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UNIVERSITY OF ALBERTA

FLOWER FORM AND POLLINATOR DIVERSITY IN THE MIDDLE EOCENE OF BRITISH COLUMBIA AND WASHINGTON

by

Sheila D. Douglas

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Science

IN

Paleobotany

DEPARTMENT OF BOTANY

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SUBMITTED BY **Sheila D. Douglas**
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF **Master of Science**
In Paleobotany.

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Date: November 15, 1990

ABSTRACT

Inflorescences, isolated flowers and insects, preserved as compression-impression fossils, were analyzed from Middle Eocene lake deposits in central British Columbia and northern Washington. Among staminate inflorescences, cluster analysis identified four multi-character similarity groups and several highly diverse outliers. Groups I and II were aments with characteristics of Betulaceae and Group III specimens showed affinities with Juglandaceae. The Republic sample was morphologically more diverse than that from Princeton. Fifty flower specimens were classified into similarity groups using cluster analysis and discriminant function analysis. Characters with the lowest variability were number of tepals (mode of 5), degree of connation of the perianth (about 60%) and length/width ratio of perianth and flower (about 1); the characters most important in differentiating between groups were perianth width, connation and tepal shape. Eleven flower form categories are described. Thirty taxa are represented in 129 specimens in four anthophilous orders of insects (Coleoptera, Hymenoptera, Diptera, Lepidoptera). Fifteen families represent new Middle Eocene records in this area and five (Cantharidae, Argidae-Diprionidae, Geometridae, Noctuidae) are the earliest records of these taxa. The most important pollinators were Mordellidae, Syrphidae, Bibionidae, Scoliidae, Vespidae, Geometridae and Noctuidae. For each flower form category, the most probable pollinating agents were selected from the fossil insect sample. Appropriate pollinators for robust, dish-shaped perianths of categories 1 and 3 are large Scarabaeidae, Cantharidae and Cerambycidae, short-haustellate, large dipterans and

non-specialized hymenopterans. Categories 4, 5, 6 and 7 were small, bowl-shaped, partially connate perianths; predicted optimal pollinators are small coleopterans, e.g. Mordellidae, Elateridae and Tenebrionidae, parasitic hymenopterans and small dipterans. Optimal pollinators of a small stereomorphic, highly connate form are long-haustellate, hovering Syrphidae and alighting Geometridae and Noctuidae. Several bowl-shaped perianths with numerous, elongate stamens have characteristics typical of pollination by small coleopterans or by wind. A staminate raceme is anemophilous and a connate perianth with a sub-apical constriction was probably pollinated by Syrphidae, Vespidae, Scoliidae, Noctuidae and Geometridae. For a large zygomorphic flower in category 8, appropriate pollinators include Syrphidae, found at British Columbia, Acroceridae, present at the coeval Green River and Meliponinae (Apidae) from the Upper Cretaceous of New Jersey; Anthophoridae and Bombylioidea, present in Europe, are also potential pollinators.

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I. INTRODUCTION

Origins of biotic pollination

The evolution of the angiosperm flower is best understood in the context of the evolution of biotic pollination. Insect pollination is ancient, probably originating as early as the Upper Carboniferous in seed plants (Dilcher 1979, Crepet 1983, Crepet and Friis 1987, Eisikowitch 1988). The current scenario is that insects visiting reproductive organs of seed ferns (pteridosperms) incidentally transported pollen to ovules. The insects may have been herbivores, feeding on reproductive structures (Dilcher 1979, Pellmyr and Thien 1986, Eisikowitch 1988) or predators searching pteridosperm foliage for invertebrate prey (Crepet 1983). There are many herbivorous or predatory neopterous insects that may have been incipient pollinators in the Paleozoic (Riek 1970).

Several important evolutionary trends in reproductive organs, that culminated during the Lower Cretaceous in the angiosperm flower, are thought to have arisen from this primitive plant-insect association: (1) the hermaphroditic condition whereby insects visiting ovules more efficiently transported pollen to other ovules, (2) progressive protection of the ovule with sterile tissue (carpels) to prevent pollinating insects from damaging ovules, (3) evolution of alternate rewards for pollinators, such as nectar, oils or excess pollen and (4) the recruitment of sterile structures to advertise and direct insects to food rewards (Crepet 1983, Dilcher 1979).

Evidence for insect pollination in the Mesozoic is found in damage to cycadeoid cones by presumed coleopteran pollinators (Crepet

1974). Early Mesozoic pollinators could also include primitive hymenopterans (Symphyta), dipterans (Tipulidae, Mycetophilidae) and thysanopterans, all present in the Jurassic fossil record (Hennig 1981, Willemstein 1987).

By the time the first angiosperms are recognizable in the fossil record (Aptian; Taylor and Hickey 1990), insect pollination of gymnosperms was presumably well-developed and there were few impediments to an adaptive shift by insects to proto-angiosperms. Adaptive radiation of flower form in angiosperms proceeded in association with its pollinators (Stebbins 1974). An important evolutionary step was "flower constancy" where floral form specifies a pollinator group and pollinators specialize on particular flowers (Faegri and van der Pijl 1979). By the end of the Cretaceous, relatively derived characters such as epigyny, syncarpy, sympetaly, weak zygomorphy and nectaries are present in fossil flowers (Friis and Crepet 1987). We know little of the extent of mosaic evolution at the time; angiosperm flowers were the product of selective pressures on pollination and seed dispersal, and probably evolved at a different rate than wood or leaves.

Pollination syndromes

In extant plants, characteristics of flowers such as size, symmetry, depth, colour patterns and scent appear to act synergistically to attract specific kinds of pollinators. In an attempt to address some of the apparent correlations between flower form and pollinators, a comprehensive categorization of flowers was made in the "functional blossom classes" of Faegri and van der Pijl (1979), in which floral shape was described in relation to its function in pollination. The corollary to these classes was formed in "pollination syndromes" which made qualitative correlations between floral characteristics and particular pollinators. Flowers were classified into discrete categories such as cantharophily (beetle-pollination), myophily (fly-pollination), bee-pollination (melittophily) and ornithophily (bird-pollination).

The functional blossom classes and pollination syndromes defined by Faegri and van der Pijl (1979) have been used as a predictive tool by paleobotanists (Crepet and Dilcher 1977, Crepet 1979a, 1979b, 1984, Crepet and Taylor 1985, Willemstein 1987). However, inferences from extant pollinators may not be entirely applicable to flower-pollinator relationships in the Cretaceous and Paleogene, a time of probable rapid co-evolutionary changes in flower form and pollinating insects. Flowers may have undergone major adaptive shifts from one pollinating agent to another, similar to the shifts made by ancient pollinating insects among pteridosperms, cycadeoids and angiosperms. Pollination syndromes in extant plants, as Macior (1971) points out, are not static end-products of co-evolution; incidental floral visitors may be incipient pollinators. For example, among mammalian pollinators, Sussman and Raven (1978) have suggested that the rarity of primate and marsupial pollinators is a result of nectarivorous bats out-competing them on co-evolved flowers.

Floral structure and pollination syndromes have been inferred from the presence of other fossil organs (foliage, pollen, fruits, wood) when flowers are not present (Crepet 1984, Willemstein 1987). The conclusions are often in disagreement with the fossil record. For example, floral syndromes indicative of ornithophily (bird-pollination) have been found in families of plants from the Upper Cretaceous (Crepet 1984). Yet the earliest fossil occurrence of hummingbirds (Trochilidae) is in Quaternary cave deposits and the fossil record of passerines (Passeriformes), to which most other nectarivorous birds belong, does not begin until the Miocene (Olson 1985).

Flower form and pollinating insects in the fossil record

The foregoing attempts at analyzing co-evolution of flowers and their pollinators have met with inconsistencies by relying heavily on the plant-insect relationships in extant groups. Although a uniformitarian approach must not be abandoned, interpretations must take into account mosaic evolution and adaptive shifts by pollinators and by flowers.

For some select stratigraphic periods, the state of knowledge of fossil plants and fossil insects is adequate enough to make inferences based primarily on fossil evidence. The Middle Eocene in North America has yielded a diversity of floral and faunal remains from western Canada and United States, primarily preserved as compression and impression fossils.

In the following chapters, I attempt to reconstruct plant/pollinator relationships in the Middle Eocene using floral and insect material available in sediments from British Columbia and northern Washington. Within the floral specimens, I describe categories of flower form, using cluster analysis to generate multi-character similarity groups and discriminant function analysis to identify the characters important in distinguishing the groups. From what is known about the pollinating behaviour of extant insects, I predict appropriate pollinators for each of the flower form categories. Using previously described insect material and specimens newly analyzed in this study, I compile a list of pollinators that were available to flowers in this area during the Middle Eocene and attempt to match fossil pollinators to fossil flower form categories. In this way, it may be possible to understand some of the selective pressures on flower form. This description of Middle Eocene flowers and insects is an important step in the evaluation of pollination syndromes from the origin of the angiosperms to the present.

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II. STUDY AREA

Localities and lithology

Specimens of inflorescences, isolated flowers and insects analyzed in this study were preserved as compression/impression fossils in a series of freshwater lakes distributed through central and southern British Columbia and northeastern Washington state during the Middle Eocene. The localities in British Columbia include Driftwood Creek (Ootsa Lake Group), Horsefly (Horsefly Beds), McAbee (Tranquille Beds, Kamloops Group), Falkland (Kamloops Group), Quilchena [Allenby Formation, Princeton Group (formerly Coldwater Group)], One Mile Creek (Allenby Formation, Princeton Group), China (Asp) Creek (Allenby Formation), Princeton Firehall (Allenby Formation), Tulameen Road (Allenby Formation) and Blakeburn Mine (Allenby Formation), and in Washington state, Republic (Klondike Mountain Formation, Tom Thumb Tuff) (Figure II-1).

Driftwood Creek is located east of Smithers in Driftwood Canyon Provincial Park (UTMG 9UXL271770); sediments are buff to yellow fine-grained laminated shales. **Horsefly** is located about 60 km east of Williams Lake on Highway 97; the site is on the Horsefly River, 6 km below the town of Horsefly (UTMG 10UFP083057). Sediments consist of laminated diatomaceous varves with alternating dark-coloured winter and light-coloured summer laminae. **McAbee** is located on the highway between Cache Creek and Kamloops on Highway 97, 1.3 km west of the point where Battle Creek crosses the highway (UTMG 10UFM264294); specimens are found in light grey to brown laminated shales. The town of **Falkland** is 106 km east of Kamloops on Highway 97; the fossil site is located west of the town on Estekwalan Mountain (UTMG 10ULF123990); specimens are found in siliceous shales. **Quilchena** locality is about 4 km south of Quilchena (Highway 5A, 15 km east of Merritt) on Quilchena Creek; sediments consist of light grey, fine-grained shales. **One Mile Creek** is 8 km north of Princeton on Highway 5, near the confluence of Allison and Summers Creek (UTMG 10UFK793897). Specimens from the One Mile Creek locality are found in a light grey-green shale consisting of laminae of silts, clays, and finely graded volcanics. **China Creek** is 1 km NW of Princeton in the west wall of China Creek ravine (UTMG 10UFK792820); sediments consist of grey, finely laminated tuffaceous shales. **Princeton Firehall** is located in the town of Princeton (UTMG 10UFK805811); sediments are brown shales. **Tulameen Road** locality lies on the north side of Tulameen Road, 4 km northwest of Princeton (UTMG 10UFK757807). Sediments are buff to yellow finely laminated and fine-grained tuffaceous shales. **Blakeburn Mine** is southwest of Coalmont (10 km NW of Princeton) (UTMG 10UFK634837); specimens are located in brown to black carbonaceous shales in an open-pit coal mine. **Republic** localities include Knob Hill (B2737) and Boot Hill (B4131), in the town of Republic, Washington (118°43'W, 48°40'N). Specimens from Republic occur in light grey fine-grained massive to laminated tuff. Information on position and lithology of localities is based on the University of Alberta Vertebrate Paleontology Collection catalogue, Wilson (1980) and M. V. H. Wilson (personal communication).

Specimens from these localities are housed in the paleobotanical (UAPC-ALTA) and paleontological (UAPAL) collections of the University of Alberta, Edmonton, the Thomas Burke Memorial Museum, University of

Washington (UWBM), the Stonerose Interpretive Centre, Republic, Washington (SR), the Canadian Museum of Nature, Ottawa (CMN), the Princeton Museum (PM) and the paleobotanical collection at Simon Fraser University, Vancouver, British Columbia (SFU).

Age of sediments

All eleven localities are Middle Eocene. Potassium-argon dating (Rouse and Mathews 1960, Hills and Baadsgaard 1967) places the Princeton area (One Mile Creek, Princeton Firehall, China Creek, Tulameen Road, Blakeburn Mine) and McAbee localities at 48 - 50 m.y. Quilchena, Horsefly, Falkland and Driftwood Creek have been correlated with the Princeton and McAbee localities using fish fauna (Wilson 1977a, 1977b), palynology (Rouse and Srivastava 1970) and mammals (Russel 1935, Gazen 1953). The Republic flora is radiometrically dated at approximately 48 - 49 m.y. (Wolfe and Wehr 1987).

Floral and faunal diversity and paleoecology

<u>Pinus</u> <u>driftwoodensis</u> Stockey, an ovulate cone with associated needles, wood and pollen cones has been described from Driftwood Creek (Stockey 1983). The flora of Horsefly includes <u>Pistillipollianthus wilsonii</u> Stockey and Manchester, a flower with possible affinities to the Euphorbiaceae (Stockey and Manchester 1988), a moss (Janssens et al. 1979) and a diversity of angiosperm leaves, fruits, seeds, flowers and wood that has yet to be described (Wilson 1980 and personal observation). Collections from McAbee include a range of angiosperm and conifer megafossils (L. V. Hills, personal communication). Taxodiaceae is represented at Quilchena (Mathewes and Brooke 1971). The fossil flora at One Mile Creek is dominated by leaves of <u>Betula</u> <u>leopoldae</u> Wolfe and

Wehr and associated infructescences, fruits and staminate inflorescences (Crane and Stockey 1987). Other angiosperm leaves, including Stonebergia columbiana (Wolfe and Wehr 1988), and conifer material are present as well (Schorn and Wehr 1986, Crane and Stockey 1987). The Republic flora now includes over 180 dicotyledonous species and several conifers (Wolfe and Wehr 1987; Wehr, personal communication). There are no published records of the flora from the other sites (Blakeburn, Tulameen Road, Princeton Firehall, China Creek and Falkland), although those near Princeton (see Figure II-1) may have been sampled in some of the early collecting in the area (Arnold 1955).

Many taxa of permineralized plants from chert layers near Princeton have been described: conifers [Metasequoia (Rothwell and Basinger 1979, Basinger 1981, 1984), Pinus (Miller 1973, Stockey 1984)], palms (Erwin 1987), several isolated flowers [Paleorosa (Basinger 1976), Princetonia (Stockey 1987), Wehrwolfea (Sapindaceae, Erwin and Stockey 1990a)], inflorescences, fruits and seeds of Princetonia (Stockey and Pigg 1989), fruits and seeds of Araceae (Cevallos-Ferriz and Stockey 1988a), Lythraceae (Cevallos-Ferriz and Stockey 1988b), Nymphaeaceae (Cevallos-Ferriz and Stockey 1989), Vitaceae (Cevallos-Ferriz and Stockey 1990a), Rosaceae (Cevallos-Ferriz and Stockey 1990c), Magnoliaceae (Cevallos-Ferriz and Stockey 1990b) and various other angiosperm remains (Robison and Person 1973, Basinger and Rothwell 1977, Erwin and Stockey 1989, 1990b, 1990c). Several bryophytes, conifers and angiosperms have been reported from compression/impression fossils from the Princeton area as well (Arnold 1955, Kuc 1972, 1974). Palynological studies have been done at Princeton, Quilchena, McAbee and Driftwood

Creek (Hills 1965, Boneham 1968).

Insects from 31 families have been identified from Middle Eocene localities, including Driftwood Creek, Horsefly, Falkland, Quilchena, Princeton and Blakeburn (Scudder 1890, Handlirsch 1910, Rice 1959, Wilson 1977b, 1978a). Several taxa of fish have been described from Driftwood Creek, Horsefly, McAbee, Quilchena, Princeton, Tulameen Road, Blakeburn and Republic (Wilson 1977a, 1978b, 1982, 1984).

Paleoecological studies have been possible at some of the localities. Seasonal variation in deposition is identifiable in lacustrine varves at Horsefly (Wilson 1977c), allowing conclusions on growth rates and sexual dimorphism in catostomid fish (Wilson 1984). Predation by piscivorous birds and fish has been inferred from coprolites and pellets found at Quilchena (Wilson 1987). Differences in diversity and composition of macrofossils at Middle Eocene localities throughout British Columbia and Washington state have been accounted for by differences in depositional micro-habitat (Wilson 1980, 1988). At Republic, Washington, substantial insight into paleoclimate and paleogeography has been achieved (Wolfe and Wehr 1987), identifying the flora as a Low Montane Mixed Coniferous forest, at a paleoaltitude of 727 - 909 m, with a mean annual temperature of 12° - 13° C (Wolfe and Wehr 1987).

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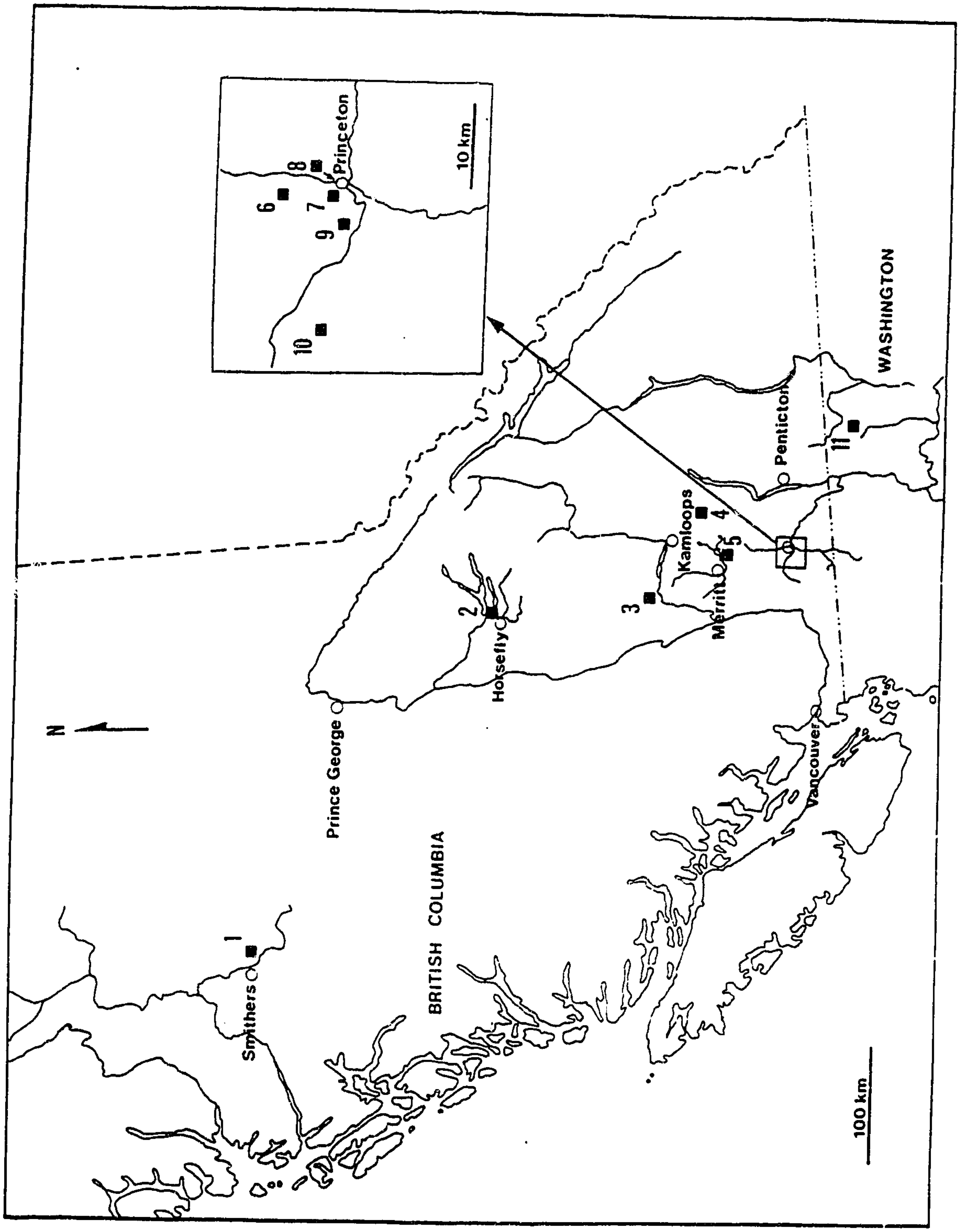
Figure II-1. Study area. Fossil localities indicated by solid square; inset = Princeton area localities. 1. Driftwood Creek; 2. Horsefly; 3. McAbee; 4. Falkland; 5. Quilchena; 6. One Mile Creek; 7. China Creek; 8. Princeton Firehall; 9. Tulameen Road; 10. Blakeburn Mine; 11. Republic.


Princeton
10 km
6
7
8
9
10
WASHINGTON
Penticton
11
Kamloops
4
5
3
Merritt
2
Horsefly
Prince George
N
BRITISH COLUMBIA
Vancouver
1
Smithers
100 km

III. MORPHOLOGICAL DIVERSITY IN STAMINATE INFLORESCENCES FROM THE MIDDLE EOCENE OF BRITISH COLUMBIA AND NORTHERN WASHINGTON[1]

INTRODUCTION

In many wind-pollinated taxa, a remarkable convergence in floral structure has confounded taxonomy. Within this diverse group, formerly referred to as the Amentiferae (Stern, 1973), the staminate inflorescences of many taxa are catkins: the lax, linear, pendulous, unisexual inflorescences are composed of small, bracteate flowers with reduced perianths; anthers are prominent and produce copious smooth, usually triporate pollen (Thorne, 1973). The overall catkin morphology, as well as characteristics of the whole plant such as presentation of catkins and timing of dehiscence, is seen as facilitating pollen dispersal by wind (Faegri and van der Pijl, 1979; Crepet, 1981). In an attempt to unravel the evolutionary relationships within the Amentiferae, the morphology and anatomy of the reproductive organs has been studied extensively (Abbe, 1935, 1974; Hjelmqvist, 1948; Endress, 1967; Zavada and Dilcher, 1986; Hufford and Endress, 1989). Recently, anthecologists have enlisted the principles of fluid dynamics to understand how pollen is released by catkins, transported in the air stream, and captured by stigmas (Whitehead, 1969, 1983; Crane, 1986; Paw U, 1989; for similar studies on conifers see Niklas and Paw U, 1982,

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1983). Combining the information on structure of catkins and mechanics of pollen dispersal, conclusions on functional morphology of catkins and their component parts (Crane, 1986) are possible.

The fossil record of the Hamamelidae (sensu Cronquist, 1988) is equivocal prior to the Late Cretaceous. By the Middle Eocene, the habit of wind dispersal of pollen was established in catkin-like staminate inflorescences of Betulaceae (Crane and Stockey, 1987), Juglandaceae (Crepet et al., 1975; Crepet et al., 1980; Wing and Hickey, 1984) and Fagaceae (Crepet, 1979; Crepet and Daghlian, 1980).

A series of contemporaneous lake deposits extending through central and southern British Columbia and northeastern Washington state has yielded valuable information on Middle Eocene biodiversity (for example, Hills, 1965; Wilson, 1977a, 1977b) and paleoecology (Wilson, 1980, 1988). Staminate catkins, preserved as compression/impression fossils at these localities, are particularly abundant at Princeton, B.C. (Allenby Formation), McAbee, B.C. (Kamloops Group) and Republic, Washington (Klondike Mountain Formation). In a sample of 40 staminate inflorescences from these discreet but coeval localities, we describe, using multivariate statistical analysis, diversity in catkin morphology. By quantifying the variation in structures for wind dispersal of pollen, insight into the state of the anemophilous syndrome (Faegri and van der Pijl, 1979) during the Eocene may be possible.

The dicotyledonous flora of Republic, Washington has been described recently (Wolfe and Wehr, 1987) and, in addition to the taxonomic conclusions, substantial insight into paleoclimate and paleogeography has been achieved. The low montane mixed coniferous forest represented by megafossils at Republic is thought to have occurred at the Princeton localities as well (Wolfe and Wehr, 1987). Although substantial progress has been made in describing the Princeton flora from permineralized material (Miller, 1973; Robison and Person, 1973; Basinger, 1976, 1981, 1984; Basinger and Rothwell, 1977; Rothwell and Basinger, 1979; Stockey, 1984, 1987; Erwin, 1987; Cevallos-Ferriz and Stockey, 1988a, 1988b, 1989), the compression flora is largely undescribed (Arnold, 1955; Kuc, 1972, 1974). A notable exception is Betula leopoldae, originally described from Republic (Wolfe and Wehr, 1987); leaves and their associated infructescences, isolated fruits, and staminate inflorescences have now been described from Princeton (One Mile Creek) (Crane and Stockey, 1987). The commonalities between the Republic and Princeton flora have yet to be validated with thorough study. By analysis of the structure of a single dispersed organ - the staminate inflorescence - from the two localities, we will be able to test assumptions about similarities between the floras.

MATERIALS AND METHODS

Study sites and specimens

Forty specimens of catkins from Middle Eocene localities in British Columbia and Washington state, preserved as compression/impression fossils, were obtained from the paleobotanical collections at UAPC, UWBM, CMN and PM. Eighteen specimens are from Princeton (One Mile Creek and Tulameen Road), British Columbia (Allenby Formation), 20 are from Republic, Washington (Klondike Mountain Formation) and 2 specimens are from McAbee, British Columbia (Kamloops Group). Details on collecting information are given in Table III-1. Lithology, age and geographic location of sites are given in Chapter II.

The fossil flora at One Mile Creek is dominated by *Betula leopoldae* leaves and associated infructescences, fruits and staminate inflorescences considered to be produced by this single fossil species (Crane and Stockey, 1987). Other angiosperm leaves and conifer material are present as well (Schorn and Wehr, 1986; Crane and Stockey, 1987). The fossil fauna consists of fish (Wilson, 1980) and insects (Douglas, unpublished data). The well-documented Republic flora includes over 180 dicotyledonous species and several conifers (Wolfe and Wehr, 1987; Wehr, personal communication). Collections from McAbee include a range of angiosperm and conifer megafossils as well as insects.

Morphological and statistical analysis

Specimens were measured with a micrometer mounted in a Wild M5 dissecting microscope and Helios dial calipers. Camera lucida drawings were made of whole specimens and details. In preparation for electron and light microscopy, pollen sacs were removed from the matrix with forceps and treated with concentrated nitric acid and household ammonia (Stockey and Manchester 1988). Length and width measurements were taken of the dehydrated pollen sacs. For scanning electron microscopy, pollen sacs were mounted whole on stubs and crushed slightly, sputter-coated with approximately 150 Å gold and analyzed and photographed with a Cambridge Stereoscan 250 at 20 kV. For transmission electron microscopy, the macerated pollen sacs were fixed with osmium tetroxide and dehydrated in ethanol. The pollen sacs were embedded in Spurr's (1969) resin, sectioned with a Reichert-Jung Ultracut E microtome and collected on copper grids. The sections were stained with uranyl acetate/lead citrate and analyzed and photographed with a Hitachi H-7000 transmission electron microscope. For analysis with the light microscope, macerated pollen sacs were stained with safranin, dehydrated in ethanol and mounted on slides; pollen sacs were crushed, liberating the pollen grains, by tapping the cover glass before the Coverbond hardened. Not all of the specimens yielded well-preserved pollen. Pore number and position was difficult to determine in many specimens and thus, only diameter and sculpturing are used as variables. However, data on pollen that is not included in the statistical analysis is later integrated into the results.

Twenty-seven characters were used for morphological description; 13 of these were numeric variables, 2 were ordinal scale variables and the remaining 12 were nominal scale data coded into present/absent dichotomies. Characters and their parameters are listed in Table III-2. Raw data on measurements of specimens are given in Appendix 1a. With the exception of pollen characteristics, characters were chosen independent of their taxonomic usefulness; rather, an attempt was made to use characters that might influence effective dispersal of pollen by wind, such as density of partial inflorescences, exsertedness of stamens and size and orientation of primary bracts.

Terms for elements of the inflorescence follow the morphogenic analysis of Betulaceae by Abbe (1935, 1974), whereby the <u>partial inflorescence</u> consists of all sterile and reproductive elements on a single peduncle arising from the inflorescence axis. He suggests that the partial inflorescence evolved from a multi-flowered cyme by reduction and fusion of bracts and perianth parts. The large and outer sterile structure that encloses the rest of the elements of the partial inflorescence is the primary bract (phyletically the subtending bract of the cyme); additional sterile structures of the partial inflorescence are secondary bracts, tertiary bracts and tepals.

Density of units within an inflorescence was expressed by calculating the number of bracts in a unit area of inflorescence (BR/MM^2). Although the majority of inflorescences had preserved stamens, the number of pollen sacs per unit area was not an accurate reflection of density: preservation state varied among the specimens, and in some, numbers of pollen sacs appeared to have been reduced considerably by taphonomic change. Thus counts of pollen sacs show only minimal numbers of anthers and are not useful for comparison between specimens.

For statistical analysis, the list of 28 characters was reduced to 15. If more than 15 specimens lacked data for a specific variable (PEDMAX, PEDX, BWIDMAX, BWIDX, SEC), it was eliminated from the analysis due to problems in handling missing data. However, DIAM, present in only 13 specimens, and SCULPT, present in 17 specimens, were retained since pollen structure is considered a good diagnostic character (Crane 1986). Correlation coefficients were calculated for nominal data variables and numeric variables; when variables were highly correlated ($r > 0.80$), one of the pair was eliminated from subsequent cluster analysis to provide a more conservative measure of association.

The 40 specimens were organized into multi-character similarity groups using a hierarchical cluster analysis (Norusis 1988). Squared Euclidean distance was based on standarized variables; specimens were clustered using the average linkage between groups (UPGMA) method and clusters were plotted as dendrograms. Analyses were run using alternate clustering techniques; these yielded similar results. Specimens with missing values were eliminated automatically from cluster analysis. This presents a problem since many characters were not measurable in all specimens. There was thus a trade-off between analyzing a large number of variables in a small sample of specimens and analyzing fewer variables in a larger sample. Consequently, a cluster analysis was initially performed using the 15 basic variables; subsequent cluster analyses were made using successively fewer variables, thus increasing the sample size. Some specimens (#1,#2,#17,#20,#27,#38,#49; see Table III-1 for specimen numbers) had so few measurable characters due to poor preservation that they appeared in none of the analyses. Specimens that clustered together at early iterations in different dendrograms were considered stable multi-character similarity groups. Each group is described by its character means and coefficient of variation of its member specimens.

RESULTS

Synopsis of morphology

The 40 specimens in the study were lax inflorescences with numerous small florets subtended by bracts. Inflorescences were linear in most (N = 36) specimens; in the remainder, one specimen (#39, Plate III-IV,4) had a narrowly triangular shape while three (#20, Plate III-III,4; #22; #27, Plate III-IV,5) consisted of dispersed partial inflorescences. Most were conspicuously staminate and unisexual, the exceptions being the immature inflorescences (#7; #8; #21,Plate III-III,4; #31, Plate III-IV,7; #37, Plate III-IV,9) and those with no visible anthers (#25, Plate III-IV,5; #30, III-IV,6). Most of the specimens were incomplete at the base, apex or both, and consequently, actual length of inflorescences, attachment and possible grouping of inflorescences were not ascertainable. However, two specimens (#26, Plate III-IV,5; #35, Plate III-II,4,5) were complete inflorescences, with lengths of 30.5 and 51.3 mm, respectively.

A summary of the univariate data for each of the characters is given in Table III-3 and form is shown in Plates III-I to III-V. Ten of the inflorescences were spikes (SPIKE), with partial inflorescences attached directly to the peduncle (e.g., Plate III-II,8; III-III,3; III-III,7; III-IV,5). Seventeen of the specimens were complex inflorescences (CINFLOR), in which the partial inflorescence (cymule) consisted of multiple florets on a peduncle arising from the inflorescence axis (e.g., Plate III-I; III-II, 1-4; III-IV,6). When pollen sacs or bracts obscured pedicel positions, the distance of primary bracts from the peduncle indicated whether or not pedicels were present. Thirteen of the specimens could not be classified for partial inflorescence structure due to immaturity (#7; #8; #37, Plate III-IV,9) or to general ambiguity from poor preservation. Inflorescence width (IWIDMAX) varied from 1.86 mm to 8.32 mm in different specimens; maximum width was highly correlated with mean width (IWIDMEAN) (Table III-6). Peduncle width (PEDMAX) was highly variable between specimens (range = 0.13 - 1.35 mm) and, similarly, the maximum width was highly correlated with the mean (PEDX).

Primary bracts were the most conspicuous sterile structures in the partial inflorescence, forming a distinct outer boundary to the inflorescence. Most were preserved in lateral view; maximum bract length within an inflorescence (BLENMAX) ranged from 1.02 to 3.16 mm; mean bract length (BLENX) was correlated positively with the inflorescence maxima. Width measurements of primary bracts (BWIDMAX, BWIDX) were possible on 17 inflorescences and showed wide variability, probably due to the bracts not being completely in face view. The form of the primary bract was classified into a number of dichotomous character states because of the wide, but distinct variation it showed in size, shape and orientation. Triangular primary bracts (BTRI) were the most common (N = 23; Plate III-I,8-9). Five of the inflorescences (#13, Plate III-II,6; #19, Plate III-III,7; #21, Plate III-III,4; #24, Plate III-II,7; #29, Plate III-II,8,9) had oval primary bracts (BOVAL), four (#22; #23, Plate III-IV,3; #33, Plate III-III,6; #39, Plate III-IV,4) had dissected primary bracts (BDIS) and two had primary bracts too small or inconspicuous to be classified (BSMAL). In 28 of 32 inflorescences in which the character could be categorized, the primary bract was the single most prominent sterile structure (BSING), although smaller and less conspicuous secondary bracts were sometimes present. In four specimens, the sterile part of the partial inflorescence consisted of multiple, similar-sized overlapping bracts (BMULT). Orientation of the bract varied from parallel to the peduncle (BPAR; Plate III-I,9) (N = 13) to an oblique angle to the peduncle (BOBL; Plate II,5) (N = 22). In many of the inflorescences (N = 21), secondary sterile structures (SEC; Plate III-I,8) were distinguishable.

Inflorescence density (BR/MM^2), equivalent to the number of partial inflorescences per unit area, ranged from 0.06 (#16, Plate III-III,2) to 4.16 (#25, Plate III-IV,5) primary bracts/mm^2. The degree to which stamens extended beyond the primary bracts (STAMEX) was variable, although most commonly, they were included entirely by the bracts. Conspicuous filaments (FIL) were present on the stamens in only 1 specimen (#39, Plate III-IV,4).

Anthers were measurable in most mature catkins (N = 33), with length (ANTHLEN) ($\bar{x}$ = 0.92 mm) highly correlated (r = 0.80) with width (ANTHWID) ($\bar{x}$ = 0.22 mm). Pollen diameter (DIAM) and the degree to which the stamens were exserted (STAMEX) exhibited the lowest variability of all characters. Mean pollen size (DIAM) showed little variability (C.V. = 0.08), ranging from 21.8 to 33.4 μm and exine sculpturing (SCULPT) was most commonly scabrate.

Pollen morphology and aperture number were not used as characters in the analysis because identification was not definitive in most specimens. The most common pollen type in the sample was a triporate grain with scabrate exine sculpturing (Table III-4; Plate III-V,4,5,7). For some specimens, only the porate nature of the pollen and scabrate exine sculpturing could be positively determined. Several specimens showed a morphology distinct from the "common" type described above; #17 and #21 were probably multiporate, #24 and #28 were not triporate and #23 had a rugulate exine (Table III-4). In specimens #9 and #34, which were sectioned for TEM, the exine had a thick foot layer, a granular interstitium and a thick tectum perforated with microchannels (Plate III-V,1).

Correlation matrices for nominal and numeric data are shown in Tables III-5 and III-6. Several variable pairs (SPIKE/CINFLOR, BSING/BMULT, BPAR/BOBL) are mutually exclusive. There were, however, non-spurious correlations that describe syndromes of co-occurring characteristics. The variables SPIKE/BOVAL/BMULT/BOBL formed a correlation complex, as did the variables CINFLOR/BTRI/BSING/BPAR (for both complexes, $r >= 0.50$, $p < 0.005$). Several correlated characters were found among the numeric variables: there was a significant negative correlation between the width of the inflorescence and the density of primary bracts, that is, wide catkins were less dense than narrow ones. This probably reflects ontogenetic changes, with a width increase accompanying elongation as the catkin matured. There was a significant negative correlation between the length of the primary bract and pollen diameter and between the width of the pollen sac and stamen exsertedness (narrower pollen sacs were associated with more exserted stamens).

Cluster analysis

Results from six cluster analyses, differing in the number of characters and number of specimens (Table III-7), are considered here. Dendrograms are presented for 3 of these (Figures III-1 to III-3); they showed similar trends in clustering of specimens, as did alternative analyses using other combinations of variables and specimens. There were specimens that consistently grouped together in all six analyses. Group I had a core of specimens 5-9-10-11-14-15-34 (Plate III-I), Group II consisted of specimens 4-6-12-35 (Plate III-II,1-5), Group III consisted of specimens 13-24-29 (Plate III-II,6-9) and Group IV was composed of specimens 16-32-36 (Plate III-III,1-3). The remaining specimens ("outliers") (Plate III-III,4-7; Plate III-IV) did not associate with these four groups in any consistent manner. Among the outliers, #3 and #26 were paired when they appeared in Dendrogram 2 and 3 and #22, #23 and #33 clustered at low coefficients in Dendrogram 3. There were two specimens (#28,#39) that consistently remained isolated and only clustered at low similarity indices. The two specimens from McAbee did not occur in any of the analyses since so few morphological characters were measurable. However, when they were compared to the character means for the four groups, neither of them, on the basis of their reduced set of characters, fit naturally into any of the groups.

Associations between variables differed in analyses A-F (Table III-7) as a function of removing selected variables. Changes in grouping are distinguished from additions to groups, which occurs as a consequence of inclusion of new specimens. Essentially, there was specimen fidelity to the four groups throughout analyses B to F; this means that the removal of characters SCULPT, STAMEX, SPIKE (representing the correlated SPIKE/CINFLOR character polarity) and ANTHWID did not alter membership in the groups. There were minor differences: in A, where groups are formed on the basis of the maximum number of characters, #12 clustered with Group I rather than Group II; when pollen diameter is excluded as a character (B-F), it clustered with Group II. The inclusion of SACWID as a character in A-E automatically excludes the immature inflorescences. When SACWID is removed in F, immature specimens (#7,#8,#31,#37) formed a cluster with specimen 10 and joined Group I at a later iteration.

A summary of the character means for the four groups is given in Table III-8. Group I specimens, which all appear to be mature inflorescences, have a mean width of 5.49 mm; the inflorescences have single, triangular primary bracts (mean length 2.18 mm) arranged parallel to the inflorescence axis; secondary bracts are also present. The inflorescences have a mean density of 0.25 primary bracts/mm^2 and stamens, which lack filaments, are always included in the margins of the primary bracts. Pollen sacs measure a mean 0.75 mm by 0.18 mm. Average pollen diameter is 26.8 μm, and sculpturing is scabrate. Pollen diameter and pollen sac size showed the lowest variability.

Group II specimens are mature inflorescences with a mean width of 8.09 mm; inflorescences are complex racemes with single, triangular primary bracts (mean length 2.51 mm) arranged at an oblique angle to the peduncle; secondary bracts are present. Density of bracts shows little variability, with a mean of 0.13 bracts/mm^2. Anthers do not extend past the bract margin of the inflorescence in any of the specimens. Mean pollen sac size is 1.01 mm by 0.24 mm; pollen diameter is 26.5 μm and in the 3 specimens for which data is available, exine sculpturing is scabrate. Group II specimens differ from Group I primarily in having wider, less dense inflorescences, primary bracts oblique rather than parallel to the peduncle and larger anthers. The three specimens that have been described as the staminate inflorescences associated with _Betula leopoldae_ (Crane and Stockey 1987) are segregated by the two groups, with one inflorescence (#5; Plate III-I,1) in Group I and two (#4, Plate III-II,1; #6, Plate III-II,2) in Group II.

The three specimens in Group III were narrow spikes (mean width 4.32 mm) with multiple oval bracts arranged at oblique angles to the peduncle. Mean length of the primary bracts was 1.78 mm and density of the inflorescences averaged 0.14 primary bracts/mm^2. Anthers extended beyond the bract margins of the inflorescence and averaged 1.30 mm by 0.31 mm. Group III differed from the two previous groups in the spikate form of the inflorescence and in the smaller, multiple, oval bracts. Inflorescence width was almost half that of Group II specimens although bract density was comparable. Anthers were larger, and stamens more exserted, than in Groups I and II.

Group IV specimens included 2 spikes and 1 complex inflorescence (mean inflorescence width 6.66 mm). The single, triangular primary bracts, averaging 1.33 mm in length, were at oblique angles to the peduncle. Inflorescences had a low density (0.08 primary bracts/mm^2) and stamens extended past the primary bracts. Mean anther length was 1.32 mm and mean width 0.45 mm. There was no pollen data for these specimens. These specimens differed from the other three groups in having the smallest mean bract length, the lowest density of bracts, the most exserted stamens and the largest anthers.

In the two specimens that consistently remained isolated from the rest, #39 (Plate III-IV,4) differed by having dissected bracts, filaments on the stamens and exserted stamens; #28 (Plate II-IV,8) differed by having the narrowest inflorescence width and inconspicuous bracts.

In order to maximize the number of specimens considered, pollen characteristics were excluded from the majority of analyses. There were, however, some trends in pollen morphology in the four groups and outliers which are worthwhile noting. Among the four groups, there were 12 specimens that had data on pollen (Table III-4). Those with triporate pollen and scabrate exine sculpturing, the most common type of pollen in the sample, were found in Group I (3 specimens), Group II (1 specimen) and Group III (1 specimen); only one specimen in the group had atypical (non-triporate) pollen. Of the specimens with unusual pollen morphology, five were among the outliers. Although the sample size is small, those specimens with unusual pollen appear to be dissimilar, from the groups and from other specimens, in other characters as well.

Locality as a factor in clustering

Although locality was not used as a variable in cluster analyses, and specimens were grouped according to morphological characters, the groups showed a strong association with locality. Specimens from Princeton formed relatively homogeneous morphological groups (I,II), while, in general, the majority of Republic specimens were outliers. Group III includes two specimens from Princeton (one from One Mile Creek and one from Tulameen Road) and one from Republic, and Group IV consists of two specimens from Republic and one from Princeton. The general pattern is illustrated in the dendrograms in Figures III-2 and III-3. Of the 17 specimens that clustered in the upper part of Dendrogram 2, 13 are from Princeton; of the 8 specimens that joined this cluster at higher distance coefficients, 6 are from Republic. Similarly, in Dendrogram 3, [illegible] of the 23 specimens forming the large upper cluster are from Princeton, and 9 of the 11 specimens that later join the cluster are from Republic.

DISCUSSION

The three Middle Eocene localities are remarkable in both the abundance of dispersed staminate inflorescences and in the high diversity shown in the catkin flora. Although 17 of the 40 specimens could be classified consistently into four multi-character similarity groups, the remaining specimens showed no consistent pattern of association with these groups; several were highly dissimilar. This taxonomic richness exceeds that reported for other Paleogene localities, although the Middle Eocene Claiborne Formation contains at least seven kinds of staminate inflorescences (Crepet et al., 1975; Crepet, 1979; Crepet and Daghlian, 1980; Crepet et al., 1980) in the Juglandaceae and Fagaceae.

Despite great morphological variability, it is possible to give a broad description of Middle Eocene staminate inflorescences from these localities. (The highly dissimilar outlier has been excluded from the description.) Unisexual staminate inflorescences from Princeton and Republic, preserved as compression/impression fossils, are linear, ranging in maximum inflorescence width 2 - 8 mm and peduncle width 0.1 - 1.4 mm. Partial inflorescences, pedicellate to sessile on the peduncle, consist of multiple stamens subtended by bract-like sterile structures. Bract shape is triangular to oval, with an entire or dissected margin, and bracts lie at an oblique angle, or parallel, to the peduncle; they are inconspicuous or absent from some inflorescences. Bracts within an inflorescence may be of similar size and texture or consist of primary and secondary bracts. There are two main character complexes: pedicellate complex inflorescences with oblique, triangular primary bracts and spike-like inflorescences with multiple, oval bracts parallel to the peduncle. Maximum bract length varies among inflorescences from 1 - 3 mm. Density of bracts varies 0.06 - 4.16 bracts/mm^2 among mature inflorescences. Filaments are absent to inconspicuous; anthers may be entirely enclosed by bracts or exserted beyond the bract margins. Pollen sacs range in width 0.2 - 0.6 mm and in length 0.5 - 1.6 mm. Pollen is triporate or multiporate; diameters vary 21.8 - 33.4 μm and sculpturing is scabrate to rugulate.

In an abbreviated form, the characters that define the staminate inflorescences of these Middle Eocene localities vary little from those that define the extant Hamamelidae. Given such an extended history to the amentiferous form of inflorescence, it seems appropriate that this complex of characters be given a distinct syndrome of pollen dispersal within anemophily and be designated "amentiflory". This inflorescence would be distinguished from other anemophilous syndromes, such as those which occur in phyletic lines committed to wind-pollination, such as most of the Juncaceae, Cyperaceae and Poaceae or in taxonomically disjunct anemophilous genera such as Thalictrum (Ranunculaceae), Sanguisorba (Rosaceae) and Ambrosia (Asteraceae), in which wind-pollination has been independently derived (Stebbins, 1974).

Most of the character states and character values of these specimens are represented in staminate inflorescences from the Middle Eocene Claiborne Formation (Eokachyra aeolius, Crepet et al., 1975; Eoengelhardia puryearensis, Crepet et al., 1980; Castaneoidea puryearensis, Crepet and Daghlian, 1980; three fagaceous catkins and 1 "Betula-Myrica" catkin, Crepet, 1979) and Golden Valley Formation

(*Platycarya americana*, Wing and Hickey, 1984). However, there are notable differences in pollen characteristics. Pollen diameter is 14.8 m in *Eoengelhardia*, 18.5 - 23.5 μm in *Platycarya americana*, a mean of 19.6 μm in *Eokachyra aeolius* and 15.0 μm by 9.0 μm in *Castaneoidea puryearensis*. Pollen is tricolporate in *C. puryearensis* and a fagaceous catkin figured in Crepet (1979) and tricolpate in 2 other fagaceous catkins (Crepet, 1979). Three-lobed primary bracts (*Eoengelhardia*, *Eokachyra aeolius*) and diminutive pollen sacs (0.24 mm length in *C. puryearensis*) are not found in the Republic and Princeton material. Taxonomically, these inflorescences can be referred to the Juglandaceae (*Eoengelhardia*, *Eokachyra aeolius*, *P. americana*) and the Fagaceae (*C. puryearensis*, 3 inflorescences figured in Crepet, 1979). It is not definitive that a "*Betula*- *Myrica*" catkin (Crepet, 1979) from Claiborne belongs in either of the genera. Taxonomic differences between the localities may account for the differences among catkins, although it cannot be excluded that such pollen characteristics are absent from the Princeton and Republic material due to pollen data from Republic being largely absent.

Within the collections from Princeton and Republic, there were four groups in which multi-character similarity was high. Three of the groups segregated according to a character complex of inflorescence type and bract structure, with Groups I and II containing partial inflorescences with large triangular primary bracts and Group III having spikate inflorescences with multiple oval bracts. Among the remaining, mostly numeric variables, there was a mosaic of character states for each group, with no consistent size or number polarity within groups. An increase in bract density coincided with a decrease in anther size between groups, but the association was only weak between the two characters in the sample as a whole.

Taxonomic description is not the purpose of this study, but taxonomic affinities of the groups can be suggested. The core taxa that produce amentiferous inflorescences are Leitneriaceae, Juglandaceae, Myricaceae, Fagaceae, Betulaceae and Salicaceae (Helmqvist, 1948; Abbe, 1974). The combination of pollen characteristics found in specimens in Groups I (porate pollen with a mean diameter of 26.8μm and scabrate exine sculpturing; thick foot layer, granular interstitium, and thick tectum with microchannels) is typical of Betulaceae (Zavada and Dilcher, 1986) as is the pedicellate partial inflorescence with a large, triangular primary bract subtending multiple florets (Abbe, 1974). Detailed morphological analysis of two of the specimens in this group (#9 and #34) showed the presence of secondary bracts and probable tepals, and maximum 21 pollen sacs per partial inflorescence, characteristics of the Betuleae; it is reasonable to apply this conclusion to Group I as a whole. One of the three catkins associated with leaves of Betula leopoldae at Princeton (Crane and Stockey, 1987) clusters with Group I. Tribe Betuleae consists of 2 genera, Alnus and Betula; although the two genera differ in inflorescence morphology (number of secondary and tertiary bracts and tepals, numbers of stamens), in some species, the differences in the genera, even in extant material, appear negligible (Abbe 1935, 1974).

The consistently reliable character for identifying Alnus is the three to seven porate pollen with arcal streaks (Bassett et al. 1978);

this pollen type was not observed in any of the specimens. However, in several staminate inflorescences from McAbee (specimens that were excluded from this analysis because of poor preservation of most characters), Alnus pollen has been identified (L.V. Hills, personal communication).

The characteristics that distinguish Group II from Group I (more robust catkin, inflorescence less dense, bracts oblique, larger anthers) do not suggest large taxonomic differences from Group I. Multi-variate comparisons with extant Betulaceae would be valuable in identifying this group, as well as other specimens in the collection. Included in Group II were two of the three catkins associated with leaves of B. leopoldae; the segregation of the catkins into two different groups is unexpected. The differences between Groups I and II could represent ontogenetic variation within a taxon. Alternatively, it may not be appropriate to identify all three catkins with the single fossil species B. leopoldae. The narrow spike-like inflorescence, and multiple, oval bracts of Group III are not betulaceous in character; the sessile partial inflorescences are suggestive of the Juglandaceae. Unlike the Claiborne Formation Engelhardieae, the specimens do not have 3-lobed bracts. There are no characteristics of Group IV specimens that are useful for placement within a family.

The juglandaceous and fagaceous catkins from other Middle Eocene localities have pollen characters that appear to exclude them from the betulaceous Groups I and II. Sessile partial inflorescences typical of Eoengelhardia, Eokachyra and Platycarya were found in Groups III and IV, and dissected bracts, characteristic of the two former genera, were present in three specimens, all from Republic. Direct comparisons with Republic specimens are difficult in that pollen is poorly preserved; multivariate comparisons using other morphological characters are necessary to substantiate any affinities between the Republic and Claiborne inflorescences.

One of the striking differences between the groups constructed by cluster analysis was in the association with locality. Groups I and II contain only specimens from Princeton; Groups III and IV have members from each of Republic and Princeton but become predominantly Republic groups as they are joined at higher distance coefficients. As well, most of the outliers are from Republic.

There are competing explanations for these differences in taxa and in diversity between the localities. If the catkin specimens are an unbiased sample of the plant communities at each of the localities, these may represent taxonomic differences in the two plant communities. The Princeton amentiferous flora would be dominated by a few taxa that were abundant in the area and the Republic flora would show high diversity in the catkin-bearing groups. However, the fossil leaf record does not indicate major differences in composition or diversity in the two floras: although <u>Betula</u> <u>leopoldae</u> is the dominant leaf type at Princeton (Crane and Stockey, 1987), several other genera are present, and are shared with the Republic flora (Wolfe and Wehr, 1987). The samples may reflect differences in microhabitat within a larger plant community. For example, in areas of disturbance such as riparian communities, monocultures may be more common through cloning; if the two localities represent samples from the extremes of a continuous deciduous community, one would conclude that the two localities differed in species composition and diversity.

Princeton and Republic are designated as early Middle Eocene based on radiometric dating and biostratigraphic studies (Hills and Baadsgaard, 1967; Pearson and Obradovich, 1977; Wolfe, 1981) as well as commonalities in angiosperm (Wolfe and Wehr, 1987) and conifer (Arnold, 1955) megafossils. A difference in catkin taxa and diversity resulting from differences in time cannot be substantiated.

Wilson (1980, 1988) attributed differences in fossil assemblages of fish, insects and plants in Middle Eocene lacustrine sites (including Princeton and Republic) to variations in the distance-from-shore and depth at which fossil-bearing sediments were deposited. Shallow water assemblages showed high diversity while deep water assemblages showed low diversity. Among plant organs used as indicators, deciduous leaves and wood characterized deep-water/off-shore deposition and taxodiaceous leaves and conifer needles characterized shallow-water/near-shore habitats. If distance-from-shore and depth are responsible for the observed differences in composition and diversity between Princeton and Republic, a prediction would be that the low diversity seen at Princeton indicates an offshore/deep-water deposition, while the high diversity at Republic would be explained by nearshore deposition. However, Republic is typified as a deep-water deposition due to abundance of leaves and sediment lithology (Wilson, 1980; Wolfe and Wehr, 1987). Although some compression fossil localities (not included in this study) near Princeton are typified as shallow, swampy areas (Wilson, 1977b), as is the Princeton permineralized plant site, the Princeton sites considered in this study (One Mile Creek and Tulameen Road) are composed of finely laminated sediments with little fragmentation of fossil material (Wilson 1980; personal observation), typical of deep, off-shore sediments. Based on these considerations, I conclude that differences in depositional habitat cannot account for differences in composition and diversity in these two localities.

There are problems in making paleoecological generalizations from such a narrow database. The disparate catkin flora in Princeton, Republic and the Claiborne and Golden Valley localities found in this study point to the need for comparisons using other fossil organs. The multivariate statistical approach taken here may prove useful in such work. There is, primarily, an urgent need for the description of the compression megafossil flora of Princeton and other British Columbia Middle Eocene sites to make such comparisons possible.

In summary, cluster analysis identified four major groups in the 40 catkins analyzed; the groups were differentiated according to characteristics of the primary bracts, inflorescence dimension and stamen morphology. Three of these groups showed clear taxonomic affinities. There were differences in diversity between Republic and Princeton. In the latter, catkins fell primarily into two similar groups; Republic catkins were highly diverse, comprising most of the outliers. It is suggested that, due to an extended history of distinct inflorescence form, the catkin be designated a separate pollination syndrome - amentiflory - within anemophily.

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Table III-1. Collecting information for specimens. CMN: Canadian Museum of Nature, Ottawa; collectors Hills, Kutluk & Hills, 1984. PM: Princeton Museum, Princeton; collectors Miller, Wehr, 1979 - 1989. UAPC: University of Alberta Paleobotany Collection, Edmonton; collectors Basinger, Douglas, Pigg, Rothwell, Stewart, Stockey, 1975 - 1989. UWBM: Thomas Burke Memorial Washington State Museum, Seattle; collectors Blackstock, Hopkins, Johnson, Nannery, Reeves, Spitz, Wehr, 1979 - 1989.

Text number	Specimen number		Locality	Plate reference
1	CMN	PB000489	McAbee	III-IV,1
2	CMN	PB000569	McAbee	
3	PM	903	Princeton Tulameen Road	III-III,5
4	UAPC	S5086	Princeton One Mile Creek	III-II,1
5	UAPC	S5345	Princeton One Mile Creek	III-I,1;III-V,8
6	UAPC	S5359	Princeton One Mile Creek	III-II,2
7	UAPC	S14091	Princeton One Mile Creek	
8	UAPC	S14089	Princeton One Mile Creek	
9	UAPC	S14238	Princeton One Mile Creek	III-I,2;III-V,3;III-V,6
10	UAPC	S26348	Princeton One Mile Creek	III-I,7
11	UAPC	S26349	Princeton One Mile Creek	III-I,4;III-I,8;III-V,2
12	UAPC	S26350	Princeton One Mile Creek	III-II,3
13	UAPC	S26351	Princeton One Mile Creek	III-II,6
14	UAPC	S26353	Princeton One Mile Creek	III-I,6;III-V,5
15	UAPC	S26363	Princeton One Mile Creek	III-I,3
16	UWBM	36001	Princeton One Mile Creek	III-III,2

Table III-1 (continued).

