

Insect Fossils from the Yukon

J.V. MATTHEWS JR. and A. TELKA

Terrain Sciences Division, Geological Survey of Canada
Ottawa, Ontario, Canada K1A 0E8

Current address of J.V. Matthews: Ohana Productions, 23 Sherry Lane
Nepean, Ontario, Canada K2G 3L4

Abstract. Many Quaternary geological exposures in the Yukon have yielded identifiable insect fossils. All groups occurring in the Yukon today except Apterygota and the pterygote orders Ephemeroptera, Mecoptera, Orthoptera, Mallophaga, Anoplura, Thysanoptera and Siphonaptera have been recorded as fossils. Coleoptera dominate, with most beetle fossils being from the Carabidae, Staphylinidae, Curculionidae and sometimes Byrrhidae.

For purposes of discussion the fossils from various sites are grouped according to age. One group includes Holocene and modern assemblages. Study of modern assemblages of insect fragments provides baseline information on taphonomy (the history of postmortal transportation and other events) and preservation. Some of the early Holocene faunas represent an intense warm period that occurred at high latitudes about 10 thousand years ago.

A second group of fossil assemblages consists of those deposited during the coldest episode of the last glaciation when large areas of the Yukon were ice free and were part of East Beringia. Some of these samples support the conclusion drawn from plant and mammal fossils that the environment at the time was steppe-like, with no modern analogue.

A third group is made up of fossils deposited between about 60 and 30 thousand years ago, an interval commonly called the mid-Wisconsinan. Some of the assemblages from this time period are very diverse; some contain unusual fossils, such as heads of noctuid moths and genital fragments of anthomyiid flies or other fossils that are exceptionally well preserved.

The fourth group—interglacial faunas—includes only 2 sites. The one most accurately referred to the last interglacial (about 125 thousand years ago) contains a few taxa that do not occur as far north as the site today, including one beetle that now lives no farther north than Alberta.

Such marked range extensions are more common in the fifth group of assemblages—those representing late Tertiary time. There are few assemblages of this age from the Yukon, but some are so close to the Yukon border that they represent the Tertiary fauna of the Yukon. Plant and insect fossils show that 3 million years ago rich coniferous forests covered at least all of central and northern Yukon and that the climate was less continental than at present. The insect fauna contained extinct species as well as some taxa now confined to the Palaearctic. The rich coniferous zone extended from eastern Siberia to Ellesmere Island and Greenland and was the last such forest connection across the Bering Straits. Subsequent intervals of dry land between Siberia and Alaska were characterized by severe arctic conditions and no forests.

Résumé. *Insectes fossiles du Yukon.* Plusieurs fouilles géologiques à des sites du Quaternaire au Yukon ont révélé la présence d'insectes fossiles identifiables. Des fossiles de tous les groupes actuels d'insectes du Yukon ont été trouvés, à l'exception des Aptérygotes et de quelques ordres ptérygotes, Ephemeroptera, Mecoptera, Orthoptera, Mallophaga, Anoplura, Thysanoptera et Siphonaptera. Les coléoptères dominent et la plupart des fossiles de cet ordre appartiennent aux familles Carabidae, Staphylinidae, Curculionidae et parfois Byrrhidae.

Pour des raisons d'ordre logistique, les fossiles des différents sites sont regroupés en fonction de l'époque. Un groupe comprend des fossiles de l'Holocène et des collections modernes. L'étude des collections modernes de fragments d'insectes a permis de tracer les grandes lignes de la taphonomie (l'histoire des déplacements après la mort et d'autres événements) et de la conservation. Certaines des faunes du début de l'Holocène reflètent une période de chaleur intense qui s'est produite aux latitudes élevées il y a environ 10 000 ans.

Un second groupe de fossiles est constitué de fragments déposés durant la période la plus froide de la dernière glaciation, période où d'importantes zones du Yukon étaient dénuées de glace et faisaient partie de la Béringie orientale. Certains de ces échantillons appuient l'hypothèse basée sur les fossiles de plantes et de mammifères et selon laquelle l'environnement à cette période était de type steppe, sans analogue moderne.

Un troisième groupe est constitué de fossiles qui remontent à environ 60 000–30 000 ans, intervalle généralement reconnu comme le Wisconsinien moyen. Certains groupes de cette période sont très diversifiés. Certains contiennent des fossiles remarquables, têtes de papillons noctuides, fragments génitaux de diptères anthomyiides, ou d'autres fossiles particulièrement bien conservés.

Le quatrième groupe—qui réunit des faunes inter-glaciaires—ne représente que deux sites. Le site daté le plus exactement remonte à environ 125 000 ans, soit la dernière période interglaciaire, et contient quelques taxons qui ne vivent plus aussi au nord maintenant, y compris un coléoptère dont la limite boréale de répartition est en Alberta.

Ce type de répartition très étendu est plus commun parmi le cinquième groupe de taxons—représentant la fin du Tertiaire. Il y a peu d'associations de cette époque au Yukon, mais certaines sont si près de la frontière du Yukon qu'elles sont considérées comme formant la faune du Tertiaire du Yukon. Les fossiles de plantes et d'insectes indiquent que de riches forêts de conifères recouvraient au moins tout le centre et le nord du Yukon il y a 3 millions d'années et que le climat à cette époque était moins continental que de nos jours. La faune des insectes contenait des espèces maintenant disparues aussi bien que des espèces maintenant strictement paléarctiques. La forêt de conifères s'étalait alors de l'est de la Sibérie jusqu'à l'île Ellesmere et au Groenland et constituait le dernier pont forestier à avoir assuré une continuité de part et d'autre de la mer de Bering. Par la suite, les liens terrestres qui ont prévalu entre la Sibérie et l'Alaska étaient caractérisés par des conditions arctiques rigoureuses et étaient dénués de toute forêt.

Introduction

Most chapters in this book concern the composition and distribution of elements of the existing insect fauna of the Yukon Territory. Fortunately, the availability of insect fossils in the Yukon makes it possible to present a more comprehensive picture of the fauna, including the all-important fourth dimension—its change with time. In this chapter we highlight some of the most important features of the history of the Yukon fauna as presently known, discussing several key faunas from the Yukon and adjacent areas in Beringia and in the Arctic Islands of the Northwest Territories (Fig. 1).

It is only possible to discuss insect fossils because the Yukon possesses innumerable geological sites that contain organic, insect-rich sediments of various ages. The existence of such sites is due in part to the fact that some of the rivers in the Yukon have cut deeply into unconsolidated Quaternary age basin-fill sediments, creating excellent exposures of fossiliferous sediments. Among the fossils are many fragments of insects, especially Coleoptera.

One particular region, the northern Yukon near the present drainages of the Porcupine and Old Crow rivers, contains literally hundreds of exposures (Fig. 2) because the rivers there have cut down into a thick sequence of basin sediments that range back in time to the late Tertiary, e.g. approximately 3 million years before present (3 ma B.P.).

In this report we discuss 3 groups of insect faunas, mostly from the Old Crow region of the northern Yukon, but including others from sites in adjacent Alaska and the Canadian Northwest Territories. The first group (Table 1) deals with insect fragments found in modern sedimentary deposits such as ponds, peatland turf and river floodplains and several fossil faunas of early Holocene age (e.g. approximately 9000 years old or 9 ka B.P.). The second group (Table 2) includes taxa identified in selected samples ranging in age from the middle Pleistocene, e.g. approximately 700 ka B.P., to 20 ka B.P. during the late Pleistocene. The third group (Table 3) includes those faunas of late Tertiary and earliest Pleistocene age. Most of the fossils in this last group come from sites other than the Yukon and are millions of years in age (ma B.P.); nevertheless, they allow some inferences to be drawn concerning the composition of the Yukon fauna during the late Tertiary.

Methods

The study of Quaternary and late Tertiary insect fossils in sediments has been going on for over thirty years, starting with the pioneering work of G.R. Coope (Elias 1994).

The insect fossils discussed in this chapter are typical of those from Quaternary deposits. Most of them refer to Coleoptera and include the heavily sclerotized pronota, heads or elytra which provide numerous characters critical for identification (though often not the characters

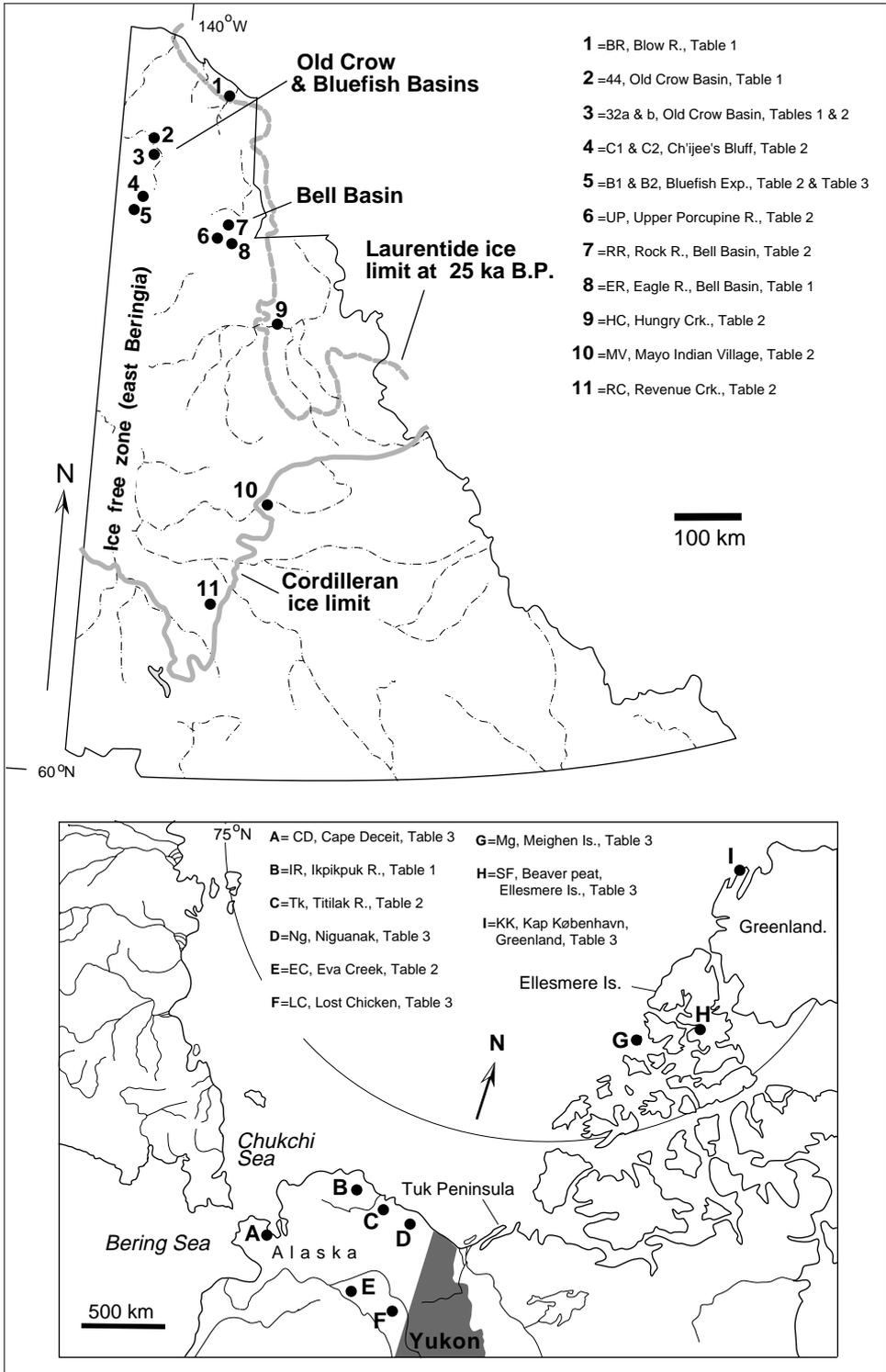


FIG. 1. Sites and localities mentioned in the text. Note that the unglaciated part of the Yukon Territory forms the eastern part of East Beringia.

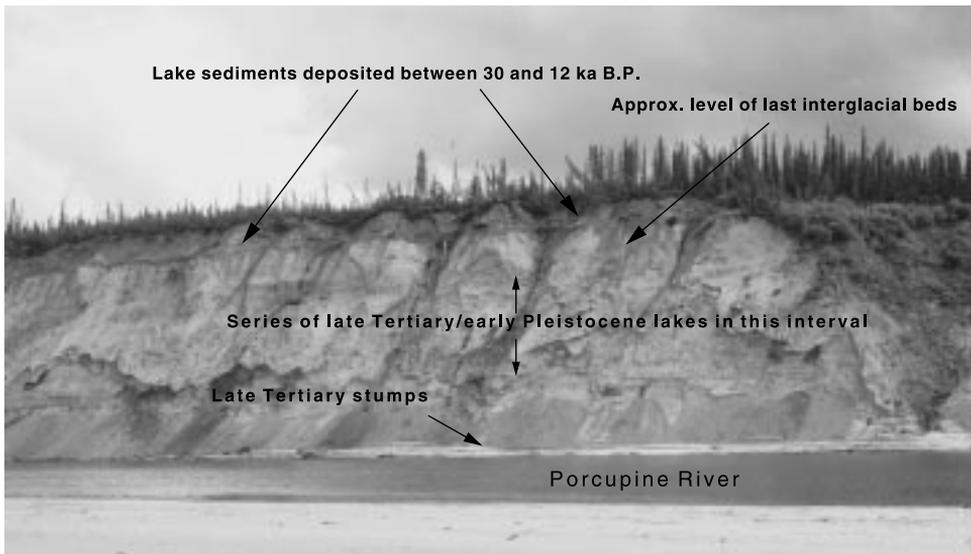


FIG. 2. Chi'jee's Bluff (site 4, Fig. 1). The photo shows only a small part of this very important Yukon river bluff exposure. The section is approximately 60 m high and extends for nearly 4 km. About 20 percent of the exposure is shown in this photo. Note the indicated level from which come the interglacial insect fossils discussed in this report.

used in keys). Fragments representing other insect and arthropod orders also occur (see discussion of specific groups), and some of these include such delicate fragments as flight wings and genitalia. Because of the presence of permafrost in the Yukon, fossil preservation is usually better than that typical of deposits in other more temperate climate regions.

Throughout this paper we specifically avoid the term "subfossil", which often is applied to remains of Quaternary insects. The use of this term is due to the excellent preservation of the fossils, but we consider it a misnomer. By definition: "A fossil is any remains, trace, or imprint of a plant or animal that has been preserved in the earth's crust since some past geologic or prehistoric time; loosely, any evidence of life" (Bates and Jackson 1984). There is no qualification as to state of preservation; only the age is qualified and this is left somewhat indefinite and ambiguous because "historic" time starts at different times in different regions. For this paper we use the term "fossil" for all remains older than the last several centuries.

In Tables 1, 2 and 3 fossils are listed either with "+", "?", or "cf." designations. The first indicates that the named taxon is present. The second signifies presence of fossils that may represent the named taxon but are not adequately preserved for a definite decision. The "cf." designation is more complex. In this report, we use it to signify fossils preserved well enough for identification but for several reasons not positively referred to the named taxon. They may indicate only that the authors have not examined enough modern reference material to come to a definite decision or, as in Table 3, that we believe specimens from the Palaearctic should be examined before a final decision is made. The designation "cf." is prevalent in Table 3 containing late Tertiary faunas. This prevalence indicates a hesitancy on our part to recognize many fossils, though well preserved, as belonging to extant species unless a large series of specimens has been examined or the fossils represent genitalia or some other definitive structure. Based on our experience and the now well known slow rate of evolution of many northern Coleoptera species (Elias 1994), we believe it is likely that

many of the “cf.” designated fossils will eventually prove to belong to the named taxon. But late Tertiary faunas also contain clear examples of extinct species and it is quite likely that with more detailed study and comparisons, or the discovery of new definitive fossils, they will also prove to be from extinct species, albeit very similar morphologically to their modern counterparts. The reader is cautioned to note carefully the taxa identified at the “cf.” degree of certainty and to avoid citing such fossils as belonging definitely to the nominal taxon in subsequent publications. To do so would potentially obscure important information on the latest evolution of many Yukon insects.

Present Environment of the Yukon

The present-day environment of the Yukon, including climatic and bioclimatic zones, is discussed by Scudder (1997). The northern Yukon, where many of the fossils discussed in this chapter were found, is very near regional treeline. The Old Crow basin itself is south of treeline, but trees are rare because of the poor drainage of the region. All sites from north of the British Mountains are located in the low-arctic tundra zone. Those from the central Yukon are within the subarctic zone, where conifer forests comprised of spruce (*Picea* spp.), rarely larch (*Larix laricina*) and jackpine (*Pinus banksiana*—as far north as Dawson City) predominate, except in extensive areas where fires have resulted in deciduous forests of birch (*Betula* spp.) and poplar (*Populus*).

The Geological and Palaeoenvironmental Context

The term “Late Tertiary” is generally accepted to refer to the Miocene and Pliocene periods, i.e. the time from about 24 million years ago (hereafter ma B.P.) to 1.8 ma B.P. The Pliocene, represented by several of the samples discussed in this chapter, covers the time from approximately 5 ma B.P. to 1.8 ma B.P. The Quaternary, which is divided into the Pleistocene and Holocene, includes all of the last 1.8 ma B.P., with the Holocene comprising approximately the last 10 thousand years. Although the “Pleistocene” is often used interchangeably with “ice ages”, major glaciation in the Northern Hemisphere actually began approximately 2.5 ma B.P., during the late Pliocene. The tempo of glaciations is now known to be driven mostly by variations in the earth’s orbit and axial tilt and precession. But during the Pleistocene the tempo changed, from a period of approximately 40 ka B.P. in the early part of the Pleistocene to an approximately 100 000 year periodicity in later Pleistocene time. During the late Pleistocene, or the last 400 ka B.P., long glacial phases were separated by relatively short interglacials during which climate was as warm or warmer than present, world ice volume was markedly reduced and sea level approached or exceeded that of the present. The Holocene, e.g. the last 10 ka B.P., is generally considered to be part of an interglacial like the others of the late Pleistocene.

At the latitude of the Yukon, earth orbital and axial tilt/precession changes caused a peak of solar radiation at about 125 ka B.P. Over most of the central and southern parts of North America the next radiation maximum occurred between 6000 and 8000 years ago—the so-called Holocene hypsithermal. However, at the latitude of the northern Yukon and northern coast of Alaska and Canadian Northwest Territories, the Holocene solar radiation maximum occurred at about 10 ka B.P. Not surprisingly, it was at this time that trees, other plants, insects and related arthropods moved north of their present limit in the Mackenzie Delta region and northern Yukon (Ritchie et al. 1983), just as they had done during the last interglacial (see below). One of the sites (Blow River: “BR”, Table 1) discussed later in this

report represents this early Holocene thermal maximum. There is little or no evidence that the northern parts of the Yukon were any warmer than at present later in the Holocene during the "Hypsithermal" of more southern regions.

Even though ice covered much of North America during the Pleistocene much of the Yukon remained ice-free (Fig. 1). This area, along with much of Alaska and the then emergent Bering and Chukchi seas, formed an unbroken corridor for exchange of Asian and North American fauna and flora. This is the region normally called "Beringia", though that term is not restricted to any particular time and does not imply any particular state of sea level. Nevertheless, the fact that Beringia was at times during the Pleistocene (and for much of the late Tertiary) a dry land connection to Asia has had great impact on the flora and fauna of both Alaska and the Yukon. During low-sea-level phases of the Pleistocene, the ice-free areas of Beringia were distributed in such a way as to make easternmost Beringia (the unglaciated Yukon) biologically more a part of Asia than of North America.

The environment of Beringia during the last major cold period has been a topic of considerable debate and discussion. The 2 sides of this controversy are best summarized by Guthrie (1990) and Ritchie (1984). Guthrie discusses a number of lines of evidence that require the existence of some type of steppe-like environment—"mammoth steppe". He bases his conclusions not only on botanical evidence but on numerous inferences drawn from the composition of the late Pleistocene mammalian fauna, which included a number of large grazing herbivores. In contrast, Ritchie's argument, based almost entirely on palaeobotanical evidence, is that the vegetation during the last cold period was a patchy tundra very much like that found in some arctic regions today. It is noteworthy that such tundra today supports a very low biomass of large grazers and many believe it could not have supported the grazers and associated carnivores that are known to have occurred in Beringia 20 000 years ago.

Dating discrepancies on the mammalian fossils, which opponents of the mammoth steppe cited in concluding that the critical mammals did not live in Beringia during the maximum of the last glaciation, have been resolved by new dates, particularly a large series of new Radiocarbon dates from the Bluefish Cave Archaeological site in the northern Yukon (Cinq-Mars 1979). This site shows that a diverse community of mammalian herbivores (including some very specialized grazers such as the saiga antelope) lived together in the northern Yukon during the coldest part of the last glaciation. Therefore, an environment having no contemporary analogue appeared to exist in late Pleistocene Beringia (Anderson et al. 1989). Some areas probably resembled present-day steppe, although clearly other regions would have appeared very much like present-day tundra. Furthermore, because the Bering land bridge was in existence at this time, the steppe-like environment probably extended well into Asia. In fact, because of the distribution of glaciers during the latest Pleistocene (Fig. 1), the Yukon was actually the eastern "cul-de-sac" of the mammoth steppe.

