

Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia – Washington State) from palynology¹

Patrick T. Moss, David R. Greenwood, and S. Bruce Archibald

Abstract: Palynofloras from the middle Early to early Middle Eocene Okanagan Highlands (northern Washington State and southern British Columbia) are used to reconstruct vegetation across a broad upland Eocene landscape. In this preliminary report, forest floristic composition is reconstructed using palynological analysis of sediments from Republic, Washington; localities of the Allenby Formation in the Princeton region (Hospital Hill, One Mile Creek and Summers Creek Road), Hat Creek, McAbee, Falkland, Horsefly, and Driftwood Canyon, British Columbia. Wind-dispersed taxa were dominant in all samples, consistent with floras preserved in lacustrine and paludal depositional environments. *Pseudolarix* was dominant in five of the floras, but *Abies* (Falkland) or *Ulmus* (Republic Corner Lot site) were dominant in individual samples for some floras. Betulaceae were dominant for McAbee (*Alnus*) and Allenby Formation (*Betula*), matching megafloreal data for these sites. Some taxa common to most sites suggest cool conditions (e.g., *Abies*, other Pinaceae; *Alnus*, other Betulaceae). However, all floras contained a substantive broad-leaved deciduous element (e.g., Fagaceae, Juglandaceae) and conifers (e.g., *Metasequoia*) indicative of mesothermal conditions. Palms were only abundant in the Hat Creek coal flora, with very low counts recorded for the Falkland, McAbee, and Allenby Formation sites, suggesting that they were rare in much of the landscape and likely restricted to specialized habitats. Thermophilic (principally mesothermal) taxa, including palms (five sites) and “taxodiaceous” conifers, may have occurred at their climatic limits. The limiting factor controlling the regional distribution of thermophilic flora, which include primarily wetlands taxa, may be either climatic or edaphic.

Résumé : Les palynoflores de l'Éocène précoce moyen à moyen précoce des hautes terres de l'Okanagan (nord de l'État de Washington, sud de la Colombie-Britannique) sont utilisées pour reconstruire la végétation à travers un vaste paysage de milieux secs datant de l'Éocène. Dans ce rapport préliminaire, la composition floristique de la forêt est reconstruite au moyen d'une analyse palynologique de sédiments provenant de : Republic, des localités de la formation Allenby dans la région de Princeton (Hospital Hill, One Mile Creek et la route de Summers Creek), Hat Creek, McAbee, Falkland, Horsefly, et Driftwood Canyon. Les taxons distribués par le vent dominaient dans tous les échantillons, ce qui concorde avec les flores préservées dans les environnements de déposition lacustres et paludéens. *Pseudolarix* dominait dans cinq des flores, mais *Abies* (Falkland) ou *Ulmus* (site de Republic Corner Lot) dominait dans les échantillons individuels pour certaines flores. Les Bétulacées dominaient pour McAbee (*Alnus*) et la Formation d'Allenby (*Betula*) concordant avec les données mégaflorales de ces sites. Quelques taxons communs à la plupart des sites suggèrent des conditions fraîches (p. ex. *Abies*, d'autres Pinacées; *Alnus*, d'autres Bétulacées). Toutefois, toutes les flores contenaient un élément substantif décidué à feuilles larges (p. ex. Fagacées, Juglandacées) et des conifères (p. ex. *Metasequoia*) indicatif de conditions mésothermes. Les palmiers étaient abondants seulement dans la flore houillère de Hat Creek, avec des comptages très faibles enregistrés pour les sites de Falkland, de McAbee et de la Formation Allenby, suggérant qu'ils étaient rares dans une grande partie du paysage et probablement restreints à des habitats spécialisés. Les taxons thermophiles (surtout mésothermes), incluant des palmiers (cinq sites) et des conifères de la famille des Taxodiacées, peuvent s'être trouvés à leurs limites climatiques. Le facteur limitatif contrôlant la distribution

Received 9 March 2004. Accepted 25 October 2004. Published on the NRC Research Press Web site at <http://cjes.nrc.ca> on 14 March 2005.

Paper handled by Associate Editor J. Jin.

P.T. Moss.² School of Geography, Planning and Architecture, The University of Queensland, Brisbane QLD 4072, Australia.

D.R. Greenwood. Environmental Science, Brandon University, 270 18th Street, Brandon, MB R7A 6A9, Canada.

S.B. Archibald. Harvard University, Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, 26 Oxford Street Cambridge, MA 02138, USA.

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

²Corresponding author (e-mail: patrick.moss@uq.edu.au).

régionale des flores thermophiles, lesquelles comprennent principalement des taxons des zones humides, peut être soit climatique ou édaphique.

[Traduit par la Rédaction]

Introduction

Early to Middle Eocene palynofloras are preserved in a series of lacustrine shales and coal deposits covering a 1000-km north–south transect in south-central British Columbia and northern Washington State (Fig. 1). These preserve a record of the local and regional plant communities of the Okanagan Highlands, an Eocene uplands landscape. Data from the spore–pollen record complement the rich regional megafloral, insect, and fish fossil record (e.g., Mathewes and Brooke 1971; Basinger 1976, 1984; Wilson 1977a, 1977b, 1980; Basinger and Rothwell 1977; Wolfe and Wehr 1987; Erwin and Stockey 1989, 1994; Cevallos-Ferriz et al. 1991; Douglas and Stockey 1996; Archibald and Mathewes 2000; Greenwood et al. 2005).

Previous palynological studies of Okanagan Highlands Eocene sites have mostly focused on providing age control and stratigraphic profiles for the various lacustrine shale and coal deposits (e.g., Boneham 1968; Rouse 1977; Rouse et al. 1970; Church 1981; Hills 1965a, 1965b; Hills and Baadsgaard 1967; Hopkins 1980). In this paper, we examine multiple sites across this series to assess the effects of climate, latitude, paleoelevation, disturbance, and edaphic factors on the Eocene plant communities of the Okanagan Highlands based primarily on new palynological analyses. These sites are arrayed across a roughly north–south transect from Driftwood Canyon in the north (present latitude of 55°N) to Republic in the south (present latitude of 48°40'N) (Fig. 1), which we assess for the effects of latitude (see later in the text). Wolfe et al. (1998) and Tribe (2005) suggest that there was a high degree of variability in paleoelevation for the Okanagan Highlands, which would be expected to impact on community dynamics across the series. Greenwood et al. (2005) provide a detailed overview of previous paleoenvironmental research based on megafloral and faunal data, which will therefore not be discussed in any detail here. Palynological data are considered here, with regards to environmental variation within and among localities (e.g., climate, disturbance, aspect, edaphic conditions, and elevation), to assess prior models for the Okanagan Highlands landscape that posited segregation of plant communities into hinterland, higher elevation coniferous forests, and deciduous dicot-rich forests occupying lakeshore, swamp, and streamside localities (Rouse 1977; Rouse et al. 1970; Wolfe and Wehr 1987).

Localities and approach

Study area and fossil localities

Outcrops of seven regional depositional basins are considered here, which we have divided into four groups based on geographic distribution to facilitate interpretation of the effects of latitude (Fig. 1): Group 1 are the northern sites at Driftwood Canyon and the Horsefly River; Group 2 are the central shale sites of Falkland and McAbee; Group 3 are the central coal deposits at Hat Creek; and Group 4 are the southern

sites of Princeton (also known as the Allenby Formation and referred to as Allenby in this paper) and Republic. The majority of these locations occupy an area of ~700 km² and are predominately clustered in central southern British Columbia. These outcrops have been dated by either direct radiometric isotope analysis, or by biostratigraphic correlation by palynology and (or) megafossil insect and plant assemblages. All localities that have new ages provided by U–Pb or ⁴⁰Ar–³⁹Ar methodologies fall within the Early Eocene (Ypresian), indicating that the series as a whole is Early Eocene (Fig. 2), however, currently undated localities may yet fall within the early Middle Eocene (Lutetian); tephra from these sites (Horsefly, McAbee, Hat Creek, and others) are currently being analysed to resolve this question (Mortensen and Archibald, current research).

Group 1: Northern sites (Driftwood Canyon and Horsefly)

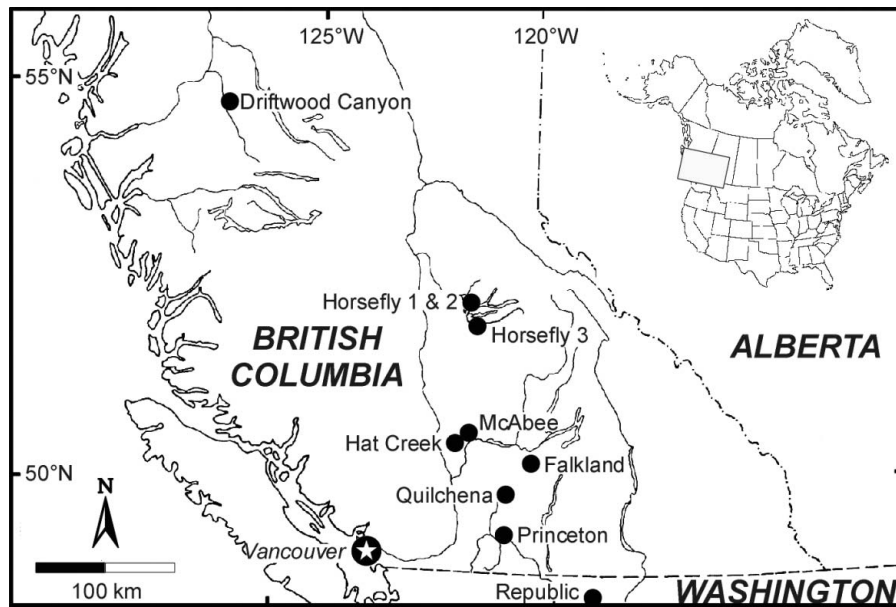
The most northerly site is Driftwood Canyon, located east of Smithers, British Columbia, in Driftwood Canyon Provincial Park, also at times referred to as Smithers (after the nearby town) and Driftwood Creek (e.g., Douglas and Stockey 1996). The sediments (Ootsa Lake Group) consist of buff to yellow fine-grained laminated shales. Two samples from Driftwood Canyon were analysed: Driftwood Canyon (Left Exposure) and Driftwood Canyon (Right Exposure). Preliminary U–Pb zircon analysis by Mortensen and Archibald (work in progress) gives an age for Driftwood Canyon of 51.77 ± 0.34 Ma.

Three samples (Horsefly 1, 2, and 3) were collected from shales of the Horsefly locality. These are exposed along the Horsefly River, about 8 km north and east of the town of Horsefly in the Cariboo region of south-central British Columbia, about 60 km east of Williams Lake on Highway 97. The Horsefly shales consist mostly of alternating dark- and light-coloured laminae, representing winter and summer deposition (Wilson 1977c), with interleaved tephra layers representing episodic volcanic eruptions. No radiometric age has been provided for the Horsefly locality, although it is considered contemporaneous with other Okanagan Highlands deposits through correlation of megafossil assemblages and palynology (Rouse et al. 1970; Wilson 1977a; Wolfe and Wehr 1987) and is, therefore, considered here to be most likely Early Eocene, although the possibility remains that it may be early Middle Eocene.

Group 2: Central shale sites (Falkland and McAbee)

The Falkland site is in the Columbia–Shuswap region of south-central British Columbia. The samples analysed, including Falkland 1a (lithified shale); Falkland 1b (unconsolidated shale or mudstone); and Falkland 2 (lithified shale), occurred in light to dark grey, often finely laminated shales and interleaved volcanics. This locality is not discussed in the literature (although it appears on a map, Fig. 1 of Wilson 1977a); we assign this shale deposit of unnamed formation

Fig. 1. Map showing the location of the fossil sites. Adapted from Wilson (1977b).



to the Kamloops Group, as it lies between Kamloops Group volcanics, and bears lithology close to that of McAbee. Preliminary U–Pb dating from zircons by Mortensen and Archibald (in progress) give an age of 50.61 ± 0.16 Ma for Falkland.

