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The Eocene Thomas Ranch flora, Allenby Formation, Princeton, British Columbia, Canada

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Abstract: A flora from Thomas Ranch near Princeton, British Columbia, Canada, is assessed for biodiversity and paleoclimate. This latest Early to early Middle Eocene flora occurs in the Allenby Formation. Seventy-six megafossil morphotypes have been recognized, representing at least 62 species, with 29 identified to genus or species. Common taxa include *Ginkgo* L., *Metasequoia* Miki, *Sequoia* Endl., *Abies* Mill., *Pinus* L., *Pseudolarix* Gordon, *Acer* L., *Alnus* Mill., *Betula* L., *Fagus* L., *Sassafras* J Presl, *Macginitiea* Wolfe & Wehr, *Prunus* L., and *Ulmus* L. More than 70 pollen and spore types are recognized, 32 of which are assignable to family or genus. The microflora is dominated by conifers (85%–97% abundance), with Betulaceae accounting for most of the angiosperms. The Climate Leaf Analysis Multivariate Program (CLAMP) calculates a mean annual temperature (MAT) of 9.0 ± 1.7 °C and bioclimatic analysis (BA) calculates a MAT of 12.8 ± 2.5 °C. Coldest month mean temperature (CMMT) was >0 °C. Mean annual precipitation (MAP) was >70 cm/year but is estimated with high uncertainty. Both the CLAMP and BA estimates are at the low end of the MAT range previously published for other Okanagan Highland localities, indicating a temperate climate consistent with a mixed conifer–deciduous forest.

Key words: Eocene, leaf morphotype, Okanagan Highlands, paleoclimate reconstruction, paleoenvironment, palynology.

Résumé : Les auteurs évaluent la biodiversité d'une flore provenant de Thomas Ranch près de Princetown en Colombie canadienne, en relation avec le paléoclimat. Cette dernière flore allant du début de l'Éocène jusqu'au début de l'Éocène moyen, se retrouve dans la formation de Allenby. Ils ont reconnu 76 morphotypes de méga fossiles, représentant au moins 62 espèces, dont 29 entités identifiées au genre ou à l'espèce. Parmi les taxa communs, on retrouve les *Ginkgo* L., *Metasequoia* Miki, *Sequoia* Endl., *Abies* Mill., *Pinus* L., *Pseudolarix* Gordon, *Acer* L., *Alnus* Mill., *Betula* L., *Fagus* L., *Sassafras* J Presl, *Macginitiea* Wolfe & Wehr, *Prunus* L., et *Ulmus* L. Ils ont également reconnu plus de 70 types de pollens et de spores, dont 32 peuvent être classifiés à l'échelle de la famille ou du genre. La microflore est dominée par des conifères (abondance de 85–97%), avec des Betulaceae constituant la plupart des angiospermes. À l'aide du programme d'analyse multivariée pour le climat et les feuilles (PAMCF), on a calculé une température annuelle moyenne (TAM) de 9.0 ± 1.7 °C et avec l'analyse bioclimatique (AB), une TAM 12.8 ± 2.5 °C avec une température moyenne du mois le plus froid (TMMF) >0 °C. Estimée avec une forte incertitude, la précipitation mensuelle moyenne (PMM) était >70 cm/an. Les estimations des PAMCF et AM se retrouvent dans le bas de l'éventail de la TAM déjà publiée pour d'autres localités des Okanagan Highland, ce qui indique un climat thermique congruent avec une forêt mixte conifères–décidus. [Traduit par la Rédaction]

Mots-clés : Éocène, morphotypes foliaires, Okanaga Highland, paléoclimat reconstruction, paléo environnement, palynologie.

Introduction

Fossil plants from the Princeton area, British Columbia, Canada, were first noted by Sir J. William Dawson in 1890, followed by a detailed description of fossils collected from the area in 1906 (Dawson 1890; Penhallow 1908). In the last 25 years, several new species have been described from leaf compression floras occurring at the following two major sites: Thomas Ranch, described here, and One Mile Creek. Species described represent genera that are Asian endemics today, including *Pseudolarix arnoldi* Gooch (Pinaceae, Gooch 1992) and the “vessel-less” angiosperm *Tetracentron hopkinsii* Pigg, Dillhoff, DeVore & Wehr (Trochodendraceae, Pigg et al. 2007; Li et al. 2011), *Betula leopoldae* Wolfe & Wehr (Crane and Stockey 1986; Wolfe and Wehr 1987) and *Palaecarpinus stonebergae* Pigg, Manchester & Wehr (Pigg et al. 2003) represent Betulaceae. Two plants from Rosaceae, *Stonebergia columbiana* Wolfe & Wehr, an extinct genus (Wolfe and Wehr 1988), and *Neviusia dunthornei* DeVore, Moore, Pigg & Wehr, are known (DeVore et al. 2004). Modern *Neviusia* has a disjunct distribution with one species from southeastern North America and the other from northern California, which the fossil species resembles more

closely. Maples are known from fruits of *Acer princetonense* Wolfe & Tanai, *Acer rousei* Wolfe & Tanai, *Acer stockeyae* Wolfe & Tanai, *Acer stonebergae* Wolfe & Tanai, *Acer toradense* Wolfe & Tanai (at Blue Flame Mine, Princeton), and *Acer wehri* Wolfe & Tanai and both leaves and fruits of *Acer stewarti* Wolfe & Tanai (Sapindaceae, Wolfe and Tanai 1987).

The Allenby Formation also hosts a diverse anatomically preserved flora in the Princeton chert, in which more than 30 taxa have been described. Many are aquatic to semiaquatic plants, such as the fern *Dennstediopsis aerenchymata* Arnold and Daugherty and members of Araceae, Nymphaeaceae, Myrtaceae, and Lythraceae (Arnold and Daugherty 1964; Cevallos-Ferriz and Stockey 1988a, 1988b, 1989; Pigg et al. 1993; Little and Stockey 2003; Smith and Stockey 2003, 2007), and *Eorhiza arnoldii* Robison & Person, a rhizomatous monocot-like dicot of uncertain taxonomic relationship (Robison and Person 1973; Stockey and Pigg 1994). Other less common taxa are “upland” elements, including several conifers (*Pinus arnoldi* Miller and *Metasequoia milleri* Basinger & Rothwell), Magnoliaceae, Lauraceae, Vitaceae, and Rosaceae, represented by *Prunus allenbyensis* Cevallos-Ferriz & Stockey, and the extinct

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Fig. 1. British Columbia map, Thomas Ranch and other Okanagan Highland localities. Redrawn from a base map provided on the Atlas of Canada website (Natural Resources Canada 2012 available at <http://atlas.gc.ca>) [accessed 30 January 2013] and Fig. 1 from Greenwood et al. (2005).



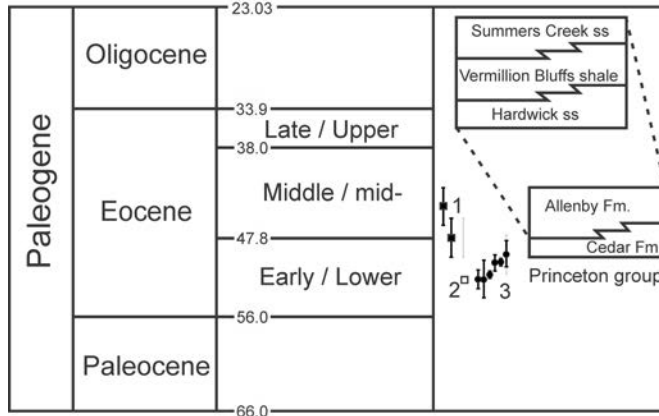
flower *Paleorosa similkameenensis* Basinger (Basinger 1976; Cevallos-Ferriz et al. 1993), several monocots (e.g., Erwin and Stockey 1994), as well as a diverse assemblage of ferns (Smith et al. 2006). An interesting array of fungi including ectomycorrhizae are also known. Reviews of the Princeton chert flora can be found in the following: Cevallos-Ferriz et al. (1991), Pigg and Stockey (1996), and Klymiuk et al. (2011).

Although the Princeton leaf compression sites have yielded several well-known individual taxa, floras have yet to be characterized as a whole or placed in paleoenvironmental context with other floras of the Okanagan Highlands province. Paleoclimate estimates and other paleoenvironmental aspects have been developed in overviews of the Okanagan Highlands floras (Greenwood et al. 2005, Moss et al. 2005; Archibald et al. 2011). Detailed paleoclimate analysis has been done for floras at McAbee (Dillhoff et al. 2005) and Falkland (Smith et al. 2009, 2012). In the present contribution we describe the mega- and micro-floras from the Thomas Ranch site, and provide a paleoclimate analysis based on both leaf physiognomic (Climate Leaf Analysis Multivariate Program (CLAMP) and leaf area analysis (LAA)) and taxonomic methods (bioclimatic analysis (BA)). Detailed studies of the individual sites within the Okanagan Highlands are providing us a better understanding of the regional floristic and paleoenvironmental diversity of this important upland temperate paleoenvironment of the Early to early Middle Eocene.

Material and methods

The Thomas Ranch locality occurs along Coalmont Road, approximately 5 km west of the town of Princeton, British Columbia, Canada (Fig. 1). Two fossiliferous areas are listed as Burke Museum of Natural History and Culture, University of Washington localities UWBM B3263 (upper level) and UWBM B4294 (lower level), and correspond to mapped megafossil localities in the Allenby Formation for this area on geological maps for south and west of Princeton (Read 1987, 2000; Massey et al. 2010). The smaller, lower site occurs immediately above the Tulameen River with beds that are nearly horizontal, in contrast to the upper, larger site, approximately 50 m higher (UWBM B3263), which consists of a small anticline that was exposed during road construction. Palynologically, the flora of the lower UWBM B4294 locality most closely matches the uppermost layers of UWBM B3263 and these exposures are characterized by the same plant megafossils. Stratigraphically (Fig. 2) the sites occur within the Early to early Middle Eocene Allenby Formation, which is part of the Princeton Group, and is represented in the Princeton and Tulameen Basins near the town of Princeton, British Columbia (Read 1987, Fig. 2), with the Cedar Formation in an outcrop also in the local area. Older reported potassium–argon (K–Ar) radiometric dates of 49 ± 4 Ma for Allenby Formation volcanic rocks just east of the Thomas Ranch locality (Read 1987, 2000; Massey et al. 2010) are consistent with a late Early Eocene to early Middle Eocene age for the

Fig. 2. Stratigraphic relationships of the Allenby Formation, Princeton Basin, based on Read (1987, 2000) and Cohen et al. (2013). Minor rock units are not shown, and the thicknesses of units shown are diagrammatic, not indicative. Available radiometric dates for Princeton Group (Cedar and Allenby Formations) samples are shown (1: K–Ar from sources cited in Read (1987, 2000); 2: Pb–U from Hardwick sandstone reported in Moss et al. (2005); 3: ^{40}Ar – ^{39}Ar from Ickert et al. (2009).