Text number	Specimen number		Locality	Plate reference
17	UWBM	36002	Princeton One Mile Creek	III-IV,2
18	UWBM	36372	Republic 4131	
19	UWBM	36381	Republic 4131	III-III,7
20	UWBM	36382A	Republic 4131	III-III,4
21	UWBM	36382B	Republic 4131	III-III,4
22	UWBM	36383	Republic 4131	
23	UWBM	36384	Republic 4131	III-IV,3
24	UWBM	36824	Republic 4131	III-II,7
25	UWBM	36825A	Republic 4131	III-IV,5
26	UWBM	36825B	Republic 4131	III-IV,5
27	UWBM	36825C	Republic 4131	III-IV,5
28	UWBM	52203	Republic 2737	III-IV,8
29	UWBM	54163	Princeton Tulameen Road	III-II,8,9
30	UWBM	54392	Republic 2737	III-IV,6
31	UWBM	54395	Republic 2737	III-IV,7
32	UWBM	54398	Republic 2737	III-III,1
33	UWBM	56630	Republic 4131	III-III,6
34	UWBM	56709	Princeton One Mile Creek	III-I,5;III-I,9; III-V,1;III-V,7
35	UWBM	56710	Princeton One Mile Creek	III-II,4,5;III-V,4
36	UWBM	56726	Republic 2737	III-III,3
37	UWBM	56787	Republic 4131	III-IV,9

Table III-1 (continued).

Text number	Specimen number	Locality	Plate reference
38	UWBM 57087	Republic 4131	
39	UWBM 74491	Republic 4131	III-IV,4
40	UWBM 74496	Republic 4131	

Table III-2. Characters measured in analysis of staminate inflorescences. Those marked with an asterix (*) were used in multivariate analysis. For variables with nominal data, the character states are 0 = character absent, 1 = character present.

*MATUR	Maturity of inflorescence 0 = unknown, 1 = immature (bracts appressed), 2 = mature (bracts spread apart, anthers visibel), 3 = overmature (partial inflorescences widely spread or disarticulated, anthers dehisced)
*SPIKE	Inflorescence a spike: primary bracts sessile; partial inflorescences originate at inflorescence axis
CINFLOR	Inflorescence with attached cymules; primary bracts stalked
*IWIDMAX	Maximum width of inflorescence (mm)
IWIDX	Mean width of inflorescence (mm)
PEDMAX	Maximum peduncle width (mm)
PEDX	Mean peduncle width (mm)
BWIDMAX	Maximum width of primary bract (mm)
BWIDX	Mean width of primary bract (mm)
*BLENMAX	Maximum length of primary bract (mm)
BLENX	Mean length of primary bract (mm)
*BDIS	Margin of primary bract dissected
*BOVAL	Primary bract oval
*BTRI	Primary bract triangular
*BSMAL	Primary bract small or inconspicuous

Table III-2 (continued).

BSING	Bract single: partial inflorescence consists of a single conspicuous bract, smaller secondary bracts may be present
BMULT	Bracts multiple: partial inflorescence consists of multiple, overlapping bracts of approximately the same size
*BPAR	Long axis of bract parallel to long axis of inflorescence
BOBL	Long axis of bract at oblique angle to long axis of inflorescence
*BR/MM^2	Density of partial inflorescences: number of bracts/mm^2
SEC	Secondary bracts present/absent
*FIL	Filaments present/absent
*ANTHWID	Mean anther width (mm)
ANTHLEN	Mean anther length (mm)
*STAMEX	Proportion of stamen enclosed by bracts (%)
*DIAM	Mean diameter of pollen (μm); measured at greatest, usually equatorial, diameter
*SCULPT	Exine sculpturing: 1 = scabrate, 2 = scabrate/rugulate; 3 = rugulate

Table III-3. Summary statistics for characters. See Table III-2 for description of acronyms. s = standard deviation; C.V. = coefficient of variation (standard deviation/mean); "-" = value not appropriate; N1 = number of specimens with non-missing data; N2 = number of specimens with non-zero data (i.e., the trait is present).

Character	$\bar{x}$ (Mode)	s	C.V.	Min.	Max.	N1	N2
LOCAL	(1)	-	-	1	5	40	40
MATUR	(2)	-	-	1	2	40	40
SPIKE	(0)	-	-	0	1	27	10
CINFLOR	(1)	-	-	0	1	27	17
IWIDMAX	5.21	1.66	0.32	1.86	8.32	39	-
IWIDX	4.49	1.43	0.32	1.75	7.46	30	-
PEDMAX	0.66	0.32	0.48	0.13	1.35	20	-
PEDX	0.58	0.29	0.50	0.13	1.29	19	-
BWIDMAX	2.01	0.99	0.49	0.62	4.68	17	-
BWIDX	1.63	1.14	0.70	0.50	4.23	8	-
BLENMAX	1.90	0.53	0.28	1.02	3.16	36	-
BLENX	1.63	0.44	0.27	0.71	2.66	36	-
BDIS	(0)	-	-	0	1	34	4
BOVAL	(0)	-	-	0	1	34	5
BTRI	(1)	-	-	0	1	34	23
BSMAL	(0)	-	-	0	1	34	2
BSING	(1)	-	-	0	1	32	28

Table III-3 (continued).

Character	$\bar{x}$ (Mode)	s	C.V.	Min.	Max.	N1	N2
BMULT	(0)	-	-	0	1	32	4
BPAR	(0)	-	-	0	1	35	13
BOBL	(1)	-	-	0	1	35	22
BR/MM^2	0.39	0.72	1.85	0.06	4.16	33	-
SEC	(1)	-	-	0	1	25	21
FIL	(0)	-	-	0	1	39	1
ANTHWID	0.28	0.10	0.36	0.15	0.55	33	-
ANTHLEN	0.99	0.30	0.30	0.51	1.62	33	-
STAMEX	94.49	17.94	0.19	39.0	100.0	34	-
DIAM	26.86	2.95	0.11	21.8	33.4	13	-
SCULPT	(1)	-	-	1	3	17	-

Table III-4. Pollen characteristics of inflorescences from scanning electron and light microscopy. Specimens 15, 19, 20, 27, 29, 30, and 33 yielded no pollen information.

Specimen	Pollen diameter (μm)	Exine Sculpturing	Aperature type
2	21.8	scabrate	porate
5	27.2		
6	26.7	scabrate	porate
9	25.2	scabrate	porate
10	24.8	scabrate	?triporate
11	30.1	scabrate/rugulate	porate
12	24.5	scabrate	porate
13	25.5	scabrate	triporate
14	28.4	scabrate	?triporate
17	28.3	scabrate	?multiporate; pores small
21	33.4	scabrate/rugulate	?multiporate
22		scabrate	
23		rugulate	
24		scabrate	probably not triporate;
28			not triporate; porate or no pores
32		scabrate	
34	24.9	scabrate	triporate
35	28.4	scabrate	triporate
36		scabrate	

Table III-5. Spearman rank correlation coefficients for dichotomous nominal data. Acronyms are described in Table III-2. N is indicated in brackets; * = $p < 0.05$; ** = $p < 0.005$; '-' = one of the characters was invariable.

	SPIKE	CINFLOR	BDIS	BOVAL	BTRI	BSMAL	BSING	BMULT	BPAR	BOBL	SEC	FIL	SCULPT
MATUR	0.07 (27)	-0.03 (27)	0.17 (34)	-0.03 (34)	-0.16 (34)	0.12 (34)	0.06 (32)	-0.06 (32)	0.43* (35)	0.43* (35)	-0.09 (25)	0.07 (39)	-0.18 (17)
SPIKE		-1.00** (27)	0.09 (25)	0.67** (25)	-0.65** (25)	-	-0.58** (25)	0.58** (25)	-0.59** (27)	0.59** (27)	-0.04 (21)	-	0.33 (15)
CINFLOR			-0.09 (25)	-0.67** (25)	0.65** (25)	-	0.58** (25)	-0.58** (25)	0.59** (27)	-0.59** (27)	0.04 (21)	-	-0.33 (15)
BDIS				-0.15 (34)	-0.53** (34)	-0.09 (34)	0.15 (31)	-0.15 (31)	-0.28 (33)	0.28 (33)	-0.10 (24)	0.48** (34)	0.50 (15)
BOVAL					-0.60** (34)	-0.10 (34)	-1.00** (31)	1.00** (31)	-0.32 (33)	0.32 (33)	0.17 (24)	-0.07 (34)	0.06 (15)
BTRI						-0.36* (34)	0.60** (31)	-0.60** (31)	0.50** (33)	-0.50** (33)	0.16 (24)	-0.25 (34)	-0.41 (15)
BSMAL							0.07 (31)	-0.07 (31)	-0.13 (33)	0.13 (33)	-0.47* (24)	-0.04 (34)	-
BSING								-1.00** (32)	0.29 (32)	-0.29 (32)	-0.17 (24)	0.07 (32)	-0.15 (14)
BMULT									-0.29 (32)	0.29 (32)	0.17 (24)	-0.07 (32)	0.15 (14)
BPAR										-1.00** (35)	0.07 (25)	-0.13 (35)	-0.12 (16)
BOBL											-0.07 (25)	0.13 (35)	0.12 (16)
SEC												0.09 (25)	0.16 (12)
FIL													-

Table III-6. Pearson correlation coefficients for numeric variables. Acronyms are described in Table III-2. N is indicated in brackets. * = $p < 0.05$; ** = $p < 0.005$. There is no coefficient for STAMEX - DIAM since all specimens with values for DIAM had STAMEX of 100%.

	IWIDX	PEDMAX	PEDX	BWIDMAX	BWIDX	BLENMAX	BLENX	BR/MM2	ANTHWID	ANTHLEN	STAMEX	DIAM
IWIDMAX	0.97** (30)	0.46* (20)	0.51* (19)	0.24 (17)	0.08 (8)	0.33* (36)	0.42* (36)	-0.55** (33)	0.23 (32)	0.31 (32)	-0.13 (34)	0.10 (13)
IWIDX		0.44 (14)	0.52 (13)	0.13 (14)	0.02 (7)	0.42* (28)	0.46* (28)	-0.58** (26)	0.24 (23)	0.37 (23)	-0.08 (28)	0.11 (9)
PEDMAX			0.97** (19)	0.18 (7)	0.27 (4)	0.37 (19)	0.46* (19)	-0.20 (18)	0.17 (18)	0.22 (18)	0.09 (17)	-0.03 (5)
PEDX				0.24 (6)	0.27 (3)	0.41 (18)	0.51* (18)	-0.23 (17)	0.23 (17)	0.34 (17)	0.10 (16)	0.05 (5)
BWIDMAX					0.99** (8)	0.28 (17)	0.23 (17)	-0.37 (15)	0.01 (12)	-0.03 (12)	-0.21 (16)	-0.49 (4)
BWIDX						0.31 (8)	0.38 (8)	-0.31 (8)	-0.64 (7)	-0.37 (7)	0.01 (8)	-1.00 (2)
BLENMAX							0.94** (36)	-0.34 (33)	-0.18 (29)	-0.06 (29)	0.13 (34)	-0.77** (12)
BLENX								-0.42* (33)	0.16 (29)	0.02 (21)	0.21 (34)	-0.80** (12)
BR/MM^2									-0.16 (28)	-0.38* (28)	0.19 (32)	0.18 (12)
ANTHWID										0.80** (33)	-0.56** (27)	0.04 (12)
ANTHLEN											-0.39* (27)	-0.07 (12)
STAMEX												

Table III-7. Parameters for cluster dendrograms. Specimen numbers are listed in Table III-1 and acronyms for variables described in Table III-2.

Variable	Dendrograms					
	A	B	C	D	E	F
MATUR	X	X	X	X	X	X
SPIKE	X	X	X	X		
IWIDMAX	X	X	X	X	X	X
BLENMAX	X	X	X	X	X	X
BDIS	X	X	X	X	X	X
BOVAL	X	X	X	X	X	X
BTRI	X	X	X	X	X	X
BSMAL	X	X	X	X	X	X
BPAR	X	X	X	X	X	X
BR/MM2	X	X	X	X	X	
FIL	X	X	X	X	X	X
ANTHWID	X	X	X	X	X	
STAMEX	X	X	X			
DIAM	X					
SCULPT	X	X				
Variables (N)	15	14	13	12	11	9
Specimens (N)	9	13	22	22	25	33

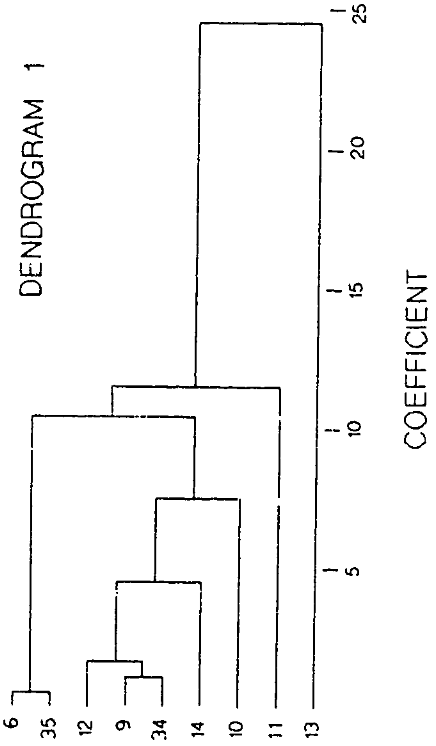
Table III-8. Summary statistics for major groups identified in cluster analysis. For description of acronyms see Table III-2. s = standard deviation; C. V. = coefficent of variation (s/x). Group I -- specimens 5-9-10-11-14-15-34; Group II -- specimens 4-6-12-35; Group III -- specimens 13-24-29; Groups IV -- specimens 16-32-36. "-" = value not appropriate; empty cell indicates no data.

	Group I				Group II				Group III				Group IV			
	x̄ (mode)	s	C.V.	N	x̄ (mode)	s	C.V.	N	x (mode)	s	C.V.	N	x̄ (mode)	s	C.V.	N
MATUR	(2)	-	-	7	(2)	-	-	4	(2)	-	-	3	(2)	-	-	3
SPIKE	(0)	-	-	7	(0)	-	-	4	(1)	-	-	3	(1)	-	-	3
CINFLOR	(1)	-	-	7	(1)	-	-	4	(0)	-	-	3	(0)	-	-	3
IWIDMAX	5.49	1.36	0.25	7	8.09	0.22	0.03	4	4.32	0.09	0.02	3	6.66	0.14	0.02	3
PEDMAX	0.87	0.44	0.51	3	0.92	0.58	0.63	2				0	0.51	0.11	0.22	3
BWIDMAX	4.68	0		1	1.59	0.01	0.01	2	1.75	0.16	0.09	2				0
BLENMAX	2.18	0.45	0.21	7	2.51	0.44	0.18	4	1.78	0.40	0.22	3	1.33	0.28	0.21	3
BDIS	(0)	-	-	7	(0)	-	-	4	(0)	-	-	3	(0)	-	-	3
BOVAL	(0)	-	-	7	(0)	-	-	4	(0)	-	-	3	(0)	-	-	3
BTRI	(1)	-	-	7	(1)	-	-	4	(0)	-	-	3	(1)	-	-	3
BSMAL	(0)	-	-	7	(0)	-	-	4	(0)	-	-	3	(0)	-	-	3
BSING	(1)	-	-	7	(1)	-	-	4	(0)	-	-	2	(1)	-	-	3
BMULT	(0)	-	-	7	(0)	-	-	4	(1)	-	-	2	(0)	-	-	3

Table III-8 (continued).

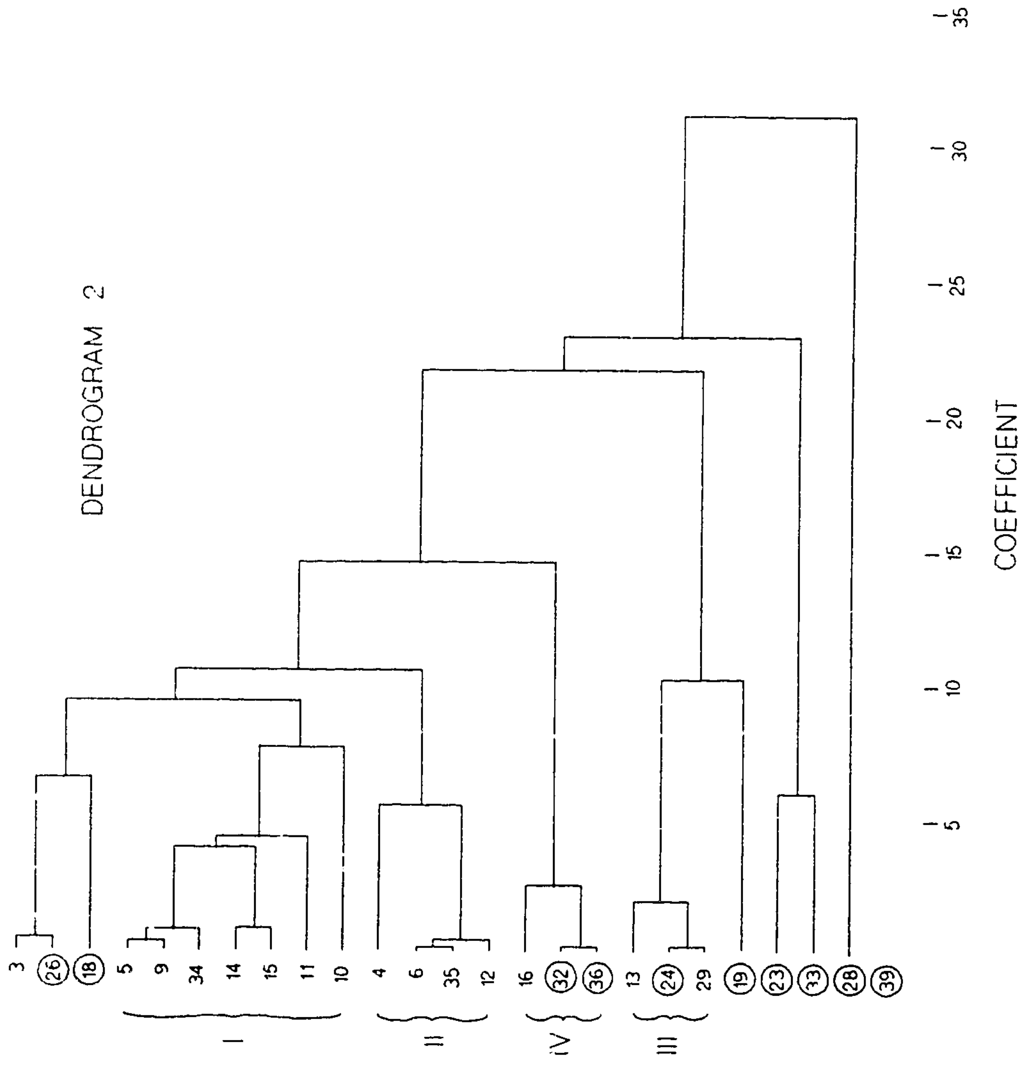
	Group I				Group II				Group III				Group IV			
	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N
BPAR	(1)	-	-	7	(0)	-	-	4	(0)	-	-	3	(0)	-	-	3
BOBL	(0)	-	-	7	(1)	-	-	4	(1)	-	-	3	(1)	-	-	3
BR/MM^2	0.25	0.19	0.76	7	0.13	0.01	0.08	4	0.14	0.09	0.64	3	0.08	0.02	0.25	3
SEC	(1)	-	-	6	(1)	-	-	4	(1)	-	-	1	(0/1)	-	-	2
FIL	(0)	-	-	7	(0)	-	-	4	(0)	-	-	3	(0)	-	-	3
ANTHWID	0.18	0.02	0.11	7	0.24	0.09	0.38	4	0.31	0.03	0.10	3	0.45	0.08	0.18	3
ANTHLEN	0.75	0.07	0.09	7	1.01	0.31	0.31	4	1.30	0.30	0.23	3	1.32	0.07	0.05	3
STAMEX	100.0	0		7	100.0	0		4	79.6	35.2	0.44	3	71.5	24.74	0.35	3
DIAM	26.8	2.18	0.08	6	26.5	1.96	0.07	3	25.5	0		1				0
SCULPT	(1)	-	-	5	(1)	-	-	3	(1)	-	-	2				0

Figure III-1. Dendrogram 1: cluster dendrogram based on 15 variables (Table III-7, Analysis A). All specimens are from Princeton. The distance coefficient is based on average linkage between groups (UPGMA).



DENDROGRAM 1

Figure III-2. Dendrogram 2: cluster dendrogram based on 11 variables (Table III-7, Analysis E). Specimens from Republic are circled. The distance coefficient is based on average linkage between groups (UPGMA). Specimen 39 joins the larger cluster at a distance coeffecient of 58.8.


DENDROGRAM 2
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19
23
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28
39
I
II
IV
III

Figure III-3. Dendrogram 3: cluster dendrogram based on 9 characters (Table III-7, Analysis F). Specimens from Republic are circled. The distance coefficient is based on average linkage between groups (UPGMA). Specimen 39 joins the larger cluster at a distance coefficient of 57.9.

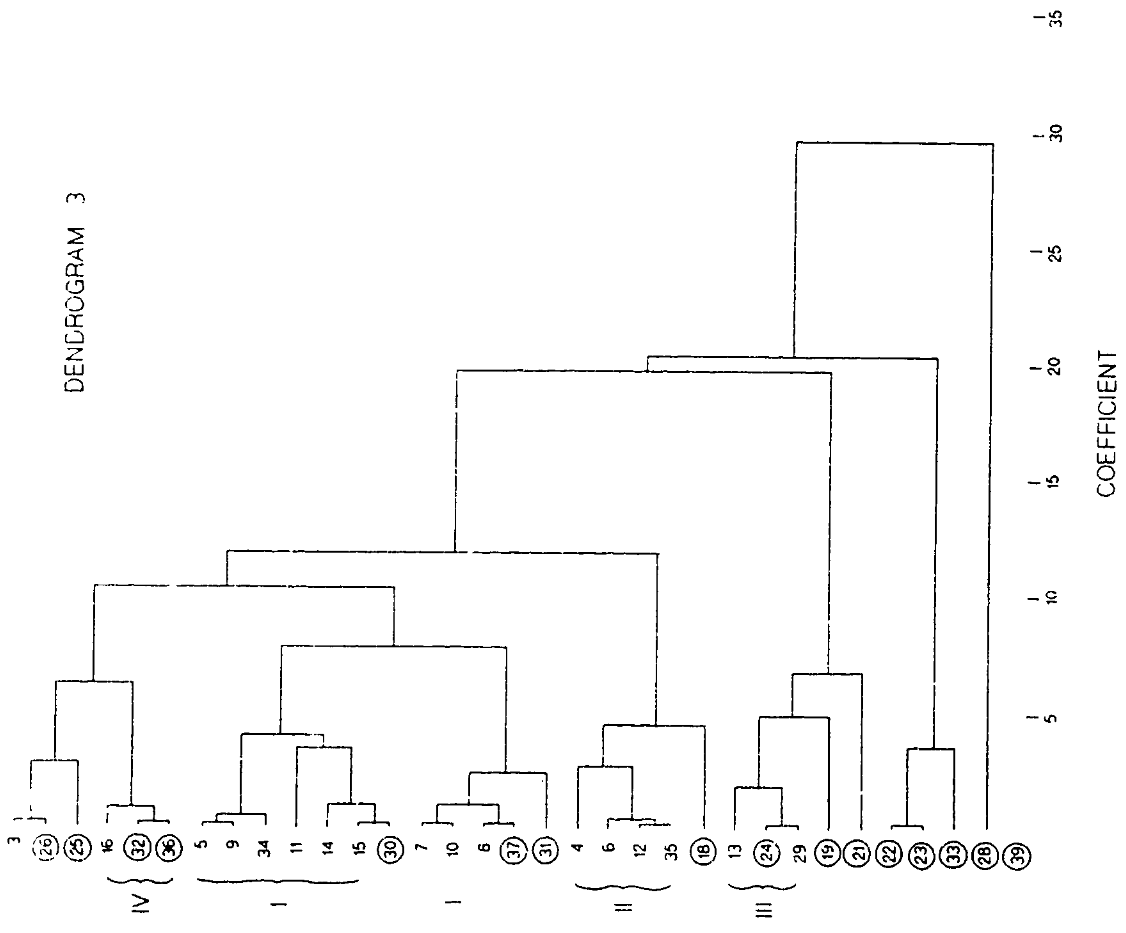
DENDROGRAM 3
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PLATE III-I. Group I catkins, One Mile Creek locality, Princeton, British Columbia.

1. Mature catkin of Betula leopoldae Wolfe and Wehr; specimen #5 (UAPC 5345); X 2.

2. Mature betulaceous catkin with widely spaced partial inflorescences, apex missing; specimen #9 (UAPC 14238); X 2.

3. Apex of mature betulaceous catkin; specimen #15 (UAPC 26363); X 2.

4. Mature betulaceous catkin with conspicuous inflorescence axis and numerous partial inflorescences; specimen #11 (UAPC 26349); X 2.

5. Mature betulaceous catkin; specimen #34 (UWBM 56709); X 2.

6. Fragment of mature catkin; specimen #14 (UAPC 26353); X 2.

7. Immature catkin apex; specimen #10 (UAPC 26348); X 2.

8. Mature partial inflorescences showing large, triangular primary bracts (P) and oval secondary bracts (S); primary bracts have long peduncles and enclose anthers; specimen #11 (UAPC 26349); X 15.

9. Mature partial inflorescences showing large primary bracts (P) parallel to the inflorescence axis; specimen #34 (UWBM 56709); X 15.


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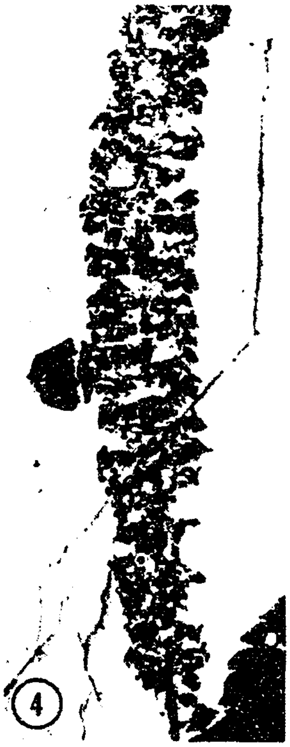
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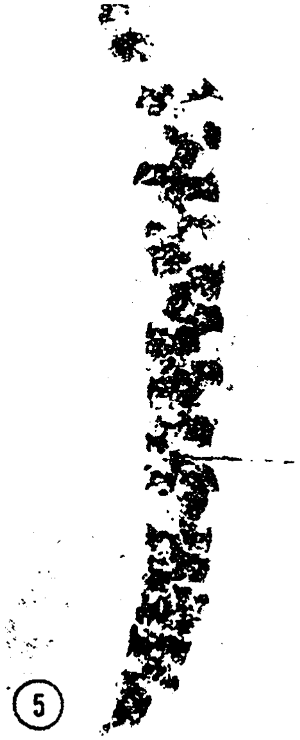
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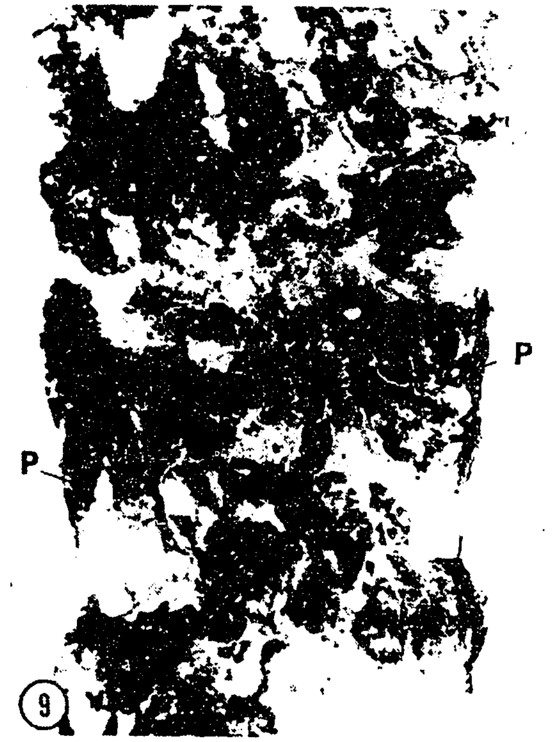

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PLATE III-II. 1-5: Group II catkins.

1. Robust partially mature catkin of Betula leopoldae; specimen #4 (UAPC 5086); One Mile Creek locality, Princeton, British Columbia; X 2.

2. Fragment of B. leopoldae catkin; specimen #6 (UAPC 5359); One Mile Creek locality, Princeton; X 2.

3. Betulaceous catkin with distorted inflorescence axis, probably missing several basal partial inflorescences; specimen #12 (UAPC 26350); One Mile Creek locality, Princeton; X 2.

4. Mature betulaceous catkin; specimen #35 (UWBM 56710); One Mile Creek locality; X 2.

5. Enlargement of specimen #35 (Plate III-II,4); mature betulaceous catkin with large primary bracts (P) at an oblique angle to the inflorescence axis; UWBM 56710; One Mile Creek locality, Princeton; X 8.

6-9: Group III catkins.

6. Fragment of narrow spikate catkin; specimen #13 (UAPC 26351); One Mile Creek locality, Princeton; X 2.

7. Whole spikate catkin with oval sessile bracts; specimen #24 (UWBM 36824); One Mile Creek locality, Princeton; X 2.

8. Enlargement of specimen #29 (Plate III-II,9), showing sessile partial inflorescences with multiple overlapping bracts; UWBM 54163; Tulameen Road locality, Princeton; X 8.

9. Mature spikate catkins with dense overlapping bracts; specimen #29 (UWBM 54163); Tulameen Road locality, Princeton; X 2.

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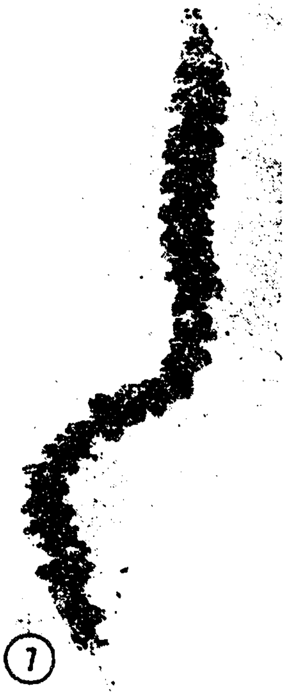

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PLATE III-III. 1-3: Group IV catkins.

1. Mature catkin with small, dark bracts and exserted, lighter coloured stamens; bracts low density; specimen #32 (UWBM 54398); Republic, Washington; X 2.

2. Overmature catkin, partially fragmented with partial inflorescences widely separate; specimen #16 (UWBM 36001); One Mile Creek locality, Princeton, British Columbia; X 2.

3. Mature catkin with small bracts and dense, exserted stamens; specimen #36 (UWBM 56726); Republic; X 2.

4-7: Catkins showing wide morphological diversity (outliers).

4. Several catkins including mature, dispersed partial inflorescences and anthers (A) and dense, spikate catkin (B); specimen #20 (A) and 21 (B) (UWBM 36382); Republic; X 2.

5. Three mature catkins on common inflorescence axis; catkins dense, narrow, with small bracts; specimen #3 (PM 903); Tulameen Road, Princeton; X 2.

6. Small narrow catkin with dissected bracts and exserted stamens; specimen #33 (UWBM 56630); Republic; X 2.

7. Mature catkin with multiple, oval bracts and large, exserted stamens; specimen #19 (UWBM 36381); Republic; X 2.


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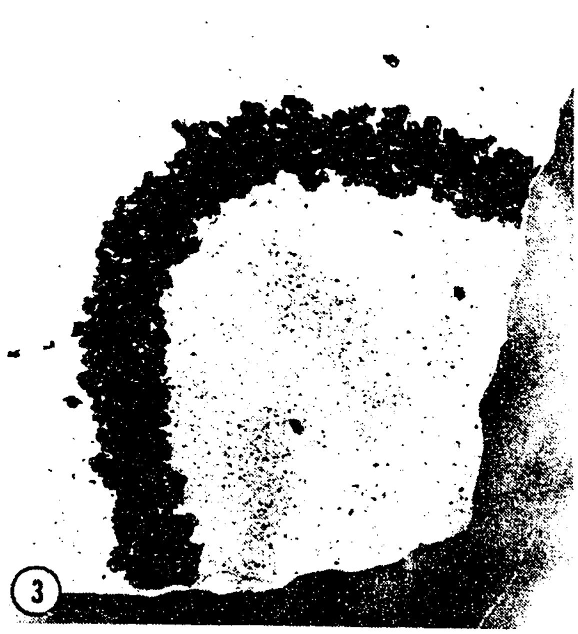
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PLATE III-IV. 1-9: Catkins showing wide morphological diversity (outliers).

1. Incomplete catkin with small bracts and exserted stamens; specimen #1 (CMN 000489); McAbee, British Columbia; X 2.

2. Complex inflorescence with partial inflorescences basally mature and dense apically; specimen #17 (UWBM 36002); One Mile Creek, Princeton, British Columbia; X 2.

3. Fragment of catkin with dissected bracts and exserted stamens; specimen #23; (UWBM 36384); Republic, Washington; X 2.

4. Non-linear staminate inflorescences with dissected bracts and anthers with filaments; specimen #39 (UWBM 74491); Republic; X 2.

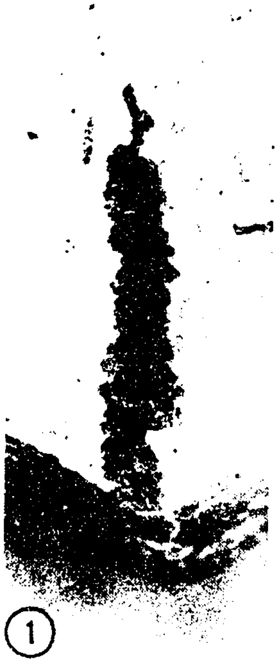
5. Groups of catkins, including dispersed partial inflorescences (A and C) and whole catkin (B) with dense bracts; specimen #25 (A), #26 (B) and #27 (C); UWBM 36825; Republic; X 2.

6. Mature catkin with primary bracts parallel to robust inflorescence axis; anthers not discernible; specimen #30 (UWBM 54392); Republic; X 2.

7. Catkin with large outer primary bracts; anther material not preserved; specimen #31 (UWBM 54395); Republic; X 2.

8. Narrow catkin fragment with inconspicuous bracts; specimen #28 (UWBM 52203); Republic; X 2.

9. Immature catkin showing tightly appressed primary bracts; specimen #37 (UWBM 56787); Republic; X 2.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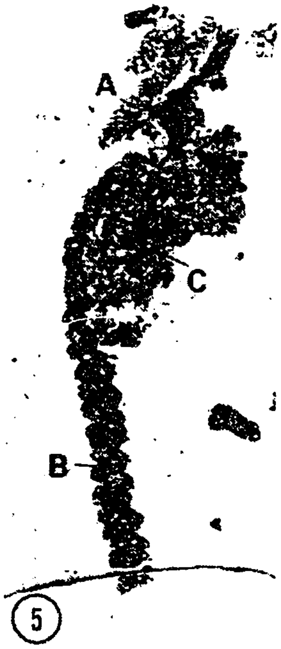
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PLATE III-V. Anthers and pollen of Group I and II catkins.

1. Transmission electron micrograph of pollen from catkin in Plate III-I,5 showing thick foot layer, granular interstitium and thick tectum; outer surface of pollen is covered in hollow Ubisch bodies; specimen #34 (UWBM 56709); Group I; One Mile Creek, Princeton; X 30,000.

2. Scanning electron micrograph of pollen from catkin in Plate III-I,4; porate pollen with scabrate/rugulate sculpturing; specimen #11 (UAPC 26349); Group I; One Mile Creek, Princeton; X 825.

3. Partial inflorescence of specimen #9 (Plate III-I,2) showing numerous clustered anthers enclosed by the primary bract; UAPC 14238; Groups I; One Mile Creek, Princeton; X 7.5.

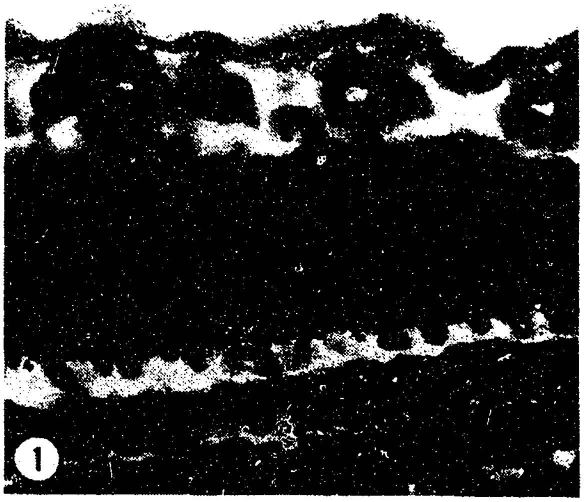
4. Scanning electron micrograph of pollen from catkin in Plate III-II, 4; pollen probably triporate; specimen #35 (UWBM 56710); Group II; One Mile Creek, Princeton; X 1250.

5. Scanning electron micrograph of pollen from catkin in Plate III-I,6; probably triporate, with scabrate sculpturing; specimen #14 (UAPC 26353); Group I; One Mile Creek, Princeton; X 900.

6. Scanning electron micrograph of scabrate, porate pollen from catkin in Plate III-I,2 and III-V,3; specimen #9 (UAPC 14238); Group I; One Mile Creek, Princeton; X 1700.

7. Scanning electron micrograph of pollen from catkin in Plate III-I,5; pollen porate with scabrate sculpturing; specimen #34 (UWBM 56709); Group I; One Mile Creek, Princeton; X 1900.

8. Scanning electron micrograph of pollen from catkin in Plate III-I,1; pollen probably triporate; specimen #5 (UAPC 5345); Group I; One Mile Creek, Princeton; X 1500.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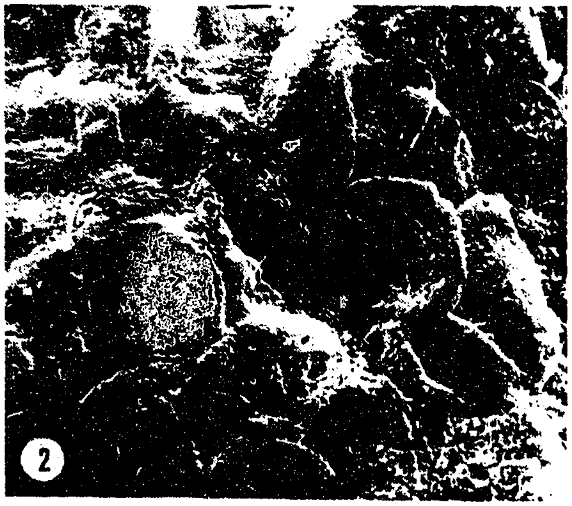
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IV. FLOWER FORM AND POLLINATION SYNDROMES IN THE MIDDLE EOCENE OF WASHINGTON STATE AND BRITISH COLUMBIA

INTRODUCTION

Faegri and van der Pijl (1979) made an important contribution to pollination studies by defining "structural blossom classes", which relate floral morphology to function in pollination, and "pollination syndromes", which identify a suite of co-occurring floral characteristics for each type of pollinating agent. Although this typological system has limited application in pollination studies, it has been put into service by paleobiologists to predict pollinating agents from floral form in fossil plants (Crepet and Dilcher 1977, Crepet 1979a, Crepet 1979b, Crepet and Taylor 1985, Willemstein 1987).

There are problems, however, in the transfer of floral form categories described by Faegri and van der Pijl to fossil flowers. Although meaningful parts of the reproductive organs and perianth may be preserved, many floral characteristics, such as color and odour, that are critical to the definition of syndromes are unrecognizable in fossils. Even in floral parts that are readily preserved, much detail may be lost or degraded through taphonomic processes. As well, paleobiologists weight characters differently than those working with extant plants, due to the narrow field of characters to choose from. The most striking example is the use of pollen morphology, a character rarely considered part of pollination syndromes of extant plants.

With such apparent discrepancies, it seems unreasonable to attempt to fit the reduced suite of floral characteristics in fossils into categories based on extant plants. The antithesis to this approach is to define the categories with reference only to preserved material. In this study, I use multivariate statistical tools to generate flower form categories in a collection of inflorescences from the Middle Eocene of British Columbia and Washington State. A similar approach was used in the analysis of staminate catkins from the area; it proved appropriate in identifying an "amentiferous" Middle Eocene pollination syndrome (Chapter III).

MATERIALS AND METHODS

Study sites and specimens

Fifty specimens of flowers and inflorescences from Middle Eocene localities in British Columbia and Washington State, preserved as compression/impression fossils, were obtained from the paleobotanical collections at UAPC-ALTA, UWBM, CMN and PM. Most specimens (N = 31) are from Republic, Washington; in British Columbia, 10 specimens are from Horsefly, 4 are from One Mile Creek, 3 are from Falkland and 2 specimens are from McAbee. Geographic location, age and lithology of sites is given in Chapter II; specimen numbers and collecting information are given in Table IV-1. The five localities are approximately contemporaneous and are part of a series of lacustrine deposits distributed through central and southern British Columbia and northeastern Washington state.

The Republic flora includes over 180 dicotyledonous species and several conifers (Wolfe and Wehr 1987; Wehr, personal communication). The diversity in staminate inflorescences is high, with betulaceous and juglandaceous groups represented (Chapter III). The flora of Horsefly includes *Pistillipollianthus wilsonii* Stockey and Manchester, a flower with some similarities to the Euphorbiaceae (Stockey and Manchester 1988) and a diversity of angiosperm leaves, fruits, seeds, flowers and wood that has yet to be described (Wilson 1980 and personal observation). The fossil flora at One Mile Creek is dominated by *Betula leopoldae* Wolfe and Wehr leaves and associated infructescences, fruits and staminate inflorescences (Crane and Stockey 1987). Other angiosperm foliage and conifer material is present as well (Schorn and Wehr 1986, Crane and Stockey 1987). Numerous staminate inflorescences are associated with *Betula leopoldae*, and although the catkins may represent several taxonomic groups, they are all betulaceous (Chapter III). The flora in sediments at Falkland is as yet undescribed. Collections from McAbee include a range of angiosperm and conifer megafossils (L.V. Hills, personal communication).

Morphological and statistical analysis

Specimens were measured with a micrometer mounted in a Wild M5 dissecting microscope and Helios dial calipers. Camera lucida drawings were made of whole specimens and details. Details of techniques for preparation of pollen for electron and light microscopy are described in Chapter III. For scanning electron microscopy, prepared anthers were mounted whole on stubs and crushed slightly, sputter-coated with 150 Å gold and examined with a Cambridge Stereoscan 250 at 20 kV. For transmission electron microscopy, the anther sections were examined with a Hitachi H-7000 transmission electron microscope. For analysis with the light microscope, the macerated and stained anthers were crushed, liberating pollen grains, by tapping the cover glass before the Coverbond hardened. Since only three of the specimens yielded well-preserved pollen, pollen characteristics are not used as variables in the statistical analysis. However, pollen information is included in the text.

Morphology of inflorescences and flowers was coded into 48 variables (Table IV-2); those describing the inflorescences (N = 8) were excluded from statistical analysis because of the small sample size. The remaining flower structure variables consisted of continuous numeric measurements of floral dimensions (27 variables) and ratios of these dimensions (6 variables), 3 nominal variables coded into presence/absence dichotomies and 4 variables describing meristic characters. The raw data for all specimens is presented in Appendix 1b.

The following measurement protocols were used. Length and width measurements were taken of the perianth, flower and tepal (Figure IV-1). It is often not possible in fossils to ascertain whether the perianth consists of corolla or calyx, and consequently, tepal is used throughout. If both calyx and corolla were present and visually distinct, the whorl with the largest dimensions was measured. Perianth length (PLENMAX, PLENX; for variable acronyms, see Table IV-2) was measurable only in specimens oriented with the side of the flower (abaxial surface) parallel to the plane of fracture (side view), whereas perianth width (PWIDMAX, PWIDX) was measurable in specimens in side view or with the adaxial surface parallel to the plane of fracture (top view). Flower dimensions (FWIDMAX, FWIDX, FLENMAX, FLENX) consisted of length and width measurements for the combined perianth and reproductive parts. Values for flower variables were the same as for perianth variables if reproductive structures were absent. The protocol applying to perianth applies to flower variables as well: flower length was measurable only in specimens in side view, but flower width was measurable from side and top view. The tepal consisted of the petal or sepal (TWIDMAX, TWIDX, TLENMAX, TLENX); in side view specimens, tepal length coincided with perianth length, whereas in top view specimens, tepal length was approximately the radius of the perianth. Shape variables (PSHAPE, FSHAPE, TSHAPE) were entered separately from dimension variables by expressing a length/width ratio for each of the three sterile floral parts. The degree of connation of sterile whorls was introduced by measuring the length and width of the connate part of the perianth; developmental connation of tepals was not distinguished from connation produced by overlapping of tepal bases. The proportion of the perianth that is connate (PCON) was calculated.

Numbers and dimensions of androecial and gynoecial structures were measured. Stamen length (STAMMAX, STAMX) was measured from the base of the perianth to the stamen tip, even though some flowers may have been epipetalous. The proportion of the reproductive organs that was enclosed by the perianth was calculated (STAMEXSE, PISEXSER). Due to taphonomic change, dimension measurements of all structures may be underestimates. As such, maximum values rather than means are more appropriate for analysis.

Univariate summary statistics (mean, mode, standard deviation, coefficient of variation) and Pearson correlation coefficients were calculated for all flower variables. For multivariate statistical analysis, the list of 40 variables was reduced to 18. Variables that had data for fewer than 15 specimens (PWIDX, PLENX, FWIDX, FLENX, ANTHWID, ANTHLEN and all 9 variables describing gynoecial structure) were eliminated due to problems in handling missing data. Since character means and maxima were highly correlated ($r > 0.95$ for all pairs: see Appendix 2 for correlation coefficients), variable means were excluded (TWIDX, TLENX and STAMX in addition to the means listed above) to provide a more conservative measure of association. Variables describing the pedicel (PCWID, PCLEN) were not included in multivariate analysis because they did not contribute to flower form.

Specimens were organized into multi-character similarity groups using a hierarchical cluster analysis (Norusis 1988). Squared Euclidean distance was based on standarized variables; specimens were clustered using the average linkage between groups (UPGMA) method and clusters were plotted as dendrograms. Analyses were done using alternate clustering techniques and the results were similar. Specimens were entered into discriminant function analysis (Norusis 1988) with group membership as the discriminating variable. Minimization of Wilks' Lambda was used to select variables for entry into stepwise discriminant analysis. Variables with small tolerances (i.e., those variables that are linear combinations of other variables) are not allowed entry into the analysis. Predictor variables that contributed to functions differentiating the groups were identified. Discriminant scores for the first three functions were used to verify group membership of specimens or to classify specimens that had not been group defined. Group centroids and specimens were plotted on the axes of the discriminant functions. Extreme outliers were identified visually on this plot. Each group is described by the variable means and coefficient of variation of its member specimens and by its position in multivariate space. Groups derived from cluster analysis and discriminant function analysis are used to construct flower form categories.

Homogeneity of groups' covariance matrices is an underlying data assumption for discriminant function analysis and is tested here with Box's M statistic (Norusis 1988).

Due to differences in preservational state, the number of characters that could be measured varied greatly among the specimens. Missing data proved to be an enormous problem in multivariate analysis. The cluster analysis and discriminant function analysis programs automatically eliminate cases with missing values. If the maximum number of morphological variables is entered into the analysis, the results are based on too few specimens. For example, in a cluster analysis that used all 25 variables (sterile and androecial structures) all cases were eliminated due to missing values for some variable. An increase in the number of cases can only occur by eliminating variables, to the detriment of multivariate accuracy. Therefore, a series of cluster analyses were performed using successively fewer variables and the concomitantly greater number of specimens and comparisons were made of the resultant dendrograms. Specimens that clustered together at early iterations in different dendrograms were considered stable multi-character similarity groups. Variable combinations that maximized specimen number yet did not sacrifice variable diversity are presented for (1) perianth characters (PNOT, PWIDMAX, PPART, PCON, PACT, FWIDMAX, TLENMAX, TSHAPE), (2) androecial characters (STAMNO, STAMMAX, FILWID, STAMEXSE), (3) variables transformed such that size variables (PLENMAX, CONWID, FWIDMAX, FLENMAX, TWIDMAX, TLENMAX) were expressed as a proportion of perianth width (PWIDMAX). In cluster analysis (1), I used variables which measured both size (PWIDMAX, FWIDMAX, TLENMAX) and shape (PNOT, PPART, PCON, PACT, TSHAPE). Although several variables had to be excluded due to small case number (PLENMAX, PSHAPE, FLENMAX, FSHAPE, TNO, TWIDMAX), all but TNO were highly correlated ($p < 0.005$) to TLENMAX and thus redundant. Discriminant function analysis was run for various sub-samples identified in cluster analysis; only the results for groups derived from (1) perianth characters and (2) androecial characters are presented. For specimens not included in cluster or discriminant analysis due to missing values, classification was made by replacing missing values with variable means. In this way, all specimens could be tentatively classified.

Terms used to describe symmetry and depth of flowers follow Leppik (1957), where actinomorphic refers to flowers with radial symmetry and parts primarily on a single plane, zygomorphic refers to those showing bilateral symmetry and stereomorphy involves some depth effect to the flower (e.g., a long corolla tube).

RESULTS

Morphological variation

Character states and variable values are summarized in Table IV-3. The characters that had the lowest variability were the number of tepals (TNO) and the degree of connation (PCON). Perianth width variables

(PWIDMAX, CONWID, FWIDMAX, TWIDMAX), which formed a correlated character complex ($r > 0.95$, $p < 0.001$ for all variable pairs) showed high variability, whereas perianth shape variables were more conservative. In 48 of the sample of 50, only one specimen (#5, Figure IV-17; see Table IV-1 for specimen numbers) had a perianth that appeared to be naturally absent; in one of the specimens, presence or absence of a perianth could not be substantiated. All specimens except #2 (Figure IV-21) were actinomorphic (PACT); perianths were incompletely fused (PPART) in all but 2 (#38, Figure IV-19; #50, Figure IV-18) of the 40 specimens in which the character could be measured. Perianth width (PWIDMAX, FWIDMAX) ranged from 1.69 mm (#35) to 43.0 mm (#18); perianth length (PLENMAX) and flower length (FLENMAX) were less variable, reaching a maximum of 19.46 mm (#2, Figure IV-21). Specimen #35 had the smallest dimensions and #18 the largest. Although tepal number (TNO) ranged from three to eight, most specimens in which tepal number was countable had 5 (17 out of 23). Tepal width (TWIDMAX) was highly variable [0.38 mm (#1) - 18.3 mm (#18)] and length (TLENMAX) was less so [1.69 mm (#35) - 21.9 mm (#18)].

Shape components of the sterile parts, measured by length:width ratios, showed that for both the perianth (PSHAPE) and the flower (FSHAPE), the average relative shape was one (length = width), although ratios ranged from 0.5 to 3.6 with #2 (Figure IV-21) having the highest ratio. Tepal shape (TSHAPE) averaged a 3:1 length:width ratio, but the maximum was close to 10:1 (#27, Figure IV-16). The proportion of the perianth that was connate (PCON) ranged from 27% (#20) to 100%, with only two specimens (#38, Figure IV-19; #50, Figure IV-18) having completely connate perianths.

Twenty-nine specimens had visible pedicels. Many of these were in inflorescences, but there were several isolated flowers in which the attached pedicels appeared to have an abscission zone at the base. There was high variability in pedicel length (PCLEN), ranging from 0.61 mm (#44) to 33.9 mm (#39, Figure IV-12).

The androecium was visible in 22 specimens. Specimen #1 had the fewest stamens (4) (STAMNO) and #38 (Figure IV-19) had the greatest number (17), the mode being 5. Maximum stamen length (STAMMAX) in different specimens ranged from 1.02 mm (#45) to 23.17 mm (#2, Figure IV-21); in the majority of specimens (15 out of 17 with stamens), stamens projected past the perianth apex (STAMEXSE). Anther length (ANTHLEN) was smallest for #31 (0.40 mm) and largest in #47 (3.51 mm). Specimen #47 had also the greatest anther width (ANTHWID), but #38 (Figure IV-19) had the smallest (0.15 mm). Anther material was removed from 6 specimens (#1,#5,#7,#9,#12,#37) for scanning electron microscopy, but only #5 (Figure IV-17) and #12 yielded pollen. Specimen #5 pollen, which was not seen singly and whole, was probably circular with a diameter of approximately 20.9 μm; pores or colpi were not apparent. The sexine was perforate, columellate and semi-tectate with scabrate sculpturing and the nexine was finely laminated. The pollen of specimen #6 (Figure IV-6) (Pistillipollianthus wilsonii holotype) is Pistillipollenites macgregorii Rouse; the grains are triporate, 22 μm average diameter, with a nanoverrucate exine sculpturing and numerous collumella-supported gemmae (Stockey and Manchester 1988). Fragments of pollen were extracted from #12; they showed a reticulate exine sculpturing. No other characters were discernible.

Gynoecial structures were present and measurable on seven specimens [#13,#21,#22(Figure IV-10),#25,#44,#45,#46]. Number of pistils (PISNO) ranged from one to three, with five of the seven specimens having a single pistil. Five had one style (STYNO) and two (both on flowers with single pistils) had a double style. Character dimensions for the pistil, style and ovary are listed in Table IV-3. Due to the small sample size for specimens with preserved gynoecia, and to the problem of size and shape changes resulting from ontogeny, the data is of little value to the study. The raw data on gynoecial characters is given in Appendix 1b.

Cluster analysis

(1) **Perianth characters:** Twenty-six specimens were included by the variables specified in cluster analysis PERI (Table IV-4). In all specimens, the perianth was present (PNOT = 0) and was dissected (PPART = 1) and actinomorphic (PACT = 1). The clustering is therefore based on the remaining five characters (PWIDMAX, PCON, FWIDMAX, TLENMAX, TSHAPE). The specimens clustered into six groups; two outlying specimens joined the groups at low similarity coefficients (Figure IV-2). Mean values for the four largest groups are given in Table IV-5. Group 1 specimens (Figure IV-4) had 5 tepals connate for three-quarters of their length. Perianth dimensions in this group were greater than for all other groups. All of the characters except for degree of connation showed low variability. The group was strongly differentiated from the other groups, joining other specimens at a low similarity coefficient (Figure

IV-2). Group 2 specimens (#1,#36; Figure IV-5) were distinguished by having a high degree of perianth connation (0.82 and 0.91, respectively), a condition that appears to be developmental rather than produced by overlapping tepal bases; in addition, the relatively small perianths had a high length-width ratio (1.19 and 2.37, respectively). Group 3 specimens (#6,#8; Figure IV-6) were 5-tepalled, robust flowers, with large perianths (perianth width = 21.38 and 19.54 mm, respectively). Among the three remaining groups, Group 4 (Figures IV-7 to IV-9) was distinguished by having the smallest mean dimensions for perianth, flower and tepal; as well, perianth connation was greater than in the other two groups. Group 5 (Figures IV-10 to IV-12) had the largest perianth dimensions and the longest tepals (highest length:width ratio for tepals) of the three. Group 6 (Figures IV-13 to IV-15) was distinct from 4 and 5 by showing little connation of the perianth, wide tepals and the least exserted stamens. There were two outliers: specimen #27 (Figure IV-16) was distinct in having the greatest number of tepals (8) and the narrowest tepals (length:width ratio = 9.64). Specimen #2 (Figure IV-21), the most divergent specimen in the dendrogram, was zygomorphic, with a long, narrow perianth (PSHAPE = 3.62), the longest tepals (19.46 mm) and little connation (0.39).

(2) **Androecial variables:** The cluster analysis based on androecial characters yielded 14 specimens, 4 of which (#2,#26,#28,#39) were shared with specimens in the perianth analysis. Of these, #2 remained the outlier (Figure IV-3), as was the case in the general perianth analysis; the other three did not have the same associations. There were three groups formed (Table IV-6). Group A (21-26-32-34-42) was distinguished

by having wide, short stamens that were fewest in number and the least exserted. Group B (28-29-39) showed intermediate characteristics for all four variables. Group C (7-12-31-38-50; Figures IV-18 and IV-19), had the greatest number of stamens, that were long, narrow and strongly exserted. When a perianth dimension variable (FWIDMAX) is added to the four androecial variables, specimens #32 and #34 form a group distinct from the other specimens.