The McAbee site is located in the Thompson–Okanagan region of south-central British Columbia on the Trans-Canada Highway between Cache Creek and Kamloops, 1.3 km west of the point, where Battle Creek crosses the highway. Samples were collected from a recent quarry site that exposed a significant outcrop of light grey to dark brown laminated shales (unnamed formation, Kamloops Group). Although tephra beds are found interleaved amongst the shale beds in all of the localities mentioned here, these beds are most frequent within the McAbee shales (Fig. 3). These (McAbee 1, 2, 3, and 5) provide a stratigraphic profile of the outcrop: McAbee 1 the youngest and McAbee 5 the oldest. McAbee has been dated by recalculation of K–Ar data as ~ 51 Ma (Ewing 1981).

Group 3: Central coal sites (Hat Creek)

The Hat Creek samples are from sub-bituminous coal (Hat Creek Coal Formation, Kamloops Group) situated between Cache Creek and Lillooet in south-central British Columbia. At about 425 m in section, this locality is one of the thickest coal deposits in the world (Church 1981), being of comparable size to the Eocene Traralgon Seam (~ 400 m in section) from the Gippsland Basin in Victoria, Australia (Holdgate et al. 2000). Samples were hand collected from two test trenches exposing portions of Deposit 1: trench A (Hat Creek samples 4–6) and trench D (Hat Creek samples 1–3).

A north-trending syncline between trenches A and D inverts the age order of the two groups of samples 1–3 and 4–6, taken sequentially from east to west (N. Church; P. Read, personal communication, 2004). In trench A, sample 6 is the oldest, and 4 the youngest, while in trench D, sample 1 is the oldest and 3 the youngest. These represent samples of three of the four coal zones recognized in the No. 1 coal deposit

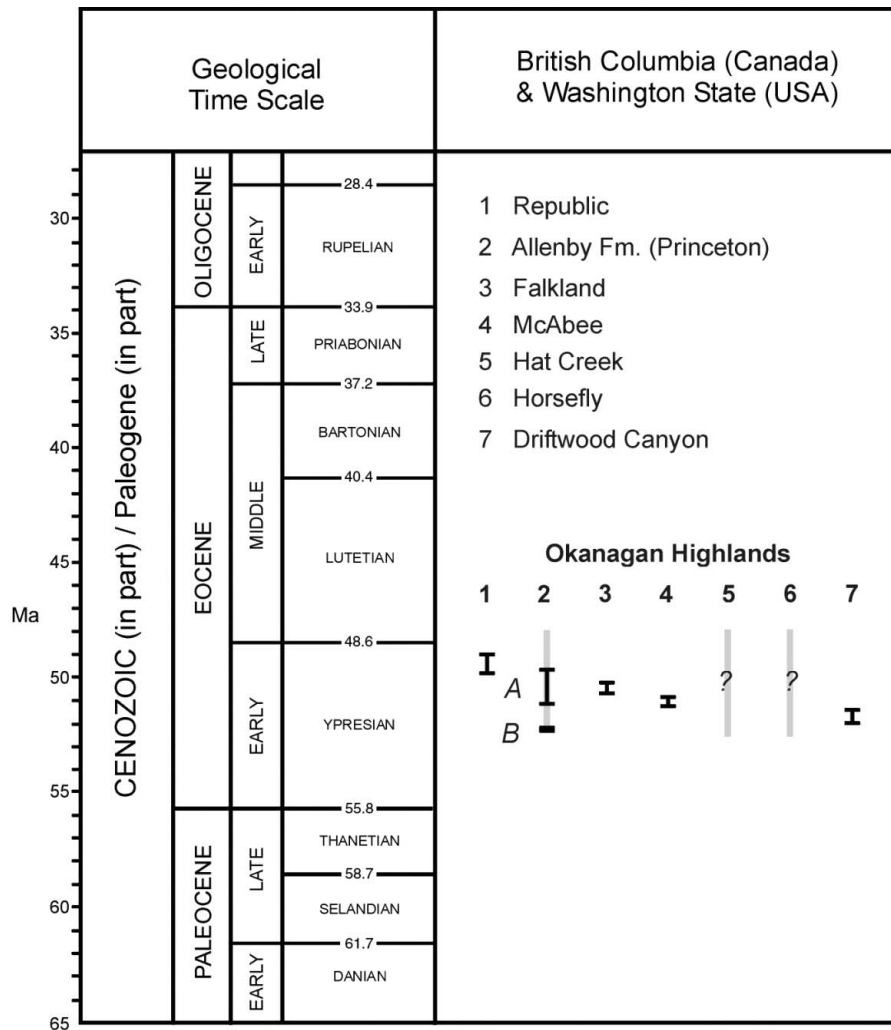
(Kim 1979; N. Church, personal communication, 2004): trench A (samples 4–6) exposes the lower part of the A zone (110–225 m thick, composed of coal and clastic material); trench D exposes the A zone at its western portion (sample 3), the B zone (sample 2) mid-trench (50–70 m, mostly coal), and the C zone (sample 1) is exposed in the eastern portion of trench D (15–60 m, mostly coal). The D zone is not represented here. Zonation of samples is further supported by lithology; the trench A samples and sample 3 from trench D are comprised of a mixture of coal and clastic sediments, and samples 2 and 1 from trench D mostly of coal. The correlation of sample 3, trench D, A zone, with the three A zone samples from trench A is not clear.

Palynological analysis suggests that deposit 1 is no older than Eocene (Church 1981). Potassium–argon dating of rhyolite overlying the Hat Creek coals indicates a minimum age of 51.2 ± 1.4 Ma (Church et al. 1979). More than 550 m of Medicine Creek lacustrine sediments lie below the dated rhyolite and above the coal (Kim 1979). Read (2000), however, states that the dated rhyolite was subsequently superimposed as a slide block over the (presently) underlying Medicine Creek Formation and coal deposits, casting doubt on an age determination for Hat Creek coal based on that of the rhyolite.

Group 4: Southern sites (Allenby and Republic)

The Allenby Formation sites (often referred to as the “Princeton flora,” e.g., Erwin and Stockey 1989; 1994) include samples taken from Hardwick sandstone unit exposures at Summers Creek Road (Allenby 1) and One Mile Creek (also known as the Princeton leaf beds) (Allenby 2) localities, both about 8 km north of the town of Princeton on Highway 5 near the confluence of Allison and Summers creeks; and at Hospital Hill (Allenby 3), an exposure of the Vermillion Bluffs shale unit within the town of Princeton, also called the “Princeton Firehall” locality (Douglas and Stockey 1996). The Allenby 1 sample was collected from poorly fissile to massive grey-green fossiliferous sandstone

Fig. 2. Stratigraphic chart showing the age of the Okanagan Highlands fossil sites, based on sources cited in the text and new radiometric ages (see text). Geological time scale is based the ICS website (<http://www.stratigraphy.org/info.htm>). Fossil localities lacking radiometric ages are shown as grey vertical lines to indicate age control based on litho- and biostratigraphy. (A) sample from Blakeburn Mine, (B) sample from Hospital Hill; (see text).



exposed in a large road cut with interleaved tephra beds exposed, the Allenby 2 sample from light grey-green fine-grained and well laminated shale (within the Hardwick sandstone) exposed on Allison Creek, and the Allenby 3 sample from dark brown fine-grained fissile shale in a limited exposure along a road cut.

A preliminary U–Pb age from zircons of 52.08 ± 0.12 Ma is determined for Hospital Hill (sample Allenby 3) (Mortensen and Archibald, current research), and, as samples Allenby 1 and 2 are from the Hardwick sandstone unit, which underlies the Vermillion Bluffs shale, these localities are constrained to an age no younger than Early Eocene. Potassium–argon studies in the 1960s (Rouse and Mathews 1961) gave an age of 48 Ma for some horizons within the Allenby Formation, suggesting that it may be early Middle Eocene in parts, although the Early–Middle Eocene boundary is now placed at 48.6 ± 0.2 Ma (International Commission on Stratigraphy 2004).

The Republic samples were collected from exposures of the Tom Thumb Tuff Member of the Klondike Mountain For-

mation at the Boot Hill and Corner Lot quarries (University of Washington, Burke Museum of Natural History and Culture locality numbers UWBMB4131 and UWBMA0307, respectively) in the town of Republic in Ferry County, north-central Washington. These samples consist of light grey fine-grained massive shale. This is the first report of relatively high concentrations of pollen extracted from Republic samples; previous environmental inferences have been based on the extensive megafossil remains found at this locality (e.g., Wolfe and Wehr 1987). An ^{40}Ar – ^{39}Ar age of 49.4 ± 0.5 Ma for Republic has been recently provided (Wolfe et al. 2003).

Palynological methodology

The samples discussed in this paper were processed for pollen and spores by the method developed by van der Kaars (1991) specifically for deep-ocean marine sediments and has been shown to be successful for the extraction of high yields of pollen from clastic samples. First, the samples were ground with a mortar and pestle, and then placed in sodium tetraphosphosphate to deflocculate the sediment. An exotic pollen

Fig. 3. Section of exposure at McAbee; arrows indicate tephra layers between fossil-bearing lacustrine shale beds.



tablet (*Eucalyptus*) was added to allow for the calculation of pollen concentrations for the samples. The samples were next sieved over a 175- μm mesh to remove coarse material (including sand grains) and then an 8- μm mesh was used to remove fine clays. The portion of the sample retained in the 8- μm mesh was kept for pollen analysis. The samples were then left to stand overnight in water to separate the solid material from the sodium tetra-pyrophosphate, which was then siphoned off and the solid material was transferred from beakers to test tubes. Hydrochloric acid was then added to dissolve any carbonate material present. Acetolysis was next undertaken to dissolve excess organic material. Heavy liquid separation using sodium polytungstate (density of 2.0) was then used to separate the organic material (including pollen and spores) from the clastic fraction. The Hat Creek samples underwent further analysis with the use of Schulze solution to remove excess organic material and were then mounted in silicon oil.

The concentrated organic samples were kept and then mounted in silicon oil and counted for pollen and spores under a light microscope at $\times 650$ magnification, with a minimum count of 300 identifiable palynomorphs or four completely counted slides. Pollen identification was aided by previous studies from the region, which provided descriptions and (or) photographs of fossil palynomorphs (Boneham 1968; Rouse 1977; Rouse et al. 1970; Hills 1965a; Hopkins 1980). The results of this pollen analysis are presented graphically using the Tilia pollen diagram software (Grimm 1991)

(Figs. 3–6). A taxon list was then generated based on previous studies (Boneham 1968; Rouse 1977; Rouse et al. 1970; Church 1981; Hills 1965a, 1965b; Hopkins 1980) and our new analyses (Table 1).

Results

The number of pollen taxa found per site in this study were: Driftwood Canyon — 32; Horsefly — 30; Hat Creek — 40; McAbee — 31; Falkland — 26; Allenby — 35; and Republic — 21 (Table 1). Several genera, including *Osmunda*, *Ginkgo*, *Abies*, *Picea*, *Pinus*, *Pseudolarix*, *Alnus*, *Betula*, *Corylus*, and *Ulmus*, are present in all sites. Other taxa that are present across nearly all sites include *Metasequoia–Sequoia* and *Tsuga*, which were absent only at Republic; *Salix*, *Acer*, Sapotaceae, and *Tilia*, which are present in all sites, except Horsefly; and Filicales and *Quercus*, which are found in all sites, except Falkland.