It would be logical to assume that a type of mammoth steppe characterized East Beringia and in particular, the Yukon, during each cold phase of the Pleistocene. However, to a degree the development of this environment and the exchange of its unique fauna and flora with other areas must have been mediated by past geographical and glacial conditions. There is now abundant evidence that the maximum advance of continental glaciers from the mid continent toward the east front of the Richardson Mountains and extending onto the northern Yukon coast occurred in latest Wisconsinan time (30–10 ka B.P.). In fact cogent arguments show the Mackenzie River in its present form is no older than latest Pleistocene and early Holocene (Duk-Rodkin and Hughes 1994). Prior to that the Mackenzie River was a relatively short watercourse originating in the Yukon and most of the water in its present southern

catchment area drained across northern North America to the Atlantic. Numerous montane glacial events occurred in the Yukon, some of them separated by intense or long interglacial periods, but with little or no continental ice extending as far as the present Mackenzie River. The migration corridor between Beringia and the rest of the North American continent must have been much more passable during all periods of the Pleistocene than it was during the latest Pleistocene. In addition to closing the passage into southern North America, late Pleistocene glaciation in the Yukon and northwestern Northwest Territories also completely rearranged the drainage system of the northern Yukon.

The Old Crow Basin and several adjacent basins form almost the only lowlands away from the arctic coast in the northern Yukon. They contain numerous fossiliferous exposures created primarily by down-cutting that started shortly after the drainage of the Porcupine river was diverted westward by glaciers moving to the flanks of the Richardson Mountains (see Laurentide ice limit shown in Fig. 1).

The basin sediments revealed by down-cutting represent times from as old as 2.5 ma B.P. to the present. The sedimentary record is not continuous, however, and because the basins were at times flooded by deep oligotrophic lakes, not all of the sediments at these exposures contain insect fossils. The last of these large lakes occupied the basin during the last glaciation; consequently, to study insect fossils from this period (40–14 ka B.P.), we are forced to turn to less informative sites located outside the basins. The result is that in this review so-called “full-glacial” faunas are touched on only briefly.

None of the Yukon faunas discussed in this chapter is of Tertiary age. Nevertheless several Tertiary arthropod faunas occur in Alaska and the Northwest Territories, and by extrapolation and interpolation of these faunas it can be shown what the late Tertiary insect fauna of the Yukon may have been like. Only a few of these Alaskan and Northwest Territories Tertiary faunas are discussed in this chapter. Matthews (unpublished) provides a comprehensive review.

Several of the conclusions drawn in that review need mention here. First, it is now clear that the earliest interruption of the Bering land bridge in the Pliocene broke the continuity of a rich coniferous forest ecosystem that extended from the Canadian High Arctic, where treeline occurred at or north of 80°N, well into eastern Siberia. In the parlance of Russian botanists this would be classed as a type of “dark” coniferous forest, much different from the light coniferous, *Larix*-dominated forest that occurs in east Siberia today. The development of light coniferous forest probably postdates the mid-Pliocene (Biske and Baranova 1984). Fossil floras from arctic North America and east Siberia suggest that there was considerable similarity of the forest flora across Beringia at this time.

Secondly, it now seems clear that the north-south width of the boreal zone in Pliocene time was considerably greater than it is today. It stretched from approximately 80°N to south of 60°N. Tundra was limited to the northernmost fringe of the Arctic Archipelago, which at the time was much less insular than at present. As well, the Alaska Range and St. Elias mountains were lower than at present (Plafker and Addicott 1976; Plafker et al. 1992). Not only would this cause interior areas to have less continental climate than at present, but it also means that the area of alpine tundra was probably much smaller than at present. There was probably no region where alpine and lowland tundra merged as it does today in the northern Yukon.

At about 2.5 ma B.P. conditions changed abruptly. Glaciers from the interior part of the continent first reached the shores of the Arctic Ocean near the present Mackenzie Delta, and shortly after the Arctic Ocean first developed its perennial ice cover, affecting all of the marginal lands. The change at 2.5 ma B.P. was a worldwide event because it is evident in

cores from nearly all of the world oceans. Undoubtedly it was accompanied by a total reorganization of the existing Pliocene flora and fauna of the Yukon, including extinction of species of plants and insects.

Taxonomic Content of Northern Fossil Assemblages

Tables 1–3 present lists of fossil insects and other arthropods from various ages and from various parts of the Yukon and adjacent regions of Alaska. Of the insect orders that occur today in the Yukon, all are represented except those in the subclass Apterygota and, of the Pterygota, Ephemeroptera, Mecoptera, Orthoptera, Mallophaga, Anoplura, Thysanoptera and Siphonaptera. The absence of some of these groups is undoubtedly due to the fact that they are not thickly sclerotized and not likely to be preserved except under exceptional circumstances (e.g. amber). However, Ephemeroptera and Orthoptera have sclerotized body parts which should preserve as fossils. This is especially true of the Orthoptera which are represented in the Yukon today by 17 species (Vickery 1997) of which at least one occurs as far north as Old Crow in the northern Yukon.

Odonata. Despite the thickly sclerotized character of certain parts of adult damselflies and dragonflies, the only fossils identified to date are the distinctive mandibles. The odonate mandibles are so distinct that there may be a potential for identification at least to the family level. Their occurrence in Yukon samples is rare mainly because many of the samples studied to date represent treeline or tundra environments, not the types of habitat in which dragonflies and damselflies are abundant. One of the samples from Rock River (Table 2) contains a fragment of the genital apparatus of an odonate, but such fossils are very rare.

Odonate larvae possess sclerotized and very distinctive mouthparts which one might expect to preserve as fossils, but to date none has been recovered from Yukon samples.

Plecoptera. About 71 species of Plecoptera occur in the Yukon (Stewart and Ricker 1997) and other arctic areas of North America (Hynes 1988), but fossils representing this group are rare in Yukon assemblages. A few nymphal heads are all that have been observed to date, and strangely even though these occur in what are presumed to be lacustrine sediments, they come from a sample thought to represent a time of maximum aridity and climatic severity in East Beringia.

Heteroptera. Many of the better studied sites in the Yukon have yielded a few hemelytral, head and pronotum fragments of Saldidae. One of the more distinctive fossils found to date (Fig. 3c) represents a partial pronotum of the species *Derephysia foliaceae* (Fallen) (Tingidae). Fragments of pentatomids, mirids, gerrids and corixids are seen in a few deposits, depending on the source of the sediments being examined.

Homoptera. Heads of Cicadellidae and Fulgoridae occur in a few Pleistocene samples. In addition leafhoppers have been found in late Tertiary sediments, such as the 3 ma B.P. site on Meighen Island (site G, Fig. 1; Matthews et al. unpublished 2) and the equally old site at Lost Chicken in east-central Alaska (site F, Fig. 1; Matthews et al. unpublished 1). Usually it is only the head and occasional hemelytra which are preserved, but many of these provide suitable characters for identification. Occasionally tergite fragments are found in the finest fraction of processed organic debris.

TABLE 1. Modern fragments and Holocene arthropod fossils found in samples from the Yukon and Alaska. All fossils are stored at the Geological Survey of Canada, Ottawa. For sites, see footnotes. For further details, see text.

Species	Modern		Holocene				
	1	2	32a	44	ER	BR	IR
INSECTA							
Odonata							
					+		
Heteroptera							
Corixidae							
Genus ?	+						
Saldidae							
Genus?					+		
Homoptera							
Cicadellidae							
<i>Driotura</i> cf. <i>gammaroides</i> (Van Duz.)							+
cf. <i>Memnomia</i>							+
Genus?	+	+					
Psyllidae							
Genus?		+					
Coleoptera							
Carabidae							
<i>Agonum consimile</i> Gyll.				1			
<i>Agonum quinquepunctata</i> Mots.				3			+
<i>Agonum sordens</i> Kby				4			
<i>Agonum</i> sp.	+		+				
<i>Amara (Celia)</i> sp.							+
<i>Amara alpina</i> Payk.							+
<i>Amara bokori</i> Csi.							+
<i>Amara erratica</i> Duft.							+
<i>Amara (Curtonotus)</i> sp.						+	
<i>Bembidion (Plataphus)</i> sp.							+
<i>Bembidion sordidum</i> Kby							+
<i>Bembidion</i> spp.				1		+	+
<i>Bembidion transparens</i> Gebl.			+	13			
<i>Bembidion umiatense</i> Lth							+
<i>Blethisa catenaria</i> Brown				1	+		+
<i>Blethisa multipunctata</i> L.				1			+
<i>Blethisa</i> sp.	+						
<i>Carabus chamissonis</i> Fisch.							+
<i>Carabus maeander</i> Fisch.				1			
<i>Carabus truncaticollis</i> Eschz.							+
<i>Chlaenius niger</i> Rand.	+						
<i>Diacheila polita</i> Fald.	+		+	1	+	+	+
<i>Dyschiriodes* frigidus</i> Mann.						+	
<i>Dyschiriodes integer</i> group			+				
<i>Dyschiriodes nigricornis</i> Mots.				23			
<i>Dyschiriodes politus</i> group							+
<i>Dyschiriodes</i> sp.	+				+		+
<i>Elaphrus clairvillei</i> Kby					+		
<i>Elaphrus lapponicus</i> Gyll.				1			+
<i>Elaphrus parviceps</i> Van Dyke							+
<i>Elaphrus</i> sp.				1			
<i>Harpalus amputatus</i> Say							+
<i>Harpalus fulvilabris</i> Mann.							cf.
<i>Harpalus</i> sp.						+	
<i>Notiophilus borealis</i> Harr.							+
<i>Notiophilus semistriatus</i> Say				1			
<i>Notiophilus</i> sp.			+				
<i>Pelophila borealis</i> Payk.							+
<i>Pterostichus agonus</i> Horn							+
<i>Pterostichus circulosus</i> Lth				3			+
<i>Pterostichus costatus</i> Men.							+

TABLE 1. (continued)

Species	Modern		Holocene				
	1	2	32a	44	ER	BR	IR
<i>Pterostichus haematopus</i> Dej.							+
<i>Pterostichus nearcticus</i> Lth							+
<i>Pterostichus sublaevis</i> J.Sahlb.							+
<i>Pterostichus vermiculosus</i> Men.							+
<i>Pterostichus (Cryobius)</i> sp.				2	+	+	+
<i>P. (Cryobius) arctica</i> Chaud.							+
<i>P. (Cryobius) brevicornis</i> Kby			+	5			+
<i>P. (Cryobius) caribou</i> Ball			+		+		+
<i>P. (Cryobius) nivalis</i> F.Sahlb.							+
<i>P. (Cryobius) parasimilis</i> Ball							+
<i>P. (Cryobius) pinguedineus</i> Eschz.				1			+
<i>P. (Cryobius) pinguedineus</i> group							+
<i>P. (Cryobius) tareumiut</i> Ball			?				?
<i>P. (Cryobius) ventricosus</i> Eschz.			+				+
<i>Sericoda quadripunctata</i> DeG.							+
<i>Trichocellus mannerheimi</i> R.Sahlb.			+	10	+		+
Haliplidae							
<i>Haliplus strigatus</i> Robys.							+
Dytiscidae							
<i>Agabus</i> spp.			?	1			+
<i>Colymbetes</i> sp.	+		+	1			+
<i>Dytiscus</i> sp.						+	
<i>Hydroporus lapponum</i> Gyll.							+
<i>Hydroporus</i> sp.		+	+	2	+		+
<i>Hygrotus</i> sp.							+
<i>Ilybius</i> sp.							+
<i>Rantus</i> sp.							+
Genus?	+			1		+	
Gyrinidae							
<i>Gyrinus</i> sp.			+	1	+		
Hydrophilidae							
<i>Cercyon herceus</i> Smet.				3	+		
<i>Cercyon marinus</i> Thoms.			+	1	+		
<i>Helophorus tuberculatus</i> Gyll.	+						
<i>Helophorus</i> spp.			+				+
<i>Hydrobius fuscipes</i> L.			cf.	4	?		
<i>Hydrophilus</i> sp.						+	
Genus?					+		+
Hydraenidae							
<i>Ochthebius</i> sp.				1			
Staphylinidae							
Aleocharinae				2			+
<i>Arpedium</i> sp.				11	+		
<i>Bledius</i> sp.							+
<i>Boreaphilus henningianus</i> C.R.Sahlb.				1			
<i>Euaesthetus</i> sp.				20			
<i>Eucnecosum brunnescens</i> (J.Sahlb.)							+
<i>Eucnecosum</i> sp.	+					+	
<i>Eucnecosum tenue</i> (LeC.)							?
<i>Gymnusa</i> sp.			+	10		+	+
<i>Holoboreaphilus nordenskiöldi</i> (Mäkl.)				9		+	+
<i>Lathrobium</i> sp.			+	9	+	+	+
<i>Micralymna brevilingue</i> Schiødt.			+				+
<i>Mycetoporus</i> sp.							+
<i>Olophrum boreale</i> (Payk.)			+				
<i>Olophrum consimile</i> Gyll.					+		
<i>Olophrum latum</i> Mäkl.				5			
<i>Olophrum marginatum</i> Mäkl.				2			

TABLE 1. (continued)

Species	Modern		Holocene				
	1	2	32a	44	ER	BR	IR
<i>Olophrum rotundicolle</i> (Sahlb.)	+			2			
<i>Olophrum</i> sp.	+					+	+
<i>Pycnoglypta</i> sp.				3			
<i>Quedius</i> sp.	+			2		+	+
<i>Stenus</i> spp.	+		+	54	+	+	+
Subfam. undet.				1	+		+
<i>Subhaida</i> sp.							+
<i>Tachinus brevipennis</i> Sahlb.			+				+
<i>Tachyporus rulomus</i> Blkw.							+
<i>Tachyporus</i> sp.	+			5	+		
Genus?			+				
Micropeplidae							
<i>Micropeplus tessera</i> Curt.				1			
Silphidae							
<i>Silpha</i> sp.			+	2		+	
<i>Thanatophilus lapponicus</i> (L.)							+
<i>Thanatophilus sagax</i> Mann.							+
Leptodiridae							
<i>Colon</i> sp.			+	1	+		
Genus?						+	
Leiodidae							
<i>Agathidium</i> sp.				+		+	
Ptiliidae							
<i>Acrotichus</i> sp.						+	
Scydmaenidae							
<i>Veraphus</i> sp.	+						
Genus?				8			
Scarabaeidae							
<i>Aegialia</i> sp.						+	+
<i>Aphodius</i> sp.				1			+
Helodidae							
<i>Cyphon</i> sp.					+		
Byrrhidae							
<i>Byrrhus</i> sp.			+				
<i>Curimopsis</i> sp.							+
<i>Cytilus alternatus</i> (Say)				3			+
<i>Morychus</i> sp.							+
<i>Simplocaria tessellata</i> (LeC.)	+		+				
<i>Simplocaria</i> sp.			+	1	+		+
Genus?	+						
Heteroceridae							
<i>Heterocerus</i> sp.				1			
Elateridae							
<i>Denticollis</i> sp.				2			
<i>Hypolithos sanborni</i> (Horn)							+
<i>Negastrius restrictulus</i> (Mann.)							+
Genus?	+					+	
Cantharidae							
<i>Podabrus deceptus</i> Brown							+
<i>Podabrus piniphilus</i> sp. group							+
Anthicidae							
Genus?			+	1			
Cryptophagidae							+
<i>Cryptophagus</i> sp.							
Coccinellidae							
Genus?							+
<i>Nephus</i> sp.							+
Lathridiidae							
Genus?	+				+	+	

TABLE 1. (continued)

Species	Modern		Holocene				
	1	2	32a	44	ER	BR	IR
Chrysomelidae							
<i>Altica</i> sp.							?
Alticinae, genus?				1		+	
<i>Chrysolina basilaris</i> (Say)							+
<i>Chrysolina</i> spp.							+
<i>Donacia</i> sp.			+	1	+		
<i>Hydrothassa boreella</i> Schf.							cf.
<i>Phratora hudsonica</i> Brown							+
<i>Plateumaris</i> sp.							+
Curculionidae							
<i>Acalyptus carpini</i> Hbst							?
<i>Apion</i> sp.				2		+	+
<i>Ceutorhynchus</i> sp.				2	+		
<i>Dorytomus alaskanus</i> Csy							+
<i>Dorytomus rufulens</i> Mann.							+
<i>Hypera</i> sp.				3			+
<i>Lepidophorus lineaticollis</i> Kby	+	+	+	3		+	+
<i>Lepyryus gemellus</i> Kby							+
<i>Lepyryus stefanssoni</i> (Leng)							+
<i>Lepyryus</i> sp.	+						
<i>Notaris aethiops</i> Fab.				2			+
<i>Rhynchaenus niger</i> (Horn)							+
<i>Rhynchaenus</i> spp.					+		+
<i>Sitona</i> sp.							+
<i>Sitona</i> large type		+					
<i>Stephanocleonus</i> sp.							+
<i>Vitavitus thulius</i> Kiss.		+					+
Genus?			+				
Scolytidae							
<i>Carphoborus</i> sp.	+						
<i>Polygraphus rufipennis</i> (Kby)			+				
<i>Scolytus piceae</i> (Swaine)			+				
Genus?	+						
Trichoptera							
Phryganeidae							
<i>Agrypnia straminea</i> Hagen							cf.
<i>Phryganea/Agrypnia</i> type							cf.
Limnephilidae							
<i>Asynarchus</i> sp.						+	
<i>Grammotaulius</i> sp.	+						
<i>Grensia praeterita</i> (Walk.)	+						+
<i>Phanocelia</i> sp.							+
Diptera							
Family?	+						+
Tipulidae							
<i>Tipula</i> sp.			+				
Chironomidae							
<i>Chironomus</i> type							+
<i>Phaenopsectra</i> type							+
<i>Glyptotendipes</i> sp.							+
Tanytarsini type							
Genus?	+						
Bibionidae							
Genus?		+					
Xylophagidae							
<i>Xylophagus</i> sp.				+			
Hymenoptera							
Ichneumonoidea, genus?				+			

TABLE 1. (continued)

Species	Modern		Holocene				
	1	2	32a	44	ER	BR	IR
Formicidae							
<i>Myrmica</i> type		+		8			
<i>Formica</i> type				3	+	+	
Genus?	+		+				
CRUSTACEA							
Cladocera							
<i>Daphnia</i> sp.	+	+					+
Notostraca							
<i>Lepiduris</i> sp.					+		
ARACHNIDA							
Acari							
Oribatida							
Ameronothridae							
<i>Ameronothrus</i> cf. <i>lineatus</i> Thorell							+
<i>Ameronothrus</i> sp.							+
Hydrozetidae							
<i>Hyrozetes</i> sp.							+
Ceratozetidae							
<i>Trichoribates/Diapterobates</i> type							+
<i>Fuscozetes/Melanozetes</i> type							+
<i>Trichobates polaris</i> Ham.							+
Mycobatidae							
<i>Mycobates</i> sp.							+
<i>Punctoribates quadrivertex</i> Herbert							+
Phenopelopidae							
<i>Eupelops</i> sp.							+
<i>Propelops canadensis</i> Ham.							+
Archipteridae							
<i>Parachipteria</i> sp.							+
Oribatulidae							
<i>Oribatula tibialis</i> (Nic.)							+
Araneae							
Lycosidae							
Genus?							+
Erigonidae							
Genus?							+

*Formerly *Dyschirius*.

Sites:

1, several samples from a thermokarst lake in the Old Crow Basin.

2, several samples from marine shoreline sites near the east end of the Tuktoyaktuk Peninsula, Northwest Territories (Fig. 1). 32a, CRH-32, Old Crow Basin, detrital organics; age: 8100±160 (GSC-1243: Lowdon and Blake 1979).

44, CRH-44, Old Crow Basin, pond sediments; age: 8460±120 (GSC-2605) and 8270±140 (GSC-1329: Lowdon and Blake 1979). Numbers show the minimum number of individuals represented by the fossils.

ER, Eagle River, Bell Basin, Yukon Territory. Samples MRA 7-9-80-33 and 7-10-80-10; age: 9970±160 (GSC-3133: Blake 1984) (site 10, Fig. 1).

BR, Blow River, northern Yukon; age: 9360±70 (TO-328); 9370±70 (TO-327) (site 1, Fig. 1) (J. Matthews 1984: unpublished fossil arthropod report ARPT 84-8).

IR, Ikpikpuk River, northern Alaska; age: 9670±130 (site B, Fig. 1) (Nelson 1976, 1982).