Thomas Ranch flora (Fig. 2). More recent Pb–U and ^{39}Ar – ^{40}Ar dating of Princeton Group samples, however, indicate that the Allenby Formation, including the Vermillion Bluffs shale that hosts the Thomas Ranch flora, is primarily Early Eocene (Moss et al. 2005; Ickert et al. 2009).

Fossils occur in a shaley tan to buff-colored matrix that can weather to produce a thin, paper shale-like matrix, whereas less weathered areas contain a thicker mudstone. Shales from some Okanagan Highlands localities have been interpreted as being derived from diagenetically altered diatomites indicative of deposition in large, deep lakes with very low levels of terrigenous sediment input (Mustoe 2005). Although some Princeton localities were so classified, Thomas Ranch (Mustoe locality P11) is indicated as clastic in composition. The shale of the upper locality (UWBM B3263) was deformed through intense folding such that complete examples of any of the larger leaves are extremely rare. Cuticle was not apparent on most specimens.

Major collections of the site were made by Wesley C. Wehr and Donald Q. Hopkins in the early 1980s and from 1989 to 2008 by Richard M. and Thomas A. Dillhoff. Specimens are deposited in the Princeton Museum, Princeton, British Columbia, Canada, and the Burke Museum of Natural History and Culture, University of Washington, Seattle, USA, with additional significant collections at the University of Alberta, Edmonton, Alberta, Canada, and the University of Saskatchewan, Saskatoon, Canada.

Dicot leaves were morphotyped using methods of the Manual of Leaf Architecture (Ellis et al. 2009) and leaf characters were scored using the CLAMP methodology developed by Wolfe (1993) and calculated using the data sets of Yang et al. (2011). CLAMP is a multivariate method that encompasses a global calibration set of modern vegetation sites (Wolfe 1993; Yang et al. 2011). Recent studies have shown that multivariate calibrations of leaf physiognomy and climate encompass regional effects caused by biogeographic history or unique attributes of regional climate (Jacques et al. 2011; Peppe et al. 2011).

Paleoclimates were estimated by the following two quantitative methods: BA and leaf physiognomic analysis (CLAMP and LAA) to allow for comparisons with estimates from these techniques that have been published for several other Okanagan Highlands sites (Greenwood et al. 2005; R. Smith et al. 2012). BA (Kershaw and Nix 1988; Kershaw 1996; Greenwood et al. 2005) is essentially equivalent to the coexistence approach of Mosbrugger and Utescher (1997), and uses “climatic profiles” (i.e., climatic parameters such

as mean annual temperature (MAT) and mean annual precipitation (MAP)) based on distributions of modern plant genera. The first step of this approach is to identify as many “nearest living relatives” (NLRs) as possible in the megafossil floras (Table 1). A library of climatic profiles is then produced for several key taxa based on such values as MAT, MAP, and coldest month mean temperature (CMMT) (Greenwood et al. 2005). The zone of overlap for a set of NLRs defines the most likely climate space occupied for an individual fossil flora.

The mean climatic values for the Thomas Ranch megafora were calculated by examining MAT, MAP, and CMMT for each NLR taxon with megafossil relatives (Table 2). To deal with outliers, taxa whose climate profile sit 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 (Greenwood et al. 2005).

The megafora contains many fragmentary leaves, confounding application of methods requiring digital scoring of leaf characters (e.g., Peppe et al. 2011). All available leaves with a nearly complete lamina, however, were measured for calculating leaf area as well as being scored for CLAMP. Because CLAMP does not estimate MAP, LAA (Wilf et al. 1998) was also applied. The direct method of Wilf et al. (1998) was used to estimate MAP, rather than using the standardized log-normal transformed leaf area (LnA) for the smallest and largest leaf size class of each leaf morphology. Because leaf size values in LAA are log-normal transformed, the error of the estimate is asymmetrical and so is expressed as a lower (–ve) and upper bound (+ve) error term. Peppe et al. (2011) provided a multivariate equation for estimating MAP based on digitized leaf traits, in addition to providing a new LAA calibration based on 92 global sites. Their new LAA calibration, however, yields a much higher standard error (0.61 vs. 0.36 as \log_e (MAP) values) than the original Wilf et al. (1998) calibration. Both estimates are provided for Thomas Ranch. Both of the leaf physiognomic methods (CLAMP and LAA) were previously applied to the Falkland megafora (Smith et al. 2009, 2012), permitting direct comparison with Thomas Ranch. To permit greater comparisons of leaf physiognomic analyses of Okanagan Highlands floras, LAA was also applied to the McAbee megafora (Dillhoff et al. 2005; Greenwood et al. 2005) and these data are presented here.

Three samples were collected at different stratigraphic horizons and processed for pollen. The sample designated B3263 Lower (see Fig. 3) was collected from steeply dipping layers near the stratigraphic base of the exposure at site UWBM 3263. Sample B3263 Upper was collected from the nearly horizontal layers near the top of the same exposure. This sample was associated with shale layers containing abundant *Azolla* megafossils. Sample B4294 was collected from the upper layers at the shale exposure below Coalmont Road. The purpose of this sampling effort was to provide an overview of the Thomas Ranch microflora; more detailed sampling would be required to construct a comprehensive biostratigraphy for the site.

Pollen samples were processed using a modification of the Faegri and Iversen (1964) method. Samples were washed and dried and then ca. 3 g of shale was crushed with a mortar and pestle and treated with 1 mol/L hydrochloric acid (HCl) to remove carbonates. Samples were centrifuged, washed, and treated again with HCl, and then 48% cold hydrofluoric acid (HF) was added to remove silicates and left overnight. Samples underwent two washes with 1 mol/L HCl followed by two with deionized water, centrifuging after each step, and were filtered and washed through 185 μm and 10 μm mesh Nitex until the water passing through the filter was clear. The sample fraction that remained on top of the 10 μm filter was treated by acetolysis to remove excess organics. Slides were prepared from the processed sample by mounting with glycerin jelly treated with 2% safranin dye. Excess sample material was stored in glycerin.

Megafossils were photographed with a Nikon D200 digital SLR and a 55 mm Micro-Nikkor lens on a lighted copystand. Microfossils were

Table 1. Thomas Ranch flora.

Group/family	Taxon	Megafossils	Pollen/spores	Figure
Bryophytes	Undetermined genus	G		Plate 1, Fig. 1
Pteridophytes				
Lycopodiaceae	<i>Lycopodium</i>		SP	Plate 5, Fig. 3
Osmundaceae	<i>Osmunda</i> L.		SP	Plate 5, Fig. 1
Schizaeaceae	<i>Anemia poolensis</i> Chandler		SP	Plate 5, Fig. 6
Filicales	Undetermined genera		SP	Plate 5, Figs. 2, 4, 5, 7
Salviniaceae	<i>Azolla primaeva</i> (Penhallow) Arnold	PL	MSP	Plate 1, Fig. 2; Plate 5, Fig. 8
Gymnosperms				
Ginkgoaceae	<i>Ginkgo dissecta</i> Mustoe	L		Plate 1, Fig. 5
	<i>Ginkgo biloba</i> L.	L		Plate 1, Figs. 3, 6
	<i>Ginkgo</i> L. sp.		P	Plate 5, Fig. 9
Cupressaceae	<i>Chamaecyparis</i> Spach sp.	LT		Plate 2, Figs. 2, 3
	<i>Cunninghamia</i> R. Br. sp.	LT		Plate 2, Fig. 1
	<i>Metasequoia occidentalis</i> (Newberry) Chaney	LT, SC		Plate 1, Figs. 4, 7
	<i>Sequoia</i> Endl.	LT, SC		Plate 1, Figs. 8, 9
	<i>Sequoiapollenites</i>		P	Not figured
	TCT pollen		P	Plate 5, Figs. 10, 11
Pinaceae	<i>Abies milleri</i> Schorn & Wehr	LT, CS, S		Plate 2, Figs. 4, 5
	<i>Abies</i> sp.		P	Plate 5, Fig. 27
	<i>Picea</i> Mill. sp.	LT, S, SC?		Plate 2, Figs. 9, 11, 12
	<i>Picea</i> Mill, sp.		P	Plate 5, Fig. 25
	<i>Pinus</i> L. sp.	L, PC, S		Plate 2, Figs. 7, 8, 10
	<i>Pinus</i> L. sp.		P	Plate 5, Fig. 24
	<i>Pseudolarix</i> Gordon sp.	CS, S		Plate 2, Figs. 13, 14
	<i>Pseudolarix</i> Gordon sp.		P	Plate 5, Fig. 26
	cf. <i>Larix</i> Phillip Miller sp./ <i>Pseudotsuga</i> Carrière sp.		P	Plate 5, Fig. 28
	<i>Tsuga</i> Carrière sp.		P	Not figured
	<i>Alisporites</i> / <i>Pityosporites</i> sp.		P	Not figured
Taxaceae	<i>Amentotaxus</i> Pilg.? sp./ <i>Torreya</i> Am.? sp.	L		Plate 2, Fig. 6
	TCT pollen		P	Plate 5, Figs. 10, 11
Unknown conifer	<i>Podocarpidites</i> / <i>Cathaya</i>		P	Plate 5, Fig. 23
Angiosperms				
Arecaeaceae	cf. <i>Sabal granopollenites</i> Rouse		P	Not figured
Betulaceae	<i>Alnus parvifolia</i> (Berry) Wolfe & Wehr	L		Not figured
	<i>Alnus</i> / <i>Betula</i> inflorescence	I		Plate 3, Fig. 4
	<i>Alnus</i> L.		P	Plate 5, Figs. 13, 14
	<i>Betula leopoldae</i> Wolfe & Wehr	L		Plate 3, Fig. 1
	<i>Betula</i> L. sp.	L	P	Plate 3, Fig. 3; Plate 5, Fig. 12
	<i>Palaeocarpinus stonebergae</i> Pigg, Manchester & Wehr	F		Plate 3, Fig. 2
	<i>Carpinus</i> L. sp.		P	Not figured
	<i>Corylus</i> L. sp.		P	Plate 5, Fig. 15
Buxaceae	<i>Erdtmanipollis pachysandroides</i> Krutzsch (cf. <i>Pachysandra</i>)		P	Plate 5, Fig. 22
Cercidiphyllaceae	cf. <i>Joffrea speirsii</i> Crane & Stockey/ <i>Cercidiphyllum</i> Sieb. & Zucc.	L		Plate 3, Fig. 10
Davidiaceae	<i>Tsakada davidifolia</i> Wolfe & Wehr	L		Not figured
Elaeagnaceae	cf. <i>Elaeagnus</i> L. sp.		P	Plate 5, Fig. 19
Ericaceae	Ericaceae pollen tetrad		P	Plate 5, Fig. 20
Fagaceae	<i>Fagus</i> L.	L		Not figured
	<i>Fagopsis undulata</i> (Knowlton) Wolfe & Wehr	L		Plate 3, Fig. 6
	<i>Castanea</i> sp.		P	Not figured
	cf. <i>Quercus</i> L. sp.		P	Not figured
Grossulariaceae	<i>Ribes</i> L. sp.	L		Plate 4, Fig. 7
Hamamelidaceae	<i>Fothergilla dunthornei</i>	L		Plate 4, Fig. 4
Juglandaceae	<i>Carya</i> Nutt. sp.		P	Not figured
	<i>Pterocarya</i> Nutt. ex Moq. sp.		P	Plate 5, Fig. 18
Lauraceae	<i>Sassafras hesperia</i> Berry	L		Plate 4, Figs. 8, 10
	Lauraceous leaf	L		Plate 4, Fig. 9
Myricaceae	<i>Comptonia columbiana</i> Dawson	L		Plate 3, Fig. 5
Platanaceae	<i>Macginitlea gracilis</i> (Lesquereux) Wolfe & Wehr	L		Plate 4, Fig. 1
	<i>Macginicarpa</i> Wolfe & Wehr	I		Plate 4, Figs. 2, 3
Rosaceae	<i>Prunus</i> L. sp. and cf. <i>Prunus</i> L. sp.	L		Plate 4, Fig. 6
	cf. <i>Rubus</i>	L		Plate 4, Fig. 5
Salicaceae	<i>Salix</i> L. sp.		P	Not figured
Sapindaceae	<i>Acer</i> sp.	F		Not figured
	<i>Acer</i> sp.	F		Plate 3, Fig. 11
	<i>Dipteronia browni</i> Manchester	F		Not figured
	<i>Acer</i> L. sp.		P	Plate 5, Fig. 16

