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Abstract: The history of plant fossil collecting in the Okanagan (Okanogan) Highlands of British Columbia and northeastern Washington is closely intertwined with the history of geological surveys and mining activities from the 1870's onward. The first descriptions of fossil plants from British Columbia were published in 1870–1920 by J.W. Dawson, G.M. Dawson and D.P. Penhallow. In the U.S.A., fossil leaves and fish were first recognized at Republic by miners in the early 1900's. Many early workers considered these floras to be of Oligocene or Miocene age. Arnold described Canadian occurrences of conifers and *Azolla* in the 1950's. Palynological studies in the 1960's by Hills, Rouse and others and those of fossil fish by Wilson in the 1970–80's provided the framework for paleobotanical research at several key localities. Permineralized plants were first described from the Princeton chert in the 1970's by Miller, Basinger and others, followed by Stockey and her students. Wehr and Johnson revitalized the study of fossils at Republic with the discovery of a diverse assemblage in 1977. In 1987 Wolfe and Wehr produced a USGS monograph on Republic and Wehr cofounded the Stonerose Interpretive Center as a venue for public collecting. Systematic studies of the Okanagan Highlands plants, as well as paleoecological and paleoclimate reconstructions from palynomorphs and leaf floras, continue to expand our understanding of this important Early Eocene assemblage.

keywords: Eocene, palaeobotany, Okanagan Highlands, history, palynology

Introduction

The Okanagan Highlands (or Okanogan Highlands in the U.S.A.) is a name coined by Wehr and Schorn (1992; Archibald and Greenwood 2005) to define an Eocene fossil-rich region of uplift of the interior Pacific Northwest that extends some 1000 km, from central to southern British Columbia, Canada, southeastward into northeastern Washington (Fig. 1). Within this regional uplift is a series of grabens and half-grabens that preserve fossiliferous lacustrine shale and coal deposits throughout its geographic extent (Archibald and Greenwood 2005; Archibald et al. 2011; DeVore and Pigg 2010). Interest in the plant fossils found in this region extends back to geological exploration of the Pacific Northwest of both Canada and the U.S.A. in the 1870s (Archibald and Greenwood 2005; Archibald et al. 2011). In this present work we review the history of paleobotanical exploration of the 'Okanagan Highlands' as they have come to be known, noting the contributions of the principal workers through to the present day. As well, we seek to provide a synthesis of the chronology and taxonomic character of these important Eocene floras, and their contribution to an understanding of Eocene phytogeography and paleoclimates.

In Canada, these fossiliferous deposits include strata within the Allenby Formation (Princeton Group) in the Princeton and Tulameen basins near Princeton, B.C., the Tranquille Formation (Kamloops Group) including Falkland, the Coldwater Beds of Quilchena and Stump Lake, several unnamed units in the Ootsa Lake Group (Driftwood Canyon), and other units including those exposed at McAbee, Chu Chua and Horsefly. In the U.S.A. sites are exposed in and near Republic, Ferry County, Washington and occur within the Tom Thumb Tuff member of the Klondike Mountain Formation.

Depositional basins differ from one another in their extent and geological history, with the Republic area alone including 3 such basins: the Republic, Curlew, and Toroda Creek basins (Gaylord et al. 1996).

The region of the Eocene Okanagan Highlands is significant because its rich flora and insect and fish faunas document the biota of higher elevation sites around the time of the Early Eocene Climatic Optimum, about 52–50 Ma (Greenwood et al. 2005; Zachos et al. 2008; Archibald et al. 2011, 2014; Smith et al. 2010, 2012). Coastal assemblages of similar age include many tropical to subtropical elements that grew under warm climates (Rouse 1962; Mustard and Rouse 1994). These include the localities at Appian Way on Vancouver Island (Mindall et al. 2009) and Burrard Inlet in B.C. (Rouse 1962; Mustard and Rouse 1994) and the Chuckanut Formation (Mustoe and Gannaway 1997; Breedlovestrout et al. 2013), the Swauk Formation (DeVore and Pigg 2010), and the Puget Group in Washington (Wolfe 1968; Burnham 1990, 1994). In contrast, the Okanagan Highlands floras are characterized by plant assemblages that include a dominant temperate component (Rouse 1962; Rouse et al. 1970; Johnson 1996; Greenwood et al. 2005). Within the Okanagan Highlands we see some of the earliest evidence of important temperate plant families, including genera within the Betulaceae, Pinaceae, Rosaceae, and Sapindaceae.

There is a considerable literature of megafossil and microfossil systematics of these sites, some of which include summaries of particular floras or complement faunal studies of fish and insects (e.g., Wolfe and Wehr 1991; Stockey 2002; Stockey and Wehr 1996; Pigg and Stockey 1996; Smith 2011; Smith et al. 2012; Dillhoff et al. 2005, 2013; Archibald et al. 2011). More recently, a greater emphasis on the paleoenvironments of the

Okanagan Highland floras has appeared both in locality studies (Dillhoff et al. 2005, 2013; Smith et al. 2009, 2010; Gushulak et al. this volume; Mathewes et al. this volume) and in studies dedicated to broader issues of paleoenvironment (Greenwood and Wing 1995; Wolfe et al. 1998, 2000; Greenwood et al. 2005; Moss et al. 2005; Smith et al. 2012; Feng and Poulsen 2016). Archibald et al. (2011) provided a preliminary synthesis of the Okanagan Highlands sites, focusing on their potential as Lagerstätten to answer questions in paleoecology incorporating both insects and plants. DeVore and Pigg (2010) included the Okanagan Highlands localities in their analysis of Eocene-Oligocene floras of western North America in context to their geological history and depositional environments (DeVore and Pigg 2010, Table 1).

Historical contributions of individual scientists have been noted in bibliographies, including those of: J.W. Dawson (Fig. 2A; Eakins and Eakins 2015); G.M. Dawson (Fig. 2B; Zeller and Avrith-Wakeam 2015); D.P. Penhallow (Fig. 2C; Zeller 2015); E.W. Berry (Cloos 1974); C.A. Arnold (Scott 1995); L.V. Hills (University of Calgary 2013); J.A. Wolfe (Spicer and Leopold 2006; Pigg and DeVore 2007; Burnham and Tonkovich 2011); and Wes Wehr (Archibald et al. 2005). The history of individual sites has been discussed for some localities (e.g., Driftwood Creek, Ludvigsen 2001; McAbee, Wilson 2008; Republic, Wolfe and Wehr 1987, Perry and Barksdale 1996, Volkman et al. 2009; Princeton chert, Pigg and Stockey 1996); however, several of these historical overviews are not easily accessible.

In the present contribution we outline the sequence of discoveries and research projects that have led to our current knowledge of the area, and provide details about individual sites. We recognize several intervals: first, the early studies from about 1870 –

1940; then several significant works in the 1950's. Later, the 1960's–70's, was a time that saw the development of a palynological and stratigraphic framework for understanding the occurrence of fossil plants, and the discovery of the significance of the Republic flora. In the final section of this review, we discuss how the 1970's–1990's were a time of many primarily taxonomic and phytogeographic studies that described the diversity and distributional history of the Okanagan Highlands plants. Finally, we present an account of how since around 2000, taxonomic studies have been presented in an increasingly phylogenetic framework, and paleoecological and paleoclimate studies have detailed the paleoenviromental history of the region.

Results

Early studies 1870-1970.

The first person to deal with the Eocene floras of British Columbia was Sir John William Dawson (1820–1899)(Fig. 2A), with a focus on sites around the Similkameen River and Tulameen River (sometimes labelled as 'North fork, Similkameen River') near Princeton (e.g., Pleasant Valley, Whipsaw Creek), Stump Lake and Quilchena near Merritt, and the Tranquille River and nearby sites around Kamloops, which he considered to be Miocene (J.W. Dawson 1879, 1880, 1890, 1883). J. William Dawson was a major figure in the development of the educational system in Canada, serving as Professor of Geology and Principal at McGill University, Montreal (1855–1893). He had friendships with Lyell and other prominent contemporaries and was among the most highly regarded geologists of his day (Eakins and Eakins 2015).

George Mercer Dawson (1849–1901), son of J. William Dawson, was equally important to the early development of Canadian geology and paleobotany (Fig. 2B).

Despite physical challenges, G.M. Dawson overcame these limitations to became one of Canada's most successful field geologists, botanists and surveyors, including work from 1872–1875 on the International Boundary Commission that marked the Canadian/U.S.A. border. G.M. Dawson’s exploration throughout British Columbia and the Yukon provided much of the fossil material for his father's work and his own publications.