Arecaceae (palms) signify mesothermal to megathermal conditions (Greenwood et al. 2005); palm pollen was found in all sites, except Republic, but was only abundant at Hat Creek (see later in the text; Fig 6). No megafossil evidence of palms was reported by Blackburn (1982) in Hat Creek coal, although he reported leaf fragments with parallel, rarely anastomosing veins that suggest palm remains, however, he noted these fossils may represent *Ginkgo*. The Hat Creek flora also contained the presence of microfossils of *Sphagnum*, *Lycopodium*, *Juglans*, *Engelhardia*, Rhamnaceae, *Nyssa*, *Typha-*

Fig. 4. Pollen profiles of Group 1 localities. “+” reflects rare taxa (<1.5% of pollen sum). D.C., Driftwood Canyon; H.F., Horsefly.

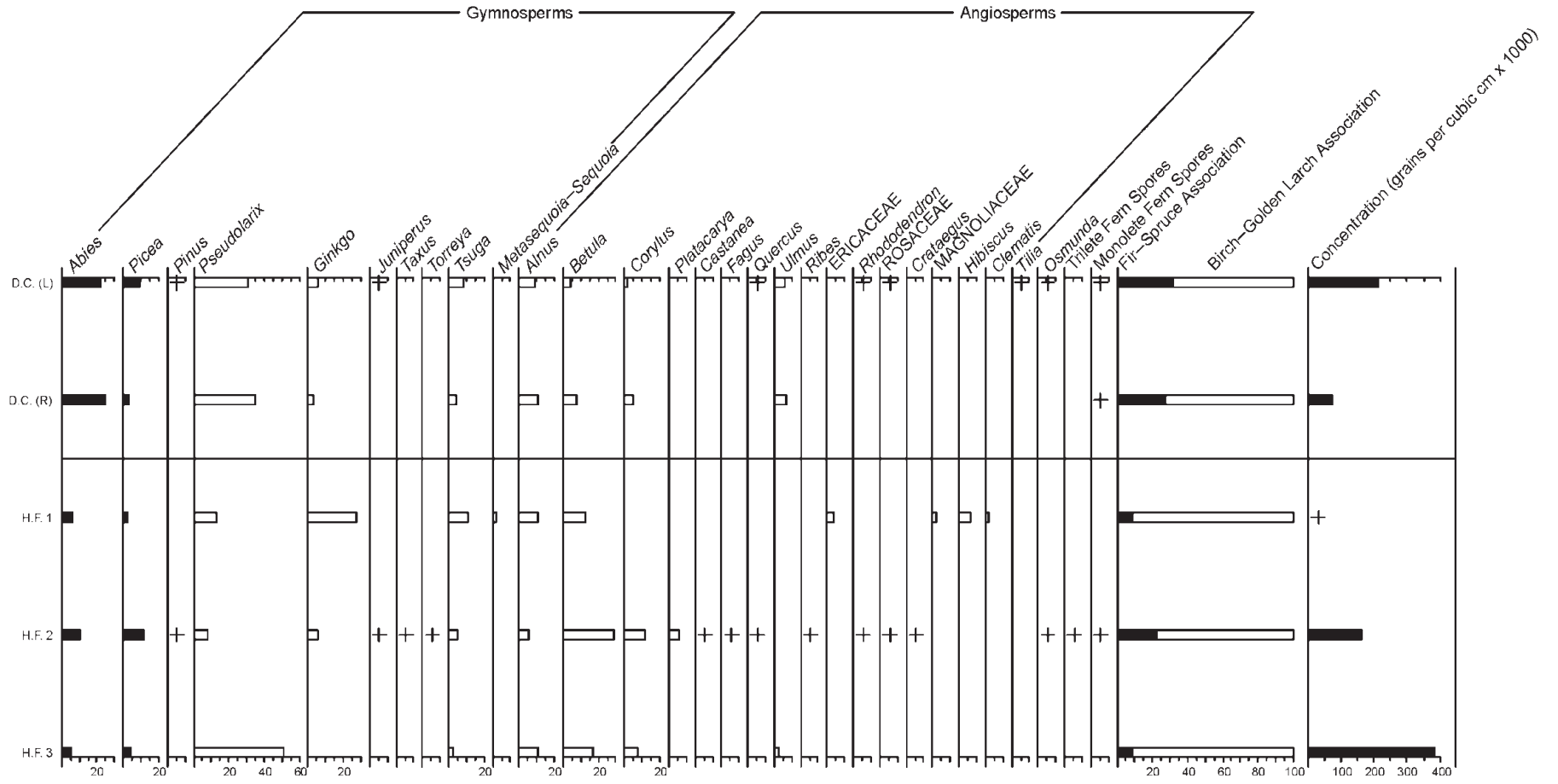


Fig. 5. Pollen profiles of Group 2 localities. “+” reflects rare taxa (<1.5% of pollen sum). Falk, Falkland.

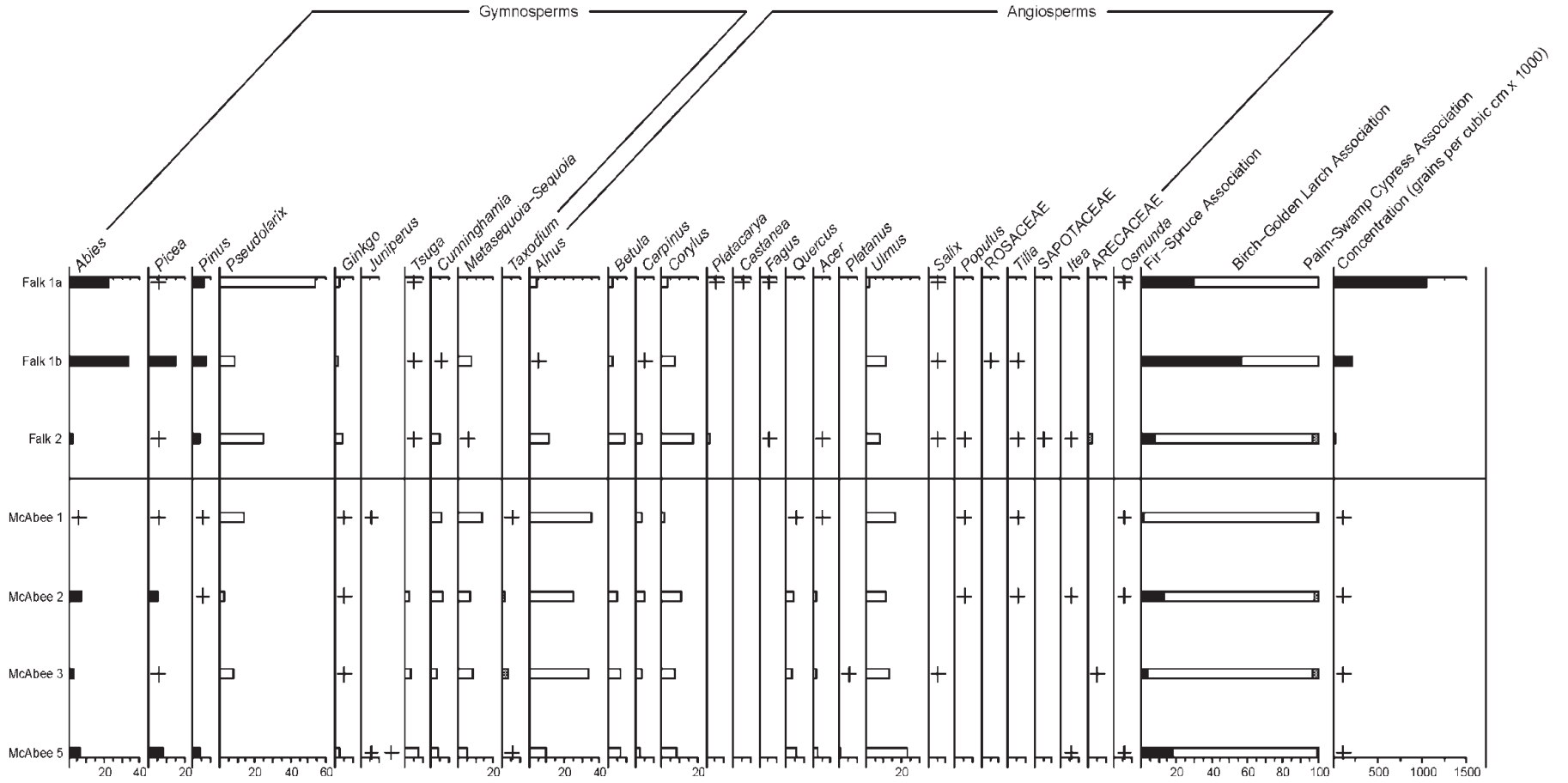
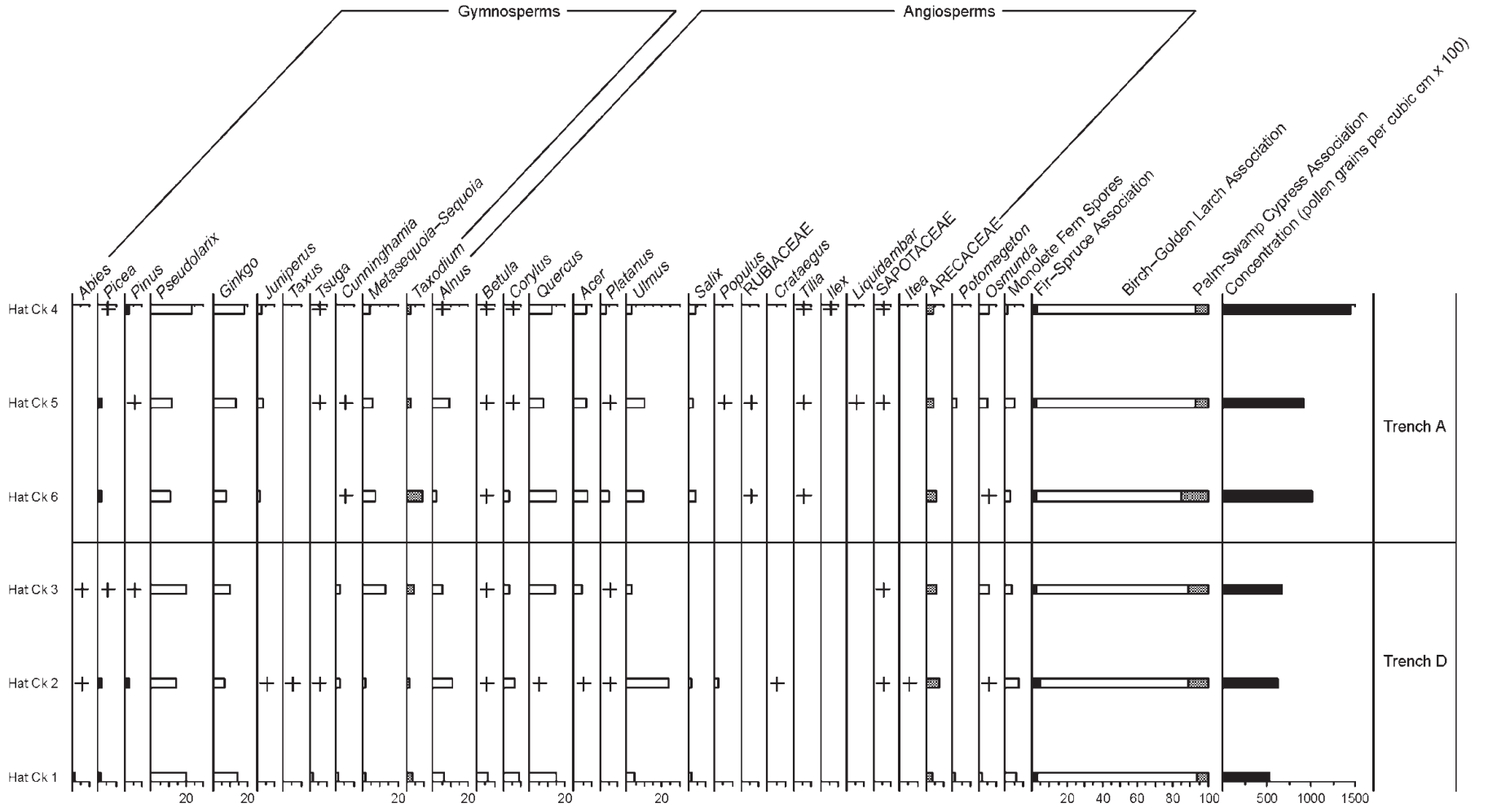


Fig. 6. Pollen profiles of Group 3 localities. “+” reflects rare taxa (<1.5% of pollen sum).