Table 1. (concluded).

Group/family	Taxon	Megafossils	Pollen/spores	Figure
Trochodendraceae	<i>Zizyphoides</i> sp.	L		Plate 3, Fig. 7
Ulmaceae	<i>Ulmus okanaganensis</i> Denk & Dillhoff	L		Not figured
	<i>Ulmus</i> L. sp.		P	Plate 5, Fig. 17
<i>Insertae sedis</i>	<i>Pistillipollenites macgregorii</i> Rouse		P	Plate 5, Fig. 21
	Pinnately compound leaf	L		Plate 3, Fig. 8
	Unknown structure	S		Plate 3, Fig. 9

Note: See text for details. CS, cone scales; F, fruits; G, gametophytes; I, infructescence or inflorescence; L, leaves; LT, leafy twigs; MSP, microspore; P, pollen; PC, pollen cone; PL, plant; S, structure; SC, seed cone; SP, spore.

Table 2. Estimates of temperature and precipitation for selected Early–Middle Eocene megafloras of the Okanagan Highlands.

Flora	MAT (°C)	MAT (°C)	CMMT (°C)	CMMT (°C)	MAP (cm/year)	MAP (cm/year)
	BA	CLAMP (±2.0 °C)	BA	CLAMP (±3.4 °C)	BA	LAA
Falkland ^{a,b}	14.7±2.1	11.9	5.2±3.0	3.0	105±48	121 –37 +52
McAbee ^{a,b,c,d}	13.5±2.5	9.5	3.5±4.4	–2.0	108±35	99 –30, +43
One Mile Creek ^{a,d,e}	13.1±3.1	7.3	5.3±2.8	–3.6	114±42	108 –33, +47
Thomas Ranch ^d	12.8±2.5	9.0	3.9±4.1	–1.2	111±40	77 –23, +33
Republic ^{a,b,e}	13.5±2.2	9.4	4.1±4.0	–0.2	115±39	135 –61 +111

Note: Abbreviations: mean annual temperature (MAT); bioclimatic analysis (BA); Climate Leaf Analysis Multivariate Program (CLAMP); coldest month mean temperature (CMMT); mean annual precipitation (MAP); leaf area analysis (LAA); CLAMP estimate errors are provided from the PhysG3brc + Met calibration (Yang et al. 2011).

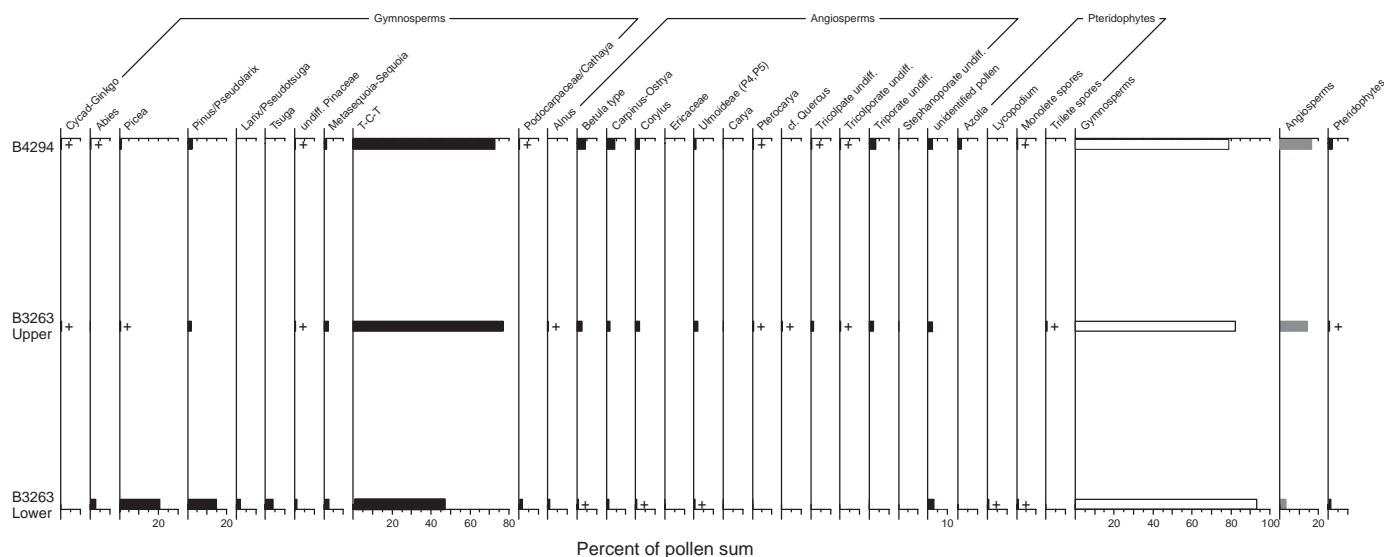
^aGreenwood et al. (2005).

^bR. Smith et al. (2009, 2012).

^cDillhoff et al. (2005).

^dThis study.

^eYang et al. (2011).

Fig. 3. Thomas Ranch pollen diagram.

photographed on a Nikon Eclipse 50i microscope utilizing a 40× objective lens and a Nikon DS-Fi1 microscope camera. Images were minimally processed with Adobe Photoshop CS2 version 9.0.2 using levels, brightness, and contrast filters, and in some cases, removing the background rock matrix for clarity.

Results

Floristic study: Taxa identified from megafossil (Plates 1–4) and palynomorph remains (Plate 5) are summarized in Table 1.

Nonvascular plants (Plate 1)

Bryophytes (Plate 1, Fig. 1)

The vegetative gametophyte of an undetermined moss has been found. Fossil mosses similar to the Thomas Ranch material have also been found at the Republic, Washington, locality; at Horsefly, British Columbia; and at the One Mile Creek site near Princeton,

British Columbia (Kuc 1974; Janssens et al. 1979). The reproductive parts of the moss sporophyte have yet to be discovered.

Pteridophytes (Plates 1, 5)

Lycopodiaceae

Lycopodium L. spores (Plate 5, Fig. 3) are found infrequently in the UWBM B3263 and UWBM B4294 horizons.

Salviniaceae

Azolla primaeva (Penhallow) Arnold (Plate 1, Fig. 2) is a common component of the flora, with individual complete plants often found together in masses, forming mats. They are locally abundant in this flora, with some layers being characterized almost exclusively by *Azolla*, including the uppermost layers of both UWBM B3263 and UWBM B4294. Well-preserved plants show the characteristic closely spaced cuplike pinnules of the floating

Plate 1. Bryophyte, pteridophyte, *Ginkgo*, and taxodiaceous conifers. (Fig. 1) Bryophyte, Loc. UWBM B3263, Spec. PB333. (Fig. 2) *Azolla primaeva*, Loc. UWBM B3263, Spec. PB9210. (Fig. 3) *Ginkgo biloba*, Princeton Museum, Spec. JP558A. (Fig. 4) *Metasequoia occidentalis*, Loc. UWBM B4294, Spec. PB9128. (Fig. 5) *Ginkgo dissecta*, Loc. UWBM B3263, Spec. 57441B. (Fig. 6) *Ginkgo biloba*, Loc. UWBM B3263, Spec. 77633. (Fig. 7) *Metasequoia occidentalis*, Loc. UWBM B4294, Spec. PB9129. (Fig. 8) *Sequoia* sp., Loc. UWBM B4294, Spec. PB8997. (Fig. 9) *Sequoia* sp., Loc. UWBM B3263, Spec. PB8996. Scale bar = 2 cm.