G.M. Dawson joined the staff of the Geological Survey of Canada in 1875, and became Director in 1895 (Jenkins and GM Dawson 2007; Zeller and Avrith-Wakeam 2015). The various papers by both J.W. and G.M. Dawson documented a diverse suite of ferns, conifers, dicot leaves and fruits and seeds, principally from southern B.C. (Fig. 1), with a particular focus on determining whether these sites were Eocene or Miocene through comparisons with the 'Laramie flora' of the U.S.A. (G.M. Dawson 1879, 1895; J.W. Dawson 1890; Penhallow 1908).

David Pearce Penhallow (1854–1910) was an assistant to preeminent American botanist Asa Gray, and a prominent botanist and educator in his own right (Fig. 2C). Penhallow was one of only a few Western scholars invited to work in Japan during the Meiji era (1868–1912), known as the "enlightenment", before Japan closed itself off from the outside world. Penhallow contributed substantially to the development of science education in Canada on his appointment to McGill University, Montreal in 1883. He was one of the first to teach evolution in the classroom and established the first marine biological station in Canada at St. Andrews, New Brunswick, and helped to build it. His particular research interests included the classification of North American gymnosperms, plant physiology, Pleistocene floras, and Devonian plants (Zeller 2015).

In reference to the sites now referred to as the Okanagan Highlands, Penhallow

(1902, 1904, 1908) built on the original work by J.W. and G.M. Dawson, recognizing many species of plants from the Okanagan Highlands (principally sites along the Similkameen River near Princeton associated with coal deposits), and describing many new taxa in a landmark monograph (Penhallow 1908). Berry (1926) described a leaf flora near Chu Chua in British Columbia (Fig. 1), and also reported plant fossils from several sites in western U.S.A., including Republic (Berry 1929). Species described by Berry (1926) from the Chu Chua flora included species named by J.W. Dawson or Penhallow as well as new names. Some of these species were discussed in studies of other floras or taxonomic monographs in subsequent years, with some of Dawson and Berry's names synonymised (e.g., Brown 1962; Wolfe and Wehr 1987; McClain and Manchester 2001; Denk and Dillhoff 2005). The Chu Chua flora is briefly reviewed later in this paper.

In the U.S.A., the Republic flora was first noted when miners with the Republic Mining Company found fossil fish and plants in and around the town of Republic during their mining operations (Umpleby 1910). The site was mentioned by E.W. Berry (1929) in his monograph on the Miocene Latah Formation, from outcrops to the east and south of Republic extending to Spokane and on into Idaho near Clarkia. Berry interpreted Republic as part of the Latah Formation. Roland W. Brown described additional specimens from Republic, including *Cercidiphyllum* in the 1930's (Brown 1935, 1937, 1939, 1940). Republic was not further studied until its rediscovery by Wehr and Johnson in the 1970s.

During the 1950s Chester A. Arnold (1901–1977), a prominent American paleobotanist, became interested in the floras from southern British Columbia. His contributions to the study of the Okanagan Highlands included description of *Azolla* *primaeva* megafossils and spores, and of conifers in 1955 from the Allenby Formation near Princeton (Arnold 1955 a, b). *Azolla* was studied further by Hills and Gopal (1967). Arnold's student Roger F. Boneham's (1968) dissertation was a landmark study on palynology of Tertiary coal basins in B.C. (including analysis of the Princeton chert). Interest in 'Tertiary' macroscopic plant fossils from British Columbia appears to have waned after Arnold's work, shifting to palynological studies, reflecting the use of palynology in combination with the then-new method of radiometric dating in stratigraphic correlation (Rouse and Mathews 1961; Hills and Baadsgaard 1967).

Leaders in Stratigraphic Palynology: 1961–1980

Palynological studies by Rouse, Hills and others in the 1960s created the framework for understanding regional stratigraphy and the recognition that the interior B.C. floras were different from the contemporaneous coastal Eocene floras (Rouse and Mathews 1961; Hills 1962, 1965; Rouse 1962; Hills 1965; Hills and Baadsgaard 1967; Boneham 1968; Rouse and Srivastava 1970; Rouse et al.1970).

In key papers, Rouse and others attempted to integrate some of the earliest radiometric dates for early Cenozoic rocks. Stratigraphic relationships were based on rare mammal fossils (Russell 1935; Gazin 1953), pollen chronological ranges, and by matching the megafloras with those found elsewhere in western North America. Critically, these pioneering papers established that the majority of the plant fossil sites in the B.C. interior from Kamloops Group and Princeton Group sediments were 'Middle Eocene' (~50 Ma, Hills and Baadsgaard 1967), and not Miocene, resolving a debate that extended back to W.A. Bell (in Duffel and McTaggart 1952), Berry (1926), Penhallow (1908) and J.W. Dawson (1879, 1883, 1890).

Hills and Baadsgaard (1967) presented a stratigraphic scheme combining K-Ar method radiometric dates, pollen and other biostratigraphy (e.g. Bisaccate, *Azolla primaeva*, and *Pistilipollenites mcgregorii* zones) for key Okanagan Highlands megaflora sites (e.g., Driftwood Creek, Quilchena, McAbee, Sunday Creek and other Allenby Formation sites near Princeton). The dating of these sites as 'Middle Eocene' has been widely cited in the literature on the Okanagan Highlands floras and faunas (e.g., Wilson 1977*c*). However, current concepts about Cenozoic geochronology place the Early-Middle (Ypresian-Lutetian) Eocene boundary later, at 47.8 Ma (Cohen et al. 2013), so that even when applying the older K-Ar dates (Hills and Baadsgaard 1967; Read 2000), the majority of the interior B.C. 'Okanagan Highlands' fossil sites should be considered Early Eocene (Greenwood et al. 2005; Moss et al. 2005; Radtke et al. 2005; Archibald et al. 2011; Dillhoff et al. 2013; Eberle et al. 2014) (Fig. 3). Newer ^{40}Ar-^{39}Ar and U-Pb methods of radiometric dating of associated volcanics reinforce this age by placing all Allenby Formation sites, including Thomas Ranch (Dillhoff et al. 2013) and several additional key sites such as Driftwood Canyon (Eberle et al. 2014) in the 53–48 Ma range, within the Ypresian stage (Early Eocene) (MacIntyre and Villeneuve 2001; Moss et al. 2005; Villeneuve and Mathewes 2005; Ickert et al. 2009). This new synthesis is presented here in Figure 3.

Rouse et al. (1970) established from comparative pollen counts of interior B.C. and coastal sites that the interior floras were a 'coniferous-hardwood flora' differing from the fern-rich coastal Eocene 'Burrard and Kitsilano formations' floras by: (1) greater amounts of Pinaceae and 'taxodiaceous' pollen; (2) higher counts and diversity of dicot trees, especially Betulaceae and Juglandaceae, including genera extant in southeastern

North America and east-central China; and (3) fewer fern spores. Absent to rare in the interior assemblages, but present in the coastal pollen floras, were warm climate indicators such as *Sabal granopollenites* (Arecaceae, palm), *Engelhardia* (Juglandaceae), ?*Nyssa*, and fern spores from the Anemiaceae-Schizeaceae group (Rouse et al. 1970, Table 2).

Rouse et al. (1970) interpreted this pollen data to indicate a cooler more continental climate for the interior Eocene (i.e., 'Princeton coal basin' /Allenby Fm., Horsefly, and Driftwood Creek), than for the coastal sites, but still 'a warm mesothermal climate', an interpretation supported by recent quantitative climate reconstructions (e.g., Greenwood et al. 2005; Smith et al. 2012; Dillhoff et al. 2013; Mathewes et al. this volume; Gushulak this volume).

Our understanding of the paleontological potential of the Eocene lake shale deposits was greatly enhanced by research on fossil fish and insects by Wilson in the 1970's – 80's, as his papers highlighted the paleobotanical potential of sites throughout the region (Wilson 1977*a*, *b*, *c*, 1978, 1980). Through Wilson's work, paleobotanists were made aware again of sites as well as material such as a silicified *Pinus* cone from Driftwood Canyon (Stockey 1984), and more recently the Falkland megaflora (Greenwood et al. 2005; Moss et al. 2005, 2016; Smith et al. 2009, 2010, 2012). Paleobotanists from the 1970s on have provided analysis of the plant fossil sites that were the focus of previous generations (e.g., works of Dawson, Penhallow, Berry, Arnold, Rouse and Hills). By applying modern methods such as phylogentic analysis, paleoecology, and paleoclimate reconstruction. In the following section we focus on the lake-deposit 'compression floras'; fossil assemblages mostly known to J.W. and G.M.