Sparganium (monads), and *Typha* (tetrads) that were not recorded in any of the other sites and are suggestive of swampy conditions. The mesothermal–megathermal taxon *Taxodium* was recorded for all sites, except Republic, Falkland, and Horsefly. *Taxodium* (as with *Arecaceae*) reached its highest abundance in the Hat Creek samples (see latter in the text). *Cunninghamia* was recorded at all sites, except Republic and Horsefly localities and was most abundant in the McAbee samples.

The mesothermal–megathermal taxon *Itea* was recorded as a megafossil at the Republic site and was also identified as pollen at Republic, Falkland, McAbee, and Hat Creek, but it is currently not recorded as a megafossil from these other localities (Greenwood et al. 2005). There are several other taxa that are known as megafossils at a number of the localities, but they were either rare or not recorded in the pollen counts. For example, *Ribes* was only found in samples from Horsefly, but megafossils (as leaves) of this taxon have been found at the Republic, Allenby, and McAbee localities (Greenwood et al. 2005). Similarly, megafossils of *Fagopsis* or *Fagus* have been found in all sites, except Driftwood Canyon, and with limited megafossil occurrences at Hat Creek, while microfossils assigned to *Fagus* have been found at Falkland, Hat Creek, and Horsefly. As mentioned earlier, *Abies*, *Picea*, *Pinus*, *Pseudolarix*, *Betula*, and *Ulmus* were present at all sites as pollen and are also recorded at all sites (except Hat Creek) as megafossils (Greenwood et al. 2005). *Acer* and *Tilia* were recorded in all sites as pollen, except Horsefly, but *Tilia* was only recorded as a megafossil at Republic and Quilchena, and *Acer* was present in all sites as megafossils, except Horsefly and Driftwood (Greenwood et al. 2005). *Populus* and *Salix* are recorded at most sites as pollen, but are poorly represented across the megaflores (Greenwood et al. 2005).

Relative abundance data of spore and pollen taxa from the present pollen analysis for the seven floras are shown in Figs. 4–7, with localities divided into four groups (as discussed earlier). Summary results of the three major vegetation associations (i.e., Fir–Spruce association; Birch–Golden Larch association; and Palm–Cypress association: see text sections “Discussion” and “Regional and local community dynamics”) are shown on the diagrams and will be examined in the discussion section. Pollen concentration values (in grains per cubic centimetre) are also recorded on the pollen diagrams.

Group 1: Northern sites (Fig. 4)

Pollen concentrations for these samples range from about 75 000 grains/cm³ in the Driftwood Canyon (right exposure) sample to around 400 000 grains/cm³ in the Horsefly 3 sample. The “+” symbol representing the Horsefly 1 sample signifies the anomalously low pollen concentrations (<1000 grains/cm³) in this sample compared with those of other localities. The three Horsefly samples differ in taxon dominance (i.e., stand out highest abundance taxon with typically > 20% representation) and by the relative contribution of other major taxa. Horsefly 1 is dominated by *Ginkgo* (~30%), with *Tsuga* (~10%), *Betula* (~10%), *Alnus* (~10%), *Hibiscus* (~5%), and *Abies* (5%) co-dominant or in moderate abundances. Horsefly 2 has a higher proportion of angiosperm taxa than any of the Horsefly and Driftwood samples, and is dominated

by *Betula* (~30%), with *Corylus* (~10%) and *Picea* (~10%) being co-dominant. *Pseudolarix* (~50%) dominated the Horsefly 3 sample, although the angiosperm taxa, *Alnus* (~10%), *Betula* (~15%), and *Corylus* (~8%), are important components. The Driftwood Canyon samples are floristically similar: both were dominated by the conifers *Abies* (~20%) and *Pseudolarix* (~20%–25%). Angiosperm taxa, such as *Alnus* (~5%–10%), *Betula* (~5%–8%), *Ulmus* (~5%–8%), and *Corylus* (~2%–5%), are other important taxa in the Driftwood Canyon samples.

Group 2: Central shale sites (Fig. 5)

Pollen concentrations ranged from 30 000 to ~1 000 000 × 10⁶ grains/cm³ in the Falkland samples to <7000 grains/cm³ in the McAbee samples (represented by the “+” symbol). Falkland 1a and 1b had similar floristic compositions, with high abundances of *Pseudolarix* (~55%), *Abies* (~20%), and *Pinus* (~8%). This result suggests that these taxa were consistently present within the local landscape at Falkland. However, Falkland 1b has lower values of *Pseudolarix* (~5%) than recorded for Falkland 1a, and Falkland 1b has higher values of *Abies* (~30%), *Picea* (~10%), *Ulmus* (~8%), *Metasequoia–Sequoia* (~5%), and *Corylus* (~5%). This might reflect the different sediment composition of each sample and thus different depositional settings, Falkland 1a from lithified shale and Falkland 1b from unconsolidated mudstone, or alternately might reflect habitat heterogeneity. Falkland 2 is dominated by *Pseudolarix* (~20%) and *Corylus* (~15%), with other important taxa, including *Alnus* (~10%), *Betula* (~8%), *Ulmus* (~5%), *Pinus* (~5%), *Cunninghamia* (~5%), and *Ginkgo* (~5%). Palms (*Arecaceae*) are also found in small, but significant amounts.

The McAbee samples provide a stratigraphic profile, with McAbee 1 the youngest and McAbee 5 the oldest. Multiple tephra beds interleave the sampled sequence, and so differences between these may reflect post-disturbance responses by the paleovegetation. In general, the most abundant taxa in the McAbee samples are *Alnus* and *Ulmus*, with other taxa present, including *Abies*, *Picea*, *Pinus*, *Pseudolarix*, *Taxodium*, *Tsuga*, *Cunninghamia*, *Metasequoia–Sequoia*, *Betula*, *Corylus*, and *Fagus*, although the values of these genera vary between samples. McAbee 5 is dominated by *Ulmus* (~25%) and has abundant amounts (> 5%) of *Abies*, *Picea*, *Pinus*, *Tsuga*, *Cunninghamia*, *Metasequoia–Sequoia*, *Alnus*, *Betula*, *Corylus*, and *Fagus*. McAbee 3 is dominated by *Alnus* (~30%), with *Ulmus* being an important component (~10%) and has abundant values (> 5%) of *Ulmus*, *Corylus*, *Betula*, *Metasequoia–Sequoia*, *Pseudolarix*, and *Taxodium*. McAbee 2 has a similar composition to McAbee 3, although *Alnus* (~20%) occurs in lower abundances and the conifer taxa *Abies* and *Picea* are more abundant (> 5%) than in McAbee 3. McAbee 1 is dominated by *Alnus* (~30%) and has abundant values (~10%) of *Ulmus*, *Pseudolarix*, *Metasequoia–Sequoia*, and *Cunninghamia*. There is no clear trend of either increase or decrease in taxon abundance or presence over time within the McAbee samples (5–1).

Group 3: Central coal sites (Fig. 6)

Concentration values range from between 50 000 and 150 000 grains/cm³. All samples were dominated by *Pseudolarix* (~10%–20%) and *Ginkgo* (~5%–20%); *Quercus* (5%–

Table 1. Plant taxa recognized in the Okanagan Eocene palynofloras (derived from Boneham 1968; Rouse 1977; Rouse et al. 1970; Church 1981; Hills 1965a, 1965b; Hills and Baadsgaard 1967; Hopkins 1980: and present pollen analysis).

Fossil palynomorph	Family	NLR	R	A	F	McA	HC	HF	DC
<i>Osmundasporites</i> sp.	Osmundaceae	<i>Osmunda</i>	*	*	*	*	*	*	*
<i>Azolla</i>	Salviniaceae	<i>Azolla</i>		*					*
<i>Sphagnum</i> sp.	Sphaganaceae	<i>Sphagnum</i>					*		
<i>Lygodiumsporites</i> sp.	Schizeaceae	<i>Lygodium</i>						*	*
<i>Lycopodium</i> sp.	Lycopodiaceae	<i>Lycopodium</i>					*		
<i>Verrucatosporites</i> sp.	Various Filicales	Filicales	*	*		*	*	*	*
<i>Cycadopites follicularis</i> ^a	Ginkgoaceae	<i>Ginkgo</i>	*	*	*	*	*	*	*
<i>Abietinaepollenites</i> sp.	Pinaceae	<i>Abies</i>	*	*	*	*	*	*	*
<i>Picea</i>		<i>Picea</i>	*	*	*	*	*	*	*
<i>Pinus</i>		<i>Pinus</i>	*	*	*	*	*	*	*
<i>Pseudolarix</i>		<i>Pseudolarix</i>	*	*	*	*	*	*	*
<i>Alisporites</i> and <i>Pityosporites</i> sp.		Pinaceae		*		*			*
<i>Taxus</i>	Taxaceae	<i>Taxus</i>		*			*	*	
<i>Torreya</i>		<i>Torreya</i>						*	
<i>Juniperus</i>	Cupressaceae–	<i>Juniperus</i>				*	*	*	*
<i>Metasequoia–Sequoia</i>	Taxodiaceae	<i>Metasequoia</i>		*	*	*	*	*	*
<i>Cunninghamia</i>		<i>Cunninghamia</i>		*	*	*	*		*
<i>Taxodiaceapollenites</i> sp.; <i>Taxodium</i>		<i>Taxodium</i>		*		*	*		*
<i>Tsuga</i>		<i>Tsuga</i>		*	*	*	*	*	*
<i>Ilex</i>	Aquifoliaceae	<i>Ilex</i>		*			*		
<i>Sabal granopollenites</i>	Arecaceae	<i>Arecaceae</i>		*	*	*	*		*
<i>Alnus</i>	Betulaceae	<i>Alnus</i>	*	*	*	*	*	*	*
<i>Betula</i>		<i>Betula</i>	*	*	*	*	*	*	*
<i>Carpinus</i>		<i>Carpinus</i>		*	*	*			*
<i>Corylus</i>		<i>Corylus</i>	*	*	*	*	*	*	*
<i>Ericaceae</i>	Ericaceae	<i>Ericaceae</i>					*	*	
<i>Rhododendron</i>		<i>Rhododendron</i>						*	*
<i>Castanea</i>	Fagaceae	<i>Castanea</i>	*	*	*		*	*	
<i>Fagus</i>		<i>Fagus</i>			*		*	*	
<i>Quercus</i>		<i>Quercus</i>	*	*	*	*	*	*	*
<i>Pistillipollenites macgregorii</i>	Gentianaceae– Euphorbiaceae	Gentianaceae– Euphorbiaceae		*	*		*	*	
<i>Itea</i>	Grossulariaceae	<i>Itea</i>	*		*	*	*		
<i>Ribes</i>		<i>Ribes</i>						*	
<i>Myriophyllum</i>	Haloragaceae	<i>Myriophyllum</i>					*		
<i>Liquidambar</i>	Hamamelidaceae	<i>Liquidambar</i>	*	*					
<i>Carya</i>	Juglandaceae	<i>Carya</i>		*		*			*
<i>Engelhardia</i> sp.		<i>Engelhardia</i>					*		
<i>Jugland</i> sp.		<i>Juglans</i>					*		
<i>Platycarya–Pterocarya</i>		<i>Platycarya</i>		*	*	*	*	*	
Magnoliaceae	Magnoliaceae	Magnoliaceae						*	
<i>Hibiscus</i>	Malvaceae	<i>Hibiscus</i>						*	*
<i>Nyssa</i>	Nyssaceae	<i>Nyssa</i>					*		
<i>Platanus</i>	Platanaceae	<i>Platanus</i>		*		*	*		
Rosaceae	Rosaceae	Rosaceae	*	*	*			*	*
<i>Crataegus</i>		<i>Crataegus</i>					*	*	
<i>Clematis</i>	Ranunculaceae	<i>Clematis</i>						*	
Rhamnaceae	Rhamnaceae	Rhamnaceae					*		
Rubiaceae	Rubiaceae	Rubiaceae					*		
<i>Populus</i>	Salicaceae	<i>Populus</i>	*		*	*	*	*	*
<i>Salix</i>		<i>Salix</i>	*	*	*	*	*		*

Table 1 (concluded).

