

Early Eocene insects from Quilchena, British Columbia, and their paleoclimatic implications

S. Bruce Archibald and Rolf W. Mathewes

Abstract: Fossil insects were examined from the Early Eocene lacustrine shale at Quilchena, British Columbia. Insects of 10 orders (Blattodea, Dermaptera, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera, Hymenoptera) were identified, bringing the known number at this site to 11. These were placed in 26 families, 22 of which are new occurrences for this locality. Specimens include early occurrences of bees and ants. Three fossils of leaves with galls were examined. Thirteen of the families are new to British Columbia, and 9 of these (Blaberidae, Haglidae, Cixiidae, Dinidoridae, Cydnidae, Staphylinidae, Panorpidae, Pipunculidae, Halictidae) are new to the region of the Okanagan Highlands. A number of taxa are earliest known occurrences. Several insects in this fauna are larger than their modern relatives and some are larger than their relatives from other Eocene locales. The presence of insects including March flies, diplopterine cockroaches, dinidorid bugs, and seed weevils confirm and perhaps exceed paleobotanical indications that in the Eocene, British Columbia was much warmer than it is today.

Résumé : Des insectes fossiles du schiste argileux lacustre du début de l'Éocène, à Quilchena, Colombie-Britannique, ont été examinés; ils appartiennent à 10 ordres (Blattodea, Dermaptera, Orthoptera, Hemiptera, Neuroptera, Coleoptera, Mecoptera, Diptera, Trichoptera, Hymenoptera) ce qui porte à 11 le nombre d'ordres rencontrés à ce site. Les insectes ont été classifiés en 26 familles, dont 22 sont des associations nouvelles à cet endroit. On peut reconnaître des abeilles et fourmis hâtives. Trois fossiles trouvés sur les feuilles avec galles ont été examinés. Treize des familles étaient des additions nouvelles en Colombie-Britannique, dont 9 étaient nouvelles aussi dans les hauteurs d'Okanagan (Blaberidae, Haglidae, Cixiidae, Dinidoridae, Cydnidae, Staphylinidae, Panorpidae, Pipunculidae, Halictidae). Certaines mentions de taxons sont parmi les plus anciennes connues. Plusieurs insectes de cette faune sont plus gros que leurs équivalents modernes et certains sont plus gros que les taxons auxquels ils sont apparentés à d'autres sites de l'Éocène. La présence de certains insectes dont les bibions, les blattes diploptérines, les punaises dinidorides et les charançons des graines confirme et parfois même dépasse les indications paléobotaniques selon lesquelles l'Éocène de Colombie-Britannique était beaucoup plus chaud que maintenant.

[Traduit par la Rédaction]

Introduction

This report summarizes our analysis of the fossil insect fauna preserved in shales of an Eocene lake at Quilchena, British Columbia. The fossils are mostly identified to family and sometimes to subfamily or genus. The primary collections are housed at Simon Fraser University, although smaller private collections were also examined. The Quilchena fossils are compared with the insect faunas of other regional Eocene sites and are analyzed and discussed in relation to their relative ages and their paleoclimatic implications.

Regional setting

The Quilchena fossil locality of south-central British Columbia (Fig. 1A) is located in a fault-bounded montane basin about 11 km long and 3 km wide (Cockfield 1948). This basin is one of several in the Merritt area that were mapped as "Coldwater beds" by Cockfield (1948). These montane basins were formed by extension faulting in the Early Eocene, beginning about 53 million years ago (mya), and were subsequently filled with clastic materials derived from nearby volcanic sources (Ewing 1981). Arkosic sandstones in the Coldwater beds show similarities to granitic rocks of the Nicola Group exposed to the north, implying southward transport by paleocurrents (Hills 1965). Conglomerate, mudstones, sandstones, and coal are all found within the basin, interspersed with bentonite and beds of fresh volcanic ash. The Coldwater beds unconformably overlie rocks of the Triassic Nicola Group, which contributed considerable detrital material to the basal conglomerates (Cockfield 1948).

Age

Recent uranium–lead dating on zircons extracted from a volcanic ash bed within the fossiliferous shales has shown this site to be of Early Eocene age, between 52 and 54.5 mya

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(R.W. Mathewes and M. Villeneuve, in preparation). Quilchena was previously thought to be of Middle Eocene age, along with other "Okanagan Highlands" sites in British Columbia and at Republic, Washington. This age assignment for the Okanagan Highlands was based on potassium-argon dating (Hills 1965; Hills and Baadsgaard 1967), palynological correlations (Hills 1965), and the presence of Middle Eocene mammal remains at Princeton, British Columbia (Russell 1935). Previous radiometric ages at Quilchena have been problematical, a Miocene age was reported by Hills (1965), along with a date of 48.9 mya on sanidine from a bentonite bed, which conforms with other Middle Eocene ages from the southern interior.

Study site

The study site is an old roadcut exposure on the northwest side of the basin, about 3 km south of Nicola Lake (50°07'40.3"N, 120°30'34.7"W). Quilchena Creek has cut into Tertiary rocks and Pleistocene overburden at this locality (Fig. 1B), exposing a southward-dipping sequence of light buff to dark brown mudstones and fissile shales derived from volcanic tuff (Mathewes and Brooke 1971; Guthrie 1995). Fossils were collected mostly along an approximately 20 m long exposure above the creek, which is divided into a finely bedded offshore lake facies at the north end and a southern more massive and sandy mudstone unit interpreted as a nearshore facies (Guthrie 1995).

A wide variety of fossils occur in rocks of both facies, including abundant fish remains, insects, and plants, and rare occurrences of molluscs, ostracods, and birds (unpublished data). Wilson (1987) noted that accumulations of small fish bones are particularly abundant at this site, and concluded that pellet regurgitation by fish-eating birds was likely responsible for these occurrences. Fossils are typically preserved as carbonaceous compressions (the "part") and corresponding impressions (the "counterpart").

Previous work

Fossil insects and plants have been collected from the Quilchena area since at least 1906, when Lawrence Lambe of the Geological Survey of Canada traveled through British Columbia by stagecoach collecting from Tertiary lacustrine sites.

The fossil plants of Quilchena have been included in a number of works on the paleobotany of British Columbia and Washington State, beginning with Penhallow (1908). Mathewes and Brooke (1971) summarized the Quilchena flora and added several new taxa of conifers and angiosperms.

Fossil insects from this area have been discussed by Handlirsch (1910), Scudder (1890), and Rice (1959). More recently, Wilson (1977), Guthrie (1995), Douglas and Stockey (1996), and Wehr (1998) have commented on fossil insects from British Columbia and Washington State, mentioning Quilchena specimens. The Quilchena insects have to date not been critically examined or published in a site-specific report.

Materials and methods

The Simon Fraser University (SFU) collection of insect, plant, and fish fossils from Quilchena has been made over the last 30 years, and includes over 450 insect specimens (many with counterparts).

This was the primary material examined, although smaller collections were also examined, including specimens collected by R. Savenye, Ken and Kenneth Dodge (father and son), and K. Naumann.

Specimens were examined under a Wild M5 dissecting microscope. Details were often made clearer by adding a small amount of distilled water to the surface of the fossil. In the case of some specimens, one side contained the dorsal aspect of the fossil and the other side the ventral aspect. At other times these aspects were partially visible on the same side. Many fossils were drawn with the aid of a Wild camera lucida attachment.

For most specimens, identification depended upon wing venation, although other features such as the legs of Auchenorrhyncha were useful. Camera lucida drawings of wings were compared with illustrations in a variety of texts, principally *The Insects of Australia* (Naumann et al. 1991), and others such as *Manual of Nearctic Diptera* (McAlpine 1981, 1987) and *Hymenoptera of the World: An Identification Guide to Families* (Goulet and Huber 1993). Features of both left and right wings (as well as from part and counterpart) were often combined. Left wings were rendered as right wings. Veins were usually drawn as simple lines in accordance with custom. Some drawings were faxed to experts in particular taxa for their opinion.

The beetle specimens vary in completeness. Many consist of an isolated elytron or a pair of elytra. Using traditional identification techniques for these specimens was therefore not possible, since keys to modern beetles depend on the use of such fragile features as tarsal segments, which are invariably missing or obscured. Workers in Quaternary paleoclimate analysis, however, have devised methods of identifying beetles by means of elytra and other robust exoskeletal features. The beetle specimens in this collection were brought to the Quaternary Entomology Laboratory in the Department of Geosciences at North Dakota State University in Fargo and examined with scientists there.

The classification system used here follows that in *The Insects of Australia* (Naumann et al. 1991), since this text takes a global approach to systematics, and some of the fossil insects of Quilchena are found today only outside North America. The only exception is the bruchid seed weevil, which reflects current thought by reporting the subfamilies of the former Bruchidae as subfamilies of Chrysomelidae (as in Farrell 1998).

Results and discussion

Over 460 specimens were examined in this study (some 450 from the SFU collection, 4 from the R. Savenye collection, 7 from K. Naumann, and a wing donated by Ken Dodge). At the order level, the numbers of identified specimens were 187 Diptera, 81 Hemiptera, 37 Coleoptera, 37 Hymenoptera, 6 Neuroptera, 3 Trichoptera, 2 Blattodea, and 1 each of Dermaptera and Mecoptera; the remainder were not identifiable to order. By far the largest family was Bibionidae, with over 160 specimens. The next largest was Gerridae, with 44 specimens. Three fossils of leaves with galls were also examined.

Systematic description

Class Insecta

Order Blattodea (cockroaches)

Family Blaberidae

Subfamily Diplopterinae

MATERIAL: Q-0040, a pair of tegmina, one atop the other (Fig. 15); Q-0048, a pair of tegmina in close association.

REMARKS: These tegmina superficially resemble beetle elytra. The venation, simplified and not distinct, is between rows of punctae, which resemble the striae of beetle elytra. The basal area is strongly convex. These features are representative of Diplopterinae, whose tegmina and hind wings (for other reasons) are considered distinctive (Rehn 1951).

The modern Diplopterinae consists of one genus, *Diploptera*, found in India, parts of Australia, Southeast Asia, and the South Pacific today (Rehn 1951). *Diploptera punctata* is associated with a number of plants, notably Cupressaceae (Roth and Willis 1960), which are represented in the Quilchena shales by at least two genera (unpublished data). The earliest Blaberidae known are from the Eocene (Labandeira 1994).

Order Dermaptera (earwigs)

Suborder Forficulina

MATERIAL: Q-0069 (*a* and *b*), a thorax and abdomen, head missing, with much of five legs, 15 mm long, female (Fig. 2).

REMARKS: This is the most complete specimen reported to date from the Okanagan Highlands Eocene. Other reported specimens are of anal forceps with a few abdominal segments only. Lewis (1994) tentatively placed Dermaptera from Republic, Washington, in Forficulidae.

Q-0069 may be placed in the suborder Forficulina because its habitus is typical of the distinctive common earwig form of this taxon (Rentz and Kevan 1991). The families of Forficulina are distinguished by features such as tarsal segments (Rentz and Kevan 1991), which are missing or obscured on this specimen. These are the remains of a female because the forceps are long and straight (Borror et al. 1989).

This specimen is the oldest known dermapteran in North America.

Order Orthoptera

Family Haglidae (hump-winged crickets)

Subfamily Prophalangopsinae

MATERIAL: Q-0101, a partial forewing preserved over a hind wing (Fig. 3).

REMARKS: The wings are 60 mm long and 29 mm wide at the widest point (although the fossil is incomplete in both length and width). Many long veins extend to the apical margin of the hind wing. Only the anterior portion is present, which is broken away and lost toward the midwing so the posterior portion of the forewing is visible. This specimen is female; male Haglidae have a large stridulatory surface on their forewings (Carpenter 1992). The basal forewing area of this fossil bears a close resemblance to the Upper Eocene Florissant *Paleorehnia maculata* Cockerell (1908*b*); illustrated in Kevan and Wighton (1983). The media and cubitus fuse for a short distance on the forewing as in *P. maculata* and the Paleocene *Albertoilus cervirufi* (Kevan and Wighton, 1983).