Plate 2. Conifers: Cupressaceae, Pinaceae, Taxaceae. (Fig. 1) *Cunninghamia* sp., leafy twig, Loc. UWBM B4294, Spec. 75604. (Fig. 2) *Chamaecyparis* sp., Loc. UWBM B3263, Spec. 54164. (Fig. 3) *Chamaecyparis* sp., Loc. UWBM B3263, Spec. PB9210. (Fig. 4) *Abies milleri* cone scale, Loc. UWBM B4294, Spec. PB6987. (Fig. 5) *Abies milleri* leafy branch, Loc. UWBM B4294, Spec. 74328. (Fig. 6) Taxaceae needle, Princeton Museum, Spec. JP623. (Fig. 7) *Pinus* sp. pollen cone, Loc. UWBM B3263, Spec. PB8993. (Fig. 8) *Pinus* sp. fascicle of five needles, Loc. UWBM B4294, Spec. PB14243. (Fig. 9) Conifer seed cone, probably *Picea*, Loc. UWBM B3263, Spec. 57437. (Fig. 10) *Pinus* sp. seed, Loc. UWBM B3263, Spec. PB3123. (Fig. 11) *Picea* sp. branch, Loc. UWBM B3263, Spec. PB20858. (Fig. 12) *Picea* sp. seed, Loc. UWBM B3263, Spec. UWBM 55023A. (Fig. 13) *Pseudolarix* sp. cone scale, Princeton Museum. (Fig. 14) *Pseudolarix* sp., Loc. UWBM B3263, Spec. PB8991. Scale bar = 2 cm.

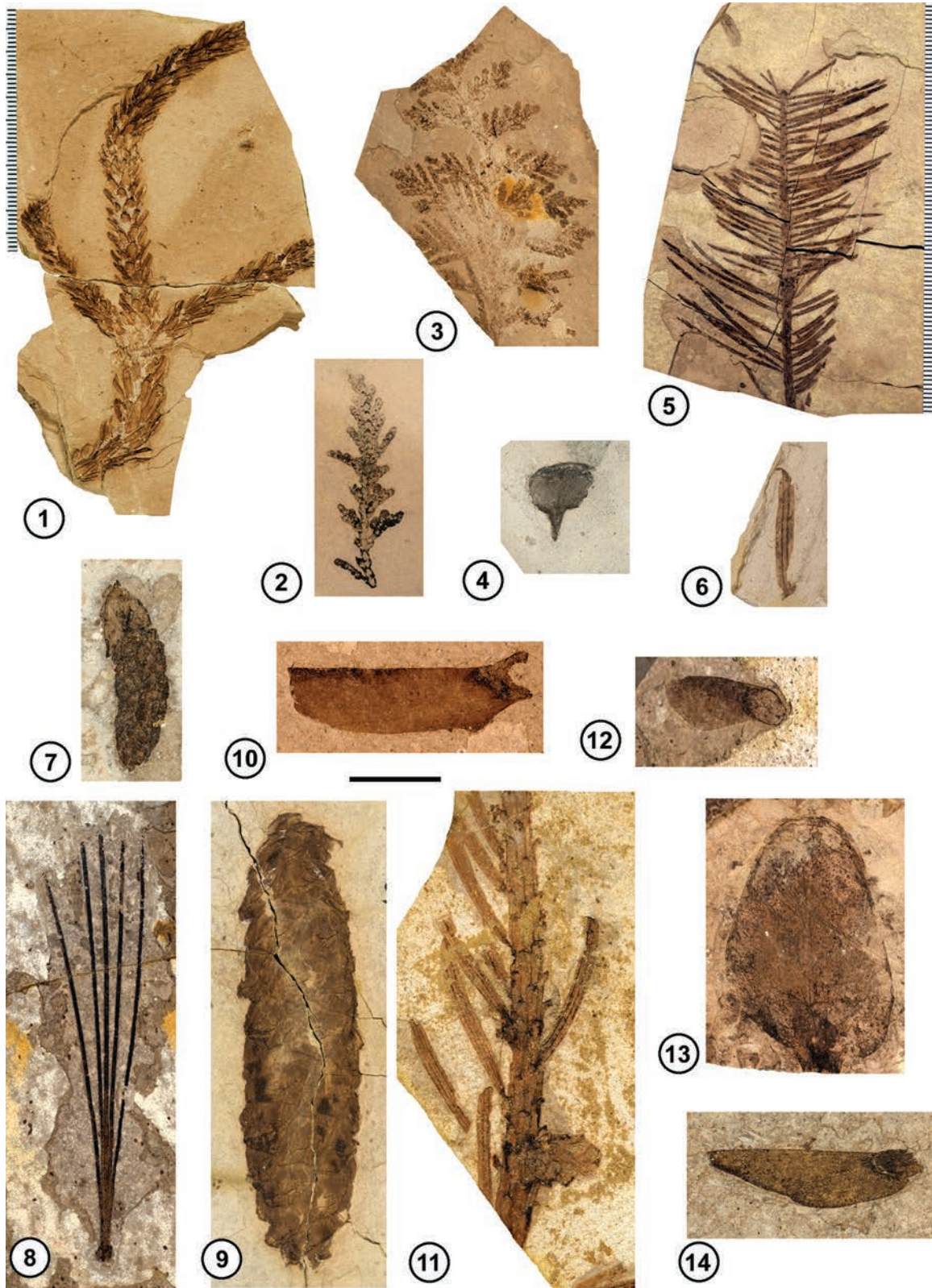


Plate 3. Dicots: Betulaceae, Zygophyllaceae, Cercidiphyllaceae, Trochodendraceae, Sapindaceae. (Fig. 1) *Betula leopoldae*, Loc. UWBM B3263, Spec. PB8985. (Fig. 2) *Palaeocarpinus stonebergae*, Loc. UWBM B3263, Spec. UWBM 56756. (Fig. 3) Betulaceae, Loc. B3263, Spec. UWBM 56284. (Fig. 4) *Alnus* sp. inflorescence, Princeton Museum. (Fig. 5) *Comptonia columbiana*, Loc. UWBM B3263, Spec. PB8928. (Fig. 6) *Fagopsis undulata*, Princeton Museum. (Fig. 7) *Zizyphoides* sp., Loc. UWBM B3263, Spec. PB8909. (Fig. 8) Unknown compound leaf, Loc. UWBM B3263, Spec. UWBM77445B. (Fig. 9) Unknown structure, Loc. UWBM B3263, Spec. UWBM54633. (Fig. 10) cf. *Joffrea* (cf. *Cercidiphyllum*) sp., UWBM Loc. B3263, Spec. PB8912. (Fig. 11) *Acer* fruit, Loc. UWBM B3263, Spec. PB8989A. Scale bar = 1 cm.

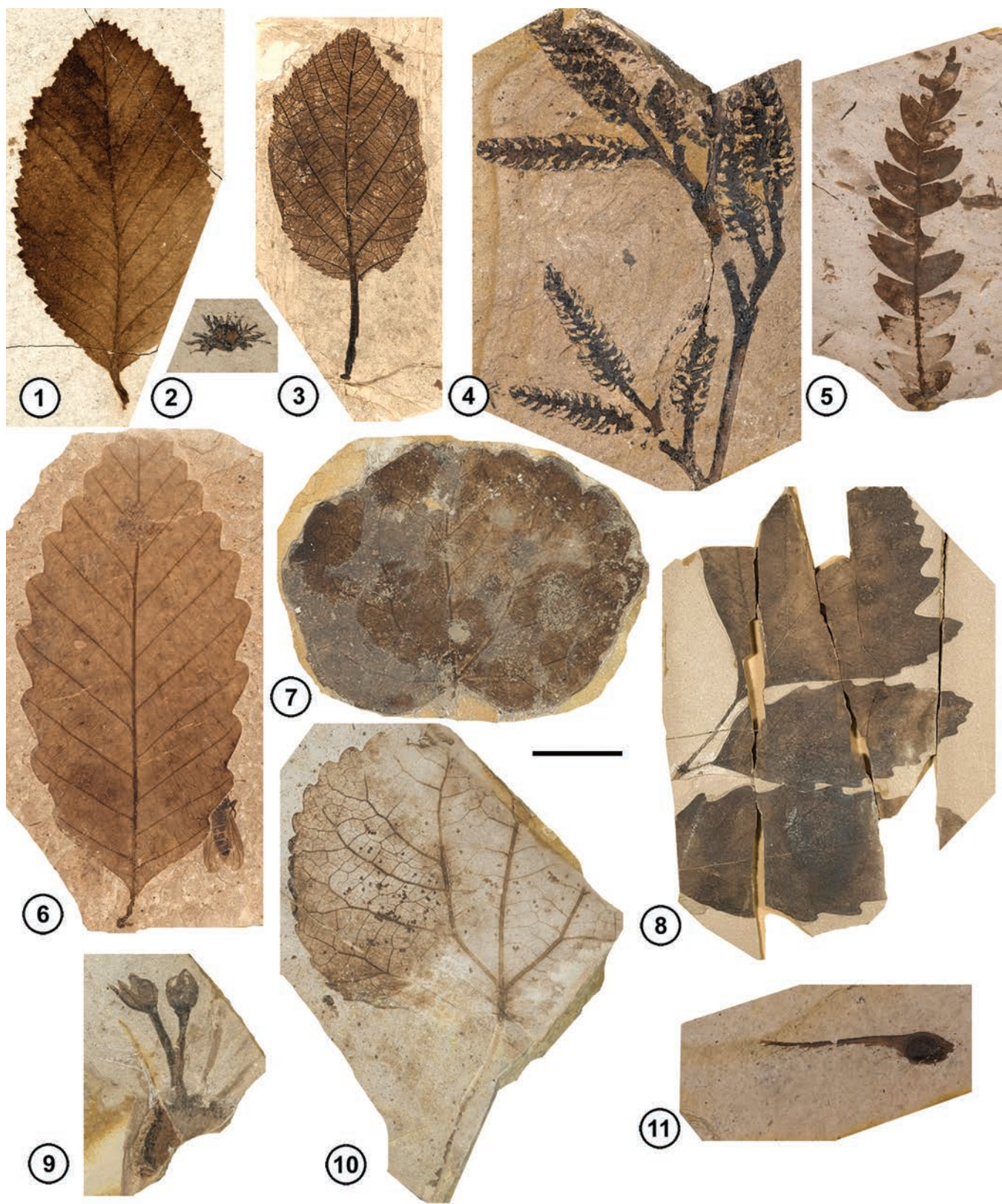


Plate 4. Dicots: Platanaceae, Hamamelidaceae, Rosaceae, Grossulariaceae, Lauraceae. (Fig. 1) *Macginitiea gracilis*, Princeton Museum, Spec. JP490. (Fig. 2) *Macginiticarpa* sp., DMNS Loc. 384. (Fig. 3) *Macginiticarpa* sp., Loc. UWBM B3263, Spec. UWBM77484A. (Fig. 4) *Fothergilla malloryi*, Princeton Museum, Spec. JP482. (Fig. 5) *Rubus* sp., DMNS Loc. 384, Spec. 9156b. (Fig. 6) *Prunus* sp., Loc. UWBM B3263, Spec. 52167. (Fig. 7) *Ribes* sp. Loc. UWBM B3263, Spec. 77689. (Fig. 8) *Sassafras hesperia*, Loc. UWBM B4294, Spec. PB9367. (Fig. 9) Lauraceous leaf, Loc. UWBM B4294, Spec. 56816A. (Fig. 10) *Sassafras hesperia*, Loc. UWBM B4294, Spec. 56815. Scale bar = 2 cm.

