

# The McAbee flora of British Columbia and its relation to the Early–Middle Eocene Okanagan Highlands flora of the Pacific Northwest<sup>1</sup>

Richard M. Dillhoff, Estella B. Leopold, and Steven R. Manchester

**Abstract:** Megafossils and pollen data are used to compare the flora found at the McAbee site, located near the town of Cache Creek, British Columbia, to six other well-collected Eocene lacustrine floras of Washington and western British Columbia. A diverse flora is found at McAbee consisting of at least 87 taxa. Gymnosperms are common, including sixteen separate species, 14 conifers and two ginkgos. A minimum of 67 angiosperm genera are represented in the flora, many yet to be described. The dominant dicotyledonous elements of the leaf assemblage at McAbee include *Fagus* (also represented by nuts and cupules) with *Ulmus* and representatives of the Betulaceae, especially *Betula* and *Alnus*. The confirmation of *Fagus*, also rarely found from sites at Princeton, British Columbia, and Republic, Washington, provides the oldest well-documented occurrence of the genus, predating the Early Oligocene records of *Fagus* previously reported for North America, Asia, and Europe. Data provided by pollen analysis broadens our knowledge of the McAbee flora. Angiosperm pollen typically predominates over gymnosperms with the Ulmoideae and Betulaceae being the most common angiosperm pollen types. Members of the Pinaceae dominate the gymnosperm pollen record. Paleoclimatic estimates for McAbee are slightly cooler than for the Republic and Princeton localities and thermophilic elements, such as *Sabal* found at Princeton or *Ensete* and Zamiaceae found at Republic are not known from McAbee.

**Résumé :** Les données provenant de mégafossiles et de pollens sont utilisées pour comparer la flore trouvée au site McAbee, à proximité de la ville de Cache Creek en Colombie-Britannique, à celles de six autres bonnes collections de flores lacustres éocènes de l'État de Washington et de l'ouest de la Colombie-Britannique. McAbee présente une flore diversifiée comprenant au moins quatre-vingt-sept taxons. Les gymnospermes y sont fréquemment trouvées, incluant seize espèces distinctes, quatorze conifères et deux ginkgos. Au moins soixante-sept genres d'angiospermes sont représentés dans la flore, dont plusieurs restent à décrire. Les éléments dicotylédones dominants de l'assemblage des feuilles à McAbee comprennent *Fagus* (aussi représenté par des noix et des cupules) et *Ulmus* et des représentants des Bétulacées, surtout *Betula* et *Alnus*. La confirmation de *Fagus*, aussi rarement trouvé à des sites à Princeton, Colombie-Britannique et Republic, Washington, fournit les plus anciennes occurrences bien documentées du genre, précédant les premiers enregistrements oligocènes de *Fagus* antérieurement rapportés pour l'Amérique du Nord, l'Asie et l'Europe. Les données fournies par les données d'analyse de pollen élargissent nos connaissances de la flore McAbee. Le pollen d'angiosperme prédomine typiquement sur les gymnospermes, les Ulmoïdées et les Bétulacées étant les types de pollens angiospermes les plus fréquents. Les membres des Pinacées dominent les pollens de gymnospermes. Les estimés paléoclimatiques pour McAbee sont légèrement plus froids que pour les localités de Republic et de Princeton et les éléments thermophiles tels que *Sabal*, trouvé à Princeton, ou *Ensete* et les Zamiacées, trouvés à Republic, ne sont pas connus à McAbee.

[Traduit par la Rédaction]

## Introduction

The fossil plants from British Columbia were first described by the members of the Geological Survey of Canada (Dawson 1890; Penhallow 1908). Botanical studies at that time focused primarily on the stratigraphic value of fossil

plants. The notion that the Paleogene deposits containing fossil plants from the interior of British Columbia were related is not exactly new. Lambe (1906), who made the collections studied by Penhallow, commented: “the view already expressed that the Tertiary shales of Horsefly, Tranquille, and Similkameen rivers are probably of the same age is sub-

Received 9 March 2004. Accepted 8 September 2004. Published on the NRC Research Press Web site at <http://cjes.nrc.ca> on 11 March 2005.

Paper handled by Associate Editor J. Jin.

**R.M. Dillhoff.**<sup>2</sup> Evolving Earth Foundation, P.O. Box 2090, Issaquah, WA 98027, USA.

**E.B. Leopold.** University of Washington, Department of Biology, Box 351800, Seattle, WA 98195-1800, USA.

**S.R. Manchester.** Paleobotany, Florida Museum of Natural History, Dickinson Hall, P.O. 117800, University of Florida, Gainesville, FL 32611-7800, USA.

<sup>1</sup>This article is one of a selection of papers published in this Special Issue on *The Okanagan Highlands: Eocene biota, environments, and geological setting*.

<sup>2</sup>Corresponding author (e-mail: [rdillhoff@evolvingearth.org](mailto:rdillhoff@evolvingearth.org)).

stantiated. That the fish and plant bearing beds in the vicinity of Quilchena have a similar age is probable”.

More recent work by Wolfe and Wehr (1987, 1991), Wehr and Schorn (1992), Wehr and Manchester (1996) at Republic, Washington and Basinger (1976, 1981), Stockey (1984), Cevallos-Ferriz and Stockey (1990), Erwin and Stockey (1994), and Stockey and Wehr (1996) at Princeton, British Columbia, focused on the botanical and paleoecological evidence these floras provide. Wehr and Schorn (1992) first applied the term “Okanagan Highlands” in print, discussing the relationship of the conifers found at Republic to those found at Princeton. The hypothesis that these localities are close in age is supported by floristic similarities and radiometric data. An understanding of the plants composing these fossil assemblages, and data on the similarities and differences among these floras, may provide important insights into regional flora and climate of the Pacific Northwest during the warmest climate interval of the Paleogene.

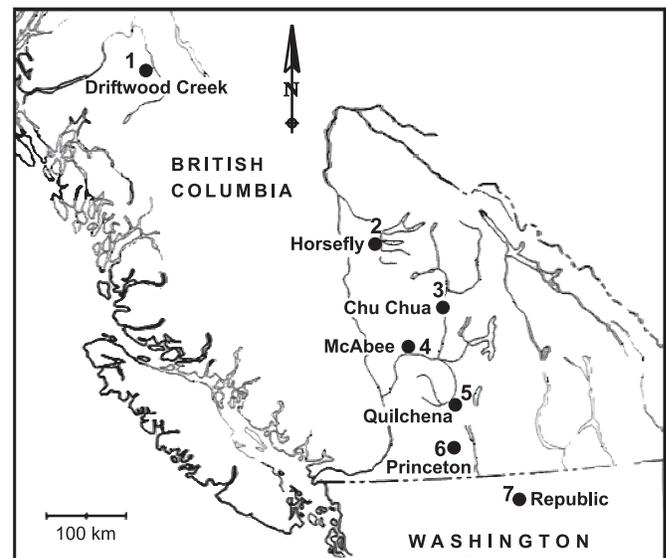
For the past eight years, we have extensively collected the McAbee flora near Cache Creek, British Columbia. Very little has been published specifically regarding the McAbee locality. It apparently escaped the notice of early workers as the first printed mention was Hills and Baadsgaard’s (1967) radiometric dating. The first published mention of fossils at McAbee was Wilson’s (1977) treatment of Middle Eocene fish from British Columbia. In this report, we will describe the flora found at McAbee based on data from both megafossils and pollen. From that information we may infer the floral structure and paleoecology of the late Early Eocene McAbee forest. We will then compare McAbee to six of the Okanagan Highlands localities that have been well enough described to provide detailed floral information (See Fig. 1).

## Geology and age of deposits

McAbee fossils are preserved as impressions and carbonaceous films in siliceous shale. The shale was deposited as diatomite (Mustoe 2005), which has been diagenetically altered. The McAbee fossil beds consist of 30 m of fossiliferous shale within an unnamed formation of the lower to middle Eocene Kamloops Group. The shale beds are capped by flow breccia and sit atop an ash-flow tuff. Tephra deposits bracketed by fossiliferous layers yielded K–Ar dates of  $49 \pm 2$  and  $52 \pm 2$  Ma from plagioclase and  $51 \pm 2$  Ma from biotite contained within a bentonitic tuff (Ewing 1981). These dates generally support the interpretation of a late Early Eocene age.

The determination that McAbee fossils were originally preserved in diatomite likely explains their preservation of fine details. A recent study of Late Eocene fossils from Florissant, Colorado (O’Brien et al. 2002) determined that those fossils were preserved within the diatomaceous component of paired couplets, which represent varves. Using scanning electron microscopy (SEM) studies the authors found evidence that diatom mats trapped floating debris and were deposited with the fossilized organisms, resulting in the preservation of fine detail at that locality. Attempts to investigate McAbee shale for a similar mechanism using SEM techniques have not yielded good results. The recrystallization of silica within the diatomite has resulted in the loss of detail at high-level magnification.

Fig. 1. Okanagan Highlands localities included in floral comparison.