Dawson, Penhallow, Berry and later workers that feature lacustrine shales (e.g., Wilson 1977b, 1980, 1988, 1993; Wilson and Barton 1996; Smith et al. 2009; Wilson and Edlund 2005). These lake shales preserved fish, insects and diatoms, as well as leaves, seeds, flowers and other plant organs preserved as impressions or with the leaf cuticle preserved as an organic film.

Studies from compression (lacustrine) sites - 1970s to present

Driftwood Canyon (Driftwood Creek or 'Smithers')

Fossil plants and insects from Driftwood Canyon (also known as the Driftwood Creek beds, or ‘Smithers’ after the nearby town 10.5 km W of the Provincial Park (Fig. 1; Fig. 3; Fig. 4A, B) were the subject of much public interest, leading to the creation of the Driftwood Canyon Provincial Park in 1967 (Ludvigsen 2001; Eberle et al. 2014). The Driftwood Creek beds are laminated shales and interbedded volcanic ashes of an unnamed formation of the Eocene Ootsa Lake Group (Driftwood beds of MacIntyre et al. 1994; Douglas and Stockey 1996; Eberle et al. 2014). Fossil fish from Driftwood Canyon in the Canadian Museum of Nature collections date to the 1930s (e.g., *Eosalmo driftwoodensis*, Wilson 1977*a*); however, early reports make reference to fossil plants from north-central British Columbia only from Finlay River and Francois Lake (e.g., Penhallow 1908), 260 and 125 km NW and S of Smithers.

Greenwood et al. (2005) summarized the megaflora at Driftwood Creek, noting common whole plants of *Azolla* (Hills and Gopal 1967), *Metasequoia* leafy shoots, *Alnus* (leaves and catkins), as well as needles, seeds and cones of *Pinus driftwoodensis* (Stockey 1983), *Pseudolarix* (LePage and Basinger 1995), *Chamaecyparis* and/or *Thuja*, *Sequoia*, and rare *Ginkgo* and *Sassafras hesperia* leaves. Rare flowers and seeds of

Ulmus (Denk and Dillhoff 2005), *Florissantia*, and fruits of *Palaeocarpinus* sp. (Pigg et al. 2003) and *Dipteronia* (McClain and Manchester 2001) are also known. Moss et al. (2005) and Eberle et al. (2014) provided brief accounts of the pollen flora from the Driftwood Canyon sites.

Driftwood Canyon is actually a series of smaller sites; two cliff faces (North and South faces of Eberle et al. 2014) that are visible from the parking area of the Provincial Park and accessible to the public, and a series of other minor outcrops along Driftwood Creek and the adjacent road, each showing some differences in sediment type. The cliff faces are prominent buff to yellow, fine-grained laminated shales and interbedded volcanic ashes and are the source of most of the plant fossils as well as important fish remains including *Eosalmo* (Wilson 1977*a*), a jaw of a primitive hedgehog (Eberle et al. 2014), and a paper shale hosting an exquisite insect fauna (Andersen et al. 1993; Douglas and Stockey 1996; Greenwood et al. 2005; Archibald et al. 2011, 2013). The creek-side outcrop includes minor coal and sandstone containing *Metasequoia* shoots and dicot leaves (Eberle et al. 2014). Most collecting has been from scree at the two cliff faces, although there is considerable evidence that amateur collecting has been focused on prying out shale from the cliff faces (Ludvigsen 2001). Ongoing work seeks to describe the Driftwood Canyon megaflora in detail based on detailed sampling in 2010–2012 (Eberle et al. 2014; D.R. Greenwood, J.F. Basinger and M.C. Brown unpublished work).

Early work dating the Driftwood Creek beds placed the site as Middle Eocene (Hills and Baadsgaard 1967; Rouse et al. 1970; Wilson, 1977*a*). However, Moss et al. (2005), placed Driftwood Canyon fossil bearing sediments as Early Eocene on the basis of an unpublished radiometric age of 51.77 ± 0.34 Ma by U-Pb zircon analysis of a prominent ash from the north cliff face exposure of the Driftwood Canyon sediments (Fig. 3). The presence of the tapiroid *Heptodon* at Driftwood Canyon is consistent with an age no older than Early Eocene (Eberle et al. 2014).

Horsefly River

The Horsefly River Beds consist in part of a sequence of finely alternating layers that have been interpreted as varved lacustrine sediments, with an estimated continuous deposition in excess of 10,000 years at one of the most productive localities (Fig. 1; Fig. 3; Fig. 4C; Wilson 1977b, 1980, 1988, 1993; Wilson and Bogen 1994; Wilson and Barton 1996). Fossils were first reported from the Horsefly River by Penhallow (1902, 1908) and Lambe (1906), and insects and fish are well known from this locality, as summarized by Wilson (1993) and Archibald et al. (2011). The Horsefly megaflora has not been reviewed in detail since Penhallow (1902, 1908), and contains around 40 plant taxa including at least 2 filicalean ferns, abundant *Metasequoia* and related Cupressaceae, and several Pinaceae. At least 3 monocots are present as are common dicots such as *Sassafras*, *Macginitea*, Cercidiphyllaceae/Trochodendraceae, Betulaceae, Rosaceae, Ulmaceae, and Sapindaceae.Greenwood et al. (2005) and Moss et al. (2005) provided preliminary summaries of the Horsefly megaflora and pollen, with Greenwood et al. (2005) reconstructing a temperate wet paleoclimate. Moss et al. (2005) recorded a rich palynoflora dominated by *Pseudolarix*, *Abies*, and Betulaceae together with ferns, other Pinaceae (*Picea*, *Pinus*, and *Tsuga*), Cupressaceae (*Metasequoia*/*Sequoia*), and several dicot families (e.g., Ericaceae, Fagaceae, Juglandaceae, Rosaceae, Sapotaceae, and Ulmaceae).

Among the plant megafossils that have been published from Horsefly since

Penhallow are the moss *Aulacomnium heterostichoides* (Janssens et al. 1979), fruits of the 'rabbit ears' *Lagokarpos lacustris*, a plant of unknown affinities (McMurran and Manchester 2010) and a flower bearing the distinctive pollen type *Pistillipollenites macgregorii*, also of uncertain affinity (Stockey and Manchester 1988). Other fruits and seeds include *Palaeocarpinus* sp. fruits similar to *P. barksdalae* from Republic (Pigg et al. 2003) and *Dipteronia* fruits (McLain and Manchester 2001)., Sapindaceae such as

The McAbee Fossil Beds

Fossil plants from the same area as the McAbee fossil beds (Cache Creek and Kamloops B.C., Fig. 4E, F) have been known since the work of G.M. Dawson (1877, 1895), J.W. Dawson (1890), and Penhallow (1908), with these authors noting conifer and dicot leaf fossils from Tranquille River and Kamloops. The prominent Canadian paleobotanist W.A. Bell (in Duffel and McTaggart 1952), noted plant fossils from several outcrops on the Ashcroft geological map, centered on Cache Creek about 13 km west of the McAbee fossil beds. In the accompanying notes, Bell listed conifers (e.g., *Sequoia langsdorfii*) and dicots (e.g., *Sapindus*, *Tilia* and *Viburnum*), and even a palm (*Sabal florisanti*?) from 'Coldwater and Tranquille sedimentary beds' (Kamloops Group) or lacustrine sediments of an unnamed unit he correlated with the Burrard Formation on the B.C. coast (Duffel and McTaggart 1952, pp. 63–68).

The McAbee fossil beds and the nearby Battle Bluffs (just west of the Tranquille River) were originally radiometrically dated from volcanic ash exposed in the lacustrine shales using the K-Ar method at ~51 Ma (Hills and Baadsgaard 1967) and most papers reference McAbee as Middle Eocene. Archibald et al. (2010) provided a radiometric date using the ^{40}Ar-^{39}Ar method of 52.9 ± 0.83 million years old. On the basis of current concepts of the Early-Middle Eocene boundary (i.e., 47.8 Ma; Cohen et al. 2013), either radiometric date places the McAbee fossil beds as Early Eocene (Fig. 3).

Research on the plant fossils of the McAbee Fossil Beds was initiated in the 1960s and early 1970s by Hills (1965) and his students who studied both the fossil spores and pollen and the leaf fossils, while fossil fish were being studied by Wilson (1977*a*, *b*, 1980). The McAbee Fossil Beds are also known for their abundant and well preserved insect fossils (Douglas and Stockey 1996; Archibald et al. 2010, 2013, 2014; Archibald and Bradler 2015).