(3) Transformed variables. This analysis yielded the same 26 specimens as did perianth analysis and the two are thus comparable. Group 1 (from the perianth analysis) retained its integrity, except for losing specimen #15, which became an outlier. Group 4 specimens remained clustered, with the addition of #39. Although there were other specimens that paired as in the full perianth analysis, Groups 5 and 6 generally clustered together.

When only size variables (PWIDMAX, PLENMAX, CONWID, CONLEN, FWIDMAX, FLENMAX, TWIDMAX, TLENMAX) were entered into cluster analysis, some pairs of specimens had the same associations and #2 remained an outlier. Apart from this, however, there was no consistency between dendrograms produced by the two analyses.

Discriminant function analysis

Discriminant function analysis used the 20 specimens of the four largest groups to construct linear combinations of variables that discriminate between the groups. For each variable, group means were significantly distinct (Table IV-7). Stepwise discriminant analysis selected the variables PWIDMAX (perianth width), PCON (connation of perianth) and TSHAPE (length/width ratio of tepal) as those which best discriminate between the four groups, and which were uncorrelated with each other. The other variables (FWIDMAX, TLENMAX) did not contribute to differences between the groups; they were, however, correlated with the predictor variable PWIDMAX ($r > 0.80$, $p < 0.001$ for both pairs). PWIDMAX was the first predictor variable selected (Wilks' Lambda = 0.08; F = 61.45; $p < 0.001$), followed by PCON (Lambda = 0.01; F = 36.81; $p < 0.001$) and TSHAPE (Lambda = 0.003; F = 37.42; $p < 0.001$). Discriminant function 1 was primarily a size function, with PWIDMAX being the variable most important in discrimination; variables PCON AND TSHAPE had approximately the same, lesser weight in specifying the function (Table IV-8). Function 2 related to shape, with PCON and TSHAPE contributing equally and PWIDMAX having little predictive value. All three variables in discriminant function 3 contributed approximately equally to defining the function. Correlations between the discriminating variables and the discriminant functions (Table IV-9) showed that a high discriminant score for function 1 is associated with high values for the correlated ($r = 0.99$; $p <0.001$) perianth width-flower width (PWIDMAX-FWIDMAX) character, that high values for function 2 are associated with a high degree of connation (PCON) and linearity of tepals (TSHAPE) and that high values for function 3 are moderately correlated with linearity of tepals, larger perianth dimensions (PWIDMAX, FWIDMAX, TLENMAX) and reduced connation. Canonical discriminant function 1 accounted for 69% of the variability between groups (Eigenvalue = 16.87) and function 2 for 24% (Eigenvalue = 5.88); although function 3 contributed significantly to group differentiation, it accounted for only 7% of the variability (Eigenvalue = 1.67).

One of the assumptions of discriminant function analysis is that the covariance matrices between groups are equal (Norusis 1988). The probability level for Box's M test is low ($p = 0.09$; $M = 44.42$; $F_{[18,562.6]} = 1.48$), indicating that covariance matrices between groups may not be equal. However, it has been suggested that homogeneity of covariance matrices is not requisite in multivariate ecological studies (McAlpine and Dilworth 1989).

Classification of specimens used in deriving the functions was 100% correct. Since, for the additional 30 specimens, variable means were used to replace missing data, the accuracy of classification will depend on the number of variables present. Six of the specimens (#5, Figure IV-17;#25,#40,#44,#46,#47) had 3 variables missing and meaningful discriminant scores could not be derived for them (all had discriminant scores of 0). When the discriminant scores for the remaining 44 specimens were plotted against the three functions, the group centroids showed strong discrimination (Figure IV-22). Group 1 was strongly differentiated along the axis of discriminant function 1, reflecting, primarily, large perianth width, and secondarily, a high degree of connation and a low tepal length:width ratio. Groups 4 and 5 were not differentiated along the axis of discriminant function 2 because they both show a high degree of connation and increased linearity of tepals. They differed mainly in the values of function 3, with Group 4 centroid reflecting smaller perianth, greater connation and less linear tepals than Group 5 centroid. Group 6 centroid was similar to Group 1 along the axis of function 3 but differentiated most strongly from Groups 4 and 5 for function 2 (showing less connation and wider tepals than Groups 4 and 5) and from Group 1 for function 1 (showing smaller perianth width and less connation). When all specimens are plotted on the axes of the first two discriminant functions (Figure IV-23), it is evident that Groups 1, 5 and 6 are differentiated from each other, while Group 4 shows overlap with both 5 and 6. Since function 1 and 2 accounted for 93% of the variability, differentiation along axis 3 may be less important for group definition. Outliers (#27,#2) and outlying pairs (#1-#36, #38-#50) were clearly evident.

Flower form categories

Using multivariate analysis, eleven categories of flower form were generated from the flower specimens. Cluster analysis based on perianth variables identified six groups and two outliers in a sub-sample of 20 flower specimens. The cluster analysis based on androecial characters identified a group with conspicuous stamens that was considered as a separate category. Of the six specimens with insufficient data for classification, there are two (#5,#11) that showed distinct morphology. A summary of the characteristics of the eleven categories is given in Table IV-10.

DISCUSSION

Fossil flowers, never abundant, are comparatively well represented in the Middle Eocene lacustrine sediments analyzed in this study. The characters used to describe floral form are necessarily fewer than those used in studies of extant plants. However, the analysis has succeeded in generating a number of distinct flower form categories that can be described by multicharacter functions.

Changes in floral characters and character complexes through time

Although this study emphasizes the larger unit of floral form, single characters may be important for understanding evolutionary trends in floral morphology. There were several character states common to most of the sample: (1) perianth present and dissected, (2) radial symmetry and (3) 5 tepals. Several characters describing shape had relatively low variability; the average values for these were: (4) perianth connation about 60% of its length,(5) length:width ratio for both perianth and flower about one and (6) length:width ratio for tepal about three. Most of these morphological states are present in the Upper Cretaceous and some date back to the Albian (100 million years BP): membraneous perianth parts are present in Platanaceous flowers from the late Albian Patapsco Formation of eastern North America (Crane et al. 1986); a robust, pentamerous and actinomorphic flower occurs in the Upper Cretaceous (Cenomanian) of Nebraska (Basinger and Dilcher 1984). Sympetally is first recorded in Actinocalyx from the Scania flora (Santonian-Cenomanian) of southern Sweden (Friis 1985). Several specimens from Scania appear to be bowl- to cup-shaped (approximately 1:1 ratio) (Friis 1984). None of the most common characteristics of these Middle Eocene flowers mark appearances of evolutionarily "new" characters; most, in fact, represent relatively ancient conditions in floral form. Stasis in these characters through time may indicate that selective pressures maintaining the morphology, presumably pollinating agents, have remained similar over that time span.

Zygomorphy was exhibited by a single specimen and stereomorphy (defined here as perianth length:width ratio > 1) in only seven of the

27 specimens in which it could be measured. Although there is continuing debate on "primitive" versus "derived" states in floral characters (Leppik 1957, 1968, Stebbins 1974, Dilcher 1979, Willemstein 1987), it is generally agreed that actinomorphy is plesiomorphic while zygomorphy and stereomorphy are derived. Raoanthus, from the Deccan Intertrappean (Maastrichtian), is slightly zygomorphic (Chitaley and Patel 1975); unequivocal zygomorphy occurs in the legume-like flower in this study (Figure IV-21) and in flowers from the Paleocene-Eocene boundary in Tennessee that show affinities with the Fabaceae (Crepet and Taylor 1985). It is difficult to choose a point on the continuum of length:width ratios at which a perianth is defined as stereomorphic, but in general, Cretaceous flowers are shallow bowl-shaped (Friis and Crepet 1987). In addition to the legume-like flowers mentioned above, funnel-shaped and tube-shaped perianths occur in the Middle Eocene Claiborne Formation (Crepet 1984) and in this study. Stereomorphy, in the form of an elongate, sympetalous corolla is sound evidence for the presence of pollinators with long mouthparts capable of obtaining nectar, while not entering the flower. An important corollary to this is that pollinators without long mouthparts are restricted from feeding and incapable of pollinating these flowers. Zygomorphy is interpreted (Stebbins 1974) as a floral form that, as a co-adaptation with specialized pollinators, orients the pollinator on a "landing platform" and brings the stamens and stigma into specific positions for depositing and receiving pollen. A review of pollinating agents with these characteristics, and predictions on pollinators of these specialized Middle Eocene flowers are given in Chapter VII.

Although there may be parts of flowers that act in isolation to facilitate pollination, anthecologists agree that character complexes, or floral "syndromes", are synergistically important in specifying appropriate pollinators. In order to identify floral syndromes that are evolutionarily "new" to British Columbia-Republic, or to the Eocene, it will be necessary to compare the flower form categories derived in this study with convergent forms in, for example, the Scania flora of southern Sweden (Friis and Skarby 1981, 1982, Friis 1984) and flowers of the Claiborne Formation of Tennessee (Crepet and Dilcher 1977, Crepet 1978, 1979a, 1984, Crepet and Daghlian 1981, 1982, Zavada and Crepet 1981, Crepet and Taylor 1985, 1986, Taylor and Crepet 1987, Taylor 1988, Herendeen and Dilcher 1990). Some of the flower form categories in this study can be qualitatively identified as evolutionarily recent, for example, those incorporating extreme zygomorphy or stereomorphy (Group 2, Figure IV-5 and Group 8, Figure IV-21) and those with a radically different morphology (Group 11, Figure IV-20). It may be more difficult, however, to identify new syndromes in flower form categories that have a more complex multivariate definition. It may be necessary to subject other samples of floral diversity (the Scania flora and the Claiborne flora) to a more quantitative, preferably multivariate statistical analysis such as is used in this study, to be able to make viable comparisons.

There are sufficiently diverse collections of flowers and inflorescences over a broad stratigraphic range (the Upper Cretaceous Scania flora, the Middle Eocene of British Columbia-Republic, Tennessee and Messel, Germany and the Late Eocene-Early Oligocene Baltic amber), that conclusions on the evolutionary trends in floral form from the Cretaceous to the Recent are possible, given a quantitative approach.

Comparisons with other Paleocene-Eocene floras

The extent to which these flower form categories are representative of the larger North American flora during the Middle Eocene can be determined by comparison with the well-documented flora of the Mississippi Embayment, Tennessee (Claiborne Formation) (Crepet and Dilcher 1977, Crepet 1978, 1979a, 1984, Crepet and Daghlian 1981, 1982, Zavada and Crepet 1981, Crepet and Taylor 1985, 1986, Taylor and Crepet 1987, Taylor 1988, Herendeen and Dilcher 1990). A summary description of specimens from the Claiborne Formation, and several other Eocene and Paleocene localities, is given in Table IV-11. Many specimens from British Columbia-Republic, although not assignable to species described from the Claiborne, show similarities in form, whether convergent or phylogenetically, with flowers from that locality. In both British Columbia-Republic and Claiborne, 5-tepalled, actinomorphic perianths are common and in each is a single, highly zygomorphic gullet/flag (see Appendix 3) flower. A small partly connate perianth with multiple, exserted stamens is shared as well. Florissantia physalis Knowlton (Group 1 in the present study) is a distinct flower widespread in western North American in the Eocene and Oligocene (Manchester 1989).

Floral characters distinct to the Claiborne specimens include sepal glands (Eoglandulosa warmanensis; Taylor and Crepet 1987), ethereal oil cells and staminal glands (Androglandulosa tennessensis; Taylor 1988), characters that may not be observable on the specimens in the present study due to poorer preservation. Several flower forms found at other Paleogene sites are not present in the British Columbia-Republic sample: a spadix with helically arranged florets (Acorites heeri; Crepet 1978), a spike with florets of 3-4 stamens (Hippomaneoidea warmanensis; Taylor and Crepet 1987), distinct trumpet-shaped corollas (Crepet 1984), a large 7-lobed funnelform-salverform corolla (Crepet and Daghlian 1981) and a 9 mm long campanulate perianth (Crepet 1979a). The only conspicuous form in the present study that is not represented in other Paleocene-Eocene collections (excepting possibly Plate VII,5 in Crepet 1979a) is the pedicellate flower in which tepals are connate, forming a bowl- to cup-shaped perianth with variable numbers of tepals and anthers (primarily Groups 4, 5 and 6; Figures IV-7 to IV-15).

The flowers in this study share many floral characters and many floral form categories with other Paleocene-Eocene fossils, yet individual specimens are rarely comparable between the areas. Similarities in floral form indicate that some pollinating agents were widespread during the early Paleogene. However, under the assumption that each of the collections is representative of the diversity of floral form in the area, the differences between the British Columbia-Republic and Claiborne samples suggest that a subset of the pollinating agents were restricted to their respective areas. Neither can be said to be typical of the larger North American anthecological habitat. Possible pollinators of the flower form categories identified in this study will be explored in Chapter VIII.

Pollination syndromes in extant plants

The structural blossom classes and pollination syndromes outlined by Faegri and van der Pijl (1979) have been used by paleoanthecologists to make inferences on pollinators based on the form of fossil flowers (Crepet and Dilcher 1977, Crepet 1979a, 1979b, Crepet and Taylor 1985, Willemstein 1987). This approach may be valid for identifying broad classes of flower types (e.g., dish-shaped, bowl-shaped, bell-shaped, gullet, flag, trumpet) and predicting pollinators at higher taxonomic levels (beetle, fly, bee, moth, butterfly, bird, bat, non-flying mammal). However, the method does not utilize all the structural detail that is available in fossil flowers, particularly dimensions. For example, in the sample of flowers analyzed in the present study, size was the most significant factor accounting for overall variation between specimens, and between groups of similar specimens. Predictions of pollinators based on the traditionally defined pollination syndromes do not account for the variability within the higher taxa of insect pollinators in pollinating behaviour nor the convergence in structure and behaviour that exists between unrelated groups of pollinators. It may be impossible to accurately predict evolutionary relationships from such generalities.

The problem is not in the inappropriate application of blossom classes and pollination syndromes to paleoanthecology, but the failure of the classification system of Faegri and van der Pijl to go beyond anecdotal and qualitative description. It may be possible to use multivariate statistical tools such as cluster analysis and discriminate function analysis to generate flower form categories in extant plants. If there were found to be strong correlations between flower form categories and specific pollinating agents, valid pollination syndromes could be defined from the associations.

Recognizing that the traditional method of categorizing blossom classes and predicting pollination syndromes has significant limitations, I will however, use the method to classify the flower form categories generated in this study to attempt to assess the validity of its conclusions.

Using the structural blossom classes and pollination syndromes of Faegri and van der Pijl (1979; see Appendix 3 for a summary of the classes and syndromes), six of the eleven categories (1,3,4,5,6 and 7) recognized by multivariate methods are classified as dish-shaped to bowl-shaped blossom classes, all of which would be encompassed by the pollination syndromes of cantharophily or myophily. Category 9 is classified as a brush blossom and would also be cantharophilous or myophilous. The single flag blossom (category 8) is melittophilous, as is category 11, a trumpet-shaped blossom. Category 2, containing bell-shaped to tube-shaped blossoms, is psychophilous or ornithophilous. The apetalous inflorescence of category 10 can be categorized into the inconspicuous blossom class and is anemophilous.

Using these classifications, all of the blossom classes, except for the strictly tubular form, are represented in the sample in this study. Most of the pollination syndromes, excluding the syndromes for pollination by moths, bats and non-flying mammals, are present. The conclusion from this analysis is that beetles, flies, bees, and butterflies are pollinators of Middle Eocene flowers in British Columbia and Republic. Crepet (1979a), in his analysis of pollination syndromes in the Middle Eocene Claiborne Formation, extrapolates in a similar manner from flower form, concluding that all syndromes except moth and bird (he does not consider bats) are present. Crepet (1979a) and Willemstein (1987) use biogeographical and phylogenetic arguments to conclude that highly derived apoid bees and other specialized groups of pollinators in other insect orders had evolved prior to the Eocene. Their absence in the fossil record is interpreted by these authors as reflecting vagaries of preservation and collecting effort.

I present an alternative method of predicting Middle Eocene pollinating agents from flower form in Chapter VII and VIII, based on a review of feeding requirements and behaviour of extant pollinating agents and their stratigraphic occurrence.

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Table IV-1. Collecting information for specimens. CMN: Canadian Museum of Nature, Ottawa; collectors Hills, Kutluk & Hills, 1984. PM: Princeton Museum, Princeton; collector Wehr, 1979. UAPC: University of Alberta Paleobotany Collection, Edmonton; collectors Douglas, Lindoe, Reimchen, Stockey, Wilson, 1975 - 1989. UWBM: Thomas Burke Memorial Washington State Museum, Seattle; collectors Blackstock, Hopkins, Johnson, Nannery, Perry, Reeves, Spitz, Wehr, Zimmerman, 1979 - 1989.

Text number	Specimen number	Locality	Figure reference
1	CMN PB000007	McAbee	
2	CMN PB000082	McAbee	IV-21
3	PM 1721	Republic	IV-4
4	PM 1722	Republic	
5	UAPC S5051	Horsefly	IV-17
6	UAPC S6557	Horsefly	IV-6
7	UAPC S6560	Horsefly	
8	UAPC S6592	Horsefly	
9	UAPC S26356	Horsefly	
10	UAPC S26357	Horsefly	
11	UAPC S26358	Horsefly	IV-20
12	UAPC S26359	Horsefly	
13	UAPC S26360	Horsefly	
14	UAPC S26361	Republic B0307	
15	UAPC S26364	Horsefly	
16	UAPC S26360	Falkland	
17	UAPC S26371	Falkland	
18	UAPC S26372	Falkland	
19	UAPC S26374	Republic	IV-13
20	UWBM 36360	Republic B4131	
21	UWBM 36370	Republic B4131	
22	UWBM 36371	Republic B4131	IV-10
23	UWBM 36374	Republic B4131	IV-7
24	UWBM 36377	Republic B4131	IV-11
25	UWBM 36380	Republic B4131	
26	UWBM 36385	Republic B4131	IV-8
27	UWBM 36386	Republic B4131	IV-16
28	UWBM 36387	Republic B4131	IV-9
29	UWBM 36388	Republic B4131	IV-14
30	UWBM 36389	Republic B4131	
31	UWBM 36395	Republic B4131	
32	UWBM 36775	Republic	

Table IV-1 (continued).

Text number	Specimen number	Locality	Figure reference
33	UWBM 36799	Republic B4131	
34	UWBM 36836	Republic B4131	
35	UWBM 37853	One Mile Creek	
36	UWBM 39397	Republic B4131	IV-5
37	UWBM 52203	Republic B2737	
38	UWBM 56531	Republic B2737	IV-19
39	UWBM 56533	Republic B2737	IV-12
40	UWBM 56735	Republic B2737	
41	UWBM 56736	Republic B2737	
42	UWBM 56737	Republic B2737	
43	UWBM 56739	Republic B2737	IV-15
44	UWBM 56785	One Mile Creek	
45	UWBM 71311	Republic B2737	
46	UWBM 74475	One Mile Creek	
47	UWBM 74476	One Mile Creek	
48	UWBM 74491	Republic B4131	
49	UWBM 74494	Republic B4131	
50	UWBM 74495	Republic B4131	IV-18

Table IV-2. Characters used in analysis of flowers and inflorescences. Those marked with an asterix (*) were used in multivariate statistical analysis. For variables with nominal data, the character states are 0 = character absent, 1 = character present. All numeric variables are in mm.

Character	Variables
Pedicel	PCWID (maximum width), PCLEN (maximum length)
Perianth	*PWIDMAX (maximum width), PWIDX (mean width), *PLENMAX (maximum length of perianth (mm), PLENX (mean length), *PSHAPE (shape: PLENMAX/PWIDMAX), *PPART (fused vs. free or partially fused), *CONWID (maximum width of connate perianth), *CONLEN (maximum length of connate part of perianth), *PCON (proportion of perianth that is connate: CONLEN/TLENMAX for specimens in side view; CONWID/PWIDMAX for apical view), *PACT (symmetry: bilateral or radial), *PNOT (perianth naturally present/absent)
Flower	*FWIDMAX (maximum width or diameter), FWIDX (mean widt or diameter), *FLENMAX (maximum length), FLENX (mean length), *FSHAPE (shape: FLENMAX/FWIDMAX)
Tepals	TNO (number), *TWIDMAX (maximum width), TWIDX (mean width), *TLENMAX (maximum length), TLENX (mean length), *TSHAPE (shape: TLENMAX/TWIDMAX)

Table IV-2 (continued).

Androecium	*STAMMNO (number of stamens), *STAMMAX (maximum length of stamens), STAMX (mean length of stamens), *FILWID (mean width of filaments), ANTHWID (mean width of anther), ANTHLEN (mean length of anther), *STAMEXSERT (proportion of stamen enclosed by perianth: PLENMAX/ STAMMAX)
Gynoecium	PISNO (number of pistils), PISLENMAX (maximum length of pistil), PISLENX (mean length of pistil), PISEXSERT (proportion of pistil enclosed by perianth: PLENMAX/ PISLENMAX), STYNO (number of styles), STYWID (mean width of style), STYLEN (mean length of style), OVWID (mean width of ovary), OVLEN (mean length of ovary)
Inflorescence	SPIKE, RACEME, PANICLE, IWIDMAX (maximum width of inflorescence), IWIDX (mean width of inflorescence), PEDMAX (maximum width of peduncle), PEDX (mean width of peduncle), PERMM2 (density of perianths: [number of perianths/mm] X IWIDMAX)

Table IV-3. Summary statistics for characters. See Table IV-2 for description of acronyms. s = standard deviation; C.V. = coefficient of variation (standard deviation/mean); "-" = value not appropriate; N1 = number of specimens with non-missing data; N2 = number of specimens with non-zero data (i.e., the trait is present).

Character	$\bar{x}$ (Mode)	s	C.V.	Min.	Max.	N1	N2
PCWID	0.79	0.41	0.52	0.12	1.70	29	-
PCLEN	7.92	6.80	0.86	0.61	33.90	29	-
PNOT	(0)	-	-	0	1	49	48
PWIDMAX	9.90	10.27	1.04	1.69	43.00	42	-
PWIDX	18.13	16.02	0.88	1.60	41.50	9	-
PLENMAX	5.23	3.64	0.70	1.69	19.46	29	-
PLENX	2.79	3.57	1.28	1.40	8.02	4	-
PSHAPE	1.02	0.68	0.67	0.50	3.62	27	-
PPART	(1)	-	-	0	1	40	38
CONWID	6.99	8.24	1.18	0.98	36.00	39	-
CONLEN	2.89	1.88	0.65	0.62	8.35	27	-
PCON	0.62	0.21	0.34	0.27	1.00	36	-
PACT	(1)	-	-	0	1	48	47
FWIDMAX	10.00	9.87	0.99	1.69	43.00	45	-
FWIDX	17.49	15.18	0.87	3.42	41.50	10	-
FLENMAX	6.26	3.66	0.58	1.69	19.46	31	-

Table IV-3 (continued)

Character	$\bar{x}$ (Mode)	s	C.V.	Min.	Max.	N1	N2
FLENX	3.93	3.57	0.91	1.40	8.02	3	-
FSHAPE	1.15	0.71	0.62	0.53	3.62	30	-
TNO	5.00	0.90	0.18	3	8	23	-
	(5)						
TWIDMAX	4.63	5.61	1.21	0.38	18.30	33	-
TWIDX	4.37	5.30	1.21	0.58	17.50	28	-
TLENMAX	7.21	5.82	0.81	1.69	21.90	42	-
TLENX	6.84	5.63	0.82	1.40	21.20	32	-
TSHAPE	2.92	1.95	0.67	1.00	9.64	33	-
STAMNO	9.39	4.71	0.50	4	17.00	18	-
	(5)						
STAMMAX	6.96	4.84	0.70	1.02	23.17	22	-
STAMX	5.73	3.47	0.61	1.04	16.76	18	-
FILWID	0.21	0.17	0.81	0.07	0.77	21	-
ANTHWID	0.31	0.19	0.61	0.15	0.77	11	-
ANTHLEN	1.29	0.82	0.64	0.40	3.51	12	-
STAMEXSER	0.70	0.37	0.53	0.29	1.61	17	-
PISNO	1.43	0.79	0.55	1	3	7	-
	(1)						
PISLENMAX	5.64	4.17	0.74	1.54	13.38	6	-
PISLENX	6.09	4.50	0.74	1.18	13.38	5	-
PISEXSER	34.50	-	-	-	-	1	-

Table IV-3 (continued)

Character	$\bar{x}$ (Mode)	s	C.V.	Min.	Max.	N1	N2
STYNO	1.29 (1)	1.13	0.88	1	2	6	-
STYWID	0.27	0.26	0.96	0.06	0.80	7	-
STYLEN	1.35	1.13	0.84	0.26	3.20	5	-
OVWID	1.30	0.53	0.41	0.53	1.71	5	-
OVLEN	2.58	1.40	0.54	1.20	4.93	5	-

Table IV-4. Parameters for cluster dendrograms. Specimen numbers are listed in Table IV-1 and acronyms for variables described in Table IV-2. T = variable transformed by division by PWIDMAX.

Variable	Dendrograms		
	PERI	AND	SHAPE
PNOT	X		X
PWIDMAX	X		X
PPART	X		X
CONWID			T
PCON	X		X
PACT	X		X
FWIDMAX	X		T
TWIDMAX			T
TLENMAX	X		
TSHAPE	X		X
STAMNO		X	
STAMMAX		X	
FILWID		X	
STAMEXSE		X	
Variables (N)	8	4	9
Specimens (N)	26	14	26

Table IV-5. Summary statistics for core groups identified in cluster analysis. For description of acronyms see Table IV-2. s = standard deviation; C. V. = coefficent of variation (s/x). Group 1 -- specimens 3-15-16-17-18; Group 4 -- specimens 13-23-26-28; Group 5 -- specimens 22-24-39-41; Groups 6 -- specimens 19-20-29-30-34-43-48. "-" = value not appropriate; empty cell indicates no data. Variables PNOT (0), PPART (1) and PACT (1) were invariable in all groups.

	Group 1				Group 4				Group 5				Group 6			
	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N
PCWID	-	-	-	0	0.74	0.30	0.41	4	1.31	0.39	0.30	4	0.65	0.23	0.35	4
PCLEN	-	-	-	0	7.14	2.38	0.33	4	14.04	13.53	0.96	4	8.47	5.90	0.70	4
PWIDMAX	33.32	7.18	0.22	5	4.13	0.68	0.16	4	6.35	1.72	0.27	4	5.81	2.46	0.42	7
PLENMAX	-	-	-	0	3.23	0.88	0.27	4	5.19	1.31	0.25	4	4.93	3.02	0.61	5
PSHAPE	-	-	-	0	0.78	0.10	0.13	4	0.85	0.23	0.27	4	0.79	0.17	0.22	5
PCON	0.77	0.05	0.64	5	0.74	0.07	0.09	4	0.51	0.09	0.18	4	0.37	0.08	0.22	7
FWIDMAX	33.32	7.18	0.22	5	4.34	0.55	0.13	4	6.80	2.47	0.36	4	6.05	2.34	0.39	7
FLENMAX	-	-	-	0	3.88	1.28	0.33	4	8.18	4.56	0.56	4	5.51	2.59	0.47	5
FSHAPE	-	-	-	0	0.89	0.21	0.24	4	1.35	1.06	0.79	4	0.87	0.14	0.16	5
	(5)	-	-	5	(3)		-	1	(5)	-	-	3	(5)	-	-	5

Table IV-5 (continued)

	Group 1				Group 4				Group 5				Group 6			
	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N
TWIDMAX	15.54	2.78	0.18	5	1.24	0.32	0.26	4	1.39	0.26	0.19	4	2.00	1.21	0.61	7
TLENMAX	18.94	2.67	0.14	5	3.26	0.87	0.27	4	5.43	1.10	0.20	4	4.34	2.82	0.65	7
TSHAPE	1.23	0.06	0.05	5	2.65	0.45	0.17	4	3.95	0.73	0.18	4	2.16	0.26	0.12	7
FILWID	-	-	-	0	0.15	0.08	0.53	2	0.31	-	-	1	0.13	0.06	0.46	3
STAMMAX	-	-	-	0	4.64	1.67	0.36	2	12.03	-	-	1	5.15	1.62	0.31	3
STAMNO	-	-	-	0	(5,9)	-	-	2	(9)	-	-	1	(7,10)	-	-	2
STAMEXSE	-	-	-	0	0.77	0.01	0.01	2	0.59	-	-	1	0.81	0.52	0.64	3

Table IV-6. Summary statistics for groups clustered according to androecial characters. For description of acronyms see Table IV-2. s = standard deviation; C. V. = coefficent of variation (s/x). Group A -- specimens 21-26-32-34-42; Group B -- specimens 28-29-39; Group C -- specimens 7-12-31-38-50. "-" = value not appropriate; empty cell indicates no data.

	Group A				Group B				Group C			
	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N	$\bar{x}$ (mode)	s	C.V.	N
FILWID	0.21	0.12	0.57	5	0.17	0.12	0.71	3	0.15	0.06	0.40	5
STAMMAX	6.13	2.19	0.36	5	[illegible]9	4.53	0.66	3	7.22	1.29	0.18	5
STAMEXSE	1.06	0.42	0.40	5	0.61	0.14	0.23	3	0.49	0.18	0.37	5
STAMNO	5.60 (6)	1.14	0.20	5	9.33 (9)	0.58	0.06	3	15.40 (17)	1.82	0.12	5

Table IV-7. Significance of differences in groups means for variables used in discriminant function analysis. See Table IV-2 for acronyms. Degrees of freedom = 3,16.

Variable	Wilks' Lambda	p
PWIDMAX	0.08	< 0.001
PCON	0.12	< 0.001
FWIDMAX	0.08	< 0.001
TLENMAX	0.09	< 0.001
TSHAPE	0.13	< 0.001

Table IV-8. Standardized canonical discriminant function coefficients. See Table IV-2 for acronyms.

Variable	Canonical discriminant function 1	2	3
PWIDMAX	0.79	-0.05	0.61
PCON	0.44	0.82	0.44
TSHAPE	-0.32	0.78	0.59

Table IV-9. Pearson correlation coefficients between variables and discriminant functions. See Table IV-2 for acronyms.

Variable	Canonical discriminant function		
	1	2	3
PWIDMAX	0.80	-0.12	0.59
FWIDMAX	0.78	-0.11	0.60
PCON	0.49	0.64	-0.59
TSHAPE	-0.47	0.60	0.65
TLENMAX	0.56	-0.01	0.60

Table IV-10. Flower form categories and summary of defining characters. Quantitative description is shown in brackets as a string of values for variables PWIDMAX-PSHAPE-TSHAPE-PCON (see Table IV-2 for acronyms); the values are means for groups identified in cluster analysis. Categories 1 - 6 correspond to groups 1 - 6 in perianth cluster analysis; category 9 corresponds to group C in gynoecial cluster analysis. n.d. = no data for the variable.

Category[a]	Description
1	large perianth with 5 broad tepals; highly connate; planar to dish-shaped (33.3 - n.d. - 1.2 - 0.8)
2	small bell-shaped perianth (stereomorphic); highly connate (2.7 - 1.8 - 6.7 - 0.9)
3	large perianth, moderate connation; 5 or 6 linear-lanceolate tepals; planar; pollen triporate, 22 m, exine nanoverrucate with gemmae (20.5 - n.d. - 2.7 - 0.7)
4	small bowl-shaped perianth; moderately connate, linear-lanceolate tepals (4.1 - 0.8 - 2.7 - 0.7)
5	bowl-shaped perianth, moderately connate; linear tepals; long pedicel (6.4 - 0.9 - 4.0 - 0.5)

Table IV-10 (continued)

Category[a]	Description
6	small, bowl-shaped perianth; linear-oval tepals with little connation (5.8 - 0.8 - 2.2 - 0.4)
7	large bowl-shaped perianth; little connation; linear tepals (9.2 - 0.8 - 9.6 - 0.4)
8	zygomorphic, highly stereomorphic perianth; linear tepals, low connation; 7 exserted stamens (5.4 - 3.6 - 6.1 - 0.4)
9	small reduced bowl-shaped perianth; highly connate; many stamens (mode = 17) with narrow filaments; stamens conspicuous, twice as long as perianth (5.4 - 0.7 - n.d. - 0.8)
10	perianth absent; anthers grouped, apical extensions to anthers, no anther filaments; pollen 21 m, perforate, scabrate, laminated nexine (n.d.)
11	highly connate perianth with sub-apical constriction and apical flare (4.5 - 2.2 - n.d. -0.9)

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a. Category 1 is composed of #3-14-15-16-17-18; category 2, #1-36; category 3, #6-8; category 4, #4-13-23-25-26-28-31-35-37-40-42-45-49; category 5, #22-24-32-39-41; category 6, #9-10-19-20-21-29-30-33-34-43-48; category 7, #27; category 8, #2; category 9, #7-12-31-38-50; category 10, #5; category 11, #11.

able IV-11. Summary of Paleocene and Eocene flowers from North America; specimens from the present study, except Pistillipollianthus wilsonii, are not included. Amentiferous inflorescenes and incontrovertably anemophilous flowers or inflorescences are excluded. The terms for floral symmetry: actinomorphic = radially symmetrical with no depth effect, stereomorphic = radially or bilaterally symmetrical with depth effect, zygomorphic = bilaterally symmetrical.

Specimen (Affinities)	Characteristics	Location (Citation)
Florissantia physalis (Malvales)	5-lobed corolla maximum 5.3 cm diameter reticulate petal venation actinomorphic	western North America (Manchester 1989)
Eoceltis dilcheri (Ulmaceae)	4 apopetalous tepals staminate, 15 stamens 9 mm diam stereomorphic	Claiborne Formation (Zavada & Crepet, 1981)
Acorites heeri (Berry) Crepet (Araceae)	spadix, 12mm long helically arranged florets	Claiborne Formation (Crepet 1978)
Protomimosoidea buchanenensis Crepet & Taylor (Leguminosae, Mimosoideae)	perianth 3.9 mm long X 1.3mm calyx connate in basal third 5 free petals 10 exserted stamens stereomorphic.	Claiborne Formation (Crepet and Taylor 1986)
Eoglandulosa warmanensis Taylor & Crepet (Malpighiaceae)	maximum 12.0 mm diameter 5 slightly connate sepals basal sepal glands petals clawed at base 10 stamens actinomorphic	Claiborne Formation (Taylor & Crepet 1987)
Androglandulosa tennessensis Taylor (Lauraceae)	maximum 5.2 mm diameter 6 tepals, basally connate short stamens ethereal oil cells, staminal glands actinomorphic	Claiborne Formation (Taylor 1988)

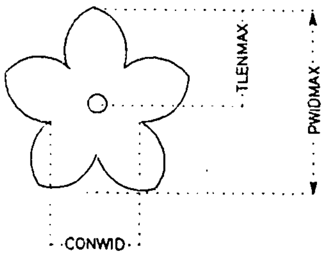
Table IV-11 (continued).

Specimen (Affinities)	Characteristics	Location (Citation)
Eomimosoidea plumosa (Leguminosae, Mimosoideae)	4-part cup-shaped corolla 2 mm long basal half connate 10 greatly exserted stamens	Claiborne Formation (Crepet & Dilcher 1977)
Hippomaneoidea warmanensis (Euphorbiaceae)	spike with cymules of 3-4 florets floret 3 mm X 2 mm 3-4 stamens/floret	Claiborne Formation (Crepet & Daghlian 1982)
undescribed (Leguminosae, Papilionoideae)	petals: standard, 2 wing, keel wing petals sculptured approximately 12 mm long zygomorphic	Paleocene/Eocene boundary (Crepet & Taylor 1985)
undescribed (?Gentianaceae)	7-lobed corolla 22 mm diam ?funnelform-salverform compressed ring of anthers *Pistillipollenites macgregorii* pollen	Wilcox Formation (Crepet and Daghlian 1981)
undescribed (Heliconiaceae)	zygomorphic	Claiborne Formation (Crepet 1984)
Crepet 1984; Figures 9,10	trumpet-shaped corollas approximately 12 mm long	Claiborne Formation (Crepet 1984)
Crepet 1979: Plates V,3; VI,1-3; VII,1	5-tepalled, large actinomorphic	Claiborne Formation (Crepet 1979)
Crepet 1979: Plates VII,3-5; VIII,1	small, low number of parts actinomorphic	Claiborne Formation (Crepet 1979)
Crepet 1979: Plate VIII,2	5 tepals approximately 6 mm diam bilaterally symmetrical, planar 2 anthers	Claiborne Formation (Crepet 1979)
Crepet 1979: Plate VIII,5	bell-shaped corolla approximately 9 mm long	Claiborne Formation (Crepet 1979)

Table IV-11 (continued).

Specimen (Affinities)	Characteristics	Location (Citation)
Princetonia allenbyensis	4 - 5 petals, 2 sepals flower 4.5 mm long X 4 mm 30+ stamens	Allenby Formation (Stockey 1987, Stockey and Pigg 1990)
Paleorosa similkameenensis (Rosaceae)	actinomorphic 5 sepals, 5 petals 7 - 19 stamens tricolporate striate pollen	Allenby Formation (Basinger 1976, Cevallos-Ferriz et al. 1990)
Pistillipollianthus wilsonii (Rosidae)	6 sepals 2.1 cm diam 6 anthers *Pistillipollenites* pollen actinomorphic	Horsefly beds (Stockey & Manchester 1988, Wing and Daghlian 1988)
Wehrwolfea striata	at least 3 sepals, up to 4 petals 3.0 - 4.5 mm long 10 stamens, anthers large interstaminary nectary disk pollen striate	Allenby Formation (Erwin and Stockey 1990)

Figure IV-1. Measuring protocol for flowers. See Table IV-2 for acronyms.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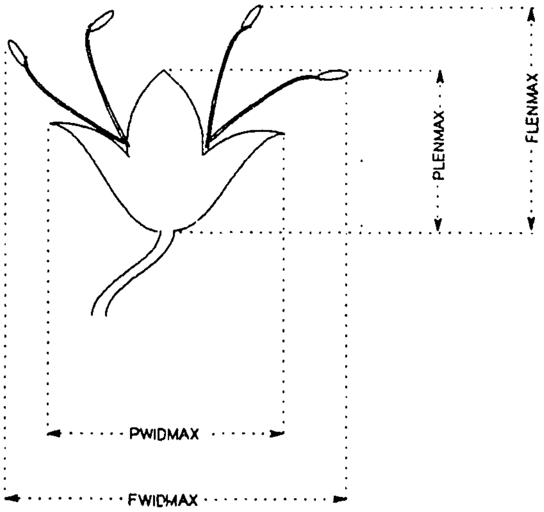
PWIDMAX
CONWID


PLENMAX
FLENMAX
PWIDMAX
FWIDMAX

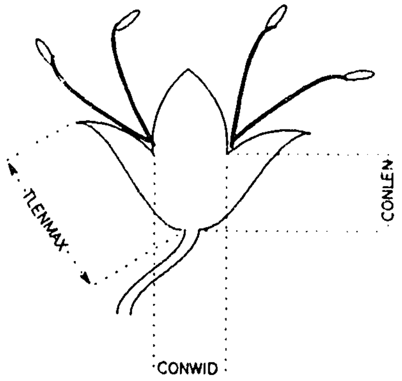

TLENMAX
CONLEN
CONWID

Figure IV-2. Cluster dendrogram based on perianth variables. Distance coefficient is based on average linkage between groups (UPGMA). Group 1 joins the larger cluster at a distance coefficient of 25.4 and specimen #2 joins at 61.9.

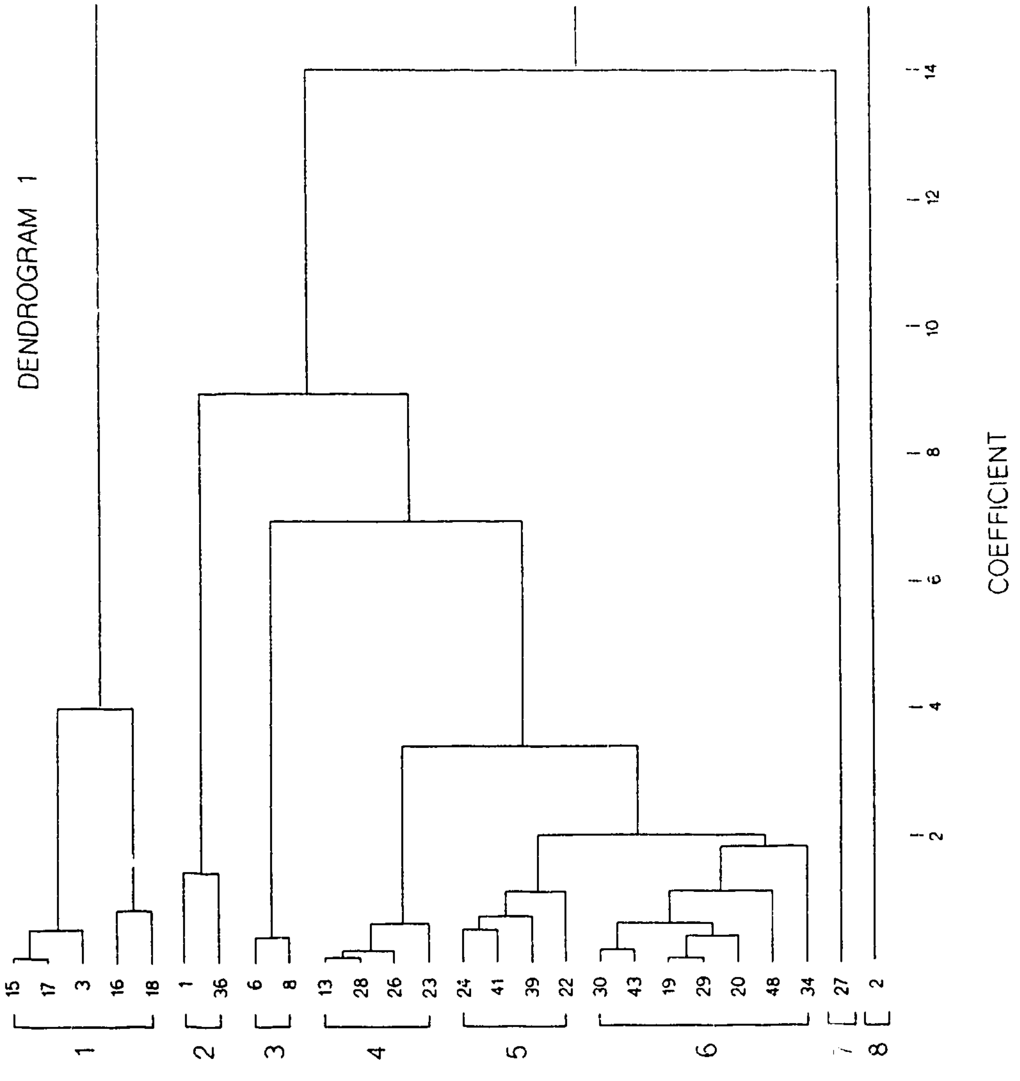
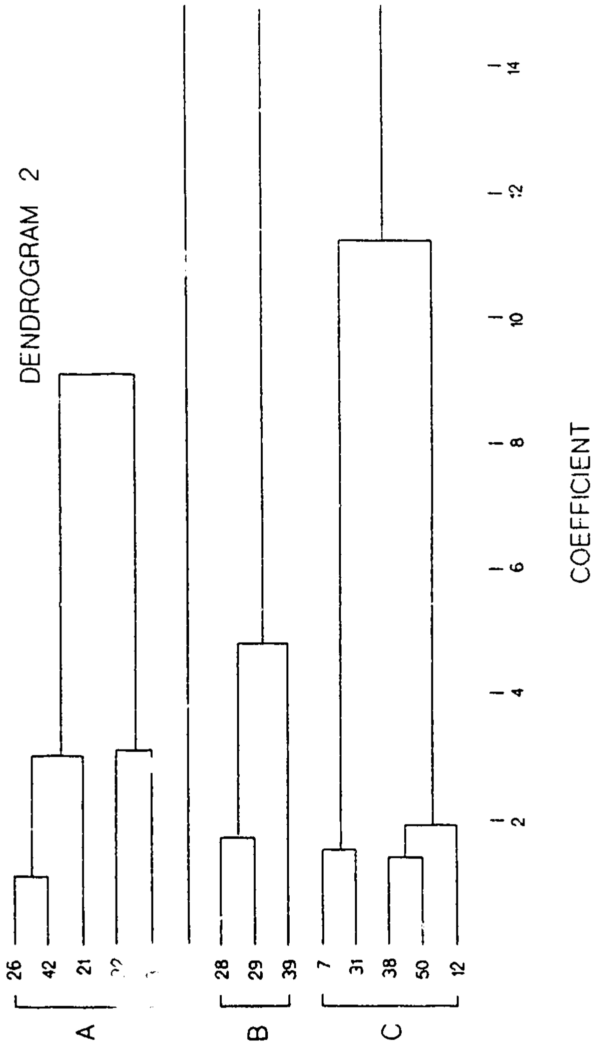

DENDROGRAM 1
COEFFICIENT
2
4
6
8
10
12
14
15
17
3
16
18
1
36
6
8
13
28
26
23
24
41
39
22
30
43
19
29
20
48
34
27
2
1
2
3
4
5
6
7
8

Figure IV-3. Cluster dendrogram based on androecial variables. Distance coefficient is based on average linkage between groups (UPGMA). Specimen #2 joins Group A at a distance coefficient of 17.3; Groups A + #2 and B join at 19.2, and Group C joins the larger cluster at 81.1.


DENDROGRAM 2
A
B
C
26
42
21
28
29
39
7
31
38
50
12
2
4
6
8
10
12
14
COEFFICIENT

FIGURES IV-4 to IV-9. Groups 1 - 4.

Figure IV-4. *Florissantia physalis* Knowlton, showing five broad, highly connate tepals; reproductive structures missing; Group 1; specimen #3 (PM 1721); Republic; X 2.

Figure IV-5. Small, stereomorphic, connate perianth of Group 2; specimen #36 (UWBM 39397); Republic; X 7.

Figure IV-6. *Pistillipollianthus wilsonii* Stockey with linear lanceolate tepals; Group 3; specimen #6 (UAPC S6557); Horsefly; X 3.4.

Figure IV-7. Connate, bowl-shaped perianth with at least 3 broad tepals; Group 4; specimen #23 (UWBM 36374); Republic; X 7.

Figure IV-8. Connate, cup-shaped perianth with 5 stamens; Group 3; specimen #26 (UWBM 36385); Republic; X 7.

Figure IV-9. Connate, cup-shaped perianth with 9 stamens; Group 3; specimen #28 (UWBM 36387); Republic; X 7.

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FIGURES IV-10 to IV-15. Groups 5 and 6.

Figure IV-10. Perianth with 5 tepals and single elongate style; Group 5; specimen #22 (UWBM 36371); Republic; X 7.

Figure IV-11. Robust, connate perianth of Group 5; specimen #24 (UWBM 36377); Republic; X 7.

Figure IV-12. Bowl-shaped flower with long pedicel, 5 tepals and 9 stamens; Group 5; specimen #39 (UWBM 56533); Republic; X 3.

Figure IV-13. Small 5-tepalled perianth; Group 5; specimen #19 (UAPC S26374); Republic; X 7.

Figure IV-14. Partially connate perianth with 5 tepals and 10 stamens; Group 6; specimen #29 (UWBM 36388); Republic; X 7.

Figure IV-15. Perianth with at least 4 broad tepals and tepal-like bract on pedicel; Group 6; specimen #43 (UWBM 56739); Republic; X 7.

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FIGURES IV-16 to IV-21. Groups 7 - 11.

Figure IV-16. Robust perianth with broad pedicel and 7 narrow tepals; Group 7; specimen #27 (UWBM 36386); Republic; X 7.

Figure IV-17. Raceme with staminate anther clusters; Group 10; specimen #5 (UAPC 5051); Horsefly; X 7.

Figure IV-18. Bowl-shaped perianth with at least 16 elongate stamens; Groups 9; specimen #50 (UWBM 74495); Republic; X 7.

Figure IV-19. Bowl-shaped, connate perianth with 17 elongate stamens; Groups 9; specimen #38 (UWBM 56531); Republic; X 7.

Figure IV-20. Stereomorphic corolla with sub-apical constriction and flared apex; Group 11; specimen #11 (UAPC S26358); Horsefly; X 6.

Figure IV-21. Zygomorphic, stereomorphic flower with 4 or 5 petals and 7 stamens; Group 8; specimen #2 (CMN PB000082); McAbee; X 3.5.

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Figure IV-22. Centroids for Groups 1, 4, 5 and 6 plotted against the first 3 discriminant functions.

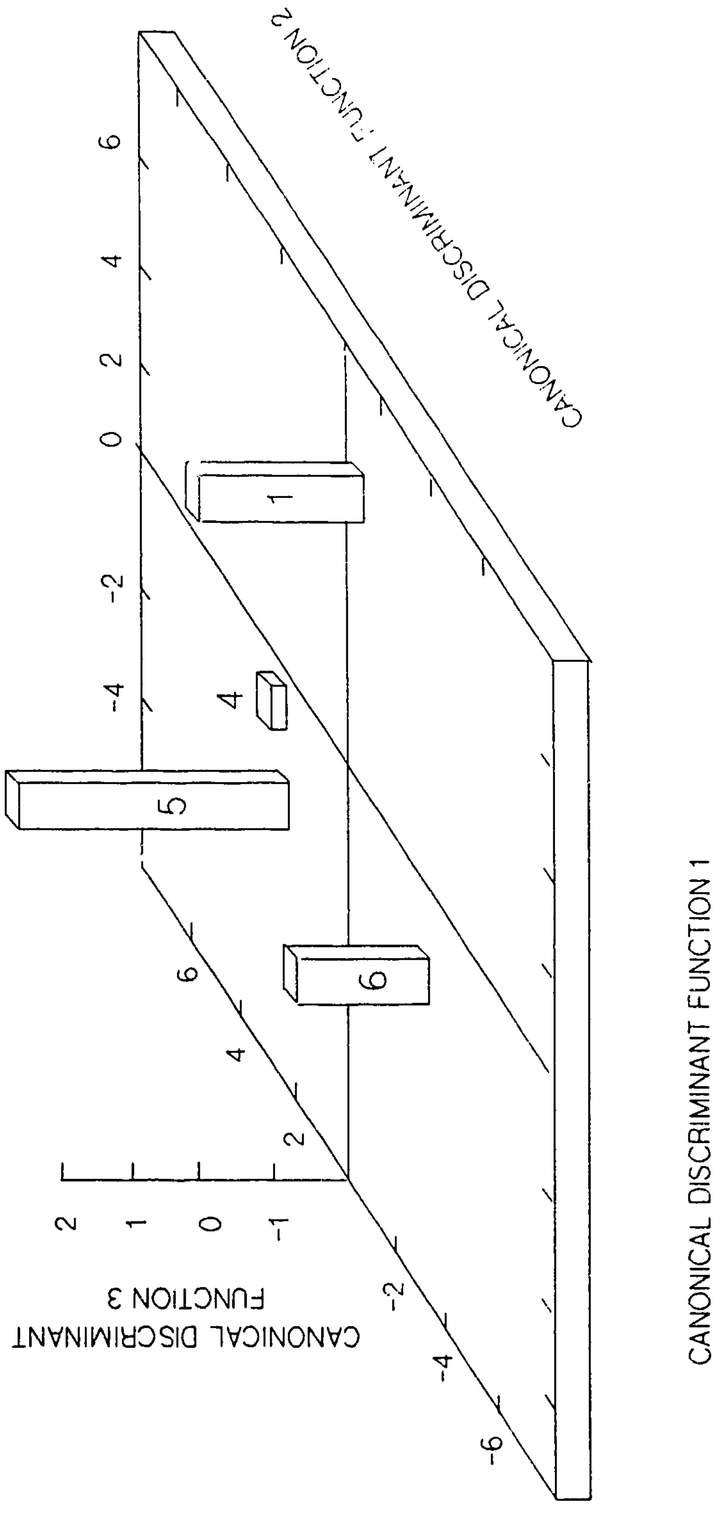
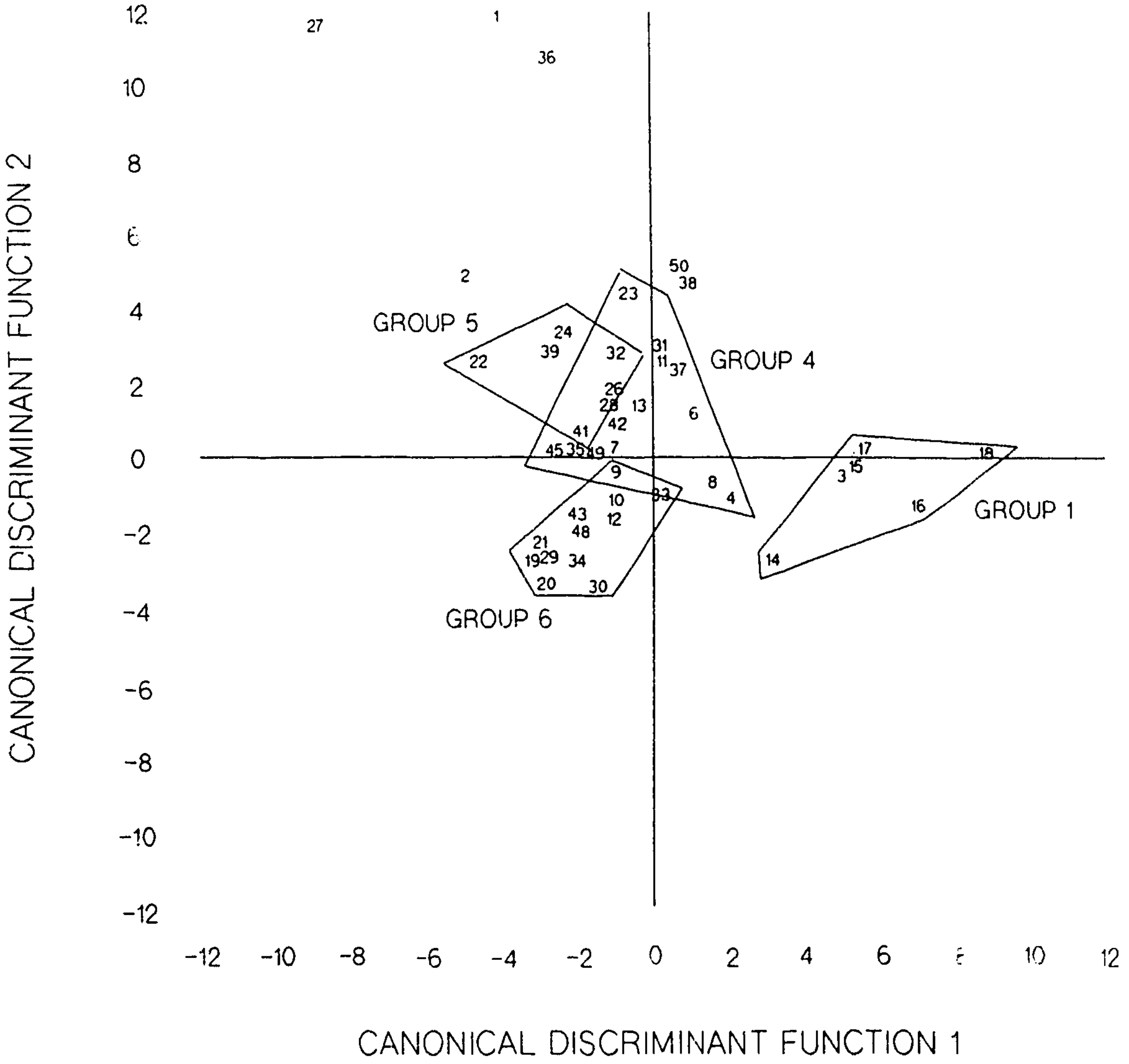

CANONICAL DISCRIMINANT FUNCTION 1
CANONICAL DISCRIMINANT FUNCTION 2
CANONICAL DISCRIMINANT FUNCTION 3
-6
-4
-2
0
2
4
6
-1
0
1
2
1
4
5
6

Figure IV-23. Specimens plotted against the first two discriminant functions. A solid line surrounds all specimens classified into a particular group and the group number is indicated.


