

Late Tertiary Plant Macrofossils from Localities in Arctic/Subarctic North America: A Review of the Data¹

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ABSTRACT. Bryophyte and vascular plant fossils occur at many late Tertiary sites in Alaska and northern Canada. A number of these floras are reviewed here. The oldest flora, possibly of late Early Miocene age, is probably the one from the Mary Sachs gravel at Duck Hawk Bluffs, Banks Island. The youngest are of early Quaternary age.

The floras are of several types. The youngest (Cape Deceit Formation) contains only plants that grow in the Arctic and Subarctic today. The Meighen Island Beaufort Formation contains a few extinct taxa (*Aracites globosa*) and fossil plants, such as *Sambucus*, *Comptonia*, and *Physocarpus*, that are not found in the present subarctic and arctic regions of North America. Some of these floras also contain fossils of a five-needle pine that may represent the Japanese Stone pine (*Pinus pumila*). A third group of floras, from Cone Bluff and Lava Camp, Alaska, usually contains more extinct plants (*Epipremnum crassum*, *Decodon* and cf. *Paliurus*) as well as fossils of pines in the subsection *Cembrae*. The Mary Sachs gravel flora, with taxa such as *Metasequoia*, *Glyptostrobus*, *Taxodium*, *Juglans*, and *Liriodendron*, stands apart from all three of the above-mentioned floral types.

The Mary Sachs gravel flora represents mixed coniferous and hardwood forests. Most of the other floras represent coniferous forests that were floristically richer than present boreal forest. Some of the richness is due to taxa now found only in Eurasia. The Meighen Island Beaufort flora and some of those from the high-level alluvium on Ellesmere Island represent forest tundra. Several lines of evidence show that the Beaufort Formation on Meighen Island in the Canadian Arctic is about 3 million years old.

Several of the younger floras contain abundant, well-preserved bryophyte fossils. Unlike the vascular plants, all of them represent extant species.

Key words: Neogene, macroflora, Arctic, Beaufort Formation, *Epipremnum*, *Aracites*, Pliocene, Miocene, Meighen Island, bryophytes

RÉSUMÉ. On trouve des fossiles de bryophytes et de plantes vasculaires dans un grand nombre de sites de la fin du tertiaire en Alaska et dans le nord du Canada. Dans le présent article, on passe en revue un certain nombre de ces flores.

La flore la plus ancienne, datant possiblement de la fin du Miocène inférieur, est probablement celle qui provient des graviers Mary Sachs, à Duck Hawk Bluff (île de Banks). Les plus récentes datent du Quaternaire inférieur.

Il existe plusieurs types de flores. La plus récente (formation de Cape Deceit) contient seulement des plantes qui, aujourd'hui, poussent dans les zones arctique et subarctique. La formation de Beaufort de l'île Meighen renferme quelques taxons aujourd'hui disparus (*Aracites globosa*) et des plantes fossiles, comme *Sambucus*, *Comptonia* et *Physocarpus*, qui ne sont actuellement pas présentes dans les régions arctiques et subarctiques de l'Amérique du Nord. Certaines de ces flores contiennent aussi les restes fossiles d'un pin dont les aiguilles sont regroupées en faisceaux de cinq, possiblement le pin nain japonais (*Pinus pumila*). Un troisième groupe de flores, correspondant à Cone Bluff et à Lava Camp, en Alaska, renferment en général plus d'espèces disparues (*Epipremnum crassum*, *Decodon* et cf. *Paliurus*) ainsi que les restes fossiles de pins appartenant à la sous-section *Cembrae*. La flore provenant des graviers Mary Sachs et renfermant des taxons comme *Metasequoia*, *Glyptostrobus*, *Taxodium*, *Juglans*, et *Liriodendron* se distingue des trois autres types de flores mentionnés précédemment.