TABLE 2. (continued)

Species	Inter-glacial		Mid-Wisconsinan			Late Wisconsinan (full glacial)					
	C1	RC	HC	C2	UP	Tk	32b	RR	MV	EC	B1
<i>Bradycellus lecontei</i> Csi.	+										
<i>Carabus chamissonis</i> Fisch.					+			+		+	
<i>Carabus truncaticollis</i> Eschz.			?		?	+		+		+	+
<i>Carabus</i> sp.					+						+
<i>Chlaenius niger</i> Rand.			+								
<i>Cymindis unicolor</i> Kby										+	
<i>Cymindis</i> sp.									+		
<i>Diacheila polita</i> Fald.	+		+	+				+			
<i>Dyschiriodes</i> * sp.	+		+		+						+
<i>D. frigidus/subarcticus</i> type				+							
<i>Dyschiriodes laevifasciatus</i> Horn	+										
<i>Elaphrus parviceps</i> Van Dyke									+		
<i>Elaphrus</i> sp.			+		+			+			+
<i>Harpalus alaskensis</i> Lth					+						
<i>Harpalus amputatus</i> Say			+		+				+		
<i>Harpalus</i> sp.	+										
<i>Loricera</i> sp.	+										
<i>Miscodera arctica</i> Payk.					+						
<i>Nebria</i> sp.	+										
<i>Notiophilus semistriatus</i> Say										+	
<i>Notiophilus sylvaticus</i> Eschz.			+								
<i>Notiophilus</i> sp.								+			
<i>Patrobus septentrionis</i> Dej.	+										
<i>Pelophila borealis</i> Payk.				+					+		
<i>Pterostichus (Cryobius)</i> spp.	+	+	+		+		8	+	+	+	+
<i>P. (Cryobius) auriga</i> Ball										?	
<i>P. (Cryobius) brevicornis</i> group			+				+			+	
<i>P. (Cryobius) brevicornis</i> Kby		+		+	+	+			+	+	
<i>P. (Cryobius) caribou</i> Ball		+			+				+		?
<i>P. (Cryobius) caribou</i> type		+									
<i>P. (Cryobius) gerstlensis</i> Ball				cf.							
<i>P. (Cryobius) hudsonicus</i> LeC.	+	+						?			
<i>P. (Cryobius) kotzebuei</i> Ball					+					+	
<i>P. (Cryobius) mandibularoides</i> Ball										+	
<i>P. (Cryobius) nivalis</i> F. Sahlb.		+			+				+	+	
<i>P. (Cryobius) ochoticus</i> subgroup										+	
<i>P. (Cryobius) parasimilis</i> Ball					+	+				+	
<i>P. (Cryobius) pinguedineus</i> Eschz.				+	+	+			?	+	+
<i>P. (Cryobius) pinguedineus</i> group						+				+	
<i>P. (Cryobius) similis</i> subgroup						+				+	
<i>P. (Cryobius) soperi</i> Ball										+	
<i>P. (Cryobius) tareumiut</i> Ball					+	+		cf.			
<i>P. (Cryobius) ventricosus</i> Eschz.					+			+		+	+
<i>Pterostichus adstrictus</i> Eschz.	+										
<i>Pterostichus haematopus</i> Dej.	+		cf.			+			+		
<i>Pterostichus nearcticus</i> Lth					+						+
<i>Pterostichus sublaevis</i> J.Sahlb.					+		1				+
<i>Pterostichus vermiculosus</i> Men.					+			+			
<i>Trechus apicalis</i> Mtsch.			+								
<i>Trechus</i> sp.			+								
<i>Trichocellus mannerheimi</i> R.Sahlb.	+			+	+			+	+	+	
<i>Trichocellus</i> sp.	+										
Dytiscidae											
<i>Agabus /Ilybius</i> type	+		+	+				+			

TABLE 2. (continued)

Species	Inter-glacial		Mid-Wisconsinan			Late Wisconsinan (full glacial)					
	C1	RC	HC	C2	UP	Tk	32b	RR	MV	EC	B1
<i>Colymbetes</i> sp.	+		+		+		1	+		+	
<i>Dytiscus</i> sp.	+										
<i>Hydroporus</i> spp.	+		+		+	+	1				
<i>Hygrotus picatus</i> (Kby)					cf.						
<i>Hygrotus</i> sp.	+										
<i>Oreodytes</i> sp.					+						+
Genus?	+				+	+	1		+		+
Noteridae											
Genus?	+		+								
Gyrinidae											
<i>Gyrinus</i> sp.	+		+								
Hydrophilidae											
<i>Cercyon herceus</i> Smet.			+								
<i>Cercyon marinus</i> Thoms.	+			+							
<i>Helophorus lacustris</i> type	+										
<i>Helophorus oblongus</i> LeC.				+							
<i>Helophorus splendidus</i> Sahlb.					+			+			+
<i>Helophorus</i> spp.	+			+	+		1				+
<i>Hydrobius</i> sp.	+			+							
<i>Hydrophilus</i> sp.	+										
Genus?	+										
Hydraenidae											
<i>Hydraena</i> sp.			+								
<i>Ochthebius kaszabi</i> Janss.	+			+							
<i>Ochthebius marinus</i> (Payk.)	+			+							
<i>Ochthebius</i> sp.	+	+	+					+			
Staphylinidae											
<i>Acidota</i> sp.	+				+						
<i>Acylophorus</i> sp.										+	
Aleocharinae	+	+		+	+	+		+		+	+
<i>Arpedium</i> sp.			+								
<i>Bledius</i> spp.	+		+								
<i>Boreaphilus henningianus</i> Sahlb.	?			+	+						
<i>Boreaphilus</i> sp.			?								
<i>Coryphiini</i> undet.					+						
<i>Coryphium hyperboreum</i> (Mäkl.)					+						
<i>Coryphium</i> sp.								+			
<i>Euaesthetus</i> sp.	?		+	+							
<i>Eucnecosum/Arpedium</i> type	+										
<i>Eucnecosum</i> sp.								+			
<i>Gymnusa</i> sp.	+		+								
<i>Lathrobium</i> sp.	+		+	+	+	+		+			
<i>Micralymma brevilingue</i> Schjødt.	+			+	+	+		+			+
<i>Micralymma</i> sp.				cf.							
<i>Olophrum boreale</i> (Payk.)	+		+								
<i>Olophrum consimile</i> Gyll.	+							+			
<i>Olophrum latum</i> Mäkl.	+	+	+		+			+		+	
<i>Olophrum rotundicolle</i> Sahlb.	+		+					?			
<i>Olophrum</i> sp.								+			
<i>Omalius</i> sp.	+										
<i>Oxytelus</i> sp.			+								
<i>Stenus</i> spp.	+	+	+	+	+		1	+	+	+	+
<i>Syntomium</i> sp.			+								
<i>Tachinus apterus</i> group					+						
<i>Tachinus brevipennis</i> J. Sahlb.			+	+	+	+	1	?		+	+
<i>Tachinus instabilis</i> Mäkl.									+		
<i>Tachinus jacuticus</i> Popp.								+			

TABLE 2. (continued)

Species	Inter-glacial		Mid-Wisconsinan			Late Wisconsinan (full glacial)					
	C1	RC	HC	C2	UP	Tk	32b	RR	MV	EC	B1
<i>Caenocara</i> sp.											+
Genus?	?										
Melyridae											
Genus?	+										
Tenebrionidae											
<i>Upis</i> sp.								?			
Cryptophagidae											
<i>Cryptophagus</i> spp.											+
Genus?		+									
Coccinellidae											
<i>Ceratomegilla ulkei</i>											
Crotch					+				+	+	
Genus?	+		+						+		
Cucujidae											
<i>Pediacus</i> sp.	+										
Lathridiidae											
Genus?	+	+			+						+
Colydiidae											
Genus?	?			+							
Mycetophagidae											
<i>Mycetophagus</i> sp.					?						
Chrysomelidae											
Alticinae, genus?	+			+							
<i>Bromius obscurus</i> (L.)	+										
<i>Cassida flaveola</i> Thunb.	?			+							
<i>Chrysolina basilaris</i> (Say)				+	+						+
<i>Chrysolina</i> spp.					+	+	1	+		+	+
<i>Chrysomela</i> sp.							1				
<i>Donacia</i> sp.				+	+			+			
<i>Hydrothassa</i> sp.					+						
<i>Phaedon</i> sp.	?										
Genus?		+						+			
Curculionidae											
<i>Apion</i> spp.	+	+	+	+	+	+			+	+	+
<i>Ceutorhynchus</i> sp.	+				+					+	+
<i>C. subpubescens</i> LeC.											+
<i>Comatichela artemisiae</i> And.				+		+	1				
<i>Dorytomus alaskanus</i> Csy										+	
<i>Dorytomus</i> sp.				?							
<i>Grypus equiseti</i> (Fab.)	+										
<i>Hylobius</i> sp.	+		+								
<i>Hypera castor</i> (LeC.)					cf.					cf.	
<i>Hypera diversipunctata</i> Schr.						+					
<i>Hypera seriata</i> (Mann.)											+
<i>Isochnus arcticus</i> (Kor.)								?			+
<i>Isochnus</i> sp.								+			
<i>Lepidophorus lineaticollis</i> Kby	+	+	+	+	+		41		+	+	+
<i>Lepyrus gemellus</i> Kby										+	
<i>Lepyrus stefanssoni</i> (Leng)						+					
<i>Lepyrus</i> sp.	+										
<i>Mecopeltus</i> sp.					+						
<i>Notaris bimaculatus</i> (Fab.)				+							
<i>Notaris</i> sp.								+	+		+
<i>Phytobius</i> (<i>Litodactylus</i> type)	+										
<i>Phytobius</i> sp.	+			+							
<i>Rhynchaenus niger</i> (Horn)						+					
<i>Rhynchaenus rufipes</i> (LeC.)				+							
<i>Rhynchaenus</i> sp.				+	+	+					+

TABLE 2. (continued)

Species	Inter-glacial		Mid-Wisconsinan			Late Wisconsinan (full glacial)					
	C1	RC	HC	C2	UP	Tk	32b	RR	MV	EC	B1
<i>Sitona</i> sp. (large group)					+						
<i>Sitona</i> sp. (small group)					+						
<i>Stephanocleonus</i> sp.	?		+		+	+		+	+		+
<i>Vitavitus thulius</i> Kiss.	+		+		+			+	+		+
Genus?								+			
Scolytidae											
<i>Carphoborus carri</i> Swaine					+			+			
<i>Carphoborus</i> sp.	+	?	+								
<i>Orthotomicus caelatus</i> (Eich.)	+										
<i>Phloeotribus piceae</i> Swaine	+							+			
<i>Phloesinus pini</i> Swaine	+										
<i>Pityophthorus opaculus</i> LeC.	+										
<i>Scolytus</i> sp.					+			+			
Genus?		+	+								
Trichoptera											
Brachycentridae											+
<i>Brachycentrus</i> type	+										
Genus?	+										
Lepidoptera											
Noctuidae					+						
<i>Agrotiphila staudingeri</i> (Mösch.)					+						
<i>Euxoa churchillensis</i> (McD.)					+						+
Family?		+			+						+
Diptera											
Tipulidae									+		
<i>Tipula</i> sp.			+						+		
Genus?	+	+			+		1	+			+
Chironomidae											
<i>Chironomus</i> type	+							+			
<i>Glyptotendipes</i> sp.	+										
Genus?					+						+
Xylophagidae											
<i>Xylophagus</i> sp.			+		+					+	+
Bibionidae											
Genus?				+	+						
<i>Cyclorrhapha</i> undet.					+						
Anthomyiidae								+			
<i>Delia hudsonica</i> Griffiths					+						
Hymenoptera											+
Symphyla											
Tenthredinidae								?	?		
Genus?	+				+						
Family?								+			
Apocrita											
Family?									+		
Braconidae											
<i>Chelonus</i> sp.											+
Ichneumonidae			+					+	+		
Genus?	+	+		+	+		2				
Formicidae											
<i>Camponotus</i> sp.	+	+									
<i>Formica</i> spp.	+	+	+	+					+		
<i>Myrmica</i> sp.	+				+						
CRUSTACEA											
Notostraca											
<i>Lepidurus</i> sp.	+				+		4				+

TABLE 2. (continued)

Species	Inter-glacial		Mid-Wisconsinan			Late Wisconsinan (full glacial)					
	C1	RC	HC	C2	UP	Tk	32b	RR	MV	EC	B1
Cladocera											
<i>Daphnia</i> sp.	+										+
ARACHNIDA											
Acari					+						
Oribatida											
Cepheidae											
<i>Cepheus</i> sp.		+	+								
Damaeidae											
<i>Epidamaeus</i> sp.	+										+
<i>E. cf. tenuissimus</i> Ham.					+						
Hydrozetidae											
<i>Hydrozetes</i> sp.	+										
Family?										+	+
Araneae											
Lycosidae											
Genus?				+	+						
Erigonidae											
<i>Erigone</i> sp.	+				+	+				+	+
Family?		+									

*Formerly *Dyschirius*.

Sites: C1, Several interglacial levels at the Ch'ijee's Bluff section (Matthews et al. 1990a) (site 4, Fig. 1); approximate age: 125 ka B.P.

RC, Revenue Creek, JJO-05-07-89-P1 to P3 (L. Jackson in prep.) (site 11, Fig. 1); approximate age 125 ka B.P. (A Telka 1995: unpublished macrofossil reports MFRT 94-101 to 94-108).

HC, Hungry Creek, Unit 2b, sample 35 (Hughes et al. 1981) (site 9, Fig. 1); 40 ka B.P., interglacial or interstadial (see text).

C2, sample A from Ch'ijee's Bluff (Matthews et al. 1990a) (site 4, Fig. 1); age: 52 ka B.P. and younger than 125 ka B.P.

UP, Upper Porcupine River sample MRA6-19-75-8 and MRA 6-19-75-5, Bell Basin, Yukon Territory (site 6, Fig. 1); age: mid Wisconsinan, i.e. approximately 36–37 ka B.P. (37430±490 yrs B.P.—TO-394; 36880±390 yrs B.P.—TO-218). Note: these dates supercede previous dates greater than ¹⁴C range published in Lowdon and Blake (1980).

RR, Rock River exposure, Bell Basin (site 7, Fig. 1); age: approx 25 ka B.P. (25460±200—TO-291). Note: this date supercedes previous dates greater than ¹⁴C range on the unit from which the sample comes (Blake 1984).

32b, CRH-32 (site 3, Fig. 1), from organic residue associated with dated sample GSC-1191 (31300±640 yrs. B.P.) (Lowdon and Blake 1979). Numbers show the minimum number of individuals represented by the fossils.

Tk, Titilak River, Alaska sample 7D15 (Nelson 1982) (site C, Fig. 1); approximate age: 30–31 ka B.P.

MV, Mayo Indian Village section, interior Yukon (Matthews et al. 1990b) (site 10, Fig. 1); age: 26.9 ka B.P.

EC, Eva Creek sample 3-3C (Matthews 1968) (site E, Fig. 1); age: 24.6 ka B.P.

B1, Bluefish exposure samples REM 76-113, REM -112, REM 75-76 and REM 75-75, (site 5, Fig. 1); age: approximately 20 ka B.P. based on date of 20800±200 (GSC-3946) from sample REM 76-113 (Blake 1987).

TABLE 3. Insect and other arthropod fossils from late Tertiary sites in Canada, Greenland and Alaska. For sites, see footnotes. For further details, see text.

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
INSECTA							
Odonata							
Family?				+	+	+	
Heteroptera							
Lygaeidae							
Genus?							+
Pentatomidae							
<i>Elasmocha</i> sp.							+
Saldidae							
<i>Chiloxanthus stellatus</i> (Curt.)	+						
<i>Saldula</i> sp.							+
<i>Teloleuca</i> sp.	+						
Tingidae, genus?		+					
Family?				+			
Homoptera							
Cicadellidae							
<i>Athysanella</i> sp.						+	
<i>Deltocephalus</i> sp.			+				
<i>Oncopsis</i> sp.						+	
Genus?	+		+	+	+	+	+
Fulgoridae							
<i>Bruchomorpha</i> sp.						+	
Psyllidae							
Genus?		+					
Aleyrodidae, genus?							+
Aphididae							
Genus?						+	
Neuroptera							
Sialidae							
<i>Sialis</i> sp.						+	+
Coleoptera							
Cicindelidae							
<i>Cicindela</i> sp.							+
Trachypachidae							
<i>Trachypachus</i> sp.						+	+
<i>Trachypachus gibbsi</i> LeC.							+
<i>Trachypachus</i> cf. <i>holmbergi</i> Mnh.		+				+	
Carabidae							
<i>Agonum</i> cf. <i>albipes</i> (Fab.)							+
<i>Agonum</i> cf. <i>exaratum</i> Mann.	+	+					+
<i>Agonum</i> cf. <i>bicolor</i> Dej.						+	
<i>Agonum</i> cf. <i>cincticolle</i> Say						+	
<i>Agonum</i> cf. <i>consimile</i> Gyll.						+	
<i>Agonum</i> sp.						+	+
<i>Amara</i> (<i>Curtonotus</i>) sp.						+	
<i>Amara alpina</i> Payk.	+		+			cf.	
<i>Amara bokori</i> Csi.	?						
<i>Amara</i> cf. <i>carinata</i> LeC.						+	
<i>Amara</i> cf. <i>colvillensis</i> Lth						+	
<i>Amara</i> cf. <i>glacialis</i> Mann.						+	+
<i>Amara hyperborea</i> Dej.	?					cf.	
<i>Amara</i> sp.							+
<i>Asaphidion alaskanum</i> Wick.				+		+	+
<i>Asaphidion yukonense</i> type A		+					
<i>Bembidion</i> (<i>Chrysobracteum</i>) sp.						+	+
<i>Bembidion</i> (<i>Hirmoplataphus</i>) sp.							+

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Bembidion (Peryphanes)</i> spp.	+						
<i>Bembidion (Plataphodes)</i> sp.	+				+		
<i>Bembidion (Plataphus)</i> spp.							+
<i>Bembidion (Trepanedoris)</i> sp.					+	+	+
<i>Bembidion</i> cf. <i>bimaculatum</i> Kby					+		+
<i>Bembidion dyschirinum</i> LeC.					+	+	cf.
<i>Bembidion grapii</i> group					+		+
<i>Bembidion grapii</i> Gyll.						+	cf.
<i>Bembidion</i> cf. <i>hasti</i> C.R.Sahlb.					+		
<i>B. honestum-lapponicum</i> type					+		
<i>Bembidion</i> cf. <i>lapponicum</i> Zett.							+
<i>Bembidion litorale/levettei</i> type							+
<i>Bembidion</i> cf. <i>mckinleyi</i> Fall							+
<i>Bembidion metallina</i> group							+
<i>Bembidion</i> cf. <i>nigripes</i> Kby					+		
<i>Bembidion nigrum</i> group							+
<i>Bembidion</i> cf. <i>nitidum</i> Kby					+		
<i>B. Notaphus-aquiliferum</i> type					+		
<i>Bembidion planatum</i> LeC.					+		cf.
<i>Bembidion</i> cf. <i>planusculum</i> Mann.							+
<i>Bembidion sordidum</i> group					+		
<i>Bembidion sordidum</i> Kby							cf.
<i>Bembidion transparens</i> Gebl.							+
<i>Bembidion</i> cf. <i>umiatense</i> Lth	+						
<i>Bembidion</i> spp.		+	+	+	+	+	
<i>Blethisa</i> cf. <i>catenaria</i> Brown					+	+	+
<i>Blethisa</i> cf. <i>multipunctata</i> L.					+		
<i>Blethisa</i> sp.		+	+				
<i>Carabus (Diocarabus)</i> sp.						+	
<i>Carabus (Pancarabus)</i> sp.							+
<i>Carabus</i> cf. <i>chamissonis</i> Fisch.					+		
<i>Carabus</i> cf. <i>nemoralis</i> type A					+		
<i>Carabus</i> cf. <i>nemoralis</i> type B		+					
<i>Carabus</i> cf. <i>taedatus</i> Fab.					+		
<i>Carabus truncaticollis</i> Eschz.	+						
<i>Carabus</i> cf. <i>vietinghoffi</i> Adams					+		
<i>Carabus</i> spp.					+		+
<i>Chlaenius</i> sp.		+			+		
<i>Diacheila matthewsi</i> Böcher		+	+		+		+
<i>Diacheila polita</i> Fald.	+						
<i>Dromius piceus</i> Dej.					cf.		+
<i>Dromius</i> sp.					+		+
<i>Dyschiriodes* frigidus</i> Mann.	+						
<i>Dyschiriodes</i> cf. <i>laevifasciatus</i> Horn					+		
<i>Dyschiriodes nigricornis</i> Mots.	+						
<i>Dyschiriodes</i> cf. <i>variens</i> Fall			+				
<i>Dyschiriodes</i> sp.		+	+		+	+	+
<i>Elaphrus americanus</i> group					+		
<i>Elaphrus angusticollis</i> Sahlb.							+
<i>Elaphrus clairvillei</i> Kby		+			cf.		
<i>Elaphrus lapponicus</i> Gyll.	+			cf.	cf.		+
<i>Elaphrus lecontei</i> Crotch							+
<i>Elaphrus</i> cf. <i>olivaceus</i> LeC.							+
<i>Elaphrus riparius</i> group					+		
<i>Elaphrus sibiricus</i> Mots.							+
<i>Elaphrus tuberculatus</i> Mäkl.							+
<i>Elaphrus</i> sp.	+				+		+
<i>Harpalus</i> cf. <i>amputatus</i> Say					+		