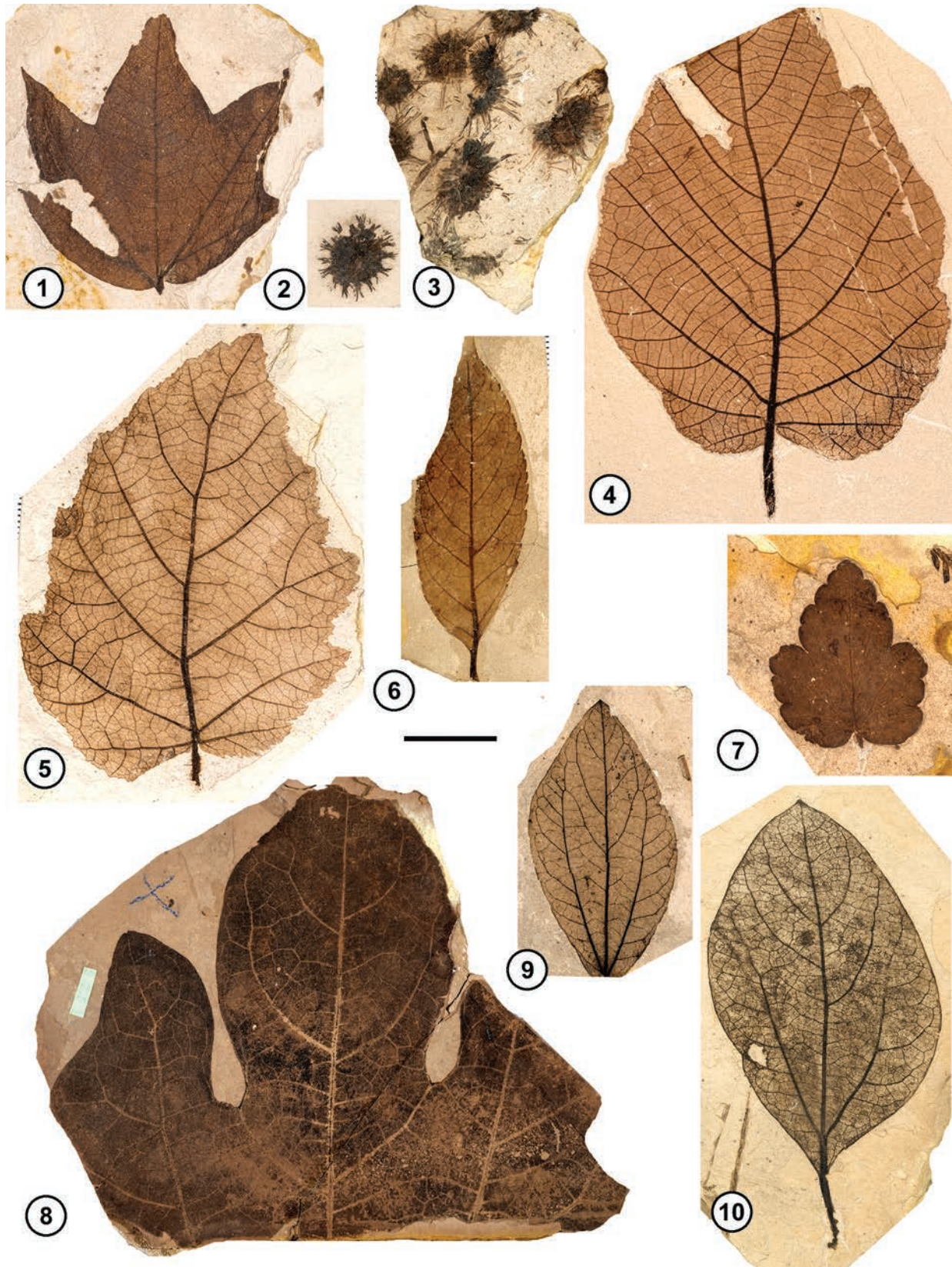
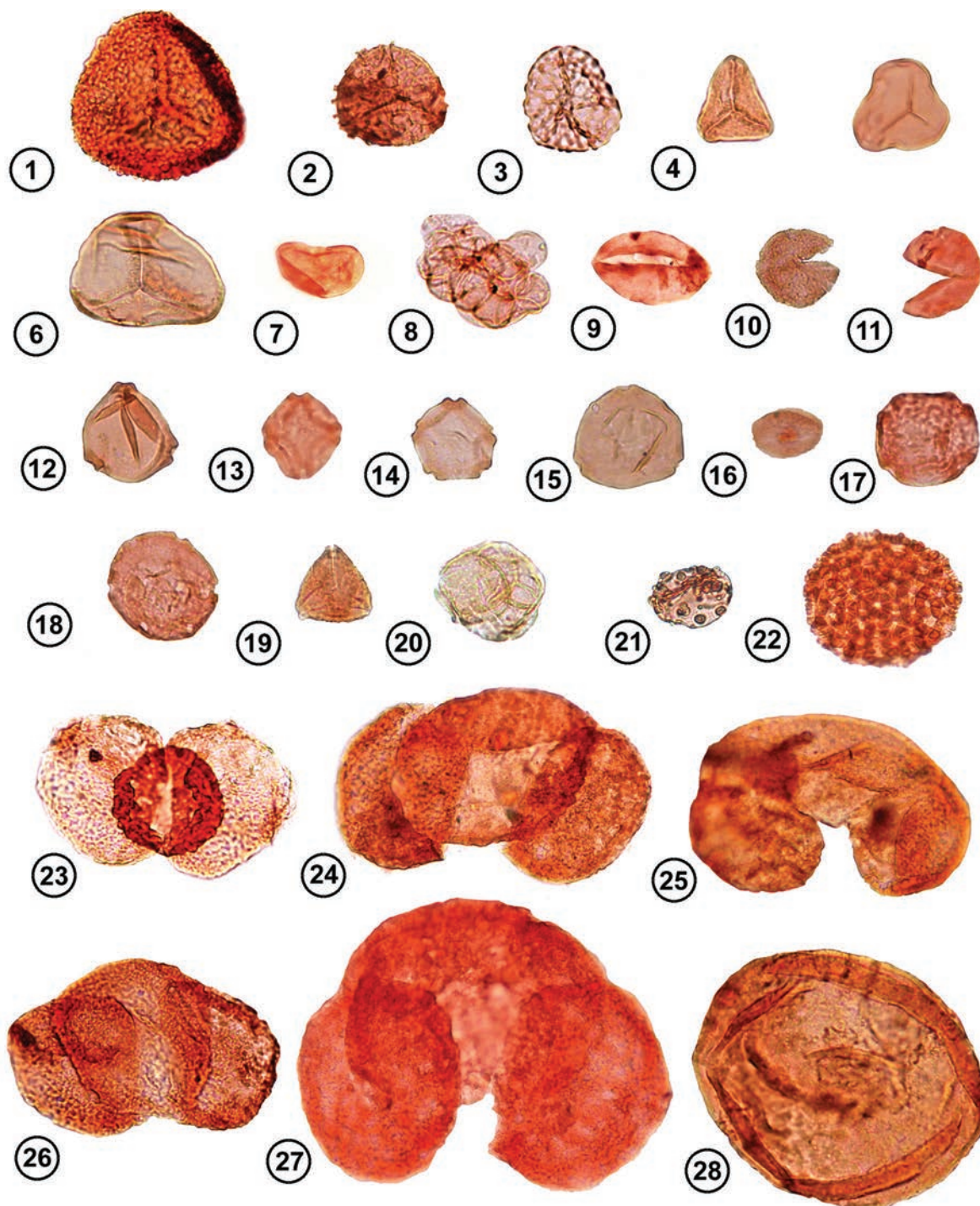


Plate 5. Pollen and Spores (catalog numbers are for the pollen slides on deposit at the University of Washington Burke Museum). (Fig. 1) *Osmunda* B3263 Lower, UWBM PB22574. (Fig. 2) Trilete granular spore B3263 Upper, UWBM PB22582. (Fig. 3) *Lycopodium* B4294, UWBM PB22577. (Fig. 4) Trilete spore B3263 Upper, UWBM PB22583. (Fig. 5) Trilete spore B3263 Upper, UWBM PB22565. (Fig. 6) *Anemia poolensis* B3263 Upper, UWBM PB22583. (Fig. 7) Monolete spore B3263 Upper, UWBM PB22563. (Fig. 8) *Azolla* microspore cluster B4294, UWBM PB22579. (Fig. 9) *Ginkgo* B3263 Upper, UWBM PB22563. (Fig. 10) TCT pollen B3263 Upper, UWBM PB22586. (Fig. 11) TCT pollen B3263 Upper, UWBM PB22563. (Fig. 12) *Betula* B3263 Lower, UWBM PB22574. (Fig. 13) *Alnus* four pores B3263 Upper, UWBM PB22563. (Fig. 14) *Alnus* five pores B3263 Lower, UWBM PB22573. (Fig. 15) cf. *Corylus* B3263 Lower, UWBM PB22571. (Fig. 16) *Acer* B3263 Upper, UWBM PB22563. (Fig. 17) *Ulmus* B3263 Upper, UWBM PB22582. (Fig. 18) *Pterocarya* B3263 Upper, UWBM PB22582. (Fig. 19) cf. *Elaeagnus* B3263 Lower, UWBM PB22573. (Fig. 20) Ericaceae B3263 Lower, UWBM PB22570. (Fig. 21) *Pistillipollenites macgregorii* B4294, UWBM PB22576. (Fig. 22) *Erdtmanipollis pachysandroides* B4294, UWBM PB22576. (Fig. 23) *Podocarpidites/Cathaya* B3263 Upper, UWBM PB22582. (Fig. 24) *Pinus* B3263 Upper, UWBM PB22566. (Fig. 25) *Picea* B3263 Upper, UWBM PB22566. (Fig. 26) *Pseudolarix* B3263 Upper, UWBM PB22586. (Fig. 27) *Abies* B3263 Upper, UWBM PB22563. (Fig. 28) *Larix/Pseudotsuga* type B3263 Lower, UWBM PB22572. Scale bar = 50 μ m.



fronds and the highly dissected submerged leaves. *Azolla primaeva* microspores preserved in clusters (Plate 5, Fig. 8) are rare at UWBM B4294 and absent from UWBM B3263, even though *Azolla* vegetative remains are locally abundant at both localities, and megaspores have not been recovered.