La flore des graviers Mary Sachs et représentative de forêts mixtes de résineux et de feuillus. La plupart des autres flores proviennent de forêts de résineux qui avaient un contenu floristique plus riche que celui de la forêt boréale actuelle. Une partie de cette richesse est attribuable à la présence de taxons que l'on ne trouve aujourd'hui qu'en Eurasie. La flore de la formation de Beaufort de l'île Meighen, ainsi que certaines des flores des alluvions atteignant un niveau élevé sur l'île d'Ellesmere, sont représentatives de la toundra forestière. Plusieurs évidences indiquent que la formation de Beaufort de l'île Meighen, située dans l'Arctique canadien, daterait d'environ 3 millions d'années.

Plusieurs des flores les plus récentes contiennent un grand nombre de fossiles de bryophytes bien préservés. Contrairement aux plantes vasculaires, ces bryophytes correspondant à des espèces qui existent encore aujourd'hui.

Mots clés: Néogène, macroflore, arctique, formation de Beaufort, *Epipremnum*, *Aracites*, pliocène, miocène, île de Meighen, bryophytes

РЕФЕРАТ. Ископаемые бриофиты и сосудистые растения встречаются во многих разрезах конца третичного периода на Аляске и на севере Канады. В настоящей работе рассматриваются некоторые из этих флор.

Наиболее древняя флора, относящаяся, предположительно, к концу раннего миоцена, представлена, повидимому, в слоях гравия Мэри Сакс в разрезе Дак Хок Блаффс на острове Банкс. Наиболее поздние флоры относятся к началу четвертичного периода.

Описываемые флоры делятся на несколько типов. Самая молодая (формация Кейп Десит) состоит исключительно из растений, произрастающих в Арктике и в субарктическом поясе в настоящее время. Формация Бофорта на острове Миен содержит несколько вымерших таксонов (*Aracites globosa*) и ископаемые растения, как, например, *Sambucus*, *Comptonia*, *Physocarpus*, которые не встречаются в наше время в субарктических и арктических районах Северной Америки. В некоторых из этих флор обнаруживаются также остатки пятихвойной сосны — возможно, кедрового стланика (*Pinus pumila*). В третьей группе флор из толщ Коун Блафф и Лава-Кэмп на Аляске содержится обычно больше вымерших растений (*Epipremnum crassum*, *Decodon* и cf. *Paliurus*), а также остатки разных видов сосны из подсекции *Cembrae*. Флора слоев гравия Мэри Сакс, в которую входят такие таксоны, как *Metasequoia*, *Glyptostrobus*, *Taxodium*, *Juglans* и *Liriodendron*, отличается от всех трех упомянутых выше типов.

Флора слоев гравия Мэри Сакс — смешанный хвойнолиственный лес. Большинство других флор представлены хвойными лесами, более богатыми по своему составу, чем бореальные леса нашего времени. Богатство состава обеспечивалось отчасти присутствием таксонов, ныне встречающихся только в Евразии. Флора формации Бофорта на острове Миен и некоторые из флор, относящихся к верхним слоям аллювия на острове Элсмир, представлены растительностью лесотундры. Имеется ряд указаний на то, что возраст формации Бофорта на острове Миен в Канадской Арктике составляет около трех миллионов лет.

Некоторые из более молодых флор содержат большое количество хорошо сохранившихся остатков бриофитов. В отличие от сосудистых растений, все они — представители существующих ныне видов.

Ключевые слова: неоген, макрофлора, Арктика, формация Бофорта, *Epipremnum*, *Aracites*, плиоцен, миоцен, остров Миен, бриофиты.

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INTRODUCTION

The Beaufort Formation in the Canadian Arctic and related late Tertiary deposits on the northern mainland of Canada and Alaska contain well-preserved plant macrofossils such as seeds and fruits. Many of the sites have also yielded fossil insects. Complete and detailed lists of the plants found in these deposits are not generally available, and the prime objective of this paper is to redress that deficiency by compiling up-to-date floristic lists. Some of the sites are still under study and others have been visited as late as the summer of 1990, so the tables and text represent at most a status report as of the spring of 1990.

The data compiled here provide the basis for the first comparison of arctic macrofloras, and as might be expected, some surprising facts have emerged. In addition, the lists show that arctic Neogene floras contained species previously known from the Tertiary of Asia, particularly the U.S.S.R., but which are extinct in North America today.