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Harpalus</i> cf. <i>cordifer</i> Not.					+		
<i>Harpalus</i> sp.		+					
<i>Harpalobrachys</i> sp.					+		
<i>Leistus</i> sp.							
<i>Miscodera arctica</i> Payk.							+
<i>Nebria</i> cf. <i>rufescens</i> Ström							+
<i>Nebria</i> sp.					+		+
<i>Notiophilus</i> cf. <i>aeneus</i> Hbst		+			+		
<i>Notiophilus aquaticus</i> L.							+
<i>Notiophilus</i> cf. <i>biguttatus</i> Fab.							+
<i>Notiophilus</i> cf. <i>directus</i> Csy					+		
<i>Notiophilus semistriatus</i> Say	+						
<i>Notiophilus</i> sp.		+		+	+		+
<i>Opisthius</i> cf. <i>richardsoni</i> Kby					+		
<i>Patrobus septentrionis</i> Dej.		+					
<i>Patrobus</i> cf. <i>stygicus</i> Chaud.							+
<i>Patrobus</i> sp.					+		+
<i>Pelophila</i> cf. <i>rudis</i> LeC.					+		
<i>Platidiolus</i> cf. <i>vandykei</i> Kurn.					+		
<i>Platynus decentis</i> Say		+					
<i>Platynus mannerheimi</i> Dej.		+					
<i>Platynus</i> sp.					+		
<i>Pterostichus</i> (<i>Derus</i>) sp.					?		
<i>Pterostichus</i> (<i>Lyperopherus</i>) sp.					+	+	
<i>P.</i> cf. <i>adstrictus</i> Eschz.							+
<i>Pterostichus</i> cf. <i>circulosus</i> Lth					+		
<i>Pterostichus costatus</i> Men.	+						
<i>Pterostichus haematopus</i> Dej.	+						+
<i>Pterostichus patruelis</i> Dej.		+	+		cf.		
<i>Pterostichus punctatissimus</i> Rand.		+					
<i>P.</i> cf. <i>sublaevis</i> J.Sahlb.					+		
<i>Pterostichus vermiculosus</i> Men.	+		cf.		+	+	cf.
<i>Pterostichus</i> (<i>Cryobius</i>) spp.	+		+	+	+	+	+
<i>P.</i> (<i>Cryobius</i>) <i>auriga</i> Ball	+						
<i>P.</i> (<i>Cryobius</i>) <i>biocryus</i> Ball	+						
<i>P.</i> (<i>Cryobius</i>) <i>brevicornis</i> group					+		+
<i>P.</i> (<i>Cryobius</i>) <i>brevicornis</i> Kby	+						cf.
<i>P.</i> (<i>Cryobius</i>) cf. <i>hudsonicus</i> LeC.					+		
<i>P.</i> (<i>Cryobius</i>) <i>kotzebuei</i> Ball	+				cf.		
<i>P.</i> (<i>Cryobius</i>) <i>mandibularoides</i> Ball	+						
<i>P.</i> (<i>Cryobius</i>) cf. <i>middendorfi</i> J.Sahlb.					+		
<i>P.</i> (<i>Cryobius</i>) <i>nivalis</i> F.Sahlb.	+				cf.		
<i>P.</i> (<i>Cryobius</i>) <i>pinguedineus</i> Eschz.	+						
<i>P.</i> (<i>Cryobius</i>) <i>similis</i> Mann.	+						
<i>P.</i> (<i>Cryobius</i>) <i>tareumiut</i> Ball	+				cf.		
<i>P.</i> (<i>Cryobius</i>) <i>tiliaceoradix</i> Ball	+						
<i>P.</i> (<i>Cryobius</i>) <i>ventricosus</i> Eschz.	+						
<i>P.</i> (<i>Cryobius</i>) <i>ventricosus</i> group					+		
<i>Pterostichus</i> sp.					+		
Haliplidae							
<i>Haliplus</i> sp.					+		+
Dytiscidae							
<i>Agabus</i> cf. <i>affinis</i> (Payk.)							+
<i>Agabus</i> cf. <i>anthracinus</i> Mann.							+
<i>Agabus bifarius</i> (Kby)					+	+	+
<i>Agabus clavicornis/serricornis</i> type							+
<i>Agabus</i> sp.	?			+	+	+	
<i>Colymbetes</i> sp.					+	+	+

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Hydroporus</i> cf. <i>morio</i> Aubé							+
<i>Hydroporus</i> sp.	+	+	+		+		+
<i>Hygrotus</i> sp.							+
<i>Ilybius angustior</i> group							+
<i>Ilybius</i> sp.	?						+
<i>Ilybius</i> cf. <i>vittiger</i> Gyll.							+
<i>Neoscutopterus</i> cf. <i>horni</i> LeC.	+						
<i>Noterus crassicornis</i> (Müll.)							+
<i>Oreodytes alpinus/laevis</i> type							+
<i>Oreodytes</i> cf. <i>sanmarki</i> (Sahlb.)							+
<i>Oreodytes</i> sp.		+			+		+
Genus?			+		+		+
Gyrinidae							
<i>Gyrinus</i> sp.						+	+
Hydrophilidae							
<i>Cercyon</i> cf. <i>herceus</i> Smet.					+		
<i>Cercyon</i> sp.						+	
<i>Helophorus</i> cf. <i>frater</i> Smet.							+
<i>Helophorus</i> cf. <i>niger</i> J. Sahlb.							+
<i>Helophorus splendidus</i> Sahlb.	+						
<i>Helophorus tuberculatus</i> Gyll.							+
<i>Helophorus</i> spp.	+		+	+	+	+	
<i>Hydrobius fuscipes</i> type					+		
<i>Megasternum obscurum</i> (Mots.)							+
Genus?					+		+
Hydraenidae							
<i>Limnebius</i> sp.		+					
<i>Ochthebius</i> sp.		+			+	+	
Georyssidae							
<i>Georyssus</i> sp.		+			+		
Staphylinidae							
<i>Acidota</i> sp.		+			+	+	+
Aleocharinae	+	+			+	+	+
<i>Arpedium</i> sp.		+			+	+	
<i>Atheta</i> sp.							cf.
<i>Bledius</i> sp.		+	+		+		+
<i>Boreaphilus</i> sp.			+		+		+
<i>Carpelimus</i> sp.					+		
<i>Coryphium hyperboreum</i> (Mäkl.)			+				
<i>Euaesthetus</i> sp.		+			+		
<i>Eucnecosum</i> sp.					+		+
<i>E.</i> cf. <i>brachypterum</i> (Grav.)							+
<i>Gymnusa</i> sp.	+			+	+	+	
<i>Holoboreaphilus</i> sp.					+		
<i>Lathrobium</i> sp.			+		+		
<i>Micralymma brevilingue</i> Schiødt.	+	+				+	
<i>Micralymma</i> type			+		+	+	+
<i>Mycetoporus</i> sp.							+
<i>Olophrum boreale</i> (Payk.)						+	
<i>Olophrum</i> cf. <i>consimile</i> Gyll.						cf.	+
<i>Olophrum</i> cf. <i>rotundicolle</i> (Sahlb.)							+
<i>Olophrum</i> sp.	+	+			+		
Omalinae, Coryphiini?		+			+	+	
Omalinae, genus?			+				+
Oxytelinae, genus				+			+
<i>Philonthus</i> sp.							+
<i>Pycnoglypta lurida</i> (Gyll.)					+		
<i>Pycnoglypta</i> sp.				+	+	+	+

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Quedius</i> spp.	+	+				+	+
<i>Q.</i> (<i>Raphirus</i>) <i>aenescens</i> group					+		
<i>Stenus</i> sp.	+	+	+	+	+	+	+
<i>Tachinus brevipennis</i> Sahlb.	+		+				
<i>Tachinus</i> cf. <i>acuticus</i> Popp.					+		
<i>Tachinus</i> sp.	+	+	+		+	+	+
<i>Tachyporus</i> cf. <i>nimbicola</i> Camp.							+
<i>T.</i> cf. <i>rulomus</i> Blackw.							+
<i>Tachyporus</i> sp.	+	+	+		+	+	
Micropeplinae							
<i>Kalissus nitidus</i> LeC.				+			
<i>Kalissus</i> sp. A					+		
<i>Micropeplus nelsoni</i> Mäkl.						+	
<i>Micropeplus sculptus</i> LeC.					+		
<i>Micropeplus tesseraula</i> Curt.						+	
Pselaphidae							
Genus?		+			+		
Elmidae							
Genus?					+		
Silphidae							
<i>Phosphuga</i> cf. <i>atrata</i> L.					+		
<i>Pteroloma forstroemi</i> (Gyll.)							+
<i>Silpha</i> cf. <i>opaca</i>					+		
<i>Silpha</i> cf. <i>ramosa</i> Say					+		+
<i>Silpha</i> sp.						+	
<i>Thanatophilus</i> sp.							+
Leptodiridae							
cf. <i>Catops</i> sp.							+
<i>Colon</i> sp.	+						
Leiodidae							
<i>Agathidium</i> sp.						+	+
cf. <i>Anisotoma</i> sp.							+
Genus?					+	+	+
Ptiliidae							
<i>Acrotrichus</i> sp.						+	
Scydmaenidae							
Genus?			+		+	+	
Histeridae							
<i>Platysoma (Cylister)</i> sp.					+		
Scarabaeidae							
<i>Aegialia</i> cf. <i>sabuleti</i> (Panz.)							+
<i>Aegialia</i> sp.		+	+	+	+	+	+
<i>Aphodius</i> sp.		+			+		+
Helodidae							
<i>Cyphon</i> sp.		+				+	
Byrrhidae							
<i>Byrrhus</i> sp.	+		+		+		
<i>Curimopsis</i> sp.					+		
<i>Cytilus alternatus</i> (Say)			+				
<i>Morychus</i> sp.		+	+		+		
<i>Simplocaria elongata</i> Sahlb.	+						
<i>Simplocaria</i> sp.		+	+		+	+	+
Genus?				+			
Buprestidae							
Genus?					+		+
Heteroceridae							
<i>Heterocerus</i> sp.			+				
Elateridae							

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Ctenicera</i> sp.					+		
<i>Hypolithus</i> cf. <i>sandborni</i> (Horn)					+		
<i>Hypnoidus</i> sp.							+
Genus?			+				
Cantharidae							
<i>Podabrus alpinus</i> (Payk.)							cf.
<i>Podabrus</i> sp.						+	
Anobiidae							
<i>Hadrobregmus</i> cf. <i>pertinax</i> (L.)							+
Genus ?		+	+		+		
Bostrichidae							
Genus?					+		
Melyridae							
cf. <i>Amecocerus</i>							+
Salpingidae							
Genus							+
Anthicidae							
<i>Anthicus</i> sp.					+		
Genus?			+				
Cucujidae							
<i>Pediacus</i> sp.	?	+					
Coccinellidae							
<i>Ceratomegilla</i> sp.					+		
Genus?		+				+	+
Lathridiidae							
Genus?	+					+	+
cf. <i>Corticaria</i> sp.							+
<i>Stephostethus</i> sp.					?		
Colydiidae							
<i>Bitoma</i> sp.					?		
Cerambycidae							
Genus?							+
Chrysomelidae							
<i>Cassida flaveola</i> Thunb.	+						
<i>Chrysolina basilaris</i> (Say)	+						
<i>Chrysolina cavigera</i> (Sahlb.)	+						
<i>Chrysolina subsulcata</i> group	+						
<i>Chrysomela</i> sp.	+						cf.
<i>Donacia</i> cf. <i>distincta-subtilis</i> group					+		
<i>Donacia</i> sp.						+	+
Donaciinae		+		+			
cf. <i>Galeruca</i> sp.							+
cf. <i>Graphops</i> sp.							+
<i>Hydrothassa</i> sp.							+
<i>Phaeodon cyanescens</i> Stål	+						
Genus?					+		+
Curculionidae							
<i>Apion</i> sp.			+		+		+
<i>Ceutorhynchus</i> sp.	+	?			cf.	?	
<i>C.</i> cf. <i>subpubescens</i> LeC.	+						
<i>Cylindrocopturus</i> sp.						+	
<i>Dorytomus</i> sp.					+		+
<i>Dryophthorus americanus</i> Bed.		+					
<i>Grypus equiseti</i> (Fab.)			+		cf.		cf.
<i>Homorosoma</i> sp.						+	
<i>Hylobius</i> sp.		+			cf.		
<i>Hypera</i> sp.	+				+		
<i>Lepidophorus lineaticollis</i> Kby		+					

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>L. cf. pumilis</i> Buchanan		+					
<i>Lepidophorus</i> sp.			cf.		+		
<i>Lepyrus</i> spp.	+				+		
<i>Lixellus</i> sp.							+
<i>Magdalus</i> sp.							+
<i>Notaris aethiops</i> Fab.				+			
<i>Notaris bimaculatum</i> type		+			+		
<i>Notaris flavipilosus</i> Chitt.	+						
<i>Notaris</i> sp.					+	+	+
<i>Otibazo</i> sp.		+					
cf. <i>Otiiorhynchus</i> spp.		+					+
<i>Phyllobius</i> sp.			+				
<i>Pissodes</i> sp.		+			cf.		+
<i>Rhynchaenus</i> sp.	+	+			+		+
<i>Rhyncolus</i> sp.							+
<i>Sitona</i> sp.							+
<i>Stephanocleonus</i> sp.	+				+		
<i>Vitavitus thulius</i> Kiss.	+	+					
<i>Vitavitus</i> sp.				+	+		
Genus?					+		+
Scolytidae							
<i>Pityophthorus</i> sp.							+
<i>Scierus</i> sp.		+			+		
<i>Scolytus</i> sp.							+
Genus?		+					+
Lepidoptera							
Family?							+
Trichoptera¹			+				
Hydropsychidae							
<i>Arctopsyche</i> cf. <i>ladogensis</i> (Kol.)					+		
Limnephilidae							
<i>Arctopora</i> cf. <i>pulchella</i> (Banks)					+		
<i>Hydatophylax</i> sp.					+		
<i>Limnephilus subcentralis</i> grp						+	
cf. <i>Limnephilus</i>					+		
Limnephilini, genus?					+		
Calamoceratidae							
<i>Heteroplectron</i> cf. <i>americanum</i> (Walk.)					+		
Molannidae							
<i>Molanna</i> cf. <i>uniophila</i> Vorh.						+	
Family??							+
Diptera			+				
Tipulidae							
<i>Tipula (Vestiplex)</i> sp.	+						
<i>Tipula</i> sp.					+		+
Chironomidae ²							
<i>Abiskomyia</i> sp.			+		+		
<i>Chironomus</i> type					+	+	+
<i>Corynocera ambigua</i> Zett.					cf.		+
<i>Diamesa</i> sp.							+
<i>Endochironomus</i> sp.							+
<i>Microspectra</i> sp.							+
Orthocladiinae, genus?							+
<i>Orthocladius</i> sp.							+
<i>Psectrocladius</i> sp.							+
<i>Sergentia</i> sp.					+		
<i>Tanypodinae</i> undet.							+
<i>Tanytarsini</i> undet.					+		

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
Genus?						+	+
Brachycera?							+
Cyclorrhapha							
Schizophora sp.							+
Xylophagidae							
<i>Xylophagus abdominalis</i> Loew	+						
<i>Xylophagus</i> sp.		+		+	+	+	
Family?			+			+	
Hymenoptera³							
Symphyla							
Tenthredinidae							
<i>Dolerus</i> sp.						?	
<i>Nematus</i> sp.	+					+	
Genus?							+
Siricidae							
<i>Urocerus</i> cf. <i>gigas</i> (L.)							+
Family?						+	
Apocrita							
Ichneumonoidea			+				
Braconidae							
Agathidinae	?						
<i>Chelonus</i> (<i>Microchelonus</i>) sp.	+						
<i>Chelonus</i> sp.	+						
<i>Ichneutes</i> sp.	+						
<i>Meteorus</i> sp.	?						
<i>Rogas</i> sp.	+						
Ichneumonidae							
Anomalinae	+			+			
<i>Atractodes</i> sp.	+						
Banchinae, genus?				+			
<i>Bathythrix</i> sp.	+						
Campopleginae, <i>Sinuphorus</i> sp.				+			
Cremastinae	+						
<i>Hyposoter</i> sp.	?						
<i>Ichneumon</i> sp.	+						
<i>Mesochorus</i> sp.	+						
<i>Phygadeuon</i> sp.	+						
Orthocentrinae, Genus?					+	+	
Pimplinae, Genus?					+		+
Chalcidae							
Genus?							+
Torymidae							
<i>Megastigmus</i> sp.							+
Pteromalidae							
Pteromalini	+						
Genus?					+		
Eurytomidae							
<i>Eurytoma gigantea</i> Walsh	+						
Megaspilidae							
<i>Conostigmus</i>					?	?	
Diapriidae							
Belytinae, genus?		+			+	+	
Genus?					+		+
Formicidae							
<i>Camponotus</i> cf. <i>herculeanus</i> (L.)							+
<i>Formica</i> type			+			+	
<i>Myrmica alaskensis</i> type ⁴					+		
<i>Myrmica</i> sp.						+	+

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
Genus?		+		+	+		
Apidae							
<i>Bombus</i> sp.					+	cf.	
<i>Pyrobombus</i> sp.					+		
Genus?					+	+	
CRUSTACEA							
Cladocera							
<i>Daphnia</i> (<i>Daphnia</i>) sp.	+						
<i>Daphnia</i> sp.		+			+	+	
Notostraca							
<i>Lepiduris</i> sp.	+		+		+		+
ARACHNIDA							
Acari							
Mesostigmata							
Gamasida (Hypoaspidae)							
<i>Hypoaspis</i> sp.						+	
Trachytidae							
cf. <i>Trachytes</i> sp.			+				
Prostigmata							
Oribatida ⁵				+			
Camisiidae							
<i>Platynothrus peltifer</i> (C.L. Koch)					+		
Cepheoidea							
<i>Cepheus corae</i> Jacot		+					
<i>Cepheus</i> sp.		+	cf.				
<i>Tritegeus</i> cf. <i>major</i> Gol. & Karp.		+					
<i>Tritegeus</i> sp.		+					
Damaeidae							
cf. <i>Epidamaeus</i> sp.					+		
<i>Epidamaeus arcticolus</i> (Ham.)					+		
<i>E. fortispinosus</i> Ham.					+		
Damaeidae undet.					+		
Megeremaeidae							
<i>Megeremaeus keewatin</i> B.-P.					+		
Eremaeidae							
<i>Eremaeus</i> sp.					+	+	
<i>E. translamellatus</i> Ham.					+		
<i>Proteremaeus macleani</i> B.-P.						+	
Astegistidae							
<i>Astegistes</i> sp.						?	
Metrioppiidae							
<i>Ceratoppia bipilis</i> (Herm.)		+			+		
<i>Ceratoppia rotundirostris</i> Drouk		?					
<i>Ceratoppia quadridentata</i> (Ham.)					+	cf.	
<i>Metrioppia helvetica</i> Grandj.		?					
Tectocephidae							
<i>Tectocephus velatus</i> (Michael)		+			+		
Hydrozetidae							
<i>Hydrozetes</i> spp.		+	+		+	+	
Limnozetestidae							
<i>Limnozetes</i> spp.					+	+	
<i>L. lustrum</i> B.-P.					+		
Zetomimidae							
<i>Heterozetes</i> sp.					+		
Ceratozetidae							
<i>Ceratozetes</i> sp.					+		
<i>Diapterobates</i> cf. <i>variabilis</i> Ham.		+					
<i>Melanozetes meridianus</i> Selln.					+	+	

TABLE 3. (continued)

Species	Alaska			YT	NT		Grn.
	CD	LC	Ng	B2	Mg	SF	KK
<i>Fuscozetes</i> sp.		+					
<i>Neogymnobates</i> sp.						+	
<i>Sphaerozetes</i> sp.					+		
<i>Sphaerozetes piriformis</i> (Nic.)					+		
<i>Sphaerozetes castaneus</i> Ham.		+					
<i>Trichoribates</i> sp.		+			+		
<i>Trichoribates polaris</i> Ham.					+	+	
Mycobatidae							
<i>Mycobates conitus</i> Ham.							+
<i>Mycobates</i> sp.		+			+		
<i>Punctoribates</i> sp.					+		
<i>P. cf. hexagonus</i> Berl.					+	+	
<i>P. quadrivertex</i> Herbert							?
Phenopelopidae							
<i>Eupelops</i> sp.		+			+		
<i>E. cf. occultus</i> (C.L. Koch)		+					
<i>Propelops groenlandicus</i> Selln.					+		
Achipteriidae							
<i>Achipteria</i> spp.		+			+		
<i>Achipteria cf. latiteca</i> (Berl.)		+					
<i>Parachiptera</i> sp.		+					
<i>Parachiptera cf. nivalis</i> Ham.							+
Tegoribatidae							
<i>Lepidozetes</i> sp.					+		
<i>Tegoribates americanus</i> Ham.					+		
Galumnidae, genus?		+					
Araneae							
Lycosidae							
Genus?							+
Linyphiidae							
<i>Erigone</i> sp.				+			

*Formerly *Dyschirius*.