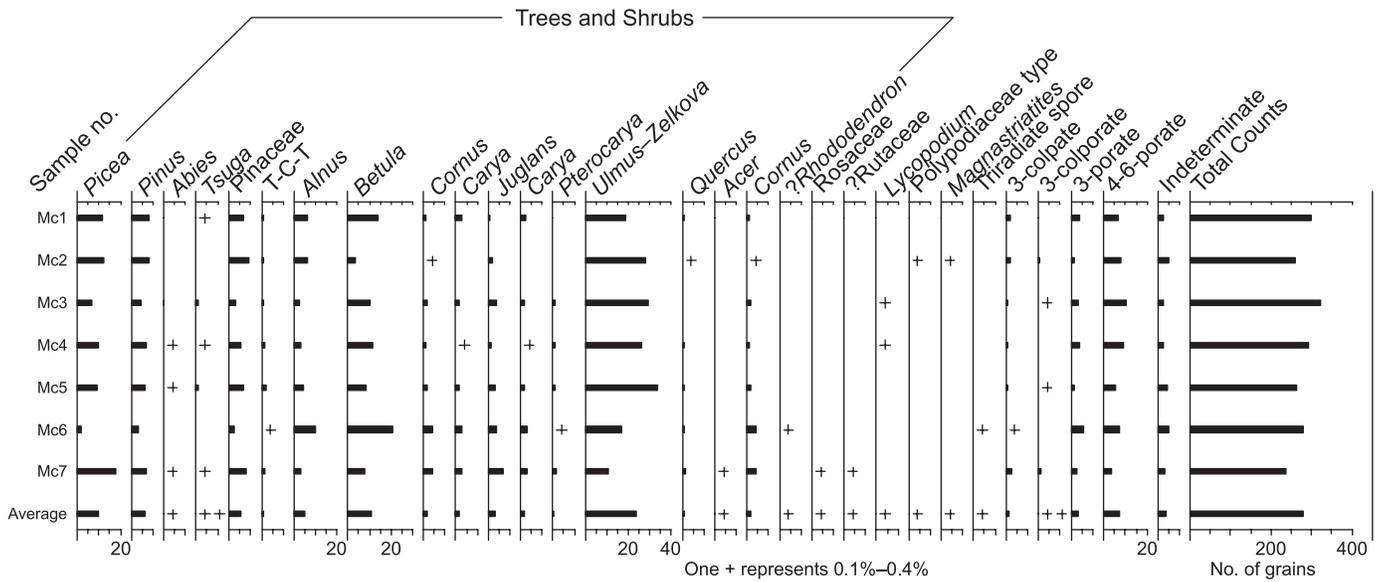
The presence of diatomite also helps to delineate the depositional environment, arguing for deep-water deposition in a substantial body of water. In modern freshwater depositional settings, diatomite does not form in the presence of significant inputs of terrigenous sediments. Wilson (1980) used the taphonomy of fish, insect, and plant remains to establish depth and distance from shore for deposits at Horsefly and Princeton. Using his construct, McAbee also appears to have been a deep-water environment based on the fact that fish remains are typically articulated, Dipteran insects are common and typically complete, and angiosperm leaves are abundant. This analysis is not unequivocal, however. The abundant bibionid flies and taxodiaceous remains at McAbee are consistent with near-shore deposition in Wilson’s model.

## Materials and methods

The McAbee site is located east of the town of Cache Creek at N50°47.818'; W121°08.568'; elevation ~650 m. Field collections made each year since 1996 provided most of the specimens used in this study. Additional material was examined at the University College of the Cariboo in Kamloops, British Columbia; The Geological Survey of Canada and The Canadian Museum of Nature in Ottawa, Ontario; the Royal Tyrrell Museum in Drumheller, Alberta; The University of Saskatchewan in Saskatoon, Saskatchewan; the Thomas Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, and additional private collections. Specimens and samples used in this study are deposited at the University of Washington, the Burke Museum (UWBM) and the University College of the Cariboo Institute for Paleontological Research (UCCIPR). Fossils are typically preserved as impressions and carbonaceous films. Leaves and fruits from exceptional specimens have excellent surface features and display detail of higher order venation, teeth, and other delicate structures. Compressed remains with well-preserved cuticle have not been found.

Pollen samples were taken at seven stratigraphic horizons ~3 m apart near the center of the deposit, with the first sample

**Fig. 2.** Eocene McAbee pollen diagram (% total pollen and spores) Cache Creek, British Columbia: measured section.



in near contact with the overlying basalt. A second sample set was taken from the bottom of a collecting pit in the middle of the series, and generally unsuccessful attempts were also made at direct extraction from preserved floral parts. Samples were crushed to pea-sized particles and placed in HCl for removal of carbonates. Treatment in HF was followed by washes with weak HCl. Schultze's solution was followed by weak KOH wash. Palynomorph preparations were made with standard techniques, following methods described by Doher (1980). Slides were mounted in glycerin jelly and residues saved in vials. Counts ranged from ~360 grains for the best materials with abundant pollen to as low as 180 for the poorest samples. Composition of spectra as shown in pollen diagrams (Figs. 2 and 3) represents percent of total pollen and spores. It should be noted that the preservation of the McAbee pollen and spores was in general only fair.

### Diversity of the McAbee flora based on fossil leaves and fruits

The identified taxa for McAbee based on megafossils include two ginkgos, 13 conifers, and 30 angiosperms, although they do not reflect the total diversity present. McAbee specimens often lack microscopic details or preserved cuticle, which can add critical diagnostic features. In many cases, a few unique specimens with particularly detailed preservation were the key to identification out of hundreds examined. Careful collecting over the last eight years has resulted in the discovery of many additional unidentified taxa. These rare taxa often lack the critical details necessary to make generic determinations, but they should be included when considering total floral diversity.

To achieve a better measure of diversity by the inclusion of unidentified taxa, the flora was characterized using the morphotyping system detailed in the Manual of Leaf Architecture (Wing et al. 1999). In this process, generic assignment is deferred but morphological and architectural details are used to separate taxa. Using this measure, we recognize two ginkgos and 14 conifers, only slightly affecting the gymno-

sperm diversity. Additional recorded conifer reproductive structures correspond with known foliage types, at least to the generic level. The effect on angiosperm diversity counts is much more dramatic. A total of at least 62 different leaf morphotypes and an additional 28 types of angiosperm reproductive structures are recorded from the flora. Thirteen of the genera known from floral parts are already included in the identified genera, but a slightly larger number remain unassigned and could represent taxa not found as leaves.

Given this information, a diversity range can be constructed. Adding equisetum, an unassigned fern and monocot, and assuming that all unassigned reproductive structures match with leaf species, the most conservative diversity estimate from megafossils would be 81 individual species. If it is assumed that two species of *Ulmus* are present, and that all the unassigned reproductive structures represent additional genera, the number rises to 97 taxa. The addition of pollen data raises the range to a minimum of 87 and as many as 103 possible species.

### Diversity of the flora based on the pollen record

A study of the pollen preserved at McAbee adds two important dimensions to the record, taxonomic and quantitative. One additional conifer, *Tsuga*, and five additional angiosperm genera: *Quercus*, *Carya*, *Juglans*, *Pterocarya*, and *Corylus*-type have been identified only from pollen remains. Pollen has also been useful for confirmation of genera identified from megafossil specimens in some cases. More importantly, pollen evidence can be used quantitatively to better understand the composition of the flora. Accurate sampling of megafossils for proportional representation is difficult and time consuming. Pollen sampling provides an alternate method for estimating relative abundance of the wind-pollinated genera that typically dominate temperate forests.

The stratigraphic pollen sample adds an important dimension to the megafossil data. The pollen diagram (Fig. 2) shows that although the percentage varied substantially, an-

**Table 1.** McAbee pollen count for measured section.

Samples:	Mc1	Mc2	Mc3	Mc4	Mc5	Mc6	Mc7	Average (%)
<b>Gymnosperm total</b>	83	79	53	69	65	21	84	26.8
<i>Picea</i>	35	32	21	28	24	5	43	11.1
<i>Pinus</i>	24	21	15	20	16	9	17	7.1
<i>Abies</i>	0	0	1	1	1	0	1	0.2
<i>Tsuga</i>	1	0	3	1	2	0	1	0.5
Pinaceae	20	24	10	15	17	6	19	6.6
TCT	3	2	3	4	5	1	3	1.2
<b>Angiosperm total</b>	133	105	165	137	145	167	98	55.0
<i>Alnus</i>	18	16	8	10	11	28	8	5.8
<i>Betula</i>	41	9	34	34	22	57	19	12.4
<i>Corylus</i> -type	4	1	5	4	4	11	10	2.3
? <i>Carpinus</i>	8	0	6	1	5	8	7	2.0
<i>Juglans</i>	3	5	13	5	9	10	16	3.6
<i>Carya</i>	1	1	2	1	1	2	1	0.5
<i>Pterocarya</i>	0	0	3	3	3	1	4	0.8
<i>Ulmus–Zelkova</i>	56	72	94	77	88	47	25	26.4
<i>Quercus</i>	2	1	0	2	2	2	4	0.8
Rosaceae	0	0	0	0	0	0	1	0.1
?Rutaceae	0	0	0	0	0	0	1	0.1
<i>Cornus</i>	0	0	0	0	0	0	1	0.1
<i>Acer</i>	0	0	0	0	0	0	1	0.1
<i>Rhododendron</i> -type	0	0	0	0	0	1	0	0.1
<b>Pteridophyte total</b>	0	2	1	1	0	1	0	0.3
<i>Lycopodium</i>	0	0	1	1	0	0	0	0.1
Polypodiaceae-type	0	1	0	0	0	0	0	0.1
<i>Magnastriatites</i>	0	1	0	0	0	0	0	0.1
Triradial spore	0	0	0	0	0	1	0	0.1
<b>Undetermined angiosperm total</b>	37	30	47	39	21	37	24	13.6
3-colpate	6	5	2	2	2	1	7	1.5
3-colporate	0	1	1	0	1	0	3	0.4
3-porate	12	4	11	11	4	16	6	3.7
4–6-porate	19	20	33	26	14	20	8	8.0
<b>Indeterminate</b>	8	14	9	8	12	15	8	4.4
<b>Total tally</b>	216	186	219	207	210	189	182	100.0

Note: Average (%) based on total pollen and spores.

giosperm pollen predominated over gymnosperms at all of the seven sample horizons. The most common angiosperm pollen taxa are Ulmaceae (*Ulmus–Zelkova*) and Betulaceae, consistent with their abundance as megafossils (Table 1). Juglandaceous pollen is present in every sample composed primarily of *Pterocarya* and *Juglans*, but *Carya* also appears as a rare element in some samples. Although juglandaceous genera are a significant portion of the pollen rain, they have yet to be found as megafossils. Like their modern counterparts, fossil juglandaceous genera were presumably efficient pollen dispersers. *Picea* pollen predominates over *Pinus* among gymnosperms with much smaller percentages of other Pinaceae and Taxodiaceous pollen designated TCT since these grains may represent Taxodiaceae, Cupressaceae, or Taxaceae.

