PALEOGENE INSECT FAUNAS OF WESTERN NORTH AMERICA[1]

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*North American Paleogene insect faunas are concentrated in lacustrine sediments of the Cordillera. They represent cool temperate to tropical paleoclimatic conditions, yet were deposited at paleolatitudes somewhat farther north than present latitudes. The more than 200 insect families recognized are listed, with supporting references. Only about 90 of these have geological ranges extending back to Paleocene or Eocene times. The faunas are dominated by Coleoptera, Hymenoptera, and Diptera, especially Bibionidae (*Plecia *spp.).*

Les insectes du Paléogène de l'Amérique du nord sont concentrés dans les sédiments lacustres de la Cordillière. Ces sédiments, déposis à des latitudes légèrement plus au nord qu'aujourd'hui ont des faunes de climat tempéré à tropical. Plus de 200 familles sont reconnues pour cette période et anotées avec leurs références. Seulement 90 de ces familles se recontrent aussi tôt que *le Paléocène ou l'Eocène. Les faunes sont dominées par les Coléoptères, les Hyménoptères, et les Diptères (particulièrement les Bibionidae du genre* Plecia).

INTRODUCTION

North American Paleogene (Early Tertiary) insect faunas were first studied comprehensively by S.H. Scudder (1890a, d, and references therein). Although more than 150 papers dealing with these faunas have since been published, the faunas have not recently been summarized.

This paper presents a summary of known Paleogene insect localities, a faunal list at the family level and a bibliography to the relevant literature. Compilation was carried out using Zoological Record searches together with cross-referencing from literature cited sections of included papers. It is hoped that this summary of the faunas will promote their further study and thus enhance their usefulness for reconstruction of paleoenvironments and faunal evolution.

PALEOGENE INSECT FAUNAS

Paleogene insect localities in North America are distributed in a broad band from British Columbia southeastward to Colorado (Fig 1). The insects are preserved as compressions in shale or other fine-grained rocks, and often occur with fossil leaves and fishes. The sediments and associated fossils indicate deposition in quiet water regions of intermontane lakes. The location, age, composition, and paleoenvironment of the major faunas are discussed below.

Paleocene Faunas

Paleocene insect localities are rare in North America and their faunas have been little studied. They occur in the Great Plains, in fine-grained phases of sedimentary formations which are otherwise predominantly coarse-grained. Brown (1957, 1962) mentioned and figured specimens of Trichoptera, Blattodea, and Odonata from localities 19, 20 and 21 respectively (Fig 1) in Fort Union strata of Montana, and mentioned coleopterous elytra as being abundant at other Paleocene localities. Also from the Fort Union of Montana, Cooper (1941) described a specimen of Cicadidae from near Bear Creek, Montana (Fig. 1, locality 27). This cicada was found in association with mammals and with plants which indicate a lowland, humid, warm-temperate paleoenvironment (Cooper, 1941). Recently insects have also been discovered in the Paleocene Paskapoo

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Formation near Red Deer, Alberta (Fig. 1, locality 22). These latter collections were obtained by D. Wighton and P. Mitchell of the University of Alberta. Taxa recognized to date from locality 22 include Odonata - Gomphidae; Homoptera - Cercopidae; Coleoptera - Carabidae, Dytiscidae, Chrysomelidae, Tenebrionidae; and some unidentified larvae (Wighton and Mitchell, pers. comm.). In addition, University of Alberta paleontologists have discovered a case of Trichoptera - Limnephilidae? associated with fishes and molluscs in the Paskapoo Formation near Robb, Alberta (Fig. 1, locality 25), a case of Trichoptera - Leptoceridae? from the same formation near Edson, Alberta (Fig. 1, locality 26), and tegmina of Homoptera - Fulgoroidea from the same formation near Sundance, Alberta (Fig. 1, locality 28). Little is known in detail about the age or paleoenvironments of most of the Paleocene faunas.

Eocene Faunas

A: Green River–The Green River Formation occurs in several sedimentary basins in Wyoming, Utah, and Colorado (Fig. 1). As there are many individual localities in the Green River Formation which are not well known they are listed below. In Wyoming, two localities occur in the Green River Basin (Fig. 1, localities 8 and 10), occupied during the Eocene by Gosiute Lake (Schaeffer and Mangus, 1965). A third locality is in the much smaller Fossil Basin (locality 9) formerly occupied by Fossil Lake (McGrew and Casilliano, 1975). Those localities in Colorado (localities 4-6) are in the Piceance Greek Basin while the locality in Utah near the Colorado border (locality 7) is in the Uinta Basin. The Piceance Creek and Uinta Basins were both occupied by Eocene Lake Uinta (Schaeffer and Mangus, 1965).

Most of the Wyoming Green River insects described by Scudder (1890a) and others apparently came from red shales at the Fish Cut locality near Green River, Wyoming (Fig. 1, locality 8). Relatively few came from the Fossil Butte locality (locality 9; McGrew and Casilliano, 1975), and only caddisfly cases are known from Leucite Mountain (locality 10; Bradley, 1924, 1974).