Ideally, a compilation of this sort should also facilitate correlation of floras; however, this is difficult when so few of the floras are dated. We present a provisional correlation scheme. It contains controversial conclusions and will probably be altered in major ways as new data emerge, but it does form a basis for further research and testing.

METHODS, IDENTIFICATION PROCEDURES AND DEFINITIONS

Except for conifer needles and occasional leaves or leaf fragments of plants such as *Dryas*, most of the fossils discussed here are bracts, cones, fruits, endocarps, nuts and achenes of vascular plants or leaves and stems of mosses. Various procedures were used to isolate the fossils and quantitative methods were not applied. Some samples yielded thousands of seeds, while others contained only a few. Furthermore, some of the fossils come from allochthonous organic debris horizons within alluvium and other samples represent autochthonous peats. Finally, some of the floras shown in the tables represent fossils from a single site in a single sample; others represent combined lists of local floras from many individual sites within a region or from several samples at a single section. While these facts mitigate against one-to-one comparisons of the floras, they do not preclude more general conclusions and comparisons.

Bryophyte identifications are based primarily on comparison with reference material and keys, checklists and descriptions in publications such as Ireland (1982), Ireland *et al.* (1987) and Steere (1978). Identification of vascular plant fossils follows from comparison with modern reference specimens in the seed collection of the Geological Survey of Canada and the collections of J. van der Burgh and reference to illustrations and descriptions in several publications, including Baranova *et al.* (1976), Bennike (1990), Buzek *et al.* (1985), Dorofeev (1963, 1972, 1988), Friis (1985), Katz *et al.* (1965), Lancucka-Srodoniowa (1966), Reid and Reid (1915) and van der Burgh (1987).

In the tables of vascular plant fossils the family names and order of families follow Lawrence (1951). Taxa below the family level are listed alphabetically. Taxa shown in bold type in some tables are those thought to be extinct. Extant genera that are presently extinct in North America are also shown in bold-face type.

The majority of bryophyte fossils listed here are within the range of variation of extant species, justifying their assignment to extant species. In contrast, few of the vascular plants are assigned unequivocally to extant or even described extinct species. Positive identifications at the species level will be possible only after the fossils have been compared with type specimens of previously described fossil species, which is beyond the scope of this paper.

Throughout this text, the term Quaternary is used in the North American sense to signify the last 1.8 million years (Ma). Early Pliocene corresponds with the Zanclean and represents the interval between 5 and 2.5 Ma; late Pliocene is from 2.5 to 1.8 Ma. Stage names from the Cook Inlet area of southern Alaska are: Seldovian — early to middle Miocene (20-13 Ma); Homerian — late Miocene (13-8 Ma); and Clamgulchian — late Miocene and early Pliocene (8 to approximately 3.1 Ma) (Wolfe, 1981). The "Beringian transgression" denotes the first appearance at about 3 Ma of a Neogene seaway between the Pacific and the Arctic oceans. This event rapidly altered the composition of the arctic molluscan fauna, providing a criterion for dating Arctic Ocean marine deposits (Hopkins and Marinovich, 1984).

FOSSIL LOCALITIES AND FOSSIL FLORAS

Figure 1 shows the regions where the sites discussed here occur. Comments on the particular sites and their floras are presented below.

Cape Deceit Formation: Cape Deceit, Seward Peninsula, Alaska

The Cape Deceit site, located a few kilometres west of the town of Deering on the north coast of Seward Peninsula (Fig. 2) is a 10-15 m high exposure nested against the dolomitic bed rock forming Cape Deceit. Fossils of plants, mammals and insects from this site have been discussed in several previous publications (Guthrie and Matthews, 1971; Matthews, 1974; Giterman *et al.*, 1982). The age of the Cape Deceit Formation, the lowest unit in the sequence, is still in dispute. Matthews (1974) originally assigned it to the middle Pleistocene. Sher (1986) believes it to be between 1.8 and 1.2 Ma, while Repenning *et al.* (1987) propose an age at least one million years older. Paleomagnetic analyses should help