CANONICAL DISCRIMINANT FUNCTION 2
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12
CANONICAL DISCRIMINANT FUNCTION 1
GROUP 5
GROUP 4
GROUP 1
GROUP 6
27
1
36
2
50
38
23
24
39
22
32
31
11
37
26
28
13
6
42
41
45
35
49
7
9
8
4
33
10
43
12
48
21
19
29
34
20
30
17
18
3
15
16
14

V. DIVERSITY OF INSECTS (COLEOPTERA, HYMENOPTERA, DIPTERA, LEPIDOPTERA) FROM THE MIDDLE EOCENE OF BRITISH COLUMBIA AND WASHINGTON WITH NEW RECORDS FOR FAMILIES.

INTRODUCTION

The Paleogene insect fauna of North America is known primarily from turn-of-the-century collections from the Green River Formation in Wyoming, Utah and Colorado (Late Early Eocene to Late Middle Eocene; Grande 1984) and the Florissant shales, Colorado (Early Oligocene; Leopold and MacGinitie 1972). The insect fauna of southern British Columbia (Middle Eocene; Wilson 1977a), although it has had a similarly long history of paleoentomological study (Scudder 1890, Handlirsch 1910, Rice 1959, Wilson 1977b), has yielded an insect fauna of much lower diversity than Green River. Collections from British Columbia show about one-third as many families as Green River; the Oligocene Florissant fauna is at least twice as diverse as that found at the Eocene localities (Wilson 1978). Paleoclimate differed between the two Eocene sites, with Green River subtropical (mean annual temperature 15° - 21° C) (Grande 1984) and the British Columbia region more temperate (mean annual temperature 12° - 13° C), being at a higher altitude as well as latitude (Wolfe and Wehr 1987). However, the extent to which differences in diversity between the two Eocene sites are a result of ecological factors cannot be addressed at this time; they may simply reflect differential collecting and classifying effort.

As part of a study on pollination in Middle Eocene angiosperms from north western North America, I examined fossil insects from four anthophilous (flower feeding) orders found at sites in British Columbia and Republic, Washington, a coeval locality in which the flora is well documented (Wolfe and Wehr 1987), but insect diversity unknown. I describe here taxonomic diversity of the sites at the family level, reviewing the important taxonomic characters for classifying fossil specimens. I summarize the stratigraphic history of the families reported and compare the insect fauna of British Columbia-Republic with that of other Paleogene localities in North America.

MATERIALS AND METHODS

Insect specimens from Middle Eocene localities in British Columbia and Washington State, preserved as compression/impression fossils, were obtained from the paleontology collections of the University of Alberta, Edmonton (UAPAL), the Thomas Burke Memorial Museum, University of Washington (UWBM), the Canadian Museum of Nature, Ottawa (CMN), Simon Fraser University, Vancouver and the Stonerose Interpretive Center, Republic, Washington (SR). Specimens belonged primarily to the orders of insects recognized as having important pollinating taxa (Coleoptera, Hymenoptera, Diptera, Lepidoptera), although those of initial uncertain identity were included for identification. Lithology, age and geographic location of sites are given in Chapter II. The number of specimens from each of the localities are: Republic (64), Driftwood Creek (72), Quilchena (55), Horsefly (51), One Mile Creek (18), Tulameen Road (8), Princeton Firehall (4), McAbee (14) and China Creek (6). The localities are approximately contemporaneous and are part of a series of lacustrine deposits distributed through central and southern British Columbia and northeastern Washington state.

Specimens were examined with a Wild M5 dissecting microscope; camera lucida drawings were made of all specimens. Distilled water was pipetted onto some of the specimens in a thin layer to emphasize cuticular parts that were obscured slightly by matrix.

Taxonomic characters

Specimens were classified initially to order (following Boudreaux 1979) and those in anthophilous orders were identified to superfamily and family where possible, using Dillon and Dillon (1961), Holland (1968), Borror et al. (1976), Richards and Davies (1977), Daly et al. (1978), Hutson et al. (1980), Day et al. (1981), McAlpine et al. (1981), Freeman (1983), Yeo and Corbet (1983), Covell (1984), Jessop (1986), McAlpine (1987), Day (1988) and Gauld and Bolton (1988). Only rarely was it possible to use standard taxonomic keys. For Hymenoptera, Diptera and Lepidoptera, identification relied heavily on wing venation patterns.

For Coleoptera, classification followed Borror et al. (1976). About half of the specimens were single or paired elytra and could not be determined to family or lower taxonomic level. Even in more complete specimens, important characters such as sternite structure, coxal attachment and number and shape of tarsal segments were preserved in few specimens. Family determination was made using characters such as antennal structure, conspicuousness of mandibles and relative size and shape of the head, pronotum, scutellum and elytra.

Hymenoptera classification follows Gauld and Bolton (1988) for the Symphyta and the parasitic Apocrita, and Daly et al. (1978) for the aculeate Apocrita. Characteristics important in identifying families within Hymenoptera were: antennal form, abdomen or alitrunk structure and shape, ovipositor presence and length, presence of hairs, leg structure (length and shape) and wing venation. Although venation could be used to distinguish some of the major groups (Symphyta, Ichneumonoidea, Formicidae, Cynipoidea) in which vein pattern and number is distinct, in the higher aculeates, there are many similarities, enough that family distinction is difficult with even slight diagenetic change. Terms for wing venation are given in Gauld and Bolton (1988).

Classification of Diptera follows McAlpine et al. (1981) and McAlpine (1987), recognizing two suborders, Nematocera and Brachycera. In the fossils, Nematocera and Brachycera were separated primarily on the basis of antennal structure. Wing venation was the most important character used and was the structure most often well-preserved. Terms for wing venation are those of McAlpine et al. (1981).

For specimens of Lepidoptera, classification and wing venation terms follow Borror et al. (1976). Only two definitive lepidopteran specimens were present in the sample. One of them, a wing fragment, was identified by venation pattern and the second, a relatively complete specimen, by characters such as distribution of hairs and scales and length and structure of the proboscis and labial palpi.

Stratigraphic occurrence of families in the four orders was surveyed using primary sources and, where appropriate, previously compiled records. The summary by Handlirsch (1908) was used for many European records previous to 1900; Wilson (1978) was used for North American Oligocene localities and Larsson (1978) for specimens in Baltic amber.

RESULTS AND DISCUSSION

Of the 292 specimens examined, there were 55 beetles, 63 wasps, 118 flies and 2 moths (Table V-1). Seven orders of insects were represented in the 54 remaining specimens. Appendix 4 lists taxonomic position and localities for all specimens. Among the Coleoptera, 18 of the specimens were classified at the family or superfamily level. Twenty-three of the specimens were single or paired elytra and no identification was possible; an additional 14 specimens could not be identified to a lower taxon.

Of the Hymenoptera, 40 were identifiable to family or superfamily. Four specimens could be identified only as aculeate apocritans. Eleven could not be identified to a taxon lower than Apocrita and in eight specimens, no identification beyond hymenopteran was possible.

During initial sorting of specimens from UAPAL, many insects that belonged to the easily identifiable dipteran family Bibionidae were not included in the sample. This has resulted in the numbers of Bibionidae and the numbers of Diptera in the sample being an underestimate. Seventy-seven specimens were classified at the family or superfamily level. There were 14 unidentifiable nematocerans and 3 unidentifiable brachycerans; 24 specimens could not be classified into a category lower than Diptera.

Taxonomic treatment

Order COLEOPTERA

Suborder Adephaga

Family Cicindelidae (Figure V-1)

Specimen: UAPAL 4523

Locality: One Mile Creek

Description: The specimen consists of the elytra, base of the abdomen, the right metathoracic leg, pronotum, head and mandibles; the remaining legs and the antennae are not present. The specimen is 10.0 mm long and 4.2 mm at the widest point of the elytra. The cuticle is well-preserved and is yellow-brown with patches of black, indicating that a colour pattern was present in the living insect. The metathoracic leg has an oval femur and slender tibia. Elytra are narrow and pointed apically (width/length ratio of elytron = 0.3), not fused and are 62% of the body length. Sculpturing is absent from the elytra as well as the rest of the body parts. The scutellum is triangular; the pronotum is slightly narrower than the elytra, broader than long, with arcuate lateral margins. The head is as wide as the pronotum; it has large lateral eyes and broad arcuate mandibles approximately 0.5 mm long.

Relationships: Arcuate mandibles are characteristic of Carabidae, rather than Cicindelidae, in which mandibles are usually sickle-shaped. However, the prominent head and eyes, probable colour pattern and lack of striae or other sculpturing on the elytra are more characteristic of Cicindelidae. The characters that distinguish the two families (shape of the clypeus and insertion of antennae) are not visible on the specimen.

Family Carabidae (Figure V-2)

Specimen: UWBM 57098

Locality: Republic

Description: The specimen (13.0 mm long and 5.3 mm wide) consists of the dorsal surface of the elytra, pronotum, head with mandibles and right antenna, and at least one of each of the pairs of legs. The femora are oval and the tibiae narrow. The elytra are slightly pointed apically, not fused at their inner margins and have widely spaced longitudinally striae (about 8 per elytron); the elytron width/length ratio is 0.34. The scutellum is small. The pronotum is narrower than the elytra, approximately square, but is constricted at its base and has sinuous lateral margins. The head is prominent, broadly attached at its posterior margin and narrower than the pronotum. The prominent mandibles are broad, arcuate, and 0.8 mm long. The filiform antenna is linear and at least 4.3 mm long.

Relationships: The specimen is classified with the Carabidae because of the combination of large arcuate mandibles, striate elytra, filiform antenna and the relative size and shape of the pronotum and head.

Family Dytiscidae (Figure V-3)

Specimen: UWBM 72302 A&B

Locality: Republic

Description: The elytra, scutellum and all three pairs of legs are present; structures anterior of the elytra are missing from the specimen (incomplete length = 15.4 mm; width = 7.52 mm). Preservation is good, with part A showing some ventral morphology, although the coxal insertion is difficult to observe. The metathoracic legs have long distal processes (either tibial spines or tarsal segments) with a fringe of fine hairs attached to the inner surfaces. The mesothoracic tibiae have longitudinal rows of cuticular bases for insertion of setae. The elytra (elytron width/length ratio = 0.36) are posteriorly truncate, exposing 2 abdominal segments. There is no apparent sculpturing or colour patterns on the elytra. The specimen has a large semi-circular scutellum.

Relationships: I have classified the specimen as Dytiscidae on the basis of the metathoracic legs, presumably an adaptation for swimming locomotion. Some Hydrophilidae closely resemble Dytiscidae; the characteristics that distinguish the two families (antennal structure, labial palpi length) are not present on the specimen. However, the specimen lacks a metasternal spine that is frequent in taxa of Hydrophilidae. Truncate elytra, as shown by this specimen, are not present in common extant taxa of Dytiscidae. The enigmatic structure of the metathoracic legs warrants examination by specialists in aquatic coleopterans.

Suborder Polyphaga

Superfamily Scarabaeoidea (Figure V-4)

Specimen: UAPAL 4635 A&B

Locality: Quilchena

Description: The specimen shows ventral abdominal and thoracic structures, including coxal insertion, the dorsal pronotum and the right prothoracic tibia. The head and its appendages, most of the legs and any elytron patterning are absent or not visible. Length of the incomplete specimen is 8.6 mm and width is 5.0 mm. The protibia is fossorial, broad with a scalloped margin. The elytra (elytron width/length ratio = 0.41) extend past the posterior tip of the abdomen. No scutellum is visible. The pronotum is posteriorally as broad as the elytra and narrows anteriorly; it is extended into blunt points posterio-laterally.

Relationships: The fossorial protibia identify the specimen as scarabaeoid, however it cannot be assigned to a family since the character used to distinguish families (antennal structure) is absent. The meso- and metathoracic legs are widely separated, typical of dung-feeding (rather than plant-feeding) Scarabaeidae.

Family Lucanidae (Figure V-5)

Specimen: UWBM 57118

Locality: Republic

Description: The ventral surface of the specimen is well preserved except for the metasternal area; morphology of the elytra and prothoracic legs is not visible. The specimen is 15.0 mm long and 4.6 mm wide. The elytra are marginally longer than the abdomen; elytron width/length ratio is 3.0. The pronotum is as wide as the elytra and narrows anteriorly. The prominent square head is narrower than the anterior pronotum with no constriction ("neck"). Mandibles are large, broad, arcuate and 0.8 mm long; 1 mm long palpi are arched inward. The lamellate antennae are 10-segmented, with the three distal lamellae widely separated.

Relationships: The combination of antennal and mandible morphology identify the specimen as belonging to the Lucanidae.

Family Elateridae (Figure V-6)

Specimen: UWBM 57095

Locality: One Mile Creek

Description: The dorsal surface of the elytra, pronotum and head and most of the legs and part of the antennae are present. The specimen (11.7 mm long and 3.3 mm wide) is all black. All leg segments are slender. The elytra are narrow (elytron width/length ratio is 0.23) and pointed apically, with longitudinal striae; they occupy 65% of the body length. The rectangular pronotum is narrower than the elytra, with the posterior lateral corners prolonged into blunt spines. The head is narrower than the pronotum and small compound eyes are visible laterally.

Relationships: The configuration of the pronotum best identifies the specimen as Elateridae.

Family Cantharidae (Figure V-7)

Specimen: UAPAL 4513

Locality: One Mile Creek

Description: The dorsal surface of most of the specimen is preserved, although the head and its appendages are not complete. The incomplete length is 11.7 mm and the width is 3.5 mm. The femora are light brown, and oval and the tibiae and tarsi are slender. The elytra (elytron width/length ratio = 0.21) have squared posterior margins and parallel sides and comprise 74% of the body length. The pronotum is square, narrower than the elytra, and coloured light brown in contrast to the elytra which are melanic. The head is broad and prominent, slightly narrower than the pronotum, with a probably forward protruding clypeus; some structural colour (iridescence) is evident on the head. The filiform antenna is 3.3 mm long.

Relationships: On the basis of the relative shape and size of the head, pronotum and elytra, the filiform antenna, and the differential coloration of the dorsal body parts, the specimen is included in the Cantharidae.

Family Cleridae (Figure V-8)

Specimen: UAPAL 4632 A&B

Locality: Quilchena

Description: The dorsal surface of the specimen (elytra, several abdominal segments, pronotum and the pro- and mesothoracic tibiae and tarsi) is preserved in part A, while the counterpart shows the ventral surface (sternites, metasternum and prosternum). The head and its appendages and the metathoracic legs are missing. The specimen has an incomplete length of 31.7 mm and a width of 14.5 mm. UAPAL 4632 was one of the few Coleoptera in which tarsal segments were well preserved: the tarsal pattern was 5-5-5 on the pro- and mesothoracic legs (metatarsi not visible). The tarsal segments are deeply lobed and each has a semicircular pad (that may be finely hairy) extending distally and between the lobes. All five tarsomeres are conspicuous and tarsal claws are present. The pronotum and elytra retain some of their original orange colour and are patterned with numerous closely spaced tubercles. The elytra are apically rounded (elytron width/length ratio 0.26); a scutellum is absent or not visible. The pronotum is as wide as the elytra, and is probably square or broadly oval.

Relationships: Based primarily on tarsal structure, the specimen was determined in the family Cleridae. The specimen is not, however, hairy, a characteristic of many clerids.

Family ?Mordellidae (Figure V-9)

Specimen: UAPAL 4551 A&B

Locality: Horsefly

Description: The specimen is oriented laterally on the plane of cleavage; although preservation is not excellent, the elytra, pronotum, head, antennae and legs are visible. The specimen is 8.2 mm long. The elytra, which occupy 70% of the body length, are covered in hairs and pointed apically. The abdomen ends in a blunt point and does not extend past the apices of the elytra. The sternites are expanded laterally, making the abdomen prominent in lateral view. The pronotum appears to be as broad as the elytra bases, square, and a lighter color than the elytra and head. The filiform antennae have >9 segments; the apical segment may be pointed.

Relationships: All of these characteristics are found in mordellids; many taxa in the family, however, have a diagnostic conical abdomen which extends posteriorly past the elytra, a characteristic not present in the specimen. The specimen is large in comparison to most extant mordellids. The specimen is tentatively placed in the Mordellidae based primarily on the fusiform body shape and its lateral orientation; the morphology of other visible parts does not contradict this designation.

Superfamily ?Chrysomeloidea (not illustrated)

Specimens: UAPAL 4511, UAPAL 4628

Locality: One Mile Creek, Quilchena

Description: Specimen UAPAL 4511 (3.7 mm long and 1.8 mm wide) is represented by the elytra, pronotum, antennae and part of the metathoracic leg. The elytra are broad (elytron width/length ratio = 0.41) and apically rounded. The pronotum is slightly narrower than the elytra, square with arcuate margins. The head is narrower than the pronotum and protrudes anterior to the insertion of the antennae. The antennae are probably 11 segmented, serrate to slightly clavate and about 1 mm long. Specimen UAPAL 4628 (13.9 mm long and 5.0 mm wide) is composed of the elytra, pronotum, head, part of an antenna, and parts of the metathoracic legs. The elytra are narrow (elytron width/length ratio = 0.26), pointed apically, with both striae and small punctae. The pronotum is narrower than the elytra and the head narrower than the pronotum, extending anteriorly past the antennal insertion. Antennae are slender (segment type is not discernible) and extend posterior to the pronotum (incomplete antenna is 5.7 mm long).

Relationships: In general morphology (shape and relative sizes of elytra, pronotum and head; antenna shape and length), the two specimens are similar to taxa in the Chrysomeloidea; preservation of important characters is too poor to give more than a tentative classification.

Family Cerambycidae (Figure V-10, V-11)

Specimens: UAPAL 4626 A&B, UWBM 57097 A&B

Locality: Quilchena, Republic

Description: The dorsal surface of UAPAL 4626 (elytra, pronotum, part of the head, left antennae) (Figure V-10) is present, although preservation is poor and the elytra are partly disarticulated. The incomplete length of the body is 9.0 mm and the width 4.0 mm. The elytra (elytron width/length ratio = 0.35) are rounded apically and have long scattered hairs. The pronotum is twice as broad as long and is as broad as the elytra bases, narrowing anteriorly. The head is prominent, with laterally projecting compound eyes; it is as wide as the anterior pronotum and extends anteriorly of the insertion of the antenna. The antennae are long (incomplete length = 10 mm) and filiform, extending past the posterior margin of the elytra.

The elytra, pronotum, part of the head and the antennae of UWBM 57097 (Figure V-11) are present, but preservation of morphological detail is poor. The specimen is 12.7 mm long and 5.7 mm wide. The elytra (elytron width/length ratio = 0.32) comprise 70% of the body length. They are broadly pointed posteriorly and patterned with bands of dense pubescence and longitudinal cuticular striations. The pronotum is as wide as the elytra, square and shield-like: the impression of a more narrow structure (posterior head?) is visible in the centre of the "shield". The head is conspicuous, narrower than the pronotum, with a process extending anterior to the antennal insertions. The antennae are serrate with elongate segments, the first or second segment about twice as long as more distal ones. There is a minimum of eight segments.

Relationships: UAPAL 4626 is classified as Cerambycidae primarily by antennal structure and length. In UWBM 57097, hairy patterned elytra, long serrate antennae and the relative size and shape of the pronotum and head are the characters used to classify the specimen in the Cerambycidae.

Family Curculionidae (Figure V-12)

Specimens: UAPAL 4532, UAPAL 4562, UAPAL 4578, UWBM 57096, UWBM 72299 A&B

Localities: Horsefly, Republic

Description: UWBM 72299 (Figure V-12) shows the legs, abdomen, elytra, pronotum and head and snout and parts of the antennae. The specimen is 6.3 mm long; elytra are 5.0 mm long and have longitudinal rows of tubercles. The head and snout are 2.3 mm long, the snout is robust (about 0.4 mm wide), slightly curved and oriented at right angles to the body. Specimen UWBM 57096 (not illustrated) shows a lateral view of the legs, abdomen, elytra, pronotum and head and snout; antennae are not visible. The specimen is 12.5 mm long; the elytra are 8.9 mm long and have longitudinal rows of punctae. The head and snout are 5.3 mm long, the snout robust and broad (about 1 mm wide), oriented at right angles to the body and relatively straight. Specimen UAPAL 4532 (not illustrated) is preserved in lateral view, with legs, elytra, pronotum and head present; the snout and antennae are poorly preserved. The specimen is 6.5 mm long and the elytra have longitudinal rows of punctae. The orientation of the head indicates that the snout projected ventrally. The legs, elytra, pronotum and head of UAPAL 4578 (not illustrated) are preserved in lateral view; the head and snout are missing. The specimen is 4.7 mm long and has the elytra and pronotum covered with tubercles. Preservation of the snout is poor, but it appears to be curved and projected ventrally. UAPAL 4562 (not illustrated) is poorly preserved, with only the elytra, pronotum and head present. The specimen is 7.1 mm long. The snout is probably incomplete and may be projected forward.

Relationships: On the basis of the presence and orientation of the snout and the general form of the body, specimens UWBM 72299, UWBM 57096, UAPAL 4532 and UAPAL 4578 are classified as curculionids. The possibility that UAPAL 4522 belongs to the Brentidae cannot be eliminated.

Order HYMENOPTERA

Suborder Symphyta

Family Tenthredinidae (Figure V-17)

Specimen: UAPAL 4500

Locality: Horsefly

Description and relationships: The family is represented by an isolated fore wing with venation typical of Tenthredinidae: a narrow costal cell, not divided by a longitudinal intercostal vein, four submarginal cells and two marginal cells (some tenthredinids have one marginal cell). Abbreviations for wing venation terminology are listed in Table V-2.

Families Argidae or Diprionidae (Figure V-18)

Specimens: UAPAL 4545, UAPAL 4548

Locality: Horsefly

Description and relationships: Specimens UAPAL 4548 (Figure V-18A) and UAPAL 4545 (Figure V-18B) each consist of well-preserved wings and an indistinct thorax. The large marginal cell, created by the absence of

2r-rs, identifies them as either Argidae or Diprionidae; morphology of the other body parts is insufficient for a more definitive classification.

Suborder Apocrita

Family Cynipidae (Figure V-19)

Specimens: UAPAL 4556, UAPAL 4581

Locality: Horsefly, Quilchena

Description: Specimen UAPAL 4556 (Figure V-19A) has both wings present and a poorly preserved body. Some iridescence is evident in the head region. The wings are incomplete in length and width, with a wing length of 4.5 mm, and are covered in fine hairs. UAPAL 4581 (Figure V-19B) as well has only fragments of the body preserved, with one incomplete wing (5.5 mm long) sparsely covered in hairs. In both specimens, vein Rs+M arises near the centre of the vein connecting R+Rs and M+Cul. This is the case only in Cynipidae and Charipidae. Since extant Cynipidae have a forewing length of 2-5 mm and Charipidae are smaller, the two specimens are designated as Cynipidae.

Superfamily Ichneumonoidea (Figure V-20)

Specimens: UAPAL 4603, UAPAL 4609, SFU 175, UWBM 179, UAPAL 5089, UAPAL 5200, UWBM 57113, UWBM 57116

Locality: Quilchena, Republic, Driftwood

Description and relationships: UAPAL 4603 (Figure V-20A) is an isolated wing; the other specimens have body parts, ranging from fragments to whole insects (e.g. UWBM 57116). The obliteration of the costal cell by fusion of vein C with vein Sc+R+Rs is an apomorphic character of

Ichneumonoidea. Specimens included here were those in which distinction between Ichneumonidae and Braconidae (see character definition under Ichneumonidae) could not be made. Hind wings were rarely preserved and were not used in identification. However, in more complete specimens, details of the antennae and presence of the ovipositor were useful in classification to the superfamily.

Family Ichneumonidae (Figure V-21)

Specimens: UAPAL 4507, UAPAL 4549, UAPAL 4580, UAPAL 4599, UAPAL 4606, UAPAL 5069, UAPAL 5093, UAPAL 5109, UAPAL 5146, UAPAL 5189, UAPAL 5714, UAPAL [illegible] UWBM 57112, UWBM 57122-A, UWBM 72311-B, CMN I00084, CMN I00092

Locality: Horsefly, Quilchena, China Creek, Driftwood, Republic, McAbee

Description and relationships: Most of the specimens were isolated fore wings, or wings with poor preservation of body parts. In only a few specimens were antennae, ovipositors or other body parts preserved (UAPAL 4507, UAPAL 5069, UAPAL 5093, UAPAL 5109, CMN I00084, CMN I00092). There are characteristics that separate Ichneumonidae from Braconidae in most taxa (Gauld and Bolton 1988): in Ichneumonidae, vein 2m-cu is usually present, the first discal cell and the first submarginal cell are confluent and an areolet (submarginal cell) is usually present. In Braconidae, vein 2m-cu is absent and the first discal and first submarginal cell are sometimes separated by a distinct vein. However, the only character that is definitive for Ichneumonidae is the presence of 2m-cu. (Similarly, the only definitive character for Braconidae is the separation of the first discal and submarginal cells).

Most specimens had confluent discal and submarginal cells in addition to the diagnostic vein 2m-cu; many had an areolet.

Family Scoliidae (Figures V-13 and V-22)

Specimen: UAPAL 4524

Locality: Tulameen Road

Description: Specimen UAPAL 4524 consists of a thorax, alitrunk, one prothoracic, one mesothoracic leg and both metathoracic legs. The fore wings from the base to distad of the pterostigma are present; the hind wings are present but venation is obscured by matrix. The head and its appendages and the distal half of the fore wings are missing. The specimen is 10.7 mm long; alitrunk length is 8.3 mm and width is 3.7 mm. The mesothoracic tibia is oval and the tarsi are slender on all legs. The metathoracic legs are long, almost as long as the apex of the alitrunk. Although fine detail is not preserved, there appear to be a few spines on the legs and the alitrunk and thorax appear to be glabrous. Basal wing venation is well preserved (Figure V-22): the costal cell is present as is a pterostigma. The specimen shows two submarginal cells (a third SMC may have been present) that are elongate parallel to the anterior wing margin. Vein 1m-cu terminates in the middle of the second submarginal cell. The basal vein (M) is strongly arched and vein cu-a is confluent with the basal vein and is angled distally.

Relationships: Although none of the wing characteristics are sufficient in themselves to specify a family, the orientation of the submarginal cells and the position of the first discal cell in relation to them is similar to wing venation in the Scoliidae. (The arched basal vein, paradoxically, is characteristic of the Halictidae.) Characteristic of the wings of Scoliidae is fine wrinkling distally; this part of the wings is missing in the specimen.

Extant scoliids are tropical to warm temperate in distribution (Gauld and Bolton 1988). Females are fossorial parasitoids of larvae of Scarabaeoidea (Day et al. 1981); males are less armed with spines.

Family Pompilidae (Figures V-14 and V-23)

Specimen: CMN I00040

Locality: McAbee

Description: Specimen CMN I00040 has a dorsal-lateral orientation with good preservation of the fore wings, thorax, propodeum, mesopleuron, and alitrunk, as well as the right meso- and metathoracic legs and one of the left legs. Notably, the head and its appendages are missing. The specimen is 12.5 mm long; the alitrunk, which is probably incomplete posteriorly, is 6.6 mm. Thoracic preservation is good, with the propodeum, scutellum and mesoscutum discernible. A faint transverse line on the mesopleuron may be the episternal groove, a character diagnostic of the Pompilidae. The body is glabrous. The right mesothoracic leg (coxa + trochanter + femur + tibia + first tarsomere) is 12.5 mm long and the right metathoracic leg (coxa + trochanter + femur + incomplete tibia) is 11.2 mm long. Pompilidae have characteristically long legs. Trochanters are large and there are two long tibial spurs on the mesothoracic leg. Fore wing venation is relatively complete (Figure V-23); the length of the right wing is 13.4 mm. There are 10 closed cells and a marked pterostigma. The costal cell is present and there are three submarginal cells. The basal vein is relatively arched and vein 2m-cu is sigmoid.

Relationships: The shape, orientation and number of cells is consistent with that of extant Pompilidae. Wing venation in the family is relatively invariable (Day 1988). Vein cu-a is postfurcal (distad of the separation of M and Cu), a character found in the subfamily Pepsinae. The specimen is unlikely to belong to the Pompilinae, since this group shows a deflection of Cu1 where it branches from Cu2 (forming a "pocket"), a character not seen in the fossil specimen. Further taxonomic work on this specimen by specialists in the family is warranted. The Pompilidae are predominantly tropical; the females actively hunt and paralyse spiders as hosts for their young and require a high ambient temperature for movement (Day 1988).

Family Formicidae (Figures V-15 and V-24)

Specimens: UAPAL 4542, UAPAL 4557, UAPAL 4558, UAPAL 4616, UAPAL 4582, UAPAL 4604, UAPAL 4610, UWBM 178

Locality: Horsefly, Quilchena, Republic

Description and relationships: Both winged and apterous specimens are present. Apterous forms were identified by the presence of a node on the pedicel and/or elbowed antennae. Winged forms had characteristically few closed cells in the fore wings, one submarginal cell and a usually reduced first discal cell. Vein cu-a arises from the basal half of the basal cell.

Order DIPTERA

Suborder Nematocera

Family Tipulidae (Figure V-25)

Specimens: UAPAL 4527, UAPAL 4530, UAPAL 4566, UAPAL 6125

Localities: Horsefly, Republic, Driftwood, Tulameen Road

Description and relationships: UAPAL 4566 is identified as Tipulidae by the long, slender legs. UAPAL 4527 consists of thorax, abdomen, partial head and most of the right wing; UAPAL 4530 (Figure V-25) is an isolated wing. The two latter specimens have the two anal veins characteristic of Tipulidae; CuA is shortened at its branching into CuA_1 and CuA_2, a characteristic of Tipulinae (Alexander and Byers 1981). In specimen UAPAL 6125, the presence of two anal veins cannot be determined since the posterior portion of the wing is missing. Configuration of the other veins indicates that it probably belongs to Tipulidae, as well.

Family Bibionidae (Figure V-26)

Specimens: UAPAL 4501, UAPAL 4502, UAPAL 4503, UAPAL 4504, UAPAL 4510, UAPAL 4540, UAPAL 4564, UAPAL 4573, UAPAL 4638, UAPAL 4640, UAPAL 4642, UAPAL 4647, UAPAL 5021-A, UAPAL 5021-B, UAPAL 5080, UAPAL 5084, UAPAL 5088, UAPAL 5090, UAPAL 5094, UAPAL 5097, UAPAL 5102, UAPAL 5123, UAPAL 5132, UAPAL 5140, UAPAL 5151, UAPAL 5159, UAPAL 5169, UAPAL 5179, UAPAL 5180, UAPAL 5204, UAPAL 5207, UAPAL 5208, UAPAL 5211, UAPAL 5222, UAPAL 5452, UAPAL 5468, UAPAL 5470, UAPAL 5479, UAPAL 5648, UWBM 57115-A, UWBM 57120, UWBM 57122-B, UWBM 57112-C, UWBM 57122-D, CMN I00013, CMN I00024, CMN I00031, CMN I00037, CMN I00042, CMN I00049, CMN I00055, CMN I00123

Localities: Horsefly, Republic, Quilchena, Driftwood, McAbee

Description and relationships: The most common taxon in the sample was Bibionidae. Numbers of specimens in the family are underrepresented in this report, since during initial sorting of specimens in collections, many that were obviously Bibionidae were not included for further study. However, in the Driftwood Creek collection, in which all specimens were tallied, the proportion of bibionids was 14%. Those specimens with only body parts present (this case was rare) were recognized by the setose body and long, setose legs. Specimens with wings, and isolated wings were classified according to the distinct bibionid venation: crossvein r-m is in the middle of the wing or distad of the middle and bm-cu (basal medial-cubital) is present, Rs is simple or branched, M is two-branched, A_1 is present but weak and A_2 and CuP are sometimes present. Unbranched and branched radial sectors were present among the specimens. Veins A_2 and CuP were rarely present; this may be the result of poorer preservation of the posterior part of the wing (due to weaker veins or obscuring of the area by the body) rather than natural absence of the veins.

Family Mycetophilidae (Figure V-27)

Specimens: UAPAL 4508, UAPAL 4529, UAPAL 4531, UAPAL 4560, UAPAL 4583, UAPAL 4595, UAPAL 4619, UAPAL 5697, UAPAL 5786

Localities: Horsefly, Quilchena, Princeton Firehall, Republic

Description and relationships: Specimens were identified by wing venation, although some had body parts preserved as well. Wing venation in the Sciaroidea can be recognized in general by the reduced number of veins, microtrichia on the wing membrane and macrotrichia on some of the anterior veins. Mycetophilidae are distinguished primarily by the position and angle of the crossvein r-m: it is slightly to greatly angled, but not continuous with R_{4+5} (see Figure V-29A). Vein R_{2+3} may be present, appearing as a cross-vein between R_1 and R_{4+5}, distad to Rs and sometimes forming a small triangle with it.

Family Sciaridae (Figure V-28)

Specimens: ?UAPAL 4509, UAPAL 4538, UAPAL 4552, UAPAL 4585, UAPAL 4590, UAPAL 4591, UAPAL 4592, UAPAL 5108

Localities: Horsefly, Quilchena, Driftwood

Description and relationships: All of the specimens consisted of wings and body fragments, except for UAPAL 4538, preservation of body parts was poor. Identification was performed using wing venation only. Wing venation in the Sciaroidea can be recognized in general by the reduced number of veins, microtrichia on the wing membrane and macrotrichia on some of the anterior veins. The characteristics that identify Sciaridae are: the costal vein ends between R_{4+5} and M, the subcosta is weak, and crossvein r-m is in line with R_5, appearing to be a longitudinal vein (Figure V-29B). A nematoceran specimen (UAPAL 4509) with long antennae, heavily spined legs and wings with macrotrichia (not illustrated) on the anterior veins is assigned to Sciaroidea; the wings are not distinct enough for placement in either Mycetophilidae or Sciaridae.

Family Rhagionidae (Figure V-30)

Specimen: UAPAL 4584

Locality: Quilchena

Description and relationships: An isolated wing is classified as Rhagionidae. Venation is complete and is typical of the family, with a central discal cell, M 3-branched and crossvein r-m basal to the center of the discal cell.

Family Empididae (Figure V-31)

Specimen: UAPAL 4646

Locality: Driftwood

Description and relationships: A single specimen with venation of both wings well preserved is present; body preservation is poor. Venation is typical of Empididae: the costal vein is continuous to R_{4+5}, a large discal medial cell is present, M is two-branched and R_{4+5} is unbranched.

Family Syrphidae (Figure V-32)

Specimen: UAPAL 4587

Locality: Quilchena

Description and relationships: The specimen is an isolated wing that is incomplete near the hind margin. Venation is characteristic of Syrphidae, with M_1 meeting R_{4+5} at the wing margin, M_2 extending into a short "stump" beyond its branching with M_1, and a pterostigma between the apex of veins Sc and R_1. The specimen differs from wings of extant forms by the absence of the spurious vein and crossvein r-m. The spurious vein is weak in some extant taxa (Vockeroth and Thompson 1987) and may not have been preserved.

Order LEPIDOPTERA

Suborder Ditrysia

Family Geometridae (Figure V-16)

Specimen: UWBM 66000 A&B

Locality: Republic

Description: Specimen UWBM 66000 is a complete lepidopteran with an estimated wing span of 28 mm. The antennae are pectinate and the visible mouthparts include porrect labial palpi and an extended proboscis. A complete description of the specimen is given in Chapter VI of this thesis.

Relationships: Due to overlapping of the front and hind wings on each side, and probable folding of the hind wing, wing venation could not be reconstructed. Thus it was necessary to use a complex of other characters (wing span, structure of antennae, size and position of labial palpi, length and scaling of proboscis, position of hairs) to determine family. On the basis of these characters, and comparison with specimens in the Strickland Museum, University of Alberta, the specimen is determined as a geometrid. Detailed classification of the specimen is given in Chapter VI of this thesis.

Family Noctuidae (Figure V-33)

Specimen: UAPAL 4579 A&B

Locality: Quilchena

Description: Specimen UAPAL 4579 is a hind wing fragment 11.2 mm wide with 8 veins present. A basal areole is formed from the fusion of $Sc+R_1$ and Rs; the junction of Rs and M_1 arises from the discal cell. M_2 arises mid-way between M_1 and M_3 (Cu appears 3-branched), slightly distad of the discal cell.

Relationships: The above combination of venation characters is found in the Noctuidae (Borror et al., 1976, Covell 1984). Both a 4-branched and 3-branched cubitus is found in this family, but when it appears 3-branched, M_2 is faint, as is the case in the fossil. Noctuids have a basal areole in the hind wing, and $Sc+R_1$ and Rs are fused for only a short distance beyond the basal areole. Rs and M_1 may be stalked at or beyond the discal cell in the family (Holland 1968). The specimen belongs to one of the smaller subfamilies of Noctuidae in which the cubitus is 3-branched. Extrapolating from the size of the wing fragment, the wing span of the whole lepidopteran would be approximately 50 mm, which is within the size range of many noctuids.

Stratigraphic record of families

The 29 taxa identified from British Columbia-Republic extend the geological history of several families back in to the Middle Eocene, and contribute new records for families in the North American Paleogene. The stratigraphic record for those families identified from British Columbia-Republic is summarized in Table V-3 and below. All records from the Middle Eocene and earlier are considered; only representative localities from later in the Paleogene are included (Baltic amber, Florissant). In the following discussion, unless otherwise indicated, the references for selected localities are: Paskapoo Formation, Alberta (Mitchell and Wighton 1979), Oligocene localities of Florissant, Ruby Paper Shales, Mormon Creek and the Creede Formation (Wilson 1978), Baltic amber (Larrson 1978), Geiseltal (Pongracz 1935) and Messel (Lutz 1987, Schaal and Ziegler 1988). Geologic time periods for all localities are given in Table V-4.

There is no Mesozoic record of Cicindelidae; the first record of the family comes from One Mile Creek in this study and a probable cicindelid from Green River (Grande 1984). The family is also represented in the Baltic amber. Carabidae has an extended fossil history, with a Mesozoic record in the Upper Jurassic of Kara Tau (Crowson 1981) and the Lower Cretaceous of Transbaikalia (Ponomarenko 1989). Paleogene records are numerous from North America [Alberta Paskapoo, Republic (this study), British Columbia, Green River, Florissant (Scudder 1890), Mormon Creek] and from Europe [Messel, Geiseltal, Baltic amber]. Dytiscidae are first recorded from the Upper Cretaceous Kazakhstan (Crowson 1981) and occur in the Alberta Paskapoo, at Republic (this study) and Green River (Scudder 1890), Florissant (Handlirsch 1908) and the Baltic amber.

The earliest records of Scarabaeidae are from British Columbia (this study and Scudder 1890) and Green River (Scudder 1890); the family is present at Florissant and the Ruby Paper Shales and at Messel and the Baltic amber (Handlirsch 1908); Scarabaeoid specimens, however, date back to the Lower Jurassic of Switzerland (Crowson 1981). The lucanid specimen from Republic in this study is the first North American record of the family; the family is also present at Florissant and in Europe at Messel and in the Baltic amber (Handlirsch 1908).

Elaterids are represented world-wide, in Mesozoic localities such as in Queensland (Upper Triassic; Tillyard and Dunstan 1923), Kara Tau

(Crowson 1981), Wealdon (Jarembowski 1984) and Lebanese amber (Crowson 1981) and in Paleogene localities in British Columbia (Scudder 1890, Handlirsch 1910, this study), at Green River (Scudder 1890, Cockerell and Levesque 1931), Florissant, and Ruby Paper Shales and Messel, Geiseltal (Pongracz 1935) and the Baltic amber. The cantharid specimen from One Mile Creek reported in this study represents the earliest stratigraphic occurrence of the family; they are also reported from Florissant (Handlirsch 1908) and the Baltic amber. Although the Cleroidea is present in the Upper Cretaceous Taimyr (Crowson 1981), the earliest record of the family Cleridae is at Quilchena in this study; clerids are also present at Florissant (Handlirsch 1908) and in Baltic amber. Mordellidae may have been present in the Upper Jurassic of Kara Tau (Crowson 1981); the family is reported from Paleogene localities of Horsefly (this study), Green River (Grande 1984), Florissant and Baltic amber.

The Chrysomeloidea has an extended fossil history, with the superfamily present in the Lower Jurassic Kara Tau (Crowson 1981) and numerous records of its three constituent families in the Paleogene. Cerambycids have also been reported from Kara Tau (Crowson 1981), as well as from the Triassic in Australia (Tillyard and Dunstan 1923) and as "Cerambycoidea" from Canadian amber (McAlpine and Martin 1969); the family occurs at sites in British Columbia and Republic (this study), Green River (Grande 1984), Florissant (Handlirsch 1908), Messel and Baltic amber.

The Curculionoidea has a similar widespread temporal and geographic distribution, the superfamily occurring in Queensland

(Tillyard and Dunstan, 1923) and Kara Tau (Crowson 1981); Curculionidae is present in the Upper Cretaceous Fox Hills (Crowson 1981) and in Paleogene strata of Alberta Paskapoo, British Columbia-Republic (this study), Green River (Scudder 1890), Florissant (Handlirsch 1908), Messel, Geiseltal and Baltic amber.

The Mesozoic history of the Tenthredinidae is uncertain, with a probable record from Bohemia (Cretaceous; Handlirsch 1908); the family is more recently reported from British Columbia (Wilson 1977b, this study), Green River (Scudder 1890), Florissant (Handlirsch 1908) and Baltic amber and there is a probable occurrence at Ruby Paper Shales. The two specimens in this study classified as Argidae-Diprionidae, both from Horsefly, represent the only fossil record of either of these symphytan families. The Cynipidae are first recorded in Canadian amber from Cedar Lake (Carpenter et al. 1937); in addition to the record from British Columbia in this study, the family has been found at Florissant (Handlirsch 1908) and in Baltic amber.

Ichneumonoids were numerous in the sample from this study, and the taxon is well represented geographically and stratigraphically. The superfamily is found in Canadian amber (Upper Cretaceous; McAlpine and Martin 1969) and Ichneumonids are common in strata in North America [British Columbia (Scudder 1890, Handlirsch 1910, Wilson 1977b, this study), Republic (this study), Green River (Scudder 1890, Cockerell and Levesque 1931), Florissant (Handlirsch 1908), Creede, Ruby Paper Shales] and Europe [Messel and Baltic amber].

The scoliid specimen described in this study is the earliest record of the family for North America; it has been reported (but not described) from Messel and also occurs at Florissant (Handlirsch 1908) and in Baltic amber. The Pompilidae specimen from this study is similar -- it is the earliest North American record of the family, but it has been identified in sediments from Messel, as well as occurring at Florissant and in Baltic amber (probably Pompilinae; Day 1988).

The earliest occurrence of Formicidae is in the Lower Cretaceous Lebanese amber (Hennig 1981); the family is common in Paleogene formations, including Sakhalin amber (Dlusskiy 1988), Alberta Paskapoo, British Columbia and Republic (Scudder 1890, Wilson 1977b, this study), Green River (Scudder 1890), Florissant (Handlirsch 1908), Ruby Paper Shales, Messel (Lutz 1986) and Baltic amber.

Tipuloidea is present in Canadian amber (McAlpine and Martin 1969) and Tipulidae is reported from Jurassic and Cretaceous strata in England (Handlirsch 1908, Jarzembowski 1984); there are numerous Paleogene records of the family [Alberta Paskapoo, British Columbia and Republic (Handlirsch 1910, Wilson 1977b, this study), Green River (Scudder 1890), Florissant (Handlirsch 1908), Mormon Creek, Creede Formation, Ruby Paper Shales, Messel and Baltic amber].

The Mesozoic record of Bibionidae is not extensive [Jurassic of England (Handlirsch 1908) and Canadian amber (McAlpine and Martin 1969, Peterson 1977)], but in virtually all North American sites the family is common and individual specimens numerous (Scudder 1890, Handlirsch 1910, Rice 1959, Wilson 1977b, Wilson 1978, this study); bibionids are present in Baltic amber as well.

The fossil record of Mycetophilidae is similar to Bibionidae, occurring in Jurassic (Handlirsch 1908) and Lower Cretaceous strata

(Jarzembowski 1984) in England and in Canadian amber (McAlpine and Martin 1969) and in British Columbia-Republic (Scudder 1890, Wilson 1977b, this study), Green River (Scudder 1890), Florissant (Cockerell 1914), Ruby Paper Shales and in Baltic amber. The earliest occurrence of Sciaridae is in Canadian amber (McAlpine and Martin 1969) and the family is present in British Columbia (Wilson 1977b, this study), Green River (Grande 1984), Florissant and Baltic amber.

The isolated rhagionid wing found in this study is the earliest North American occurrence of the family; it is found as well in the Oligocene of Florissant and the Baltic amber. The Mesozoic history of the Rhagionidae consists of Upper Jurassic (James and Turner 1981) and Lower Cretaceous (Jarzembowski 1984) taxa. Empididae are represented in the Lower Cretaceous Wealdon beds (Jarzembowski 1984) and Canadian amber (McAlpine and Martin 1969) and in the Paleogene in British Columbia (Handlirsch 1910, Wilson 1977b, this study), Green River (Grande 1984), Florissant and the Baltic amber. There is no Mesozoic record of the Syrphidae; in the Paleogene, however, the family is represented in strata from British Columbia (Wilson 1977b, this study), Green River (Scudder 1890, Cockerell and Levesque 1931, James 1932), Florissant, Creede Formation, Ruby Paper Shales, Messel and Baltic amber.

The two lepidopteran taxa reported in this study, Geometridae (Republic) and Noctuidae (Quilchena), are the earliest occurrence of the families in the stratigraphic record. A lepidopteran egg from the Upper Cretaceous in Massachusetts classified as Noctuidae (Gall and Tiffney 1983) is considered suspect by Whalley (1986) since egg characteristics are not diagnostic at the family level. Geometers are found in the

Oligocene at Florissant and in Baltic amber (Handlirsch 1908).

Comparison with other Middle Eocene collections from North America

Insects from Middle Eocene sites in British Columbia have been studied by Scudder (1890, 1895), Handlirsch (1910), Rice (1959) and, more recently, by Wilson (1977b), covering the same localities as this study (Blakeburn, Quilchena, Horsefly, Driftwood Creek) and other coeval sites (Pleasant Valley, Whipsaw Creek, Nicola, Tranquille). Although many insect specimens from Republic have been collected, with some taxonomic classification accomplished [illegible] Wehr, unpublished data), there are no published accounts of the diversity. These previous records from British Columbia, compiled by Wilson (1977b), total 19 families (Coleoptera - 7 families, Hymenoptera - 5, Diptera - 7, Lepidoptera - 0), 7 of which were not found in my study (Hydrophilidae, Buprestidae, Tenebrionidae, Chrysomelidae, Ptychopteridae, Braconidae and Vespidae). Of the 30 taxa identified in my study, 15 are new records for families in the Middle Eocene of British Columbia and Washington state (Cicindelidae, Dytiscidae, Lucanidae, Cantharidae, Cleridae, Mordellidae, Cerambycidae, Curculionidae, Argidae-Diprionidae, Cynipidae, Scoliidae, Pompilidae, Rhagionidae, Geometridae, Noctuidae). Significant for the study of paleoanthecology are the first records of Lepidoptera from the area. When these data are added to previous records, the insect fauna from the Middle Eocene of British Columbia-Republic is increased to 34 families in the four anthophilous orders.

Twenty of the 34 families found at British Columbia-Republic are also present in insect beds at Green River, an approximately contemporaneous (Late Early Eocene to Late Middle Eocene; Grande 1984) locality in Wyoming, Utah and Colorado. However, nine of the families described in the present study have not been found at Green River and remain the earliest occurrences of the taxa in the Middle Eocene of North America. These are Lucanidae, Cantharidae and Cleridae in the Coleoptera, Argidae-Diprionidae, Scoliidae and Pompilidae in the Hymenoptera, Rhagionidae in the Diptera and Geometridae and Noctuidae in the Lepidoptera. Of these, Lucanidae, Scoliidae and Pompilidae have been reported from Messel, Germany (Middle Eocene), but have yet to be described and Rhagionidae has been found at Wealdon, England (Lower Cretaceous; Jarzembowski 1984). The remaining 5 taxa (Cantharidae, Cleridae, Argidae-Diprionidae, Geometridae, Noctuidae) are the earliest known occurrences of the respective families in the stratigraphic record.

This study has doubled the number of known insect families at British Columbia-Republic, indicating that part of the previous discrepancy in diversity between Green River and British Columbia-Republic was due to differences in collecting effort. However, the difference in taxonomic richness remains substantial (34 families for British Columbia-Republic vs. 59 for Green River) and additional factors are necessarily involved. It is worthwhile to note that taxonomic overlap between the faunas is low: only 20 families (in the orders studied) are shared by the two areas. The 14 families found only at British Columbia-Republic show no obvious commonalities that suggest reasons for their restricted distribution. Several of the taxa (Lucanidae, Diprionidae, Scoliidae, Pompilidae), however, are primarily tropical groups with limited distribution in northern areas (Jessop

1986, Gauld and Bolton 1988). To suggest that the northerly locality may have been more tropical than Green River contradicts conclusions on paleoclimate for the two areas; British Columbia-Republic is inferred to have had a more temperate climate than Green River during the Eocene (Grande 1984, Wolfe and Wehr 1987). Whether the remaining disparity between the two insect faunas is a biotic phenomenon or is largely due to taphonomic processes and depositional regime (for example, Wilson 1980, 1988) requires further study.

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Table V-1. Taxonomic identity of Middle Eocene insect specimens of Coleoptera, Hymenoptera, Diptera and Lepidoptera. ? = determination not definitive.

Order	Suborder	Superfamily	Family	Number of specimens
COLEOPTERA	Adephaga		Cicindelidae	1
			Carabidae	1
			Dytiscidae	1
	Polyphaga	Scarabaeoidea		1
			Lucanidae	1
		Elateroidea	Elateridae	1
		Cantharoidea	Cantharidae	1
		Cleroidea	Cleridae	1
		Melooidea	?Mordellidae	1
		?Chrysomeloidea		2
			Cerambycidae	2
		Curculionoidea	Curculionidae	5
	elytra			23
	unidentified coleopteran			14
HYMENOPTERA	Symphyta	Tenthredinoidea	Tenthredinidae	1
			Argidae-Diprionidae	2
	Apocrita	Cynipoidea	Cynipidae	2
		Ichneumonoidea		8
			Ichneumonidae	17
		Scolioidea	Scoliidae	1

Table V-1 (continued).

Order	Suborder	Superfamily	Family	Number of specimens
HYMENOPTERA	(continued)	Pompiloidea	Pompilidae	1
		Formicoidea	Formicidae	8
	unidentified aculeate apocritans			4
	unidentified apocritans			11
	unidentified hymenopteran			8
DIPTERA	Nematocera	Tipuloidea	Tipulidae	5
		Bibionoidea	Bibionidae	52
		Sciaroidea		1
			Mycetophilidae	9
			Sciaridae	7
	Brachycera	Tabanoidea	Rhagionidae	1
		Empidoidea	Empididae	1
		Syrphoidea	Syrphidae	1
	unidentified nematocerans			14
	unidentified brachycerans			3
	unidentified dipterans			24
LEPIDOPTERA	Dytrisia	Geometroidea	Geometridae	1
		Noctuoidea	Noctuidae	1

Table V-2. Abbreviations used in wing venation terminology.

Veins

A	anal
bm-cu	basal medial-cubital
bv	basal vein
C	costa
Cu	cubitus
cu-a	cubital-anal
CuA	anterior branch of cubitus
CuP	posterior branch of cubitus
M	media
m-cu	medial-cubital
R	radius
r-m	radial-medial
r-rs	radial-sectorial
Rs	radial sector
Sc	subcosta

Cells

BC	basal cell
C	costal cell
d	discal cell (Diptera)
DC	discal cell (Hymenoptera)
dm	discal medial cell
MC	marginal cell
SMC	submarginal cell

Wing areas

ar	areolet
ba	basal areolet
pt	pterostigma

Table V-3. Stratigraphic occurrence of insect families found in Middle Eocene localities in British Columbia and northern Washington. Records previous to Upper Cretaceous are plotted on the far left of the chart. Dashed line indicates questionable record, * = records of families found in this study that are the earliest occurrence of the taxa in North America.

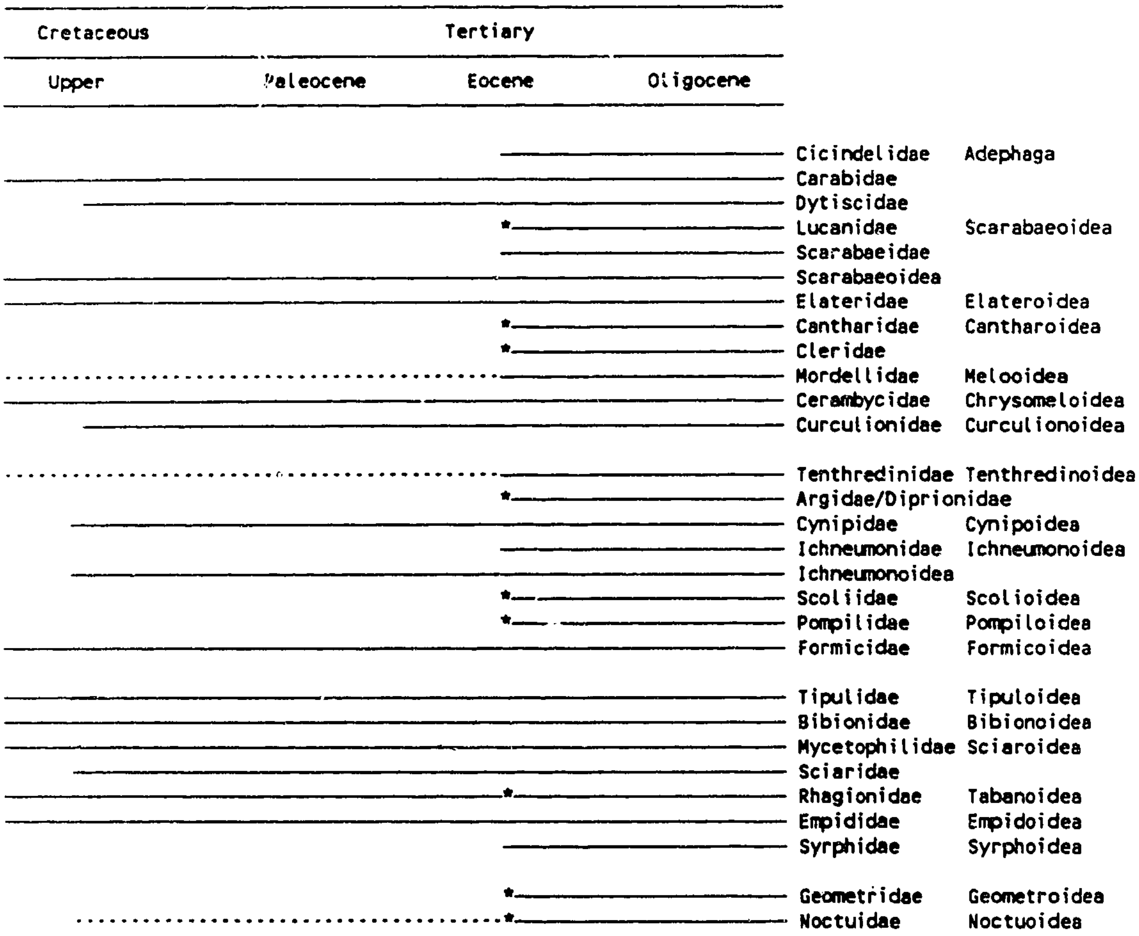

Table V-4. Stratigraphic range of Mesozoic and Paleogene localities referred to in text.