The second pollen sample set (Table 2, Fig. 3) taken from

the bottom of a collecting pit shows higher conifer values than the average stratigraphic sample. Pollen counts for the four samples are shown in Table 2, and their average values are shown on the right. *Pinus* predominated over *Picea* in this case, accounting for nearly one quarter of the grains observed. The most common angiosperm pollen type in the pit sample is the Ulmoideae, comprising approximately 40% of the count. The 4–5-pored pollen is assigned to *Ulmus–Zelkova* type, and the 3-pored pollen to Ulmaceae. Other *Ulmoideipites* are poorly preserved types. Betulaceae includes several temperate types, *Betula*, *Alnus*, *Corylus*-type, and *Ostrya–Carpinus*, in that order of importance. *Corylus* type may represent the extinct genus *Palaocarpinus*, based on in situ coryloid pollen recovered from aments found at localities near Republic (Pigg et al. 2003).

**Table 2.** McAbee pollen count for pit samples.

Samples:	McA 2-II	McA 3-II	McA 5-II	McA 7-II	Average (%)
<b>Gymnosperm total</b>	100	87	164	147	40.7
<i>Pinus</i>	65	57	83	89	24.0
<i>Picea</i>	14	16	51	34	9.4
<i>Abies</i>	2	0	2	2	0.5
<i>Tsuga</i>	0	0	1	0	0.1
TCT	3	1	1	1	0.5
Pinaceae	16	13	26	21	6.2
<b>Angiosperm total</b>	135	128	175	158	48.7
<i>Alnus</i>	1	1	0	2	0.3
<i>Betula</i>	4	7	24	9	3.6
<i>Carpinus–Ostrya</i>	3	4	5	6	1.5
<i>Juglans</i>	2	1	2	4	0.7
<i>Pterocarya</i>	3	0	4	3	0.8
? <i>Carya</i>	0	0	0	1	0.1
<i>Quercus</i>	3	2	1	1	0.6
<i>Ulmus</i>	112	101	126	122	37.7
<i>Ulmus</i> (3p)	2	4	7	6	1.6
<i>Ulmoideipites</i>	3	2	1	3	0.7
3-colpate	0	1	1	1	0.2
3-colporate	0	2	0	0	0.2
3-porate	2	3	4	0	0.7
<b>Pteridophyte total</b>	0	0	1	0	0.1
Polypodiaceasporites sp.	0	0	1	0	0.1
<b>Others (ungrouped) total</b>	32	21	28	48	10.5
<i>Inaperturopollenites</i> sp.	7	1	1	0	0.7
Unknown pollen	4	3	1	3	0.9
Undetermined pollen	8	3	8	2	1.7
Indetermined pollen	13	14	18	43	7.2
<b>Total tally</b>	267	236	368	353	100.0
<b>Miscellaneous total</b>	30	32	43	52	
Algae (granulate)	14	21	30	36	
Algae (smooth)	16	10	13	14	
Fungal spores	0	1	0	2	

**Note:** Average (%) based on total pollen and spores.

Pollen of Fagaceae is rare. *Fagus* was not recovered using standard processing techniques, in spite of common occurrence of *Fagus* megafossils, and only a few *Quercus* pollen grains are present. Use of an alternate pollen preparation method for another study that did not employ Schultz solution and KOH resulted in the recovery of recognizable *Fagus* pollen (Manchester and Dillhoff 2004). Many unidentifiable dicot grains are present; some are placed in morphological categories, 3-pored, 4-pored, and so on, and these suggest there is far more diversity to this flora than is evident from the pollen preparations we have available. Fern spores are rare.

### McAbee floral list

Using the combined data set from megafossils and the

pollen record, a much more complete picture of the McAbee flora emerges. The following floral list incorporates both, indicating which plant organ was used in the diagnosis:

### Gymnospermae

#### Ginkgoaceae

*Ginkgo biloba* Linnaeus (Foliage)

*Ginkgo dissecta* Mustoe (Foliage)

#### Cupressaceae sensu lato

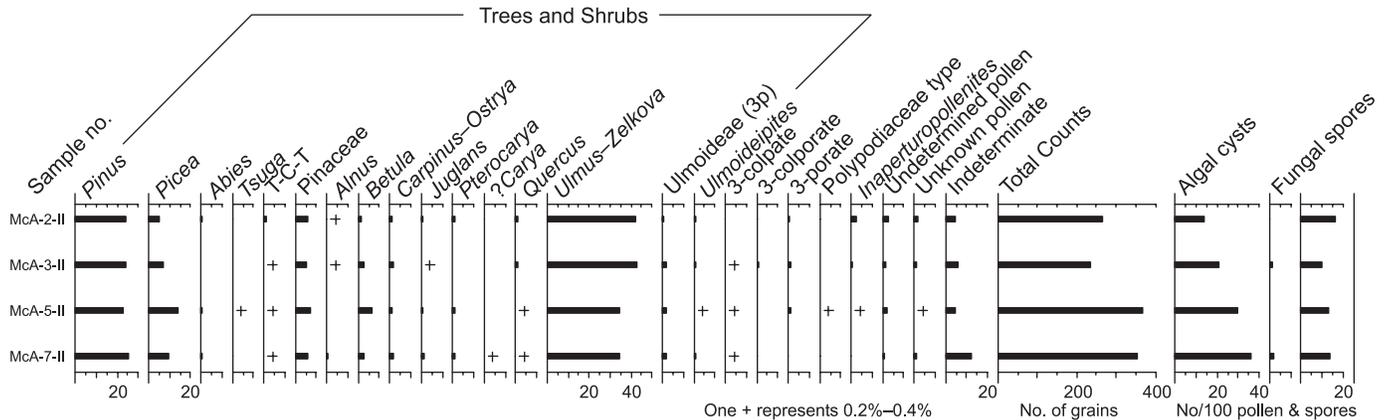
cf. *Calocedrus* sp. (Leafy twigs)

*Chamaecyparis* sp. (Leafy twigs, cones)

*Cunninghamia* sp. (Leafy twigs, cones)

*Metasequoia occidentalis* (Newberry) Chaney (Leafy twigs, cones)

*Sequoia* sp. (Leafy twigs, cones)

**Fig. 3.** Eocene McAbee pollen diagram (% total pollen and spores) Cache Creek, British Columbia: pit sample.

cf. *Thujopsis* sp. (Leafy twigs)  
*Thuja* sp. (Leafy twigs, cones)

#### Pinaceae

*Abies milleri* Schorn and Wehr (Leafy twigs, cone scales, winged seeds, and *Abies* pollen)  
*Picea* sp. (Leafy twigs, winged seeds, cones, and pollen)  
*Pinus* sp. (Leafy twigs, foliage, cones, winged seeds, and pollen)  
*Pseudolarix* sp. (Cones, foliage, and winged seeds)  
*Tsuga* sp. (Pollen)

#### Taxaceae

cf. *Amentotaxus* – cf. *Torreya* sp. (Leafy twigs, foliage)

#### Angiospermae

##### Lauraceae

*Sassafras hesperia* Berry (Foliage)

##### Platanaceae

*Macginitiea gracilis* (Lesquereux) Wolfe and Wehr (Foliage)

##### Trochodendraceae

*Trochodendron* sp. (Leafy twigs, foliage, and fruits)  
*Zizyphoides* sp. (Foliage)

##### Cercidiphyllaceae

*Joffrea* sp. (Foliage, fruits)

##### Hamamelidaceae

*Langeria magnifica* Wolfe and Wehr (Foliage)

##### Grossulariaceae

*Ribes* sp. (Foliage)

##### Salicaceae

*Populus* sp. (Foliage)

##### Vitaceae

cf. *Vitis* sp. (Foliage)

##### Rosaceae

cf. *Crataegus* sp. (Foliage)  
cf. *Prunus* sp. (Foliage)

##### Ulmaceae

*Ulmus* sp. (Leafy twigs, foliage, fruit, and *Ulmus-Zelkova* pollen)

##### Fagaceae

*Fagus langevinii* Manchester and Dillhoff (Leafy twigs, foliage, cupules, nuts, and *Fagus* pollen)

*Quercus* sp. (Pollen)

##### Myricaceae

*Comptonia columbiana* Dawson (Foliage)

##### Juglandaceae

*Carya* sp. (Pollen)

*Juglans* sp. (Pollen)

*Pterocarya* sp. (Pollen)

##### Betulaceae

*Alnus parvifolia* (Berry) Wolfe and Wehr (Foliage, ovulate cones, and *Alnus* pollen)

*Alnus* sp. 2 (Cones)

*Betula leopoldae* Crane and Stockey (Foliage, aments, and *Betula* pollen)

cf. *Corylus* sp. (Corylus-type pollen)

##### Malvaceae

*Florissantia quilchenensis* Manchester (Flowers)

##### Sapindaceae

*Acer rousei* Wolfe and Tanai (Fruits)

*Acer stewarti* Wolfe and Tanai (Fruits)

*Acer wehri* Wolfe and Tanai (Fruits)

*Acer* sp. (Foliage)

*Aesculus* sp. (Foliage)

