

# Great Canadian *Lagerstätten* 1. Early Eocene *Lagerstätten* of the Okanagan Highlands (British Columbia and Washington State)

S. Bruce Archibald, David R. Greenwood, Robin Y. Smith, Rolf W. Mathewes et James F. Basinger

Volume 38, numéro 4, december 2011

URI : [https://id.erudit.org/iderudit/geocan38\\_4ser01](https://id.erudit.org/iderudit/geocan38_4ser01)

[Aller au sommaire du numéro](#)

Éditeur(s)

The Geological Association of Canada

ISSN

0315-0941 (imprimé)

1911-4850 (numérique)

[Découvrir la revue](#)

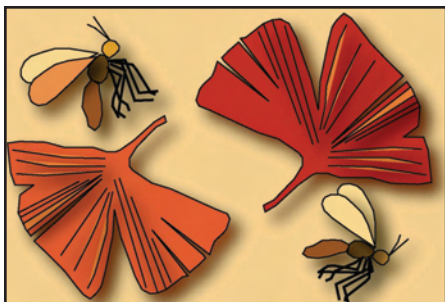
Citer cet article

Archibald, S. B., Greenwood, D. R., Smith, R. Y., Mathewes, R. W. & Basinger, J. F. (2011). Great Canadian *Lagerstätten* 1. Early Eocene *Lagerstätten* of the Okanagan Highlands (British Columbia and Washington State). *Geoscience Canada*, 38(4), 155–164.

Résumé de l'article

La série de dépôts lacustres de schiste et de charbon du début de l'Éocène des hautes terres d'Okanagan, aux confins de l'ouest de l'Amérique du Nord, constituent un groupe important de sites fossiles particulièrement bien conservés de suites d'organismes diverses (*Lagerstätten*). De nos jours, ces sites forment en une bande d'environ 1 000 kilomètres, depuis le sud de la Colombie-Britannique jusqu'au nord de l'État de Washington. Dans le contexte de réchauffement climatique, c'est l'occasion ou jamais d'étudier la paléoenvironnement de communautés terrestres dans des conditions climatiques modérées dans un paysage de montagne à faible saisonnalité. Les sites des hautes terres d'Okanagan représentent un cadre de comparaison sans pareil permettant d'étudier les effets de ce tournant majeur sur le développement des principales caractéristiques modernes de la communauté terrestre.

# SERIES



## Great Canadian *Lagerstätten* 1. Early Eocene *Lagerstätten* of the Okanagan Highlands (British Columbia and Washington State)

S. Bruce Archibald<sup>1,2</sup>, David R.  
Greenwood<sup>3,4</sup>, Robin Y. Smith<sup>4</sup>, Rolf  
W. Mathewes<sup>1</sup> and James F.  
Basinger<sup>4</sup>

<sup>1</sup>Department of Biological Sciences  
Simon Fraser University  
Burnaby, BC, Canada, V5A 1S6  
E-mail: sba48@sfu.ca

<sup>2</sup>Royal British Columbia Museum,  
Victoria, BC, Canada; and  
Museum of Comparative Zoology,  
Cambridge, MA, USA

<sup>3</sup>Department of Biology,  
Brandon University,  
Brandon, MB, Canada

<sup>4</sup>Department of Geological Sciences,  
University of Saskatchewan,  
Saskatoon, SK, Canada

### SUMMARY

The Early Eocene Okanagan Highlands series of lacustrine shale and coal

deposits, in far western North America, constitutes a significant group of fossil sites with exceptional preservation of a diverse suite of organisms (*Lagerstätten*). With contemporaneous basins arrayed across about 1000 kilometres of southern British Columbia and northern Washington, these sites offer a unique opportunity to examine the paleoecology of terrestrial communities spanning a temperate, low-seasonality landscape in a montane setting during a time of generally warm temperatures across the globe. The Okanagan Highlands sites provide an unparalleled comparative framework within which to examine this major turning point in terrestrial community development during the emergence of their broad modern character.

### SOMMAIRE

La série de dépôts lacustres de schiste et de charbon du début de l'Éocène des hautes terres d'Okanagan, aux confins de l'ouest de l'Amérique du Nord, constituent un groupe important de sites fossiles particulièrement bien conservés de suites d'organismes diverses (*Lagerstätten*). De nos jours, ces sites forment en une bande d'environ 1 000 kilomètres, depuis le sud de la Colombie-Britannique jusqu'au nord de l'État de Washington. Dans le contexte de réchauffement climatique, c'est l'occasion ou jamais d'étudier la paléoécologie de communautés terrestres dans des conditions climatiques modérées dans un paysage de montagne à faible saisonnalité. Les sites des hautes terres d'Okanagan représentent un cadre de comparaison sans pareil permettant d'étudier les effets de ce tournant majeur sur le développement des principales caractéristiques modernes de la communauté terrestre.

### INTRODUCTION

*Lagerstätten* (*Konservat-Lagerstätten* in particular) are fossil assemblages that combine fine preservation of features not typically fossilized (e.g., soft tissues, hairs, colour patterns) with high biological diversity, providing exceptional records of past life (Seilacher 1970). Famous examples include the Eocene sites at Florissant, Colorado (Meyer 2003) and Messel, Germany (Schaal and Ziegler 1992), and the Cambrian Burgess Shale of British Columbia (Gould 1989). A series of Early Eocene sites collectively called the Okanagan Highlands also fits this description well. These occur across an approximately 1000 km transect, stretching from northern Washington State to central British Columbia (Fig. 1), in depositional basins where lacustrine shales and coal deposits fill grabens associated with uplift and regional volcanism (Ewing 1980). The deposits reveal ancient forest, lake and swamp life in temperate upland communities within the context of a warm and seasonally equable world, including a rich suite of plants, insects, fish, feathers, and (rarely) bird and mammal skeletal remains (Figs. 2, 3), as well as microfossils such as diatoms and pollen. Megafossils are commonly spectacularly well preserved as compressions featuring colour patterns on insects' wings, exquisite whole flowers of *Florissantia*, and delicate ferns like the floating *Azolla* (Fig. 4), and showing minute details of epidermal cell patterns of leaves (Fig. 5) and membrane hairs on the wings of tiny fungus gnats (Fig. 6). These fossils reveal communities in their environmental contexts some fifteen million years after the end-Cretaceous mass extinction event, affording an unprecedented



**Figure 1.** Map showing the Okanagan Highlands fossil sites in British Columbia and Washington.

opportunity to examine the origin and development of large-scale patterns of diversity, biogeography, evolution and climate.

### HISTORY OF WORK

Until the latter part of the 20<sup>th</sup> century, the remoteness of the Okanagan Highlands hampered its scientific study compared with more accessible contemporaneous localities, such as those near railway lines in mid-continental USA (e.g. Meyer 2003). When British Columbia entered Confederation in 1871, following a series of gold rushes, the federal government sent geologists to assess its coal and mineral wealth. Among them was George Mercer Dawson (1879, 1895), who reported plant and insect fossils in sedimentary rocks of the Interior, later called the Okanagan Highlands (earliest use apparently by Wehr and Schorn 1992). These early collections resulted in a variety of studies in paleoentomology (Scudder 1877; Handlirsch 1910); paleobotany (e.g. J.W. Dawson 1879, 1883, 1891; Penhallow 1908; Berry 1926, 1929; Brown 1935, 1937, 1939, 1940); and rare mammals (two teeth; Russell

1935; Gazin 1953).