The first taxonomic overview of the McAbee megaflora was included in an unpublished M.Sc. thesis by Hill's student K. Verschoor (1974). Subsequent taxonomic studies have revealed a well preserved flora of up to 76 genera of plants, based on abundant leaves, shoots, seeds (e.g., *Pseudolarix*; LePage and Basinger 1995), flowers, and cones (Dillhoff et al. 2005; Greenwood et al. 2005).

Fossil plants described from the McAbee fossil beds include rare flowers and fruits such as *Dipteronia* (McClain and Manchester 2001), Betulaceae such as *Palaeocarpinus* (Pigg et al. 2003), maple samaras (*Acer rousei*; Wolfe and Tanai 1987), and fruits and leaves of a beech (*Fagus langevinii*; Manchester and Dillhoff 2004), *Ulmus chuchuanus* and *U. okanaganensis* (Denk and Dillhoff 2005), *Trochodendron drachukii* and associated leaves (Pigg et al. 2007), and a reproductive structure of unknown affinities named *Dillhoffia cachensis* (Manchester and Pigg 2008). Both Greenwood et al. (2005) and Dillhoff et al. (2005, 2013) provided paleoclimate reconstructions for McAbee (see Gushulak et al. this volume), and both Dillhoff et al. (2005) and Moss et al. (2005) presented pollen count data that indicated a diverse flora. While primarily focused on insects in his study of McAbee, Archibald et al. (2010) used rarefaction analysis of a small collection (< 200 leaves) to show plant diversity in the Early Eocene comparable to tropical rainforest sites, corroborating an extensive and detailed assessment of insect diversity. These data, in combination with data from Republic (Wilf et al. 2003, 2005) and Falkland (Smith et al. 2012) have demonstrated high plant and insect diversity for the Okanagan Highlands fossil sites, which Archibald et al. (2010, 2013) proposed was caused by low temperature seasonality rather than high tropical-character temperatures.

Chu Chua (Joseph Creek)

Berry (1926) and several more recent authors reference a site named Chu Chua or Joseph Creek (Fig. 1; Fig. 3), about 85 km N of Kamloops B.C. (Arnold 1955; Brown 1962; Wolfe and Tanai 1987; Gooch 1992; Wolfe et al. 1998, 2000; McClain and Manchester 2001; Denk and Dillhoff 2005; Dillhoff et al. 2005; Villeneuve and Mathewes 2005; Feng and Poulsen 2016). It is likely the various authors citing either Chu Chua or Joseph Creek refer to multiple separate outcrops exposed near the villages by the same names which are about 15 km apart along the North Thompson River, north of Kamloops on Provincial Highway 5 (Fig. 1), as Berry refers to 3 separate sites near Chu Chua, Joseph Creek, and small floras from Darlington Creek (3 species) and Newhykulston Creek (11 species). Wolfe and Tanai (1987) cite a Geological Survey of Canada locality number (G.S.C. plant loc. 4821) as Chu Chua Creek which is just on the south edge of the village by the same name, whereas Joseph Creek is 12.5 km north of Chu Chua village. The G.S.C. Ottawa collections from Chu Chua are catalogued under four main locality numbers corresponding to the separate areas of outcrop from which Berry (1926) described taxa. Ewing (1981) refers coal-bearing sediments in this area to the Early Eocene Chu Chua Formation, noting similarities to the Coldwater beds near Merritt that include the Quilchena flora. Wolfe et al. (1998) suggested an age of 48–50 Ma for the Chu Chua flora (Fig. 3).

Some of the principal species from Berry's (1926) work are reproduced from the original plates in Figure 5. The synonymies and previously published suggested nomenclatural updates of Berry's taxa (e.g., Brown 1962; Wolfe and Wehr 1987; Gooch 1992; McLain and Manchester 2001; Denk and Dillhoff 2005) are provided in the caption for this figure. Berry (1926) noted 29 species of plants at Joseph Creek and area, ranging from *Equisetum*, *Ginkgo* and taxodioid Cupressaceae (*Glyptostrobus*, *Sequoia*, '*Taxodium' occidentalis*), to Pinaceae, dicots (e.g., *Acer*, *Comptonia*, *Sassafras*, *Trochodendroides*, others) as both seeds and leaves, and monocots (Fig. 5). Wolfe and Wehr (1987) when describing *Bohlenia insignis* from Republic noted the common presence of *Dipteronia* fruits with leaflets matching *Bohlenia* Wolfe et Wehr in both the Republic and Chu Chua floras (i.e., '*Myrica uglowi*', Fig. 5 C). Wolfe et al. (1998) recorded 24 dicot leaf morphotypes for Chu Chua, including; *Alnus* (Fig. 5 B), *Betula leopoldae*, *Bohlenia insignis* (Fig. 5 C), *Carya* (Fig. 5 C), *Comptonia* (Fig. 5 A), *Cornus*, *Corylus*, *Fagus*/*Castanea*, *Joffrea*, *Langeria magnifica* (Fig. 5 C), *Prunus*, *Physocarpus*, *Sassafras hesperia* (Fig. 5 D), *Ulmus* (Fig. 5 B) and various indeterminate taxa. Fruits of *Acer wehri* (Wolfe and Tanai 1987) and *Pseudolarix* (Gooch 1992; LePage and Basinger 1995) are recorded from Chu Chua, as are leaves of *Ulmus chuchuanus* (Denk and Dillhoff 2005, who refer to the site as equivalent to Joseph Creek). McClain and Manchester (2001) recorded fruits of *Dipteronia* from Joseph Creek, and also reported a limited pollen flora containing *Pinus*, taxodioid Cupressaceae, *Alnus*, *Corylus*, *Ulmus*, and occasional *Tiliaeopollenites*, and *Pistillipollenites*. Berry's (1926) type material is in the Canadian Museum of Nature, and additional material is housed in the G.S.C. collections in Ottawa.

Quilchena and Falkland

The Quilchena fossil site (Fig. 1; Fig 3; Fig. 4 D) has been known since before 1890 (Penhallow 1904, 1908; references cited in Archibald and Mathewes 2000). Fossil plants were first reported from the Coldwater Beds at the Quilchena site and nearby by Penhallow (1908). Mathewes and Brooke (1971) reviewed these records and described several conifers and dicots. These observations were updated briefly in Greenwood et al. (2005) and Dillhoff et al. (2005), and Denk and Dillhoff (2005) listed specimens of *Ulmus okanaganensis* from Quilchena. Mathewes et al. (this volume) provide an update on the megaflora, describe the palynoflora, and provide new paleoclimate estimates. As is the case for many of these sites, a diverse insect fauna is also known (e.g., Wilson 1977*b*; Douglas and Stockey 1996; Archibald and Mathewes 2000; Archibald et al. 2010, 2014). Hills and Baadsgaard (1967) dated Quilchena as Middle Eocene based on the K-Ar method; however, a more recent ^{39}Ar-^{40}Ar date by Villeneuve and Mathewes (2005) from a bentonite that is interleaved within the shales dated the Quilchena sediments at 51.5 ± 0.4 Ma, so Early Eocene (Mathewes et al. this volume) (Fig. 3). The Coldwater Beds are correlated with the Allenby Formation (Read 2000), so are close in age to the Princeton area localities (e.g., Similkameen and Tulameen River sites such as the Princeton Chert, Tulameen Road, Thomas Ranch, as well as One Mile Creek).

The Falkland site (Fig. 1; Fig. 6 B) was known primarily from insect (Rice 1959; Archibald 2005) and fish fossils described from there (Wilson 1977*a*), with Greenwood et al. (2005) and Moss et al. (2005) providing initial summaries of the megaflora and palynoflora respectively. *Ulmus okanaganensis* was reported from Falkland (as 'Falklands' *sic*) by Denk and Dillhoff (2005). Falkland has been dated to 50.61 ± 0.16 Ma (Fig. 3), using U–Pb analysis of zircons from a prominent volcanic ash layer within the fossil beds (Moss et al. 2005), which are an unnamed lacustrine shale member within the Tranquille Formation (Smith et al. 2009 and references cited therein).

Robin Smith intensively sampled the site for a paleocological study of the megaflora (Smith et al. 2009, 2010, 2012; Smith 2011; Moss et al. this volume). Smith described a highly diverse megaflora rich in both conifers (Pinaceae and Cupressaceae) as seeds, cones, and foliage, as well as a diverse monocot and dicot leaf and seed flora including new records of *Dipteronia brownii* (McClain and Manchester 2001). She figured several ferns including *Azolla* and two unidentified pinnate terrestrial ferns.