*Dipteronia brownii* McClain and Manchester (Foliage?, fruits)

*Koelreuteria arnoldi* Becker (Fruits)

##### Cornaceae

*Cornus* sp. (Foliage, pollen)

##### Ericaceae

cf. *Rhododendron* sp. (Foliage?, large Ericaceous pollen)

##### Araliaceae

cf. *Aralia* sp. (Foliage)

cf. *Paleopanax* sp. (Fruits)

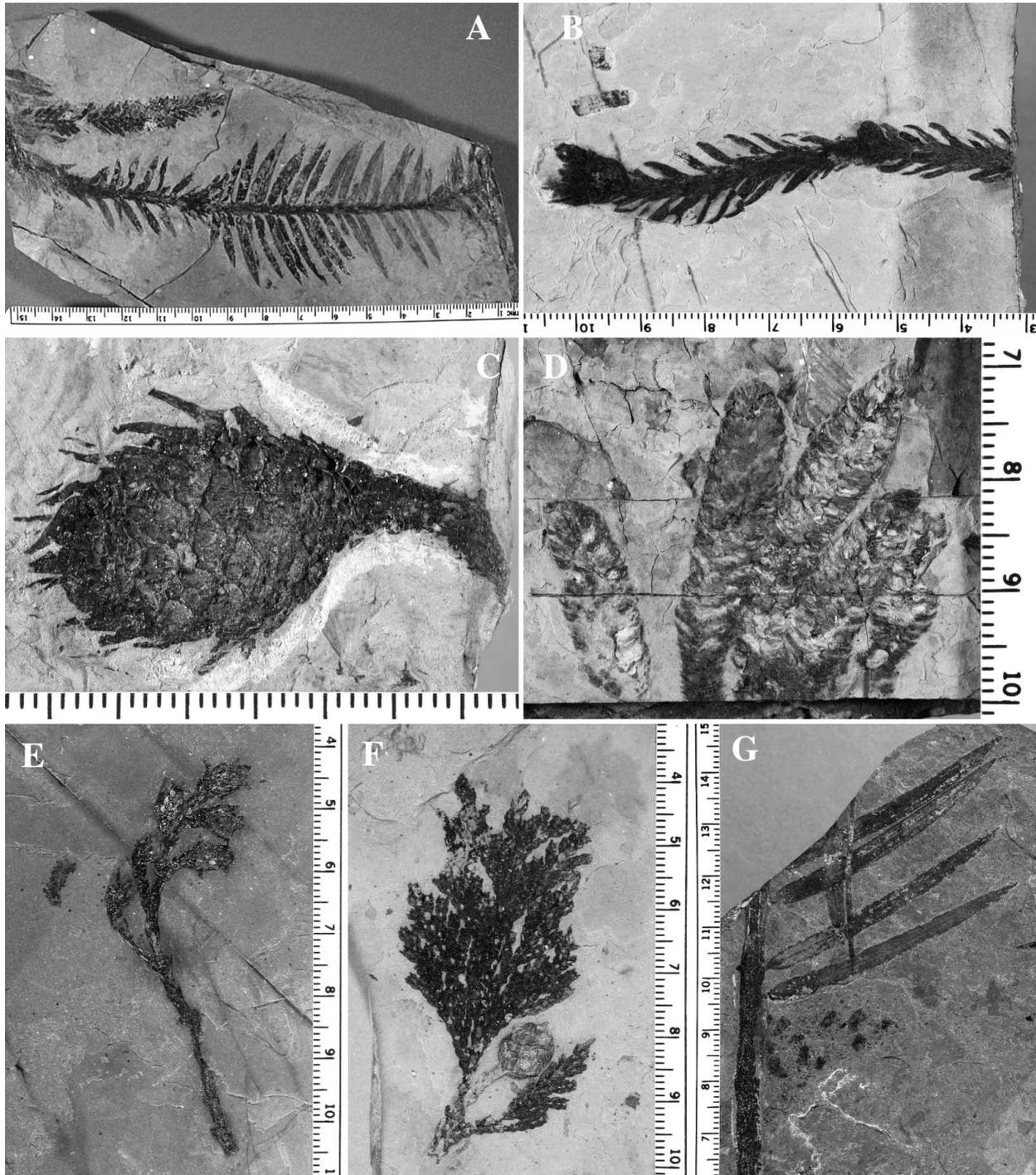
##### Uncertain affinity

*Chaneya tenuis* (Lesquereux) Wang and Manchester (Flower)

*Averrhoites* sp. (Foliage)

We have not been able to determine whether specimens of large taxaceous needles represent *Amentotaxus* or *Torreya* or both. Attempts to prepare cuticle to resolve this question have not been successful, and both genera have been reported in literature at Okanagan Highland localities. In either case, the Taxaceae were clearly present. The leaf type previously assigned by previous authors to *Cercidiphyllum* has been assigned to the extinct genus *Joffrea* in this study. Only a single specimen of fruits from Republic (Wehr and Manchester 1996) has been tentatively assigned to modern genus

**Plate 1.** Conifer examples. (A) *Cunninghamia* foliage (juvenile) UWBM 97604. (B) *Cunninghamia* foliage (mature) UWBM 97626. (C) *Cunninghamia* ovulate cone UWBM 97664. (D) *Cunninghamia*? Staminate cones UWBM 97665. (E) *Thuja* foliage and cones UWBM 97666. (F) *Chamaecyparis* foliage and cones UCCIPRL 18F1090. (G) Unidentified Taxaceous foliage UWBM 97667.



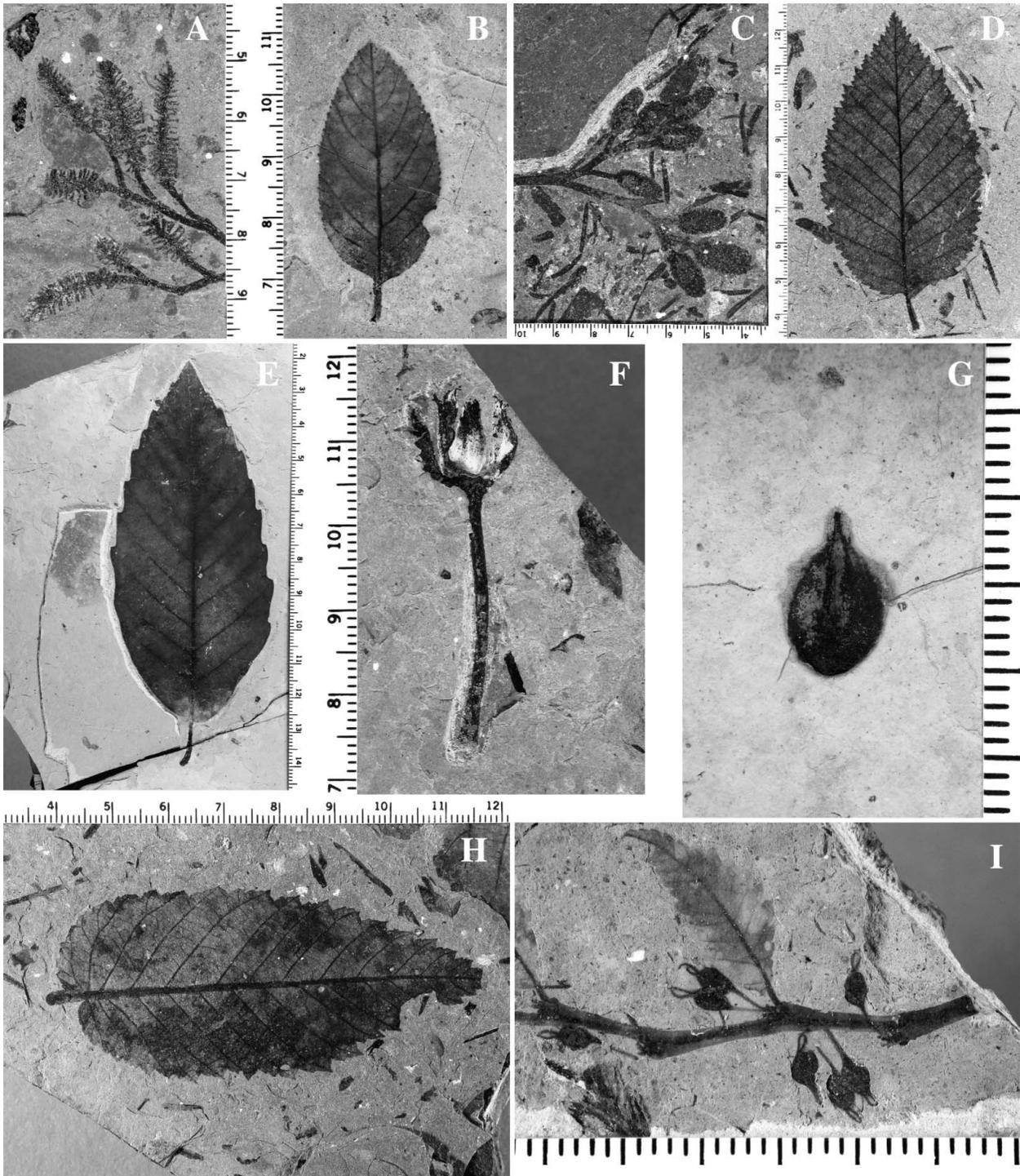
*Cercidiphyllum*. Fruits found at McAbee and the other Okanagan Highlands localities conform to the description for *Joffrea* (Crane and Stockey 1985) or *Nyssidium* (Crane 1984). Although not all of the required elements are present to confirm a diagnosis for *Joffrea*, the leaves associated with this fruit type in the Okanagan Highlands localities more closely match the description of *Joffrea* than the *Trochodendroides*

leaves that have been found in association with *Nyssidium* fruits.