Osmundaceae

Osmunda L. (Plate 5, Fig. 1) is known only from the microflora, which is found as rare, well-preserved spores from all three sample horizons. This large spore has a prominent trilete mark and granulate ornamentation.

Schizaeaceae

The Schizaeaceae is represented by spores of *Anemia poolensis* Chandler (Plate 5, Fig. 6). These spores are relatively large trilete grains with a thin, folded psilate exine. Hills (1965) reported spores of this type throughout the Princeton Basin.

Other Pteridophytes

Several other spore types (Plate 5, Figs. 2–5, 7) are found in the Thomas Ranch microflora, suggesting a reasonably diverse pteridophyte assemblage. They include trilete spores with a rounded amb with granular or reticulate ornamentation (Plate 5, Fig. 2), triangular trilete spores with a smooth exine (Plate 5, Figs. 4, 5), and small monolet spores with a smooth exine (Plate 5, Fig. 7). The spores are rare and megafossils are absent.

Gymnosperms (Plates 1, 2, 5)

Ginkgoaceae

Ginkgo biloba L. leaves range from unlobed to bifurcating (Plate 1, Figs. 3, 6) and *Ginkgo dissecta* Mustoe leaves are highly dissected (Plate 1, Fig. 5). Leaves assigned to *Ginkgo biloba* are assigned occasionally to *Ginkgo adiantoidies* (Unger) Heer. *Ginkgo dissecta* was established for leaves with a highly divided lamina and distinctive cuticle (Mustoe 2002). Whether these forms are distinct species or variants from similar trees remains unclear, since modern *Ginkgo* leaves are quite variable on a single tree, with juvenile forms often being highly dissected (Smith et al. 2010). Leaves of the *Ginkgo dissecta* type predominate at the Thomas Ranch locality. *Ginkgo* pollen (Plate 5, Fig. 9) is present but rare in all samples.

Cupressaceae

Four genera are known: *Metasequoia occidentalis* (Newberry) Chaney (Plate 1, Figs. 4, 8); *Sequoia* Endl. (Plate 1, Figs. 7, 9); *Cunninghamia* R. Br. (Plate 2, Fig. 1); and *Chamaecyparis* Spach. (Plate 2, Figs. 2, 3). *Metasequoia* is among the most common foliage type in the flora (Plate 1, Figs. 4, 7), with *Sequoia* also being present, but less frequently encountered (Plate 1, Figs. 8, 9). *Cunninghamia*, today an Asian endemic and commonly planted ornamental, is not common in the Okanagan Highlands except at the McAbee locality. Here it is known from a robust branching specimen thickly clothed with small scalelike leaves (Plate 2, Fig. 1). *Chamaecyparis* branches have tightly imbricate scale-like leaves (Plate 2, Figs. 2, 3). Cupressaceous pollen (Plate 5, Figs. 10, 11) is very common at all sample locations, accounting for up to 75% of the total pollen count.

Pinaceae

The pine family megafossils at Thomas Ranch include *Abies milleri* Schorn & Wehr (fir; Plate 2, Figs. 4, 5), *Pinus* L. (pine; Plate 2, Figs. 7–10); *Picea* Mill. sp. (spruce; Plate 2, Figs. 11, 12), and *Pseudolarix* Gordon sp. (Plate 2, Figs. 13, 14). *Abies milleri*, a species described originally from the Republic flora, is represented here by leafy branches with long slender needles and rare individual cone scales (Plate 2, Figs. 4, 5). This occurrence contrasts with those at other sites, where it is typically known from a combination of cone scales, seeds, and leafy branches. Pines are known from five-needled leaf fascicles, pollen cones, and dispersed, winged seeds

(Plate 2, Figs. 7, 8, 10). In this flora, the seed body of *Pinus* is often torn from its wing, and the wings found alone, bearing the opened area once occupied by the seed (Plate 2, Fig. 10). Spruces have distinctive branches with individual leaves attached helically, rounded leaf scars, and short shoots (Plate 2, Fig. 11). Their seeds have a much smaller, ovoid wing than those of *Pinus* (compare Plate 2, Figs. 10, 12). A conifer seed cone, probably assignable to *Picea*, is also known (Plate 2, Fig. 9). *Pseudolarix* is known from ovoid cone scales and seeds with narrow, elongate wings (Plate 2, Figs. 13, 14).

The Pinaceae are also well represented in the pollen samples. The most common bisaccate types are *Picea* (Plate 5, Fig. 25) and *Pinus* (Plate 5, Fig. 24), whereas *Abies* (Plate 5, Fig. 27) and *Pseudolarix* (Plate 5, Fig. 26) are less common. *Larix/Pseudotsuga* (Plate 5, Fig. 28) and *Tsuga* (not figured) are also found in the microflora. These types are only common in the lower UWBM B3263 sample; they are rare in the other two samples. Pollen of *Larix* and *Pseudotsuga* is very similar, and thus is reported as a single palynomorph. Neither genus is known from megafossils in the Thomas Ranch deposits.

Taxaceae

Members of Taxaceae include a few long flattened leaves with the characteristic parallel stomatal furrows (Plate 2, Fig. 6).

Other conifers

Pollen referred to *Podocarpidites/Cathaya* (Plate 5, Fig. 23) is rare, but present from all three sample locations. The following two distinct types were noted: a large grain type 95–133 μm long (Plate 5, Fig. 23) and a smaller type 60–76 μm long. The taxonomic assignment of these types in the Tertiary of western North America currently is controversial. Although some authors assign this type to *Podocarpidites* (Hills 1965; Reininck-Smith and Leopold 2005), others recognize it as *Cathaya* (Pinaceae, Liu and Basinger 2000; Zetter et al. 2011). Zetter et al. (2011) state that the most definitive characters for positive identification of *Cathaya* pollen are only visible under SEM. To date, there have been no confirmed megafossils of either *Cathaya* or Podocarpaceae in the Okanagan Highlands floras.

Angiosperms (Plates 3–4)

Areaceae

Rare, monocolpate pollen (not figured) has been found that is similar to *Sabal granopollenites* Rouse, a form that has been reported from other Okanagan Highlands localities (Hills 1965; Moss et al. 2005) and from the Eocene Burrard Formation in western British Columbia (Rouse 1962). Palm megafossils have not been found. The Thomas Ranch pollen is not well enough preserved to provide positive identification, however, if this occurrence can be verified with additional samples, palm pollen would have significant implications for the minimum CMMT.

Betulaceae

The birch family is represented by megafossils in both subfamily Betuloideae (two types of *Betula* leaves, *Betula leopoldae* and *Betula* sp., and *Alnus parvifolia* (Berry) Wolfe & Wehr), and subfamily Coryloideae (*Palaeocarpinus stonebergae* Pigg, Manchester & Wehr, Plate 43, Figs. 1–4). Leaves of *Betula leopoldae* (Plate 3, Fig. 1) and a second form (Plate 3, Fig. 3) are common, while those of *Alnus* (not figured) are less often encountered. Catkins assignable to *Alnus* are also known (Plate 3, Fig. 4). In the Coryloideae the small winged fruits of *Palaeocarpinus stonebergae* are present (Plate 3, Fig. 2).

Pollen of *Alnus*, *Betula*, *Ostrya-Carpinus*, and *Corylus* is also found. *Betula* pollen (Plate 5, Fig. 12) is less common but is in all three sample horizons. As with the megafossils, *Alnus* pollen is relatively rare. It occurs most commonly as four- and five-pored grains (Plate 5, Figs. 13, 14), although a few, rare six-pored grains are found. As

Hills (1965) noted, *Carpinus* and *Corylus* pollen grains (Plate 5, Fig. 15) from this formation are very similar and difficult to separate from each other reliably, except in the best preserved examples. These are the most common betulaceous pollen types in the assemblage.

Within subfamily Coryloideae, *Palaeocarpinus stonebergae* is also known at Thomas Ranch, but is distinct from *Palaeocarpinus barksdaleae* Pigg, Manchester & Wehr from Republic, and other unnamed forms from several other Okanagan Highlands sites (Pigg et al. 2003). *Corylus* megafossils have not been reported previously from the Allenby Formation, but *Corylus johnsoni* Pigg, Manchester & Wehr was described from infructescences and fruits at Republic (Pigg et al. 2003).

Buxaceae

A single, well-preserved grain of buxaceous pollen assignable to the Cretaceous/Tertiary *sporae dispersae* palynomorph *Erdtmanipollis pachysandroides* Krutsch has been found in the Thomas Ranch samples (Plate 5, Fig. 22). This grain has the distinctive wedge-shaped and rectangular sculptural units of *Erdtmanipollis pachysandroides* (Zetter et al. 2011). It is morphologically quite similar to the pollen of modern *Pachysandra* Michx., today a disjunct genus with species native to eastern Asia and southeastern North America. The Tertiary history of *Pachysandra* in western North America based on pollen remains was reviewed by Gray and Sohma (1964), who reported a single partial grain of this type in the Allenby Formation from a railway cut approximately 2.5 km south of the former mining town of Allenby, British Columbia. Our specimen is of similar size and morphology to the one described by Gray and Sohma (1964), who did not formally name their material. It can thus be considered the second confirmed report of this type from the Allenby Formation.

Cercidiphyllaceae

A leaf type assignable to either cf. *Joffrea* Crane & Stockey or cf. *Cercidiphyllum* is characterized by three prominent central veins, a regular crenulate margin and a long petiole (Plate 3, Fig. 10). *Joffrea speirsii* is used in the strict sense to refer to the Late Paleocene whole plant from the Late Paleocene Joffre Bridge, Alberta, site (Crane and Stockey 1985), but leaves and fruits with morphology similar to *Joffrea* are commonly found in the Okanagan Highlands floras.

