Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape[1]

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

Abstract: The late Early to early Middle Eocene Okanagan Highlands fossil sites, spanning ~1000 km north–south (northeastern Washington State, southern British Columbia) provide an opportunity to reconstruct biotic communities across a broad upland landscape during the warmest part of the Cenozoic. Plant taxa from these fossil sites are characteristic of the modern eastern North American deciduous forest zone, principally the mixed mesophytic forest, but also include extinct taxa, taxa known only from eastern Asian mesothermal forests, and a small number of taxa restricted to the present-day North American west coast coniferous biome. In this preliminary report, paleoclimates and forest types are reconstructed using collections from Republic in Washington State, USA., and Princeton, Quilchena, Falkland, McAbee, Hat Creek, Horsefly, and Driftwood Canyon in British Columbia, Canada. Both leaf margin analysis (LMA) and quantitative bioclimatic analysis of identified nearest living relatives of megaflora indicated upper microthermal to lower mesothermal moist environments (MAT ~10–15 °C, CMMT > 0 °C, MAP > 100 cm/year). Some taxa common to most sites suggest cool conditions (e.g., *Abies*, other Pinaceae; *Alnus*, other Betulaceae). However, all floras contain a substantive broadleaf deciduous element (e.g., Fagaceae, Juglandaceae) and conifers (e.g., *Metasequoia*) with the bioclimatic analysis yielding slightly higher MAT than LMA. Thermophilic (principally mesothermal) taxa include various insects, the aquatic fern *Azolla*, palms, the banana relative *Ensete*, taxodiaceous conifers, *Eucommia* and *Gordonia*, taxa which may have occurred near their climatic limits. The mixture of thermophilic and temperate insect and plant taxa indicates low-temperature seasonality (i.e., highly equable climate).

Résumé : Les sites fossiles des hautes terres de l'Okanagan (Éocène précoce tardif à moyen précoce) s'étendent sur ~1000 km nord–sud (nord-est de l'État de Washington, sud de la Colombie-Britannique) et fournissent l'occasion de reconstruire les communautés biotiques à travers un vaste paysage de zones sèches durant la partie la plus chaude du Cénozoïque. Les taxons des plantes provenant de ces sites fossilifères sont caractéristiques de la zone moderne de forêts décidues du nord-est de l'Amérique du Nord, principalement la forêt mixte mésophile, mais ils comprennent aussi des taxons éteints, des taxons connus seulement dans les forêts mésothermes de l'est de l'Asie et un petit nombre de taxons restreints au biome conifère actuel de la côte ouest de l'Amérique du Nord. Dans ce rapport préliminaire, les paléoclimats et les types de forêts sont reconstruits à partir des collections de Republic dans l'État de Washington, É.-U., et Princeton, Quilchena, Falkland, McAbee, Hat Creek, Horsefly et le canyon Driftwood en Colombie-Britannique, Canada. L'analyse des bordures de feuilles ainsi que l'analyse bioclimatique quantitative des plus proches parents vivants identifiés de la mégaflore indiquent des environnements humides microthermes supérieurs à mésothermes inférieurs (TMA ~10–15 °C, température moyenne des mois les plus froids > 0 °C, PMA > 100 cm/an). Quelques taxons communs aux sites humides suggèrent des conditions fraîches (p. ex. *Abies*, d'autres Pinacées; *Alnus*, d'autres Bétulacées). Toutefois, toutes les flores contiennent un élément substantif de décidu à feuille large (p. ex. Fagacées, Juglandacées) et de conifères (p. ex. *Metasequoia*) avec une analyse bioclimatique qui donne des TMA plus élevées que l'analyse de la bordure des feuilles. Les taxons thermophiles (surtout mésothermes) comprennent la fougère aquatique *Azolla*, des palmiers, *Ensete*, parent de la banane, des conifères de la famille des Taxodiacées, *Eucommia* et *Gordonia*, des taxons qui étaient possiblement à leur limite

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D.R. Greenwood.[2] Environmental Science Program, 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.
R.W. Mathewes. Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
P.T. Moss. School of Geography, Planning and Architecture, University of Queensland, Brisbane, QLD 4072, Australia.

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[2]Corresponding author (e-mail: greenwoodd@brandonu.ca).

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climatique. Le mélange de taxons thermophiles et tempérés de plantes et d'insectes indique une saisonnalité de basse température (c'est-à-dire un climat hautement tempéré).

[Traduit par la Rédaction]

Introduction

The Eocene is recognized from paleontological and isotopic evidence worldwide as the warmest part of the Cenozoic, with peak warmth in the Early Eocene Climatic Optimum (Wolfe 1985; Wing and Greenwood 1993; Basinger et al. 1994; Zachos et al. 2001; Greenwood et al. 2003). Paleontological evidence demonstrates Eocene forests and a diverse biota well beyond their present day latitudinal extent, including sites in the high Arctic (Basinger et al. 1994; Markwick 1994). At North American middle latitudes, Early to Middle Eocene taxa include "temperate" elements that occur alongside crocodilians and other thermophilic vertebrates, various insect taxa, and plant groups, such as palms, gingers, and tree ferns, that are today either restricted to or most diverse in frost-free tropical and subtropical environments (Wolfe and Wehr 1987; Wing and Greenwood 1993; Greenwood and Wing 1995; Markwick 1994; Archibald and Mathewes 2000). The Okanagan Highlands assemblages occur in a series of lacustrine shales and coal deposits that extend ~1000 km northwest from Republic, in northeastern Washington State, to Driftwood Canyon, in west-central British Columbia (Fig. 1). Multiple sites in these basins preserve a rich Early to Middle Eocene plant and insect record, as well as vertebrates (e.g., Mathewes and Brooke 1971; Basinger 1976, 1981, 1984; Wilson 1977*a*, 1977*b*, 1980; Basinger and Rothwell 1977; Guthrie 1985; Wolfe and Wehr 1987; Erwin and Stockey 1989, 1994; Cevallos-Ferriz et al. 1991; Douglas and Stockey 1996; Pigg and Stockey 1996; Stockey et al. 1998; Archibald and Mathewes 2000).

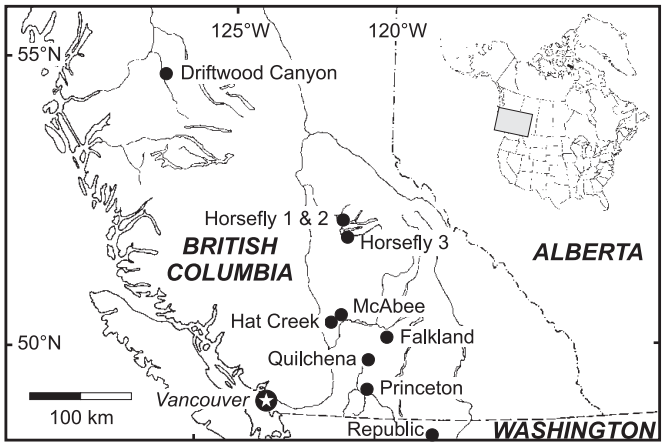
The Republic compression flora assemblages and the Princeton Chert permineralized flora contain a mixture of taxa that includes both thermophilic tropical elements (e.g., a cycad, the banana-relative *Ensete*, the palm *Uhlia*, and other arboresecent monocots, and various dicots, such as *Gordonia*), as well as those associated with temperate climates today (e.g., *Abies*, *Larix* and other Pinaceae; *Betula* and other Betulaceae; Fagaceae; *Ulmus* and other Ulmaceae) (Basinger 1984; Crane and Stockey 1987; Wolfe and Wehr 1987; Erwin and Stockey 1994; Pigg and Stockey 1996; Schorn and Wehr 1996; Wehr and Manchester 1996; Hopkins and Johnson 1997; Wehr 1998). Indeed, many of the genera reported as fossils are characteristic of the deciduous forest biome of eastern North America (e.g., *Betula*, *Carya*, *Castanea*, *Fagus*, *Juglans*, *Liquidambar*, *Liriodendron*, *Ostrya–Carpinus*, *Tilia*, and others; Greller 1988), implying that the Okanagan Highlands Eocene floras may represent the antecedents of this biome type (e.g., Wolfe 1985, 1987). Wolfe and Wehr (1987), however, argued on taphonomic grounds that dicot leaves were over-represented relative to the conifer remains, and stressed the high conifer diversity of the Republic flora, suggesting an analogy with the mixed coniferous forest (sensu Wolfe 1979) of the Pacific Northwest of North America. More recent systematic studies of the Republic flora have highlighted, however, the high diversity of broadleaf taxa, including Rosaceae (e.g., Johnson 1996; Wehr 1998; Pigg and Wehr 2002; DeVore et al. 2005). Phytogeographic analyses have also pointed to the presence of plant genera in these floras that are restricted today to east Asian forests or shared between east Asia and eastern North America (Manchester 1999; DeVore et al. 2005).

That the Okanagan region was an upland in the Eocene is suggested by regional history of tectonic uplift (Ewing 1980), geomorphology (Tribe 2005), and comparison with presumably coeval coastal lowland fossil localities with floras that indicate higher mean annual temperatures (Rouse et al. 1971; Wolfe and Wehr 1987; Wolfe 1994; Schorn and Wehr 1996; Wolfe et al. 1998). Differences between the floristic composition and leaf physiognomy of the coeval Okanagan Highlands and Puget Group fossil floras are consistent with an altitudinal difference between them of 0.7–1.2 km (Wolfe and Wehr 1987; Wolfe 1994; Schorn and Wehr 1996).

Wilson (1977*c*) considered the Eocene Horsefly fossil biotas, and the sedimentology of the varved lake sediments, indicative of a warm temperate climate, with wet summers and dry winters; however, he equivocated on whether seasonal temperature fluctuations were sufficient to allow some winter ice cover on the lakes. Based on the classification of the Republic flora as mixed coniferous forest, and the presence of a broadleaved evergreen element, Wolfe (Wolfe 1987; Wolfe and Wehr 1987) interpreted the Republic, Princeton, and coeval floras from British Columbia as microthermal, and suggested a MAT for Republic of 12 to 13 °C and cold month mean temperature (CMMT) in the range of –2 to <1 °C. Okanagan Highlands sites analysed by taxon-free leaf physiognomic analyses (Wing and Greenwood 1993; Greenwood and Wing 1995; Wolfe 1994; Wolfe et al. 1998) have also consistently indicated microthermal climates (where megathermal MAT > 24 °C, mesothermal MAT is 13–24 °C, and microthermal MAT < 13 °C sensu Wolfe 1979). Coeval coastal megafloras from the Puget Group in Washington State yielded estimates of 15–18.6 °C (Wolfe 1994; Wolfe et al. 1998; Mustoe 2002), indicating mesothermal climates at low elevations in the late Early to early Middle Eocene.

Wolfe and his co-workers have derived several estimates for the paleoelevation of the Republic and other Okanagan Highlands floras using paleobotanical inference, ranging in chronological order from 0.7 to 0.9 km for Republic (Wolfe and Wehr 1987), 0.9 to 1.7 km for Republic and 1.1 to 2 km for One Mile Creek (Wolfe 1994), and 2.5 km and 2.9 km (±0.9 km), respectively, for these two floras (Wolfe et al. 1998). The latter two sets of estimates (Wolfe 1994; Wolfe et al. 1998) overlap at the extremes of the error of the estimates, and support the idea that the Okanagan Highlands in the region around Republic and Princeton was at a paleoelevation > 1 km in the Early Eocene, comparable to, but higher than, the present altitude (~0.8 km). Tribe (2005) interprets the Eocene landscape as resembling its modern counterpart with highlands, plains, and deeply incised drainages, where relief

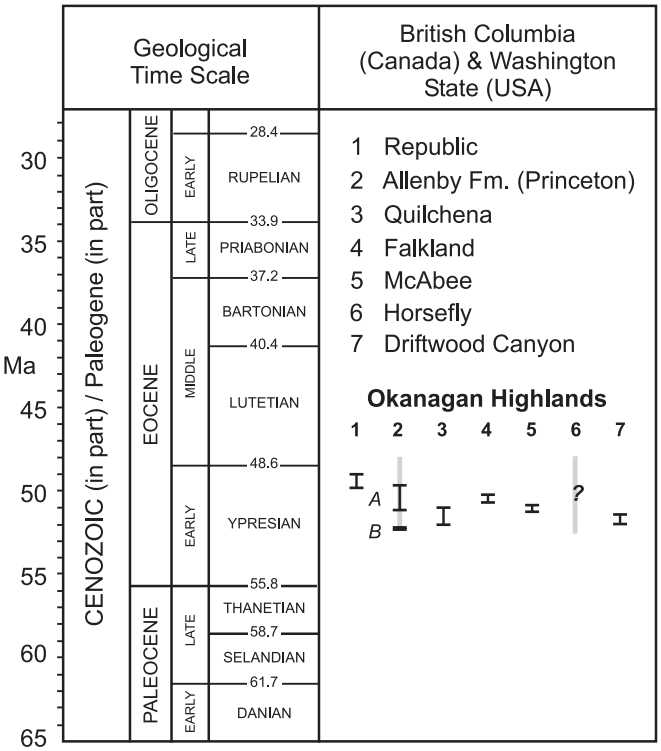
Fig. 1. Map showing the location of the fossil sites. Adapted from Wilson (1977*b*).



ranged from 400 to 1500 m, and the regional base level was in the range of 400–1200 m. In an area the size of the Okanagan Highlands, spanning ~1000 km north–south (~7 °C of latitude; Fig. 1), variation in elevation can be expected across the landscape. Based on an estimate that the Eocene meridional temperature gradient in North America was 0.4–0.6 °C/1 °C latitude (Greenwood and Wing 1995), at constant elevation a difference in MAT of ~3–4 °C can be expected between the southernmost (Republic) and northernmost (Driftwood Canyon) of the Okanagan Highlands floras. The biota arrayed across this landscape would, therefore, have had available to it in the Early Eocene a range of climatic zones, reflecting both the latitudinal and the altitudinal range present within the region. Within the present-day deciduous forest biome of eastern North America, and also within the southeastern coastal plain, canopy dominance by key tree genera and the overall floristic composition and structure of stands varies locally across the landscape between ridges and swales, and regionally with elevation, and along east–west rainfall and north–south temperature gradients (Christensen 1988; Greller 1988).