Sites:

CD, Cape Deceit Formation, Cape Deceit site (site A, Fig. 1), western Alaska; age: 1.8 ma B.P.?

LC, Lost Chicken site (site F, Fig. 1), east central Alaska; age: 3 ma B.P. (late Pliocene).

Ng, Niguanak exposure (site D, Fig. 1), Alaska North slope; age: Pliocene?

B2, Bluefish exposure, Old Crow region of Yukon (site 5, Fig. 1); age: Pliocene?

SF, Beaver pond deposit, Strathcona Fiord (site H, Fig. 1), Ellesmere Is., Northwest Territories; age: Pliocene?

Mg, Meighen Island, Queen Elizabeth group (site G, Fig. 1), Northwest Territories; Combination of sites approx. 3 ma (late early Pliocene) (Matthews et al. unpublished 2).

KK, Kap København site (site I, Fig. 1), northern Greenland; age: 2–2.5 ma B. P. (late Pliocene). For a complete list with extended comments see Böcher (1995).

¹ Identified by N. Williams, Scarborough College, University of Toronto, Ontario.

² Identified by I. Walker, Queens University, Ontario.

³ Identified by W. Mason, Biosystematics Research Institute, Ottawa, Ontario.

⁴ Identified by André Francoeur, Université du Québec à Chicoutimi, Chicoutimi, Québec.

⁵ Identified by V. Behan-Pelletier, Biological Resources Division, Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, Ontario.

A few Psyllidae are represented in fossil assemblages by flight wings and some can be identified to genus on the basis of wing venation. The tiny heads of the psyllids are much rarer.

Only in exceptional instances are fossils of aphids found, and none of the sites is from the Yukon. However, the deposits on Meighen Island show that in certain contexts, aphid fossils as old as 3 ma B.P. (Fig. 3h) occur. Of course, they are not preserved as well as aphids found in amber.

Neuroptera. The distinctive mandibles of alderflies (*Sialis*) have been seen in a few subarctic northern samples and can be expected to occur eventually in Yukon assemblages, particularly those representing warmer-than-present climates. None has yet been found in Yukon assemblages.

Coleoptera. Beetles dominate most fossil assemblages largely due to the fact that their bodies are thickly sclerotized. The fragments represent all parts of the coleopteran body with pronota, heads and elytra providing the best characters for identification.

On rare occasions, beetle fossils are preserved as nearly whole individuals, allowing the examination of genitalia and potential studies of gut contents and other soft tissues. This type of preservation is typical of specimens from autochthonous peats. Even the Yukon fossils that consist of disarticulated fragments exhibit excellent preservation because the prevalence of permafrost in the Yukon assures that most of them have probably been frozen since shortly after their deposition. The protective aspects of burial in permafrost are undoubtedly responsible for some examples of exceptional preservation of isolated fragments. At one site in western Alaska, many of the elytra of the staphylinid beetle *Tachinus apterus* contained the flight wing attached to the underside. This condition occurred in samples ranging from early Pleistocene to late Pleistocene, enabling the documentation of flight-wing reduction over a span of some 1.0–1.5 million years (Matthews 1974, 1975).

Fossils of beetle larvae are relatively rare, though they do occur in most assemblages where a great number of fossils have been examined. The most commonly encountered larval fossils are mandibles and fragments of heads. At the late Pliocene Lost Chicken site near the Alaska/Yukon border (site F, Fig. 1), nearly complete silphid larvae occur in an autochthonous peat that also contains articulated fossils of adult beetles. Such good preservation of larvae is a rarity, even for autochthonous peats, and may be due to the fact that the peat in question is partly cemented (Matthews et al. unpublished 1).

Coleopteran fossils occur in almost every sample studied to date. The composition of the fossil assemblages is dictated largely by the origin of the sediments in which the fossils occur and by taphonomy (postmortal history of transportation, degradation, burial, etc.). Autochthonous peats, as the name implies, contain mostly insects and other arthropods that occupied the site of peat formation, but in many instances the abundance of fossils is low compared to allochthonous deposits, such as river alluvium, which potentially can contain fossils representing all of the biotopes or environments within the drainage basin. Fossil assemblages from alluvium are usually dominated by local taxa, i.e. those that presently live on river banks and adjacent habitats; however, taphonomic factors may also skew their composition. For example, some of the fossils in any assemblage may be rebedded from older sediments deposited when climate conditions were different from those prevailing during deposition of the majority of fossils. Secondly, some fossils have shapes which cause them to be readily sorted when transported by water. The weevil *Lepidophorus lineaticollis* lives along sandy floodplains beneath willows where it likely feeds on roots. Because of this

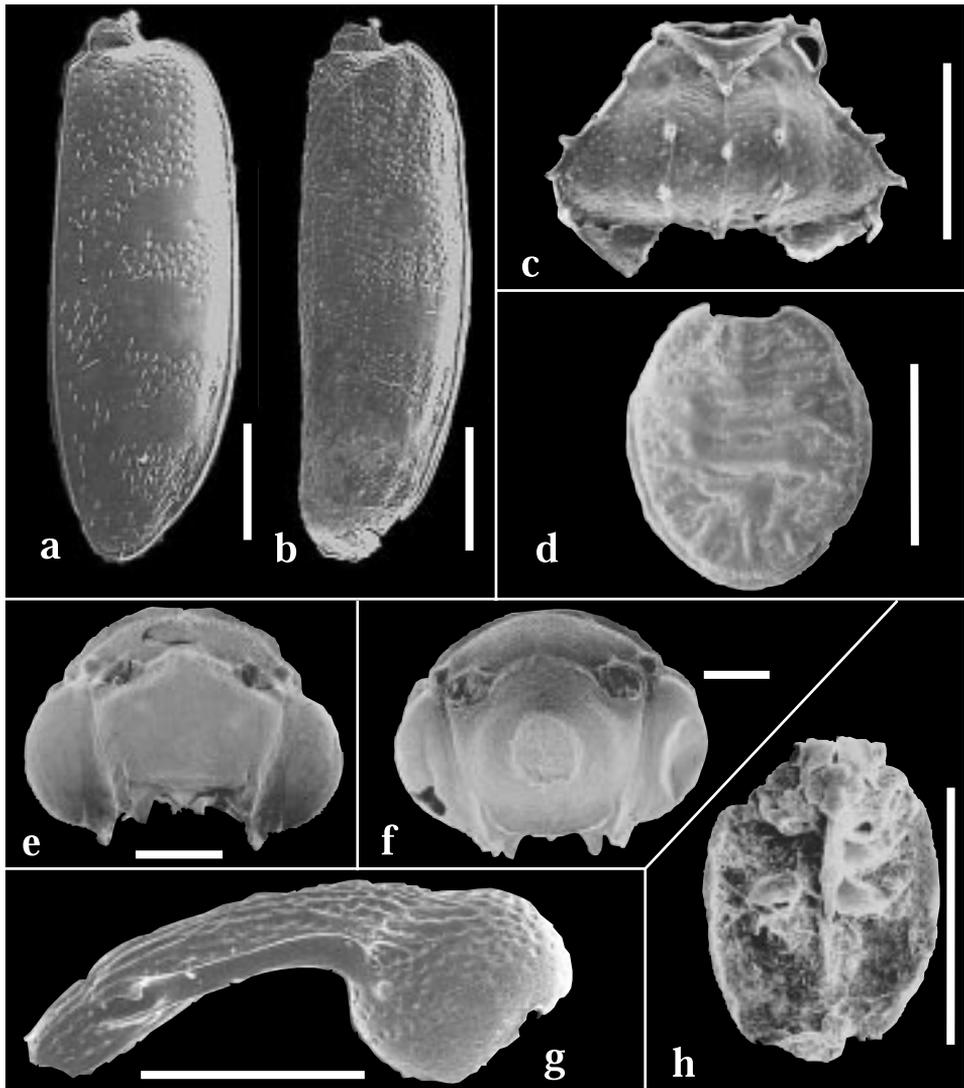


FIG. 3. a, Right elytron of modern *Asaphidion yukonense* Wickham (Coleoptera: Carabidae) compared with fossil elytron (b) from the Lost Chicken mine (site F, Fig. 1)—note the less developed bare patch on the Lost Chicken specimen, which also has microsculpture, unlike *A. yukonense*; c, *Derefphysia foliacea* (Fallén) (Heteroptera: Tingidae), pronotal fragment, Bluefish exposure (site 5, Fig. 1), late Pleistocene; d, Whitefly (Homoptera: Aleyrodidae), Beaver Peat (site H, Fig. 1), Ellesmere Island, Pliocene; e, *Agrotiphila staudingeri* (Möschler) (Lepidoptera: Noctuidae), head, Upper Porcupine site (site 6, Fig. 1), mid Wisconsinan (e.g. approx. 38 ka B.P.); f, *Euxoa churchillensis* (McDunnough) (Lepidoptera: Noctuidae), head, Upper Porcupine site (site 6, Fig. 1), mid Wisconsinan; g, *Otibazo* sp. (Coleoptera: Curculionidae), head showing slightly developed eye, Lost Chicken (site F, Fig. 1), Pliocene (3 ma B.P.); h, Aphididae (Homoptera), ventral view of nearly whole specimen, Meighen Island (site G, Fig. 1), Pliocene (approx. 3.2 ma B.P.). Scale bars 0.5 mm.

habit, its fossils are abundant in most Yukon assemblages derived from alluvium; but in some, heads dominate; in others elytra or pronota dominate.

Trichoptera. Nancy Williams (e.g. Williams and Morgan 1977) has been at the forefront in showing that fossils of larval head capsules of caddisflies can be identified, often to genus

and species. Such fossils occur rarely in Yukon samples, probably because most of the samples studied to date do not come from lacustrine sediments, and larval fragments are unlikely to be buoyant enough to be flushed into alluvial systems. There are mountain-stream species (Wiggins 1997), but that biotope is rarely represented in the fossil record.

Fossil caddisfly cases occur more commonly than the frontoclypeal fragments. Some of these cases can be identified tentatively to family or superfamily groups. To date fossils of adult caddisflies have not been observed except in recent samples (see Table 1 and below).

Lepidoptera. Many Yukon samples contain nondescript mandibles of larval Lepidoptera, but identifiable fragments, of either larvae or adults, are rare. One exception to this statement are the delicate yet well preserved heads of *Euxoa* (Fig. 3f). While they lack scales, the heads nevertheless retain delicate structures such as the pilifers. The noctuid fossils from one of the sites show that it is not always necessary to obtain species determinations in order to derive palaeoenvironmental data. For example, all of the noctuid fossils from the upper Porcupine sample (site 6, Fig. 1; Table 2) have ellipsoid eyes, a character typical of tundra species (Lafontaine and Wood 1988). One of them (Fig. 3f) can definitely be referred to the treeline species *Euxoa churchillensis*. A few samples contain an unusual abundance of lepidopteran larval mandibles; the most notable of these is the sample from the late Pleistocene part of the Bluefish exposure (site 5, Fig. 1; Table 2). Noctuids (cutworms) are known to undergo plague-like outbreaks, even in northern areas, and this may be what is indicated by the abundance of mandibles in some samples.

Diptera. The tables show that Yukon fossil assemblages almost always contain some fragments of Diptera. Chironomid larval head capsules are usually present, but with rare exceptions and not in the numbers typical of lake sediments. More informative chironomid faunas come from lake cores, such as those collected for pollen analysis. None of the assemblages discussed here comes from cores and in general the study of chironomids from lake sediment cores in the Yukon has not progressed as far as at more southern sites, e.g. British Columbia (Walker 1987).

Ovipositors of crane flies or the caudal plates of the larvae of *Xylophagus* occur in many samples. Many samples also contain a few puparia. Some sediments associated with frozen carcasses and bones contain literally thousands of calliphorid puparia. In at least one instance (Guthrie 1990) the absence of such puparia around a frozen carcass provides as much information on the history of the carcass as their presence. Most calliphorid puparia seen in carrion-related samples are empty. A few, however, contain the remains of unemerged flies—either the calliphorid adults or possibly even tachinid parasites. Such fossils remain to be studied in detail by dipterists.

Some samples from pond and alluvial sediments contain a few fragments of other Diptera—heads and flight wings of bibionid flies and thoracic and head fragments of higher flies. An exceptional fossil is the male hypopygium with well preserved gonostyli and mesolobus of the anthomyiid fly *Delia hudsonica* (Griffiths 1993).

Hymenoptera. Heads, mandibles and thoracic fragments of Formicidae occur in almost every sample, and some of these can be identified by appropriate experts. Also present in most samples are heads and thoracic fragments of ichneumonids and braconids, and rarely other families such as the Diapriidae. There is great potential for identification of such fossils when studied by appropriate specialists. As with all of the groups mentioned here, once Hymenopteran fossils are studied in detail, they too will reveal distributional and taxonomic surprises.

Arachnida. A few of the sites discussed in this chapter contain fossils of spiders, usually parts of the cephalothorax. In rare instances male palps have been found, potentially enabling specific determinations. More detailed study of the finer fractions of samples would undoubtedly result in discovery of more spider fossils, but they will always be rare compared to the other major arachnid group represented by fossils—oribatid mites.

Study of fossil oribatids is well advanced in Russia (Golosova et al. 1985; Krivolutsky and Druk 1986). Such efforts are in their infancy on this continent. Nevertheless, the oribatid fossils (identified by V. Behan-Pelletier, Biological Resources Division, Agriculture Canada) listed in the tables clearly reveal the potential for such studies in arctic and subarctic regions. In particular, the find of *Proteremaeus macleani* from a late Tertiary sample in the arctic (Behan-Pelletier and Ryabinin 1991) shows that oribatid fossils have the same potential as do fossil Coleoptera for revealing major, and sometimes totally unexpected, distributional changes through time.

In addition to oribatid mites, rare finds of other types of mites have been made, mostly from sites located outside the Yukon. One of the most spectacular finds is a nearly complete gamasid mite (Mesostigmata) from the 3–4 ma B.P. Beaver Peat site on Ellesmere Island (site H, Fig. 1) (Matthews unpublished). Though much rarer than oribatid mites, fossils representing other mesostigmatid mites have been found at some sites quite near the Yukon. One such fossil comes from the Niguanak site (site D, Fig. 1).

Selected Faunas

A complete recounting of all available data on fossil insects from the Yukon is beyond the scope of this chapter. Instead we discuss selected faunas of different ages and origins. Many of the faunas come from riverbank exposures such as the one in Fig. 2. Such sites are abundant in the northern Yukon due to its unique geological history.

Because this book is concerned primarily with the extant fauna, the discussion will proceed from the extant fauna backwards in time rather than from oldest to youngest as is the norm for geological studies. The starting point of the discussion is the extant fauna, or rather the way in which the extant fauna is represented in the modern sedimentary record.

Extant Faunal Remains. It is important to emphasize that the study of fossils cannot be conducted without an adequate knowledge of the present-day fauna. A step removed from the modern fauna is the modern fauna as represented in a postmortal state. It can be very enlightening for understanding fossil assemblages to begin by examining recently dead insects, after they have become disarticulated, setae and scales fallen off and all soft, lightly-sclerotized tissues decayed. Such fragments occur in many modern sediments such as recently deposited river alluvium.

During the past decade an important part of our study of the environmental history of the Yukon and adjacent areas of Alaska and the Northwest Territories has been the collection and study of insect and plant fragments found in recently deposited sediments. The insect fauna from 2 such samples is shown in Table 1. Sample 1 comes from the organic detritus along the shoreline of several thermokarst or “thaw lakes” in the Old Crow Basin. The second (sample 2, Table 1) represents finely disseminated debris occurring along a marine shoreline east of the Tuktoyaktuk Peninsula in the Northwest Territories.

Thaw lakes or thermokarst lakes, such as the one that yielded sample 1 in Table 1, are a special type of aquatic environment that is prevalent in regions underlain by permafrost. The combination of ice-rich organic sediments and shallow-water wave action causes parts

of the lake shoreline to be littered with wave-washed debris derived from the eroded sediments. The process gives thaw-lake fossil faunas and floras very distinctive characteristics. They may contain a few fossils of aquatic insects, but are dominated by terrestrial forms that lived on or in the terrain that the thaw lake has eroded. The number of strictly aquatic organisms is low because of the abundance of terrestrial fossils entering the system plus the fact that thaw lakes are normally turbid and freeze to the bottom, limiting the diversity of the resident aquatic community. Sample 1 in Table 1 exemplifies a typical thaw-lake assemblage.

Thaw-lake samples are worthy of examination by entomologists studying the modern fauna of a region, because the sorted debris represents many square metres of a terrestrial environment and some samples contain rare species. For example, the fauna of sample 1 contained an elytron of the ground beetle *Chlaenius niger*, a species not previously known to occur in the Yukon (Lindroth 1961–69).

Holocene Faunas. The Holocene interval encompasses approximately the last 10 000 years (10 ka B.P.) and is considered to represent an interglacial warm period similar to but certainly not identical to the other interglacial periods of the Quaternary.

Northern Yukon and Alaskan Coastal Plain. Two of the samples in Table 1 (BR and IR, locs. B and 1, Fig. 1) represent the early Holocene on the arctic coastal plain about 9600 years ago. As discussed earlier, that was a time when solar insolation peaked at latitude 60°N (Ritchie et al. 1983; Ritchie 1984). Treeline expanded somewhat and poplars (*Populus*) grew as far north as the northern coast of Alaska and the Yukon. The few isolated poplar stands that remain there today are probably relicts of this early Holocene warm period.

Nelson (1987) tabulated more than 1000 individual beetles, representing more than 100 taxa (60 named species) at the Ikpikpuk site. It resembles the BR assemblage, containing a few of the same southern species. Unlike the Ikpikpuk assemblage, the Blow River list includes a number of non-coleopterous fossils such as larval Trichoptera, the larval chironomid *Glyptotendipes* (Fig. 3), adult leafhoppers (*Driotura* and possibly *Memnonia*) as well as a large number of hymenopteran fragments.

Old Crow Basin. Sample 44 in Table 1 (site 2, Fig. 1) comes from autochthonous deposits of a wet depression that formed between 8.2 and 8.5 ka B.P. The numbers listed in the Table are the minimum number of specimens of each taxon in the sample. Even though the total number of Coleoptera individuals is much smaller than in the Ikpikpuk fauna, the aquatic and near-aquatic nature of the sediments is clearly shown by the abundance of beetles such as *Euaesthetus*, *Stenus*, *Gymnusa*, *Dyschiriodes nigricornis* and *Bembidion transparens*. Rarer are the carabid *Bembidion sordidum* and the weevil *Lepidophorus lineaticollis*, both beetles that live near river margins. Most of the species in the assemblage occur today both within and outside treeline; though a few, such as the beetles *Heterocerus*, *Micropeplus tesseraula* and *Agonum quinquepunctatum* are more common within forested regions and show that treeline was probably close by. This conclusion is not so clearly indicated by the plant fossils, which are dominated by seeds of shrub birch. Like some of the others in Table 1, the 44 assemblage contains a few fossils of rare beetles. Two important examples are the carabids, *Pterostichus circulosus* and *Carabus maeander*. Either these species are rarer now than they were 8000 ago or they are simply rarely collected today.

Sample 32a (site 3, Fig. 1) is also from the Old Crow basin and is approximately the same age (8 ka B.P.) as sample 44. Its fauna is much less diverse. Only half of its taxa (minimum of 36 species) also occur in the 44 assemblage, which is only several hundred

years older. However, many of these are species or genera typical of drier sites. Among the 2 samples are several fossils of bark beetles, which undoubtedly means that trees were growing near the site, a fact confirmed by the presence of many spruce fossils. Both samples 32a and 44 accumulated in a former lake basin which was already partly dissected by an early version of the Old Crow River. If wetlands existed, they were the type normally associated with permafrost phenomena such as thaw lakes and other wet sites formed where ice wedges grow and melt. The difference between the 2 sites may be as subtle as one being located near a grove of conifers in a largely treeless region, a common condition today, while the other was in an open tundra-like site well away from trees. Alternatively, site 32a may have been closer to or within regional treeline, whereas site 44 was beyond treeline. Pollen data from the 2 sites show marked differences in the percentage of spruce. Pollen and plant macrofossils from other sites near the Old Crow basin confirm that 8 ka B.P. was a time of expanding treeline (Ovenden and Brassard 1989; Cwynar 1982).

Eagle River. Like sample 32a, the Eagle River assemblage (ER, Table 1) is a small sample collected primarily for ^{14}C dating. The sediments represent organics deposited in a depression formed partly by local thawing starting around 9 ka B.P. The entire 10 metres of fill of this depression is available for study, but so far only the basal organics have been examined (Blake 1984). In general, the insects agree with the plant macrofossils in portraying a poorly drained depression which was occasionally filled with water (note several dytiscids and *Gyrinus*). The importance of this sample is that it represents the time immediately before the movement of spruce into the region. Detailed study of an entire suite of samples from this site could potentially reveal the same type of differential climatic response by plants and insects as was shown in the classic report by Coope and Brophy (1972). The plants from the ER site hint that a detailed study of the insects might yield some surprises. Among the plant fossils are achenes of *Bidens*, a weed considered by most botanists to be introduced (e.g. Hultén 1968).