Order Hemiptera

Suborder Auchenorrhyncha (hoppers)

Superfamily Cercopoidea (froghoppers, spittle bugs)

MATERIAL: Q-0083, a complete body with partial wings and a hind leg (Fig. 4A); Q-0077, a tegmen and hind wing in close association (Fig. 4B).

REMARKS: On Q-0077 the venation on the hind wing agrees with that of fossil *Aphrophora* sp. in Scudder (1895) and Handlirsch (1910). The pronotum is not present, so it cannot be seen whether the posterior margin is W-shaped, as in Aphrophoridae (Carver et al. 1991), or straight. Insects with the same hind-wing venation have been placed (Wilson 1977) in Cercopidae, as the posterior border of the pronotum is straight, not W-shaped. Carpenter (1992) includes Aphrophoridae in his section on Cercopidae "...because of the difficulty of recognizing the distinguishing features in fossils." The tegmen is 20 mm long and appears uniformly darkly coloured.

On Q-0083 the hind tibia (see Fig. 4A) shows several stout spines, and a ring of spines at the distal end. The first tarsus also has a ring of spines. This is characteristic of Cercopoidea (Borror et al. 1989). The posterior margin of the pronotum is obscured (this specimen shows primarily the ventral aspect). The partial hind wings appear identical with Q-0077.

Family Cicadellidae (leafhoppers)

MATERIAL: Q-0201, a complete specimen (Fig. 4C); Q-0075 and Q-0085 (Fig. 4D), isolated tegmina.

REMARKS: The smallest of the Auchenorrhyncha found are Q-0085 (a wing, 5.5 mm long) and Q-0201 (a whole insect, 11 mm long). On Q-0201, the hind tibia shows a row of numerous small spines characteristic of Cicadellidae (Carver et al. 1991). Q-0085 shows M_{1+2} apically fused with RP as in Cicadellidae (Carver et al. 1991).

Q-0075 is a large tegmen, 25 mm long. R and M join basally. There are traces of coloration.

Family Cixiidae (cixiid planthoppers)

MATERIAL: Q-0076, a pair of tegmina, one complete, attached to a partial thorax (Fig. 4F).

REMARKS: The tegmina are 23 mm long. The anal veins are apically confluent (Carver et al. 1991).

The preserved pronotum and tegmina are dark chocolate brown with two wide bands of light coloration. The same colour pattern is seen on other Quilchena Auchenorrhyncha of unknown families. Three banded cicadellid wings are known (see Fig. 3 of Wilson 1977) from the Driftwood Creek site.

Family Ricaniidae

MATERIAL: Q-0102, a partial tegmen, 13 mm long, with colour patterns (Figs. 4E, 16).

REMARKS: R, M, and especially CuA branch many times, and although most of the costal margin is missing, the part present shows the numerous cross-veins as in Ricaniidae (Carpenter 1992; see especially Fig. 153, *Hammapteryx* sp.).

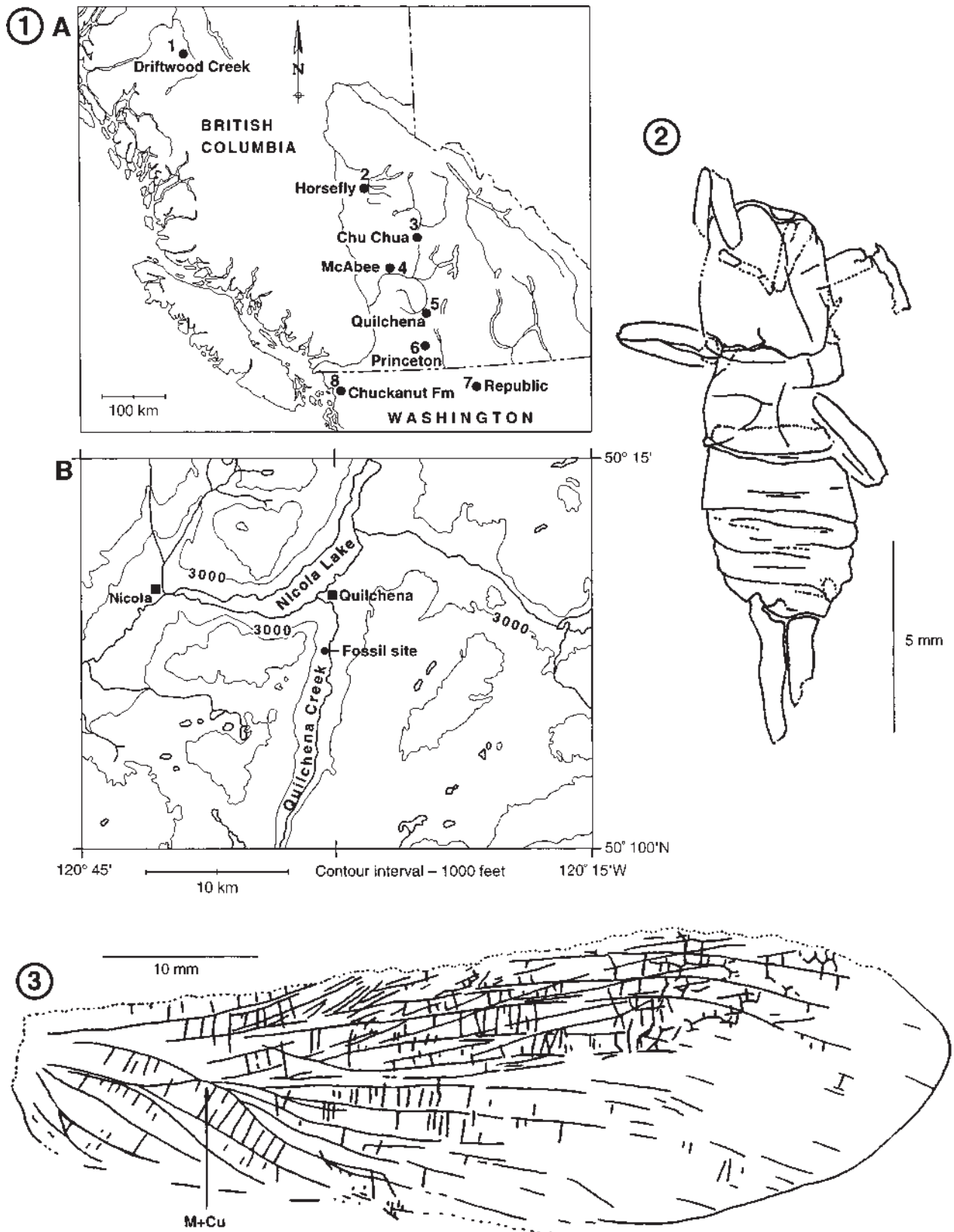
Ricaniidae are poorly known from the Okanagan Highlands. *Ricania antiquata* was described in Scudder (1895) from a fragmentary specimen collected by George Mercer Dawson on the Similkameen River (Princeton, B.C.) in 1888.

Family unknown

MATERIAL: Q-0078, a large, coloured tegmen with a partial hind wing beneath.

REMARKS: This tegmen is one of the larger specimens (28 mm), with distinct banding. Unlike in Q-0083 and Q-0077 above, M_{1+2} splits near the peripheral vein on the hind wing (Fig. 4G).

Abbreviations in Figs. 3–14 are as follows: T, spinose hind tarsus; for veins: A, anal; B, basal; C, costa; Cu, cubitus; CuA, anterior branch of the cubitus; CuP, posterior branch of the cubitus; M, media; R, radius; r-m, radial-medial; Rs, radial sector; Sc, subcosta; for cells: cup, posterior cubital cell; dc, discoidal cell; dm, discal medial; 1D, first discal cell; **Fig. 1.** (A) Regional setting. (B) Site locality. **Fig. 2.** Dermaptera (specimen Q-0069). **Fig. 3.** Orthoptera: Haglidae (Q-0101).



Suborder Sternorrhyncha

Family Aphididae (aphids)

MATERIAL: Q-0391 (*a* and *b*), a forewing (Fig. 5); Q-0125, most of an alate body with partial legs and one partial forewing.

REMARKS: The wing (Q-0391) shows the characteristic venation of Aphididae (Carver et al. 1991). There is a stout stigma from which issues a small curved Rs. M is branched twice. Although the wing is not complete, the extrapolated overall length is about 9 mm, very large for an aphid.

The wing of the largest (extant or fossil) aphid known, *Longistigma caryae* Harris (the hickory or giant bark aphid), is also about 9 mm long (Heie and Friedrich 1971). Today *L. caryae* lives in eastern North America. The body has been measured at 7.19 mm long (Heie and Friedrich 1971). A fossil of this species has been found in Miocene deposits of northwestern Iceland (Heie and Friedrich 1971); the wing is also about 9 mm long and the body 7.82 mm long. The wing venation of *L. caryae* is distinctive, the pterostigma being pointed, curved, and narrow and Rs quite straight and short (Heie and Friedrich 1990), different from the *Quilchena* specimen.

Suborder Heteroptera (bugs)

Family Gerridae (water striders)

MATERIAL: Q-0205, Q-0207, Q-0208, Q-0209, Q-0210, Q-0211, and other specimens in varying levels of completeness.

REMARKS: A fossil gerrid was the first insect fossil described from the *Quilchena* area. It was collected on July 26, 1906, by Lawrence Lambe of the Geological Survey of Canada.

They are typical water striders, with the very long middle and hind legs adapted for skimming on the surface of water. Some specimens appear to be apterous, but when the counterpart is examined, wings are clearly seen (cf. Q-0214 *a* and *b*, Q-0218 *a* and *b*). In other apparently apterous specimens the wings may be on the missing counterpart. If the wings can pull away evenly from one side, perhaps they can pull away from *both* sides of the rock upon being split.

On one piece of shale (Fig. 19), five gerrids (Q-0207 to Q-0211) are lined up in close association, possibly by taphonomic sorting due to water currents, amid the water fern *Azolla primaeva*.

Fossil water striders are relatively common at *Quilchena* and Driftwood Creek, but not elsewhere in the Okanagan Highlands, although there are sporadic occurrences from Blakeburn Mine, B.C. (Wilson 1977), and elsewhere in the Princeton, B.C., area (Scudder 1890).

Family Dinidoridae (dinidorid bugs)

Subfamily Megymeninae

MATERIAL: Q-0195 (*a* and *b*), a body 19 mm long, with parts of the forelegs (Fig. 17).

REMARKS: The head is broad, with hornlike anteocular processes over each eye. Coarse punctae cover the head and pronotum, with finer punctae on the abdomen. There are projections pointing anteriolaterally on the pronotum. The abdomen has a series of lateral lobes extending around the margin as is characteristic of the subfamily Megymeninae (Schuh and Slater 1995).

This is the earliest known occurrence of Dinidoridae. The only other known fossil dinidorid is *Dinidorites margiformis* (Cockerell 1921) from Upper Eocene Florissant.

Family Cydnidae (burrowing bugs)

MATERIAL: Q-0194 (*a* and *b*); a fairly complete insect, 15 mm long, with several partial legs and an antenna (Fig. 18).

REMARKS: This is an insect of robust, pentatomoid form. The legs have strong spines along the tibia. Such heavily spinose legs are characteristic of Cydnidae (Schuh and Slater 1995), which dig amongst and feed upon roots (Schuh and Slater 1995). The corium appears to extend beyond the scutellum (in presumed resting posture), as in some Cydnidae. The pronotum has a cydnid-like habitus, with its rounded anterior.

cf. Family Pentatomidae (stink bugs)

MATERIAL: Q-0257 (*a* and *b*), partial thorax and abdomen; Q-0402 (*a* and *b*); pronotum and scutellum, with a small bit of abdomen; Q-0268, ventral aspect of an abdomen.

These heteropterans are too fragmentary to assign to a family, yet they appear similar to Pentatomidae. Pentatomid fossils are known from other Eocene sites in British Columbia (Wilson 1977; unpublished data) and other western North American sites (Table 1).

