Modernisation of the Hymenoptera: ants, bees, wasps, and sawflies of the early Eocene Okanagan Highlands of western North America

S. B. Archibald,[1] Alexandr P. Rasnitsyn, Denis J. Brothers, Rolf W. Mathewes

Abstract—Most major modern families of Hymenoptera were established in the Mesozoic, but the diversifications within ecologically key trophic guilds and lineages that significantly influence the character of modern terrestrial ecosystems – bees (Apiformes), ants (Formicidae), social Vespidae, parasitoids (Ichneumonidae), and phytophagous Tenthredinoidea – were previously known to occur mostly in the middle to late Eocene. We find these changes earlier, seen here in the early Eocene Okanagan Highlands fossil deposits of western North America. Some of these may have occurred even earlier, but have been obscured by taphonomic processes. We provide an overview of the Okanagan Highlands Hymenoptera to family level and in some cases below that, with a minimum of 25 named families and at least 30 when those tentatively assigned or distinct at family level, but not named are included. Some are poorly known as fossils (Trigonalidae, Siricidae, Peradeniidae, Monomachidae), and some represent the oldest confirmed occurrences (Trigonalidae, Pompilidae, Sphecidae *sensu stricto*, Peradeniidae, Monomachidae, and possibly Halictidae). Some taxa previously thought to be relictual or extinct by the end of the Cretaceous (Angarosphecidae, Archaeoscoliinae, some Diapriidae) are present and sometimes abundant in the early Eocene. Living relatives of some taxa are now present in different climate regimes or on different continents.

Introduction

The Hymenoptera – ants, bees, wasps, and sawflies – have been tremendously successful, increasing their taxonomic and morphological diversity, filling ecospace by assuming a wide range of trophic roles, and saturating communities with great numbers of individuals across the globe. They are one of four hyperdiverse insect orders today, along with the Diptera, Lepidoptera, and Coleoptera. Hymenoptera comprise over 153 000 named species, perhaps almost 10% of all described species of life, and if unnamed species are considered, there might be four or more times that number (Gaston 1991; Sharkey 2007; Davis *et al.* 2010; Aguiar *et al.* 2013; Klopfstein *et al.* 2013). Today they are major elements of modern terrestrial ecosystems, acting across a broad spectrum of feeding guilds as predators, parasitoids, and hyperparasitoids of other arthropods, scavengers, pollinators, and herbivores consuming plant organs both externally and internally, including pollen and nectar feeding, galling, leaf chewing and mining, and wood and stem boring. Some also tend phytophagous insects in return for fluid excretions, farm fungi for food, and engage in other symbiotic activities. In these ways, they regulate populations of plants and arthropods,

S.B. Archibald,[1] Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada; Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts, 02138, United States of America; and Royal British Columbia Museum, 675 Bellvelle Street, Victoria, British Columbia, V8W 9W2, Canada

A.P. Rasnitsyn, A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow 117647, Russia; Invertebrate Palaeontology Department, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom

D.J. Brothers, School of Life Sciences, University of KwaZulu-Natal (Pietermaritzburg), Private Bag X01, Scottsville, 3209, South Africa

R.W. Mathewes, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada

[1]Corresponding author (e-mail: sba48@sfu.ca).

© 2018 Entomological Society of Canada

affecting their community interactions, reproduction, diversities, and distributions.

Most major modern hymenopteran trophic guilds and lineages to the family level were established in the Mesozoic, but expansion of ecologically key groups below this level – notably of social Hymenoptera (ants, some bees, and some Vespidae), parasitoids (Ichneumonidae), and phytophagous Tenthredinoidea – is first seen in the Eocene, showing the onset of their rise to become the major elements of terrestrial ecosystems that they are today.

Hymenoptera were amongst the first Ypresian (early Eocene) Okanagan Highlands insects collected by Geological Survey of Canada geologists George Mercer Dawson in 1877 (Dawson 1879) and Lawrence Lambe in 1906 (Handlirsch 1910) in the decades immediately after British Columbia entered Confederation in 1867. The specimens were sent to Samuel Scudder in Cambridge, Massachusetts, United States of America (*e.g.*, Scudder 1877, 1878, 1879, 1890) and Anton Handlirsch in Vienna, Austria (Handlirsch 1910). Much of the interior of British Columbia, however, remained remote and difficult to reach due to rough terrain and dense forests until well into the 20th century, and research on its fossil Hymenoptera after this initial interest was sporadic (*e.g.*, Rice 1968), lagging behind work on European Eocene deposits such as Baltic amber and those in the mid-continental United States of America that were easily accessed by railway, such as the Green River (Grande 1984) and Florissant (Meyer 2003) Formations. The known Okanagan Highlands Hymenoptera were summarised by Cameron (1917) as four species of Ichneumonidae, two of Braconidae, and three of Formicidae. Very little was written about them for the next 60 years, and they only began to receive intensive attention in the final decades of the century, primarily sparked by the works of Wilson (1977a, 1978a, 1978b, 1982), followed by Douglas and Stockey (1996), and in the first reports of insects from the rich deposits at the southernmost Okanagan Highlands locality in Republic, Washington, United States of America by Lewis (1992), Wehr and Barksdale (1996), and Wehr (1998). While some works treated Hymenoptera among insects in general (*e.g.*, above references, and Archibald and Mathewes 2000), relatively a few focussed on them until recently (Rice 1968; Dlussky and Rasnitsyn 1999, 2003;

Pulawski *et al.* 2000; Engel and Archibald 2003; Archibald *et al.* 2006; Archibald and Rasnitsyn 2015), and knowledge of the order in the Okanagan Highlands has not kept pace with the potential provided by increasingly large collections of their fossils in recent years. Here, we provide an overview of the rich, but understudied, Ypresian fossil Hymenoptera assemblage of the Okanagan Highlands of British Columbia, Canada and Washington, United States of America (Archibald *et al.* 2010, 2011a), in light of recent collecting, and evaluate its signficance in the modernisation of the order.

Materials and methods

The fossiliferous lacustrine shales of the Okanagan Highlands often consist of fine, easily splitting laminae, which have been found, in cases where tested, usually to consist of sapropel and siliceous laminae of diatomaceous origin (Wilson 1977b; Mustoe 2005, 2015; Wolfe and Edlund 2005). This presumably promoted fine-level preservation and increased fidelity of the fossil assemblage to the life assemblage (Archibald and Makarkin 2006, based on taphonomic processes modelled at Florissant by McLeroy and Anderson 1996; Harding and Chant 2000; O'Brien *et al.* 2002, 2008). Amber is also present at some sites such as Hat Creek, where it is usually clear to yellow, in pieces up to 3–4 cm in diameter, found *in situ* within coal beds.

The Okanagan Highlands (Fig. 1) deposits occur in former lake and swamp basins scattered from west-central British Columbia, Canada across ~1000 km to north-central Washington, United States of America (Archibald *et al.* 2011a). All major localities bear Hymenoptera fossils (Fig. 1; Table 1). These include the Klondike Mountain Formation exposures at Republic, Washington, United States of America; and in British Columbia, Canada, the Allenby Formation at Princeton, Coldwater Beds at Quilchena, unnamed formations at Falkland, McAbee (often informally called "Tranquille Shales"), Hat Creek, and Horsefly River, and in the Ootsa Lake Group shales at Driftwood Canyon Provincial Park near Smithers. The location near the town of Quesnel in the central Cariboo region of British Columbia where fossil insects were collected by G.M. Dawson in the 1870s (Scudder 1877, 1878: see Ichneumonoidea and ants, below) is currently

Fig. 1. Map of the Okanagan Highlands, British Columbia, Canada and Washington, United States of America, with localities mentioned in the text.
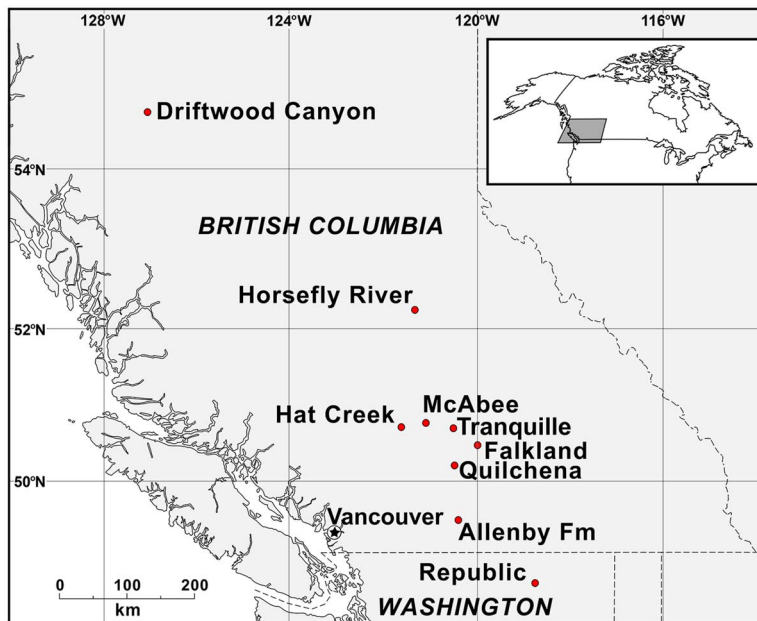
unknown, but it appears to be part of the Okanagan Highlands series. Dawson also sent Scudder insects from an exposure of the Allenby Formation on a branch of the Similkameen River that is today called the Tulameen. The Tranquille locality (see Handlirsch's species of Ichneumonidae, below) is on the north shore of Kamloops Lake between Kamloops and McAbee.

While some genera and species described by Scudder (1877, 1878, 1879) and Handlirsch (1910) over a century ago are in need of revision, we mostly agree with their determinations of Hymenoptera fossils to the family level (see below). The Okanagan Highlands insect taxon lists of Wehr and Barksdale (1996) and Wehr (1998) do not associate specimens with taxa; therefore, as the identities of individual specimens are revised, the status of some listed families has become unclear. As we examined all specimens that we presume they based their lists on, the Hymenoptera portions of those are superseded here. For some families where large numbers of specimens are known, we list exemplars, as noted.

Specimens were borrowed from institutional collections or collected by Archibald and Mathewes, and a few were evaluated from published illustrations as indicated. Our goal here is to provide a family-level overview, with determinations below this in some cases. Several higher groups, including "Symphyta", "Parasitica", and "Spheciformes" are generally recognised as paraphyletic and are thus informal, but nevertheless useful in discussion. We will not burden the text by indicating them between quotation marks hereafter. Recent molecular analyses further suggest that groups such as Vespoidea, Crabronidae, and Tenthredinidae might also be paraphyletic (Pilgrim *et al*. 2008; Song *et al*. 2016 and references therein; Branstetter *et al*. 2017; Peters *et al*. 2017); we prefer to take a conservative position until consensus is achieved, and so we generally follow the systematic arrangement of Aguiar *et al*. (2013) without further comment, except that we recognise Scelionidae as a distinct family (see discussion of McKellar and Engel 2012) and do not recognise Aulacidae, which appears insufficiently distinguishable from the Gasteruptiidae in the Mesozoic (Townes 1950). Furthermore, these molecular studies include dated phylogenies that differ in their estimated times of origin of various groups, and we will not attempt to comment on these, but rather refer to actual fossil occurrences for dating.

Table 1. Distribution of Okanagan Highlands Hymenoptera families.

		R	A	Q	F	M	Hc	Hf	D
Symphyta									
Megalodontoidea	Pamphiliidae	X							
Cephoidea	Cephidae					X		X	
Siricoidea	Siricidae	X				X			
Tenthredinoidea	Tenthredinidae	X	RI	X		X		X	X
	Cimbicidae	X	X			X			
Apocrita									
Ceraphronoidea	Megaspilidae						X		
Trigonalyoidea	Trigonalyidae			X	X				
Ichneumonoidea	Ichneumonidae	X	DS?	X		X		X	X
	Braconidae	X	X	X		X		X	X
Mymarommatoidea	*Incertae sedis*						X		
Proctotrupoidea	Diapriidae	X				X		X	X
	Proctotrupidae	X				X		X	X
	Heloridae					X			
	Peradeniidae					X			
	Roproniidae	X							
	Near Roprioniidae					X			
Cynipoidea	Cynipidae (?)			DS?				DS?	
	Figitidae					X			
Chalcidoidea	*Incertae sedis*					X	X		X
Chrysidoidea	Chrysididae					X			
Vespoidea	Pompilidae	X				DS			
	Scoliidae	X	X						
	Vespidae	X	X	X		X			X
	Formicidae	X	X	X	X	X	X	X	X
Spheciformes	Angarosphecidae	X	X	X		X			X
	Sphecidae (*sensu stricto*)	X				X			X
Apiformes	Apidae					X			
	Halictidae (?)	X		X		X			
	Megachilidae	X				L		X	
	Incertae sedis	X				X			X

Notes: X, new records, new specimens, and previously reported with specimens examined by us (see text). Previously reported only, specimens not seen by us, but confirmed by photographs and/or drawings: RI, Rice (1968); L, Labandeira (2002); DS, Douglas and Stockey (1996) and DS?, questionable records in that work (Cynipidae) or occurrence based on specimens that were not illustrated nor seen by us (Allenby Ichneumonidae).

R, Republic and surrounding localities of the Klondike Mountain Formation; A, Allenby Formation, Princeton and surrounding localities; Q, Quilchena; F, Falkland; M, McAbee; Hc, Hat Creek amber; Hf, Horsefly; D, Driftwood Canyon.

Institutional abbreviations for particular specimens examined or cited are: CDM, the Courtenay and District Museum and Archives, Courtenay, British Columbia, Canada; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; GSC, Geological Survey of Canada, Ottawa, Ontario, Canada; DMNH, the Denver Museum of Nature and Science, Denver, Colorado, United States of America; KM, Kelowna Museums, Kelowna, British Columbia, Canada; RBCM, Royal British Columbia Museum, Victoria, British Columbia, Canada; PMF, the Princeton and District Museum and Archives, Princeton, British Columbia, Canada; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; SFU, Simon Fraser University, Burnaby, British Columbia, Canada; SR, SRUI, the Stonerose Interpretive Center, Republic, Washington, United States of America; TRU, Thompson Rivers University, Kamloops, British Columbia, Canada; UAPAL, University of Alberta, Edmonton, Alberta, Canada; UWBM, University of Washington,

Burke Museum, Seattle, Washington, United States of America. Type and other specimens referred to with these prefixes to their catalogue numbers are housed in these institutions. "SBA-" numbers were collected by Archibald and are housed at Simon Fraser University; "SBA-" specimens from the Driftwood Canyon locality in Driftwood Canyon Provincial Park are the property of BC Parks (British Columbia Ministry of Environment), and are also housed at Simon Fraser University until BC Parks establishes a permanent repository. Many shale specimens include both the "part" and "counterpart", *i.e.*, both sides of a split piece of shale with a fossil on one side and its mirror image on the other. The part is designated the "a" side and the counterpart the "b" side where this is specified on accession numbers, and this appears where relevant in the text.

Ages, names, and spellings of Cretaceous amber deposits follow Rasnitsyn *et al*. (2016). We follow Smith *et al*. (2003, 2004) in considering the Green River Formation insects as deposited at sites ranging through the second half of the Ypresian, *i.e.*, contemporaneous with those of the Okanagan Highlands; Lenz *et al*. (2015) in considering the lacustrine shale at Messel, Germany, to be latest Ypresian into the Lutetian; Kodrul (1999) in considering Sakhalin amber to be Lutetian (early middle Eocene); Dilcher (1973) and Dockery (1996) in considering the Cockfield Formation (formerly clays of the Wilcox Formation) to be Bartonian (late middle Eocene); and Perkovsky *et al*. (2007) in considering Baltic amber as Priabonian (late Eocene).

Family Pamphiliidae (Symphyta: Pamphilioidea)

Figure 2C.

Specimens. Republic: UWBM 77532, holotype, *Ulteramus republicensis* Archibald and Rasnitsyn.

Remarks. Today the Pamphiliidae has 291 described species in the subfamilies Pamphiliinae, Cephalciinae, and Juralydinae, distributed in temperate and boreal Eurasia and North America (Taeger *et al*. 2010; Aguiar *et al*. 2013). Their larvae spin silk, living either singly or in groups, and feed on foliage of the Pinaceae (Cephalciinae) or on angiosperm leaves, which they roll (Pamphiliinae) (Goulet 1993). Their fossil record extends to the late

Jurassic with the subfamily Juralydinae, previously thought to be extinct, but which was recently expanded to include an extant genus (Wang *et al*. 2014b, 2016). *Ulteramus republicensis* appears to belong to one of the two other subfamilies, previously unknown before the early Oligocene (summary: Archibald and Rasnitsyn 2015).

Family Cephidae (Symphyta: Cephoidea)

Figure 2B.

Specimens. Horsefly River: Cephinae species A (Archibald and Rasnitsyn 2015): RBCM.EH2015. 005.0001.001 and RBCM.EH2015.005.0001.002; McAbee: *Cuspilongus cachecreekensis* Archibald and Rasnitsyn, holotype (Cuspilonginae): TRU F-1545 (part) and TRU F-1546 (counterpart).

Remarks. The family has 160 described modern species (Aguiar *et al*. 2013), almost all of which are members of the Cephinae. They are predominantly temperate/boreal Holarctic, with a few species ranging into lower latitudes (summary: Archibald and Rasnitsyn 2015). Their larvae mostly feed inside grass stems or within the twigs of woody plants (Goulet 1993). The fossil record of the Cephidae is sparse: outside of the Okanagan Highlands, there are three species of unassigned subfamily affinity from the early Cretaceous of Asia (one at Baissa and two from Obeschchayushchiy), one from Mongolia (Bon-Tsagaan) belonging to the Cuspilonginae along with the McAbee species (Kopylov and Rasnitsyn 2016), and two more in the Priabonian (one each in Florissant shale and Baltic amber), both belonging to the Cephinae; the two species described by Heer (1847) in the Miocene of Oeningin, Germany are ants (Formicidae) (Archibald and Rasnitsyn 2015).

Family Siricidae (Symphyta: Siricoidea)

Figure 2A.

Specimens. McAbee: RBCM.EH2015.004. 0001.001A&B, holotype, *Ypresiosirex orthosemos* Archibald and Rasnitsyn, in subfamily Siricinae (as defined therein). Republic: SRUI 99-97-08.1.

Remarks. Siricidae has 111 described modern species (Aguiar *et al*. 2013). They are primarily

Fig. 2. Symphyta: Siricidae (**A**), Cephidae (**B**), Pamphiliidae (**C**), Cimbicidae (**D–M**). **A,** RBCM. EH2015.004.0001.001A, holotype of *Ypresiosirex orthosemos* Archibald and Rasnitsyn, McAbee. **B,** TRU F-1545, holotype of *Cuspilongus cachecreekensis* Archibald and Rasnitsyn, McAbee. **C,** UWBM 77532, holotype forewing of *Ulteramus republicensis* Archibald and Rasnitsyn, Republic. **D,** SBA-2990, McAbee. **E,** TRU F-848, McAbee. **F,** RBCM.EH2007.002.0001, Allenby Formation. **G,** TRU F-771, McAbee. **H,** TRU F-1565b, McAbee. **I,** TRU F-1563, McAbee. **J,** TRU F-1182, McAbee. **K,** TRU F-1564a, McAbee. **L,** UWBM-54840, Republic. **M,** SR 92-18-08, Republic. **N,** SBA-2418, McAbee. **D–N,** to same scale.
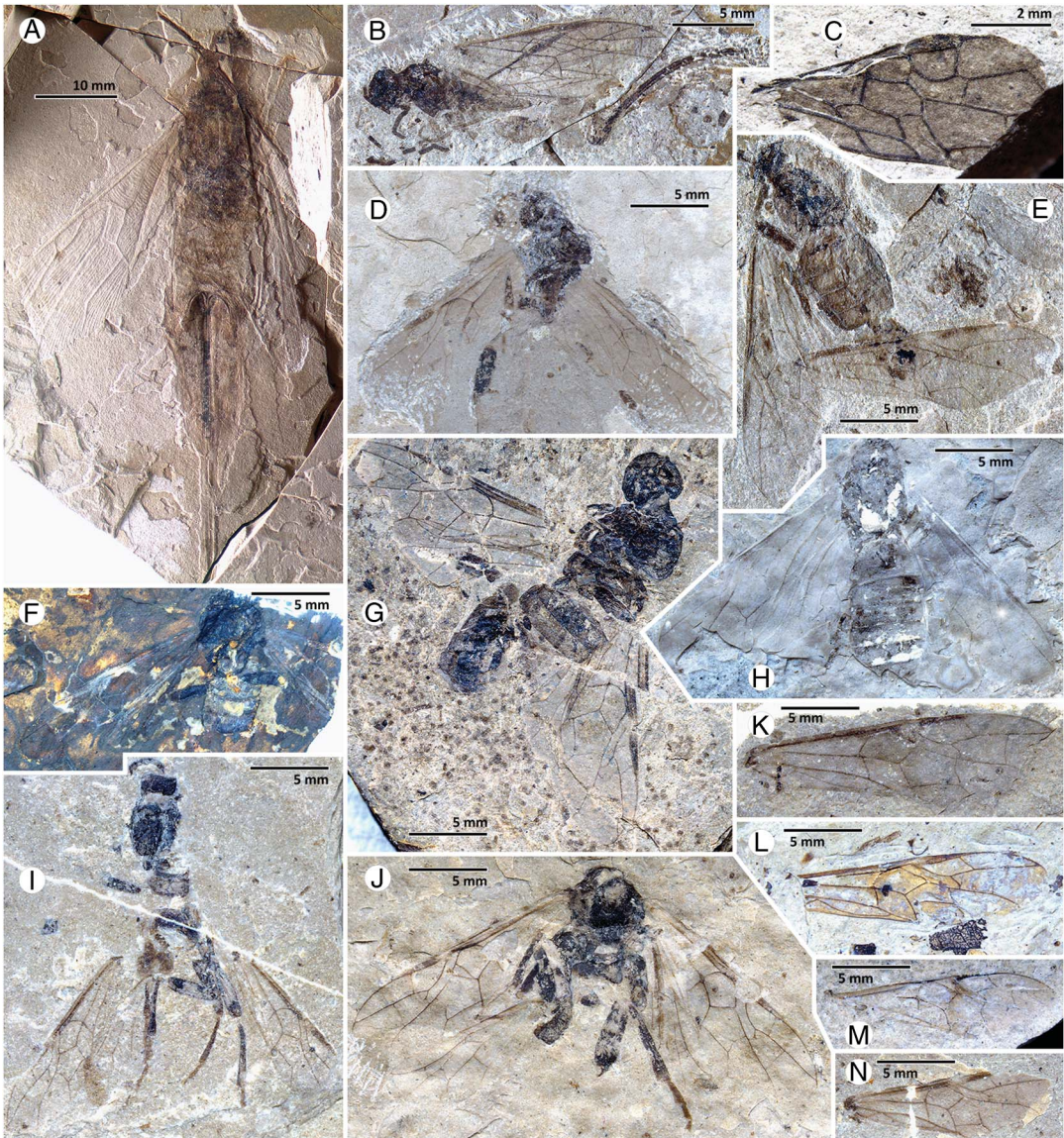
Holarctic, with a few species that are native to lower latitudes, and some introduced in the Southern Hemisphere (review: Archibald and Rasnitsyn 2015). Their larvae bore through wood feeding on fungus, which they grow in galleries, killing the tree (Schiff *et al.* 2012). A group of siricids (*sensu lato*) assigned to currently loosely defined extinct subfamilies or to none, extend from the Pliensbachian (early Jurassic) (Rasnitsyn 1968) to the Albian (latest early Cretaceous)

(Gromov *et al*. 1993). Siricidae *sensu stricto* (= Siricinae, *sensu* Rasnitsyn 1968, *i.e*., which includes those currently assigned to the Tremicidae: see also Wedmann 1998; Wedmann *et al*. 2014; Archibald and Rasnitsyn 2015) has a modest fossil record beginning in the Albian.

Family Tenthredinidae (Symphyta: Tenthredinoidea)

Figure 3.

Specimens. Driftwood Canyon: SBA-3155, SBA-5134. Horsefly: SBA-5151, SBA-5421, SBA-5525, SBA-5559. McAbee, many, *e.g*., TRU F-803, TRU F-1548, TRU F-1567, TRU F-1568, TRU F-1569, TRU F-1570, TRU F-1571, TRU F-1572, TRU F-1573, TRU F-1581, SBA-2000, SBA-2374, SBA-2618, SBA-2794, UWBM 7522A, UWBM 77545, UWBM PB-4087; the following subfamilies identified at McAbee (Archibald 2007): Tenthredininae: SBA-192, SBA-227, SBA-329, SBA-375, SBA-536, SBA-2185, SBA-2497, SBA-2524, SBA-2959; Allantinae: SBA-82, SBA-244, SBA-248, SBA-2186, SBA-2388; Blennocampinae: SBA-2828; Nematinae: SBA-108, SBA-2831, SBA-1966, SBA-2559. Quilchena: SFU Q-5147.

Fig. 3. Symphyta: Tenthredinidae (**A–M, O–R**) and Tenthredinoidea *incertae sedis* **N. A,** SBA-82A, McAbee. **B,** UWBM 7522A, McAbee. **C,** UWBM 77545, McAbee. **D,** TRU F-1581A, McAbee. **E,** TRU F-1548, McAbee. **F,** TRU F-1569, McAbee. **G,** TRU F-1567, McAbee. **H,** SBA-192, McAbee. **I,** TRU F-803, McAbee. **J,** TRU F-1568, McAbee. **K,** SBA-227A, McAbee. **L,** SBA-248B, McAbee. **M,** TRU F-1573a, McAbee. **N,** PMF.2016.0824.002, Allenby Formation. **O,** SRUI 99-90-50, Republic. **P,** SBA-5421, Horsefly River. **Q,** SBA-5151, Horsefly River. **R,** SFU Q-5147A, Quilchena. All to same scale, except for **N**.
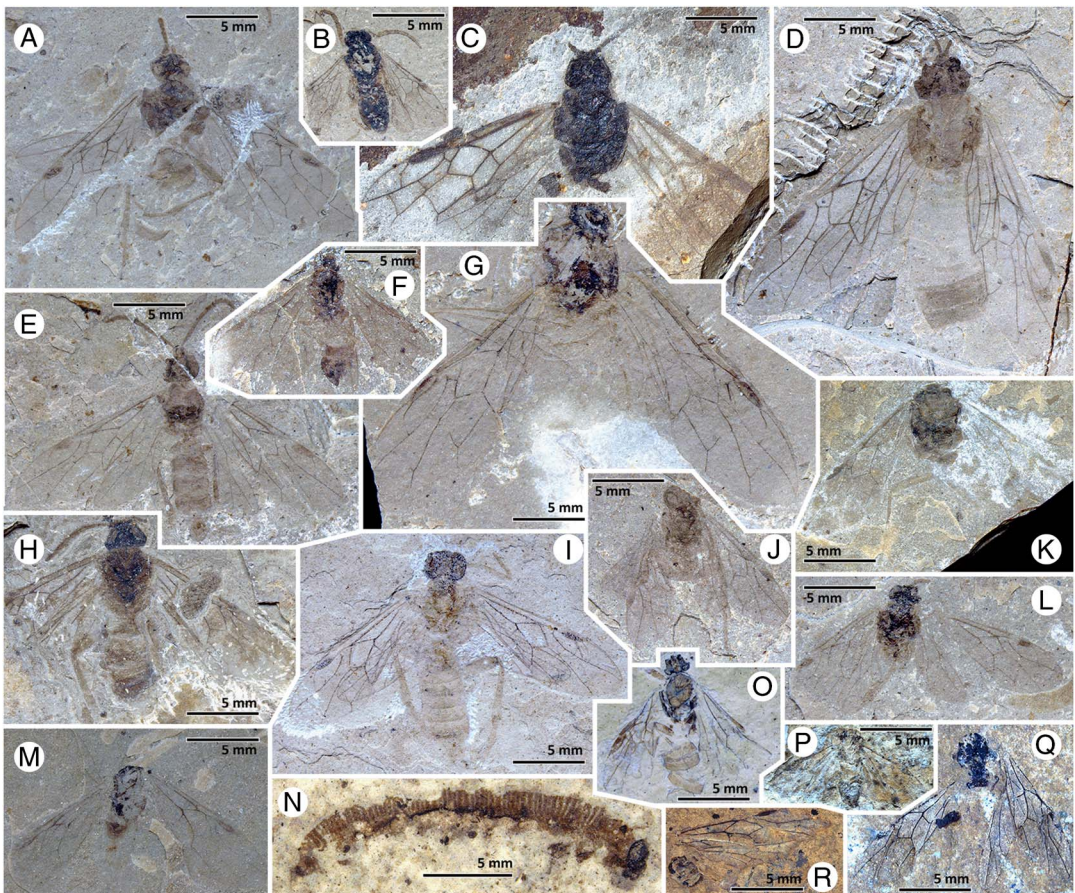
Republic: SRUI 99-90-50, SR 05-03-02, SR 99-90-80.2.

Previous records. Allenby Formation: GSC 22688 *Eriocampa tulemeenensis* Rice (Allantinae). Horsefly River: GSC 22689 *Pseudosiobla campbelli* Rice (Allantinae), both described by Rice (1968). Douglas and Stockey (1996) reported specimens UAPAL 4500, 4548, and 4545 from Horsefly River as tenthredinids; however, we agree with Nel (2004) that these are too poorly preserved to confidently assign to a family.

Remarks. The Tenthredinidae is today the largest family of phytophagous Hymenoptera, with 5500 described species that primarily inhabit Holarctic regions as far north as plant growth, although a small number is found in the Southern Hemisphere (Goulet 1993; Smith 2003; Aguiar *et al.* 2013). They mostly feed externally on leaves, but some are stem or twig borers, or leaf miners. *Palaeathalia layangensis* Zhang from the Laiyang Formation (roughly correlated with the Barremian-Aptian Yixian Fm) in northeast China (Zhang 1985) confidently belongs to the family, and there are undescribed undoubted tenthredinid species from the Aptian of Mongolia and the Ola Formation of northeast Russia, dated Santonian or possibly early Campanian (A.P.R., personal observation) (see further discussion, below). They are described from the Paleocene of Menat, and then found in various Okanagan Highlands localities (above) and in the Priabonian at Florissant and in Baltic amber and younger deposits (reviewed by Vilhelmsen and Engel 2012).