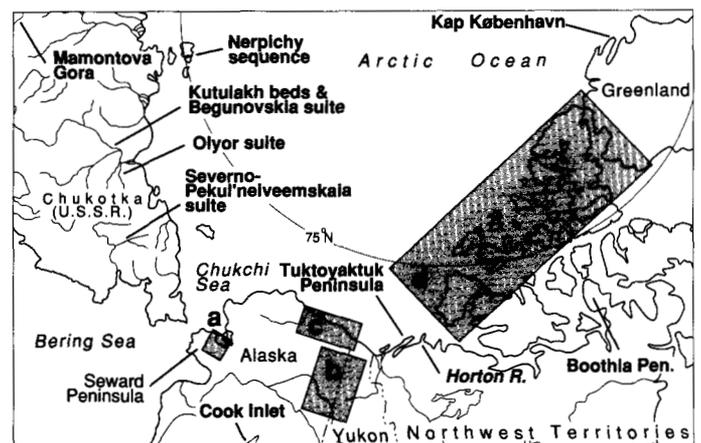


FIG. 1. Distribution of sites and geographical features mentioned in the text. Boxes indicate locations of more detailed maps. Siberian localities are from Baranova and Biske (1979).

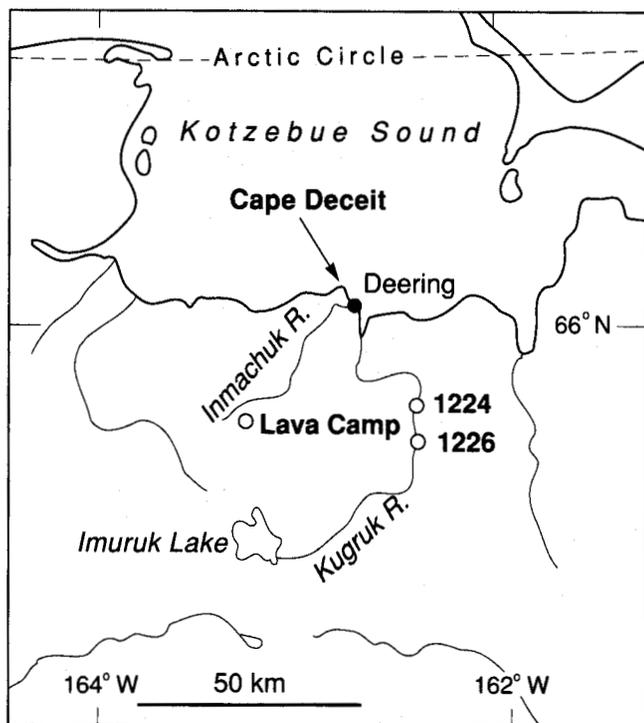


FIG. 2. Seward Peninsula, Alaska, sites.

to resolve this controversy, but detailed studies have yet to be done.

Cape Deceit is currently slightly west of the regional spruce-dominated tree line. Part of the Cape Deceit Formation represents westward movement of a *Larix laricina*-dominated tree line. This warm event was followed by cooling and development of tundra conditions. A single pollen sample from a unit below beach level suggests that the spruce tree line existed near the site (Matthews, 1974). However, it is no longer clear that the buried horizon with high spruce pollen percentages and the zone dominated by *Larix* macrofossils represent two distinct episodes of warmer climate. Even if they do, they may not differ greatly in age. Moreover, since the Cape Deceit site is very close to the present tree line, it may be wrong (Matthews, 1974; Repenning *et al.*, 1987) to interpret the slight westward movement of the tree line recorded by the fossils as an indication of worldwide climate warming.

For this report, the large collection of macrofloral remains originally studied by Matthews (1974) was re-examined. The assemblage of vascular plant taxa (not shown in the lists) lacks the southern forms and extinct plants that seemingly characterize many of the other late Tertiary assemblages discussed in this paper. The absence of *Aracites globosa* (Reid and Reid) Benn., a plant whose seeds are readily incorporated into alluvial and pond deposits, is particularly noteworthy.