In the Piceance Basin of Colorado, locality 4 (Fig. 1) represents a large number of sites in the Roan Plateau area, including Piceance Creek of Carpenter (1928, 1931, 1955), Kimball Creek of James (1932). and the Brushy Creek Canyon, Parachute Creek, Roan Mountain, Rifle, Eask Alkali Gulch, Camp Gulch, and Bear Gulch sites of Cockerell (1909d, 1921a-c, 1923a, 1925a, 1925c, 1928, 1933, 1941) and Cockerell and LeVeque (1931.) Locality 5 is Hay Gulch of Cockerell (1917a), and locality 6 represents the Smith's Ranch, Little Duck Creek, and Cathedral Bluffs sites of Cockerell (1921a, b, 1925a), and the Douglas Pass site (University of Alberta collections).

Scudder described many insects from a locality he termed "White River", a designation which is unfortunate because of possible confusion with the Oligocene White River Group of Colorado. Scudder's "White River" collections, some of which were described by Cockerell (1921a, b) came from Green River Formation localities along the White River near the Colorado-Utah border (locality 7). These may correspond in part to the Evacuation Creek localities of Cockerell (1916) and Carpenter (1955) in the Uinta Basin.

The Green River Formation strata are dated by their intercalation with the mammal-bearing Wasatch and Bridger Formations. Recent stratigraphic studies indicate that the Green River Formation in the Green River, Fossil and Piceance Basins ranges in age from Late Early Eocene (Lostcabinian) to Late Middle Eocene (Bridgerian C-D), or from about 52Ma to about 47Ma BP (Roehler, 1972). Some Green River strata in the Uinta Basin may be slightly younger.

Table 1 gives the composition to family level of the Green River Formation fauna. A total of 83 families has been recorded. By 1921 Cockerell could mention 279 species (Cockerell 1921a). In number of individuals, Cockerell noted the abundance of Coleoptera, Diptera, Hymenoptera, and Homoptera (especially Fulgoridae; Cockerell 1917c, 1921a). Scudder (1890c) earlier tabulated the results of a single summer's collecting effort and showed that the majority of specimens from the Green River localities were Coleoptera (63%), followed by Diptera (22%) Hemiptera - Homoptera (9%), and Hymenoptera (3%). Lepidoptera are rare, and bees have yet

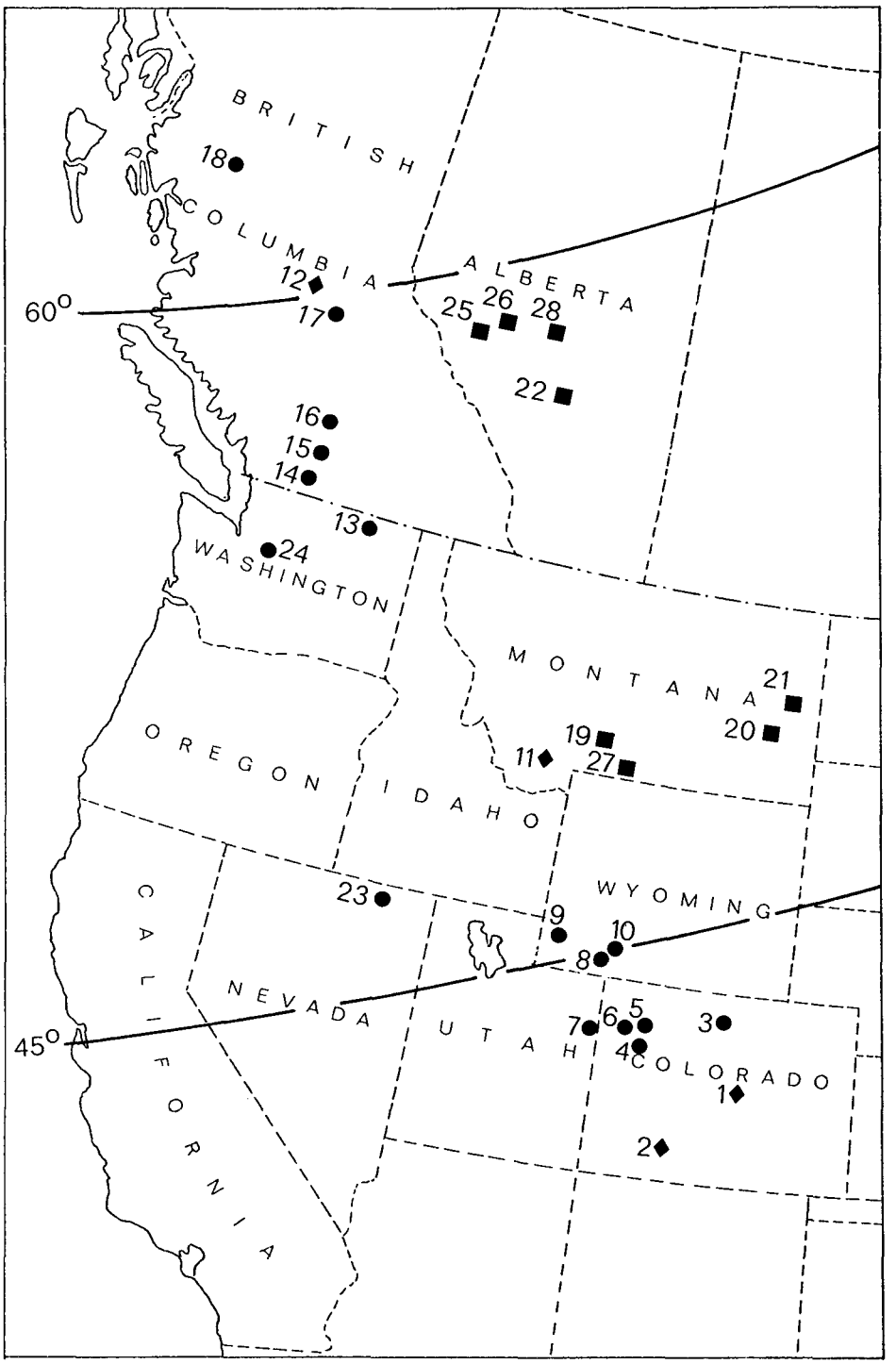

Fig. 1. Distribution of Paleogene insect localities in western North America. Squares are Paleocene localities, circles are Eocene localities, and diamonds are Oligocene localities. Heavy oblique lines are reconstructed Eocene latitudes. Locality numbers are referred to in text.

