

SYSTEMATICS AND BIOGEOGRAPHY OF SELECTED MODERN AND FOSSIL
DIPTERONIA AND *ACER* (SAPINDACEAE)

By

AMY MARIE MCCLAIN

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2000

Copyright 2000

by

AMY MARIE MCCLAIN

ACKNOWLEDGMENTS

I would like to thank the many people who have helped me throughout the last few years. My committee chair, Steven R. Manchester, provided continual support and assistance in helping me become a better researcher. The members of my committee, David L. Dilcher and Walter S. Judd, have spent much time and effort teaching me in their areas of expertise. The University of Florida Herbarium (FLAS) staff, including Kent Perkins and Trudy Lindler, were of great assistance. I also thank the Harvard Herbarium (A, GH) staff, especially Emily Wood, David Boufford, Kancheepuram Gandhi, and Timothy Whitfeld, as well as those at the Beijing Herbarium (PE) and Zhiduan Chen, who helped to arrange my visit to China. I thank David Jarzen for help with the University of Florida fossil plant collections. I appreciate the access to fossil specimens provided to Steven Manchester and me by Amanda Ash, Melvin Ashwill, James Basinger, Lisa Barksdale, Richard Dillhoff, Thomas Dillhoff, Diane Erwin, Leo Hickey, Kirk Johnson, Linda Klise, Wesley Wehr, and Scott Wing. Thanks go to Richard and Thomas Dillhoff for providing measurements of additional fossil specimens. I especially thank my husband, Rob McClain, for his patience, help, and support, and my parents for their love and encouragement. This work was funded in part by a research assistantship from the Florida Museum of Natural History.

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	iii
LIST OF TABLES	vi
ABSTRACT	vii
INTRODUCTION	1
<i>Dipteronia</i>	3
<i>Acer</i>	4
MATERIALS AND METHODS	7
<i>Dipteronia</i>	7
<i>Acer</i>	16
<i>DIPTERONIA</i>	26
Morphology	26
Modern	26
Fossil	27
Previous Nomenclature	28
<i>Dipteronia brownii</i> , McClain et Manchester, sp. nov.	30
Discussion of <i>Dipteronia brownii</i> sp. nov.	31
Biogeography	34
Phylogeny	35
<i>ACER</i>	43
Morphology	43
Modern	43
Fossil	49
Biogeography	51
Phylogeny	52
CONCLUSIONS	76

LIST OF REFERENCES	78
BIOGRAPHICAL SKETCH	83

LIST OF TABLES

	<u>Page</u>
Table 1: Localities for <i>Dipteronia</i> fossil fruits in the Northern Hemisphere, giving the estimated geologic ages, sources of age estimates, geographic coordinates, and example specimens cited.	10
Table 2: Species included in <i>Acer</i> section <i>Macrantha</i> by various authors.....	19
Table 3: <i>Acer</i> sections and series as circumscribed by de Jong, 1994.	20
Table 4: <i>Acer</i> Section <i>Macrantha</i> as circumscribed by de Jong, 1994, with modern range...	23

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

SYSTEMATICS AND BIOGEOGRAPHY OF SELECTED MODERN AND FOSSIL
DIPTERONIA AND *ACER* (SAPINDACEAE)

By

Amy Marie McClain

December 2000

Chairman: Steven R. Manchester

Major Department: Botany

Dipteronia and its sister genus *Acer* form the traditional family Aceraceae, now interpreted as a subgroup of the Sapindaceae. These two genera have fossil records that extend back to the Paleocene or Eocene. In this thesis, I evaluate the fossil records of *Dipteronia* based on fruits and those of *Acer* section *Macrantha* based on leaves. Although confined to China today, the record of *Dipteronia* fruits ranges from the Paleocene to the Oligocene in western North America. Leaves of *Acer* section *Macrantha* have a similar pattern of distribution, with fossils from both North America and Asia. *Acer* section *Macrantha* has a more limited fossil record than reported in the literature, but can be confirmed from the Eocene of Alaska and the Miocene and Pliocene of Japan.

INTRODUCTION

Maple trees are common elements in forests across the Northern Hemisphere. *Dipteronia* and *Acer* are both well represented in the fossil record with occurrences in the Tertiary of North America and Asia. *Acer* is additionally well represented in the European Tertiary. Although the two genera have long been considered to be sister taxa, they have had quite different histories since their divergence. The fossil record of both consists primarily of fruits and leaves, but *Dipteronia* and *Acer* present different challenges to understanding their fossil record. *Dipteronia* has distinctive fruits, but the compound leaflets are difficult to distinguish from various other sapindalean genera. Previous reports of *Dipteronia* fossils have included both fruits and equivocal foliage, which confuses the history. This study was designed to incorporate only those reports where I am confident that the genus has been identified correctly. *Acer* is easily recognized in the fossil record from both leaves and fruits, although the fruits are similar to some other Sapindaceae and to Malpighiaceae. The main difficulty within the genus has been determining the infrageneric relationships of the fossils. Because there are over one hundred modern species, monographers have separated the genus into sections, many of which have been consistently recognized by various authors over time. However, the specific leaf characters for these sections have been described only in vague terms. Other characters such as flowers (de Jong, 1976) or bud scales and wood anatomy (Ogata, 1967) have often been given more attention.

This study comprises two parts. The first is an analysis of extant and fossil *Dipteronia* fruits, designed to determine the historical biogeography of the genus as represented by the distinctive fruits. The second examines the genus *Acer*, which is easily identified in the fossil record from both leaves and fruits. Only the leaf morphology of *Acer* is studied here, but future work will include fruits. To further understand the biogeography of *Acer*, it is necessary not only to recognize the genus, but also to assess the infrageneric relationships of the fossils. Although previous researchers (Pax, 1902; Akhmetiev, 1971; Walther, 1972; Tanai and Ozaki, 1977; Wolfe and Tanai, 1987; Ozaki, 1991) have often placed fossil taxa in fossil and modern sections of the genus, the characters upon which such assignments are based have often not been truly diagnostic and the fossils, as described, sometimes also match in morphology more than one section.

Dipteronia and *Acer* have long been considered sister taxa, as indicated by their traditional placement in the bigeneric family Aceraceae (Pax, 1902; Pojarkova, 1949). Both share the characters of opposite, exstipulate leaves, flowers with five sepals, five nonappendaged petals, a nectariferous disc, eight stamens, tricolporate pollen, two carpels and two ovules per carpel with only one seed developing per carpel and schizocarpic winged fruits borne in pairs. Recent phylogenetic investigations continue to support the close phylogenetic relationship between *Dipteronia* and *Acer* (Judd, Sanders, and Donoghue, 1994; Gadek et al., 1996). However, these analyses also indicate that these taxa are nested within the Sapindaceae; therefore the traditional recognition of Aceraceae at the family level renders the Sapindaceae paraphyletic. It is more

appropriate to treat the *Dipteronia-Acer* clade as a subfamily (Aceroidae) or lower rank within the Sapindaceae.

The two genera are readily distinguished on morphological grounds. *Dipteronia* has distinctive fruits in which the wing fully encircles the seed. It also differs from *Acer* in lack of bud scales and much larger inflorescences of over 400 flowers (Ogata, 1967; de Jong, 1976; van Gelderen, de Jong, and Oterdoom, 1994). The pinnately compound leaves of *Dipteronia* differ from the leaves of most *Acer* species, which are typically simple and palmately lobed. *Acer* may also be palmately compound, trifoliolate or, as in *Acer negundo*, pinnately compound with only 5-7 leaflets instead of the 7-15 common in *Dipteronia*.

Dipteronia and *Acer* are both well represented in the fossil record with occurrences of *Dipteronia* in the Tertiary of North America and *Acer* throughout the Northern Hemisphere. Although the fossil record of *Acer* is well documented in the Tertiary of North America (Brown, 1935, 1937; Wolfe and Tanai, 1987), Europe (Walther, 1972), and Asia (Akhmetiev, 1971; Tanai and Ozaki, 1977; Manchester, 1999), that of *Dipteronia* has received relatively little attention and some of the previously published reports refer to isolated leaflet impressions of equivocal diagnostic value (Brown, 1935, 1937; MacGinitie, 1974). The fossil record of *Dipteronia* may complement that of *Acer*, providing a better understanding of the geographic origins and timing of the radiation of the *Acer-Dipteronia* clade.

Dipteronia

Dipteronia Oliver (1889) is an extant genus endemic to southern and central China with two living species, *D. sinensis* Oliver (1889) and *D. dyerana* Henry (1903).

The genus is distributed in broadleaved deciduous forests, along stream margins at altitudes from 1450 to 2400 m, sometimes as low as 1000 m, in the Chinese provinces Gansu, Guizhou, Henan, Hubei, Hunan, Shaanxi, Sichuan, and Yunnan (Ying, Zhang, and Boufford, 1993). In the *Dipteronia* chapter of this thesis, I review the diagnostic characters of the fruits of the two extant species as a basis for recognizing fossil remains from western North America. I attempt to unravel the complicated nomenclature of North American fossil *Dipteronia* and *Bohlenia*. Although fossil fruits of *Dipteronia* have been illustrated from the Tertiary of North America, they were always attributed to species that were based on detached leaves of uncertain affinity to *Dipteronia* (Brown, 1935, 1937). I recognize a new species, *Dipteronia brownii* sp. nov., based on characteristic fruit remains, review its stratigraphic and geographic distribution and compare its morphology with that of extant species. The significance of fossil remains as a basis to understand the evolutionary and biogeographic history of the *Acer-Dipteronia* clade is discussed.

Acer

Acer L. is distributed throughout the Northern Hemisphere, in a variety of environments. The genus is usually deciduous, but some species in warmer areas are evergreen. There are at least 120 modern species, more according to some taxonomists. The first comprehensive monograph of the genus was that of Pax (1885, 1886, 1902). Systematic treatments of *Acer* have also been published by Pojarkova (1949), Momotani (1962), Fang (1966), Ogata (1967), Murray (1970), de Jong (1976), Delendick (1981), and Mai (1984).

Acer fossils are found throughout the Northern Hemisphere from the Eocene to the Recent (Walther, 1972; Tanai and Ozaki, 1977; Wolfe and Tanai, 1987), and perhaps as early as the Paleocene (Brown, 1962; Wolfe and Tanai, 1987; Crane, Manchester, and Dilcher, 1990). The most complete summary of the fossil record of *Acer* in North America is the 1987 paper by Wolfe and Tanai. They described and illustrated 21 previously established *Acer* species from North America as well as 62 new species, two new combinations, and six undetermined species, based on leaf and fruit fossils. They placed these fossils in 21 modern and 12 fossil sections. However, I believe important work still remains. There has not been sufficient analysis as to the reliability of the infrageneric assignments of many of these species. The unique character combinations that define each modern and fossil section have yet to be described. Another problem is that detached fruits and leaves hypothesized to represent the same species have often been formally merged and given the same name, which creates difficulties for paleobotanists. By analyzing a single, easily identifiable section of *Acer*, I hope to provide a more reliable basis for determining whether or not fossil *Acer* leaves belong to that section.

I surveyed the modern and fossil *Acer* literature to determine which modern sections may be reliably diagnosed based on leaf morphology. I determined that some species in the section *Macrantha* had a distinctive leaf type not found in any other modern section. I surveyed the circumscription of the section *Macrantha* by the major monographers of *Acer* in order to determine which modern species to study. Fruit morphology also may be used in the future, as fruits are also common *Acer* fossils.

The section *Macrantha* was first described by Pax in 1885. Most monographers have considered the type species to be *A. pennsylvanicum* L., but Delendick (1981) believes that the first species to be identified as the type following the ICBN may actually be *A. rufinerve* Sieb. et Zucc. as published by Fang (1966). I have not yet studied the nomenclature in enough detail to evaluate this and other nomenclatural problems. In this thesis I will generally follow de Jong (1994), the most recent classification, which appears to work fairly well within the section *Macrantha*. This section has been recognized by all the monographs since it was first described (Pax, 1885). The group seems very likely to be monophyletic, based on putatively synapomorphic morphological characters such as striped bark, stalked bud scales (also present in section *Glabra*, series *Glabra*), and poorly developed inflorescence bracts. Recent molecular analyses of *Acer* show support for the monophyly of the section *Macrantha* (Hasebe, Ando, and Iwatsuki, 1998), or for at least most of the taxa sampled (Ackerly and Donoghue, 1998). However, a comprehensive molecular analysis of the genus *Acer* has not been attempted.

Wolfe and Tanai (1987) include five fossil species in section *Macrantha* based on leaves and fruits from North America: *A. clarnoense* Wolfe et Tanai, *A. dettermani* Wolfe et Tanai, *A. castorrivularis* Wolfe et Tanai, *A. latahense* Wolfe et Tanai, and *A. palaeorufinerve* Tanai et Onoe. To determine if these species were appropriately assigned to section *Macrantha*, I surveyed the morphology of modern section *Macrantha* leaves in order to determine which characters available in the fossil record could be used to identify the group.

MATERIALS AND METHODS

Dipteronia

The winged fruits of *Dipteronia* occur as impressions in lacustrine shales at localities where fossil dicotyledonous leaves are abundant. Specimens are usually recovered in the process of splitting the sediment in search of leaf impressions.

Dipteronia fruits were examined from all known North American localities, from Colorado to British Columbia (Table 1, Fig. 1). Specimens cited in this paper are housed at the Florida Museum of Natural History, Gainesville, (UF), Burke Museum in Seattle, Washington (UWBM), Smithsonian Institution, Washington DC (USNM), Peabody Museum of Natural History, New Haven, Connecticut (YPM), the University of California at Berkeley (UCMP), and the University of Saskatoon, Saskatchewan (USASK). The literature and major museum collections in Europe and Asia were studied by S. Manchester (cited in Manchester, 1999) in search of *Dipteronia* fruits.

The geographic distribution of extant and fossil occurrences of *Dipteronia* (Fig. 1) were plotted using the “Online Map Creation” web page (http://www.aquarius.geomar.de/omc/omc_intro.html) application of Generic Mapping Tools by entering the latitudes and longitudes of individual sites. Table 1 provides the geographic coordinates and stratigraphic position of localities from which *Dipteronia* fossil fruits have been studied and indicates the references upon which the geologic age is based. In some instances the age determinations are based on stratigraphic proximity to

radiometrically dated units; in other instances the age is simply an approximation based on floristic correlations (Table 1; localities 1, 9-11, and 13). The earliest known *Dipteronia* fruits are two fragmentary specimens collected by Manchester from the Paleocene Fort Union Formation at Hell's Half Acre, Wyoming. These megafossils were collected from the same stratigraphic sequence used by Nichols and Ott (1978) as the basis for establishing a palynological zonation that is now widely used in biostratigraphic investigations of Paleocene sediments in Wyoming and adjacent states. The *Dipteronia* fruits were found at the level of pollen zone P-4 sensu Nichols and Ott (1978), which is considered to be middle Paleocene (Nichols and Flores, 1993), or ~ 60-63 million years old.

Middle Eocene localities include West Branch Creek and White Cliffs Sr., Oregon; Republic, Washington; Joseph Creek, McAbee, and One Mile Creek, British Columbia (Table 1: localities 2-7). There are many Late Eocene localities, including Sumner Spring, Teater Road, White Rock Gulch, and White Cap Knoll in Oregon; Ruby River Basin, Montana; and Florissant, Colorado (Table 1: localities 8-13). The youngest specimen is from the early Oligocene shales of Bridge Creek, Oregon (Brown, 1959; Meyer and Manchester, 1997).

Modern comparative material was examined from herbaria at A, FLAS, and PE. Fruit length is the longest line parallel to the primary vein leading to the seed. Fruit width is the longest line perpendicular to the length (Fig. 2). Measurements cited in the text are for the largest measurement of each fruit, as the fruits are usually very similar in each dimension.

Fossil *Dipteronia* fruits were measured to determine whether they could be divided into two or more groups based on size. There were no gaps along width or length for the fossils (Fig. 3). Length and width appear to be highly correlated. The modern fruits are generally larger than most fossils. When fossils were incomplete, size measures are conservative estimates. Because the wing is fairly symmetrical on either side of the seed body, these estimates should be reasonably accurate. Because the ratio of length vs. width was highly correlated, I used the maximum dimension to represent the overall size of the fruits. I graphed maximum dimension over time (Fig. 4), but because of limited stratigraphic information, the time axis is poorly resolved.

Table 1: Localities for *Dipteronia* fossil fruits in the Northern Hemisphere, giving the estimated geologic ages, sources of age estimates, geographic coordinates, and example specimens cited.

Locality	Age	Locality age assignment	Latitude/ Longitude	Illustrations or cited specimens
1. Hell's Half Acre, Wyoming	Late Paleocene	Nichols and Ott, 1978	43°00.88'N 107°04.84'W	Fig. 24
2. McAbee, British Columbia	Mid Eocene	Stockey and Wehr, 1996	50°47'N 121°08'W	Fig. 33
3. Joseph Creek, British Columbia	Mid Eocene	Wolfe and Wehr, 1987	~50°N ~120°W	Fig. 26
4. One Mile Creek, Princeton, British Columbia	Mid Eocene	Stockey and Wehr, 1996	49°21' N ~120°19.98'W	Figs. 18, 19, 31, 32; Stockey and Wehr, 1996
5. Republic, Washington	Mid Eocene	Wolfe and Wehr, 1987	48°39.10'N 118°44.33'W	Figs. 13, 16, 25, 34; Brown, 1935; Wolfe and Wehr, 1987, as <i>Bohlenia</i> ; Wehr, 1995, as <i>Bohlenia</i>
6. White Cliffs Sr., Oregon	Mid Eocene	Manchester, 1990	44°44.302'N 120°28.376'W	Fig. 29
7. West Branch Creek, Oregon	Mid Eocene	Manchester, 1990	44°35.44'N 120°15.51'W	Fig. 35
8. Whitecap Knoll, Oregon	Late Eocene	Manchester, 2000	44°50.195'N 120°25.074'W	Manchester, 2000
9. White Rock Gulch, Oregon	Late Eocene	Manchester estimate	44°43.245'N 120°28.443'W	Fig. 27
10. Sumner Spring, Oregon	Late Eocene	Smith et al., 1998	44°25.833'N 121°07.018'W	Figs. 20, 36, 37; McFadden, 1986
11. Teater Road, Oregon	Late Eocene	Wolfe and Tanai, 1987 as Sheep Rock Creek	44°10.039'N 120°14.856'W	Fig. 28

Table 1—continued.