Late Wisconsinan. The samples grouped under the heading “Late Wisconsinan” (Table 2) refer to the time between approximately 30 ka and 10 ka B.P. and represent the transition from interstadial, or moderately warm climates of the Wisconsinan glacial period, to the maximum cold of about 20 ka B.P. Sample Tk (Table 2; site C, Fig. 1) is from the North Slope of Alaska, the same region from which the Holocene IR sample (Table 1) comes (see Fig. 1 and Nelson 1976, 1982). Its age is approximately 30–31 ka B.P.

Northern Yukon. Sample 32b (Table 2; site 3, Fig. 1) comes from the same Old Crow Basin section as 32a (Table 1; Fig. 1, site 3). Although the number of individuals represented in 32b is small, fragments of one species of weevil, *Lepidophorus lineaticollis*, dominate. Comparison of the plant macrofossil assemblages reveals even greater differences: virtually no spruce fossils occur in 32b, but they are abundant in 32a.

The Rock River section (RR, Table 2; site 7, Fig. 1) is only one of several in the Bell Basin that have yielded abundant insect fossils. A nearby site is the “Upper Porcupine Section” from which comes one of the richest insect assemblages yet discovered in the Yukon (see below: Mid-Wisconsinan assemblages). Though most of the Upper Porcupine fossils discussed here are of mid-Wisconsinan rather than late Wisconsinan age, one fossiliferous level at Upper Porcupine is dated at 13.5 ka B.P., which places it at the end of the late Pleistocene—a time when climate was starting to warm rapidly and shrub birches were again growing in the northern Yukon. Only a summary of insects (grouped as ecological categories) from that level has been published (Hughes et al. 1981; Matthews 1982, 1983),

and even though the use of such ecological groups for interpretation of fossil insect data is subject to certain biases (Elias 1994), ecological composition of the 13.5 ka B.P. material shows clearly that it lacks a modern analogue. Apparently it represents a dry, possibly cold environment that was almost steppe-like in places. Plant macrofossils from the sample support this conclusion. Among them are seeds of various grass species as well as several representing the chenopod *Corispermum* (bugseed), a dry-site plant that is very rare in the present-day Yukon.

Another important late Wisconsinan site from the Yukon is the Bluefish section in the Bluefish Basin near Old Crow (B1, Table 2; site 5, Fig. 1). The sediments were deposited by a low-gradient stream emptying into the glacial lake that occupied Old Crow and Bluefish Basins during the late Pleistocene. The assemblage of fossil insects in this sample is rich, including fragments representing groups such as the Plecoptera and noctuid moths. As with other late Pleistocene assemblages, fossils of the byrrhid beetle *Morychus* sp. and the weevil *Lepidophorus lineaticollis* dominate, indicating prevalence of dry local conditions. What is most interesting about this particular sample is that the associated plant fossils provide the best evidence available for existence of steppe-like conditions in East Beringia. The sample is unique, for example, in containing florets of *Artemisia*, some of which match those of *A. frigida*. Modern *Artemisia frigida* grows exclusively on south-facing slopes and is considered to be a relict of former steppe-lands of late-Pleistocene Beringia (Yurtsev 1982). Among the other plant fossils are abundant seeds of *Chenopodium* and other taxa that might be expected to grow in a dry, scantily vegetated environment.

One of the unique insect fossils from this unit is a pronotum of the lace bug *Derephysia foliaceae* (Fallén) (Heteroptera: Tingidae) (Fig. 3c). This species was found only recently in North America (Lattin 1987). It has been collected in alpine meadows in western Oregon. The fossil find shows that this species was probably distributed through Beringia during the late Pleistocene, and this is the time and the route for its most recent arrival in western North America. Furthermore, its occurrence today in alpine meadows is intriguing, because such meadows may be the one habitat that comes closest to mimicking the extinct steppe-like habitat that we believe existed over parts of Beringia during the late Pleistocene (Guthrie 1990).

Central Yukon. The Mayo Indian Village assemblage (MV, Table 2; site 10, Fig. 1), ¹⁴C dated at 26.9 ka B.P., is also comprised of fossils deposited as detritus in a river. Its taxa do not display the obvious incongruities of the Rock River and Upper Porcupine assemblages and probably, like the associated plant fossils, represent a time when climate was too cold for forests in the region. Aside from this, the assemblage is of limited entomological interest because of its low diversity. Though the diversity of insect fossil assemblages can be expected to be partly a function of climatic severity, it does not follow that all samples from times known to be severely cold will be equally impoverished. For example, a fossil fauna from Alaska (Eva Creek : EC, Table 2; site E, Fig. 1), is much richer in species than the Mayo Indian Village fauna, but represents a time when climate was equally cold and limiting (Matthews 1968). The higher diversity probably results from the fact that the Eva Creek sediments represent a greater number of local habitats or biotopes than Mayo Indian Village beds.

The carabid subgenus *Cryobius* contains a number of very similar species that are the predominant ground beetles in arctic regions (Ball 1963, 1966). Fossils of this group occur in almost every insect assemblage from the Yukon and Alaska. The diversity of species is particularly high at Alaskan sites, such as the late Wisconsinan Eva Creek sample

(EC, Table 2), and the 12 ka B.P. Cape Deceit fauna (Matthews 1974). Eva Creek fossils accumulated in a different manner than most of the fossils in assemblages from the Yukon. However, this difference probably is not the complete explanation for the difference in diversity of *Cryobius* at Yukon and Alaskan sites. During glacial periods, the Yukon was a cul-de-sac for dispersing organisms. The unglaciated parts of the Yukon are predominantly upland. In contrast, unglaciated landscapes in Alaska were more varied, signifying a greater diversity of tundra-like environments than existed in the Yukon. This distinction may also explain other differences between Alaskan and Yukon late Wisconsinan faunas.

Carcass Samples. Several fossil insect faunas from the Yukon and adjacent Alaska are associated with the remains of Pleistocene mammals. In one instance, the fossils are in the sediments containing bones of a mammoth which, according to ^{14}C dating, likely died of old age more than 39 900 years ago. Abundant fly puparia and the presence of fragments of carrion feeders such as *Silpha lapponica* show that the carcass was available for scavenging for some time after death of the old mammoth. In contrast, none of the insects from the famous mid-Wisconsinan "Blue Babe" *Bison* (Guthrie 1990) were carrion feeders, supporting other evidence that shows the animal died in winter and was buried and frozen prior to the following summer. Other insect faunas have been recovered from the cranial cavity of a bison which was believed to have drowned in the lake occupying Old Crow basin 12.1 ka B.P.

Archaeological sites have also yielded informative insect faunas, some sites providing very rich assemblages that include elements of the fauna that normally are rare. The only such site in the Yukon at which insects have been studied is Bluefish Cave in the Old Crow region (Cinq-Mars 1979). The fossils in that small assemblage appear to indicate the same type of arid cold conditions that are suggested by the "mammoth fauna". One of the dominant taxa is the byrrhid *Morychus* sp., which in east Siberia is considered an indicator of steppe conditions. Along with *Morychus* the Bluefish Cave fauna included remains of the weevil *Vitavitus thulius*, another beetle typical of very dry sites, such as fell-field, today (Anderson 1997). It probably inhabited a type of steppe-meadow during the late Pleistocene. As mentioned earlier, numerous ^{14}C dates on bones from the caves (J. Cinq-Mars, pers. comm. 1994) show that the members of the complex "mammoth fauna" actually did live together in East Beringia. The small insect fauna associated with the bones is also of the type expected of a cold dry steppe-like site.

Mid-Wisconsinan Assemblages. The mid-Wisconsinan covers the interval of time from about 80 ka B.P. to a little less than 30 ka B.P. It was a time of variable climate. Overall, it was warmer than during the previous and following (late Wisconsinan) cold intervals, but seldom, if at any time, as warm as the present and certainly not as warm as the last interglacial. The variability of climate over the 50 000 years of this interval has resulted in distinctly different and rich fossil insect faunas and floras. Some of these faunas are among the most taxonomically diverse seen from any Quaternary site in the Yukon or Alaska.

Ch'ijee's Bluff. Ch'ijee's bluff (C2, Table 2; site 4, Fig. 1) is an important fossil locality near Old Crow (Fig. 2). It has yielded important palaeoenvironmental information including a number of rich fossil insect assemblages. Some of these come from an autochthonous peat of probable mid-Wisconsinan age (e.g. approximately 60 ka B.P.) (Matthews et al. 1990b). Among a number of fossils, it contains the distinctive caudal plates of larvae of *Ctenicera sjaeandica*, an elaterid beetle. Such fossils of immature insects, especially the thickly sclerotized parts, occur in a few Yukon insect assemblages.

Upper Porcupine Locality. One of the richest fossil insect assemblages from the Yukon comes from a section on the Upper Porcupine River in the Bell Basin (UP, Table 2; Fig. 1, site 6) dated at approximately 38 ka B.P. As with many of the assemblages discussed here, the fossils are allochthonous, having accumulated in river sediments. According to both insect and plant macrofossils (Matthews unpublished data), the environment at the time of deposition was a spruce parkland with numerous dry treeless openings. Although the dry, treeless openings were not true tundra, they may have harboured a number of tundra insects. Some of them, e.g. noctuid moths, have rarely been seen as fossils (Fig. 3e, f).

Another unique fossil from this assemblage represents the fly *Delia hudsonica* Griffiths (Anthomyiidae). This find in particular is interesting both because it shows that this species existed in Beringia as part of the Beringian fauna, well west of its present known limit (Griffiths 1993), but also because of the unusual nature of the fossils. The fossil consists of a “male hypopygium with gonostyli and mesolobus well preserved” (G.C.D. Griffiths, pers. comm. 1993). Preservation of such delicate fossils is rare in most Yukon assemblages, but not the ones from the Upper Porcupine locality. For example, in spite of the fact that the deposits are water-lain, some of the fossils are articulated—even possessing antennal fragments, while others, such as some of the weevils, still possess the scales which clothe the animal in life. For example, while weevil fossils are common in Yukon and Alaskan Pleistocene faunas, the fossils seldom preserve the delicate scales that often clothe weevils. Many specimens from the UP assemblage possess such scales.

Hungry Creek. Another relatively rich mid-Wisconsinan insect assemblage from farther south in the Yukon comes from the Hungry Creek section (HC, Table 2; site 9, Fig. 1). The fossiliferous sediments have been variously referred to a mid-Wisconsinan interstadial and the last interglacial, a difference of up to 90 000 years. All that is known for certain is that they are definitely older than 39 900 years (Hughes et al. 1981) and hence clearly not of late Wisconsinan full-glacial age.

The HC fossils come from what appear to be deltaic sediments deposited near the shore of a large lake; consequently, the fossil assemblage is diverse, representing many different biotopes. It contains a mixture of arctic and boreal forms, much like the Upper Porcupine locality.

Presence of fossils of arctic insects does not rule out the possibility that climate was warmer than present. It probably means only that open, well drained sites were abundant, unlike present boreal forest. Such conditions might be promoted by a climate warm enough to cause significant degradation of permafrost. Fossils of beetles such as *Chlaenius niger*, *Notiophilus sylvaticus*, *Gyrinus*, *Syntomium*, *Micropeplus laticollis*, *Hylobius*, and *Carphoborus* in the HC assemblage indicate strongly that climate was as warm or warmer than at present. The fact that climate can warm drastically yet habitats still persist that are suitable for arctic insects is perhaps a clue as to why some Coleoptera have evolved so slowly. Even during periods when regional climate was unfavourable, almost any area would have contained a few sites suitable for survival of species not otherwise expected to occur in the region. Of course this would not be the case for phytophagous insects that were linked to a particular plant. One might expect to see evidence of evolution within those groups, even during the Quaternary.

Fossils of the carabid beetle *Notiophilus sylvaticus* at Hungry Creek are a great surprise. Today, this distinctive species has a coastal distribution, but ascends to alpine sites (Lindroth 1961–69; Lindroth 1969). It probably disappeared from the central Yukon as a result of late Pleistocene climate. The late Pleistocene with its severe climate was undoubtedly a severe

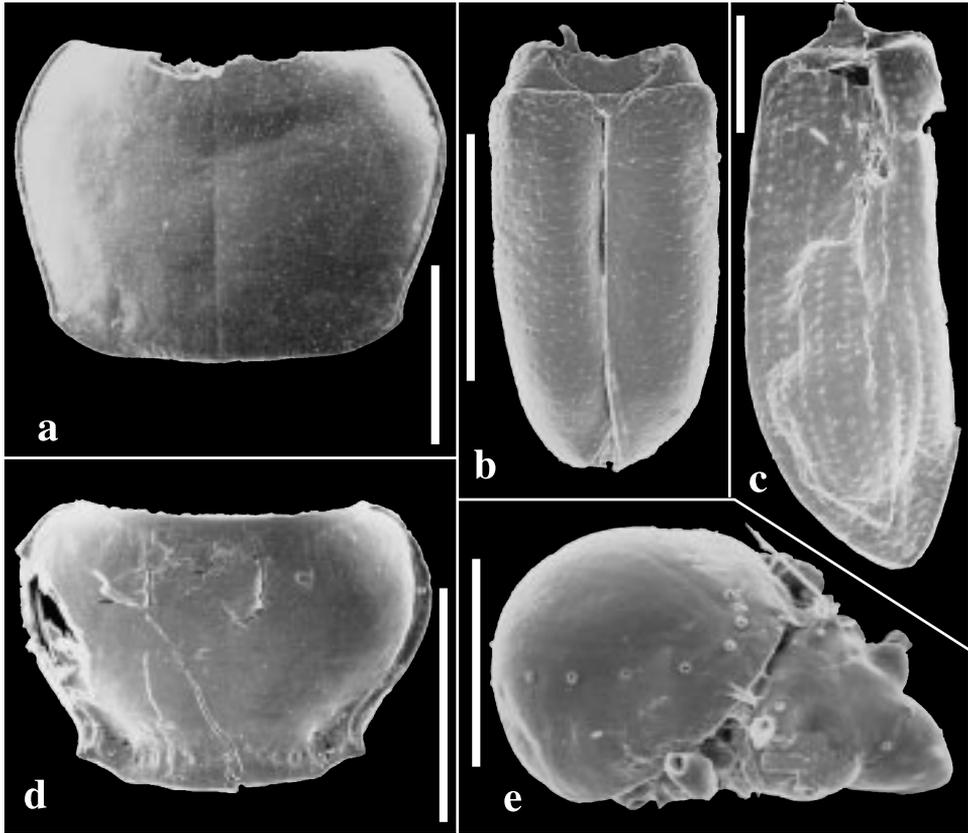


FIG. 4. Selected arthropod fossils from the interglacial beds at Ch'ijee's Bluff (site 4, Fig. 1). a, Pronotum of *Bradycellus lecontei* Csiki (Coleoptera: Carabidae) (GSC-98847)—the small white dots on the pronotal surface mark post-mortal pits that characterize the degradation of insect cuticle; b, Fused elytra of the bark beetle *Pityophthorus opaculus* LeConte (Coleoptera: Scolytidae); c, Right elytron from *Phloesinus pini* (?) Swaine (Coleoptera: Scolytidae); d, Pronotum of the beetle *Bembidion quadrimaculatum* LeConte (Coleoptera: Carabidae); e, Nearly complete individual of an oribatid mite, *Epidamaeus* cf. *tenuissimus* Hammer (Acari: Damaeidae) (GSC-98844). Scale bars 0.5 mm except e, 0.25 mm.

bottleneck to survival in Beringia of many insects, perhaps even more of a threat than warm climate was for tundra species. However, as Guthrie (1990) has shown using mammals, late Pleistocene Beringia was not as uniformly bleak and unproductive as some authors have suggested.

Last Interglacial

Ch'ijee's Bluff. Only one sample of all of those from the northern Yukon is unequivocally of the last interglacial (C1, Table 2; site 4, Fig. 1), i.e. approximately 125 ka B.P. in age. It comes from the same Ch'ijee's Bluff mentioned previously (Matthews et al. 1990a) and shown in Fig. 2. We know the age of the critical beds so precisely because of the combination of ^{14}C dates and the fact that they are underlain by Old Crow tephra, a volcanic ash whose date of eruption pre-dates the last interglacial by only several tens of thousands of years. Thus, by default, the only time that the C1 assemblage could represent is the peak of the last interglacial.

The C1 fauna is quite diverse. A few of the fossils are shown in Fig. 4. In contrast to other rich faunas like Upper Porcupine and Hungry Creek, none of the beetle species from the Ch'ijee's Bluff interglacial deposits is today an obligate tundra inhabitant. Moreover, some of these species now have northern limits well south of the site (Fig. 5). These are the ways in which true interglacial insect faunas from the Yukon can be expected to differ from those of mid-Wisconsinan age.

Revenue Creek. Another possible interglacial site is located in the southern Yukon near Carmacks (RC, Table 2; site 11, Fig. 1). Fossils come from the base of a 13 m placer-mine exposure comprising approximately 3 m of fluvial deposits. The age of the RC beds is not known with as much certainty as the Ch'ijee's C1 interglacial beds; we cannot unequivocally state that RC is interglacial; however, limited evidence suggests they are about the same age (L. Jackson, pers. comm. 1995). Because the RC site is much farther south than Ch'ijee's Bluff, well within the boreal forest, its fossils are less valuable for showing response to climatic warming than the more northern Ch'ijee's Bluff site, which is presently situated very near northern treeline. Indeed, unlike the Ch'ijee's C1 assemblage, all of the insects from the RC site live in the Carmacks area today.

The combined plant and insect fossil evidence from Revenue Creek suggests that the environment, at the time of deposition, was a spruce forest with dry treeless openings. The assemblage contains insect fossils of scolytids and bostrichids as well as many specimens of the forest-leaf-litter mite *Cepheus*. The insect fossil assemblage contains 2 tundra ground beetles, *Pterostichus (Cryobius) caribou* and *Pterostichus (Cryobius) nivalis*. Rather than posing a special interpretational problem, they probably indicate, as for the Hungry Creek assemblage, that open sites superficially similar to tundra existed within the forests of the time (A. Telka 1995: unpublished macrofossil report MRPT 94-108).

Late-Tertiary Faunas. Except for unusually rich assemblages such as the one from the Upper Porcupine locality or the warm, interglacial fauna from Ch'ijee's Bluff, fossil insect assemblages from the Yukon tend to be very similar to one another. Nearly all of them contain abundant fossils of carabids, chiefly *Pterostichus* and *Amara*, an abundance of omaliine staphylinids (2 to 3 genera), some byrrhids and dytiscids and many fragments of weevils, most of which represent some combination of the genera *Lepidophorus*, *Lepyrus* and *Vitavitus*. In contrast, late Tertiary assemblages, even at sites well north of the Yukon, are dramatically richer. As well they contain a few extinct species and many of the taxa do not occur today in the Yukon. A few are not even resident in North America today.

To date, late Tertiary beds at the Bluefish exposure (B2, Table 3; site 5, Fig. 1) in the northern Yukon, are the only ones that have yielded insect fossils. The age is not known exactly, but is probably Pliocene (Matthews and Ovenden 1990; Matthews unpublished) (see below).

A number of late Tertiary sites in Alaska and the Canadian Northwest Territories have insect fossils. Some of them, such as Lost Chicken, are so close to the Yukon that they can be taken to represent Yukon faunas. Others, such as Meighen Island and Kap København (Fig. 1), are much more distant, but even so, their faunas provide valuable hints on the probable character of the Yukon fauna during the late Tertiary.

Table 3 is modified from a recent review of Tertiary floras and insect faunas in the North American arctic (Matthews unpublished). For additional details on the sites listed below see that review. Appendix 2 of that paper is the most up-to-date list of arthropod fossils from late Tertiary sites in Alaska, the Yukon and arctic Canada.