to be discovered. Cockerell remarked on the absence of really large specimens, the average size being smaller than the insects of the Florissant shales. He also commented on the relatively few species in common between the Green River Basin and the Colorado-Utah basins.

It has been thought until recently that much of the oil shale and varved fossiliferous marl of the Green River Formation was deposited in the deeper regions of stratified lakes (Bradley, 1948; McGrew, 1975). More recently playa-lake (Eugster and Surdam, 1973) and near-shore depositional environments (Bradley, 1974; Baer, 1969; Buchheim and Surdam, 1977) have been proposed, and many workers now feel that much of the Green River Formation represents playa-lake deposition (Eugster and Hardie, 1975); Surdam and Wolfbauer, 1975). Even if this is true, both deep and shallow phases are undoubtedly represented, as evidenced by major differences between such fish faunas as those of the Fossil Butte locality (McGrew, 1975) and others near Green River, Wyoming (Buchheim and Surdam, 1977). It is not known what proportion of the insect fauna occurs in the deep water deposits. Paleobotanical evidence suggests that climates during deposition of the Green River Formation varied from tropical to subtropical (Leopold and MacGinitie, 1972). Paleolatitudes reconstructed from Eocene paleomagnetic pole positions relative to North America (Jurdy and Van Der Voo, 1975) suggest that the Green River Formation localities were at a latitude of about 45°during the Eocene (Fig. 1). The Green River Formation is also famous for its fossil fishes (McGrew and Casilliano, 1975; Buchheim and Surdam, 1977).

B. British Columbia.—The Eocene insect fauna of British Columbia has recently been summarized with specific locality information by Wilson (1977b). There are numerous localities, representing isolated Eocene lakes, scattered through the interior plateau region of the province (Fig. 1, localities 14-18). Early studies of the fauna were by Scudder (1890a, 1895) and Handlirsch (1910); more recent studies were by Rice (1959, 1968).

Associated mammal teeth and palynomorphs, and K-Ar dating of interbedded volcanics indicate that the sediments are Middle Eocene or about 47-52 Ma old (Wilson, 1977b).

The fauna contains representatives of 30 families in seven orders (Table 1). In numbers of individuals it is dominated by Bibionidae of the genus *Plecia,* although locally Gerridae, large Homoptera, and Ichneumonidae are abundant. Coleoptera are rare except at one locality (Fig. 1, locality 15), from which they are the only order so far reported.

Specimens are preserved in fine-grained tuffaceous shales which appear to represent both deep off-shore and shallow, near-shore paleoenvironments. The varved insect-bearing sediments in the Horsefly area (Fig. 1, locality 17) were deposited in deep water in the hypolimnion of a stratified lake (Wilson, 1977a). Associated fossils such as molluscs, fishes, and coal at other localities indicate shallow, swampy conditions (Wilson, 1977b). The local insect faunules appear to reflect these paleoenvironmental differences (Wilson, 1977b).

According to paleobotanical evidence, the Middle Eocene climate in British Columbia was warm temperate, with wet summers and dry winters, and more continental aspects than Eocene coastal climates at the same latitude (Rouse et al., 1971). Eocene forests in British Columbia are believed to have been of a mixed deciduous-coniferous composition. Reconstructed paleolatitudes (Fig. 1) suggest that the area was at a latitude of about 60°N during the Eocene, or about 15°farther north than the area of the approximately contemporaneous Green River fauna. The insects occur with leaves, fishes, molluscs, and rare spiders, birds, and mammals (Wilson, 1977b, 1977c).

C: Republic, Washington—Insects are also known from the Middle Eocene Klondike Mountain Formation near Republic, Washington (Fig 1, locality 13). A few specimens were obtained by R.C. Pearson of the U.S. Geological Survey in the 1960's. In addition, a sizable collection was obtained by the present author during fossil fish collecting expeditions in 1976 and 1977. This collection is now at the University of Albera. No studies of the Republic insects have yet

been published.

The Republic flora, described by Berry (1929) and Brown (1937), was believed until recently to be Oligocene. Its Middle Eocene age is based on a number of K-Ar determinations on interbedded volcanics (R.C. Pearson, pers. comm., 1976). The fossil fishes are consistent with this interpretation (Wilson, in press). The Republic fauna is the same age as the British Columbia fauna, and is probably best interpreted as a southward extension of it.

The University of Alberta collections have yet to be studied in detail, but like the contemporaneous British Columbia fauna they contain numerous specimens of Bibionidae (*Plecia*) and large-winged Homoptera.

Sedimentology and study of associated fossil fishes indicate the presence of both deep water and shallow water conditions. In other aspects the paleoenvironment is probably similar to the British Columbia conditions of the time.

D: Coalmont Formation.—Cockerell (1916) described Eocene insects from the North Park Colorado, near Big Muddy (or Araphahoe) Pass. In 1977 the author obtained a collection, now at the University of Alberta, from the Coalmont Formation in this area.