### Discussion of gymnosperm taxa

The initial impression from the common megafossils occurring at McAbee is of a conifer-dominated forest with a

**Plate 2.** Common angiosperm tree samples. (A) *Alnus* ovulate cones type 2 UWBM 97688. (B) *Alnus parvifolia* leaf UWBM 97669. (C) *Alnus* ovulate cones type 1 UWBM 97670. (D) *Betula leopoldae* leaf UWBM 97671. (E) *Fagus langevinii* leaf UWBM 97593. (F) *Fagus langevinii* cupule UWBM 97583. (G) *Fagus langevinii* nut UWBM 97590. (H) *Ulmus* leaf UWBM 97672. (I) *Ulmus* branch with fruits UWBM 97673.



few simple hardwood constituents. Conifers are quite common and diverse composing at least 14 genera represented by individual needles, winged seeds, occasional cones and rarely, articulated branches. Cones occur both as compressions and as three-dimensional, zeolitized, carbonaceous replace-

ments, which although they are clearly pinaceous, typically fall apart as they hydrate and are seldom identifiable to genus. Isolated needles of *Pinus* and shoots of Cupressaceae (including the formerly recognized Taxodiaceae) are the most commonly encountered vegetative remains. Seeds of *Picea*

are the most common conifer reproductive remains, followed by seeds and cone scales of *Abies*, *Pinus*, and, less commonly, *Pseudolarix*.

The material here recognized as *Cunninghamia* (Plate 1) has been variously assigned to *Cryptomeria* (Wehr 1998) and *Araucaria* (Verschoor 1974). Typically, this foliage type has been found as short branch segments at other localities, but McAbee has produced rare articulated branches, as well as ovulate and staminate cones. The assignment to *Cunninghamia* is based on the morphology of cones found in attachment with foliage and the architecture of disarticulated cone scales. Both juvenile foliage with lanceolate needles up to 2.3 cm and mature foliage with blunt overlapping needles ~ 1 cm long are recognized, as in the modern genus. Modern *Cunninghamia* is unique among conifers in the presence of minute marginal teeth on the juvenile leaves, but these have not been observed on the McAbee material to date.

*Thuja* and *Chamaecyparis* (Plate 1) are both present at McAbee, based on specimens with cones in attachment to foliage, but we cannot determine their relative abundance since many foliage specimens are not well enough preserved to distinguish between the two. No diagnostic fossils of *Tsuga* have been recognized among megafossils, but the presence of the genus is confirmed by pollen. *Thujopsis* and *Calocedrus* specimens are extremely rare, and these assignments must be considered tentative until better diagnostic material is found. Taxaceae were present, but the genera are uncertain.

Two types of *Ginkgo* leaves are found at many Okanagan Highland sites, one similar to modern *Ginkgo biloba* and the other, an extinct form, *Ginkgo dissecta*, which has deeply dissected lobes (Mustoe 2002). Although most attempts to recover cuticle from McAbee have failed, the tough, well-preserved cuticle of *Ginkgo* was successfully recovered. This has allowed recognition of both *G. biloba* and *G. dissecta*, the latter being more common at McAbee.

## Discussion of angiosperm taxa

The most common angiosperm megafossil genera are elms (*Ulmus*), birch, and alder, members of the Betulaceae, and beech (*Fagus*) (Plate 2). The importance of these taxa is also generally reflected in the pollen record — *Ulmus–Zelkova* is dominant among angiosperm pollen, closely followed by the Betulaceae. Although *Fagus* pollen grains were not found in our investigation, they were recovered using a less destructive process in another study (Manchester and Dillhoff 2004).

Two types of ulmaceous foliage are recognized: small, simply toothed forms, and larger leaves with typically compound teeth. Because some extant elms have differing leaf morphologies on vegetative versus reproductive branches, these fossils may represent a single species, and further study is required. Some of the small simply toothed leaves have been attributed to *Zelkova* (Wolfe and Wehr 1987). However, no fruits similar to *Zelkova* have been found at any of the Okanagan Highlands localities, and these leaves have now been found in attachment with ulmus fruits. Fruits similar to modern *Ulmus mexicana* and *U. alata* have been found in attachment to branches bearing these leaves at McAbee and One Mile Creek near Princeton. No other ulmaceous fruits have been found at McAbee, and the larger leaf form has not been found in attachment with fruits. Ulmoideae 4–5-pored

pollen is assigned to *Ulmus–Zelkova*, as pollen of these genera are indistinguishable.

The Betulaceae at McAbee are common and diverse, and include two forms of *Alnus* based on ovulate cones, two types of *Betula*, based on pollen size, and possibly other genera, including either *Corylus*, and *Carpinus* based on pollen types. Leaves matching the description for *Betula leopoldae* (Crane and Stockey 1987) are common, but the reproductive bracts associated with those leaves at the type locality have not been found at McAbee.

The large leaves of *Fagus* are among the most common angiosperm remains found at McAbee. The co-occurrence of well-preserved cupules and nuts confirms, for the first time, the presence of this genus in the Middle Eocene. *Fagus* leaves are also present, although less common at Princeton, and Republic has produced a single nut in addition to rare leaves. Pollen data indicate the fagaceous genus *Quercus* was present in the vicinity of McAbee, although no recognizable leaves have been found. Although *Castanophyllum* is reported at other Okanagan Highland localities, a continuous series of forms from round-toothed to leaves with attenuate teeth occur at McAbee, suggesting these leaves also could be *Fagus*.

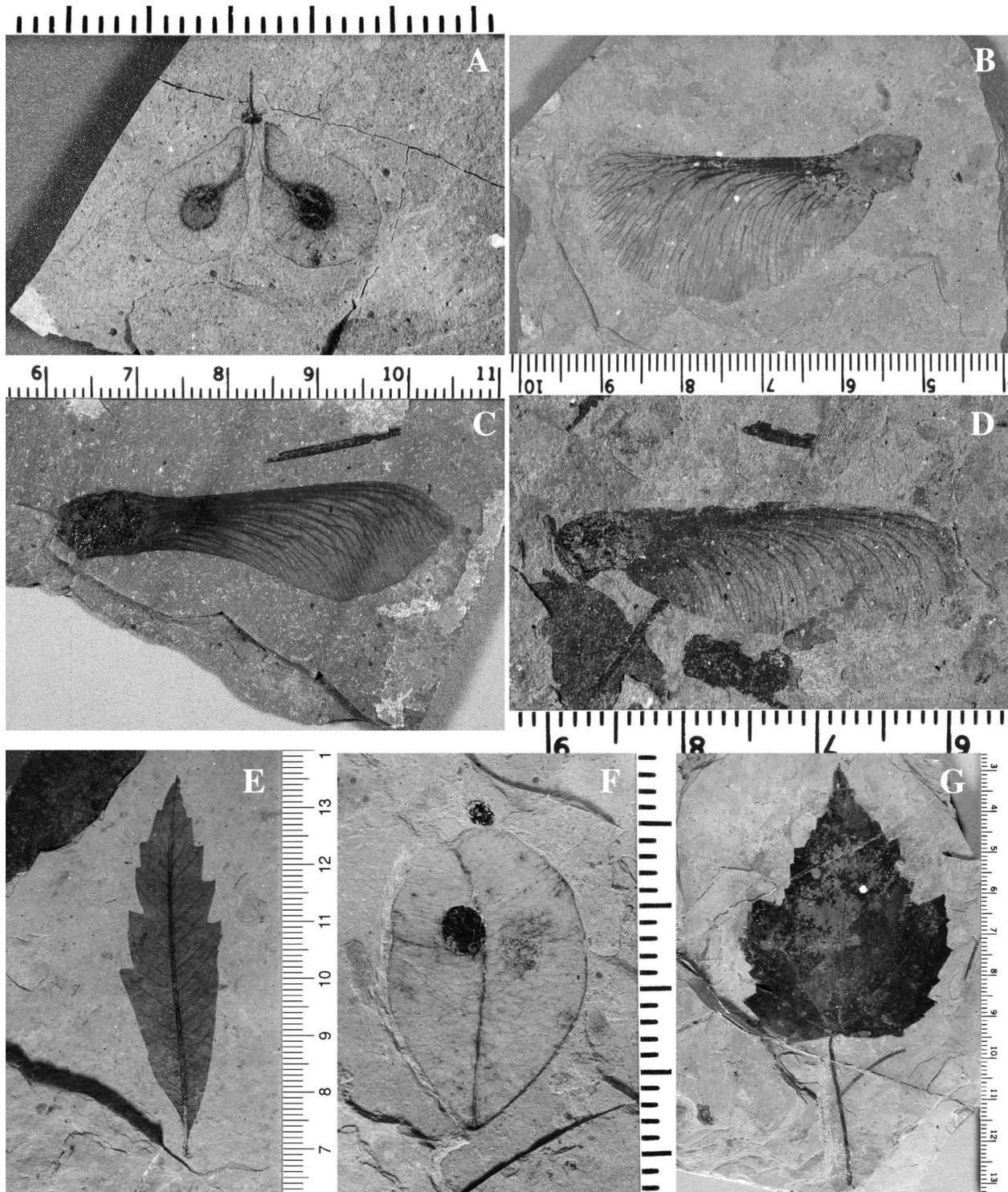
Other commonly occurring angiosperm taxa include *Sassafras*, *Zizyphoides*, cf. *Prunus*, cf. *Crataegus*, and *Acer*. All of these are identified solely on the evidence of leaf fossils, with the exception of *Acer*. Three species of *Acer* are recognized from fruits and leaves, along with three other members of the Sapindaceae — *Aesculus*, *Dipteronia*, and *Koelreuteria* (Plate 3). *Dipteronia* fruits from McAbee and other Eocene sites of western North America were described and illustrated by McClain and Manchester (2001). The extinct sapindalean genus *Deviacer* has been reported from Republic and Quilchena (Wehr 1998) but is not recognized at McAbee.