Elaeagnaceae

A single grain of cf. *Elaeagnus* L. was identified from the flora (Plate 5, Fig. 19). Fossil pollen of the Elaeagnaceae have been reported from the Middle Eocene Green River Formation and the Late Eocene Florissant Formation (Leopold et al. 2008), but this is the first report from the Eocene Okanagan Highlands floras. As this identification is based only upon a single well-preserved pollen grain, it should be considered tentative until such time as it can be confirmed by additional finds. Extant *Elaeagnus* is found in temperate to tropical zones, with highest diversity in China.

Ericaceae

The Ericaceae is represented by a single distinctive pollen tetrad (Plate 5, Fig. 20). Many modern representatives of this family have pollen grains that remain in tetrads at maturity (Erdtman 1952).

Fagaceae

The beech family includes leaves assignable to *Fagopsis undulata* (Knowlton) Wolfe & Wehr (Plate 3, Fig. 6) and *Fagus* L. sp. (not figured). *Fagopsis* and true *Fagus* L. are both known from a combination of leaves and fruits at the McAbee and Republic sites (Manchester and Dillhoff 2004). *Fagus* pollen has not been found in any of the samples, although very rare pollen of *Castanea* L. and *Quercus* L. types (not figured) was noted.

Grossulariaceae

The family Grossulariaceae is represented by leaves assignable to the gooseberry *Ribes* L. (Plate 4, Fig. 7). These leaves are common at Republic, where they display two morphologies. The Thomas Ranch form has rounded lobes.

Hamamelidaceae

Fothergilla malloryi Radtke, Pigg & Wehr was described from a single leaf from the One Mile Creek locality. Since then, additional specimens have appeared at Republic (K. Pigg, unpublished data), as well as here at Thomas Ranch (Plate 4, Fig. 4; Radtke et al. 2005).

Juglandaceae

Although megafossils of Juglandaceae are not known at Thomas Ranch, and are generally fairly rare at other Okanagan Highlands sites, the family is represented in the Thomas Ranch microflora by *Carya* pollen (not figured) and by six- to eight-pored pollen of the *Pterocarya* type (Plate 5, Fig. 18). Both of these types are present in all pollen samples from Thomas Ranch, but make up only a small percentage of the microflora. These finds are consistent with those reported from other Okanagan Highlands floras (Moss et al. 2005).

Lauraceae

Sassafras hesperia Berry (Plate 4, Figs. 8, 10) and a second lauraceous leaf form are known (Plate 4, Fig. 9). *Sassafras* leaves can be quite large and are among the largest leaves found at Thomas Ranch. Many are found as fragmentary remains. They are 2–3 lobed or unlobed, similar to their modern counterparts.

Myricaceae

Comptonia columbiana Dawson (Plate 3, Fig. 5) is a relatively common component of the Okanagan Highlands floras and the Thomas Ranch flora is no exception.

Platanaceae

The sycamores are represented by both *Macgnittea gracilis* Wolfe & Wehr leaves (Plate 4, Fig. 1) and *Macginicarpa* Wolfe & Wehr infructescences (Plate 4, Figs. 2, 3).

Rosaceae

Rosaceous leaves are common components of Okanagan Highlands floras. At Thomas Ranch we find both leaves assignable to cf. *Rubus* L. (Plate 4, Fig. 5) and to *Prunus* L. (Plate 4, Fig. 6). Rosaceae are commonly present throughout the Okanagan Highlands localities and much higher in diversity in the Republic flora.

Sapindaceae

Acer samaras of at least two types are known (Plate 3, Fig. 11, and a second form that is not figured), as is a single fruit of *Dipteronia browni* Manchester (not figured, McClain and Manchester 2001). Only two grains of *Acer* pollen (Plate 5, Fig. 16) have been found at this locality.

Trochodendraceae

Zizyphoides Newberry sp. leaves (Plate 3, Fig. 7) are similar to those present at Republic (Pigg et al. 2001; DeVore and Pigg 2013) and several other Okanagan Highlands sites. They are characterized by broad, irregular teeth and are often wider than long.

Ulmaceae (not figured)

Elms are assigned to *Ulmus okanaganensis* Denk & Dillhoff (Denk and Dillhoff 2005). Both *Ulmus okanaganensis* and a second species, *Ulmus chuchuanus* (Berry) LaMotte are known at other Okanagan Highlands sites. The Ulmaceae is represented in the pollen record by both four- and five-pored grains (Plate 5, Fig. 17). It is present in all samples and makes up a small but significant percentage of the assemblage.

Incertae sedis

Two distinctive megafossil types with undetermined taxonomic relationships are known from Thomas Ranch; one a pinnately compound leaf (Plate 3, Fig. 8), and the other an unusual structure originally interpreted as an inflorescence (Plate 3, Fig. 9). The leaf is one of the most common components of the Thomas Ranch flora, although most specimens are quite fragmentary and no complete leaves are known. Individual leaflets have a thin petiole and an elliptical to ovate lamina with an irregular lobed margin (Plate 3, Fig. 8). Jack Wolfe illustrated this leaf (Wolfe 1989, Fig. 5.1E).

The other fossil currently under study is made up of a stalked ovoid structure bearing two to several pedicellate radially symmetrical structures each with 4–5 fused parts (Plate 3, Fig. 9). Several faint elongate appendages surround these structures. Similar specimens are known from Republic and McAbee.

In the microflora, three grains of *Pistillipollenites macgregorii* were observed (Plate 5, Fig. 21). This palynomorph has been found throughout the Okanagan Highlands, and although its taxonomic affinity is uncertain, it is an important biostratigraphic indicator species.

Paleoclimate estimates

Using 19 assigned NLRs, MAP was estimated using BA as 116 ± 45 cm/year. Using LAA based on 31 leaf morphotypes, the MAP for Thomas Ranch was estimated at 77 cm/year -23 cm, $+33$ cm using the Wilf et al. (1998) equation (Table 2). Using the Peppe et al. (2011) LAA equation, MAP was estimated as 117 cm/year -54 cm, $+99$ cm. The growing season precipitation (GSP) estimate using CLAMP is 68.06 cm. Using the same NLRs, MAT was estimated using BA as 12.8 ± 2.5 °C versus 9.0 °C using CLAMP, and a CMMT of 3.9 ± 4.1 °C from BA versus -1.2 °C using CLAMP (Table 2). A few leaf types (e.g., *Macginitia gracilis*) are observed to have large individual specimens that were too fragmentary to be measured, resulting in a smaller than actual mean leaf size for these morphotypes, and so the estimate of MAP using LAA should be seen as a minimum estimate, as per the recommendations of Wilf et al. (1998). Using the Peppe et al. (2011), the LAA equation yielded very high errors of the estimate, reflecting the poor regression statistics from their analysis of 92 global sites (i.e., $r^2 = 0.23$ vs. 0.76 for Wilf et al. 1998); however, both estimates overlap within the respective errors and indicate a mesic to humid climate.

Discussion

Megafossils

Nonvascular plants are represented by a single type of bryophyte, and the only pteridophyte megafossil discovered is that of *Azolla*, found in mats at the B4294 locality and in the upper layers of the UWBM B3263 site. The dominant megafossils are of taxodiaceous conifers (*Sequoia*, *Metasequoia*), along with fragmentary betulaceous leaves. A total of 20 gymnosperm morphotypes are recognized, eight of which are reproductive organs that match up to corresponding leaf morphotypes, resulting in a total gymnosperm diversity of 12 types. The majority of these are assignable at least to genus, including two species of *Ginkgo*, *Metasequoia*, *Sequoia*, *Chamaecyparis* Spach. *Cunninghamia* R. Br. (Cupressaceae), *Abies*, *Pinus*, *Picea*, *Pseudolarix* (Pinaceae), and one representative of Taxaceae. Of these, the forms common to other Okanagan Highlands flora are well represented (*Metasequoia*, *Chamaecyparis*, *Pinus*, *Picea*, *Pseudolarix*). *Abies milleri* is present but not common, and *Cunninghamia* is represented by a stout branching specimen with short, presumably adult foliage. The presence of *Cunninghamia* is interesting as it is known only from two other Okanagan Highlands sites, McAbee and Republic. Although uncommon, this genus has a long record in the Pacific Northwest, with an early occurrence in the Late Cretaceous of British Columbia (Brink et al. 2009).

There are 51 angiosperm morphotypes, six of which are assignable to the same genus as leaf specimens, resulting in a total diversity of 45 angiosperm types. Seventeen are assignable to genus or species, reflecting their incomplete preservation and the difficulty of identification of fragmentary leaves. Fruits and seeds are uncommon, with the exception of *Palaeocarpinus* fruits. The Betulaceae dominate the angiosperm megafloora, both in common occurrence and diversity, with at least four genera. The relative rarity of *Alnus* in both the megafossil and palynomorphs is interesting and probably reflects local conditions (Moss et al. 2005). The presence and abundance of *Palaeocarpinus stonebergae* is notable as this species is currently known only at one other locality, Coalmont Bluff. A different species, *Palaeocarpinus barksdala*, is common at Gold Canyon, in the Republic flora, and several other differing types of *Palaeocarpinus* occur at other Okanagan Highlands sites (Pigg et al. 2003). The diversity of this genus has yet to be fully recognized.

Other relatively common leaf types include *Comptonia*, *Fagopsis*, cf. *Joffrea* Crane & Stockey (cf. *Cercidiphyllum* Sieb. & Zucc.), *Macginitia*, *Sassafras*, and *Zizyphoides*. One of the most common leaf types, apparently unique to this site, was described and figured by Wolfe (1989) as “an undescribed taxon from Princeton, British Columbia; this taxon probably represents an extinct order that has chloranthoid teeth and pinnately compound foliage” (Plate 3, Fig. 8). The megafloora assemblage at Thomas Ranch is less diverse than most other well-known Okanagan Highland floras but shares many taxa with the nearby One Mile Creek locality.

Palynomorphs

All samples from the Thomas Ranch site were rich in pollen, although preservation was sometimes less than optimal, especially from the upper UWBM B3263 sample location. More than 70 different spore and pollen types were found, of which 32 are identifiable to the family or genus level. The microflora adds considerable diversity not represented in the megafossils, including the club moss *Lycopodium*, at least three additional ferns, three additional conifers, and 12 angiosperms.