Locality	Age	Locality age assignment	Latitude/ Longitude	Illustrations or cited specimens
12. Ruby River Basin, Montana	Late Eocene	Wolfe and Wehr, 1987	45°13.13'N 112°12.50'W	Becker, 1960, 1961; Manchester, 1999
13. Florissant, Colorado	Late Eocene	Wolfe and Wehr, 1987	38° 55'N 105°16'W	Brown, 1937; MacGinitie, 1953
14. Bridge Creek, Oregon (Painted Hills)	Early Oligocene	Meyer and Manchester, 1997; Bestland et al., 1999	44°38.48'N 120°17.25'W	Brown, 1959; Meyer and Manchester, 1997

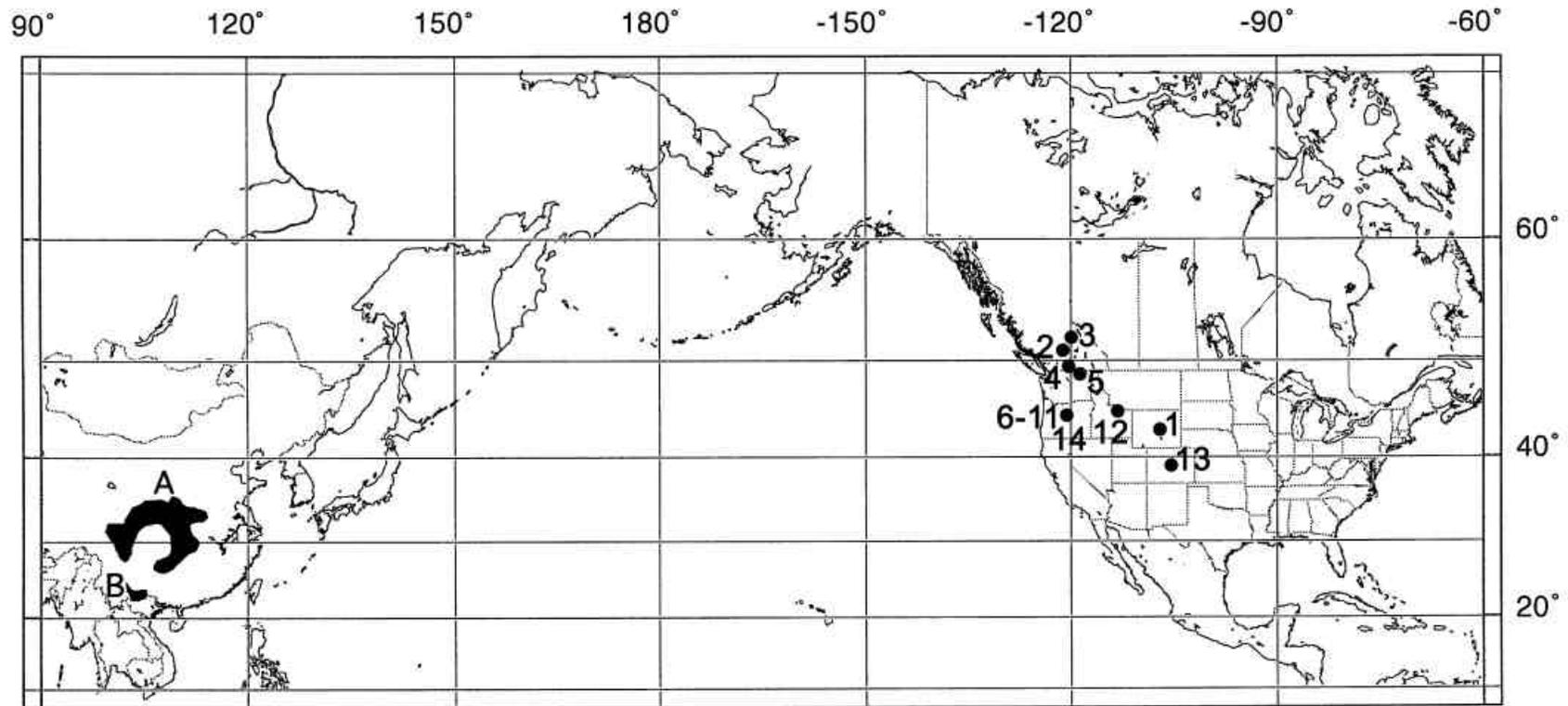


Figure 1. Map showing the distribution of modern and fossil *Dipteronia*. Modern ranges of (A) *D. sinensis* and (B) *D. dyerana* following Ying, Zhang, and Boufford (1993). Fossil occurrences are indicated by solid dots with numbers corresponding to the localities indicated in Table 1. The oldest and youngest occurrences are (1) Paleocene of Hell's Half Acre, Wyoming, and (14) Oligocene of Painted Hills, Oregon. All other sites are middle to late Eocene in age.

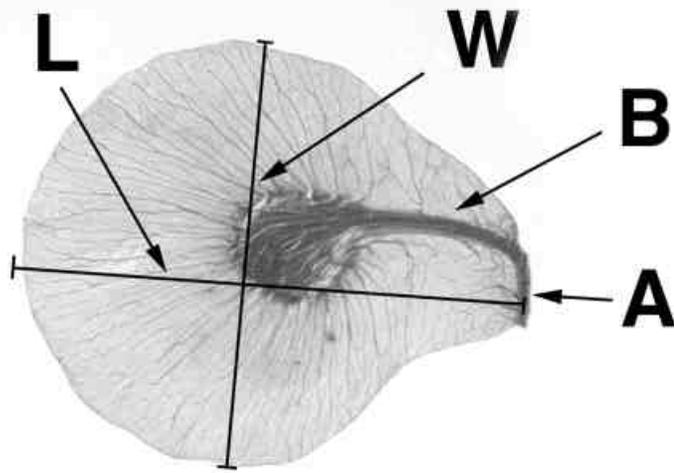


Figure 2. Photograph of extant mericarp of *Dipteronia sinensis* showing the orientations used for measuring length and width. The length (L) is measured parallel to the primary vein (B) that diverges from the detachment scar (A). The width is measured perpendicular to the axis of length (A: B. Bartholomew et al., 1063, Hubei).

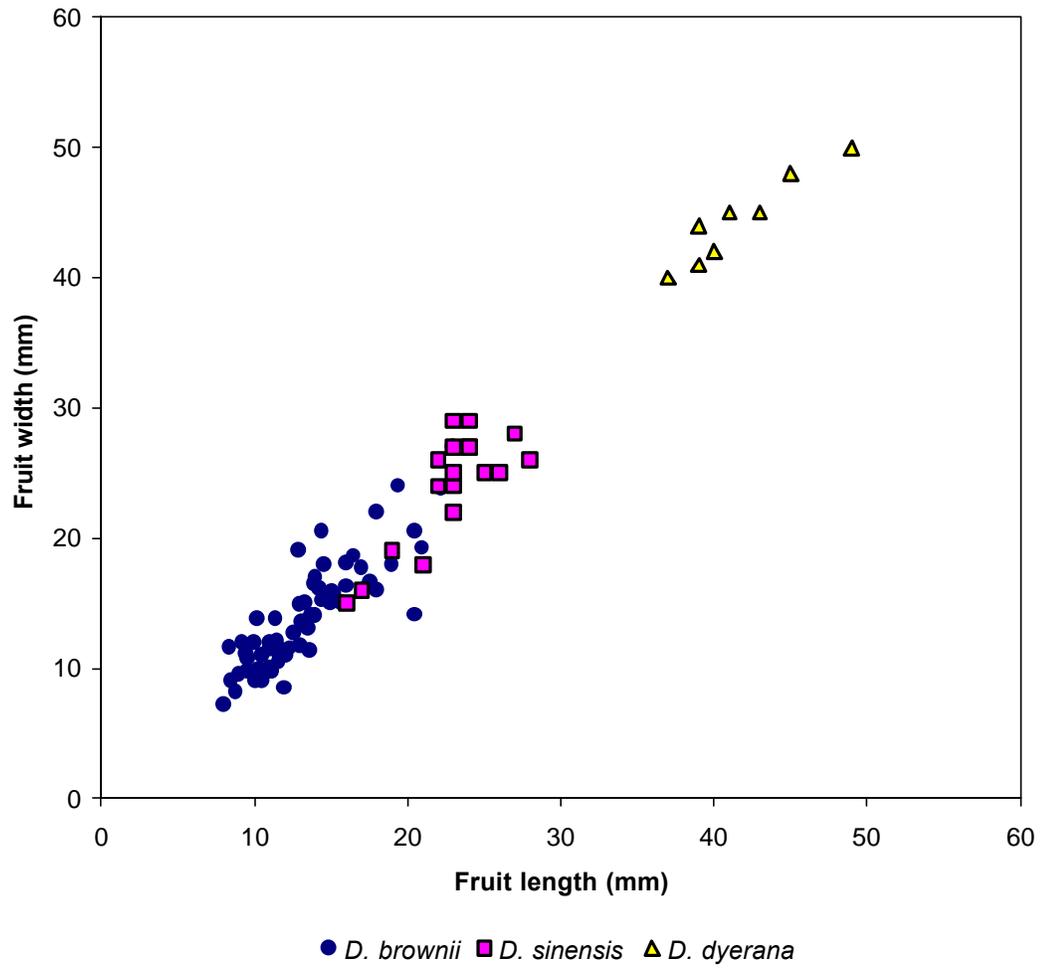


Figure 3. Modern and fossil *Dipteronia* fruits length vs. width.

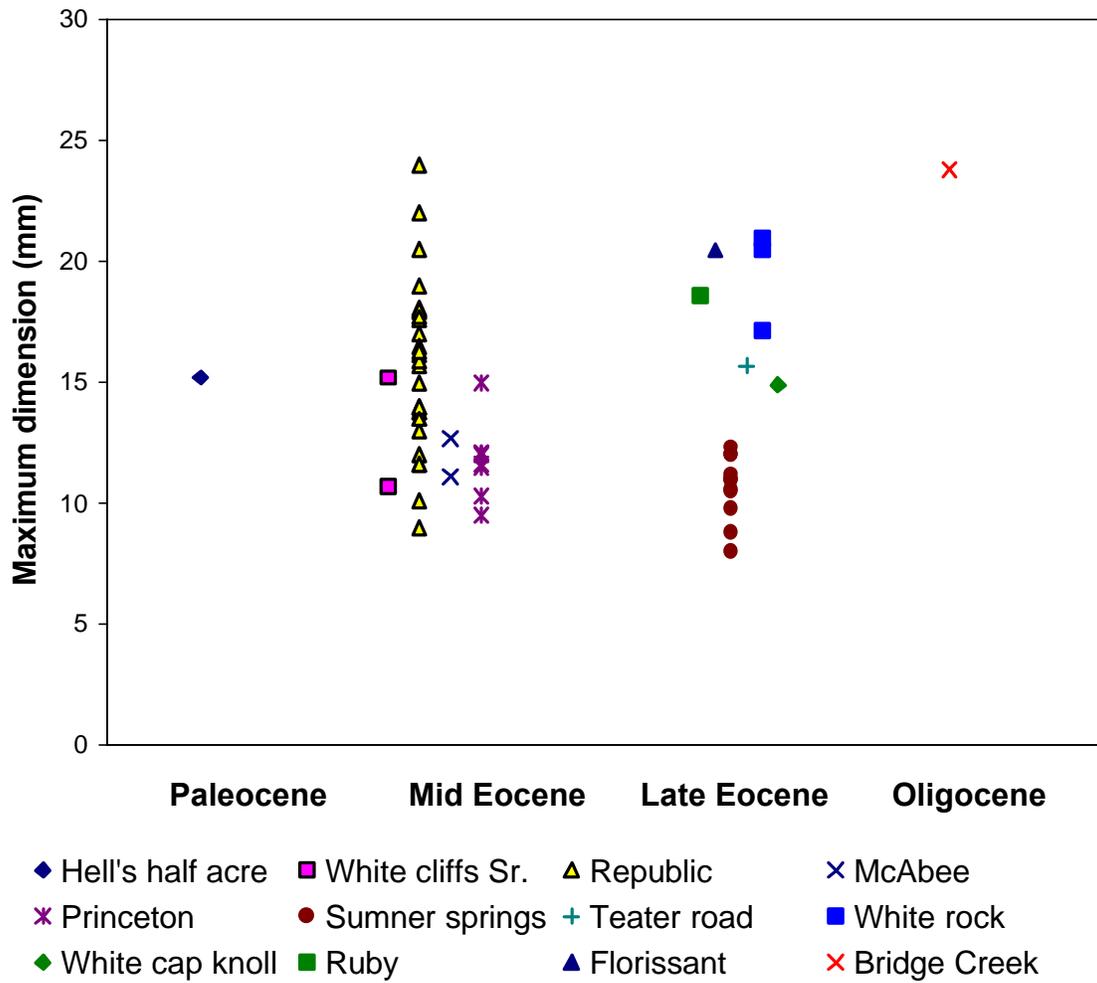


Figure 4. Maximum dimension of fossil *Dipteronia* mericarps across time.

Acer

As the majority of *Acer* leaf fossils reported in the literature are palmately lobed, I surveyed approximately 60 extant species in the genus that normally produce leaves of this kind, using herbarium collections at Harvard (A, GH), Beijing (PE), and the University of Florida (FLAS). I analyzed major morphological characters such as number of primary veins, number of lobes, characters of secondary veins and marginal condition to identify sections of *Acer* with similar leaves. Based on this preliminary analysis, I determined that *Acer* section *Macrantha* could be identified solely on leaf characters. I then surveyed the literature to compare how *Acer* section *Macrantha* has been characterized by various monographers and workers on the genus, including Pax (1885, 1886, 1902), Pojarkova (1949), Fang (1939, 1966), Ogata (1965, 1967), Murray (1970), de Jong (1976, 1994), Delendick (1981, 1990), and Mai (1984). Table 2 summarizes the taxa included in *Acer* section *Macrantha* section by various authors, accounting for nomenclatural changes. The modern distribution of each taxon is also noted.

In order to determine the synapomorphies for *Acer* section *Macrantha* and to establish criteria for the recognition of fossil representatives, variation in the section was studied using modern leaves. The classification I used in this thesis basically follows that of de Jong (1994). Table 3 lists the species recognized by de Jong (1994) and the sections and series in which he places them. Further studies will attempt to clarify the nomenclature, but here I provide all of the names currently used and some of the historical names. Many herbaria still catalogue the species according to names used by Fang (1939) or older monographs, so it is important to know under which names to look.

Table 4 lists the species studied from *Acer* section *Macrantha*, as well as some synonyms.

Additionally, the following species were studied; these have leaves somewhat similar to those in section *Macrantha*: *Acer nipponicum* (section *Parviflora*, series *Parviflora*), *A. spicatum* and *A. caudatum* ssp. *ukurunduense* (section *Parviflora*, series *Caudata*), *A. argutum* (section *Glabra*, series *Arguta*), and *A. wardii* (section *Wardiana*).

I analyzed leaves of these species using the general leaf characters described by Hickey (1973), Wolfe and Tanai (1987), and the Leaf Architecture Working Group (1999). For those characters specific to palmately lobed leaves, I am following the terminology of Wolfe and Tanai (1987), which I will clarify here.

The thickest vein of the lamina continuous with the petiole of the leaf is the medial primary (Fig. 5A). Other primary veins that arise at an angle to the medial primary are termed lateral primaries (Fig. 5B). Secondary veins that branch from the medial primary are termed medial secondaries (Fig. 5C) and those that branch from the lateral primaries are lateral secondaries (Fig. 5D).

The sinus between the lobes is termed the lobal sinus. The origin of the veins that surround the sinus on either side (lobal sinus bracing) is a character stressed by Wolfe and Tanai (1987). This character is not emphasized here due to variability within species.

Tooth shape terminology follows the Leaf Architecture Working Group (1999). The upper and lower shapes of each tooth are determined to be convex (CV), straight (ST), concave (CC), flexuous (FL), or retroflexed (RT). Flexuous is defined as basally convex and apically concave and retroflexed is the inverse. The abbreviations are written

with the apical shape first. For example, CC/CV would mean that the apical side of the tooth was concave and the basal side was convex.

The Leaf Architecture Working Group (1999) describes lobes as indentations along the margin that reach at least $\frac{1}{4}$ of the distance to the midvein, measured parallel to the main vein of the lobe, or the axis of symmetry of the lobe. I have modified this definition to better describe the degree of lobing. Shallow lobes are indentations up to $\frac{1}{3}$ of the distance along a lateral primary to the medial primary. Medium lobing varies from $\frac{1}{3}$ to $\frac{2}{3}$ the length and deeply lobed leaves have indentations greater than $\frac{2}{3}$ the length of the lateral primary.

The term lobation is used, as in Wolfe and Tanai (1987), to describe a very large tooth or group of teeth that subdivides a major lobe of the leaf.

Higher order venation, as studied by Tanai (1978), is not stressed in this study, although it may prove useful for differentiating other species of *Acer*.

Epidermal anatomy may be useful for some sections (Walther, 1972). However, because fossils with cuticle are most often studied in Europe and *Acer* section *Macrantha* does not appear in the modern European flora or the European fossil record, section *Macrantha* has not been studied for cuticular characters. Further work may be useful for resolving relationships among extant species, although the majority of *Acer* leaf fossils in North America do not have cuticle preserved.

Table 2: Species included in *Acer* section *Macrantha* by various authors.

	Pax 1902	Fang 1966	Ogata 1967	Murray 1970	Mai 1984	Delen- dick 1981	de Jong 1994
<i>A. pensylvanicum</i>	X	X	X	X	X	X	X
<i>A. capillipes</i>	X	X	X	X	X	X	X
<i>A. rufinerve</i>	X	X	X	X	X	X	X
<i>A. tegmentosum</i>	X	X	X	X	X	X	X
<i>A. caudatifolium</i>	-- ¹	X ³	X ⁶	X	X	X ¹¹	X
<i>A. crataegifolium</i>		X	X	X	X	X	X
<i>A. pectinatum</i>	X ²	X ⁴	X ⁷	X ⁹	X ¹⁰	X ¹²	X
<i>A. rubescens</i>	-- ¹	X	X	X		X	X
<i>A. sikkimense</i>		X	X ⁸	X ⁸	X ⁸	X ⁸	X
<i>A. wardii</i>	-- ¹	X	X	X	X		
<i>A. micranthum</i>	X	X	X	X	X	X	X
<i>A. tschonoskii</i>	X	X	X	X	X	X	X
<i>A. davidii</i>		X ⁵	X ⁵	X	X ⁵	X ⁵	X
<i>A. morifolium</i>	-- ¹	X	X		X		X
<i>A. metcalfii</i>	-- ¹	X	X	X		X	
<i>A. laisuense</i>	-- ¹	X					X

1 Species described after publication

2 As *A. maximowiczii* Pax and *A. pectinatum*

3 As *A. kawakamii*

4 As *A. forrestii*, *A. laxiflorum*, *A. maximowiczii* Pax, and *A. taronense*

5 As *A. davidii* and *A. grosseri*

6 As *A. insulare* and *A. kawakamii*

7 As *A. chienii*, *A. laxiflorum*, *A. maximowiczii*, and *A. pectinatum*

8 As *A. hookeri* and *A. sikkimense*

9 As *A. laxiflorum*, *A. maximowiczii* Pax, *A. pectinatum*, and *A. taronense*

10 As *A. laxiflorum*, *A. maximowiczii* Pax, and *A. pectinatum*

11 As *A. caudatifolium* and *A. morrisonense*

12 As *A. forrestii*, *A. laxiflorum*, *A. maximowiczii* Pax, *A. pectinatum*

Table 3: *Acer* sections and series as circumscribed by de Jong, 1994.