In this paper, we examine multiple sites to assess the extent to which variation at the scale of the landscape is reflected in the fossil floras, arrayed across the north–south transect from Republic in the south to Driftwood Canyon in the north (Fig. 1). These biotic assemblages are from sites that have been dated within an increasingly narrow range of about 3 Ma emerging from modern geochronological methodologies in recent years (Mathewes 2003; Wolfe et al. 2003) and the work in progress of Mortensen and Archibald (Fig. 2). The effects of climate change over this time interval are likely to be over-ridden by altitude and latitude differences across the Okanagan Highlands in the late Early Eocene to early Middle Eocene as global temperatures were relatively stable through this time (Zachos et al. 2001). The biogeographical relationships of North American Paleogene and Neogene floras, including in part those of the Okanagan Highlands, have been considered by Manchester (1999), Dillhoff et al. (2005) and DeVore et al. (2005), and so are not discussed in detail here. However, Wolfe's (1987; Wolfe and Wehr 1987) comparison of the Okanagan Highlands floras with the mixed coniferous forest of the Pacific Northwest of North America

Fig. 2. Stratigraphic chart showing the age and relationship of the Okanagan Highlands fossil sites, based on sources cited in the text and new radiometric ages from the work in progress of Mortensen and Archibald. Geological time scale from International Commission on Stratigraphy (2004). *A*, Blakeburn Mine; *B*, Hospital Hill.



is assessed, vis a vis the deciduous forest zone of eastern North America, and the mixed broadleaf deciduous – broadleaf evergreen forests of Meso-American highlands.

Localities and approach

Fossil localities

Regional setting

The fossil assemblages analysed here are from outcrops of the Okanagan Highlands series of deposits, which extend from north-central Washington State through the Thompson–Okanagan, Cariboo, and Bulkley Valley regions of southern British Columbia (Fig. 1), of Early Eocene (Ypresian) to early Middle Eocene (Lutetian) age (Fig. 2). The sites therefore provide a north–south transect, extending in an ~1000 km north-northwest line from a current latitude of 48°40′N (Republic) to 55°N (Driftwood Canyon). The majority of the sites are clustered in southern British Columbia, spanning an area of ~700 km^2. Outcrops of eight regional depositional basins are considered here: Republic in northeastern Washington State, USA.; One Mile Creek (Allenby Formation), Quilchena, Falkland, McAbee, Hat Creek, Horsefly, and Driftwood Canyon in British Columbia, Canada. Additional fossil sites are known, but are not considered here. Site descriptions presented here are in part modified from Wilson (1977*c*), Wolfe and Wehr (1987), Douglas and Stockey (1996), and Stockey et al. (1998).

Depositional basins

The Driftwood Canyon site is located east of Smithers, B.C., in Driftwood Canyon Provincial Park. Shales of an unnamed formation of the Ootsa Lake Group are exposed in cliff faces along Driftwood Creek. The ongoing work of Mortensen and Archibald gives a preliminary age for the Driftwood Canyon sediments of 51.77 ± 0.34 Ma by U–Pb zircon analysis. The fossiliferous Horsefly shale outcrops on the Horsefly River, about 8 km north and east of the town of Horsefly in the Cariboo region of south-central British Columbia (Fig. 1). No radiometric age has been reported for this unnamed formation of an unnamed group, but tephra from beds within the shale sequence is currently being analysed by Mortensen and Archibald.

The Hat Creek fossils are from sub-bituminous coal (Hat Creek Formation, Kamloops Group) situated between Cache Creek and Lillooet in south-central British Columbia (Fig. 1). Rare fragmentary leaf impressions were encountered in iron-stained baked shale on a recent reconnaissance (SBA and DRG), but otherwise the megaflora at Hat Creek is restricted to fragmentary leaf cuticle (Blackburn 1982) and massive, partly silicified tree stumps in the coal. 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. This outcrop (unnamed formation of the Kamloops Group) has been dated at ~51 Ma (Ewing 1981). The Falkland site is in the Columbia–Shuswap region of south-central British Columbia (Fig. 1). The Falkland megaflora is reported here for the first time. Preliminary U–Pb dating from zircons by Mortensen and Archibald give an age of 50.61 ± 0.16 Ma.

The Quilchena site is about 3 km south of the town of Quilchena on Quilchena Creek. Sediments consist of light gray to buff fine-grained shales. Current radiometric analysis (^{40}Ar–^{39}Ar) of sanidine from Quilchena tephra (Villeneuve, Geological Survey of Canada and RWM) gave a radiometric age of 51.5 ± 0.4 Ma. Two sites of the Allenby Formation near the town of Princeton in southern British Columbia are considered here: One Mile Creek and the Princeton Chert. The One Mile Creek site is 8 km north of the town of Princeton on Highway 5, near the confluence of the Allison and Summers Creek. Specimens were collected from a light grey-green shale consisting of laminae of silts, clays, and finely graded volcanics occurring within the Hardwick sandstone unit. A preliminary age determined by Mortensen and Archibald of 52.08 ± 0.12 Ma (U–Pb from zircons) for the Hospital Hill locality (see Moss et al. 2005) in the Vermillion Bluffs shale unit overlying the Hardwich sandstone, constrains One Mile Creek to no younger than the Ypresian. The Princeton Chert locality is on the east side of the Similkameen River, about 8.4 km south of the town of Princeton. The outcrop consists of at least 49 interbedded layers of chert and coal with an occasional thin ash bed replacing a chert layer. The locality has been referred to as locality "I" (Boneham 1968) and the "Princeton Chert" (Basinger and Rothwell 1977; Stockey et al. 1998). Chert layers and interbedded coal seams are part of the Princeton Group, Allenby Formation and are located 630 m above the Princeton–Black coal seam (Boneham 1968).

The Republic flora was collected from the Tom Thumb Tuff Member of the Klondike Mountain Formation in a series of quarries in and around the town of Republic in Ferry County, northeastern Washington (Wolfe and Wehr 1987). Republic has been assigned an age of 49.42 ± 0.54 Ma by ^{40}Ar–^{39}Ar (Wolfe et al. 2003). Further detailed discussion of localities, lithologies and the age determinations is provided in Moss et al. (2005).

Collections examined

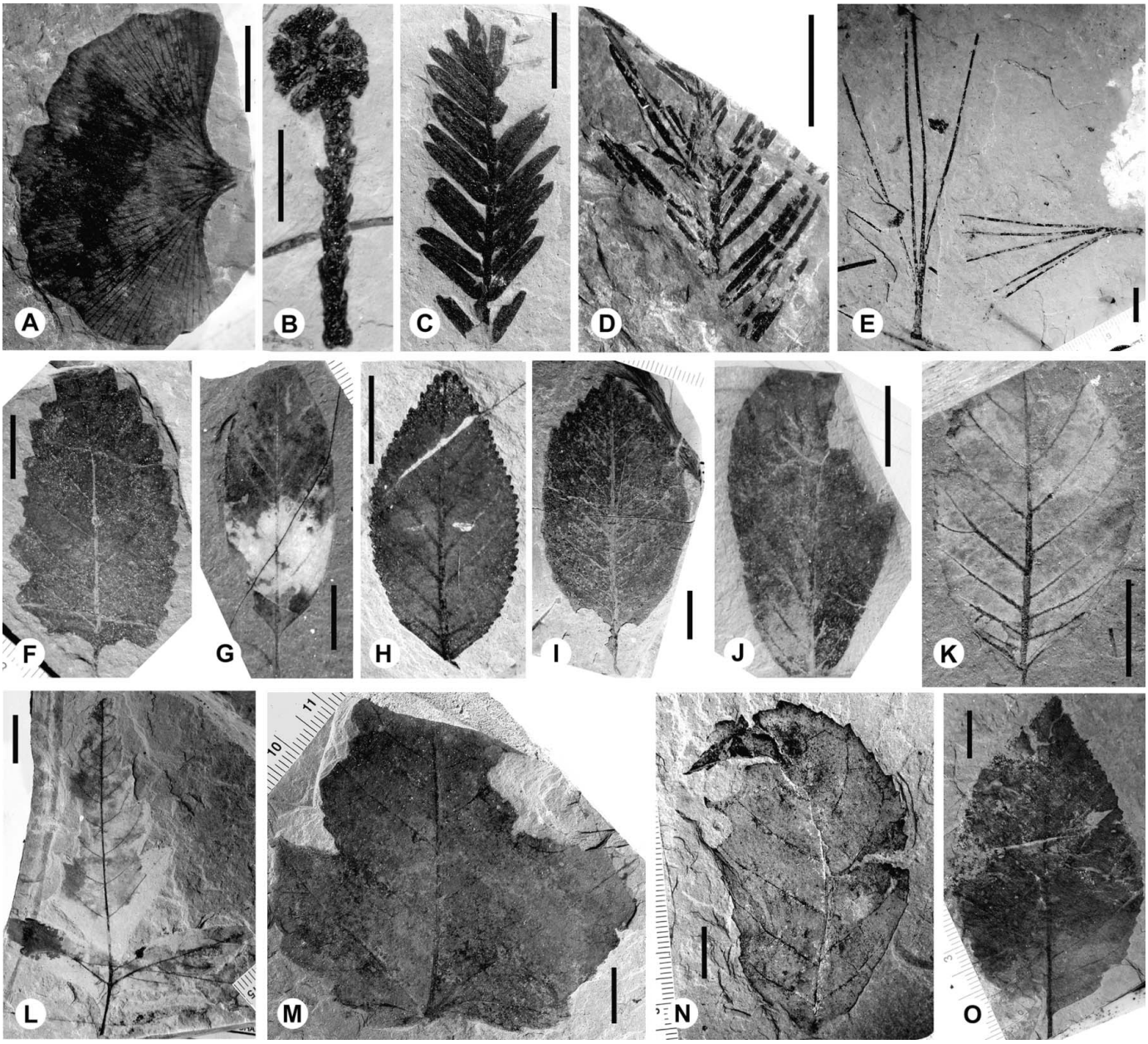
A number of existing collections were used in this study. Leaf collections from McAbee and the One Mile Creek locations were examined from the Department of Geological Sciences, University of Saskatchewan, Saskatoon (collected by J.F. Basinger), and specimens from these sites photographed from collections in the Department of Biological Sciences, University of Alberta, Edmonton (collected by M.V.H. Wilson, R.A. Stockey and colleagues). Data from Republic were primarily from photographs of the collections in the Stonerose Interpretive Center, Republic, and the Burke Museum, Seattle, Washington and published sources (e.g., Wolfe and Wehr 1987; Pigg and Wehr 2002). Data from Quilchena are from collections at Simon Fraser University, Burnaby, British Columbia (RWM). Fossils from Princeton (One Mile Creek), Falkland, McAbee, Horsefly, and Driftwood Canyon were collected by one of us (SBA) specifically for this study (Fig. 3). Concomitantly collected samples for palynological analysis from these same localities (and others, including Hat Creek and Republic) are reported by Moss et al. (2005).

Systematic relationships of megafloral taxa and their inferred nearest living relatives are based on Wehr (1998), Pigg and Wehr (2002), and Manchester (1999; McClain and Manchester 2001), with some data on McAbee from Dillhoff et al. (2005). Nomenclature for modern plants used in this paper follows usage in the online edition of the Flora of North America (Flora of North America Editorial Committee 1993; Anonymous 2003). Following the latter work, the Cupressaceae encompasses the former "Taxodiaceae," *Acer* and *Aesculus* are placed in the Sapindaceae, *Nyssa* in Cornaceae, and the Mexican elm (section *Chaetoptelea*) is placed within *Ulmus*.