Smith's study was the first to apply a quantitative sampling methodology called 'census sampling' to a Canadian Okanagan Highlands megaflora, allowing comparison with a largely unpublished quantitative study of the Republic flora (Passmore et al. 2002; Wilf et al. 2003) and diversity at other Early Eocene sites in North and South America (Smith et al. 2012). This approach yielded high quality data on plant taxon occurrence and abundance through a 3 m sampled vertical sequence at Falkland (Fig. 6 B), demonstrating concomitant changes in the Early Eocene lake-side forest composition in parallel with changes in climate with stratigraphic depth over time (about 6000–8000 years) from leaf and taxon-based climate proxies, and falling atmospheric CO_2 levels estimated from *Ginkgo* leaf stomatal frequency (Smith et al. 2010, 2012). A parallel pollen-based study of floristic change within the sequence sampled by Smith is reported by Moss et al. (this volume). The pattern of diversity over the sampled sequence, using either leaves (Smith et al. 2012) or pollen (Moss et al. 2016), is consistent with landscape-scale disturbance by volcanism as a factor promoting high diversity in the Falkland fossil flora.

Princeton compression floras: One Mile Creek, Thomas Ranch

The richness of paleobotanical resources from the Princeton Basin was first reported extensively by Penhallow (1908). Several shale compression fossil localities occur throughout the Princeton area (Fig. 1), including Pleasant Valley (from coal mine tailings, also the source of the mammal fossil used in Allenby Formation biostratigraphy; Russell 1935; Gazin 1953), One Mile Creek, China or Asp Creek, sites along the Similkameen River (Allenby, Ashnola shale, Whipsaw Creek), and sites along the Tulameen River (also known as the north fork of the Similkameen River in old reports) such as Tulameen Road, Thomas Ranch, and Vermillion Bluffs.

One Mile Creek (Fig. 1; Fig 6 F) is a site located approximately 9 km north of Princeton in outcrop of the Hardwick Sandstone unit of the Allenby Formation on the west side of Provincial Highway 5A, near the confluence of Allison and Summers creeks. Greenwood et al. (2005) considered One Mile Creek to be Early Eocene based on a U-Pb date of 52.08 ± 1.2 Ma for outcrop at Hospital Hill in Princeton of the Vermillion Bluffs shale unit (Moss et al. 2005), which overlies the Hardwick sandstone (Read 2000) (Fig. 3). Beautifully preserved plants are found in a light gray-tan matrix. Fossils from this locality cannot be split easily along the bedding planes like the typical lacustrine deposit shales. The matrix is very hard and, instead, slabs of shale are excavated and then left to weather, eventually allowing for "pop-outs" of leaves and other remains.

The One Mile Creek site is well known for its whole plant reconstruction of *Betula leopoldae* (Crane and Stockey 1987), a plant represented by abundant leaves, fruits, and pistillate and staminate catkins, suggesting it may have been a dominant taxon here. Additionally five species of *Acer* fruits were described from One Mile Creek in Wolfe and Tanai's 1987 monograph on fossil *Acer*; *A. wehri*, *A. hillsi*, *A. rousei*, *A. spitzi* and *A. stonebergae.* Manchester (2001) noted leaves of *Aesculus* were present. Other plants initially named from One Mile Creek include *Neviusia dunthornei* (Rosaceae, DeVore et al. 2004), and *Tetracentron hopkinsii* (Trochodendraceae, Pigg et al. 2007). A diverse flora, yet to be formally described, includes mosses (Kuc 1972, 1974), many Rosaceae including *Rubus*, *Stonebergia*, *Amelanchier*, several species of *Prunus*, as well as *Cercidiphyllum*, *Fagus*, *Sambucus*, *Tsukada*, *Pterocarya*, *Ulmus*, *Pseudodolarix arnoldii* (Gooch 1992; LePage and Basinger 1995), and well preserved *Pinus* needle fascicles, seeds and seed cones.

Another site referred to as Thomas Ranch (Fig. 1; Fig 6 E) was recently detailed by Dillhoff et al. (2013). This site is very close to the Tulameen Road site (Penhallow 1908, Wilson 1977*c*; Douglas and Stockey 1996) and certainly samples the same sediments (Vermillion Bluffs shale), and is likely the same site (DeVore and Pigg 2010). Dillhoff et al. (2013) considered the Thomas Ranch site Early Eocene based on recent radiometric dates for Allenby Formation in the area (Fig. 3). Thin paper shales from the Tulameen Road site and nearby with abundant *Azolla* have been known from the time of Penhallow (in J.W. Dawson 1890), who referred to them as *Azollophyllum primaevum.* They were later renamed *Azolla primaeva* by Arnold (1955). This is also the site for *Palaeocarpinus stonebergae*, named for Margaret Stoneberg, former curator of the

Princeton and District Museum (Pigg et al. 2003).

In addition to these taxa, Dillhoff et al. (2013, Table 1) described a total of 76 megafossil morphotypes, taxa including a bryophyte, both typical *Ginkgo* and the highly dissected form first figured by Verschoor (1974) and referred to *Ginkgo dissecta* by Mustoe (2002), *Metasequoia*, *Cunninghamia*, *Abies milleri*, a 5-needled *Pinus* and seeds, seeds and branches of *Picea*, and *Pseudolarix* cone scales and seeds (Gooch 1992). Among the dicots are *Betula*, *Macginitiea* and *Macginicarpa*, one type of *Acer* samara, *Cercidiphyllum*, *Fothergilla*, *Rhus*, *Rubus*, *Prunus*, *Comptonia*, *Sassafras hesperia* and other lauraceous leaves, *Fagopsis*, an unusual pinnately compound leaf and an unnamed fruiting structure. Dillhoff et al. (2013) also studied the palynomorphs from Thomas Ranch and found they included an abundance of conifers, with the most common angiosperm types being Betulaceae.

The Republic Flora

In northeastern Washington, the Republic flora was known from the early 1900's, as fossil leaves and fish were recovered during mining operations. Early studies by Berry (1929) and Brown (1935, 1937, 1939) described Republic fossils but the site was regarded as conifer-dominated, relatively depauperate and of Oligocene to Miocene age. Wilf et al. (2003, 2005) and Radtke et al. (2005) considered the Republic flora to be Early Eocene, the latter authors citing an unpublished ^{40}Ar-^{39}Ar date of 49.4 ± 0.5 Ma (Fig. 3).

The Republic flora remained poorly known scientifically after its initial discovery in the early 1900's and the studies of the 1920's and 1930's. In 1977, it gained considerable new significance, when Wes Wehr, Affiliate Curator of the Burke Museum, University of Washington in Seattle, and Kirk R. Johnson discovered a highly productive layer of fossils at the "Corner Lot" at the north end of Clark Street, the main street in Republic (Archibald et al. 2005).

Wehr brought the site to the attention of Jack Wolfe, who incorporated Republic into the localities that fueled his research on paleoclimate and leaf physiognomy. Together he and Wehr produced a U.S.G.S. monograph on the dicot flora of Republic (Wolfe and Wehr 1987). This monograph described 24 taxa including new species named for many colleagues and personal mentors including Elso Barghoorn (*Barghoornia*), Ann Bohlen (*Bohlenia*), Kirk R. Johnson (*Tilia johnsoni*), Suzanne Langer (*Langeria magnifica*), and Virginia Page (*Photinia pagae*), among others.

Also in 1987, Wehr and Republic city commissioner Bert Chadwick established the Stonerose Interpretive Center (Perry and Barksdale 1996), and collecting was made officially open to the public (Joseph 1987). Stonerose was initially funded by the city of Republic, and it is currently governed by a board of directors known as the Friends of Stonerose Interpretive Center and Eocene Fossil Site (Perry and Barksdale 1996; Sternberg et al. 2014).

Wehr continued to promote the Republic flora as a public venue by conducting biennial informal workshops at the site until his death in 2004. He published a series of short papers in *Washington Geology*, the journal of the Washington Department of Natural Resources (Wehr 1995; Wehr and Manchester 1996; Wehr and Hopkins 1994; Pigg and Wehr 2002). At the same time Wehr was promoting Republic to the general public as a tool for informal education and outreach he was busily supplying the scientific community with numerous research-quality specimens of Republic plants and insects. He continued these efforts from his unsalaried position at the Burke Museum, and was honored by the Paleontological Society with the Harrel R. Strimple Award in 2003.