Family Cimbicidae (Symphyta: Tenthredinoidea)

Figure 2D–N.

Specimens. McAbee: TRU F-771, TRU F-848, TRU F-1182, TRU F-1563, TRU F-1564, TRU F-1565, TRU F-1566, SBA-530, SBA-2990; Cimbicinae: SBA-1975, SBA-1139; Coryninae or Pachylostictinae: SBA-2418 (subfamilies as in Archibald 2007). Allenby: RBCM.EH2007.002.0001. Republic: SR 92-18-08, UWBM-54840.

Remarks. Cimbicids range through much of the Holarctic, in the Western Hemisphere as far south as the United States of America, except for a subfamily native to Brazil, Argentina, and

Paraguay (Smith 1988). They comprise 182 described modern species of sometimes-large sawflies, whose larvae feed on the leaves of a variety of dicot angiosperms (Goulet 1993; Taeger *et al.* 2010; Aguiar *et al.* 2013). Their earliest recorded occurrence is *Cenocimbex menatensis* Nel from the Paleocene of Menat, France (Nel 2004). *Eopachylosticta byrami* Cockerell from the Green River Formation is roughly contemporaneous with the Okanagan Highlands, and all other published occurrences are younger, in the Priabonian of Florissant and a variety of Miocene localities (Taeger *et al.* 2010).

Family *incertae sedis* (Symphyta: Tenthredinoidea)

Figure 2N.

Specimen. Allenby: PMF.2016.0824.002
Remarks. This caterpillar belongs to the Tenthredinidae, Cimbicidae, or Diprionidae, based on the numerous (six or seven) annulets per segment (other larval Symphyta have at most four annulets), but cannot be assigned to any of these on the characters preserved.

## Family Megaspilidae (Apocrita: Parasitica: Ceraphronoidea)

Figure 4B.

Specimens. Hat Creek amber. SBA-HC-9.
Remarks. The Megaspilidae has 299 described modern species (Aguiar *et al.* 2013). They are small, cosmopolitan parasitoids and hyperparasitoids whose hosts are little known, although some are reported to attack Coccoidea, Neuroptera, Diptera, or Boreidae (Mecoptera), and some are hyperparasitoids of aphids through braconid wasps (Masner 1993a). Megaspilids are rare as fossils before Okanagan Highlands time: undescribed species recorded in Burmese and Vendean Cretaceous amber (compiled by Rasnitsyn *et al.* 2016, supplementary information table 1), two described species in Santonian Taimyr amber (one specimen each) and one in Campanian Canadian amber (two specimens); after Okanagan Highlands time they become more numerous, with eight species from Priabonian Baltic amber and two from Burdigalian shale

Fig. 4. Parasitica: Trigonalidae (**A, C**), Megaspilidae (**B**), Diapriidae (**D–K**). **A,** SFU Q-5086, Quilchena. **B,** SBA-HC-9, Hat Creek amber. **C,** SBA-2993, Falkland. **D,** SBA-3124, Driftwood Canyon. **E,** SBA-3478, Driftwood Canyon. **F,** SBA-4814, Driftwood Canyon. **G,** SBA-5723, Driftwood Canyon. **H,** SBA-5718, Driftwood Canyon. **I,** SBA-3697, Driftwood Canyon. **J,** SBA-228, McAbee. **K,** SRUI 99-97-09, Republic. Scales differ, except **D–K** to same scale.
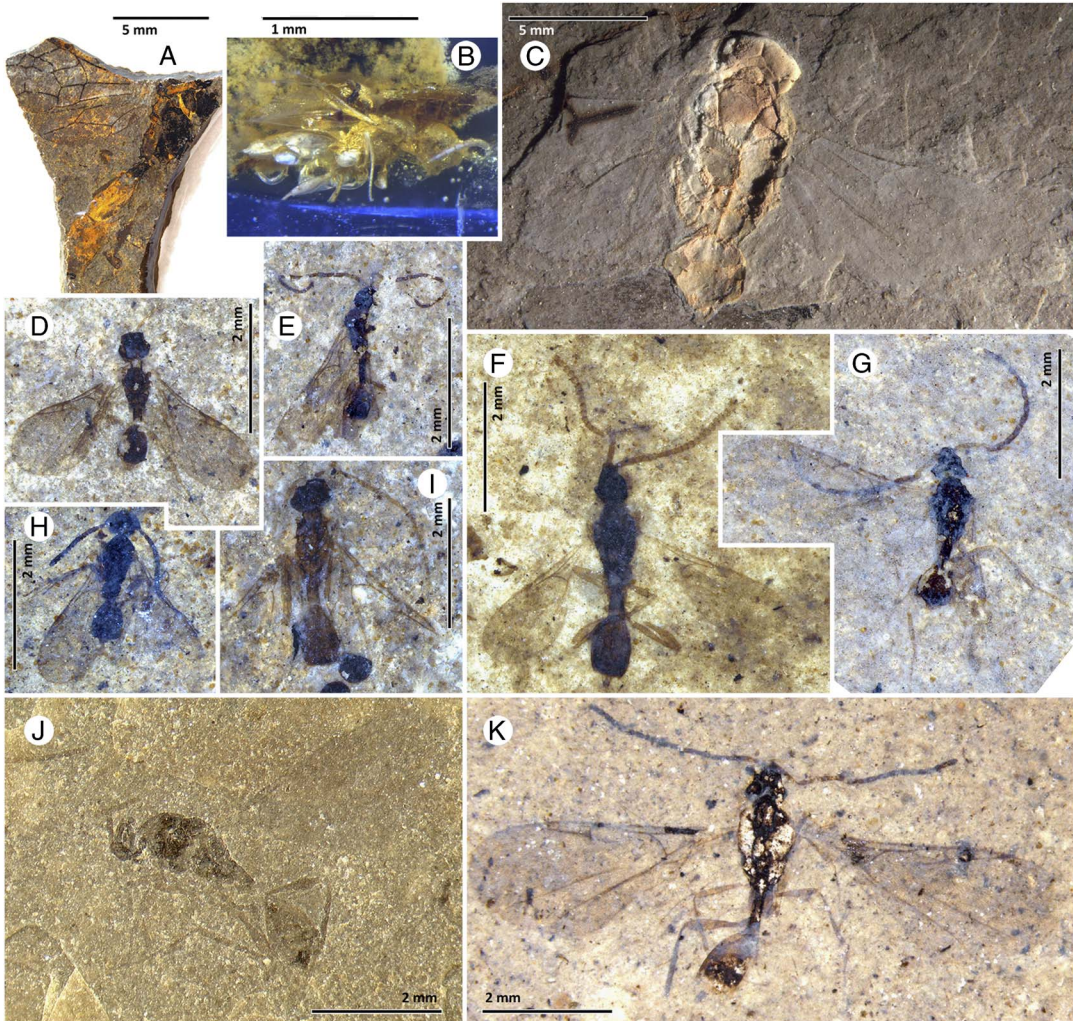
of Spain (reviewed by McKellar and Engel 2011, 2012).

Family Trigonalidae (Apocrita: Parasitica: Trigonaloidea)

Figure 4A, C.

Specimens. Falkland: SBA-2993. Quilchena: SFU Q-5086

Remarks. The Trigonalidae is a small group of 92 rare modern species (Aguiar *et al*. 2013). They are cosmopolitan, but predominantly tropical and subtropical, inhabiting a range of environments, but mostly montane forests (Carmean 1991; Weinstein and Austin 1991; Carmean and Kimsey 1998). They may have complex life histories that include sequential hosts: symphytan or lepidopteran caterpillars consume their tiny eggs deposited on leaves, and they then become hyperparasitoids within their conspecifics or other parasitoids (*e.g.*, Ichneumonidae or Tachinidae (Diptera)). They may even change hosts again to a

predatory wasp that consumes the caterpillar + parasitoids (or + hyperparasitoids); the final instar feeds externally (Weinstein and Austin 1991). These records are the oldest confident fossils of the family, as all currently reported fossils need confirmation (Cretaceous and Paleogene: *e.g.*, Nel *et al.* 2003; Poinar 2005), except *Trigonalys bischoffi* Statz from the Aquitanian of Rott, which undoubtedly belongs to it. The majority of Cretaceous records compiled by Rasnitsyn *et al.* (2016, supplementary information table 1), actually refer to the misinterpreted extinct family Maimetshidae, except for *Albiogonalys* Nel *et al.*, which most probably belongs to another extinct family, the Praeaulacidae (A.P.R., personal observation).

Family Ichneumonidae (Apocrita: Parasitica: Ichneumonoidea)

Figure 5.

Specimens. Driftwood Canyon: SBA-3719, SBA-3920, SBA-4367, SBA-4425, SBA-4469, SBA-4474, SBA-4484, SBA-4505, SBA-4540, SBA-4665, SBA-4857, SBA-5013, SBA-5025, SBA-5079, SBA-5248, SBA-5249, SBA-5255, SBA-5269, SBA-5303, SBA-5719, SBA-5724. Horsefly River: SBA-5845. McAbee: SBA-250, SBA-254, SBA-387, SBA-388, SBA-389, SBA-470, SBA-632, SBA-652, SBA-1801, SBA-2272, SBA-2560, SBA-3002, TRU F-1575. Quilchena: SFU Q-0018, SFU Q-5252. Allenby: PMF.2017.0134.001. Republic: UWBM-77457, SRUI 99-85-75, SR 01-08-18, SR 05-11-18, SR 06-01-29, SR 06-08-06, SR 06-62-08, SR 09-18-03, SR 09-18-05, SR 87-61-10.

Previous records. Samuel Scudder (1877) described *Pimpla saxea* Scudder, *P. decessa* Scudder, and *P. senecta* Scudder from the shales at Quesnel, and Handlirsch (1910) described *Xylonomus lambei* Handlirsch from the Tranquille River. Wings of the following were figured by Archibald (2007), all from McAbee: SBA-110, SBA-138, SBA-140, SBA-146, SBA-349, SBA-378, SBA-394, SBA-412, SBA-563, SBA-605, SBA-638, SBA-668, SBA-684, SBA-767, SBA-1927, SBA-1988, SBA-2023, SBA-2096, SBA-2097, SBA-2106, SBA-2107, SBA-2109, SBA-2110, SBA-2155, SBA-2156, SBA-2200, SBA-2214, SBA-2258, SBA-2263, SBA-2416,

SBA-2417, SBA-2428, SBA-2433, SBA-2444, SBA-2499, SBA-2551, SBA-2558, SBA-2710, SBA-2783, SBA-2820, SBA-2839, SBA-2848, SBA-2859, SBA-2953, SBA-2975, SBA-3001. Douglas and Stockey (1996) report UAPAL 4599 and UWBM 57112 as ichneumonids from the Allenby Formation, but they are not illustrated and we have not seen them.

Remarks. There are 24 025 described modern species of Ichneumonidae (Aguiar *et al.* 2013), distributed across the globe. Although there is debate whether their species richness lies in mid-latitudes (Janzen 1981; Quicke 2012; Veijalainen *et al.* 2012), there is some evidence supporting this notion (see Discussion section). They are parasitoids and hyperparasitoids, overwhelmingly of the larvae or pupae of holometabolous insects (most commonly Symphyta and Lepidoptera) and in some cases of the adults or eggs of Chelicerata, either internally or externally (Gauld 1988). They may feed upon immobilised, paralysed prey (idiobionts) or allow their host to remain active (koinobionts), in close synchrony with them, often exerting control over their development. As endoparasites they employ sophisticated chemical control of their hosts' immune response. They may attack prey that are exposed or concealed within plant tissue. They first appear in the early Cretaceous, but remain a small group, becoming diverse and numerous only in the Eocene (see Discussion, below) (Grimaldi *et al.* 2000; Rasnitsyn 2002; Zherikhin 2002; Kopylov 2010; Kopylov *et al.* 2010; McKellar *et al.* 2013). Ichneumonids are among the most numerous insects found at McAbee after March flies (Diptera, Bibionidae, *Plecia* Wiedemann species) and Auchenorrhyncha (Hemiptera) (Archibald *et al.* 2010), and are anecdotally so throughout the Okanagan Highlands. Exemplars of their many specimens are listed here.

## Family Braconidae (Apocrita: Parasitica: Ichneumonoidea)

Figure 6.

Specimens. Driftwood Canyon: SBA-3004, SBA-3466, SBA-3567, SBA-3688, SBA-3698, SBA-3732, SBA-4477, SBA-4403, SBA-4567, SBA-4613. Horsefly River: SBA-756. McAbee: TRU F-1090, TRU F-237; Quilchena: SFU Q-5088. Republic: SR 06-59-03, SR 11-31-01.

Fig. 5. Parasitica: Ichneumonidae. **A,** TRU F-1575, McAbee. **B,** SBA-2820A, McAbee. **C,** SFU Q-0018, Quilchena. **D,** PMF.2017.0134.001, Allenby Formation. **E,** SBA-140, McAbee. **F,** SBA-5845, Horsefly River. **G,** SBA-389A, McAbee. **H,** SBA-2097B, McAbee. **I,** SFU Q-5252, Quilchena. **J,** SBA-388B, McAbee. **K,** SR 87-61-10, Republic. **L,** SBA-605, McAbee. **M–W,** all from Driftwood Canyon: **M,** SBA-5013; **N,** SBA-3920; **O,** SBA-4474; **P,** SBA-4665; **Q,** SBA-5079; **R,** SBA-5255A; **S,** SBA-5303; **T,** SBA-5719; **U,** SBA-5248A; **V,** SBA-4425; **W,** SBA-4505. **X,** SRUI 99-85-75B; **Y,** SR 05-11-18; **Z,** SR 06-01-29A; **AA,** SR 01-08-18B; **BB,** SR 06-62-08, Republic. **A–L** and **X–BB** to same scale; **M–W,** to same scale.
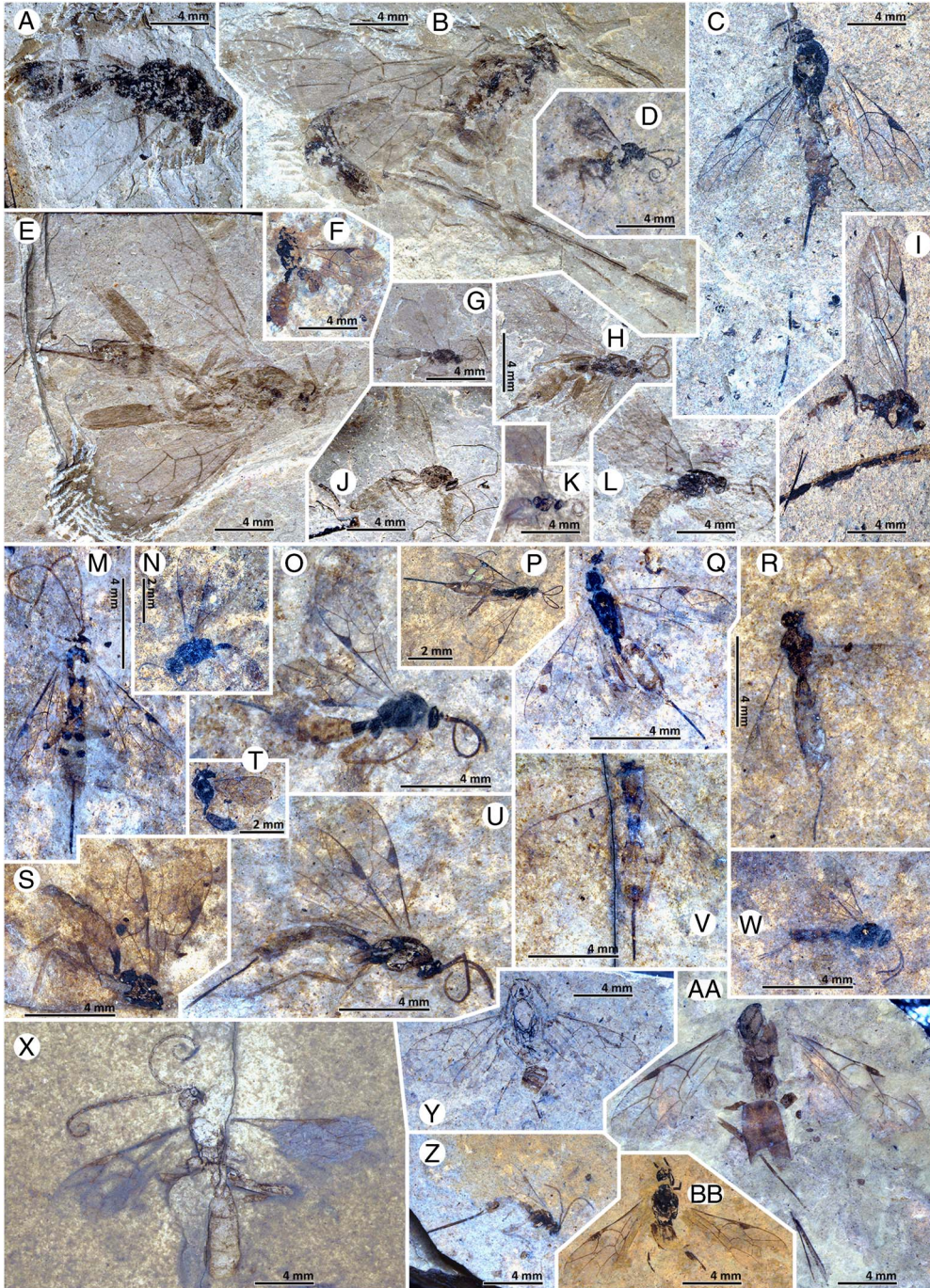
Fig. 6. Parasitica: Braconidae. **A,** TRU F-237, McAbee. **B,** SR 11-31-01, Republic. **C,** TRU F-1090, McAbee. **D,** SFU Q-5088, Quilchena. **E,** SBA-756, Horsefly River. **F,** SBA-3698, Driftwood Canyon. **G,** SBA-3466, Driftwood Canyon. **H,** SBA-4613, Driftwood Canyon. **I,** SBA-3004, Driftwood Canyon. **J,** SBA-3567, Driftwood Canyon. **K,** SBA-4403, Driftwood Canyon. **L,** SBA-3732, Driftwood Canyon. **M,** SR 06-59-03A, Republic. **A–D, K,** and **M** to same scale; **E–F** and **I–J** to same scale; **G–H** and **L** to same scale.
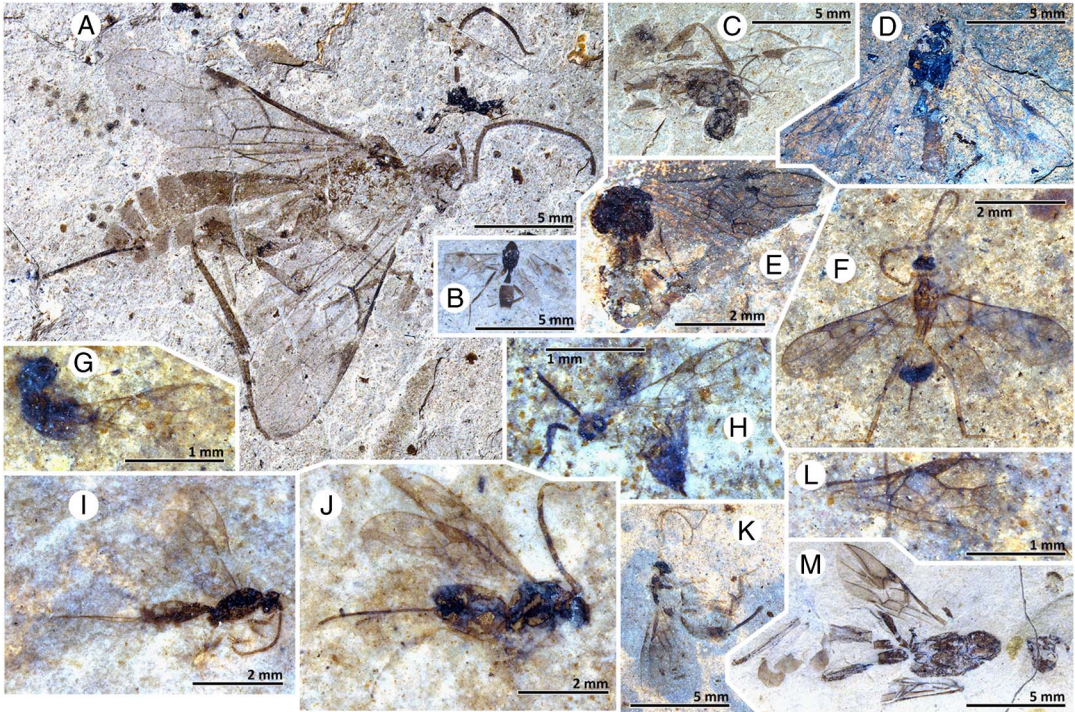
Previous records. Scudder (1879) reported several specimens (Geological Survey of Canada numbers GSC 69 and 78) as *Bracon* Fabricius species from an Allenby Formation exposure on the Tulameen River ("north fork of the Similkameen": see Introduction). Scudder (1877) also described *Calyptites antediluvianum* Scudder from the shales at Quesnel as belonging to the Braconidae, but this insect was later considered to be an ant by Wheeler (1911), and as having an unresolved family position by Bolton (2003).

Remarks. Braconids are generally considered the second-most diverse family of Hymenoptera after the Ichneumonidae, with 19 205 described modern species, distributed across the globe (Wahl and Sharkey 1993; Aguiar *et al.* 2013). They are most often endoparasitic idiobionts, and, unlike ichneumonids, many attack nymphal Hemimetabola, are not known to prey upon Araneae (spiders), and are less frequently hyperparasitoids (Gauld 1988; Wahl and Sharkey

1993). They have a small Cretaceous fossil record beginning in the Berriassian of Mongolia, and are first seen as diverse and numerous in the Priabonian (Rasnitsyn 2002; Perrichot *et al.* 2009; Ortega-Blanco *et al.* 2011a; Belokobylskij 2012; McKellar and Engel 2012; Li *et al.* 2017) (further detail: see Discussion, below).

Family Monomachidae (Apocrita: Parasitica: Diaprioidea)

Figure 7B.

Specimens. McAbee: TRU F-1549.

Remarks. Monomachidae are rare today, with 30 species, mostly inhabiting the New World tropics extending north into tropical Mexico, but also in New Guinea and Australia (Masner 1993b; Johnson and Musetti 2012; Aguiar *et al.* 2013). Their natural history is poorly known, but a few species are known to be parasitoids of

Fig. 7. Parasitica: Mymarommatoidea family *incertae sedis* (**A**), Monomachidae (**B**), Peradeniidae (**C**), Proctotrupidae (**D–F**), Figitidae (**G**), Roproniidae *sensu lato*. (**H**), Chalcidoidea family *incertae sedis*. (**I**), Heloridae (**J**), near Roproniidae (**K**). **A,** SBA-HC-10.1, Hat Creek amber. **B,** TRU F-1549, McAbee. **C,** SBA-2855, McAbee. **D,** SBA-4102, Driftwood Canyon. **E,** TRU F-1550, McAbee. **F,** SBA-3960, Driftwood Canyon. **G,** SBA-507, McAbee. **H,** SR 04-08-05, Republic. **I,** SBA-HC-7, Hat Creek amber. **J,** TRU F-1057, McAbee. **K,** TRU F-1552, McAbee. Scales differ throughout.
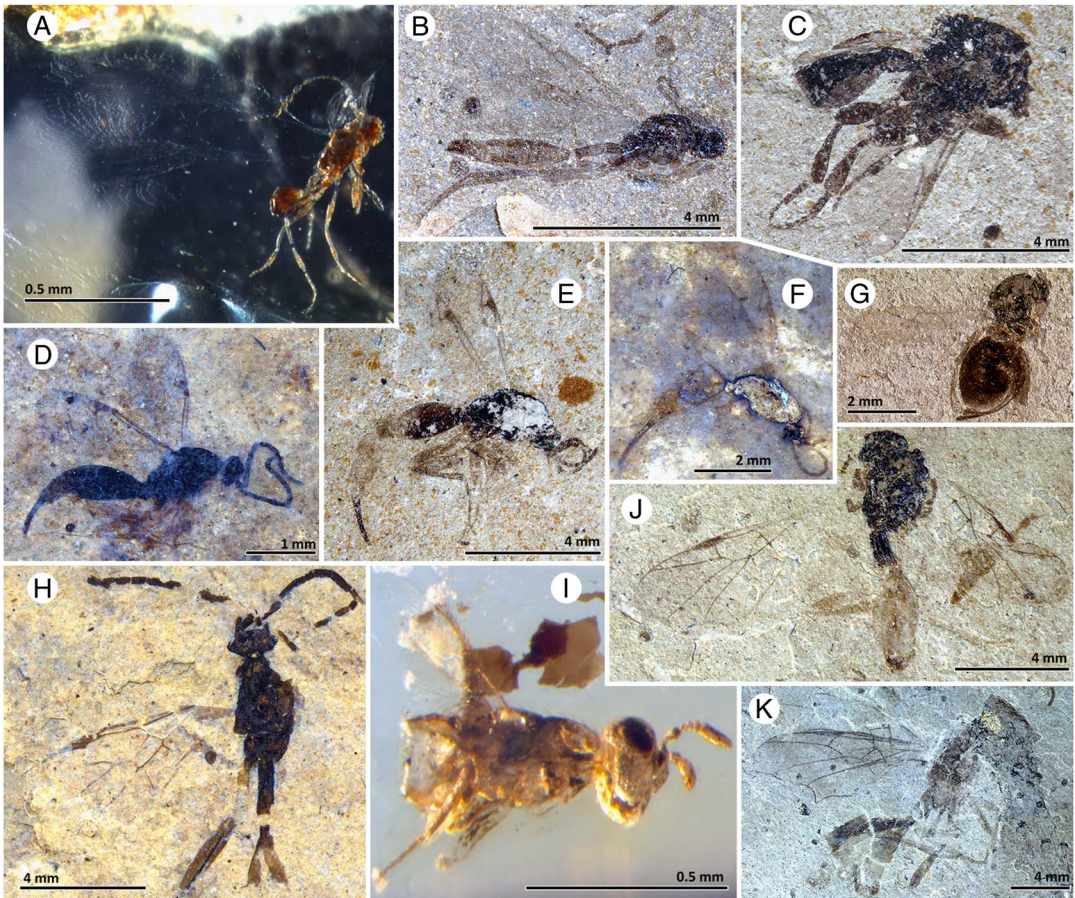
Stratiomyidae (Diptera). This is the only confirmed fossil record of the family beyond a tentative re-identification (by Rasnitsyn 1990a) of one of the paratypes of *Westratia nana* Jell and Duncan, an early Cretaceous fossil from the Koonwarra fossil beds in Australia (Jell and Duncan 1986, fig. 66F).

Family Diapriidae *sensu lato* (Apocrita: Parasitica: Diaprioidea)

Figure 4D–K.

Specimens. Driftwood Canyon: SBA-3124, SBA-3478, SBA-3685, SBA-3697, SBA-4660, SBA-4812, SBA-4814, SBA-5718, SBA-5723, SBA-5902. Horsefly River: SBA-760, SBA-5179, SBA-5585. McAbee: SBA-228, SBA-720. Republic: SRUI 99-75-03, and SRUI 99-97-09.

Remarks. The Diapriidae *sensu lato* (the Diapriidae and Ismaridae of Sharkey *et al.* 2012) are generally small wasps that are distributed globally. They are mostly endoparasitic in Diptera, but are also known to feed upon some other groups. Their adults are most common in moist, shaded habitats in forests, near water, or in soil (Masner 1993b). As small to very small wasps, they are mostly known as fossils from ambers (see appendix 1 of Perrichot and Nel 2008 and Engel *et al.* 2013b).

Sharkey *et al*. (2012) recognised the subfamily Ismarinae as a separate family, with a single genus and 29 species (Aguiar *et al*. 2013). It has a small fossil record of a few species restricted to the Cretaceous, beginning in Aptian Chosi amber of Japan (Skidmore 1999; Perrichot and Nel 2008, appendix 1; Engel *et al*. 2013b). The remaining Diapriidae *sensu stricto* has 2048 described modern species (Aguiar *et al*. 2013). The earliest undoubted occurrence of Diapriidae *sensu stricto* is in Albian French amber (Perrichot and Nel 2008), although a stem diapriid was described as an ant from the Aptian of Koonwarra, Australia (*Cretacoformica explicata* Jell and Duncan) and putative Diapriidae were described from the Berriasian of England (Rasnitsyn *et al*. 1998). Diapriids *sensu lato* of unknown affinities have been reported from Cenomanian Burmese amber, and other ambers through Florissant shale (Perrichot and Nel 2008; Rasnitsyn *et al*. 2016). Until recently, when a number of belytine diapriids were reported from Lutetian Kishenehn Formation of Montana (Greenwalt *et al*. 2015), Diapriidae *sensu lato* were thought rare until the Priabonian, and diverse and abundant from that time on (Zherikhin 2002; Perrichot and Nel 2008).

We tentatively assign SBA-3124, SBA-4814, SBA-5723, and possibly SBA-5718 to the Diapriidae *sensu stricto* (*sensu* Sharkey *et al*. 2012). We consider all of the remaining as Diapriidae *sensu lato* (Diapriidae, but possibly also Ismaridae; *i.e*., Diaprioidea except Monomachidae, Maamingidae, and Spathiopter-ygidae). Of those, SBA-228, SBA-720, SBA-760, SBA-3478, SBA-3697, SRUI 99-97-09, SRUI 99-75-03, and SBA-4812 are distinct from all modern and almost all fossil members by their short second metasomal segment. This condition is found in the similar Cretaceous wasps *Iberopria* Engel *et al*. from Albian Spanish (Álava) amber and *Cretacoformica* Jell and Duncan from the early Cretaceous of Australia. *Iberopria* was placed in the Diapriidae *sensu lato* as a stem-group member based on this morphology (Engel *et al*. 2013b), and the enigmatic *Cretacoformica* also shares this (considered a member of various groups including the Diapriidae: reviewed by Perrichot and Nel 2008). SBA-3685, SBA-660, SBA-5902, SBA-5179, and SBA-5585 are wings only.