Order Neuroptera (lacewings)

Family unknown

MATERIAL: Q-0422 (*a* and *b*), a large forewing, 45 mm long (Figs. 6A, 20); Q-0094, the anterior apical portion of two wings overlapping; Q-0421, a forewing with colour patterns, about 45 mm long (Figs. 6B, 21); Q-0379, a presumed portion of the posterior margin of a forewing.

REMARKS: On Q-0422 the wing is long and ovate, as in many Osmyliidae, e.g., the Florissant *Lithosmylus columbianus* and *Osmylidia requieta* (Carpenter 1943). The costal area is broad, with many small accessory veins, which branch (sometimes several times) and are connected by a series of gradate cross-veins (unlike the Florissant osmylids, which have much simpler cross-veins in the costal area). There are numerous fine longitudinal branches of the radial sector, which are connected by many small cross-veins in the main body of the wing. These cross-veins are not organized into any series. There is, however, an outer gradate series of cross-veins connecting the numerous longitudinal branches of the radial sector. These cross-veins form a line that parallels the posterior margin of the wing just proximad of the fine distal branching of the longitudinal veins.

In general shape this wing also resembles those of Polystoechotidae, which is also known from Florissant (Cockerell 1908a). In Polystoechotidae, however, the number of cross-veins is greatly reduced (Comstock 1918). Q-0422 has many such cross-veins (more like Osmyliidae). Because the important characteristics of the basal portions of the wing are obscured by matrix, Polystoechotidae is also a possible determination.

This wing was collected by Kenneth Dodge, who, along with his father, Ken Dodge, generously donated it to the SFU collection.

Q-0094 is a partial wing fragment, but appears similar to Q-0422.

Fig. 4. Auchenorrhyncha. (A) Cercopoidea, hind tarsus (Q-0083). (B) Cercopoidea (Q-0077). (C) Cicadellidae (Q-0201). (D) Cicadellidae (Q-0085). (E) Ricaniidae (Q-0102). (F) Cixiidae (Q-0076). (G) Auchenorrhyncha incertae sedis (Q-0078).
Fig. 5. Sternorrhyncha, Aphididae (Q-0391).

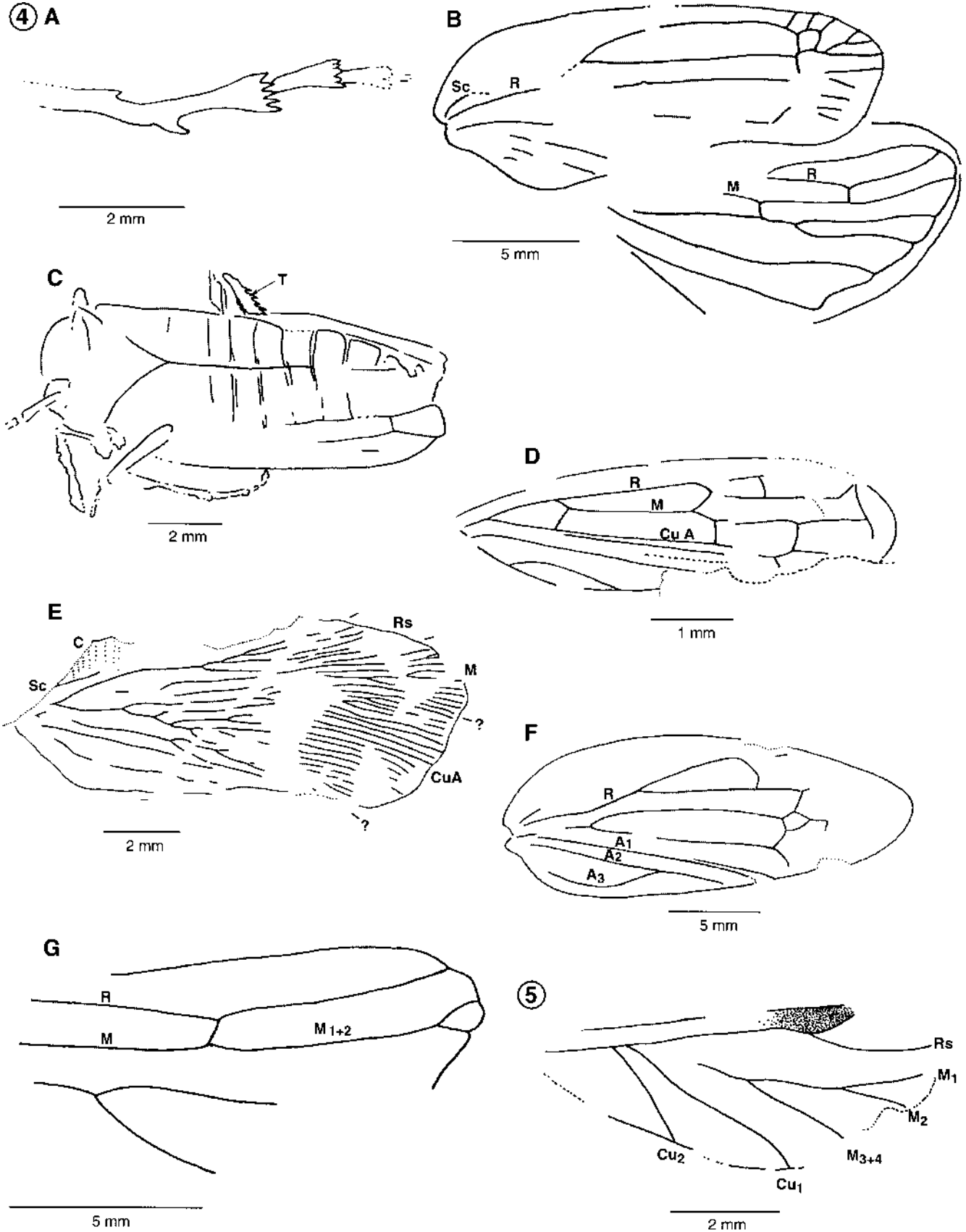


Table 1. Systematic list of fossil insects found at Quilchena, with published occurrences of these taxa elsewhere in the western North American Eocene.

Order or suborder	Family or subfamily	Quilchena	British Columbia	Republic	Green River	Florissant
Blattodea (cockroaches)	Blaberidae: Diplopterinae	×				
Dermaptera (earwigs)	Family unknown ^d	×		WB, L		W78
Orthoptera (grasshoppers, crickets, katydids)	Haglidae (hump-backed crickets)	×				Cc08
Hemiptera/Auchenorrhyncha (hoppers, cicadas)	Cercopoidea (spittle bugs)	×	W78	WB, L	G	W78
	Cicadellidae (planthoppers)	×	W78		G	W78
	Cixiidae (cixiid planthoppers)	×			G	W78
	Ricaniidae (ricaniid planthoppers)	×	Sc95		G	
Hemiptera/Sternorrhyncha (aphids and others)	Aphididae (aphids)	×		WB, L	G	W78
Hemiptera/Heteroptera (bugs)	Dinidoridae (dinidorid bugs)	×				Cc21
	Cydnidae (burrowing bugs)	×			G	W78
	cf. Pentatomidae (stink bugs)	×	W78	WB, L	G	W78
	Gerridae (water striders)	×	W78		G	W78
Neuroptera (lacewings, ant lions, and others)	Family unknown	×		WB ^b		C43 ^c
	Hemerobiidae (brown lacewings)	×		WB		W78
Coleoptera (beetles)	Carabidae (ground beetles)	×	W78, DS	WB, L, DS	G	W78
	Staphylinidae (rove beetles)	×			G	W78
	Scarabaeoidea (scarab beetles)	×	W78		G	W78
	cf. Erotylidae (pleasing fungus beetles)	×			G	W78
	Cerambycidae? (long-horned beetles)	DS		WB, L	G	W78
	Chrysomelidae (leaf beetles)	×	W78	WB	G	W78
	Pachymerinae (seed weevils) ^d				G	W78
	Curculionidae (weevils)	×	DS	WB, L, DS	G	W78
Mecoptera (scorpionflies)	Panorpidae (common scorpionflies)	×				W78
Diptera (two-winged flies)	Tipulidae (crane flies)	×	W78, DS	WB, L, DS	G	W78
	Bibionidae (March flies)	×	W78, DS	WB, L, DS	G	W78
	Sciaridae ^e (dark-winged fungus gnats)	DS	W78, DS		G	W78
	Mycetophilidae (fungus gnats)	×, DS	W78, DS	WB, L, DS	G	W78
	Rhagionidae (snipe flies)	DS				W78
	Pipunculidae (big-headed flies)	×				
	Syrphidae (hover flies)	×	W78		G	W78
Trichoptera (caddisflies)	Phryganeidae (large caddisflies)	×		WB, L		W78
Lepidoptera (butterflies and moths)	Noctuidae (noctuid moths)	DS				
Hymenoptera (ants, bees, and wasps)	Ichneumonidae (ichneumon wasps)	×, DS	W78, DS	WB, L, DS	G	W78
	Cynipidae (gall wasps)	DS				W78
	Vespididae (hornets, potter wasps)	×	W78	L		W78
	Formicidae (ants)	×, DS	W78, DS	WB, L, DS	G	W78
	Sphecidae (digger wasps)	×		WB	G	W78
	Halictidae (halictid bees)	×				W78

Note: ×, this study; C43, Carpenter 1943; Cc08, Cockerell 1908b; Cc21, Cockerell 1921; DS, Douglas and Stockey 1996; G, Grande 1984; L, Lewis 1992; Sc95, Scudder 1895; WB, Wehr and Barksdale 1996; W78, Wilson 1978. Wilson (1978) and Grande (1984) are compilations of previous references.

^bOsmylidae.

^cOsmylidae and Polystoechotidae (see text).

^dSeed weevils are recorded here for the first time in the Okanagan Highlands; however, they are considered to be nested within the family Chrysomelidae (which has the previous record noted above) rather than as Bruchidae.

^eFor some early writers (e.g., Scudder 1890), Sciaridae was within Mycetophilidae.

In venation, Q-0421 and Q-0422 are similar. The central area of wing Q-0421, with its many longitudinal veins connected by many cross-veins, appears very much like that of wing Q-0422. They are also about the same size (large). These two fossils differ, however, in that Q-0422 is elongate and ovate (over twice as long as wide), whereas Q-0421 is roughly triangular.

Q-0421 shows striking colour patterns (Fig. 21).

The fragment Q-0379 shows many small veins arising from longitudinal veins at an oblique angle, and resembles the presumably similar area of the posterior margin of Q-0421. It is blackened without colour patterning, although this may be an artifact of preservation.

It is not possible to rule out other "osmylid-like" families (Lambkin 1988) such as Nymphidae and Myrmeleontidae. In general habitus, however, these fossils most resemble Poly-stoechotidae and Osmylidae.

Family Hemerobiidae (brown lacewings)

MATERIAL: Q-0092; a wing, missing only the most basal portion (Fig. 6C).

REMARKS: R_1 branches five times. Although modern hemerobiids commonly branch two to four times (Borror et al. 1989), such branching of R_1 is not unknown in modern brown lacewings such as *Hemerobius nitidulus* (Meinander 1962). As in Hemerobiidae, Sc and R are not fused apically (Meinander 1962). Cross-veins are in gradate series. M is forked near the base of the wing but Cu is not preserved. Costal accessory veins branch, and the costal area widens basally.

Brown lacewings have not been known previously from the Eocene of the Okanagan Highlands. They are, however, recorded from the Oligocene of Quesnel (Handlirsch 1910).

Order Coleoptera (beetles)

Family Carabidae (ground beetles)

MATERIAL: Q-0380 and Q-0059, pairs of elytra; Q-0055?, an elytron; Q-0045, a thorax with abdomen and elytra, articulated.