Locality	Stratigraphic range
Alberta Paskapoo	Paleocene
Baltic amber	Late Eocene
Bohemia	Cretaceous
British Columbia	Middle Eocene
Canadian (Cedar Lake) amber	Upper Cretaceous
Claiborne Formation	Middle Eocene
Creede Formation, Colorado	Late Oligocene
Florissant, Colorado	Early Oligocene
Geiseltal, Germany	Middle Eocene
Green River	Late Early Eocene-Late Middle Oligocene
Kara Tau	Upper Jurassic
Kazakhstan	Upper Jurassic-Upper Cretaceous
Lebanese amber	Lower Cretaceous
Massachusetts	Upper Cretaceous
Messel, Germany	Middle Eocene
Mormon Creek, Montana	Late Eocene or Early Oligocene
Queensland, Australia	Upper Triassic
Republic, Washington	Middle Eocene
Ruby Paper Shales, Montana	Late Oligocene

Table V-4 (continued)

Locality	Stratigraphic range
Sakhalin amber	Paleocene?
Switzerland	Lower Jurassic
Taimyr, Siberia	Upper Cretaceous
Transbaikalia	Lower Jurassic-Lower Cretaceous
Wealdon	Lower Cretaceous

FIGURES V-1 to V-9: Coleoptera.

Figure V-1. Cicindelidae; elytra with patterning; prominent head and large arcuate mandibles; UAPAL 4523; One Mile Creek; X 4.

Figure V-2. Carabidae with filiform antenna, large arcuate mandibles and striate elytra; UWBM 57098; Republic; X 4.

Figure V-3. Dytiscidae; metathoracic legs have fringes of long hairs; UWBM 72302; Republic; X 7.

Figure V-4. Scarabaeoidea, showing fossorial protibia; UAPAL 4635; Quilchena; X 4.

Figure V-5. Lucanidae with large mandibles and 10-segmented lamellate antennae; UWBM 57118; Republic; X 4.

Figure V-6. Elateridae; posterior lateral corners of pronotum extend into blunt spines; UWBM 57095; One Mile Creek; X 4.

Figure V-7. Cantharidae with colour pattern still evident; filiform antennae; UAPAL 4513; One Mile Creek; X 4.

Figure V-8. Cleridae with prothoracic and mesothoracic tarsal pattern of 5-5-5; UAPAL 4632; Quilchena; X 2.

Figure V-9. Beetle with laterally compressed fusiform body tentatively classified as Mordellidae; UAPAL 4551; Horsefly; X4.


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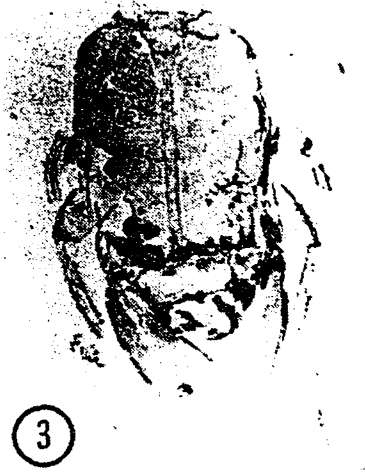
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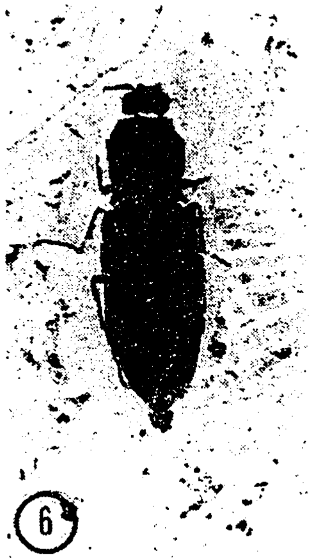
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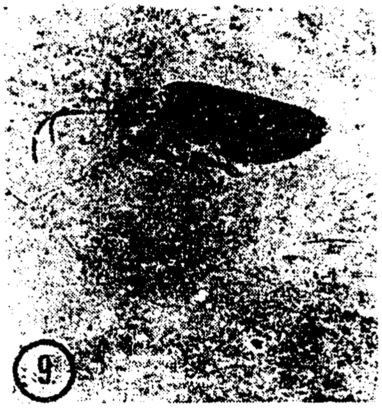
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Figures V-10 to V-12: Coleoptera.

Figure V-10. Cerambycidae showing long antennae, prominent head and broad pronotum; UAPAL 4626; Quilchena; X 4.

Figure V-11. Cerambycidae showing long antennae, conspicuous head, shield-like pronotum; bands of pubescence present on elytra; UWBM 57097; Republic; X 4.

Figure V-12. Curculionidae with conspicuous snout and lateral orientation to body; UWBM 72299; Republic; X 4.

Figures V-13 to V-15: Hymenoptera.

Figure V-13. Scoliidae; UAPAL 4524; Tulameen Road; X 4.

Figure V-14. Pompilidae with characteristically long legs; CMN I00040; McAbee; X 4.

Figure V-15. Formicidae, winged, showing elbowed antenna and broad alitrunk; UWBM 178; Republic; X 2.

Figure V-16. Lepidoptera; complete specimen of Geometridae; UWBM 66000; Republic; X 3.5.

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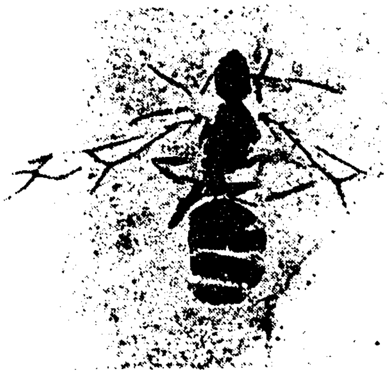

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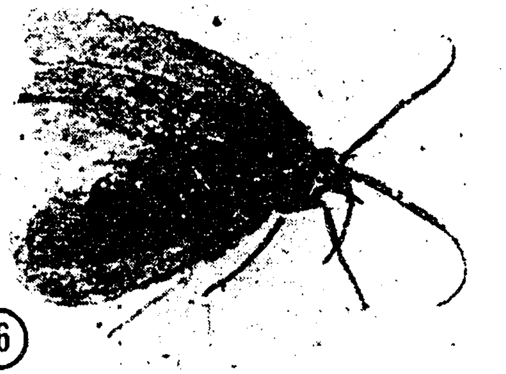

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FIGURES V-17 to V-19: Hymenoptera.

Figure V-17. Tenthredinidae; UAPAL 4500; Horsefly.

Figure V-18. Argidae/Diprionidae; (A) UAPAL 4548; Horsefly. (B) UAPAL 4545; Horsefly.

Figure V-19. Cynipidae; (A) UAPAL 4556; Horsefly. (B) UAPAL 4581; Quilchena.

Abbreviations: Cu, cubitus; M, media; MC, marginal cell; SMC, submarginal cell; R, radius; Rs, radial sector.

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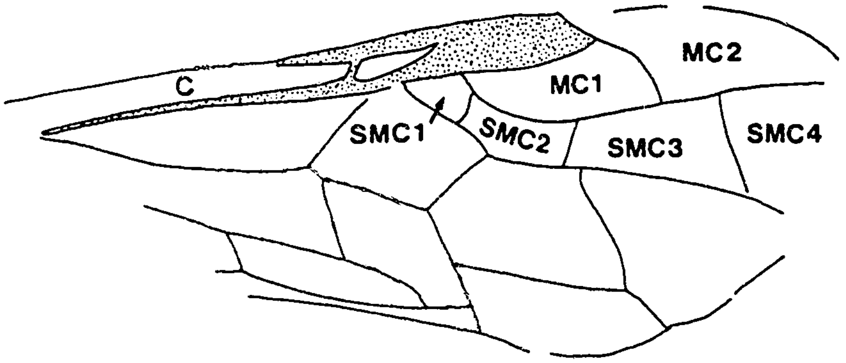

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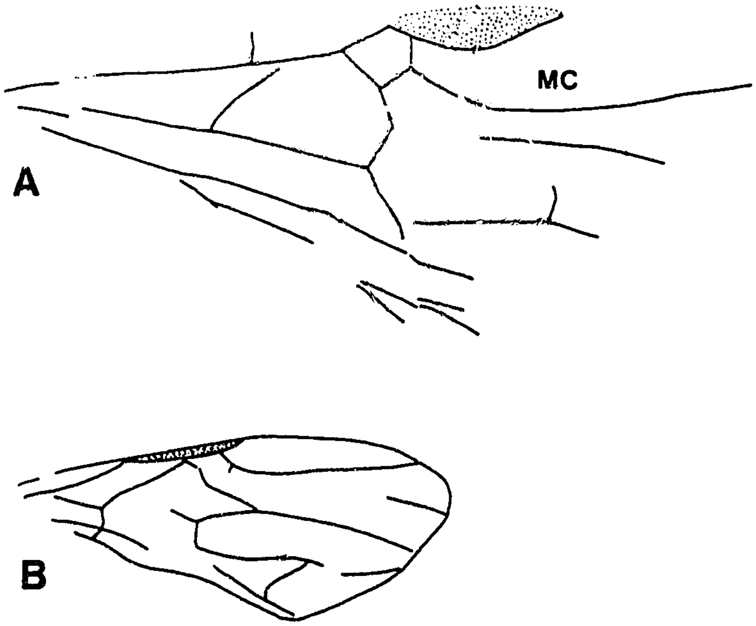

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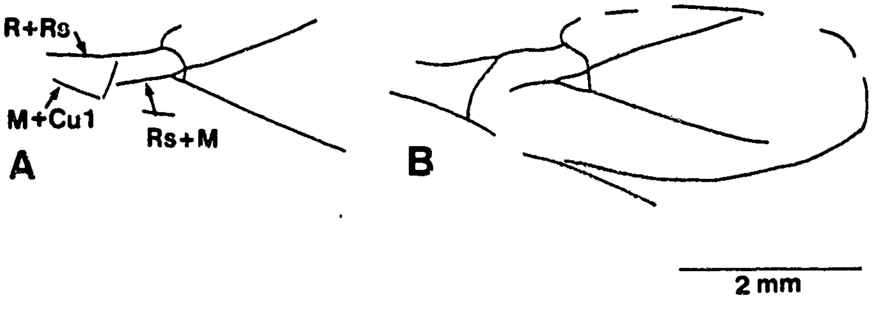

FIGURES V-20 to V-21: Hymenoptera.

Figure V-20. Ichneumonoidea; (A) UAPAL 4603; Quilchena. X. (B) SFU 175; Quilchena.

Figure V-21. Ichneumonidae; (A) UAPAL 4549; Horsefly. (B) UAPAL 4580; Quilchena. (C)UAPAL 5069; Driftwood. (D) CMN 100092; McAbee. (E) UAPAL 5714; Republic.

Abbreviations: ar, areolet; DC, discal cell; m-cu, medial-cubital; SMC, submarginal cell.

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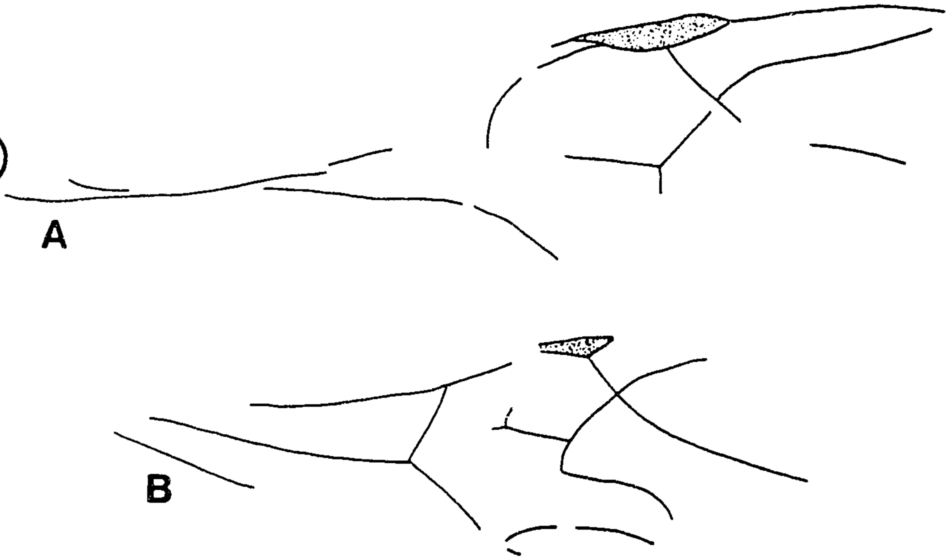

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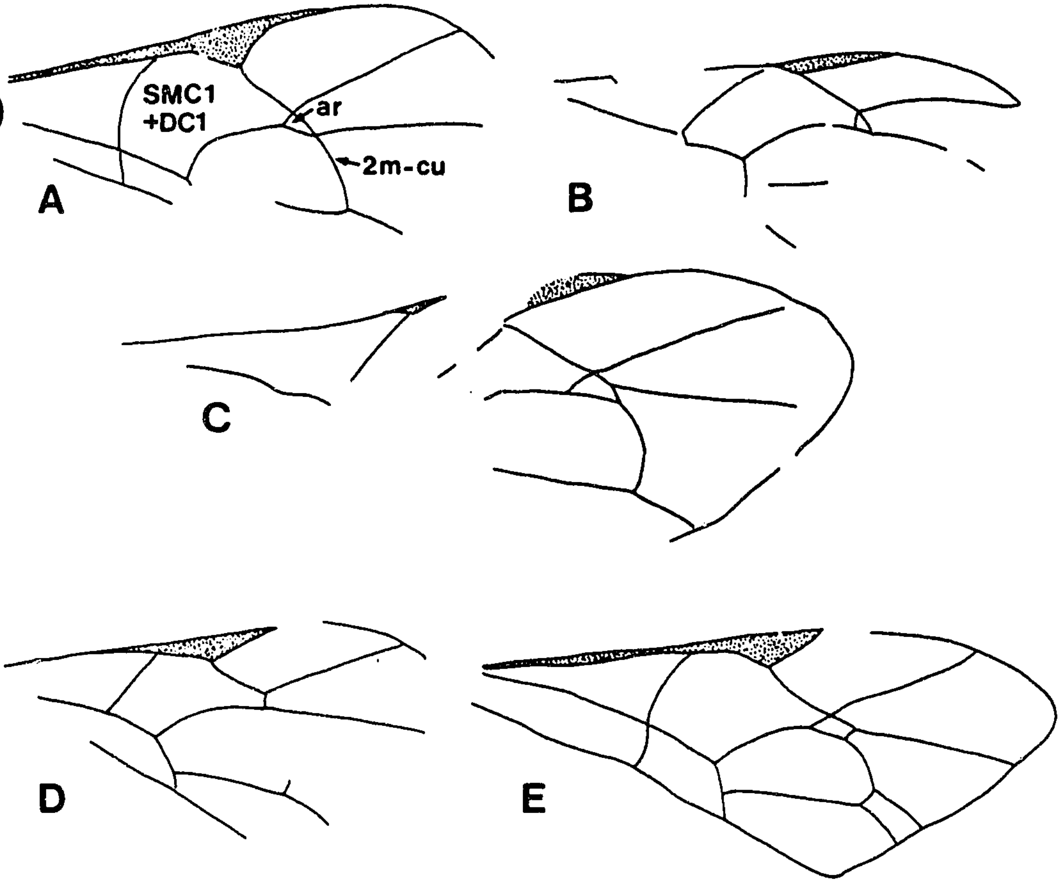


FIGURES V-22 to V-25: Hymenoptera.

Figure V-22. Scoliidae; UAPAL 4524; Tulameen Road.

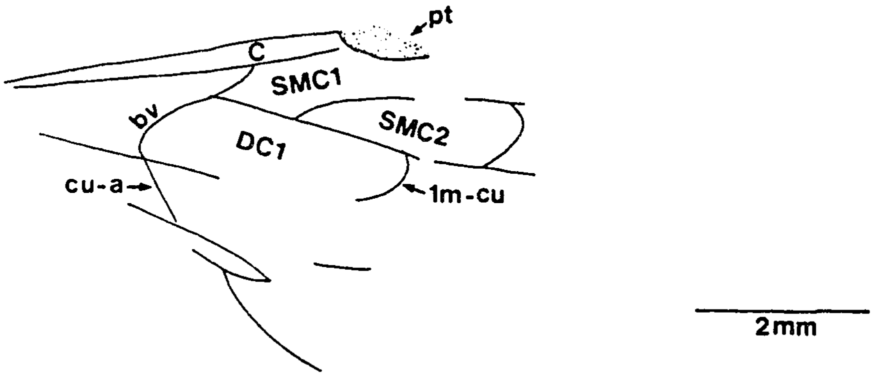
Figure V-23. Pompilidae; CMN I00040; McAbee.

Figure V-24. Formicidae; (A) UAPAL 4557; Horsefly. (B) UAPAL 4558; Horsefly. (C) UAPAL 4610; Quilchena. (D) UAPAL 4604; Quilchena.

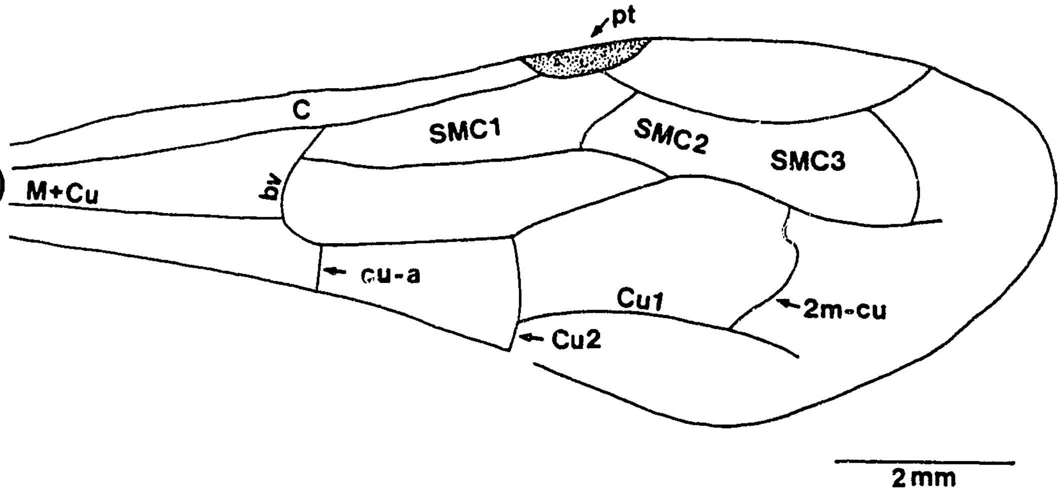
Figure V-25. Diptera; Tipulidae; UAPAL 4530; Horsefly.

Abbreviations: BC, basal cell; bv, basal vein; C, costal cell; Cu, cubitus; CuA, anterior branch of cubitus; cu-a, cubital-anal; DC, discal cell; M, media; m-cu, medial-cubital; SMC, submarginal cell; pt, pterostigma.

㉒


pt
C
SMC1
SMC2
bv
DC1
cu-a
1m-cu
2mm

㉓


pt
C
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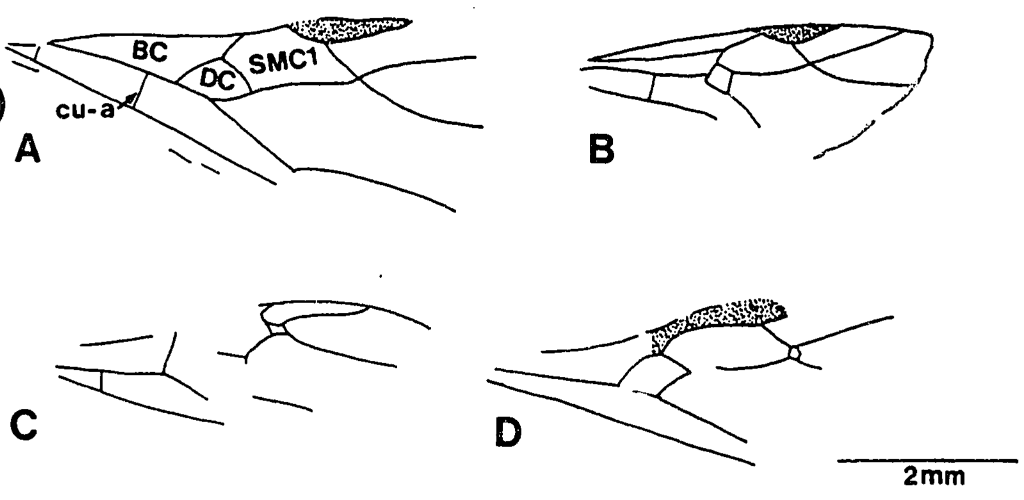
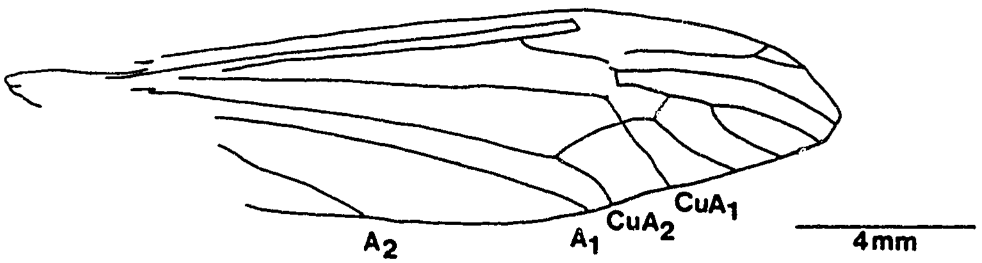
SMC3
M+Cu
bv
cu-a
Cu1
2m-cu
Cu2
2mm

㉔


BC
DC
SMC1
cu-a
A
B
C
D
2mm

㉕


A2
A1
CuA2
CuA1
4mm

FIGURES V-26 TO V-29: Diptera.

Figure V-26. Bibionidae; (A) UAPAL 4640; Horsefly. (B) UAPAL 5021; Tulameen Road. (C) UWBM 57122B; Republic. (D) UWBM 57122C; Republic. (E) CMN I00013; McAbee. (F) CMN I00012З; McAbee.

Figure V-27. Mycetophilidae; (A) UAPAL 4529; Horsefly. (B) UAPAL 4583; Quilchena.

Figure V-28. Sciaridae; (A) UAPAL 4538; Horsefly; additional longitudinal veins are a result of the two wings being superimposed asymmetrically. (B) UAPAL 4552; Horsefly.

Figure V-29. Basal vein configuration in (A) Mycetophilidae and (B) Sciaridae.

Abbreviations: bm-cu, basal medial-cubital; CuP, posterior branch of cubitus; M, media; R, radius; r-m, radial-medial; Rs, radial sector.

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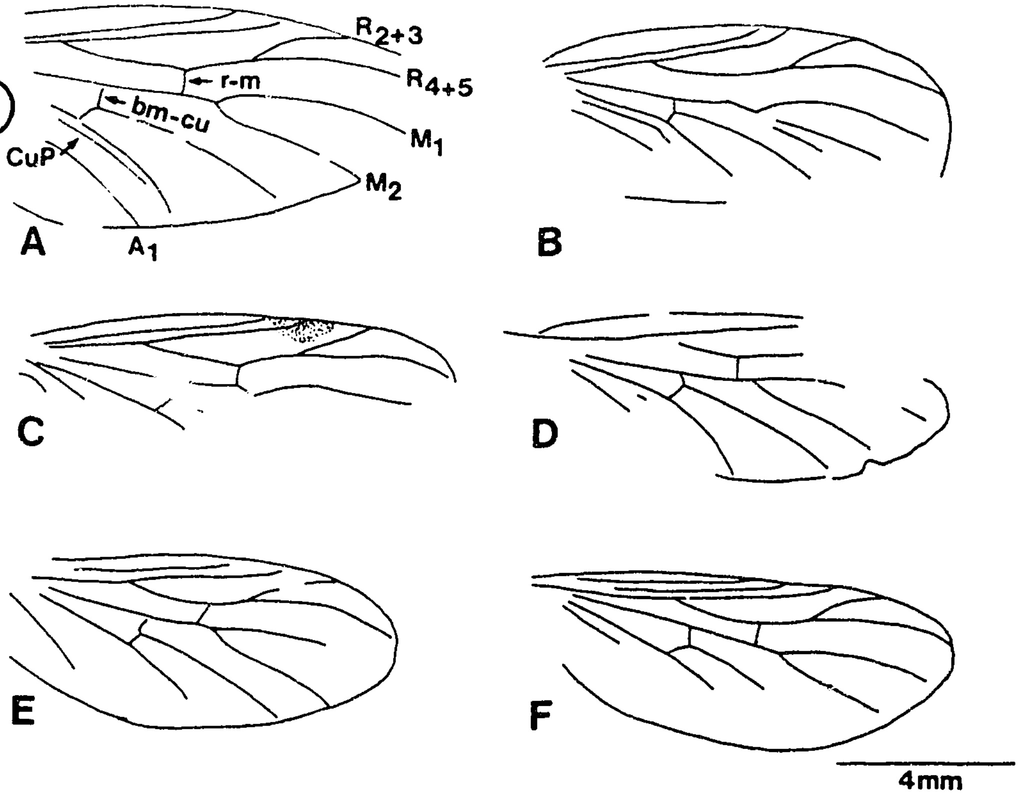
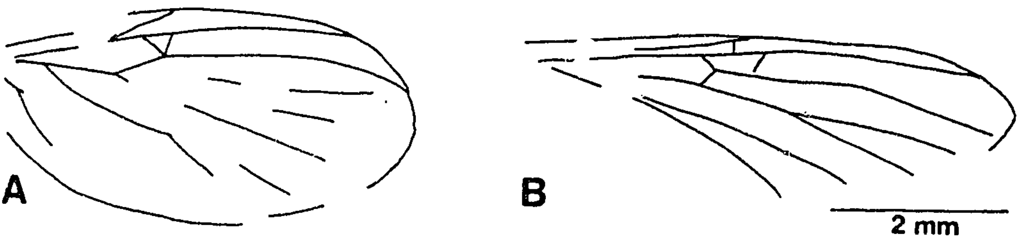
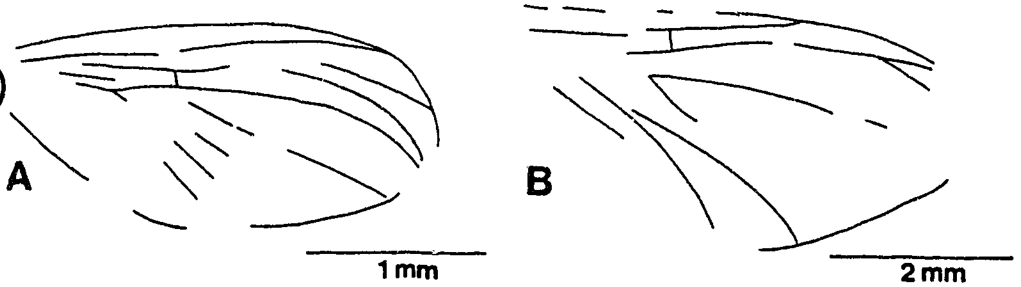

R_{2+3}
r-m
R_{4+5}
bm-cu
M_1
CuP
M_2
A
A_1
B
C
D
E
F
4mm

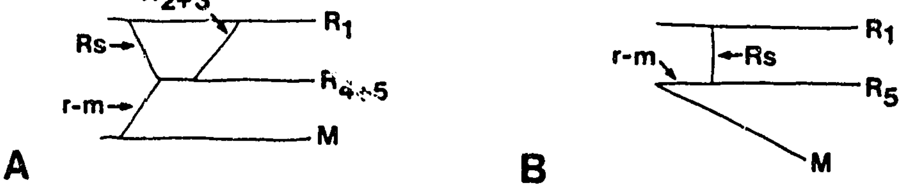
㉗


A
B
2 mm

㉘


A
B
1 mm
2 mm

㉙


R_{2+3}
Rs
R_1
R_{4+5}
r-m
M
A
R_1
r-m
Rs
R_5
M
B

FIGURES V-30 to V-32: Diptera.

Figure V-30. Rhagionidae; UAPAL 4584; Quilchena.

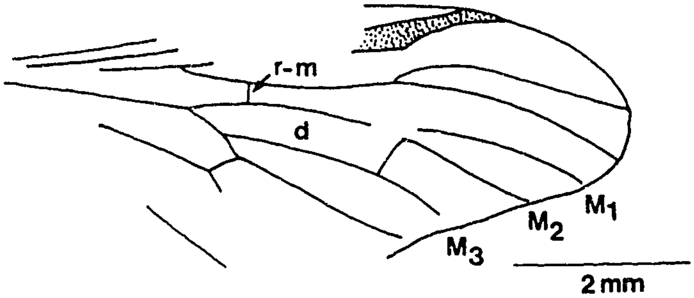
Figure V-31. Empididae; UAPAL 4646; Driftwood; Additional veins between R_1 and R_{2+3} are a result of the two wings being superimposed asymmetrically.

Figure V-32. Syrphidae; UAPAL 4587; Quilchena.

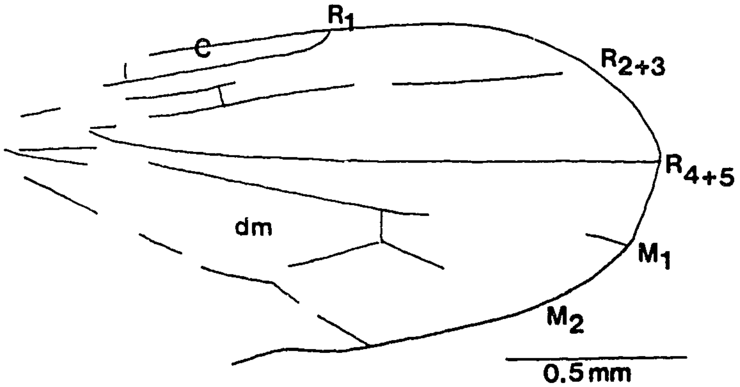
Figure V-33. Lepidoptera: Noctuidae; UAPAL 4579; Quilchena.

Abbreviations: A, anal; ba, basal areale; C, costal cell; Cu, cubitus; d, discal cell; dm, discal medial cell; M, media; pt, pterostigma; R, radius; Rs, radial sector; r-m, radial-medial; Sc, subcosta.

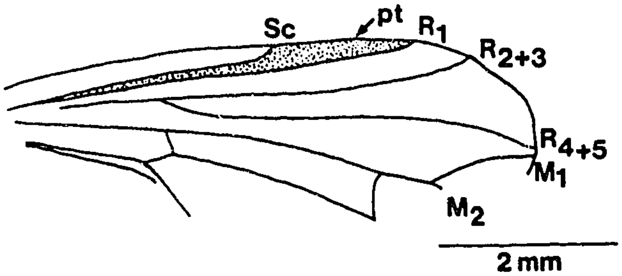
㉚


r-m
d
M$_1$
M$_2$
M$_3$
2 mm

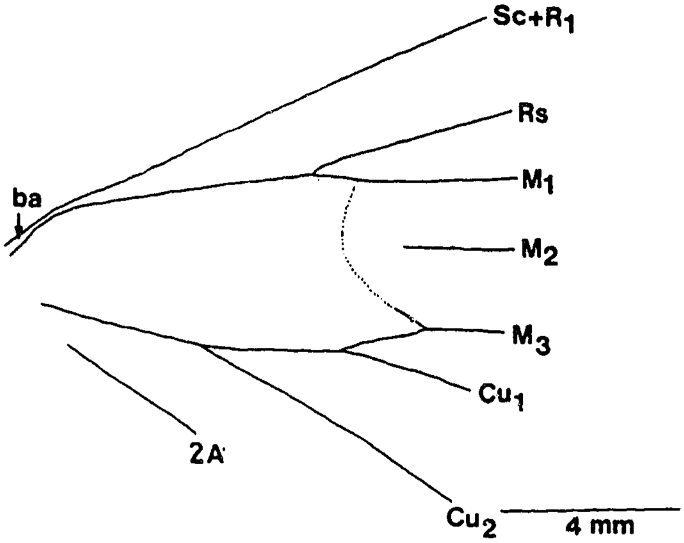
㉛


R$_1$
c
R$_{2+3}$
R$_{4+5}$
dm
M$_1$
M$_2$
0.5 mm

㉜


Sc
pt
R$_1$
R$_{2+3}$
R$_{4+5}$
M$_1$
M$_2$
2 mm

㉝


Sc+R$_1$
Rs
M$_1$
ba
M$_2$
M$_3$
Cu$_1$
2A
Cu$_2$
4 mm

VI. TWO NEW LEPIDOPTERA (GEOMETRIDAE, NOCTUIDAE) FROM THE MIDDLE EOCENE OF NORTH AMERICA

INTRODUCTION

The fossil history of the Lepidoptera has important implications for anthecology. Extant plants pollinated by lepidopterans have flowers with distinct characteristics (pollination syndromes); these syndromes are assumed to be the result of co-evolution between the two groups (Faegri and van der Pijl 1979). Two syndromes are recognized, psychophily or butterfly (Papilionoidea and Hesperioidea) pollinated flowers and phalaenophily or moth (all other Ditrysia) pollinated flowers, which differ according to behaviour of the pollinators, such as diel activity, olfactory and colour sensitivity and flight characteristics (Faegri and van der Pijl 1979).

Fossil flowers from the Eocene with funnel-shaped perianths are inferred to be pollinated by lepidopterans (Crepet and Friis 1987) and fossils belonging to highly derived lepidopteran families (Papilionidae, Lycaenidae) have been found in strata from the same epoch (Durden and Rose 1978). It is assumed that a proboscis appropriate for feeding on deeply-recessed nectar had evolved by this time, although mouthpart structure is not described for any fossil lepidopterans. It is important to establish a time frame for the origin of nectar-feeding lepidopterans in order to understand the selective pressures acting on flower form.

Lepidopterans are relatively rare as fossils, the most diverse fauna being from Baltic amber (Larsson 1978, Willemstein 1987) and the North American Oligocene Florissant shales (Wilson 1978). In this study, I describe two lepidopteran specimens from the Middle Eocene of British Columbia and Republic, Washington. Their importance to evolution of plant-pollinator systems is discussed, as well their relevance to the phylogeny of Lepidoptera.

MATERIALS AND METHODS

The two compression/impression specimens were examined with a Wild M5 dissecting microscope and measurements made with an ocular micrometer or Helios dial calipers. Composite measurements and drawings were made using the two counterparts of the fossil. UWBM 66000, a relatively complete specimen, is from Republic, Washington and is housed in the Thomas Burke Museum, University of Washington. UAPAL 4579, a wing fragment, is from Quilchena, British Columbia and is housed in the paleontological collection of the University of Alberta. An age of 48 - 50 m. y. has been established for the two sites by radiometric dating (Wolfe and Wehr 1987) and correlation with fish fauna (Wilson 1977).

Specimen UAPAL 4579 has most of the basal veins intact and was identified to family on venation pattern using Borror et al. (1976) and Covell (1984). Specimen UWBM 66000 has wings partly spread, such that the anterior veins of the front wing are visible but the posterior front wing venation and all of the hind wing venation is obscured. Probable folding of the hind wing has compounded the problem. It was not possible, even with composite camera lucida drawings, to reconstruct wing venation. Rather, it was necessary to use a complex of characters visible on the fossil specimen and compare it to extant specimens and descriptions. The characters used were: (1) wing span, (2) presence and location of hairs on wings, (3) form and size of labial palpi, (4) antennal type, (5) presence and form of proboscis, (6) presence and length of hairs on vertex. Family descriptions in Daly et al. (1978), Richards and Davies (1977), Borror et al. (1976), Holland (1968) and Covell (1984) were reviewed. Extant specimens in the Strickland Entomological Museum, University of Alberta, were examined in the following taxa: Incurvariidae (1 genus), Prodoxidae (3 genera), Tineidae (2), Oecophoridae (3), Coleophoridae (1), Gelechiidae (5), Cosmopterigidae (4), Olethreutidae (7), Epermeniidae (1), Glyphipterigidae (1), Plutellidae (2), Yponomeutidae (1), Douglasiidae (1), Cossidae (1), Tortricidae (1), Limacodidae (1), Pyralidae (48 genera in 8 subfamilies), Thyatiridae (1), Drepanidae (1), Geometridae (43 genera in 2 subfamilies), Epiplemidae (1) and Lasiocampidae (1). Many Noctuidae (Phalaenidae) were examined for antennal and proboscis characteristics. Where character states were available at the family level from the literature, they were used, supplemented by information from the specimens. Where no information was available from the literature, characteristics of museum specimens were assumed to be representative of the family. Those families in which one or more of the characters did not match the fossil were eliminated from consideration. The lepidopteran specimens at the Strickland Museum are primarily from western Canada and the literature encompasses mostly North American and European taxa.

RESULTS

A. UWBM 66000 (Figure VI-1)

Description

The head has a maximum diameter of 1.5 mm. The frons has a dense zone of hairs between and slightly anterior to the antennae. The hairs appear to be grouped in tufts closer to the antennal sockets; individual hairs are a maximum of 0.4 mm long. There are scattered hairs on the vertex and genae. The frontalclypeal suture appears as a distinct black line. Individual ommatidia are distinguishable in an impression of the right compound eye on one of the counterparts. Eye diameter measured anterio-ventrally is 0.5 mm, although this may represent a minimum since it is difficult to discern a posterior edge to the eye.

The antennae (Figure VI-1, ant) are 8.8 mm long. They appear to be unipectinate, but may be bipectinate with one set of projections at right angles to the plane of fracture and embedded in matrix. The pectinations are club-shaped (maximum 0.6 mm long and 0.1 mm wide), arranged on the inner surface of the antennae. Pectinations are reduced in size apically and are absent from the apical third of the right antenna and the apical 4/5 of the left antenna. There are 32 pectinations on the left antenna and 19 on the right.

The proboscis (Figure VI-1, p)is extended, with the distal part split into the two component galeae. The measurable length is 2.2 mm, but the actual length will be slightly greater since the base is obscured. Width is 0.04 mm. Labial palpi (Figure VI-1,lp) are extended porrect to slightly upward in front of the head. The right palpus is elbowed between the first and second segment; the left palpus is fully extended. The right palpus, measured from the supposed base of the second segment to the apex is 1.0 mm long and 0.1 mm wide at its widest part. Scattered hairs are visible on the ventral surface of the right labial palpus. There is preserved material in the vicinity of the mouthparts that is extraneous to the palpi, proboscis and left prothoracic leg; no structures can be discerned here, but may represent maxillary palpi. Numerous hairs are present in this area as well.

Leg morphology was reconstructed from the counterparts and paired appendages. In the prothoracic legs (Figure VI-1,pro), the tibia is 2.8 mm long. In the mesothoracic legs (mes), the femur is 2.2 mm long, the tibia 1.8 mm and the tarsi are 3.0 mm (left) and 3.1 mm long (right). The segments of the metathoracic legs (met) are not measurable. On the mesothoracic legs, the femur has tufts of hairs near the inner base, outer center and inner apex; the apex of the left femur has short spines that point distally. The base of the tibia on the left mesothoracic leg has a spur extending obliquely from the posterior surface; there is as well an apical tibial spur on the right mesothoracic leg. On the mesothoracic legs, the tarsus is composed of 5 tarsomeres and a pair of pretarsal claws. Each tarsomere has one or two small apical spines; as well, there are one or two apical projections to the tarsomeres whereby a broad point overlaps the successive tarsomere. The basitarsus is the longest segment, occupying 40% of the whole tarsus. There are no scales on any of the legs. The coxa and femur of the right prothoracic leg have scattered hairs on their facing surfaces.

The mesoscutum is 1.5 mm between wing attachment and 1.8 mm long and has a dense covering of long (0.5 mm) hairs. The combined length of the thorax and abdomen is 10.6 mm; the abdomen 3.8 mm at its widest point. Seven abdominal segments are delineated by bars of dark material. No hairs are visible on the abdomen. There is a dark bar that lies inside the right margin of the abdomen that may be part of the genitalia or gut.

Wing span is 27.8 mm. Width of wings is not measurable since they are not fully spread. The front wings have squared off distal margins. The anterior and distal margin of the right wing and the distal margin of the left wing has a fringe of linear scales oriented at right angles to the wing margin. Scales and hairs occur at a position that probably corresponds with where the posterior margins of the hind wings meet. Hairs are dense and are oriented parallel to the body axis in a band that extends from the approximate anterior edge of the abdomen to half-way down its length. Posterior to this, there are numerous isolated hairs and scales scattered from the middle of the abdomen to the distal wing margins, being more dense anteriorly. Where the basal right wing margin has broken off there is a dense band of obliquely-oriented scales or hairs that corresponds to the base of the sub-costal vein. This may be the retinaculum, although it is entirely absent from the left wing.

Identification

The families which were excluded from consideration because they showed one or more critical characteristics not found in the fossil are as follows. Small forms (< 20 mm wing span) with narrow or lanceolate wings were eliminated (Nepticulidae, Opostegidae, Tischeriidae, Heliozelidae, Lyonetiidae, Gracillariidae, Elaschistidae, Blastobasidae, Coleophoridae, Momphidae, Agonexidae, Scythrididae, Epermeniidae, Glyphipterigidae, Argyresthiidae, Douglasiidae, Acrolepiidae, Heliodinidae). Cosmopterigidae were eliminated by virtue of the long, narrow wings, Alucitidae and Pterophoridae due to plume-like wings and Carposinidae, Plutellidae, Choreutidae and Epipyropidae due to very small size. Eriocraniidae was eliminated because taxa have aculeae on the wings (as does Hepialidae, Nepticulidae and Incurvariidae). Families in which wing scales are entirely absent (Sesiidae) or absent in patches (Thyrididae, Apatelodidae) were not included. Drepanidae was eliminated because of the characteristic hooked tips to the fore wings.

Families in which the proboscis is vestigial or absent were excluded (Micropterygidae, Hepialidae, Psychidae, Cossidae, Cochylidae, Limacodidae, Bombycidae, Lasiocampidae); Epiplemidae was not considered because it apparently has vestigial labial palpi. Superfamilies and families with antennae not pectinate were eliminated (Hepialidae, Incurvariidae, Tineidae, Oschenheimeriidae, Oecophoridae, Coleophoridae, Gelechiidae, Olethreutidae, Yponomeutidae, Hesperioidea, Papilionoidea, Hyblaeidae, Thyatiridae, Sphingoidea). There were several families (Aconthopteroctetidae, Momphidae, Copromorphidae, Dalceridae, Sematuridae, Uraniidae, Dioptidae) in which no information on the characters was available; these were excluded from consideration.

Characteristics of the 11 remaining families are shown in Table VI-1. Of these, only five families (Tortricidae, Zygaenidae, Geometridae, Arctiidae, Noctuidae) match several of the characteristics of the fossil. In the Tortricidae, the apical segment of the labial palpus is turned down, the head has rough scales, there are no long hairs on the wings and the proboscis is short to vestigial, characteristics that differ from the fossil; as well, the family usually has filiform antennae. In the Zygaenidae, labial palpi are short and upturned, rather than long and porrect as in the fossil. Taxa in the Pyralidae have conspicuously long, narrow legs and long tibial spurs, usually filiform antennae and have the base of the labial palpi conspicuously scaled; this combination of characteristics is not found in the fossil. In the Arctiidae, labial palpi are short and the proboscis is usually reduced, as opposed to the long palpi and proboscis seen in the fossil. Noctuidae are robust and heavily scaled, unlike the more gracile fossil, and have upturned labial palpi. In the Geometridae, labial palpi are upturned, unlike the porrect structure in the fossil.

Of the extant specimens examined, only taxa in the Geometridae exhibited characteristics of the proboscis, antennae and head that closely resembled the fossil specimen. Although there was a range of lengths for the proboscis in different geometrids, it was uniformly unscaled, a distinct characteristic in the fossil. The maximum length of the labial palpi observed in the extant specimens was about 1.5 times the head diameter; in the fossil specimen, labial palpi were shorter than the head diameter, and thus within the range seen in extants. Only in the Geometridae were there extant specimens with pectinate antennae in which the pectinations were similar in shape and number to the fossil. For example, in Anacamptodes lanaria (Subfamily Ennominae), there were 34 pectinations arranged 4/5 of the length of the antennae, with the pectinations in the middle of the antennae longest and those at the apex and base of decreasing size. Several species (for example, Dasyfidonia avuncularia) in the subfamily have elongate hairs on the vertex rather than short or broad scales. Long hairs were present on the side and dorsal thorax in a few specimens. There are two noteworthy differences between the fossil and the extant specimens examined: extant proboscides appear thicker than that of the fossil and secondly, most of the extant species had a subcostal frenulum hook rather than the probable retinaculum seen on the fossil. On the basis of the close match between the structure of the fossil and many of the extant specimens examined, UAPAL 66000 is classified in the Geometridae.

Stratigraphic occurrence

Specimen UAPAL 66000 is the earliest known Geometridae in the fossil record. The family is reported from the late Eocene Baltic amber (Handlirsch 1908) and the Oligocene of the Florissant shales (Wilson 1978).

B. UAPAL 4579

Description and identification

Specimen UAPAL 4579 (Figure VI-2) is a hind wing fragment 11.2 mm wide with 8 veins present. A basal areole is formed from the fusion of $Sc+R_1$ and Rs; the junction of Rs and M_1 arises from the discal cell. M_2 arises mid-way between M_1 and M_3 (Cu appears 3-branched), slightly distad of the discal cell. This combination of characters is found in the Noctuidae (Borror et al. 1976, Covell 1984). Both a 4-branched and 3-branched media is found in this family, but when it appears 3-branched, M_2 is faint, as is the case in the fossil. Noctuids have a basal areole in the hind wing, and $Sc+R_1$ and Rs are fused for only a short distance beyond the basal areole. Rs and M_1 may be stalked at or beyond the discal cell in the family (Holland 1968). The specimen belongs to one of the smaller subfamilies of Noctuidae in which the cubitus is 3-branched. Extrapolating from the size of the wing fragment, the wing span of the whole lepidopteran would be approximately 50 mm, which is within the size range of many noctuids.

Stratigraphic occurrence

This is the earliest report of the Noctuidae in the stratigraphic record. A lepidopteran egg from the Upper Cretaceous in Massachusetts classified as Noctuidae (Gall and Tiffney 1983) is considered suspect by Whalley (1986) since egg characteristcs are not diagnostic at the family level.

DISCUSSION

Although Lepidoptera is one of the taxonomically most well-studied orders of insects, phylogenetic relationships, especially among the more derived superfamilies, are still uncertain. There is at present general agreement that the order consists of five monophyletic suborders (Brock 1971, Common 1975), the primary character separating them being the structure of the female genitalia. Feeding structures differ in the suborders as well and are crucial to the behaviour of lepidopterans as pollinators (Common 1975). The Zeugloptera have the least derived mouthparts, with functional mandibles and no proboscis. Dacnonypha, Exoporia and Monotrysia show a range in feeding structures between the primitive mandibulate condition and the sucking haustellate mouthparts. In the Ditrysia, the mandibles are usually vestigial and the galeae are modified into a proboscis for sucking liquids. There may be secondary reduction or loss in the proboscis in ditrysians.

The term microlepidoptera refers to the four primitive orders and to the small-sized taxa in Ditrysia, while macrolepidoptera is a polyphyletic group of ditrysians which include the butterflies and some of the large, more derived moths (Papilionoidea, Bombycoidea, Geometroidea, Noctuoidea) (Brock 1971). The phylogeny of Brock (1971) for Ditrysia has been generally accepted: of the primitive ditrysians (Tineoidea, Yponomeutoidea, Gelechioidea, Copromorphoidea and Tortricoidea), a tortricoid form radiated into the Castnioidea, Cossoidea, Pyraloidea, Zygaenoidea and Aegerioidea. The macrolepidopterans evolved independently from these groups, Papilionoidea diverging from Castnioidea, Bombycoidea from Cossoidea and Geometroidea and Noctuoidea from Pyraloidea. The two specimens described here (Geometroidea, Noctuoidea), in addition to the Papilionoidea (Durden and Rose 1978), put a time frame on the reconstructed phylogeny, demonstrating that the diversification of the ditrysians, at least at the level of superfamily, had occurred by the Middle Eocene.

Triassic fossils from Australia (*Eocorona*, *Eoses triassica*; Tindale 1945, 1980) that have been attributed to Lepidoptera are now considered to belong to Trichoptera or Mecoptera (Whalley 1986). *Archaeolepis*, from the Jurassic of England may be a primitive lepidopteran (Whalley 1985) and *Eolepidopterix* is placed in the extinct family Eolepidopterigidae, closely related to the Zeugloptera (Whalley 1986). Most of the Cretaceous lepidopterans belong to the primitive, non-ditrysian suborders: *Undopterix* (Zeugloptera) from Transbaikalia (Skalski 1979), Incurvariidae scales (Monotrysia) and *Parasabatinca*

(Zeugloptera) from Lebanese amber (Whalley 1977), a caterpillar and 3 imagines (Incurvariina, Monotrysia) from Siberian amber (Zherikhin and Sukacheva 1973) and zeuglopteran scales from French amber (Kuhne et al. 1973). Also in the Cretaceous are Daiopterix from the USSR in the extinct Eolepidopterigidae (Skalski 1984) and a possible Tineidae (Ditrysia, Tineoidea) head capsule from Canadian amber (MacKay 1970). The preponderance of groups with primitive, mandibulate mouthparts among Jurassic and Cretaceous fossils suggests that lepidopterans may not have been important pollinators prior to the Tertiary.

There are no extensive Paleocene insect faunas known and by the Middle Eocene, representatives of highly derived Ditrysia (Thyrididae, Papilionidae, Lycaenidae, Geometridae and Noctuidae) are present, as well as the primitive ditrysian Yponomeutidae (Durden and Rose 1978, Wilson 1978, this study). Extant taxa in these families feed on floral nectar; the Geometridae specimen described here with its well-developed proboscis is direct evidence for nectar feeding on flowers with narrow, stereomorphic corollas. The late Cretaceous and early Paleogene may have been a period of rapid evolutionary change among the lepidoptera, with a shift from chewing to sucking mouthparts and a concomitant dependency on floral nectar for adult diet.

By the end of the Paleogene, lepidopteran diversity was high, with about half of the modern microlepidopteran families and the majority of macrolepidopteran superfamilies represented (Scudder 1889, Cockerell 1907, 1933, Cockerell and Levesque 1931, Handlirsch 1908, Forbes 1931, Kinzelbach 1970, Larsson 1978, Wilson 1978, Willemstein 1987).

This is the first report of a fossil proboscis, and its significance in setting the upper time bracket for the origin of flower feeding in lepidopterans is apparent. The proboscis appeared to be substantially narrower than those in extant specimens. It is difficult to make definitive statements on the significance of the differences since they may be a result of the small geographical range in the extant collection. Examination of a broad geographical and taxonomic range of specimens in the family will determine whether the differences represent variability among extant taxa or actual evolutionary changes over time.

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Table VI-1. Characteristics of extant families of Lepidoptera in comparison to specimen UAPAL 66000. Classification follows Covell (1984). Porrect = projecting forward; "-" = no data available on the character.

Family	Wing span (mm)	Labial palpi	Antennae	Proboscis
fossil specimen	27.8	long, extended, with hairs	unipectinate or bipectinate	long, naked
Tortricidae	10-33	porrect with apical segment turned down	usually filiform	naked or scaled, short or vestigial
Zygaenidae	16-28	short, porrect	bipectinate	naked
Megalopygidae	24-40	reduced	bipectinate	reduced
Pyralidae	9-62	long, porrect	usually simple	scaled at base
Geometridae	10-60	short, porrect	filiform, bipectinate or unipectinate	naked, short to long porrect to upturned
Mimallonidae	20-50	reduced	bipectinate	reduced
Saturniidae	30-150	small	unipectinate, bipectinate or 4-pectinate	reduced or absent
Notodontidae	23-62	-	bipectinate	developed or reduced
Arctiidae	12-70	short	bipectinate	absent to developed
Lymantriidae	15-67	well-developed	bipectinate	reduced to absent
Noctuidae	12-170	usually long, upturned	simple to bipectinate	developed

Figure VI-1. UWBM 66000; Klondike Mountain Formation, Republic, Washington; X 12. Abbreviations: ant, antennae; lp, labial palpus; mes, mesothoracic leg; met, metathoracic leg; p, proboscis; pro, prothoracic leg;

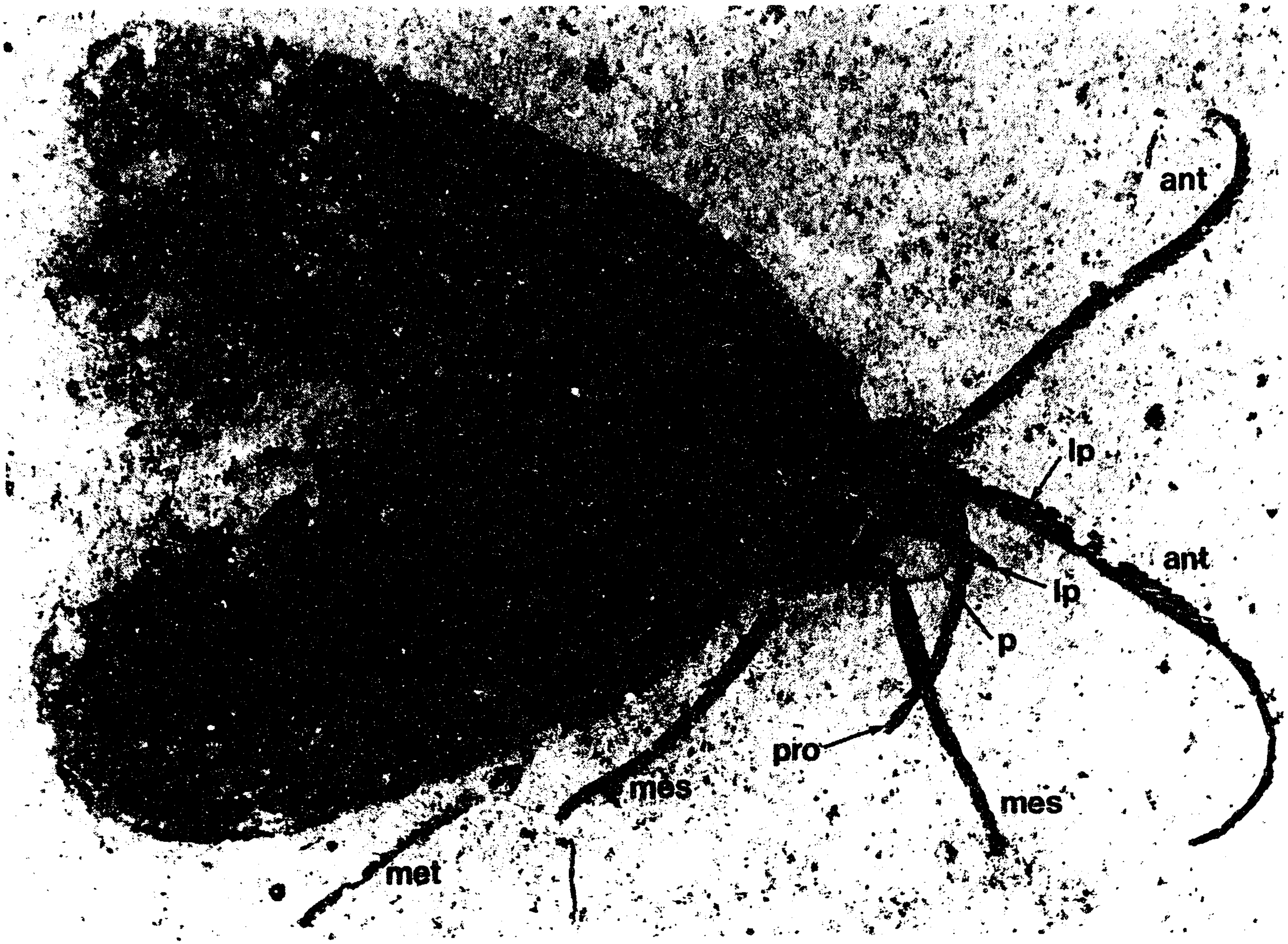
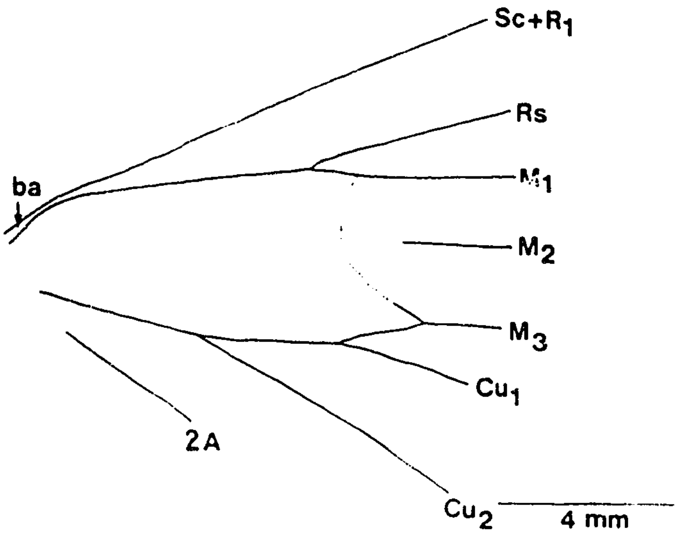

ant
lp
ant
lp
p
pro
mes
mes
met

Figure VI-2. UAPAL 4579; Allenby Formation, Quilchena, British Columbia. Abbreviations: A, anal; ba, basal areale; Cu, cubitus; M, media; R, radius; Rs, radial sector; Sc, subcosta.