Section <i>Parviflora</i>	
Series <i>Parviflora</i>	
<i>A. nipponicum</i>	
Series <i>Distyla</i>	
<i>A. distylum</i>	
Series <i>Caudata</i>	
<i>A. caudatum</i>	<i>A. spicatum</i>
Section <i>Palmata</i>	
Series <i>Palmata</i>	
<i>A. ceriferum</i>	<i>A. circinatum</i>
<i>A. duplicatoserratum</i>	<i>A. japonicum</i>
<i>A. palmatum</i>	<i>A. pauciflorum</i>
<i>A. pseudosieboldianum</i>	<i>A. pubipalmatum</i>
<i>A. robustum</i>	<i>A. shirasawanum</i>
<i>A. sieboldianum</i>	
Series <i>Sinensia</i>	
<i>A. calcaratum</i>	<i>A. campbellii</i>
<i>A. chapaense</i>	<i>A. confertifolium</i>
<i>A. elegantulum</i>	<i>A. erianthum</i>
<i>A. fenzelianum</i>	<i>A. kuomeii</i>
<i>A. kweilinense</i>	<i>A. lanpingense</i>
<i>A. linganense</i>	<i>A. mapienense</i>
<i>A. miaoshanicum</i>	<i>A. olivaceum</i>
<i>A. oliverianum</i>	<i>A. schneiderianum</i>
<i>A. shangszeense</i>	<i>A. sichourense</i>
<i>A. sunyiense</i>	<i>A. taipuense</i>
<i>A. tonkinense</i>	<i>A. tutcheri</i>
<i>A. wuyuanense</i>	<i>A. yaoshanicum</i>
Series <i>Penninervia</i>	
<i>A. cordatum</i>	<i>A. crassum</i>
<i>A. erythranthum</i>	<i>A. eucalyptoides</i>
<i>A. fabri</i>	<i>A. hainanense</i>
<i>A. kiukiangense</i>	<i>A. laevigatum</i>
<i>A. lucidum</i>	<i>A. oligocarpum</i>
<i>A. sino-oblongum</i>	<i>A. yinkunii</i>
Section <i>Wardiana</i>	
<i>A. wardii</i>	

Table 3—continued.

Section <i>Macrantha</i>	
<i>A. capillipes</i>	<i>A. caudatifolium</i>
<i>A. crataegifolium</i>	<i>A. davidii</i>
<i>A. laisuense</i>	<i>A. micranthum</i>
<i>A. morifolium</i>	<i>A. pectinatum</i>
<i>A. pensylvanicum</i>	<i>A. rubescens</i>
<i>A. rufinerve</i>	<i>A. sikkimense</i>
<i>A. tegmentosum</i>	<i>A. tschonoskii</i>
Section <i>Glabra</i>	
Series <i>Glabra</i>	
<i>A. glabrum</i>	
Series <i>Arguta</i>	
<i>A. acuminatum</i>	<i>A. argutum</i>
<i>A. barbinerve</i>	<i>A. stachyophyllum</i>
Section <i>Negundo</i>	
Series <i>Negundo</i>	
<i>A. negundo</i>	
Series <i>Cissifolia</i>	
<i>A. cissifolium</i>	<i>A. henryi</i>
Section <i>Indivisa</i>	
<i>A. carpinifolium</i>	
Section <i>Acer</i>	
Series <i>Acer</i>	
<i>A. caesium</i>	<i>A. heldreichii</i>
<i>A. pseudoplatanus</i>	<i>A. velutinum</i>
Series <i>Monspessulana</i>	
<i>A. hyracanum</i>	<i>A. monspessulanum</i>
<i>A. obtusifolium</i>	<i>A. opalus</i>
<i>A. sempervirens</i>	
Series <i>Sacharodendrom</i>	
<i>A. saccharum</i>	
Section <i>Pentaphylla</i>	
Series <i>Pentaphylla</i>	
<i>A. pentaphyllum</i>	
Series <i>Trifida</i>	
<i>A. buergerianum</i>	<i>A. coriaceifolium</i>
<i>A. discolor</i>	<i>A. fengii</i>
<i>A. oblongum</i>	<i>A. paxii</i>
<i>A. shihweii</i>	<i>A. sycopseoides</i>
<i>A. wangchii</i>	<i>A. yuii</i>

Table 3—continued.

Section <i>Trifoliata</i>	
Series <i>Grisea</i>	
<i>A. griseum</i>	<i>A. maximowiczianum</i>
<i>A. triflorum</i>	
Series <i>Mandshurica</i>	
<i>A. mandshuricum</i>	<i>A. sutchuenense</i>
Section <i>Lithocarpa</i>	
Series <i>Lithocarpa</i>	
<i>A. diabolicum</i>	<i>A. leipoense</i>
<i>A. sinopurpurascens</i>	<i>A. sterculiaceum</i>
Series <i>Macrophylla</i>	
<i>A. macrophyllum</i>	
Section <i>Platanoidea</i>	
<i>A. campestre</i>	<i>A. cappadocicum</i>
<i>A. longipes</i>	<i>A. miyabei</i>
<i>A. mono</i>	<i>A. nayongense</i>
<i>A. platanoides</i>	<i>A. tenellum</i>
<i>A. tibetense</i>	<i>A. truncatum</i>
Section <i>Pubescentia</i>	
<i>A. pentapomicum</i>	<i>A. pilosum</i>
Section <i>Ginnala</i>	
<i>A. tataricum</i>	
Section <i>Rubra</i>	
<i>A. pycnanthum</i>	<i>A. rubrum</i>
<i>A. saccharinum</i>	
Section <i>Hyptiocarpa</i>	
<i>A. garrettii</i>	<i>A. laurinum</i>

Table 4: *Acer* Section *Macrantha* as circumscribed by de Jong, 1994, with modern range.

<i>A. capillipes</i> Maximowicz (1867)	Japan
Synonym <i>A. pensylvanicum</i> ssp. <i>capillipes</i> (Maximowicz) Wesmael (1890)	
<i>A. caudatifolium</i> Hayata (1911)	Taiwan
Synonyms <i>A. insulare</i> Makino (1910)	
<i>A. kawakamii</i> Koidzumi (1911)	
<i>A. morrisonenese</i> Hayata (1911)	
<i>A. ovatifolium</i> Koidzumi (1911)	
<i>A. pectinatum</i> ssp. <i>formosanum</i> Murray (1977)	
<i>A. crataegifolium</i> Siebold et Zuccarini 1845	Japan
<i>A. davidii</i> Franchet (1885) ssp. <i>davidii</i>	China
Synonym <i>A. cavaleriei</i> Léveillé (1912)	
<i>A. davidii</i> ssp. <i>grosseri</i> (Pax) de Jong (1994) (not studied)	China
Basionym <i>A. grosseri</i> Pax (1902)	
Synonyms <i>A. pavolinii</i> Pampanini (1910)	
<i>A. hersii</i> Rehder (1922)	
<i>A. tegmentosum</i> ssp. <i>grosseri</i> (Pax) Murray (1966)	
<i>A. laisuenae</i> Fang et Hu (1966) (not studied)	China
<i>A. metcalfi</i> Rehder 1933 [<i>A. sikkimense</i> ssp. <i>metcalfi</i> (Rehder) de Jong (1994)]	China
Synonym <i>A. kiangsiense</i> Fang et Fang f. (1966)	
<i>A. micranthum</i> Siebold et Zuccarini (1845)	Japan
<i>A. morifolium</i> Koidzumi (1914)	Japan
Synonyms <i>A. insulare</i> auct. non Makino (1910)	
<i>A. caudatum</i> sensu Ito et Matsumura (1920) non Wallich	
<i>A. capillipes</i> ssp. <i>insulare</i> (Makino) Murray (1977)	
<i>A. pectinatum</i> Wallich ex Nicholson (1881) ssp. <i>pectinatum</i>	China
<i>A. pectinatum</i> ssp. <i>forrestii</i> (Diels) Murray (1977)	China
Basionym <i>A. forrestii</i> Diels (1912)	
Synonym <i>A. laxiflorum</i> sensu Rehder (1911) non Pax	
<i>A. pectinatum</i> ssp. <i>laxiflorum</i> (Pax) Murray (1977)	China
Basionym <i>A. laxiflorum</i> Pax (1902)	
<i>A. pectinatum</i> ssp. <i>maximowiczii</i> (Pax) Murray (1977)	China
Basionym <i>A. maximowiczii</i> Pax (1889)	
Synonym <i>A. urophyllum</i> Maximowicz (1889)	
<i>A. pectinatum</i> ssp. <i>taronense</i> (Handel-Mazzetti) Murray (1977)	China
Basionym <i>A. taronense</i> Handel-Mazzetti (1924)	
Synonym <i>A. chienii</i> Hu et Cheng (1948)	
<i>A. chloranthum</i> Merrill (1941)	
<i>A. pensylvanicum</i> L. (1753)	Eastern North America
Synonyms <i>A. striatum</i> Duroi (1771)	
<i>A. canadense</i> Marshall (1758)	
<i>A. tricuspifolium</i> Stokes (1812)	

Table 4—continued.

<i>A. rubescens</i> Hayata (1911)	Taiwan
Synonym <i>A. morrisonense</i> sensu Li (1963), non Hayata	
<i>A. rufinerve</i> Siebold et Zuccarini (1845)	Japan
Synonyms <i>A. pennsylvanicum</i> ssp. <i>rufinerve</i> (Siebold et Zuccarini) Wesmael (1890) <i>A. cucullobracteatum</i> Léveillé et Vaniot (1906)	
<i>A. sikkimense</i> Miquel (1867) ssp. <i>sikkimense</i>	China
Synonym <i>A. hookeri</i> Miquel (1867)	
<i>A. tegmentosum</i> Maximowicz (1857)	East Asia
Synonym <i>A. pennsylvanicum</i> ssp. <i>tegmentosum</i> (Maximowicz) Wesmael (1890)	
<i>A. tschonoskii</i> Maximowicz (1886) ssp. <i>tschonoskii</i>	East Asia
Synonym <i>A. pellucidobracteatum</i> Léveillé et Vaniot (1906)	
<i>A. tschonoskii</i> ssp. <i>koreanum</i> Murray (1977) (not studied)	East Asia
Synonym <i>A. komarovii</i> Pojarkova (1949)	

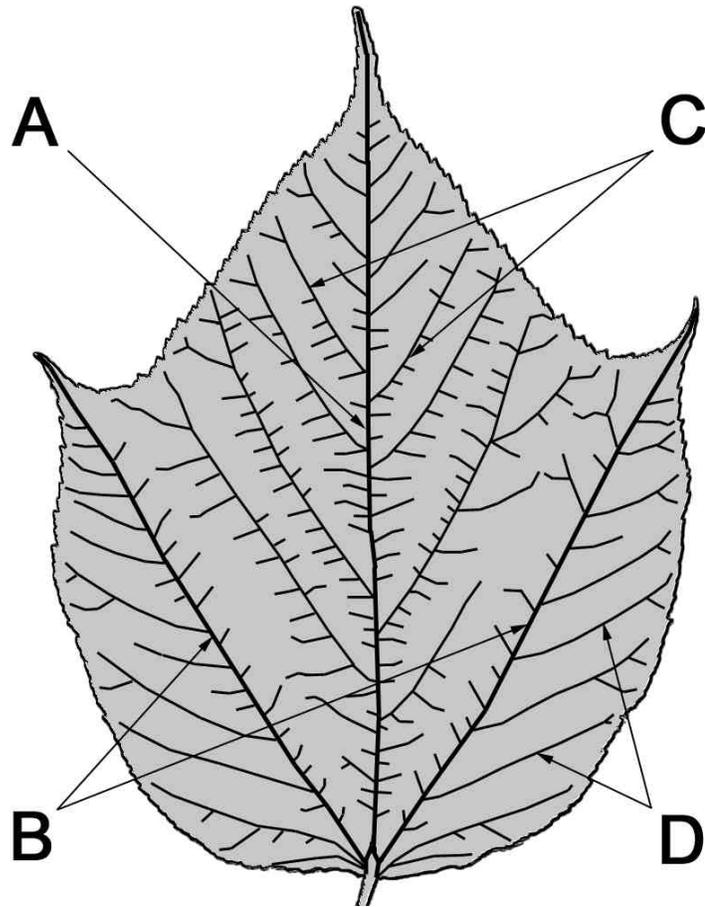


Figure 5. Diagram of a generalized *Acer* leaf showing terms used here. (A) Medial primary vein, (B) lateral primary vein, (C) medial secondary vein, (D) lateral secondary vein.

DIPTERONIA

Morphology

Modern

Dipteronia fruits are distinctive winged schizocarps composed typically of two subelliptical mericarps (Fig. 6). The mericarps are joined to each other at their proximal edges along an axis continuous with the pedicel. Each schizocarp produces a single style that arises apically from the junction of the mericarps (Fig. 10). The perianth and disk are found at the junction between the pedicel and the fruit (Fig. 6). The schizocarps split apart along the median axis, typically leaving a flat proximal detachment scar on each mericarp. A prominent vascular trace extends along the attachment scar (Fig. 2A), then deflects toward the centrally positioned elliptical seed of each mericarp (Fig. 2B). When this large primary vein reaches the seed, it ramifies into smaller secondary veins that form a reticulum covering the pericarp (Fig. 9). These veins give rise to tertiary veins that radiate out from the seed body area to vascularize the encircling wing. These tertiary veins dichotomize and anastomose and terminate directly at the margin of the wing. Quaternary veins form a fine reticulum of polygonal areoles throughout the wing with few or no free-ending veinlets (Figs. 11, 12).

The two modern species of *Dipteronia* differ in overall size and in the thickness of the pericarp around the seed. *Dipteronia dyerana* (Fig. 8) mericarps average ~ 4.5-6.0 cm in diameter, significantly larger than *D. sinensis* (Figs. 6, 7) fruits (2.0-2.5 cm). The

general appearance of the fruit is different, because *D. dyerana* fruits have a noticeably thicker pericarp layer around the seed body and the wing is thicker. This results in a less distinct boundary between the pericarp and wing. In the few *D. dyerana* herbarium specimens studied, I observed an increased tendency for the fruits to develop only one mature mericarp per pair, resulting in a more circular fruit (Fig. 8). Also, the attachment scar between the two fruits is proportionally smaller than in *D. sinensis*.

Fossil

All of the fossil *Dipteronia* fruits appear to fall within a single species, below named *D. brownii* sp. nov. Compared to the two living species, the fossil fruits more closely resemble *D. sinensis*. The most obvious difference from either modern species is their smaller size. The fossil mericarps studied range from 0.8 to 2.4 cm in diameter (Fig. 3), with the majority of specimens between 1 and 2 cm, compared to the larger ranges of the modern species, as described above. *Dipteronia brownii* fruits have approximately the same range of variation in general shape as modern *D. sinensis* fruits. Fossil fruits are readily distinguished from *D. dyerana*, because they are significantly smaller, the attachment scar is larger in proportion to the body of the wing and the pericarp does not appear to be as thick.

Mericarps of the modern species almost always occur in pairs, although tricarpellate fruits have been reported (Hall, 1961). The fruits of the fossil species were borne both in twos (Figs. 14, 20, 21) and in threes (Figs. 13, 15, 16, 17). Complete undetached schizocarps of *Dipteronia* are rarely preserved as fossils--currently eight schizocarps are known from the Eocene of western North America. Four of them clearly show the attachment of three mericarps to a shared pedicel (Figs. 13, 15, 16, 17), three

show only two mericarps (Figs. 14, 20, 21), and one is equivocal (Figs. 18, 19). Most of these schizocarps are from the intensively collected locality of Republic, Washington.

I am uncertain whether the two-mericarp specimens were original pairs, or whether they might represent triplets that had already shed one mericarp prior to deposition. I favor the interpretation that *D. brownii* bore both bi- and tricarpellate fruits.

The pattern of venation is the same in the fossils as in the modern, including the very fine reticulation between the radiating veins of the wing (Fig. 23).

I have been unable to detect any consistent differences between *Dipteronia* fruits from different geological localities and ages ranging from the Late Paleocene through the Oligocene. Morphologically, the species appears not to have changed greatly during this time in its fruit characters, although it would be interesting to know if the foliage also remained constant. The youngest fossil fruit, a single specimen from the Oligocene Bridge Creek flora, is one of the largest of the fossil specimens, measuring 2.38 cm (Meyer and Manchester, 1997). Based on its large size, it falls close to the average size of the extant *D. sinensis*. With only one specimen, I cannot evaluate the population variability for the Bridge Creek occurrence and my placement of the specimen with the older fossils of *D. brownii* is only provisional.

Previous Nomenclature

Roland Brown (1935) was the first to recognize *Dipteronia* from fruits in the Tertiary of western North America. Unfortunately, the specific names that he applied to the fruits have priority for unrelated leaf fossils and the nomenclature has become confused. In 1935, he described a new species *Dipteronia americana* Brown from Republic, Washington and included both leaves and fruits in his concept of the species,

although neither has ever been found attached. Brown figured one fruit and one unattached leaflet and cited a previously described leaflet from Berry (1929, pl. 50, Fig. 5 [USNM 38094]) in synonymy, but he did not designate a holotype. Wolfe and Wehr (1987) subsequently designated Berry's leaflet specimen as the lectotype for Brown's species. At the same time they transferred this species into their new extinct genus *Bohlenia*. Wolfe and Wehr (1987) included both leaves and fruits in their concept of *Bohlenia americana* (Brown) Wolfe and Wehr, although the fruits have never been found attachment to the *Bohlenia* foliage. However, the fruits cannot be distinguished morphologically from modern *Dipteronia*, except they are usually smaller and might be more commonly in threes, as discussed above. The possibility that the fossil population may have had fruits in threes may be used to differentiate species, but does not constitute the generic distinction made by Wolfe and Wehr (1987). Because fossil *Dipteronia* fruits have never been found attached to any type of foliage, I restrict the name *Bohlenia americana* to the foliage upon which it is based.