After this initial burst of activity, only sporadic studies were published until a renaissance in the latter half of the 20<sup>th</sup> century, beginning with work on pollen in the 1960s (Rouse and Mathews 1961; Mathews 1964; Hills 1965; Hills and Baadsgaard 1967), then gaining momentum in the 70s with the first description of the McAbee flora (Verschoor 1974) and examination of the exquisitely detailed three-dimensional plant fossils of the Princeton chert (Miller 1973; Basinger 1976, 1984; Basinger and Rothwell 1977; Cevallos-Ferriz et al. 1991; Erwin and Stockey 1991; Stockey et al. 1999; Smith and Stockey 2007; and others). The scope of research expanded with work on fish and insects (Wilson 1977a, b, 1978, 1980) and paleobotanical study focusing on the Republic site (e.g. Wolfe and Wehr 1987), leading to a series of papers with a broader regional view, often inspired by talented amateur American paleobotanist Wes Wehr's promotion of Okanagan Highlands paleontology (e.g. Lewis 1992; Reed 1996; see also Archibald et al. 2005a for Wes Wehr's obituary). In

recent years, interest in Okanagan Highlands fossils has continued to grow (e.g. Basinger et al. 1996; Stockey and Wehr 1996; Wilson 1996a, b; Archibald and Greenwood 2005 and references therein).

### PRESERVATION OF FOSSILS

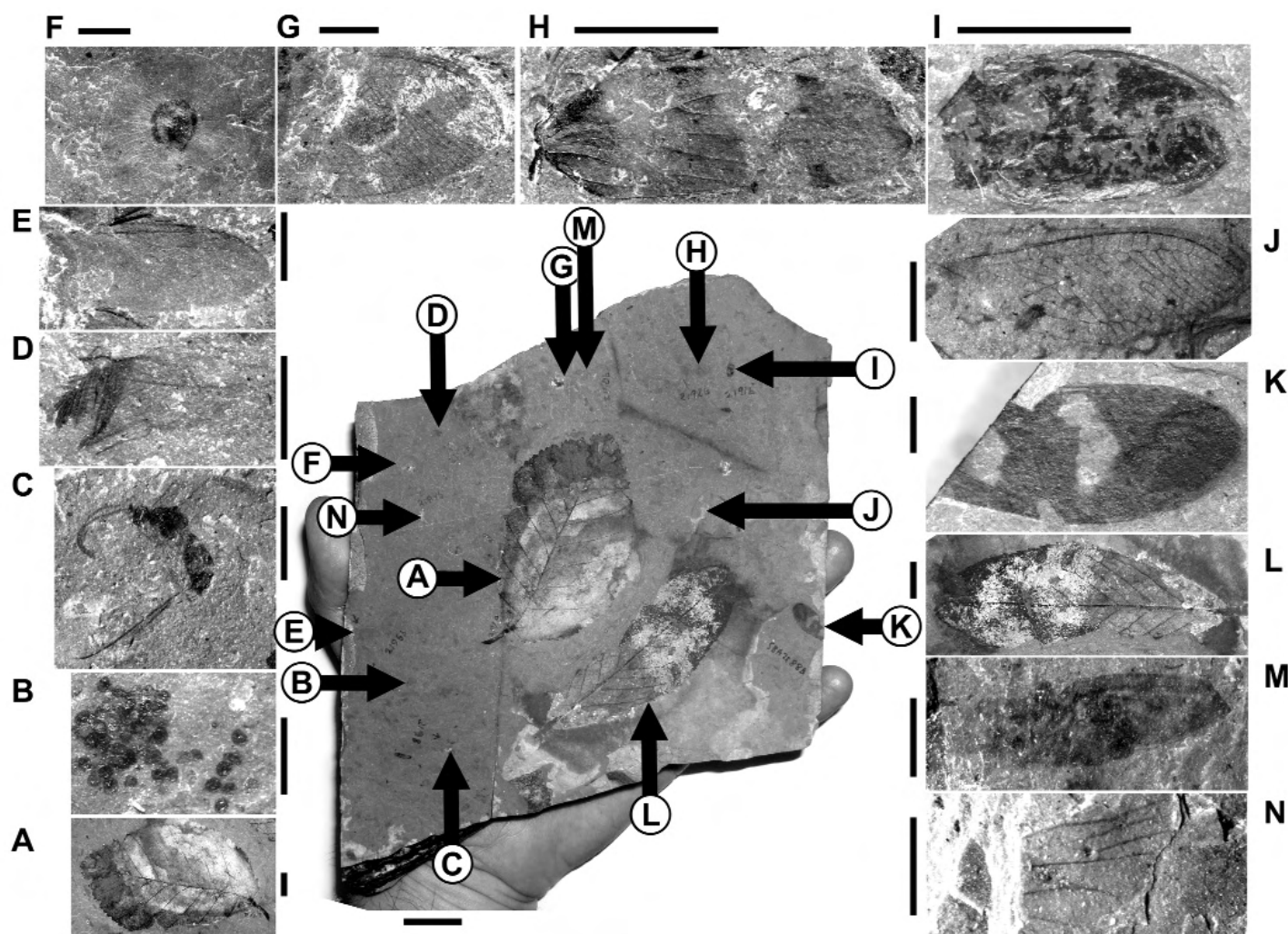
Fossils of the Okanagan Highlands are typically preserved in lacustrine shales. Preservation of the stunning detail often seen in these fossils (Figs. 2-6) may be related, at least in part, to their entrapment in diatom blooms and subsequent coating by biofilms, as inferred for Eocene lacustrine-shale *Lagerstätten* elsewhere (Harding and Chant 2000; Mustoe 2005). Archibald and Makarkin (2006) also suggest that biofilm coating may have lessened taphonomic sorting of insect assemblages by surface area/mass during flotation on the lake surface, thereby increasing fidelity of the fossil assemblages to the original community compositions. Research into lake environments, depositional settings and taphonomic processes in the Okanagan Highlands has resulted in highly influential papers (e.g. Wilson 1980; Barton and Wilson 2005), particularly from work at the Horsefly site, which will be specifically treated by M.V.H. Wilson in a subsequent paper in this Canadian *Lagerstätten* series.

### LIFE AT THE DAWN OF THE RECENT

Early workers considered these deposits to be Oligocene or Miocene (Scudder 1878, 1895; G.M. Dawson 1879, 1896). J.W. Dawson (1891) provisionally agreed, but suggested that they might also be Eocene. This was later supported by teeth of the tillodont mammal *Trogosus* found in the Allenby Formation near Princeton (Russell 1935), then confirmed by K–Ar dating, which indicated Middle Eocene ages throughout the region (Rouse and Mathews 1961). Recent  $Ar^{40}/Ar^{39}$  and U–Pb analyses have pushed back their ages a bit further into the latter half of the Early Eocene (Villeneuve and Mathews 2005; Moss et al. 2005; Mortensen and Archibald, personal communication).