The age of this fauna is probably Early Eocene. Palynomorphs studied by Leopold (Leopold and MacGinitie, 1972) indicate that the Coalmont Formation is Paleocene and Early Eocene. Fossil leaf occurrences in the Coalmont Formation are believed to be Eocene (Hail, 1965).

Cockerell's (1916) insects were assigned to two species of Coleoptera. The University of Alberta collection has yet to be studied, but it is dominated by Coleoptera as well.

Contemporaneous floras in Wyoming indicate a humid, subtropical paleoclimate (Leopold and MacGinitie, 1972). The insects occur in association with fishes (University of Alberta collections).

E. Additional Eocene faunas.—Other Eocene faunas have been collected by this author, but as yet have been little studied. So far only coleopterous elytra have been found.

These faunas include the Copper Basin fauna which occurs in the Dead Horse Tuff near Jarbidge, Nevada (Fig. 1, locality 23). Its Late Eocene age is based on a K-Ar date of 40 Ma BP (Axelrod, 1966). The Copper Basin flora is dominated by conifers and small-leaved angiosperms, representing a cool-temperate upland habitat (Axelrod, 1966).

The Roslyn fauna occurs in the Roslyn Formation near Cle Elum, Washington (Fig. 1, locality 24). It is considered to be Middle Eocene based on a single fossil fish and two turtle carapaces (Foster, 1960). The insects occur with leaves and molluscs in shales roofing a coal seam, indicating shallow, swampy depositional conditions.

Oligocene Faunas

A: Florissant.— The Forissant fauna is the best known, most prolific, and most diverse of the North American Paleogene insect faunas. There are a number of localities within a small intermontane basin (Scudder, 1882) once occupied by a small lake near South Park, Colorado (Fig. 1, locality 1). Many people, including Scudder and Cockerell, have published descriptions of Florissant insects.

The shales of the Florissant basin are generally agreed to be Early Oligocene. This age is based on study of plants (Leopold and MacGinitie, 1972) and of a marsupial (Gazin, 1935).

The fauna as presently known includes representatives of 192 families (Table 1). According to Scudder (1882, 1890c) there are many specimens of Formicidae and Ichneumonidae among the Hymenoptera, and of Bibionidae among the Diptera.

The Florissant shales seem to have been deposited in part in the hypolimnion of a stratified lake (McLeroy and Anderson, 1966). The Early Oligocene climate of the Florissant area was warm temperate to subtropical according to the evidence of fossil floras (Leopold and Macginitie, 1972). The insect evidence is in accord with this interpretation, but the evidence is

conflicting as to whether the climate was wet or dry. For example, James (1939) felt that some of the Diptera were indicative of a humid climate, whereas the abundance of Bombyliidae (Hull, 1973) suggests an arid climate. The small intermontane basin is indicative of a more upland location than the older Green River lakes. The paleolatitude of the Florissant shales was probably little different from that of the Green River Formation (Fig. 1).

B: Mormon Creek.—The Mormon Creek fauna (Fig. 1, locality 11) is the smaller of two known from the Passamari Formation of the Ruby Basin, Montana (Dorr and Wheeler, 1964). The Mormon Creek sediments cover only a small area and specimens are obtained primarily from a single excavation site.

The Flora is indicative of a Late Eocene or Early Oligocene age (Leopold and MacGinitie, 1972) although ages as old as Late Early Eocene have been suggested (Becker, 1960).

Only a few insects from this fauna have been reported. They include Carabidae, Tipulidae, and Ichneumonidae (Becker, 1960).

The plants indicate a humid, warm temperate to subtropical climate and moderate elevation (Becker, 1960). The Mormon Creek fauna also includes fish scales (Becker 1960; University of Alberta collections).

C: Ruby Paper Shales.—The Passamari Formation of the Ruby Basin, Montana (Fig. 1, locality 11), contains a second insect fauna believed to be Late Oligocene (Leopold and MacGinitie, 1972; Dorr and Wheeler, 1964). The Ruby Paper shales are found at a number of excavation sites in a small area between Mormon and Peterson Creeks in the Upper Ruby River Basin (Becker, 1961).

The insect fauna includes representatives of 29 families in 13 orders, according to Becker (1961, 1965), Hull (1960, 1962), Lewis (1971a, 1971b, 1972, 1975, 1976), and Zuidema (1950, 1955). Recognized are: Ephemeroptera - Baetidae; Odonata; Dermaptera; Plecoptera; Orthoptera - Acrididae; Hemiptera - cf Coreidae; Homoptera - Cicadellidae, Fulgoridae; Megaloptera - Sialidae, Corydalidae; Coleoptera - Silphidae?, Scarabeidae, Psephenidae, Elateridae; Diptera - Tipulidae, Chironomidae, Bibionidae, Mycetophilidae, Therevidae, Asilidae, Bombyliidae, Diopsidae, Syrphidae; Mecoptera; Trichoptera; Lepidoptera - Psychidae?; Hymenoptera - Tenthredinidae?, Ichneumonidae, Apidae, Formicidae. Bibionidae are the most abundant Diptera (Hull, 1960), as at many other Paleogene localities.

According to Becker (1961, 1966) and Leopold and MacGinitie (1972) the Ruby flora records cooler conditions than at Florissant, but still warmer, more moderate, and more moist than in the modern Ruby Basin. The insects occur in association with the diverse Ruby Paper Shale flora (Becker, 1961, 1966) and with fishes and a bird (Becker, 1961; Dorr and Wheeler, 1964).