Brown (1937) also recognized a second fossil species of *Dipteronia*, *D. insignis* (Lesq.) Brown, when he transferred an isolated leaf impression previously called *Myrica insignis* by Lesquereux from Florissant, Colorado into the genus *Dipteronia*. Although Brown implied that the name should be applied both to fruits and foliage, the epithet *insignis* is based on leaf remains of equivocal relationship to *Dipteronia*. Hence, the name is inappropriate for accommodating the fossil fruits. Wolfe and Wehr (1987) established the new combination *Bohlenia insignis* (Lesquereux) Wolfe & Wehr for this species.

In my opinion, the name *Bohlenia* should be applied exclusively to foliage. The true systematic affinities of this foliage remain elusive because similar kinds of leaflets are produced by more than one extant genus of sapindales. Accordingly, all fossil fruits previously associated with the names *Dipteronia* and *Bohlenia* foliage are orphaned and need to be placed into a new fossil fruit species. Although Brown considered the fossil fruits to represent two species, I regard them all as variants of the single species described below.

Dipteronia brownii, McClain et Manchester, sp. nov.

Diagnosis. Fruits schizocarpic, composed of 3 (or sometimes 2) mericarps, usually dispersed singly. Pedicel slender, broadened with disk and perianth at junction with fruit. One style, extending apically between the mericarps. Each mericarp with a central flattened elliptical to pyriform pericarp 3-8 mm diameter surrounded by a flat, subelliptical wing 8-24 mm in diameter. Wing margin entire, rounded, except for a flat proximal edge representing the detachment scar. Primary vein extending from the pedicel, 1.6-5.6 mm to the apical end of the attachment scar, then deflecting sharply at 90-135 degrees and extending straight 2-8 mm to the centrally positioned seed of each mericarp (Fig. 25). Secondary veins forming a coarse reticulum over the pericarp (Figs. 13, 17). Tertiary veins radiating from the seed body, dichotomizing and anastomosing enroute to the wing margin. Quaternary veins forming a fine reticulum of polygonal areoles throughout the wing with few or no free-ending veinlets (Fig. 23).

Holotype. UWBM 39729, Fig. 13, from middle Eocene of Republic, Washington (UWBM locality A0307).

Other specimens. Figure 24 (Paleocene, Hell's Half Acre, WY; UF locality 15740), Fig. 33 (Middle Eocene, McAbee, BC; US 38-9734), Figs. 18, 30, 31, 32 (One Mile Creek, Princeton BC; UWBM locality 3389), Figs. 13-17, 21-23, 25, 34 (Republic, WA, UF localities 18048, 18152; UWBM localities A0307, B2737, B4131), Fig. 29 (White Cliffs Sr., OR UF locality 00262), Fig. 35 (West Branch Creek, OR; USGS locality 8637), Fig. 27 (White Rock Gulch, OR UF locality 00237), Figs. 20, 36, 37 (Sumner Spring, OR; UF 00075, 00283), Fig. 28 (Teater Road, OR; UF locality 00256), Fig. 26 (Joseph Creek, BC, UCMP 168335); Not figured: YMP 37270 (Florissant, CO); Not figured: USNM locality 8641 (Bridge Creek, OR).

Number of specimens examined: over 65

Etymology: The epithet acknowledges the work of Roland Brown in describing the first known *Dipteronia* fossils from North America.

Discussion of *Dipteronia brownii* sp. nov.

Dipteronia brownii mericarps have a ratio of length to width that ranges from 0.68 to 1.45, but commonly they are more or less orbicular. If only a few of the specimens were studied, one might interpret the morphological differences to indicate that more than one species is represented. However, at localities where numerous specimens are available, e.g., Republic, Washington (25 specimens), One Mile Creek, BC (eight specimens) and Sumner Spring (25 specimens), it becomes clear that there is a wide and continuous range in size and shape of the wing and even the proportion of pericarp size to wing size. Some specimens have a shallow concavity in the wing on the basal side adjacent to the attachment scar (Figs. 27, 30, 33, 36), whereas others from the same localities are only convex along the basal wing margin.

In some specimens the proximal margin of the schizocarp continues straight well beyond the attachment scar before rounding (Figs. 28, 30); in others the corresponding margin becomes convex immediately beyond the attachment scar (Figs. 27, 33). Some specimens show a small circular area within the pericarp (Figs. 27, 30). This could be interpreted as the immature seed, or possibly the second aborted ovule, although aborted ovules in *Acer* are much smaller. It is possible that, similar to some *Acer* species, the pericarp may be fully developed although the seed is still growing.

The reticulum of quaternary veins forming a mesh between the radiating tertiary veins is well preserved in only a few specimens (Figs. 22, 23). It corresponds to that observed in the modern species (Figs. 11, 12).

No consistent morphological differences were noted in North American fossils across time or between localities. There are some differences in mean fruit size between localities, but the ranges overlap. Smaller fruits tend to occur in the populations at One Mile Creek (9.5 to 15.0, average 11.8 mm, N = 8) and at Sumner Spring (8.0-13.5, average 11.0 mm, N = 25), but at Republic there is both a greater range of size and greater mean size (10-18, average 16.0 mm, N = 25). From most localities only one or a few specimens are available, making it difficult to determine the “typical” fruits of those populations. For example, at McAbee, the five specimens range from 11.1 to 14.2 mm (average 12.8 mm).

The range of variation in fruit size does appear to increase through time (Fig. 4). However, it is difficult to interpret whether the increase in size range throughout time represents the true evolution or is only an artifact due to small sample size during the Paleocene. One hypothesis that may be suggested based on these results is that

Dipteronia was more diverse during the Eocene, with either more species or more morphological variation in fruit size than today. The small fruits from Sumner Spring may be explained by the hypotheses that they represent a species or population that became extinct and that only the species or population producing larger fruits migrated to, or continued to exist in, Asia.

I have adopted a broad circumscription of *Dipteronia brownii*, which accommodates the full range of morphological variability seen at the type locality (Republic) and other sites ranging from Paleocene to Oligocene. It is possible that if the corresponding foliage were available, I could distinguish more than one species, but the associated leaflets remain speculative. Fruits in twos vs. threes could possibly have been used as a basis to recognize two species, but because the schizocarps are very rarely preserved intact, most fossil mericarps would be unassignable to a species. I have so far found only eight complete schizocarps, half of which show three mericarps (Figs. 13, 15, 16, 17), three fossils show two mericarps (Figs. 14, 20, 21), and one is equivocal (Figs. 18, 19). In my view, a distinction based on merosity would be artificial, because carpel number was probably a variable feature in the population; even today fruits of *D. sinensis* occasionally develop from tricarpellate ovaries (Hall, 1961). Tricarpellate schizocarps can also be found on modern *Acer* trees (Pax, 1885; de Jong, 1976). Wolfe and Wehr (1987) cited the occurrence of three carpels as a basis for distinguishing a separate genus and argued that the taxon be moved from Aceraceae (two carpels) to Sapindaceae (usually three carpels). However, the clade containing *Acer* and *Dipteronia* likely originated within the Sapindaceae, from an ancestor with the primitive sapindalean trait of three carpels. Therefore, the three-fruited specimens merely call into question the

level of universality of the bicarpellate fruit character. A reduction from three to two carpels may not have occurred at the base of the Aceroideae clade, but higher up. This reduction may have occurred gradually over time, so some populations could have been polymorphic. If this hypothesis is true, combining the two- and three-fruited fossils may possibly result in a paraphyletic species. However, because this is mostly conjecture and number of carpels is not usually known in the fossils, I adopt a broad circumscription for *Dipteronia brownii*.

Biogeography

The earliest known *Dipteronia* fruits are two specimens from the Paleocene Fort Union Formation of Hell's Half Acre, central Wyoming (Fig. 24), ~ 60-63 million years old. Surprisingly, the distinctive fruits have not been recovered from other Paleocene localities, which are widely distributed and well collected in Wyoming, Montana and North Dakota (Brown, 1962; Hickey, 1977; Crane, Manchester, and Dilcher 1990; Wing, 1994) and they have not yet been observed in early Eocene sites. However, they are well represented at middle and late Eocene localities. Middle Eocene localities are distributed in Washington, Oregon, and British Columbia. Late Eocene occurrences are known from Colorado, western Montana, and Oregon. The only locality of certain Oligocene age is from the Bridge Creek flora of Oregon, ~ 32 million years old.

The Asian fossil record is undoubtedly incomplete and more collections need to be made. In Europe, however, where paleobotanical study has been more intense, *Dipteronia* fruits have not been described in the literature and are not present in major museum collections (personal communication from H. Walther, Staatliches Museum für Mineralogie und Geologie, Dresden and Z. Kvacek, Charles University, Prague to S.

Manchester). Therefore, my current hypothesis assumes the genus has been limited to Asia and North America throughout its history.

This leads to the supposition that the genus evolved in one of these continents and emigrated to the other. Taking the fossil record as it is currently known, one might conclude that the genus first appeared in North America in the Paleocene and migrated to Asia soon after. At this time, both continents were at higher latitudes, but the climate was warmer and a land bridge was present (Tiffney, 1994). Although the literature suggests there are records of *Dipteronia* in the Miocene of North America (LaMotte, 1952), this information is based on either erroneous taxonomic assignments or inaccurate age dates. I am not aware of any valid occurrences in North America subsequent to the lower Oligocene. From this I infer that *Dipteronia* went extinct in North America by the end of the Oligocene.

The fossil record of *Dipteronia* is nearly continuous from the Paleocene through the Oligocene in North America, but because of the lack of fossil fruits in Asia, it is uncertain whether the genus inhabited the continent prior to the Recent. My interpretation is that Chinese fossil fruits have not been found because they are rare. *Dipteronia* fruits are never very common fossils, except perhaps at Republic, Washington and Sumner Springs, Oregon.

Phylogeny

Judd, Sanders, and Donoghue (1994) suggest that *Acer* and *Dipteronia* diverged from a “winged samaroid clade” of the Sapindaceae including members of the tribes *Thouiniaceae* (*Athayana*, *Bridgesia*, *Diatenopterys*, and *Thouinia*) and *Paulinieae* (*Serjania* and *Thinouia*). The divergence of aceroids from other Sapindaceae follows a

pattern of temperate taxa diverging from large tropical families (Judd, Sanders, and Donoghue, 1994). Judging from the Paleocene occurrences of *Acer* and *Dipteronia*, the divergence of the clade probably occurred during the Late Cretaceous or Early Paleocene.

It is interesting that *Dipteronia* fruits have remained essentially the same from the Paleocene to the Recent, perhaps only just recently forming two distinct species.

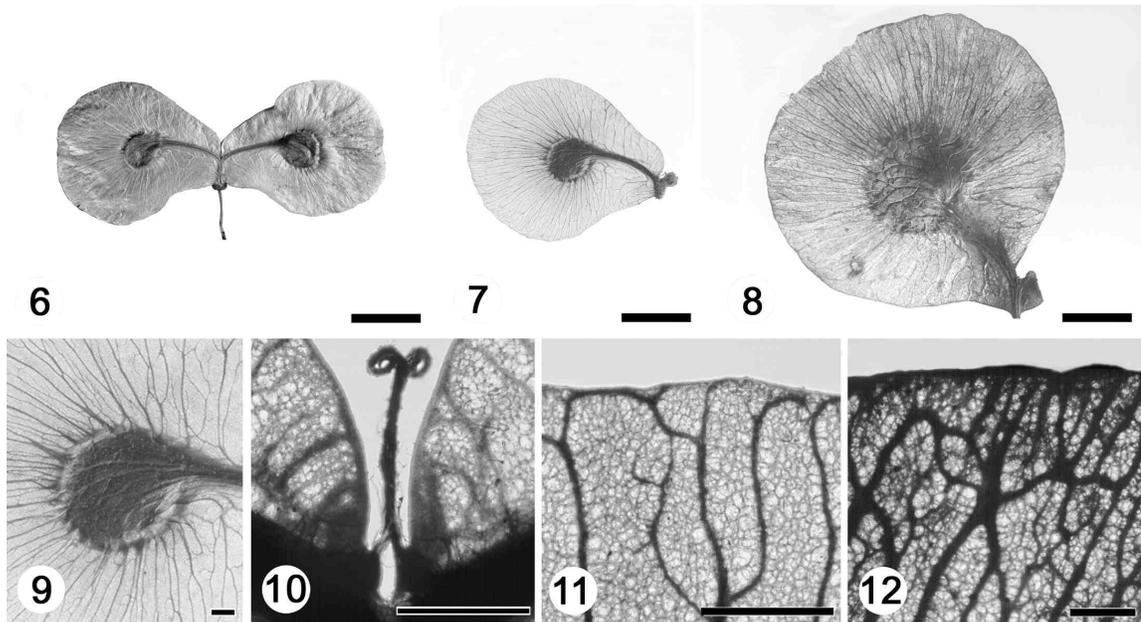
Although it is unknown if there has been similar stasis in other parts of the plant, clearly the genus has not diversified as much as its sister taxon, *Acer*. Although the two genera have existed for the same amount of time, there are now only two living species of *Dipteronia* and over 120 species of *Acer* (van Gelderen, de Jong, and Oterdoom, 1994).

It is essential that the fossil representatives of *Dipteronia* be understood from a “whole plant” perspective so that they can be used in a cladistic analysis of *Acer* and *Dipteronia*. Once *Dipteronia* is well understood, the modern and fossil representatives can be included in phylogenetic analyses of the clade and possibly be used as an outgroup for the genus *Acer*.

To gain a better understanding of the phylogeny of *Dipteronia*, it is necessary to obtain more characters from other organs. It is likely that leaves of *Dipteronia* are also present at some of the localities where the fruits occur, but detailed comparative studies to show how to distinguish *Dipteronia* leaves from other similar sapindalean genera have not been published. It would be of interest to know if the leaves from the Eocene of China more closely resemble those of the extant species, or those of the North American Eocene representatives. In addition, an understanding of foliage variability within the genus would provide a better understanding of the evolution of leaf characters in comparison with other species of both *Dipteronia* and *Acer*.

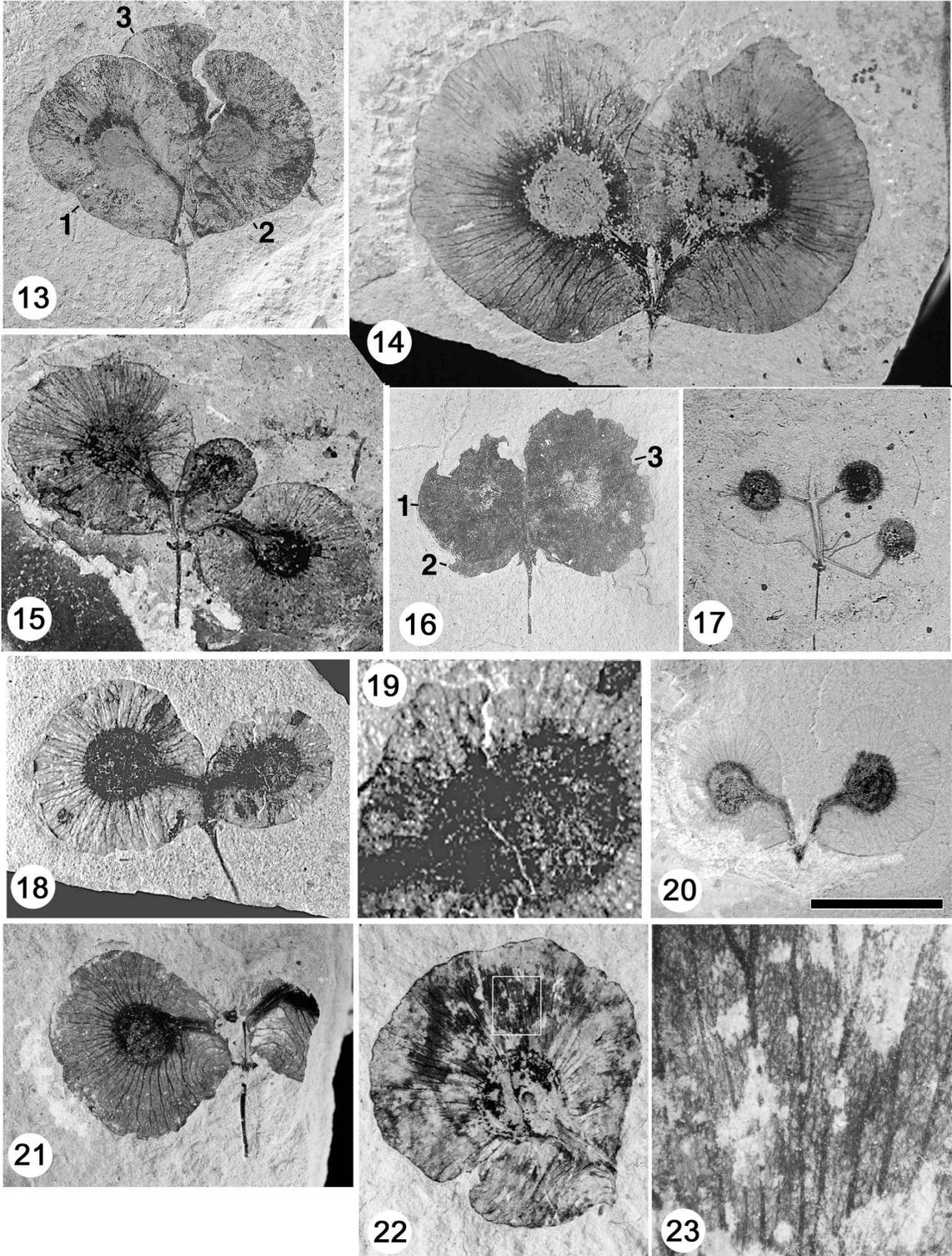
Bohlenia foliage appears to be sapindalean, but does not closely resemble modern *Dipteronia* leaflets. The leaflets of *Bohlenia* are much smaller, have rounder teeth and may have bohleneoid venation, where alternating secondary veins terminate at a sinus instead of a tooth. In fact, I believe the *Bohlenia* leaflets figured by Wolfe and Wehr (1987, Plate 13, Figs. 1, 3) are more similar to the modern *Koelreuteria elegans* (Seem.) A.C. Sm. *Koelreuteria* is also represented at the same site by fruit remains (Wolfe and Wehr, 1987).

In this thesis, I have attempted to clarify the fossil record of *Dipteronia* in North America. Because *Acer* leaf and fruit fossils are known from Tertiary localities in North America, Europe, and Asia, I focused my biogeographic study of *Dipteronia* in these areas. However, I did not find any valid *Dipteronia* specimens from Europe or Asia. I believe that the lack of European *Dipteronia* fossils is significant, because *Acer* fossils are known from many European localities. However, the Asian plant fossil record is not as well understood as that of North America and Europe for many plant taxa. Because *Dipteronia* lives in China today, it is likely that fossils will be found if localities are collected further.