Family *incertae sedis* (Apocrita: Parasitica: Mymarommatoidea)

Figure 7A.

Specimens. Hat Creek: SBA-HC-10.1 and SBA-HC-01.2, two specimens as syninclusions in a piece of amber. A precise family-level identification is prevented by imperfect preservation, particularly of the head and wings.

Remarks. The Mymarommatoidea and its fossil record were treated in detail by Gibson *et al*. (2007), Engel and Grimaldi (2007), and Ortega-Blanco *et al*. (2011b). The fossil record of these extremely tiny wasps – some as small as 0.3 mm in length – is entirely in amber. The superfamily consists of the extant Mymarommatidae, with a fossil record from Albian Spanish amber through Miocene Sicilian amber, and two extinct, early Cretaceous families: the Alvarommatidae, with one species from Albian Spanish amber, and the Gallorommatidae, with five species from Cenomanian Taimyr, Burmese, and French Bezonnais ambers. They may be parasites of insect eggs, but their natural history is essentially unknown. They have 10 described extant species distributed widely across the globe, but these minute microhymenoptera are assumed to be greatly undercollected and understudied.

Family Proctotrupidae (Apocrita: Parasitica: Proctotrupoidea)

Figure 7D–F.

Specimens. Driftwood Canyon: SBA-3960, SBA-4102, SBA-4452, SBA-4874, SBA-4903 (tentatively in the Proctotrupidae). Horsefly River: SBA-5868. McAbee: SBA-485 (tentatively), SBA-2902, TRU F-1550, TRU F-1551. Republic: SRUI 09-99-91.

Remarks. Proctotrupids are cosmopolitan today, but most diverse in the Holarctic, with 403 described species (Aguiar *et al*. 2013). Adults are found in damp, shaded habitats, *e.g*., forests, marshes, near water, or in soil. They are mostly endoparasitoids of Coleoptera, but also of Diptera (Mycetophilidae, Sciaridae), Lepidoptera (Oecophoridae), and centipedes (Chilopoda: Lithobiidae) (Masner 1993b; Kolyada and Perkovsky 2011). Their earliest occurrence is in

the early Cretaceous, when their fossils are more numerous than at any time later; their previously reported Cenozoic record begins in the Priabonian of Baltic and Rovno ambers, Florissant, and the Bembridge Marls (Kolyada and Mostovski 2007; Kolyada 2009; Kolyada and Perkovsky 2011; Antropov *et al.* 2014).

Family Heloridae (Apocrita: Parasitica: Proctotrupoidea)

Figure 7J.

Specimens. McAbee: TRU F-1057.
Remarks. Heloridae has 12 rare modern species, distributed around the world, but mostly in the Holarctic and apparently absent from the lowland tropics (Masner 1993b; Achterberg 2006; Aguiar *et al.* 2013). They are solitary endoparasitoids of Chrysopidae. The previously known fossil record of the family includes 15 species from the late middle Jurassic to the early Cretaceous of Asia (Shih *et al.* 2011; Shi *et al.* 2013, 2014).

Family Peradeniidae (Apocrita: Parasitica: Proctotrupoidea)

Figure 7C.

Specimens. McAbee: SBA-2855.
Remarks. Peradeniidae is a little-known family with two rare modern species in one genus known only from Tasmania and Victoria, Australia, and whose ecology and hosts are unknown (Naumann and Masner 1985; Masner 1993b). One specimen of *Peradenia galerita* Johnson *et al.* from Priabonian Baltic amber is the only other known fossil of the family (Johnson *et al.* 2001).

Family Roproniidae *sensu lato* (Apocrita: Parasitica: Proctotrupoidea)

Figure 7H.

Specimens. Republic: SR 04-08-05.
Remarks. The distinction between Roproniidae *sensu stricto* (20 extant species, Holarctic and Oriental: Aguiar *et al.* 2013) and Proctorenyxidae (three species, eastern Palearctic: Kim *et al.* 2016)

needs confirmation in our opinion, and here we treat these together as Roproniidae *sensu lato*. These are parasitoids with little-known hosts, except in one case reared from the cocoons of Symphyta (Masner 1993b). Its fossil record (all Roproniidae *sensu stricto*) includes two species from the middle Jurassic of China and undescribed specimens from the middle Jurassic of Mongolia, early Cretaceous (Neocomian to Aptian) of Transbaikalia and Mongolia, the mid-late Cretaceous of the Russian Far East near Magadan (Rasnitsyn 1990b), and five species from the middle to late Jurassic of China (review: Zhang and Zhang 2000).

Family *incertae sedis* (Apocrita: Parasitica: Proctotrupoidea)

Figure 7K.

Specimens. McAbee: TRU F-1552.
Remarks. TRU F-1552 is evidently near Roproniidae *sensu lato*, however, it does not belong to that group, as the hind wing possesses a closed cell that distinguishes it from those and is more like the condition found in the Monomachidae.

Family Cynipidae (?) (Apocrita: Parasitica: Cynipoidea)

Previous records. Horsefly: UAPL 4556 (Douglas and Stockey 1996). Quilchena: UAPL 4581 (Douglas and Stockey 1996), galls (Archibald and Mathewes 2000).

Remarks. Cynipids have 1412 modern species, distributed across the world (Aguiar *et al.* 2013). They are the only phytophagous Cynipoidea, their larvae feeding in galls that they induce or as inquilines in those of others (Ritchie 1993). Cynipoids are rare in the fossil record; there is an equivocal cynipid in Turonian New Jersey amber, and they are first established in Campanian Canadian amber, and known again in the Priabonian of Florissant and Baltic amber and in younger deposits (Grimaldi *et al.* 2000; Grimaldi and Engel 2005; Liu *et al.* 2007; and see Ronquist *et al.* 2015). We consider all of the Okanagan Highlands records to be tentative: the drawings of Douglas and Stockey (1996) of the wings from Horsefly River and Quilchena are consistent with

Cynipidae, but some doubt remains, and the galls reported by Archibald and Mathewes (2000) are equivocal.

Family Figitidae (Apocrita: Parasitica: Cynipoidea)

Figure 7G.

Specimens. McAbee: SBA-507, SBA-24. The specimen SBA-24 lacks wings, but the body as preserved indicates that, while not conspecific with SBA-507, they appear closely related.

Remarks. The Figitidae has 1571 modern species (Aguiar *et al*. 2013). They are cosmopolitan, primarily parasitoids of Diptera, but also of lacewings (Neuroptera: Hemerobiidae and Chrysopidae), and some are hyperparasitoids of Braconidae or Chalcidoidea within Aphididae and Psyllidae (Ritchie 1993; Liu *et al*. 2007). Their known fossil record begins in the late Cretaceous of Turonian New Jersey amber, Santonian Taimyr amber of Russia, and Campanian Canadian amber. In the Cenozoic, they are reported in the Priabonian of Baltic amber and Florissant shale, and in younger deposits (Liu *et al*. 2007; and see Buffington *et al*. 2012).

Family *incertae sedis* (Apocrita: Parasitica: Chalcidoidea)

Figure 7I.

Specimens. Driftwood Canyon: SBA-3082, SBA-4524, SBA-5720. Hat Creek amber: SBA-HC-7. McAbee: RBCM.EH.2004.001.1972.

Remarks. Chalcidoids are cosmopolitan, with some 20 997 described modern species distributed in habitats from equatorial forests to the northernmost tundra, and from deserts to wetlands (Gibson 1993; Aguiar *et al*. 2013). They are small wasps, which attack a wide number of insect orders and sometimes Arachnida (Araneae and Acari), mostly as parasitoids or hyperparasitoids and rarely as predators; a few are phytophagous, gall formers or seed eaters, and may be inquilines in the galls of other species (Gibson 1993). The oldest record of the superfamily is in earliest Cretaceous Mongolian shale (Rasnitsyn *et al*. 2004), and they have been reported in Albian through Campanian Cretaceous ambers (Rasnitsyn

et al. 2016, supplementary information table 1), but are never diverse until the Priabonian in Baltic amber (Heraty and Darling 2009).

Family Chrysididae (Apocrita: Aculeata: Chrysidoidea)

Specimens. McAbee: SBA-225 (Chrysidinae).

Remarks. The Chrysididae is a moderately large family of 2500 modern described species (Aguiar *et al*. 2013). They are cosmopolitan, with a greatest diversity in temperate deserts of both hemispheres (Finnamore and Brothers 1993). Their larvae are parasitoids of insect eggs and larvae, or cleptoparasites. They are known from the Cretaceous in Barremian Lebanese amber, late Barremian-early Aptian Turga shale, early Albian Álava amber, Cenomanian Burmese amber (age: Shi *et al*. 2012), Turonian New Jersey amber, Santonian Taimyr amber, Campanian Canadian amber (summarised by Rasnitsyn *et al*. 2016, supplementary information table 1); and then not until the Priabonian (*e.g*., Cockerell 1907) and younger (*e.g*., Engel 2006). The Chrysidinae, its largest subfamily, are usually brightly metallic coloured cleptoparasites in the nests of bees and wasps (Finnamore and Brothers 1993).

### Family Pompilidae (Apocrita: Aculeata: Vespoidea)

Figure 8C.

Specimen. Republic: SR 14-001-002.

Previous records. McAbee: CMN100040 (Douglas and Stockey 1996).

Remarks. The Pompilidae has 4855 modern species (Aguiar *et al*. 2013). They are a cosmopolitan, but predominantly tropical family (Brothers and Finnamore 1993). Each larva consumes a single paralysed spider (seldom other Arachnida) usually in a constructed cell, sometimes in another's cell or in a cavity, rarely on an active spider. Their fossils were not previously established older than the numerous species described from the Priabonian of Baltic and Rovno ambers and Florissant shale, and subsequently in the Oligocene and Miocene of Europe (reviewed by Engel and Grimaldi 2006; Rodriguez *et al*. 2016). Rodriguez *et al*. (2016) removed the Cretaceous *Bryopompilus interfector* Engel and Grimaldi from

Fig. 8. Aculeata: Scoliidae (**A, B**), Pompilidae (**C**), aculeates of unknown affinity (**D, E**). **A**, SR 96-04-03, Republic. **B**, SR 09-13-01, Republic. **C**, SR 14-001-002, Republic. **D**, TRU F-1556, McAbee. **E**, TRU F-1557, McAbee. Scales differ throughout. TRU F-1557, McAbee. Scales differ throughout.
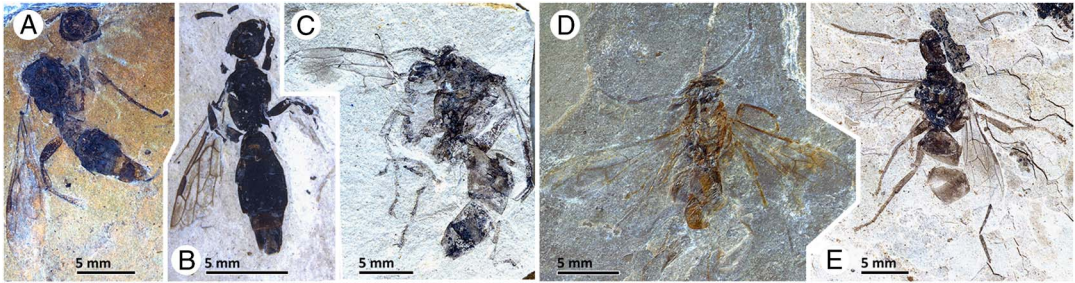
Pompilidae and placed it in the family Bryopompilidae, although mistakenly claiming to establish this as a new family despite Engel and Grimaldi (2006) having established the tribe Bryopompilini for it. A.P.R. recently restudied the type, and we agree that the fossil represents a family of its own (Bryopompilidae Engel and Grimaldi), not closely related to Pompilidae. We agree with Douglas and Stockey's (1996) determination of CMN100040 as a pompilid from examination of the figures provided.

Family Scoliidae (Apocrita: Aculeata: Vespoidea)

Figure 8A–B.

Specimens. Republic: SR 09-13-01, SR 96-04-03 (both Archaeoscoliinae).
Previous records. Allenby: UAPL 4524 (Douglas and Stockey 1996) (here treated as belonging to the Archaeoscoliinae).
Remarks. The Scoliidae has 560 described modern species (Aguiar *et al*. 2013) with a cosmopolitan, predominantly tropical distribution. Their larvae are ectoparasitoids of soil-dwelling Coleoptera larvae, usually Scarabaeoidea (Brothers and Finnamore 1993). Their fossils have been found throughout the Cretaceous, beginning in the Barremian of Spain (Rasnitsyn 1993; Rasnitsyn and Martínez-Delclòs 1999; Zhang *et al*. 2002, 2015). In the Cenozoic, they first appear in the Lutetian at Messel, Germany, and then the Priabonian at Florissant and the Bembridge Marls (Lutz 1990; Rasnitsyn 1993; Antropov *et al*. 2014). The extinct subfamily Archaeoscoliinae is known from the Barremian of

Spain, Aptian of Bon Tsagaan, Turonian of northern Kazakhstan, Campanian of northeast Siberia, and the Priabonian of Florissant (Rasnitsyn 1993; Zhang *et al*. 2002).

## Family Vespidae (Apocrita: Aculeata: Vespoidea)

Figure 9.

Specimens. Driftwood Canyon: SBA-3070, SBA-4897. McAbee: SBA-1094, TRU F-1020/1021, SBA-593, TRU F-1553. Quilchena: SFU Q-5879. Republic: SR 05-03-03, SR 06-21-03, SR 02-01-12, SR 99-07-20, SR 06-01-01.
Previous records. Allenby Formation, Blakeburn Mine: ROM 31319 (Wilson 1977a). Quilchena: SFU Q-0037 (Archibald and Mathewes 2000).
Remarks. The Vespidae has 4932 species today (Aguiar *et al*. 2013), with a cosmopolitan, but predominantly tropical distribution. Most species are solitary, but many are social, from semi-social to the highly organised eusocial societies of the subfamilies Stenogastrinae (hover wasps), Vespinae (hornets and yellowjackets), and Polistinae (paper wasps) (Brothers and Finnamore 1993). Larvae of solitary species feed on those of other insects, rarely on pollen and nectar, which are deposited in a cell constructed by the adult female; those of social species are continuously fed on masticated insects provided by the adults, or rarely on their glandular secretions. A few species are cleptoparasites in nests of social species (Brothers and Finnamore 1993).

They first appear in the Cretaceous, where they are known from Asia (Valanginian Baissa, late Barremian-early Aptian Turga shale, Aptian

Fig. 9. Aculeata: Vespidae. **A,** SBA-3070, Driftwood Canyon. **B,** SR 06-21-03, Republic. **C,** SFU Q-5897, Quilchena. **D,** TRU F-1553, McAbee. **E,** TRU F-1021, McAbee. **F,** SBA-1094, McAbee. **G,** SR 99-07-20A, Republic. **H,** SFU Q-0037, Quilchena. All to same scale.
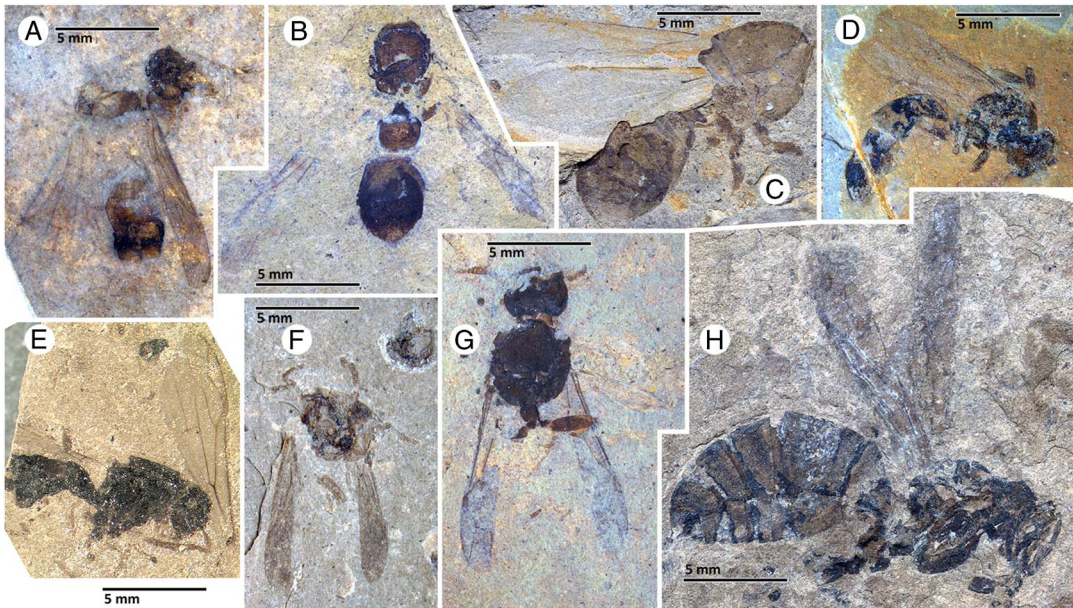
Bon-Tsagaan, Cenomanian Burmese amber, Turonian Kzyl-Zhar), Africa (Turonian Orapa shale of Botswana), and North America (Turonian New Jersey amber), all belonging to non-social taxa; however, a nest from Utah indicates the presence of social Vespidae in the Cretaceous (Carpenter and Rasnitsyn 1990; Wenzel 1990; Brothers 1992; Carpenter 2000; Perrard *et al.* 2017). Similar nests have been described from the Coniacean of Central Asia (Nesov 1985, 1995), which, however, were not necessarily made by social wasps.

The body fossils of eusocial vespids are first confidently known from a vespine and a polistine from the Paleocene of Menat, France, found with non-social vespids (Piton 1940; Nel and Auvray 2006). Vespidae (social and non-social) are then known in the Ypresian from the Okanagan Highlands (Allenby Formation and Quilchena), the Green River Formation (United States of America) and the Tadushi Formation (Rasnitsyn 1980: the Tadushi called Zerkal'naya); the Lutetian of Messel, Germany; the Priabonian of Florissant, the Bembridge Marls (United Kingdom), and Baltic amber; and various Oligocene and Miocene localities (Burnham 1978;

Wilson 1978a; Lutz 1990; Archibald and Mathewes 2000; Meyer 2003; Poinar 2005; Nel and Auvray 2006; Antropov *et al.* 2014). In all, 14 of the Okanagan Highlands specimens are confidently members of the Vespidae, 12 of which we assign to the Vespinae and/or Polistinae, *i.e.*, were eusocial. The remaining two (SBA-1094, SR 05-03-03) likely belong to the non-eusocial Eumeninae.

Family Formicidae (Apocrita: Aculeata: Vespoidea)

Figures 10–12.

Specimens. Ants are known from all major sites. Driftwood Canyon: SBA-5781. Horsefly River: SBA-5849, SBA-5866. Hat Creek: SBA-HC-1, SBA-HC-2, SBA-HC-3, SBA-HC-6, KM NH998015004, KM NH998015008, KM NH998015010, KM NH998015011. McAbee: SBA-109, SBA-331, SBA-460, SBA-1137, SBA-5926, TRU F-260, TRU F-789, TRU F-990, TRU F-1554, TRU F-1574, TRU F-1576, TRU F-1577, TRU F-1578, TRU F-1579, TRU F-1580. Quilchena: SFU Q-0001, SFU Q-0002, SFU Q-0003, SFU Q-0005, SFU Q-0006,

Fig. 10. Aculeata: Formicidae. **A,** SFU Q-0409, Quilchena. **B,** SFU Q-0007, Quilchena. **C,** SFU Q-0400A, Quilchena. **D,** SFU Q-0002, Quilchena. **E,** PMF.2016.0001.001, Allenby Formation. **F,** SFU Q-0015, Quilchena. **G,** SBA-5781, Driftwood Canyon. **H,** NH998015004, Dolichoderinae, Hat Creek amber. **I,** SBAHC-4, Myrmicinae, *Leptothorax* species (Poinar *et al*. 1999) or possibly *Tetramorium* species (Radchenko and Dlussky 2015), Hat Creek amber. **J,** SBA-HC-3, Formicinae *incertae sedis* (not Dolichoderinae, Technomyrmex as stated by Poinar *et al*. 1999), Hat Creek amber. **K,** SBA-HC-1, Dolichoderinae, *Dolichoderus* species, Hat Creek amber. **L,** NH998014008, Dolichoderinae, Hat Creek amber. **M,** Myrmeciinae, *Myrmeciites* (?) *tabanifluviensis* Archibald *et al*., 2003.2.10.CDM034, Horsefly River. **N,** 2003.2.9.CDM.033a, Myrmeciinae, *Myrmeciites incertae sedis*, Falkland. **A–G, M–N** to same scale; **H–L,** to same scale.
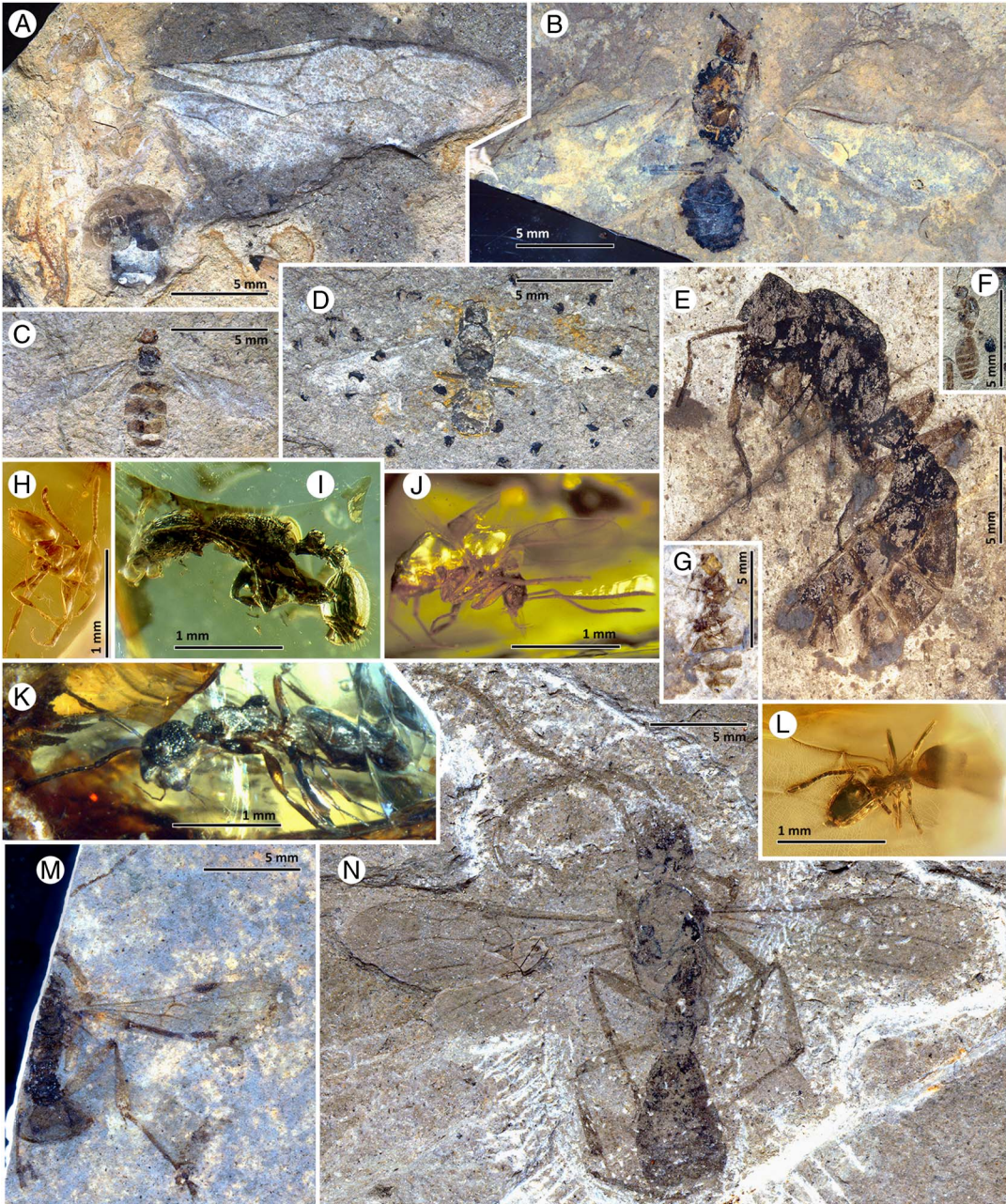
Fig. 11. Aculeata: Formicidae, McAbee. **A,** TRU F-1574, Myrmeciinae, likely *Myrmeciites* (?) *goliath* Archibald *et al.* **B,** Myrmeciinae, TRU F-260. **C,** SBA-331A. **D,** TRU F-1554. **E,** TRU F-789, Myrmeciinae. **F,** SBA-5926. **G,** TRU F-990. **H,** SBA-109A. **I,** SBA-460. All to same scale.
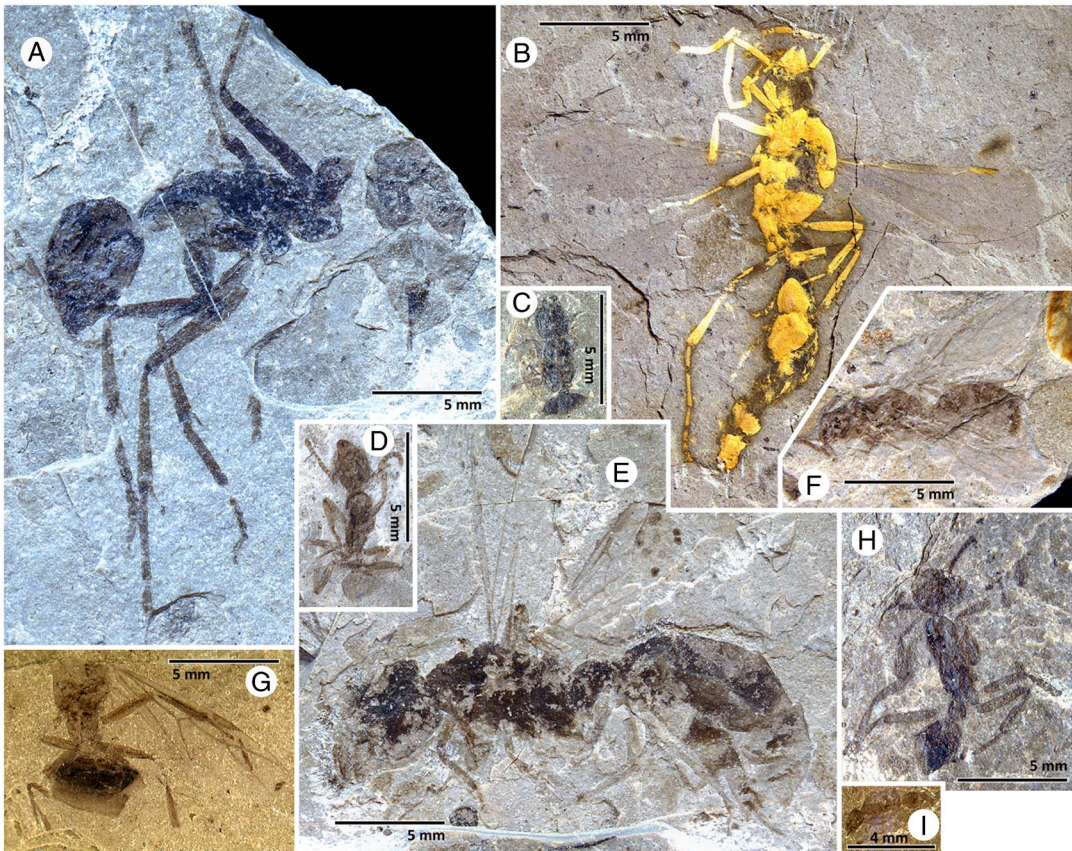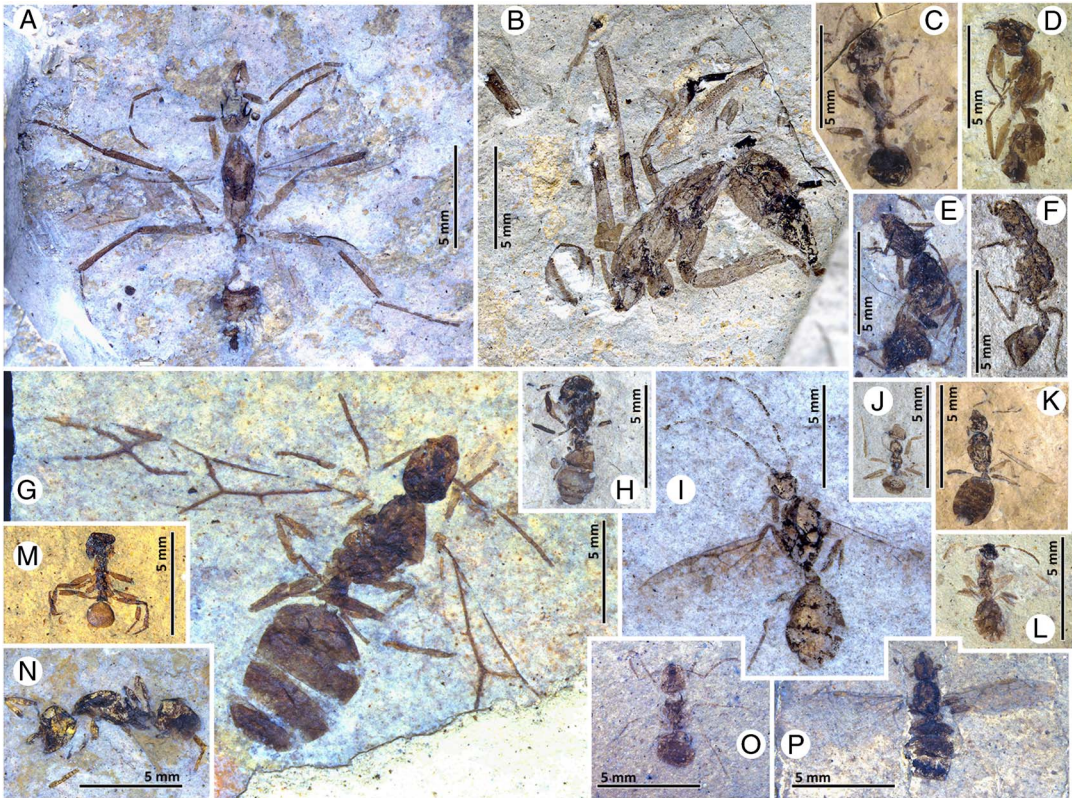

SFU Q-0010, SFU Q-0012, SFU Q-0013, SFU Q-0015, SFU Q-0019, SFU Q-0258, SFU Q-0366, SFU Q-0412, SFU Q-0453, SFU Q-0456, SFU Q-0485, SFU Q-0492, SFU Q-0510, SFU Q-0517, SFU Q-5880, SFU Q-5881, SFU Q-5882. Allenby Formation: PMF.2016.0001.001. Republic: DMNH-27804, DMNH-27805, SR 00-02-01, SR 03-02-01, SR 04-01-01, SR 05-03-09, SR 05-03-14, SR 05-03-17, SR 05-03-22, SR 06-01-03, SR 07-03-09, SR 07-05-06, SR 08-35-06, SR 09-11-02, SR 10-41-12, SR 11-02-01, SR 11-58-09, SR 11-58-10, SR 99-14-08, SR 99-82-54, SRUI 07-03-01, SRUI 08-03-03, SRUI 99-75-55, SRUI 99-82-54, SRUI 99-84-27, SRUI 99-84-78, SRUI 99-85-52, SRUI 99-90-08, SRUI 99-92-24.