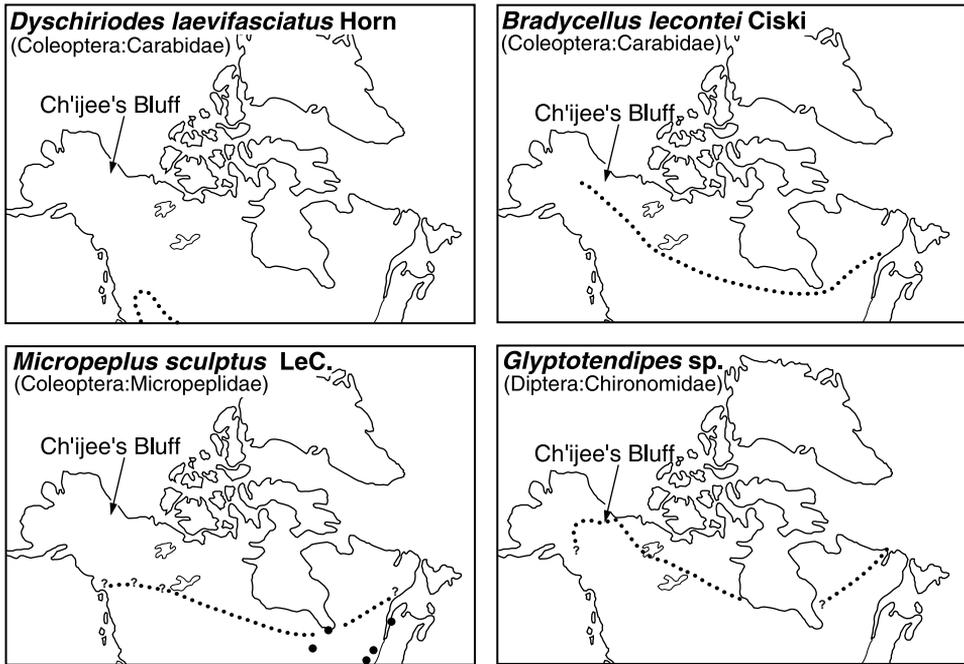


FIG. 5. Present distribution of some of the insects from the interglacial beds at Ch'ijee's Bluff (site 4, Fig. 1). Although these four taxa form only a small part of the rich assemblage, they show, by their present northern limit (dashed line), that the climate at the time was likely warmer than at present (see Matthews et al. 1990a).

Cape Deceit Formation. According to recent evaluations (McDougall 1995), the Cape Deceit fauna (CD, Table 3; site A, Fig. 1) from the Cape Deceit Formation at Cape Deceit in western Alaska is approximately 1.8 million years old. This places it in the earliest part of the Pleistocene, within an interval that was mostly as warm or warmer than today (Repenning and Brouwers 1992). The Cape Deceit Formation insect fauna is extremely diverse, probably due to the unusually large volumes of sediment that were sampled and processed. For the most part, it represents low-arctic tundra similar to that at the site today.

The Cape Deceit fauna is one half to nearly a million years younger than the Kap København fauna from northern Greenland (Böcher 1995). Both represent treeline sites, but the Cape Deceit fauna contains no obvious extinct species. The only potential evidence that the Coleoptera of that region have evolved over the last 1.8 million years is that fossils of one of the staphylinid beetles show slightly different elytral proportions compared to their modern counterparts, a difference related to non-functional flight wings being slightly longer in the fossils (Matthews 1974).

Another intriguing characteristic of the Cape Deceit fauna is that it lacks fossils of the weevil *Lepidophorus*, one of the most common genera in late Pleistocene assemblages. This absence may mean that the species did not evolve and become a common weevil of northern dry sites until after the early Pleistocene. The hypothesis needs testing, because if confirmed it would make fossils of *L. lineaticollis* very important for dating early Quaternary deposits. Of interest is that despite the thousands of fossils recovered at Kap København, Böcher (1995) does not record the presence of *Lepidophorus*. It is true that some of the other late Tertiary assemblages from Alaska and the Northwest Territories contain the odd head or

elytral fragment of *Lepidophorus* (Matthews unpublished), but none of the fossils is clearly from *L. lineaticollis*.

What would an early Pleistocene insect fauna from the Yukon look like? It would probably contain some of the species seen at Cape Deceit though be much less diverse. Most, if not all, of the Yukon at 1.8 ma B.P. was probably densely forested; whereas, some lowland tundra existed in Alaska, at least near the Bering land bridge and possibly also along the arctic coast. This difference would have caused early Pleistocene faunas in the Yukon to deviate even more from those at sites in western Alaska.

Lost Chicken. As indicated above, the Lost Chicken site (LC, Table 3; Fig. 1, site F) is located so close to the Yukon that its fossils essentially constitute a Yukon fauna. As such it is a valuable window on the character of the Yukon insect fauna 3 million years ago during the early part of the late Pliocene. At that time the central Yukon would have been part of a latitudinally broad boreal zone stretching from a southern limit south of the central Yukon to at least 80°N on the Arctic Islands (at that time much less insular) where treeline occurred (Matthews and Oveden 1990; Matthews unpublished). The boreal forest in central Yukon 3 ma B.P. was much richer in plant species than today. Instead of the current 2 species of spruce, *Larix laricina*, *Pinus contorta* and *Abies* (at higher elevations), the lowland coniferous flora consisted of a 2-needle pine, probably from a species similar to *P. contorta*, a 5-needle pine more closely related to some now growing in Asia than to any in North America, lowland *Abies*, 2 types of spruce and an extinct species of *Larix*. Fossils of the latter (*L. groenlandi* Bennike) have been found at many arctic sites of late Tertiary age. Among the flowering plants were many taxa that occur in the Yukon today in addition to extinct plants such as a species very closely related to *Myrica gale*, 2 extinct arums, the closest relative of one of which now grows in tropical regions, and other plants such as elderberry (*Sambucus*) that were well north of their current range.

The presence of plants like elderberry and fossils of unusual species of *Sphagnum* is evidence that climate was not as continental in the late Tertiary as it is at present. The reason for this is that the mountain barrier between the Yukon and the Pacific was hundreds of metres lower in the late Pliocene (Plafker and Addicott 1976; Plafker et al. 1992).

The LC insect fauna is rich. It is made up mostly of Coleoptera, but includes a few fossils of tingids and cicadellids, and many oribatid mites (Matthews et al. unpublished 1). Several of the LC insect fossils provide hints as to the character of the Yukon fauna during the late Pliocene.

One of these represents the nearly blind, soil-inhabiting weevil *Otibazo*. Today the genus is found only in Japan. Its presence at Lost Chicken shows that we should expect the middle-Pliocene fauna of the Yukon to have included a few taxa that are now restricted to the Palaearctic region—perhaps even *Otibazo*. Other sites listed in Table 3 support this conclusion, because most of them are north and east of the Yukon and also contain fossils of Palaearctic plants and/or insects.

Another significant fossil from Lost Chicken represents an extinct species closely related to the contemporary subarctic carabid *Asaphidion yukonense*. The Lost Chicken fossil elytron (*A. yukonense* type A, Table 3; Fig. 3b) clearly shows the bare (impunctate) patches that characterize the extant species (Lindroth 1961–1969) but the patches are less developed and elytral microsculpture better developed than in the extant species. Fossils similar to *Asaphidion yukonense* occur at other late Tertiary sites from the arctic but some of those are even more primitive with respect to elytral characteristics than the Lost Chicken species. Though the relationships of these extinct *Asaphidion* species and *A. yukonense* could

be interpreted in various ways, one alternative is to consider them as stages in the evolution of a single lineage. If so, the fossils not only are of interest because of what they show about the rate of evolution of some carabids; they also have value for dating and correlation—the traditional geological use of fossils.

Several well preserved elytra and head fragments from Lost Chicken represent an extinct species closely related to the mesic-tundra carabid *Diacheila polita*. Apparently the same species occurs in the Kap København fauna in northern Greenland (Böcher 1995). Böcher has described them as *Diacheila matthewsi*. *D. matthewsi* occurs at a number of Tertiary sites, including the Niguanak site on the northern Alaskan coast (see below and Matthews unpublished); hence it almost certainly once lived in the Yukon. The Lost Chicken record of *D. matthewsi* is significant because the associated plant fossils indicate that the species lived within dense forest, quite unlike its modern counterpart. Similar examples of contemporary tundra beetles having close extinct relatives that occupied lowland forests (e.g. *Carabus* cf. *truncaticollis* from Lava Camp in western Alaska: Matthews 1979) hints at the origin of at least some elements of the modern tundra insect fauna. Other elements likely had alpine origins.

Oribatid mites from Lost Chicken have been studied by Alexander Druk (Matthews et al. unpublished 1). They represent an unusual fauna quite different from any that exists today in the present subarctic region.

Bluefish. The Bluefish site (B2, Table 3; site 5, Fig. 1) has yielded extinct plants as well as other plants such as *Sambucus* and *Brasenia* that do not occur in the Yukon today. These plant fossils establish that the site is late Tertiary in age, but also that it represents a climate much less continental and most likely warmer than at present.

The fossil arthropod assemblage from the Bluefish Tertiary beds has a distinctly more modern cast than the 3 ma B.P. Lost Chicken fauna. In fact, the only insect fossils that suggest a pre-Quaternary age are an elytron similar to that of the carabid beetle *Notiophilus aeneus*, a species now confined to the eastern part of North America, and a pronotal fragment similar to pronota of the extinct hydrophilid beetle *Helophorus meighensis* (Matthews 1976).

Niguanak. Like Lost Chicken, the Niguanak site (Ng, Table 3; site D, Fig. 1) in Alaska on the North Slope of the Brooks Range, is also close enough to the Yukon to serve as a proxy for the late Tertiary northern Yukon fauna. The plant fossils include a 5-needle pine that may have been similar to the Asian shrub pine, *Pinus pumila*. The same pine species probably grew throughout the present North American arctic region during the late Tertiary (see below and Matthews unpublished).

The Niguanak fauna is not precisely dated, but it is certainly no younger than late Pliocene, and may be as old as the early Pliocene. Associated plant fossils provide us with a hint of what the Pliocene might have been like in the northernmost Yukon. Clearly, it was forested (though perhaps with open forests in some areas), and the forests probably included a number of conifers not found in contemporary boreal forest, among them 2 or more species of *Tsuga* (R. Nelson, pers. comm. 1989). That climate was both warmer and less continental than at present is suggested by fossils of *Lonicera* (honeysuckle).

Niguanak insect fossils remain to be studied in detail, but preliminary examination reveals an unusual fauna. For example, it contains the leafhopper *Deltocephalus*, the mesostigmatid mite *Trachytes*, the extinct carabid *Diacheila matthewsi* (Böcher 1995) and some specimens of the hydrophilid genus *Helophorus* that probably represent an Asian species group. This last characteristic suggests that when the Niguanak fauna is better studied

it will exhibit some of the same Asian affinities as seen in other late Tertiary insect faunas and floras.

Taglu and Kumak Boreholes, Mackenzie Delta. In 1992 the Geological Survey of Canada with industry support drilled 3 geotechnical boreholes in the Mackenzie Delta. The sediments of each have been sampled and analyzed for arthropod and plant fossils. Some of the samples, though small by comparison with most of the others discussed here, contain an abundance of fossils (not listed in Table 3; see “Fossils” section of the multimedia CD presentation of the Mackenzie Delta Borehole Project: Dallimore and Matthews 1997).

Two of the boreholes, Kumak and Taglu, extend into the late Tertiary and therefore provide additional hints on the Tertiary fauna of the adjacent areas of the northern Yukon. The plant fossils show, like other sites, that late Tertiary forests, though coniferous, were more diverse than at present. The Taglu borehole contains fossils of *Larix*, *Abies*, *Picea* and both 2-needle and 5-needle pines. According to the Taglu borehole sequence, the extinct carabid *Diacheila matthewsi* Böcher probably lived in the delta region during the late Pliocene. Because fossils of this species have been found at such widely spaced sites as Lost Chicken and Kap København, this is really not surprising. What is more remarkable is a single elytron of the beetle *Pteroloma* (Agyrtidae) from the Taglu borehole. This taxon has not been encountered before in Alaskan or Yukon assemblages and it is not a resident of the modern fauna. Böcher (1995) records the boreo-alpine European species *P. forsstromii* from the Kap København beds in northern Greenland (see below). The Taglu fossil is not well enough preserved for a specific determination.

Meighen Island. Meighen Island at 80°N is located so far north of the Yukon Territory that one might wonder why its fauna bears mentioning in a book on Yukon insects. But the Meighen Island sites (Mg, Table 3; site G, Fig. 1) are reliably dated at about 3 ma (Matthews et al. unpublished 2; Fyles et al. 1991), which makes them about the same age as the Lost Chicken site. And since Meighen Island was very near the northern limit of trees 3 million years ago, it and the Lost Chicken site delimit a boreal zone much broader latitudinally than today. South-to-north climatic and species-diversity gradients must have been much less steep than now, which means that virtually all of what is today the northern Yukon probably had an insect fauna similar to that at Lost Chicken.

Meighen Island deposits are part of the widespread sedimentary unit known as the Beaufort Formation (Fyles 1990). Nearly all Beaufort deposits contain plant and insect fossils, but those on Meighen Island are especially rich. To date, approximately 215 arthropod taxa have been identified. Even though these taxa are predominantly Coleoptera, the assemblage also includes fossils of Hymenoptera, Cicadellidae and other Homoptera, Diptera, Trichoptera, Heteroptera and oribatid mites.

Many of the insects and oribatid mites from Meighen Island display biogeographical affinities similar to those shown by plants, e.g. an abundance of taxa closely related to present-day subarctic and low-arctic tundra species with an admixture of fossils whose extant relatives occur now only in eastern North America or in east Asia. One of the leafhoppers—*Athysanella*—is an extreme example of Asian affinities because its closest living relative is now found in the Himalayan region (K.G.A. Hamilton, pers. comm. 1972).

Beaver Peat, Strathcona Fiord, Ellesmere Island. Although the Meighen Island arthropod flora is one of the richest yet recovered from northern Canada, the so-called “Beaver Peat site” (SF, Table 3; Fig. 1, site H) at Strathcona Fiord on Ellesmere Island offers a more

complete picture of the total biota because in addition to arthropods and plants and even a few molluscan fossils, it also includes fossil vertebrates. The site is positioned high on a valley side, probably higher in elevation than at the time of deposition. It pre-dates the formation of the existing system of fiords, inlets and passages of Ellesmere Island. Although its exact age is not known, some of the plant fossils and vertebrate fossils point to its being slightly older than Meighen Island deposits, e.g. older than 3.3 ma B.P., but clearly younger than the late Miocene at 5 ma B.P.

The Beaver Peat *sensu stricto* is a mass of semi-autochthonous peat, compact enough to form a vertical wall within the alluvial deposit. Other organic deposits, probably of about the same age but not deposited in the same manner, occur within a kilometre. When their fossils are combined with those from the Beaver Peat, they provide a very detailed picture of the flora and fauna (arthropod and vertebrate) of Ellesmere Island during the late Tertiary.

Although the macrofossil and arthropod assemblages from the several Beaver Peat sites include a few species that are now found far to the south, even south of the boreal-forest zone, the overall composition of the flora and fauna is similar to that of a forest-tundra site. Among the beetle fossils are several that are common in tundra regions, such as the ground beetle *Carabus truncaticollis*. Treeline may have crossed Ellesmere Island at the time of deposition, representing a significantly warmer climate than at present.

Like many late Tertiary organic sites, those associated with the Beaver Peat contain oribatid mites and one of them, *Proteremaeus macleani*, is a species previously known only from Asia (Behan-Pelletier and Ryabini 1991). In Asia *P. macleani* is found in habitats dominated by *Pinus pumila*, and remarkably, one of the sites associated with the Beaver Peat contains seeds and leaves of *P. pumila* or a closely related (extinct?) species.

Some of the organic deposits associated with the Beaver Peat contain fossils of insects that are seldom seen in fossil assemblages. One particular pond deposit contains many specimens of whiteflies (Aleyrodidae). The same sediments also yielded a nearly complete specimen of the gamasid mite *Hypoaspis*. While such finds have little importance for predicting the composition of the Yukon fauna of the early Pliocene, they do show that rare deposits can provide a more diverse picture of a former arthropod fauna than most of those discussed here.

However, the Beaver Peat fauna does allow some potential characteristics of a Yukon fauna of the same age to be predicted. Like many of the others, including Lost Chicken, it has an Asian component. The same can be expected of a Yukon fauna of the same age, especially since the Bering land bridge was in existence at that time. Some of the Beaver Peat fossils, e.g. the small beetle *Micropeplus nelsoni*, also show that the early Pliocene Yukon fauna probably contained taxa whose modern counterparts occupy the mountains of the North American Pacific Northwest (Campbell 1989).

Kap København. The Kap København insect fauna (Böcher 1995) comes from the Kap København site (KK, Table 3; site 1, Fig. 1) in northernmost Greenland. Its estimated age is approximately 2–2.5 ma B.P. At the time of deposition regional treeline nearly reached the northern coast of Greenland (Bennike 1990). Much of the rest of Greenland and perhaps large areas of what are today the Arctic Islands of Canada probably were also forested, most likely with larches predominating. However, fossils from at least one site, on Ellesmere Island, slightly south of the latitude of Kap København, show that tundra did exist in some parts of the arctic (Fyles et al. 1997).

No arctic arthropod fauna has been treated in as much detail as the one from Kap København (Böcher 1995), and this will likely be so for years to come, making the Kap

København fauna a reference against which all others from the arctic are compared. An interesting aspect of the Kap København flora and fauna is that they postdate the first major glaciation in the arctic region. If repeated Northern-Hemisphere glaciation was one of the primary forces in the formation of the present-day impoverished fauna and flora, then we should expect the Kap København assemblages to be less diverse than those from older sites at the same latitude. Indeed, this appears to be so. The Beaufort Formation on Meighen Island is older than Kap København only by about 500 to 700 thousand years, but it pre-dates the first major glaciation in the arctic region. The environmental conditions on Meighen Island were probably similar to those at Kap København, so differences between the 2 faunas are probably due to the deleterious effects of the first glacial climatic event. The differences between the 2 faunas are subtle but exactly of the type expected. For example, one result of a climatic crisis such as regional cooling and glaciation would be depletion of faunal diversity. The Kap København fauna is slightly less diverse than that from Meighen Island. Some important groups, e.g. histerid beetles, are present on Meighen Island, but not at Kap København. Furthermore, the Meighen Island fauna appears more archaic, i.e. it has more fossils that presumably represent extinct species. Meighen Island, for example, contains several species of the genus *Carabus*, one of them probably extinct. No specimens of *Carabus* have been found at Kap København. The Kap København assemblages contain remains of the tiny beetle *Kalissus nitidus*. Fossils of *Kalissus* also occur on Meighen Island, but they are clearly not *K. nitidus* and probably represent an extinct species.

There are other distinctions (Böcher 1995), but these alone show that the Meighen Island assemblages have a more archaic character than those from Kap København. In other words, the arctic insect fauna, though quite diverse compared to present at about 2–2.5 ma B.P., had already suffered some depletion as a result of the first glaciation of the region. Even though much of the northern Yukon was never glaciated, we can expect that the climatic changes associated with the initial glacial events also had a depleting effect on the late Pliocene Yukon fauna.

The Yukon Insect Fauna and the History of Beringia

A Reconstructed Yukon Pliocene Fauna. The faunas mentioned above allow us to make some reasoned assessments of the character of the Yukon insect fauna during the late Pliocene. First, it is clear that 3 ma ago the Yukon was within a broad boreal zone stretching from near 80°N to south of 65°N. It was characterized by a much richer coniferous and angiosperm flora than exists in the boreal region today, and because the mountain barriers to the west were significantly lower, climate was not only warmer but much less continental.

Judging from sites like Lost Chicken, the central Yukon would have had an insect fauna made up of many of the genera seen in the boreal region today, in addition to other species whose present relatives are today restricted either to the more southern parts of North America, east and west, or to eastern Asia. Absence of permafrost would have promoted a much richer soil fauna.

At 3 ma B.P. there would have been no lowland tundra in the Yukon and the only areas that might have supported a nascent tundra fauna would have been some upland areas, but it is doubtful that many of these uplands were high enough to develop significant tracts of alpine tundra. Thus the present tundra fauna did not exist, though the progenitors of some current tundra species probably lived either in the Pliocene forests or in alpine areas. The extinct beetle *Diacheila matthewsi* is an example of a forest species that even in the Pliocene

was living near sites that mimic present-day tundra, and its probable extant sister species (or descendant) is currently found almost exclusively on tundra.

In many respects the rich Pliocene boreal forests growing in central and northern Yukon represent the “true” boreal forest—a biome in which plant and animal communities had developed over millions of years. The start of major Northern Hemisphere glaciations, about 2.5 million years ago, severely disrupted the biome, causing extinction of some species and radically changing the distributions of others. The disappearance of a connection with Asia only a short time before the first glacial events must have placed further strain on the fauna and flora of the Yukon and Alaska (see below). Warm periods occurred after the initial down-turn of climate—as witnessed by Kap København—but they were brief compared to the long time over which the biome had developed, and by the latter half of the Pleistocene drastic climatic changes occurred with a frequency of only 100 000 years or less. However, it would be wrong to assume that the diversity of the East Beringian fauna (which includes the Yukon) declined by an equal amount during each cold phase. Judging from sites like Cape Deceit, the change to an essentially modern fauna was complete by 1.8 ma B.P. Thus even as early as 1.8 million years ago, the Yukon insect fauna had become a pale imitation of what existed there during the late Pliocene.

The only hint that the elements of the original boreal fauna might have persisted longer comes from the boreholes in the Mackenzie Delta which suggest that larch (*Larix*) may have been more common when forests reached that area during the Pleistocene. Unlike modern boreal forest, some of these treeline forests in the Mackenzie Delta region (and possibly the northern Yukon) may even have contained *Abies* (Matthews and Telka 1997). If such fossils are proxies for other as yet undocumented differences in Pleistocene forests, then we must assume that the insect fauna of the time also differed from that of the present.