Paleoenvironmental analysis

Paleoclimates were estimated using two quantitative approaches: bioclimatic analysis and leaf margin analysis (Greenwood et al. 2003). Bioclimatic analysis (Kershaw and Nix 1988; Kershaw 1996) is essentially the same as the co-existence approach of Mosbrugger and Utescher (1997), and requires the development of "climatic profiles" (i.e., climatic parameters such as MAT and MAP) using the climate associated with the distributions of modern plant genera. The first step of this approach is to identify as many "nearest living relatives" (NLRs) as possible in the fossil floras (megaflora; Table 2). A library of climatic profiles is then produced for several key taxa based on climatic values, such as mean annual temperature (MAT), mean annual precipitation (MAP), and coldest month mean temperature (CMMT) (Kershaw and Nix 1988; Kershaw 1996; Moss and Kershaw 2000; Greenwood et al. 2003). The climatic profiles used here were from two sources; a study of North American tree genera (Thompson et al. 1999) and the PALAEOFLORA database (PALAEO-

Fig. 3. Examples of leaves of taxa from the Falkland fossil flora. Scale bars = 1 cm. (A) *Ginkgo*, (B) *Sequoia*, (C) *Metasequoia*, (D) *Abies*, (E), *Pinus*, (F) unidentified dicot, (G) cf. Lauraceae, (H) cf. *Prunus*, (I) indeterminate Rosaceae, (J) unidentified dicot, (K) indeterminate Rosaceae, (L) cf. *Acer*, (M–O) unidentified dicots.



FLORA database 2003; Mosbrugger and Utescher 1997), which includes a wider range of extant plant genera than the North American database and also includes European and Asian distribution records. The zone of overlap for a set of NLRs defines the most likely climate space occupied for an individual fossil flora (Kershaw and Nix 1988; Kershaw 1996; Mosbrugger and Utescher 1997; Greenwood et al. 2003). The mean climatic values for each site (Republic, One Mile Creek (Allenby Formation), Quilchena, Falkland, McAbee, Horsefly, and Driftwood Canyon) were calculated by examining the climatic variables (e.g., MAT, MAP, and CMMT) for each NLR taxon found at that location. Greenwood et al. (2003) calculated mean climate values for fossil sites based on the range of the individual climatic variable for the 25th to 75th percentile values for each of the NLR taxa and divided these values by the total number of NLRs found at each site. However, Kershaw and Nix (1988) had previously rejected this approach, on the grounds that climate profiles can be highly skewed with some genera having the majority of their distribution at one extreme of the total climate range. Accordingly, in the current study the climate envelope or zone of coexistence that accommodated a majority of taxa was determined for all sites in the present study (Kershaw and Nix 1988; Mosbrugger and Utescher 1997). To deal

Table 1. Leaf physiognomy-based estimates of MAT (°C) for Okanagan Highlands floras.

Flora site	CLAMP	CLAMP-MLR	*r*	LMA (1)	LMA (2)
Republic	11.4[1], 10.0[2]	8.0[3]	28[3]	9.1[3]	9.4±2.0[3]
			45	8.8±2.0	9.2±2.0
One Mile Creek	9.3[1], 8.3[2]	5.1	26	3.5±2.0	5.1±2.0
Quilchena	—	—	52	15.3±2.1	14.8±2.0
Falkland	—	—	24	9.4±2.8	10.0±2.2
McAbee	9.5[4]	10.7[3]	21	10.0[3]	10.4±2.4
				10.1±3.0	
Horsefly	—	—	24	10.1±3.0	10.4±2.2
Driftwood Canyon	—	—	6	6.2±4.7	7.3±3.7

Note: Data sources: [1] Wolfe (1994); [2] Wolfe et al. (1998); [3] Wing and Greenwood (1993), Greenwood and Wing (1995); [4] Dillhoff et al. (2005). No data is provided for Hat Creek, as this site has not yielded leaves. Minimum error of the estimate in all cases is ±2 °C (Wilf 1997). LMA, leaf margin analysis; MLR, multiple linear regression (Wing and Greenwood 1993; Greenwood and Wing 1995).

with outliers, taxa whose climate profile sits outside of the zone of overlap of the majority of taxa, the zone of overlap was calculated using the 10th percentile (lower limit) and 90th percentile (upper limit) of the total range for all taxa recorded for a single flora.

Leaf margin analysis (LMA) has been widely applied to North American Paleogene floras (Wolfe 1979; Greenwood and Wing 1995; Wilf 1997). Data from South and North America and East Asia produce essentially the same statistical relationship between leaf margin proportion and MAT (i.e., the same slope and essentially the same intercept). Two LMA equations are used for the present study: (1) that derived from Wolfe (1979) by Wing and Greenwood (1993), and (2) the regression equation derived from the CLAMP "warm sites" data set by Wilf (1997). The equations are

$$[1] \qquad \mathrm{MAT}_{\mathrm{LMA\text{-}78}} = 11.41 + (30.6 \cdot P_{\mathrm{margin}})$$

$$[2] \qquad \mathrm{MAT}_{\mathrm{LMA\text{-}CLAMP}} = 3.25 + (24.4 \cdot P_{\mathrm{margin}})$$

where P_{margin} is the proportion of dicot species where the leaf margin lacks teeth ($0 < P_{\mathrm{margin}} < 1$).

Applying the method of Wilf (1997), the error of the estimate for LMA is expressed here as the binomial sampling error

$$[3] \qquad \sigma[\mathrm{LMA}] = c\sqrt{(P_{\mathrm{margin}}(1 - P_{\mathrm{margin}} / r}$$

where c is the slope from the LMA regression equation, P_{margin}, as defined in eq. [1], and r is the number of species scored for leaf margin type for the individual flora (Table 1).

Fossil biota

Floristics

The Republic, One Mile Creek, and Princeton Chert floras (and related sites in the Allenby Formation) are the most collected and studied of the Okanagan Highland Eocene floras, although Quilchena and McAbee also have significant data available (Mathewes and Brooke 1971; Wolfe and Wehr 1987; Pigg and Stockey 1996; Wehr 1998; Manchester 1999; McClain and Manchester 2001; Pigg and Wehr 2002; Mathewes 2003; Dillhoff et al. 2005). Assigning fossils to extant genera based on leaves alone is often problematic, as diagnostic characters for extant genera may be restricted to reproductive organs (e.g., *Betula leopoldae*, One Mile Creek), and the leaves of closely related genera in some cases cannot be separated (e.g., *Betula* and other Betulaceae), or may even be confused with the leaves of unrelated extant genera (Manchester 1999; Pigg et al. 2003). In other cases, however, megafloral taxa can be identified to subgeneric rank (e.g., *Alnus parvifolia* is closest to the extant Meso-American species *A. incana* of subgenus *Alnus*, Wolfe and Wehr 1987, p. 15). Because of the concentration of systematic effort and taphonomic factors (including differences in preservation, e.g., the Princeton Chert is a permineralized 3-dimensional flora, whereas all others are impression–compression floras), the number of identifications and overall diversity for Republic and Princeton is much higher than for the other floras, with a significant number of taxa known from only one of these two floras (Table 2). For this report, identifications of taxa for most of the floras are largely based on Wehr (1998), the review of North American Tertiary floras by Manchester (1999) and Pigg and Wehr (2002), and our analysis of available collections. For McAbee, the identifications listed by Dillhoff et al. (2005) are used, including their confirmation of *Fagus* from nuts and cupules at McAbee, Princeton, and Republic (see also Pigg and Wehr 2002). Hat Creek is not considered fully here, as leaf fossils from this site are rare and fragmentary (Blackburn 1982).

A suite of diverse gymnosperms occurs throughout these floras, with *Ginkgo*, *Metasequoia*, and several genera of Pinaceae (*Abies*, *Picea*, *Pinus*, and *Pseudolarix*) found in each. *Sequoia* is known from foliage (±cones) from all but one of the seven floras. Blackburn (1982) reported that coal samples from Hat Creek were dominated by leaf cuticle of *Glyptostrobus* and (or) *Metasequoia*, with rare *Ginkgo*. There are several conifers that are known from only a single locality (*Cephalotaxus* and *Taxus*, Republic; *Calocedrus* and *Taxodium*, Quilchena), while others are known from two or three localities (e.g., *Amentotaxus* and *Chamaecyparis* — Republic, Quilchena, and One Mile Creek; *Cryptomeria* — Republic and McAbee; *Glyptostrobus* — Republic, Quilchena, and Falkland). The conifer diversity in the southernmost sites of Republic (16 genera) and Princeton (11 genera) is significantly higher than in the northernmost site, Driftwood Canyon (6 genera). Moss et al. (2005) and Dillhoff et al. (2005) reported a number of conifer taxa as pollen that were not recorded as megaflora

Table 2. Plant taxa recognized in the Okanagan Eocene megafloras (i.e., leaves and (or) reproductive structures) that were used for bioclimatic analysis[a] and genera typical of modern sites of the mixed coniferous forest of the Pacific Northwest (Wolfe 1979; Franklin 1998), the deciduous forest zone (principally the mixed mesophytic forest, but also swamp forests) of modern eastern North America[b] (Christensen 1998; Greller 1998), and cool uplands in Meso-America (Hartshorn 1998).

			Okanagan Highlands Eocene Floras							Modern forest zones					
Fossil taxon	Family	NLR	R	OM–P	Q	F	McA	H	DC	1	2	3	4	5	6
Osmunda	Osmundaceae	*Osmunda*		*				*	*				*		
Azolla	Salviniaceae	*Azolla*	*	*	*	*		*							
Schizeaceae	Schizeaceae	*Lygodium*	*	*											
cycads	Zamiaceae	cycads	*										*		
Ginkgo	Ginkgoaceae	*Ginkgo*	*	*	*	*	*	*	*						
Abies	Pinaceae	*Abies*	*	*	*	*	*	*	*	*		*		*	*
Keteleeria		*Keteleeria*			*										
Picea		*Picea*	*	*	*	*	*	*	*	*	*	*			*
Pinus		*Pinus*	*	*	*	*	*	*	*	*		*	*	*	*
Pseudolarix		*Pseudolarix*	*	*	*	*	*	*	*						
Tsuga		*Tsuga*	*	*	*		*	*	*	*	*	*			*
Amentotaxus	Taxaceae	*Amentotaxus*	*	*	*		?								
Taxus		*Taxus*	*				?	*		*			*	*	*
Torreya		*Torreya*	*		?			*					*		
Calocedrus	Taxodiaceae	*Calocedrus*			*		?								*
Chamaecyparis	Cupressaceae	*Chamaecyparis*	*	*	*		*			*			*		*
Cryptomeria		*Cryptomeria*	*				*								
Glyptostrobus		*Glyptostrobus*	*		*	*									
Juniperus		*Juniperus*		*				*		*				*	
Metasequoia		*Metasequoia*	*	*	*	*	*	*	*						
Sequoia		*Sequoia*	*	*	*	*	*	*							*
Taxodium		*Taxodium*			*					*			*	*	
Thuja		*Thuja*	*	*	*		*								*
Rhus	Anacardiaceae	*Rhus*	*	*	*		?			*			*		*
Ilex	Aquifoliaceae	*Ilex*	*							*	*	*	*		
Uhlia	Arecaceae	*Sabal*		*									*	?	
Alnus	Betulaceae	*Alnus*	*	*	*		*	*	*				*	*	*
Betula		*Betula*	*	*	*	?	*		*	*	*	*		?	
Corylites		*Corylus*	*	*		*	*	*	*	*				*	*
Joffrea – Nyssydium – Trochodendroides	Cercidiphyllaceae	*Cercidiphyllum*	*	*	*	*	*								
Cornus	Cornaceae	*Cornus*	*	*	*		*			*		*	*	*	*
	(Nyssaceae)	*Nyssa*			*					*			*	*	
Arbutus	Ericaceae	*Arbutus*	*												*
Rhododendron		*Rhododendron*	*												
Eucommia	Eucommiaceae	*Eucommia*	*		*										
Castaneophyllum	Fagaceae	*Castanea*	*	*	?					*	*	*			
Fagus		*Fagus*	*	*			*			*	*	*	*		
Quercus		*Quercus*	*	*			*	*	*	*	*	*	*	*	*
Ribes	Grossulariaceae	*Ribes*	*	*			*			*					*
Corylopsis	Hamamelidaceae	*Corylopsis*	*	*	*										
Hamamelis		*Hamamelis*								*					
Itea	Iteaceae	*Itea*	*										*		
Carya	Juglandaceae	*Carya*	*				*	*		*	*	*	*		
Juglans		*Juglans*	*							*	*				
Pterocarya		*Pterocarya*	*	*			*								
Lindera	Lauraceae	*Lindera*		*						*			*		
Phoebe		*Phoebe*	*	*			*							*	
Sassafras		*Sassafras*	*	*		*	*			*		*			
Liriodendroxylon	Magnoliaceae	*Liriodendron*		*						*		*	*		
Talauma		*Magnolia*	*							*	*	*	*		
Morus	Moraceae	*Morus*	*							*	*		*		
Ensete	Musaceae	*Musa*	*												
Comptonia	Myricaceae	*Comptonia*	*	*	*		*								
Fraxinus	Oleaceae	*Fraxinus*			*		*			*	*		*		*
Macginitea – Macginicarpa	Platanaceae	*Platanus*	*	*	*	*	*	*						*	
Amelanchier	Rosaceae	*Amelanchier*		*	*		*			*		*			
Crataegus		*Crataegus*	*				*	*		*			*		

Table 2 (*concluded*).