Life in the Early Eocene was making a large step toward modernization following events such as the great extinction at the end of the Cretaceous and the brief, intense interval of global





**Figure 2.** A single piece of shale (about 25 by 20 cm) from McAbee, BC, bearing seven orders and at least ten new species of insects (including insects not illustrated here) as well as bird and plant remains: A. birch (*Betula*) leaf; B. seed cluster; C. parasitoid wasp (Hymenoptera); D. an unidentified feather; E. a march fly wing (Diptera: Bibionidae); F. *Dipteronia* fruit; G. a green lacewing wing (Neuroptera: Chrysopidae); H. a plant hopper forewing (Hemiptera: Auchenorrhyncha: Cercopoidea); I. a beetle (Coleoptera); J. a second species of green lacewing; K. an undescribed family of scorpionfly (Mecoptera); L. leaf, possibly cherry (cf. *Prunus*) leaf; M. mayfly nymph wing pad (Ephemeroptera); N. plant hopper hind wing. Also, there are several poorly preserved small insects, conifer needles, and other fossils not indicated here. Scale bar for A. and L. = 10 mm; scale bar for central rock image = 2 cm. All other scale bars 2 mm.

warming at the Paleocene–Eocene boundary (Zachos et al. 2008). Here, in the Okanagan Highlands, numerous groups of animals and plants make their first appearances in the fossil record; for example, genera such as hazel (*Corylus*) and hornbeam (*Carpinus*) in the birch family (Betulaceae); the oldest known service-berry (*Ame-lanchier*), snow-wreath (*Neviusia*), and cherry (*Prunus*) in the rose family (Rosaceae); winter-hazel (*Corylopsis*) and witch-alder (*Fothergilla*) in the witch-hazel family (Hamamelidaceae); and beech (*Fagus*) in the beech family (Fagaceae) (e.g. Wolfe and Wehr 1987;

Wehr and Hopkins 1994; Manchester and Dillhoff 2004; Radtke et al. 2005; DeVore and Pigg 2007, 2010). We see the oldest records of such insects as seed weevils (Coleoptera: Chrysomelidae: Bruchinae), sweat bees (Hymenoptera: Halictidae), and panorpoid scorpionflies (Mecoptera: Panorpidae) (Archibald and Mathewes 2000; Engel and Archibald 2003); and the earliest salmonid fish (Wilson and Li 1999).

Mixed with these modern elements were such extinct taxa as the ubiquitous and often beautifully preserved *Florissantia* (Fig. 4A) and bizarre

holcorpid scorpionflies (Archibald 2010), reminding us that this was still a world in transition. These communities were organized in distinctly different manners than we would expect to see today, molded, in large part, by their particular climatic setting.

### EARLY EOCENE UPLANDS CLIMATE

In the Early Eocene, the world experienced the highest temperatures of the Cenozoic, notably during hyperthermal events, when atmospheric carbon dioxide greatly exceeded modern levels (Zachos et al. 2008; Smith et al. 2010). This was the acme of the ‘greenhouse





**Figure 3.** Representative taxa from the Falkland flora. Scale bars = 1 cm. A. *Metasequoia occidentalis* foliage; B. *Ginkgo adiantoides* foliage; C. *Pinus* seed; D. *Abies milleri* seed; E. *Tetracentron* sp. foliage; F. *Pseudolarix* seed; G. betulaceous staminate inflorescence; H. ?*Adiantum* fern pinna (close-up of portion of I); note the preservation of sori (arrow); I. ?*Adiantum* fern pinna; J. *Alnus parvifolia* foliage; K. *Alnus parvifolia* pistillate inflorescence; L. *Ulmus* sp. samara; note preservation of narrow wing (arrow); M. *Ulmus* sp. samara; note preservation of peripheral hairs (arrow); N. *Ulmus okanaganensis* foliage; O. *Prunus* sp. flower; note preservation of remnant stamens and style of carpel (arrow); P. *Photinia pagae* foliage; Q. *Koelreuteria arnoldi* samara; and R. *Acer* sp. samara.

world' global climatic regime of warm temperatures and mild winters before the climatic downturn initiating our current 'icehouse world' after the close of the Eocene (Zachos et al. 2008).

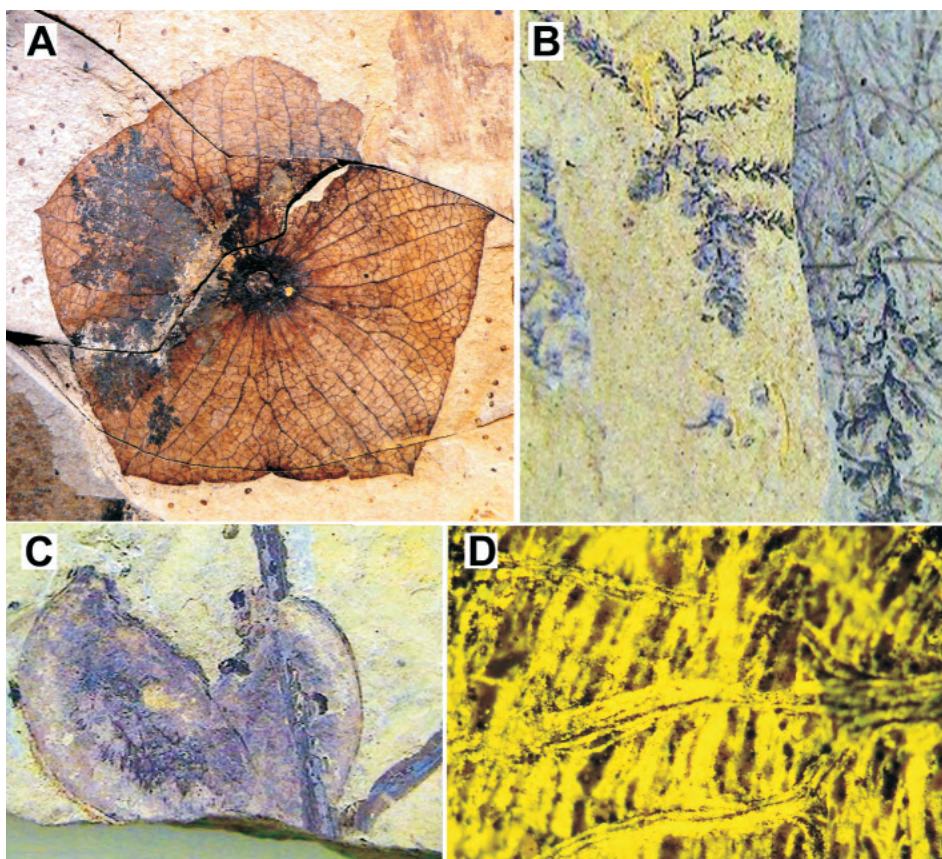
Multiple geologic and paleontological indicators suggest that this region was a temperate upland in this warm world (e.g. Greenwood et al. 2005; Smith et al. 2009; and references therein), with upper microthermal to lower mesothermal mean annual temperatures, similar to those of modern

coastal southern British Columbia roughly through Oregon. The southern British Columbia region underwent significant uplift in the Early Eocene (Ewing 1980), reflected in the contrast between the Okanagan Highlands and coeval warmer, subtropical-character forests in nearby lowland coastal regions (Rouse et al. 1971). The Okanagan Highlands climate has been determined by taxon-independent leaf physiognomy data from variables such as the size and shape of dicot leaves