Previous records. Scudder (1877) described a series of ants from Quesnel, which he named

Formica arcana Scudder, *Aphaenogaster longaeva* Scudder, and Hypoclinea *obliterata* Scudder (these determinations below family level are in need of revision). In the same paper, he described *Calyptites antediluvianum* Scudder, also from Quesnel, as a member of the Braconidae, but it was later considered to be an ant (Wheeler 1911), and subsequently as belonging to an undetermined family (Bolton 2003). Douglas and Stockey (1996) illustrated SR 88-11-12 from Republic (subsequently named *Camponotites kraussei* Dlussky and Rasnitsyn, see below), UAPAL 4557 and UAPAL 4558 from Horsefly River, UAPAL 4610 and UAPAL 4604 from Quilchena (all of which we agree are ants, judging from their figures), and further listed (which we have not seen) UAPAL 4542 from Horsefly River and UAPAL 4616 and UAPAL 4582 from

Fig. 12. Aculeata: Formicidae, Republic. **A,** SR 07-03-09, Myrmeciinae. **B,** SR 07-05-06A, Myrmeciinae. **C,** SR 11-58-10. **D,** SR 08-35-06. **E,** SR 05-03-14. **F,** SRUI 99-84-78. **G,** SR 88-11-02, holotype, *Camponotites kraussei* Dlussky and Rasnitsyn. **H,** SR 10-41-12. **I,** SR 03-02-01. **J,** SR 99-14-08. **K,** SR 06-01-03. **L,** SR 94-05-07, holotype, *Klondikia whiteae* Dlussky and Rasnitsyn. **M,** DMNH-27804. **N,** SR 04-01-01. **O,** DMNH-27805. **P,** SRUI 99-92-24. All to same scale.

Quilchena. Archibald and Mathewes (2000) reported, but did not describe, ants from Quilchena, illustrating three (SFU Q-0409, SFU Q-0007, SFU Q-0400), listing a further eight (SFU Q-0008, SFU Q-0011, SFU Q-0014, SFU Q-0019, SFU Q-0021, SFU Q-0410, SFU Q-0271) and mentioning that there are numerous others. Dlussky and Rasnitsyn (1999) described the formicine *Camponotites kraussei* Dlussky and Rasnitsyn (holotype: UWBM-78047, part, SR 88-11-02, counterpart; *Camponotites* Steinbach a form genus), and subsequently (2003) *Klondikia whiteae* Dlussky and Rasnitsyn (holotype: SR 94-04-24, part, SR 94-05-07, counterpart; subfamily indet.), both from Republic. A myrmicine in Hat Creek amber (SBA-HC-4) was illustrated by Poinar *et al*. (1999), which they called *Leptothorax* Mayr, but which Radchenko and Dlussky (2015) thought might be a species of *Tetramorium* Mayr. They also illustrated an ant that they determined as *Technomyrmex* Mayr (SBA-HC-5), and mentioned the presence of *Dolichoderus* Lund (not figured). Archibald *et al*. (2006) described the Myrmeciinae of the Okanagan Highlands, naming *Ypresiomyrma orbiculata* Archibald *et al*. (holotype: TRU F-749, part, TRU F-750, counterpart), *Ypresiomyrma bartletti* Archibald *et al*. (holotype: GSC 127632a,b, part and counterpart), *Avitomyrmex elongatus* Archibald *et al*. (holotype: 2003.2.8CDMM032, part only), *Avitomyrmex mastax* Archibald *et al*. (holotype: TRU F-850, paratype: TRU F-929), *Avitomyrmex systenus* Archibald *et al*. (holotype: 2003.2.11CDM035, part only; paratype: TRU F-989, part only; additional specimen: TRU F-825, part only. TRU F-825 tentatively assigned

to this species), *Macabeemyrma ovata* Archibald *et al.* (holotype: TRU F-844, part, TRU F-856, counterpart), and *Myrmeciites herculeanus* Archibald *et al.* (holotype: TRU F-974, part only; *Myrmeciites* Archibald *et al.*, a form genus), all from McAbee; placing two species tentatively in the Myrmeciinae, *Myrmeciites* (?) *tabanifluviensis* Archibald *et al.* (holotype: 2003.2.10CDM034, part only) from Horsefly River, and *Myrmeciites* (?) *goliath* Archibald *et al.* (holotype: TRU F-999, part, TRU F-1000, counterpart) from McAbee; and treating two further myrmeciines as *Myrmeciites incertae sedis*: a male from Falkland (2003.2.9CDM033a, b, part and counterpart) and a female (worker or queen) from Republic (SR 05-03-01). Archibald (2007) illustrated the forewings of Dolichoderinae (SBA-367), Formicinae (SBA-390, SBA-2292) and Myrmeciinae (SBA-2832, SBA-2111 possibly a myrmeciine), and an ant not determined to subfamily (SBA-2996) at McAbee. Here, we recognise *Propalosoma gutierrezae* Dlussky and Rasnitsyn from Republic (holotype: part: SR 93-08-04, counterpart: UWBM 77524) as a myrmeciine ant.

Remarks. Ants comprise 12 199 described modern species (Aguiar *et al.* 2013). They are cosmopolitan, but predominantly tropical, highly social, and occupy a wide variety of habitats and niches: as mutualists tending aphids and other Sternorrhyncha, Auchenorrhyncha, the caterpillars of Lycaenidae (Lepidoptera), and some other insects for their exudates; as scavengers of dead arthropods; as active predators; as herbivores; and as fungivores (Brothers and Finnamore 1993; Pierce *et al.* 2002; Wilson and Hölldobler 2005).

If *Armania* Dlussky species and their relatives are considered as within the Formicidae, the fossil record of ants extends to the Albian (Dlussky 1999). This group has just over a dozen species, which are abundant as individuals from the outset at Khetana into the late Cretaceous (Dlussky 1999; Rasnitsyn 2002; Zherikhin 2002, review of Engel and Grimaldi 2005). Their status as ants has been the subject of debate (Armaniinae within the Formicidae, *e.g.*, Bolton 2003; Armaniidae, *e.g.*, Grimaldi and Engel 2005; treated as "stem ants" along with the Sphecomyrminae by Ward 2014).

Uncontroversial ant fossils appear in Albian-Cenomanian French and Cenomanian Burmese amber (Nel *et al.* 2004; Perrichot 2015). The 19 species of the primitive, extinct Sphecomyrminae are

widespread throughout the Cretaceous from the early Cretaceous at Baikura amber (northern Siberia – distinct from nearby "Taimyr amber") through latest Albian – earliest Cenomanian French amber (Perrichot 2015), earliest Cenomanian Burmese amber (Dlussky 1996; Engel and Grimaldi 2005), Turonian New Jersey amber (Wilson *et al.* 1967; Grimaldi *et al.* 1997; Engel and Grimaldi 2005), the Turonian of Kazakhstan (Dlussky 1983), Santonian Taimyr amber (Dlussky 1987), and in Campanian Canadian amber (Wilson 1985; McKellar and Engel 2012). None of these primitive ants (or close ant relatives) is known to have survived into the Cenozoic.

After crown-group ants are first seen in mid-Cretaceous amber, they are known from a small number of individuals reported through the remainder of the Cretaceous, never diverse and always rare. Of these, four species have unknown or extinct subfamily affinities, and fewer than 10 are assigned to modern subfamilies (Dlussky *et al.* 2004; Engel and Grimaldi 2005; Perrichot *et al.* 2008a, 2008b; McKellar and Engel 2012; LaPolla *et al.* 2013; McKellar *et al.* 2013; Perrichot 2015; and references therein). The early Cenozoic history of ants is reviewed below in the Discussion section.

Spheciformes (Apocrita: Aculeata: Apoidea)

The Spheciformes is a paraphyletic group composed of those apoids that are not bees. The Okanagan Highlands spheciform wasp assemblage presents an unusual challenge in that many specimens are indistinct at the family level, even some that are quite clearly preserved – a surprising situation. We can say, however, that a feature of these is that they almost doubtlessly not only reveal the presence, but also an abundance and diversity of Angarosphecidae, an extinct group not known to persist into the Cenozoic before the description of *Eosphecium naumanni* Brothers and Archibald (Pulawski *et al.* 2000) in the Okanagan Highlands at Quilchena.

Family Angarosphecidae (Apocrita: Aculeata: Apoidea: Spheciformes)

Figure 13.

Specimens. *Eosphecium* Pulawski and Rasnitsyn species: Driftwood Canyon: SBA-2988.

Fig. 13. Aculeata: Angarosphecidae and possible Angarosphecidae (see text). **A,** SR 02-25-02, Republic. **B,** TRU F-1560, McAbee. **C,** UWBM PB-3823, McAbee. **D,** UWBM 57297, Allenby Formation. **E,** TRU F-1561, McAbee. **F,** SFU Q-0423, Holotype, *Eosphecium naumanni* Brothers and Archibald, Quilchena. **G,** SRUI 99-82-01, Republic. **H,** UWBM 57128, Allenby Formation. **I,** SR 10-18-27, Republic. **J,** UWBM-74301, Republic. **K,** SR 05-03-11A, Republic. All to same scale.
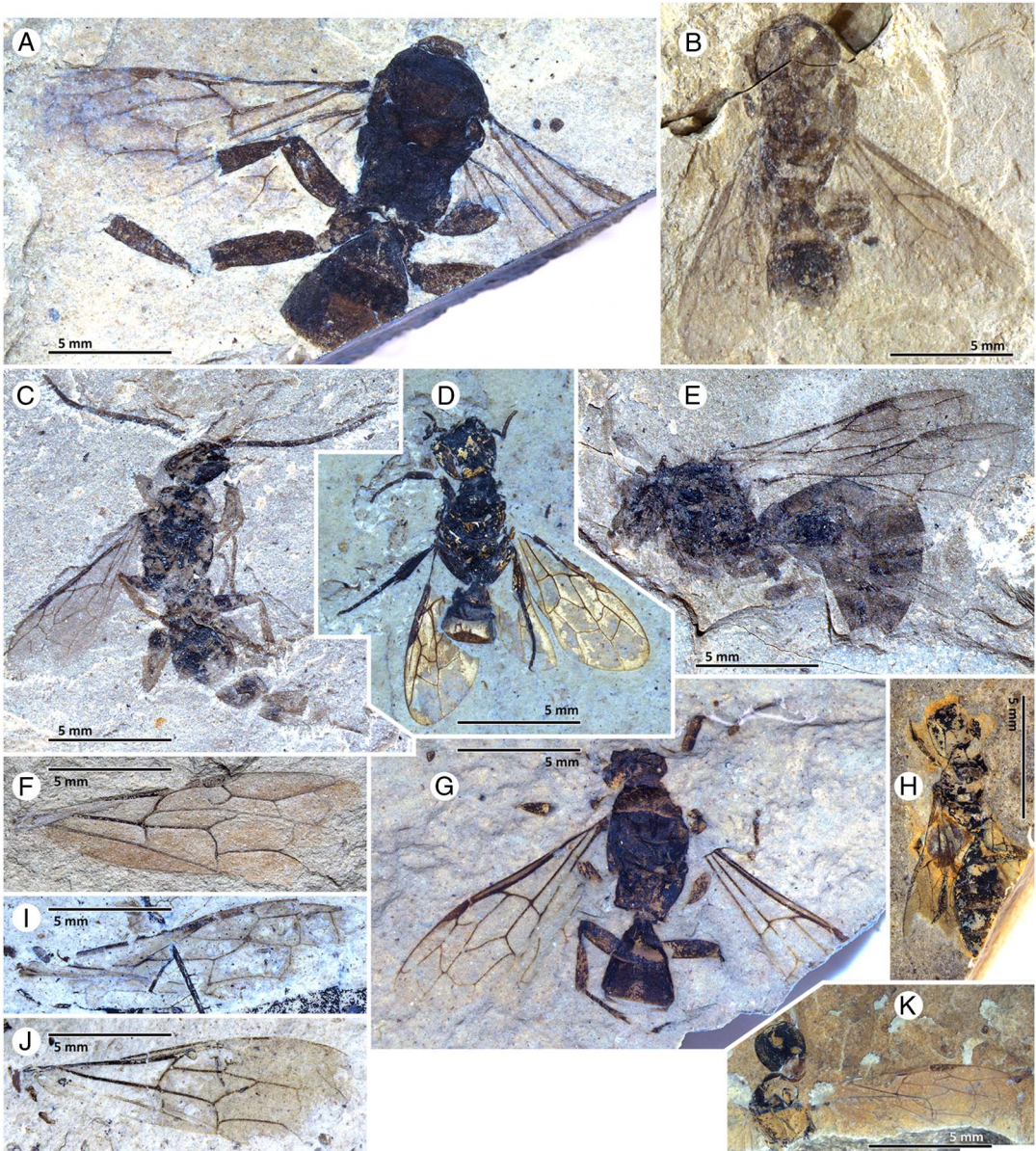
McAbee: UWBM PB-3823/4104. Republic: SR 05-03-11, UWBM 74301. *Eosphecium* species or near: McAbee: TRU F-1560. Republic: SR 02-25-02, SRUI 99-82-01. Almost certainly Angarosphecidae: McAbee: UWBM PB-3909. Allenby Formation (One Mile Creek): UWBM 57297, UWBM 57128. Possibly Angarosphecidae: McAbee: TRU F-1561, TRU F-1562. Republic: SR 10-18-27, SR 12-004-004, SR 92-02-23.

Previous records. Quilchena: SFU Q-0423 *Eosphecium naumanni* Brothers and Archibald (Pulawski *et al*. 2000).

Remarks. The Angarosphecidae as currently understood represents an extinct group that is supposedly basal in Apoidea and perhaps paraphyletic with regard to the rest. They are among the most abundant Hymenoptera found in the early Cretaceous (Rasnitsyn *et al*. 1999). Their fossil record begins in the early Berriassian of Dorset, United Kingdom; and then they are found in the Hauterivian–Valanginian Purbeck Limestones (United Kingdom); the Valanginian of Transbaikalia; the early Barremian of Spain; Barremian or Aptian of Shandong, China; the Aptian of Russia, Mongolia, and Brazil (reviewed by Rasnitsyn *et al*. 1998, and see Pulawski *et al*. 2000; Rasnitsyn and Ansorge 2000). After a lengthy hiatus, the family is reported again with a single species in the Ypresian, described from Quilchena in the Okanagan Highlands (Pulawski *et al*. 2000).

With the wide morphological range of the wasps that we associate with that family here (confidently or tentatively to various degrees), the group becomes more difficult to define with clearly diagnostic character states, in particular any that easily separate its species from those of the Ampulicidae and Crabronidae. They remain more or less distinct from the Sphecidae, Heterogynaidae, and the apiform families. As a working definition, we associate those wasps listed above with the Angarosphecidae based on a rather straight alignment of the forewing vein sections of RS + M and M combined with the presence of notauli (and isolated wings whose morphology is close to those of more complete specimens that possess notauli), and we group them by likelihood of being closely related to *Eosphecium* and allied Cretaceous wasps. We will address this issue in detail in ongoing research.

Family Sphecidae *sensu stricto* (Apocrita: Aculeata: Apoidea: Spheciformes)

Figure 14A–B.

Specimens. McAbee: TRU F-692, TRU F-258. Republic: SR 14-001-001.

Remarks. Today, the Sphecidae (*sensu stricto*) are cosmopolitan, medium to large wasps, with 724 described species, which have a wide range of behaviours from parasitoid-like to primitively social nest building or crevice dwelling (Finnamore and Michener 1993; Aguiar *et al*. 2013). They provision their young with prey that includes spiders, orthopteroids, and Lepidoptera larvae.

No previously known fossil Sphecidae (*sensu stricto*) is older than the Priabonian, where they are reported from Florissant and the Bembridge Marls: *Hoplisidea kohliana* Cockerell (transferred to the Sphecidae by Menke and Rasnitsyn 1987) and *Protosceliphron brevior* (Cockerell) (revised by Antropov *et al*. 2014). We associate the fossils listed above confidently with the Sphecidae *sensu stricto*.

Family *incertae sedis* (Apocrita: Aculeata: Apoidea: Spheciformes)

Specimens. Driftwood Canyon: SBA-4905; SBA-3505; SBA-3550; SBA-4390. Hat Creek amber: SBA-HC-8. McAbee: UWBM PB-2747. Republic: SR 09-11-06.

**Remarks.** These specimens might belong to the Angarosphecidae, Sphecidae, or Crabronidae.

Apiformes (Apocrita: Aculeata: Apoidea)

Modern bees (Apiformes or Anthophila) have 19 844 described, almost entirely pollinivorous, solitary, and semi-social to eusocial species that range across the globe outside of the polar regions (Michener 2007; Aguiar *et al*. 2013). Most dig or construct external nests, which are complex in some species.

The oldest reported putative bee, *Melittosphex burmensis* Poinar and Danforth, from Cenomanian Burmese amber, comprises the extinct family Melittosphecidae (Poinar and Danforth 2006). It is now, however, considered to be an apoid wasp in an unresolved position near bees and crabronids (Michener 2007; Ohl and Engel 2007; Danforth and Poinar 2011). An advanced apid was described from putative Maastrichtian New Jersey amber (Michener and Grimaldi 1988; Engel 2000); however, the amber piece that contains it was found unlabelled in a drawer, leaving its provenance in doubt, and other insects found as syninclusions are consistent with it being of much

Fig. 14. Aculeata: Spheciformes (**A–B**) and Apiformes (**C–I**). **A**, TRU F-258, Sphecidae *sensu stricto*, McAbee. **B**, SR 14-001-001, Sphecidae *sensu stricto*, Republic. **C**, SR 04-08-06, Halictidae, Republic. **D**, SFU Q-0424, Halictidae, *Halictus savenyei* Engel and Archibald, Quilchena. **E**, SR 06-22-01, Republic. **F**, TRU F-1555, Halictidae, McAbee. **G**, TRU F-263, Apidae, McAbee. Megachilidae leaf cutting damage (oval cuts) (**H** and **I**): **H**, SR 94-05-31, Republic, on a *Prunus* leaf. **I**, SBA-5195, Horsefly River. Scales differ, except (**C–G**) to same scale.
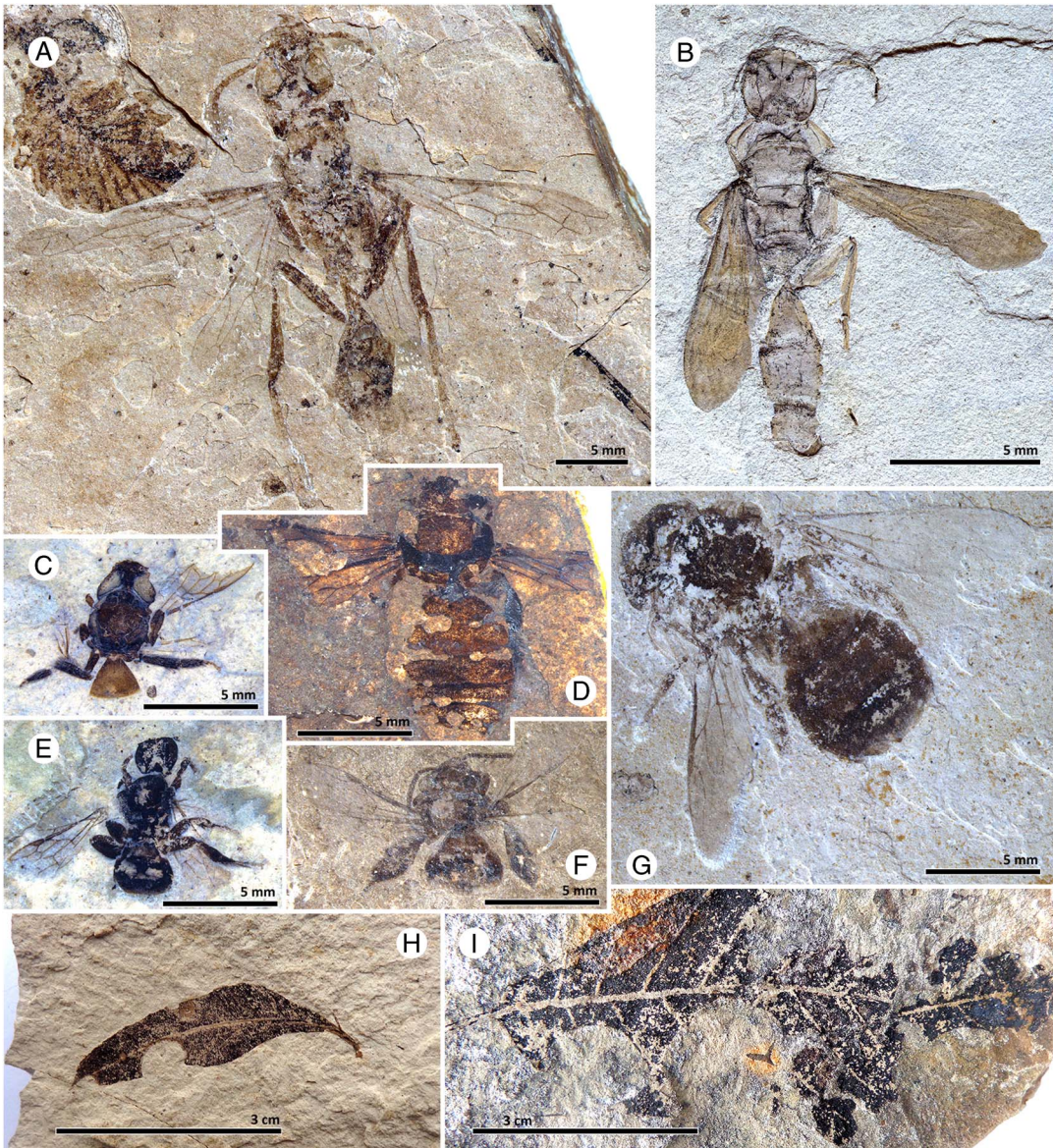
younger Cenozoic age, which we find most reasonable (discussion: Rasnitsyn and Michener 1991; Grimaldi 1999; Zherikhin 2002). An ichnofossil from Uruguay was described as a Cretaceous bee nest (Roselli 1939); however, Zeuner and Manning (1976) concluded that while its structure does bear some resemblance to that of bee cells, it may not be Cretaceous. The Cenozoic record of bees is reviewed in the Discussion section, below.

Family Apidae (Apocrita: Aculeata: Apoidea: Apiformes)

Figure 14G.

Specimen. McAbee: TRU F-263.

Remarks. The Apidae is one of the most speciose families of bees today, with 5749 described species widespread across the globe, and includes most eusocial bees (*e.g.*, the honey bee, *Apis mellifera* Linnaeus), as well as many less social and solitary species (Michener 2007; Aguiar *et al.* 2013). The fossil record of the family is reviewed in the Discussion section, below.

Family Megachilidae (Apocrita: Aculeata: Apoidea: Apiformes)

Figure 14H–I.

Specimen. Horsefly River: SBA-5195, a leaf with megachilid cutting (Fig. 14I).

Previous records. Leaf-cutting damage was reported from Republic by Lewis (1994): UWBM-57529a, b on a *Prunus* Linnaeus (Rosaceae) leaf, one side subsequently designated SR 94-05-31 (Fig. 14H); and Labandeira (2002): UWBM 95726 on an *Ulmus* Linnaeus (Ulmaceae) leaf. Labandeira (2002, and see Wedmann *et al.* 2009) reported such damage on a *Ginkgo* Linnaeus (Ginkgoaceae) leaf from McAbee (UWBM 77597).

Remarks. The Megachilidae is a large family of bees today, with 4096 described species, inhabiting all continents except Antarctica (Gonzalez *et al.* 2012; Aguiar *et al.* 2013). They may use the abandoned nests of other insects or construct their own, either openly, in cavities, or digging tunnels in soil, which they may line with a variety of materials, sometimes leaf pieces cut in arcs from angiosperm leaves (but see an instance of *Ginkgo*, above) (Finnamore and Michener 1993; Engel 1999).

The earliest body fossil of a member of the Megachilidae is from the Paleocene of Menat (Nel and Petrulevičius 2003), and others subsequently in the Eocene from the Priabonian in Baltic and Rovno ambers and at Florissant (see review by Engel and Perkovsky 2006). The earliest occurrences of their distinctive leaf damage are in the Okanagan Highlands and the Green River Formation (Republic: Lewis 1994; Labandeira 2002; McAbee: Wedmann *et al.* 2009; Green River Formation: Labandeira 2002), and then from the Lutetian of Argentina (Sarzetti *et al.* 2008) and Eckfelt Maar in Germany (Wappler and Engel 2003), the Bartonian Cockfield (Wilcox) Formation of Kentucky and Tennessee, United States of America (Berry 1931; Brooks 1955), the Priabonian of Florissant (Cockerell 1910), and in younger deposits (reviewed: Wappler and Engel 2003; Wedmann *et al.* 2009).

Family Halictidae (?) (Apocrita: Aculeata: Apoidea: Apiformes)

Figure 14C–D, F

Specimens. McAbee: TRU F-1555; Republic: SR 04-08-06.

Previous records. Quilchena: SFU Q-0424, *Halictus*? *savenyei* Engel and Archibald.

Remarks. Sweat bees, the Halictidae, have 4327 described species today (Aguiar *et al.* 2013), spread over much of the globe. They include many eusocial species and a wide variety of social to solitary, cleptoparasitic, and socially parasitic species among the remainder, and nest by burrowing in soil and sometimes rotting wood (Michener 2007; Danforth *et al.* 2013).

The oldest fossil ascribed to the Halictidae is *Halictus*? *savenyei* from the Okanagan Highlands locality at Quilchena (Engel and Archibald 2003) and the rest of the fossil record is Priabonian (Baltic amber, one species; Florissant, six species) and younger (reviewed by De Meulemeester *et al.* 2012). Although *Halictus*? *savenyei* was described as a halictid, possibly a species of *Halictus* Latreille, here we consider this and the other Okanagan Highlands specimens to be likely, but unconfirmed members of the family, and so the Halictidae is tentatively present there.

Family *incertae sedis* (Apocrita: Aculeata: Apoidea: Apiformes)

Figure 14E.

Specimens. Driftwood Canyon: SBA-4534. McAbee: SBA-2994. Republic: SR 06-22-01.

Vespoidea or Spheciformes family *incertae sedis* (Apocrita: Aculeata: Apoidea)

Figure 8D–E.

Specimens. McAbee: UWBM PB-4332, TRU F-1556ab, TRU F-1557, TRU F-1558, TRU F-1559. Republic: SR 08-33-04, SRUI 09-95-31.1.

Remarks. The wing venation of these seven wasps is similar to that of *Paleorhopalosoma menatensis* Nel *et al.* from the Paleocene of Menat (Nel *et al.* 2010). However, we question the attribution of *P. menatensis* to Rhopalosomatidae, as its wing venation strongly differs from the very characteristic venation of other Rhopalosomatidae and is similar to that of, *e.g.*, *Pompilopterus corpus* Rasnitsyn *et al.* from the Barremian of the United Kingdom (Rasnitsyn *et al.* 1998). The female tarsi are only slightly widened in *P. menatensis*, unlike the condition found in unquestionable Rhopalosomatidae. In addition, the Okanagan Highlands fossils, which have a great similarity to *P. menatensis* and are probably related to it, show a comparatively long pronotum with a straight hind margin (specimen TRU F-1557: Fig. 8E) and a triangular area comparable with a propodeal enclosure (TRU F-1559). This suggests that a more logical attribution of *P. menatensis* as well as these Okanagan Highlands fossils is to the Spheciformes, possibly near or in the Angarosphecidae. SR 08-33-04 is known from an isolated wing with similar venation, except that cell 1 mcu is somewhat longer and 3 rm is slightly shorter; it may be closely related to the above species. Finally, specimen UWBM PB-4332 has a somewhat similar general appearance. Its propodeum bears a structure suggesting a propodeal enclosure, and cell 2 rm has an odd form, with the only analogue being in *Pompilopterus wimbledoni* Rasnitsyn *et al.* (1998) from the Berriasian of the United Kingdom. It may be a member of the above assemblage or closely related.

Discussion

We find a minimum of 25 named families, or at least 30 including those tentatively assigned (Cynipidae and Halictidae) and those that are distinct at the family level but not currently associated with named families (*e.g.*, Chalcidoidea and Mymarommatoidea family *incertae sedis*), and surely a number of others (*e.g.*, see in the Apoidea) in collections of Okanagan Highlands Hymenoptera examined and confirmed in literature reviewed (Table 1).