Fossil taxon	Family	NLR	Okanagan Highlands Eocene Floras							Modern forest zones					
			R	OM–P	Q	F	McA	H	DC	1	2	3	4	5	6
Malus		*Malus*	*												
Photinia		*Photinia*	*	*											
Prunus		*Prunus*	*	*	*	*	*			*	*	*	*		*
Rubus		*Rubus*	*	*											
Sorbus		*Sorbus*	*	*			*			*		*	*		
Spiraea		*Spiraea*	*	*											
Clematis	Ranunculaceae	*Clematis*	*					*							
Populus	Salicaceae	*Populus*	*		*		*			*					*
Salix		*Salix*	*				?			*					
Acer	Sapindaceae	*Acer*	*	*	*	*	*			*	*	*	*		*
Aesculus		*Aesculus*	*	*			*			*	*	*			
Bohlemia – Dipteronia		*Dipteronia*	*	*	*	*	*								
Koelreuteria		*Koelreuteria*	*				*								
Gordonia	Theaceae	*Gordonia*	*		*		*						*		
Ternstroemites		*Ternstroemia*	*												
Tilia	Tiliaceae	*Tilia*	*		*					*	*	*	*		
Ulmus	Ulmaceae	*Ulmus*	*	*	*	*	*		*	*	*		*	*	
Zelkova		*Zelkova*	*		?		*								
Ampelocissus – Cissus – Vitis	Vitaceae	*Vitis*	*	*		*	*			*					

Note: R, Republic; OM–P, One Mile – Princeton Creek; Q, Quilchena; F, Falkland; McA, McAbee; H, Horsefly; DC, Driftwood Canyon. 1, mixed mesophytic forest; 2, central Appalachians; 3, southern Appalachians; 4, southeast coastal plain; 5, northern Meso-America (>1000 m); 6, Pacific Northwest. ? denotes uncertain records that were not used in the bioclimatic analysis. Comparisons with Asian forest types are provided in Dillhoff et al. (2005).

[a]Data on fossil occurrences from Mathewes and Brooke (1971), Wehr (1998), Manchester (1999), Mathewes (2003), Dillhoff et al. (2005), various sources cited in the text and this study. However, this is not an exhaustive list. Some taxa were omitted as either NLRs could not be determined, or a climate profile could not be obtained for a fossil taxon's NLR. Not all taxa had climate profiles for each climate parameter.

[b]Some genera may occur within the Pacific Northwest or the deciduous forest zone but were not specifically cited by Franklin (1988), Greller (1988), and Hartshorn (1988), so were not included here. Taxa such as *Ginkgo*, *Amentotaxus*, and *Cercidiphyllum* are exclusively present today in East Asia.

for some sites (e.g., *Taxus* from Allenby Formation sites and Hat Creek; *Taxodium* from Allenby Formation sites, McAbee, and Hat Creek; *Juniperus* from McAbee and Hat Creek; and *Tsuga* at McAbee).

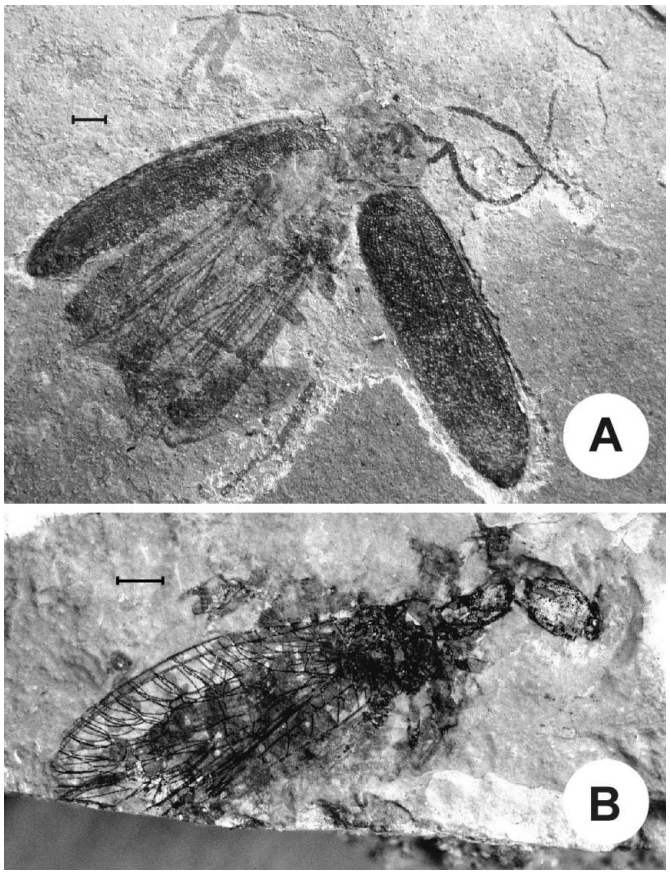
A number of dicot taxa are known from all or the majority of megafloras; e.g., *Acer*, *Alnus*, *Betula*, *Cercidiphyllum*, *Sassafras*, *Comptonia*, and *Ulmus* (including "*Chaetoptelea*" at One Mile Creek, Quilchena, and Republic), and others (Table 2). These taxa together with the common gymnosperms appear to constitute the main forest elements across most of the Eocene landscape of the Okanagan Highlands. The extinct taxon *Florissantia* is also found in the majority of floras (Wehr 1998; this study). A small number of dicot taxa are known from a single locality (e.g., *Ilex*, *Rhododendron*, and *Ternstroemia*, Republic; *Nyssa*, Quilchena); however, most taxa are known from two or more fossil localities (e.g., *Cornus*, *Eucommia*, *Fagus*, *Gordonia*, *Rhus*, *Ribes*, *Tilia*, and *Zelkova*). Some of these taxa are likely to be detected in additional sites as further sampling occurs and as systematic understanding of all of the floras improves, particularly as some are recorded as pollen for sites where they are absent as megafossils (Dillhoff et al. 2005; Moss et al. 2005).

At Hat Creek, Blackburn (1982) reported that the carbonaceous claystones and shaly beds at Hat Creek, representing open water semi-lacustrine as opposed to paludal environments, yielded leaf cuticle assemblages with *Equisetum*, unspecified ferns, *Typha*, Betulaceae, and unspecified other angiosperms together with *Metasequoia*. Semi-quantitative data are available for One Mile Creek (Allenby Formation), Republic, and McAbee, and these sites appear to show differences in the dominant leaf taxa, between floras and also between quarry sites within floras. Wolfe and Wehr (1987, p. 10) reported that the Republic megaflora was dominated by dicot leaves, with several dicot taxa that were "represented by more than 20 specimens…", including *Alnus*, *Cercidiphyllum*, *Sassafras*, and *Comptonia*. However, these authors pointed to differences in dominance between individual quarries and lithotypes in the Republic area, with for example *Cercidiphyllum*, *Macginitea*, and *Comptonia* leaves abundant at Resner Canyon, whereas *Fagopsis* leaves dominated Graphite Creek. McAbee collections surveyed in this study, and on site, are dominated by leaves of *Fagus* (with attached nuts and cupules: Pigg and Wehr 2002; Dillhoff et al. 2005), *Ginkgo*, and *Sassafras*, whereas One Mile Creek collections are dominated by leaves of *Betula* and *Cercidiphyllum*. *Metasequoia* twigs are very common at all sites, and *Pinus* needles are common at several. This anecdotal evidence suggests that quantitative sampling yielding specimen counts > 300 leaves (e.g., Greenwood and Basinger 1994; Wilf et al. 2003) may indicate greater differences among the Okanagan Highlands Eocene megafloras than presence–absence data (e.g., Table 2) alone indicates. Palynological data also demonstrated patterns of differing taxon dominance between samples within a flora and between floras (Dillhoff et al. 2005; Moss et al. 2005).

Fauna

The fossil fauna of the Okanagan Highlands is dominated by its insect assemblage (Fig. 4), both rich in specimens and taxonomically diverse, with over 80 families in 17 orders determined from both compression fossils in shale and Hat Creek amber (e.g., Wilson 1977*a*; Wehr 1998; Poinar et al.

Fig. 4. Climatically indicative insects from the Okanagan Highlands Eocene sites. Scale bars = 1 mm. (A) A cockroach (Blattodea: Blaberidae: Diplopterinae) from McAbee; its nearest living relative ranges almost exclusively tropical regions (SBA999a). (B) A snakefly (Raphidioptera) from One Mile Creek; its nearest living relative inhabits cool regions of the Holarctic (higher altitudes in southern portion of range) (UWBM77544).



1999). Despite this known richness at the family level, the insect fossil record of the region has remained understudied since it was first discovered in the 1870s (Scudder 1879). Therefore, the taxon count is steeply rising as these insects are analysed in detail; the significance of this entomofauna is becoming increasingly apparent. Other arthropods include spiders and rare crayfish specimens.

Fish are not diverse but are commonly found throughout the region, both as loose scales and as skeletons (Wilson 1977*b*). Only one extant genus has been found, the bowfin, *Amia*, which is today restricted to the southeastern United States (Wilson 1996).

The skeletal remains of vertebrates other than fish are exceedingly rare. Cevallos-Ferriz et al. (1991) illustrated turtle bones from an Allenby Formation locality on the Similkameen River. Birds are mostly known from loose feathers, which are found with regularity at McAbee and occasionally at other localities, such as Quilchena (Guthrie 1985). The "cough-up pellet" coprolites of birds are also quite common, particularly at Quilchena, and consist mostly of partially digested fish bones (Wilson 1987), although pellets containing insect remains have also been recovered (SBA). Less than a half dozen bird skeletons are known; these have not been definitively studied. The avian fauna, therefore, remains poorly known even though coprolites and feathers are relatively common. Mammals are known only from two Tillodont teeth recovered from an Allenby Formation outcrop on the Similkameen River (Russell 1935; Gazin 1953). These were bear-sized mammals, whose position within the class is unknown.

Plants and paleoclimates

All lines of evidence indicate that the Okanagan Highlands in the late Early Eocene to early Middle Eocene experienced a microthermal to lower mesothermal mesic climate (Tables 1, 3). The results from leaf margin analysis (eqs. [1] and [2]) for all sites, except Quilchena, provided an estimated MAT in the range 3.5–10.4 °C (Table 1). The LMA estimates for Republic and McAbee were consistent with previously published estimates for these floras (Table 1), based on either LMA (Wing and Greenwood 1993) or multivariate physiognomic analyses (Wing and Greenwood 1993; Wolfe 1994; Greenwood and Wing 1995; Wolfe et al. 1998; Dillhoff et al. 2005). Our LMA estimates for MAT from One Mile Creek and Horsefly are based on a small, low-diversity sample in each instance (Table 1), and the estimate of 3.5 ± 2.0 °C for One Mile Creek using equ. [1] is significantly lower than estimates using CLAMP for this site (Wolfe 1994; Wolfe et al. 1998). Our estimate of 5.1 ± 2.0 °C for One Mile Creek using eq. [2] is within the lower bounds of the error of the estimate for previous studies, but nonetheless appears low. Ongoing research on the One Mile Creek megaflora is revealing a greater diversity of dicot taxa than is represented in the samples used in the present analysis (Dillhoff et al. 2005; DeVore et al. 2005), and LMA based on the scoring of a more diverse One Mile Creek sample may yield a different MAT estimate to that provided here.