D: Creede.—The Creede Formation of Colorado (Fig. 1, locality 2) is believed to be latest Oligocene or earliest Miocene in age (Leopold and MacGinitie, 1972).

Insects from the formation include Isoptera - Rhinotermitidae; Megaloptera - Raphidiidae; Neuroptera - Chrysopidae; Diptera - Tipulidae, Bibionidae, Syrphidae; Hymenoptera - Ichneumonidae (Carpenter, 1935, 1936; Carpenter et al., 1938; Cockerell, 1941). The Chrysopidae, Tipulidae, and Bibionidae are among the most abundant based on lists of specimens in Carpenter *et al.* (1938).

Floral evidence suggests a high altitude paleoenvironment (Leopold and MacGinitie, 1972). According to Carpenter *et al.* (1938) this is reflected in the low specific diversity of the insect fauna.

E: Quesnel.—Tertiary insects from the Fraser River Valley near Quesnel, British Columbia (Fig. 1, locality 17) were described by Scudder (1890a, 1895) and Handlirsch (1910).

There has been no dating of the specific fossil localities. However, Late Early Oligocene mammal teeth and palynomorphs occur in Fraser Valley sediments south of Quesnel (Piel, 1971).

Table 1. Systematic list of insect families known from three Paleogene faunas. References for each family are combinations of the last two digits of the year of publication, and the author's surname abbreviated as follows: Ben: Benson; Be: Bequaert; Br: Bradley; Bn: Brown; B: Brues; Ca: Carpenter; C: Cockerell; CC: Cockerell and Custer; CL: Cockerell and LeVeque; Co: Cooper; E: Emerson; F: Forbes; Ha: Handlirsch; H: Hull; J: James; M: Melander; MC: McGrew and Casilliano; Ri: Rice; R: Rohwer; S: Scudder; Sn: Snyder; W: Wickham; Wi: Wilson; ZM: Zeuner and Manning.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Thysanura					
Lepismatidae	silverfish	x			C13d, S90a
Ephemeroptera					
Baetidae	small may flies	x			C23b
Ephemeridae	burrowing mayflies	x			C08j, C13d, S86, S90a
Odonata					
Platycnemididae	platycnemidid damselflies	x			C08i, S92a
Coenagrionidae	narrow-winged damselflies	x			BMC54, C21a, C25b
Chlorocyphidae	chlorocyphid damselflies		x		C25a
Calopterygidae	broad-winged damselflies	x	x		C07d, C08a, C08i, C08q, C08t, C09d, C10 C13d, C16, C21a, C25b, C40, S90a
Aeshnidae	darners	x			C07d, C13c, C13d, S90a
Gomphidae	clubtails	x			S92a
Libellulidae	common skimmers	x	x		C21b, S78, S90a
Blattodea					
Blattidae	cockroaches	x	x	x	Bn57, Ca47, C09g, C13d, S86, S90a
Mantodea					
Mantidae	mantids	x			C08f, C13d
Dermaptera					
Forficulidae	common earwigs	x			C25a, S86, S90a
Orthoptera					
Gryllacrididae	leaf-rolling grasshoppers	x			C09h, S90a
Tettigoniidae	long-horned grasshoppers	x			C08m, C09h
Gryllidae	crickets	x	x		C08a, C21b, S78, S86, S90a
Acrididae	short-horned grasshoppers	x	x	x	C08a, C09h, C10, C14b, C26b, Ha10, S78, S86, S90a
Phasmatodea					
Phasmatidae	walking sticks	x			C13d, S86, S90a
Embioptera					
Embiidae	webspinners	x			C08j, C13d
Isoptera					
Mastotermitidae	mastotermitids			x	Wi77b
Kalotermitidae	dry-wood, damp-wood, powder-post termites	x			E33, E69, S90a, Sn25, Sn50
Termopsidae	true damp-wood termites	x			E33, Sn25
Hodotermitidae	rotten-wood termites	x			C13e, S86, S90a, Sn25, Sn50