Rare leaves and a single panicle of fruits resembling *Trochodendron aralioides* have been identified at McAbee and will be described in a separate publication. *Zizyphoides* leaves, from an extinct member of the Trochodendraceae that survived into the Miocene are quite common. A single possible *Nordenskioldia* fruit, which has been found in association with *Zizyphoides* leaves at northwest Miocene localities (Manchester et al. 1991), has been found at McAbee. Rare *Nordenskioldia* fruits have also been collected at Republic in association with similar leaves (Wehr 1995). *Trochodendron* is the only broad-leaved evergreen identified with confidence at McAbee. A few rare leaves and two fruits document the presence of Araliaceae, which is also poorly known from rare specimens found at Republic. Most members of this family are also evergreen.

## The McAbee forest

Challenges remain to a reconstruction of the Eocene flora at McAbee. Because so many of the existing genera are still found in similar associations in temperate Asia today, those forests provide possible modern equivalents for the McAbee forest. Possible analogues are the Mixed Northern Hardwood forests of Northeast China (Wang 1961) or Northern New England (Wolfe 1979). Important genera to the Mixed Northern Hardwood forests of Northeast China flora that are

**Plate 3.** Sapindaceae. (A) *Dipteronia brownii* fruits UWBM 97675. (B) *Acer rousei* UWBM 76628A. (C) *Acer stewarti* UWBM 97677. (D) *Acer wehri* UWBM 97678. (E) *Dipteronia?* Leaflet UWBM 97679. (F) *Koelreuteria arnoldi* fruit UWBM 97676. (G) *Acer* leaf UCCIPRL 18 1089.



also found at McAbee include *Acer*, *Betula*, *Pinus*, *Quercus*, *Juglans*, and *Ulmus*. It differs from the McAbee flora in the absence of *Fagus* and low diversity of conifers present in the modern association. The Mixed Mesophytic Forests of southern central China also contain a similarly diverse an-

giosperm and conifer flora, but they also contain a significant component of broad-leaved evergreens that are rare at McAbee. These Chinese forests also lack *Picea*, which is the dominant conifer in the McAbee stratigraphic pollen record. The generic list is basically that of a deciduous hardwood

forest with diverse conifer genera, many of which grow today in both New England, USA and in Southeast Sichuan, China.

Taphonomic evidence supports the idea that McAbee represents the sorted litter of more than one forest zone. Among the gymnosperms, the Pinaceae, including *Pinus*, *Abies*, *Pseudolarix* and *Tsuga*, are represented primarily by organs that transport well: pollen, winged seeds, and individual needles. *Picea*, the most common conifer in pollen samples, is extremely rare as articulated twigs among megafossils, but winged seeds of *Picea* that ended up in the rivers that fed Lake McAbee are common. Cupressaceae, such as *Chamaecyparis*, *Cunninghamia*, *Metasequoia*, *Sequoia*, and *Thuja*, are primarily found as small, articulated branches, although it must also be noted that some Cupressaceae characteristically shed small branches seasonally. In the Mixed Mesophytic forests of central China, these genera, along with *Pinus*, commonly occur within the deciduous component of that forest. A picture emerges of a more distant upland forest dominated by Pinaceae and a more diverse deciduous forest containing cupressaceous conifers and hardwoods growing at lower elevations closer to the lake.

Modern regional plant associations vary at any given location due to microclimate, topography, north-south orientation, and random chance. Extinction adds another dimension to the puzzle. Overall, the plant families found at McAbee are surprisingly modern in aspect given its early middle Eocene age. The percentage of extinct genera is hard to measure considering the number of unassigned taxa. For those genera that have been identified, eight or nine angiosperms represent extinct genera, 27%–30% of the angiosperm families identified. At least that percentage of the unidentified taxa can be expected to represent extinct genera.

### Climatic interpretation

Two of the commonly accepted methods of estimating climatic parameters from plant communities are LMA (leaf margin analysis) and NLR (nearest living relative) comparisons. Multivariate analysis of dicotyledonous leaves was performed using the most recent iteration of CLAMP program designed by Jack Wolfe (Wolfe 1993). Based on a sample of 45 angiosperm leaf types, estimated mean annual temperature (MAT) was 9.5 °C and cold month mean temperature (CMMT) was estimated to be -2 °C. This analysis does not provide an annual precipitation estimate but suggests growing season precipitation to have been ~121 cm/year. The margin of error for CLAMP MAT estimates is indicated to be ±1.7 °C by Wolfe. Margin of error for other parameters measured by CLAMP is not given. The estimated MAT was ~1 °C cooler and, more significantly, the CMMT is nearly 4 °C cooler than estimates published previously (Greenwood and Wing 1995).

Recently calculated NLR estimates for McAbee were provided by Greenwood (Greenwood 2005) based on the most recent McAbee floral list, of which 35 taxa had data available for modern analogues. MAT is estimated to have been 13.5 (±2.5) °C and the CMMT is 3.5 (±4.4) °C. The precipitation estimate is substantially lower at 108 (±35) cm/year.

A discussion of the limitations of estimating past climate is beyond the scope of this paper, but estimates based on

multivariate analysis have been shown to be too low in some instances. One analysis evaluated CLAMP estimates for extant wetland plant communities, which tend to be especially well represented in lacustrine depositional settings, and determined that temperature estimates calculated using CLAMP were 2.5–10 °C lower than actual recorded temperatures (Kowalski and Dilcher 2003). Also, particularly at high latitudes, use of the NLR method has resulted in higher temperature estimates than those arrived at by multivariate analysis (Greenwood and Wing 1995).

From the perspective of the flora, the two discrepancies that are most important are the CMMT and precipitation regime. Palms are often used as indicator species because modern palms do not survive prolonged freezes (Sakai and Larcher 1987). Today palms generally occur in climates that have a MAT > 10 °C and a CMMT > 5 °C (Greenwood and Wing 1995). Both methods indicate a CMMT lower than the threshold that supports modern palms. Sabal palms are found at Princeton but to date no palynological or megafossil evidence of the presence of members of the *Arecaceae* exists for McAbee. Estimates of precipitation also vary widely between the two methods. The absolute amount of precipitation would not have been as important as seasonality if the comparison to the mixed mesophytic and Northern Hardwood forests is accurate. Such broad-leaved deciduous forests require a summer-wet climate regime.

### Comparison with other Okanagan Highland floras

A series of Early to Middle Eocene fossil deposits occur in the southernmost area of the Okanagan Highlands, found near Republic, Washington, followed by Princeton in extreme southern British Columbia; the Quilchena locality near Merritt; the subject of this report; McAbee; on Joseph Creek near Chu Chua; at the Horsefly Mine in the Quesnel District; and on Driftwood Creek near Smithers (Fig. 1). These deposits record the fish, insects, and plants that lived in the lake basins and adjacent uplands of the early Eocene of the Okanagan Highlands.

Making meaningful comparisons between the localities is not a straightforward task. The intensity of collecting, amount of scientific study, size of the study area, and taphonomy of sites all vary substantially. At one end of the scale Republic has been intensively collected for more than 30 years. Many publications have discussed elements of the flora, and the floral list compiled runs over one hundred species based on collections at several localities. Horsefly data, on the other hand, is compiled from a single site, with a small sample available for study; the latest published floristic treatment was by Penhallow in 1908. Wherever possible the data used in this study was updated with recent investigations, some of them not yet published. To focus on the regional flora, taxa found only at one locality were excluded. Diagnostic taxa that were eliminated from the comparison will be included in the discussion that follows. Table 3 compares 62 genera found in at least two of the described Okanagan Highland localities.

Approximately 10% of the common genera are found at all localities, except Chu Chua: *Ginkgo*, *Metasequoia*, *Pinus*, *Betula*, *Joffrea*, *Florissantia*, and *Ulmus*. Genera representing

**Table 3.** Genera common to the floras of the Okanagan Highlands.

Sites:	McAbee <sup>a</sup>	Republic <sup>b</sup>	Princeton <sup>c</sup>	Quilchena <sup>d</sup>	Chu Chua <sup>e</sup>	Horsefly <sup>f</sup>	Smithers <sup>g</sup>
<b>A. Gymnospermae</b>							
<b>Ginkgoaceae</b>							
<i>Ginkgo</i>	M	M	M	M	M	M	M
<b>Cupressaceae</b>							
<i>Calocedrus</i>	M?	M					
<i>Chamaecyparis</i>	M	M	M	M			
<i>Cunninghamia</i>	M	M	M				M
<i>Glyptostrobus</i>		M		M	M		
<i>Metasequoia</i>	M	M	M	M		M	M
<i>Sequoia</i>	M	M	M	M	M		M
<i>Taxodium</i>			M	M	M		
<i>Thujaopsis</i>	M						M
<i>Thuja</i>	M	M	M	M			
<b>Pinaceae</b>							
<i>Abies</i>	M P	M	M	M			M
<i>Picea</i>	M P	M	M	M			
<i>Pinus</i>	M P	M	M	M	M	M	M
<i>Pseudolarix</i>	M	M	M	M			M
<i>Tsuga</i>	P	M	M				
<b>Taxaceae</b>							
<i>Amentotaxus</i>	M?	M		M			M?
<i>Torreya</i>	M?	M					M?
<b>B. Angiospermae</b>							
<b>Anacardiaceae</b>							
<i>Rhus</i>		M	M				
<b>Araliaceae</b>							
<i>Aralia</i>	M?	M					
<b>Betulaceae</b>							
<i>Alnus</i>	M P	M		M	M		M
<i>Betula</i>	M P	M	M	M	M	M	M
<i>Corylus</i>	P?	M	M	M	M		
<i>Palaeocarpinus</i>	P?	M	M			M	M
<b>Cercidiphyllaceae</b>							
<i>Joffrea</i>	M	M	M	M	M	M	M
<b>Cornaceae</b>							
<i>Cornus</i>	M P	M		M	M	M	
<i>Tsukada</i>		M	M				
<b>Ericaceae</b>							
<i>Rhododendron</i>	M P	M					
<b>Fagaceae</b>							
<i>Fagus</i>	M P	M	M		M		
<i>Fagopsis</i>		M	M			M	M
<i>Quercus</i>	P	M	M	M			
<b>Grossulariaceae</b>							
<i>Ribes</i>	M	M	M				