Several fossiliferous sites are known in and around Republic (Wolfe and Wehr 1987; Gaylord et al. 1996). Within the town are the Corner Lot site originally studied by Wehr and Johnson and the Boot Hill site (Fig. 6 A), which is particularly productive and is the locality where managed public collecting is mediated by Stonerose Interpretive Center staff. Pigg et al. (2011) provided an informational guidebook for the Republic flora, available through the Stonerose Interpretive Center. Also within the Republic Basin are sites at Gold Mountain or "Grandpa's Fossil Patch", the source of *Palaeocarpinus barksdalae* (Pigg et al. 2003), Knob Hill, and the Golden Promise Mine. North of Republic in the Curlew Basin is Mount Elizabeth, a locality that produces a variety of taxa, including the heterosporous water fern *Salvinia*. To the north and west is the Toroda Creek Basin, which has several localities no longer accessible and others on privately owned land. Several of Wolfe and Wehr's (1987) specimens are from the Toroda Creek area.

The Republic flora has been estimated conservatively to have around 250 taxa (DeVore and Pigg 2010), but more recent estimates are considerably larger (M. Sternberg, personal communication, 2015). Below we highlight some of the well documented genera. Filcalean ferns are generally rare, although *Osmunda* and at least one additional fern bearing fertile sori are known. As with much of the Okanagan Highlands, *Azolla* can be often abundant on layers of thin paper shales. *Salvinia* is known only at Mt. Elizabeth. A cycad with *Zamia*-like pinnae described from two fragmentary leaves by Hopkins and Johnson (1997) is now known from a dozen specimens and is currently under study. *Ginkgo* leaves are not particularly common; however, both the more typical shallowly bilobed and more deeply lobed forms are present (Mustoe 2002). Conifers are well represented at Republic, with *Metasequoia* foliage among the most common plant fossils found. Other conifers include *Sequoia* and related forms, *Chamaecyparis*, *Taiwania, Sciadopitys,* well preserved leaves, seed and pollen cones and seeds of several types of *Pinus*, *Picea*, *Abies milleri* (Schorn and Wehr 1986,1996) and two species of *Pseudolarix* based on cones, cone scales and seeds (Gooch 1992).

The most common dicots at Republic are leaves of *Alnus parvifolia* (Wolfe and Wehr 1987; Wang and Manchester 2015). Betulaceae is also represented by *Betula leopoldae* similar to the One Mile Creek material (Crane and Stockey 1986). Fruits of *Corylus johnsoni*, *Carpinus reedae, Palaeocarpinus barksdalae* and variations of *Palaeocarpinus* sp. pollen catkins, and additional leaves of Betulaceae (Pigg et al. 2003). Trochodendraceae is represented by *Trochodendron nastae* leaves and associated *Trochodendron* sp. infructesences as well as *Zizyphoides* sp. leaves (DeVore and Pigg 2013), a fruit of *Nordenskioldia* (Pigg et al. 2001), and *Tetracentron* sp. leaves now identifiable to *T. hopkinsii* (Pigg et al. 2007). Additional *Trochodendron*-like and *Tetracentron* fruits are currently under study.

Platanaceae fossil taxa include *Macgnitiea* and *Macginicarpa* (Manchester 1986). Hamamelidaceae include leaves of *Fothergilla dunthornei* and *Corylopsis reedae* (Radtke et al. 2005). *Fagopsis* (Manchester and Crane 1983) and *Fagus* (Manchester and Dillhoff 2004) are known from both leaves and fruits, as are two types of elms, *Ulmus chuchuanus* and *U. okanaganensis* described primarily from McAbee by Denk and Dillhoff (2005). Sapindaceae are well represented by several *Acer* species (Wolfe and

Tanai 1987), *Dipteronia* (McClain and Manchester 2001), at least two types of *Koelreuteria* (Wang et al. 2013), and a wide range of foliage types.

Among the most diverse families found at Republic is the Rosaceae. Published taxa include flowers of *Prunus cathybrownae* and *Oemleria janhartfordae* (Benedict et al. 2011) and leaves of *Photinia pagae* (Wolfe and Wehr 1987). Other forms are similar to extant genera of *Spiraea*, *Sorbus*, *Amelanchier*, and *Crataegus*, among other genera as reviewed by DeVore and Pigg (2007). Among these rosaceous leaves are forms that show morphological features of the type found in modern rosaceous hybrids, in particular of the genus *Sorbus*. An analysis of these putative hybrid Eocene leaves is provided by DeVore and Pigg (this volume).

Additional significant plant remains found at Republic include: *Florissantia* (Manchester 1999); *Eucommia* (Call and Dilcher 1997); two forms of *Ribes*; *Rhus* and other Anacardiaceae foliage types; *Cornus*; *Comptonia*; *Tilia johnsoni* (Wolfe and Wehr 1987); *Itea* (Hermsen 2013); representatives of Bignoniaceae, Magnoliaceae, Melastomataceae (Renner et al. 2001); Myrtaceae; and Lauraceae including *Sassafras* and other forms. *Nuphar carlquistii* (DeVore et al. 2015) was recently published on the basis of fossil fruit and seed remains. Several monocots are also recognized at Republic, including a distinctive sedge. Many additional unidentified forms remain to be studied.

The Princeton chert

Along with the leaf compression sites described above, the Princeton chert is a second type of plant fossil site - permineralized plant organs preserved in 3 dimensions - that has provided additional information about the Okanagan Highlands plants (Fig 6 C, D). Boneham (1968) included the Princeton chert in his pollen analyses, and enumerated the cyclic layers of coal and chert in the main deposit, a practice continued by Stockey and her students (Fig 6 D).

The Princeton chert is recognized as part of the Ashnola shale (or Ashnola chert in Wilson 1980) in the Allenby Formation (Read 2000) and previously has been considered Middle Eocene based on regional correlations utilizing mammal fossils, pollen, and radiometric dates (Boneham 1968; Basinger and Rothwell 1977; Read 2000; Mustoe 2011). Initial radiometric dates of 49–50 Ma were based on the K-Ar method for volcanic sediments at Allenby near the chert site (Hills and Baadsgaard 1967). Little et al. (2009) (also see DeVore and Pigg 2010) cite an unpublished radiometric date of 48.7 Ma (without an age uncertainty value) for ash layer #22 in the Princeton Chert, placing the Princeton chert as latest Early Eocene (i.e., Early Eocene - Middle Eocene boundary at 47.8 Ma; Cohen et al. 2013) (Fig. 3). This value is consistent with recent regional radiometric dating of Allenby Formation volcanics (Ickert et al. 2009). As the Ashnola shale is stratigraphically high in the Allenby Formation (Boneham 1968; McMechan 1983; Read 2000), the Princeton chert appears to be the youngest of the Okanagan Highlands floras, as either latest Early Eocene or earliest Middle Eocene.

The Princeton chert comprises 49 main and other minor layers of interbedded cherts and coals that extend out into the Similkameen River (Boneham 1968; Basinger and Rothwell 1977; Mustoe 2011) (Fig. 6 C, D). Much of this material can be prepared with the cellulose acetate peel technique as modified by Basinger and Rothwell (1977) using hydrofluoric acid to dissolve the silicates. Interestingly, chert blocks of seemingly identical nature, occurring only a few meters above the river, cannot be peeled.

The first megafossils described from the Princeton chert were *Pinus* cones and leaves (Miller 1973) and the rhizomatous plant *Eorhiza arnoldii* (Robison and Person 1973). Basinger described *Paleorosa* (1976*a*) and along with Rothwell provided early overviews of the flora and descriptions of and *Metasequoia milleri* (Basinger 1976*b*, 1981, 1984; Basinger and Rothwell 1977; Rothwell and Basinger 1979). A sustained series of papers by Stockey with her students and colleagues from the early 1980s on described additional dicots, monocots, ferns, and fungi.

Plants known from the Princeton chert include five filicalean ferns: *Osmunda*, *Dennstaedtiopsis aerenchymata*, and the blechnoid *Trawetsia princetonensis* (Smith et al. 2006); *Makotopteris* (Stockey et al. 1999) and *Dickwhitea* (Karafit et al. 2006). The *Dennstaedtiopsis* fern is fairly common and typically represented by its vegetative rhizome and higher level frond segments. It has abundant aerenchyma in its ground tissues, keying it as an aquatic plant (Cevallos-Ferriz et al. 1991).

Conifers include *Metasequoia milleri,* for which stems, leaves, seed and pollen cones are known (Rothwell and Basinger 1979; Basinger 1981, 1984) and several species of *Pinus*, based on leaves, seed cones, and seeds (Miller 1973; Stockey 1984). *Pinus arnoldii* has been reconstructed as a "whole plant" (Klymiuk et al. 2011).