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Rhinotermitidae	subterranean and damp-wood termites	x			S90a, Sn25, Sn50
Termitidae	soldierless, desert and nasutiform termites	x			C13d, Sn25
Psocoptera	booklice, psocids		x		S90a
Hemiptera					
Miridae	leaf (plant) bugs	x			C13d, S90a
Tingidae	lace bugs	x			C14a, S90b
Reduviidae	assassin bugs	x	x		S78, S90a
Coreidae	leaf-footed bugs	x	x		C09d, S90a, S90b
Saldidae	shore bugs		x		S90a
Lygaeidae	seed bugs	x	x		S78, S90a, S90b
Pyrrhocoridae	red bugs or stainers	x			S90a
Cydnidae	burrower bugs	x	x		C09d, S90a
Pentatomidae	stink bugs	x	x	x	C09g, C26c, S78, S90a, Wi77b
Gerridae	water striders	x	x	x	C13d, Ha10, S90a, S95, Wi77b
Veliidae	ripple bugs	x		x	S90a, Wi77b
Gelastocoridae	toad bugs		x		S90a
Notonectidae	back swimmers	x			S90a
Belostomatidae	giant water bugs	x			C08j
Corixidae	water boatmen	x			S90a
Homoptera					
Cixiidae	cixiid planthoppers	x	x		S90a
Delphacidae	delphacid planthoppers		x		C25a, S90a
Fulgoridae	planthoppers	x	x	x	C09d, C09g, C21a, C21c, CL3l, S78, S90a, S95
Achilidae	achilid planthoppers	x			S90a, S90b
Ricaniidae	ricaniid planthoppers		x		S90a
Flatidae	flatid planthoppers		x		C21a, S90a
Dictyopharidae	dictyopharid planthoppers	x			S90a
Cercopidae	froghoppers, spittlebugs	x	x	x	C08s, C21a, Ha10, S90a, S90b, S95, Wi77b
Cicadidae	cicadas	x			C06a, C08h, C11, C13d, C17b, Co41, S92a
Cicadellidae	leafhoppers	x	x	x	Ca47, C13d, C21a, C25a, S78, S90a, S95 Wi77b
Psyllidae	psyllids or jumping plantlice	x			C11, C14b, S90a
Aphididae	aphids or plantlice	x	?		C08n, C09g, S90a
Pemphigidae	woolly and gall-making aphids	x	x		S90b
Coccidae	wax and tortoise scales	x			C13d, S90a
Thysanoptera					
Aeolothripidae	broad-winged or banded thrips		x		S90a
Megaloptera				x	Wi77b
Sialidae	alderflies	x			S90a
Raphidiidae	raphidiid snakeflies	x		x	Ca36, C07a, C09g, C12, C13d, C14a, C17b, CC25, Ha10, R09

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Inocelliidae	inocelliid snakeflies	x			Ca36, CC25
Neuroptera					
Hemerobiidae	brown lacewings	x			C08a, C08e, S90a
Chrysopidae	green lacewings	x			Ca35, C08c, C09e, C14a, S90a
Nemopteridae	nemopterids	x			C07b, C08r
Coleoptera					
Carabidae	ground beetles	x	x	x	C08h, C13d, C21a, C21b, C25a, S78, S90a, S92a, S95, S00, W09, W11, W13, W14b, W17, W20
Cicindelidae	tiger beetles		x?		C21a
Dytiscidae	predaceous diving beetles	x	x		S90a, S00, W09, W11, W13, W14b, W20
Hydrophilidae	water scavenger beetles	x	x	x	S78, S90a, S95, S00, W09, W11, W14b, W20
Silphidae	carrion beetles	x			C08a, S00, W13, W14b, W20
Staphylinidae	rove beetles	x	x		S90a, S00, W11, W13, W14b, W20,
Lucanidae	stag beetles	x			W11, W13, W20
Scarabeidae	scarab beetles	x	x	x	Ha10, S90a, S95, S00, W09, W11, W13, W14a, W14b, W20
Helodidae	marsh beetles	x			W20
Dascillidae	soft-bodied plant beetles	x			W11, W14b, W20
Byrrhidae	pill beetles	x			S92a, W13, W14b, W20
Nosodendridae	wounded-tree beetles		x		S90a, S00
Psephenidae	water penny beetles	x			W20
Chelonariidae	chelonariid beetles	x			W20
Dryopidae	long-toed water beetles	x			S00, W11, W14b
Buprestidae	metallic wood-boring beetles	x		x	C26c, S90a, S95, S00, W13, W14a, W16, W17, W20
Elateridae	click beetles	x	x	x	C14b, CL31, Ha10, S78, S90a, S95, S00, W08, W14b, W16, W20
Eucnemidae	false click beetles	x			W20
Trixagidae	throscid beetles	x			W14a, W20
Lampyridae	lightningbugs or fireflies	x			S00, W13, W14b, W17, W20
Cantharidae	soldier beetles	x			W09, W20
Lycidae	net-winged beetles	x			W20
Melyridae	soft-winged flower beetles	x			C13d, W14b, W17
Dermestidae	dermestid or skin beetles	x			S00, W14b, W20
Anobiidae	death watch beetles	x	x		W20
Ptinidae	spider beetles	x	x		S78, S90a, S92b, S00, W14a, W14b, W17