Republic and the southern British Columbia sites include thermophilic elements, such as the banana relative *Ensete* (Musaceae) and a cycad, both at Republic, and the palm *Uhlia* and other "tropical" monocots of the Princeton Chert (Allenby Formation). Other thermophilic taxa found in the southern sites include *Dipteronia* (Falkland, McAbee, Republic, and Quilchena), *Eucommia* (Republic and Quilchena), and *Gordonia* (Republic, McAbee, and Quilchena). However, the majority of taxa known from Republic and (or) Allenby Formation sites and other southern British Columbia floras are warm temperate (i.e., upper microthermal to lower mesothermal), and include *Acer* and *Aesculus* (Sapindaceae), *Castaneophyllum–Fagus–Quercus* (Fagaceae), *Liriodendroxylon* (Magnoliaceae), *Tilia–Craigia* (Tiliaceae), *Sassafras*, and other Lauraceae, *Ilex* (Aquifoliaceae), *Arbutus* and *Rhododenron* (Ericaceae), *Fraxinus* (Oleaceae), Vitaceae (*Ampelocissus–Cissus–Vitis*), *Cercidiphyllum–Joffrea–Nyssydium–Trochodendroides* (Cercidiphyllaceae), Magnoliaceae, *Platanus–Macginitea–Macginicarpa* (Platanaceae), *Carya–Juglans* and *Pterocarya* (Juglandaceae), *Photinia* (Theaceae), *Rhus* (Anacardiaceae), *Ulmus* and *Zelkova* (Ulmaceae), and others. In addition, there are commonly found taxa that are typical of, but not restricted to, cool temperate to even boreal climates (i.e., microthermal zones), such as *Abies*, *Picea* and other Pinaceae, and *Alnus* and *Betula* (Betulaceae). Wolfe

Table 3. Bioclimatic-based estimates[a] of climate for Okanagan Highlands Early Eocene-Middle Eocene floras, based on the megafloral lists in Table 2.

Flora site	MAT (°C)	CMMT (°C)	MAP (cm/year)
Republic	13.5±2.2 (51)	4.1[b]±4.0 (52)	115±39 (52)
One Mile–Princeton	13.1±3.1 (39)	5.3[b]±2.8 (40)	114±42 (40)
Quilchena	15.0±0.6 (32)	5.8±2.0 (33)	126±28 (33)
Falkland	14.7±2.1 (21)	5.2±3.0 (21)	105±48 (22)
McAbee	13.5±2.5 (36)	3.5±4.4 (35)	108±35 (35)
Horsefly	13.3±1.9 (20)	5.3±2.8 (20)	105±47 (20)
Driftwood Canyon	12.3±1.9 (13)	2.7±5.6 (12)	102±63 (12)

Note: MAT, mean annual temperature; CMMT, cold month mean temperature; MAP, mean annual precipitation. The number of taxa used for each estimate is given in parentheses.

[a]The estimate is the zone of overlap or coexistence interval (Kershaw and Nix 1988; Utescher and Mosbrugger 1997), calculated as the mean of the upper bound and lower bound of the total range all values for each taxon, constrained to the 10th–90th percentiles of each climate value to remove outliers. The error of the estimates is the upper bound and lower bound of the total range across all of the climate profiles for all taxa represented in each flora.

[b]The presence of a cycad at Republic (Hopkins and Johnson 1997), and a palm in the Princeton Chert (Erwin and Stockey 1994), constrains CMMT > 5 °C for these two sites (Wing and Greenwood 1993; Greenwood and Wing 1995).

(1987) considered the Okanagan Highlands climate to be microthermal because of the presence of these taxa. Although these genera have peak diversity in microthermal climates, they may include mesothermal species.

Bioclimatic analysis provided information on seasonal temperature extremes (as CMMT) and mean annual precipitation (MAP), as well as mean annual temperature (MAT) (Table 3). The number of taxa available for bioclimatic analysis for each flora ranged from 52 (Republic) to 12 (Driftwood Canyon). Where the systematic resolution of the fossils did not permit separation of related extant genera (e.g., *Palaeocarpinus* and *Corylus–Carpinus*: Manchester 1999; Pigg et al. 2003), the climate profile used both modern genera combined. Few taxa were found in common among all floras (in the preceding text, and Table 2). MAT estimates using bioclimatic analysis based on all taxa varied across the range 12.3–15.0 °C (Fig. 5A), with similar errors of the estimate (±0.6–2.5 °C) to those for LMA (Table 1). Allowing for errors in both methods, estimates for most floras overlap at the upper bound of the LMA estimate and the lower bound of the bioclimatic estimate. For the majority of the floras where both LMA and bioclimatic estimates of MAT were available, the latter were on average higher by 3–5 °C, with the exception of Quilchena, which was comparable, and One Mile Creek, where the LMA estimates of MAT was 8.3 °C cooler than the bioclimatic estimate. The warmest bioclimatic estimates were for the southern sites (Republic, Quilchena, and Falkland), although the differences among all floras are not significant.

All sites had bioclimatic estimates of CMMT > 0 °C, in the range 2.7–5.8 °C, with the coolest site being Driftwood Canyon, but with most estimates overlapping within their errors; therefore, the differences between sites are not meaningful. The presence of a cycad (Hopkins and Johnson 1997) and a palm (Erwin and Stockey 1994) at Republic and the Princeton Chert respectively, further constrain CMMT > 5 °C for these two sites (Wing and Greenwood 1993; Greenwood and Wing 1995). At the lower bounds of the constrained estimates for CMMT, winter snow-falls and potential killing frosts are possible for the northernmost Driftwood site and for McAbee — climates that could not support key taxa (e.g., palms known from the Princeton Chert, palm pollen abundant at Hat Creek; Moss et al. 2005). The co-occurrence of some thermophilic taxa at all sites, with a significant number of microthermal taxa at the upper bound of their modern climatic range, likely reflects the skewed modern distribution of a significant number of North American taxa present in each of the floras; taxa that are today typical of, and most speciose in, microthermal climates and mesothermal climates with CMMT < 0 °C in North America (e.g., Pinaceae (*Abies*, *Picea*, and *Tsuga*), Betulaceae (*Alnus* and *Betula*), and Fagaceae). This skew towards cold-adapted members may reflect the restriction in the database to species found in Europe, Asia, Canada, and the USA (Mosbrugger and Utescher 1997; Thompson et al. 1999). However, some of these taxa also have microthermal–mesothermal members in the upland forests of Meso-America (e.g., *Alnus acuminata*, *Cornus* spp., Fagaceae (including *Quercus oleoides* and *Q. copeyensis*), and *Ulmus mexicana*), and the high mountains (>2000 m) of Guatemala include a high diversity of conifers (e.g., *Abies*, *Cupressus*, *Juniperus*, *Pinus*, *Taxodium*, and *Taxus*) (Hartshorn 1988) (Table 2). Meso-American highlands sites (i.e., >1000 m) experience microthermal–mesothermal climates but with much higher CMMT than sites at higher latitudes at the same MAT.

In the present analysis, constraining the bioclimatic analysis of CMMT by deriving the zone of overlap exclusive of outliers (sensu Mosbrugger and Utescher 1997) removed the weighting of those taxa with markedly warm profiles (i.e., taxa where the CMMT 25th percentile > 5 °C; *Sequoia*, cycads, and palms; Fig. 5B). Further, *Sequoia* is clearly relictual today. Other relictual taxa, such as *Ginkgo* and *Metasequoia* were not included in the constrained bioclimatic analyses, as their present distribution is not indicative of their potential modern range. These constrained estimates of CMMT are consistent with Wolfe and Wehr's (1987) estimate for Republic. The presence of a significant number of thermophilic taxa (e.g., cycads or palms at two sites, "Taxodiaceae" at all sites) also suggests CMMT was > 5 °C for both the Princeton Chert (Allenby Formation) and Republic, and supports CMMT

Fig. 5. Bioclimatic profiles for selected fossil sites using taxa known from each megaflora (Table 2). *Taxodium* is plotted in place of *Metasequoia* for all sites, as the latter is relictual, and the climate profile of *Taxodium* is wider than that of extant *Metasequoia* and so provides a more conservative comparison. Similarly, *Platanus* is used as a proxy for *Macginitea*. The climate profile of extant Australian *Cycas* (Cycadaceae) + *Macrozamia* (Zamiaceae) is used as a proxy for all cycads, and the palms *Livistona* (a pan-Australian highly speciose genus) and *Sabal palmetto* (a widespread North American species) are used as proxies for *Uhlia* (Arecaceae) from the Princeton Chert. (A) Bioclimatic profiles for MAT. (B) Bioclimatic profiles for CMMT. (C) Bioclimatic profiles for MAP.

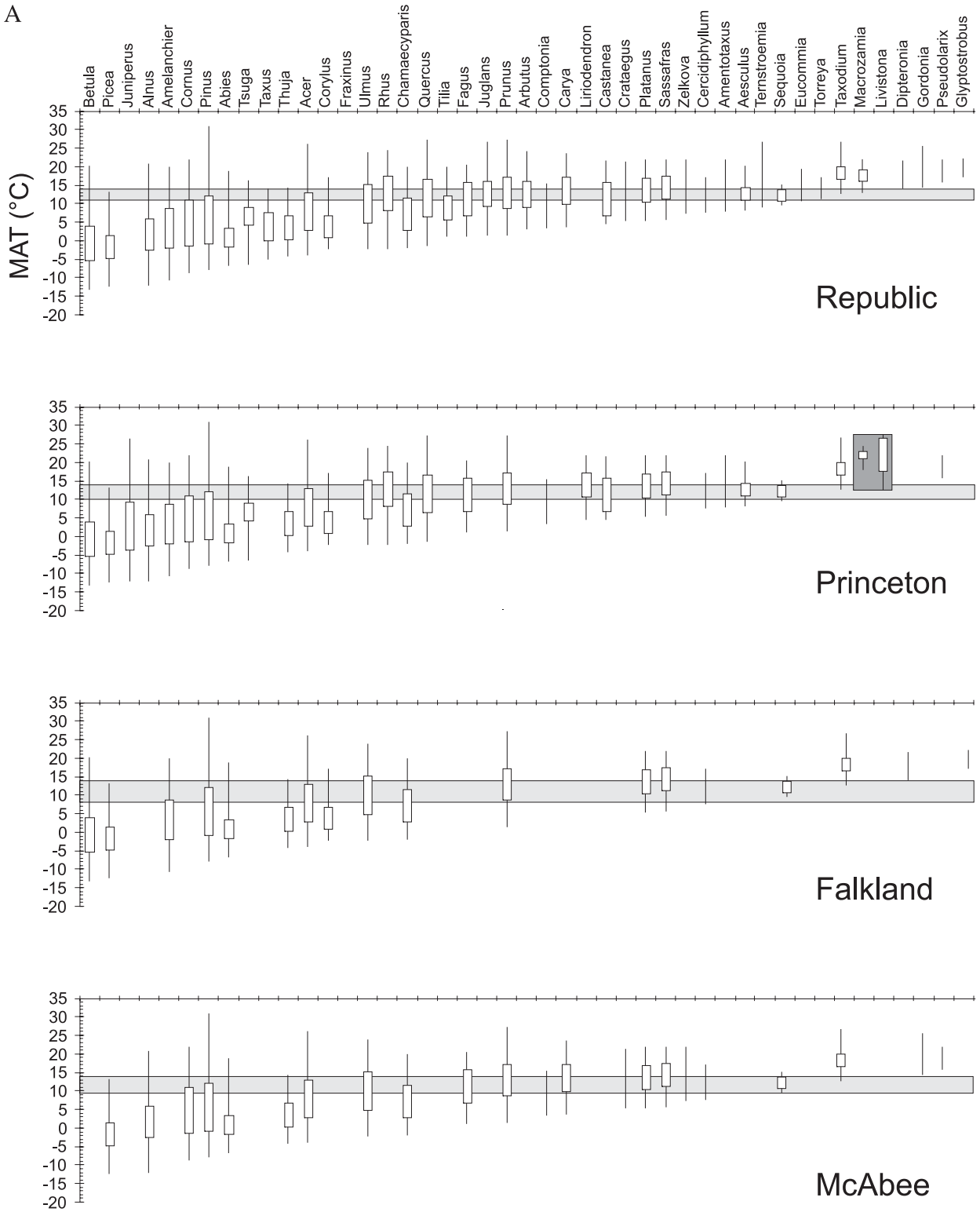
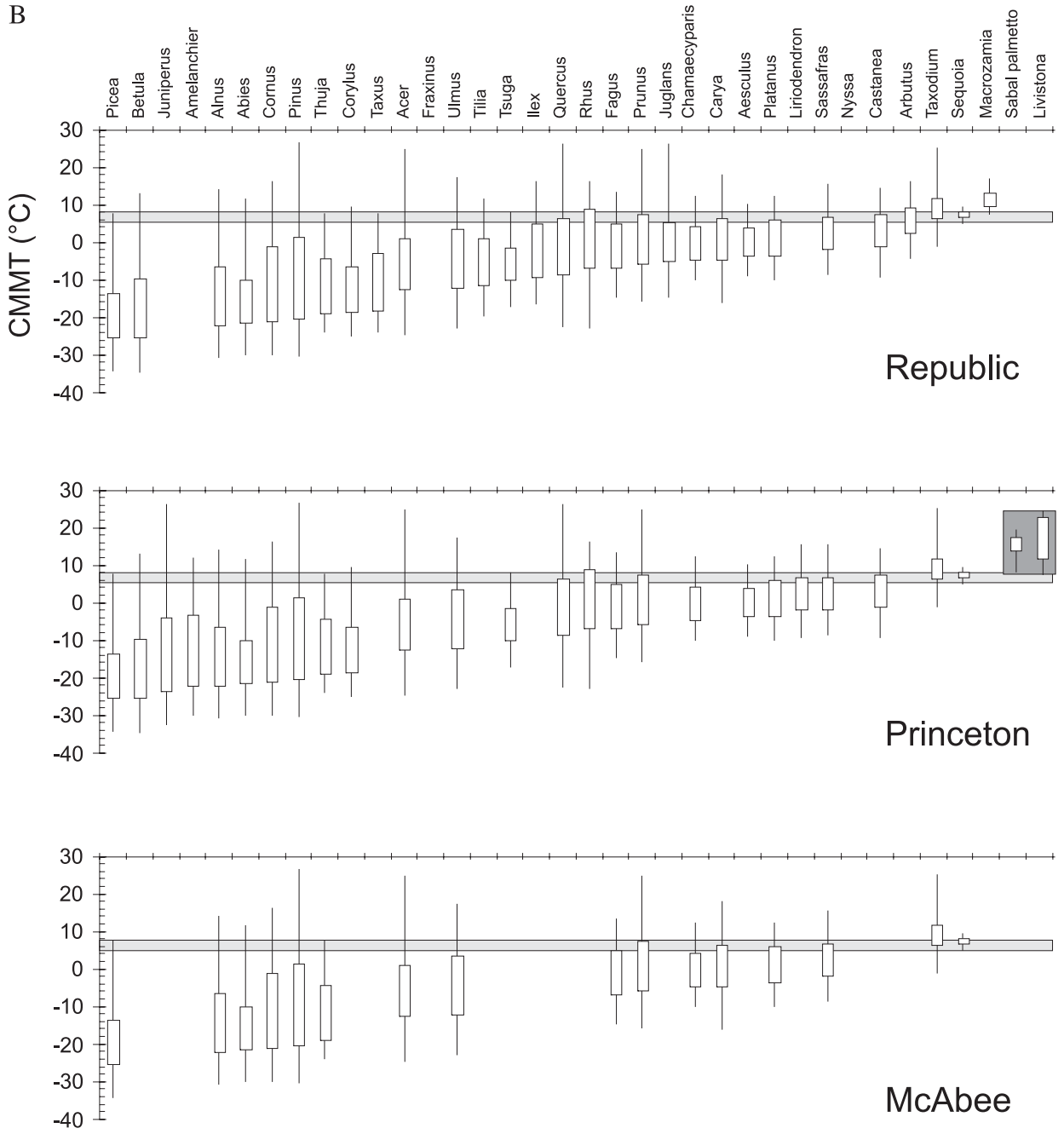