Fossil palynomorph	Family	NLR	R	A	F	McA	HC	HF	DC
<i>Acer</i>	Sapindaceae	<i>Acer</i>	*	*	*	*	*		*
<i>Aesculus</i>		<i>Aesculus</i>		*		*			*
Sapotaceae	Sapotaceae	Sapotaceae	*	*	*	*	*		*
<i>Tilia</i>	Tiliaceae	<i>Tilia</i>	*	*	*	*	*		*
<i>Ulmus</i>	Ulmaceae	<i>Ulmus</i>	*	*	*	*	*	*	*
<i>Typha–Sparganium</i> (monads)	Typhaceae	<i>Typha–Sparganium</i>					*		
<i>Typha</i> (tetrads)		<i>Typha</i>					*		
<i>Potamogeton</i>	Zosteraceae	<i>Potamogeton</i>		*		*	*		*

Note: R, Republic; A, Allenby; F, Falkland; McA, McAbee; HC, Hat Creek; HF, Horsefly; DC, Driftwood Canyon. NLR, nearest living relative.

^a*Cycadopiites follicularis* grains from the Republic sediments may also include cycads. Cycad pollen, in addition to Ginkgo pollen, is consistent with this pollen type (R.W. Mathewes, personal communication, 2005) and cycad foliage has been recorded in the Republic macroflora but is unknown at all the other sites, while Ginkgo leaves are recorded at all sites (Greenwood et al. 2005).

15%) has relatively high abundance in all samples, except Hat Creek 3. *Metasequoia–Sequoia* (~5%–8%) and *Acer* (~10%) abundance were successively higher in the Hat Creek 3–6 samples relative to the Hat Creek 1 and 2 samples. Values for *Ulmus* were highest in the Hat Creek 2 (~25%), 5 (~10%), and 6 (~10%) samples. *Alnus* and *Corylus* have higher abundances (~5%–10%) in the trench D samples, while *Salix* values (~5%) have higher abundances in the trench A samples than in the trench D samples. *Taxodium*, and *Arecaceae* maintain low but significant values throughout all samples for both trench A and D samples. Pteridophytes have much higher abundance in the Hat Creek samples than in any of the other Okanagan Highlands Eocene sites surveyed in this study. The Hat Creek samples also have the lowest representation of Pinaceae pollen grains (~5% to <20%); the highest representation of deciduous dicots (*Alnus*, *Corylus*, *Quercus*, *Ulmus*, *Acer*, and *Salix*) and mesothermal gymnosperms (*Pseudolarix*, *Ginkgo*, and *Metasequoia–Sequoia*) (~70%–90%); and palm (*Arecaceae*), evergreen dicot (e.g., *Sapotaceae*), and *Taxodium* (~5%–10%) pollen grains of all Okanagan Highlands sites surveyed here.

This differences between Hat Creek and all of the other sites likely reflect their contrasting environmental settings — a coal-forming swamp (local) versus lacustrine (local + regional) setting — reflecting differing components of the local and regional landscapes reflected in the pollen rain found in the sampled sediments (McAndrews and Wright 1969). Mesofossil evidence from the Hat Creek coal (Blackburn 1982) showed abundant *Glyptostrobus* and *Metasequoia* (and possibly *Ginkgo*), reinforcing the idea that these taxa dominated the swamp vegetation and that Pinaceae were not in the swamps. Wind-dispersed pollen (such as bisaccate Pinaceae) is typically over-represented in open-water environments; swamps (based on actualistic studies) show a strong local signal (as the local vegetation filters out the externally sourced pollen), so anything in low counts in the swamp sediments is either rare in that environment or was growing externally to the swamp (Jansson 1966; Williams et al. 1998).

Group 4: Southern sites (Fig. 7)

The pollen concentration of the Allenby samples range from nearly 6000 to ~26 000 grains/cm³, while pollen concentrations in the Republic samples are < 2700 grains/cm³. Allenby 1 and 2 are dominated by *Abies* (~15%), *Picea* (~5%–10%), *Alnus* (~5%–15%), and *Betula* (~10%–20%),

while particular gymnosperms (*Pseudolarix* (~10%–15%), *Ginkgo* (~5%–8%), and *Taxus* (3–5%)) have higher abundances in Allenby 2 and 3 than in Allenby 1. *Tsuga* (5%) reaches its highest representation in Allenby 2. Allenby 3 also shows higher abundances of *Metasequoia–Sequoia* (~10%), *Corylus* (~5%), *Quercus* (~5%), *Acer* (~5%), and *Ulmus* (~5%), and lower abundances (generally <5%) of *Abies*, *Picea*, and *Alnus* and the presence of *Arecaceae*.

The Republic Boot Hill sample is dominated by *Pseudolarix* (~40%), with abundant presence (~5%) of *Abies*, *Picea*, *Pinus*, *Ginkgo*, *Betula*, *Sapotaceae*, and *Itea*. *Ulmus* (~35%) dominates the Republic Corner Lot sample, with *Pseudolarix*, *Ginkgo*, and *Castanea* occurring in relatively high abundances (~10%).

Discussion

Biostratigraphy

The presence of the stratigraphically diagnostic taxa *Tilia* (Driftwood Canyon, Falkland, McAbee, Hat Creek, Allenby, and Republic), *Quercus* (Driftwood Canyon, Horsefly, McAbee, Hat Creek, Allenby, and Republic), *Ilex* (Hat Creek and Allenby), and *Platycarya* (Horsefly, Falkland, McAbee, Hat Creek, and Allenby) denotes a post Late Paleocene age (Manchester 1987; Harrison et al. 1999). The Early to Middle Eocene biostratigraphically diagnostic taxon *Pistillipollenites macgregorii* was found at the Allenby, Horsefly, Hat Creek, and Falkland sites. *Pistillipollenites macgregorii* is common in the Upper Paleocene to Middle Eocene, first appearing in chron 25n in western Canada (Rouse 1977; Harrison et al. 1999). This distinctive palynomorph was not included in the relative abundance data, as it occurred only in low abundances, and there is some debate about its taxonomic affinities, either Gentianaceae or Euphorbiaceae (Crepet and Daghighian 1981; Stockey and Manchester 1988; Collinson et al. 2003).

Gothanipollis pollen is indicative of Late Eocene and Oligocene ages, and its absence in all Okanagan Highlands samples analysed indicates the samples are older than Late Eocene (Rouse 1977; Long and Sweet 1994; Ridgway et al. 1995). Another important palynomorph, indicative of an Early to Middle Eocene age, *Platycarya* (Rouse 1977), was found at all sites, except Republic and Driftwood Canyon. The results of this study (in terms of diagnostic taxa and floristic assemblages) support an Early to Middle Eocene age for all localities (Fig. 2), which would be included in Rouse's (1977) E1 biozone. These data, therefore, are con-

Fig. 7. Pollen profiles of Group 4 localities. "+" reflects rare taxa (<1.5% of pollen sum). Rep., Republic.