Lava Camp: Seward Peninsula, Alaska

Lava Camp is a placer gold mine located on the Seward Peninsula (Fig. 2) in the valley of the Immachuk River. The gold-bearing alluvial gravel at the mine is capped by a reversed polarity lava flow K-Ar dated at 5.7 ± 0.2 Ma (Hopkins *et al.*, 1971). In the late 1960s, pollen, plant macrofossils and insects were isolated from detrital organic zones within the gravel exposed in the wall of an adit extending nearly 100

m beneath the lava flow (Hopkins *et al.*, 1971; Matthews, 1970a, 1976, 1977a). The charred character of the organics shows they are essentially the same age as the overlying basalt.

Plant macrofossils picked from samples collected by Matthews in 1968 were studied by J. Wolfe, of the U.S. Geological Survey (Hopkins *et al.*, 1971). Remaining, unstudied portions of the 1968 sample were examined by Matthews for this report.

Table 1 presents the most up-to-date list of plant fossils from Lava Camp. *Larix* leaves and short shoots are the most abundant plant macrofossils. Wolfe (in Hopkins *et al.*, 1971) noted the presence of needles resembling those of the western white pine *Pinus monticola*. *P. monticola* belongs to the group of pines characterized by having external resin canals in the needles (Critchfield, 1986). Some of the newly isolated pine needles possess resin canals in the medial position (Harlow, 1931), as shown in Figure 3:4 (see Discussion). This allies them with other Asian species in the subsection *Cembrae* rather than with the group (subsection *Eustrobi*) containing *P. monticola* (Critchfield, 1986). If Wolfe's original *P. monticola* determination is correct, the new fossils show that the Lava Camp flora contained at least two types of five-needle pine. One poorly preserved fascicle from the newly studied material resembles that of a two-needle pine, confirming Wolfe's pollen record of two-needle type pine pollen (*Haploxylon* type).

Another plant new to the Lava Camp flora is represented by distinctive fruits similar to those illustrated in Figures 4:1 and 4:2. They are tentatively referred to the genus *Paliurus* (Rhamnaceae) and are similar to but smaller than *Paliurus* fruits illustrated by van der Burgh (1987) and Dorofeev (1963). Closer in size to the fossils discussed here are specimens of *Carpolithus szaferi* V. Nikitin, which Nikitin (in Baranova *et al.*, 1976) compares to *Paliurus*. Fossils from the Omoloy lowland (U.S.S.R.) referred by Dorofeev (1972) to *Paliurus* are similar both in size and other features to the *Paliurus* from Lava Camp.

The updated Lava Camp macrofossil assemblage (Table 1) lacks bryophytes as well as several of the other taxa, e.g., *Epipremnum crassum* (Araceae) (Fig. 3:2), *Decodon* (Lythraceae) (Fig. 4:8) and *Aracites globosa* (Araceae), which occur at other sites discussed here. These omissions may be due to a sampling bias or small sample size.

Because it is independently dated, the small Lava Camp flora is one of the most important ones discussed here. Like some of the other radiometrically dated sites mentioned below, it should have high priority for future study.

Kugruk River Sites: Seward Peninsula, Alaska

The Kugruk River valley is located on the Seward Peninsula immediately east of the Immachuk valley and Lava Camp (Fig. 2). Several low bluffs along the river expose gravel units similar to those at Lava Camp. D.M. Hopkins and R.R. Rosé sampled organic horizons within the gravel at two sites (1226 and 1224, Fig. 2). At the time, they believed that the gravel from both sites was correlative to the Lava Camp sediments, but as indicated below and in Matthews (1977b), this seems to be only partly true.

The vascular flora from site 1226 (Table 1) contains only a few poorly preserved fossils. Nevertheless, the presence of *Comptonia* (Myricaceae) allies it with other Tertiary seed floras (Matthews, 1987; Dorofeev, 1963; Nikitin, in Baranova

TABLE 1. Plant macrofossils from Seward Peninsula localities (Alaska)