**Table 3** (continued).

Sites:	McAbee <sup>a</sup>	Republic <sup>b</sup>	Princeton <sup>c</sup>	Quilchena <sup>d</sup>	Chu Chua <sup>e</sup>	Horsefly <sup>f</sup>	Smithers <sup>g</sup>
<b>Hamamelidaceae</b>							
<i>Langeria</i>	M	M		M	M		
<b>Icacinaceae</b>							
<i>Paleophytocrene</i>		M		M			
<b>Juglandaceae</b>							
<i>Carya</i>	P	M		M P	M		
<i>Juglans</i>	P			M P			
<i>Pterocarya</i>	P	M	M				
<b>Lauraceae</b>							
<i>Sassafras</i>	M	M	M	M	M		M
<i>Phoebe</i>		M	M				
<b>Lythraceae</b>							
<i>Decodon</i>		M	M				
<b>Malvaceae</b>							
<i>Florissantia</i>	M	M	M	M		M	M
<b>Myricaceae</b>							
<i>Comptonia</i>	M	M	M	M	M		
<b>Myrtaceae</b>							
<i>Paleomyrtinaea</i>		M	M				
<b>Platanaceae</b>							
<i>Macginitiea</i>	M	M		M		M	
<b>Rosaceae</b>							
<i>Amelanchier</i>		M	M				
cf. <i>Crataegus</i>	M	M	M				
<i>Neviusia</i>		M	M				
<i>Photinia</i>		M	M				
aff. <i>Physocarpus</i>		M	M				
<i>Prunus</i>	M	M	M	M	M		
<i>Rubus</i>		M	M				
aff. <i>Sorbus</i>		M	M			M	
<i>Spiraea</i>		M	M				
<b>Salicaceae</b>							
<i>Populus</i>	M	M		M			
<i>Pseudosalix</i>		M					M
<b>Sapindaceae</b>							
<i>Acer</i>	M	M	M	M			M
<i>Aesculus</i>	M	M	M				
<i>Deciacer</i>		M		M		M	
<i>Dipteronia</i>	M	M	M		M	M	M
<i>Koelreuteria</i>	M	M				M	
<b>Trochodendraceae</b>							
<i>Trochodendron</i>	M	M					
<i>Zizyphoides</i>	M	M				M	M
<i>Nordenskioldia</i>	M?	M	M				

Table 3 (concluded).

Sites:	McAbee <sup>a</sup>	Republic <sup>b</sup>	Princeton <sup>c</sup>	Quilchena <sup>d</sup>	Chu Chua <sup>e</sup>	Horsefly <sup>f</sup>	Smithers <sup>g</sup>
<b>Ulmaceae</b>							
<i>Cedrelospermum</i>		M		M			
<i>Ulmus</i>	M P	M	M	M	M	M	M
<b>C. Uncertain affinity</b>							
<i>Averrhoites</i>	M	M				M	
<i>Chaneya</i>	M		M				
<b>D. Total number of genera</b>							
66	47	62	43	32	18	17	22

<sup>a</sup>Results of this investigation.

<sup>b</sup>Wehr 1998. Does not include more than 80 angiosperm genera reported only from Republic.

<sup>c</sup>Wehr 1998; Pigg and Wehr, personal communication, 2003.

<sup>d</sup>Wehr 1998, Mathewes and Brooke 1971, Guthrie 1995.

<sup>e</sup>Berry 1926; Wolfe, personal communication, 2004.

<sup>f</sup>Manchester and Stockey, personal communication, 2003.

<sup>g</sup>Dillhoff, unpublished data, 2004.

the families Fagaceae and Sapindaceae are also common to all sites. Of the common genera, *Joffrea* and *Florissantia* are extinct so do not provide useful climatic information, and the natural climatic parameters for *Ginkgo* and *Metasequoia* are unknown. The remaining common genera are widespread both geographically and in physiognomic tolerances today but are primarily temperate plant families.

The conifer genera are common to almost all sites with a few exceptions. The only information available for conifers at Chu Chua was Berry (1926), when elements such as *Metasequoia* were not yet recognized. The Horsefly record is the least complete, but the low number of conifer taxa there is striking, especially given that these taxa are usually among the most common specimens encountered at the other sites. Other than the questionable record for Horsefly, the genera *Glyptostrobus* and *Taxodium* are only significant conifer genera that are not common to most sites. Today they both grow in locations that are at least seasonally flooded and their presence or absence may reflect taphonomy rather than abundance or rarity. The reports of *Thujopsis* at McAbee and Smithers and *Calocedrus* at McAbee and Republic are based on a few very rare finds so these genera do not appear to have been major constituents of the flora.

Among the Eocene angiosperms of the Okanagan Highlands, the Betulaceae and Sapindaceae are the most taxonomically diverse families present. Five genera of Sapindaceae, one extinct today, are each found in at least three localities. At least four genera of Betulaceae are recognized, including one extinct genera; *Palaeocarpinus*. The Fagaceae and Ulmaceae were also common to the region but less diverse. The Ulmaceae are represented by one or two of *Ulmus* species, and the extinct *Cedrelospermum*. Three representatives of Fagaceae occur. The extinct genus *Fagopsis* is found at Republic and Princeton, while the genus *Fagus* is only common at McAbee. *Quercus* is not common at any locality and is confirmed only by pollen at McAbee.

*Sassafras* is the only common member of the Lauraceae found at most localities. Its presence is a useful indicator since modern *Sassafras* grows in the summer-wet forests of eastern North America, China, and Taiwan. A similar disjunct distribution is the case for the Juglandaceae and Cornaceae,

which occur today in North America and Asia. Both are rare elements of the fossil floras where they are found, and the Juglandaceae are only confirmed at McAbee through the presence of pollen.

A tremendous diversity of Rosaceae is reported at Republic. Many of the oldest occurrences of rosaceous genera come from Republic, where 16 genera occur. Eleven genera are recognized from Princeton, two from McAbee, and three at Chu Chua. No members of the Rosaceae are known from Driftwood Creek, and only a single genus is recognized at Horsefly and Quilchena. This pattern suggests that the diversity of Rosaceae decreased at higher latitudes, but we need better characterization of the floras at Horsefly and Driftwood Creek to understand if this pattern has significance. There are also unidentified genera that appear to be rosaceous at McAbee.

This comparison also excluded thermophilic plants, such as *Ensete* (banana) (Wehr 1998) and Zamiaceae (cycad) (Hopkins and Johnson 1997) found at Republic. The flora at Republic also includes a number of broad-leaved evergreen angiosperm genera, associated with warm temperate to subtropical climates, such as the Magnoliaceae and Lauraceae. The Princeton chert locality contains unique permineralized remains that allow anatomical studies which confirm the presence of thermophilic taxa for the two southernmost localities. The Princeton chert records Arecaceae (palm) (Erwin and Stockey 1994), as well as representatives of the Magnoliaceae and Lauraceae (Cevallos-Ferriz and Stockey 1990; Stockey and Pigg 1991). Although McAbee records only one certain broad-leaved evergreen genus from megafossils; the unidentified pollen grains may represent additional genera.

## Conclusion

Based on the inclusion of rare and unidentified taxa and the quantitative information provided by the pollen record, the McAbee flora records a diverse early middle Eocene angiosperm-dominated forest. Although angiosperms predominated, gymnosperms were also common and diverse, especially the Pinaceae and Cupressaceae (including the formerly recognized Taxodiaceae). The Sapindaceae and

Betulaceae were the most common and diverse angiosperm families, followed by Fagaceae and members of the Ulmaceae. Broad-leaved evergreen taxa are rare, and thermophilic taxa such as palms and cycads, have not been identified, indicating that cold month temperatures could drop below freezing.

A comparison of the flora at McAbee to other Okanagan Highlands floras reveals many similarities. By focusing on the taxa common to these localities, we find a consistent, diverse conifer assemblage and a common basic angiosperm flora dominated by members of the Betulaceae, Fagaceae, Sapindaceae, and Ulmaceae throughout the Okanagan Highlands. With a better defined regional flora, the plants present at specific localities may answer questions about past floral associations and localized climate regimes. Patterns, such as the diversity of Rosaceae at Republic and Princeton, the extent of thermophilic taxa in the region, and the evolutionary history of important temperate tree families, are just beginning to emerge.

Meaningful comparisons between localities are difficult because of differences in collecting history, taxonomic study, and the extent of depositional basins. Each locality provides a unique window to a specific geographical setting at a short interval in time. The physical setting, from the location where plants grew to the transport mechanisms to the depositional setting itself, act as taphonomic filters, which determine what ultimately enters the record. The occurrence of so many localities that are close in time and geographic space provides a rare opportunity to reconstruct a regional flora and its components.