McAbee (19 named families, maybe more than 24) and Republic (14 named families, maybe more than 16) show the greatest family diversities. Driftwood Canyon has a moderate family representation (nine named families, maybe more than 10), as do the localities at Horsefly River (seven named families, maybe more than eight), Quilchena (seven named families, maybe more than nine), and in the Allenby Formation (eight named families, maybe more than eight), about half or less of the family diversities of McAbee and Republic. The Falkland locality (four families) is much more difficult to access than the others, and its insects have been infrequently collected. Hat Creek amber has hardly been examined to date (three named families, maybe more than five), and, as expected, contains the smallest identified specimens, *e.g.*, Mymarommatoidea. These numbers among shale sites likely reflect differential collecting intensities to some degree, but McAbee does appear to be exceptional.

The recent rate of discovery is high – only three families had been recognised in the Okanagan Highlands fauna until the late 1950s and eight by the mid-1990s (Douglas and Stockey 1996). This will certainly continue to increase through the near future, not only from new compression fossils, but particularly as Okanagan Highlands amber is thoroughly examined. The Okanagan Highlands Hymenoptera can now be seen as among the more diverse family assemblages older than that in Baltic amber (Tables 2–3). The family numbers of these deposits reflect differential histories of attention to some degree (*e.g.*, insects of Baltic amber and Florissant shales have been treated in detail for over a century), and some include old records with identifications that are not to modern standards or which employ outdated family concepts, and so should be taken as generalities only. Still, informative patterns are emerging, and the formation and character of the Okanagan Highlands Hymenoptera community can be set in the context of preceding crises and opportunities in an increasingly angiosperm-dominated world punctuated by large-scale extinction, recovery, and dispersal events.

Table 2. Hymenoptera family numbers in major Cretaceous through Eocene deposits.

Paleogene (part)				
Eocene	Priabonian		Bembridge Marls, United Kingdom	20
			Florissant, Colorado, United States of America	37
			Baltic amber	55
			Rovno amber, Ukraine	30–31
	Lutetian		Eckfelt, Germany	6
			Messel, Germany	11
			Kishenehn Formation, United States of America	17
			Sakhalin amber, Russia	12
	Ypresian		Oise amber, France	13
			Fushun amber, China	12
			Cambay amber, India	6–8
			Green River Formation, United States of America	21
			Okanagan Highlands, Canada, United States of America	25–30
			Fur Formation, Denmark	6
Paleocene	Thanetian		Menat, France	10
Cretaceous				
Campanian			Canadian amber	31
Santonian			Kheta Formation amber, Russia	26
Turonian–Santonian?			Charentese amber, France	17
Turonian			Raritan amber, United States of America	18
			Orapa shale, Botswana	9–16
Cenomanian			Burmese amber	30
Albian			Spanish Albian amber	21
Hauterivian–Barremian			Levantine amber	17

References: Cretaceous ambers: Rasnitsyn *et al.* (2016); Orapa, Botswana: Brothers and Rasnitsyn (2003); Menat, France: Piton (1940) and Nel (1992, 2004), plus Formicidae, recognised here; Fur Formation, Denmark: Rust (1990, 1998); Green River Formation: summaries of Wilson (1978a), Grande (1984), Dehon *et al.* (2014), and A.P.R. (personal observation); Oise amber, France: Nel and Brasero (2010); Fushun amber, China: Wang *et al.* (2014a); Indian Cambay amber: Rust *et al.* (2010); Sakhalin amber, Russia: Zherikhin (1978), Simutnik (2014), and A.P.R. (personal observation); Kishenehn Formation: Huber and Greenwalt (2011), Greenwalt and Engel (2014), LaPolla and Greenwalt (2015), and D. Greenwalt (personal communication); Messel, Germany: Lutz (1990), Wappler and Engel (2003); Eckfelt, Germany: Wappler (2003); Rovno amber: Perkovsky *et al.* (2010); Baltic amber: see updated list Table 3 and references therein; Florissant: Meyer (2003); Bembridge Marls: Antropov *et al.* (2014).

Context

The establishment of angiosperm-dominated ecosystems. Perhaps the most profound biotic interactions that form and maintain modern terrestrial ecosystems are between angiosperms and Hymenoptera. Flowering plants are first confidently seen in the early Cretaceous and begin to define most terrestrial ecosystems by the mid-Cretaceous (Heimhofer *et al.* 2005; Doyle 2015), but the transition to an overwhelmingly angiosperm flora was only completed around Okanagan Highlands time (Niklas *et al.* 1983; Cleal and Cascales-Miñana 2014). Today, they comprise almost 90% of land-plant species (Pennisi 2009).

The Cretaceous-Paleogene extinction crisis. The end-Cretaceous extinction event appears to have had little or no effect on insects at the family level (*e.g.*, Grimaldi and Engel 2005; Rasnitsyn

et al. 2016; Perkovsky and Węgierek 2017). At lower taxonomic levels, however, ichnofossil evidence indicates that they suffered a significant disruption and losses in North America (with few exceptions), stabilising and recovering diversity by the end of the Paleocene (Labandeira *et al.* 2002; Wilf *et al.* 2006; Currano *et al.* 2008). Outside this region, however, insect–plant interactions appear to have suffered less, had a quicker recovery, or both (Wilf *et al.* 2005b; Iglesias *et al.* 2007; Wappler and Denk 2011; Wappler *et al.* 2012; Donovan *et al.* 2016). Plants suffered extensive impacts, of apparently differing intensities and durations across the globe (*e.g.*, Wilf and Johnson 2004; Wilf *et al.* 2005a; Iglesias *et al.* 2007; Barreda *et al.* 2012; Wappler *et al.* 2012). Changes in leaf morphologies suggest a shift in forest ecosystem functioning (Blonder *et al.* 2014). The Okanagan

Table 3. Hymenoptera families present in Baltic amber.

Symphyta		Cephoidea	Cephidae[A,B]
		Orussoidea	Orussidae[C]
		Siricoidea	Siricidae[A]
		Tenthredinoidea	Diprionidae[B]
			Electrotomidae[B]
			Tenthredinidae[A,D]
Apocrita	Parasitica	Trigonaloidea	Trigonalidae[B]
		Megalyroidea	Megalyridae[A,B]
		Stephanoidea	Stephanidae[A,B]
		Ceraphronoidea	Ceraphronidae[E]
			Megaspilidae[A]
		Evanioidea	Evaniidae[A,B]
			Gasteruptiidae[B]
		Mymarommatoidea	Mymarommatidae[A]
		Proctotrupoidea	Pelecinidae[A,B]
			Peradeniidae[B]
			Proctotrupidae[A,B]
		Diaprioidea	Diapriidae[A,B]
		Platygastroidea	Platygastridae[F]
			Scelionidae[A,B]
		Cynipoidea	Cynipidae[A,B]
			Figitidae[A,B]
			Ibaliidae[B]
		Chalcidoidea	Aphelinidae[G]
			Chalcididae[A]
			Encyrtidae[A]
			Eucharitidae[B]
			Eupelmidae[A,B]
			Mymaridae[A]
			Perilampidae[B]
			Pteromalidae[A]
			Tanaostigmatidae[B]
			Tetracampidae[A]
			Torymidae[A,B]
			Trichogrammatidae[G]
		Ichneumonoidea	Ichneumonidae[A,B]
			Braconidae[A,B]
	Aculeata	Chrysidoidea	Bethylidae[A,B]
			Chrysididae[A,B]
			Dryinidae[A,B]
			Embolemidae[A,B]
			Scolebythidae[A,B]
		Vespoidea	Formicidae[A,B]
			Mutillidae[A,B]
			Pompilidae[A,B]
			Tiphiidae[B]
			Vespidae[A,B]
		Apoidea	Ampulicidae[A]
			Andrenidae[A,B]
			Apidae[A,B]
			Crabronidae[A]
			Halictidae[B]
			Megachilidae[B]
			Melittidae[A,B]
			Paleomelittidae[B]

Note: Modified from Weitschat and Wichard ([A]1998, [B]2010), with additional information from [C]Schedl (2011), [D]Vilhelmsen and Engel (2012), [E]Kupryjanowicz (2001), [F]Buhl (2002), and [G]Burks *et al*. (2015). Gasteruptiidae appears in Weitschat and Wichard (2010) as Aulacidae.

Highlands shows forests that had rebounded to high, modern tropical levels of plant diversity (woody dicotyledons) (Wilf *et al*. 2003; Archibald *et al*. 2010; Smith *et al*. 2012).

The Paleocene/Eocene transition. The Ypresian was a time of Holarctic intercontinental dispersal, explaining some biogeographic patterns. Land connections between North America, Europe, and East Asia facilitated large-scale dispersal of plants and mammals (Manchester 1999; Tiffney 2000; Bowen *et al*. 2002). Insects share numerous closely related taxa between northern continents in the Eocene (Archibald 2005, 2009; Archibald *et al*. 2005, 2006, 2011b; Archibald and Makarkin 2006; Petrulevičius *et al*. 2007; Makarkin and Archibald 2013; Dlussky *et al*. 2015). This follows a brief hyperthermal spike in global temperatures by at least 5 °C at the Paleocene/Eocene boundary (Zachos *et al*. 2008).

The Okanagan Highlands. In the Ypresian of far-western North America, the Okanagan Highlands depositional basins were formed as tectonic uplift raised the interior of southern British Columbia and northern Washington (Ewing 1980), an upland of considerable elevation (estimates: Wolfe *et al*. 1998; Tribe 2005; Smith *et al*. 2009) spanning about 1000 km north to south (Archibald *et al*. 2011a). These localities are mostly coincident with the early Eocene Climatic Optimum, an interval of several million years with the highest sustained (*i.e*., excepting brief hyperthermal events) global temperatures of the Cenozoic (Zachos *et al*. 2008). The montane Okanagan Highlands localities, however, mostly had upper microthermal (≤13 °C) mean annual temperature at all sites except at Quilchena, which is estimated to have been a few degrees warmer (Mathewes *et al*. 2016). Winters were mild, with coldest-month mean temperatures ⩾8 °C indicated at most localities, implying low temperature seasonality (Archibald *et al*. 2010, 2014). Only the coeval Tadushi Formation of Pacific coastal Russia might also represent an Ypresian insect assemblage preserved in such a cooler upland (Archibald *et al*. 2005; age of the Tadushi: Popov and Grebennikov 2001), although some others may have had a mixture of source communities possibly including such an environment (*e.g*., the Fur Formation: Archibald and Makarkin 2006).

The Tadushi, however, contains fewer and less diverse Hymenoptera than the Okanagan Highlands despite large collections, a fact that cannot easily be explained as a taphonomic artefact, and may then represent a community with a genuinely smaller component of the order. Insect-bearing localities of the Kishenehn Formation (Montana) and at Florissant (Colorado) of the United States of America also represent uplands, but these were younger, after the Ypresian and the early Eocene Climatic Optimum (Meyer 2003; Fan *et al*. 2017).

The temperate, seasonally equable, and mesic sites of the Okanagan Highlands supported closed canopy forests that were in many ways like those of the modern eastern deciduous forest of North America. It was composed in large part of plant genera that today inhabit forests of this region, and some that range in low latitudes or in East Asia, as well as others that are now extinct (Greenwood *et al*. 2005; Moss *et al*. 2005; Archibald *et al*. 2011a). Insect alpha diversity has been measured at McAbee as similar to that of a modern lowland Neotropical rainforest, and there was high insect beta diversity across the series (Archibald *et al*. 2010, 2013). Its mild winters allowed frost-intolerant plants now restricted to low latitudes to coexist with temperate-climate flora characteristic of its mean annual temperature values, *e.g*., palms (Arecaceae) and spruce (Pinaceae) (Archibald and Farrell 2003; Archibald *et al*. 2011a, 2014). It records the first appearances and expansions of numerous genera of prominent plant families associated with temperate latitudes today (DeVore and Pigg 2007, 2009). Graham (2011) speculated that the Okanagan Highlands might represent the origin of boreal forests that subsequently spread into the lowlands by about 10 million years ago in the globally cooler Neogene.

The Hymenoptera assemblages

All 22 modern superfamilies of Hymenoptera were in existence by Okanagan Highlands times, 15 of which we find in these collections. There are no known extinct superfamilies of the order in the Cenozoic. Okanagan Highlands absences are mainly in the Parasitica: the Evanioidea, Megalyroidea, Platygastroidea, and Stephanoidea, but also a few in the Symphyta: the Xyeloidea, Xiphydrioidea, and Orussoidea. Many absent Parasitica are very small, and we suspect that some might appear as Okanagan Highlands amber is more thoroughly investigated. Other missing

groups might have been regionally absent, unsuited for the temperate, mesic upland environment; *e.g.*, the lack of Scelionidae, well represented in some Cretaceous and Priabonian assemblages, might be explained by their preference for warmer, drier habitats (Zherikhin *et al*. 2009). Some specimens belong to families for which few fossils are known, such as Trigonalidae, Siricidae, Peradeniidae, and Monomachidae (its single confirmed fossil, see above), and these may have been rare within the landscape.

Biogeography. As with plants, Okanagan Highlands insects constitute a mixture of those that are today associated with various climates of differing latitudes, which can also be explained by the combination of mostly microthermal mean annual temperature values with mild winters; *i.e.*, low temperature seasonality in a temperate setting (Archibald and Farrell 2003; Archibald *et al*. 2010). In plants, this is most clearly seen at lower taxonomic levels; although here we examine Hymenoptera families, these show broad trends consistent with this pattern (Benson 1946; Smith 1988; Brothers and Finnamore 1993; Finnamore and Michener 1993; Gibson 1993; Goulet 1993; Masner 1993a, 1993b; Mason 1993; Michener 1993; Ritchie 1993; Sharkey 1993; Wahl 1993; Schiff *et al*. 2012):

Cosmopolitan: Cimbicidae, Megaspilidae, Trigonalidae, Ichneumonidae, Braconidae, Diapriidae, Mymarommatoidea, Proctotrupidae, Cynipidae, Figitidae, Chalcidoidea, Sphecidae (*sensu stricto*), Megachilidae, Apidae, Vespidae, Formicidae;

Cosmopolitan, trending to temperate: Heloridae, Chrysididae;

Temperate and predominantly temperate: Cephidae, Pamphiliidae, Siricidae, Tenthredinidae, Peradeniidae, Roproniidae;

Predominantly tropical: Monomachidae, Pompilidae, Scoliidae.

Along with the expected presence of groups with predominantly modern northern distributions, such as various Symphyta, we see taxa like the Peradeniidae and Myrmeciinae (Formicidae) that join other Okanagan Highlands insects that are today native to the Australia/Southeast Asia region, like *Megymenum* Guérin-Méneville (Hemiptera:

Dinidoridae), and species of Nymphidae (Neuroptera) and Mastotermitidae (Isoptera). Monomachidae are today restricted to the Southern Hemisphere north into tropical Mexico (Johnson and Musetti 2012). Some groups show deeper biogeographic patterns, *e.g.*, the myrmeciine ants include species found in the Green River Formation of mid-continental United States of America, the Lutetian of Patagonia, and Baltic amber, and the extinct genus *Ypresiomyrma* is also known from the Ypresian Fur Formation of Denmark and the Priabonian Bol'shaya Svetlovodnaya (Biamo) of Pacific-coastal Russia, showing wide-spread Eocene dispersal before the later restriction of Myrmeciinae to the Australian region (Archibald *et al*. 2006 and references therein; Dlussky *et al*. 2015). The sole living genus of Peradeniidae, *Peradenia* Naumann and Masner, today restricted to Australia, is also known from Baltic amber (Johnson *et al*. 2001) (the McAbee specimen is not yet determined to genus).

Last occurrences/relictual taxa. Some taxa that were previously only known from the Cretaceous or were prominent then are last seen or are unexpectedly well represented in the Okanagan Highlands. *Cuspilongus cachcreekensis* Archibald and Rasnitsyn (Symphyta: Cephidae) from McAbee bears a distinctive, exceptionally long ovipositor (Fig. 2B), a trait shared within the family only by its sole congener and only other member of the Cuspilonginae, *C. ghilarovi* Rasnitsyn from the Aptian of Bon-Tsagaan, and so represents the single occurrence of this ancient lineage persisting into the Ypresian (Archibald and Rasnitsyn 2015; Kopylov and Rasnitsyn 2016). We find three specimens (Republic and Allenby Formation) belonging to the Archaeoscoliinae (Scoliidae), in contrast to only one reported from the very large, extensively collected Florissant assemblage. These are the only known occurrences of archaeoscoliines in the Cenozoic, a group that was diverse through the Cretaceous, found in Kazakhstan, Brazil, China, Spain, Siberia, and Mongolia (summarised: Rasnitsyn and Martínez-Delclòs 1999; Zhang 2004). Several Okanagan Highlands diaprioids from Driftwood Canyon, Horsefly River, and McAbee appear to belong to basal Diapriidae *sensu lato* not previously known after the early Cretaceous. There is an unexpectedly large representation of

angarosphecid Spheciformes, which were prominent in the early Cretaceous (see family treatment above) and were previously unknown in the Cenozoic outside of a single species in the Okanagan Highlands. Further, it is surprising that so large a number of other Okanagan Highlands Hymenoptera cannot be easily attributed to any family, which is unusual for the Cenozoic, more typical of the Mesozoic.

Earliest occurrences/taxon expansions. These fossils include the oldest confirmed occurrences of Monomachidae (but see a possible early Cretaceous occurrence, above), Trigonalidae, Peradeniidae, Pompilidae, and Sphecidae (*sensu stricto*), and perhaps others such as the Halictidae, although these await confirmation. Importantly, they also show the earliest evidence of notable diversifications within other families that were previously minor community elements. We discuss these below by trophic guilds, grouping fungivores with herbivores and separate from pollinivorous bees, treating parasitoids apart from predators, and considering ants separately by their wide range of roles.

Herbivores, fungivores

Fossils of siricomorph Symphyta are rare in the Okanagan Highlands – two of Siricidae, one of Pamphiliidae, and three of Cephidae – and are generally rare in the fossil record, and so new specimens are important (Archibald and Rasnitsyn 2015 and references therein). Okanagan Highlands forests contained many of the plant genera that they are associated with today, including some within the angiosperm families Rosaceae, Betulaceae, Cornaceae, Sapindaceae, Fagaceae, Juglandaceae, Oleaceae, Salicaceae, Ulmaceae, and Grossulariaceae, and the conifer families Pinaceae and Cupressaceae; many are characteristic of modern northern temperate latitudes, and some are early or earliest-known occurrences (Pigg *et al*. 2003; DeVore and Pigg 2007, 2009). These, together with a climatic regime of mean annual temperature values, provide the first appearance of the combination of conditions in the Okanagan Highlands that these Symphyta overwhelmingly prefer today.

The major diversity of modern herbivorous Hymenoptera is found in the Tenthredinoidea, which today has 7169 described species in six extant families (Aguiar *et al*. 2013). Tenthredinoid families associated with angiosperms are its most species-rich: the Argidae, Cimbicidae, Pergidae, and Tenthredinidae (except Selandriinae). The Tenthredinidae overwhelmingly dominate the superfamily with 5500 species (Aguiar *et al*. 2013; Isaka and Sato 2015). Molecular analysis indicates that the basal host plants of tenthredinoids were angiosperms, with a few groups subsequently switching to gymnosperms (Diprionidae) or pteridophytes (Blasticotomidae and Selandriinae) (Isaka and Sato 2015); however, while the fossil record of Blasticotomidae is not older than Florissant, they are morphologically closest to the predominantly Jurassic (and therefore pre-angiosperm) Xyelotomidae (Gao *et al*. 2009) implying the likelihood of a long ghost lineage. It further suggests that higher-level Tenthredinoidea would have been largely in place well before Okanagan Highlands time, although there are no fossils reported for Diprionidae older than Baltic amber (Schedl 2008) and for Argidae and Blasticotomidae older than Florissant (Zhelochovtzev and Rasnitsyn 1972, but a tentative argid from the Paleocene of Menat, France was reported by Nel 2004), and there is only equivocal fossil evidence of Pergidae (Krogmann *et al*. 2013).

The Mesozoic record of Tenthredinidae is small and little known. *Palaeathalia laiyangensis* Zhang from the early Cretaceous of Laiyang, China (Barremian to early Aptian) (Zhang 1985) was placed in the family, and leaf damage attributed to tenthredinids was described from the late Cretaceous (Turonian) Ora Formation of Israel (Krassilov and Rasnitsyn 2008). Grimaldi and Engel (2005) and Vilhelmsen and Engel (2012) subsequently considered all Mesozoic specimens assigned to the superfamily to be most conservatively treated as putative stem-group Tenthredinoidea. We believe *P. laiyangensis* to be a confident tenthredinid, however, which is supported by further undescribed fossils from the Cretaceous of Mongolia (Rasnitsyn 1980: Bon Tsagaan: Aptian; 17 specimens, possibly six others), Transbaikalia (Baissa: Valanginian; one to three specimens), and the Ola Formation (Obeshchayushchiy, Magadan Region, southeastern Siberia: Santonian to mid-Campanian; six to seven specimens) (A.P.R., personal observation). From this preliminary examination, it appears that these all either belong to *Palaeathalia* Zhang or differ slightly and are surely closely related, with little

variation within each site assemblage, consistent with low Mesozoic diversity within the family.

In the Paleocene, there is one described species of Tenthredinidae from Menat, France (Piton 1940; see review of Vilhelmsen and Engel 2012). We know of no undescribed Paleogene specimens older than the Okanagan Highlands, when the explosive species radiation within the family is now seen, a diversification that was previously thought to take place in the Priabonian (*e.g.*, see Florissant: Meyer 2003). In the Okanagan Highlands, two workers collecting an unbiased insect sample for about three weeks in a very limited portion of the McAbee recovered 26 tenthredinids (13% of Hymenoptera), which included 20 undescribed species assigned to the Tenthredininae, Allantinae, Blennocampinae, and Nematinae (Archibald *et al.* 2010). Rice (1968) reported further species of Allantinae at Horsefly River and in the Allenby Formation. The family has also been found elsewhere throughout the Okanagan Highlands, at Driftwood Canyon, Quilchena, and Republic (numerous specimens, exemplars listed above). In collections from the coeval Tadushi Formation (eastern Sikhote-Alin, Russian Far East: Ypresian) there are 26 tenthredinoid fossils (about 30% of Hymenoptera), with 12 wings that can be assigned to the Tenthredinidae in at least several unidentified subfamilies; although determination of Tadushi tenthredinid morphospecies diversity is difficult, as they are of varied preservation quality and all are incomplete, they preliminarily appear modern and diverse compared with the Cretaceous fossils discussed above (A.P.R., personal observation).

The oldest described species of Cimbicidae is from the Paleocene (Nel 2004), and no undescribed specimens pre-date this to our knowledge. This is followed by a species from the Green River Formation (Cockerell 1925) and those reported here from the coeval Okanagan Highlands, which include specimens from McAbee, the Allenby Formation, and Republic (above). McAbee specimens are assigned to the subfamilies Cimbicinae and Coryninae or Pachylostictinae (Archibald 2007). The unbiased McAbee sample has six specimens (3% of Hymenoptera) (Archibald *et al.* 2010); including these, we found a total of 14 in all collections examined.

Pollinators: bees

Bees are well known for their essential role today as the most important angiosperm pollinators (*e.g.*, Regal 1977; Michener 2007). Confident bee fossils first appear with three species with one specimen each from the Paleocene of Menat: *Paleoepeolus micheneri* Dehon *et al.* (Apidae), *Probombus hirsutus* Piton (Megachilidae), and *Paleohabropoda oudardi* Michez and Rasmont (Apidae) (Piton 1940; Nel and Petrulevičius 2003; Michez *et al.* 2009; Dehon *et al.* 2017). Molecular analyses support an older, cryptic Cretaceous record, but these were calibrated with fossils that include the advanced bee *Cretotrigona prisca* (Michener and Grimaldi) as Cretaceous, which we consider most likely younger (Cenozoic) and some using a Lutetian age for the rich record of Priabonian Baltic amber bees (*e.g.*, Rehan *et al.* 2010; Cardinal and Danforth 2013; Martins *et al.* 2014), or including the Cenomanian *Melittosphex burmensis* Poinar and Danforth, now considered to be in an unresolved position near crabronids and bees (Branstetter *et al.* 2017).

Proxy evidence supporting the existence of bees deep into the Cretaceous is provided by Turonian flowers with morphology today associated with bee pollination (Crepet and Nixon 1998; Crepet 2008). There was a variety of lineages of Jurassic and Cretaceous insect pollinators of various orders, some not associated with pollination today, some pre-dating angiosperms and associated with other plant groups, and others with angiosperms or stem-group proangiosperms (*e.g.*, Ren 1998; Krassilov and Rasnitsyn 1999; Krassilov *et al.* 2003; Ren *et al.* 2009; Labandeira 2010; Peñalver *et al.* 2015; Labandeira *et al.* 2016; Lu *et al.* 2016; Makarkin 2016). It is thought that the onset of angiosperms was associated not only with extinctions of some of these insect groups, but also with lateral transfer to angiosperm pollination in others, and origins of new angiosperm pollinators, some of which subsequently went extinct. This raises the possibility that one or more of these extinct insect groups might have been originally associated with these floral structures, which could have then been later exploited by bees as floral exaptations and so are today exclusively associated with them.

After the Paleocene, we see a rapid expansion of bee fossils beginning in Okanagan Highlands time, *i.e.*, the latter half of the Ypresian. Okanagan

Highlands bees include seven body fossils: the previously reported *Halictus*? *saveneyi* (Engel and Archibald 2003) from Quilchena (a possible halictid), and six new body-fossil specimens reported here from Republic (one possible halictid, one of undetermined family), McAbee (one apid, one possible halictid, one of undetermined family) and Driftwood Canyon (one of undetermined family). None appears to be conspecific. Ichnofossil evidence further indicates the presence of Megachilidae at Republic, McAbee, and Horsefly River (see above, Fig. 14H–I). Coeval specimens in Green River Formation shale (leaf damage, Megachilidae: Labandeira 2002; one body specimen, Apidae: Dehon *et al.* 2014), French Oise amber (one specimen, Melittidae: Michez *et al.* 2007), Indian Cambay amber (four specimens, three species in Apidae belonging to Electrapini and Melikertini: Engel *et al.* 2013a), and Chinese Fushun amber (one specimen, Apidae: Engel and Michener 2013), broaden the Ypresian record.

The Paleocene *P. micheneri* from Menat has morphology characteristic of cleptoparasitism (Dehon *et al.* 2017), and the Ypresian Oise melittid and some Lutetian German bees possess structures indicating specialised relationships with flowers (Michez *et al.* 2007; Wappler *et al.* 2015). These either support the notion of a long, cryptic, Cretaceous presence of bees, or alternatively that they had a later origin, burst of diversification, and rapid evolution of specialised behaviour and sophisticated pollination syndromes in concert with the onset of early Paleogene angiosperm modernisation.

Predators

Okanagan Highlands spheciform Apoidea include three specimens that are the earliest records of the Sphecidae (*sensu stricto*), previously known in Priabonian and younger deposits (see above). The superfamily is dominated by the Angarosphecidae, perhaps a paraphyletic grade of stem-apoids. These were plentiful and diverse in the later early Cretaceous and were thought to be long extinct by Okanagan Highlands time until *Eosphecium* was reported at Quilchena (Pulawski *et al.* 2000). The extent of the representation of these primitive wasps in the Okanagan Highlands reported here is unexpected.

In the Vespoidea, the Scoliidae and Pompilidae are present, but rare. The McAbee pompilid is the oldest confident record of its family. The Vespidae is well represented, with 14 specimens distributed among most major Okanagan Highlands localities: at Driftwood Canyon (two), McAbee (four), Quilchena (two), the Allenby Formation (one), and at Republic (five). It is a surprise that they are so well represented in the Okanagan Highlands, and a greater one yet that we can refer 12 to eusocial subfamilies. Because of their conservative wing morphology, a precise estimate of their species diversity is premature here; however, their relative sizes, shapes, and venations indicate that a number of species is represented, and that they are not repeated specimens of the same or a few species. Depending on the finalised number, this could be a larger representation of eusocial Vespidae than at any other site or site group (*e.g.*, Baltic amber) in the fossil record. The plentiful and diverse Formicidae are treated separately, below.

Parasitoids

About 75% of insect parasitoids belong to the Hymenoptera, most in the paraphyletic Parasitica, which constitutes the largest number of described species of the order (LaSalle and Gauld 1992; LaSalle 1993). Perhaps 77–99% remain undescribed, however, and they may represent some 80–85% of Hymenoptera and 20% of all insects (LaSalle and Gauld 1992). It is thought that food chains consisting of green plants, insect herbivores and the Parasitica contain over half of all metazoan species (May 1988). A typical English garden was found to have over 500 species of Ichneumonidae alone (Owen *et al.* 1981). They include many keystone species essential in regulating phytophagous insect populations and so maintaining plant diversity and ecosystem stability (Pimm and Lawton 1978; Hawkins and Lawton 1987; LaSalle and Gauld 1992; Hawkins 1993; LaSalle 1993).

The fossil record shows prominent parasitoid taxa undergoing major diversifications in the Paleogene, notably within the Chalcidoidea, Diaprioidea, and Ichneumonoidea (general overviews by Rasnitsyn 2002; Zherikhin 2002; of individual groups by Grimaldi and Engel 2005), and with major changes within the Platygastroidea.

Platygastroidea. Platygastroids are tiny (mostly 1–2 mm in length) endoparasitoids of insect eggs (Masner 1993c). The Platygastridae (*sensu stricto*) underwent a burst of diversification in the

© 2018 Entomological Society of Canada

Cenozoic, in contrast to the Scelionidae, which flourished in the Cretaceous (Rasnitsyn 1975; Ortega-Blanco *et al.* 2014). Neraudeau *et al.* (2008) reported four undescribed specimens of Platygastridae from uppermost Albian-lowermost Cenomanian French amber, but they meant Platygastridae (*sensu lato*), and the specimens referred to belong to Scelionidae (V. Perrichot, personal communication). Therefore, the earliest confident record of Platygastridae (*sensu stricto*) is in the Lutetian Kishenehn Formation (Talamas and Buffington 2015). They subsequently appear in Priabonian Baltic (four genera) and Scandanavian (three genera) ambers, and then in Miocene Dominican amber (25 genera) (Scandanavian: Buhl 2002; Baltic and Dominican: Talamas and Buffington 2015). Talamas and Buffington (2015) suggest that many of the species-level records of these are in need of revision. Platygastroids are currently unknown in the Okanagan Highlands.