Beringia—Its Early History. The Yukon is currently the eastern end of Beringia—loosely defined as the land and shelf areas stretching between the Mackenzie River on the east and the Lena River on the west. While it is well known that the Bering land bridge between Alaska and Siberia existed up until the Pliocene and intermittently thereafter in response to eustatic changes, our knowledge of what the Pliocene land bridge was like has been vague. Entomologists seeking to explain distributional and taxonomic patterns in the Holarctic region have simply assumed that the land bridge was in existence and that it must have been suitable for the transfer of the organisms under study, regardless of their probable habitat requirements.

Some of the late Tertiary faunas and floras mentioned above allow us to be more precise in defining the character of Beringia at various times of the late Tertiary. For example, though it is remote from Beringia today, the Beaufort Formation flora and fauna from Meighen Island adds to our knowledge of the character of the late Pliocene land-bridge environment. Hopkins et al. (1971) postulated that cool climates and treeless vegetation existed on the land bridge in late Miocene time (Hopkins et al. 1971), creating a barrier to migration of forest forms. This filter was proposed to explain what appeared in 1971 to be distinct and long-standing differences between the arboreal floras on either side of the Bering land bridge. But fossils, particularly macrofossils, from Tertiary sites in Alaska and many of the Canadian sites discussed here have refuted that hypothesis. The fossils show that diverse coniferous forests existed as far north as 70°N during the mid-Miocene, and that similar forests existed on the eastern and western doorsteps to the land bridge as late as 3 ma B.P., making it difficult to argue that a tundra barrier blocked continuity of Tertiary forests between Siberia and Alaska. The Bering land bridge existed as a dispersal corridor for forest insects until it was

breached by a seaway in the Pliocene. Thereafter, the land bridge was in place intermittently in response to lowered sea level during periods of cold climate, meaning that the forests on the land bridge just before the final breach 3 million years ago were the last ones to occupy the land bridge, i.e. it was the last time for exchange of obligate forest insects between East Asia and Alaska and the Yukon.

Pliocene forests on the Bering land bridge may have resembled those which grew at the Lost Chicken site. If so, the Pliocene Bering land bridge contained not only spruce and larch, but also 2- and 5-needle pines and possibly even *Abies*. They would have been the type of forests that Russian botanists class as “dark coniferous”. In Siberia the present northern limit of dark coniferous forests is far south of the land-bridge region. According to some workers (Laukhin 1993a), light coniferous forest, dominated by larch, first appeared in eastern Siberia in the latter part of the early Pliocene, prior to the generally accepted time of formation of a major seaway across Beringia. Thus the breach in the land bridge, though it almost certainly interrupted continuity of forests, may only have punctuated a partitioning of the Holarctic coniferous realm that was already well underway by the late Pliocene. Evolution of the North American spruces and some of the other northern North American species that currently have no representatives in East Siberia may have started well before a seaway developed with a retreat of the dark coniferous realm to the southwest in Asia and to the east in Alaska.

A corollary to the above conclusions concerning Pliocene forests on the Bering land bridge is that tundra did not start to form in that region (or in the Yukon) until after the land bridge had been breached, possibly not until about 2.5 ma B.P. (Repenning and Brouwers 1992). Contrary to statements in some reviews (Laukhin 1993b), no definite evidence exists from North American sites of a tundra phase at the Miocene/Pliocene boundary. Some Russian scientists believe tundra is indicated by pollen data from East Siberia, but plant macrofossils from both Russian and North American sites clearly suggest that during Miocene/Pliocene time (about 5 ma B.P.), eastern Siberia and Alaska possessed diverse conifer forests.

Mid-Miocene floras from the Canadian arctic (about 16 ma B.P.), especially those from northern and southern Banks Island (Fyles et al. 1994; Matthews unpublished) contain northern hardwood plants such as *Juglans* and *Liriodendron*. Mid-Miocene floras from approximately the same latitude as the Bering land bridge contain even more such species (e.g. *Quercus*) (Leopold and Liu 1994; White and Ager 1994). Clearly this implies that the land bridge itself was probably suitable for more temperate-adapted insects than the boreal forms that would have used the land bridge during the Pliocene. The Yukon would have been one of the regions in which these temperate insects lived, even though we have very little fossil evidence of their presence.

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This report is dedicated to the memory of Owen Hughes, a colleague and friend of all who have worked in the northern Yukon and perhaps the last true naturalist to work on the bluffs of Yukon rivers.

The study of fossil insects from the Northern Yukon has been facilitated by the fact that the Old Crow region has been the site of intensive palaeoenvironmental and archaeological studies. Two major research projects, the Northern Yukon Research Program and the Yukon Refugium Project, were active during the decade of the 1970s and early 80s. Both projects had, as their principal objective, the discovery of early man sites. The last named project,

led by a remarkably innovative and curious scientist—R.E. Morlan (Canadian Museum of Civilization)—was designed to gather all information on environmental change in the northern Yukon, even if some of the information was of no immediate relevance to archaeological questions. Morlan's enlightened approach is responsible for much of what we report here. We also owe a debt of gratitude to our many colleagues at Agriculture Canada. Over the years they have shown great patience for people coming to them with bits and pieces of fossil insects.

References

- Anderson, P.M., P.J. Bartlein, L.B. Brubaker, K. Gajewski, and J.C. Ritchie. 1989. Modern analogs of late-Quaternary pollen spectra from the western interior of North America. *J. Biogeogr.* 16:573–596.
- Anderson, R.S. 1997. Curculionidea (excluding Scolytinae and Platypodinae) of the Yukon. pp. 523–562 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Ball, G.E. 1963. The distribution of the species of the beetle genus *Cryobius* (Coleoptera, Carabidae, *Pterostichus*): with special reference to the Bering Land Bridge and Pleistocene refugia. pp. 133–149 in J.L. Gressitt (Ed.), *Pacific Basin Biogeography*. Bishop Museum Press, Honolulu, Hawaii. 563 pp.
- . 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). *Opusc. ent.* 28:1–166.
- Bates, R.L. and J.A. Jackson. 1984. *Dictionary of Geological Terms*. Anchor Press/Doubleday, Garden City. 571 pp.
- Behan-Pelletier, V.M. and N.A. Ryabinin. 1991. Taxonomy and biogeography of *Proteremaeus* (Acari: Oribatida: Eremaeidae). *Can. Ent.* 123:559–565.
- Bennike, O. 1990. The Kap København Formation: stratigraphy and palaeobotany of a Plio-Pleistocene sequence in Peary Land, North Greenland. *Meddr Grønland* 23:1–85.
- Biske, S.F. and Yu.P. Baranova. 1984. Main paleogeographic features of Beringia in the pre-Quaternary Cenozoic. pp. 154–163 in V.L. Kontrimavichus (Ed.), *Beringia in the Cenozoic Era*. Oxonian Press, New Delhi, India. 724 pp.
- Blake, W., Jr. 1984. Geological Survey of Canada Radiocarbon dates XXIV. *Geol. Surv. Can. Pap.* 84(7):1–35.
- . 1987. Geological Survey of Canada Radiocarbon dates XXVI. *Geol. Surv. Can. Pap.* 86(7):1–60.
- Böcher, J. 1995. Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland. *Meddr Grønland* 33:1–82.
- Campbell, J.M. 1989. *Micropeplus nelsoni*, a new species from the Cascade Range of Washington (Coleoptera: Micropeplidae). *Coleopt. Bull.* 43:305–310.
- Cinq-Mars, J. 1979. Bluefish Cave I: A late Pleistocene eastern Beringian cave deposit in the northern Yukon. *Can. J. Archaeol.* 3:1–32.
- Coope, G.R. and J.A. Brophy. 1972. Late glacial environmental changes indicated by a Coleopteran succession from North Wales. *Boreas* 1:97–142.
- Cwynar, L.C. 1982. A late-Quaternary vegetation history from Hanging Lake, Northern Yukon. *Ecol. Monogr.* 52:1–24.
- Dallimore, S.R. and J.V. Matthews Jr. 1997. Overview of the Mackenzie Delta Borehole Project. in S.R. Dallimore and J.V. Matthews Jr. (Eds.), *Mackenzie Delta Borehole Project*. Compact Disc issued by the Geological Survey of Canada.
- Duk-Rodkin, A. and O.L. Hughes. 1994. Tertiary-Quaternary drainage of the pre-Glacial Mackenzie Basin. pp. 221–241 in T.A. Ager, J.M. White, and J.V. Matthews Jr. (Eds.), *Tertiary Quaternary Boundaries*. *Quaternary Int.* 22/23. 241 pp.
- Elias, S.A. 1994. *Quaternary Insects and their Environments*. Smithsonian Institution Press, Washington, D.C. 284 pp.
- Fyles, J.G. 1990. Beaufort Formation (Late Tertiary) as seen from Prince Patrick Island, Arctic Canada. *Arctic* 43:393–403.
- Fyles, J.G., L. Marincovich Jr., J.V. Matthews Jr., and R.W. Barendregt. 1991. Unique mollusc find in the Beaufort Formation (Pliocene) Meighen Island, Arctic Canada. *Current Res., Part B, Geol. Surv. Can. Pap.* 91-1B:105–111.
- Fyles, J.G., L.V. Hills, J.V. Matthews Jr., R.W. Barendregt, J. Baker, E. Irving, and H. Jetté. 1994. Ballast Brook and Beaufort Formations (Late Tertiary) on northern Banks Island, Arctic Canada. pp. 141–171 in T.A. Ager, J.M. White, and J.V. Matthews Jr. (Eds.), *Tertiary Quaternary Boundaries*. *Quaternary Int.* 22/23. 241 pp.
- Fyles, J.G., D.H. McNeil, J.V. Matthews Jr., R.W. Barendregt, L. Marincovich Jr., E. Brouwers, L.E. Ovensen, J. Bednarski, J. Baker, and E. Irving. 1997. Geology of Hvitland Beds (Late Pliocene), White Point Lowland, Ellesmere Island, Northwest Territories. *Geol. Surv. Can. Bull.* 512. in press.

- Golosova, L.D., A.Y. Druk, E. Karppinen, and S.V. Kiselyov. 1885. Subfossil oribatid mites (Acarina, Oribatei) of Northern Siberia. *Annls ent. fenn.* 51:3–18.
- Griffiths, G.C.D. 1993. Anthomyiidae. Flies of the Nearctic Region 8(2), No. 10. pp. 1417–1632.
- Guthrie, R.D. 1990. Frozen Fauna of the Mammoth Steppe. Univ. Chicago Press, Chicago. 323 pp.
- Hopkins, D.M., J.A. Wolfe, J.V. Matthews Jr., and M.L. Silberman. 1971. A Pliocene flora and insect fauna from the Bering Strait region. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 9:211–231.
- Hughes, O.L., C.R. Harington, J.J. Janssens, J.V. Matthews Jr., R.E. Morlan, N.W. Rutter, and C.E. Schweger. 1981. Upper Pleistocene stratigraphy, paleoecology, and archaeology of the northern Yukon interior, eastern Beringia, 1. Bonnet Plume Basin. *Arctic* 34:329–365.
- Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford Univ. Press, Menlo Park. 1008 pp.
- Hynes, H.B.N. 1988. Biogeography and origins of the North American stoneflies (Plecoptera). pp. 31–37 in J.A. Downes and D.H. Kavanaugh (Eds.), Origins of the North American Insect Fauna. *Mem. ent. Soc. Can.* 144. 168 pp.
- Jackson, L.E., Jr. in prep. Terrain Inventory and Quaternary History of the Carmacks Map Area. *Geol. Surv. Can. Bull.*
- Krivolutsky, D.A. and A.Y. Druk. 1986. Fossil oribatid mites. *A. Rev. Ent.* 31:533–545.
- Lafontaine, J.D. and D.M. Wood. 1988. A zoogeographic analysis of the Noctuidae (Lepidoptera) of Beringia, and some inferences about past Beringian habitats. pp. 109–123 in J.A. Downes and D.H. Kavanaugh (Eds.), Origins of the North American Insect Fauna. *Mem. ent. Soc. Can.* 144. 168 pp.
- Lattin, J.D. 1987. *Derphysia foliacea* (Fallén), a Tingidae new to North America (Hemiptera: Heteroptera). *Jl N.Y. ent. Soc.* 95:76–80.
- Laukhin, S.A. 1993a. Climatic changes in northeast Asia during the Pliocene-Pleistocene. Stratigraphy and Geological Correlation. English translation by *Interperiodica* 1(6):620–625.
- 1993b. Tertiary paleoclimates of Northeastern Asia. pp. 171–176 in E. Planderova, M. Konzalova, Z. Kvacek, V. Sitar, P. Snopkova, and D. Suballyova (Eds.), Paleofloristic and Paleoclimatic Changes during Cretaceous and Tertiary, Proceedings of an International Symposium. Geologicky Ustav Dionyza Stura, Bratislava.
- Leopold, E.B. and G. Liu. 1994. A long pollen sequence of Neogene age, Alaska Range. pp. 103–140 in T.A. Ager, J.M. White, and J.V. Matthews Jr. (Eds.), Tertiary Quaternary Boundaries. *Quaternary Int.* 22/23. 241 pp.
- Lindroth, C.H. 1961–69. The ground-beetles of Canada and Alaska, parts 1–6. *Opusc. ent. Suppl.* 20, 24, 29, 33, 34, 35. 1192 + XLVIII pp.
- 1969. An analysis of the carabid beetle fauna of the refugium. pp. 195–210 in T.N.V. Karlstrom and G.E. Ball (Eds.), The Kodiak Island Refugium: Its Geology, Flora, Fauna and History. Boreal Institute of North America, Edmonton, Alberta. 262 pp.
- Lowdon, J.A. and W. Blake Jr. 1979. Geological Survey of Canada Radiocarbon dates XIX. *Geol. Surv. Can. Pap.* 79 (7):1–57.
- McDougall, K. 1995. Age of the Fishcreekian Transgression. *Palaios* 10:199–220.
- Matthews, J.V., Jr. 1968. A paleoenvironmental analysis of three late Pleistocene coleopterous assemblages from Fairbanks, Alaska. *Quaest. ent.* 4 :202–224.
- 1974. Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): evolution of a tundra ecosystem. *Geol. Soc. Am. Bull.* 85:1353–1385.
- 1975. Use of late Cenozoic beetle fossils for dating and correlation. Abstracts; Quaternary non-marine paleoecology conference, Univ. Waterloo, Waterloo, Ontario, May 12–13.
- 1976. Evolution of the subgenus *Cyphelophorus* (Genus *Helophorus*, Hydrophilidae, Coleoptera): description of two new fossil species and discussion of *Helophorus tuberculatus* Gyll. *Can. J. Zool.* 54:652–673.
- 1979. Late Tertiary Carabid fossils from Alaska and the Canadian Arctic Archipelago. pp. 425–445 in G.E. Ball, T.E. Erwin, and D.R. Whitehead (Eds.), Carabid Beetles: their Evolution, Natural History, and Classification. W. Junk, The Hague. 635 pp.
- 1982. East Beringia during Late Wisconsin time: a review of the biotic evidence. pp. 127–150 in D.M. Hopkins, J.V. Matthews Jr., C.E. Schweger, and S.B. Young (Eds.), Paleocology of Beringia. Academic Press, New York. 489 pp.
- 1983. A method for comparison of northern fossil insect assemblages. *Géogr. phys. quaternaire* 37:297–306.
- (unpublished) Late Cenozoic plant and insect macrofossils from Alaska and Arctic/Subarctic Canada: new data, intercontinental comparisons and correlations. *Geol. Surv. Can. Bull.*
- Matthews, J.V., Jr. and L.E. Ovenden. 1990. Late Tertiary plant macrofossils from localities in Arctic/Subarctic North America (Alaska, Yukon and Northwest Territories): a review of the data. *Arctic* 43:364–392.
- Matthews, J.V., Jr., C.E. Schweger, and J.J. Janssens. 1990a. The last (Koy-Yukon) interglaciation in the northern Yukon Territory: evidence from Unit 4 at Ch'ijee's Bluff exposure, Bluefish Basin. *Géogr. phys. quaternaire* 44:341–362.
- Matthews, J.V., Jr., C.E. Schweger, and O.L. Hughes. 1990b. Plant and insect fossils from the Mayo Indian Village Section (Central Yukon): new data on mid-Wisconsinan environments and glaciation. *Géogr. phys. quaternaire* 44:15–26.

- Matthews, J.V., Jr., A.Y. Druk, J.A. Westgate, and L.E. Ovenden. (unpublished ms 1) Fossils of plants and arthropods from the upper pit of the Lost Chicken gold mine (east central Alaska): a late Pliocene window on the environment of East Beringia. *Geol. Surv. Can. Bull.*
- Matthews, J.V., Jr., J.G. Fyles, L.E. Ovenden, R.A. Barendregt, E.C. Irving, J. Brigham-Grette, L. Marincovich, E. Brouwers, and V. Behan-Pelletier. (unpublished ms 2) Biostratigraphy and environment during deposition of the mid-Pliocene Beaufort Formation in the Bjaere Bay region of Meighen Island, Canadian Arctic Archipelago. *Geol. Surv. Can. Bull.*
- Matthews, J.V., Jr. and A. Telka. 1997. Plant and Arthropod Fossils. in S.R. Dallimore and J.V. Matthews Jr. (Eds.), Mackenzie Delta Borehole Project. Compact Disc issued by the Geological Survey of Canada.
- Nelson, R.E. 1976. Mid-Wisconsin aridity in northern Alaska: incongruity of a mesic pollen record and xeric insect indicators. *Curr. Res. Pleistocene* 3:57–59.
- 1982. Late Quaternary Environments of the Western Arctic Slope, Alaska. PhD. thesis, Univ. Washington, Seattle. 90 pp.
- 1987. Paleoenvironmental analysis of insects and extralimital *Populus* from an early Holocene site on the Arctic Slope of Alaska, U.S.A. *Arct. Alp. Res.* 19:230–241.
- Ovenden, L.E. and G.R. Brassard. 1989. Wetland vegetation near Old Crow, northern Yukon. *Can. J. Bot.* 67:954–960.
- Plafker, G. and W.O. Addicott. 1976. Glaciomarine deposits of Miocene through Holocene age in Yakataga Formation along the Gulf of Alaska margin, Alaska. pp. Q1–Q22 in T.P. Miller (Ed.), Recent and Ancient Sedimentary Environments in Alaska. *Proc. Alaska geol. Soc. Symp.* April 12–14, 1975. Alaska Geological Society, Anchorage.
- Plafker, G., C.W. Naeser, R.A. Zimmerman, J.S. Lull, and T. Hudson. 1992. Cenozoic uplift history of the Mt. McKinley area in central Alaska Range based on fission-track dating. pp. 202–212 in D.C. Bradley and C. Dusel-Bacon (Eds.), Geological Studies in Alaska by the U.S. Geological Survey. *Bull. U. S. geol. Surv.* 2041.
- Repenning, C.A. and E.M. Brouwers. 1992. Late Pliocene-Early Pleistocene ecologic changes in the Arctic Ocean borderland. *Bull. U. S. geol. Surv.* 2036:1–37.
- Ritchie, J.C. 1984. Past and Present Vegetation of the Far Northwest of Canada. Univ. Toronto Press, Toronto, Canada. 251 pp.
- Ritchie, J.C., L.C. Cwynar, and R.W. Spear. 1983. Evidence from north-west Canada for an early Holocene Milankovitch thermal maximum. *Science* 305:126–128.
- Scudder, G.G.E. 1997. Environment of the Yukon. pp. 13–57 in H.V. Danks and J.A. Downes (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Stewart, K.W. and W.E. Ricker. 1997. Stoneflies (Plecoptera) of the Yukon. pp. 201–222 in H.V. Danks and J.A. Downes (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Vickery, V.R. 1997. Orthopteroid insects (Orthoptera) of the Yukon. pp. 223–239 in H.V. Danks and J.A. Downes (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Walker, I.B. 1987. Chironomidae (Diptera) in paleoecology. *Quaternary Sci. Rev.* 6:29–40.
- White, J.M. and T.A. Ager. 1994. Palynology, paleoclimatology and correlation of Middle Miocene beds from Porcupine River (Locality 90-1), Alaska. pp. 43–77 in T.A. Ager, J.M. White, and J.V. Matthews Jr. (Eds.), Tertiary Quaternary Boundaries. *Quaternary Int.* 22/23. 241 pp.
- Wiggins, G.B. and C.R. Parker. 1997. Trichoptera of the Yukon, with analysis of the Beringian and Holarctic species of North America. pp. 787–866 in H.V. Danks and J.A. Downes (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Williams, N.E. and A.V. Morgan. 1977. Fossil caddisflies (Insecta: Trichoptera) from the Don Formation, Toronto, Ontario, and their use in paleoecology. *Can. J. Zool.* 55:519–527.
- Yurtsev, B.A. 1982. Relics of the xerophyte vegetation of Beringia in Northeastern Asia. pp. 157–177 in D.M. Hopkins, J.V. Matthews Jr., C.E. Schweger, and S.B. Young (Eds.), Paleocology of Beringia. Academic Press, New York. 489 pp.