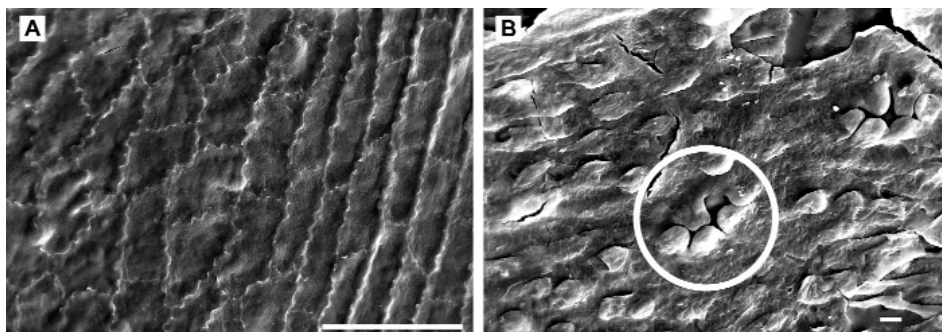
and by taxon-dependent analyses of the nearest-living-relative climatic associations of plant micro- and megafossils and insects (Figs. 2, 3; e.g. Rouse et al. 1971; Wolfe and Wehr 1987; Wolfe 1994; Wolfe et al. 1998; Archibald and Mathewes 2000; Greenwood et al. 2005; Dillhoff et al. 2005; Moss et al. 2005; Archibald 2007; Smith et al. 2009; Smith 2011). Paleobotanical indicators show mesic levels of precipitation.

Fine preservation of leaf





**Figure 4.** Quilchena, BC. A. *Florissantia quilchenensis*; B. whole *Azolla* plant (floating water fern); C. *Eucommia* fruits; D. epifluorescence image of latex from a *Eucommia* fruit.



**Figure 5.** Scanning electron photomicrographs of fossil *Ginkgo adiantoides* cuticle from Falkland. Scale bars: A. = 100 µm and B. = 10 µm. A. Adaxial (non-stomatal bearing) cuticle, inner surface, showing epidermal cells with obvious undulate walls diagnostic of *Ginkgo*; B. Abaxial cuticle, outer surface, showing stomata and papillate epidermal cells (one of two visible stomata circled). Source: Smith et al. (2010).

compression fossils to the cellular level allows evaluation of other aspects of the paleoenvironment, including levels of atmospheric carbon dioxide ( $p\text{CO}_2$ ). Estimates of Early Eocene  $p\text{CO}_2$  vary widely, from near modern-day levels to an order of magnitude greater (Royer 2006; Smith et al. 2010). Resolving these is a key task in determining whether climate and  $p\text{CO}_2$  were then

coupled. The stomatal frequency of fossil plants is one proxy measure that can be used to estimate paleo- $p\text{CO}_2$ , as the frequency of stomata on the leaf surface is regulated, at least in part, by levels of  $\text{CO}_2$  (Woodward 1987; Royer 2001). The 'living fossil' *Ginkgo biloba* is often used in the application of this proxy measure, as the fossil *Ginkgo adiantoides* is indistinguishable from the

living species, and indicates that this lineage has persisted with little change in gross morphology since the Cretaceous (Royer et al. 2003). The exceptional preservation of *Ginkgo* with intact cuticle at the Okanagan Highlands Falkland locality (Fig. 5) has provided the opportunity to estimate  $p\text{CO}_2$  during the critical window of the Early Eocene. Stomatal counts on fossil *Ginkgo* leaves at Falkland indicate that  $p\text{CO}_2$  was  $>2\times$  modern-day levels during the Early Eocene (Smith et al. 2010). Furthermore, evidence of cooling temperatures over time at Falkland is correlated with a trend toward decreasing  $p\text{CO}_2$ , suggesting that they were coupled (Smith et al. 2010).

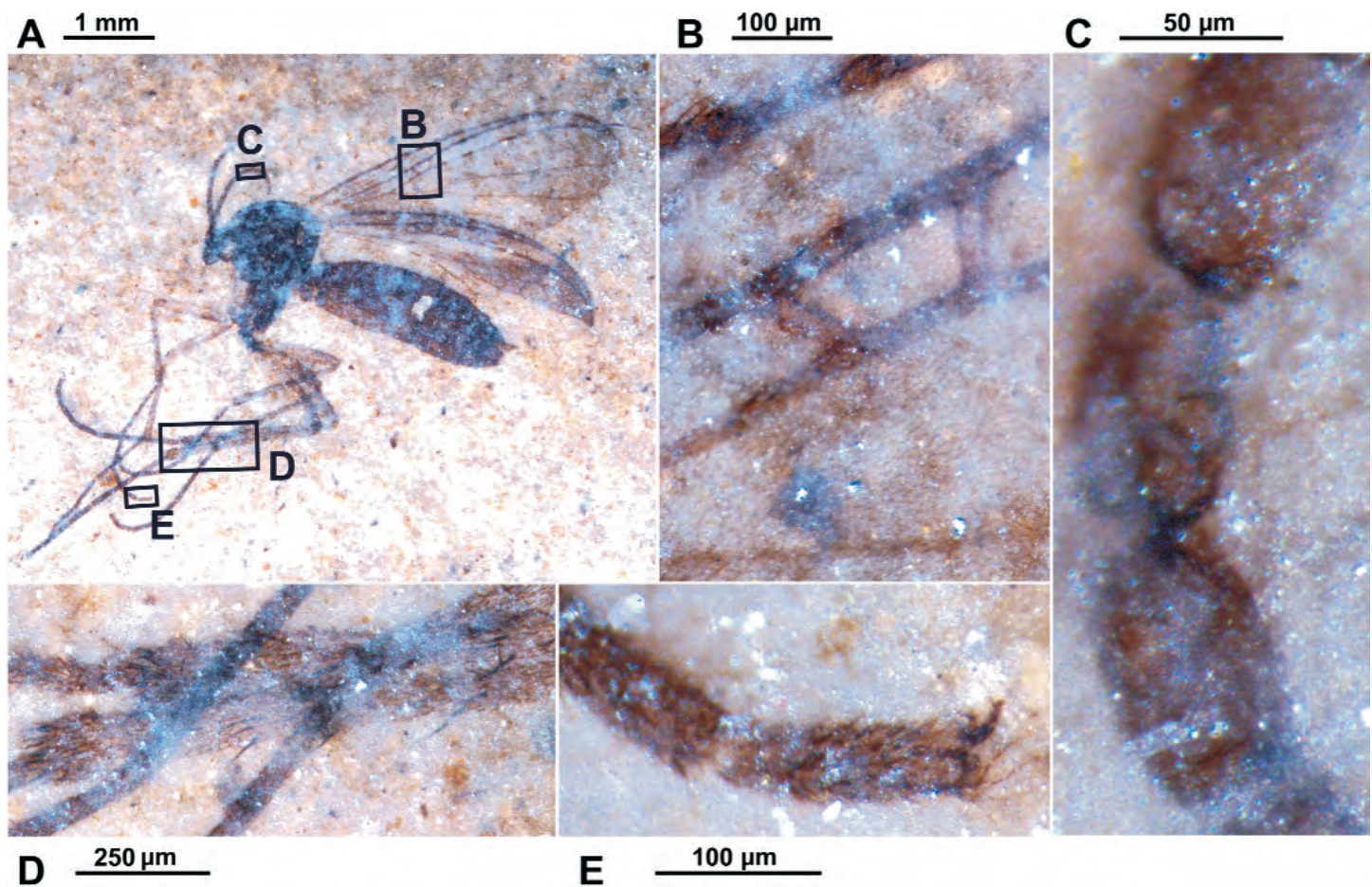
The Eocene was also a time of seasonally equable temperatures, with mild winters extending into high latitudes, unlike today when such low seasonality is most associated with low latitudes (Greenwood and Wing 1995; Zachos et al. 2008; Shellito et al. 2009).