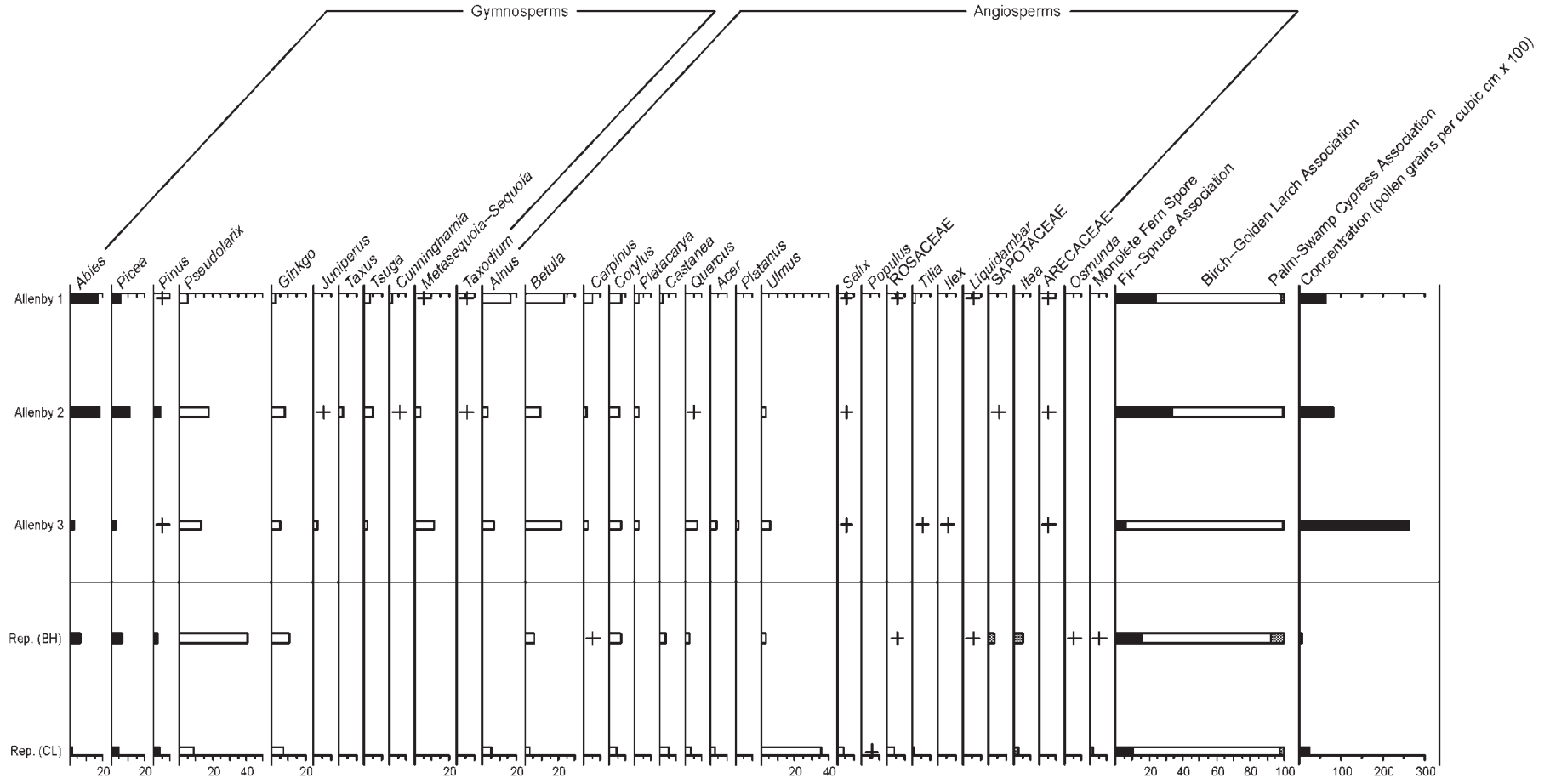
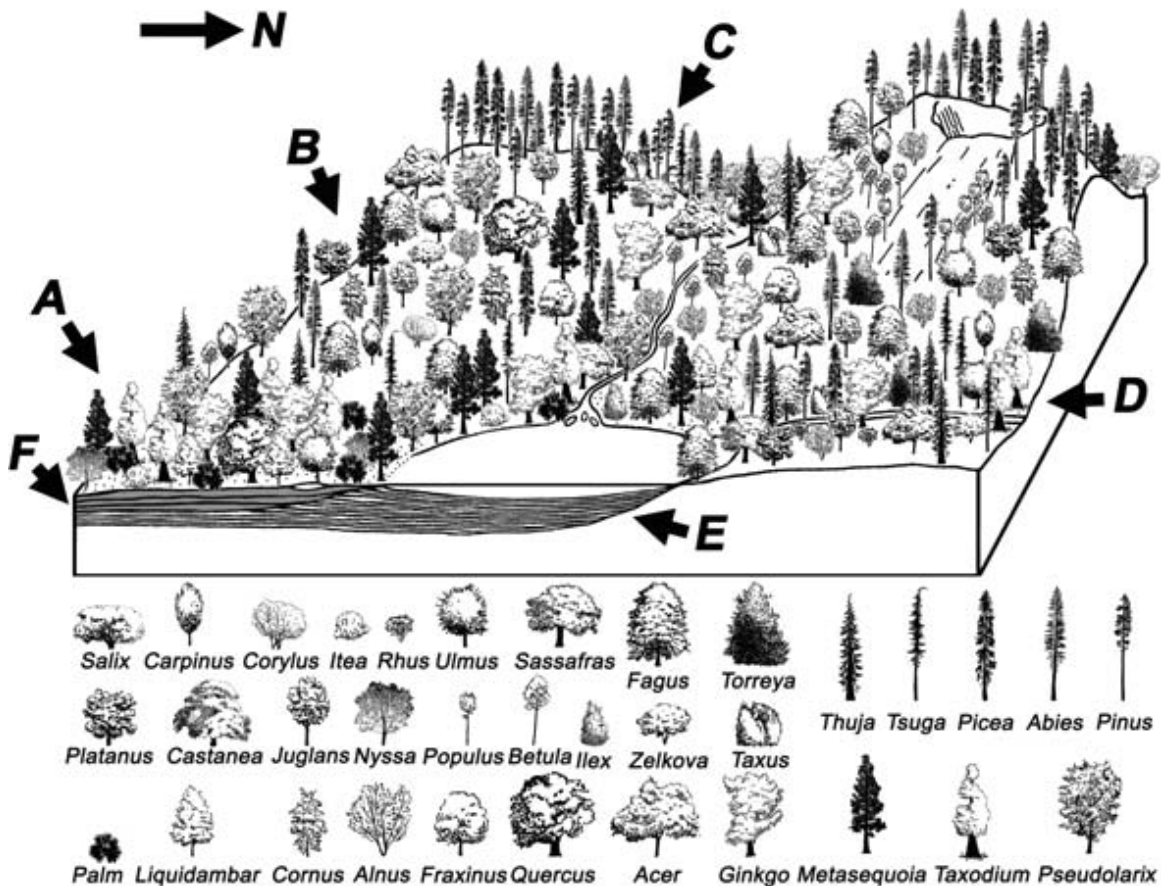


Fig. 8. Reconstruction of generalized Okanagan Highlands forest structure and depositional setting: (A) Palm–Swamp Cypress association dominant in low wet areas; (B) Birch–Golden Larch association mixed with Fir–Spruce association on better drained ground and hillsides; (C) Fir–Spruce association dominant on higher ridges and north aspects; (D) Birch–Golden Larch association dominant streamside; E, lacustrine shale formation; (F) coal formation. N, north. Some tree symbols after Pojar and Meidinger (1991).



sistent with radiometric ages from tephra, where available (see text section “Localities and approach” and Fig. 2).

Floristics

Previously, pollen analyses have been undertaken of the One Mile Creek (Allenby Formation), McAbee, Driftwood Canyon, and Hat Creek localities (Boneham 1968; Rouse 1977; Rouse et al. 1970; Church 1981; Hills 1965a, 1965b; Hopkins 1980). The results of these analyses, along with those of this study are presented in Table 1. Both this and previous studies give a similar environmental signal, with key differences in the presence or absence of relatively minor taxa (in terms of relative abundances). The variation in the presence–absence of taxa between the present study and earlier works may relate to the different focus of the present study, which is primarily presenting an environmental reconstruction based on the relative abundances of taxa for the region during the Early–Middle Eocene epoch, compared with the past studies, which placed an emphasis on providing biostratigraphic control among sites. Rouse (1977) discussed this strategy by suggesting that indicator palynomorphs occur in relatively small numbers and required extensive searching of slides to locate one or two specimens. Therefore, while these taxa are recorded by such studies at these sites, their low occurrences rendered them not recognized in the present

analysis, which was based on a sequential count of grains. In addition, previous studies (Hills 1965a, 1965b) identified *Alisporites* sp. (Pinaceae) and *Pityosporites* sp. (Pinaceae–Podocarpaceae), which the present investigation may have recorded at a higher taxonomic resolution (i.e., genus rather than family) and recorded these taxa as one of the bisaccate Pinaceae genera (*Abies*, *Picea*, *Pinus*, and *Pseudolarix*).

In general, the results of palynological analyses (previous and present) support previous megaflora-based findings (Mathewes and Brooke 1971; Wehr and Manchester 1996; Pigg and Stockey 1996; Wehr 1998; Manchester 1999; McClain and Manchester 2001; Mathewes 2003; Dillhoff et al. 2005; Greenwood et al. 2005) that the Okanagan Highlands supported forest communities that reflect upper microthermal to lower mesothermal conditions, with mainly mesic conditions (Greenwood et al. 2005). A diverse set of gymnosperm and angiosperm taxa is observed throughout the region (see Table 1), and while taxon occurrences and abundances do vary between sites (as would be expected over such a broad area), this is likely reflecting differences in latitude, microhabitat, disturbance and (or) elevation (discussed later in the text). In general, all sites record the presence of bisaccate Pinaceae taxa, which previous studies of Okanagan Highlands Eocene sites have interpreted as probably derived from hinterland, higher elevation coniferous forests, while the deciduous di-

cots occupied lakeshore, swamp, and streamside localities (Rouse 1977; Rouse et al. 1970; Wolfe and Wehr 1987).

Abundant megafloreal remains of most Pinaceae in each of the lacustrine localities, however, are inconsistent with such clear segregation within the landscape (Greenwood et al. 2005). The presence of ferns (*Osmunda* and other spore taxa); the gymnosperms *Ginkgo*, *Pseudolarix*, *Metasequoia-Sequoia*, and *Tsuga*; and the deciduous dicots *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Quercus*, *Salix*, *Acer*, and *Tilia* in the palynofloras from nearly all sites indicates that these taxa were the principal members of the forest communities across the regional landscape. In addition, the presence of palms (Arecaceae), evergreen dicot trees (e.g., *Ilex*, *Itea*, *Liquidambar*, and Sapotaceae), and the mesothermal–megathermal conifer, *Taxodium*, have been interpreted in previous studies as indicating the regional presence of lowland forest communities reflective of mesothermal–megathermal conditions (Rouse 1977; Rouse et al. 1970; Wolfe and Wehr 1987). However, a narrow seasonal range of temperature, that is, a highly equable climate with warm winters (i.e., CMMT > 2 °C) under upper microthermal to lower mesothermal conditions, would permit all of these taxa to occur within the same climate zone (Greenwood et al. 2005).

Regional and local community dynamics

Regional forest type

Our results support the interpretation of megafossil evidence by Greenwood et al. (2005) that the Okanagan Highlands landscape supported forest communities and floristic associations that constitute the antecedent of the modern North American eastern deciduous forest biome. These authors compared the floristics of the Okanagan Highlands megaflores with regional landscape elements of the eastern deciduous forest biome, and discussed the similarity of hypothesized effect on Okanagan Highland floras of slope, elevation, aspect, edaphic conditions, and seral history influencing local floristic composition, attributes that control floristics in the extant eastern North American deciduous forest zone (Greller 1988).

Forest associations

We reconstruct three forest types within the local and regional landscape (Fig. 8). The (1) Fir–Spruce association is characterized primarily by fir and spruce and also including pine; (2) Birch–Golden Larch association was dominated by deciduous dicots (alder, birch, hazel, elm, oak, willow, maple, and basswood), but also contains gymnosperms (e.g., ginkgo, golden larch, redwood – dawn redwood, and hemlock); and the (3) Palm–Swamp Cypress association included such taxa as palms (Arecaceae), evergreen dicot trees (e.g., *Ilex*, *Itea*, *Liquidambar*, and Sapotaceae), and swamp cypress. The relative abundances of these vegetation associations are recorded on Figs. 4–7. Most taxa would appear to not have been faithful to a single forest association, but rather were more abundant in habitat types more suited to their requirements. Community floristics were also labile, reflecting local history (i.e., succession in response to disturbance, such as volcanic eruptions and (or) forest fires) and microhabitat. The exception to this pattern was likely the Palm–Swamp Cypress association

(3), members of which are inferred by their nearest living relatives to have had the narrowest autecological parameters.

Community structure: elevation and latitude

The present study indicates the effects of latitude and elevation on Okanagan Highlands taxon occurrence and abundance, and association dominance. Microthermal–mesothermal and mesothermal–megathermal taxa are more abundant and diverse at the expense of microthermal taxa at southerly localities (e.g., Republic and Allenby) and (or) hypothesized lower elevation sites, which may produce differing edaphic and (or) microclimate settings (e.g., Hat Creek), as seen today in the eastern deciduous forest zone (Greller 1988). Further factors influencing the observed community associations sampled across the region may include change in water tables, volcanic and fire disturbance, and short-term, recent and regional climatic events.

We model the Fir–Spruce association (1) as being dominant in higher ridge and cooler north aspect slope communities with elements of association, (2) persisting in these communities to a lesser degree, and (3) with the Palm–Swamp Cypress association absent in such areas. The Fir–Spruce association was likely present, to a more or less degree, throughout the landscape, including lower lying lakeshore regions (consistent with megafossil evidence) (Greenwood et al. 2005), perhaps as a seral element, but association (2) was dominant in local lakeshores, streambanks, swamps, and adjoining communities. Association (3) consists primarily of mesothermal–megathermal taxa, and may have been limited to such specialized habitats where such taxa could occur (i.e., within the lower parts of the landscape, upland swamps, or warmer south-facing slopes), with these habitats occupying decreasing portions of the landscape with increasing latitude and (or) elevation.