	Lava Camp ¹		Kugruk River sites ²			Lava Camp ¹		Kugruk River sites ²	
			1226	1224				1226	1224
Fungal Sclerotia	+				Polygonaceae				
VASCULAR PLANTS					<i>Rumex</i> sp.				+
Equisetaceae					Caryophyllaceae				
<i>Equisetum</i> sp.				+	genus?				+
Pinaceae					Nymphaeaceae				
<i>Larix</i> sp.	+		+		<i>Nuphar</i> sp.				+
<i>Picea</i> sp.			+		Ranunculaceae				
<i>P. glauca</i> (Moench) Vos.	+ ⁴			+	<i>Ranunculus</i> sp.				+
<i>P. mariana</i> (Mill.) B.S.P.	+ ⁴				<i>R. abortivus</i> L.				?
<i>P. sitchensis</i> (Bong.)					<i>R. hyperboreus</i> Rottb.				+
Carr	cf. ⁴				<i>R. lapponicus</i> L.				?
<i>Pinus</i> two-needle type					Cruciferae				
undiff.	?				<i>Rorippa islandica</i>				
<i>Pinus</i> five-needle type					(Oeder) Borbas				+
<i>P. monticola</i> Dougl.	+ ⁴				Rosaceae				
<i>P. subsect. Cembrae</i> ³	+				<i>Geum</i> sp.				+
<i>Tsuga heterophylla</i> (Raf.)					<i>Potentilla</i> sp.				+
Sarg	+ ⁴				<i>P. palustris</i> (L.) Scop.				+
Cupressaceae					<i>Potentilla anserina</i> L.				+
<i>Thuja</i> sp.	?				<i>Rubus arcticus</i> L.				?
Sparganiaceae					Empetraceae				
<i>Sparganium hyperboreum</i>					<i>Empetrum nigrum</i> L.				+
Laest.				+	Rhamnaceae				
Potamogetonaceae					<i>Pallurus</i> sp.	cf.			
<i>Potamogeton filiformis</i>					Haloragaceae				
Pers.				?	<i>Myriophyllum spicatum/</i>				
<i>P. Richardsonii</i> (Benn.)					<i>exalbescens</i> type				+
Rydb.			+		Hippuridaceae				
Cyperaceae					<i>Hippuris</i> sp.	+		+	
<i>Carex aquatilis</i> Wahlenb.				+	Cornaceae				
<i>Carex rostrata</i> Stokes				cf	<i>Cornus stolonifera</i> Michx.	cf.		cf.	
<i>Cyperus</i> spp.	+ ⁴				Ericaceae				
<i>Eriophorum</i> sp.				+	<i>Andromeda polifolia</i> L.				+
Salicaceae					<i>Arctostaphylos alpina/rubra</i>				
<i>Populus</i> sp.				+	type				+
<i>Salix</i> sp.				+	<i>Ledum</i> sp.				+
Myricaceae					<i>Vaccinium</i> sp.	+			
<i>Comptonia</i> sp.			+		Gentianaceae				
Betulaceae					<i>Menyanthes trifoliata</i> L.	+			+
<i>Betula</i> sp.			?		<i>Menyanthes small form</i>			+	
<i>Betula</i> dwarf shrub type				+	Caprifoliaceae				
					<i>Symphoricarpos</i> sp.	+ ⁴			

¹Lava Camp — Inmachuk River, Seward Peninsula, Alaska; U.S. Geological Survey paleobotany locality 11190 (see Hopkins *et al.*, 1971).

²1226 — Kugruk River valley at Reindeer Creek, Seward Peninsula, Alaska (65°50.62'N; 162°26.03'W); 1224 — Kugruk River valley, downstream from Chicago Creek (65°54.33'N; 162°28.2'W). Fossils from sites 1226 and 1224 were picked by R.E. Nelson from field samples collected by D.M. Hopkins and R. Rosé.

³Taxa shown in bold-face type either represent extinct genera (at least in North America) or the fossils referred to the taxon probably represent extinct species.

⁴Signifies taxa identified by J.A. Wolfe in Hopkins *et al.* (1971).

et al., 1976, and below). The single extant species of *Comptonia* (*C. asplenifolia*) is found in eastern North America (Scoggan, 1978). The fossils from sample 1226 differ from *C. asplenifolia* by having well-developed ribs and represent an extinct species.