Fig. 5 (*continued*).



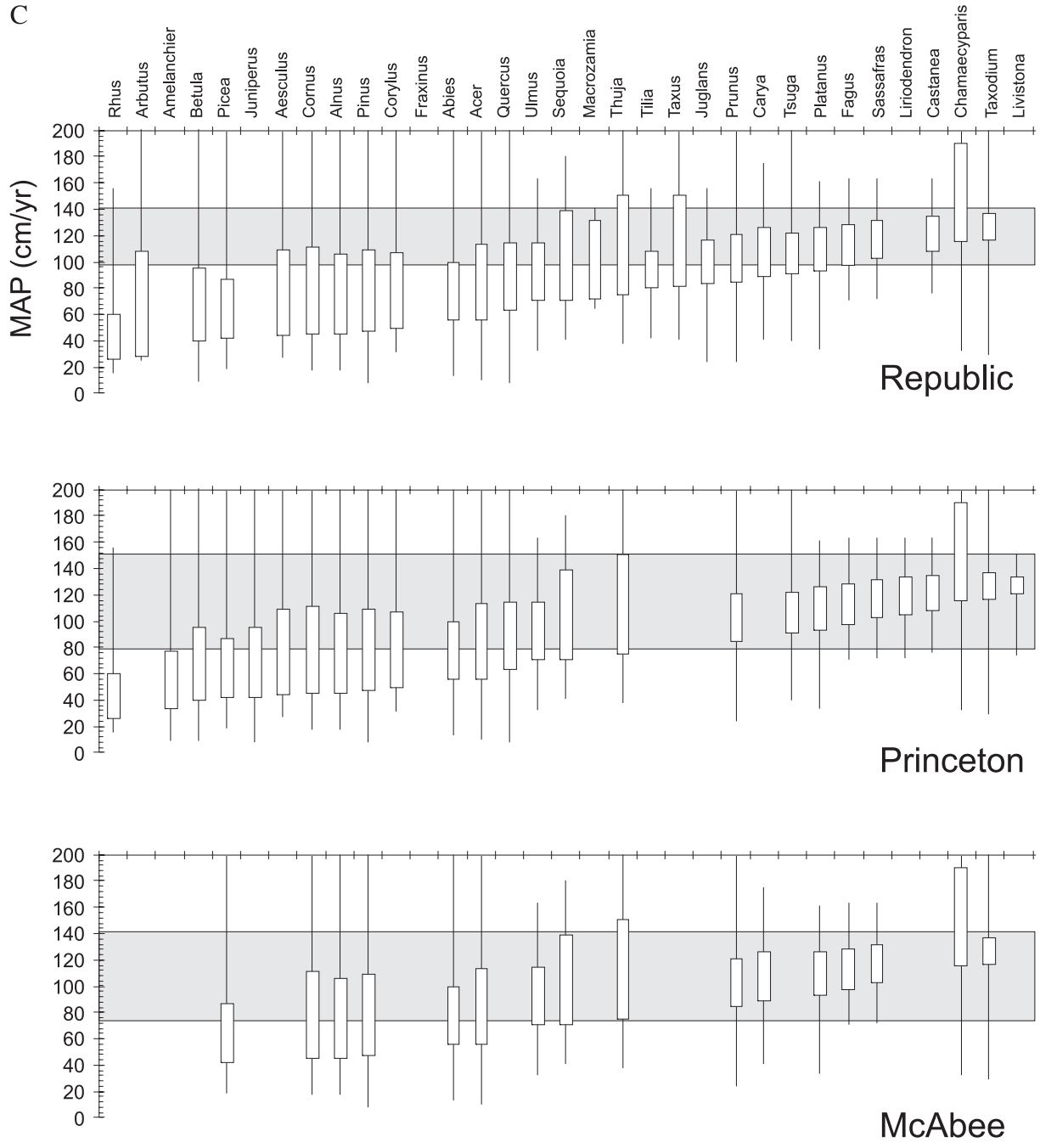
≥ 0 °C for all sites. Recent experimental trials growing key taxa (e.g., palms and "Taxodiaceae") under high pCO_2 (800 ppmv), indicated that NLR-based estimates of CMMT may underestimate this parameter by 1.5–3 °C for times when atmospheric pCO_2 was high, such as in the Early Eocene (Royer et al. 2002). Greater refinement of the bioclimatic estimates of both MAT and CMMT may be possible with greater taxonomic precision for the matching of fossil and extant NLRs (e.g., *Alnus parvifolia* cf. subgenus *Alnus*), and particularly the development of climate profiles for Meso-American species of the microthermal taxa.

All sites gave bioclimatic estimates of MAP that indicate a mesic climate (i.e., MAP 102–126 ± 35–48 cm/year; Fig. 5C) (Table 3). As rainfall at its lower limit is most likely to control the distribution of most of the plant genera present, the lower limit of the MAP estimate is considered to be representative of the Early to Middle Eocene climates of the Okanagan Highlands.

Insects and paleoclimates

The bulk of the taxonomic work on the Okanagan Highlands insect fauna has been at the family level (e.g., Wilson 1977*a*; Lewis 1992; Douglas and Stockey 1996; Wehr 1998; Archibald and Mathewes 2000). The climatic affinities of their nearest living relatives, and their biogeographical, ecological, and evolutionary implications will become increasingly apparent as their systematic positions are determined

Fig. 5 (*concluded*).



to finer taxonomic levels. Some patterns, however, are becoming evident. For example, as in Eocene entomofaunas of Baltic amber and other deposits (Archibald and Farrell 2003), insects whose nearest living relatives are considered both thermophilic and cool-associated are present together in Okanagan Highlands assemblages (Figs. 5A, 5B).

Cockroaches of the blaberid subfamily Diplopterinae were reported from Quilchena (Archibald and Mathewes 2000) and have recently been determined (SBA) from Republic and McAbee (Fig. 4B). These Okanagan Highlands fossil Diplopterinae are probably congeneric with the distinctive beetle-like *Diploptera*, the single extant genus of this subfamily, which ranges from the Indian Ocean through Pacific Ocean regions, almost exclusively in the tropics (but also on Easter Island). Bruchid seed weevils (Coleoptera: Chrysomelidae, Pachymerinae), which have been reported from Quilchena (Archibald and Mathewes 2000), are closely allied to extant pachymerines of the Indian Ocean region (determination: G. Morse). This subfamily in general is tropical or subtropical today (Kingsolver 1965). New bruchids have been collected at Driftwood Canyon and McAbee (SBA). A dinidorid (Hemiptera: Heteroptera) of the genus *Megymenum* was also reported from Quilchena (Archibald and Mathewes 2000). *Megymenum* today ranges from tropical Southeast Asia to tropical–subtropical regions of northern Australia. Termites of the family Mastotermitidae (Isoptera) have been

reported from Horsefly (Wilson 1977*a*); other termites from McAbee, Princeton and Falkland are likely congeneric. Extant mastotermitids are native to tropical northern Australia and have been introduced to areas of New Guinea (Watson and Gay 1991). March flies (Diptera: Bibionidae) in 22 species of *Plecia* and *Penthetria* are extremely common fossils throughout the Okanagan Highlands and are the most common insects at most localities (Rice 1959, Wilson 1977*a*, Wehr 1998). These insects are most diverse in low latitudes today, with the genus *Plecia* ranging as far north as subtropical and warm-temperate regions of the southeastern United States.

A cool-climate insect signal is also apparent throughout the region. All extant snakeflies (Raphidioptera) range exclusively in cool regions of the Holarctic (Aspök and Aspök 1991). Fossil snakeflies are known from One Mile Creek, McAbee, and Republic (Wehr 1998; new material) (Fig. 4A). A brown lacewing of the genus *Wesmaelius* (Neuroptera: Hemerobiidae) was described from Quilchena (Makarkin et al. 2003). Of the 60 or so extant species of this genus, about 50 have exclusively Palearctic and Nearctic distributions. All those remaining species that range into lower latitudes live in mountainous regions at cooler high elevations, except one, *Wesmaelius nubilus*, which alone may inhabit areas of tropical lowland heat (Makarkin et al. 2003).

Several insect taxa are notable exceptions to the well-documented latitudinal gradient of species richness, namely parasitoid ichneumon wasps (Hymenoptera: Ichneumonidae) and aphids (Hemiptera: Aphididae). Both groups are most diverse in temperate mid-latitudes (aphids in the Northern Hemisphere in particular) rather than in the tropics, where they are depauperate (Heie 1967, 1994; Janzen 1981; Dixon et al. 1987; Popov et al. 2001). An increasingly diverse assemblage of both of these groups is emerging from the Eocene Okanagan Highlands. Ichneumons are among the most plentiful insect fossils after March flies at most sites, with an increasingly evident taxonomic diversity regionally; a variety of aphids are becoming well known at various localities, presumably where taphonomic factors allow (particularly in extremely fine-grained matrix, such as characterizes some beds at Driftwood Canyon).

Discussion

Paleoclimates

The estimates of MAT from our study (Tables 1, 3), with one exception (Allenby Fm. sites), were consistent with previously published reconstructions for Okanagan Highlands Eocene sites (e.g., Wilson 1977*c*; Wolfe 1987, 1994; Wolfe and Wehr 1987; Wing and Greenwood 1993; Greenwood and Wing 1995; Wolfe et al. 1998; Dillhoff et al. 2005). All lines of evidence point to upper microthermal to lower mesothermal climates (MAT ~10–15 °C; i.e., "warm temperate") in the Okanagan Highlands in the late Early Eocene to early Middle Eocene, with lower mesothermal conditions indicated by bioclimatic analysis. The estimates of Eocene CMMT and MAP presented in this paper typically have large errors associated with them (Table 3). However, the estimates of rainfall are consistent with general expectations from earlier qualitative and narrative analyses, in that the Okanagan Highlands are reconstructed as being mesic, with rainfall > 100 cm/year. The calculated bioclimatic estimates of CMMT ~3 °C at the northernmost Driftwood Canyon site, at the lower bounds of the estimate, indicates a climate that experienced winters cold enough to experience snow-lie for at least part of the time — conditions that would kill some of the plant taxa present (e.g., some "Taxodiaceae," palms known from pollen: Moss et al. 2005); however the CMMT estimates for most of the floras would allow the presence of taxa, such as palms, based on the anatomy and physiology of living examples (Wing and Greenwood 1993; Greenwood and Wing 1995). Moss et al. (2005) have reported palm pollen in trace amounts at most sites, including Driftwood, but only in Hat Creek samples was palm pollen abundant. The mix of thermophilic taxa together with clearly microthermal taxa (plants and insects) in most of the fossil assemblages appears anomalous in comparison to the modern North American middle latitudes. However, this outcome would appear to be a consequence of the restriction in the modern reference database for climate profiles for the NLR plant genera that are biased towards North American and European records of current distribution (Mosbrugger and Utescher 1997; Thompson et al. 1999), to the exclusion of uplands Meso-American records of plant genera such as *Ulmus* (i.e., section *Chaetoptelea*), *Abies*, *Alnus*, and other "microthermal" lineages. This modern distribution is, therefore, skewed (Kershaw and Nix 1988), as it excludes areas where these living taxa experience low MAT combined with low mean annual range of temperature (and thus higher relative CMMT). For example, the Australian palm genus *Livistona* has a lower MAT yet comparable CMMT lower limit as the North American palm *Sabal palmetto* (Figs. 5A, 5B), reflecting the more equable Australian climate; CMMT is the primary factor limiting palm distribution (Greenwood and Wing 1995). Nonetheless, the CMMT estimates of the Okanagan Eocene floras can accommodate the majority of taxa (i.e., 2.7 ± 5.6 °C to 5.8 ± 2.0 °C; Fig. 5B), indicating a highly equable climate, and is consistent with other lines of evidence and prior estimates (e.g., Wolfe and Wehr 1987).