REMARKS: Because remains of beetles of the family Carabidae are often useful as proxy indicators for modeling the Quaternary paleoclimate, the identifying features of disarticulated parts such as elytra have been carefully studied by paleoecologists. The distinctive elytral striae and the ridge across the elytral base are diagnostic features of Carabidae (D. Schwert, personal communication). Q-0380 and Q-0059 exhibit these features and are assigned to Carabidae. Q-0055 is lacking the base and so assignment of this specimen to Carabidae is tentative.

Q-0045 is cf. genus *Amara*, a "large, extremely difficult genus" (Lindroth 1968). It has a ridge across the elytral base; the pronotum is quadrate and wider than long, with a medial suture, basal fovea, and lateral reflexion. A setigerous puncture is visible on the right lateral posterior corner of the pronotum (Fig. 22).

Family Staphylinidae (rove beetles)

Subfamily Omaliinae

MATERIAL: Q-0047, a body with hind femora and most of one antenna (Fig. 7A); Q-0046, a body, lacking legs, with partial antenna.

REMARKS: Q-0047 has a slender body and the elytra are short as in Staphylinidae. Six abdominal segments appear exposed behind the elytra. The antenna is filiform. Two ocelli are present and are indicative of the subfamily Omaliinae (White 1983).

Q-0046 has a long, slender body, tapering posteriorly. The elytra are short, with seven abdominal segments visible. Short segments of a filiform antenna are visible.

Superfamily Scarabaeoidea (scarab beetles)

MATERIAL: Q-0037, a whole beetle with most of five legs; Q-0057, a fairly complete beetle with right hind wing exposed through broken-away elytron (Fig. 23); Q-0062, a whole beetle with parts of four legs; Q-0204?, ventral aspect of a whole beetle with much of five legs visible.

REMARKS: These are specimens of different taxa of scarabs. They are all robust, with a very wide oval body and strong fossorial legs with tooth-like projections on the tibia. The pronota have forward-facing projections extending to the sides of the head.

cf. Family Erotylidae (pleasing fungus beetles)

MATERIAL: Q-0205, a pair of elytra, separate (Fig. 24).

REMARKS: The elytra are smooth and elongate, with transverse colour patterns as in some Erotylidae. Modern erotylids are commonly black with red, orange, or yellow patterning, or are metallic; some are smooth like this specimen (Lawrence and Britton 1991; White 1983).

Family Chrysomelidae (leaf beetles)

Subfamily Pachymerinae (pachymerine bruchids)

MATERIAL: Q-0061, a very complete specimen with most of one antenna and parts of legs (Fig. 25).

REMARKS: The hind femora of Q-0061 are heavy ($>5 \times$ tibia width); the tibiae are strongly curved inward with carinae. The abdomen protrudes beyond the elytra, with a widely exposed pygidium (although this may be due in part to preservational distortion of the specimen); antenna clavate; the elytra have 10 deep striae bearing elongate fossae.

The pronotal disc is subpentagonal and the postocular lobes are long, as in the tribe Caryopemini, Old World seed weevils indigenous to India, East Asia, and Madagascar.

This is the first bruchid seed weevil from the Okanagan Highlands, and the earliest known occurrence.

Family Curculionidae (snout beetles)

MATERIAL: Q-0043 and Q-0063 (Fig. 26), complete beetles; Q-0052, robust pair of elytra; other elytra, single and paired.

REMARKS: The two relatively complete specimens (Q-0063 and Q-0043) show the distinctive weevil snout. Q-0063 shows scales on the pronotum, a delicate feature to be preserved in shale fossils.

Q-0052, a pair of elytra, shows heavily impressed striae with transverse lines across the striae, very large hinge attachments, and a slight pinch at the apical end.

Family unknown

MATERIAL: Q-0044 and Q-0157, whole beetles.

REMARKS: Q-0044 has the long (11 mm), gracile habitus and elytra with pinched-in tips that are found in buprestid beetles. The head, pronotum, elytra, and legs are heavily

punctate. Unlike in Buprestidae, the antenna is distinctly capitate, terminating in a three-segmented ball.

Q-0157 is a small beetle, 6 mm long, that is in close association with a March fly over twice as long (Fig. 7B). This beetle appears to be attached to the fly's legs, which may be an example of phoresy, where one organism is attached to another for transport, and no parasitism or other negative effect is involved. There are a limited number of examples of phoresy in the fossil record (Boucot 1990). Beetles of the families Limulodidae and Histeridae travel on and live with ants (Boucot 1990).

Order Mecoptera (scorpionflies)

Family Panorpididae (common scorpionflies)

MATERIAL: Q-0096, a hind wing, complete except for the apical region (Fig. 8).

REMARKS: There are very few cross-veins. Both R and M have five branches. CuA joins M basally and is unbranched. At the point of juncture between Cu₁ and M, a cross-vein connects M + Cu₁ to Cu₂. Cu₂ appears to branch early, beyond this, but this is the separation of Cu₂ + A₁, which have joined together basally. Cu₂ + A₁ is joined to A₂ by a short cross-vein, and there is a very short A₃.

The fusion in the hind wing of M + Cu₁ basally and the fusion of Cu₂ + A₁ also basally are considered distinctive features of Mecoptera (Byers 1989).

Q-0096 appears close to the panorpid *Holcorpa* sp. from Florissant (Scudder 1890). Scudder (1890) noted that the wings of *Holcorpa* sp. lack cross-veins except at the base, as appears to be the case in this (incomplete, however) fossil. He noted that the wing is shorter and wider than in *Panorpa* sp., and Q-0096 was evidently even shorter and wider than *Holcorpa* sp. There is no previously recorded fossil occurrence of Mecoptera west of Florissant.

Order Diptera (flies)

Suborder Nematocera ("long-horned" flies)

Family Tipulidae (crane flies)

MATERIAL: Q-0065 (Fig. 9A) and Q-0187 (and others), loose wings; Q-0375, wings plus abdomen.

REMARKS: Q-0065 is a large wing (30 mm) showing characteristics typical of Tipulidae: there are 2 complete anal veins, 11 (or 12; end of Sc is indistinct) veins that reach the margin, and basal cells over half the length of the wing (Alexander and Byers 1981). In Q-0187, Sc ends by joining R and the specimen can therefore be placed in the subfamily Tipulinae (Colless and McAlpine 1991). In other specimens this end of Sc is obscured or not preserved. Q-0187 and Q-0065 both show M divided into three branches.

Q-0375 has most of two wings and the abdomen, which shows distinct colour patterning.

Family Bibionidae (March flies)

Subfamily Pleciinae

MATERIAL: Q-0155, Q-0138, and many other specimens (Fig. 9B).

REMARKS: Well over a third of the SFU collection are March flies, which were previously known to predominate in the Quilchena fauna (Wilson 1987) and are by far the most common insect at most sites in the Okanagan Highlands (Wilson

1977; Wehr 1998). They are well known throughout the western North American Tertiary.

Rice (1959) placed the British Columbia Tertiary Bibionidae in 20 species of *Plecia* and two of *Penthetria*, which are "extremely difficult" to tell apart (Wilson 1977), as they are separated by only slight variations in venation. The venation is characteristic of Pleciinae (Hardy 1981); R splits once into R₂₊₃ and R₄₊₅ as in *Plecia*, *Penthetria*, and *Hesperinus*. *Hesperinus*, however, has long, easily distinguishable antennae. All specimens reported from the Okanagan Highlands have short antennae.

Family Mycetophilidae (fungus gnats)

MATERIAL: Q-0186, Q-0193, Q-0272, Q-0276, Q-0376, and Q-0398, small flies, some with clear wing venation (Fig. 9C).

REMARKS: These are all small flies; the wing of Q-0186 (3.7 mm) is representative. The venation is typical of Mycetophilidae (cf. Figs. 14–50 and 14–51 in Vockeroth 1981). The short cross-vein r-m branches from M in the proximal 1/3 to 1/4 of the wing, and meets Rs at an angle. The similarly short Rs branches downward from R. They join, then R₄₊₅ continues to the apical margin. A short cross-vein connects Sc to R close to the base of the wing. M branches once, as does CuA. A short anal vein does not reach the margin. The subcosta is not weak and does not end free as in Sciaridae, but reaches the costa as in Mycetophilidae. The base of the abdomen, when present, is constricted as in fungus gnats (Colless and McAlpine 1991).

Suborder Brachycera

Family Pipunculidae (big-headed flies)

MATERIAL: Q-0397, a thorax and abdomen with both wings (Fig. 9D); Q-0188, a thorax, an abdomen, and wings.

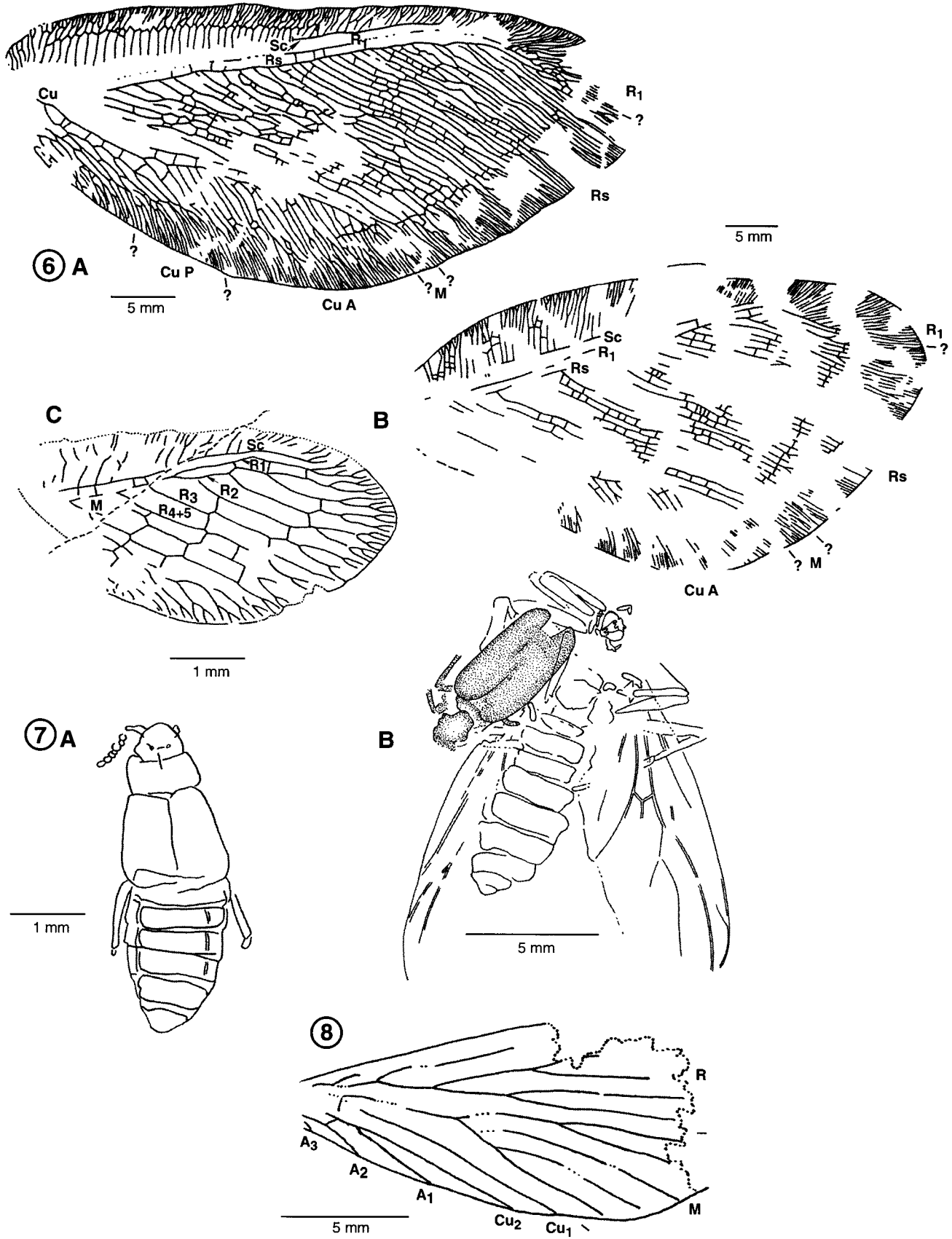
REMARKS: The wings are slender and show typical pipunculid venation (Hardy 1987). Rs is two-branched, R₂₊₃ and R₄₊₅ are divergent, and R₄₊₅ and M₁ are convergent, terminating close to each other at the wing margin. CuA₂ and A₁ join near the wing margin, forming cell cup, which is long and pointed. Cross-vein r-m is visible on only one wing of one of the specimens (Q-0937), and may not have been easily preserved. The pterostigma between Sc and R₁ is visible on both of these fossils.