Further, there is a high degree of variability in terms of local representation of each of these vegetation associations at each site. These sub-regional differences probably reflect the influence of local environmental factors (e.g., aspect, moisture availability, volcanic activity, and (or) fire), as well as possible variation in depositional settings and differential pollen preservation affecting pollen representation. Previous studies investigating the effects of variation in depositional setting on pollen representation during the Eocene environments of the Bighorn Basin (Wyoming) suggest that lacustrine sediments have a significantly higher proportion of aerial-transported pollen types (e.g., bisaccate conifer pollen), while swamp deposits have higher values of local fluvially transported palynomorphs (e.g., *Alnus*, *Fagaceae*, and *Taxodium*) (Farley 1990; Farley and Traverse 1990). The results of the Wyoming study would appear to support our findings from the Eocene Okanagan Highlands, with higher values of the Fir–Spruce association in the lacustrine-derived shale samples (Driftwood Canyon, Horsefly, Falkland, McAbee, Allenby, and Republic) and higher abundances of the Birch–Golden Larch and Palm–Swamp Cypress associations in the swamp-derived coal samples of Hat Creek.

The Driftwood Canyon samples show high similarity (in both taxon occurrence and relative abundance), with the pollen assemblage indicating a mixture of the Birch–Golden Larch forest association (65%–70% relative abundance), probably occupying lakeshore, warmer low-lying areas, or southerly

aspects (and thus warmer sites), and the Fir–Spruce associations (30%–35% relative abundance), which dominated areas of higher elevations or cooler northerly aspects. The high values of the Birch–Golden Larch association suggest that they were probably derived from the local lakeshore vegetation, as the leaves from these taxa are common in the megafossil record (Greenwood et al. 2005). The Horsefly samples reflect a broadly similar environment to that reconstructed for Driftwood Canyon. The differences that do exist between them may be the result of diverse depositional environments recording variation in community composition.

Wilson (Wilson 1977c, 1980; also see Barton and Wilson 2005) suggested that the Horsefly locality reflects a deep-water offshore lacustrine environment and perhaps the variation in taxa may reflect samples that are taken at differing distances from the paleo-lake shore, and thus differing depositional settings. That is, the Horsefly 1 and 3 samples provide a signal indicative of local lakeshore environments with higher abundances of the Birch–Golden Larch association (~90%) and lower values of the Fir–Spruce association (~10%). In contrast, the Horsefly 2 sample may represent a site further from shore than the other two samples, providing a greater insight into regional environments, with a greater representation of the Fir–Spruce association (~20%) derived from highland and northerly aspects of the landscape.

The Falkland samples demonstrate a great deal of variation in the relative abundance of the three vegetation associations. The close proximity of their collection laterally and in vertical section within the outcrop indicates that floristic differences must reflect changes in patchiness in the local vegetation linked to different microhabitats (caused by variation in water table depth or other edaphic factors) over the short time period represented by these samples, or perhaps seral stages in response to disturbance (e.g., fire), rather than larger scale climate change, difference in elevation, or north versus south facing slopes. It would appear that Falkland 1a and 1b have relatively similar vegetation based on the vegetation association data (i.e., Fir–Spruce association ~35%–55% and Birch–Golden Larch association ~45%–65%). However, there is a great deal of variation in taxon representation, in particular, Falkland 1b has a much higher proportion of *Abies* (fir), *Picea* (spruce), and *Pinus* (pine) pollen grains, while *Pseudolarix* (golden larch) is more abundant in the Falkland 1a sample. In addition, the Falkland 1b sample has a greater proportion of mesothermal angiosperm taxa (elm and hazel) and the mesothermal taxa *Metasequoia–Sequoia* (dawn redwood – redwood) compared with Falkland 1a. The difference in pollen representation between these two samples may reflect contrasting depositional environments or diagenesis, as the Falkland 1a and 2 assemblages were from samples of lithified shale, whereas the Falkland 1b sample was from an unconsolidated matrix. These different sediment types may reflect a variation in pollen signal during the time of deposition, or be the result of differential pollen preservation after deposition.

The Falkland 2 sample was taken in close proximity to Falkland 1a and 1b, but records a different pollen signal for these samples, with significantly lower abundances of the Fir–Spruce association (~5%) and higher values of the Birch–Golden Larch association (~92%), and the presence of the Palm–Swamp Cypress association (~3%), which are

suggestive of warmer conditions that may reflect a favourable microhabitat for the occurrence of mesothermal–megathermal taxa or represent a different seral stage in the landscape.

The McAbee samples provide a stratigraphic profile through part of the late Early Eocene that may reflect vegetation succession after repeated volcanic activity. An intense pulse of volcanism was concurrent with tectonism and regional basin development of the Okanagan Highlands during the Early–Middle Eocene (Ewing 1981). The shale exposure at McAbee has numerous interleaved tephra beds (Fig. 3). Here, differences in vegetation association values may represent increased disturbance pressure resulting from greater local effects of volcanism, and therefore in samples representing differing seral communities. A great deal of variability is observed in vegetation association data across the stratigraphic profile. McAbee 1 and 3 have values for the Birch–Golden Larch associations of ~90%–95%, while McAbee 2 and 5 have higher abundances of the Fir–Spruce association (~15%–20%). These shifts in vegetation association abundances suggest a series of random seral stages from multiple disturbance events, with a predominantly alder–elm forest replacing a mixed conifer–elm forest after periods of volcanic activity.

Alternatively, the expansion of a community rich in alders may be in response to changes in water table levels, which may have increased towards the top of the McAbee section (i.e., McAbee samples 3 to 1) and are unrelated to constant volcanism. Representation of the Palm–Swamp Cypress association remains constantly low in all samples (~1%–3%) and is suggestive of a regional presence of this association occurring in lowland areas and (or) upland swamps. A high-resolution analysis of the McAbee locality would facilitate evaluation of the apparent differences in community dynamics through the stratigraphic profile.

Hat Creek has the highest representation of the Palm–Swamp Cypress (between 5% and 10%) and the Birch–Golden Larch (between 85% and 90%) associations and the lowest abundances of Fir–Spruce associations (between ~1% and 3%) of any of the Okanagan Highland sites. In our community model (see earlier in the text) these results would suggest that this site would lie lower in the landscape and, therefore, be warmer than any other Okanagan Highlands locality surveyed here, which have less or no presence of the Palm–Swamp Cypress association (MAT estimates are not provided for Hat Creek in Greenwood et al. 2005, because of insufficient megafossil data).

The key difference observed in the Allenby Formation samples is a decrease in the Fir–Spruce association (from ~25%–30% to < 5%) and increase in the Birch–Golden Larch association (from ~60%–70% to ~90%) from Allenby 1 to Allenby 3. This may represent alterations in plant taxon abundances linked to differences in relative paleoelevation, with the Allenby 1 (Summers Creek Road) and 2 (One Mile Creek) samples reflecting higher elevation environments dominated by Fir–Spruce forests and the Allenby 3 sample (Hospital Hill) representing lower elevation mixed forest community, with a greater abundance of Birch–Golden Larch forest.

The samples analysed from the Republic sites indicate high abundances of the Birch–Golden Larch association (~75%–85%), suggesting warmest conditions among the lacustrine localities, supporting the influence of latitude on

the Okanagan Highlands' climate. Slight differences in elevation, or between north versus south facing slopes, may affect pollen representation between the two sites, with the strata sampled at the Boot Hill locality possibly representing an environment more exposed to winds, therefore, providing a regional representation of the Fir–Spruce association (~15%) and the Palm–Swamp Cypress association (~5%) and that of the Corner Lot site reflecting more local environmental conditions (higher values (~85%) of the Birch–Golden Larch association).

Community structure: edaphic factors

Alternatively, the landscape model of Tribe (2005), places the paleoelevation of Hat Creek at about 900–1200 m, higher than either McAbee, at about 500–800 m, and Horsefly at about 800 m. Only the Allenby (Princeton) locality, at about 600–1100 m, is modelled by Tribe as having significant overlap in elevation with Hat Creek (paleoelevation estimates are not provided for other localities discussed here). Therefore, a factor controlling the range of the Palm–Swamp Cypress association other than lower elevation warmth must be considered.

Many of the taxa considered here as members of the Palm–Swamp Cypress association are not only thermophilic, but in the southeastern USA. are today restricted to, or are most abundant and diverse in, wetlands (Greller 1988; Christensen 1988). Swamp cypress and the modern sweetgum (*Liquidambar*) generally prefer moist habitats, while Sapotaceae and palms achieve their greatest representation in wet, lowland forests. If the presence of these taxa at Hat Creek was determined in large part by habitat ground moisture, then the correlation of thermophily with these taxa is somewhat a conflating issue. By this model, the relative rarity of Palm–Swamp Cypress association taxa at most localities, e.g., McAbee, indicates less extensive swamplands surrounding these lakes, or a greater distance to such areas from the sample location.

The present pollen analysis of the Hat Creek samples suggests fairly stable conditions throughout the length of the record, providing support for the assertion of Hopkins (1980), Kim (1979), and Blackburn (1982) that community changes at Hat Creek were caused by alteration in the water table through time. The results of this study are interpreted as showing that the trench A section of the Hat Creek samples and sample 3 of trench D reflect drier conditions caused by lower water table levels compared with samples 2 and 1 from trench D. This is supported by the higher amounts of clastic sediments and the increased representation of massive tree types, such as dawn redwood – redwood, oak, maple, sycamore, and elm in the trench A section and dawn redwood – redwood, oak, and maple in sample 3 of the trench D section, which probably reflects the development of a drier swamp. The increased representation of willow (*Salix*) pollen in the A section probably represents the development of a clearly defined stream network across the Hat Creek landscape, although this was not observed in sample 3 of the trench D section and probably suggests that this sample reflects a different time period. In contrast, samples 2 and 1 of the trench D section reflect wetter conditions, with a lower representation of massive tree types and comprising mostly organic material, which suggests higher water table level and a wetter

swamp environment. Further, high-resolution research is indicated to investigate in greater detail alterations in community dynamics at Hat Creek and to clarify the stratigraphic relationship between the trench A samples and sample 3 of the trench D section.

The results of this study have implications for the reconstruction of Okanagan Highlands (and by extension, Eocene) climate. Greenwood et al. (2005) estimated a MAT for McAbee of about 10 °C by leaf margin analysis, and about 13 °C by bioclimatic (nearest living relative) analysis. By this reconstruction, the presence of palms at McAbee would indicate a CMMT of > 5 °C, to allow for the survival of all life-history stages of palms (Greenwood and Wing 1995). At values near 5 °C, however, palms would be near the limit of their climatic tolerance, and their presence would be minimal, as is supported by the pollen signal. The palm line (MAT < 5 °C, i.e., where frost occurrence eliminates palms; Greenwood and Wing 1995) would then be upslope, perhaps at altitudes not much higher than the depositional lake at McAbee. If, however, Hat Creek was at a higher (and perhaps significantly higher) altitude than McAbee, where palms were not only present, but flourishing, then the palm line (MAT < 5 °C) would have to be significantly higher than in the McAbee depositional basin, requiring that equability was increased (seasonality decreased) by a much greater degree than previously posited.

Acknowledgments

We thank Lisa Barksdale, Neil Church, Rosemary Doughty, Brian Farrell, Cornie Froese, Jim Haggart, Andrew Legun, Rolf Mathewes, Terry McCullough, Jim Mortensen, Jack and Sonja Powell, Peter Read, Terrence O'Sullivan, Art Sweet, Robin Webb, and Ken Zimmer (and others at British Columbia Parks in Smithers). We also thank Owen Davis, Jisuo Jin, and Douglas J. Nichols for their extremely helpful comments on the originally submitted manuscript. Partial support for this research was provided by an Australian Research Council Grant to P. T. Moss and D. R. Greenwood, and by a travel grant to D.R. Greenwood by the Faculty of Science, Engineering and Technology, Victoria University (Melbourne, Australia). P.T. Moss is grateful for the support of the Department of Geography and Center for Climate Research at the University of Wisconsin — Madison in providing access to laboratory space and microscopes. S.B. Archibald gratefully acknowledges funding provided by a Natural Sciences and Engineering Research Council of Canada scholarship and a Putnam Expeditionary Grant. We also acknowledge the patience and support of our partners, Belinda, Cathy, and Shelley.