Forest communities

Wolfe and Wehr's (1987) match of the Republic flora (and by inference, the Okanagan Highlands) to the lower montane mixed coniferous forest type of the Pacific Northwest of North America was based primarily on the high conifer diversity of the Republic flora (and palynofloras with 70%–80% bisaccate Pinaceae (Wolfe and Wehr 1987, p.10; see also Moss et al. 2005), mix of evergreen dicots (minor element, e.g., *Gordonia*, *Phoebe*, *Photinia*, *Republica*, and *Ternstroemites*), and deciduous dicots (dominant element, e.g., *Alnus*, *Cercidiphyllum*, *Sassafras*, *Rhus*, Ulmoideae, *Macginitiea*, and *Comptonia* – but also a diverse suite of Rosaceae). They stressed, however that the phylogenetic distance between the identified fossil taxa and their species prominent in the modern forests, and the presence of taxa no longer present in the Pacific Northwest.

Wolfe and Wehr (1987, p. 10) downplayed the role of the dicots in the Republic flora, arguing that the conifer remains had largely been deposited in nearshore facies, rather than in the dicot-rich fine-grained sediments deposited "a considerable distance from shore" that were typically sampled. They also

presented a local landscape model where (1) a diverse conifer element dominated the hinterland, (2) deciduous dicots and deciduous gymnosperms (e.g., *Ginkgo*, *Glyptostrobus*, *Metasequoia*) occupied the lake shore and streamsides, and (3) a minor forest element, including both deciduous dicot shrubs and evergreen dicot trees was also present. The high degree of similarity among most of the Okanagan Highlands floras suggests that this model, or some variation of it, may apply across the Okanagan Highlands in the Early Eocene to early Middle Eocene. However, it is also reasonable to assume that megafossils of some conifer taxa could have been transported from nearby highpoints to lakes below (e.g., Spicer and Wolfe 1987; Greenwood 1992; Steart et al. 2002). Further, wind-dispersed pollen, such as Betulaceae and the bisaccate Pinaceae, are produced in abundance and will travel greater distances than other types and so will be over-represented in lake sediments (McAndrews and Wright 1969; Moss et al. 2005). Dillhoff et al. (2005) discussed taphonomic evidence that more than one forest zone was represented by the conifer foliage and pollen in the McAbee megaflora. In addition, a number of taxa found in both the Republic flora and the modern eastern North American deciduous forests are absent from extant Pacific Northwest mixed coniferous forest (viz. *Taxodium*, *Comptonia*, *Gordonia*, *Itea*, *Sassafras*, *Tilia*, and *Ulmus*: Wolfe 1987; Table 2).

Qualitative assessment of the megafloras suggests that dicots were diverse (e.g., Pigg and Wehr 2002; DeVore et al. 2005) and that their leaves, and typically 1–3 species (e.g., *Fagus*, *Fagopsis*, and *Sassafras* at McAbee), dominate southern British Columbia floras. Conifers (with the exception of *Metasequoia*), while diverse, were not numerically dominant in the Okanagan Highlands Eocene megafloras. Wolfe (1987) proposed that the Okanagan Highlands floras represented the origination of forest ecosystems dominated by deciduous microthermal lineages, such as Pinaceae (e.g., *Abies* and others), *Acer*, *Quercus*, and others. It may, therefore, be the case that a better analogy than the mixed coniferous forest is found in forest types where deciduous woody dicots play a significant role, such as the eastern North America deciduous forest (e.g., Table 2). Other reports have stressed taxonomic links and floristic analogy with forests that persist today in eastern Asia (Manchester 1999; DeVore et al. 2005), and certainly, the evidence is clear that exchange of taxa did occur between North America and Europe–Asia.

We do not suggest here that the Okanagan Highlands Eocene floras represent deciduous forest as currently expressed in eastern North America. But like Wolfe (1987), we do propose that the antecedents of the eastern North America deciduous forest were growing in the Okanagan Highlands in the Eocene, under a climate that while in the mid-range of MAT for this forest type (i.e., 10–15 °C vs. 7–18 °C), differed primarily from that prevailing in eastern North America by the lack of sustained freezing conditions in winter (i.e., CMMT ~3–6 °C vs. –7 to 10 °C). Today, the deciduous forest zone covers the eastern third of North America, and the main forest type is the mixed mesophytic forest (Greller 1988). The southeastern coastal plain overlaps the deciduous forest zone and shares many taxa with it, but has a greater representation of broad-leaved evergreen taxa than forests to the north (Christensen 1988). Canopy dominance by key tree genera in the modern eastern North American deciduous forest varies between the central and southern Appalachians, with some taxa exclusive to the southeastern coastal plain (Table 2).

According to Greller (1988, p. 290), the eastern North American deciduous forest has no pre-Quaternary North American fossil record (or at best, no pre-Miocene record), apart from pollen and rare megafossils in Eocene floras of the characteristic genera of the deciduous forest (e.g., *Betula*, *Carya*, *Castanea*, *Fagus*, *Juglans*, *Liriodendron*, *Ostrya–Carpinus*, *Tilia*, and others) co-occurring with distinctive broad-leaved evergreen taxa typical of the southeastern coastal plain (e.g., *Gordonia*; Christensen 1988). The Okanagan Highlands, however, would appear to have supported a flora in the Early to early Middle Eocene that contained nearly all of the key tree genera (or their near fossil relatives) that are characteristic of the modern deciduous forests of eastern North America (Table 2). The point made by Wolfe and Wehr (1987) remains valid, however, that the phylogenetic distance between the Eocene taxa and those present today in eastern North America is significant. Furthermore, some taxa in the Okanagan Highlands Eocene floras are today restricted to east Asian forests (some represented by a single extant species, e.g., *Eucommia ulmoides*) or found in common between North America and Asia (Manchester 1999; DeVore et al. 2005). The greatest floristic differences between the present-day eastern North American deciduous forest and the Okanagan Highlands flora are the presence in the Eocene of taxa that are today (1) restricted to the Pacific Northwest and west coast region of North America (e.g., *Arbutus*, *Sequoia*); (2) extinct within North America but still found in East Asia (e.g., *Ginkgo*, various conifers, such as *Amentotaxus*, *Glyptostrobus*, *Metasequoia*, and *Pseudolarix* and dicots, such as *Cercidiphyllum*, *Dipteronia*, *Eucommia*, *Koelreuteria*, *Photinia*, *Pterocarya*, and *Zelkova*); and (3) only known as fossils (e.g., *Florissantia* and *Palaeocarpinus*). Taxa absent today from North America or from eastern North America (and extant in east Asia) are mostly intolerant of sustained freezing conditions (e.g., Wolfe 1987; Wolfe and Wehr 1987). Wolfe and Wehr (1987) recognized only four dicot taxa in common between Republic and the mixed coniferous forests of the Pacific Northwest, whereas ~30 dicot taxa (or their near relatives) are found in common between the Okanagan Eocene floras and the deciduous forest zone of North America (Table 2).

Forests with similar floristic composition to the eastern North American deciduous forests and the Okanagan Eocene floras also occur today in cool uplands in Meso-America (Wolfe 1987; Hartshorn 1988) (Table 2) and, as noted earlier in the text, in east Asia (Manchester 1999; DeVore et al. 2005). The Meso-American uplands lack sustained freezing winter temperatures. Just as today, where microthermal elements, such as *Abies*, are largely restricted to highpoints and highlands within the landscape of the deciduous forest zone and cool uplands in Meso-America (Greller 1988; Hartshorn 1988). Taxa, such as microthermal Pinaceae (i.e., *Abies* and *Picea*), *Taxus*, and other conifers, likely dominated high points but also occurred sufficiently close to the Eocene lakes that their foliage and reproductive structures were transported and deposited by streams into the lakes (e.g., Spicer and Wolfe 1987; Steart et al. 2002; Dillhoff et al. 2005). Tribe

(2005) proposed that the Eocene landscape of the Okanagan Highlands looked much like it does today, with highlands, plains, and deeply incised drainages and relief across these valleys from 400–1500 m.

The mixture of insects with warm- and cool-adapted NLRs in the Okanagan Highlands fauna is echoed in other Eocene faunas (Archibald and Farrell 2003). In Baltic amber, both circumpolar and tropical genera of ants are found preserved in the same pieces of amber, precluding time averaging as an explanation for this co-occurrence. Although thermophilic winged insects may be episodically blown upslope to a cool upland, or cool-associated winged insects carried downslope to a warmer depositional environment, wingless worker ants of taxa with such mutually exclusive autecological parameters are found as syn-inclusions in Baltic amber, lessening the probability of transport as an explanation. Dillhoff et al. (2005) note that the delicate nature and abundance of some of the conifer remains also suggests a local origin for these taxa.

Such tropical–temperate mixture of insect fauna is seen today in the case of tropical mountainous regions, where cool MAT is combined with low-temperature seasonality (Archibald and Farrell 2003). For example, in highlands of tropical Mexico at ~1500 m altitude, both temperate and tropical ant genera coexist (Archibald and Farrell 2003), a pattern replicated by plant genera in the same area, as noted earlier (Hartshorn 1988).

Summary

The overall impression provided by the leaf physiognomic evidence (LMA), the bioclimatic analysis from plants, and the modern geographical distribution of the Eocene insect taxa is that climate was fairly uniformly microthermal–mesothermal and equable (i.e., no extremes of temperature) and mesic along the 1000 km north–south transect and across the 700 km^2 of the Okanagan Highlands in the late Early Eocene to early Middle Eocene. In part, this result reflects the restriction of fossil sites to lake and coal swamp sediments; sites likely to have sat in low points in the landscape and where water was not a limiting factor for plant growth (Wolfe and Wehr 1987; Cevallos-Ferriz et al. 1991). Some of the foliage of microthermal conifers (e.g., some Pinaceae, such as *Abies*) may have been transported to these lakes via streams from nearby high points in the landscape (e.g., Spicer and Wolfe 1987), but the character of much of the conifer remains, such as *Chamaecyparis*, *Cunninghammia*, *Metasequoia*, *Sequoia*, and *Thuja*, suggests a more local source (Dillhoff et al. 2005). It is unlikely that the leaves of dicots encountered in the sediments reflect anything other than the local flora, as chartaceous leaves have not been found transported more than a few hundreds of metres down streams (Greenwood 1992; Steart et al. 2003).

The mixture of fossil insect taxa in the Okanagan Highlands whose NLRs are both thermophilic and temperate-associated is consistent with the plant-based bioclimatic analysis of moderate MAT (i.e., MAT 10–15 °C) together with mild winters (i.e., low seasonality, CMMT > 2 °C and likely > 5 °C), as may be found today in low-latitude montane regions. This mixture conforms to data from other biota and other regions worldwide in the Paleogene (see earlier references), and is most easily explained by heightened equability. Further analysis is required to establish whether plant taxon dominance varies from sites to site, and therefore across the Okanagan Eocene landscape.

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References

Anonymous. 2003. Flora of North America. Available from http://hua.huh.harvard.edu/FNA/index.html (accessed 27 April 2003).

Archibald, S.B., and Farrell, B.D. 2003. Wheeler's Dilemma. Proceedings of the 2nd Paleoentomological Congress, Acta Zoologica Crakoviensia, **46**(Supplement on Fossil Insects): pp. 17–23.

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.

Aspök, H., and Aspök, U. 1991. Raphidioptera (Snake-flies, camelneck-flies): The Insects of Australia: a textbook for students and research workers. Vol. 1. Commonwealth Scientific and Industrial Research Organisation, Canberra, and Cornell University Press, Ithaca, N.Y., pp. 521–524.