## COMMUNITIES: FAMILIAR AND STRANGE

The particular Okanagan Highlands mixture of temperate upland mean annual temperatures, and winters with few if any frost days, may have been of key importance in determining the distinctive character of its forests (Archibald and Farrell 2003; Greenwood et al. 2005). The paleoclimate appears to have allowed plant and insect taxa that are today associated with sub-tropical to tropical temperatures to co-exist with more typically temperate elements. Here, forests contained palms (*Ublia*) and cycads, at some localities mixed with taxa such as spruce (Erwin and Stockey 1991; Greenwood et al. 2005).

Not only were these communities notable for their tropical-temperate mixture of organisms, but they possessed differing patterns of species richness than we would expect in modern temperate, mid-latitude forests. Diversity of insects (McAbee) and plants (Falkland, McAbee, Republic) has been shown to be surprisingly high; it is comparable to that found in modern tropical forests (Archibald et al. 2010; Smith et al. 2011), and the Falklands flora matches the hyperdiverse floras of Eocene South America (Wilf et al. 2005; Smith et al. 2011).





**Figure 6.** Driftwood Canyon. Fine-level preservation of fungus gnat (Diptera: Mycetophilidae): A. whole insect; B. detail of wing showing veins and microtrichia (minute hairs) on wing membrane; C. detail of antenna showing individual flagellomeres; D. legs, showing coarse and fine hairs; and E. tip of leg, showing tarsal claw morphology. Detailed preservation may be due to encasement in diatom mats (see text).

Perhaps oddly, this tropical level of diversity seen in insects and plants is not reflected in fish.

Some Okanagan Highlands plant and insect lineages are now native to distant regions such as Chile or Australia (e.g. Wing and Greenwood 1993; Archibald and Mathewes 2000; Archibald and Farrell 2003; Greenwood et al. 2005; Archibald et al. 2005b, 2006). In the Early Eocene, North America was connected to Europe across the Arctic via Greenland, and to East Asia via Beringia (Manchester 1999). Patterns of Okanagan Highlands insect and plant fossil occurrences have helped reveal the histories of particular lineages that have disjunct distributions in the modern world (e.g. DeVore et al. 2005; Archibald and Makarkin 2006; Archibald 2009; DeVore and Pigg 2007, 2010). The Okanagan Highlands forests show similarities to those of

modern eastern USA, but also include many taxa that today occur in East Asia and the Pacific Northwest, alongside some that are now extinct, helping elucidate the origins and history of lineages characteristic today of microthermal broad-leaved deciduous and coniferous forests (Wolfe 1987; Manchester 1999). For example, taxa that are characteristic of the eastern hardwood forests of North America today and also represented in the Okanagan Highlands flora include elm (*Ulmus*, Fig. 3L–M), beech (*Fagus*), hazel (*Corylus*), hornbeam (*Carpinus*), birch (*Betula*), maple (*Acer*, Fig. 3R) and others. Relict taxa that are today restricted to East Asia, but were more widespread in the Early Eocene, include typical Okanagan Highlands taxa such as dawn redwood (*Metasequoia*, Fig. 3A), maidenhair tree (*Ginkgo*, Fig. 3B), and golden larch (*Pseudolarix*, Fig. 3F), as well as more rare occur-

rences of *Dipteronia*, *Eucommia* (Fig. 6C), *Koelreuteria* (Fig. 3Q), *Tetracentron* (Fig. 3E) and *Photinia* (Fig. 2P). Genera that are found today in the Pacific Northwest of North America, and that were also present during the Early Eocene, include cedar (*Thuja*), redwood (*Sequoia*), spruce (*Picea*), fir (*Abies*, Fig. 3D), pine (*Pinus*, Fig. 3C), alder (*Alnus*, Fig. 3J–K), cherry (*Prunus*, Fig. 3O) and others.

## CONCLUSIONS

While *Lagerstätten* such as the Late Eocene Florissant and Middle Eocene Messel preserve an extraordinary range of life in fine detail (Meyer 2003; Schaal and Ziegler 1992), they reflect the environments around single lakes. The multiple Early Eocene deposits of the Okanagan Highlands, however, preserve a profusion of life surrounding a series of lakes spanning about 1000 kilometres north to south, pro-



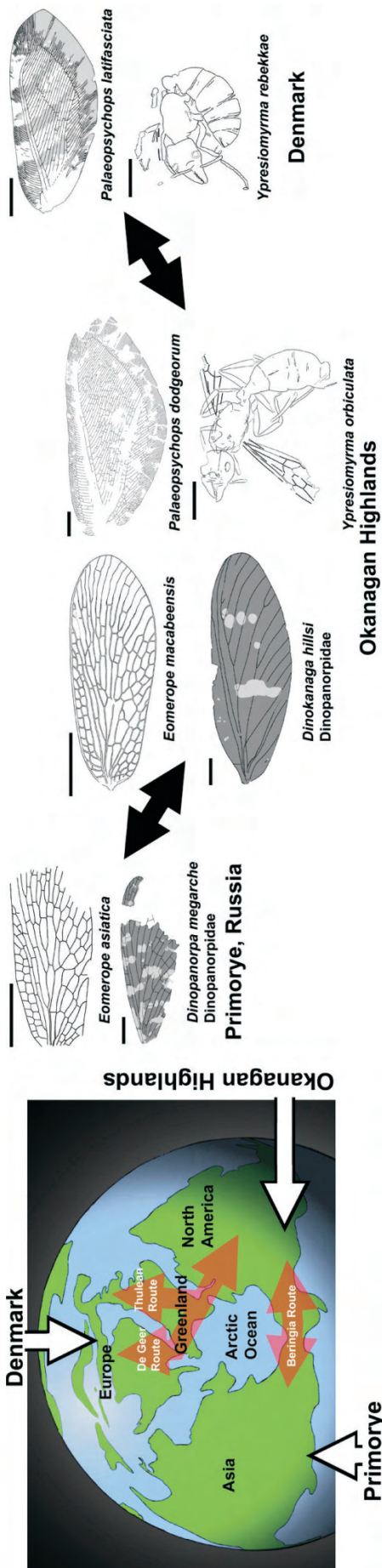


Figure 7. Polar view of the Earth in Okanagan Highland times, with insects indicating dispersal between Denmark and Pacific coastal Russia and the Okanagan Highlands (after Archibald et al. 2011). All scale bars 5 mm.

viding an unprecedented opportunity to examine an extended transect of temperate uplands in a warm world. These fossils were deposited at a key moment in the emergence of modern terrestrial lineages and communities before the onset of our current icehouse world climate, an ancient world with a mixture of familiar and strange life forms and environments. The extraordinary *Lagerstätten* of the Okanagan Highlands offer an exceptional window into the formation of life in our modern world and constitute a unique comparative framework within which to examine the processes that govern its nature.