References

- Archibald, S.B., and Mathewes, R.W. 2000. Early Eocene insects from Quilchena, British Columbia, and their paleoclimatic implications. *Canadian Journal of Zoology*, **78**: 1441–1462.
- Barton, D.G., and Wilson, M.V.H. 2005. Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10 000 years of environmental change. *Canadian Journal of Earth Sciences*, **42**: This issue.
- Basinger, J.F. 1976. *Paleorosa similkameensis*, gen. et sp. nov.,

- permineralized flowers (Rosaceae) from the Eocene of British Columbia. *Canadian Journal of Botany*, **54**: 2293–2305.
- Basinger, J.F. 1984. Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. *Canadian Journal of Botany*, **62**: 281–289.
- Basinger, J.F., and Rothwell, G.W. 1977. Anatomically preserved plants from the Middle Eocene (Allenby Formation) of British Columbia. *Canadian Journal of Botany*, **55**: 1984–1990.
- Blackburn, D.T. 1982. Palaeobotany of coal-bearing strata from the Cretaceous and Tertiary of western Canada and Ellesmere Island. Unpublished report to the Geological Survey of Canada. Institute of Sedimentary and Petroleum Geology, pp. 1–128.
- Boneham, R.F. 1968. Palynology of three Tertiary coal basins in central British Columbia. Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, Mich.
- Cevallos-Ferriz, S.R.S., Stockey, R.A., and Pigg, K.B. 1991. The Princeton Chert — evidence for in situ aquatic plants. *Review of Palaeobotany and Palynology*, **70**: 173–185.
- Christensen, N.L. 1988. Vegetation of the Southeastern coastal plain. *In North American terrestrial vegetation. Edited by M.G. Barbour and W.D. Billings.* Cambridge University Press, Cambridge, UK., Ch. 11, pp. 317–364.
- Church, B.N. 1981. Further studies of the Hat Creek coal deposit (921/12, 13E). *In Geological fieldwork 1980.* British Columbia Ministry of Energy, Mines and Petroleum Resources, Paper 921/12, 13E, pp. 99–118.
- Church, B.N., Matheson, A., and Hora, Z.D. 1979. Combustion metamorphism in the Hat Creek area, British Columbia. *Canadian Journal of Earth Sciences*, **16**: 1882–1887.
- Collinson, M.E., Hooker, J.J., and Gröcke, D.R. 2003. Cobham Lignite Bed and pencontemporaneous macrofloras of southern England: A record of vegetation and fire across the Paleocene–Eocene Thermal Maximum. *In Causes and consequences of globally warm climates in the early Paleogene. Edited by S.L. Wing, P.D. Gingerich, B. Schmitz, and E. Thomas.* Geological Society of America, Special Paper 369, pp. 333–349.
- Crepet, W.L., and Daghlian, C.P. 1981. Lower Eocene and Paleocene Gentianaceae: Floral and palynological evidence. *Science*, **214**: 75–77.
- Dillhoff, R.M., Leopold, E.B., and Manchester, S.R. 2005. The McAbee flora of British Columbia and its relation to the Early–Middle Eocene Okanagan Highlands flora of the Pacific Northwest. *Canadian Journal of Earth Sciences*, **42**: This issue.
- Douglas, S.D., and Stockey, R.A. 1996. Insect fossils in Middle Eocene deposits from British Columbia and Washington State: faunal diversity and geological range extensions. *Canadian Journal of Zoology*, **74**: 1140–1157.
- Erwin, D.M., and Stockey, R.A. 1989. Permineralized monocotyledons from the Middle Eocene Princeton (Allenby Formation) of British Columbia — Alismataceae. *Canadian Journal of Botany*, **67**: 2636–2645.
- Erwin, D.M., and Stockey, R.A. 1994. Permineralized monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia — Arecaceae. *Palaeontographica Abteilung, Series B*, **234**: 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.
- Farley, M.B. 1990. Vegetation distribution across the Early Eocene depositional landscape from palynological analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **79**: 11–27.
- Farley, M.B., and Traverse, A. 1990. Usefulness of palynomorph concentrations in distinguishing Paleogene depositional environments in Wyoming (USA). *Review of Palaeobotany and Palynology*, **64**: 325–329.
- Greenwood, D.R., and Wing, S.L. 1995. Eocene continental climates and latitudinal gradients. *Geology*, **23**: 1040–1048.
- Greenwood, D.R., Archibald, S.B., 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.
- Greller, A.M. 1988. Deciduous forest. *In North American terrestrial vegetation. Edited by M.G. Barbour and W.D. Billings.* Cambridge University Press, Cambridge, UK. pp. 288–316.
- Grimm, E. 1991. Tilia 2.0. IBM Computer Pollen Diagram Program.
- Harrison, J.C., Mayr, U., McNeil, D.H., Sweet, A.R., McIntyre, D.J., Eberle, J.J., Harington, C.R., Chalmers, J.A., Dam, G., and Nøhr-Hansen, H. 1999. Correlation of Cenozoic sequences of the Canadian Arctic region and Greenland; implications for the tectonic history of northern North America. *Bulletin of Canadian Petroleum Geology*, **47**: 223–254.
- Hills, L.V. 1965a. Palynology and age of Early Tertiary basins, interior of British Columbia. Ph.D. dissertation, University of Alberta, Calgary, Alta.
- Hills, L.V. 1965b. Source of the Allenby Formation, Princeton coalfield, British Columbia. *Bulletin of Canadian Petroleum Geology*, **13**: 271–279.
- Hills, L.V., and Baadsgaard, H. 1967. Potassium–Argon dating of some Lower Tertiary strata in British Columbia. *Bulletin of Canadian Petroleum Geology*, **15**: 138–149.
- Holdgate, G.R., Wallace, M.W., Gallagher, S.J., and Taylor, D. 2000. A review of the Traralgon Formation in the Gippsland Basin — a world class brown coal resource. *International Journal of Coal Geology*, **45**: 55–84.
- International Commission on Stratigraphy (SIS: Working Group on Stratigraphic Information System) 2004. Available from <http://www.stratigraphy.org> (accessed 24 January 2004).
- Hopkins, W.S., Jr. 1980. Palynology of the 75-106 core hole, Hat Creek coal basin, British Columbia. Geological Survey of Canada, Open File 547, pp. 1–27.
- Jansson, C.R. 1966. Recent pollen spectra from the deciduous and coniferous–deciduous forests of northeastern Minnesota: a study in pollen dispersal. *Ecology*, **47**: 804–825.
- Kim, H. 1979. Depositional Environment and Stratigraphic Subdivision — Hat Creek No. 1 Deposit, B.C. Canada. 4th Annual Meeting, Canadian Institute of Mining and Metallurgy, British Columbia Hydro and Power Authority.
- Long, D.G.F., and Sweet, A.R. 1994. Age and depositional history of the Rock River coal basin, Yukon Territory, Canada. *Canadian Journal of Earth Sciences*, **31**: 865–880.
- Manchester, S.R. 1987. The fossil history of Jungandaceae. *In Monograph in systematic botany.* Missouri Botanical Gardens, St Louis, Mo., pp. 1–137.
- Manchester, S.R. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Gardens*, **86**: 472–522.
- Mathewes, R.W. 2003. An Early Eocene flora from Quilchena, British Columbia and its paleoenvironmental significance. Geological Association of Canada – Mineralogical Association of Canada – Society Economic Geologists, Joint Annual Meeting. Abstracts **28**: abstract 736. (CD-ROM.)
- Mathewes, R.W., and Brooke, R.C. 1971. Fossil Taxodiaceae and new angiosperms from Quilchena, British Columbia. *Syesis*, **4**: 209–216.
- McAndrews, J.H., and Wright, H.E., Jr. 1969. Modern pollen rain

- across the Wyoming basin and the northern Great Lakes (USA). *Review of Palaeobotany and Palynology*, **9**: 17–43.
- McClain, A.M., and Manchester, S.R. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroidae. *American Journal of Botany*, **88**: 1316–1325.
- Pigg, K.B., and Stockey, R.A. 1996. The significance of the Princeton Chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. *Washington Geology*, **22**: 32–36.
- Pojar, J., and Meidinger, D. 1991. British Columbia: the environmental setting. *In Ecosystems of British Columbia*. Edited by D. Meidinger and J. Pojar. British Columbia Ministry of Forests, special report series 6, pp. 39–67.
- Read, P.B. 2000. Geology and industrial minerals of the Tertiary basins, south-central British Columbia. British Columbia Ministry of Energy and Mines. GeoFile 2000-3, pp. 1–110.
- Ridgway, K.D., Sweet, A.R., and Cameron, A.R. 1995. Climatically induced floristic changes across the Eocene–Oligocene transition in the northern high latitudes, Yukon Territory, Canada. *Geological Society of America Bulletin*, **107**: 676–696.
- Rouse, G.E. 1977. Paleogene palynomorph ranges in western and northern Canada. *In Contributions of stratigraphic palynology*. Edited by W.D. Elsik. *Cenozoic Palynology*, **1**: 48–65.
- Rouse, G.E., and Mathews, W.H. 1961. Radioactive dating of Tertiary plant-bearing deposits. *Science*, **133**: 1079–1080.
- Rouse, G.E., Hopkins, W.S., and Piel, K.M. 1970. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. *In Symposium on palynology of the Late Cretaceous and Early Tertiary*, San Francisco, Calif., 1966. Edited by R.M. Kossack and A.T. Cross. *Geological Society of America, Special Paper 127*, pp. 213–246.
- Stockey, R.A., and Manchester, S.R. 1988. A fossil flower with *in situ Pistillipollenites* from the Eocene of British Columbia. *Canadian Journal of Botany*, **66**: 313–318.
- Tribe, S. 2005. Eocene paleo-physiography and drainage directions, southern Interior Plateau, British Columbia. *Canadian Journal of Earth Sciences*, **42**: This issue.
- van der Kaars, W.A. 1991. Palynology of eastern Indonesian marine piston cores: A Late Quaternary vegetational and climatic record from Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **85**: 239–302.
- 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**: 25–27.
- Williams, M., Dunkerley, D., De Deckker, P., Kershaw, P., and Chappell, J. 1998. *Quaternary Environments*. 2nd ed. Arnold, London, UK.
- Wilson, M.V.H. 1977a. New records of insect families from the freshwater Middle Eocene of British Columbia. *Canadian Journal of Earth Sciences*, **14**: 1139–1155.
- Wilson, M.V.H. 1977b. Middle Eocene freshwater fishes from British Columbia. *Life Sciences Contributions 113*. Royal Ontario Museum, Toronto, Ont., pp. 1–51.
- Wilson, M.V.H. 1977c. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. *Canadian Journal of Earth Sciences*, **14**: 953–962.
- Wilson, M.V.H. 1980. Eocene lake environments: depth and distance from shore variation in fish, insect and plant assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **32**: 21–44.
- Wolfe, J.A., and Wehr, W. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. *US Geological Survey Bulletin 1597*, pp. 1–25.
- Wolfe, J.A., Forest, C.E., and Molnar, P. 1998. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. *Geological Society of America Bulletin*, **110**: 664–678.
- Wolfe, J.A., Gregory-Wodzicki, K.M., Molnar, P., and Mustoe, G. 2003. Rapid uplift and then collapse in the Eocene of the Okanogan? Evidence from paleobotany. *Geological Association of Canada – Mineralogical Association of Canada – Society Economic Geologists, Joint Annual Meeting. Abstracts 28*: abstract No. 533 (CD-ROM.)