The most abundant plant remains in the Princeton chert, occurring in many of the chert layers, are aquatic to semi-aquatic plants such as the rhizomatous stem *Eorhiza arnoldii*. Rhizomes of *Eorhiza* were described by Robison and Person (1973) and later the vegetative plant was reconstructed in more detail by Stockey and Pigg (1994). Young inflorescences, flowers, mature fruits and senescent fruits of *Princetonia allenbyensis* (Stockey 1987; Stockey and Pigg 1991) were thought possibly to be the flowers and fruits of this plant, but organic attachments have yet to be found.

Other remains that occurred along with *Eorhiza* are *Allenbya collinsae*, a waterlily seed in the *Victoria* Lindley lineage (Nymphaeaceae; Cevallos-Ferriz and Stockey 1989), *Keratosperma* (Araceae; Cevallos-Ferriz and Stockey 1988b; Smith and Stockey 2003); and Lythraceae, represented by *Decodon* fruits, seeds, stems and roots, and *Duabanga*-like leaves (Cevallos-Ferriz and Stockey 1988a; Little 2003, 2005; Little et al. 2004). Small lauraceous flowers and fruits (Little et al. 2009), flowers of Piperales (Smith and Stockey 2007), and fruits and seeds of *Paleomyrtinaea* (Myrtaceae, Pigg et al. 1993) are often associated with the aquatic plant remains.

Considerably less common are plant remains from 'upland' sites. Whereas thousands of seeds are known for some of the aquatic plants like *Allenbya*, the 'upland' plants are based on only a handful of specimens. These include *Prunus* fruits and wood (Cevallos-Ferriz and Stockey 1990b, 1991), twigs of Magnoliaceae (Cevallos-Ferriz and Stockey 1990*a*, and seeds of Vitaceae (Cevallos-Ferriz and Stockey 1990*c*). Other more rarely occurring forms are the flowers of *Paleorosa similkameenensis* (Rosaceae; Basinger 1976*b*; Cevallos-Ferriz et al. 1993) and the sapindaceous flower *Wehrwolfea striata* (Erwin and Stockey 1990).

The Princeton chert is also known for its diverse array of monocots that include palms, Alismataceae, Juncaceae/Cyperaceae, and Liliales (Erwin and Stockey 1989, 1991*a*, *b,* 1992, 1994; Smith and Stockey 2003). A rich assemblage of fungi have been described from the Princeton chert (Currah et al. 1991, 1998; LePage et al. 1994, 1997; Klymiuk et al. (2015*a*, *b*).

As a site with permineralized plant remains, the Princeton chert has offered a distinct opportunity to compare anatomical structures of Eocene plants with other permineralized floras of contemporary age. Regionally, these include the Clarno Nut Beds from central Oregon (Manchester 1994; Wheeler and Manchester 2002) and the related flora at Post, Oregon and the Appian Way flora of Vancouver Island, B.C. (Mindell et al. 2009). In a broader context these floras can be compared with the Middle Eocene Messel of Germany (Collinson et al. 2012) and the Lower Eocene London Clay (Reid and Chandler 1933; Collinson 1983).

Summary

In this contribution we have traced the history of the paleobotany of the Okanagan Highlands, its researchers, its localities and its fossils. We have seen that these floras serve to address a wide array of questions, both directly about the floras and questions of interest to the broader community of scientists. Highlights include the following:

1. Proxies for climate reconstruction. Since the works of Dawson and Penhallow, and Rouse through to present researchers, the Okanagan Highlands sites have been recognized as having a cooler climate than the Eocene floras of the coastal lowlands (Rouse 1962; Rouse et al. 1970; Johnson 1996; Greenwood et al. 2005). Several authors have quantified this perception, applying both leaf physiognomy and nearest living relative analysis to reconstruct microthermal (MAT 10–15° C) and wet environments (MAP > 100 $cm.a^{-1}$) (Greenwood et al. 2005; Smith et al. 2009, 2012; Dillhofff et al. 2013; Gushulak et al. this volume; Mathewes et al. this volume).

2. Comparative biodiversity. From the time of the Wolfe and Wehr (1987) monograph, the Republic flora especially has been noted as a highly diverse flora (Wolfe and Wehr 1987; Smith et al. 2012; Wilf et al. 2003). Archibald et al. (2010) using a small leaf fossil

sample showed high plant diversity for McAbee also, and proposed that the 'tropical style' diversity of McAbee insects and plants was due to low temperature seasonality in the Early Eocene. Smith et al. (2012) showed that the Falkland site may be of even higher diversity, and proposed that patch dynamics and succession due to landscape-scale disturbance (e.g., area volcanism) may have played a role in generating this diversity. Republic and McAbee were used as the proxy for Northern Hemisphere temperate floras in comparative studies of the highly diverse tropical floras of Early Eocene Patagonia and their relationship to insect diversity (Wilf et al. 2003, 2005; Archibald et al. 2010, 2013). 3. Contribution to taxonomic and phylogenetic studies of many important families. The Okanagan Highlands has provided significant and sometimes the oldest records for key temperate families including Rosaceae, Pinaceae, Betulaceae, Sapindaceae (Basinger 1976*b*;Wolfe and Tanai 1987; Wolfe and Wehr 1987; Cevallos-Ferriz et al. 1993; Manchester 1999; DeVore et al. 2005; DeVore and Pigg 2007). 4. Paleobiogeography of Northern Hemisphere Eocene plants. The Okanagan Highlands plants have figured into numerous studies of the paleobiogeography of many groups. Many of the plants in the Okanagan Highlands floras occur only in Asia today (e.g., *Pseudolarix*, *Trochodendron*, *Tetracentron*, *Cercidiphyllum*, *Corylopsis*, *Eucommia*, *Dipteronia*; Manchester 1999; McClain and Manchester 2001; DeVore et al. 2005) or are closely related to the extant Asian forms of larger taxa (e.g., *Corylus*, *Carpinus*, Pigg et al. 2003; *Neviusia,* DeVore et al. 2004). Others document taxa with wider Northern Hemisphere distributions (Manchester 1999; DeVore and Pigg 2010).

5. Researchers have used the Republic flora as the prime example of a temperate flora in the fossil record for use when looking at physiological responses to different types of

environments. For example, Royer et al. (2007) used Republic for this purpose in modelling leaf economics of temperate vs. tropical plants, and DeVore and Pigg (2014) have documented the presence of heterophyllous leaves and branch dimorphism as dormancy responses in some taxa.

6. Examples of evolutionary innovation. The value of morphological and physiological innovations to evolutionary adaptation can be documented in the Okanagan Highlands floras, particularly at Republic. In more recent work it has been demonstrated that distinctive leaf morphologies and venation patterns that are consistently found in modern leaves of hybridized plants also occur in the Eocene at Republic (DeVore and Pigg, this volume). This suggests that mechanisms of evolutionary change that occur today in disturbed habitats among such families as Rosaceae and Anacardiaceae were significant in Eocene paleoenvironments of the Okanagan Highlands.

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Figure captions

Figure 1. Map showing the Early Eocene Okanagan Highlands fossil sites (open circles) and nearby cities (small filled circles). Modified from Dillhoff et al. (2013, Fig. 1).

Figure 2. Early paleobotanists who studied the Okanagan Highlands floras. (A). J. William Dawson. (B). George Mercer Dawson. (C). David Penhallow. Reproduced with permission from the McCord Museum, Montreal.

Figure 3. Simplified stratigraphy of Allenby Formation (Princeton Basin), and Okanagan Highlands fossil sites. (A) K-Ar dates from Allenby Fm. from sources cited in Read (1987, 2000). (B) ^{40}Ar-^{39}Ar of Princeton Group volcanics from Ickert et al. (2009). (C) Rock unit relationships adapted from Read (2000); minor units not shown. (D) ^{40}Ar-^{39}Ar and Pb-U from tephra reported in Villeneuve and Mathewes (2005), Moss et al. (2005), Archibald et al. (2010), DeVore & Pigg (2010), and summarised in the text; *A* 48.7 Ma from ash layer #22 from the Ashnola Shale / Princeton Chert; *B* Vermillion Bluffs shale; *C* Hardwick sandstone. (E) Epoch and Stage Ages from Cohen et al. (2013). Hyperthermals: EECO - Early Eocene Climatic Optimum; ETM2 - Eocene thermal maximum 2; PETM - Paleocene-Eocene thermal maximum.