Sc+R1
Rs
ba
M1
M2
M3
Cu1
2A
Cu2
4 mm

VII. INSECT POLLINATION IN MIDDLE EOCENE ANGIOSPERMS OF BRITISH COLUMBIA AND WASHINGTON STATE

INTRODUCTION

Evidence for intimate paleoecological associations between species is uncommon; scattered examples occur such as parasitism of spiders by Ichneumonidae larvae preserved in Dominican amber (Poinar 1987) and predatory fish preserved with prey in their mouths in the Eocene Green River Formation (Grande 1984). In paleoanthecology, evidence for pollinator-plant interactions are rare as well. Pollen identifiable to genus has been found in the digestive tracts of beetles preserved in Baltic amber (Willemstein 1987), indicating a floral association. A lepidopteran with a well-developed proboscis is present in the Middle Eocene strata at Republic (Chapter VI).

However, most conclusions on interactions between taxa are made on uniformitarian principles. Inferences on pollinators of Paleogene flowers have been made (Crepet and Dilcher 1977, Crepet 1979a, 1979b, 1985, Crepet and Taylor 1985, Willemstein 1987) based on broad flower form categories used to describe extant plants (Faegri and van der Pijl 1979). Phylogenetic information such as the occurrence of sister-groups has also been used as evidence for the presence of taxa not yet found in the fossil record (Willemstein 1987).

In the Middle Eocene of British Columbia and Republic, northern Washington, there is a diversity of flowers and inflorescences (Chapters III and IV); insect specimens representing 34 families in the four anthophilous orders (Coleoptera, Hymenoptera, Diptera, Lepidoptera) are also present (Chapter V, Wilson 1978). The purpose of this paper is to define the constellation of pollinating agents available to Middle Eocene flowers of this area. I will review the degree to which insects in the four orders are dependent on nectar and pollen. The stratigraphic occurrence of anthophilous families will be compiled, and insect taxa coeval with fossil flowers of this area will be ranked according to their predicted importance in pollination. Phylogenetic and biogeographical evidence for presence of taxa not represented by fossils will also be examined. Although insects are probably the primary biotic pollinating agents in the Paleogene (Willemstein 1987), the potential of birds and mammals as pollinators will also be discussed.

METHODS

Classification of Coleoptera follows Borror et al. (1976). Hymenoptera classification follows Gauld and Bolton (1988) for the Symphyta and the parasitic Apocrita and Daly et al. (1978) for the aculeate Apocrita. I follow Gauld and Bolton (1988) in retaining the informal distinction between the parasitic Apocrita and the aculeate Apocrita because of its usefulness in discussing the different feeding behaviours of the two groups. For the same reasons -- facilitating recognition of behavioural differences between groups -- I do not reduce the number of aculeate superfamilies, as has been suggested by several taxonomists (Brothers 1975, Gauld and Bolton 1988). The taxonomic classification used reflects the phylogeny of the Hymenoptera, as it is understood today, well enough that inferences on the geological appearance of groups can be made from the classification.

Classification of Diptera follows McAlpine et al. (1981) and McAlpine (1987), recognizing the two suborders Nematocera and Brachycera. For Lepidoptera, classification follows Borror et al. (1976) and Covell (1984), in which five suborders (Zeugloptera, Dacnonypha, Exoporia, Monotrysia, Ditrysia) are recognized. The informal designation of microlepidoptera refers to the four most primitive orders plus several families of small, primitive Ditrysia, while macrolepidoptera refers to a polyphyletic group of Ditrysia which includes the butterflies and some of the larger, more derived moths (Superfamilies Papilionoidea, Bombycoidea, Geometroidea, Noctuoidea).

The flower feeding habits and the degree of specialization on pollen, nectar or other floral rewards was assessed at the family level (and occasionally subfamily) using various sources (Dillon and Dillon 1961, Hocking 1968, Holland 1968, Free 1970, Cruden 1972, Kevan 1972, Borror et al. 1976, Smith and Snow 1976, Stelleman and Meeuse 1976, Richards and Davies 1977, Stevenson and Thomas 1977, Daly et al. 1978, Willson and Bertin 1979, Ackerman and Mesler 1979, Faegri and van der Pijl 1979, Hutson et al. 1980, Crowson 1981, McAlpine et al. 1981, Motten 1982, Grant and Grant 1983, Covell 1984, Travis 1984, Thien et al. 1985, Jessop 1986, McAlpine 1987, Willemstein 1987, Gauld and Bolton 1988). Families in which no information is available are excluded. For lepidopterans, the presence of a proboscis was considered as positive evidence for nectar feeding. Citations for flower feeding in birds and mammals are included in the text.

Stratigraphic occurrence of families within the four orders of insects was surveyed using primary sources and, where appropriate, using previously compiled records. The summary by Handlirsch (1908) was used for many of the European records previous to 1900; Wilson (1978) was used for North American Oligocene localities and Larsson (1978) for specimens in Baltic amber. The compilation by Crowson (1981) was used for many Coleoptera families. In discussion of the stratigraphic occurrence of families, all records from the Middle Eocene and earlier are considered; only representative localities from later in the Paleogene are included (Baltic amber, Florissant). Appendix 5 lists the fossil localities and references for all insect families; the ages of localities is given in Appendix 6. Sources for the stratigraphic tables are: Scudder 1889, 1890, 1895, Cockerell 1907a, 1907b, 1907c, 1908a, 1908b, 1914a, 1914b, 1933, Handlirsch 1908, 1910, Tillyard and Dunstan 1923, Cockerell and Levesque 1931, Forbes 1931, James 1932, Pongracz 1935, Carpenter et al. 1937, Rice 1959, Evans 1969, 1973, McAlpine and Martin 1969, MacKay 1969, Kinzelbach 1970, McAlpine 1970, 1987, Teskey 1970, Saunders et al. 1974, Peterson 1977, Rasnitsyn 1977, Whalley 1977, 1986, Wilson 1977, 1978, Durden and Rose 1978, Larsson 1978, Skalski 1979, Mitchell and Wighton 1979, Crowson 1981, Hennig 1981, McAlpine et al. 1981, Beach 1982, Gall and Tiffney 1983, Grande 1984, Jarzembowski 1984, Lutz 1986, 1987, Zeitsev 1986, Day 1988, Dlusskiy 1988, Grogan and Szadziewski 1988, Ruttner 1988, Schaal and Ziegler 1988, Forster 1989.

RESULTS AND DISCUSSION

Anthophily and pollinating behaviour among extant insects

Coleoptera

There are at least forty-one families of extant coleopterans in which some taxa feed on nectar or pollen (Table VII-1a). The majority of anthophilous taxa feed on pollen, having primarily chewing mouthparts. Only adults are anthophilous; none are known to store pollen or nectar or to provision larvae. A few groups visit carrion-scented flowers or collect at flowers for mating (Faegri and van der Pijl 1979, Beach 1982). Specialized mouthparts for feeding on pollen and nectar (prognathy, long or spatulate setae on the maxillae or labium facilitating capture of pollen) are found in some Dascillidae, Cantharidae, anthophilous Scarabaeidae, Melyridae, Oedemeridae, Mordellidae, Meloidae and Cerambycidae (Crowson 1981, Willemstein 1987). Although the habit of generalist pollen feeding is taxonomically widespread, trends towards specialization have occurred in only a few clades (Melooidea and Chrysomeloidea), but not to exclusivity.

The pollen feeding behaviour of coleopterans is, on the whole, unspecialized, landing on open flowers and chewing easily-accessible pollen (Faegri and van der Pijl 1979). Nectar feeding may be more widespread than is commonly acknowledged; beetles from seven families were found to lap nectar from nectaries in unspecialized flowers in the Liliaceae and five species carried large pollen loads (Travis 1984). Nemognatha is a specialized nectar feeder, with the galeae modified into a sucking tube up to 7.5 mm long (Daly et al. 1978). As far as is known, there are no coleopterans that hover while they feed on flowers.

Coleopterans are generally regarded as sub-optimal pollinators, probably since many floral visits are incidental to pollination; this does not negate the presence of several specialized, pollen-carrying beetles among extant groups.

The stratigraphic occurrence of anthophilous coleopterans is given in Table VII-1b. Of the ten families that have specialist flower-feeding taxa (that is, with morphological modifications for feeding on pollen or nectar, or that have been identified in the literature as having taxa that are obligate flower feeders), half have a fossil record extending back into the Mesozoic (Dascillidae, Nitidulidae, Oedemeridae, Cerambycidae, Chrysomelidae); Scarabaeidae, Cantharidae and Mordellidae are first recorded from the Middle Eocene while Melyridae and Meloidae are not present as fossils until the Oligocene. However, there appears to be no information from fossils that morphological structures or behaviour for specializing on pollen or nectar were present in the Eocene or previously. Reticulate tricolporate pollen typical of entomophilous flowers has been found on a fossil mordellid from the Baltic amber (Willemstein 1987).

Eleven anthophilous families of coleopterans are represented at the Middle Eocene British Columbia-Republic localities (see Table VII-1b); five of these belong to the specialist families defined above (Scarabaeidae, Cantharidae, Mordellidae, Cerambycidae, Chrysomelidae). An additional five families, one of them with specialist flower-feeders (Nitidulidae), are represented in the Middle Eocene Green River rmation (Table VII-1b). All of the families except the Mordellidae have taxa that are non-obligate flower feeders, so the possibility exists that pollen- and nectar-feeding and pollen transport by coleopterans was minimal at the time. However, considering the diversity of anthophilous coleopterans available to Middle Eocene flowers, I conclude that pollination by generalist and at least one specialist (Mordellidae) group of coleopterans was present.

Hymenoptera

At least 29 families of Hymenoptera are known to be anthophilous (Table VII-2a). Nectar and pollen feeding is widespread in the Symphyta and parasitic Apocrita, but with the exception of the Agaonidae, anthophilous taxa are not wholly dependent on flowers for food. In the aculeate Apocrita, a range of flower dependency exists. The most derived of the Hymenoptera, the Apoidea, are obligate flower feeders as adults and larvae, the adults feeding on nectar and the larvae provisioned with pollen and nectar, and in some groups (Anthophoridae, Melittidae), oils produced by floral elaiophores. There are several groups in which cleptoparasitism occurs (Halictidae, Megachilidae and Anthophoridae), but larvae are still maintained on floral foods. Characteristics associated with pollen collection and transport (branched or plumose hairs, corbiculae or scopae) (Michener et al. 1978, Thorp 1979) have evolved in the Apoidea concomitant with obligate flower feeding. Eusociality, in which cooperative brood care, reproductive castes, and overlap of generations in the colony is found (Wilson 1971), have evolved in the Halictini (Halictidae), Ceratini (Anthophoridae) and Apidae. In the non-apoid aculeate apocritans, flower feeding is common in adults, but adults provision larvae with insect prey and show a range of brood care behaviour and sociality. In some of the non-apoid hymenopterans (Chrysididae, Masarinae and Sphecidae), the proboscis is elongate, comparable to that of the apoids. In the Masarinae (Vespidae), obligate flower feeding occurs, with adults provisioning the nests with pollen and nectar.

Among many of the aculeate Apocrita, and incontrovertibly in the Apoidea, behaviours that optimize recognition of flowers, manipulation of flowers to obtain food, and optimal ways of foraging for nectar and pollen have evolved (Faegri and van der Pijl 1979). All hymenopterans alight on flowers rather than hover; in visits to actinomorphic flowers, pollen collects ventrally on the body and in highly stereomorphic flowers with narrow corolla openings, pollen collects ventrally or is deposited dorsally on the head and thorax, depending on the orientation of the insect to the anthers. The length of the proboscis varies, for example, with Adrenidae, Colletidae and Halictidae having relatively short "tongues" and Megachilidae, Anthophoridae and Apidae with long tongues. In Bombus (Bombini, Apidae), proboscis length ranges between species and between castes of the same species; for example, B. terricola queens have a mean tongue length (prementum + glossa) of 9.4 mm and B. fervidus queens a mean length of 13.3 mm, while workers of B. terricola have tongues 65% shorter than queens (Heinrich 1976)). The length of the proboscis determines the depth of corollas that are accessible for nectar (Heinrich 1976, Ranta and Lundberg 1980). The pollen carrying capacity of hymenopterans is high in the Apoidea, where branched or plumose hairs (an autapomorphy of Apoidea) facilitate pollen adhesion.

The stratigraphic occurrence of Hymenoptera is shown in Table VII-

2b. The only records of obligate flower feeders (Agaonidae, Apoidea) prior to the Baltic amber (Late Eocene-Early Oligocene) are a Meliponinae (Apidae) from New Jersey amber (Michener and Grimaldi 1988a, 1988b) and an Anthophoridae, reported but not described, from Middle Eocene Messel, Germany. There is also a questionable record of Anthophoridae from the Green River Formation. Non-apoid aculeate families whose extant members are dependent on nectar as adults and that have elongate proboscises (Scoliidae, Vespidae, Sphecidae) are present by the Middle Eocene. Many of the symphytan and parasitic apocritan families that have taxa feeding on nectar and pollen have a pre-Oligocene fossil record.

Since the Apoidea are the most important insect pollinators of extant flowers, it is necessary to look at their geological history in greater detail. The earliest apoid hymenopteran is Trigona (Meliponinae, Apidae) from New Jersey amber (Michener and Grimaldi 1988a, 1988b). Anthophoridae is reported from the Middle Eocene of Messel, Germany (Schaal and Ziegler 1988). The Andrenidae and Apidae are present in Baltic amber (Late Eocene or Early Oligocene); the Apidae are represented by several species of Trigona and Electrapis, the latter considered to be a group of species ancestral to all recent Apidae (Ruttner 1988). Compression specimens of Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae and Apidae (Bombinae) have been identified from the Lower Oligocene Florissant Shales. Specimens assignable to Apis are not found until the Early Miocene of Rott (Ruttner 1988).

Michener (1979) has argued that the widespread tropical distribution of extant Trigona and its allies in South America and southern Africa indicates that the subfamily originated in western Gondwana and underwent adaptive radiation during or shortly after the breakup of the supercontinent; he considers South America and Africa to be close enough for faunal dispersal until the Early Paleocene. The Meliponinae is the oldest subfamily in the Apidae (Ruttner 1988); its Upper Cretaceous occurrence does not preclude a much later origination of the other subfamilies (Apinae and Bombinae).

There is compelling floral evidence for the presence of oil-collecting apoid bees during the Middle Eocene. Fossil flowers with paired sepal glands (Eoglandulosum warmanensis, Malpighiaceae) have been described from the Middle Eocene Claiborne Formation of Tennessee (Taylor and Crepet 1987). In many extant species of Malpighiaceae, oils produced by sepal elaiophores are collected by solitary anthophorid bees (Anthophorinae), mixed with pollen and transported to the nest. Some melittid bees also collect floral oils (Gauld and Bolton 1988).

Eight families of anthophilous Hymenoptera are present at British Columbia-Republic; only two (Scoliidae, Vespidae) are dependent as adults on floral food (nectar). There are seven families of anthophilous Hymenoptera reported from Green River; only one of these, a questionable report of Anthophoridae, is an obligate flower-feeder at all life stages. The Upper Cretaceous Trigona from New Jersey is an important addition to the pollinator diversity of North America. Although there are hymenopterans that feed exclusively on nectar as adults, and could potentially effect pollination by transporting pollen, the fossil record for North America indicates that the groups of hymenopterans that are dependent on floral foods at all life stages, have adaptations for collecting and transporting pollen and are capable of obtaining food from complex flowers (the Apoidea) were present in low diversity and numbers. Hymenopteran pollination at British Columbia-Republic, however, consisted of a more generalist, less flower-constant constellation of insects.

Diptera

At least 48 families of Diptera contain anthophilous taxa (Table VII-3a). The majority of anthophilous taxa are nectarivorous, but there are a few that chew pollen; nectar and pollen are not used as larval foods. In the Nematocera, nectar feeding is widespread and common but there are few obligate nectar feeders (male Culicidae and Ceratopogonidae and some Bibionidae). Extant Bibionidae are important pollinators of fruit crops (Free 1970), feeding on nectar. Among several brachyceran families (Apioceridae, Tabanidae, Nemestrinidae, Acroceridae, Bombyliidae, Pipunculidae, Syrphidae, Conopidae, Tachinidae), there are specialist flower feeders with elongate mouthparts; among the tropical tabanids and nemestrinids are taxa which hover at flowers while feeding (Faegri and van der Pijl 1979, Daly et al. 1978). Extant nearctic Syrphidae feed on both pollen and nectar and are able to hover at flowers (Vockeroth and Thompson 1987). Other brachycerans that show some dependence on floral foods are the Stratiomyidae, Mydidae, Empididae, Lonchopteridae and Lauxaniidae. For many groups, both nematoceran and brachyceran, nectar feeding is part of a generalist behaviour for insects with a sponging or sucking haustellum and mainly liquid diet. There are no strong evolutionary trends towards specialization in any clades except the Bombylioidea and the Syrphoidea.

Taxa that alight on flowers collect pollen ventrally. Those that hover are capable of feeding from stereomorphic flowers that do not have perianth parts to land on or grasp, collecting pollen on the face and head. Those with elongate haustelli are able, similar to bees, to feed on nectar in flowers with a narrow perianth opening; pollen will collect on the head or, if the pollinator crawls into the flower, ventrally or dorsally depending on the position of the insect in relation to the anthers (Faegri and van der Pijl 1979). Although dipterans do not have plumose hairs specialized for pollen adherence, many are setose.

The stratigraphic appearance of anthophilous Diptera is shown in Table VII-3b. The Bombylioidea have a Mesozoic history, although there is no fossil evidence for the early evolution of long haustellate mouthparts. The oldest Syrphoidea are from the Middle Eocene in both North America and Europe. Only four of the remaining 12 families that have floral dependent groups are pre-Eocene. It is probable that the Bombylioid lineage had an early radiation (Mesozoic) into floral feeding and could be expected to be the earliest dipteran group to have evolved an elongate haustellum in association with increasing floral stereomorphy. The other groups may have originated flower feeding later in the Mesozoic or in the Paleogene.

Seven of the 48 families of Diptera categorized as anthophilous are present at British Columbia-Republic; only three of these (Bibionidae, Empididae, Syrphidae) show a high degree of dependence on floral foods. Many syrphids are important pollinators (Free 1970, Kevan 1972, Stelleman and Meeuse 1976, Motten 1982, Douglas 1983, Travis 1984, Vockeroth and Thompson 1987). Specimens belonging to the Bibionidae were the most common fossils in a sample of insects from British Columbia and Republic analyzed in Chapter V. Their abundance in other North American Paleogene sediments has been noted (Rice 1959, Wilson 1978). In extant bibionids, Bibio and Doliphus are "supplementary" pollinators of fruit crops, apoid bees being the most important (Free 1970). Bibio is the primary pollinator in a population of Nemophila (Hydrophyllaceae) in which its usual pollinators, apoid bees, are absent. Although anthophilous diptera do not have the energy requirements and larval dependents of apoid bees, they are effective pollinators by sheer numbers (Faegri and van der Pijl 1979).

Nineteen families of anthophilous dipterans are represented at Green River; eight of these (Bibionidae, Culicidae, Stratiomyidae, Acroceridae, Empididae, Syrphidae, Conopidae, Tachinidae) are dependent to a greater extent on floral foods. The presence of the Acroceridae is an important element in the pollinator constellation of Green River, in addition to the syrphids and bibionids.

I conclude that syrphids and bibionids are significant dipteran pollinators in the Middle Eocene of British Columbia-Republic and that a low number of incidental pollinators have a lesser part in pollination. The dipteran pollination regime for North America as a whole is more diverse, with the important addition of the Acroceridae and numerous non-specialist nectar feeders from Green River.

Lepidoptera

Thirty-eight families of Lepidoptera are known in which imagines have a well-developed proboscis and presumably are obligate nectarivores

(Table VII-4a). Zeugloptera have the least derived mouthparts with functional mandibles and no proboscis. The three suborders, Dacnonypha, Exoporia and Monotrysia, show a range in feeding structures between the primitive mandibulate condition and the sucking haustellate mouthparts. In the Ditrysia, the mandibles are usually vestigial and the galeae are modified into a proboscis for sucking liquids. In several families, there has been secondary reduction or loss of the proboscis and some adults are non-feeding.

The ditrysian proboscis, with extreme lengths of 12 cm for the sphingid Manduca quinquemaculata (Daly et al. 1978), allows access to recessed nectaries in stereomorphic flowers with restrictive perianth openings. The Sesiidae (Clear-winged moths) and Sphingidae (Hawk moths) are known to hover at flowers while feeding.

The fossil record of the Lepidoptera is less extensive than the other three orders (Table VII-4b). Of the four primitive suborders, Zeugloptera, Dacnonypha and Monotrysia have a Mesozoic record; there is no fossil record of the Exporia. Except for Tineoidea, the ditrysian record begins in the Eocene; for many families in this suborder, no fossils have been found.

Two lepidopteran families have been reported from British Columbia-Republic (Chapter VI). The Geometridae is a large family (about 1400 species in North America alone; Covell 1984) of small- to medium-sized nocturnal lepidopterans. The proboscis is unscaled, and rarely reduced or absent. The Noctuidae is the largest family of lepidopterans (almost 3000 North American species); the proboscis is usually well-developed and they show a wide size range. Both families have pollinating groups (for example, Kevan 1972, Stephenson and Thomas 1977, Willson and Bertin 1979). The geometer specimen from Republic is the first record of the family and the first instance of a fossil proboscis; the proboscis is unscaled, narrow and 2 mm long (Chapter VI).

Four families of lepidopterans are reported from Green River. The Yponomeutidae are small moths with the proboscis unscaled; the Thyrididae are small- to medium-sized moths with a well-developed, unscaled proboscis. There are reports of flower feeding for both of the families (Willemstein 1987). Three species of macrolepidopterans, *Prepapilio colorado* and *P. gracilis* (Prepapilioninae, Papilionidae) and *Riodinella nympha* (Riodininae, Lycaenidae) have been described (Durden and Rose 1978). Both families are medium-sized to large diurnal lepidopterans with naked proboscises. Extant members of both families feed on nectar and have been reported as pollinators (for example, Smith and Snow 1976, Travis 1984).

Although the diversity of lepidopteran families is low for both British Columbia-Republic and Green River, the families that are present contain important pollinating taxa. Both diurnal and crepuscular-noctural lepidopterans are concluded to be a component of the pollination regime of the North American Middle Eocene.

Vertebrate pollinators

Birds

There are several families of birds that have independently evolved nectarivorous feeding habitats. This includes the New World Trochilidae (hummingbirds)and Coerebidae (honeycreepers and quits), the Hawaiian Drepanididae (Hawaiian honey-creepers), the Indo-Australian

Meliphagidae (honey-eaters), Acanthizidae (thornbills), Zosteropidae (silvereye) and Trichoglossidae (lorikeets) and the African and Asian Nectariniidae (sun-birds) (Sussman and Raven 1978, Faegri and van der Pijl 1979, Johnsgard 1983, Vanstone and Paton 1988). None of these families have a pre-Pleistocene fossil record (Sussman and Raven 1978, Olson 1985, Willemstein 1987). There is opportunistic feeding on flowers by taxa in many other passerine families (see Faegri and van der Pijl 1979); there are no definitive records of Passeriformes prior to the Miocene (Olson 1985).

Although pollination by birds is excluded from this study, being of too recent origin, it is relevant to note that plants with the tubular, sympetalous dicotyledonous flowers that are pollinated by hummingbirds are thought to have a homeoplastic origin, evolving independently from numerous different taxa with bee-pollinated flowers (Grant and Grant 1968).

Bats

Although bat-pollination (chiropterophily) is recognized as a single syndrome (Faegri and van der Pijl 1979), anthophily in bats is a convergent feeding habit, having evolved independently in the Old World megachiropterans (Macroglossinae, Pteropodidae) and the New World microchiropterans (Glossophaginae and Brachyphyllinae of the Phyllostomidae) (Hill and Smith 1984). There may be reasons to establish a subset of chiropterophily for each of the clades, since they differ in some aspects of feeding behaviour, the pteropodids landing on flowers or flower heads and the phyllostomids capable of hovering while feeding.

The earliest bat fossils are from the Eocene in Germany and Green

River, North America, although the order is thought to have originated in the Paleocene or Late Cretaceous (Hill and Smith 1984). *Icaronycteris index* from the Green River Formation (Jepsen 1966) is, on the evidence of tooth morphology, an insectivorous microchiropteran (Hill and Smith 1984). The morphological features of nectar and pollen feeding bats include modifications of the teeth, mandibles and wings (Heithaus 1982) which would presumably be recognizable in fossils. Due to the absence of such specialized structures in fossil bats, I conclude that anthophilous bats may not have been were not present during the Middle Eocene and can probably be eliminated as prospective pollinators.

Non-flying mammals

There are several taxa of nectarivorous small mammals that act as pollinators for extant plants, the best-documented being the marsupial honey possum (*Tarsipes*, Tarsipedidae) and pygmy possums (Burramyidae) in Australia (Hopper and Burbidge 1982, Turner 1982, Wooller et al. 1983) and nocturnal lemurs (Lemuridae) in Madagascar (Sussman and Raven 1978). The honey possum and lemurs are Recent, while the range of pygmy possums extends back to the Miocene (Nowak and Paradiso 1983). There is, however, a number of extinct marsupials and prosimians that may have fed on nectar and pollen during the Paleogene (Sussman and Raven 1978). Some of these families have been found at Green River (Adaphidae, Anaptomorphidae, Didelphidae; Grande 1984), but their feeding habitats are unknown. Faegri and van der Pijl (1979) have stated that there is no pollination syndrome for non-flying anthophilous mammals. A "marsupial pollination syndrome" has been proposed, but the characters used to define it (open flowers, nocturnal, strong odour, abundant nectar and pollen, dull- or light-coloured) are too general to be predictive and may well also describe chiropterophily. It has been proposed that anthophilous non-flying mammals may have been competitively displaced by nectarivorous bats in the Miocene (Sussman and Raven 1978). Although the possibility of pollination by small, non-flying mammals exists for North American Middle Eocene flowers, there is not sufficient information to assess the importance of this group.

SUMMARY

A summary of insect pollinators that are available to Middle Eocene flowers in British Columbia-Republic and in North America as a whole is given in Table VII-5. Based on the habits of extant insects, the families that would be the most important pollinators are Mordellidae, Syrphidae, Bibionidae, Scoliidae, Vespidae and all four families of large lepidopterans (Geometridae, Noctuidae, Papilionidae, Lycaenidae). Several apoid hymenopterans (Anthophoridae and Meliponinae) were present in North America and may have been critical pollinators. Many pollinating families found in Mesozoic strata in Europe, Asia and Australia could be expected to be present in North America, barring any restrictions of climate, food plants or geographic barriers. These are the coleopteran Dascillidae and Dermestidae, the symphytan Xyelidae and Pamphilidae, the dipteran Psychodidae, Nemestrinidae and Bombyliidae and the microlepidopteran Incurvariidae. Of these, nemestrinids and bombyliids would be a significant addition to the pollinator constellation of North America. Bird and bat pollinators are absent from the Middle Eocene, but possibly small marsupials and prosimians were pollinators. From the diversity of amentiferous staminate inflorescences (catkins), it is apparent that pollination by wind was widespread (Chapter III).

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Table VII-1a. Degree of specialization among anthophilous Coleoptera; adult feeding habits only. Taxa in which no flower associations are recorded are excluded. Classification follows Borror et al. (1976).

Taxa Suborder	 Superfamily	 Family	Floral reward[a]	Dependency on flowers[b]	Degree of anthophily[c]
POLYPHAGA	Histeroidea	Histeridae	c	-	-
	Staphylinoidea	Staphylinidae	c p	2	3
		Silphidae	c	-	-
	Dascilloidea	Dascillidae	r	2	-
	Scarabaeoidea	Lucanidae	r	2	3
		Scarabaeidae	n p	1	2
	Dryopoidea	Ptilodactylidae	r	-	-
	Buprestoidea	Buprestidae	p	2	3
	Elateroidea	Elateridae	n p	2	2
		Throscidae	r	2	3
	Cantharoidea	Lampyridae	p	2	3
		Cantheridae	p n	2	-
		Lycidae	r	2	3
	Dermestoidea	Derodontidae	p	2	3
		Dermestidae	n p c	2	3
	Bostrichoidea	Anobiidae	p	2	-
		Ptinidae	p	2	3
	Cleroidea	Cleridae	p	2	2
		Melyridae	n	2	2?

Table VII-1a (continued)

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
	Cucujoidea	Nitidulidae	n p	1?	2
		Cryptophagidae	r	2	2
		Languriidae	p	2	2
		Phalacridae	r	2	3
		Coccinellidae	r	2	3
		Endomychidae	r	2	-
		Lathridiidae	r	2	-
		Byturidae	r	-	2
	Tenebrionoidea	Tenebrionidae	p	2	3
		Lagriidae	r	2	3
		Alleculidae	p	2	2
		Pyrochroidae	r	2	2
		Oedemeridae	p	2	1?
		Melandryidae	r	2	2
	Melooidea	Mordellidae	n p	1	1
		Rhipiphoridae	r	2	2
		Meloidae			
		<u>Nemognatha</u> spp.	n	1	1
		Anthicidae	r	2	2
	Chrysomeloidea	Cerambycidae[d]	n p	1	1
		Bruchidae	r	2	3
		Chrysomelidae	n p	1	3

Table VII-la (continued)

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
	Curculionoidea	Anthribidae	r	2	3
		Curculionidae	p	2	3

a. p = pollen; n = nectar; r = floral reward unspecified.

b. 1 = obligate flower feeding (eutropic, eulectic) exists for some taxa within the family; 2 = some taxa within the family obtain food from flowers, but are not dependent on it (hemitropic, hemilectic, allotropic) and obligate flower feeding is absent; ? = categorization not definitive; - = insufficient information to categorize.

c. 1 = high (all taxa obtain food from flowers); 2 = moderate; 3 = low (only a few species feed at flowers). ? = categorization not definitive; - = insufficient information to categorize.

d. Subfamilies Lepturinae, Cerambycinae, Lamiinae.

Table VII-1b. Stratigraphic occurrence of anthophilous Coleoptera. Records previous to Upper Cretaceous are plotted on the far left of the chart. 1 = British Columbia-Republic; 2 = Green River. Record beginning in Upper Eocene is Baltic amber and beginning in Lower Oligocene is Florissant. Dashed line indicates questionable record.

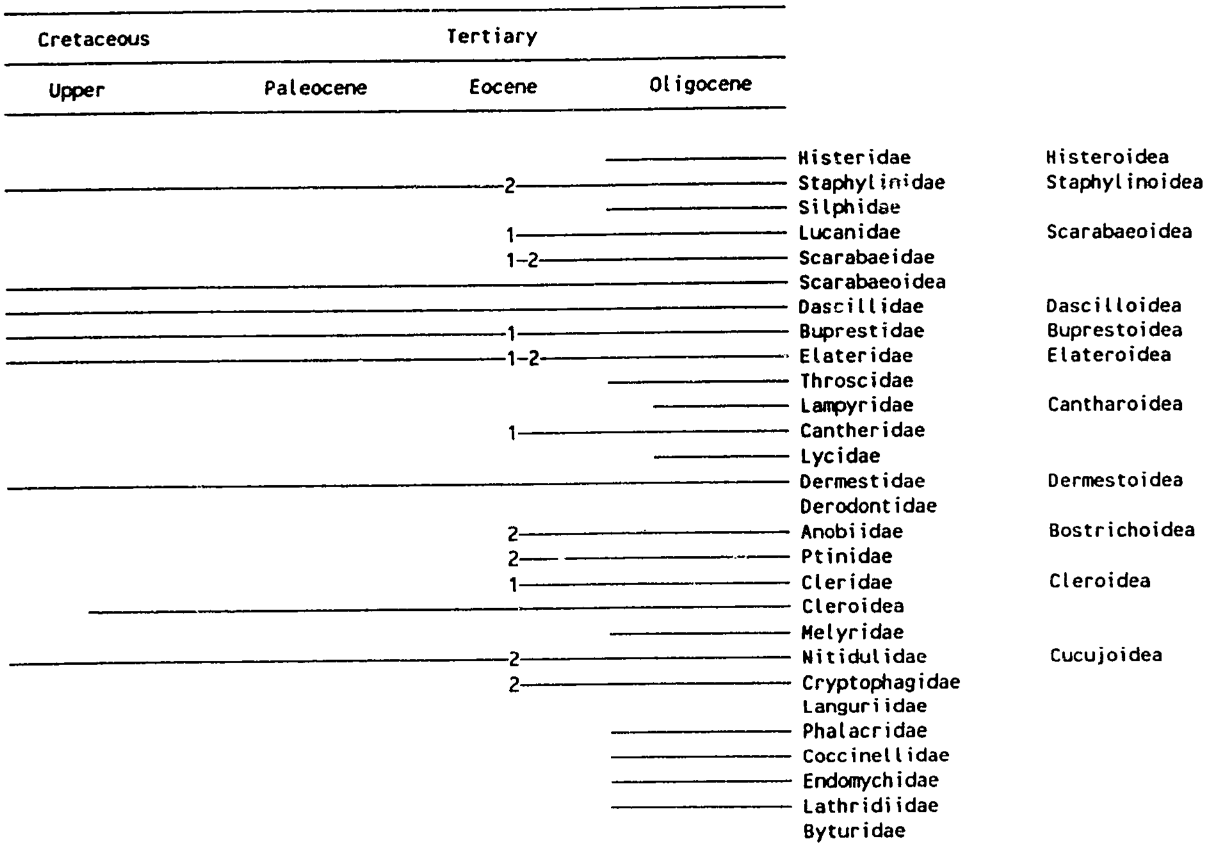

Table VII-1b (continued).

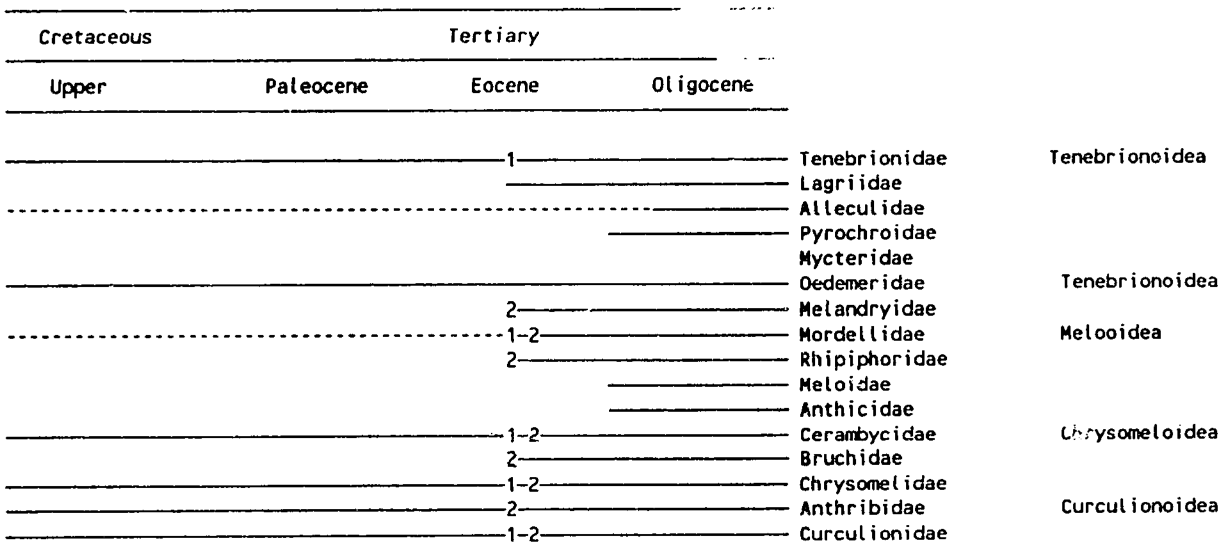

Table VII-2a. Degree of specialization among anthophilous Hymenoptera. Taxa in which no flower associations are recorded are excluded. Classification of Symphyta and parasitic Apocrita follows Gauld and Bolton (1988) and classification of aculeate Apocrita, Daly et al. (1978).

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
SYMPHYTA	Xyeloidea	Xyelidae	p	2	-
	Megalodontoidea	Pamphiliidae	r	2	3
		Megalodontidae	n p	2	2
	Tenthredinoidea	Argidae	r	2	3
		Cimbicidae	r	2	2
		Tenthredinidae	n p	2	3
		Pergidae	r	2	3
	Cephoidea	Cephidae	r	2	-
APOCRITA	Evanioidea	Gasteruptiidae	n	2	-
(parasitic)	Cynipoidea	Cynipidae	r	2	-
	Chalcidoidea	Chalcididae	r	2	3
		Agaonidae	p	1A	1
	Ichneumonoidea	Ichneumonidae	n	2	2
		Braconidae	n	2	-
APOCRITA	Chrysidoidea	Chrysididae	n	1B	2
(aculeate)	Scolioidea	Tiphiidae	n	2	-
		Mutillidae	n	2	-
		Scoliidae	n	1B	1

Table VII-2a (continued).

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
APOCRITA	Pompiloidea	Pompilidae	n	2	-
(aculeate)	Formicoidea	Formicidae	n	2	1
	Vespoidea	Vespidae	n	1B-2	1
		Masarinae	n p	1A	1
	Sphecoidea	Sphecidae	n	1B	1
	Apoidea	Colletidae	n p	1A	1
		Halictidae	n p	1A	1
		Andrenidae	n p	1A	1
		Melittidae	n p o	1A	1
		Fideliidae	n p	1A	1
		Megachilidae	n p	1A	1
		Anthophoridae	n p o	1A	1
		Apidae	n p	1A	1

a. p = pollen; n = nectar; o = floral oils; r = reward unspecified.

b. 1A = adults and larvae dependent on pollen, nectar and/or oils for complete diet (eutropic, eulectic); 1B = pollen, nectar and/or oils form primary diet of adults, larvae fed on different foods; 2 = food from flowers is a non-obligate part of diet (hemitropic, hemilectic, allotropic).

c. 1 = high (all taxa obtain food from flowers); 2 = moderate; 3 = low (only a few species feed at flowers). - = insufficient information for categorization.

Table VII-2b. Stratigraphic occurrence of anthophilous Hymenoptera. Records previous to Upper Cretaceous are plotted on the far left of the chart. 1 = British Columbia-Republic; 2 = Green River. Record beginning in Upper Eocene is Baltic amber and beginning in Lower Oligocene is Florissant.

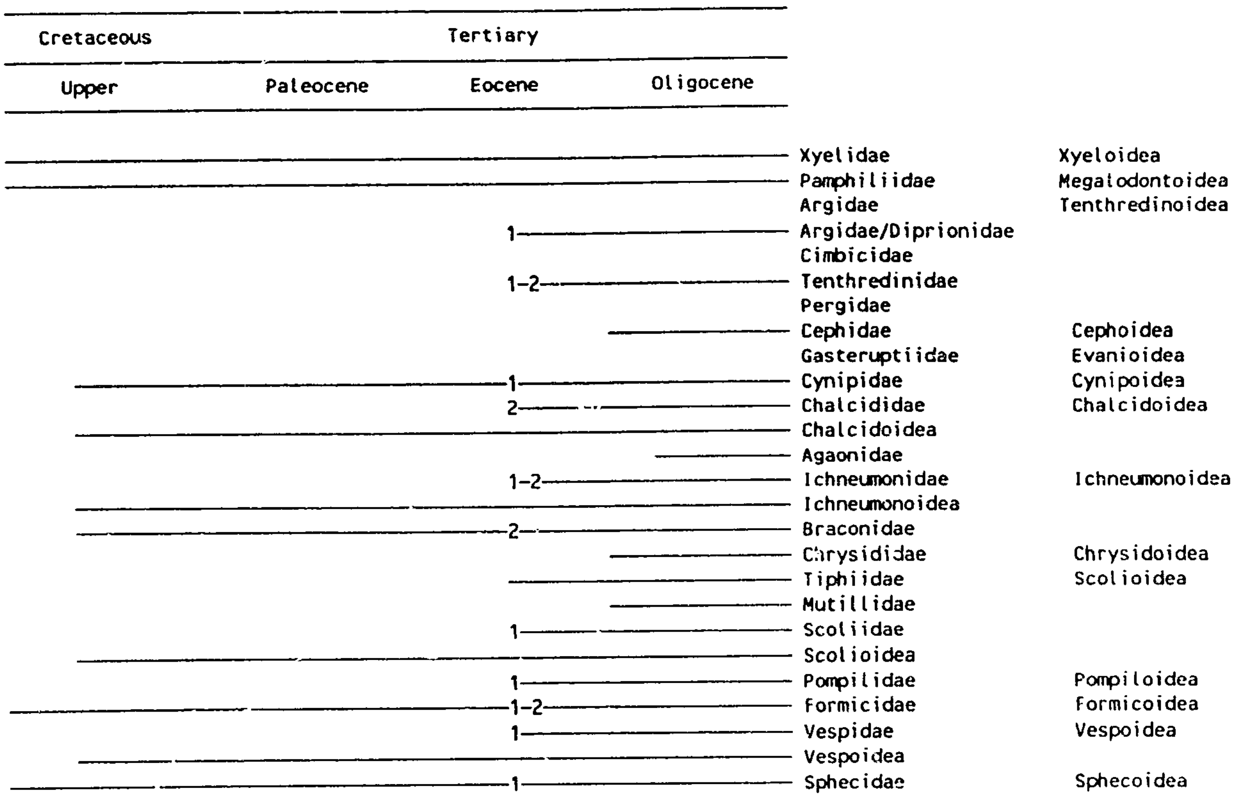

Table VII-2b (continued).

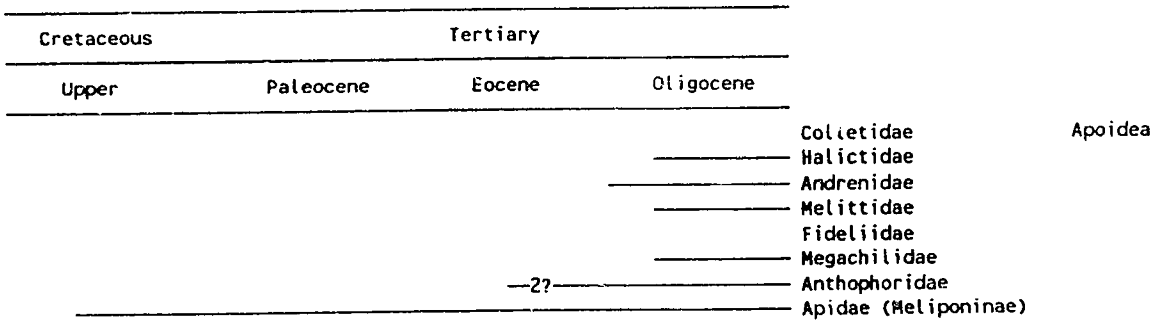

Table VII-3a. Degree of specialization among anthophilous Diptera; only adults considered. Taxa in which no flower associations are recorded are excluded. Classification follows McAlpine et al. (1981) and McAlpine (1987).

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
NEMATOCERA	Tipuloidea	Tipulidae	n	2	2
	Bibionoidea	Bibionidae	n p	1?-2	2?
	Sciaroidea	Mycetophilidae	n	2	2
		Sciaridae	n	2	2?
		Cecidomyiidae	n	2	2?
	Psychodoidea	Psychodidae	n	2	2
	Anisopodoidea	Anisopodidae	n	2	2
	Scatopsoidea	Scatopsidae	n	2	2
	Culicoidea	Culicidae	n	1-2[d]	1
	Chironomoidea	Ceratopogonidae	n	1-2[d]	1
		Chironomidae	n	2	3
BRACHYCERA	Tabanoidea	Pelecorhynchidae	r	2	3
		Tabanidae	n	1	3
		Rhagionidae	n	2	-
	Stratiomyoidea	Stratiomyidae	n p	1	1?
	Asiloidea	Therevidae	n	2	3
		Vermileonidae	n	2	-
		Mydidae	n	1	2
		Apioceridae	n	1	-

Table VII-3a (continued).

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
BRACHYCERA	Bombylioidea	Acroceridae	n	1	2
		Nemestrinidae	n	1	2
		Bombyliidae	n	1	1
	Empidoidea	Empididae	n	1[e]	1
		Dolichopodidae	n	2	3?
	Lonchopteroidea	Lonchopteridae	n	1	1
	Platypezoidea	Phoridae	r	2	3
	Syrphoidea	Syrphidae	n p	1	1
		Pipunculidae	n	1	2?
	Conopoidea	Conopidae	n	1	1?
	Diopsoidea	Diopsidae	n	2	-
	Tephritoidea	Platystomatidae	n	2	-
	Opomyzoidea	Clusiidae	n	2	-
		Agromyzidae	r	-	-
		Milichiidae	n	2	3
	Sciomyzoidea	Dryomyzidae	n	2	-
		Sepsidae	r	2	-
	Lauxanioidea	Lauxaniidae	n	1?	1?
	Sphaeroceroidea	Heleomyzidae	n	2	-

Table VII-3a (continued).

Taxa			Floral	Dependency	Degree of
Suborder	Superfamily	Family	reward[a]	on flowers[b]	anthophily[c]
BRACHYCERA	Ephydroidea	Drosophilidae	n	2	3
		Ephydridae	n	2	3
		Chloropidae	r	2	-
		Tethinidae	r	2	3
	Muscoidea	Anthomyiidae	n p	2?	-
		Muscidae	n p	2	3
	Oestroidea	Calliphoridae	n	2	-
		Sarcophagidae	p	2	-
		Tachinidae	n	1	2?

a. p = pollen; n = nectar; r = floral reward unspecified.

b. 1 = obligate flower feeding (eutropic, eulectic) exists for some taxa within the family; 2 = some taxa within the family obtain food from flowers, but are not dependent on it (hemitropic, hemilectic, allotropic) and obligate flower feeding is absent; ? = categorization not definitive; - = insufficient information to categorize.

c. 1 = high (all taxa obtain food from flowers); 2 = moderate; 3 = low (only a few species feed at flowers). ? = categorization not definitive; - = insufficient information to categorize.

d. adult males feed on nectar; adult females feed on blood and sometimes nectar.

e. adult males supplement female diet with insects.

Table VII-3b. Stratigraphic occurrence of anthophilous Diptera. Records previous to Upper Cretaceous are plotted on the far left of the chart. 1 = British Columbia-Republic; 2 = Green River. Record beginning in Upper Eocene is Baltic amber and beginning in Lower Oligocene is Florissant. Dashed line indicates questionable record.

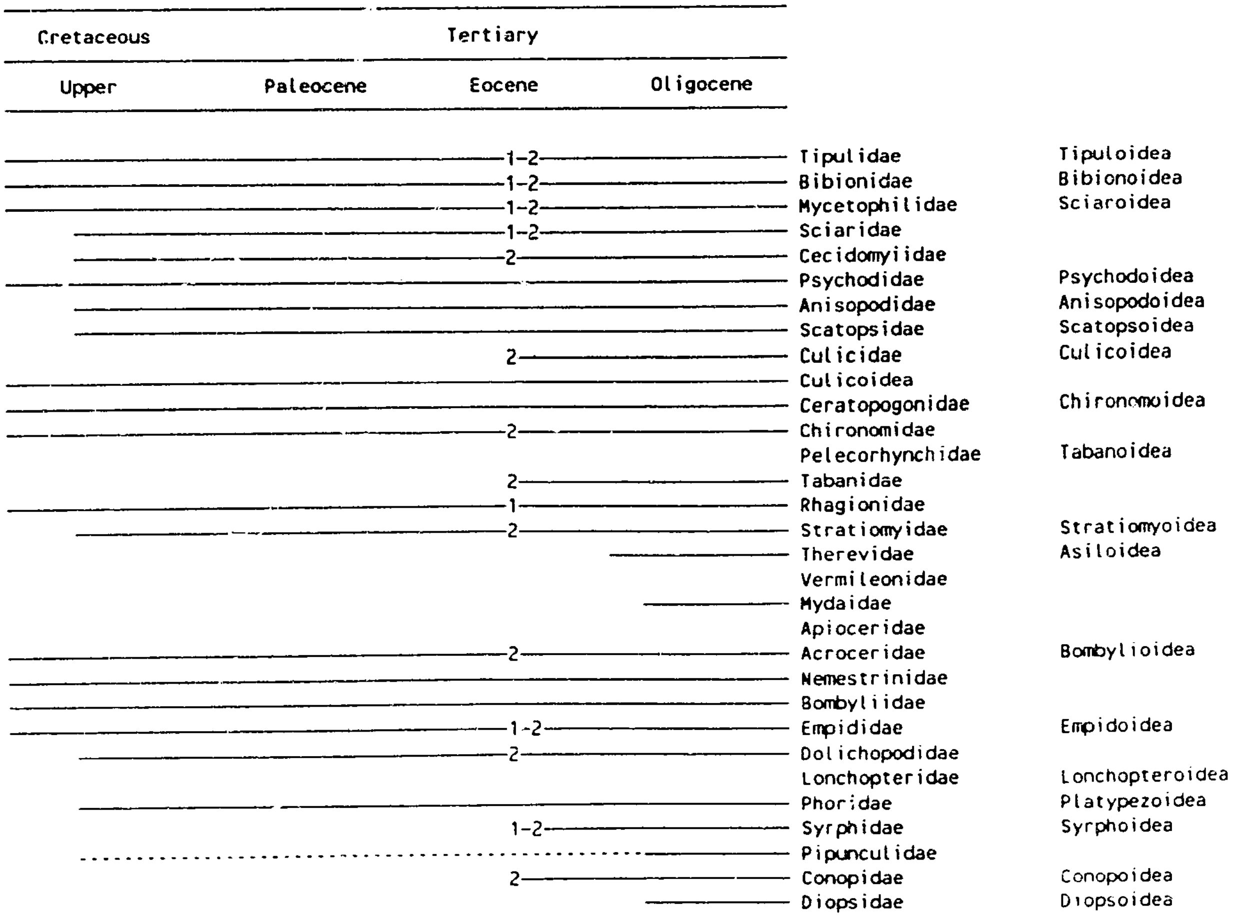

Table VII-3b (continued).

Cretaceous	Tertiary				
Upper	Paleocene	Eocene	Oligocene		
				Platystomatidae	Tephritoidea
		2—	—	Tephritidae	
				Clusiidae	Opomyzoidea
			—	Milichiidae	
			—	Dryomyzidae	Sciomyzoidea
			—	Sepsidae	
			—	Lauxaniidae	Lauxanioidea
		2—	—	Heleomyzidae	Sphaeroceroidea
			—	Drosophilidae	Ephydroidea
				Ephydridae	
—	—	—	—	Chloropidae	
				Tethinidae	
		2—	—	Anthomyiidae	Muscoidea
		2—	—	Muscidae	
—	—	—	—	Calliphoridae	Oestroidea
				Sarcophagidae	
		2—	—	Tachinidae	

Table VII-4a. Degree of specialization among anthophilous Lepidoptera. Families in which no data on floral rewards or feeding structure is available are excluded. Classification follows Covell (1984), except for classification of Hesperioidea and Papilionoidea, which follows Borror et al. (1976).

Taxa			Floral	Feeding
Suborder	Superfamily	Family	reward[a]	structure[b]
ZEUGLOPTERA	Micropterigoidea	Micropterigidae	p	m
DACNONYPHA	Eriocranioidea	Eriocraniidae	-	r
EXOPORIA	Hepialoidea	Hepialidae	-	r
MONOTRYSIA	Nepticuloidea	Nepticulidae	-	r
		Opostegidae	-	r
		Tischeriidae	-	p
	Incurvarioidea	Incurvariidae	p n	p t
		Heliozelidae	-	r
DITRYSIA	Tineoidea	Tineidae	-	p
		Lyonetiidae	-	r
		Gracillariidae	-	r
	Gelechioidea	Oecophoridae	-	r
		Elaschistidae	-	r
		Coleophoridae	-	r
		Scythrididae	-	p
		Gelechiidae	-	r

Table VII-4a (continued).

Taxa Suborder	 Superfamily	 Family	Floral reward[a]	Feeding structure[b]
	Copromorphoidea	Copromorphidae	-	p
		Alucitidae	-	p
		Carposinidae	-	p
		Epermeniidae	-	r
		Glyphipterigidae	n	p
	Yponomeutoidea	Yponomeutidae	n	p
		Douglasiidae	n	p
		Heliodinidae	n	p
	Sesioidea	Sesiidae	n	p
		Choreutidae	-	p
	Tortricoidea	Tortricidae	n	p
		Cochylidae	-	r
	Hesperioidea	Hesperiidae	n	p
		Megathymidae	n	p
	Papilionoidea	Lycaenidae	n	p
		Pieridae	n	p
		Papilionidae	n	p
		Danaidae	n	p
		Nymphalidae	n p	p

Table VII-4a (continued).

Taxa			Floral	Feeding
Suborder	Superfamily	Family	reward[a]	structure[b]
	Zygaenoidea	Zygaenidae	n	p
		Megalopygidae	-	r
		Limacodidae	-	r
	Pyraloidea	Pyralidae	n	p
		Thyrididae	-	p
		Hyblaeidae	-	p
	Drepanoidea	Thyatiridae	-	p
		Drepanidae	-	r
	Geometroidea	Geometridae	n	p
		Epiplemidae	-	p
		Sematuridae	-	p
		Uraniidae	n?	p
	Mimallonoidea	Mimallonidae	-	r
	Bombycoidea	Apatelodidae	-	r
		Lasiocampidae	n	p
	Sphingoidea	Sphingidae	n	p

Table VII-4a (continued).

Taxa			Floral	Feeding
Suborder	Superfamily	Family	reward[a]	structure[b]
	Noctuoidea	Ctenuchidae	n	p
		Notodontidae	-	p
		Arctiidae	n	p
		Lymantriidae	-	r
		Noctuidae	n	p

a. p = pollen; n = nectar; - = no feeding records found.

b. p = well-developed proboscis present in part or all of family; r = proboscis reduced or short in all of family; m = mandibles used for feeding; t = maxillary tentacles present; - = feeding structur unknown. Proboscis is absent in all taxa in the ditrysian Psy Cossidae, Bombycidae, Lasiocampidae and Saturnidae and prob food is taken in the adult stage.

Table VII-4b. Stratigraphic occurrence of anthophilous Lepidoptera. Records previous to Upper Cretaceous are plotted on the far left of the chart. 1 = British Columbia-Republic; 2 = Green River. Record beginning in Upper Eocene is Baltic amber and beginning in Lower Oligocene is Florissant. Dashed line indicates questionable record.