#### ACKNOWLEDGEMENTS

Funding for this research was provided by NSERC through Discovery Grants to DRG, JFB and RWM, a Canada Graduate Scholarship to RYS and a Post-Doctoral Fellowship to SBA, and by facilities funded by a Canada Foundation for Innovation grant to DRG. We wish to acknowledge Richard Hebda of the Royal BC Museum for permission to collect at the BC sites, and John Howard and Scott McMillan of BC Parks for facilitating work at Driftwood Canyon Provincial Park (under BC Parks permit). We also acknowledge the generous assistance of Catherine Brown and Karl Volkman of the Stonerose Interpretive Center in Republic, WA. We thank Marlow Pellatt (Parts Canada) for access to microphotography equipment. We thank our colleagues for their advice and input. We thank David Rudkin and Graham Young for their efforts in organizing both the *Lagerstätten* symposium at GeoCanada 2010 in Calgary, Alberta, and this series, and further thank them, Mark Wilson, and Mike Wilson for their helpful comments on this manuscript.

#### REFERENCES

Archibald, S.B., 2007, Climate and

- Species Diversity: The Eocene Okanagan Highlands Insect View, v. 1–2: Ph.D. thesis, Harvard University, Cambridge, MA, 623 p.
- Archibald, S.B., 2009, New Cimbrophlebiidae (Insecta: Mecoptera) from the Early Eocene, McAbee, British Columbia, Canada, and Republic, Washington, USA: *Zootaxa*, v. 2249, p. 51–62.
- Archibald, S.B., 2010, A revision of the scorpionfly family Holcorpidae (Mecoptera), with description of a new species from Early Eocene McAbee, British Columbia, Canada: *Annales de la Société Entomologique de France*, v. 46, p. 173–182.
- Archibald, S.B., and Farrell, B.D., 2003, Wheeler's dilemma: Proceedings of the Second Paleoentomological Congress, *Acta Zoologica Crakoviensia*, v. 46 (supplement, fossil insects), p. 17–23.
- Archibald, S.B., and Greenwood, D.G., 2005, Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: Climates and ecosystems across an Eocene landscape: *Canadian Journal of Earth Sciences*, v. 42, p. 167–185.
- Archibald, S.B., and Makarkin, V.N., 2006, Tertiary giant lacewings (Neuroptera: Polystoechotidae) revision and description of new taxa from western North America and Denmark: *Journal of Systematic Paleontology*, v. 4, p. 119–155.
- Archibald, S.B., and Mathewes, R.W., 2000, Early Eocene insects from Quilchena, British Columbia and their paleoclimatic implications: *Canadian Journal of Zoology*, v. 78, p. 1441–1462.
- Archibald, S.B., Bossert, W.H., Greenwood, D.R., and Farrell, B.D., 2010, Seasonality, the latitudinal gradient of diversity, and Eocene insects: *Paleobiology*, v. 36, p. 374–398.
- Archibald, S.B., Cover, S.D. and Moreau, C.S., 2006, Bulldog Ants of the Eocene Okanagan Highlands, and the history of the subfamily (Hymenoptera: Formicidae: Myrmecinae): *Annals of the Entomological Society of America*, v. 99, 487–523.
- Archibald, S.B., Johnson, K.R., Mathewes, R.W., and Greenwood, D.R., 2011, Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals: *Proceedings of the Royal Society B, Biological Sciences*, v. 278, p. 3679–3686, doi: 10.1098/rspb.2011.0729.
- Archibald, S.B., Pigg, K.B., Greenwood, D.R., Manchester, S.R., Barksdale, L.L., Johnson, K.R., Sternberg, M.E.,



