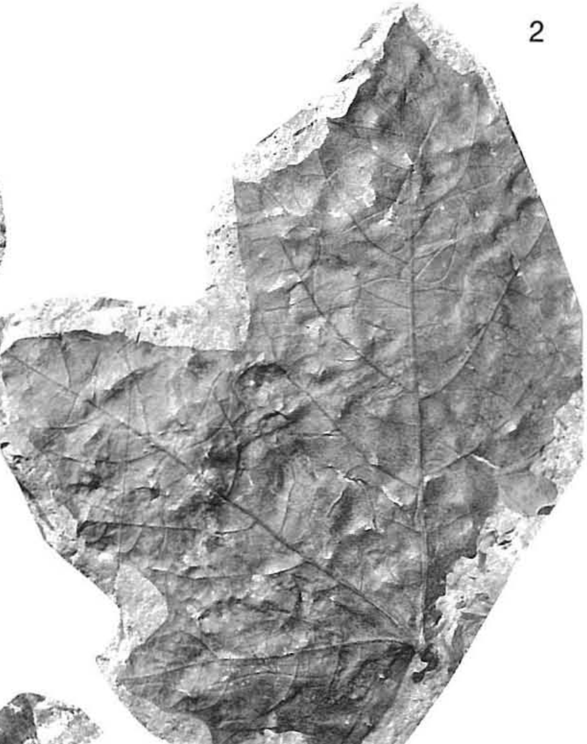

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Acer tyrellense	Weyerhauser	USGS 9997	leaf	USNM 396206
	Hog Creek	USGS 8923	fruit	USNM 396207A, B; 39608, 396209
	Almaden	UCMP P6001	leaf	UCMP 9197
	Trapper Creek	UCMP P571	fruit	UCMP 8473-8475, 8480-8482
	Niles Canyon	UCMP PA-129	leaf	UCMP 9198
Acer washingtonense	Republic/Knob Hill	UWBM B-2737	leaf	UWBM 56253A, B
			fruit	UWBM 56255, 71135A, B
	Republic/Resner Canyon	USGS 11018	fruit	USNM 396011
	Republic	UWBM A-0307	fruit	UWBM 54308
Acer wehri	Republic	UWBM A-0308	fruit	UWBM 39728A, B
		UWBM A-0307	fruit	UWBM 56257, 56260
		USGS 7870	fruit	USNM 396039
	Princeton/One Mile Creek	UWBM B-3389	fruit	UWBM 54108A, B
	Chu Chua Creek	GSC 4821	fruit	GSC 82970A, B
Acer whitebirdense	Latah/Brickyard	USGS 7884	fruit	USNM 396109
	Latah/SP&S Cut	——	fruit	USNM 396110, 396111
	Grand Coulee	USGS 9078	fruit	USNM 396112
	Whitebird	USGS 8444	leaf	USNM 396113-396117
		UCMP PA-97	leaf	UCMP 9100
		——	leaf	UWBM 56258
		USGS 8444	fruit	USNM 39669, 316329, 396118-396121
		——	fruit	UWBM 18484
	Baker	USGS 8171	leaf	USNM 396122, 396123
			fruit	USNM 396124
	Stinking Water	UCMP P4120	fruit	UCMP 9101
Acer sp. 1	Tsadaka Canyon	USGS 9359	leaf	USNM 396012A, B
Acer sp. 2	Rex Creek	USGS 9928	fruit	USNM 396013
Acer sp. 3	Princeton/Whipsaw Creek	GSC 4573	leaf	GSC 82969
Acer sp. 4	Copper Basin	UCMP P3918	leaf	UCMP 20113
Acer sp. 5	Elko	UCMP 22261	leaf	UCMP 9170
Acer sp. 6	Bridge Creek/Twickenham	UCMP P5603	fruit	UCMP 9171A, B
Acer spp. indet. (series Saccharodendron)	Cape Blanco	USGS9743	leaf	USNM 396210
	Mulholland	UCMP P-386	leaf	UCMP 1662
	Denton Creek	UCMP P5602	leaf	UCMP 9200
	Mint Canyon	UCMP P40	leaf	UCMP 9201

(Manuscript received on Sept. 10, 1986; and accepted on Oct. 29, 1986).