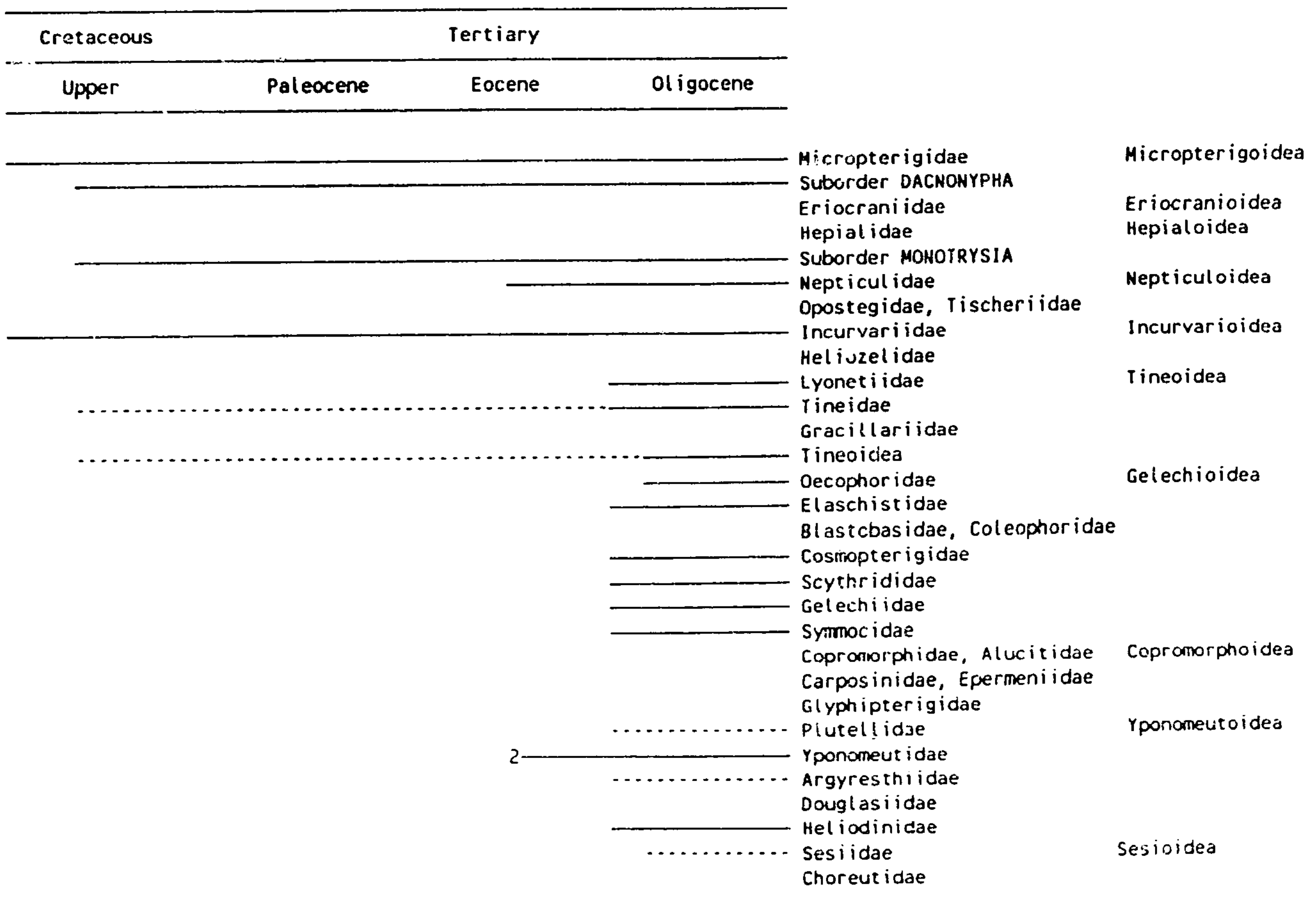

Table VII-4b (continued).

Cretaceous	Tertiary				
Upper	Paleocene	Eocene	Oligocene		
			——	Tortricidae	Tortricoidea
				Cochylidae	
			——	Hesperiidae	Hesperioidea
				Megathymidae	
		2——	——	Lycaenidae	Papilionoidea
				Riodinidae	
			——	Pieridae	
		2——	——	Papilionidae	
				Parnassiidae	
			——	Libytheidae	
				Danaidae, Satyridae, Heliconiidae	
			——	Nymphalidae	
			——	Zygaenidae	Zygaenoidea
				Megalopygidae, Limacodidae	
				Epipyropidae, Dalceridae	
			——	Pyralidae	Pyraloidea
		2——	——	Thyrididae	
				Hyblaeidae	
				Pterophoridae	Pterophoroidea
				Thyatiridae, Drepanidae	Drepanoidea
		1——	——	Geometridae	Geometroidea
				Epiplemidae, Sematuridae	
				Uraniidae	
				Mimallonidae	Mimallonoidea
				Apatelodidae	Bombycoidea
		——	——	Sphingidae	Sphingoidea
				Notodontidae, Dioptidae	Noctuoidea
		——	——	Arctiidae	
				Lymantriidae	
- - - - - -	- - - - - -	- - -1——	——	Noctuidae	

Table VII-5. Insect pollinators available to Middle Eocene flowers in North America. 1 = British Columbia-Republic; 2 = Green River; 3 = Greenland (Eocene); 4 = Canadian amber (Upper Cretaceous); 5 = Alberta (Upper Cretaceous); 6 = New Jersey.

Order	Families with taxa dependent on nectar/pollen/oils	Families with taxa mainly generalist flower feeders	
COLEOPTERA	Scarabaeidae^{1,2}	Staphylinidae^{2}	Tenebrionidae^{1}
	Cantheridae^{1}	Lucanidae^{1}	Melandryidae^{2}
	Nitidulidae^{2}	Buprestidae^{1}	Rhipiphoridae^{2}
	Oedemeridae^{3}	Elateridae^{1,2}	Bruchidae^{2}
	Mordellidae$^{1?,2}$	Anobiidae^{2}	Anthribidae^{2}
	Cerambycidae^{1,2}	Ptinidae^{2}	Curculionidae^{1,2}
	Chrysomelidae^{1,2}	Cryptophagidae^{2}	
HYMENOPTERA	Scoliidae^{1}	Argidae$^{1?}$	
	Vespidae^{1}	Tenthredinidae^{1,2}	
	Sphecidae^{2}	Cynipidae^{1}	
	Anthophoridae$^{2?}$	Chalcididae^{2}	
	Apidae (Meliponinae)^{6}	Ichneumonidae^{1,2}	
		Braconidae^{1,2}	
		Pompilidae^{1}	
		Formicidae^{1,2}	

Table VII-5 (continued).

Order	Families with taxa dependent on nectar/pollen/oils	Families with taxa mainly generalist flower feeders	
DIPTERA	Bibionidae[1,2]	Tipulidae[1,2]	Dolichopodidae[2]
	Culicidae[2]	Mycetophilidae[1,2]	Phoridae[4]
	Ceratopogonidae[4]	Sciaridae[1,2]	Tephritidae[2]
	Stratiomyidae[2]	Cecidomyiidae[2]	Heleomyzidae[2]
	Acroceridae[2]	Anisopodidae[4]	Chloropidae[4]
	Empididae[1,2]	Scatopsidae[4]	Anthomyiidae[2]
	Syrphidae[1,2]	Chironomidae[2]	Muscidae[2]
	Conopidae[2]	Tabanidae[2]	Calliphoridae[5]
	Tachinidae[2]	Rhagionidae[1]	
LEPIDOPTERA	Yponomeutidae[2]		
	Thyrididae[2]		
	Papilionidae[2]		
	Lycaenidae[2]		
	Geometridae[1]		
	Noctuidae[1]		

VIII. POLLINATION SYNDROMES AND POLLINATING AGENTS

Predictions of pollinators from flower form

For each of the eleven flower form categories defined in Chapter IV, it is possible to extrapolate a "pollination syndrome" (Table VIII-1): those characters that will be important in specifying a particular pollinator. The characters used are perianth size, connation, symmetry, and depth, and where the structures are present, pollen presentation. For each syndrome, optimal pollinating agents are predicted. The optimum for the plant is assumed to be the efficient transport of pollen to another stigma of the same species; this involves the provision of appropriate floral rewards (nectar, pollen, oils, mating sites) to the animal pollinator.

As well as providing appropriate, accessible rewards, flower form may specify a pollinator by restricting access to food rewards; long, narrow corolla tubes, spurs or constricted corolla apices limit successful feeding to pollinators with elongate mouthparts (Faegri and van der Pijl 1979). However, specifying a particular pollinator does not imply that there are no other animals that feed on pollen or nectar in the particular flower (Macior 1971, Faegri and van der Pijl 1979). For example, specialized, long-tongued insects visit and feed from flowers that require no manipulation or long mouthparts. Similarly, small non-specialized insects may inhabit and feed on bell- or tube-shaped flowers that are pollinated by apoid hymenopterans or alighting lepidopterans. These "sub-optimal" pollinators are not included in the discussion below, even though they may transport pollen.

Description of floral form categories is given in Chapter IV and data for floral feeding behaviour and stratigraphic occurrence of pollinators in Chapter VII.

The predicted optimal pollinators for category 1, Florissantia physalis, are non-specialized, robust coleopterans and dipterans and large non-apoid hymenopterans. The most effective pollinators are those that alight and pick up pollen by brushing ventrally against the anthers. Hovering groups would be unlikely to effect pollination; elongate mouthparts are not necessary. Large perianths indicate long-range conspicuousness and probably specify a more robust pollinator with high food requirements. The pollinators of category 3 flowers have the same qualifications as category 1; any predicted differences would be in the pollinator attractedness to polypetalous versus more connate perianths. The pollinators that exhibit these characteristics from British Columbia-Republic during the Middle Eocene are large Scarabaeidae, Cantharidae, Cerambycidae and Chrysomelidae, short-haustellate Syrphidae, Empididae and Bibionidae and non-specialized Scoliidae and Vespidae, as well as generalist hymenopterans, including Tenthredinidae, Ichneumonidae, Braconidae and Pompilidae.

The optimal pollinators for category 2 flowers are hovering animals with elongate mouthparts to feed on nectar; however if the haustellum or bill is longer than the corolla, the head of the pollinator will not come in contact with the anthers and no pollen will be transported. Hovering lepidopterans and hovering dipterans are the optimal pollinators, provided the haustellum is not longer than 7 mm, the length of the corolla; small insects with elongate mouthparts may be able to feed while grasping the corolla apex. The only taxa at British Columbia-Republic that has members capable of hovering is Syrphidae. The Geometridae specimen from Republic has a 2 mm proboscis and was probably incapable of reaching nectar from a corolla of this length; Noctuidae, and other taxa of Geometridae, may be pollinators if proboscides are long enough.

The predicted optimal pollinators for categories 4, 5 and 6 are small non-specialized dipterans and coleopterans and small parasitic hymenopterans. The size of the flower probably limits the amount of nectar produced and the conspicuousness of the flowers (unless flowers were grouped in inflorescences). No specialized mouthparts are necessary. Many of the groups having high metabolic requirements (birds, bats, apoid bees, large dipterans and lepidopterans) may be excluded, as would more robust agents; hovering taxa would not effect pollination. Category 7 differs from the three previous primarily in its large size and long tepals; it could be predicted, similarly, to accommodate larger taxa of generalist dipterans, coleopterans and hymenopterans. At British Columbia-Republic, the pollinators that exhibit these characteristics are Mordellid beetles and small generalist coleopterans, such as Elateridae, Tenebrionidae and Curculionidae, small hymenopterans with no modifications for feeding on flowers (Cynipidae, Ichneumonidae, Braconidae and Formicidae) and small dipterans (Bibionidae, Syrphidae, Empididae, Mycetophilidae, Sciaridae). When the Green River insect fauna is considered as well, a wide range of small coleopteran, hymenopteran and dipteran families is added to the pollinator spectrum.

The pollination syndrome of category 9 is similar to the foregoing in perianth size and shape, with the exception that the numerous exserted anthers probably offer pollen as the attractant and food reward. As such, mandibulate rather than haustellate pollinators are appropriate. Small coleopterans (Mordellidae, Elateridae, Tenebrionidae, Curculionidae) are likely pollinators at British Columbia-Republic. Alternatively, exsertedness of the stamens may indicate wind-dispersal of pollen.

In the large, highly stereomorphic flower of category 8, pollen is deposited on the pollinator as it alights or hovers at the apex of the corolla, contacting the anthers dorsally while feeding with elongate mouthparts on basal nectar. Apoid hymenopterans, large lepidopterans, large, specialized dipterans and hummingbirds are probable pollinators. A proboscis or bill in the range of 15 - 20 mm would allow pollen deposition on the head or back of the agent. The flower shows characteristics similar to Fabaceae, Caesalpiniaceae or Polygalaceae; many extant taxa of Fabaceae are pollinated by apoid bees and occasionally, nectarivorous birds (Faegri and van der Pijl 1979). Neither of these pollinating agents is present in the Eocene sediments of British Columbia-Republic. There are two interpretations for the presence of the pollination syndrome represented by the legume-like flower: (1) long-tongued apoid bees are present and well-developed by the Middle Eocene in British Columbia-Republic but have not yet been found as fossils, or (2) an alternate group of long-tongued pollinators, already present in the fossil record, pollinated legume-like flowers. At British Columbia-Republic, the families of insects that have taxa with elongate proboscises are the Scoliidae, Vespidae and Syrphidae. As far as is known, only the Syrphidae have an haustellum of a length appropriate for feeding on the flower. Present at the coeval, more southerly Green River is the Acroceridae, which has taxa with proboscis lengths capable of feeding on such flowers and a possible Anthophoridae. As well, Meliponinae are present in Upper Cretaceous amber of New Jersey, Nemestrinidae and Bombyliidae occur in Mesozoic strata in Europe and anthophorid bees are recorded from the Middle Eocene of Germany. Flowers with oil-producing glands, which in extant taxa are pollinated by anthophorid bees, are present in the Middle Eocene of Tennessee. There is range of pollinators present in the fossil record capable of feeding from and pollinating the legume-like flower; it is not necessary to argue for the presence of the most derived Apidae (Bombinae and Apinae) not yet found as fossils. Pollinators with elongate mouthparts, such as the apoid Anthophoridae and Meliponinae and the Syrphidae, Acroceridae, Nemestrinidae and Bombyliidae, were appropriate pollinators of highly stereomorphic flowers.

The discovery of high diversity in Upper Cretaceous or early Paleocene apoid hymenopterans will be the best evidence for a long association between derived flowers and these pollinators. Anthecological data on extant associations between bombylioid pollinators and highly derived flower forms will be suggestive of a more ancient co-evolved system. Direct evidence for flower feeding will be found in preserved mouthparts of probable pollinators. The only definitive evidence for pollination, not yet found in compression fossils or in amber, is the presence of identifiable pollen on appropriate pollen collecting structures of fossil insects.

The numerous pollen sacs and reduced perianth parts of the contracted inflorescence in category 10 is indicative of anemophily. The highly connate, stereomorphic corolla of category 11 will restrict pollinators to those with elongate mouthparts. Successful deposition of pollen on the agent is possible with proboscid lengths of about 7 mm. The apical flare allows pollinators to alight, but depending on the length of the proboscis or bill, hovering agents could also effect pollination. Optimal pollinators include apoid bees, lepidopterans, hummingbirds and specialized non-apoid hymenopterans or dipterans. The discussion of apoid and dipteran pollinators of the legume-like corolla (category 8) are applicable here as well, except that the optimal proboscid length is less. In British Columbia-Republic, long-tongued Syrphidae, Vespidae and Scoliidae and the lepidopteran families of Noctuidae and Geometridae are available pollinators. When Green River fauna are considered, the pollinator constellation includes the Sphecidae, Acroceridae and four lepidopteran families (Yponomeutidae, Thyrididae, Papilionidae and Lycaenidae); Meliponinae are present in the Upper Cretaceous of New Jersey and Bombylioidea and Anthophoridae are present by the Middle Eocene in Europe.

Conclusions

The fossil record of pollinators is sufficient to account for flower form in the Middle Eocene of British Columbia and Republic, Washington. The absence of the majority of families of apoid Hymenoptera does not equate with the absence of specialized pollinators for highly derived (stereomorphic and zygomorphic) flowers. Flower feeders such as syrphid flies, bibionids and non-apoid wasps are often considered as minor pollinators of extant flowers, due to the efficiency of apoid hymenopterans (Free 1970). However, in the absence of bees, these may be significant pollinating agents. Many of the fossil flowers from British Columbia and Republic fit into a broad pollination syndrome defined by small, bowl-shaped perianths of varying size, connation and tepal length. A wide range of small, non-specialized coleopterans, dipterans and hymenopterans are available to these flowers. Finer divisions within this broad syndrome, and more detailed predictions of pollinators, are probably not possible with the range of characters preserved in flower specimens from this area.

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Macior, L. W. 1981. Co-evolution of plants and animals - systematic insights from plant-insect interactions. Taxon 20:17-28.

Free, J. B. 1970. Insect pollination of crops. Academic Press, London.

Table VIII-1. Flower form categories and predicted pollinators. Category numbers refer to groups in Table IV-10.

Category	Floral characteristics	Inferred pollination syndrome	Predicted optimal pollinators
1	large perianth, conspicuous venation	conspicuous over large distances, food conspicuous	-robust coleopterans, dipterans
	planar to dish-shaped, highly connate	pollinator alighting, can be robust	-non-apoid, non-specialist
		pollen collects ventrally on pollinator	hymenopterans
		no special mouthparts needed	
2	perianth stereomorphic, highly connate,	elongate mouthparts, response to visual cues	-hovering lepidopterans
	nectar concealed		-hovering dipterans
	flowers small, no corolla rim	pollinator hovering; if alighting, small	-small, alighting lepidopterans
	anthers at corolla mouth on one specimen	pollen collected on head, dorsal/ventral	
3	large perianth	conspicuous over long distances, food conspicuous	-non-specialist robust dipteran
		pollinator alighting, may be robust	-non-apoid, non-specialist
	planar, moderate connation	no specialized mouthparts needed	hymenopterans
		pollen collects ventrally	
4	small, bowl-shaped perianth, long tepals	pollinator alighting, small	-small dipterans, coleopterans
		food rewards accessible	and non-specialist hymenopterans
		no specialized mouthparts needed	

Table VIII-1 (continued).

5	small, bowl-shaped perianth, long tepals	pollinator alighting, small	-small dipterans, coleopterans
		food rewards accessible	and non-specialist hymenopterans
		no specialized mouthparts needed	
6	small, bowl-shaped perianth, lobed tepals	pollinator alighting, small	-small dipterans, coleopterans
		food rewards accessible	and non-specialist hymenopterans
		no specialized mouthparts needed	
7	large bowl-shaped perianth, linear tepals	pollinator alighting, may be robust	-large or small generalist
		long-distance conspicuousness	dipterans and coleopterans
		food rewards accessible	-non-apoid,non-specialist
		no specialized mouthparts needed	hymenopterans
		pollen collects dorsally or ventrally	
8	zygomorphic, stereomorphic, long tepals	pollinator alighting	-long-tongued, apoid hymenopterans
	perianth length 19.5 mm	elongate mouthparts	-hovering birds
		manipulation of flower probably needed	-robust, long-tongued dipterans
		nectar rewards concealed	
	long stamens on upper part of flower	pollen deposited dorsally	

Table VIII-1 (continued)

9	small cup-like flowers, perianth reduced	no long-distance conspicuousness	-small dipterans, coleopterans
		pollinator alighting	and non-specialist hymenopterans
	many, long conspicuous stamens	pollen presentation is attractant	-possibly wind
		food rewards (pollen) accessible, conspicuous	
		no specialized mouthparts needed	
		pollen collects ventrally	
10	no perianth	no visual attractant	-wind
	inflorescence of clustered anthers	no nectar, copious pollen	
11	stereomorphic, highly connate	food rewards concealed	-long-tongued, apoid hymenopterans
	corolla constricted sub-apically	elongate mouthparts needed	-lepidopterans
		pollen collects on head	-specialized non-apoid
	expanded corolla rim	pollinator alighting	hymenopterans and dipterans
			-hovering birds

IX. SUMMARY: FLOWER FORM AND POLLINATOR DIVERSITY IN THE MIDDLE EOCENE OF BRITISH COLUMBIA AND WASHINGTON

Study area

The floral and insect material analyzed in this study are from sediments deposited during the Middle Eocene in a series of lakes located in central British Columbia and northern Washington. The specimens are compression-impression fossils in fine grained, laminated shales from eleven localities. Potassium-argon dating and biostratigraphic correlation dates the sites at 48 - 50 m. y. (Rouse and Mathews 1960, Hills and Baadsgaard 1967, Wilson 1977a, 1977b, Wolfe and Wehr, 1987).

Staminate inflorescences

Diversity was high among forty specimens of staminate inflorescences ("catkins") from British Columbia (Princeton and McAbee) and Republic, Washington. Four multicharacter similarity groups were generated for seventeen of the specimens using cluster analysis; the remaining specimens ("outliers") were highly diverse and did not consistently associate with any of the four groups. Groups I and II consisted of complex inflorescences with large triangular primary bracts, the two groups differing in width and density of the catkin, angle of the primary bracts and pollen sac size. Group III specimens were narrow spikes with multiple oval bracts and exserted stamens and Group IV specimens had the smallest and least dense bracts, the most exserted stamens and largest pollen sacs of all groups. Groups I and II had characteristics similar to the Betulaceae; three catkins associated with leaves of the fossil Betula leopoldae are in these groups. Group III showed affinities with the Juglandaceae. There was a striking locality factor in the grouping. Groups I and II contain only specimens from Princeton; Republic is represented in Groups III and IV and in the majority of outliers. The higher diversity at Republic cannot be accounted for by differences in age or in depositional habitat, and may be the result of microhabitat differences.

Flower form

Fifty specimens of flowers and inflorescences from British Columbia (Horsefly, One Mile Creek, Falkland, McAbee) and Republic were classified into multicharacter similarity groups using cluster analysis and discriminant function analysis. The characters with the lowest variability were the number of tepals (mode of 5), the degree of connation of the perianth (about 60%) and the length/width ratio of both perianth and flower (about 1). Cluster analysis generated 6 similarity groups among twenty-six of the specimens; using discriminant function analysis, the characters that were most important in differentiating between the groups proved to be perianth width, perianth connation and shape of the tepals. An additional five floral form categories were added: a group identified by cluster analysis based on androecial characters and 4 outlying specimens. Groups 1 and 3 consisted of large, robust perianths of Florissantia physalis and Pistillipollianthus wilsonii. Groups 4, 5 and 6 were small, bowl-shaped, partially connate perianths that varied independently in the three predictor variables; Group 7 differed from these three groups primarily in perianth size. The remaining flower form categories include a small stereomorphic, highly connate form (Group 2), a large zygomorphic flower (Group 8), a number of bowl-shaped perianths with numerous, exserted stamens (Group 9), a staminate raceme (Group 10) and a connate perianth with a sub-apical constriction (Group 11).

The sample of flowers from British Columbia-Republic shares many floral characters and many floral form categories with other samples of Paleocene-Eocene flowers, notably those from the Claiborne formation of Tennessee; however, each area has distinct forms as well, indicating that there may be differences in the diversity of pollinating agents.

Insect diversity

Insect specimens in the four anthophilous orders (Coleoptera, Hymenoptera, Diptera, Lepidoptera) were examined from nine localities (Driftwood Creek, Quilchena, Horsefly, One Mile Creek, Tulameen Road, Princeton Firehall, McAbee, China Creek and Republic) in British Columbia and Washington. Thirty taxa (at the family or superfamily level) were represented in 129 specimens, with the most common families being Bibionidae and Ichneumonidae. Almost half of the coleopteran specimens were isolated elytra and identification was not possible. Coleoptera was the most diverse of the four orders, with specimens identified in 10 families and 2 superfamilies. Fifteen of the families identified are new records for the Middle Eocene of British Columbia-Republic, bringing the diversity of insects in these four orders in the area to 34 families. Nine families (Lucanidae, Cantharidae, Cleridae, Argidae-Diprionidae, Scoliidae, Pompilidae, Rhagionidae, Geometridae, Noctuidae) represent the earliest occurrences of the taxa in North America and five (Cantharidae, Cleridae, Argidae-Diprionidae, Geometridae, Noctuidae) are the earliest records of the respective families in the stratigraphic record. Significant for the study of paleoanthecology are the new records for lepidopterans. The insect diversity of British Columbia-Republic (34 families in the four orders) is lower than at the more southerly, contemporaneous Green River (59 families) (Wilson 1978); only 20 families are present in both areas.

Pollinator diversity

Based on a literature review of the feeding habits of insects, at the family level, in the four anthophilous orders (Coleoptera, Hymenoptera, Diptera and Lepidoptera) and of their stratigraphic occurrence, a "short list" of potential pollinators of Middle Eocene flowers was compiled. At least 28 families of pollinating insects were available to flowers analyzed in this study; the most important are Mordellidae, Syrphidae, Bibionidae, Scoliidae, Vespidae, Geometridae and Noctuidae. In addition, Acroceridae, Papilionidae and Lycaenidae are present at Green River (Wilson 1978, Durden and Rose 1978) and Meloponinae occurs in New Jersey (Michener and Grimaldi 1988a, 1988b). Anthophoridae, found in Middle Eocene Germany (Schaal and Zeigler 1988) and Nemestrinidae and Bombyliidae, present in Mesozoic strata in Europe (McAlpine et al. 1981, Zeitsev 1986), may have been important pollinators in North America as well. Bird (Olson 1985) and bat (Hill and Smith 1984) pollinators are absent from sediments in or previous to the Middle Eocene, but there is a possibility that small marsupials and mammals were pollinators (Sussman and Raven 1978).

Pollination syndromes and pollinating agents

For each of the flower form categories, the most probable pollinating agents were selected from the range of anthophilous families present at British Columbia-Republic in the Middle Eocene. The larger pollinator fauna available in North America and world-wide at the time is also considered. The pollinators appropriate to categories 1 and 3 are large Scarabaeidae, Cantharidae, Cerambycidae and Chrysomelidae, short-haustellate Syrphidae, Empididae and Bibionidae and non-specialized Scoliidae and Vespidae, as well as large generalist hymenopterans. The optimal pollinators for category 2 flowers are long-haustellate, hovering Syrphidae, as well as alighting Geometridae and Noctuidae. The predicted optimal pollinators for categories 4, 5, 6 and 7 are Mordellid beetles and small generalist coleopterans, such as Elateridae, Tenebrionidae and Curculionidae, small hymenopterans with no modifications for feeding on flowers (Cynipidae, Ichneumonidae, Braconidae and Formicidae) and small dipterans (Bibionidae, Syrphidae, Empididae, Mycetophilidae, Sciaridae). When the Green River insect fauna is considered as well, a wide range of small coleopteran, hymenopteran and dipteran families are added to the pollinator spectrum. Among Category 9 flowers, the most probably pollinators are small coleopterans (Mordellidae, Elateridae, Tenebrionidae, Curculionidae); exsertedness of the stamens may indicate wind-dispersal of pollen. Wind as a pollinating agent is the most probable scenario for the non-amentiferous category 10 inflorescence. The optimal pollinators available to the highly connate corolla of category 11 are Syrphidae, Vespidae, Scoliidae, Noctuidae and Geometridae; present at Green River are Sphecidae, Acroceridae and four lepidopteran families (Wilson 1978, Durden and Rose 1978) and in New Jersey, Meliponinae. Other Bombylioidea and Anthophoridae are present by the Middle Eocene in Europe (McAlpine et al. 1981, Zeitsev 1986, Michener and Grimaldi 1988a, 1988b, Schaal and Zeigler 1988).

In the large legume-like flower of category 8, a proboscis of 15 - 20 mm is necessary to reach the base of the flower. Apoid hymenopterans, which pollinate extant flowers of similar form, are not present as fossils in British Columbia-Republic. There are, however, several groups of specialized pollinators with elongate mouthparts present in North America during the Middle Eocene, notably the Syrphidae, found at British Columbia-Republic, Acroceridae, present at the coeval Green River (Wilson 1978) and Meliponinae, present in New Jersey in the Upper Cretaceous (Michener and Grimaldi 1988a, 1988b). Appropriate pollinators also include Nemestrinidae and Bombyliidae, present in Mesozoic strata in Europe (Zeitsev 1986, Schaal and Zeigler 1988) and an anthophorid bee from the Middle Eocene of Europe (Schaal and Zeigler 1988).

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APPENDIX 1a. Morphological data for staminate inflorescences analyzed in Chapter III. For acronyms and character definition, see Table III-2.

TEXTNO	SPEC	LOCAL	MATUR	SPIKE	CINFLOR	IWIDMAX	IWIDX	ILENMAX	ILENX
1	489	5	0			5.25	4.83	24.96	
2	569	5	2			3.07	2.82	16.9	
3	903	2	2			3.71	3.14	18.43	18.18
4	5086	2	2	0	1	8.18	7.46	42.25	
5	5345	2	2	0	1	6.06	5.4	38.41	
6	5359	2	2	0	1	8.05		16.37	
7	14091	2	1			4.5	4.5	15.5	
8	14098	2	1			3.9	3.9	14	
9	14238	2	2	0	1	6.58		30.8	
10	26348	2	1	0	1	4	3.5	18.87	
11	26349	2	2	0	1	7.6	6.1	49	
12	26350	2	2	0	1	7.81	6.7	20.8	
13	26351	2	2	1	0	4.4	4.26	29.06	
14	26353	2	2	0	1	3.98		12.02	
15	26363	2	2	0	1	4.68	4.6	10.69	
16	36001	2	2	0	1	6.78	6.72	31	
17	36002	2	2	0	1	5.63	4.29	47.7	
18	36372	1	2	0	1	3.46		11.52	
19	36381	1	2	1	0	6.02	4.81	42.6	
20	36382A	1	2			4.99			
21	36382B	1	1	1	0	3.71	3.11	25.7	
22	36383	1	2			6.14			
23	36384	1	2	1	0	5.89	4.88	13.3	
24	36824	1	2	1	0	4.35	3.53	47.2	
25	36825A	1	2			1.86	1.75	10.37	
26	36825B	1	2	1	0	3.01	2.92	30.5	
27	36825C	1	2						
28	52203	1	2			3.46	3.16	11.52	
29	54163	2	2	1	0	4.22	3.76		
30	54392	1	2	0	1	5.12	4.52	42.2	
31	54395	1	1	0	1	4.4	4.1	44.8	
32	54398	1	2	1	0	6.5	5.6	103.1	
33	56630	1	2	0	1	3.33	2.84	30.1	
34	56709	2	2	0	1	5.5		51.9	
35	56710	2	2	0	1	8.32	6.57	51.3	
36	56726	1	2	1	0	6.7	5.5	52.5	
37	56787	1	1			3.2	2.98	30.2	
38	57087	1	2			7.68	6.42	39	
39	74491	1	2			6.4		14.08	
40	74496	1	2	1	0	4.86		28	

APPENDIX 1a (continued).

TEXTNO	PEDMAX	PEDX	PCWID	PCLEN	BWIDMAX	BWIDX	BLENMAX	BLENX
1	0.77				1.41	1.17	1.41	1.03
2								
3	0.38	0.3			1.34	0.9	1.79	1.44
4	1.33	1.29			1.6	1.27	3.16	2.66
5							2.49	2.12
6					1.58		2.41	2.22
7					1.15		2.3	2.26
8							1.79	1.73
9	1.35	0.99	0.57				2.52	2.29
10					4.68	4.23	2.24	1.98
11	0.77	0.64	0.32				1.66	1.42
12	0.51	0.51					2.24	2.19
13					1.64	1.46	2.24	1.95
14							2	1.76
15	0.48	0.44					1.58	1.33
16	0.45	0.43	0.26				1.02	0.96
17	0.38	0.35	0.19				1.73	1.37
18	0.32	0.29	0				3.07	2.02
19			0		3.01		2.75	2.15
20	0.38	0.38	0					
21	0.9	0.79	0		1.54		1.66	1.44
22	1.02	1.02	0		3.58		1.92	1.53
23	0.51	0.42	0		2.24		1.92	1.76
24					1.86	1.56	1.55	1.27
25					0.62	0.5	1.02	0.71
26							1.71	1.38
27								
28	0.13	0.13	0				1.47	1.35
29			0				1.54	1.34
30	0.77	0.6	0.26				1.54	1.44
31					1.92		1.28	1.19
32	0.64	0.54	0				1.41	1.4
33			0		1.6		1.41	1.27
34							2.77	2.18
35							2.24	1.88
36	0.45	0.41	0				1.57	1.42
37					1.66		1.79	1.67
38								
39	0.77	0.71	0.64	2.37	2.69	1.91	1.6	1.35
40	0.83	0.72	0	0			1.54	1.36

APPENDIX 1a (continued).

TEXTNO	BDIS	BOVAL	BTRI	BSMAL	BSING	BMULT	BPAR	BOBL	PERMM2
1									0.25
2									
3	0	0	1	0	1	0	0	1	0.44
4	0	0	1	0	1	0	0	1	0.15
5	0	0	1	0	1	0	1	0	0.14
6	0	0	1	0	1	0	0	1	0.13
7	0	0	1	0	1	0	1	0	
8	0	0	1	0	1	0	1	0	
9	0	0	1	0	1	0	1	0	0.122
10	0	0	1	0	1	0	1	0	0.65
11	0	0	1	0	1	0	1	0	0.132
12	0	0	1	0	1	0	0	1	0.128
13	0	1	0	0	0	1	0	1	0.07
14	0	0	1	0	1	0	1	0	0.3
15	0	0	1	0	1	0	1	0	0.26
16	0	0	1	0	1	0	0	1	0.059
17							1	0	0.195
18	0	0	1	0	1	0	0	1	0.176
19	0	1	0	0	0	1	0	1	0.1
20	0	0	0	1					
21	0	1	0	0	0	1	0	1	0.431
22	1	0	0	0	1	0	0	1	
23	1	0	0	0	1	0	0	1	0.102
24	0	1	0	0			0	1	0.11
25	0	0	1	0			0	1	4.16
26	0	0	1	0	1	0	0	1	0.75
27									
28	0	0	0	1	1	0	0	1	0.405
29	0	1	0	0	0	1	0	1	0.237
30	0	0	1	0	1	0	1	0	0.293
31	0	0	1	0	1	0	1	0	0.318
32	0	0	1	0	1	0	0	1	0.077
33	1	0	0	0	1	0	0	1	1.23
34	0	0	1	0	1	0	1	0	0.145
35	0	0		0	1	0	0	1	0.12
36	0	0	1	0	1	0	0	1	0.104
37	0	0	1	0	1	0	1	0	0.843
38									
39	1	0	0	0	1	0	0	1	0.08
40					1	0	0	1	0.21

APPENDIX 1a (continued).

TEXTNO	SEC	FIL	FILWID	STAMMAX	ANTHWID	ANTHLEN	STAMEX	DIAM	SCULPT
1		0	0		0.24	0.9	68		
2					0.18	0.61		21.8	1
3	1	0	0		0.24	0.78	100		
4	1	0	0		0.37	1.47	100		
5	1	0	0		0.18	0.86	100	27.2	
6	1	0	0		0.2	0.86	100	26.7	1
7		0	0				100		
8		0	0				100		
9	1	0	0		0.23	0.82	100	25.2	1
10		0	0		0.15	0.71	100	24.8	1
11	1	0	0		0.18	0.65	100	30.1	2
12	1	0	0		0.18	0.87	100	24.5	1
13		0	0		0.28	1.62	100	25.5	1
14	1	0	0		0.19	0.74	100	28.4	1
15	1	0	0		0.19	0.73	100		
16	1	0	0		0.36	1.24	100		
17	1	0	0		0.19	0.69	100	28.3	1
18	1	0	0		0.19	0.59	76.6		
19	1	0	0		0.55	1.45	71.7		
20		0	0		0.34	1.33			
21	1	0	0				100	33.4	2
22	1	0	0		0.36	1.31			1
23	1	0	0		0.32	1.21	70		3
24		0	0		0.31	1.04	39		1
25		0	0				100		
26	1	0	0		0.19	0.51	100		
27		0	0		0.25	0.74			
28	0	0	0		0.22	1.07	100		
29	1	0	0		0.34	1.23	100		
30	0	0	0				100		
31		0	0				100		
32	0	0	0		0.48	1.38	58.9		1
33	0	0	0		0.35	0.89	91.4		
34	1	0	0		0.17	0.72	100	24.9	1
35	1	0	0		0.21	0.85	100	28.4	1
36		0	0		0.51	1.35	55.6		1
37		0	0				100		
38		0	0		0.36	1.17			
39	1	1	0.1	3.52	0.32	1.29	45.5		
40		0	0		0.34	1.02			

APPENDIX 1b. Morphological data for inflorescences and flowers analyzed in Chapter IV. For acronyms and character description, see Table IV-2.

TEXTNO	SPEC	LOCAL	VIEW	MATUR	PCWID	PCLEN	PNOT	PWIDMAX	PWIDX
1	7	5	1	[illegible]	0.51	5.57	0	2.37	
2	82	5	1	2			0	5.38	
3	1721	1	2	2			0	26	
4	1722	1	2	2			0		
5	5051	3	1	2			1		
6	6551	3	2	2			0	21.38	
7	6560	3	1	2	0.7	3.2	0	5.76	
8	6592	3	2	2			0	19.54	
9	26356	3	2	2	0.12	1.74	0	4.42	
10	26357	3	2	2			0	3.78	3.62
11	26358	3	1	2			0	4.48	
12	26359	3	1	2	1.15	3.2	0	7.55	
13	26360	3	1	3	0.77	4.48	0	3.65	
14	26361	1	2	3			0	25.6	
15	26364	3	2	2			0	29.5	28.8
16	26370	4	2	2			0	38.7	37.3
17	26371	4	2	2			0	29.4	29.4
18	26372	4	2	0			0	43	41.5
19	26374	1	2	2			0	3.65	
20	36360	1	2	0			0	7.28	6.98
21	36370	1	1	3	0.45	3.14	0	3.[illegible]	
22	36371	1	1	3	1.66	5.12	0	4.48	
23	36374	1	1	2	1.15	8.45	0	4.35	
24	36377	1	1	2	1.28	5.76	0	5.44	
25	36380	1	1	2			0		
26	36385	1	1	2	0.51	9.73	0	4.99	
27	36386	1	1	2	1.28	16.26	0	9.22	
28	36387	1	1	2	0.51	5.89	0	3.52	
29	36388	1	1	2	0.32	6.4	0	3.84	
30	36389	1	2	3			0	7.68	
31	36395	1	1	2	0.74	6.96	0	5.53	
32	36775	1	1	2	1.7	19.72	0	12.42	11.49
33	36799	1	2	2	0.9	9.09	0	10.88	
34	36836	1	1	2	0.85	16.4	0	9.36	
35	37853	2	3	2	0.39	1.95	0	1.69	1.6
36	39397	1	1	0	0.65	4.03	0	3.06	
37	52203	1	1	2	0.9	5.38	0		
38	56531	1	1	2	0.59	3.12	0	5.07	
39	56533	1	1	2	1.54	33.9	0	8.32	
40	56735	1	1	1	0.77	10.75	0		
41	56736	1	1	2	0.77	11.39	0	7.17	
42	56737	1	1	2	0.64	9.6	0	3.46	
43	56739	1	1	2	0.77	8.7	0	6.14	
44	56785	2	1	3	0.26	0.61	0		
45	71311	1	2	2			0	4.67	
46	74475	2	1	3			0		
47	74476	2	1	2					
48	74491	1	1	2	0.64	2.37	0	2.75	2.45
49	74494	1	1	2	0.27	6.63	0	4.03	
50	74495	1	1	2			0	3.12	

APPENDIX 1b (continued).

TEXTNO	PLENMAX	PLENX	PSHAPE	PPART	CONWID	CONLEN	CONSHAPE	PCON	PACT
1	2.82		1.19	1	1.66	2.3	1.38	0.82	1
2	19.46		3.62	1	2.56	7.68	3	0.39	0
3				1	19.4			0.75	1
4				1				0.72	1
5									
6				1	6.18			0.57	1
7	2.88		0.5		3.74	1.66	0.44	0.58	1
8				1	6.51			0.58	1
9				1					1
10				1	1.91				1
11	9.86		2.2	1	3.01	8.35	2.77	0.85	1
12	6.4		0.85		6.85	3.34	0.49	0.52	1
13	2.82		0.77	1	3.74	2.08	0.56	0.74	1
14				1	21.49				1
15				1	23			0.78	1
16				1	27			0.7	1
17				1	23.5			0.8	1
18				1	36			0.84	1
19				1	1.19			0.33	1
20				1	1.95			0.27	1
21	2.82		0.89	1	1.83	1	0.55	0.35	1
22	5.12		1.14	1	3.15	1.99	0.63	0.39	1
23	2.94		0.68	1	3.82	2.57	0.67	0.84	1
24	4.48		0.82	1	4.07	2.99	0.73	0.61	1
25									1
26	4.54		0.91	1	3.9	3.07	0.79	0.68	1
27	7.42		0.8	1	3.32	2.66	0.8	0.36	1
28	2.62		0.74	1	3.57	1.83	0.51	0.7	1
29	2.47		0.64	1	3.49	0.83	0.24	0.34	1
30	4.99		0.65	1	4.07	1.74	0.43	0.37	1
31	2.86		0.52	1	5.53	2.34	0.42	0.82	1
32	10.24	8.02	0.82	1					1
33				1	5.48				1
34	9.49		1.01	1	7.15	3.25	0.45	0.33	1
35	1.69	1.4	1						1
36	7.28		2.37	1	3.06	6.63	2.17	0.91	1
37	4.99			1		3.49		0.72	1
38	2.47		0.49	0	5.07	2.47	0.49	1	1
39	7.04		0.85	1	6.51	3.67	0.56	0.52	1
40	5.76								1
41	4.1		0.57	1	3.65	2.32	0.64	0.5	1
42	3.71		1.07	1	3.4	2.91	0.86	0.71	1
43	5.76		0.94	1	3.17	2.51	0.79	0.43	1
44					1.62	0.62	0.38		1
45				1	3.01				1
46									1
47									
48	1.92	1.73	0.7	1	0.98	0.94	0.96	0.51	1
49									1
50	2.86		0.92	0	3.12	2.86	0.92	1	1

APPENDIX 1b (continued).

TEXTNO	FWIDMAX	FWIDX	FLENMAX	FLENX	FSHAPE	TNO	TWIDMAX	TWIDX	TLENMAX
1	3.33		4.03		1.21		0.38		2.82
2	5.38		19.46		3.62		3.2	2.88	19.46
3	26					5	11.52	11.2	15.3
4							13.8		13.8
5									
6	21.38					6	3.34	3.07	10.86
7	7.17		6.4		0.89				
8	19.54					5	5.34	4.27	11.19
9	4.42					5	0.96	0.79	1.98
10	3.78	3.62				5	1.22	0.94	2.11
11	4.48		9.86		2.2				
12	10.5		8.45		0.8				6.4
13	3.65		3.46		0.95		1.34	1.31	2.82
14	25.6					5	12.5	11.75	13
15	29.5	28.8				5	15.4	14.1	18.3
16	38.7	37.3				5	18	17.5	21.2
17	29.4	29.4				5	14.5	14.5	18
18	43	41.5				5	18.3	15	21.9
19	3.65					5	0.78	0.66	1.86
20	7.28	6.98				4	1.69	1.58	3.9
21	4.23		2.82		0.67				2.82
22	4.48		13.01		2.9	5	1.09	0.74	5.12
23	4.35		2.94		0.68	3	0.96	0.77	3.07
24	5.44		4.48		0.82		1.28	1.28	4.93
25	5.12		5.89		1.15				
26	4.99		5.77		1.16		1.66		4.54
27	9.22		6.4		0.69	8	0.77	0.58	7.42
28	4.35		3.33		0.77		1.02		2.62
29	5.63		4.99		0.89	5	1.09	0.9	2.47
30	7.68		4.99		0.65	5	2.69	2.23	4.74
31	5.85		4.75		0.81				2.86
32	12.42	11.49	10.42	8.02	0.84	4	2.69	2.34	10.24
33	10.88	10.82				5	3.46	3.2	6.4
34	9.36		9.49		1.01		4.16	3.77	9.75
35	1.69	1.6	1.69	1.4	1				1.69
36	3.77		7.28		1.93		1.24	1.24	7.28
37			4.99				1.66		4.86
38	12.09		6.37		0.53				2.47
39	10.11		11.14		1.1	5	1.66	1.47	7.04
40	5.5		5.76		1.05				5.76
41	7.17		4.1		0.57	6	1.54	1.15	4.61
42	4.35		4.48		1.03				4.1
43	6.14		5.76		0.94	4	2.56	2.31	5.82
44	3.84	3.42	2.75	2.38	0.72				
45	4.67					5			2.69
46									
47									
48	2.62		2.3		0.88		1.02	0.78	1.86
49	4.03								
50	3.12		6.37		2.04				2.86

APPENDIX 1b (continued).

TEXTNO	TLENX	TSHAPEX	TSHAPE	FILWID	STAMMAX	STAMX	STAMNO	ANTHWID	ANTHLEN
1		2	7.42		4.22	4.14	4	0.52	1.38
2		2	6.08	0.19	23.17	16.76	7	0.3	1.48
3	14.2	4	1.33						
4		4	1						
5								0.19	1.28
6	10.46	5	3.25	0.34	4.98	4.09	5	0.18	1.63
7				0.16	7.04	6.22	13	0.15	0.83
8	10.42	5	2.1		2.57			0.28	1.6
9	1.92	2	2.06						
10	1.97	3	1.73						
11									
12	3.89			0.15	8.32	5.68	17	0.31	0.83
13	2.66	3	2.1						
14	12	4	1.04						
15	15.8	4	1.19						
16	21.2	4	1.18						
17	16.7	4	1.24						
18	20.9	4	1.2						
19	1.7	2	2.38						
20	3.59	2	2.31						
21	2.53			0.08	3.84	3.31	4		
22	4.62	1	4.7						
23	2.98	4	3.2						
24	4.8	4	3.85						
25				0.15	3.52	2.66	15		
26		4	2.73	0.2	5.82	5.7	5		
27	6.81	3	9.64						
28		3	2.57	0.09	3.46	3.29	9		
29	2.33	3	2.27	0.1	5.19	4.68	10		
30	3.92	3	1.76						
31		3		0.07	5.4	4.57	14		0.4
32	8.02	5	3.81	0.41	9.52	6.82	6		
33	5.81	4	1.85						
34	9.56	3	2.34	0.2	6.75	5.82	7		
35	1.4								
36		1	5.87	0.48	7.48				
37	4.86		2.93						
38				0.16	8.58	6.79	17	0.15	0.82
39	6.74	4	4.24	0.31	12.03	10.94	9		
40									
41	4.03	4	2.99						
42	3.72	4		0.16	4.74	4.43	6		
43	5.66	5	2.27						
44									
45	2.38	3		0.12	1.02	1.04	5	0.24	0.43
46									
47				0.77	15.21			0.77	3.51
48	1.43		1.82	0.1	3.52			0.32	1.29
49									
50				0.23	6.76	6.12	16		

APPENDIX 1b (continued).

TEXTNO	STAMEXERT	PISLENMAX	PISLENX	PISNO	PISEXERT	STYWID	STYLEN	STYNO	OVWID	OVLEN
1	0.67									
2	0.84									
3										
4										
5										
6										
7	0.41									
8										
9										
10										
11										
12	0.77									
13		4.16	4.16	1		0.17	1.44	2	0.96	2.18
14										
15										
16										
17										
18										
19										
20										
21	0.73	6.14	5.95	1		0.15	1.16	2	1.66	4.93
22		13.38	13.38	1	34.5	0.26		1		
23										
24										
25		5.76	5.76	1		0.8	3.2	1	1.66	2.56
26	0.78									
27										
28	0.76									
29	0.48									
30										
31	0.53									
32	1.61									
33										
34	1.41									
35										
36	0.97									
37										
38	0.29									
39	0.59									
40										
41										
42	0.78									
43										
44		1.54	1.18	3		0.08	0.26	1	0.53	1.2
45				1		0.38		1		
46		2.86		2		0.06	0.7	1	1.71	2.04
47										
48	0.55									
49										
50	0.42									

APPENDIX 2. Pearson correlation coefficients for numeric variables. Acronyms are described in Table IV-2. N is indicated in brackets. * = $p < 0.05$; ** = $p < 0.005$.

	PCLEN	PWIDMAX	PLENMAX	PSHAPE	PPART	PCON	PACT	FWIDMAX	FLENMAX
PCWID	0.59**	0.62**	0.68**	-0.02	0.13	0.07	-	0.53**	0.72**
	(29)	(26)	(26)	(23)	(23)	(42)		(28)	(26)
PCLEN		0.65**	0.64**	-0.06	0.17	-0.28	-	0.54**	0.56**
		(26)	(25)	(23)	(23)	(22)		(28)	(26)
PWIDMAX			0.47*	-0.15	0.14	0.21	0.07	0.99**	0.41*
			(27)	(27)	(38)	(34)	(42)	(42)	(27)
PLENMAX				0.79**	0.22	-0.12	-0.75**	0.31	0.87**
				(27)	(25)	(27)	(29)	(28)	(29)
PSHAPE					0.15	0.02	-0.77**	-0.23	0.67**
					(24)	(25)	(27)	(27)	(27)
PPART						-0.45*	-0.04	0.07	0.01
						(34)	(40)	(38)	(25)
PCON							0.19	0.24	-0.25
							(36)	(34)	(26)
PACT								0.07	-0.67**
								(45)	(31)
FWIDMAX									0.38*
									(30)

APPENDIX 2 (continued).

	FSHAPE	TNO	TWIDMAX	TLENMAX	TSHAPE	FILWID	STAMMAX	STAMNO	STAMEXSE
PCWID	0.31	0.22	0.19	0.65**	0.32	0.64*	0.79**	0.09	0.61*
	(25)	(16)	(19)	(26)	(19)	(15)	(15)	(13)	(16)
PCLEN	-0.04	0.32	0.36	0.65**	0.21	0.46	0.67*	-0.28	0.39
	(25)	(16)	(19)	(26)	(19)	(14)	(15)	(13)	(15)
PWIDMAX	-0.20	0.34	0.96**	0.88**	-0.42*	0.47*	-0.02	-0.17	0.64*
	(30)	(30)	(31)	(39)	(31)	(18)	(20)	(17)	(17)
PLENMAX	0.63**	-0.01	0.66**	0.99**	0.36	0.48	0.89**	-0.25	0.60*
	(28)	(16)	(19)	(27)	(19)	(17)	(17)	(15)	(18)
PSHAPE	0.83**	-0.28	0.29	0.76**	0.42	0.37	0.74**	-0.32	0.26
	(27)	(16)	(18)	(25)	(18)	(16)	(17)	(15)	(17)
PPART	-0.03	.	.	0.19	.	0.02	-0.08	-0.78**	0.47
	(24)	(30)	(33)	(39)	(33)	(16)	(18)	(15)	(15)
PCON	0.02	-0.29	0.43*	0.14	-0.14	0.43	-0.18	0.44	0.04
	(25)	(24)	(28)	(34)	(28)	(17)	(18)	(15)	(17)
PACT	-0.66**	0.29	0.05	-0.33*	-0.29	0.01	-0.83**	0.13	-0.08
	(30)	(30)	(33)	(42)	(33)	(19)	(21)	(18)	(17)
FWIDMAX	-0.28	0.34	0.96**	0.87**	-0.41*	0.41	0.03	0.01	0.31
	(30)	(30)	(31)	(40)	(31)	(19)	(21)	(18)	(17)
FLENMAX	0.76**	0.05	0.52*	0.87**	0.34	0.42	0.95**	-0.05	0.35
	(30)	(16)	(19)	(27)	(19)	(17)	(18)	(16)	(17)
FSHAPE		-0.17	0.19	0.59**	0.34	0.30	0.75**	-0.11	0.08
		(16)	(18)	(26)	(18)	(17)	(18)	(16)	(17)

APPENDIX 2 (continued).

	FSHAPE	TNO	TWIDMAX	TLENMAX	TSHAPE	FILWID	STAMMAX	STAMNO	STAMEXSE
TNO			0.23	0.18	0.13	0.30	-0.25	-0.03	-0.07
			(27)	(30)	(27)	(10)	(11)	(10)	(8)
TWIDMAX				0.87**	-0.50*	0.23	0.14	-0.14	0.71*
				(33)	(33)	(10)	(12)	(9)	(10)
TLENMAX					-0.20	0.48	0.71**	-0.23	0.55
					(33)	(17)	(19)	(16)	(16)
TSHAPE						0.62	0.48	-0.46	-0.01
						(10)	(12)	(9)	(10)
FILWID							0.47*	-0.24	0.60*
							(20)	(17)	(17)
STAMMAX								0.07	0.15
								(18)	(17)
STAMNO									-0.53
									(15)

APPENDIX 3. Structural blossom classes and pollination syndromes from Faegri and van der Pijl (1979). Pollination syndromes have been edited to include only those characteristics relevant to fossil material.

STRUCTURAL BLOSSOM CLASSES

Dish to bowl shaped : depth effect none or little; insect alights on open flower, pollen collects sternotribically; "mess and soil" pollination.

Bell (concave) or funnel/beaker (sides straight/concave): generally has a rim on which pollinator alights; pollen collects dorsally if it climbs down corolla, or on abdomen if it holds on to central reproductive organs.

Head or brush shaped: outermost parts of the reproductive structures form the surface for alighting; perianth reduced or filiform; pollen collects sternotribically or on head for non-alighting pollinators.

Gullet: sex organs on upper side of flower; pollen deposited on the back of the head or the dorsum of the pollinator; lower lip usually has landing platform.

Flag: sex organs on lower part of flower; insects carry pollen sternotribically.

Tube shaped: narrow shape excludes pollinators without elongate mouthparts; pollen collected on front of body.

Trumpet shaped: tube shaped flower with rim for pollinators to alight.

POLLINATION SYNDROMES

Cantharophily (beetle pollination): no definite shape, no depth effect, large, flat shallow bowl-shaped; attractants (pollen or nectar) easily accessible; sexual organs exposed.

Myophily (fly pollinated): regular, simple, no depth effect; nectar easily accessible; sexual organs exposed.

Melittophily (bee pollination): zygomorphic, great depth effect; surface for alighting; intricate, nectar hidden; sexual organs concealed, stamens few.

Psychophily (butterfly pollination): erect, radial, narrow rim not much dissected; nectar hidden in tubes or spurs.

Phalaenophily (moth pollination): horizontal or pendent, no rim for alighting, perianth lobes dissected; nectar deeply hidden.

Ornithophily (bird pollination): tubate, rim absent or curved back; nectar deeply hidden;filaments stiff or united.

Chiropterophily (bat pollination): large-mouthed, strong, single flowers or strong inflorescences of brush flowers; large or many anthers.

APPENDIX 4. Classification and locality of insect specimens. UAPAL = Paleontology Collection, University of Alberta, Edmonton; UWBM = Thomas Burke Memorial Museum, University of Washington, Seattle; CMN = Canadian Museum of Nature, Ottawa; SFU = Simon Fraser University, Vancouver; e = elytron. British Columbia, collectors: J.W. Basinger, S.D. Douglas, L. V. Hills, Kutluk, A. Lindoe, J. Mathewes, R. Mathewes, T.E. Reimchen, G. Rothwell, W.N. Stewart, R.A. Stockey, W. Wehr, M.V.H. Wilson, 1976-1989. Republic, Washington: A0307 = 10th and Clark, B2737 = Knob Hill, B4131 = Boot Hill; collectors: B. Blackstock, D. Hopkins, C. Jenkins, K. Johnson, R. Krausse, K. Nannery, D. Paulson, M. Perry, M. Reeves, D. Silva, M. Spitz, J. Weeks, W. Wehr, 1981 - 1989.