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order / Family	Common Name	Florissant	Green River	British Columbia	References
Bostrychidae	branch and twig borers	x			W14b, W20
Trogossitidae	bark-gnawing beetles	x			C13d, W13, W20
Cleridae	checkered beetles	x			W14a, W14b, W20
Lymexylidae	ship-timber beetles	x			W11, W20
Nitidulidae	sap beetles	x	x		S78, S90a, S00, W20
Cucujidae	flat bark beetles	x	x		S90a, S00, W13, W14a, W14b, W20
Cryptophagidae	silken fungus beetles	x	x		C26c, S78, S90a, S00, W13, W14b, W20
Erotylidae	pleasing fungus beetles	x	x		S78, S90a, S00, W20
Coccinellidae	ladybird beetles	x			S00, W14b, W17, W20
Lathridiidae	minute brown scavenger beetles	x			W14a, W14b, W20
Mycetophagidae	hairy fungus beetles	x			W20
Colydiidae	bark beetles	x			W14b, W20
Tenebrionidae	darkling beetles	x		x	S90a, S95, S00, W13, W14a, W20
Alleculidae	comb-clawed beetles	x			W14a, W14b, W20
Pythidae	narrow-waisted bark beetles	x			W20
Melandryidae	false darkling beetles	x	x		C25a, W11, W20
Mordellidae	tumbling flower beetles	x	x		C25a, W09, W14a, W14b, W20
Rhipiphoridae	wedge-shaped beetles	x	x		S78, S90a, S00, W20
Oedermeridae	false blister beetles	x			W14b, W20
Meloidae	blister beetles	x			S00, W14b, W20
Anthicidae	antlike flower beetles	x			W14b, W20
Cerambycidae	long-horned beetles	x	x		C08a, C08i, C16, C25a, S00, W11, W13, W14a, W14b, W17, W20
Bruchidae	seed beetles	x	x		S90a, S00, W13, W14b, W17, W20
Chrysomelidae	leaf beetles	x	x	x	C21a, S78, S90a, S95, S00, W11, W13, W14a, W14b, W20
Anthribidae	fungus weevils	x	x		S78, S90a, S92b, S93, W11, W14b, W20
Attelabidae	leaf-rolling beetles	x	x		C13d, S90a, S92b, S93, W11
Curculionidae	snout beetles	x	x		C09i, C13d, C21b, C26c, S78, S90a, S92b, S93, W11, W13, W14b, W17, W20
Scolytidae	bark or engraver and ambrosia beetles	x	x		S78, S90a, S92b, S93, W11, W20
Mecoptera					
Meropeidae	earwigflies	x			C09b
Panorpidae	common scorpionflies	x			Ca31, C07b, C08g, C13d, S90a,
Bittacidae	hangingflies	x	x		Ca28, Ca31, Ca55, C09b
Diptera					
Tipulidae	crane flies	x	x	x	C08a, C08j, C09h, C10, C21a, C25a, Ha10, M49, S78, S90a, S94, Wi77b
Ptychopteridae	phantom crane flies	x		x	C10, Ha10
Culicidae	mosquitoes		x		C21a, S90a

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Chironomidae	midges	x	x		C10, S78, S90a,
Scatopsidae	minute black scavenger flies	x			M49
Bibionidae	March flies	x	x	x	C09d, C11, C14b, C16, C17a, C17b, C21a, C25a, Ha10, H60, J39 M49, Ri59, S90a, Wi77b
Cecidomyiidae	gall gnats	x	x		C08a, S90a
Sciaridae	dark-winged fungus gnats	x	x	x	C16, M49, S90a Wi 77b
Mycetophilidae	fungus gnats	x	x	x	C06d, C09a, C11, C14b, Ci4f, C21a, C25a, M49, S78, S90a, Wi77b
Rhagionidae	snipe flies	x			C08d, C09a, C09g, C11, C13d, C14e, M49
Tabanidae	horse and deer flies	x	x?		C09g, C16, M46, MC75
Stratiomyidae	soldier flies	x	x		C10, C11, C13d, C17d, J37, J39, S90a
Nemestrinidae	tangle-veined flies	x			Be47, BeCa36, C08k, C08o, C08p, C10 C14a, M49
Acroceridae	small-headed flies		x		S90a
Therevidae	stiletto flies	x			C09c, C09g, C16, C21a, M49
Asilidae	robber flies	x	x		C08d, C09f, C09g, C10, C11, C13b, C13d, C14a, C14b, C14e, C17b, C21a, H57, J39, M46, M49, S78
Mydaidae	mydas flies	x			C13a
Bombyliidae	bee flies	x			C09a, C09c, C09g, C10, C11, C14a, C14b, C14e, C16, C17a, C17d, H73, M46, M49
Empididae	dance flies	x	x	x	C14b, C15, C16, C17a, C21a, Ha10, J37, J39, M49, Wi77b
Dolichopodidae	long-legged flies		x		S78, S90a
Platypezidae	flat-footed flies	x	x		C09a, C11, S90a
Phoridae	humpbacked flies	x			B08a, C13c, M49
Syrphidae	hover or flower flies	x	x	x	C09a, C09a, C09f, C09g, C14a, C16, C21a, C24, C25a, CL3l, H45, H49, H60, J32, M49, S78, S90a, Wi77b
Conopidae	thick-headed flies		x		S90a
Otitidae	picture-winged flies	x			C16, C17a, M49
Tephritidae	fruit flies		x		C25a
Sepsidae	black scavenger flies	x			M49
Sciomyzidae	marsh flies	x	x		C09c, S78, S90a
Lauxaniidae	lauxaniid flies	x			M49
Heleomyzidae	helomyzid flies	x	x		C14b, M49, S90a
Piophilidae	skipper flies	x			M49
Agromyzidae	leaf miner flies	x			M49