- Stockey, R.A., DeVore, M.L., and Rothwell, G.W., 2005a, Wes Wehr dedication: Canadian Journal of Earth Sciences, v. 42, p. 115-117.
- Archibald, S.B., Rasnitsyn, A.P., and Akhmetiev, M.A., 2005b, The ecology and distribution of Cenozoic Eomeropidae (Mecoptera), and a new species of *Eomerope* Cockerell from the Early Eocene McAbee locality, British Columbia, Canada: Annals of the Entomological Society of America, v. 98, 503-514.
- Barton, D.G., and Wilson, M.V.H., 2005, Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10 000 years of environmental change: Canadian Journal of Earth Sciences, v. 42, p. 137-149.
- Basinger, J.F., 1976, *Paleorosa similkameensis*, gen. et sp. nov., permineralized flowers (Rosaceae) from the Eocene of British Columbia: Canadian Journal of Botany, v. 54, p. 2293-2305.
- Basinger, J.F., 1984, Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia: Canadian Journal of Botany, v. 62, p. 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, v. 55, p. 1984-1990.
- Basinger, J.F., McIver, E., and Wehr, W.C., 1996, Eocene conifers of the Interior, in Ludvigsen, R., (ed.) Life in Stone: A Natural History of British Columbia's Fossils: University of British Columbia Press, p. 248-258.
- Berry, E.W., 1926, Tertiary floras from British Columbia: Geological Survey of Canada, Bulletin 42, p. 91-116.
- Berry, E.W., 1929, A revision of the flora of the Latah Formation: United States Geological Survey Bulletin, No. 1597, p. 225-265.
- Brown, R.W., 1935, Miocene leaves, fruits, and seeds from Idaho, Oregon, and Washington: Journal of Paleontology, v. 9, p. 572-587.
- Brown, R.W., 1937, Additions to some fossil floras of the western United States: United States Geological Survey Professional Paper, v. 186-J, p. 163-187.
- Brown, R.W., 1939, Fossil leaves, fruits, and seeds of *Cercidiphyllum*: Journal of Paleontology, v. 13, p. 485-499.
- Brown, R.W., 1940, New species and changes of name in some American fossil floras: Journal of the Washington Academy of Science, v. 30, p. 344-356.
- Cevallos-Ferriz, S.R.S., Stockey, R.S., and Pigg, K.B., 1991, The Princeton chert: Evidence for *in situ* aquatic plants: Review of Palaeobotany and Palynology, v. 70, p. 173-185.
- Dawson, G.M., 1879, Preliminary report on the physical and geological features of the southern portion of the Interior of British Columbia: Geological Survey of Canada, Report of Progress 1877-1878, Dawson Brothers, Montreal, p. 112-133.
- Dawson, G.M., 1895, Report on the area of the Kamloops map-sheet, British Columbia: Geological Survey of Canada, Annual Report 1894, Vol. VII, p. 3B-427B.
- Dawson, G.M., 1896, Report on the Kamloops map-sheet, British Columbia (New Ser.): Geological Survey of Canada Annual Report for 1894, v. 7, p. 1-427.
- Dawson, J.W., 1879, List of Tertiary plants from localities in the southern part of British Columbia, with the description of a new species of *Equisetum*: Geological Survey of Canada, Annual Report 1877-1878, Appendix B, p. B186.
- Dawson, J.W., 1883, On the Cretaceous and Tertiary floras of British Columbia and the Northwest Territories: Proceedings and Transactions of the Royal Society of Canada, v. I (Section IV), p. 15-34.
- Dawson, J.W., 1891, On fossil plants from the Similkameen Valley and other places in the Southern Interior of British Columbia: Transactions of the Royal Society of Canada, ser. 1, 8 (1890), section 4, p. 75-91.
- DeVore, M.L., and Pigg, K.B., 2007, A brief review of the fossil history of the family Rosaceae with a focus on the Eocene Okanagan Highlands of eastern Washington State, USA, and British Columbia, Canada: Plant Systematics and Evolution, v. 266, p. 45-57.
- DeVore, M.L., and Pigg, K. B., 2010, Floristic composition and comparison of Middle Eocene to Late Eocene and Oligocene floras in North America: Bulletin of Geosciences, v. 85, p. 51-74.
- 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, v. 42, p. 205-214.
- 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, v. 42, p. 155-166.
- Engel, M.S., and Archibald, S.B., 2003, An Early Eocene bee (Hymenoptera: Halictidae) from Quilchena, British Columbia: The Canadian Entomologist, v. 135, p. 63-69.
- Erwin, D.M., and Stockey, R.A., 1991, Silicified monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia, Canada: Review of Palaeobotany and Palynology, v. 70, p. 147-162.
- Ewing, T.E., 1980, Paleogene tectonic evolution of the Pacific Northwest: Journal of Geology, v. 88, p. 619-638.
- Gazin, C.L., 1953, The Tillodontia: An early order of mammals: Smithsonian Miscellaneous Collections, v. 121, no., 10, p. 1-110.
- Gould, S.J., 1989, Wonderful Life: The Burgess Shale and the Nature of History: W.W. Norton and Co., New York, 347 p.
- Greenwood, D.R., and Wing, S.L., 1995, Eocene continental climates and latitudinal temperature gradients: Geology, v. 23, p. 1044-1048.
- Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T., 2005, Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: Climates and ecosystems across an Eocene landscape: Canadian Journal of Earth Sciences, v. 42, p. 167-185.
- Handlirsch, A., 1910, Canadian fossil insects: Geological Survey Branch, Canada Department of Mines, Contributions to Canadian Paleontology, Memoire 12-P, v. II, Part III.
- Harding, I.C., and Chant, L.S., 2000, Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant Lake Beds, Colorado, United States: Geology, v. 28, p. 195-198.
- Hills, L.V., 1965, Palynology and Age of Early Tertiary Basins, Interior British Columbia: Ph.D. thesis, University of Alberta, Edmonton, AB, 189 p.
- Hills, L.V., and Baadsgaard, H., 1967, Potassium-argon dating of some lower Tertiary strata in British Columbia: Bulletin of Canadian Petroleum Geology, v. 15, p. 138-149.
- Lewis, S.E., 1992, Insects of the Klondike Mountain Formation, Republic, Washington: Washington Geology, v. 20, p. 15-19.
- Manchester, S.R., 1999, Biogeographical relationships of North American Tertiary floras: Annals of the Missouri Botanical Garden, v. 86, p. 472-522.
- Manchester, S.R., and Dillhoff, R.M., 2004, *Fagus* (Fagaceae) fruits, foliage, and pollen from the Middle Eocene of