Family Syrphidae (hover flies)

MATERIAL: Q-0251, a head, a thorax, and an abdomen and two wings (Fig. 9E); Q-0199?, a thorax, an abdomen, and a small distal part of one wing.

REMARKS: Q-0251, M₁ bends forward and is convergent with R₄₊₅ at the wing margin. They join just before the apex as in Syrphidae (Vockeroth and Thompson 1987). The cup cell is closed near the wing margin by the joining of CuA₂ and A₁ (as in Pipunculidae, but the head is not enlarged as in Pipunculidae). The presence of the spurious vein between R₄₊₅ and M is difficult to determine. Vockeroth and Thompson (1987) note that this vein may be faint at times. These venational features may also be present in Conopidae (e.g., see Figs. 15.8–15.10 in Smith and Peterson 1987). Cross-vein dm-cu is roughly subparallel with the posterior margin as in some illustrated wings of Syrphidae (see Vockeroth and Thompson 1987), not at a sharper angle as in those Conopidae whose venation resembles that of Syrphidae. The abdomen of Q-0251 does not show any

Fig. 6. Neuroptera. (A) Incertae sedis (Q-0422). (B) Incertae sedis (Q-0421). (C) Hemerobiidae (Q-0092). **Fig. 7.** Coleoptera. (A) Staphylinidae: Omaliinae (Q-0047). (B) Phoresy?; unknown beetle (Q-0157) in association with a March fly. **Fig. 8.** Mecoptera (Q-0096).



colour patterning; if present, it was not preserved (conopids, like syrphids, may mimic wasps).

The abdomen of Q-0199, however, does show colour patterning as in Syrphidae, and the small part of the extant wing is not in disagreement with Syrphidae, but Conopidae cannot be ruled out for this fossil.

Order Trichoptera (caddisflies)

Family Phryganeidae (large caddisflies)

MATERIAL: Q-0098, a forewing (Fig. 10A).

REMARKS: The anal veins join apically to form two Y veins near the base of the wing and Cu_1 forks into Cu_{1a} and Cu_{1b} , as is characteristic of the forewings of Trichoptera (Borrer et al. 1989). Cu_2 does not branch (although the apical portion of the wing is not present). M forks once into M_{1+2} , and M_{3+4} , then these fork again into M_1 , M_2 , M_3 , and M_4 . The radial sector branches similarly, once into R_{2+3} , and R_{4+5} and then each branch again into R_2 , R_3 , R_4 , and R_5 . Sc continues without branching, although it may have done so on the missing portion. A small part of the costa is present. There are various connecting cross-veins. These features are characteristic of the trichopteran wing (Borrer et al. 1989).

The discoidal (= radial in Carpenter 1992) cell is closed and is longer than the Rs, with R_{2+3} (Rs_{1+2} in Carpenter 1992) forking well before the distal end of the discoidal cell. This places Q-0098 in Phryganeidae (Carpenter 1992).

Family unknown

MATERIAL: Q-0424, a forewing with the posterior margin missing (Fig. 10B); Q-0097, a wing (Fig. 10C); Q-0401, a caddisfly larval case.

REMARKS: In Q-0424 the discoidal cell is closed, with the connecting cross-vein very short to the point of giving the appearance of R_3 and R_4 joining in an "X," creating a diamond-shaped discoidal cell. The Rs cell extends apicad of the discoidal cell, where it terminates with cross-vein r-rs. R_5 is joined to M_{1+2} (M_1 ?) by cross-vein r-m at the point where there is a branching of the media to M_{3+4} (M_2 ?). The posterior region of the wing is missing. This fossil was collected by Ken Naumann, who generously donated it to the SFU collection.

In Q-0097 the discoidal cell is shorter than in Q-0098, and R_{2+3} diverges near the distal end of this cell, therefore this specimen is not a phryganeid. M_{1+2} and M_{3+4} do not branch further before the obscured end of the wing. M is joined to CuA by cross-vein M-Cu. CuA branches to CuA_1 and CuA_2 , as would be expected, and is joined to CuP by a cross-vein immediately after this branching. This appears to be a hind wing because the three anal veins do not converge (although this area is poorly preserved).

Q-0401 is a caddisfly larval case about 2.5 cm long, made up of small bits of rubble. This compares to illustrated larval cases of Limnephilidae (Borrer et al. 1989), although it is also possibly Philanisidae (Boucot 1990), Oeconesidae, or Leptoceridae (Neboiss 1991). Even modern larval cases may not always be attributable to family (Boucot 1990): only a few types may be placed to family with certainty.

Order Hymenoptera (sawflies, ants, bees, and wasps)

Suborder Apocrita

Family Ichneumonidae (ichneumon wasps)

MATERIAL: Q-0018 (Fig. 27), Q-0026, Q-0192, Q-0023, Q-0020, Q-0022, Q-0016, and other specimens, in varying degrees of completeness.

REMARKS: The costal cell is absent (Naumann et al. 1991) as in (almost all) Ichneumonoidea. The distinctive ichneumon "horse's head" cell is present (Borrer et al. 1989), formed by the joining of the first discoidal and first submarginal cells in the forewing as a result of the loss of vein Rs + M (Borrer et al. 1989). The areolet cell (second submarginal cell) is present on most specimens. The ovipositor of Q-0018 is at least 13 mm long, as long as the body. There are six distinct types, based on forewing venation.

Family Vespidae (yellow jackets, hornets, and paper, mason, and potter wasps)

MATERIAL: Q-0034, a robust wasp in lateral aspect, with folded wings (Figs. 11 and 28).

REMARKS: The wings of Vespidae are folded longitudinally when at rest (Naumann et al. 1991), as in this fossil. Of the other families that fold their wings longitudinally, (e.g., Leucospidae, Gasteruptiidae, some Pompilidae) (Naumann et al. 1991), only vespids are large, robust, and short-legged in this manner (Naumann et al. 1991). The venation could be examined by drawing the folded wings and then comparing this with drawings of folded and unfolded modern vespid wings. In this way the ancient wasp wings were "graphically unfolded" (Fig. 11). The first discal cell of the forewing is longer than the basal cell, as in Vespidae (Brothers and Finnamore 1993).

Fossil Vespidae are only rarely found in the Okanagan Highlands.

Family Formicidae (ants)

MATERIAL: Q-0409, Q-0410, Q-0021, Q-0011, Q-0007, Q-027, and 29 other specimens (many with counterparts), some fairly complete, and many loose wings (Fig. 12).

REMARKS: Ant fossils are rare at other Eocene Okanagan Highlands sites. Only at Quilchena does there seem to be an extensive and diverse ant fauna. I will refer to them informally as types A, B, and C for ease of discussion.

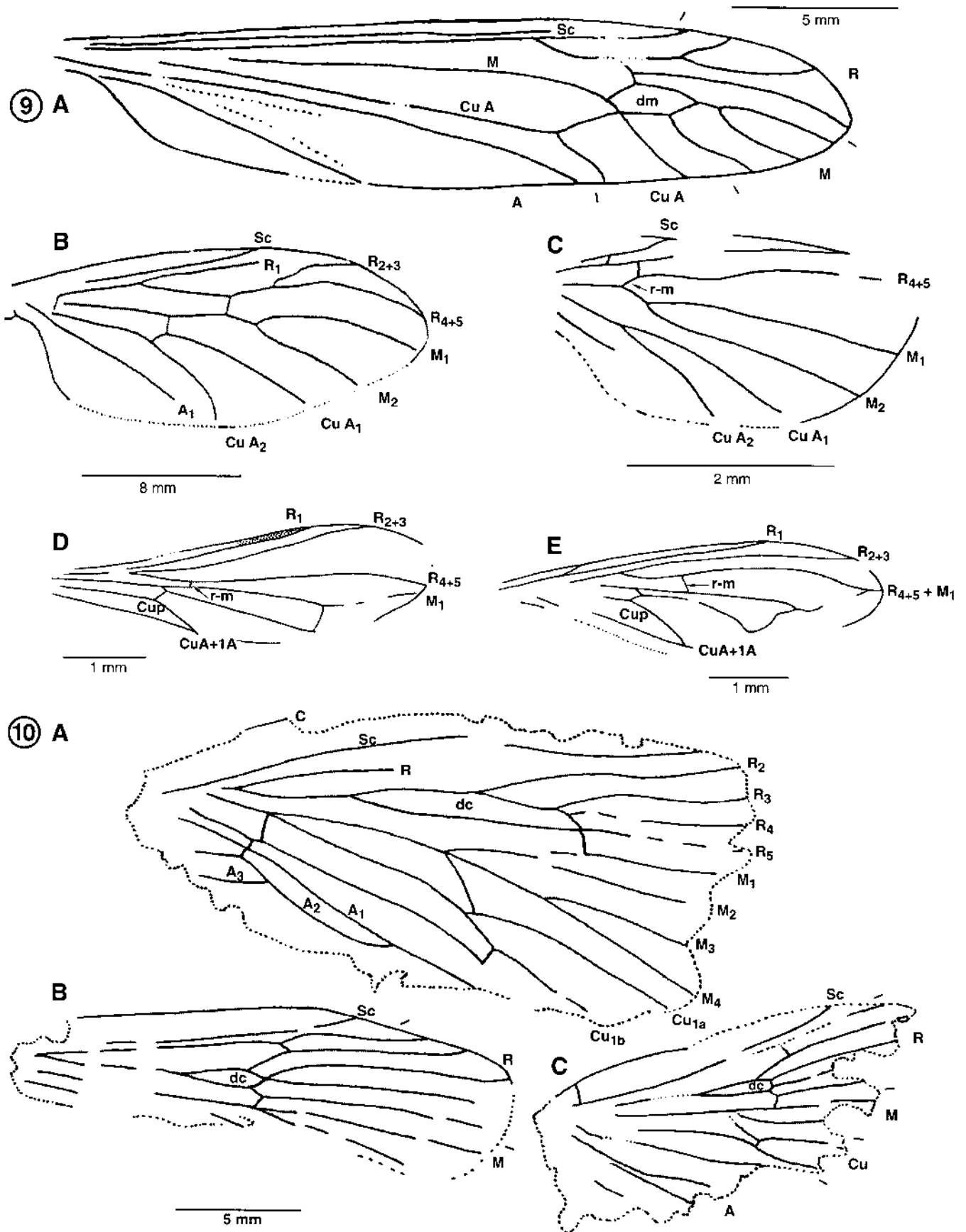
Type A (Fig. 12A) are large-winged ants. Q-0271, Q-0011, and Q-0409 are all about 17 mm long (although the distal end of the gaster is somewhat obscured in these specimens). Q-0271 had an estimated total wingspan of approximately 50 mm.

The gaster is large and subspheroidal (although it possibly swelled after death; see Rust and Andersen 1999). There is a distinct formicoid waist (particularly visible on Q-0011, but faintly preserved, if at all, on others) and the alitrunk is robust. Unfortunately, in none of these specimens is the entire antenna preserved, although in several (e.g., Q-0011, Q-0409a) the scape is present.

These ants are similar to *Camponotites kraussei* Dlussky and Rasnitsyn (1999) (also see Douglas and Stockey 1996) from the early Middle Eocene of Republic, Washington State, just south of Quilchena.