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. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern Bristish Columbia. Canadian Journal of Botany, **59**: 2379–2410.

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.

Basinger, J.F., Greenwood, D.R., and Sweda, T. 1994. Early Tertiary vegetation of Arctic Canada and its relevance to palaeoclimatic interpretation. *In* Cenozoic plants and climates of the Arctic.

Edited by M.C. Boulter and H.C. Fisher. NATO ASI Series, Vol. 27, I. Springer-Verlag, Berlin, Germany, pp. 176–198.

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.

Boneham, R.F. 1968. Palynology of three Tertiary coal basins in central British Columbia. Ph.D. thesis, 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., Chap. 11, pp. 317–364.

Crane, P.R., and Stockey, R.A. 1987. *Betula* leaves and reproductive structures from the Middle Eocene of British Columbia. Canadian Journal of Botany, **65**: 2490–2500.

DeVore, M.L., Pigg, K.B., and Wehr, W.C. 2005. Systematics and phytogeography of selected Eocene Okanagan Highlands plants. Canadian Journal of Earth Sciences, **42**: this issue.

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.

Dixon, A.F.G., Kindlmann, P., Leps, J., and Holman, J. 1987. Why are there so few species of aphids, especially in the tropics? American Naturalist, **29**: 580–592.

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 B Palaeophytologie, **234**: 19–40.

Ewing, T.E. 1980. Paleogene tectonic evolution of the Pacific Northwest. Journal of Geology, **88**: 619–638.

Ewing, T.E. 1981. Regional stratigraphy and structural setting of the Kamloops Group, south-central British Columbia. Canadian Journal of Earth Science, **18**: 1464–1477.

Flora of North America Editorial Committee (*Editors*). 1993. Flora of North America North of Mexico. 7+ Vols. New York and Oxford.

Franklin, J.F. 1988. Pacific northwest forests. *In* North American terrestrial vegetation. *Edited by* M.G. Barbour and W.D. Billings. Cambridge University Press, Cambridge, UK., pp. 103–130.

Gazin, C.L. 1953. The Tillodontia: an early order of mammals. Smithsonian Miscellaneous Collections 121, no. 10, pp 1–110.

Greenwood, D.R. 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. Review of Palaeobotany and Palynology, **71**: 142–196.

Greenwood, D.R., and Basinger, J.F. 1994. The paleoecology of high latitude Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic. Review of Palaeobotany and Palynology, **81**: 83–97.

Greenwood, D.R., and Wing, S.L. 1995. Eocene continental climates and latitudinal gradients. Geology, **23**: 1040–1048.

Greenwood, D.R., Moss P.T., Rowett, A.I., Vadala, A.J., and Keefe, R.L., 2003, Plant communities and climate change in southeastern Australia during the early Paleogene. *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. 365–380.

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.

Guthrie, G.H. 1985. A high resolution palaeoecological analysis of an Eocene fossil locality from Quilchena, British Columbia. M.Sc. thesis, Simon Fraser University, Burnaby, B.C.

Hartshorn, G.S. 1988. Tropical and Sub-tropical vegetation of Meso-America. *In* North American terrestrial vegetation. *Edited by* M.G. Barbour and W.D.Billings. Cambridge University Press, Cambridge, UK., pp. 365–390.

Heie, O.E. 1967. Studies on fossil aphids (Homoptera: Aphoidea). Spoia Zoologica Musei Hauniensis, **26**: 1–247.

Heie, O.E. 1994. Why are there so few aphid species in the temperate areas of the southern hemisphere? European Journal of Entomology, **91**: 127–133.

Hopkins, D.J., and Johnson, K.R. 1997. First record of cycad leaves from the Eocene Republic flora. Washington Geology, **25**: 37.

International Commission on Stratigraphy (SIS: Working Group on Stratigraphic Information System). 2004. Available from http://www.stratigraphy.org (accessed 24 January 2004).

Janzen, D.H. 1981. The peak in North American ichneumonid species richness lies between 38° and 42° N. Ecology, **62**: 532–537.

Johnson, K.R. 1996. The role of the Republic flora in documenting the floristic evolution of the Northern Hemisphere. Washington Geology, **24**: 41–42.

Kershaw, A.P. 1996. A bioclimatic analysis of Early to Middle Miocene brown coal floras, Latrobe Valley, southeastern Australia. Australian Journal of Botany, **45**: 373–83.

Kershaw, A.P., and Nix, H.A. 1988. Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. Journal of Biogeography, **15**: 589–602.

Kingsolver, J.M. 1965. A new fossil bruchid genus and its relationship to modern genera (Coleoptera: Bruchidae: Pachymerinae). Coleopterists' Bulletin, **19**: 25–30.

Lewis, S.E. 1992. Insects of the Klondike Mountain Formation, Republic, Washington. Washington Geology, **20**: 15–19.

Manchester, S.R. 1999. Biogeographical relationships of North American Tertiary floras. Annals of the Missouri Botanical Gardens, **86**: 472–522.

Makarkin, V.N., Archibald, S.B., and Oswald, J.D. 2003. New Early Eocene Brown Lacewings (Neuroptera: Hemerobiidae) from Western North America. The Canadian Entomologist, **135**: 637–653.

Markwick, P.J. 1994. "Equability", continentality, and Tertiary "climate": The crocodilian perspective. Geology, **22**: 613–616.

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 Aceroideae. American Journal of Botany, **88**: 1316–1325.

Mosbrugger, V., and Utescher, T. 1997. The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Paleogeography, Palaeoclimatology, Palaeoecology, **134**: 61–86.

Moss, P.T., and Kershaw, A.P. 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record. Palaeogeography, Palaeoclimatology, Palaeoecology, **155**: 155–176.

Moss, P.T., Greenwood, D.R., and Archibald, S.B. 2005. Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia – Washington State) from palynology. Canadian Journal of Earth Sciences, **42**: This issue.

Mustoe, G.E. 2002. *Hydrangea* fossils from the Early Tertiary Chuckanut Formation. Washington Geology, **30**: 17–20.

PALAEOFLORA database. 2003. Paleoclimate Reconstructions using Tertiary Plant Taxa. The Paleobotanical Workgroup of Volker Mosbrugger at Tübingen University. Available from http://www.geologie.uni-bonn.de/Palaeoflora/Palaeoflora_home.htm (accessed April–December 2003).

Pigg, K.B., and Stockey, R.A. 1994. The significance of the Princeton Chert permineralized flora to the Middle Eocene upland biota of the Okanogan Highlands. Washington Geology, **22**: 32–36.

Pigg, K.B., and Wehr, W.C. 2002. Tertiary flowers, fruits and seeds of Washington State and adjoining areas — Part III. Washington Geology, **30**: 3–16.

Pigg, K.B., Manchester, S.R., and Wehr, W.C. 2003. *Corylus*, *Carpinus* and *Palaeocarpinus* (Betulaceae) from the middle Eocene Klondike Mountain and Allenby Formations of northwestern North America. International Journal of Plant Sciences, **164**: 807–822.

Poinar, G.O., Jr., Archibald, S.B., and Brown, A. 1999. New amber deposit provides evidence of Early Paleogene extinctions, paleoclimates, and past distributions. The Canadian Entomologist, **131**: 171–177.

Popov, S.V., Akhmetiev, M.A., Bugrova, E.M, Lopatin, A.V., Amitrov, O.V., Andreeva-Grigorovich, A.S., Zherikhin, V.V., Zaporozhets, N.I., Nikoleva, I.A., Krasheninnikov, V.A., Kuzmicheva, E.I., Sytchevskaya, E.K., and Shcherba, I.G. 2001. *In* Biogeography of the Northern Peri-Tethys from the Late Eocene to the Early Miocene: Part 1. Late Eocene. *Edited by* L.A. Nevesskaya. Paleontological Journal [English translation of Paleontologicheskii Zhurnal] **35**(Supplement 1): 1–68.

Rice, H.M.A. 1959. Fossil Bibionidae (Diptera) from British Columbia. Geological Survey of Canada, Bulletin 55, pp. 1–37.

Rouse, G.E., Hopkins, W.S., and Piel, K.M. 1971. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geological Society of America, Special Paper 127, pp. 213–246.

Royer, D.L., Osborne, C.P., and Beerling, D.J. 2002. High CO_2 increases the freezing sensitivity of plants: Implications for paleoclimatic reconstructions from fossil floras. Geology, **30**: 963–966.

Russell, L.S. 1935. A Middle Eocene mammal from British Columbia. American Journal of Science, **29**: 54–55.

Schorn, H.E., and Wehr, W.C. 1994. The conifer flora from the Eocene uplands at Republic, Washington. Washington Geology, **22**: 22–24.

Scudder, S.H. 1879. Appendix A. The fossil insects collected in 1877 by Mr. G.M. Dawson, in the interior of British Columbia. Report of Progress of the Geological Survey of Canada 1877–1878, pp. 176B–185B.

Spicer, R.A., and Wolfe, J.A. 1987. Taphonomy of Holocene deposits in Trinity (Clair Engle) Lake, Northern California. Paleobiology, **13**: 227–245.

Stockey, R.A., LePage, B.A., and Pigg, K.B. 1998. Permineralized fruits of *Diplopanax* (Cornaceae, Mastixioideae) from the middle Eocene Princeton chert of British Columbia. Review of Palaeobotany and Palynology, **103**: 223–234.

Steart, D.C., Boon, P.I., Greenwood, D.R., and Diamond, N.T. 2002. Transport of leaf litter in upland streams of south-eastern Australian *Eucalyptus* and *Nothofagus* forests. Archiv für Hydrobiologie, **156**: 43–61.

Thompson, R.S., Anderson, K.H., and Bartlein, P.J. 1999. Atlas of Relations Between Climatic Parameters and Distributions of Important Trees and Shrubs in North America. US. Geological Survey, Professional Paper 1650 A&B. Online Version 1.0, 14 December 1999.

Tribe, S. 2005. Eocene paleo-physiography and drainage directions, southern Interior Plateau, British Columbia. Canadian Journal of Earth Sciences, **42**: This issue.

Watson, J.A.L., and Gay, F.J. 1991. Isoptera (termites). *In* The insects of Australia: a textbook for students and research workers. Vol. 1. Commonwealth Scientific and Industrial Research Organization, Canberra, and Cornell University Press, Ithaca, N.Y., pp. 330–347.

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.

Wilf, P. 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. Paleobiology, **23**: 373–390.

Wilf, P., Cúneo, N.R., Johnson, K.R., Hicks, J.F., Wing, S.L., and Obradovich, J.D. 2003. High plant diversity in Eocene South America: Evidence from Patagonia. Science, **300**: 122–125.

Wilson, M.V.H. 1977*a*. new records of insect families from the freshwater middle Eocene of British Columbia. Canadian Journal of Earth Science, **14**: 1139–1155.

Wilson, M.V.H. 1977*b*. Middle Eocene freshwater fishes from British Columbia. Life Sciences Contributions 113, Royal Ontario Museum, Toronto, Ont., pp. 1–51.

Wilson, M.V.H. 1977*c*. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Science, **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.

Wilson, M.V.H. 1987. Predation as a source of fish fossils in Eocene lake sediments. Palaios, **2**: 497–504.

Wilson, M.V.H. 1996. Fishes from Eocene lakes of the interior. *In* Life in stone: a natural history of British Columbia's fossils. *Edited by* R. Ludvigsen. The University of British Colimbia Press, Vancouver, B.C., pp. 212–224.

Wing, S.L., and Greenwood, D.R. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. *In* Paleoclimates and their modeling with special reference to the Mesozoic Era. *Edited by* J.R.L. Allen, B.J. Hoskins, B.W. Sellwood, and R.A. Spicer. Philosophical Transactions of the Royal Society (of London), Series B, **341**: 243–253.

Wolfe, J.A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the

northern hemisphere and Australasia. US. Geological Survey Professional Paper 1106, pp. 1–37.

Wolfe, J.A. 1985. The distribution of major vegetational types during the Tertiary. *In* The carbon cycle and atmospheric CO_2: natural variations Archean to Present. *Edited by* E.T. Sundquist and W.S. Broecker. American Geophysical Union, Geophysical Monograph 32, pp. 357–375.

Wolfe, J.A. 1987. An overview of the origins of the modern vegetation and flora of the northern Rocky Mountains. Annals of the Missouri Botanical Gardens, **74**: 785–803.

Wolfe, J.A. 1994. Tertiary climatic changes at middle latitudes of western North America. Palaeogeography, Palaeoclimatology, Palaeoecology, **108**: 195–205.

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 Okanagan? Evidence from paleobotany. Geological Association of Canada – Mineralogical Association of Canada – Society Economic Geologists, Joint Annual Meeting, Abstracts **28**: abstract No. 533. (CD-ROM.)

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, **292**: 686–693.