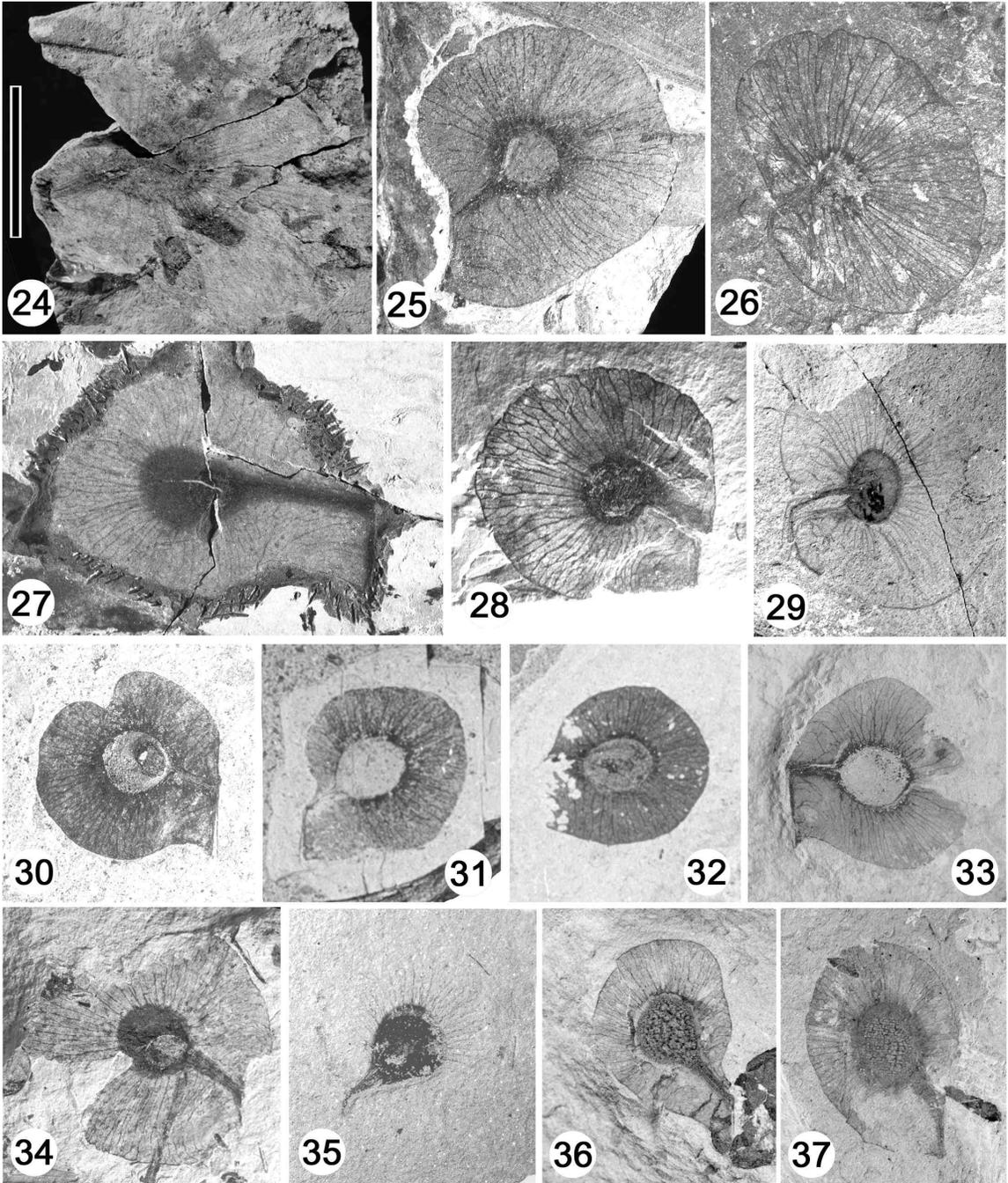


Figures 6-12. Extant fruits of *Dipteronia*. Figs. 6-8, by combined transmitted and reflected light, scale bar = 1 cm. **6.** Typical schizocarp of *D. sinensis* with two fully developed mericarps (A: B. Bartholomew et al., 1063, Hubei). **7.** Another specimen from the same collection showing an enlarged schizocarp (left) and an undeveloped one (right). **8.** *Dipteronia dyerana* showing large fruit size (A: H. T. Tsai, 51524, Yunnan). **9.** *Dipteronia sinensis* detail from Fig. 7, showing secondary veins over the pericarp and radiating tertiary veins (scale bar = 1 mm). **10.** *Dipteronia sinensis* enlargement from Fig. 6, showing the pair of recurved styles arising apically from the pair of mericarps (scale bar = 1 mm). **11.** Enlargement from Fig. 6, showing the reticulum of quaternary veins between the tertiaries (scale bar = 1 mm). **12.** Enlargement of specimen in Fig. 7, showing the higher order venation (scale bar = 1 mm).

Figures 13-23. Schizocarps and mericarps of *Dipteronia. brownii* sp. nov. from the Eocene of western Canada and western USA (scale bar = 1 cm). **13.** HOLOTYPE, from Republic, Washington, showing three attached mericarps. Previously illustrated as *Bohlenia americana* by Wolfe and Wehr (1987). UWBM 39729 (locality A0307). **14.** Schizocarp with two attached mericarps from Republic, Washington, SR 96-08-07. **15.** Schizocarp with three attached mericarps from Republic, Washington, SR 92-20-3A. **16.** Schizocarp with remnants of perianth at junction of pedicel with fruit. Specimen shows three mericarps: two in face view and a third with the margin of its wing protruding on the lower left. Republic, Washington, UWBM 71380 (locality B2737). **17.** Schizocarp with three attached mericarps. Republic, Washington UWBM 26006 (locality B4131). **18.** Schizocarp showing two attached mericarps, pedicel expanded to form a disk at junction with the fruit. One Mile Creek, Princeton, British Columbia, UWBM 56575A (locality B3389). **19.** Enlargement of Fig. 18 showing possibly two mericarps. Note the margin of seed body is not continuous, indicating one partial mericarp may be appressed to another underneath. **20.** Incompletely detached mericarps from Sumner Spring, Gray Butte, Oregon, UF 00283-31375. **21.** Schizocarp with two attached mericarps from Republic Washington, UF 18152-32028. **22.** Mericarp from the type locality showing pyriform pericarp, presumably containing one enlarged seed, with the impression of a small, perhaps immature, seed in the center, UF 18048-30283. **23.** Enlargement of Fig. 22 showing venation.



Figures 24-37. *Dipteronia brownii* mericarps from various localities of western North America and eastern Asia (scale bar = 1 cm). **24.** Hell's Half Acre, Wyoming, UF 15740-23086. **25.** Republic, Washington, UWBM 55044 (locality B4131). **26.** Joseph Creek, British Columbia, UCMP 168335. **27.** White Rock Gulch, Oregon, UF 00237-30301. **28.** Teater Road, Oregon, UF 00256-20862. **29.** White Cliffs, Sr., Oregon, UF 00262-30303. **30.** One Mile Creek, British Columbia, UWBM 57496A (locality B3389). **31.** One Mile Creek, British Columbia, UWBM 97007 (locality B3389). **32.** One Mile Creek, British Columbia, UWBM 57497. **33.** McAbee, British Columbia, US 38-9734. **34.** Republic, Washington, UWBM. **35.** West Branch Creek, Oregon, USNM 509800 (USGS locality 8637). **36.** Sumner Spring, Oregon, UF 00283-31376. **37.** Sumner Spring, Oregon, UF 00275-21691.



ACER

Morphology

Modern

The character used consistently by most monographers to unite *Acer* section *Macrantha* is striped bark. The appearance of vertical white stripes on the bark gives the common name to the group, the snakebark maples. The inflorescence bracts are poorly developed in this section and the buds are often stalked (Ogata, 1967). The rays in the wood are very narrow, usually only three cells wide, with a fairly irregular outline (Ogata, 1967). The group has two pairs of bud scales, leading some researchers to believe that it is fairly primitive, as the sister genus, *Dipteronia*, has no bud scales (van Gelderen, de Jong, and Oterdoom, 1994). Other groups with very few bud scales are section *Parviflora* (called *Spicata* by some authors), series *Parviflora*, *Caudata*, and *Distyla*, section *Wardiana*, section *Glabra*, series *Glabra* and *Arguta*, section *Negundo*, series *Negundo* and *Cissifolia*. Of these, the sections with three to five lobed leaves have sometimes been placed close to *Macrantha*. That is, sections *Parviflora*, *Caudatum*, *Wardiana*, *Glabra*, and *Arguta*. These taxa may be related to section *Macrantha*, but they have leaf forms distinct from *Acer* section *Macrantha*. In this thesis, I will explain how the three to five lobed leaves of these groups can be distinguished from similar leaves in the *Macrantha* group.

Pax (1902) used staminal position as the primary character to delimit his sections. Species with intermediate staminal insertion (*Perigyna*) were placed in section *Macrantha* while species with an intrastaminal nectar disc (*Intrastaminalia*) were placed in section *Indivisa*, which resulted in an artificial classification. Pojarkova (1949) divided section *Macrantha* into four series: *Parviflora*, *Tegmentosa*, *Macrantha*, and *Crataegifolia*, based on number of leaf lobes. However, her groupings did not make sense with the normal range of leaf variation found in the taxa. Momotani (1962) rearranged the species of section *Macrantha* based on fruit characters, which are not evaluated here, but may be useful. Fang (1966) divided section *Macrantha* into three series: *Crataegifolia*, *Tegmentosa*, and *Maximowicziana*. Ogata (1967) also distinguished three series in section *Macrantha*, series *Macrantha*, *Micrantha*, and *Rufinerve* based primarily on bud characters. Murray (1970) basically followed Pojarkova's divisions, although he excluded series *Parviflora*. Tanai (1978) found no fine venation characters to help him distinguish any subgroups within section *Macrantha*, although he did mention that all the leaves of members of section *Macrantha* did not stain well compared with those of other sections. Mai (1984) studied fruit anatomy and divided section *Macrantha* into three series, *Macrantha*, *Rufinerve*, and *Wardiana*.

As summarized in Table 4, I studied the following species in *Acer* section *Macrantha*: *A. capillipes*, *A. caudatifolium*, *A. crataegifolium*, *A. davidii*, *A. metcalfi*, *A. micranthum*, *A. morifolium*, *A. pectinatum*, *A. pennsylvanicum*, *A. rubescens*, *A. rufinerve*, *A. sikkimense*, *A. tegmentosum*, and *A. tschonoskii*. From the leaf characters investigated, I have determined that within *Acer* section *Macrantha*, there is a "Core section *Macrantha*" consisting of *A. pennsylvanicum* (Figs. 38, 58), *A. tegmentosum* (Figs. 39, 59),

A. rufinerve (Figs. 40, 60), *A. capillipes* (Figs. 41, 61), and *A. morifolium* (Figs. 42, 43, 62, 63). The leaves of these species are difficult to distinguish from one another. The leaves are usually shallowly 3-5 lobed, with small basal lobes. *Acer morifolium* normally has unlobed leaves. However, when it does occasionally produce lobed leaves, they are very similar to the others in this group.

Leaves of the “Core section *Macrantha*” differ from those of other section *Macrantha* species in their vein and margin characters. Venation is craspedodromous, with distinct, straight medial secondary veins that do not branch until very close to the leaf margin. The medial secondaries and lateral primary veins are similar in size, shape, and spacing. The margin is very finely serrate, usually with 5-15 teeth/cm. The most common tooth shapes are CC/CV and CC/ST. The leaves have acuminate apices. When *A. morifolium* produces lobed leaves, they are very similar, although the teeth are usually FL/FL. However, normally the leaves are unlobed, which makes them very easy to distinguish from the other members of the “Core section *Macrantha*”. When unlobed, the venation is not very different, except that there are usually only three primary veins. *Acer morifolium* leaves are distinguishable from other unlobed leaves in the section *Macrantha* because the venation is craspedodromous, while the venation is brochidodromous in other species of section *Macrantha* that have unlobed leaves.

Acer metcalfi (Figs. 46, 64) and *A. rubescens* (Figs. 47, 67) have the most similar leaf types to the “Core section *Macrantha*”. The leaves are usually medium 5-lobed, with deeper lobar sinuses than the core group. The lateral primary veins are more distinct from the medial secondary veins in the core group. The venation of medial secondaries in these two species is craspedodromous, but not very strongly, as the veins curve up as

they get close to the leaf margin and fade as they branch increasingly. Both species have teeth: CC/CV, ST/CV, and ST/ST, which are much larger and fewer than in the core group. The leaves usually have only 3-4 teeth/cm.

Leaf morphology supports the retention of *A. metcalfi* as a species distinct from *A. sikkimense* (Figs. 45, 65), whereas de Jong (1994) regards it as a subspecies of the latter. The two clearly have different leaf forms, where *A. sikkimense* has unlobed leaves and *A. metcalfi* has 3-lobed leaves. In my opinion, the leaves of these two taxa are also distinguishable based on venation. *Acer sikkimense* has clear brochidodromous venation while *A. metcalfi* has weak craspedodromous to weak brochidodromous venation.

The leaves of *Acer micranthum* (Figs. 48, 68) and *A. tschonoskii* (Figs. 49, 69) are very similar to one another. They are distinct from the core group in that they have many lobations along the margin. The medial secondary veins are fewer in number than in the core group and are broadly curving upwards. The leaves resemble “Core section *Macrantha*” because they are usually medium five lobed, with a finely serrate margin with teeth of the CC/CV type. *Acer tschonoskii* leaves tend to have deeper lobations, although the leaves of the two species are often virtually indistinguishable.

The subspecies of *A. pectinatum* have leaves very similar to one another, with overlapping ranges of variation. Therefore, I will focus on *A. pectinatum* ssp. *pectinatum* (Figs. 50, 70) here. The leaves of *A. pectinatum*, *A. crataegifolium* (Figs. 52, 71), and *A. caudatifolium* (Figs. 51, 72) differ from “Core section *Macrantha*” in overall shape. The lateral primaries are significantly smaller than the primary vein, resulting in two small, shallow lateral lobes. The medial secondaries of these species are more broadly curving than the core group, with poor craspedodromous to weak brochidodromous venation.

The leaves are similar to the core group in their finely serrate margin and usually three or five shallowly lobed leaves. Leaves of *A. pectinatum* have teeth of the CC/CV type; those of *A. crataegifolium* have CC/CV, FL/CV, and FL/FL teeth; those of *A. caudatifolium* have ST/ST teeth. Of the three species, *A. crataegifolium* leaves tend to have venation closer to brochidodromous. In all, venation type is difficult to categorize because the medial secondary veins become very faint towards the leaf margin. Therefore, it is important to carefully observe this area.

Leaves of *A. davidii* (Figs. 44, 64) and *A. sikkimense* (Figs. 45, 46) are easily distinguished from the “Core section *Macrantha*” by their unlobed leaves. The leaves are similar to the core group in their finely serrate margin. The medial secondaries, however, are not as well defined and less straight than as in the core group and venation is brochidodromous.

I also studied species of other *Acer* sections whose leaves may be similar to leaves of section *Macrantha* species: *A. wardii*, *A. spicatum*, *A. caudatum* ssp. *ukurunduense*, *A. nipponicum*, and *A. argutum*.

Acer wardii leaves differ from the leaves of species of section *Macrantha* in that they are deeply three-lobed with elliptical shaped lobes. The medial secondary veins are well defined, but broadly curving, and branch before reaching the margin. The serrate teeth are CC/CV.

Acer spicatum leaves (Figs. 54, 74) resemble those of members of section *Macrantha* in their venation but not margin characters. The straight, fairly well defined medial secondary veins are similar to those in leaves of members of section *Macrantha*.

In contrast, the margin of leaves of *Acer spicatum* has teeth that are larger in proportion to the leaf size. There are 2-3 teeth/cm of the FL/FL and CC/CV types.

Acer caudatum ssp. *ukurunduense* (Figs. 55, 75) leaves are similar to leaves of species in the “Core section *Macrantha*” because of their distinct, straight medial secondary veins. However, these veins are fewer in number and more irregularly spaced. The margin is very different, with fewer, larger teeth, although they are of the same shape as many in section *Macrantha*, ST/ST, CC/ST, and CC/CV. The leaves are usually medium 5-lobed.

Leaves of *A. nipponicum* (Figs. 56, 76) are very similar to those of members of the “Core section *Macrantha*”. They are shallowly 5-lobed, with distinct, straight medial secondary veins. The margin is finely serrate as in the core group, with ~ 10 teeth/cm. The teeth are ST/ST and CC/CV. The teeth may be more incised than in the core group, although the leaves are otherwise indistinguishable from the core group based on margin and venation characters.

Leaves of *A. argutum* (Figs. 57, 77) resemble those of *A. tschonoskii* and *A. micranthum* in their overall shape, with five medium lobes and acuminate apices. The medial secondary veins of leaves of *A. argutum* resemble those of the “Core section *Macrantha*” in their even spacing and distinct appearance. However, they are more broadly curving than those in the core group. Teeth are ST/ST and CC/CV. The margin has lobations, although they are not as incised as in *A. tschonoskii* and *A. micranthum*.

There is no single leaf character that can be used to place a species in section *Macrantha*. However, there are smaller groups within section *Macrantha* whose species have combinations of characters that can be used to place a species into the group based

on leaf characters, as I have described. Most of the leaves of species that do not belong to section *Macrantha* can be distinguished from the leaves of section *Macrantha*, although this might not be possible for *A. nipponicum*.

Fossil

In order to assign a fossil leaf to *Acer* section *Macrantha*, the margin and the secondary venation need to be preserved. The leaf does not have to be complete, although it would be useful to see the lobes and the apices to provide additional support for the sectional placement. I studied the five fossil species assigned to section *Macrantha* by Wolfe and Tanai (1987) in their review of the North American *Acer* fossil record. I also reviewed the Asian fossil leaves assigned to the section by Tanai and Ozaki (1977), Tanai (1983), and Ozaki (1991). I analyzed the leaves for the vein and margin characters, described in the Materials and Methods chapter, to determine if the fossils could be placed in the modern section *Macrantha*.

Leaves of *A. castorriularis* (Fig. 78) are three-lobed with straight, well-defined medial secondary veins. The margin is not well preserved in the holotype (Wolfe and Tanai, 1987). In one section of the margin near the petiole, there appears to be only one or two teeth along an otherwise entire margin. This is markedly different from the modern species of *Macrantha*, in which the core group all have a finely serrate margin with lots of small teeth. Based on the margin characters shown in this fossil, the species appears closer to section *Parviflora*, than to section *Macrantha*.