Chalcidoidea. The chalcidoids are very small (3–5 mm or less in length), species-rich but poorly known wasps that are found in a wide variety of habitats worldwide (Gibson 1993). Although their fossil record extends to the earliest Cretaceous, they remained a relatively small group until they are found in greater abundance in the Priabonian, diversifying towards their modern ecological importance, perhaps in concert with their known primary hosts, Lepidoptera and brachyceran flies (Zherikhin 2002; Rasnitsyn *et al.* 2004; Zherikhin *et al.* 2009). Consistent with their minute size, their fossil record is almost entirely in amber, rarely in shale (Grimaldi and Engel 2005). In the Okanagan Highlands, they are known not only from the single specimen in Hat Creek amber, but also in shale, with one from McAbee and three from Driftwood Canyon, where small to minute insects are commonly preserved.

Diaprioidea. Today the superfamily is among the more speciose of the Parasitica (although far smaller than the Ichneumonoidea), and is dominated by the Diapriidae, which has 2048 of its 2109 species (Aguiar *et al.* 2013). They were scarcely known before the Priabonian (Rasnitsyn 2002; Zherikhin 2002), until large numbers of Belytinae were reported in the Lutetian Kishenehn Formation of Montana (Greenwalt and Labandeira 2013). However, it is currently

undetermined if these constitute many or few species. In the Okanagan Highlands assemblage, many appear modern: three belong to the diapriid subfamily Belytinae, and a further one may also be a belytine, but might also belong to the Ismaridae, and five wing specimens belong to the Diapriidae *sensu lato* (Diapriidae + Ismaridae: Sharkey *et al.* 2012). Seven surprisingly primitive specimens are apparently allied to early Cretaceous basal Diapriidae *sensu lato* (see above). From our preliminary observations, we estimate conservatively that there is a minimum of 10 species of the family in these collections.

Ichneumonoidea. The Ichneumonoidea are widely considered to be the most important group of entomophagous insects today (LaSalle and Gauld 1992). They comprise the great majority of described modern Parasitica, and dominate the Hymenoptera in species numbers: Ichneumonidae have some 24 025 described species and Braconidae some 19 205 (Aguiar *et al.* 2013), which is thought to be a small portion of a much greater total diversity of both – the Ichneumonidae alone may have more than 100 000 species (Rasnitsyn 1978).

The fossil record of the superfamily begins in the early Cretaceous, with all families present: the extant Ichneumonidae and Braconidae, and its extinct groups Praeichneumonidae (five described species), possibly paraphyletic with regard to extant Ichneumonoids (Kopylov 2012); and the Tanychorinae (22 species), described as a subfamily of the Ichneumonidae, but probably basal to Ichneumonidae + Braconidae (Kopylov 2010). The Ichneumonidae (excluding the Tanychorinae) have 37 described Cretaceous species, 12 in the early Cretaceous and 25 in the late Cretaceous (recently summarised by Menier *et al.* 2004; Li *et al.* 2017). These are represented by numerous specimens in shale deposits; all 12 early Cretaceous species, and 15 of the late Cretaceous species (Li *et al.* 2017). At Baissa, they are 1.1% of Hymenoptera; at Khasurtyi, 0%; at Bon-Tsagan, 10.1%; at Obeshchayushchii, 29%; and at Orapa, 4.6% (here, Tanychorinae are excluded, altering slightly the data provided by Kopylov 2010 and Brothers and Rasnitsyn 2003). In the Paleocene, a single species is known from Menat (Piton 1940), and in a collection of 2000 insects from the earliest Ypresian Fur Formation of Denmark there were 23 ichneumonids, all belonging to a single

named species (Rust 1990), with a few other unnamed ones found in subsequently examined collections (Rust 1999). They were previously known to be diverse first in the Priabonian (Bembridge Marls: Antropov *et al.* 2014; Florissant: Meyer 2003; further, see checklist of Menier *et al.* 2004), but here we see them both plentiful and diverse in the Okanagan Highlands. In samples taken from unbiased collecting (Archibald) at Driftwood Canyon, Horsefly River and McAbee, and from the SFU Quilchena collections (Mathewes) and the Stonerose Interpretive Center collection of Republic insects, there were 117 ichneumonid specimens with 94 morphospecies, almost three times the known species from the Cretaceous (Archibald *et al.* 2010, 2013).

The Braconidae (including the Eoichneumonidae) have ~36 species in the Cretaceous (Perrichot *et al.* 2009; Ortega-Blanco *et al.* 2011a; Belokobylskij 2012), but this is difficult to enumerate with precision because of undescribed specimens in current collections (A.P.R., personal observation) and many questionable published identifications in need of revision (Belokobylskij 2012). However, they reasonably appear to have a similar species richness in the Cretaceous as the Ichneumonidae. They are also seen as diverse first in the Priabonian (Baltic amber, Bembridge Marls, and Florissant: reviewed by Belokobylskij 2014). While they are present in the Okanagan Highlands, Braconidae are much less well represented than the Ichneumonidae in both species and number of specimens. The unbiased McAbee sample contains only six specimens, two of which were complete enough to assign to two species. The upland Tadushi Formation also has a small number of braconid specimens relative to ichneumonids (A.P.R., personal observation), but the reverse is true for the hot, lowland Green River Formation (A.P.R., personal observation: 21 Braconidae, 11 Ichneumonidae, unbiased collection in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; 105 versus 83 respectively, general collection in the National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, United States of America, A.P.R. determined in 1988). Ichneumonidae dominate in the Lutetian Kishenehn Formation of Montana (125 versus 67 Braconidae: D. Greenwalt, personal

communication). It is not yet determined whether these braconid fossils contain a few or many species. The differing patterns of relative abundance of Braconidae and Ichneumonidae among these localities may be due to a regionally varying factor such as climate, *e.g.*, the cooler Okanagan Highlands versus the warmer Green River Formation. Today, Ichneumonidae far outnumber Braconidae in cool, wet northern Siberia (S. Belokobylskij and D. Kasparyan, personal communication), and in samples from Harvard Forest in Massachusetts there were about three times the ichneumonid specimens as braconids, but in the tropical lowland forest at La Selva, Costa Rica, braconids were about double the number of ichneumonids (Archibald *et al.* 2010). Li *et al.* (2017) found this same pattern present in the Cretaceous, with Braconidae distributed widely across latitudes and Ichneumonidae prevalent outside of the tropics.

Ants: predators, herbivores, fungivores

The diversification of ant species and their increase in abundance in communities would have marked an important event in the development of modern terrestrial ecosystems. Today, they are ubiquitous, prospering in a wide variety of ecological niches worldwide, excluding the polar regions and isolated Pacific islands, comprising about 15–20% of global animal biomass, and about 25% in the tropics; in the Amazon *terra firme* rainforest, each hectare is thought to support over eight million individual ants; 43 species in 28 genera were recovered from a single tree in the Peruvian Amazon (Fittkau and Klinge 1973; Wilson 1987; Hölldobler and Wilson 1990; Schultz 2000). Ants are extremely efficient foragers, with large numbers of workers constantly monitoring large areas and rapidly mass-recruiting nest mates to exploit discovered food items. They are among the leading invertebrate predators in most terrestrial habitats, and in the tropics dead insects are scavenged within minutes (Carroll and Janzen 1973; Leston 1973; Hölldobler and Wilson 1990 and references therein). Ant predation protects plants from their herbivores: a colony of *Formica rufa* Linnaeus fed upon 21 700 caterpillars (Lepidoptera and Symphyta) in a day, and one of *F. polyctena* Förster took about six million prey items per year from a 0.33 ha plot (Hölldobler and Wilson 1990 and references therein). Leaf-cutter

ants are among the major herbivores of the Neotropics, as shown by recently measured consumption rates on Barro Colorado Island in Panama (Herz *et al.* 2007). They transport large amounts of nutrients in the form of leaf cuttings up to 6 m underground, modifying soil composition and facilitating deep root growth, and act as soil turners in many regions, in some surpassing termites and earthworms (reviewed by Hölldobler and Wilson 1990; LaSalle and Gauld 1993). In the humid tropics, keystone ant mosaics control rates of insect herbivory, defending against it in return for rewards (*e.g.*, domatia, extrafloral nectaries), or promoting it by tending herbivores (*e.g.*, aphids, caterpillars) (Leston 1978; Gilbert 1980; Pierce 1985). These relationships are highlighted by the evolution of ant domatia in over 90 genera of 36 plant families, and of extrafloral nectaries in at least 68 angiosperm families (Elias 1983; Hölldobler and Wilson 1990). In some regions, they are the principle granivores, dispersing seeds of many plants, reducing their competition, buffering the effects of local disturbance, and promoting growth in the nutrient-rich soils of their nests (Hölldobler and Wilson 1990; LaSalle and Gauld 1993). In New York State, United States of America, they disperse 37–48% of aboveground herbaceous biomass, half of all stems (Handel *et al.* 1981). Major insect pollinators (bees, some Diptera) may have flourished in this role at least in part through resistance to predation by ants (Leston 1973), and flowers may have evolved characters to exclude them (Faegri and van der Pijl 1979). In these ways, ants strongly influence differential floral and invertebrate patchiness, taxon compositions and diversities across the landscape, and so are a major factor controlling overall biotic composition, diversity, and distributions (Leston 1978; Gilbert 1980; Majer 1983).

While molecular analyses indicate that many higher-level ant taxa were established in the Cretaceous, only a few are confirmed by fossils (Engel and Grimaldi 2005; Moreau *et al.* 2006; LaPolla *et al.* 2013). Most recent hypotheses on the diversification of ants use "diversification" to mean divergence of their higher-level sub-taxa, although a few concern increase of richness at lower levels, which we mean here (*e.g.*, see differing meanings by Leston 1973; Wilson and Hölldobler 2005; Moreau *et al.* 2006; Dunn *et al.* 2007; Dlussky and Wedmann 2012; Lucky *et al.*

2013; Ward 2014). The Cretaceous fossil record suggests a low community presence and impact of small numbers of individuals and species (Zherikhin 2002; Barden and Grimaldi 2016). Cretaceous ants are discussed further in the family treatment above. Paleocene ants are little known, apart from *Ancistrocerus berlandi* Piton at Menat, described as a member of the Eumenidae (see Piton 1940: fig. 91) but which is surely an ant, and possible fragmentary evidence from the Paskapoo Formation of Alberta, Canada (Mitchell and Wighton 1979).

Ants first appear common and diverse in the Ypresian. A single ant species has been reported from the earliest Ypresian Fur Formation of Denmark (Rust and Andersen 1999) and 40 species in French Oise amber (approximately coeval with McAbee) (Aria *et al.* 2011; LaPolla *et al.* 2013); 27 species in Chinese Fushun amber (Hong 2002); 16 species from the Green River Formation (Dlussky and Rasnitsyn 2003); and a diverse collection of ants in Cambay amber, but with no estimation of species number (Rust *et al.* 2010). In the Okanagan Highlands, ants have been previously reported from a variety of sites (see family treatment above). Here, we conservatively find a preliminary estimate of about 50 Okanagan Highlands ant species in the collections examined and the above references, excluding numerous wing specimens and others that may well be recognised as distinct species in the future. We expect this number to grow, particularly as Okanagan Highlands amber is thoroughly examined.

Conclusions

The Okanagan Highlands show Hymenoptera in transition, with the last or among the last occurrences of some taxa that were diverse in, or were previously only known in the Mesozoic (*e.g.*, Angarosphecidae, Archaeoscoliinae, Cuspilonginae, some Diaprioidea), and the first appearances of some modern taxa (*e.g.*, Sphecidae *sensu stricto*, Pompilidae, Cephinae).

Biogeography

The mixture of taxa that today inhabit both temperate and low-latitude tropical climates is consistent with mostly upper microthermal mean annual temperatures combined with mild, likely frost-free winters, and is also seen in plants.

The community is also consistent with Holarctic dispersals through intercontinental connections as seen in plants and mammals. There is also a component that is today restricted to the Australian region.

Diversifications within ecologically key carnivore and herbivore groups

Phytophagous Hymenoptera species numbers increased towards modern prominence at a time of completion of the transition to angiosperm-dominated ecosystems, and the first evidence of temperate northern forests that would later spread through northern latitudes and the first appearances of many plant genera that characterise those forests today. This combination of climate and flora that Symphyta are mostly associated with today is not seen before the Okanagan Highlands. There is a great increase of species within the Tenthredinoidea, most importantly in the Tenthredinidae (at least 20 species in four subfamilies at McAbee alone), but also in the less diverse Cimbicidae. The beginning of the expansion of bees is seen in the latter half of the Ypresian, from three in the Paleocene to 14: seven in the Okanagan Highlands plus numerous specimens of Megachilidae leaf damage, one in the Green River Formation plus Megachilidae damage, one in Oise amber, four in Indian Cambay amber, and one in Fushun amber, indicating a shift towards modern pollination relationships.

Carnivorous Hymenoptera show notable diversifications within the Parasitica, in the Diapriodea and significantly in the highly ecologically important Ichneumonidae, with almost three times the number of species in the Okanagan Highlands as is known from the Cretaceous. Predators show diversifications within Vespidae (14 specimens, perhaps a few if any conspecific, 12 placed in eusocial subfamilies; only two specimens in two Paleocene species of eusocial Vespidae predate this) and ants (a minimum 50 species in the Okanagan Highlands, 30 in Oise amber; 27 in Fushin amber, 16 in the Green River Formation, and an unknown number in Indian Cambay amber; all earlier records are low diversity).

Diversifications within eusocial Hymenoptera

The establishment of the dominance of social insects is a major turning point in terrestrial ecology. May (1988) noted that, to a first order of approximation, insects comprise all animal life on Earth, and Hölldobler and Wilson (1990), taking a similarly broad point of view, went further to say that essentially all insects today are social insects. Engel *et al.* (2009, 2016) showed six termite species with various castes in Cenomanian Burmese amber, although they speculated that termites may not have begun their ascent to ecological prominence until the Priabonian, not achieving it until the Miocene. Rasnitsyn and Ross (2000), however, found a higher presence of termites in Burmese amber (about 91 of 1198 insects), indicating that they may have been prominent as far back as the mid-Cretaceous.

The record of eusocial Hymenoptera in the Cretaceous, however, is limited. Ants are found deep into the Cretaceous, but with a small presence, and eusocial wasps are indicated only by a single late Cretaceous fossil paper-wasp nest (Carpenter and Rasnitsyn 1990). It is not yet known if any Okanagan Highlands bees belong to social taxa. The oldest evidence of eusocial bees is the Ypresian Meliponini from Fushun amber and Electrapini and Melikertini from Cambay amber (Engel and Michener 2013; Engel *et al.* 2013a).

Might these diversifications of ecologically key Hymenoptera groups be older, masked by preservational bias?

The insect-rich Danish Fur Formation, immediately following the Paleocene/Eocene boundary in the earliest Ypresian, has no reported bees or social vespids, but bears plentiful specimens of ants and ichneumonids. Of the 2000 insects examined by Rust and Andersen (1999) in Fur Formation collections, however, all of the 101 ant specimens belong to the myrmeciine species *Ypresiomyrma rebekkae* (Rust and Andersen), and the ichneumons were also all placed in a single species by Rust (1990), who later estimated a few further, undescribed species in new collections (Rust 1999). The Fur, however, is a marine formation, and may have been highly selective for the subset of its source insect communities that flew near the shore at elevations and perhaps times of year with favourable winds to transport them to offshore depositional sites coinciding with the diatom blooms within which they are preserved. We know little about Paleocene insects apart from ichnofossil evidence, as they are barely

represented in insect body-fossil localities. The richest Paleocene insect fossil record at Menat suggests that while bees, social Vespidae, ants, Ichneumonidae, Tenthredinidae, and Cimbicidae were present, they were not important community elements. The Menat record is, however, poor for Hymenoptera in general (Piton 1940; Nel and Auvray 2006) and appears unexpectedly unbalanced, perhaps for unknown taphonomic reasons. The only Hymenoptera reported from the Paleocene insect assemblage of the Paskapoo Formation in Alberta, Canada are possible ant fragments (Mitchell and Wighton 1979).

If the lower-level diversifications of these key groups were earlier than the second half of the Ypresian, perhaps masked in the Fur and Paskapoo Formations and at Menat by taphonomic factors specific to those sites, they might also have been obscured in late Cretaceous deposits by yet other taphonomic processes. The Maastrichtian lacks insect localities except for North Dakota (United States of America) amber, which is little known (Rasnitsyn *et al.* 2016). The next oldest is Campanian Canadian amber, which is strongly biased towards smaller species (McKellar and Engel 2012). Late Cretaceous Hymenoptera are primarily known in amber. Even in larger-sized ambers, however, there appears to be a tendency to capture smaller insects relative to shale deposits (A.P.R., personal observation), potentially under-representing such groups as Symphyta, non-chrysidoid Aculeata and Ichneumonidae.

There are, however, some indirect reasons to suspect that at least some of the diversifications of these ecologically key hymenopteran taxa commenced in or soon before Okanagan Highlands times. Low-diversity Paleocene forests, at least in North America, diversifying to high, modern tropical levels of species diversity seen in various regions such as the Okanagan Highlands, coupled with the appearance of new forest types and diversifications of temperate plant families preferred by Symphyta, and the bottleneck and re-establishment of plant-insect interactions indicated by the North American leaf-damage record, would be consistent with diversification of phytophagous Hymenoptera and then others at higher trophic levels in the Ypresian. The aftermath of the Paleocene-Eocene Thermal Maximum shows diversifications in other organisms (*e.g.*, mammals: Gingerich 1987; Rea *et al.* 1990), associated not only with its dramatic and brief spike in global temperature, but also with Holarctic intercontinental dispersals.

The Ichneumonidae feed on a wide variety of immature holometabolous insects and various Chelicerata, but most commonly upon larvae of the Symphyta and Lepidoptera. We know that the most diverse symphytans, the Tenthredinidae, were at least somewhat numerous as individuals in the Cretaceous (above), and their high species richness is first seen in the Okanagan Highlands; however, they are scarcely known in amber – even in Priabonian Baltic amber after they are seen to be diverse in shale deposits (Vilhelmsen and Engel 2012) – and so their species diversity is unknown between their presence in the Santonian to mid-Campanian Ola Formation shale (see above) and the Okanagan Highlands. The fossil record shows Lepidoptera since the later early Jurassic, and a few rare specimens of diverse higher taxa of moths since the middle Jurassic (Zhang *et al.* 2013); molecular analyses indicate that its higher-level clades were in place during the Cretaceous, followed by a burst of diversification of modern lineages below that level in the Paleogene (Lepidoptera in general: Wahlberg *et al.* 2013; butterflies: Wahlberg *et al.* 2009; Heikkilä *et al.* 2012).

The argument for a post-Campanian diversification of ant lower taxa appears stronger, as Canadian amber should show this, but does not. The Fur and Menat records are suggestive, but inconclusive that high ant species diversity was not in place before the mid-Ypresian. An earlier history and cryptic diversity of bees is possible, as many are small, which, like ants, could have been preserved in Cretaceous ambers even of smaller size. Ants and bees are common and diverse in Priabonian Northern European and Miocene Dominican and Mexican ambers. Although the Maastrichtian and Paleocene insect body fossil record is depauperate, there is a good leaf record, and the characteristic leaf damage of megachilids first appears in the Ypresian of the Okanagan Highlands and the Green River Formation, soon after the oldest megachilid body fossil from Menat. Modernisation of angiosperm communities in the early Paleogene could be consistent with a concomitant diversification of bees. The tiny Diapriidae should be well represented, but have a small fossil record in Cretaceous ambers (see family treatment above).

For these reasons, while a mid to later Ypresian diversification of bees, ants, social vespids, Tenthredinoidea, Diaprioidea, and Ichneumonidae is possible, it remains somewhat speculative, perhaps clouded by differential taphonomic factors influencing fossil assemblage compositions between it and the late Cretaceous, and resting on the assumptions discussed above. Confirmation awaits future discoveries of Paleocene and more comparable late Cretaceous insect localities. What is clear now, however, is that these events were all underway at least as early as the mid-late Ypresian.

The Okanagan Highlands. If this diversification was a phenomenon of the latter half of the Ypresian, did the Okanagan Highlands play a particular role? Ants are also plentiful and diverse in some coeval deposits discussed above; however, there is scant evidence of higher species diversities of other key hymenopteran groups discussed until later. If the Okanagan Highlands were different beyond possessing a favourable taphonomic setting promoting unusually high fidelity of fossil assemblage to community representation, *i.e.*, if it was in fact composed of communities where at least some of these changes were first occurring, then why? The unique combination of an Ypresian temperate upland in a warm early Eocene Climatic Optimum world with a diversifying modern temperate flora and high-diversity insect and plant community at a time of large-scale intercontinental dispersal immediately presents itself for consideration. Detailed comparison of Okanagan Highlands Hymenoptera with other taphonomically equivalent assemblages of the later half of the Ypresian might suggest answers, *e.g.*, of Okanagan Highlands ambers with Oise, Cambay, and Fushun ambers, bearing in mind that we know none of these to have represented temperate, montane communities, nor do we know any such in the Paleocene or late Cretaceous.

The lower-level diversifications in these ecologically key Hymenoptera groups represent the onset of a major phase in insect evolution, not by the appearance of new body plans or higher-level taxa, but of the great lower-level expansion and impact of key functional groups within communities, ones that profoundly affect modern terrestrial ecosystems. While this change or parts of it may have commenced undetected in the later Cretaceous or the Paleocene, we now see the broad sweep of it certainly in place by the latter half of the Ypresian, most clearly in the diverse, temperate uplands of the Okanagan Highlands.

Acknowledgements

References

Achterberg, C.V. 2006. European species of the genus *Helorus* Latreille (Hymenoptera: Heloridae), with description of a new species from Sulawesi (Indonesia). Zoologische Mededelingen, **80**: 1–12.

Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T., *et al.* 2013. Order Hymenoptera. *In* Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (Addenda 2013). *Edited by* Z.-Q. Zhang. Zootaxa, **3703**: 51–62.

Antropov, A.V., Belokobylskij, S.A., Compton, S.G., Dlussky, G.M., Khalaim, A.I., Kolyada, V.A., *et al.* 2014. The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (late Eocene) of the Isle of Wight, UK. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **104**: 335–446.

Archibald, S.B. 2005. New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada; Washington State, USA). Canadian Journal of Earth Sciences, **42**: 119–136.

Archibald, S.B. 2007. Climate and species diversity: the Eocene Okanagan Highlands insect view. Volumes 1–2. Ph.D. thesis. Harvard University, Cambridge, Massachusetts, United States of America.

Archibald, S.B. 2009. New Cimbrophlebiidae (Insecta: Mecoptera) from the early Eocene at McAbee, British Columbia, Canada and Republic, Washington, USA. Zootaxa, **2249**: 51–62.

Archibald, S.B., Bossert, W.H., Greenwood, D.R., and Farrell, B.D. 2010. Seasonality, the latitudinal gradient of diversity, and Eocene insects. Paleobiology, **36**: 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: Myrmeciinae). Annals of the Entomological Society of America, **99**: 487–523.

Archibald, S.B. and Farrell, B.D. 2003. Wheeler's dilemma. Acta Zoologica Cracoviensia, **46**: 17–23. (supplement: fossil insects).

Archibald, S.B., Greenwood, D.R., and Mathewes, R.W. 2013. Seasonality, montane beta diversity, and Eocene insects: testing Janzen's dispersal hypothesis in an equable world. Palaeogeography, Palaeoclimatology, Palaeoecology, **371**: 1–8.

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

Archibald, S.B., Johnson, K.R., Mathewes, R.W., and Greenwood, D.R. 2011b. Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. Proceedings of the Royal Society B, **278**: 3679–3686.

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 Palaeontology, **4**: 119–155, 307 (errata).

Archibald, S.B. and Mathewes, R.W. 2000. Early Eocene insects from Quilchena, British Columbia and their paleoclimatic implications. Canadian Journal of Zoology, **78**: 1441–1462.

Archibald, S.B., Morse, G.E., Greenwood, D.R., and Mathewes, R.W. 2014. Fossil palm beetles refine upland winter temperatures in the early Eocene Climatic Optimum. Proceedings of the National Academy of Sciences of the United States of America, **111**: 8095–8100.

Archibald, S.B. and Rasnitsyn, A.P. 2015. New early Eocene Siricomorpha (Hymenoptera: Symphyta: Pamphiliidae, Siricidae, Cephidae) from the Okanagan Highlands, western North America. The Canadian Entomologist, **148**: 209–228.

Archibald, S.B., Rasnitsyn, A.P., and Akhmetiev, M.A. 2005. 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, **98**: 503–514.

Aria, C., Perrichot, V., and Nel, A. 2011. Fossil Ponerinae (Hymenoptera: Formicidae) in early Eocene amber of France. Zootaxa, **2870**: 53–62.

Barden, P. and Grimaldi, D.A. 2016. Adaptive radiation in socially advanced stem-group ants from the Cretaceous. Current Biology, **26**: 515–521.

Barreda, V.D., Cúneo, N.R., Wilf, P., Currano, E.D., Scasso, R.A., and Brinkhuis, H. 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. Public Library of Science One, **7**: e52455.

Belokobylskij, S.A. 2012. Cretaceous braconid wasps from the Magadan Province of Russia. Acta Palaeontologica Polonica, **57**: 351–361.

Belokobylskij, S.A. 2014. Family Braconidae Nees, 1812. *In* The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (late Eocene) of the Isle of Wight, UK. Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **104**: 360–392.

Benson, R.B. 1946. Classification of the Cephidae (Hymenoptera Symphyta). Transactions of the Royal Entomological Society of London, **96**: 89–108.

Berry, E. W. 1931. An insect-cut leaf from the Lower Eocene. American Journal of Science, **21**: 301–304.

Blonder, B., Royer, D.L., Johnson, K.R., Miller, I., and Enquist, B.J. 2014. Plant ecological strategies shift across the Cretaceous–Paleogene boundary. Public Library of Science Biology, **12**: e1001949.

Bolton, B. 2003. Synopsis and classification of Formicidae. American Entomological Institute, Gainesville, Florida, United States of America.

Bowen, G.J., Clyde, W.C., Koch, P.L., Faircloth, B.C., Ward, P.S., Buffington, M.L., *et al.* 2002. Mammal dispersal at the Paleocene/Eocene boundary. Science, **295**: 2062–2065.

Branstetter, M.G., Danforth, B.N., Pitts, J.P., Faircloth, B.C., Ward, P.S., Buffington, M.L., *et al.* 2017. Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. Current Biology, **27**: 1019–1025.

Brooks, H. K. 1955. Healed wounds and galls on fossil leaves from the Wilcox deposits (Eocene) of western Tennessee. Psyche, **62**: 1–9.

Brothers, D.J. 1992. The first Mesozoic Vespidae from the Southern Hemisphere, Botswana. Journal of Hymenoptera Research, **1**: 119–124.

Brothers, D.J. and Finnamore, A.T. 1993. Superfamily Vespoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 161–278.

Brothers, D.J. and Rasnitsyn, A.P. 2003. Diversity of Hymenoptera and other insects in the late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. African Entomology, **11**: 221–226.

Buffington, M.L., Brady, S.G., Morita, S.I., and Van Noort, I. 2012. Divergence estimates and early evolutionary history of Figitidae (Hymenoptera: Cynipoidea). Systematic Entomology, **37**: 287–304.

Buhl, P.N. 2002. On the Baltic amber collection of Platygastridae and Diapriidae. Entomologiske Meddelelser, **70**: 57–61.

Burks, R.A., Heraty, J.M., Pinto, J.D., and Grimaldi, D. 2015. Small but not ephemeral: newly discovered species of Aphelinidae and Trichogrammatidae (Insecta: Hymenoptera: Chalcidoidea) from Eocene amber. Systematic Entomology, **40**: 592–605.

Burnham, L. 1978. A survey of social insects in the fossil record. Psyche, **85**: 85–133.

Cameron, A.E. 1917. Fossil insects, with special reference to those of Tertiary lake deposits of the Similkameen Valley, BC. Proceedings of the Entomological Society of British Columbia, **10**: 21–29.

Cardinal, S. and Danforth, B.N. 2013. Bees diversified in the age of eudicots. Proceedings of the Royal Society B, **280**: 20122686.

Carmean, D. 1991. Biology of the Trigonalyidae (Hymenoptera), with notes on the vespine parasitoid *Bareogonalos canadensis*. New Zealand Journal of Zoology, **18**: 209–214.

Carmean, D. and Kimsey, L. 1998. Phylogenetic revision of the parasitoid wasp family Trigonalidae (Hymenoptera). Systematic Entomology, **23**: 35–76.

Carpenter, J.M. 2000. A vespid wasp from New Jersey amber. *In* Studies in fossil amber, with particular reference to the Cretaceous of New Jersey. *Edited by* D. Grimaldi. Backhuys Publishers, Leiden, The Netherlands. Pp. 333–337.

Carpenter, J.M. and Rasnitsyn, A.P. 1990. Mesozoic Vespidae. Psyche, **97**: 1–20.

Carroll, C.R. and Janzen, D.H. 1973. Ecology of foraging by ants. Annual Review of Ecology and Systematics, **4**: 231–257.

Cleal, C.J. and Cascales-Miñana, B. 2014. Composition and dynamics of the great Phanerozoic evolutionary floras. Lethaia, **47**: 469–484.

Cockerell, T.D.A. 1907. Some fossil arthropods from Florissant, Colorado. Bulletin of the American Museum of Natural History, **23**: 605–616.

Cockerell, T.D.A. 1910. A tertiary leaf-cutting bee. Nature, **82**: 429.

Cockerell, T.D.A. 1925. Fossil insects in the United States National Museum. Proceedings of the United States National Museum, **64**: 1–15.

Crepet, W.L. 2008. The fossil record of angiosperms: requiem or renaissance? Annals of the Missouri Botanical Garden, **95**: 3–33.

Crepet, W.L. and Nixon, K.C. 1998. Fossil Clusiaceae from the late Cretaceous (Turonian) of New Jersey and implications regarding the history of bee pollination. American Journal of Botany, **85**: 1122–1133.