Type B ants are winged but smaller than type A; Q-0007 and Q-0008 are 11 mm long (Fig. 12B). Unfortunately, the venation is incompletely preserved. Q-0007 appears to preserve the scape element of the antenna. Some (e.g., Q-0008) appear apterous, although a possible faint trace of a wing is

Fig. 9. (A) Tipulidae (Q-0065). (B) Bibionidae (Q-0164). (C) Mycetophilidae (Q-0186). (D) Pipunculidae (Q-0397). (E) Syrphidae (Q-0251). **Fig. 10.** Trichoptera. (A) Phryganeidae (Q-0098). (B) Incertae sedis (Q-0424). (C) Incertae sedis (Q-0097).



visible. Q-0008 has a subspheroidal gaster, a distinct waist, and robust alitrunk.

Q-0400 represents type C an even smaller (6 mm) winged form. The gaster is proportionately large, and more ovate than in the other types. The alitrunk is separated from the gaster by a gap in which there is no visible waist. Possible antennal elements may actually be fragmentary leg parts. With neither a waist nor an antenna with a recognizably formicid scape and funiculus, this specimen cannot be definitely assigned to Formicidae, yet its habitus leaves no better place to tentatively assign it (Fig. 12C). There are other small specimens (Q-0019, Q-0014) that have a relatively larger, more robust alitrunk than Q-0400.

There has been controversy about all ants reported from the Mesozoic. Dlussky (1988) stated that Formicoidea of the Upper Cretaceous should not be assigned to Formicidae, but rather to either Sphecomyrmidae or Armaniidae. Baroni Urbani (1989) placed *Sphecomyrma freyii* from Upper Cretaceous New Jersey amber in Sphecomyrmidae rather than Formicidae because of such features as its relatively short scapus in relation to the funiculus. Clearly, however, there is more to be said (see Grimaldi et al. 1997). Unfortunately, the funiculus is not preserved on any of the Quilchena ants examined.

It cannot reasonably be expected that other important features considered synapomorphic for ants (Baroni Urbani 1989), such as the metapleural gland, will be visible on ants fossilized in shale. It is therefore possible that none of these are ant fossils, but are members of an ant-like, or remnant pre-ant, group of wasps. Ants assigned to modern genera, however, have been discovered in amber from the Hat Creek coal beds (Poinar et al. 1999), which are Early to early Middle Eocene in age, similar to Quilchena (Poinar et al. 1999). The extant ant genus *Pachycondyla* has been reported from the 55-mya Fur Formation of Denmark (Rust and Andersen 1999). Based on the established existence of Formicidae at this time, the formicoid waist (types A and B), and the similarity of type A to slightly younger ants from Republic (Dlussky and Rasnitsyn 1999), placement of at least some of the Quilchena types in Formicidae seems reasonable.

Family Sphecidae (digger wasps)

MATERIAL: Q-0423, a forewing.

REMARKS: The forewing has 10 closed cells arranged as in aculeate wasps. This specimen was collected by K. Naumann, who generously donated it to the SFU collection. It is currently being described (Pulawski et al. 2000).

Superfamily Apoidea (bees)

Family Halictidae

MATERIAL: Q-0424, a body, one partial leg, and part of fore and hind wings (Figs. 13 and 29).

REMARKS: The body is robust and the head, thorax, and abdomen are relatively wide for a hymenopteran, as in Apoidea. The wing venation is consistent with that of Apoidea, although as Darling and Sharkey (1990) state in their discussion of Mesozoic Hymenoptera, "It is extremely difficult to assign a fossil to either Sphecidae or Apidae.... There appear to be no diagnostic differences in wing venation, and the traditional differentiae, plumose hairs and expanded hind basitarsus, are either unlikely to be preserved in mineral replacement fos-

sils, or subtle." It is, then, fortunate to see the partial leg in this specimen with an enlarged basitarsus as in Apoidea, bearing scopae (Figs. 29a and 29b). Long hairs are also visible just posterior to where the leg appears to go beneath the body.

There is strong arcuation of the basal vein as in Halictidae (M. Engel, personal communication). This bee most resembles those of subfamily Halictinae (M. Engel, personal communication).

This is the first bee body fossil known from the Eocene Okanagan Highlands (megachilid leaf damage has been reported from Republic), and one of few bee fossils known from before the Middle Eocene.

Q-0424 was collected and generously donated to the SFU collection by R. Savenye.

Incertae sedis

MATERIAL: Q-0093, a single wing (basalmost area obscured); Q-0392, parts of at least two wings and perhaps some of the body, all partial and obscure (Fig. 14A). Q-0095, the apical portion of a wing (Fig. 14B).

REMARKS: Q-0093 and Q-0392 appear superficially similar to some Plecoptera, yet the subcosta reaches the apical margin and the enlarged basal area of the costal region is unlike Plecoptera (B. Stark, personal communication). These wings also resemble those of the megalopteran genus *Sialis*, yet it is not in the neuropteroid orders (J. Oswald, personal communication).

Q-0095 is the apical portion of a wing with a pectinately branched (presumed) radial sector with many cross-veins.

Fossil galls

cf. Hymenoptera: Cynipidae/Diptera: Cecidomyiidae

MATERIAL: Q-0262, Q-0396 (Fig. 30), and Q-0395 (Fig. 31), dicot leaves with galls.

REMARKS: Q-0262 and Q-0396 appear to be the same type of gall and Q-0395 appears to be of a different type. Q-0262 has five galls, two pairs of two touching and a lone one, all on the same leaf. These are subcircular, about 4–4.5 mm in diameter. They appear to have a distinct structure with an inner circle of tissue. Some of this apparent structure may be due to the compression of an originally spherical gall. Q-0396 appears similar. It is a lone gall on a leaf, but the leaf is incomplete and there may have been others present.

Q-0395 represents a different type of gall. It is smaller; the outer ring is about 2.5 mm in diameter. It has an inner raised area about 1.3 mm in diameter.

Illustrations of recent and fossil galls (e.g., Hoffman 1932; Eady and Quinlan 1963; Borror et al. 1989; Larew 1992) show galls of similar form resulting from both cynipid wasps and cecidomyiid flies. It would appear, in particular, that Q-0395 resembles the cecidomyiid galls shown in Fig. 32 in chapter 32 of Borror et al. (1989) in apparent size and morphology, and that Q-0262 and Q-0396 resemble the galls of cynipid wasps (Figs. 341–351 of Eady and Quinlan 1963).

However, it should be noted that fossil galls of very similar appearance to Q-0262 and Q-0396 are illustrated in Hoffman (1932) from the Miocene of Douglas Canyon, Washington. These galls are 0.3–0.4 cm in diameter, a bit smaller than Q-0262 and Q-0396, but not much. Hoffman stated that they are "characterized by a dot-like protuberance at their

Fig. 11. Hymenoptera: Vespidae(Q-0034). **Fig. 12.** Hymenoptera: Formicidae. (A) "Type A" (Q-0409). (B) "Type B" (Q-0007). (C) "Type C" (Q-0400). **Fig. 13.** Hymenoptera: Apoidea: Halictidae (Q-0424). **Fig. 14.** Incertae sedis. (A) Q-0093. (B) Q-0095.

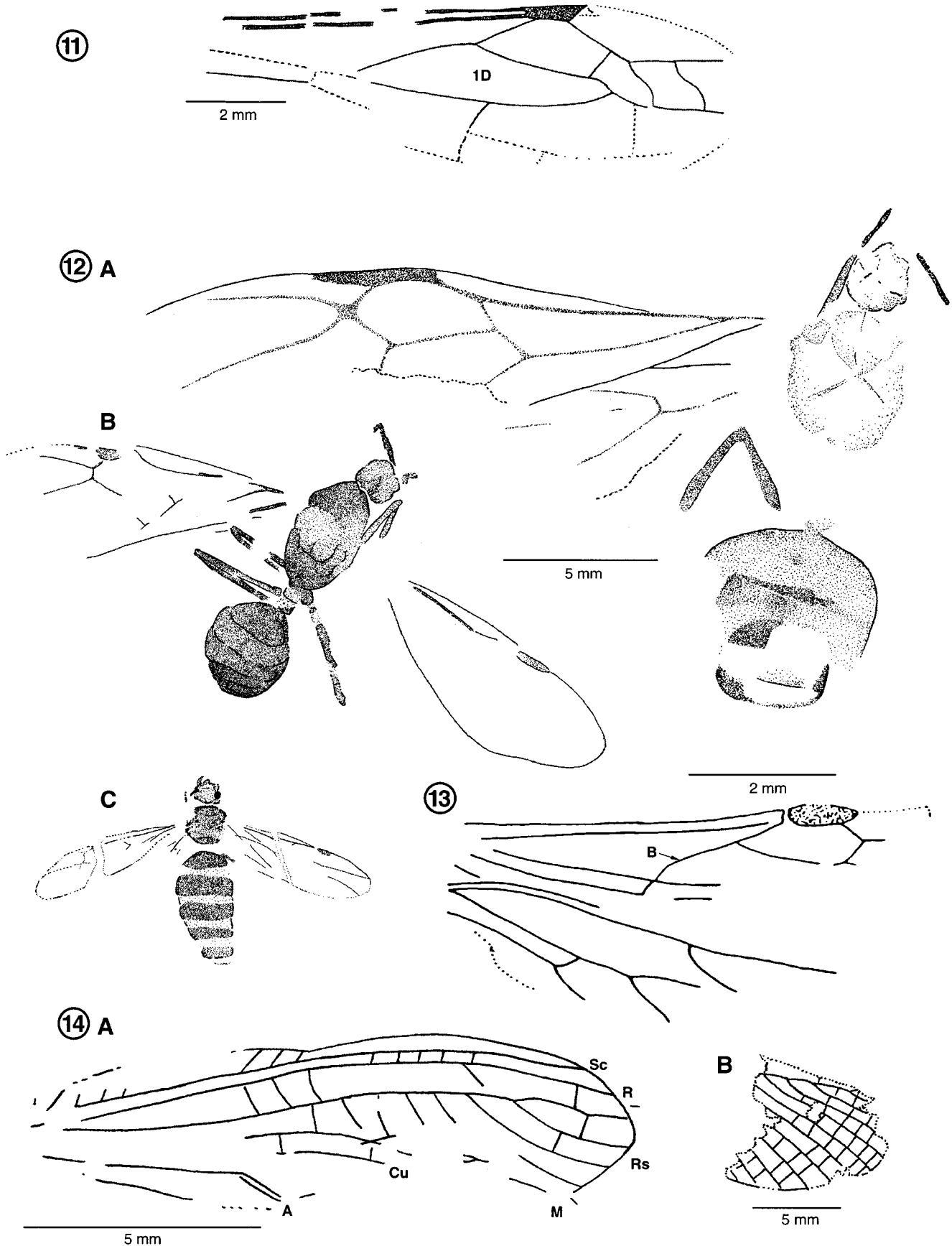
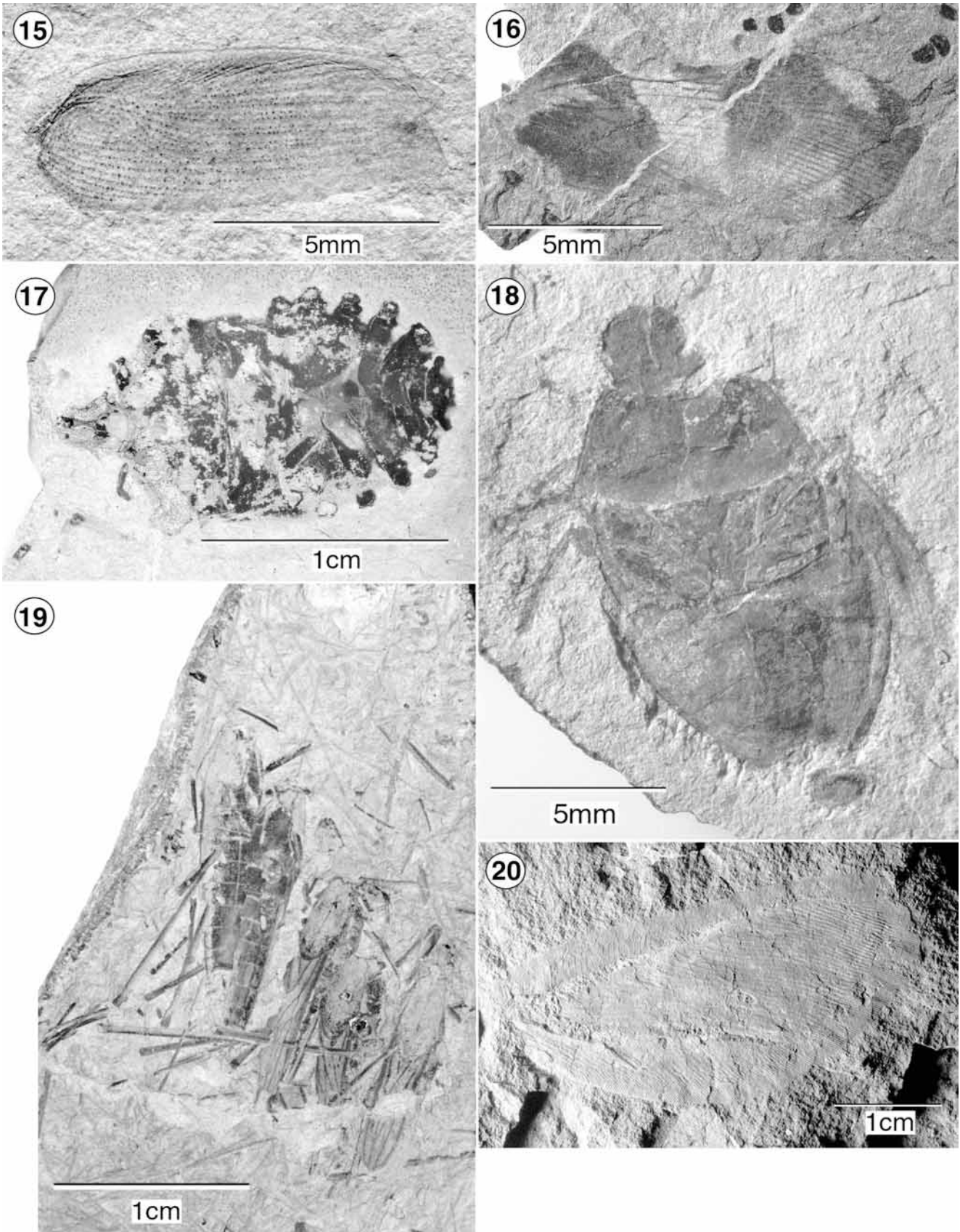