Acer palaeorufinerve has only been reported in North America from fossil fruits (Wolfe and Tanai, 1987). The validity of fossil fruit assignments are not addressed here. *Acer palaeorufinerve* leaf fossils were originally described from the Late Miocene of Japan (Tanai and Onoe, 1961). As described in Tanai and Ozaki (1977), *A.*

palaeorufinerve does appear to belong to section *Macrantha*. The leaf has three large lobes and two small basal lobes, all shallowly lobed. The medial secondaries are fairly strong, but the margin does not appear to be well preserved. Ozaki (1991) also placed fossils from the Pliocene of Honshu, Japan in *A. palaeorufinerve*. These leaf remains do seem to belong to section *Macrantha*, although the teeth seem rather large.

Acer uemurae is suggested by Tanai and Ozaki (1977) to be most closely related to *A. micranthum* and *A. tschonokii*. Leaves of *A. uemurae* do resemble the leaves of these modern species in the five medium lobed leaf shape with lobations. There are few medial secondary veins that broadly curve upwards. The margin is finely serrate, similar to the modern species. This species clearly fits into the section *Macrantha*.

Ozaki (1991) refers one Pliocene fossil leaf to the modern species *A. crataegifolium*. Although it is not given a formal name, this leaf does appear to be closely related to *A. crataegifolium*, based on its overall leaf shape and finely serrate margin.

Acer koreanum is a fossil fruit species described by Endo (1950) from a single North Korean specimen. Fruits are not analyzed here, so the placement in section *Macrantha* cannot be evaluated at this time.

Leaves of *A. clarnoense* (Figs. 80, 83), described by Wolfe and Tanai (1987), do not fit into the “Core section *Macrantha*”. The leaves are shallowly 3-lobed, with few, indistinct, broadly curving medial secondary veins. The serrate margin is different from any species in the modern section *Macrantha*. There are very few teeth, even in proportion to the small size of the leaf.

Acer dettermani Wolfe et Tanai (1987) (Fig. 81) does fit into the “Core section *Macrantha*”, although the specimens of this species have fragmentary preservation.

Medial secondary veins are well defined and fairly straight. Portions of the margin that are preserved are finely serrate.

Leaves of *A. latahense* (Figs. 79, 82), described by Wolfe and Tanai (1987), have distinct, straight medial secondary veins and a serrate margin, which may warrant the placement of this species in the “Core section *Macrantha*”. The leaves are shallow to medium three-lobed. However, the margin has larger teeth than the modern species in “Core section *Macrantha*”. The teeth are of the CC/CV shape. The large teeth indicate closer similarity to section *Parviflora* than to section *Macrantha*.

Biogeography

The modern species of *Acer* section *Macrantha* are concentrated in eastern Asia, except for one species in eastern North America. The distribution of each species is given in Table 4.

The leaf fossils that fit into section *Macrantha* based on vein and margin characters are *A. dettermani* from the middle or late Eocene of Alaska, *A. uemurae* from the Late Miocene of Japan, *A. palaeorufinerve* from the Late Miocene and Pliocene of Japan, and *A. crataegifolium* from the Pliocene of Japan. Species placed in section *Macrantha* by Wolfe and Tanai (1987) but excluded here are *A. clarnoense* from the middle to late Eocene of Oregon, *A. castorrivularis* from the latest Eocene of Montana, and *A. latahense* from the early to middle Miocene of Washington and Oregon.

Based on the leaf fossils accepted here, section *Macrantha* dates back to the Eocene in Alaska, with younger occurrences in the Miocene of Japan.

Two possible explanations are suggested by the presence of fossils with “Core section *Macrantha*” leaf characters in only Asia and Alaska. The core group may have diverged in eastern Asia and only recently migrated to North America. This could explain why the modern diversity is higher in Asia in the core group (for example, three species versus one in North America). It is hypothesized that this section has always been limited to North America and Asia. I have not seen any reports of European *Acer* species that I would place in section *Macrantha*. Alternatively, the section could have been present in North America, but represented by species with leaf morphologies different from the modern taxa. The modern leaf characters of straight medial secondary veins with a finely serrate margin may be derived, and therefore the fossils could not be assigned to the modern section *Macrantha*, based on those characters.

Phylogeny

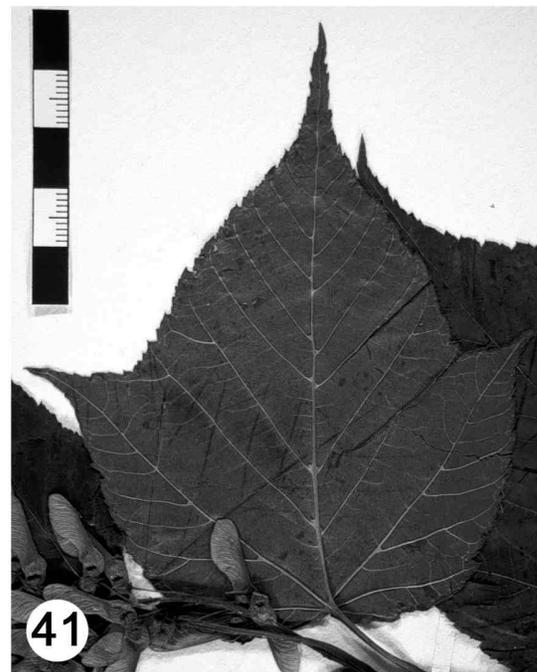
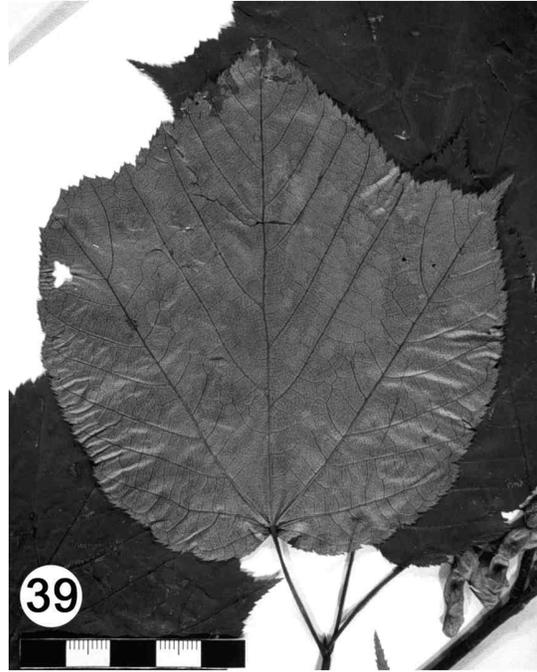
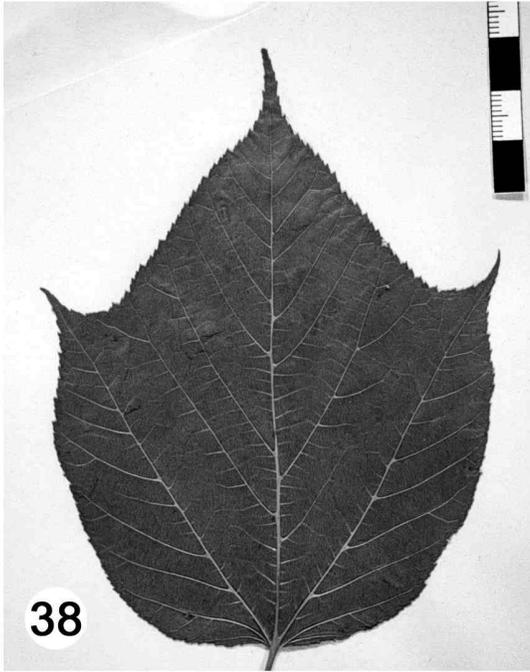
Acer section *Macrantha* is resolved as monophyletic according to Hasebe, Ando, and Iwatsuki (1998), in a molecular study using chloroplast DNA restriction fragment length polymorphisms. However, the resolution of the cladogram is poor because it is the consensus tree of 398 equally parsimonious trees. A significant problem with the Hasebe, Ando, and Iwatsuki (1998) study is their choice of an outgroup, *A. spicatum* and *A. ukurunduense* [*A. caudatum* ssp *ukurunduense* (Traut. & Meyer) Murray]. *Acer spicatum* is nested high in the cladograms in the ITS analysis of Ackerly and Donoghue (1998), not basally as hypothesized by Hasebe, Ando, and Iwatsuki (1998). Ackerly and Donoghue (1998) chose *Dipteronia sinensis* as their outgroup.

Acer section *Macrantha* is paraphyletic in the consensus tree of two most parsimonious trees of Ackerly and Donoghue (1998), although the species *A.*

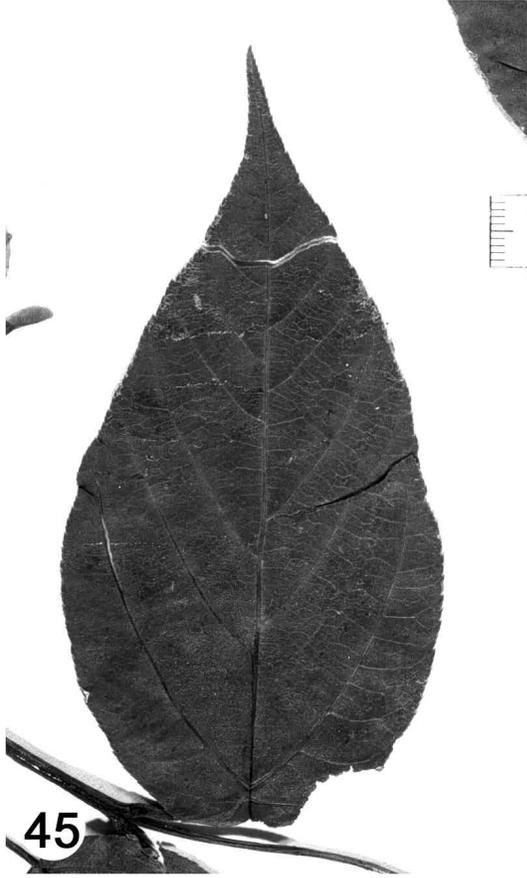
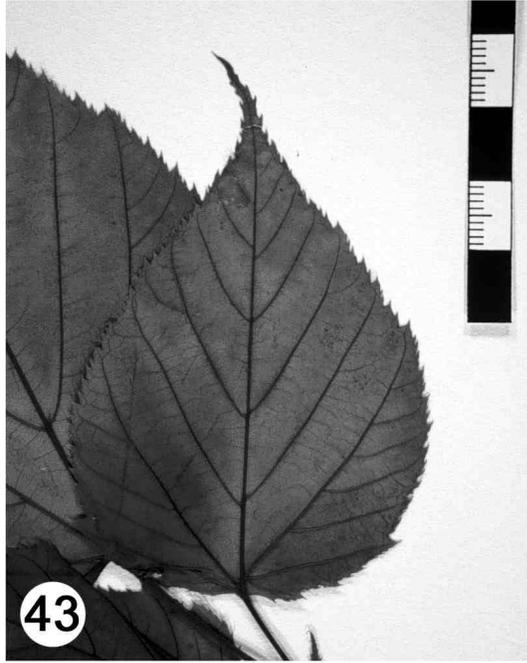
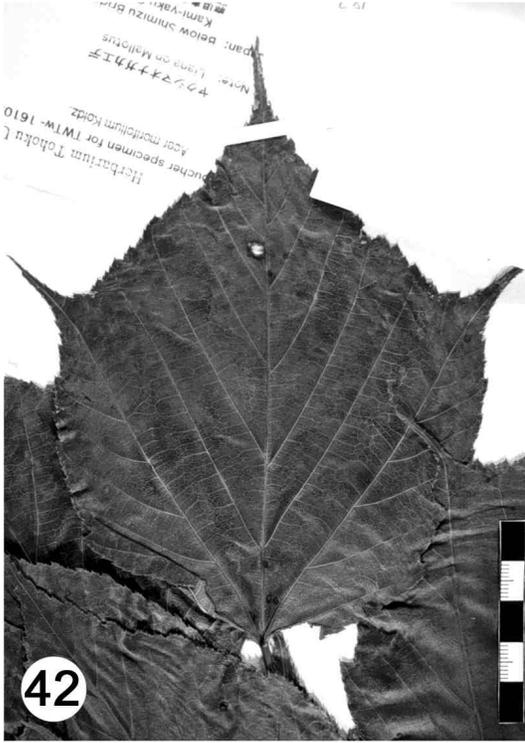
tegmentosum, *A. rufinerve*, *A. crataegifolium*, and *A. pensylvanicum* form a monophyletic group. *Acer tschonoskii* and *A. micranthum* are phylogenetically adjacent, but section *Macrantha* does not form a monophyletic group in their analysis. However, a comprehensive analysis has not yet been undertaken. Future analyses may help to clarify these relationships. It is interesting that Ackerly and Donoghue's (1998) analysis of selected *Acer* species grouped the section *Macrantha* species studied (*A. tschonoskii*, *A. micranthum*, *A. tegmentosum*, *A. rufinerve*, *A. crataegifolium*, and *A. pensylvanicum*) with the sections *Glabra* (*A. glabrum*), *Negundo* (*A. negundo*), *Parviflora* (*A. spicatum*, *A. nipponicum*, and *A. distylum*), and *Ginnala* (*A. ginnala*). With the exception of *A. negundo*, these species all produce palmately lobed simple leaves.

Pax (1902) included *A. nipponicum* [as *A. crassipes* Pax and *A. parviflorum* Franch et Sav.] and *A. caudatum* ssp. *multiserratum* [as *A. erosum* Pax] in his circumscription of section *Macrantha*.

Figures 38-41. Modern *Acer* leaves (scale bar = 1 cm). **38.** *Acer pensylvanicum*, A: I. W. Anderson, August 16, 1915. **39.** *Acer tegmentosum*, A: V. Komarov, 1053. **40.** *Acer rufinerve*, A: T. Azuma et al., 201. **41.** *Acer capillipes*, A: Y. Kadota, 2302.



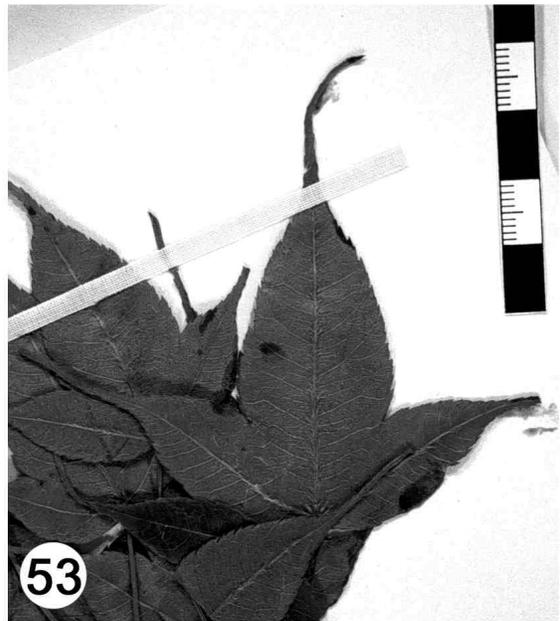
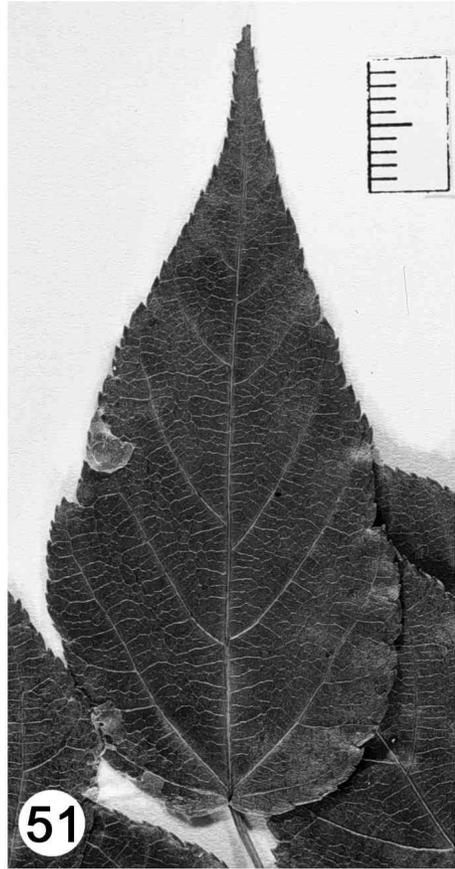
Figures 42-45. Modern *Acer* leaves (scale bar = 1 cm). **42.** *Acer morifolium*, lobed leaf, A: M. Suzuki et al., E462. **43.** *Acer morifolium*, unlobed leaf, A: T. Yahara et al., 9183. **44.** *Acer davidii*, A: Q. X. Wang and J. L. Sun, 13020. **45.** *Acer sikkimense*, A: A. Henry, 10640.



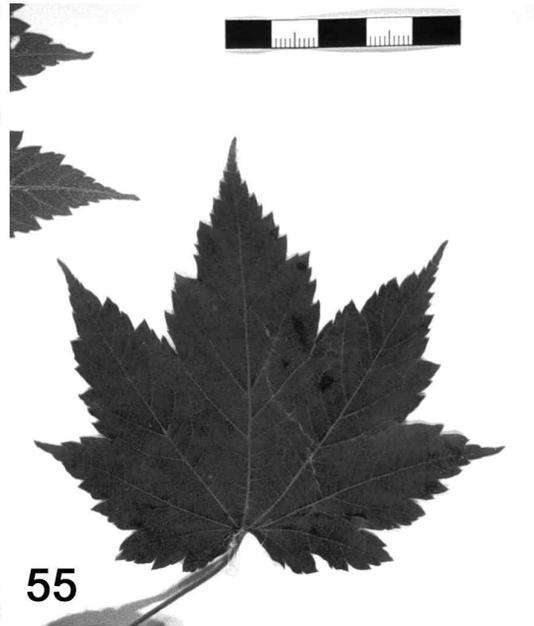
Figures 46-49. Modern *Acer* leaves (scale bar = 1 cm). **46.** *Acer metcalfii*, A: Y. W. Taam, 593. **47.** *Acer rubescens*, A: W.-H. Hu, 1429. **48.** *Acer micranthum*, A: M. Furuse, August 21, 1962. **49.** *Acer tschonoskii*, A: C.-S. Chang, 884.