Some of the *Menyanthes* seeds from sample 1224 are indistinguishable from the extant buckbean, *Menyanthes trifoliata*, but others are much smaller than *M. trifoliata* and are listed in the table as "*Menyanthes* small form." A similar type of *Menyanthes* occurs in many of the other samples discussed here. An extinct species having seeds less than 2 mm in diameter has been described in Europe as *Menyanthes carpatica* (Jentys-Szaferowa and Truchanowicz, 1953), but we refrain from use of this name until detailed comparisons are made.

The plant macrofossil assemblage from sample 1224 (Table 1) is more diverse and the fossils are better preserved than from sample 1226. *Picea* is the only conifer, and extralimital

and/or extinct taxa are absent. These distinctions plus the differences of the fossil insect faunas from the two sites (Matthews, 1977b) show that the site 1224 sediments are probably significantly younger (Quaternary?) than those from 1226. In an earlier report (Matthews, 1977b) one of the fossils from sample 1224 was referred to *Alisma*. Re-examination of the specimen shows it represents an unidentified species of *Ranunculus*.

Lost Chicken Mine: East Central Alaska

The Lost Chicken placer gold mine, located in the Forty-mile District of eastern Alaska (Fig. 5), is best known for its mammalian fossils (Harrington, 1980; Porter, 1988). The bones come from "muck" exposures near the valley floor. All of the plant macrofossils discussed here come from an "old cut" located on a bench well up the side of the valley.

The "old cut" reveals auriferous gravel overlain by approximately 30 m of silt, peat and pebbly gravel. Two prominent