## Acknowledgments

Many individuals contributed to this study. Special thanks are due to Thomas Dillhoff of the Evolving Earth Foundation for photography and morphotyping; Gengwu Lui of the Nanjing Institute for pollen studies and George Mustoe of Western Washington University for his understanding of the McAbee sediments. George Mustoe and David Greenwood graciously provided access to unpublished findings, contained in their papers published in this Special Issue. Jack Wolfe, Ruth Stockey, Kathleen Pigg, and Wes Wehr provided unpublished floral lists. David Langevin and Robert Drachuk were especially generous in providing access to the site and their extensive collections. Many of the unique taxa that have been found are the result of their efforts to preserve unusual specimens. Ken Klein at the University College of the Cariboo in Kamloops, British Columbia; Wes Wehr at the Burke Museum in Seattle, Washington; Len Hills at the University of Calgary, Alberta; and Bruce Archibald at Harvard University in Cambridge, Massachusetts provided access to specimens. Thomas Dillhoff, John Fraser, David Morgan, David Langevin, and Robert Drachuk donated specimens that were used in this investigation. The comments of Jisuo Jin, Diane Erwin, Rolf Mathewes, Kathleen Pigg, George Mustoe, and Thomas Dillhoff provided critical feedback. Samantha Dillhoff edited the manuscript and formatted it for publishing. Our thanks to you all. This project was funded in part by the National Science Foundation (grant EAR 0174295) and the Evolving Earth Foundation.

## References

- Basinger, J.F. 1976. *Paleorosa similkameenensis*, gen. Et sp. Nov., permineralized flowers (Rosaceae) from the Eocene of British Columbia. *Canadian Journal of Botany*, **54**(20): 2293–2305.
- Basinger, J.F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of Southern British Columbia. *Canadian Journal of Botany*, **59**: 2379–3410.
- Berry, E. 1926. Tertiary Floras from British Columbia. Canada, Department of Mines, Geological Survey, Bulletin 42, pp. 91–116.
- Cevallos-Ferriz, S.R.S., and Stockey, R.A. 1990. Vegetative remains of the Magnoliaceae from the Princeton chert (middle Eocene) of British Columbia. *Canadian Journal of Botany*, **68**(6): 1327–1339.
- Crane, P.R. 1984. A re-evaluation of *Cercidiphyllum*-like plant fossils from the British early tertiary. *Botanical Journal of the Linnean Society*, **89**: 199–230.
- Crane, P.R., and Stockey, R.A. 1985. Growth and Reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the late Paleocene of Alberta, Canada. *Canadian Journal of Botany*, **63**: 340–364.
- Crane, P.R., and Stockey, R.A. 1987. *Betula* leaves and reproductive structures from the Middle Eocene of British Columbia, Canada. *Canadian Journal of Botany*, **65**: 2490–2500.
- Dawson, W.J. 1890. On fossil plants from the Similkameen valley and other places in the Southern interior of British Columbia. *Transactions of the Royal Society of Canada*, **VIII**: 75–90.
- Doher, I.L. 1980. Palynomorph preparation procedures currently used in the Paleontology and Stratigraphy laboratories, US. Geological Survey. United States Geological Survey, Circular 830.
- Erwin, D.M., and Stockey, R.A. 1994. Permineralized monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia, Canada — Arecaceae. *Paleontographica*, **234**(B): 19–40.
- Ewing, T.E. 1981. Regional stratigraphy and structural setting of the Kamloops Group, South-central British Columbia. *Canadian Journal of Earth Sciences*, **18**: 1464–1477.
- Greenwood, D.R., and Wing, S.L. 1995. Eocene continental climates and latitudinal temperature gradients. *Geology*, **23**(11): 1044–1048.
- Greenwood, D.R., Archibald, B.S., Mathewes, R.W., and Moss, P.T. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northern Washington State: climates and ecosystems across an Eocene landscape. *Canadian Journal of Earth Sciences*, **42**: This issue.
- Guthrie, G.H. 1995. A high resolution paleoecological analysis of an Eocene fossil locality from Quilchena, British Columbia. Project submitted in partial fulfillment, M.Sc. thesis, Simon Fraser University, Burnaby, B.C., April 1995.
- Hills, L.V., and Baadsgaard, H. 1967. Potassium-argon dating of some Lower Tertiary strata in British Columbia. *Canadian Petroleum Geologists Bulletin*, **15**: 138–149.
- Hopkins, D.J., Jr., and Johnson, K.R. 1997. First record of cycad leaves from the Eocene Republic flora. *Washington Geology*, **25**(4): 38.
- Kowalski, E.A., and Dilcher, D.L. 2003. Warmer paleotemperatures for terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **100**(1): 167–170.
- Lambe, L.M. 1906. Summary Report of the Geological Survey Department of Canada for the Calendar Year 1906. S.E. Dawson, Ottawa, Ont.
- Manchester, S.R., and Dillhoff, R.M. 2004. *Fagus* (Fagaceae) fruits, Foliage and pollen from the Middle Eocene of Pacific North-

- western North America. *Canadian Journal of Botany*, **82**(10): 1509–1517.
- Manchester, S.R., Crane, P.R., and Dilcher, D.L. 1991. *Nordenskiöldia* and *Trochodendron* (Trochodendraceae) from the Miocene of Northwestern North America. *Botanical Gazette*, **152**(3): 357–368.
- Mathewes, R.W., and Brooke, R.C. 1971. Fossil Taxodiaceae and new angiosperm macrofossils from Quilchena, British Columbia. *Syesis*, **4**: 209–216.
- McClain, A.M., and Manchester, S.R. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroideae. *American Journal of Botany*, **88**(7): 1316–1325.
- Mustoe, G.E. 2002. Eocene *Ginkgo* leaf fossils from the Pacific Northwest. *Canadian Journal of Botany*, **80**: 1078–1087.
- Mustoe, G.E. 2005. Diatomaceous origin of siliceous shale in Eocene lake beds of central British Columbia. *Canadian Journal of Earth Sciences*, **42**: This issue.
- O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A.M., and Maguire, S. 2002. Microbial taphonomic processes in the fossilization of insects and plants in the late Eocene Florissant Formation, Colorado. *Rocky Mountain Geology*, **37**(1): 1–11.
- Penhallow, D. 1908. Report on Tertiary plants of British Columbia. Geological Survey Branch, Department of Mines, Ottawa, Ont., Report No.1013.
- Pigg, K.B., Manchester, S.R., and Wehr, W.C. 2003. *Corylus*, *Carpinus* and *Palaeocarpinus* (Betulaceae) from the Middle Eocene Klondike Mountain and Allenby Formations of Northwestern North America. *International Journal of Plant Sciences*, **164**(5): 807–822.
- Sakai, A., and Larcher, W. 1987. Frost survival of plants: Responses and adaptation to freezing stress. Springer-Verlag, Berlin, Germany, pp. 1–321.
- Stockey, R.A. 1984. Middle Eocene *Pinus* remains from British Columbia. *Botanical Gazette*, **145**: 262–274.
- Stockey, R.A., and Pigg, K.B. 1991. Flowers and fruits of *Princetonia allenbyensis* (Magnoliopsida; family indet.) from the middle Eocene Princeton Chert of British Columbia. Review of Paleobotany and Palynology.
- Stockey, R.A., and Wehr, W.C. 1996. Flowering plants in and around Eocene lakes. In *Life in stone: A natural history of British Columbia's fossils*. Edited by R. Ludvigsen. The University of British Columbia Press, Vancouver, B.C., pp. 234–247.
- Verschoor, K. van R. 1974. Paleobotany of the Tertiary (Early Middle Eocene) McAbee beds, British Columbia. Unpublished thesis, Department of Geology, University of Alberta, Calgary, Alta.
- Wang, C.W. 1961. The forests of China with a survey of grassland and desert vegetation. Maria Moors Cabot Foundation, Publication #5, Harvard University Press, Cambridge, Mass.
- Wehr, W.C. 1995. Early Tertiary flowers, fruits and seeds of Washington State and adjacent areas. *Washington Geology*, **23**(3): 3–16.
- Wehr, W.C. 1998. Middle Eocene insects and plants of the Okanogan highlands. In *Contributions to the paleontology and geology of the West Coast; in honor of V. Standish Mallory*. Edited by J.E. Martin. Thomas Burke Memorial Washington State Museum, Research Report 6, pp. 99–109.
- Wehr, W.C., and Manchester, S.R. 1996. Paleobotanical Significance of Eocene Flowers, Fruits and Seeds from Republic, Washington. *Washington Geology*, **24**(2): 25–27.
- Wehr, W.C., and Schorn, H.E. 1992. Current research on Eocene conifers at Republic, Washington. *Washington Geology*, **20**(2): 20–23.
- Wing et al. 1999. Manual of Leaf Architecture — morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms by Leaf Architecture Working Group. Smithsonian Institution, Washington, D.C.
- Wilson, M.V.H. 1980. Eocene lake environments: depth and distance from shore variation in fish, insect and plant assemblages. *Paleogeography, Paleoclimatology, Paleoecology*, **32**: 21–44.
- Wolfe, J.A. 1979. Temperature Parameters of Humid to Mesic Forests of Eastern Asia and Relation to Forests of other regions of the Northern Hemisphere and Australasia. US. Geological Survey, Professional Paper 1106.
- Wolfe, J.A. 1993. A method of obtaining climatic parameters from leaf assemblages. US. Geological Survey, Bulletin 2040.
- Wolfe, J.A., and Tanai, T. 1987. Systematics, Phylogeny, and Distribution of *Acer* (Maples) in the Cenozoic of Western North America. *Journal of Faculty Science, Hokkaido University*, **22**, 1–246.
- Wolfe, J.A., and Wehr, W.C. 1987. Middle Eocene dicotyledonous plants from Republic, Northeastern Washington. US. Geological Survey, Bulletin 1597.
- Wolfe, J.A., and Wehr, W.C. 1991. The significance of the Eocene fossil plants at Republic, Washington. *Washington Geology*, **19**: 18–24.