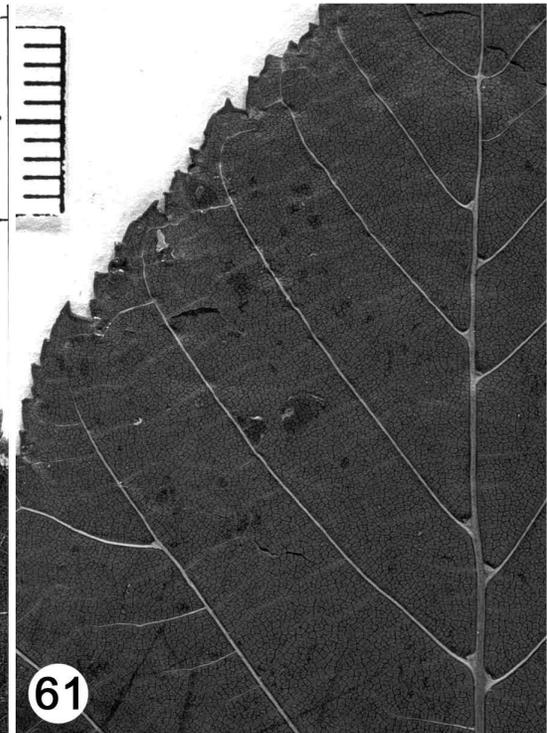
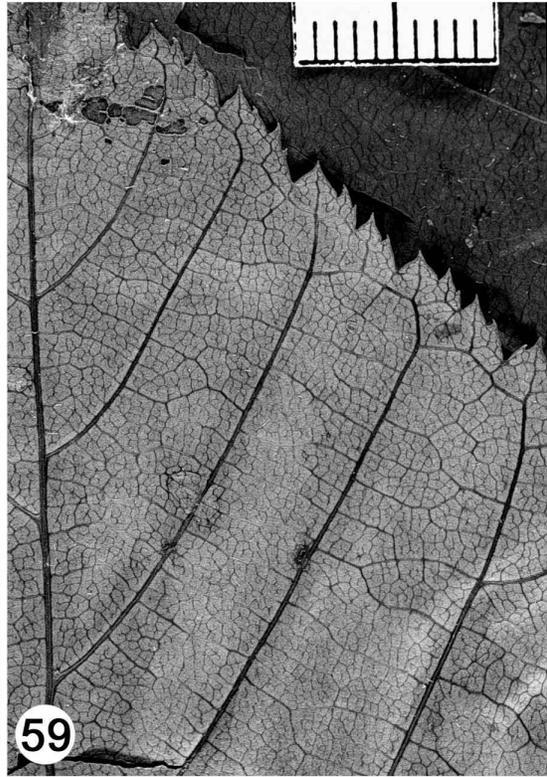
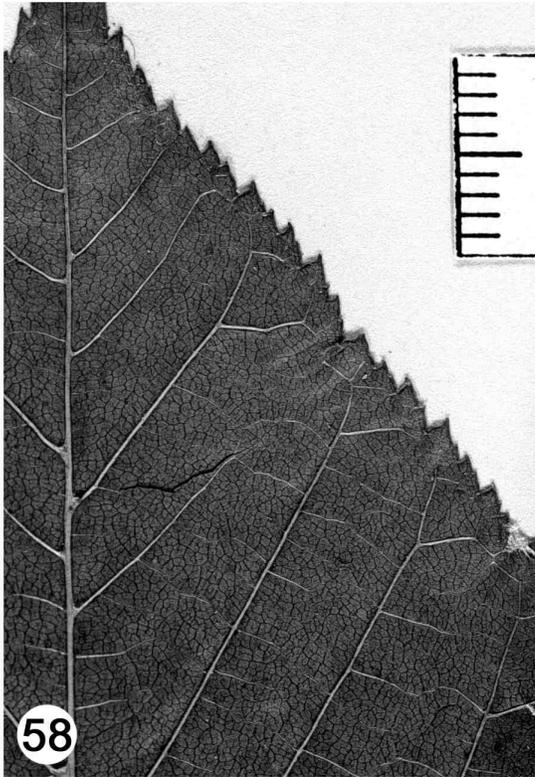
Figures 50-53. Modern *Acer* leaves (scale bar = 1 cm). **50.** *Acer pectinatum*, A: T. T. Yu, 6788. **51.** *Acer caudatifolium*, A: C.-C. Wang, 1052. **52.** *Acer crataegifolium*, A: T. Fukuda et al., 73. **53.** *Acer wardii*, A: T. T. Yu, 22080.



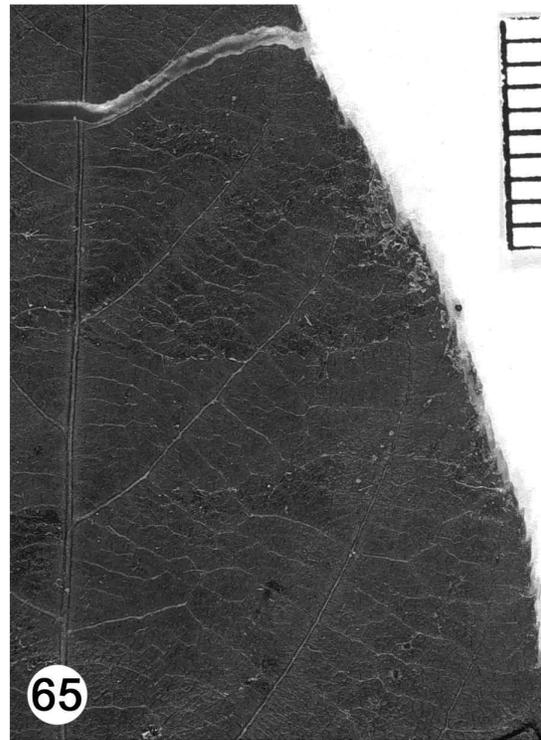
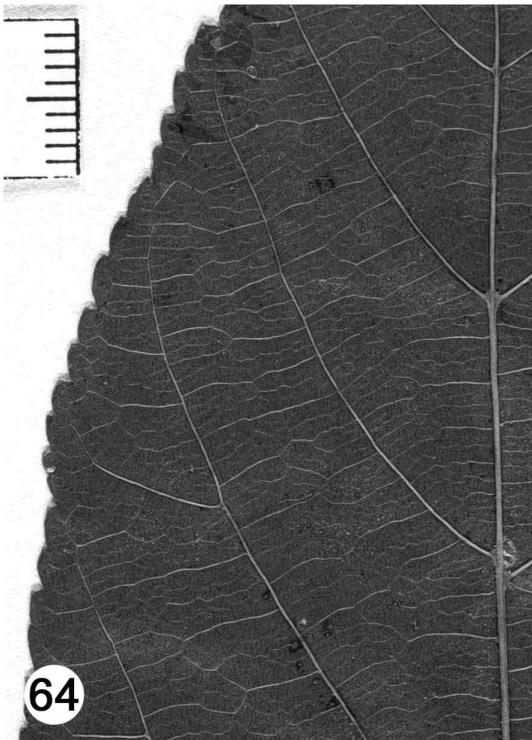
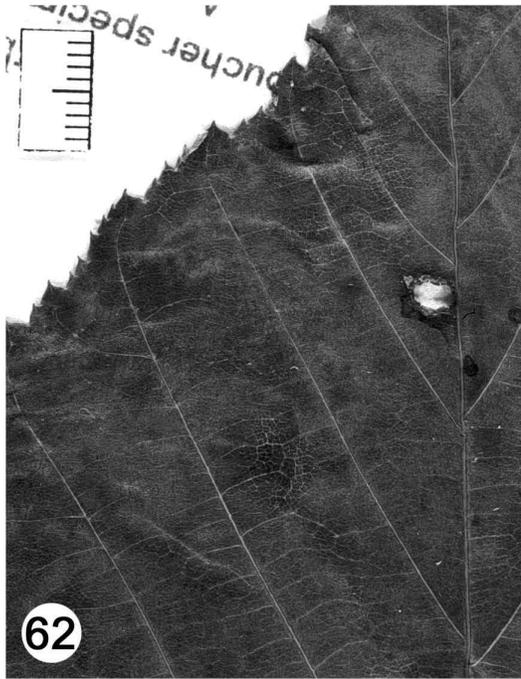
Figures 54-57. Modern *Acer* leaves (scale bar = 1 cm). **54.** *Acer spicatum*, A: E. L. Palmer, 775. **55.** *Acer caudatum* ssp. *ukurunduense*, A: M. Furuse, June 23, 1960. **56.** *Acer nipponicum*, A: S. Suzuki, 398020. **57.** *Acer argutum*, A: Y. Kadota, 2408.



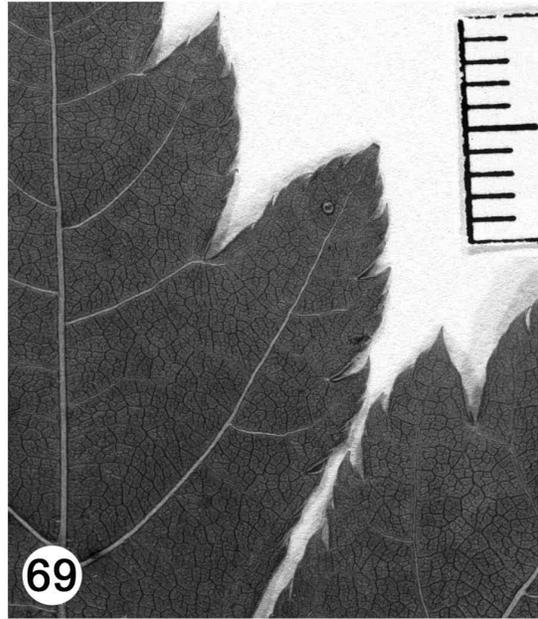
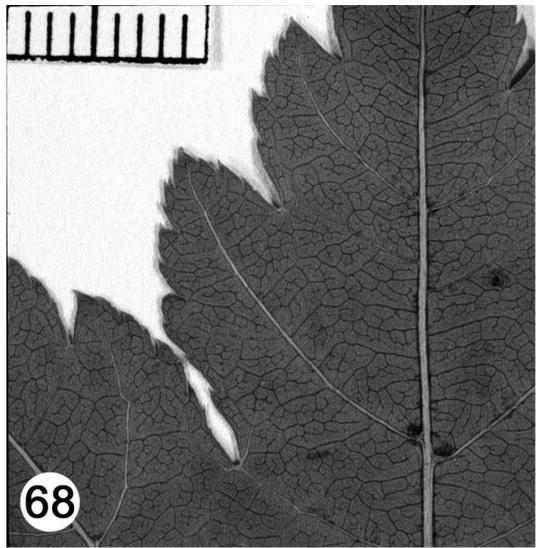
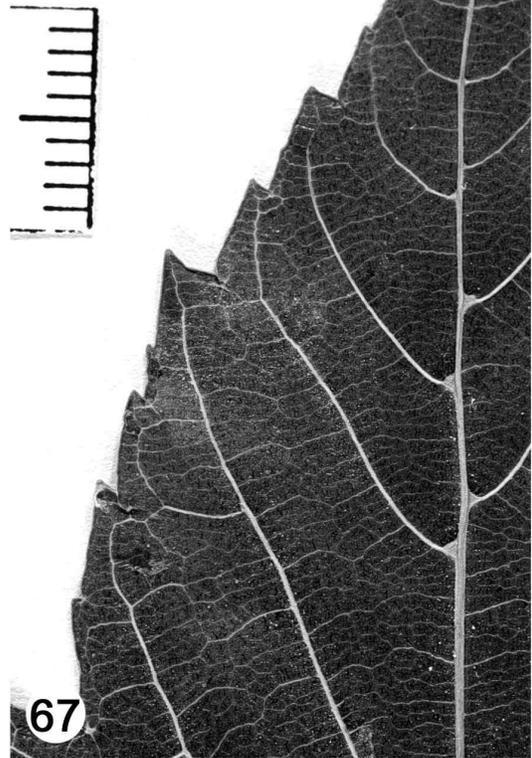
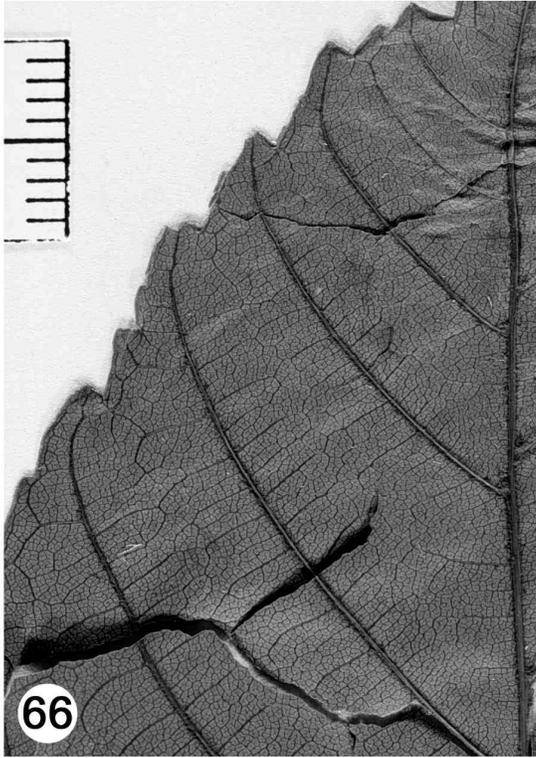
Figures 58-61. Modern *Acer* leaves (scale bar = 1 cm). **58.** *Acer pensylvanicum*, A: I. W. Anderson, August 16, 1915. **59.** *Acer tegmentosum*, A: V. Komarov, 1053. **60.** *Acer rufinerve*, A: T. Azuma et al., 201. **61.** *Acer capillipes*, A: Y. Kadota, 2302.



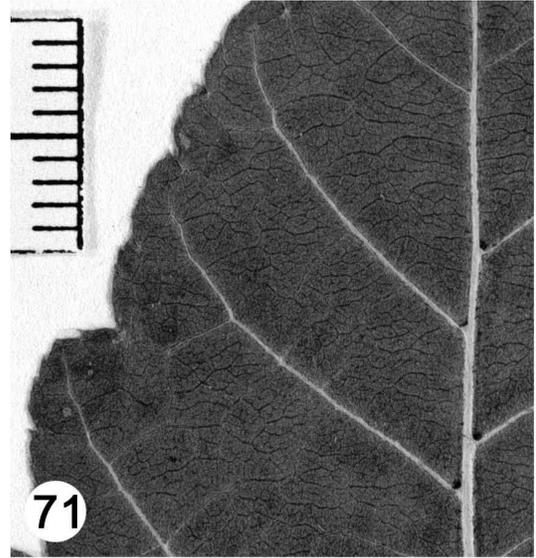
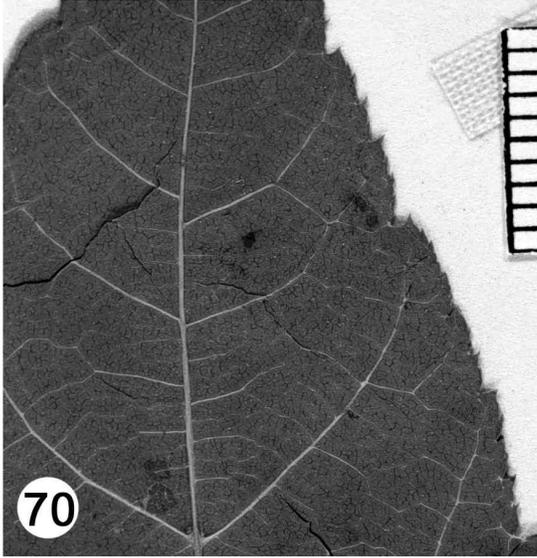
Figures 62-65. Modern *Acer* leaves (scale bar = 1 cm). **62.** *Acer morifolium*, lobed leaf, A: M. Suzuki et al., E462. **63.** *Acer morifolium*, unlobed leaf, A: T. Yahara et al., 9183. **64.** *Acer davidii*, A: Q. X. Wang and J. L. Sun, 13020. **65.** *Acer sikkimense*, A: A. Henry, 10640.



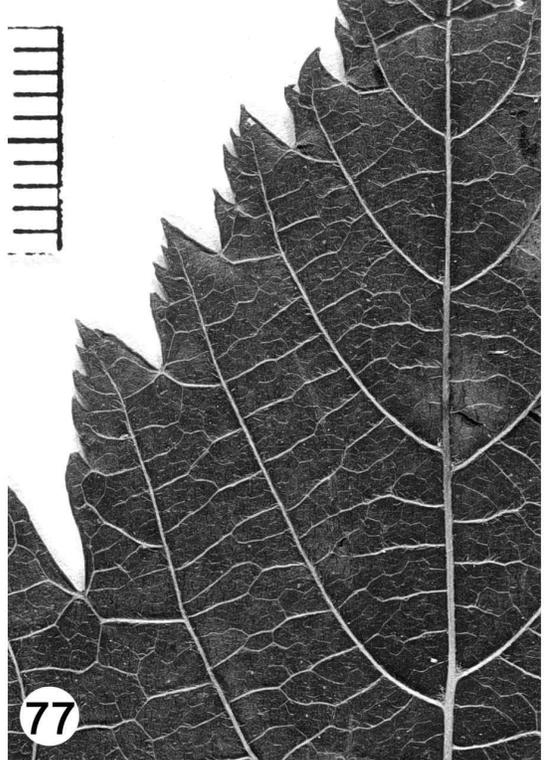
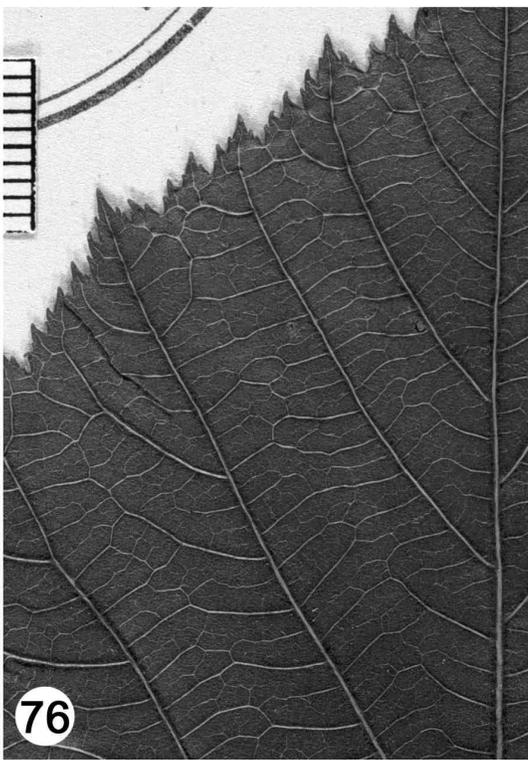
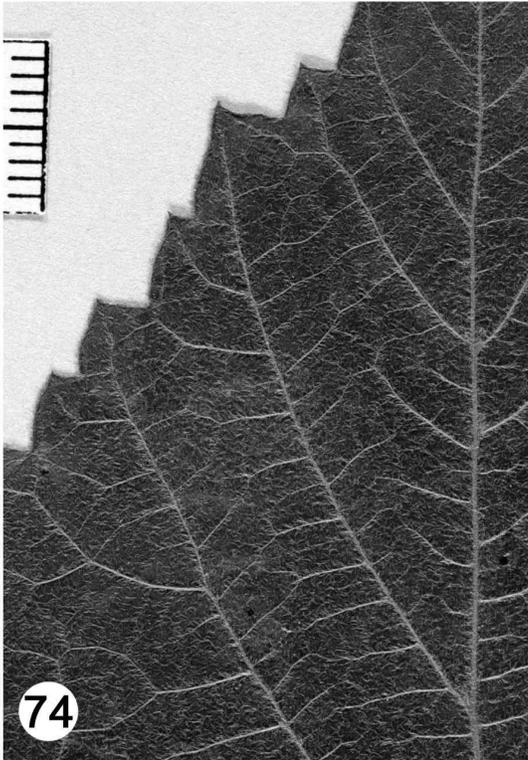
Figures 66-69. Modern *Acer* leaves (scale bar = 1 cm). **66.** *Acer metcalfii*, A: Y. W. Taam, 593. **67.** *Acer rubescens*, A: W.-H. Hu, 1429. **68.** *Acer micranthum*, A: M. Furuse, August 21, 1962. **69.** *Acer tschonoskii*, A: C.-S. Chang, 884.