Currano, E.D., Wilf, P., Wing, S.L., Labandeira, C.C., Lovelock, E.C., and Royer, D.L. 2008. Sharply increased insect herbivory during the Paleocene–Eocene thermal maximum. Proceedings of the National Academy of Sciences of the United States of America, **105**: 1960–1964.

Danforth, B.N., Cardinal, S., Praz, C., Almeida, E.A.B., and Michez, D. 2013. The impact of molecular data on our understanding of bee phylogeny and evolution. Annual Review of Entomology, **58**: 57–78.

Danforth, B.N. and Poinar, G.O. 2011. Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoidea: Melittosphecidae) and implications for early bee evolution. Journal of Paleontology, **85**: 882–891.

Davis, R.B., Baldauf, S.L., and Mayhew, P.J. 2010. The origins of species richness in the Hymenoptera: insights from a family-level supertree. BMC Evolutionary Biology, **10**: 109.

Dawson, G.M. 1879. Preliminary report on the physical and geological features of the southern portions of the interior of British Columbia, 1877. *In* Report of progress for 1877–1878. Geological Survey of Canada, Montréal, Québec, Canada. Pp. 1–187B.

Dehon, M., Michez, D., Nel, A., Engel, M.S., and De Meulemeester, T. 2014. Wing shape of four new bee fossils (Hymenoptera: Anthophila) provides insights to bee evolution. Public Library of Science One, **9**: e108865.

Dehon, M., Perrard, A., Engel, M.S., Nel, A., and Michez, D. 2017. Antiquity of cleptoparasitism among bees revealed by morphometric and phylogenetic analysis of a Paleocene fossil nomadine (Hymenoptera: Apidae). Systematic Entomology, **42**: 543–554.

De Meulemeester, T., Michez, D., Aytekin, A.M., and Danforth, B.N. 2012. Taxonomic affinity of halictid bee fossils (Hymenoptera: Anthophila) based on geometric morphometrics analyses of wing shape. Journal of Systematic Palaeontology, **10**: 755–764.

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 Okanogan Highlands of eastern Washington State, USA, and British Columbia, Canada. Plant Systematics and Evolution, **266**: 45–57.

DeVore, M.L. and Pigg, K.B. 2009. Floristic composition and comparison of middle Eocene to late Eocene and Oligocene floras in North America. Bulletin of Geosciences, **85**: 111–134.

Dilcher, D.L. 1973. Vegetation and vegetational history of northern Latin America. *Edited by* A. Graham. Elsevier, Amsterdam, The Netherlands. Pp. 39–59.

Dlussky, G.M. 1983. A new family of upper Cretaceous Hymenoptera – an "intermediate link" between the ants and the scolioids. Paleontological Journal, **17**: 65–78.

Dlussky, G.M. 1987. New Formicoidea (Hymenoptera) of the upper Cretaceous. Paleontological Journal, **21**: 146–150.

Dlussky, G.M. 1996. Ants (Hymenoptera: Formicidae) from Burmese amber. Paleontological Journal, **30**: 449–454.

Dlussky, G.M. 1999. The first find of the Formicoidea (Hymenoptera) in the lower Cretaceous of the Northern Hemisphere. Paleontological Journal, **33**: 274–277.

Dlussky, G.M., Brothers, D.J., and Rasnitsyn, A.P. 2004. The first late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. Insect Systematics & Evolution, **35**: 1–13.

Dlussky, G.M. and Rasnitsyn, A.P. 1999. Two new species of aculeate hymenopterans (Vespida = Hymenoptera) from the middle Eocene of the United States. Paleontological Journal, **33**: 546–549.

Dlussky, G.M. and Rasnitsyn, A.P. 2003. Ants (Hymenoptera: Formicidae) of Formation Green River and some other middle Eocene deposits of North America. Russian Entomological. Journal, **11**: 411–436.

Dlussky, G.M., Rasnitsyn, A.P., and Perfilieva, K.S. 2015. The ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (late Eocene of Sikhote-Alin, Russian Far East). Caucasian Entomological Bulletin, **11**: 131–152.

Dlussky, G.M. and Wedmann, S. 2012. The poneromorph ants (Hymenoptera: Amblyoponinae, Ectatomminae, Ponerinae) of Grube Messel, Germany: high biodiversity in the Eocene. Journal of Systematic Palaeontology, **10**: 725–753.

Dockery, D.T. 1996. Toward a revision of the generalized stratigraphic column of Mississippi. Mississippi Geology, **17**: 1–8.

Donovan, M.P., Iglesias, A., Wilf, P., Labandeira, C.C., and Cúneo, R.N. 2016. Rapid recovery of Patagonian plant–insect associations after the end-Cretaceous extinction. Nature Ecology & Evolution, **1**: 0012.

Douglas, S.D. and Stockey, R.A. 1996. Insect fossils in middle Eocene deposits from British Columbia and Washington State: faunal diversity and geological range extensions. Canadian Journal of Zoology, **74**: 1140–1157.

Doyle, J.A. 2015. Recognizing angiosperm clades in the early Cretaceous fossil record. Historical Biology, **27**: 414–429.

Dunn, R.R., Gove, A.D., Barraclough, T.G., Givnish, T.J., and Majer, J.D. 2007. Convergent evolution of an ant–plant mutualism across plant families, continents, and time. Evolutionary Ecology Research, **9**: 1349–1362.

Elias, T.S. 1983. Extrafloral nectaries: their structure and distribution. *In* The biology of nectaries. *Edited by* B. Bentley and T. Elias. Columbia University Press, New York, United States of America. Pp. 174–203.

Engel, M.S. 1999. *Megachile glaesaria*, the first megachilid bee fossil from amber (Hymenoptera: Megachilidae). American Museum Novitates, **3276**: 1–13.

Engel, M.S. 2000. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). American Museum Novitates, **3296**: 1–11.

Engel, M.S. 2006. A new cuckoo wasp of the genus *Ceratochrysis* in amber from the Dominican Republic (Hymenoptera: Chrysididae). Polskie Pismo Entomologiczne, **75**: 499–504.

Engel, M.S. and Archibald, S.B. 2003. An early Eocene bee (Hymenoptera: Halictidae) from Quilchena, British Columbia. The Canadian Entomologist, **135**: 63–69.

Engel, M.S., Barden, P., Riccio, M.L., and Grimaldi, D.A. 2016. Morphologically specialized termite castes and advanced sociality in the early Cretaceous. Current Biology, **26**: 522–530.

Engel, M.S. and Grimaldi, D.A. 2005. Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). American Museum Novitates, **3485**: 1–23.

Engel, M.S. and Grimaldi, D.A. 2006. The first Cretaceous spider wasp (Hymenoptera: Pompilidae). Journal of the Kansas Entomological Society, **79**: 359–368.

Engel, M.S. and Grimaldi, D.A. 2007. New false fairy wasps in Cretaceous amber from New Jersey and Myanmar (Hymenoptera: Mymarommatoidea). Transactions of the Kansas Academy of Science, **110**: 159–168.

Engel, M.S., Grimaldi, D.A., and Krishna, K. 2009. Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. American Museum Novitates, **3650**: 1–27.

Engel, M.S. and Michener, C.D. 2013. A minute stingless bee in Eocene Fushan amber from northeastern China (Hymenoptera: Apidae). Journal of Melittology, **14**: 1–10.

Engel, M.S., Ortega-Blanco, J., Nascimbene, P.C., and Singh, H. 2013a. The bees of early Eocene Cambay amber (Hymenoptera: Apidae). Journal of Melittology, **25**: 1–12.

Engel, M.S., Ortega-Blanco, J., Soriano, C., Grimaldi, D.A., and Delclòs, X. 2013b. A new lineage of enigmatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). American Museum Novitates, **3771**: 1–23.

Engel, M.S. and Perkovsky, E.E. 2006. An Eocene bee in Rovno amber, Ukraine (Hymenoptera: Megachilidae). American Museum Novitates, **3506**: 1–11.

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

Faegri, K. and van der Pijl, L. 1979. The principles of pollination ecology, 3rd edition, Pergamon Press, Oxford, New York, United States of America.

Fan, M., Constenius, K.N., and Dettman, D.L. 2017. Prolonged high relief in the northern Cordilleran orogenic front during middle and late Eocene extension based on stable isotope paleoaltimetry. Earth and Planetary Science Letters, **457**: 376–384.

Finnamore, A.T. and Brothers, D.J. 1993. Superfamily Chrysidoidea. In Hymenoptera of the world. Edited by H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 130–160.

Finnamore, A.T. and Michener, C.D. 1993. Superfamily Apoidea. In Hymenoptera of the world. Edited by H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 279–357.

Fittkau, E.J. and Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica, **5**: 2–14.

Gao, T., Ren, D., and Shih, C. 2009. The first Xyelotomidae (Hymenoptera) from the middle Jurassic in China. Annals of the Entomological Society of America, **102**: 588–596.

Gaston, K.J. 1991. The magnitude of global insect species richness. Conservation Biology, **5**: 283–296.

Gauld, I.D. 1988. Evolutionary patterns of host utilization by ichneurnonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). Biological Journal of the Linnean Society, **35**: 351–377.

Gibson, G.A.P. 1993. Superfamilies Mymarommatoidea, and Chalcidoidea. In Hymenoptera of the world. Edited by H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 570–655.

Gibson, G.A.P., Read, J., and Huber, J.T. 2007. Diversity, classification and higher relationships of Mymarommatoidea (Hymenoptera). Journal of Hymenoptera Research, **16**: 51–146.

Gilbert, L.E. 1980. Food web organization and the conservation of Neotropical diversity. In Conservation biology: an evolutionary–ecological perspective. Edited by M.E. Soulé and B.A. Wilcox. Sinauer Associates, Sunderland, Massachusetts, United States of America. Pp. 11–33.

Gingerich, P.D. 1987. Evolution and the fossil record: patterns, rates, and processes. Canadian Journal of Zoology, **65**: 1053–1060.

Gonzalez, V.H., Griswold, T., Praz, C.J., and Danforth, B.N. 2012. Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. Systematic Entomology, **37**: 261–286.

Goulet, H. 1993. Superfamilies Cephoidea, Megalodontoidea, Orussoidea, Siricoidea, Tenthredinoidea, and Xyeloidea. In Hymenoptera of the world. Edited by H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 101–129.

Graham, A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. American Journal of Botany, **98**: 336–351.

Grande, L. 1984. Paleontology of the Green River Formation, with a review of the fish fauna, 2nd edition. Bulletin of the Geological Survey of Wyoming 63. Geological Survey of Wyoming, Laramie, Wyoming, United States of America.

Greenwalt, D. and Engel, M.S. 2014. A diminutive pelecinid wasp from the Eocene Kishenehn Formation of northwestern Montana (Hymenoptera: Pelecinidae). Novitates Paleoentomologicae, **8**: 1–9.

Greenwalt, D. and Labandeira, C. 2013. The amazing fossil insects of the Eocene Kishenehn Formation in northwestern Montana. Rocks and Minerals, **88**: 434–441.

Greenwalt, D.E., Rose, T.R., Siljestrom, S.M., Goreva, Y.S., Constenius, K.N., and Wingerath, J.G. 2015. Taphonomic studies of the fossil insects of the middle Eocene Kishenehn Formation. Acta Palaeontologica Polonica, **60**: 931–947.

Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northern Washington State: climates and ecosystems across an Eocene landscape. Canadian Journal of Earth Sciences, **42**: 167–185.

Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. Annals of the Missouri Botanical Gardens, **86**: 373–406.

Grimaldi, D.A., Agosti, D., and Carpenter, J.M. 1997. New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. American Museum Novitates, **3208**: 1–43.

Grimaldi, D.A. and Engel, M.S. 2005. Evolution of the insects. Cambridge University Press, Cambridge, United Kingdom.

Grimaldi, D., Shedrinsky, A., and Wampler, T. 2000. A remarkable deposit of fossiliferous amber from the upper Cretaceous (Turonian) of New Jersey. *In* Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. *Edited by* D. Grimaldi. Backhuys Publishers, Leiden, The Netherlands. Pp. 1–76.

Gromov, V.V., Dmitriev, V.Y., Zherikhin, V.V., Lebedev, E.L., Ponomarenko, A.G., Rasnitsyn, A.P., and Sukaczewa, I.D. 1993. Melovye entomofauny basseina r. Ul'ia (Zapadtoe Priokhot'ie) [Cretaceous insects from Uljya-river Basin (West Okhot Region)]. *In* Mezozoiskie nasekomye I ostrakody Azii [Mesozoic insects and ostracods from Asia]. *Edited by* A.G. Ponomarenko. Trudy Paleontologicheskogo instituta Rossiiskoi Akademii Nauk SSSR [Transactions of the Paleontological Institute, Russian Academy of Sciences of the Union of Soviet Socialist Republics], **252**: 5–60. [In Russian].

Handel, S.N., Fisch, S.B., and Schatz, G.E. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. Bulletin of the Torrey Botanical Club, 430–437.

Handlirsch, A. 1910. Canadian fossil insects. Contributions to Canadian Paleontology, **2**: 5, Insects from the Tertiary lake deposits of the southern interior of British Columbia, collected by Mr. Lawrence M. Lambe in 1906. Geological Survey of Canada Memoir, **12**: 93–129.

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 (Boulder), **28**: 195–198.

Hawkins, B.A. 1993. Refuges, host population dynamics and the genesis of parasitoid diversity. *In* Hymenoptera and biodiversity. *Edited by* J. LaSalle and I.D. Gauld. CAB International, Wallingford, United Kingdom. Pp. 235–256.

Hawkins, B.A. and Lawton, J.H. 1987. Species richness for parasitoids of British phytophagous insects. Nature, **326**: 788–790.

Heer, O. 1847. Die Insektenfauna der Tertiärgebilde von Oeningen und Rodoboj in Croatien. W. Engelmann, Leipzig, Germany.

Heikkilä, M., Kaila, L., Mutanen, M., Peña, C., and Wahlberg, N. 2012. Cretaceous origin and repeated tertiary diversification of the redefined butterflies. Proceedings of the Royal Society of London B Biological Sciences, **279**: 1093–1099.

Heimhofer, U., Hochuli, P.A., Burla, S., Dinis, J.M.L., and Weissert, H. 2005. Timing of early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. Geology, **33**: 141–144.

Heraty, J.M. and Darling, D.C. 2009. Fossil Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea) from Baltic amber. Zootaxa, **2306**: 1–16.

Herz, H., Beyschlag, W., and Hölldobler, B. 2007. Herbivory rate of leaf-cutting ants in a tropical moist forest in Panama at the population and ecosystem scales. Biotropica, **39**: 482–488.

Hölldobler, B. and Wilson, E.O. 1990. The ants. Harvard University Press, Cambridge, Massachusetts, United States of America.

Hong, Y.C. 2002. Amber insect of China. Beijing Science and Technology Press, Beijing, China.

Huber, J.T. and Greenwalt, D. 2011. Compression fossil Mymaridae (Hymenoptera) from Kishenehn oil shales, with description of two new genera and review of Tertiary amber genera. *In* Advances in the systematics of fossil and modern insects: honouring Alexandr Rasnitsyn. *Edited by* D.E. Shcherbakov, M.S. Engel, and M.J. Sharkey. ZooKeys, **130**: 473–494.

Iglesias, A., Wilf, P., Johnson, K.R., Zamuner, A.B., Cúneo, N.R., Matheos, S.D., and Singer, B.S. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. Geology, **35**: 947–950.

Isaka, Y. and Sato, T. 2015. Was species diversification in Tenthredinoidea (Hymenoptera: Symphyta) related to the origin and diversification of angiosperms? The Canadian Entomologist, **147**: 443–458.

Janzen, D.H. 1981. The peak in North American ichneumonid species richness lies between 38° and 48°N. Ecology, **62**: 532–537.

Jell, P.A. and Duncan, P.A. 1986. Invertebrates, mainly insects, from the freshwater, lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *In* Plants and invertebrates from the lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria. *Edited by* P.A. Jell and J. Roberts. Association of Australian Palaeontologists, Sydney, Australia. Pp. 111–205.

Johnson, N.F. and Musetti, L. 2012. Genera of the parasitoid wasp family Monomachidae (Hymenoptera: Diaprioidea). Zootaxa, **3188**: 31–41.

Johnson, N.F., Musetti, L., and Janzen, J.-W. 2001. A new fossil species of the Australian endemic genus *Peradenia* Naumann & Masner (Hymenoptera: Proctotrupoidea, Peradeniidae) from Baltic amber. Insect Systematics and Evolution, **32**: 191–194.

Kim, C.-J., Lelej, A.S., Park, B., and Lee, J.-W. 2016. Review of the family Proctorenyxidae (Hymenoptera: Proctotrupoidea), with description of new species from South Korea. Zootaxa, **4103**: 94–100.

Klopfstein, S., Vilhelmsen, L., Heraty, J.M., Sharkey, M., and Ronquist, F. 2013. The Hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. Public Library of Science One, **8**: e69344.

Kodrul, T.M. 1999. Fitostratigrafiia paleogena yuzhnogo Sakhalina [Phytostratigraphy of the Paleogene of southern Sakhalin]. Trudy Geologicheskogo Instituta Rossiyskoy Akademii Nauk [Proceedings of the Geological Institute of the Russian Academy of Sciences], **519**: 1–150. [In Russian].

Kolyada, V.A. 2009. Revision of some parasitic wasps (Hymenoptera: Proctotrupoidea *sensu lato*) from the Florissant locality, United States. Paleontological Journal, **43**: 191–196.

Kolyada, V.A. and Mostovski, M.B. 2007. Revision of Proctotrupidae (Insecta: Hymenoptera) described by Ch. T. Brues from Baltic amber. Zootaxa, **1661**: 29–38.

Kolyada, V. and Perkovsky, E.A. 2011. New species of the genus *Disogmus* Förster (Hymenoptera, Proctotrupoidea, Proctotrupidae) from the Eocene Rovno amber. Zookeys, **130**: 455–459.

Kopylov, D.S. 2010. Ichneumonids of the subfamily Tanychorinae (Insecta: Hymenoptera: Ichneumonidae) from the lower Cretaceous of Transbaikalia and Mongolia. Paleontological Journal, **44**: 179–186.

Kopylov, D.S. 2012. New species of Praeichneumonidae (Hymenoptera, Ichneumonoidea) from the lower Cretaceous of Transbaikalia. Paleontological Journal, **46**: 66–72.

Kopylov, D.S., Brothers, D.J., and Rasnitsyn, A.P. 2010. Two new labenopimpline ichneumonids (Hymenoptera: Ichneumonidae) from the upper Cretaceous of southern Africa. African Invertebrates, **51**: 423–430.

Kopylov, D.S. and Rasnitsyn, A.P. 2016. Cephidae (Hymenoptera) of the Mesozoic. Euroasian Entomological Journal, **15**(supplement 1): 78–83.

Krassilov, V.A. and Rasnitsyn, A.P. 1999. Plant remains from the guts of fossil insects: evolutionary and paleoecological inferences. Proceedings of the First Palaeoentomological Conference Moscow 1998. Bratislava. AMBA/AM/PFICM98/1.99. AMBA Projects Publication, Bratislava, Slovakia. Pp. 65–72.

Krassilov, V.A. and Rasnitsyn, A.P. (editors). 2008. Plant-arthropod interactions in the early angiosperm history: evidence from the Cretaceous of Israel. Pensoft and Brill, Sofia, Bulgaria.

Krassilov, V., Tekleva, M., Meyer-Melikyan, N., and Rasnitsyn, A. 2003. New pollen morphotype from gut compression of a Cretaceous insect, and its bearing on palynomorphological evolution and palaeoecology. Cretaceous Research, **24**: 149–156.

Krogmann, L., Engel, M.S., Bechly, G., and Nel, A. 2013. Lower Cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta). Journal of Systematic Palaeontology, **11**: 83–89.

Kupryjanowicz, J. 2001. Arthropods in Baltic amber and their photographic record. *In* The amber treasure trove: part I, the Tadeusz Giecewicz's collection at the Museum of the Earth, Polish Academy of Sciences, Warsaw. *Edited by* B. Kosmowska-Ceranowicz. Museum of the Earth Documentary Studies 18. Museum of the Earth, Warsaw, Poland. Pp. 19–72, 36 plates.

Labandeira, C.C. 2002. Paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: a preliminary report. Rocky Mountain Geology, **37**: 31–59.

Labandeira, C.C. 2010. The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects. Annals of the Missouri Botanical Garden, **97**: 469–513.

Labandeira, C.C., Johnson, K.R., and Wilf, P. 2002. Impact of the terminal Cretaceous event on plant–insect associations. Proceedings of the National Academy of Sciences of the United States of America, **99**: 2061–2066.

Labandeira, C.C., Yang, Q., Santiago-Blay, J.A., Hotton, C.L., Monteiro, A., Wang, Y.J., *et al*. 2016. The evolutionary convergence of mid-Mesozoic lacewings and Cenozoic butterflies. Proceedings of the Royal Society B, **283**: 20152893.

LaPolla, J.S., Dlussky, G.M., and Perrichot, V. 2013. Ants and the fossil record. The Annual Review of Entomology, **58**: 609–630.

LaPolla, J.S. and Greenwalt, D.E. 2015. Fossil ants (Hymenoptera: Formicidae) of the middle Eocene Kishenehn Formation. Sociobiology, **62**: 163–174.

LaSalle, J. 1993. Parasitic Hymenoptera, biological control and biodiversity. *In* Hymenoptera and biodiversity. *Edited by* J. LaSalle and I.D. Gauld. CAB International, Wallingford, United Kingdom. Pp. 197–215.

LaSalle, J. and Gauld, I.D. 1992. Parasitic Hymenoptera and the biodiversity crisis. Redia, **74**: 315–334.

LaSalle, J. and Gauld, I.D. 1993. Hymenoptera: their diversity, and impact on the diversity of other organisms. *In* Hymenoptera and biodiversity. *Edited by* J. LaSalle and I.D. Gauld. CAB International, Wallingford, United Kingdom. Pp. 1–26.

Lenz, O. K., Wilde, V., Mertz, D. F., and Riegel, W. 2015. New palynology-based astronomical and revised ^{40}Ar/^{39}Ar ages for the Eocene maar lake of Messel (Germany). International Journal of Earth Sciences, **104**: 873–889.

Leston, D. 1973. The ant mosaic – tropical tree crops and the limiting of pests and diseases. Pest Articles & News Summaries, **19**: 311–341.

Leston, D. 1978. A Neotropical ant mosaic. Annals of the Entomological Society of America, **71**: 649–653.

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

Lewis, S.E. 1994. Evidence of leaf-cutting bee damage from the Republic sites (middle Eocene) of Washington. Journal of Paleontology, **68**: 172–173.

Li, L., Kopylov, D.S., Shih, C., and Ren, D. 2017. The first record of Ichneumonidae (Insecta: Hymenoptera) from the upper Cretaceous of Myanmar. Cretaceous Research, **70**: 152–162.

Liu, Z., Engel, M., and Grimaldi, D.A. 2007. Phylogeny and geological history of the cynipoid wasps (Hymenoptera: Cynipoidea). American Museum Novitates, **3583**: 1–48.

Lu, X.M., Zhang, W.W., and Liu, X.Y. 2016. New long-proboscid lacewings of the mid-Cretaceous provide insights into ancient plant-pollinator interactions. Scientific Reports, **6**: 25382.

Lucky, A., Trautwein, M.D., Guenard, B.S., Weiser, M.D., and Dunn, R.R. 2013. Tracing the rise of ants – out of the ground. Public Library of Science One, **8**: e84012.

Lutz, H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. Courier Forschungsinstitut Senckenberg, **124**: 1–165.

Majer, J.D. 1983. Ants: bioindicators of minesite rehabilitation, land use and land conservation. Environmental Management, **7**: 375–383.

Makarkin, V.N. 2016. Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera, Sisyridae) from Burmese amber imply nectarivory or hematophagy. Cretaceous Research, **65**: 126–137.

Makarkin, V.N. and Archibald, S.B. 2013. A diverse new assemblage of green lacewings (Insecta, Neuroptera, Chrysopidae) from the early Eocene Okanagan Highlands, western North America. Journal of Paleontology, **87**: 123–146.

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

Martins, A.C., Melo, G.A., and Renner, S.S. 2014. The corbiculate bees arose from New World oil-collecting bees: implications for the origin of pollen baskets. Molecular Phylogenetics and Evolution, **80**: 88–94.

Masner, L. 1993a. Superfamily Ceraphronoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 566–569.

Masner, L. 1993b. Superfamily Proctotrupoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 537–557.

Masner, L. 1993c. Superfamily Platygasteroidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 558–565.

Mason, W.R.M. 1993. Superfamilies Evanioidea, Stephanoidea, Megalyroidea, and Trigonalyoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 510–520.

Mathewes, R.W., Greenwood, D.R., and Archibald, S.B. 2016. Paleoenvironment of the Quilchena flora, British Columbia, during the early Eocene Climatic Optimum. Canadian Journal of Earth Sciences, **53**: 574–590.

May, R.M. 1988. How many species are there on Earth? Science, **241**: 1441–1449.

McKellar, R.C. and Engel, M.S. 2011. New Stigmaphronidae and Megaspilidae (Hymenoptera: Ceraphronoidea) from Canadian Cretaceous amber. Cretaceous Research, **32**: 794–805.

McKellar, R.C. and Engel, M.S. 2012. Hymenoptera in Canadian Cretaceous amber (Insecta). Cretaceous Research, **35**: 258–279.

McKellar, R.C., Kopylov, D.S., and Engel, M.S. 2013. Ichneumonidae (Insecta: Hymenoptera) in Canadian late Cretaceous amber. Fossil Record, **16**: 217–227.

McLeroy, C.A. and Anderson, R.Y. 1996. Laminations of the Oligocene Florissant Lake deposits, Colorado. Geological Society of America Bulletin, **77**: 605–618.

Menier, J.-J., Nel, A., Waller, A., and De Ploëg, G. 2004. A new fossil ichneumon wasp from the lowermost Eocene amber of Paris Basin (France), with a checklist of fossil Ichneumonoidea *sl* (Insecta: Hymenoptera: Ichneumonidae: Metopiinae). Geologica Acta, **2**: 83–94.

Menke, A.S. and Rasnitsyn, A.P. 1987. Affinities of the fossil wasp *Hoplisidea kohliana* Cockerell (Hymenoptera: Sphecidae: Sphecinae). Psyche, **94**: 35–38.

Meyer, H.W. 2003. The fossils of Florissant. Smithsonian Books, Washington, District of Columbia, United States of America.

Michener, C.D. 1993. Series Apiformes. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 307–321.

Michener, C.D. 2007. The bees of the world, 2nd edition, Johns Hopkins University Press, Baltimore, Maryland, United States of America.

Michener, C.D. and Grimaldi, D.A. 1988. A *Trigona* from late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). American Museum Novitates, **2917**: 1–10.

Michez, D., De Meulemeester, T., Rasmont, P., Nel, A., and Patiny, S. 2009. New fossil evidence of the early diversification of bees: *Paleohabropoda oudardi* from the French Paleocene (Hymenoptera, Apidae, Anthophorini). Zoologica Scripta, **38**: 171–181.

Michez, D., Nel, A., Menier, J.-J., and Rasmont, P. 2007. The oldest fossil of a melittid bee (Hymenoptera: Apiformes) from the early Eocene of Oise (France). Zoological Journal of the Linnean Society, **150**: 701–709.

Mitchell, P. and Wighton, D. 1979. Larval and adult insects from the Paleocene of Alberta, Canada. The Canadian Entomologist, **111**: 777–782.

Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., and Pierce, N.E. 2006. Phylogeny of the ants: diversification in the age of angiosperms. Science, **312**: 101–104.

Moss, P.T., Greenwood, D.R., and Archibald, S.B. 2005. Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia/Washington State) from palynology. Canadian Journal of Earth Sciences, **42**: 187–204.

Mustoe, G.E. 2005. Diatomaceous origin of siliceous shale in Eocene lake beds of central British Columbia. Canadian Journal of Earth Sciences, **42**: 231–241.

Mustoe, G.E. 2015. Geologic history of Eocene Stonerose Fossil Beds, Republic, Washington, USA. Geosciences, **5**: 243–263.

Naumann, I.D. and Masner, L. 1985. Parasitic wasps of the proctotrupoid complex: a new family from Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). Australian Journal of Zoology, **33**: 761–783.

Nel, A. 1992. Révision du statut de *Manevalia pachyliformis* Piton, 1940 (Insecta, Heteroptera, Hymenoptera). Entomologica Gallica, **3**: 76–77.

Nel, A. 2004. New and poorly known Cenozoic sawflies of France (Hymenoptera, Tenthredinoidea, Pamphilioidea). Deutsche Entomologische Zeitschrift, **51**: 253–269.

Nel, A. and Auvray, F. 2006. The oldest Vespinae from the Paleocene of Menat (France) (Hymenoptera: Vespidae). Zootaxa, **1344**: 59–62.

Nel, A., Azar, D., and Hevret, S. 2010. A new rhopalosomatid wasp in the Paleocene of France (Hymenoptera). Annales de la Société Entomologique de France, **46**: 211–215.

Nel, A. and Brasero, N. 2010. Oise amber. *In* Biodiversity of fossils in amber from the major world deposits. *Edited by* D. Penney. Siri Scientific Press, Manchester, United Kingdom. Pp. 137–148.

Nel, A., de Ploëg, G, Millet, J., Menier, J.-J., and Waller, A. 2004. The French ambers: a general conspectus and the lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. Geologica Acta, **2**: 3–8.

Nel, A., Perrault, G., Perrichot, V., and Néraudeau, D. 2004. The oldest ant in the lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). Geologica Acta, **2**: 23–29.

Nel, A., Perrichot, V., and Néraudeau, D. 2003. The oldest trigonalid wasp in the late Albian amber of Charente-Maritime (SW France) (Hymenoptera: Trigonalidae). Eclogae Geologicae Helvetiae, **96**: 503–508.

Nel, A. and Petrulevičius, J.F. 2003. New Palaeogene bees from Europe and Asia. Alcheringa, **27**: 277–293.

Neraudeau, D., Perrichot, V., Colin, J.-P., Girard, V., Gomez, B., Guillocheau, F. 2008. A new amber deposit from the Cretaceous (uppermost Albian-lowermost Cenomanian) of southwestern France. Cretaceous Research, **29**: 925–929.