Fig. 15. Blattodea: Blaberidae: Diplopterinae (Q-0040). **Fig. 16.** Auchenorrhyncha: Ricaniidae (Q-0102). **Fig. 17.** Heteroptera: Dinidoridae (Q-0195). **Fig. 18.** Heteroptera: Cydnidae (Q-0194). **Fig. 19.** Heteroptera: Gerridae (Q-0207 to Q-0211). **Fig. 20.** Neuroptera incertae sedis (Q-0422).



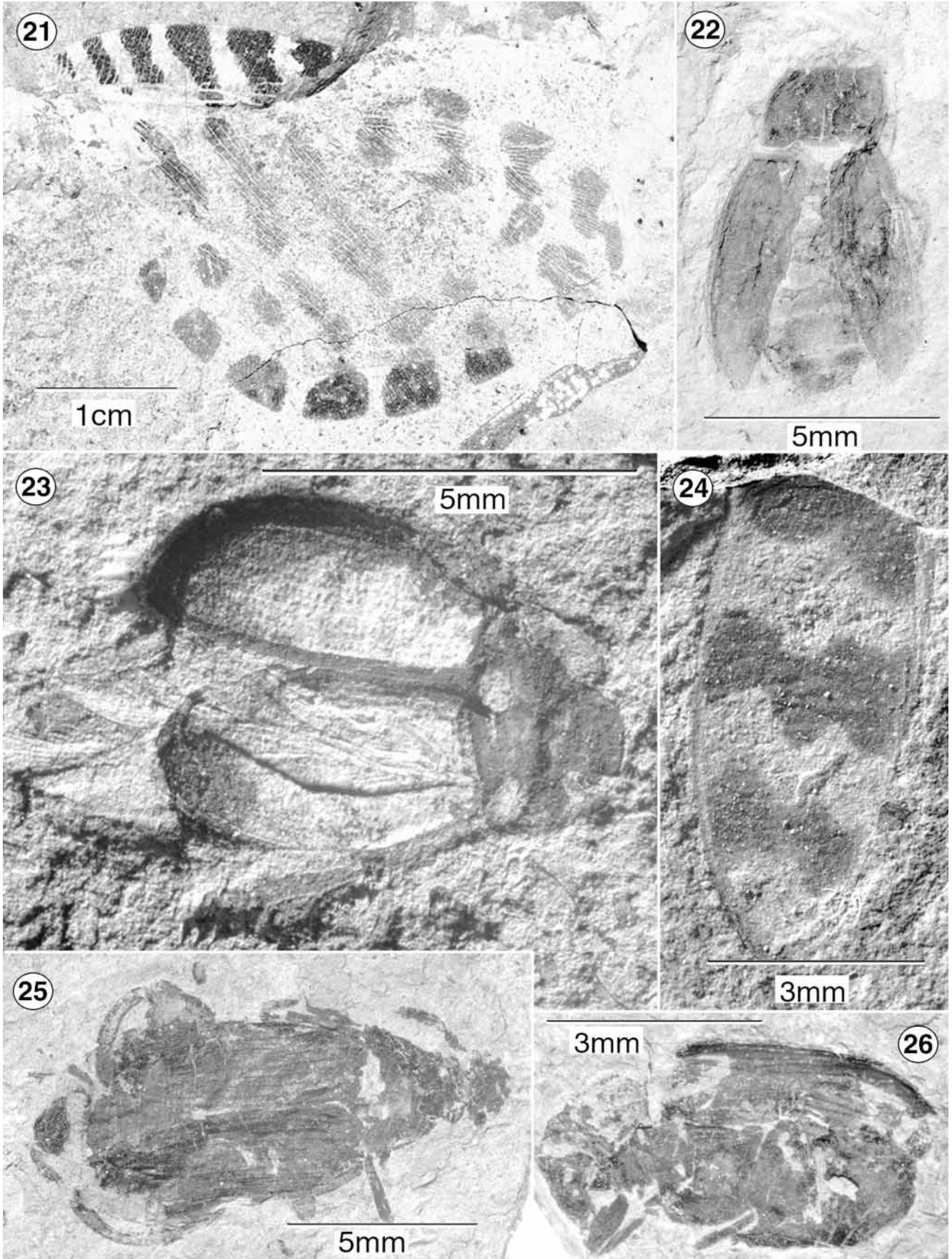


Fig. 21. Neuroptera incertae sedis (Q-0421). **Fig. 22.** Coleoptera: Carabidae, cf. *Amara* sp. (Q-0045). **Fig. 23.** Coleoptera: Scarabaeoidea (Q-0057). **Fig. 24.** Coleoptera: cf. Erotylidae (Q-0205). **Fig. 25.** Coleoptera: Chrysomelidae: Bruchinae: Pachymerinae (Q-0061). **Fig. 26.** Coleoptera: Curculionidae (Q-0063).

centers...” (see his Fig. 1), similar to the central area of the Quilchena fossils. Hoffman (1932) notes that these galls resemble both cynipid and cecidomyiid galls.

The oldest known insect galls (Larew 1992) from the Upper Cretaceous of Maryland resemble Q-0262 and Q-0396. They are assigned to Cynipidae.

Many gall-inducing insects are dedicated to their host plant. Unfortunately, the leaves associated with the galls in this collection are too incomplete to identify beyond being dicots, and so do not help in identification or in analyzing insect–plant interaction.

Douglas and Stockey (1996) record the presence of Cynipidae from Quilchena, and Cecidomyiidae are known from the Eocene of Florissant and The Green River Formation (Wilson 1978). Both of these taxa are known as far back as the Cretaceous (Labandeira 1994).

It is noted from all of the above authors (as well as Whittlake 1981 and Boucot 1990), that identifying the insect inducer of fossil galls is very difficult. It is possible that these fossils are either cecidomyiid- and (or) cynipid-induced galls.

Size of insects

Some of the insects in the Quilchena fauna are larger than might be expected when compared with other Eocene fossils and extant relatives. The significance of this is unclear.

Neuroptera

Wings Q-0422 and Q-0421 are about 45 mm long. The modern Kempyninae are known to be “the largest and most spectacular Osmylidae” (New 1983). Their wings reach 37 mm long (New 1991), significantly shorter than wing Q-0422. The Florissant Osmylidae are smaller as well. The wing of *O. requita* is 14–15 mm long (Carpenter 1943) and that of *L. columbianus* (in Kempyninae) is 28 mm long (Carpenter 1943) (25 mm in Cockerell 1908a).

Modern Polystoehotidae have wingspans of up to 75 mm (Borror et al. 1989), but this still places the forewing at about 37 mm.

Formicidae

Type A ants are large. Q-0271, Q-0011, and Q-0409 are all about 17 mm long (the end of the gaster is obscured, limiting precision). Q-0271 is about 25 mm from the presumed wing tip to the centre of the thorax, making a total wingspan of approximately 50 mm. The wings of several specimens (Q-0004, Q-0272) may have been a few millimetres longer.

Much larger ants are known from the Middle Eocene of Messel, Germany; their wingspan reached 16 cm (Lutz 1992)! Ants recently reported from the early Tertiary Fur Formation of Denmark (Rust and Andersen 1999) reach a body length of 25 mm. While the Quilchena specimens are smaller than these fossil European ants, they are still relatively large compared with modern ants. The giant ant (*Camponotus herculeanus*) is the largest extant ant in central and northern Europe (Stanek 1969). The queens are 16–18 mm long (Stanek 1969),

probably the same size as the Quilchena ants. While the bodies of the Quilchena ants appear marginally longer than *C. kraussei* from the early Middle Eocene of Republic (Dlussky and Rasnitsyn 1999), there is possible and variable postmortem swelling (Rust and Andersen 1999). The size of the forewing of the Quilchena ant, however, indicates that it was larger than the Republic ant.

Aphididae

The Quilchena aphids are estimated to be the equivalent in size to the largest aphids known, the modern and fossil (Miocene) *L. caryae* (the hickory, or giant bark aphid) (Heie and Friedrich 1971).

Auchenorrhyncha

There are various Auchenorrhyncha in the Quilchena fauna that are large compared with modern representatives of their families. Some isolated tegmina (e.g., Q-0086 and Q-0084) are 25 mm long. Large Auchenorrhyncha are well known elsewhere in the Eocene of North America. Handlirsch (1910) called the Princeton, British Columbia, *Aphrophora* sp. “a very large species,” and notes, “There is not doubt that this species belongs in the genus *Aphrophora* in the strict sense, yet today this genus includes only small forms.”

Scudder commented several times on the size of these insects. He writes of the Tertiary Cercopoidea of North America (1890) that “...some of them are gigantic, nearly all large...” and of British Columbian specimens (1895) that “...we are struck by the great size of these insects” and “...the most striking feature of this fauna is the size of the individuals which compose it.”