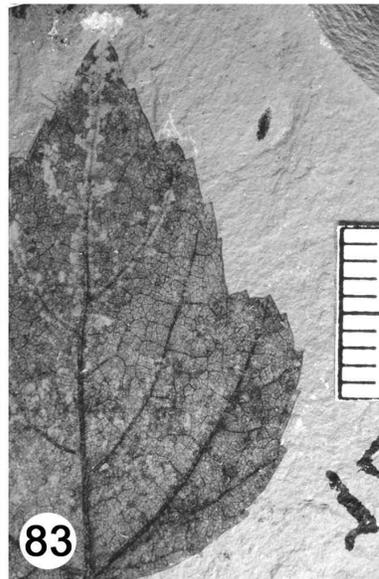
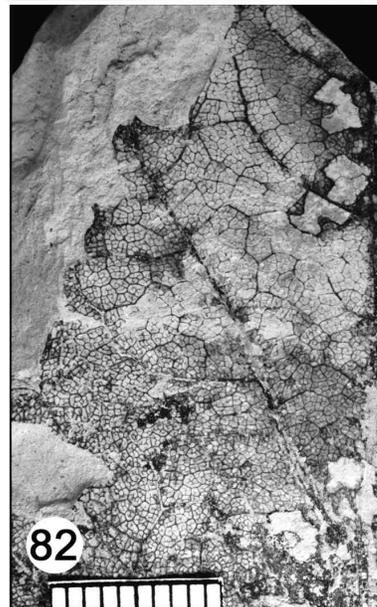
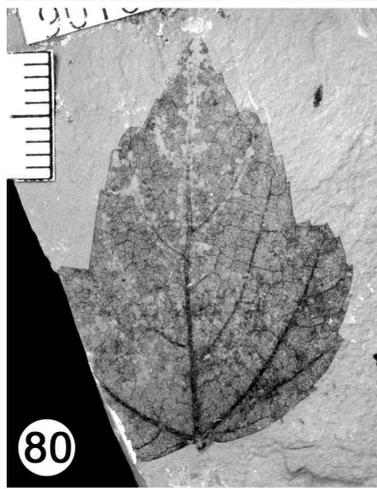
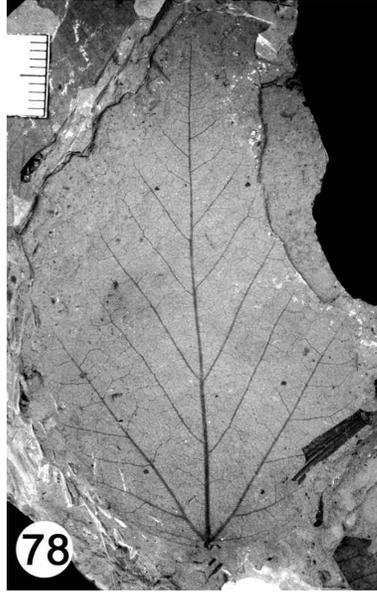
Figures 70-73. Modern *Acer* leaves (scale bar = 1 cm). **70.** *Acer pectinatum*, A: T. T. Yu, 6788. **71.** *Acer crataegifolium*, A: T. Fukuda et al., 73. **72.** *Acer caudatifolium*, A: C.-C. Wang, 1052. **73.** *Acer wardii*, A: T. T. Yu, 22080.



Figures 74-77. Modern *Acer* leaves (scale bar = 1 cm). **74.** *Acer spicatum*, A: E. L. Palmer, 775. **75.** *Acer caudatum* ssp. *ukurunduense*, A: M. Furuse, June 23, 1960. **76.** *Acer nipponicum*, A: S. Suzuki, 398020. **77.** *Acer argutum*, A: Y. Kadota, 2408.



Figs. 78-83. Fossil *Acer* leaves (scale bar = 1 cm). **78.** *Acer castorrivularis*, UCMP 9310. **79.** *Acer latahense*, USNM 396136. **80.** *Acer clarnoense*, UCMP 9010. **81.** *Acer dettermani*, USNM 396034. **82.** *Acer latahense*, USNM 396136. **83.** *Acer clarnoense*, UCMP 9010.



CONCLUSIONS

The fossil records for *Dipteronia* and *Acer* section *Macrantha* are more limited, in my opinion, than reported previously in the literature. The fossil record of *Dipteronia* may be expanded in the future if leaves are confirmed to be diagnostic for the genus.

The *Dipteronia* fossil record, based on fruits, extends from the Paleocene to the Oligocene in North America. *Dipteronia* may have been present in North America earlier or later, but today occurs only in China. The Asian fossil record is unfortunately not as well known. Therefore, the place of origin for *Dipteronia*, the direction of intercontinental migration, and the age of its initial appearance in Asia are unknown.

Leaves remain to be analyzed to determine if they can be reliably be assigned to the genus *Dipteronia*. The leaves could provide additional evidence for the existence of the genus in areas where the fruits are not commonly preserved. This could possibly be important in Asia, where there are no known fossil *Dipteronia* fruits.

In order to determine if a fossil *Acer* leaf fits into section *Macrantha*, the secondary venation and margin need to be preserved. The medial secondary veins in section *Macrantha* are fairly regularly spaced and straight to broadly curved. They generally do not branch until very close to the margin. The margin in leaves of section *Macrantha* is finely serrate, with three or more orders of teeth. The teeth are very small in relation to the size of the leaf, with 5-15 teeth/cm. The teeth are irregularly spaced and many are of the CC/CV shape as defined by the Leaf Angiosperm Working Group (1999).

The remaining modern sections of *Acer* still need to be studied and described in order to determine if these sections are present in the fossil record. Additionally, the fossil sections of *Acer* need to be analyzed to determine if they exhibit characters or sets of characters not present in any modern section. The fossil fruits could also be analyzed in the same way to provide additional evidence and to determine if different organs show the same rates of evolution. It is hoped that by providing a character-based recognition system for leaves of the modern sections, neo- and paleobotanists will be better able to assign *Acer* fossils at the sectional level and, thus, to learn more about the biogeography and evolutionary patterns within the genus.

LIST OF REFERENCES

- Ackerly, D. D., and M. J. Donoghue. 1998. Leaf Size, Sapling Allometry, and Corner's Rules: Phylogeny and Correlated Evolution in Maples (*Acer*). American Naturalist 152: 767-791.
- Akhmetiev, M.A. 1971. Tertiary maples of eastern Asia. Paleontological Journal 5: 362-371.
- Becker, H. F. 1960. Additions to the Tertiary Ruby Paper Shale flora of Southwestern Montana. Bulletin of the Torrey Botanical Club 87: 386-396.
- Becker, H. F. 1961. Oligocene plants from the Upper Ruby River Basin, Southwestern Montana. Geological Society of America Memoir 82: 1-127.
- Berry, E. W. 1929. A revision of the flora of the Latah Formation. U. S. Geological Survey Professional Paper 154-H: 225-265.
- Bestland, E. A., P. E. Hammond, D. L. S. Blackwell, M. A. Kays, G. J. Retallack, and J. Stimac. 1999. Geologic framework of the Clarno Unit, John Day Fossil Beds National Monument, central Oregon. Oregon Geology 61: 3-19.
- Boulter, M. C., J. N. Benfield, H. C. Fisher, D. A. Gee, and M. Lhotak. 1996. The evolution and global migration of the Aceraceae. Philosophical Transactions of the Royal Society of London B, Biological Sciences 351: 589-603.
- Brown, R. W. 1935. Miocene leaves, fruits, and seeds from Idaho, Oregon, and Washington. Journal of Paleontology 9: 572-587.
- Brown, R. W. 1937. Additions to some fossil floras of the Western United States. U. S. Geological Survey Professional Paper 186-J: 163-206.
- Brown, R. W. 1959. A bat and some plants from the Upper Oligocene of Oregon. Journal of Paleontology 33: 125-129.
- Brown, R. W. 1962. Paleocene Flora of the Rocky Mountains and Great Plains. U. S. Geological Survey Professional Paper 375: 1-119.
- Crane, P. R., S. R. Manchester, and D. L. Dilcher. 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte

- Formation (Paleocene) near Almont, North Dakota. Fieldiana Geology, new series, 20: 1-63.
- de Jong, P. C. 1976. Flowering and sex expression in *Acer* L. A biosystematic study. Mededelingen Landbouwhogeschool Wageningen 76: 1-201.
- de Jong, P. C. 1994. Chapter 6 In van Gelderen, D. M., P. C. de Jong, and H. J. Oterdoom. Maples of the world, 69-103. Timber Press, Portland, Oregon, USA.
- Delendick, T. J. 1981. A systematic review of the Aceraceae. Ph. D. thesis, City University of New York, New York.
- Delendick, T. J. 1990. A survey of foliar flavonoids in the Aceraceae. Memoirs of the New York Botanical Garden 54:1-129.
- Endo, S. 1950. On the fossil *Acer* from Japan, Korea, and south Manchuria. Short Papers, Institute of Geology and Paleontology, Sendai 1: 11-17.
- Fang, W.-P. 1939. A monograph of Chinese Aceraceae. Contributions from the Biological Laboratory of the Chinese Association for the Advancement of Science, section botany, 11: 1-346.
- Fang, W.-P. 1966. Revisio taxorum Aceracearum Sinicarum. Acta Phytotaxonomica Sinica 11: 139-189.
- Gadek, P. A., E. S. Fernando, C. J. Quinn, S. B. Hoot, T. Terrazas, M. C. Sheahan, and M. W. Chase. 1996. Sapindales: molecular delimitations and infraordinal groups. American Journal of Botany 83: 802-811.
- Hall, B. A. 1961. The floral anatomy of *Dipteronia*. American Journal of Botany 48: 918-924.
- Hasebe, M., T. Ando, and K. Iwatsuki. 1998. Intrageneric Relationships of maple trees based on the chloroplast DNA restriction fragment length polymorphisms. Journal of Plant Research 111: 441-451.
- Henry, A. 1903. Chinese maples. Gardeners' Chronicle, series III, 33: 21-22, 62-63, 100.
- Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. American Journal of Botany 60: 17-33.
- Hickey, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. Geological Society of America Memoir 150: 1-183.

- Judd, W. S., R. W. Sanders, and M. J. Donoghue. 1994. Angiosperm family pairs: preliminary phylogenetic analyses. Harvard Papers in Botany 1(5): 1-51.
- LaMotte, R. S. 1952. Catalogue of the Cenozoic plants of North America through 1950. Geological Society of America Memoir 51: 1-381.
- Leaf Architecture Working Group. 1999. Manual of Leaf Architecture - morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms. Published privately. Washington, D. C. 1-65.
- MacGinitie, H. D. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Institution of Washington Publication 599: 1-198.
- MacGinitie, H. D. 1974. An early middle Eocene flora from the Yellowstone – Absaroka volcanic province, northwestern Wind River Basin, Wyoming. University of California Publications in the Geological Sciences 108: 1-103.
- Mai, D. H. 1984. Die Endokarprien bei der Gattung *Acer* L. (Aceraceae) – Eine biosystematische Studie. Gleditschia 11: 17-46.
- Manchester, S. R. 1990. Eocene to Oligocene floristic changes recorded in the Clarno and John Day Formations, Oregon, USA. In E. Knobloch and Z. Kvacek [eds.], Symposium Proceedings, paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary, 183-187. Geological Survey Press, Prague, Czech Republic.
- Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. Annals of the Missouri Botanical Gardens 86: 472-522.
- Manchester, S. R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. Oregon Geology 62: 51-63.
- McFadden, J. J. 1986. Fossil flora near Gray Butte, Jefferson County, Oregon. Oregon Geology 48: 51-58.
- Meyer, H. W., and S. R. Manchester. 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. University of California Publications in the Geological Sciences 141: 1-195.
- Momotani, Y. 1962. III. System of Aceraceae. Memoirs of the College of Science; Kyoto Imperial University, series B, biology 29: 177-189.
- Murray, A. E. 1970. A Monograph of the Aceraceae. Ph. D. thesis, Pennsylvania State University.

- Nichols, D. J., and H. L. Ott. 1978. Biostratigraphy and evolution of the *Momipites-Caryapollenites* lineage in the early Tertiary in the Wind River Basin, Wyoming. Palynology 2: 93-112.
- Nichols, D. J., and R. M. Flores. 1993. Palynostratigraphic correlation of the Fort Union Formation (Paleocene) in the Wind River Reservation in the Waltman Area, Wind River Basin, Wyoming. In W. R. Keefer, W. J. Metzger, and L. H. Godwin [eds.], Wyoming Geological Association Special Symposium on Oil and Gas and other resources of the Wind River Basin, Wyoming, 175-189. Pioneer Printing, Cheyenne, Wyoming, USA.
- Ogata, K. 1965. A dendrological study on the Japanese Aceraceae, with special reference to the geographical distribution. Bulletin of the Tokyo University Forests 60: 1-99.
- Ogata, K. 1967. A systematic study of the Aceraceae. Bulletin of the Tokyo University Forests 63: 89-206.
- Oliver, D. 1889. *Dipteronia sinensis*. Hooker's Icones Plantarum, Third series, vol. 9. Plate 1898.
- Ozaki, K. 1991. Late Miocene and Pliocene floras in Central Honshu, Japan. Bulletin of Kanagawa Prefectural Museum Natural Science Special Issue: 1-244.
- Pax, F. 1885. Monographie der Gattung *Acer*. Botanische Jahrbuch 6: 287-347.
- Pax, F. 1886. Monographie der Gattung *Acer*. Botanische Jahrbuch 7: 177-263.
- Pax, F. 1902. Aceraceae. In A. Engler [ed.], Das Pflanzenreich, series IV, 163: 8: 1-89.
- Pojarkova, A. I. 1949. Aceraceae. Flora USSR 14: 443-476 (English translation by Israel Program for Scientific Translation, Jerusalem).
- Smith, G. A., S. R. Manchester, M. Ashwill, W. C. McIntosh, and R. M. Conrey. 1998. Late Eocene-early Oligocene tectonism, volcanism, and floristic change near Gray Butte, central Oregon. Geological Society of America Bulletin 100: 759-778.
- Stockey, R. A., and W. C. Wehr. 1996. Flowering Plants in and around Eocene Lakes of the Interior. In R. Ludvigsten [ed.], Life in stone, a natural history of British Columbia's fossils, 234-247. UBC Press, Vancouver, British Columbia, Canada.
- Tanai, T. 1978. Taxonomical investigation of the living species of the genus *Acer* L., based on vein architecture of leaves. Journal of the Faculty of Science, Hokkaido University, series IV, 18: 243-282.

- Tanai, T. 1983. Revisions of Tertiary *Acer* from East Asia. Journal of the Faculty of Science, Hokkaido University, series IV, 20: 291-390.
- Tanai, T., and Onoe, T. 1961. A Mio-Pliocene flora from the Ningyotoge area on the border between Tottori and Okayama Prefecture, Japan. Geological Survey of Japan Report 187: 1-62.
- Tanai, T., and K. Ozaki. 1977. The Genus *Acer* from the Upper Miocene in Tottori Prefecture, Western Japan. Journal of the Faculty of Science Hokkaido University, series IV, 17: 575-606.
- Tiffney, B. H. 1994. An estimate of the early Tertiary paleoclimate of the southern Arctic. In M. C. Boulter and H. C. Fisher, [eds.], *Cenozoic plants and climates of the Arctic*, 267-295. Springer-Verlag, New York, New York, USA.
- van Gelderen, D. M., P. C. de Jong, and H. J. Oterdoom. 1994. *Maples of the world*. Timber Press, Portland, Oregon, USA.
- Walther, H. 1972. Studien über tertiäre *Acer* Mitteleuropas. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie 19: 1-309.
- Wehr, W. 1995. Early Tertiary flowers, fruits and seeds of Washington State. Washington Geology 23: 3-16.
- Wing, S. L. 1994. Fossil plant localities. In T. M. Bown, K. D. Rose, E. L. Simons, and S. L. Wing, [eds.], *Distribution and stratigraphic correlation of Upper Paleocene and Lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman Formations, southern Bighorn Basin, Wyoming*. U. S. Geological Survey Professional Paper 1540: 1-103.
- Wolfe, J. A., and T. Tanai. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of western North America. Journal of the Faculty of Science of Hokkaido University, series IV, 22: 1-246.
- Wolfe, J. A., and W. Wehr. 1987. Middle Eocene dicotyledonous plants from Republic, Northeastern Washington. U. S. Geological Survey Bulletin 1597: 1-25.
- Ying, T.-s., Y.-l. Zhang, and D. E. Boufford. 1993. *The endemic genera of seed plants in China*. Science Press, Beijing, P. R. China.

BIOGRAPHICAL SKETCH

Amy Marie McClain was born in Lansing, Michigan, on July 22, 1976. She graduated from Michigan State University with a Bachelor of Science in botany and plant pathology in 1998. Her positive undergraduate research experience and encouragement from many people in the Department of Botany and Plant Pathology led her to pursue a master's degree. Her interest in studying evolution through the fossil record brought her to the University of Florida to work with Steven Manchester and David Dilcher. She will continue her research on modern and fossil *Acer* as a doctoral student with Dr. Steven Manchester in the Department of Botany at the University of Florida.