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Anthomyiidae	anthomyiid flies	x	x		C13f, C17a, C21a
Eophlebomyiidae and Glossinidae	tsetse flies	x	x		C17d, C25a, C25c
Muscidae	muscid flies	x	x		C07b, C07h, C08a, C09j, S90a
Tachinidae	tachinid flies		x		S78, S90a
Oestridae	warble and bot flies	x	x		C16, S92a
Trichoptera				x	Wi77b
Hydropsychidae	net-spinning caddisflies	x	x		C07a, C09b, C09g, C10, S90a
Hydroptilidae	micro-caddisflies		x		C21a
Limnephilidae	northern caddisflies	x	x		C07a, C10, C21a, S90a
Phryganeidae	large caddisflies	x			C07a, C14a, S90a
Leptoceridae	long-horned caddisflies	x			S90a
Odontoceridae	odontocerids	x			C09b
Sericostomatidae	sericostomatids		x		Br24, Br74
Lepidoptera					
Cossidae	carpenter and leopard moths	x			C26a
Tortricidae	tortricid moths	x			C07g, C16, C22b
Tineidae	clothes moths etc.	x			S90a
Yponomeutidae	ermine moths		x		C33, CL31, F31
Oecophoridae	oecophorid moths	x			C13d
Ethmiidae	ethmiid moths	x			C22b
Thyrididae	window-winged moths		x		C33
Papilionidae	swallowtails	x			S87
Pieridae	whites, sulphurs and orange-tips	x			C13d, C22b
Nymphalidae	brush-footed butterflies	x			C08a, C22b, S87, S92a
Libytheidae	snout butterflies	x			C22b
Geometridae	measuring worms	x			C22b
Saturniidae	giant silkworm moths	x			C22b
Hymenoptera					
Orussidae	parasitic wood wasps	x			B06
Siricidae	horntails	x			B08b
Tenthredinidae	common sawflies	x	x	x	B08b, C06b, C07a, C07b, C08g, C09f, C10, C11, C14b, C14d, C16, C17a, C17b, C22a, Ri68, R08b, R08c, S92a
Blasticotomidae	blasticotomid sawflies	x			Ben42, B08b, R08b,
Xyelidae	xyelid sawflies	x			C13d
Pamphilidae	web-spinning and leaf-rolling sawflies	x			B08b, C13d, R08b, R08c
Cephidae	stem sawflies	x			C14a
Stephanidae	stephanids	x			B10a
Ichneumonidae	ichneumonid wasps	x	x	x	B06, B10a, B10b, C06d, C19, C21a, C24, C41, CL31, Ha10, S09a, Wi77b
Braconidae	braconid wasps	x	x	x	B06, B10a, B10b, S78, S90a, Wi77b
Evaniidae	ensign wasps	x			B10a, B10b, C16
Proctotrupidae	proctotrupids	x			B10a, B10b
Scelionidae	scelionid wasps	x			C14b

Table 1. (Continued.) Systematic list of insect families known from three Paleogene faunas. Abbreviations p. 19.

Order Family	Common Name	Florissant	Green River	British Columbia	References
Diapriidae	diapriid wasps	x			B06, B10a, B10b, C13d
Figitidae	figitids	x			B10a
Cynipidae	gall wasps	x			B10a, B10b
Agaonidae	fig wasps	x			B10a, B10b
Mymaridae	fairyflies	x			B10b
Chalcididae	chalcidid wasps	x	x		B10a, C07a, S90a
Eurytomidae	seed chalcids	x			B10a, B10b
Torymidae	torymids	x			B10a, B10b
Pteromalidae	pteromalids	x			B10a, B10b
Chrysididae	cuckoo wasps	x			C07a, R09
Bethylidae	bethylid wasps	x			B06, B10a, B10b
Pompilidae	spider wasps	x			C06d, C08j, C14a, C41
Scoliidae	scoliid wasps	x			C07j
Tiphiidae	tiphiid wasps	x			C10, C13b
Vespidae	vespid wasps	x		x	C06d, C07a, C11, C14b, C23c, Wi77b
Eumenidae	potter wasps	x			C09f, C13d, C14b
Sphecidae	sphecid wasps	x	x		C06d, C07a, R08a, R08d, R09. S90a
Halictidae	halictid bees	x			C06d, ZM76
Andrenidae	andrenid bees	x			C06d, C081, C11, C14b, ZM76
Melittidae	melittid bees	x			ZM76
Megachilidae	leaf-cutting bees	x			C06d, C08b, C08f, C081, C17a, C23c, ZM76
Anthophoridae	digger bees	x	x?		Bn34, Bn35, C06c, C081, ZM76
Apidae	honey bees	x			C081, C08t, ZM76
Formicidae	ants	x	x	x	Ca47, C06c, C21c, C23a, C41, S78, S90a

Insects recorded from the fauna are: Odonata - Libellulidae; Hemiptera - Pentatomidae; Homoptera - Aphididae; Neuroptera - Hemerobiidae; Coleoptera - Nitidulidae; Diptera - Chironomidae, Mycetophilidae, Dolichopodidae, Otitidae, Sciomyzidae, Heleomyzidae, Pallopteridae, Lonchaeidae, Anthomyzidae; Hymenoptera -Ichneumonidae, Braconidae, Formicidae. According to Scudder (1890a) most specimens are Diptera and Hymenoptera.

The flora records a humid, warm temperate to near subtropical climate (Piel, 1971). The Oligocene paleolatitude of the Quesnel area was presumably intermediate between its Eocene latitude of about 60° N and its present latitude of 53° N.

CONCLUSIONS

North American Paleogene insect faunas are known from a large number of localities extending from British Columbia in the north-west to Colorado in the south-east. Paleocene faunas are few and are confined to the Great Plains. Eocene and Oligocene faunas are numerous and occur in the intermontane basins of the Cordillera. The faunas occur predominantly in fine-grained lacustrine sediments in association with compression fossils of leaves and fishes. Inferred paleoclimates vary from temperate to tropical, based mostly on paleobotanical evidence. Latitudes ranged from about 43° N to more than 60° N during deposition of the faunas. To date only limited use has been made of the insects for paleoenvironmental reconstruction.

More than 200 families of insects have been recognized to date. Of these 90 are known from Eocene formations and about 190 from Oligocene formations. Only a few families are recorded from the Paleocene. In numbers of individuals the faunas are dominated by Coleoptera, Diptera, and Hymenoptera, with Bibionidae of the genus *Plecia* and parasitic Hymenoptera such as Ichneumonidae being especially abundant.

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