- Pacific Northwestern North America: Canadian Journal of Botany, v. 82, p. 1509-1517.
- Mathews, W.H., 1964, Potassium-argon age determination of Cenozoic volcanic rocks from British Columbia: Geological Society of America Bulletin, v. 75, p. 465-468.
- Meyer, H.W., 2003, The Fossils of Florissant: Smithsonian Books, Washington, 258 p.
- Miller, C.N., 1973, Silicified cones and vegetative remains of *Pinus* from the Eocene of British Columbia: Contributions from the Museum of Paleontology, The University of Michigan, v. 24, p. 101-118.
- 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, v. 42, p. 187-204.
- Mustoe, G.E., 2005, Diatomaceous origin of siliceous shale in Eocene lake beds of central British Columbia: Canadian Journal of Earth Sciences, v. 42, p. 231-241.
- Penhallow, D.P., 1908, A report on Tertiary plants of British Columbia, collected by Lawrence M. Lambe in 1906 together with a discussion of previously recorded Tertiary floras: Canada Department of Mines, Geological Survey Branch, Report 1013, p. 1-167.
- Radtke, M.G., Pigg, K.B., and Wehr, W.C., 2005, Fossil *Corylopsis* and *Fothergilla* leaves (Hamamelidaceae) from the lower Eocene flora of Republic, Washington, U.S.A., and their evolutionary and biogeographic significance: International Journal of Plant Sciences, v. 166, p. 347-356.
- Reed, K.M., (ed.), 1996, Republic Centennial Issue: Featuring articles about the geology of the Republic area, the Republic Mining District, and Eocene fossil deposits: Washington Geology, v. 24(2), 48 p.
- Rouse, G.E., and Mathews, W.H., 1961, Radioactive dating of Tertiary plant-bearing deposits: Science, v. 133, p. 1079-1080.
- Rouse, G.E., Hopkins, W.S., Jr., 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, p. 213-246.
- Royer, D.L., 2001, Stomatal density and stomatal index as indicators of paleoatmospheric CO<sub>2</sub> concentration: Review of Palaeobotany and Palynology, v. 114, p. 1-28.
- Royer, D.L., 2006, CO<sub>2</sub>-forced climate thresholds during the Phanerozoic: Geochimica et Cosmochimica Acta, v. 70, p. 5665-5675.
- Royer, D.L., Hickey, L.J., and Wing, S.L., 2003, Ecological conservatism in the 'living fossil' *Ginkgo*: Paleobiology, v. 29, p. 84-104.
- Russell, L.S., 1935, A Middle Eocene mammal from British Columbia: American Journal of Science, v. 29, p. 54-55.
- Schaal, S., and Ziegler, W., (eds.), 1992, Messel – An insight into the history of the life and of the Earth: Oxford University Press (Clarendon Press), 328 p.
- Scudder, S.H., 1877, The insects of the Tertiary beds at Quesnel (British Columbia): Report of progress of the Geological Survey of Canada 1875-1876, p. 266-280.
- Scudder, S.H., 1878, Additions to the insect fauna of the Tertiary beds at Quesnel (British Columbia): Report of progress of the Geological Survey of Canada 1876-1877, p. 457-464.
- Scudder, S.H., 1895, Canadian fossil insects. 1. The Tertiary Hemiptera of British Columbia: Geological Survey of Canada 2, part 1, 5-26.
- Seilacher, A., 1970, Begriff und Bedeutung der Fossil-Lagerstätten: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1970, p. 34-39.
- Shellito, C.J., Lamarque, J.-F., and Sloan, L.C., 2009, Early Eocene Arctic climate sensitivity to pCO<sub>2</sub> and basin geography: Geophysical Research Letters, v. 36, L09707, p. 1-5.
- Smith, R.Y., 2011, The Eocene Falkland fossil flora, Okanagan Highlands, British Columbia: Paleoclimate and plant community dynamics during the Early Eocene Climatic Optimum: Ph.D. thesis, University of Saskatchewan, Saskatoon, SK. 303 p.
- Smith, R.Y., Basinger, J.F., and Greenwood, D.R., 2009, Depositional setting, fossil flora and paleoenvironment of the Early Eocene Falkland site, Okanagan Highlands, British Columbia: Canadian Journal of Earth Sciences, v. 46, p. 811-822.
- Smith, R.Y., Basinger, J.F., and Greenwood, D.R., 2011, Early Eocene plant diversity and dynamics in the Falkland flora, Okanagan Highlands, British Columbia, Canada: Palaeobiodiversity and Palaeoenvironments, DOI: 10.1007/s12549-011-0061-5.
- Smith, R.Y., Greenwood, D.R., and Basinger, J.F., 2010, Estimating paleoatmospheric pCO<sub>2</sub> during the Early Eocene Climatic Optimum from stomatal frequency of *Ginkgo*, Okanagan Highlands, British Columbia, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 293, p. 120-131.
- Smith, S.Y., and Stockey, R.A., 2007, Establishing a fossil record for the perianthless Piperales: *Saururus tuckerae* sp. nov. (Saururaceae) from the Middle Eocene Princeton Chert: American Journal of Botany, v. 94, p. 1642-1657.
- Stockey, R.A., and Wehr, W.C., 1996, Flowering plants in and around Eocene lakes of the Interior, in Ludvigsen, R., ed., Life in Stone: A Natural History of British Columbia's Fossils: University of British Columbia Press, p. 234-247.
- Stockey, R.A., Nishida, H., and Rothwell, G.W., 1999, Permineralized ferns from the middle Eocene Princeton chert. I. *Makotopteris princetonensis* gen. et sp. nov. (Athyriaceae): International Journal of Plant Science, v. 160, p. 1047-1055.
- Verschoor, K. van R., 1974, Paleobotany of the Tertiary (early Middle Eocene) McAbee Beds, British Columbia: M.Sc. thesis, University of Calgary, Calgary, AB, 128 p.
- Villeneuve, M., and Mathewes, R., 2005, An Early Eocene age for the Quilchena fossil locality, southern British Columbia: Geological Survey of Canada, Current Research 2005-A4, 7 p.
- Wehr, W.C., and Hopkins, D.Q., 1994, Eocene orchards and gardens of Republic, Washington: Washington Geology, v. 22, p. 27-34.
- Wehr, W.C., and Schorn, H.E., 1992, Current research on Eocene conifers at Republic, Washington: Washington Geology, v. 20, p. 20-23.
- Wilf, P., Johnson, K.R., Cúneo, N.R., Smith, M.E., Singer, B.S., and Gandolfo, M.A., 2005, Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina: The American Naturalist, v. 165, p. 634-650.
- Wilson, M.V.H., 1977a, Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia: Canadian Journal of Earth Sciences, v. 14, p. 953-962.
- Wilson, M.V.H., 1977b, New records of insect families from the freshwater Middle Eocene of British Columbia: Canadian Journal of Earth Sciences, v. 14, p. 1139-1155.
- Wilson, M.V.H., 1978, *Eobiodon woodruffi* n. sp. (Teleostei, Hiodontidae), from the Middle Eocene Klondike Mountain Formation near Republic, Washington: Canadian Journal of Earth Sciences, v. 15, p. 679-686.
- Wilson, M.V.H., 1980, Eocene lake environments: depth and distance from



shore variation in fish, insect, and plant assemblages: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 32, p. 21-44.

Wilson, M.V.H., 1996a, Fishes from Eocene lakes of the Interior, *in* Ludvigsen, R., *ed.*, *Life in Stone: A Natural History of British Columbia's Fossils*: University of British Columbia Press, p. 212-224.

Wilson, M.V.H., 1996b, Insects near Eocene Lakes of the Interior, *in* Ludvigsen, R., *ed.*, *Life in Stone: A Natural History of British Columbia's Fossils*: University of British Columbia Press, p. 225-233.

Wilson, M.V.H., and Li, G.-Q., 1999, Osteology and systematic position of the Eocene salmonid *Eosalmo driftwoodensis* western North America: *Zoological Journal of the Linnean Society*, v. 125, 279-311.

Wing, S.L., and Greenwood, D.R., 1993, Fossils and fossil climate: the case for equable continental interiors in the Eocene: *Philosophical Transactions of the Royal Society of London B*, v. 341, p. 243-252.

Wolfe, J.A., 1987, Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous Event: *Paleobiology*, v. 13, p. 215-226.

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

Wolfe, J.A., and Wehr, W.C., 1987, Middle Eocene dicotyledonous plants from Republic, Northeastern Washington: *United States Geological Survey, Bulletin* 1597, 25 p.

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*, v. 110, p. 664-678.

Woodward, F.I., 1987, Stomatal numbers are sensitive to increases in CO<sub>2</sub> from pre-industrial levels: *Nature*, v. 327, p. 617-618.

Zachos, J.C., Dickens, G.R., and Zeebe, R.E., 2008, An early Cenozoic perspective on greenhouse warming and carbon cycle dynamics: *Nature*, v. 451, p. 279-283.

---

## CORPORATE MEMBERS

### PATRONS

Alberta Geological Survey  
Anglo American Exploration Canada  
Memorial University of Newfoundland  
Ministère de Ressources naturelles et de la Faune  
Natural Resources - Government of Newfoundland and Labrador  
Northwest Territories Geoscience Office  
Yukon Dept. of Energy Mines & Resources

### SPONSORS

Northern Geological Survey  
Royal Tyrrell Museum of Palaeontology

### SUPPORTERS

Activation Laboratories Ltd.  
Barrick Gold Corp.  
Franklin Geosciences Limited  
IBK Capital Corp.  
Johnson GEO CENTRE  
Silver Spruce Resources Inc.  
SRK Consulting  
Vale

### UNIVERSITIES

Acadia University  
CASP, University of Cambridge  
Institut national de la recherche scientifique (INRS)  
McGill University  
Utah State University  
University of Calgary  
University of New Brunswick  
University of Toronto  
University of Waterloo  
Université du Québec à Montréal  
Université Genève

---

Received May 2011

Accepted as revised October 2011