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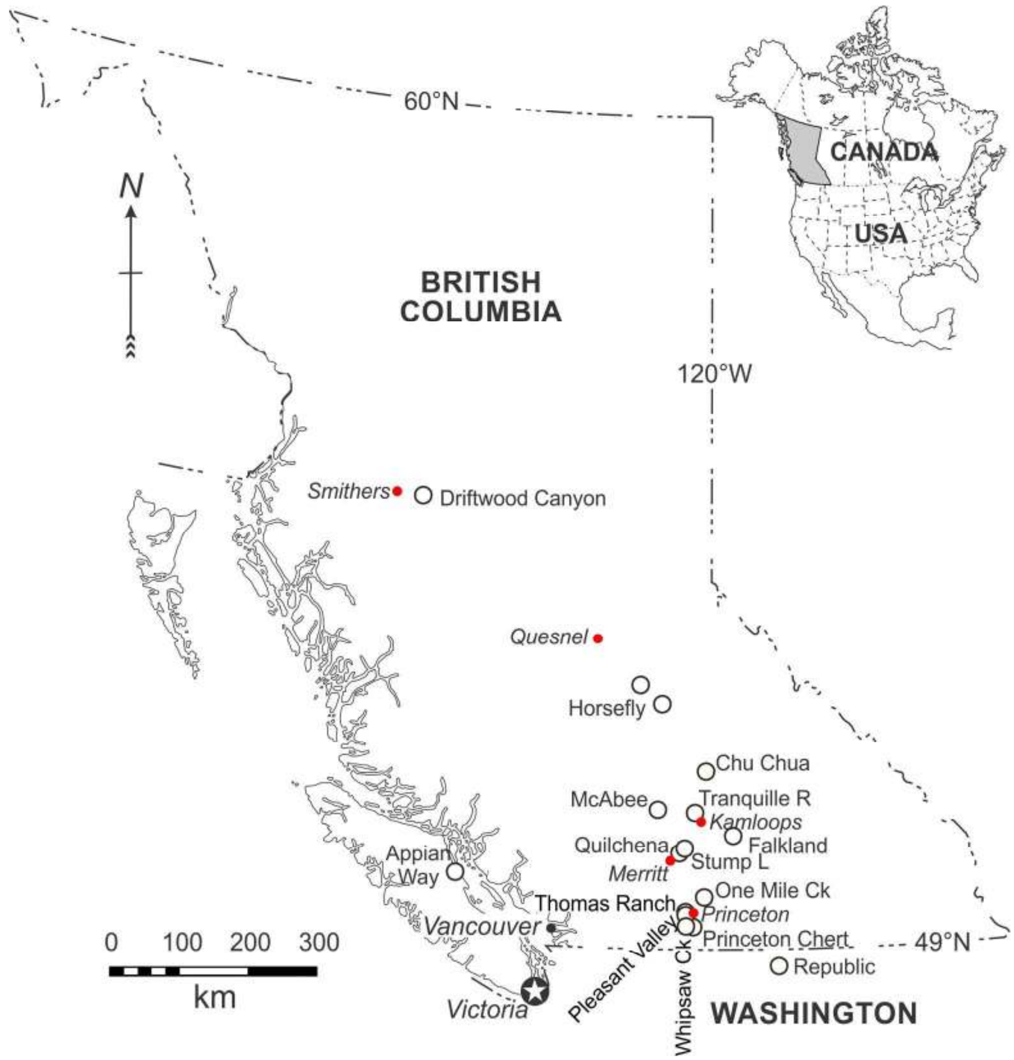

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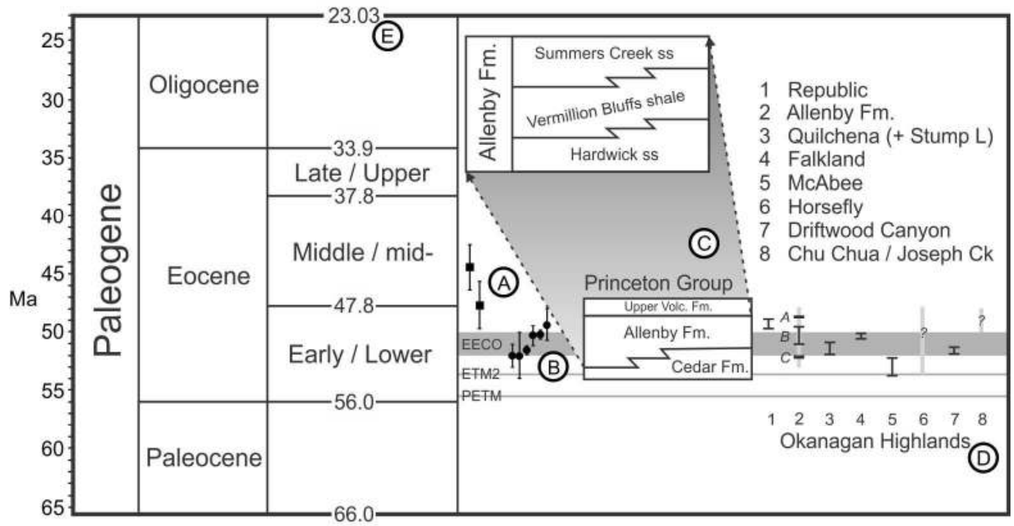

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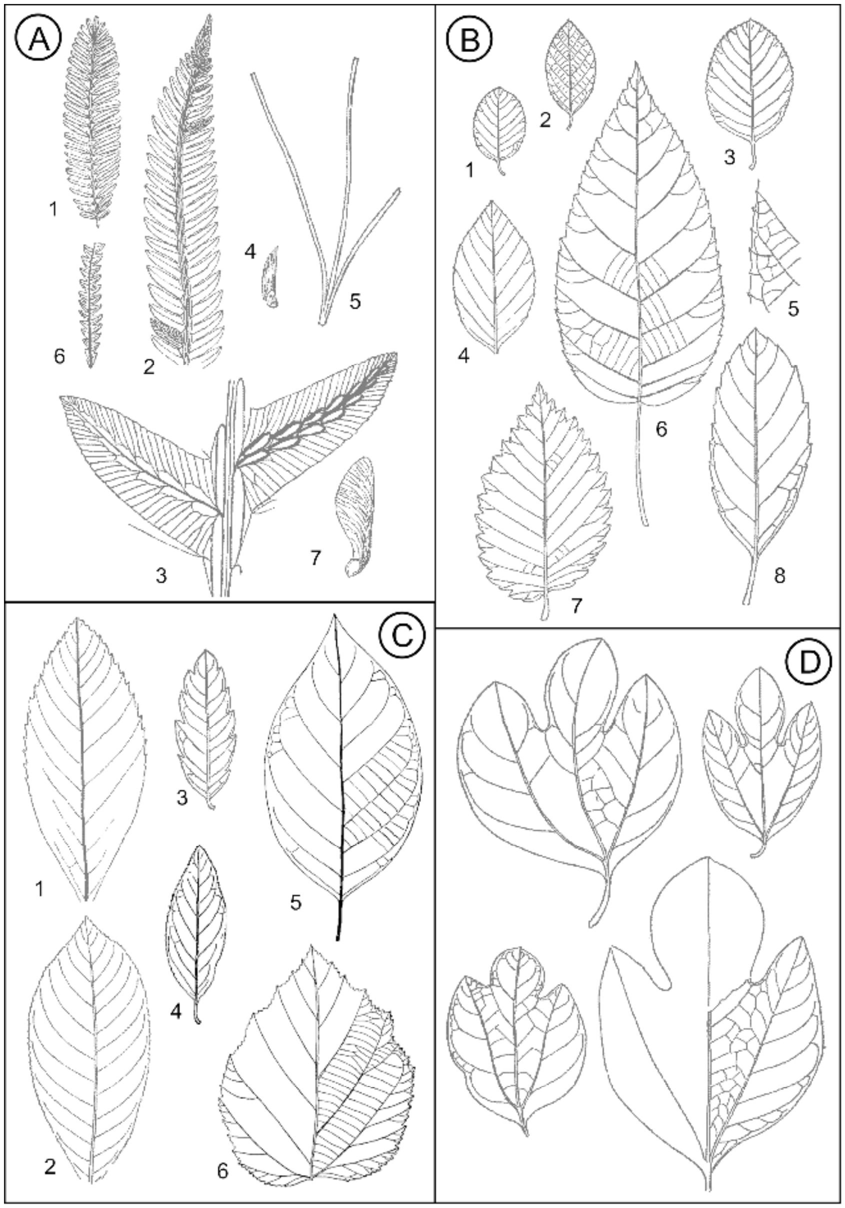

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