The Thomas Ranch palynoflora is similar to assemblages from the Princeton area that were included in regional treatments of Early and Middle Eocene palynofloras from central British Columbia and northeastern Washington state (Hills 1965; Boneham 1968; Moss et al. 2005; Zetter 2006). Conifer pollen representing Pinaceae and Cupressaceae is dominant with angiosperms being significantly diverse, particularly within Betulaceae. The presence of *Pistillipollenites macgregorii* Rouse, sometimes recognized as a biostratigraphic indicator species, supports the assignment of an Early to Middle Eocene age to the flora. *Erdtmanipollis pachysandroides* Krutzsch is known from a single grain from the Thomas Ranch site, providing only the second published report of this taxon from the Allenby Formation (Gray and Sohma 1964).

Figure 3 shows the percentage distribution of major palynomorphs found at each sample location. Conifer pollen was heavily dominant in all samples. Undifferentiated Taxodiaceae–Cupressaceae–Taxaceae (TCT) pollen was a major contributor in all samples, with just under 50% at the lower UWBM B3263 site and over 70% at the upper UWBM B3263 site and the UWBM B4294 site. Some previous authors (Hills 1965; Moss et al. 2005) separated inaperturate gymnosperm pollen into *Cunninghamia*, *Taxodium*, and *Taxus* types. Hills (1965) used Wodehouse's (1933) identification of *Taxodium hiatipites*, but acknowledged that the name could actually represent other genera within the Cupressaceae. Because of the difficulty in distinguishing between these genera, especially using light microscopy, we chose to use the undifferentiated TCT classification. *Metasequoia/Sequoia* type pollen can be separated from TCT by the presence of a single papilla on the pollen grain, and this type was observed in all samples.

Where possible, *Pinus* and *Pseudolarix* pollen was differentiated based on the methods described in Zanni and Ravazzi (2007), but

Table 3. Palynomorphs recognized from the Allenby Formation in previous studies (as compiled by Moss et al. 2005) versus palynomorphs recognized in Thomas Ranch samples.

Family	Palynomorph	Nearest living relative (NLR)	Reported from Allenby Fm in previous studies	Recognized from Thomas Ranch
Lycopodiophytes				
Lycopodiaceae	<i>Lycopodium</i> sp.	<i>Lycopodium</i>	—	*
Pteridophytes				
Azollaceae	<i>Azolla</i>	<i>Azolla</i>	*	*
Osmundaceae	<i>Osmundasporites</i> sp.	<i>Osmunda</i>	*	*
Schizaceae	<i>Anemia poolensis</i>	<i>Anemia</i>	*	*
Various Filicales	Various	Filicales	*	*a
Gymnosperms				
Ginkgoaceae	<i>Cycadopites follicularis</i>	<i>Ginkgo</i>	*	*
Cupressaceae	<i>Cunninghamia</i>	<i>Cunninghamia</i>	*	TCT ^b
	<i>Sequoiapollenites</i>	<i>Metasequoia-Sequoia</i>	*	*
	<i>Taxodiaceapollenites</i> sp., <i>Taxodium</i>	<i>Taxodium</i>	*	TCT ^b
Pinaceae	<i>Abietinaepollenites</i> sp.	<i>Abies</i>	*	*
	cf. <i>Larix/Pseudotsuga</i>	<i>Larix/Pseudotsuga</i>	*	*
	<i>Picea</i>	<i>Picea</i>	*	*
	<i>Pinus</i>	<i>Pinus</i>	*	*
	<i>Pseudolarix</i>	<i>Pseudolarix</i>	*	*
	<i>Tsuga</i>	<i>Tsuga</i>	*	*
	<i>Alisporites</i> and <i>Pityosporites</i> sp.	Pinaceae	*	*
Taxaceae	<i>Taxus</i>	<i>Taxus</i>	*	TCT ^b
Incertae sedis	<i>Podocarpidites</i> sp.	Podocarpaceae/ <i>Cathaya</i>	*	*c
Angiosperms				
Aquifoliaceae	<i>Ilex</i>	<i>Ilex</i>	*	*
Arecaceae	cf. <i>Sabal granopollenites</i>	Arecaceae	*	*
Betulaceae	<i>Alnus</i>	<i>Alnus</i>	*	*d
	<i>Betula</i>	<i>Betula</i>	*	*
	<i>Carpinus</i>	<i>Carpinus</i>	*	*
	<i>Corylus</i>	<i>Corylus</i>	*	*
Buxaceae	<i>Erdtmanipollis pachysandroides</i>	<i>Pachysandra</i>	*e	*
Elaeagnaceae	cf. <i>Elaeagnus</i>	<i>Elaeagnus</i>	—	*
Ericaceae	Ericaceae	Ericaceae	—	*
Fagaceae	<i>Castanea</i>	<i>Castanea</i>	*	*
	cf. <i>Quercus</i>	<i>Quercus</i>	*	*
Hamamelidaceae	<i>Liquidambar</i>	<i>Liquidambar</i>	*	—
Juglandaceae	<i>Carya</i>	<i>Carya</i>	*	*
	<i>Pterocarya</i>	<i>Pterocarya</i>	*	*f
Platanaceae	<i>Platanus</i>	<i>Platanus</i>	*	—
Rosaceae	Rosaceae	Rosaceae	*	—
Salicaceae	<i>Salix</i>	<i>Salix</i>	*	*
Sapindaceae	<i>Acer</i>	<i>Acer</i>	*	*
	<i>Aesculus</i>	<i>Aesculus</i>	*	—
Sapotaceae	Sapotaceae	Sapotaceae	*	—
Tiliaceae	<i>Tilia</i>	<i>Tilia</i>	*	—
Ulmaceae	<i>Ulmus</i>	<i>Ulmus</i>	*	*g
Zosteraceae	<i>Potamogeton</i>	<i>Potamogeton</i>	*	—
Incertae sedis	<i>Pistillipollenites macgregorii</i>	Gentianaceae-Euphorbiaceae	*	*

^aAt least three forms recognized from Thomas Ranch, including two monoete spore types and one trilete spore type.

^bWe do not believe that we can adequately separate most genera in the Taxodiaceae–Cupressaceae–Taxaceae (TCT) pollen type and thus chose to report this type as undifferentiated TCT.

^cTwo types of cf. *Podocarpidites* pollen are present in Thomas Ranch samples.

^d*Alnus* pollen from Thomas Ranch occurs most commonly in four-pored and five-pored forms, although rare six-pored grains were also noted.

^eNot reported in Moss et al. (2005), but a single partial grain of *Pachysandra* was previously reported from a railway cut ~1 mile (1 mile = 1.60934 km) south of Allenby, British Columbia (Gray and Sohma 1964).

^fMoss et al. (2005) report this as *Platycarya–Pterocarya* with the nearest living relative as *Platycarya*, but the Thomas Ranch type has 6–8 pores and is more like modern *Pterocarya* pollen.

^gBoth four- and five-pored types are present.

the two are often difficult to distinguish because of an overlap in size range, preservational issues, and the need to see the grains in proper orientation on mounted slides. Because of this, we chose to report them together in Fig. 3.

At the lower UWBM B3263 sample site, pollen from a number of genera within the Pinaceae was codominant with TCT. Pinaceous pollen was less common in the other two horizons. Other gymnosperm pollen includes *Ginkgo* L., cf. *Larix* Phillip Miller sp. *Pseudotsuga*

Carrière sp., and *Podocarpidites* Cookson ex. Couper/*Cathaya* Chun & Kuang.

Among angiosperms, the Betulaceae are the best represented, making up approximately 3% of the total palynoflora in the lower UWBM B3263 sample and approximately 10% of the other two samples. Other relatively common angiosperms include four- and five-pored ulmaceous pollen and pollen of the Juglandaceae, including *Carya* Nutt. and *Pterocarya* Nutt. ex Moq. sp. types.

As shown in Table 3, the Thomas Ranch pollen–spore assemblage correlates well with other microfloras reported from the Allenby Formation by previous authors (Hills 1965; Boneham 1968; Moss et al. 2005), with only minor differences in the rarer elements.

Hills (1965) offered stratigraphic pollen zones for the Princeton and Coalmont deposits, and extended them to other Eocene deposits in British Columbia. In this zonation system by Hills, the basalmost bisaccate zone is followed by the *Azolla primaeva* zone, and lastly the *Pistillipollenites macgregorii* zone. In comparison, the Thomas Ranch palynomorph assemblage correlates loosely with two of the zone definitions. The sample from the stratigraphically lower layers of UWBM B3263 includes a significant percentage of bisaccate forms and the minor constituents match well with Hills' bisaccate zone. However, the high proportion of TCT pollen is anomalous. Hills also notes that an abundance of *Tsuga* suggests correlation with the bisaccate zone, and *Tsuga* makes up nearly 4% of the lower UWBM B3263 sample at Thomas Ranch.

Samples from the upper layers at UWBM B3263 and from UWBM B4294 are very similar to each other in composition, and the presence of layers with abundant megafossils of *Azolla primaeva* suggests that these may be equivalent to Hills' *Azolla primaeva* zone. However, neither pollen sample shows a high proportion of *Azolla* microspores, and the proportions of TCT and bisaccate forms do not match well with Hills' criteria. *Pistillipollenites macgregorii* is present in both of these samples, but is very rare with only three grains identified in the 25 slides examined. In Hills' uppermost zone, *Pistillipollenites macgregorii* constitutes approximately 5% of the total pollen count, and rare occurrences of *Tilia*, *Psilodiporites*, and *Verrucosiporites* are found. The paucity of *Pistillipollenites* and the absence of the rare elements indicate that this zone is not represented at the Thomas Ranch locality.

Given the distribution seen in the Thomas Ranch pollen assemblage and the presence of layers in the upper portion of the deposit with abundant *Azolla* megafossils, it is postulated that this deposit represents Hills' bisaccate zone, grading up into the *Azolla primaeva* zone. This suggests that the Thomas Ranch site is in the lower part of the Allenby Formation. Additional pollen sampling would be required to substantiate this conclusion.

In common with the other Okanagan Highland megafloras with bioclimatic estimates (Table 2), Thomas Ranch is reconstructed as having an upper microthermal climate (MAT in the range 10–15 °C), with limited or no frost in winter (CMMT 0–5 °C), and moderate to high precipitation (MAP >70 cm/year, likely >100 cm/year). The leaf physiognomic methods derived estimates for Thomas Ranch are comparable to estimates of temperature and precipitation across these other Okanagan Highlands megafloras. The very low MAT estimate for One Mile Creek from LMA reflects both the use of the Wolfe (1979) calibration as derived by Wing and Greenwood (1993), and the small sample used for the analysis by Greenwood et al. (2005); the estimate derived from BA is considered more reliable. Differences in estimated precipitation between individual megafloras are not significant as they all overlap within their respective errors of the estimate.

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