Climatic implications

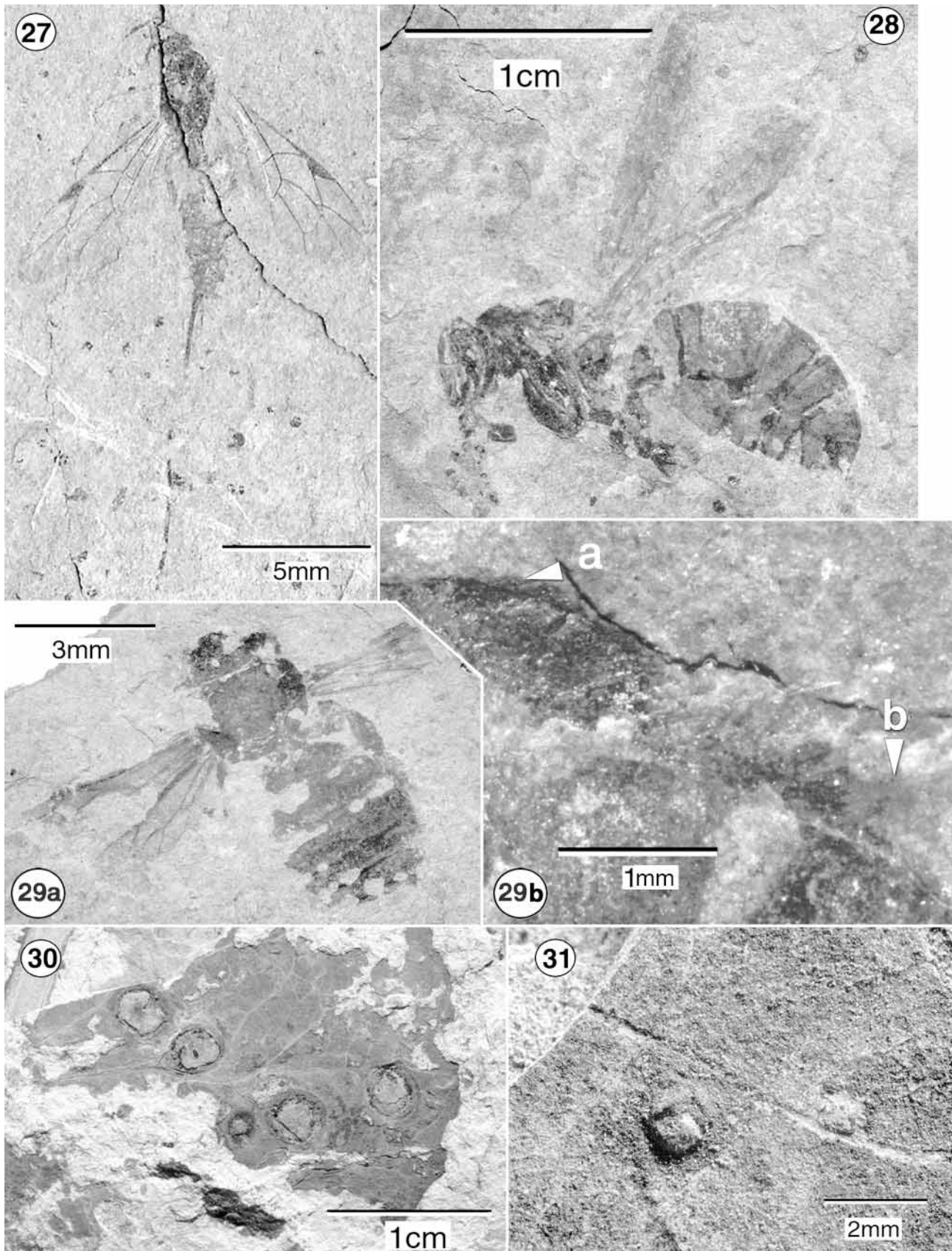
It might be intuitively thought that large size would be causally linked with a warm climate. However, a relationship between size and climate has not been established with insects. In the case of the giant bark aphid, the modern range is in temperate eastern North America. The Miocene aphids of this species lived in Iceland, which also had a temperate climate. Large size in this case (at least for modern representatives) is the result of the need for large mouthparts, because these aphids feed upon trees. In the case of living ants, the largest specimens reported are from the tropics, although the largest of the Quilchena ants are comparable in size to the largest modern European ants. Scudder certainly equated the large hoppers with the Neotropics (although not necessarily because of size).

Although the climatic implications of insect size are equivocal, certain taxa at Quilchena do suggest much warmer climatic conditions than today, based on analogy with distributions of nearest living relatives. These include the following:

Blattodea: Blaberidae

The family Blaberidae is principally tropical (Borror et al. 1989), with North American representatives found almost

Fig. 27. Hymenoptera: Ichneumonidae (Q-0018). **Fig. 28.** Hymenoptera: Vespidea (Q-0034). **Fig. 29.** (A) Hymenoptera: Halictidae (Q-0424). (B) The same as A, enlarged. Note the hairs on leg, *a*, and body? (or leg behind body, *b*?). **Fig. 30.** Galls on leaf (Q-0396). **Fig. 31.** Gall on leaf (Q-0395).



entirely in the subtropical southern United States (Borror et al. 1989). Modern cockroaches of the subfamily Diplopterinae are certainly tropical (Zimmerman 1948; Roth and Willis 1960). They are native to India, Sri Lanka, Singapore, Australia, Fiji, Samoa, Society Islands, Marquesas Islands, and Easter Island (Zimmerman 1948).

Auchenorrhyncha: Cercopoidea

Scudder (1890) writes of Tertiary Cercopoidea of Florissant, Wyoming, and British Columbia (Princeton; although it is likely that many or most Princeton Cercopoidea are of the same taxa as those at Quilchena) that “some of them are gigantic, nearly all large, and by far the greater part of them allied to types now found only in the tropics of the New World....”

Hemiptera: Dinidoridae

Q-0195 is very close to and possibly congeneric with *Megymenum*. This genus is today found in only the Oriental biotic region and Australia, in areas of subtropical to tropical climate (G. Gross, personal communication).

Coleoptera: Chrysomelidae: Pachymerinae

Seed weevils of the subfamily Pachymerinae are mostly tropical and subtropical today (Kingsolver 1965). Q-0061 is likely in the tribe Caryopemini, which today ranges in India, East Asia, and Madagascar (Nilsson 1992), all areas with a warm climate.

Diptera: Bibionidae

The fossil genera found at Quilchena (*Plecia* and *Penthetria*) are known today only from warm-climate areas, extending as far north as the warm-temperate – subtropical southern U.S.A. (Rice 1959).

The fossil insects reported here thus have a strongly thermophilous component, and so far there are no taxa that are presently restricted to microthermal climates. These examples of insect taxa with subtropical to tropical affinities parallel similar discoveries in other Eocene localities in the Okanagan Highlands. Megapodagrionid damselflies, which are presently entirely tropical in distribution, have been found at Republic, and the tropical termite family Mastotermitidae is recorded at Horsefly (Wehr 1998). Insects in Early to early Middle Eocene amber at Hat Creek (near McAbee; Fig. 1A) include tropical–subtropical taxa such as cockroaches of the subfamily Corydiinae (Polyphagidae) and ants of the presently essentially tropical genus *Technomyrmex* (Poinar et al. 1999).

Such insect indicators of mesothermal (mean annual temperature (MAT) 13–20°C) to possibly megathermal (MAT >20°C) conditions (as defined by Wolfe 1987) are at odds with interpretations of Okanagan Highlands sites, where paleoclimatic reconstructions using the Climate-Leaf Analysis Multivariate Programme (CLAMP) indicate microthermal (MAT <13°C) conditions (Wolfe 1994). For example, the Okanagan Highlands floras indicate that Republic had a MAT of 11.4°C, while the McAbee site in British Columbia had a MAT of 10.7°C (Greenwood and Wing 1995). One Mile Creek (near Princeton) and Chu Chua are estimated to be cooler yet, only 9.3 and 9.2°C, respectively (Table 2 in Wolfe 1994).

The much cooler conditions inferred for the Okanagan Highlands localities compared with warmer lowland coastal sites have been attributed to increasing elevation due to tectonic uplift of the Cordillera (Wolfe 1987; Wehr 1988).

The Early Eocene age of Quilchena places it near the warmest climatic episode of the Cenozoic, the Early Eocene thermal maximum (Wing and Greenwood 1993; Wolfe 1994). Quilchena was then near the beginning of regional uplift and therefore at a lower elevation and with a warmer climate than other possibly younger and higher Okanagan Highlands sites. Eocene lowland forests in the coastal Pacific Northwest were interpreted as megathermal rain forests (Wolfe 1987). In earlier members of the Eocene coastal lowland Chuckanut Formation (Fig. 1A), vegetation includes palms and abundant subtropical plants such as tree-ferns (Mustoe and Gannaway 1997). CLAMP, which has not yet been done at Quilchena, may reveal temperatures higher than at other Okanagan Highlands sites. It is also possible, however, that further radiometric dating of other Okanagan Highlands sites will reveal that they are as old as Quilchena. Early paleobotanical comparisons (Penhallow 1908; Hills 1965) suggest that the plant macrofossil assemblages of the Princeton region were similar enough to those of Quilchena and related Coldwater beds near Merritt to assign to them the same age.

If CLAMP analysis also reveals a microthermal climate for Quilchena, then the occurrences of “anomalously warm adapted” insects might be explained in several ways. Flying insects may have been transported from warmer lowlands by upslope winds or storms, or conversely, leaves of microthermal taxa may have been imported from cooler uplands, possibly by river transport. It might be expected, however, that long-distance transport would result in more damage to the leaves than is present. An apparently warm-adapted insect assemblage may also reflect a local microthermal community that contained relict representatives of taxa that are now restricted to mesothermal and (or) megathermal environments through evolutionary change or extinction of cold-tolerant variants.

It may also be that methods of estimating temperature using leaf physiognomy are less accurate than was previously thought (Wiemann et al. 1998; Wilf 1997; and others). This possibility must be considered in light of some recent discoveries in Middle Eocene Okanagan Highlands sites. For example, Erwin and Stockey (1991) identified vegetative organs of coryphoid (= sabaloid) fan-leaved palms as the most common elements of the Middle Eocene Princeton chert flora. Pollen grains similar to those of the palm *Sabal* have been found at Quilchena and a number of Okanagan Highlands sites (Princeton, Coalmont, Tranquille, McAbee, and Driftwood Creek) by Hills (1965). Palms have long been recognized as good indicators of warm climates with limited frost, and low monthly mean temperatures above 5–7°C (Wing and Greenwood 1993). With a MAT of 10.7°C and a mean annual range of temperature (MART) of 13.3°C (Greenwood and Wing 1995), the McAbee site would have a low monthly mean temperature of about 4°C, a little lower than the 5–7°C limit for palms cited by Wing and Greenwood (1993). Cycads are another well-recognized warm-climate indicator group (Wing and Greenwood 1993), and the first cycad leaf fossil was recently published from Republic (Hopkins and Johnson

1997). Other probably thermophilous plants of the Okanagan Highlands are listed in Wehr (1998).

Another possibility is that the presence of warm-adapted insects and plants is not in conflict with a low MAT, but rather that their ranges are limited by the lowest winter temperatures. Palms and other plants and insects may have ranged into areas of lower MAT than at present because of a more equable climate (lower MART) in the Eocene (Wolfe and Wehr 1991; Wing and Greenwood 1993). They were not subjected to the severe winter stress they would experience at the same MAT today. The "palm line" is the latitudinal boundary that defines the northern limits of palms today, since the soft, water-rich manoxylic wood of palms (along with other morphological characteristics) cannot stand more than a few days a year of freezing conditions (Wing and Greenwood 1993; Greenwood and Wing 1995). Eocene crocodiles have been discovered on Ellesmere Island in the Canadian Arctic (Markwick 1994). As with thermophilous plants, it is possible that the low monthly mean temperature may have been the limiting factor on crocodylian distribution this far north, rather than MAT (Markwick 1994). The mean annual range of temperature at the early Middle Eocene McAbee site is given as 13.3°C (Greenwood and Wing 1995). The present-day mean annual range of temperature for the Interior Douglas-fir biogeoclimatic zone (in which modern *Quilchena* lies) is 24–26°C (Krajina 1969), about twice as high.

Future work with leaf-margin and CLAMP analyses at *Quilchena*, and further radiometric dating of Okanagan Highlands sites in general is required in order to make a meaningful comparison of their insects, plants, and other fossils with their Eocene paleoenvironments.

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