Nesov, L.A. 1985. NBovye mlekopitayushchie mela Kyzulkumov [New mammals in the Cretaceous of Kyzylkum]. Vestnik of St. Petersburg State University, Biology Series, **17**: 8–18. [In Russian].

Nesov, L.A. 1995. Dinozavry Severnoi Evrazii: Novye dannye o sostave kompleksov, ekologii I paleogeografii [Dinosaurs of the northern Eurasia: new data on the composition of assemblages, ecology and paleobiogeography]. Institut zemnoi kory St. Peterburgskogo Gosudarstvennogo Universiteta [Earth Crust Institute of St. Petersburg State University], St. Petersburg, Russia. [In Russian].

Niklas, K.J., Tiffney, B.H., and Knoll, A.H. 1983. Patterns in vascular land plant diversification. Nature, **303**: 614–616.

O'Brien, N.R., Meyer, H.W., and Harding, I.C. 2008. The role of biofilms in fossil preservation, Florissant Formation, Colorado. *In* Paleontology of the upper Eocene Florissant Formation, Colorado. *Edited by* H.W. Meyer and D.M. Smith. Boulder, Colorado, United States of America. Geological Society of America Special Papers, **435**: 19–31.

O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A.M., and Maguire, S. 2002. Microbial taphonomic processes in the fossilization of insects and plants in the late Eocene Florissant Formation, Colorado. Rocky Mountain Geology, **37**: 1–11.

Ohl, M and Engel, M.S. 2007. Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). Denisia, **20**: 687–700.

Ortega-Blanco, J., Delclòs, X., and Engel, M. 2011a. A Protorhyssaline wasp in early Cretaceous amber from Spain (Hymenoptera: Braconidae). Journal of the Kansas Entomological Society, **84**: 51–57.

Ortega-Blanco, J., McKellar, R.C., and Engel, M.S. 2014. Diverse scelionid wasps from early Cretaceous Álava amber, Spain (Hymenoptera: Platygastroidea). Bulletin of Geosciences, **89**: 553–571.

Ortega-Blanco, J., Peñalver, E., Delclòs, X., and Engel, M. 2011b. False fairy wasps in early Cretaceous amber from Spain (Hymenoptera: Mymarommatoidea). Palaeontology, **54**: 511–523.

Owen, J., Townes, H., and Townes, M. 1981. Species diversity of Ichneumonidae and Serphidae (Hymenoptera) in an English suburban garden. Biological Journal of the Linnean Society, **16**: 315–336.

Peñalver, E., Arillo, A., Pérez-de la Fuente, R., Riccio, M.L., Delclòs, X., Barrón, E., and Grimaldi, D.A. 2015. Long-proboscid flies as pollinators of Cretaceous gymnosperms. Current Biology, **25**: 1917–1923.

Pennisi, E. 2009. On the origin of flowering plants. Science, **324**: 28–31.

Perkovsky, E.E., Rasnitsyn, A.P., Vlaskin, A.P., and Taraschuk, M.V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. African Invertebrates, **48**: 229–245.

Perkovsky, E.E. and Węgierek, P. 2017. Aphid-*Buchnera*-ant symbiosis, or why are aphids rare in the tropics and very rare further south? Earth and Environmental Science Transactions of the Royal Society of Edinburgh, in press.

Perkovsky, E.E., Zosimovich, V.Y., and Vlaskin, A.P. 2010. Rovno amber. *In* Biodiversity of fossils in amber from the major world deposits. *Edited by* D. Penney. Siri Scientific Press, Manchester, United Kingdom. Pp. 116–136.

Perrard, A., Grimaldi, D., and Carpenter, J.M. 2017. Early lineages of Vespidae (Hymenoptera) in Cretaceous amber. Systematic Entomology, **42**: 379–368.

Perrichot, V. 2015. A new species of *Baikuris* (Hymenoptera: Formicidae: Sphecomyrminae) in mid-Cretaceous amber from France. Cretaceous Research, **52**: 585–590.

Perrichot, V., Lacau, S., Néraudeau, D., and Nel, A. 2008a. Fossil evidence for the early ant evolution. Naturwissenschaften, **95**: 85–90.

Perrichot, V. and Nel, A. 2008. A new belytine wasp in Cretaceous amber from France (Hymenoptera: Diapriidae). Alavesia, **2**: 203–209.

Perrichot, V., Nel, A., Néraudeau, D., Lacau, S., and Guyot, T. 2008b. New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). Naturwissenschaften, **95**: 91–97.

Perrichot, V., Nel, A., and Quicke, D.L.J. 2009. New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea. Zoologica Scripta, **38**: 79–88.

Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., *et al.* 2017. Evolutionary history of the Hymenoptera. Current Biology, **27**: 1013–1018.

Petrulevičius, J.F., Nel, A., Rust, J., Bechly, G., and Kohls, D. 2007. New Paleogene Epallagidae (Insecta: Odonata) recorded in North America and Europe. Biogeographic implications. Alavesia, **1**: 15–25.

Pierce, N.E. 1985. Lycaenid butterflies and ants: selection for nitrogen-fixing and other protein-rich food plants. The American Naturalist, **125**: 888–895.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B., and Travassos, M.A. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology, **47**: 733–771.

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

Pilgrim, E.F., Von Dohlen, C.D., and Pitts, J.P. 2008. Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. Zoologica Scripta, **37**: 539–560.

Pimm, S.L. and Lawton, J.H. 1978. On feeding on more than one trophic level. Nature, **275**: 542–544.

Piton, L.-E. 1940. Paléontologie du Gisement Éocène de Menat (Puy-de-Dôme) (flore et faune). Mémoires de la Société d′Histoire Naturelle d′Auvergne, **1**: 1–303 + 2 unnumbered.

Poinar, G. 2005. Fossil Trigonalidae and Vespidae (Hymenoptera) in Baltic amber. Proceedings of the Entomological Society of Washington, **107**: 55–63.

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

Poinar, G.O. and Danforth, B.N. 2006. A fossil bee from early Cretaceous Burmese amber. Science, **314**: 614.

Popov, V.K. and Grebennikov, A.V. 2001. Novye dannye o vozraste effuzivov bogopol'skoi svity v Primorye [New data on the age of effusives from the Bogopol Formation in Primorye]. Tikhookeanskaya Geologiya [Pacific Geology], **3**: 47–54. [In Russian].

Pulawski, W.J., Rasnitsyn, A.P., Brothers, D.J., and Archibald, S.B. 2000. New genera of Angarosphecinae: *Cretosphecium* from early Cretaceous of Mongolia and *Eosphecium* from early Eocene of Canada (Hymenoptera: Sphecidae). Journal of Hymenoptera Research, **9**: 34–40.

Quicke, D.L.J. 2012. We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology. Public Library of Science One, **7**: e32101.

Radchenko, A.G. and Dlussky, G.M. 2015. First record of fossil species of the genus *Tetramorium* (Hymenoptera, Formicidae). Vestnik zoologii, **49**: 311–316.

Rasnitsyn, A.P. 1968. Novye Mezozojskie Pilil'shhiki (Hymenoptera, Symphyta). [New Mesozoic sawflies (Hymenoptera, Symphyta)]. *In* Jurskie Nasekomye Karatau [Jurassic insects of Karatau]. *Edited by* B.B. Rodendorf. Nauka, Moskow, Russia. Pp. 190–236. [In Russian].

Rasnitsyn, A.P. 1975. Vysshie pereponchatokrylye mezozoya [Hymenoptera Apocrita of Mesozoic]. Trudy Paleontologicheskogo instituta Akademii Nauk SSSR [Transactions of the Palaeontological Institute of the Academy of Sciences of the Union of Soviet Socialist Republics], **147**: 1–134, 8 plates. [In Russian].

Rasnitsyn, A.P. 1978. Predislovie [Introduction]. *In* Vostochnopalearkticheskie pereponchatokrylye nasekomye podsemeistva Ichneumoninae [Eastern Palearctic Ichneumoninae]. *Edited by* G.H. Heinrich. Nauka PressLeningradskoe otdelenie [Leningrad Branch], Leningrad, Union of Soviet Socialist Republics. Pp. 3–5. [In Russian].

Rasnitsyn, A.P. 1980. Proiskhozhdenie I evolutsiia pereponchatokrylykh nasekomykh [The origin and evolution of Hymenoptera]. Trudy Paleontologicheskogo instituta Akademii Nauk SSSR [Transactions of the Paleontological Institute of the Academy of Sciences of the Union of Soviet Socialist Republics], **174**: 1–192. [In Russian].

Rasnitsyn, A.P. 1990a. Novye pereponchatokrylye semeistva Praeaulacidae iz rannego mela Buriatii I Mongolii [New Hymenoptera of the family Praeaulacidae from the early Cretaceous in Buriatia and Mongolia]. Vestnik Zoologii, **1990**: 27–31. [In Russian].

Rasnitsyn, A.P. 1990b. Otryad Vespida. Pereponchatokrylye [Order Vespida. Hymenopterans]. *In* Pozdnemezozoiskie nasekomye Vostochnogo Zabaikalya [Late Mesozoic insects of eastern Transbaikalia]. *Edited by* A.P. Rasnitsyn. Nauka, Moscow, Russia. Trudy Paleontologicheskogo instituta Akademii Nauk SSSR [Transactions of the Paleontological Institute of the Academy of Sciences of the Union of Soviet Socialist Republics], **239**: 177–205. [In Russian].

Rasnitsyn, A.P. 1993. Archaeoscoliinae, an extinct subfamily of scoliid wasps (Insecta: Vespida = Hymenoptera: Scoliidae). Journal of Hymenoptera Research, **2**: 85–95.

Rasnitsyn, A.P. 2002. Superorder Vespidea, Laicharting, 1781. Order Hymenoptera Linne, 1758 (= Vespida, Laicharting, 1781). *In* History of insects. *Edited by* A.P. Rasnitsyn and D.L.J. Quicke. Kluwer Academic Publishers, Dordrecht, The Netherlands. Pp. 242–254.

Rasnitsyn, A.P. and Ansorge, J. 2000. New early Cretaceous hymenopterous insects (Insecta: Hymenoptera) from Sierra del Montsec (Spain). Paläontologische Zeitschrift, **74**: 335–341.

Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Y.A., *et al.* 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). Cretaceous Research, **61**: 234–255.

Rasnitsyn, A.P., Basibuyuk, H.H., and Quicke, D.L.J. 2004. A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. Insect Systematics and Evolution, **35**: 123–135.

Rasnitsyn, A.P., Jarzembowski, E.A., and Ross, A.J. 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. Cretaceous Research, **19**: 329–391.

Rasnitsyn, A.P. and Martínez-Delclòs, X. 1999. New Cretaceous Scoliidae (Vespida = Hymenoptera) from the lower Cretaceous of Spain and Brazil. Cretaceous Research, **20**: 767–772.

Rasnitsyn, A.P. and Michener, C.D. 1991. Miocene fossil bumble bee from the Soviet Far East with comments on the chronology and distribution of fossil bees (Hymenoptera: Apidae). Annals of the Entomological Society of America, **84**: 583–589.

Rasnitsyn, A.P., Pulawski, W.J., and Martínez-Delclòs, X. 1999. Cretaceous digger wasps of the new genus *Bestiola* Pulawski and Rasnitsyn (Hymenoptera: Sphecidae: Angarosphecinae). Journal of Hymenoptera Research, **8**: 23–34.

Rasnitsyn, A.P. and Ross, A.J. 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. Bulletin of the Natural History Museum, Geological Series, **56**: 21–24.

Rea, D.K., Zachos, J.C., Owen, R.M., and Gingerich, P.D. 1990. Global change at the Paleocene–Eocene boundary: climatic and evolutionary consequences of tectonic events. Palaeogeography, Palaeoclimatology, and Palaeoecology, **79**: 178–128.

Regal, P.J. 1977. Ecology and evolution of flowering plant dominance. Science, **196**: 622–629.

Rehan, S.M., Chapman, T.W., Craigie, A.I., Richards, M.H., Cooper, S.J., and Schwarz, M.P. 2010. Molecular phylogeny of the small carpenter bees (Hymenoptera: Apidae: Ceratinini) indicates early and rapid global dispersal. Molecular Phylogenetics and Evolution, **55**: 1042–1054.

Ren, D. 1998. Flower-associated Brachycera flies as fossil evidence for Jurassic angiosperm origins. Science, **280**: 85–88.

Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A., Shih, C., Bashkuev, A., *et al.* 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. Science, **326**: 840–847.

Rice, H.M.A. 1968. Two tertiary sawflies (Hymenoptera-Tenthredinidae) from British Columbia. Geological Survey of Canada Paper, **67–59**: i–vi, 1–21.

Ritchie, A.J. 1993. Superfamily Cynipoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 521–536.

Rodriguez, J., Waichert, C., von Dohlen, C.D., Poinar, G., and Pitts, J.P. 2016. Eocene and not Cretaceous origin of spider wasps: fossil evidence from amber. Acta Palaeontologica Polonica, **61**: 89–96.

Ronquist, F., Nieves-Aldrey, J.-L., Buffington, M.L., Liu, Z., Liljeblad, J., and Nylander, J.A.A. 2015. Phylogeny, evolution and classification of gall wasps: the plot thickens. Public Library of Science One, **10**: e0123301.

Roselli, F.L. 1939. Apuntes de geología y paleontología Uruguaya y sobre insectos del Cretácico del Uruguay o descubrimentos de admirables instintos constructivos de esa época. Boletin de la Sociedad Amigos de las Ciencias Naturales 'Kraglievich-Fontana', **1**: 72–102.

Rust, J. 1990. Insekten aus der Fur-Formation von Dänemark (Moler, Ob. Paleozän/Unt. Eozän?). 3 Hymenoptera. Meyniana, **42**: 25–45.

Rust, J. 1999. Fossil insects from the Fur and Olst Formations ("Mo Clay") of Denmark (Upper Paleocene/Lowermost Eocene). Proceedings of the First International Palaeoentomological Conference, Moscow 1998. AMBA/AM/PFICM98/1.99. AMBA Projects Publication, Bratislava, Slovakia. Pp. 135–139.

Rust, J. and Andersen, N.M. 1999. Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae). Zoological Journal of the Linnean Society, **125**: 331–348.

Rust, J., Singh, H., Rana, R.S., McCann, T., Singh, L., Anderson, K., *et al*. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proceedings of the National Academy of Sciences of the United States of America, **107**: 18360–18365.

Sarzetti, L.C., Labandeira, C.C., and Genise, J.F. 2008. A leafcutter bee trace fossil from the middle Eocene of Patagonia, Argentina, and a review of megachilid (Hymenoptera) ichnology. Palaeontology, **51**: 933–941.

Schedl, W. 2008. Nachweis eines Männchens von *Eodiprion* sp. aus dem baltischen Bernstein (Hymenoptera: Symphyta: Diprionidae). Berichte des naturwissenschaftlichmedizinischen Vereins in Innsbruck, **95**: 77–80.

Schedl, W. 2011. Eine Orussidae aus dem baltischen Bernstein (Hymenoptera: Symphyta). Zeitschrift der Arbeitsgemeinschaft österreichischer Entomologen, **63**: 33–36.

Schiff, N.M., Goulet, H., Smith, D.R., Boudreault, C., Wilson, A.D., and Scheffler, B.E. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. Canadian Journal of Arthropod Identification, **21**: 1–305.

Schultz, T.R. 2000. In search of ant ancestors. Proceedings of the National Academy of Sciences of the United States of America, **97**: 14028–14029.

Scudder, S.H. 1877. The insects at the tertiary beds at Quesnel. Appendix to Mr. George Mercer Dawson's report. Report of Progress to the Geological Survey of Canada, 1875–1876: 266–280.

Scudder, S.H. 1878. Additions to the insect fauna of the Tertiary beds at Quesnel (British Columbia). Report of Progress to the Geological Survey of Canada, 1876–1877: 457–464.

Scudder, S.H. 1879. Appendix A: The fossil insects collected in 1877 by Mr. G. M. Dawson, in the interior of British Columbia. Report of Progress for the Geological Survey of Canada, 1877–1878: 175B–185B.

Scudder, S.H. 1890. The tertiary insects of North America. United States Geological Survey of the Territories, Washington, District of Columbia, United States of America.

Sharkey, M.J. 1993. Family Braconidae. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 362–395.

Sharkey, M.J. 2007. Phylogeny and classification of Hymenoptera. Zootaxa, **1668**: 521–548.

Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., *et al*. 2012. Phylogenetic relationships among superfamilies of Hymenoptera. Cladistics, **28**: 80–112.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, M., *et al*. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research, **37**: 155–163.

Shi, X., Zhao, Y., Shih, C., and Ren, D. 2013. New fossil helorid wasps (Insecta, Hymenoptera, Proctotrupoidea) from the Jehol Biota, China. Cretaceous Research, **41**: 136–142.

Shi, X., Zhao, Y., Shih, C., and Ren, D. 2014. Two new species of *Archaeohelorus* (Hymenoptera, Proctotrupoidea, Heloridae) from the middle Jurassic of China. ZooKeys, **369**: 49–59.

Shih, C., Feng, H., and Ren, D. 2011. New fossil Heloridae and Mesoserphidae wasps (Insecta, Hymenoptera, Proctotrupoidea) from the middle Jurassic of China. Annals of the Entomological Society of America, **104**: 1334–1348.

Simutnik, S.A. 2014. The first record of Encyrtidae (Hymenoptera, Chalcidoidea) from the Sakhalin Amber. Paleontological Journal, **48**: 621–623.

Skidmore, R.E. 1999. Checklist of Canadian amber inclusions in the Canadian National Collection of Insects. Electronic Publication. Research Branch Agriculture and Agri-food Canada, Ottawa, Ontario, Canada. Available from http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.616.5680 [accessed 30 October 2017].

Smith, D.R. 1988. A synopsis of the sawflies (Hymenoptera: Symphyta) of America south of the United States: introduction, Xyelidae, Pamphiliidae, Cimbicidae, Diprionidae, Xiphydriidae, Siricidae, Orussidae, Cephidae. Systematic Entomology, **13**: 205–261.

Smith, D.R. 2003. A synopsis of the sawflies (Hymenoptera: Symphyta) of America south of the United States: Tenthredinidae (Nematinae, Heterarthrinae, Tenthredininae). Transactions of the American Entomological Society, **129**: 1–45.

Smith, M.E., Singer, B., and Carroll, A. 2003. ^{40}Ar/^{39}Ar geochronology of the Green River Formation, Wyoming. Geological Society of America Bulletin, **115**: 549–565.

Smith, M.E., Singer, B.S., and Carroll., A.R. 2004. Discussion and Reply: ^{40}Ar/^{39}Ar geochronology of the Green River Formation, Wyoming (reply). Geological Society of America Bulletin, **116**: 251–256.

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, **46**: 811–822.

Smith, R.Y., Basinger, J.F., and Greenwood, D.R. 2012. Early Eocene plant diversity and dynamics in the Falkland flora, Okanagan Highlands, British Columbia, Canada. Palaeobiodiversity and Palaeoenvironments, **92**: 309–328.

Song, S.N., Tang, P., Wei, S.J., and Chen, X.X. 2016. Comparative and phylogenetic analysis of the mitochondrial genomes in basal hymenopterans. Scientific Reports, **6**: 20972.

Taeger, A., Blank, S.M., and Liston, A.D. 2010. World catalog of Symphyta (Hymenoptera). Zootaxa, **2580**: 1–1064.

Talamas, E. and Buffington, M. 2015. Fossil Platygastroidea in the National Museum of Natural History, Smithsonian Institution. Journal of Hymenoptera Research, **47**: 1–52.

Tiffney, B.H. 2000. Geographic and climatic influences on the Cretaceous and tertiary history of Euramerican floristic similarity. Acta Universitatis Carolinae Geologica, **44**: 5–16.

Townes, H.K. 1950. The Nearctic species of Gasteruptiidae (Hymenoptera). Proceedings of the United States National Museum, **100**: 85–145.

Tribe, S. 2005. Eocene paleo-physiography and drainage directions, southern Interior Plateau, British Columbia. Canadian Journal of Earth Sciences, **42**: 215–230.

Veijalainen, A., Wahlberg, N., Broad, G.R., Erwin, T. L., Longino, J.T., and Sääksjärvi, I.E. 2012. Unprecedented ichneumonid parasitoid wasp diversity in tropical forests. Proceedings of the Royal Society B, **279**: 4694–4698.

Vilhelmsen, L. and Engel, M.S. 2012. *Sambia succinica*, a crown group tenthredinid from Eocene Baltic amber (Hymenoptera: Tenthredinidae). Insect Systematics & Evolution, **43**: 271–281.

Wahl, D.B. 1993. Family Ichneumonidae. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 395–442.

Wahl, D.B. and Sharkey, M.J. 1993. Superfamily Ichenumonoidea. *In* Hymenoptera of the world. *Edited by* H. Goulet and J.T. Huber. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. Pp. 358–509.

Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L., and Brower, A.V.Z. 2009. Nymphalid butterflies diversify following near demise at the Cretaceous/tertiary boundary. Proceedings of the Royal Society B, **276**: 4295–4302.

Wahlberg, N., Wheat, C.W., and Peña, C. 2013. Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). Public Library of Science One, **8**: e80875.

Wang, B., Rust, J., Engel, M.S., Szwedo, J., Dutta, S., Nel, A., *et al.* 2014a. A diverse paleobiota in early Eocene Fushun amber from China. Current Biology, **24**: 1606–1610.

Wang, M., Rasnitsyn, A.P., Li, H., Shih, C., Sharkey, M.J., and Dong, R. 2016. Phylogenetic analyses elucidate the inter-relationships of Pamphilioidea (Hymenoptera, Symphyta). Cladistics, **32**: 239–260.

Wang, M., Rasnitsyn, A.P., Shih, C.K., and Ren, D. 2014b. A new fossil genus in Pamphiliidae (Hymenoptera) from China. Alcheringa, **38**: 1–7.

Wappler, T. 2003. Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. Mainzer Naturwissenschaftliches Archiv, **27**: 1–234, 18 plates.

Wappler, T., De Meulemeester, T., Aytekin, A.M., Michez, D., and Engel, M.S. 2012. Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae). Systematic Entomology, **37**: 784–792.

Wappler, T. and Denk, T. 2011. Herbivory in early tertiary Arctic forests. Palaogeography, Palaeoclimatology, Palaeoecology, **310**: 283–295.

Wappler, T. and Engel, M.S. 2003. The middle Eocene bee faunas of the Eckfeld Maar and Messel, Germany (Hymenoptera: Apoidea). Journal of Paleontology, **77**: 908–921.

Wappler, T., Labandeira, C.C., Engel, M.S., Zetter, R., and Grímsson, F. 2015. Specialized and generalized pollen-collection strategies in an ancient bee lineage. Current Biology, **25**: 1–7.

Wappler, T., Labandeira, C.C., Rust, J., Frankenhäuser, H., and Wilde, V. 2012. Testing for the effects and consequences of mid Paleogene climate change on insect Herbivory. Public Library of Science One, **7**: e40744.

Ward, P.S. 2014. The phylogeny and evolution of ants. Annual Review of Ecology, Evolution, and Systematics, **45**: 23–43.

Wedmann, S. 1998. First records of fossil tremicine hymenopterans. Palaeontology, **41**: 929–938.

Wedmann, S., Pouillon, J.-M., and Nel, A. 2014. New Palaeogene horntail wasps (Hymenoptera, Siricidae) and a discussion of their fossil record. Zootaxa, **3869**: 33–43.

Wedmann, S., Wappler, T., and Engel, M.S. 2009. Direct and indirect fossil records of megachilid bees from the Paleogene of Central Europe (Hymenoptera: Megachilidae). Naturwissenschaften, **96**: 703–712.

Wehr, W.C. 1998. Middle Eocene insects and plants of the Okanagon Highlands. *In* Contributions to the paleontology and geology of the West Coast: in honor of V. Standish Mallory. *Edited by* J.E. Martin. Burke Museum, Research Report, **6**: 99–109.

Wehr, W.C. and Barksdale, L.L. 1996. A checklist of fossil insects from Republic, Washington. Washington Geology, **24**: 29.

Weinstein, P. and Austin, A.D. 1991. The host relationships of trigonalyid wasps (Hymenoptera: Trigonalyidae), with a review of their biology and catalogue to world species. Journal of Natural History, **25**: 399–433.

Weitschat, W. and Wichard, W. 1998. Atlas der Pflanzen und Tiere im Baltischen Bernstein. Dr. Friedrich Pfeil, Munich, Germany.

Weitschat, W. and Wichard, W. 2010. Baltic amber. *In* Biodiversity of fossils in amber from the major world deposits. *Edited by* D. Penney. Siri Scientific Press, Manchester, United Kingdom. Pp. 80–115.

Wenzel, J.W. 1990. A social wasp's nest from the Cretaceous Period, Utah, USA, and its biogeographical significance. Psyche, **97**: 21–29.

Wheeler, W.M. 1911. A list of the type species of the genera and subgenera of Formicidae. Annals of the New York Academy of Sciences, **21**: 157–175.

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

Wilf, P. and Johnson, K.R. 2004. Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record. Paleobiology, **30**: 347–368.

Wilf, P., Johnson, K.R., Cúneo, N.R., Smith, M.E., Singer, B.S., and Gandolfo, M.A. 2005a. Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. The American Naturalist, **165**: 634–650.

Wilf, P., Labandeira, C.C., Johnson, K.R., Cúneo, N.R., and Dilcher, D.L. 2005b. Richness of plant-insect associations in Eocene Patagonia: a legacy for South American biodiversity. Proceedings of the National Academy of Sciences of the United States of America, **102**: 8944–8948.

Wilf, P., Labandeira, C.C., Johnson, K.R., and Ellis, B. 2006. Decoupled plant and insect diversity after the end-Cretaceous extinction. Science, **313**: 1112–1115.

Wilson, E.O. 1985. Ants from the Cretaceous and Eocene amber of North America. Psyche, **92**: 205–216.

Wilson, E.O. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. Biotropica, **19**: 245–251.

Wilson, E.O., Brown, W.L., and Carpenter, F.M. 1967. The first Mesozoic ants, with the description of a new subfamily. Psyche, **74**: 1–19.

Wilson, E.O. and Hölldobler, B. 2005. The rise of the ants: a phylogenetic and ecological explanation. Proceedings of the National Academy of Sciences of the United States of America, **102**: 7411–7414.

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

Wilson, M.V.H. 1977b. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Canadian Journal of Earth Sciences, **14**: 953–962.

Wilson, M.V.H. 1978a. Paleogene insect faunas of western North America. Quaestiones Entomologicae, **14**: 13–34.

Wilson, M.V.H. 1978b. Evolutionary significance of North American Paleogene insect faunas. Quaestiones Entomologicae, **14**: 35–42.

Wilson, M.V.H. 1982. Early Cenozoic insects: paleoenvironmental biases and evolution of the North American insect fauna. Proceedings of Third North American Paleontological Convention, **2**: 585–588.

Wolfe, A.P. and Edlund, M.B. 2005. Taxonomy, phylogeny, and paleoecology of *Eoseira wilsonii* gen. et sp. nov., a middle Eocene diatom (Bacillariophyceae: Aulacoseiraceae) from lake sediments at Horsefly, British Columbia, Canada. Canadian Journal of Earth Sciences, **42**: 243–257.

Wolfe, J.A., Forest, C.E., and Molnar, P. 1998. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. Geological Society of America Bulletin, **110**: 664–678.

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

Zeuner, F.E. and Manning, F.J. 1976. A monograph on fossil bees (Hymenoptera, Apoidea). Bulletin of the British Museum (Natural History). Geology, **27**: 149–268, 4 plates.

Zhang, H.C., Rasnitsyn, A.P., and Zhang, J.F. 2002. The oldest known scoliid wasps (Insecta, Hymenoptera, Scoliidae) from the Jehol biota of western Liaoning, China. Cretaceous Research, **23**: 77–86.

Zhang, H.C. and Zhang, J. 2000. Proctotrupoid wasps (Insecta, Hymenoptera) from the Yixian Formation of western Liaoning Province. Acta Micropalaeontologica Sinica, **18**: 11–28.

Zhang, J. 2004. New representatives of *Cretoscolia* (Insecta: Hymenoptera: Scoliidae) from eastern China. Cretaceous Research, **25**: 229–234.

Zhang, J.-F. 1985. New data of the Mesozoic fossil insects from Laiyang in Shandong. Geology of Shandong, **1**: 23–39. [In Chinese, abstract in English].

Zhang, Q., Zhang, H., Rasnitsyn, A.P., and Jarzembowski, E. 2015. A new genus of Scoliidae (Insecta: Hymenoptera) from the lower Cretaceous of northeast China. Cretaceous Research, **52**: 579–584.

Zhang, W., Shih, C., Labandeira, C.C., Sohn, J.-C., Davis, D.R., Santiago-Blay, J.A., *et al.* 2013. New fossil Lepidoptera (Insecta: Amphiesmenoptera) from the middle Jurassic Jiulongshan Formation of Northeastern China. Public Library of Science One, **8**: e79500.

Zhelochovtzev, A.N. and Rasnitsyn, A.P. 1972. On some tertiary sawflies (Hymenoptera: Symphyta) from Colorado. Psyche, **79**: 315–327.

Zherikhin, V.V. 1978. Razvitie I smena melovykh I kainozoiskikh faunisticheskikh kompleksov (trakheinye i khelitserovye) [Development and changes of the Cretaceous and Cenozoic faunal assemblages (Tracheata and Chelicerata)]. Trudy Paleontologicheskogo instituta Akademii Nauk SSSR [Transactions of the Paleontological Institute of the Academy of Sciences of the Union of Soviet Socialist Republics], **165**: 1–198. [In Russian].

Zherikhin, V.V. 2002. Ecological history of the terrestrial Insects. *In* History of insects. *Edited by* A.P. Rasnitsyn and D.L.J. Quicke. Kluwer Academic Publishers, Dordrecht, The Netherlands. Pp. 331–338.

Zherikhin, V.V., Sukacheva, I.D., and Rasnitsyn, A.P. 2009. Arthropods in contemporary and some fossil resins. Paleontological Journal, **43**: 987–1005.