Specimen number	Locality	Order	Superfamily (Suborder)	Family
SFU 175	Quilchena	Hymenoptera	Ichneumonoidea	
SFU 176	Quilchena	Hymenoptera		
SFU 177	Quilchena	Hymenoptera		
SR 88-11-1	Republic B4876	Hymenoptera	Ichneumonoidea	
SR 88-11-2	Republic	Hymenoptera	Formicoidea	Formicidae
UAPAL 4500	Horsefly 3	Hymenoptera	Tenthredinoidea	Tenthredinidae
UAPAL 4501	Horsefly 3	Diptera	Bibionoidea	Bibionidae
UAPAL 4502	Horsefly 3	Diptera	Bibionoidea	Bibionidae
UAPAL 4503	Horsefly 3	Diptera	Bibionoidea	Bibionidae
UAPAL 4504	Horsefly 3	Diptera	Bibionoidea	Bibionidae
UAPAL 4505	Horsefly 3	Coleoptera[e]		
UAPAL 4506	Horsefly 3	Hymenoptera	(Apocrita)	
UAPAL 4507	Horsefly 3	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL 4508	Horsefly 3	Diptera	Sciaroidea	Mycetophilidae
UAPAL 4509	Horsefly 3	Diptera	Sciaroidea	
UAPAL 4510	One Mile Creek	Diptera	Bibionoidea	Bibionidae
UAPAL 4511	One Mile Creek	Coleoptera	?Chrysomeloidea	
UAPAL 4512	One Mile Creek	Coleoptera[e]		
UAPAL 4513	One Mile Creek	Coleoptera	Cantharoidea	Cantharidae
UAPAL 4514	One Mile Creek	Coleoptera		
UAPAL 4515	One Mile Creek	Hymenoptera	(Apocrita)	
UAPAL 4516	One Mile Creek	Coleoptera		
UAPAL 4517	One Mile Creek	Diptera	(Nematocera)	
UAPAL 4518	One Mile Creek	Hemiptera	(Homoptera)	
UAPAL 4519	One Mile Creek	Hymenoptera		
UAPAL 4520	One Mile Creek	Coleoptera[e]		
UAPAL 4521	One Mile Creek	Diptera	Brachycera	
UAPAL 4522	One Mile Creek	Coleoptera[e]		
UAPAL 4523	One Mile Creek	Coleoptera	(Adephaga)	Cicindelidae
UAPAL 4524	Tulameen Road	Hymenoptera	Scolioidea	Scoliidae
UAPAL 4525	Tulameen Road	Diptera	(Nematocera)	
UAPAL 4526	Tulameen Road	Diptera		
UAPAL 4527	Horsefly	Diptera	Tipuloidea	Tipulidae
UAPAL 4528	Horsefly	Isoptera		
UAPAL 4529	Horsefly	Diptera	Sciaroidea	Mycetophilidae
UAPAL 4530	Horsefly	Diptera	Tipuloidea	Tipulidae
UAPAL 4531	Horsefly	Diptera	Sciaroidea	Mycetophilidae
UAPAL 4532	Horsefly	Coleoptera	Curculionoidea	Curculionidae
UAPAL 4533	Horsefly	Hemiptera	(Homoptera)	Cicadellidae
UAPAL 4534	Horsefly	Coleoptera[e]		
UAPAL 4535	Horsefly	Hemiptera		
UAPAL 4536	Horsefly	Diptera	(Nematocera)	
UAPAL 4537	Horsefly	Hymenoptera	(aculeate Apocrita)	
UAPAL 4538	Horsefly	Diptera	Sciaroidea	Sciaridae
UAPAL 4539	Horsefly	Coleoptera[e]		
UAPAL 4540	Horsefly	Diptera	Bibionoidea	Bibionidae
UAPAL 4541	Horsefly	Diptera	(Nematocera)	
UAPAL 4542	Horsefly	Hymenoptera	Formicoidea	Formicidae
UAPAL 4543	Horsefly	Coleoptera[e]		
UAPAL 4544	Horsefly	Coleoptera[e]		
UAPAL 4545	Horsefly	Hymenoptera	Tenthredinoidea	Argidae/Diprionidae

UAPAL	4546	Horsefly	Hemiptera	Aphidoidea	Aphididae
UAPAL	4547	Horsefly	Hymenoptera	(Apocrita)	
UAPAL	4548	Horsefly	Hymenoptera	Tenthredinoidea	Argidae/Diprionidae
UAPAL	4549	Horsefly	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	4550	Horsefly	Diptera		
UAPAL	4551	Horsefly	Coleoptera	Melooidea	Mordellidae
UAPAL	4552	Horsefly	Diptera	Sciaroidea	Sciaridae
UAPAL	4553	Horsefly	Thysanoptera		
UAPAL	4554	Horsefly	Hymenoptera	(aculeate Apocrita)	
UAPAL	4555	Horsefly	Diptera	(Nematocera)	
UAPAL	4556	Horsefly	Hymenoptera	Cynipoidea	Cynipidae
UAPAL	4557	Horsefly	Hymenoptera	Formicoidea	Formicidae
UAPAL	4558	Horsefly 2	Hymenoptera	Formicoidea	Formicidae
UAPAL	4559	Horsefly 2	Hymenoptera	(aculeate Apocrita)	
UAPAL	4560	Horsefly 2	Diptera	Sciaroidea	Mycetophilidae
UAPAL	4561	Horsefly	Coleoptera^e		
UAPAL	4562	Horsefly 2	Coleoptera	Curculionoidea	?Curculionidae
UAPAL	4563	Republic	Hemiptera		
UAPAL	4564	Republic	Diptera	Bibionioidea	Bibionidae
UAPAL	4565	Tom Thumb	Hemiptera	(Homoptera)	Aphidae
UAPAL	4566	Republic	Diptera	Tipuloidea	Tipulidae
UAPAL	4567	Republic	Coleoptera^e		
UAPAL	4568	Republic	Coleoptera^e		
UAPAL	4569	Republic	Coleoptera		
UAPAL	4570	Republic	Coleoptera^e		
UAPAL	4571	Republic	Hemiptera		
UAPAL	4572	Republic	Hemiptera		
UAPAL	4573	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	4574	Republic	Diptera	(Nematocera)	
UAPAL	4575	Republic	Hymenoptera	(Apocrita)	
UAPAL	4576	Republic	Coleoptera		
UAPAL	4577	Republic	Hymenoptera	(Apocrita)	
UAPAL	4578	Republic	Coleoptera	Curculionoidea	Curculionidae
UAPAL	4579	Quilchena	Lepidoptera	Noctuoidea	Noctuidae
UAPAL	4580	Quilchena	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	4581	Quilchena	Hymenoptera	Cynipoidea	Cynipidae
UAPAL	4582	Quilchena	Hymenoptera	Formicoidea	Formicidae
UAPAL	4583	Quilchena	Diptera	Sciaroidea	Mycetophilidae
UAPAL	4584	Quilchena	Diptera	Tabanoidea	Rhagionidae
UAPAL	4585	Quilchena	Diptera	Sciaroidea	Sciaridae
UAPAL	4586	Quilchena	Hemiptera	(Homoptera)	
UAPAL	4587	Quilchena	Diptera	Syrphoidea	Syrphidae
UAPAL	4588	Quilchena	Hemiptera	(Heteroptera)	
UAPAL	4589	Quilchena	Diptera		
UAPAL	4590	Quilchena	Diptera	Sciaroidea	Sciaridae
UAPAL	4591	Quilchena	Diptera	Sciaroidea	Sciaridae
UAPAL	4592	Quilchena	Diptera	Sciaroidea	Sciaridae
UAPAL	4593	Princeton "F"	Coleoptera^e		
UAPAL	4594	Princeton "F"	Hemiptera	(Homoptera)	
UAPAL	4595	Princeton "F"	Diptera	Sciaroidea	Mycetophilidae
UAPAL	4596	Princeton "F"	Hymenoptera	(Apocrita)	
UAPAL	4597	China Creek	Hemiptera	Aphidoidea	Aphidae
UAPAL	4598	China Creek	Trichoptera		
UAPAL	4599	China Creek	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	4600	China Creek	Hymenoptera		
UAPAL	4601	China Creek	Hemiptera	Aphidoidea	Aphidae
UAPAL	4602	China Creek	Diptera	(Nematocera)	
UAPAL	4603	Quilchena	Hymenoptera	Ichneumonoidea	
UAPAL	4604	Quilchena	Hymenoptera	Formicoidea	Formicidae
UAPAL	4605	Quilchena	Trichoptera		
UAPAL	4606	Quilchena	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	4607	Quilchena	Trichoptera		
UAPAL	4608	Quilchena	Hemiptera	Aphidoidea	
UAPAL	4609	Quilchena	Hymenoptera	Ichneumonoidea	
UAPAL	4610	Quilchena	Hymenoptera	Formicoidea	Formicidae

UAPAL	4611	Quilchena	Trichoptera		
UAPAL	4612	Quilchena	Odonata		
UAPAL	4613	Quilchena	Coleoptera[e]		
UAPAL	4514	Quilchena	?Hemiptera		
UAPAL	4615	Quilchena	Hemiptera	Aphidoidea	Aphididae
UAPAL	4616	Quilchena	Hymenoptera	Formicoidea	Formicidae
UAPAL	4617	Quilchena	Diptera		
UAPAL	4618	Quilchena	Neuroptera		
UAPAL	4619	Quilchena	Diptera	Sciaroidea	Mycetophilidae
UAPAL	4620	Quilchena	Hemiptera	Aphidoidea	
UAPAL	4621	Quilchena	Hemiptera	Aphidoidea	Aphidae
UAPAL	4622	Quilchena	Coleoptera		
UAPAL	4623	Quilchena	Coleoptera[e]		
UAPAL	4624	Quilchena	Coleoptera		
UAPAL	4625	Quilchena	Coleoptera		
UAPAL	4626	Quilchena	Coleoptera	Chrysomeloidea	Cerambycidae
UAPAL	4627	Quilchena	Coleoptera		?Scarabaeidae
UAPAL	4628	Quilchena	Coleoptera	?Chrysomeloidea	
UAPAL	4629	Quilchena	Coleoptera		
UAPAL	4630	Quilchena	Coleoptera		
UAPAL	4631	Quilchena	Coleoptera		
UAPAL	4632	Quilchena	Coleoptera	Cleroidea	Cleridae
UAPAL	4633	Quilchena	Hemiptera	Aphidoidea	Aphidae
UAPAL	4634	Quilchena	Hymenoptera	(Apocrita)	
UAPAL	4635	Quilchena	Coleoptera	Scarabaeoidea	
UAPAL	4636	Quilchena	Diptera	(Nematocera)	
UAPAL	4637	Quilchena	Diptera	(Nematocera)	
UAPAL	4638	Quilchena	Diptera	Bibionoidea	Bibionidae
UAPAL	4639	Quilchena	Diptera	(Nematocera)	
UAPAL	4640	Horsefly 2	Diptera	Bibionoidea	Bibionidae
UAPAL	4641	Horsefly 3	Diptera	(Nematocera)	
UAPAL	4642	Horsefly 3	Diptera	Bibionoidea	Bibionidae
UAPAL	4643	One Mile Creek	Odonata	(Anisoptera)	
UAPAL	4644	Horsefly	Trichoptera		
UAPAL	4645	Driftwood	Diptera		
UAPAL	4646	Driftwood Creek	Diptera	Empidoidea	Empididae
UAPAL	4647	One Mile Creek	Diptera	Bibionoidea	Bibionidae
UAPAL	5016	Driftwood	Diptera		
UAPAL	5017	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5021a	Tulameen Road	Diptera	Bibionoidea	Bibionidae
UAPAL	5021b	Tulameen Road	Diptera	Bibionoidea	Bibionidae
UAPAL	5036	Horsefly	Diptera	(Nematocera)	
UAPAL	5069	Driftwood	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5080	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5084	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5087	Driftwood	Hemiptera	(Heteroptera)	
UAPAL	5088	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5089	Driftwood	Hymenoptera	Ichneumonoidea	
UAPAL	5090	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5093	Driftwood	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5094	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5096	Driftwood	Hemiptera	(Heteroptera)	
UAPAL	5097	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5098	Driftwood	Isoptera		
UAPAL	5102	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5103	Driftwood	Hymenoptera		
UAPAL	5105	Driftwood	Hemiptera	(Homoptera)	Aphidae
UAPAL	5106	Driftwood	Diptera		
UAPAL	5108	Driftwood	Diptera	Sciaroidea	Sciaridae
UAPAL	5109	Driftwood	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5112	Driftwood	Diptera	(Nematocera)	
UAPAL	5115	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5116	Driftwood	Diptera		
UAPAL	5119	Driftwood	Diptera		
UAPAL	5120	Driftwood	Diptera	(Nematocera)	

UAPAL	5121	Driftwood	Diptera		
UAPAL	5123	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5129	Driftwood	Diptera		
UAPAL	5130	Driftwood	Diptera		
UAPAL	5131	Driftwood	Hymenoptera		
UAPAL	5132	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5133	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5135	Driftwood	Diptera		
UAPAL	5136	Driftwood	Diptera		
UAPAL	5137	Driftwood	Diptera		
UAPAL	5139	Driftwood	Hymenoptera	(Apocrita)	
UAPAL	5140	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5143	Driftwood	Diptera		
UAPAL	5144	Driftwood	Hemiptera	(Heteroptera)	
UAPAL	5145	Driftwood	Isoptera		
UAPAL	5146	Driftwood	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5150	Driftwood	Hymenoptera	(Apocrita)	
UAPAL	5151	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5154	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5157	Driftwood	Diptera		
UAPAL	5159	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5160	Driftwood	Coleoptera		
UAPAL	5161	Driftwood	Hemiptera	(Heteroptera)	
UAPAL	5165	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5169	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5172	Driftwood	Diptera		
UAPAL	5179	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5180	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5181	Driftwood	Diptera		
UAPAL	5189	Driftwood	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5192	Driftwood	Diptera		
UAPAL	5196	Driftwood	Hymenoptera		
UAPAL	5200	Driftwood	Hymenoptera	Ichneumonoidea	
UAPAL	5204	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5206	Driftwood	Hymenoptera		
UAPAL	5207	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5208	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5211	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5214	Driftwood	Hemiptera	(Heteroptera)	Gerridae
UAPAL	5222	Driftwood	Diptera	Bibionoidea	Bibionidae
UAPAL	5223	Driftwood	Diptera		
UAPAL	5225	Driftwood	Hemiptera	(Heteroptera)	
UAPAL	5452	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	5468	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	5470	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	5479	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	5648	Republic	Diptera	Bibionoidea	Bibionidae
UAPAL	5695	Republic	?Hemiptera		
UAPAL	5697	Republic	Diptera	Sciaroidea	Mycetophilidae
UAPAL	5714	Republic	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5781	Republic	Hymenoptera	Ichneumonoidea	Ichneumonidae
UAPAL	5786	Republic	Diptera	Sciaroidea	Mycetophilidae
UAPAL	6122	Tom Thumb	Hemiptera	(Homoptera)	
UAPAL	6123	Tulameen Road	Diptera		
UAPAL	6125	Tulameen Road	Diptera	Tipulomorpha	?Tipulidae
UAPAL	6126	Tulameen Road	Diptera		
UWBM	57095	One Mile Creek	Coleoptera	Elateroidea	Elateridae
UWBM	57096	Republic	Coleoptera	Curculionoidea	Curculionidae
UWBM	57097	Republic	Coleoptera	Chrysmeloidea	Cerambycidae
UWBM	57098	Republic B2737	Coleoptera	(Adephaga)	Carabidae
UWBM	57100	Republic A0307	Coleoptera[e]		
UWBM	57101	Republic	Coleoptera[e]		
UWBM	57102	Republic A0307	Coleoptera[e]		
UWBM	57103	Republic	Coleoptera[e]		
UWBM	57104	Republic	Coleoptera[e]		

UWBM	57105	Republic	Coleoptera[e]		
UWBM	57106	Republic B4131	Coleoptera[e]		
UWBM	57107	Republic	Hemiptera	(Heteroptera)	
UWBM	57108	Republic	Coleoptera[e]		
UWBM	57110	Republic	Hemiptera	(Heteroptera)	
UWBM	57111	Republic B2737	Hymenoptera	(Apocrita)	
UWBM	57112	One Mile Creek	Hymenoptera	Ichneumonoidea	Ichneumonidae
UWBM	57113	Republic	Hymenoptera	Ichneumonoidea	
UWBM	57114	Republic	?Hemiptera		
UWBM	57115A	Republic	Diptera	Bibionoidea	Bibionidae
UWBM	57116	Republic B2737	Hymenoptera	Ichneumonoidea	
UWBM	57117	Republic B2737	Coleoptera		
UWBM	57118	Republic B2737	Coleoptera	Scarabaeoidea	Lucanidae
UWBM	57120	Republic B2737	Diptera	Bibionoidea	Bibionidae
UWBM	57122A	Republic A0308	Hymenoptera	Ichneumonoidea	Ichneumonidae
UWBM	57122B	Republic A0308	Diptera	Bibionoidea	Bibionidae
UWBM	57122C	Republic A0308	Diptera	Bibionoidea	Bibionidae
UWBM	57122D	Republic A0308	Diptera	Bibionoidea	Bibionidae
UWBM	57123	Republic B4131	Hymenoptera	Sphecoidea	Sphecidae
UWBM	57124	Republic B2737	Diptera		
UWBM	57125	Republic	Hemiptera	Aphidoidea	
UWBM	66000	Republic	Lepidoptera	Geometroidea	Geometridae
UWBM	72299	Republic A0308	Coleoptera	Curculionoidea	Curculionidae
UWBM	72302	Republic	Coleoptera	(Adephaga)	Dytiscidae
UWBM	72307	Republic	Hemiptera	(Heteroptera)	Gerridae
UWBM	72311	Republic	Hymenoptera	Ichneumonoidea	Ichneumonidae
UWBM	72312	Republic A0307	Hymenoptera	(Apocrita)	
UWBM	72321	Republic A0308	Hemiptera		
CMN	100013	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100024	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100031	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100037	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100040	McAbee	Hymenoptera	Pompiloidea	Pompilidae
CMN	100042	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100044	McAbee	Hemiptera	(Heteroptera)	
CMN	100049	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100055	McAbee	Diptera	Bibionoidea	Bibionidae
CMN	100084	McAbee	Hymenoptera	Ichneumonoidea	Ichneumonidae
CMN	100085	McAbee	Hemiptera	(Heteroptera)	
CMN	100089	McAbee	Orthoptera		
CMN	100092	McAbee	Hymenoptera	Ichneumonoidea	Ichneumonidae
CMN	100123	McAbee	Diptera	Bibionoidea	Bibionidae

APPENDIX 5. Stratigraphic occurrence of families of insects (Coleoptera, Hymenoptera, Diptera, Lepidoptera). Families are arranged alphabetically within orders. For additional families for Florissant and Green River, see Wilson (1978). All records previous to and including the Eocene are listed below and in Wilson (1978); only representative Oligocene records are listed. Neogene records are not included. Citations are listed in Chapter VI, pp. 189-192 and Chapter VII, pp. 214-224. Stratigraphic position of localities is given in Appendix 6 or, for less common records, included with the reference below.

COLEOPTERA

Aderidae	Baltic amber	Larsson 1978
Alleculidae	Karatau	Crowson 1981
Anaspidae	Baltic amber	Larsson 1978
Anobiidae	Florissant	Handlirsch 1908
Anobiidae	Baltic amber	Handlirsch 1908, Larsson 1978
Anobiidae	Green River	Handlirsch 1908, Grande 1984
Anthicidae	Baltic amber	Handlirsch 1908, Larsson 1978
Anthribidae	Baltic amber	Handlirsch 1908, Larsson 1978
Anthribidae	Florissant	Handlirsch 1908
Anthribidae	Green River	Scudder 1890, Grande 1984
Anthribidae	Karatau	Crowson 1981
Apionidae	Lower Cretaceous	Crowson 1981
Archecoleoptera	Upper Permian	Crowson 1981
Artematopidae	Baltic amber	Larsson 1978
Aspidiophoridae	Baltic amber	Larsson 1978
Attelabidae	Green River	Grande 1984
Belidae	Karatau	Crowson 1981
Bostrychidae	Baltic amber	Handlirsch 1908, Larsson 1978
Bruchidae	Baltic amber	Larsson 1978
Bruchidae	Green River	Grande 1984
Buprestidae	Baltic amber	Handlirsch 1908, Larsson 1978
Buprestidae	Italy Mid Eocene, England Mid Eocene	Handlirsch 1908
Buprestidae	Quesnel, Ninemile, Similkameen, Vancouver Island	Handlirsch 1910
Buprestidae	Nicola	Scudder 1890
Buprestidae	Queensland	Tillyard and Dunstan 1923
Buprestidae	Messel	Schaal and Ziegler 1988
Buprestidae	Karatau	Crowson 1981
Buprestidae	Geiseltal	Pongracz 1935
Byrridae	Florissant	Handlirsch 1908
Byrridae	Green River	Scudder 1890
Byrridae	Baltic amber	Handlirsch 1908, Larsson 1978
Cantheridae	Florissant	Handlirsch 1908
Cantheridae	Baltic amber	Handlirsch 1908, Larsson 1978
Carabidae	Florissant,Nicola	Scudder 1890
Carabidae	Green River	Scudder 1890, Grande 1984
Carabidae	Alberta Paskapoo	Mitchell and Wighton 1979
Carabidae	Baltic amber	Handlirsch 1908, Larsson 1978
Carabidae	Claiborne	Saunders et al. 1974
Carabidae	Mongolia (Up.Jurassic, Low Cret), Transbaikalia (Low Cret)	Ponomarenko 1989
Carabidae	Mormon Creek	Wilson 1978
Carabidae	Messel	Schaal and Ziegler 1988
Carabidae?	Geiseltal	Pongracz 1935
Carabidae	Karatau	Crowson 1981
Carabidae	Florissant	Handlirsch 1908
Cerambycidae	Baltic amber	Handlirsch 1908, Larsson 1978
Cerambycidae	Queensland	Tillyard and Dunstan 1923
Cerambycidae	Messel	Schaal and Ziegler 1988
Cerambycidae	Green River	Grande 1984
Cerambycidae	Karatau	Hennig 1981
Cerambycidae	Geiseltal	Pongracz 1935
Cerambycoidea	Canadian amber	McAlpine and Martin 1969
Cerophytidae	Taimyr	Crowson 1981
Chrysomelidae	Florissant, Greenland Eocene, Similkameen	Handlirsch 1908
Chrysomelidae	Ninemile	Scudder 1890
Chrysomelidae	Alberta Paskapoo	Mitchell and Wighton 1979

Chrysomelidae	Baltic amber	Handlirsch 1908, Larsson 1978
Chrysomelidae	Geiseltal	Pongracz 1935
Chrysomelidae	Green River	Scudder 1890, Grande 1984
Chrysomeloidea	Karatau	Crowson 1981
Cicindellidae	Baltic amber	Larsson 1978
Cicindellidae	Green River	Grande 1984
Ciidae	Baltic amber	Handlirch 1908
Circaeidae	Baltic amber	Larsson 1978
Clambidae	Baltic amber	Larsson 1978
Cleridae	Florissant	Handlirsch 1908
Cleridae	Baltic amber	Handlirsch 1908, Larsson 1978
Cleroidea	Taimyr	Crowson 1981
Coccinellidae	Florissant	Handlirsch 1908
Coccinellidae	Baltic amber	Handlirsch 1908, Larsson 1978
Colydiidae	Baltic amber	Handlirsch 1908, Larsson 1978
Colydiidae	Florissant	
Corlylophidae	Baltic amber	Larsson 1978
Cryptophagidae	Baltic amber	Handlirsch 1908, Larsson 1978
Cryptophagidae	Green River	Scudder 1890
Cucujidae	Baltic amber	Handlirsch 1908, Larsson 1978
Cucujidae	Florissant	Handlirsch 1908
Cucujidae	Green River	Scudder 1890
Cucujoidea	Karatau	Crowson 1981
Cupedidae	Baltic amber	Handlirsch 1908, Larsson 1978
Cupedidae	Karatau	Crowson 1981
Curculionidae	Geiseltal	Pongrasz 1935
Curculionidae	Central Asia (Low Cret)	Crowson 1981
Curculionidae	Fox Hills	Crowson 1981
Curculionidae	Baltic amber	Handlirsch 1908, Larsson 1978
Curculionidae	Florissant, England	Handlirsch 1908
Curculionidae	Alberta Paskapoo	Mitchell and Wighton 1979
Curculionidae	Queensland	Tillyard and Dunstan 1923
Curculionidae	Messel	Schaal and Ziegler 1988
Curculionidae	Green River	Scudder 1890, Grande 1984
Curculionoidea	Karatau	Crowson 1981
Dascillidae	Baltic	Handlirsch 1908
Dascillidae	Queensland	Tillyard and Dunstan 1923
Dascillidae	Messel	Schaal and Ziegler 1988
Dermestidae	Baltic amber	Handlirsch 1908, Larsson 1978
Dermestidae	Florissant	Handlirsch 1908
Dermestidae	Queensland	Tillyard and Dunstan 1923
Dermestidae	Lebanese amber	Crowson 1981
Dryopidae	Florissant	Handlirsch 1908
Dytiscidae	Florissant	Handlirsch 1908
Dytiscidae	Alberta Paskapoo	Mitchell and Wighton 1979
Dytiscidae	Baltic amber	Handlirsch 1908, Larsson 1978
Dytiscidae	Kazakhstan	Crowson 1981
Dytiscidae	Green River	Scudder 1890, Grande 1984
Elateridae	Baltic amber	Handlirsch 1908, Larsson 1978
Elateridae	Similkameen	Handlirsch 1910
Elateridae	Geiseltal	Pongracz 1935
Elateridae	Ruby Paper Shales	Wilson 1978
Elateridae	Lebanese amber	Crowson 1981
Elateridae	Karatau	Crowson 1981
Elateridae	USSR (Low Jura)	Crowson 1981
Elateridae	Nicola	Scudder 1890
Elateridae	Green River	Scudder 1890, Cockerell and Levesque 1931
Elateridae	Wealdon (LowCret)	Jarzembowski 1984
Elateridae	Queensland	Tillyard and Dunstan 1923
Elateridae	Messel	Schaal and Ziegler 1988
Elateridae?	Alberta Paskapoo	Mitchell and Wighton 1979
Endomychidae	Baltic amber	Handlirsch 1908, Larsson 1978
Eobelidae	Karatau	Crowson 1981
Erotylidae	Baltic amber	Handlirsch 1908
Erotylidae	Green River	Scudder 1890

Eucnemidae	White River	Handlirsch 1908
Eucnemidae	Baltic amber	Handlirsch 1908, Larsson 1978
Glaphyropteridae	Geiseltal	Pongracz 1935
Gyrinidae	Baltic amber	Handlirsch 1908, Larsson 1978
Gyrinidae	Karatau	Crowson 1981
Helodidae	Alberta Paskapoo	Mitchell and Wighton1979
Helodidae	Baltic amber	Larsson 1978
Heteroceridae	Baltic amber	Larsson 1978
Histeridae	Baltic amber	Handlirsch 1908, Larsson 1978
Histeridae	Florissant	Handlirsch 1908
Hydraenidae	USSR (Low Jura)	Crowson 1981
Hydrophilidae	Florissant	Handlirsch 1908
Hydrophilidae	Nicola	Scudder 1890
Hydrophilidae	Baltic amber	Larsson 1978
Hydrophilidae	Queensland	Tillyard and Dunstan 1923
Hydrophilidae	Green River	Scudder 1890, Grande 1984
Lagriidae	Greenland Eocene	Handlirsch 1908
Lagriidae	Baltic amber	Handlirsch 1908, Larsson 1978
Lathridiidae	Baltic amber	Handlirsch 1908, Larsson 1978
Lathridiidae	Taimyr	Crowson 1981
Limnichidae	Baltic amber	Larsson 1978
Lucanidae	Baltic	Handlirsch 1908
Lucanidae	Messel	Schaal and Ziegler 1988
Lyctidae	Baltic amber	Handlirsch 1908, Larsson 1978
Lymexylonidae	Baltic amber	Handlirsch 1908, Larsson 1978
Meloidae	Florissant	Handlirsch 1908
Meloidae	Baltic amber	Handlirsch 1908, Larsson 1978
Melandryidae	Baltic amber	Handlirsch 1908, Larsson 1978
Melandryidae	Green River	Grande 1984
Melyridae	Baltic amber	Handlirsch 1908, Larsson 1978
Mordellidae	Baltic amber	Handlirsch 1908, Larsson 1978
Mordellidae	Green River	Grande 1984
Mordellidae?	Karatau	Crowso 1981
Mycetophagidae	Provence	Handlirsch 1908
Mycetophagidae	Baltic amber	Larsson 1978
Nitidulidae	Baltic amber	Handlirsch 1908, Larsson 1978
Nitidulidae	Florissant	Handlirsch 1908
Nitidulidae	Quesnel	Scudder 1890
Nitidulidae	Green River	Scudder 1890, Grande 1984
Nitidulidae	Karatau	Hennig 1981
Nosodendridae	Florissant	Handlirsch 1908
Nosodendridae	Green River	Handlirsch 1908, Grande 1984
Noteridae?	Alberta Paskapoo	Mitchell and Wighton 1979
Nemonychidae	Karatau	Crowson 1981
Oedemeridae	Baltic amber	Handlirsch 1908, Larsson 1978
Oedemeridae	Karatau	Hennig 1981
Ommadidae	USSR (Low Jura)	Crowson 1981
Ostomatidae	Karatau	Hennig 1981
Ostomidae	Greenland Eocene	Handlirsch 1908
Ostomidae	Baltic amber	Handlirsch 1908, Larsson 1978
Otiorhynchidae	Green	Scudder 1890
Oxycorynidae	Karatau	Crowson 1981
Paussidae	Baltic amber	Handlirsch 1908, Larsson 1978
Pedilidae	Baltic amber	Larsson 1978
Phalacridae	Baltic	Handlirsch 1908
Platypodidae	Baltic amber	Larsson 1978
Praemordellidae	Karatau	Hennig 1981
Protocoleoptera	Ural Mtns (Low Permian)	Crowson 1981
Pselaphidae	Baltic amber	Handlirsch 1908, Larsson 1978
Psephenidae	Ruby Paper Shales	Wilson 1978
Ptilinidae	Baltic amber	Larsson 1978
Ptilodactylidae	Baltic amber	Larsson 1978
Ptinidae	Green River	Scudder 1890, Grande 1984
Pyrochroidae	Baltic amber	Handlirsch 1908, Larsson 1978
Pythidae	Baltic amber	Handlirsch 1908

Rhipiphoridae	Florissant	Scudder 1890
Rhipiphoridae	Baltic amber	Handlirsch 1908, Larsson 1978
Rhipiphoridae	Green River	Grande 1984
Rhynchitidae	Green River	Scudder 1890
Salpingidae	Baltic amber	Larsson 1978
Scaphidiidae	Baltic amber	Handlirsch 1908, Larsson 1978
Scarabaeidae	Baltic amber	Handlirsch 1908
Scarabaeidae	Ninemile	Scudder 1890
Scarabaeidae	Messel	Schaal and Ziegler 1988
Scarabaeidae	Green River	Scudder 1890, Grande 1984
Scarabaeidae	Ruby Paper Shales	Wilson 1978
Scarabaeoidea	Switzerland (Low Jura)	Crowson 1981
Scolytidae	Baltic amber	Handlirsch 1908, Larsson 1978
Scolytidae	Florissant, White	Handlirsch 1908
Scolytidae	Green River	Scudder 1890, Grande 1984
Scraptiidae	Baltic amber	Larsson 1978
Scydmaenidae	Baltic amber	Handlirsch 1908, Larsson 1978
Scydmaenidae	Lebanese amber	Crowson 1981
Scydmaenidae	Cedar Lake amber	McAlpine and Martin 1969
Silphidae	Florissant, Germany	Handlirsch 1908
Silphidae	Baltic amber	Larsson 1978
Silphidae	Ruby Paper Shales	Wilson 1978
Spercheidae	Karatau	Crowson 1981
Staphylinidae	Florissant	Scudder 1890
Staphylinidae	Baltic amber	Handlirsch 1908, Larsson 1978
Staphylinidae	Magadan (East USSR, UpCret)	Ryvkin 1988
Staphylinidae	Cedar Lake amber	McAlpine and Martin 1969
Staphylinidae	Messel	Schaal and Ziegler 1988
Staphylinidae	Green River	Scudder 1890, Grande 1984
Staphylinidae	Karatau	Crowson 1981
Tenebrionidae	Baltic amber	Handlirsch 1978, Larsson 1978
Tenebrionidae	Florissant, Greenland Eocene, England Eocene	Handlirsch 1908
Tenebrionidae	Ninemile, White	Scudder 1890
Tenebrionidae	Alberta Paskapoo	Mitchell and Wighton 1979
Tenebrionidae	Queensland	Tillyard and Dunstan 1923
Tenebrionidae	Geiseltal	Pongracz 1934
Tetraphaleridae	USSR (Low Jura)	Crowson 1981
Throscidae	Baltic amber	Handlirsch 1908, Larsson 1978
Trachypachidae	Mongolia (Up. Jurassic, Low Cret)	Ponomarenko 1989
Trichopterygidae	Baltic amber	Handlirsch 1908
Xylophilidae	Baltic amber	Handlirsch 1908

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Adrenidae	Baltic	Handlirsch 1908
Adrenidae	Baltic amber	Handlirsch 1908, Larsson 1978
Aulacidae	Baltic amber	Larsson 1978
Aphelidae	Baltic amber	Larsson 1978
Anthophoridae	Messel	Schaal and Ziegler 1988
Apidae (Adrena, Bombus, Melipona, Trigona)	Baltic, Florissant	Handlirsch 1908
Apidae(Meliponinae, Trigona)	Baltic amber	Larsson 1978, Ruttner 1988
Apidae(Electrapis, no subfamily)	Baltic amber	Larsson 1978, Ruttner 1988
Apidae	Ruby Paper Shales	Wilson 1978
Baissodidae(extinct fam)	Wealden	Jarzembowski 1984
Belytidae	Baltic amber	Larsson 1978
Bethylidae	Baltic amber	Handlirsch 1908, Larsson 1978
Bethylidae	Taimir	Evans 1973
Bethyloidea	Cedar L. amber	Evans 1969
Braconidae	Driftwood, BC	Wilson 1977
Braconidae	Florissant	Handlirsch 1908
Braconidae	Baltic amber	Handlirsch 1908, Larsson 1978
Braconidae	Green River, Quesnel, Similkameen	Scudder 1890
Braconidae	Cedar Lake amber	Carpenter et al. 1937, McAlpine and Martin 1969
Calliceratidae	Cedar Lake amber	Carpenter et al. 1937
Cecidomyiidae	Baltic amber	Larsson 1978
Cephidae	Baltic amber	Larsson 1978

Ceraphronidae	Baltic amber	Larsson 1978
Ceraphronidae	Cedar Lake amber	Carpenter et al. 1937, McAlpine and Martin 1969
Chalcididae	Baltic, Florissant	Handlirsch 1908
Chalcididae	Green River	Scudder 1890
Chalcididae	Messel	Schaal and Ziegler 1988
Chalcidoidea	Canadian amber	McAlpine and Martin 1969
Chrysididae	Florissant	Handlirsch 1908
Chrysididae	Baltic amber	Handlirsch 1908, Larsson 1978
Cleptidae(Chrysididae)	Cedar Lake amber	Evans 1969
Cleptidae	Taimir(UpCret)	Evans 1973
Cretevaniidae	Wealden (LowCret)	Jarzembowski 1984
Cynipidae	Florissant	Handlirsch 1908
Cynipidae	Cedar Lake amber	Carpenter et al. 1937
Cynipidae	Baltic amber	Handlirsch 1908, Larsson 1978
Diapriidae	Baltic amber	Larsson 1978
Diapriidae	Canadian amber	McAlpine and Martin 1969
Dryinidae	Baltic amber	Larsson 1978, Ponomarenko 1988
Embolemidae	Baltic amber	Larsson 1978
Encyrtidae	Baltic amber	Larsson 1978
Ephialtitidae	Spain Jurassic	Handlirsch 1908
Eulophidae	Baltic amber	Larsson 1978
Eumenidae	Messel	Schaal and Ziegler 1988
Eurytomidae	Baltic amber	Larsson 1978
Evaniidae	Baltic amber	Larsson 1978
Evanioidea	Karatau	Crowson 1981
Formicidae	Florissant	Handlirsch 1908
Formicidae	Baltic amber	Handlirsch 1978, Larsson 1978
Formicidae	Quesnel	Scudder 1890
Formicidae	Alberta Paskapoo	Mitchell and Wighton 1979
Formicidae	Sakhalin amber (Paleocene?)	Dlussiy 1988
Formicidae	Green River	Scudder 1890, Grande 1984
Formicidae	Messel	Lutz 1986, Schaal and Ziegler 1988
Formicidae	Ruby Paper Shales	Wilson 1978
Formicidae	Claiborne	Saunders et al. 1974
Formicidae	Lebanese amber	Hennig 1981
Ichneumonidae	BC	Wilson 1977
Icheumonidae	Florissant	Handlirsch 1908
Ichneumonidae	Baltic amber	Handlirsch 1908, Larsson 1978
Ichneumonidae	Tranquille	Handlirsch 1910
Ichneumonidae	Quesnel	Scudder 1890
Ichneumonidae	Green River	Scudder 1890, Cockerell and Leveque 1931, Grande 1984
Ichneumonidae	Messel	Schaal and Ziegler 1988
Ichneumonidae	Mormon Creek	Wilson 1978
Ichneumonidae	Ruby Paper Shales	Wilson 1978
Ichneumonidae	Creede Formation	Wilson 1978
Ichneumonoidea	Canadian amber	McAlpine and Martin 1969
Karataidae	Kazakhstan	Rasnitsyn 1977
Lophyridae	Baltic amber	Larsson 1978
Megachilidae	Florissant	Cockerell 1908
Megalyridae	Azerbaydzhanian SSR (UpCret)	Rasnitsyn 1977
Mymaridae	Cedar Lake amber	Carpenter et al. 1937, McAlpine and Martin 1969
Mymaridae	Baltic amber	Larsson 1978
Mymaridae	Claiborne	Saunders et al. 1974
Mymarommidae	Baltic amber	Larsson 1978
Myrmisidae(Pseudosiricidae)	Messel	Schaal and Ziegler 1988
Myrmosidae	Baltic amber	Larsson 1978
Mutillidae	Baltic amber	Handlirsch 1908, Larsson 1978
Orussidae	Taimir (UpCret)	Rasnitsyn 1977
Pamphiliidae	Transbaikalia (Mid-Up Jur)	Rasnitsyn 1977
Pompilidae	Florissant	Handlirsch 1908
Pompilidae	Baltic amber	Handlirsch 1908, Larsson 1978, Day et al. 1988
Pompilidae	Messel	Schaal and Ziegler 1988
Proctotrupidae	Baltic amber	Handlirsch 1908, Larsson 1978
Proctotrupoidea	Canadian amber	McAlpine and Martin 1969
Pseudosiricidae	Solnhofen	Handlirsch 1908

Pteromalidae	Baltic amber	Larsson 1978
Sapygidae	Baltic amber	Handlirsch 1908, Larsson 1978
Scelionidae	Cedar Lake amber	Carpenter et al. 1937
Scelionidae	Baltic amber	Larsson 1978
Scolebythidae(extinct fam)	Taimir (UpCret)	Evans 1973
Scoliidae	Florissant	Handlirsch 1908
Scoliidae	Baltic amber	Handlirsch 1908, Larsson 1978
Scoliidae	Messel	Schaal and Ziegler 1988
Scolioidea (Cretavus) (Up Cret)		Evans 1969
Serphitidae	Cedar Lake amber	Carpenter et al. 1937
Siricidae	Baltic amber	Larsson 1978
Siricoidea	Solnhofen	Hennig 1981
Sphecidae	Baltic amber	Handlirsch 1908, Larsson 1978, Nemkov 1988
Sphecidae	Florissant	Handlirsch 1908
Sphecidae	Green River	Scudder 1890
Sphecidae	England (LowCret)	Evans 1969
Sphecidae	Cedar Lake amber	Evans 1969
Sphecidae	Taimir (UpCret)	Evans 1973
Sphecidae	Wealden (LowCret)	Jarzembowski 1984
Sphecidae	Messel	Schaal and Ziegler 1988
Tenthredinidae	Florissant	Handlirsch 1908
Tenthredinidae	Green River	Scudder 1890
Tenthredinidae	Baltic amber	Handlirsch 1908, Larsson 1978
Tenthredinidae?	Bohemia Cretaceous	Handlirsch 1908
Tenthredinidae?	Ruby Paper Shales	Wilson 1978
Tiphiidae	Messel	Schaal and Ziegler 1988
Torimidae	Baltic amber	Larsson 1978
Trigonalidae	Taimir (UpCret)	Rasnitsyn 1977
Trichogrammatidae	Baltic amber	Larsson 1978
Vanhorniidae?	Canadian amber	McAlpine and Martin 1969
Vespidae	Blakeburn, BC	Wilson 1977
Vespidae	Baltic, Florissant	Handlirsch 1908
Vespoidea	Kazakhstan	Willemstein 1987
Xyelidae	Transbaikalia (LowCret)	Rasnitsyn 1977
Xyelotomidae	Transbaikalia (LowCret)	Rasnitsyn 1977

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Acanthomenidae	Baltic	Handlirsch 1908
Acartophthalmidae	Baltic amber	Larsson 1978
Acroceridae	Baltic amber	Larsson 1978
Acroceridae	White River	Handlirsch 1908
Acroceridae	Green River	Grande 1984
Acroceridae	Karatau	McAlpine et al. 1971
Anosopodidae	Canadian amber	McAlpine and Martin 1969
Anthericidae	Baltic amber	Larsson 1978
Anthericidae	Messel	Schaal and Ziegler 1988
Anthomyidae	Quesnel	Scudder 1890
Anthomyidae	Green River	Grande 1984
Anthomyzidae	Baltic amber	Larsson 1978
Asilidae	Baltic amber	Handlirsch 1908, Larsson 1978)
Asilidae	Florissant	Handlirsch 1908, Cockerell 1908, Cockerell 1914
Asilidae	Similkameen	Scudder 1890
Asilidae	Ruby Paper Shales	Wilson 1978
Asilidae	Green River	Scudder 1890, Grande 1984
Asteiidae	Baltic amber	Larsson 1978
Aulacigastridae	Baltic amber	Larsson 1978
Bibionidae	BC (many sites)	Rice 1959
Bibionidae	Baltic amber	Handlirsch 1908, Larsson 1978
Bibionidae	BC	Wilson 1977
Bibionidae	England Jurassic	Handlirsch 1908
Bibionidae	Similkameen	Scudder 1890
Bibionidae	Horsefly, Tulameen	Handlirsch 1910
Bibionidae	Cedar Lake amber	Peterson 1977
Bibionidae	Canadian amber	McAlpine and Martin 1969
Bibionidae	Green River	Scudder 1890, Grande 1984

Bibionidae	Ruby Paper Shales	Wilson 1978
Bibionidae	Creede Formation	Wilson 1978
Bombyliidae	Baltic amber	Larsson 1978
Bombyliidae	Taimir	Zeitsev 1986
Bombyliidae	Ruby Paper Shales	Wilson 1978
Borboridae	Baltic, Green, Florissant, Quesnel, White	Handlirsch 1908
Borboridae	Quesnel	Handlirsch 1910
Calobatidae	Baltic amber	Larsson 1978
Calliphoridae	Edmonton Fm (Up Cret)	McAlpine 1970
Camillidae	Baltic amber	Larsson 1978
Carnidae	Baltic amber	Larsson 1978
Cecidomyiidae	Baltic amber	Handlirsch 1908, Larsson 1978
Cecidomyiidae	Green River	Scudder 1890
Cecidomyiidae	Canadian amber	McAlpine and Martin 1969
Ceratopogonidae	Baltic amber	Larsson 1978
Ceratopogonidae	Cedar Lake amber	Carpenter et al. 1937, McAlpine and Martin 1969
Ceratopogonidae	New Jersey (Upper Cret)	Grogan and Szadziewski 1988
Ceratopogonidae	Lebanese amber	McAlpine et al. 1981
Chamaemyiidae	Baltic amber	Larsson 1978
Chironomidae	Baltic amber	Handlirsch 1908, Larsson 1978
Chironomidae	Florissant	Handlirsch 1908
Chironomidae	Cedar Lake amber	Carpenter et al. 1937, McAlpine and Martin 1969
Chironomidae	Green River	Scudder 1890, Grande 1984
Chironomidae	Quesnel	Handlirsch 1910
Chironomidae	Messel	Schaal and Ziegler 1988
Chironomidae	Ruby Paper Shales	Wilson 1978
Chironomidae	Lebanese amber	McAlpine et al. 1981
Chloropidae	Baltic amber	Larsson 1978
Chloropidae	Canadian amber	McAlpine and Martin 1969
Chyromyidae	Baltic amber	Larsson 1978
Clusiidae	Baltic amber	Larsson 1978
Conopidae	Baltic	Handlirsch 1908
Conopidae	Green River	Scudder 1890
Cryptochetidae	Baltic amber	Larsson 1978
Culicidae	Florissant	Handlirsch 1908
Culicidae	Baltic amber	Handlirsch 1908, Larsson 1978
Culicidae	Green River	Scudder 1890, Grande 1984
Culicoidea	Wealdon	Jarzembowski 1984
Cypselosomatidae	Baltic amber	Larsson 1978
Cyrtidae	White River	Scudder 1890
Diastatidae	Baltic amber	Larsson 1978
Diopsidae	Baltic amber	Larsson 1978
Diopsidae	Ruby Paper Shales	Wilson 1978
Dixidae	Baltic amber	Handlirsch 1908, Larsson 1978
Dolichopodidae	Baltic amber	Handlirsch 1908, Larsson 1978
Dolichopodidae	Green River	Scudder 1890
Dolichopodidae	Guennel	Handlirsch 1910
Dolichopodidae	Canadian amber	McAlpine and Martin 1969
Drosophilidae	Baltic amber	Larsson 1978
Dryomyzidae	Baltic amber	Larsson 1978
Empididae	Tulameen	Handlirsch 1910
Empididae	Baltic amber	Handlirsch 1908, Larsson 1978
Empididae	Driftwood,BC	Wilson 1977
Empididae	Wealdon	Jarzembowski
Empididae	Canadian amber	Legg 1942 in McAlpine and Martin 1969, McAlpine and Martin 1969
Empididae	Green River	Grande 1984
Eophlebomyiidae	Green River	Grande 1984
Eoptychopteridae	Transbaikalia (Low-Mid Jurassic)	Kalugina 1989
Eremochaetidae	Kazakhstan (UpJur), Mongolia (LowCret), Transbaikalia (LowCret)	Kovalev 1989
Heleomyzidae	Baltic amber	Larsson 1978
Heleomyzidae	Green River, Quesnel	Scudder 1890
Ironomyiidae	Canadian amber	McAlpine and Martin 1969
Lauxaniidae	Baltic amber	Larsson 1978
Leptidae(Rhagionidae)	Baltic	Handlirsch 1908
Leptidae(Rhagionidae)	Florissant	(Cockerell 1908, 1914)

Limoniidae	Baltic amber	Larrson 1978
Limoniidae	Messel	Schaal and Ziegler 1988
Lonchaeidae	Baltic amber	Larsson 1978
Lonchaeidae	Quesnel	Scudder 1890
Megamerinidae	Baltic amber	Larsson 1978
Midasidae	Baltic, Florissant	Handlirsch 1908
Milichiidae	Baltic amber	Larsson 1978
Muscidae	Baltic, Green Florissant, Quesnel	Handlirsch 1908
Muscidae	Green River	Scudder 1890
Mycetophilidae	Baltic amber	Handlirsch 1908, Larsson 1978
Mycetophilidae	BC	Wilson 1977
Mycetophilidae	England Jurassic	Handlirsch 1908
Mycetophilidae	Quesnel	Scudder 1890
Mycetophilidae	Florissant	Cockerell 1914
Mycetophilidae	Wealden (LowCret)	Jarzembowski 1984
Mycetophilidae	Canadian amber	McAlpine and Martin 1969
Mycetophilidae	Green River	Scudder 1890, Grande 1984
Mycetophilidae	Ruby Paper Shales	Wilson 1978
Nemestrinidae	Florissant	Handlirsch 1908
Nemestrinidae	Karatau	McAlpine et al. 1981
Odiniidae	Baltic amber	Larsson 1978
Ortalidae	Quesnel	Scudder 1890
Oestridae	Green River	Grande 1984
Otitidae	Quesnel	Wilson 1978
Pallopteridae	Baltic amber	Larsson 1978
Pallopteridae	Quesnel	Wilson 1978
Phoridae	Canadian amber	McAlpine et al. 1981
Phoridae	Baltic amber	Handlirsch 1908, Larsson 1978
Pipunculidae	Baltic amber	Handlirsch 1908, Larsson 1978
Pipunculidae?	Canadian amber	McAlpine and Martin 1969
Platypezidae	Baltic amber	Larsson 1978, Handlirsch 1908
Platypezidae	Green River	Scudder 1890
Platypezidae	Canadian amber	McAlpine and Martin 1969
Proneottiophilidae	Baltic amber	Larsson 1978
Pseudopomyzidae	Baltic amber	Larsson 1978
Psilidae	Baltic amber	Larsson 1978
Psychodidae	Baltic amber	Handlirsch 1908, Larsson 1978
Psychodidae	Siberia, England Jurassic	Handlirsch 1908
Psychodidae	Canadian amber	McAlpine et al. 1981
Psychodidae	Lebanese amber	McAlpine et al. 1981
Ptychopteridae	Baltic	Handlirsch 1908
Ptychopteridae	Tulameen	Handlirsch 1908
Rachiceridae	Baltic amber	Larsson 1978
Rhagionidae	Baltic amber	Larsson 1978
Rhagionidae	Wealdon	Jarzembowski 1984
Rhagionidae	Up Jurassic	McAlpine et al. 1981
Rhyphidae	Baltic	Handlirsch 1908
Scatopsidae	Baltic amber	Larsson 1978
Scatopsidae	Canadian amber	McAlpine and Martin 1969
Sciadoceridae	Baltic amber	Larsson 1978
Sciadoceridae	Canadian amber	McAlpine and Martin 1966 in McAlpine and Martin 1969
Sciaridae	Baltic amber	Larsson 1978
Sciaridae	BC	Wilson 1977
Sciaridae	Canadian amber	McAlpine and Martin 1969
Sciaridae	Green River	Grande 1984
Sciomyzidae	Baltic amber	Larsson 1978
Sciomyzidae	Quesnel	Scudder 1890
Sciomyzidae	Green River	Scudder 1890
Sepsidae	Baltic amber	Larsson 1978
Simulidae	Baltic amber	Handlirsch 1908, Larsson 1978
Solvidae	Baltic amber	Larsson 1978
Stratiomyidae	Green, Florissant	Handlirsch 1908
Stratiomyidae	Baltic amber	Handlirsch 1908, Larsson 1978
Stratiomyidae	Green River	Scudder 1890, Grande 1984
Stratiomyidae	Cedar Lake amber	Teskey 1970

Stratiomyidae	Canadian amber	McAlpine and Martin 1969
Syrphidae	Baltic amber	Handlirsch 1908, Larsson 1978
Syrphidae	Florissant	Handlirsch 1908
Syrphidae	Horsefly, BC	Wilson 1977
Syrphidae	Ruby Paper Shales	Wilson 1978
Syrphidae	Creede Formation	Wilson 1978
Syrphidae	Green River	Scudder 1890, Cockerell and Levesque 1931, James 1932, Grande 1984
Syrphidae	Messel	Schaal and Ziegler 1988
Tabanidae	Baltic amber	Handlirsch 1908, Larsson 1978
Tabanidae	Messel	Schaal and Ziegler 1988
Tabanidae	Green River	Grande 1984
Tachinidae	Green River	Scudder 1890
Tanyderidae	Baltic amber	Larsson 1978
Tephritidae	Green River	Grande 1984
Therevidae	Baltic amber	Handlirsch 1908, Larsson 1978
Therevidae	Ruby Paper Shales	Wilson 1978
Tipulidae	Alberta Paskapoo	Mitchell and Wighton 1979
Tipulidae	Baltic amber	Handlirsch 1908, Larsson 1978
Tipulidae	Florissant, White	Handlirsch 1908
Tipulidae	Mormon Creek	Wilson 1978
Tipulidae	Creede Formation	Wilson 1978
Tipulidae	Ruby Paper Shales	Wilson 1978
Tipulidae	Driftwood, BC	Wilson 1977
Tipulidae	England, Jurassic	Handlirsch 1908
Tipulidae	Green River	Scudder 1890, Grande 1984
Tipulidae	Tulameen	Handlirsch 1910
Tipulidae	Wealdon	Jarzembowski 1984
Tipulidae	Messel	Schaal and Ziegler 1988
Tipuloidea	Canadian amber	McAlpine and Maring 1969
Trichoceridae	Baltic amber	Larsson 1978
Xylophagidae	Baltic amber	Handlirsch 1908, Larsson 1978

LEPIDOPTERA

Archeolepis	England (Jura)	Whalley 1985
Arctidae	Baltic amber	Handlirsch 1908
Argyresthiidae?	Baltic amber	Willemstein 1987
Cosmopterygidae	Baltic amber	Willemstein 1987
Eocoronidae	Queensland	Tindale 1980
Eolepidopterygidae	USSR (Low Cret)	Skalski 1984
Eolepidopterygidae	USSR (Up Jura)	Rasnitsyn 1983
Elaschistidae	Baltic amber	Willemstein 1987
Gelechiidae	Baltic amber	Willemstein 1987
Geometridae	Baltic amber	Handlirsch 1908
Helodiniidae	Baltic amber	Willemstein 1987
Incurvariidae	Baltic amber	Larsson 1978
Incurvariidae	Siberian amber (Up Cret)	Zherikhin and Sukacheva 1973
Incurvariidae	Lebanese amber	Whalley 1977
Libytheidae	Florissant (Libytheinae)	Scudder 1889
Lithosiidae	England Oligo	Handlirsch 1908
Lycaenidae	Baltic	Handlirsch 1908
Lycaenidae	Green River	Durden and Rose 1978
Lyonetiidae	Baltic amber	Willemstein 1987
Micropterygidae	Baltic amber	Larsson 1978
Micropterygidae	Transbaikal	Skalski 1979
Micropterygidae	Lebanese amber	Whalley 1977
Nepticulidae	Messel	Kinzelbach 1970
Nymphalidae	Florissant	Handlirsch 1908
Nymphalidae	Florissant	Scudder 1889, Cockerell 1907
Oecophoridae	Baltic amber	Larsson 1978
Paleontinidae	Jurassic	Handlirsch 1908
Papilionidae	Green River	Durden and Rose 1978
Pieridae	Florissant	Handlirsch 1908
Pieridae	Florissant	Scudder 1889
Plutellidae?	Baltic amber	Larsson 1978
Psychidae	Baltic amber	Handlirsch 1908, Larsson 1978

Psychidae?	Ruby Paper Shales	Wilson 1978
Pyralidae	Florissant	Handlirsch 1908
Scythrididae	Baltic amber	Willemstein 1987
Sesiidae?	Provence Oligo	Handlirsch 1908
Sphingidae	Baltic amber	Handlirsch 1908
Symmocidae	Baltic amber	Willemstein 1987
Thyrididae	Green River	Cockerell 1933
Tineidae	Baltic amber	Handlirsch 1908, Larsson 1978
Tineidae	Florissant	Scudder 1890
Tineidae?	Canadian amber	MacKay 1970
Tortricidae	Baltic amber	Handlirsch 1908, Larsson 1978
Tortricidae	Florissant	Cockerell 1907
Yponomeutidae	Baltic amber	Larsson 1978
Yponomeutidae	Green River	Cockerell and Levesque 1931, Forbes 1931
Zeugloptera	French amber (Up Cret)	Kuhne et al. 1973
Zygaenidae	Germany (Miocene)	Bielefeld 1987

APPENDIX 6. Stratigraphic position of fossil insect localities referred to in Appendix 5.

Locality	Stratigraphic range
Alberta Paskapoo	Paleocene
Baltic amber	Late Eocene
Bohemia	Cretaceous
British Columbia (Ninemile, Similkameen, Nicola, Driftwood, Tranquille, Blakeburn, Horsefly, Tulameen)	Middle Eocene
Canadian (Cedar Lake) amber	Upper Cretaceous
Claiborne Formation	Middle Eocene
Creede Formation, Colorado	Late Oligocene
Florissant, Colorado	Early Oligocene
Fox Hills, Dakota	Upper Cretaceous
Geiseltal, Germany	Middle Eocene
Green River	Late Early Eocene-Late Middle Oligocene
Karatau	Upper Jurassic
Kazakhstan	Upper Jurassic-Upper Cretaceous
Lebanese amber	Lower Cretaceous
Massachusetts	Upper Cretaceous
Messel, Germany	Middle Eocene
Mormon Creek, Montana	Late Eocene or Early Oligocene
Provence, France	Oligocene
Queensland, Australia	Upper Triassic
Quesnel, British Columbia	Late Early Oligocene
Republic, Washington	Middle Eocene

APPENDIX 6 (continued)

Ruby Paper Shales, Montana	Late Oligocene
Sakhalin amber	Paleocene?
Solnhofen	Jurassic
Switzerland	Lower Jurassic
Taimyr, Siberia	Upper Cretaceous
Transbaikalia	Lower Jurassic-Lower Cretaceous
White River (Handlirsch)	Oligocene
White River (Scudder)	Middle Eocene
Wealdon	Lower Cretaceous