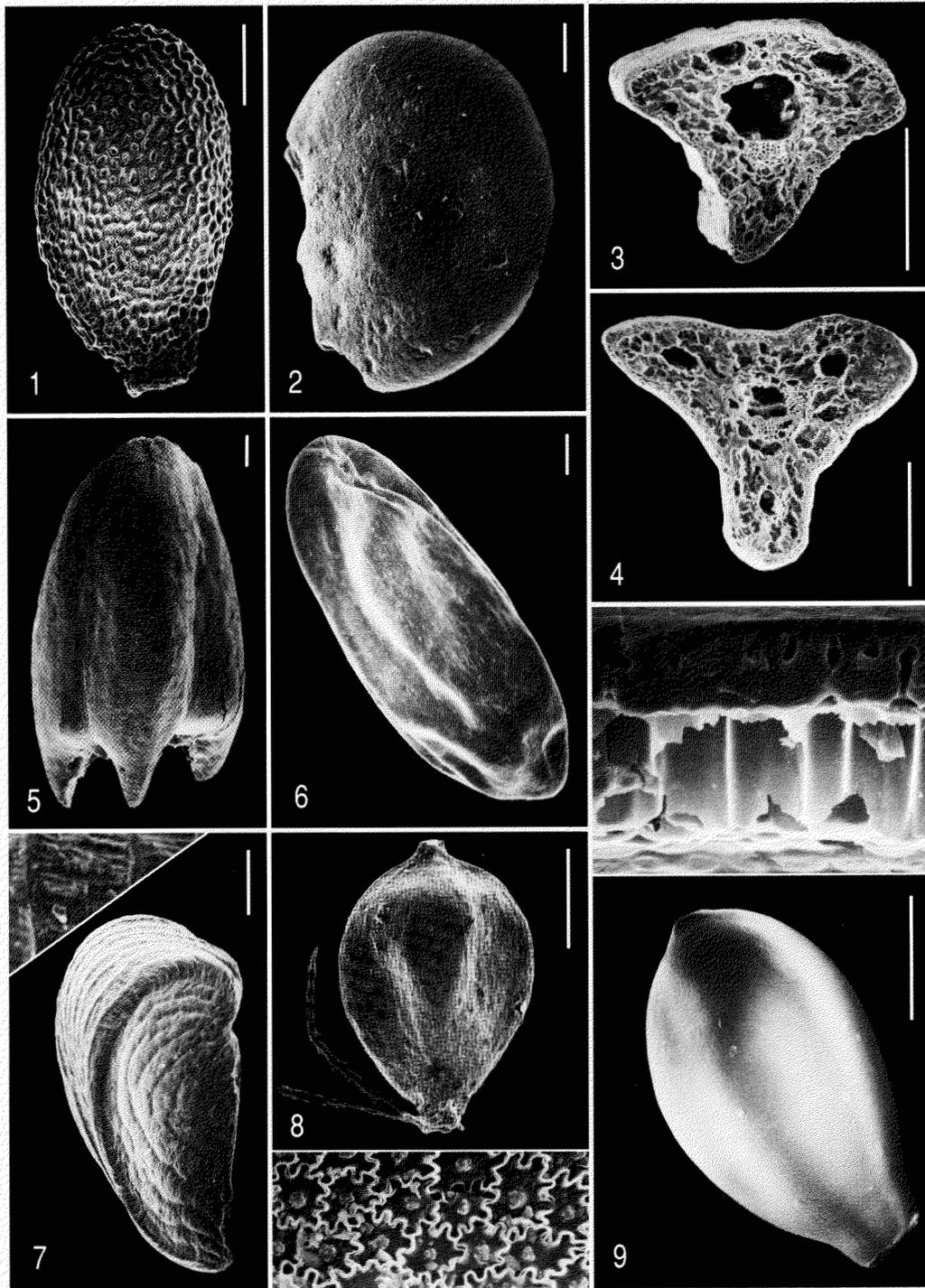


FIG. 3. Scanning Electron Micrographs of selected fossils. Scale bar = 300 μ m, unless otherwise noted. 1) *Actinidia* sp. (Actinidiaceae): seed. GSC-99130. Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample MRA 7-7-88-1 (SEM 41.319). 2) *Epipremnum crassum* Reid & Reid: seed. GSC-85358 Beaufort Formation (*sensu stricto*), Ballast Brook, Banks Island, N.W.T. Sample JVM 3-73 (SEM 40.809). 3) *Pinus* subsect *Eustrobi* Engelm: cross-section of needle. GSC-99131 High-level alluvium (Beaver Peat site, Figs. 10, 11), Ellesmere Island, N.W.T. Sample FG 88-51b (SEM 41.442). Photograph shows central fibrovascular bundle and two external (i.e., adjacent to dermal region) resin canals. 4) *Pinus* subsect *Cembrae* Engelm. (Pinaceae): cross-section of needle. GSC-99132. Beaufort Formation, Prince Patrick Island, N.W.T. Sample FG 87-17b (SEM 41.534). Note the three resin canals, all of which are in the medial position (surrounded by mesophyll parenchyma). 5) Cyperaceae type A: fruit? GSC-99133 High-level alluvium, Vendom Fiord region, Ellesmere Island, N.W.T. Sample FG 89-31c (SEM 41.001). Longitudinal cross-section intersects two vascular bundles (?) located near the inner margin of the parenchyma tissue, as in the specimen illustrated in Plate 25 (7-9) of Friis (1985). 6) *Scheuchzeria* sp. (Scheuchzeriaceae): seed. GSC-99134 High-level alluvium (beaver pond locality), Ellesmere Island, N.W.T. Sample: FG 88-8b (SEM 41.261). 7) *Phyllanthus* (*Phyllanthus*) sp. (Euphorbiaceae): seed. GSC-99135 Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample: MRA 7-7-88-1 (SEM 41.249). Magnified inset (SEM 41.216) shows the transverse ridges bridging the main ridges on the outer face of the seed. 8) *Scirpus microcarpus* Presl. (Cyperaceae): achene with remains of filaments. GSC-99136 High-level alluvium (Beaver Peat site, Figs. 10, 11), Ellesmere Island, N.W.T. Sample FG-88-8b (SEM 41.356). Magnified inset (SEM 31.358) shows distinctive epidermal cells with central projection in each lumen. 9) *Aldrovanda* sp. (Droseraceae): seed. GSC-99137. Upper Ramparts site on the upper ramparts of the Porcupine River, Alaska. Sample MRA 7-20-80-3 (SEM 41.512). Micropylar end at lower right. Magnified inset (SEM 41.517) shows a cross-section of the wall.

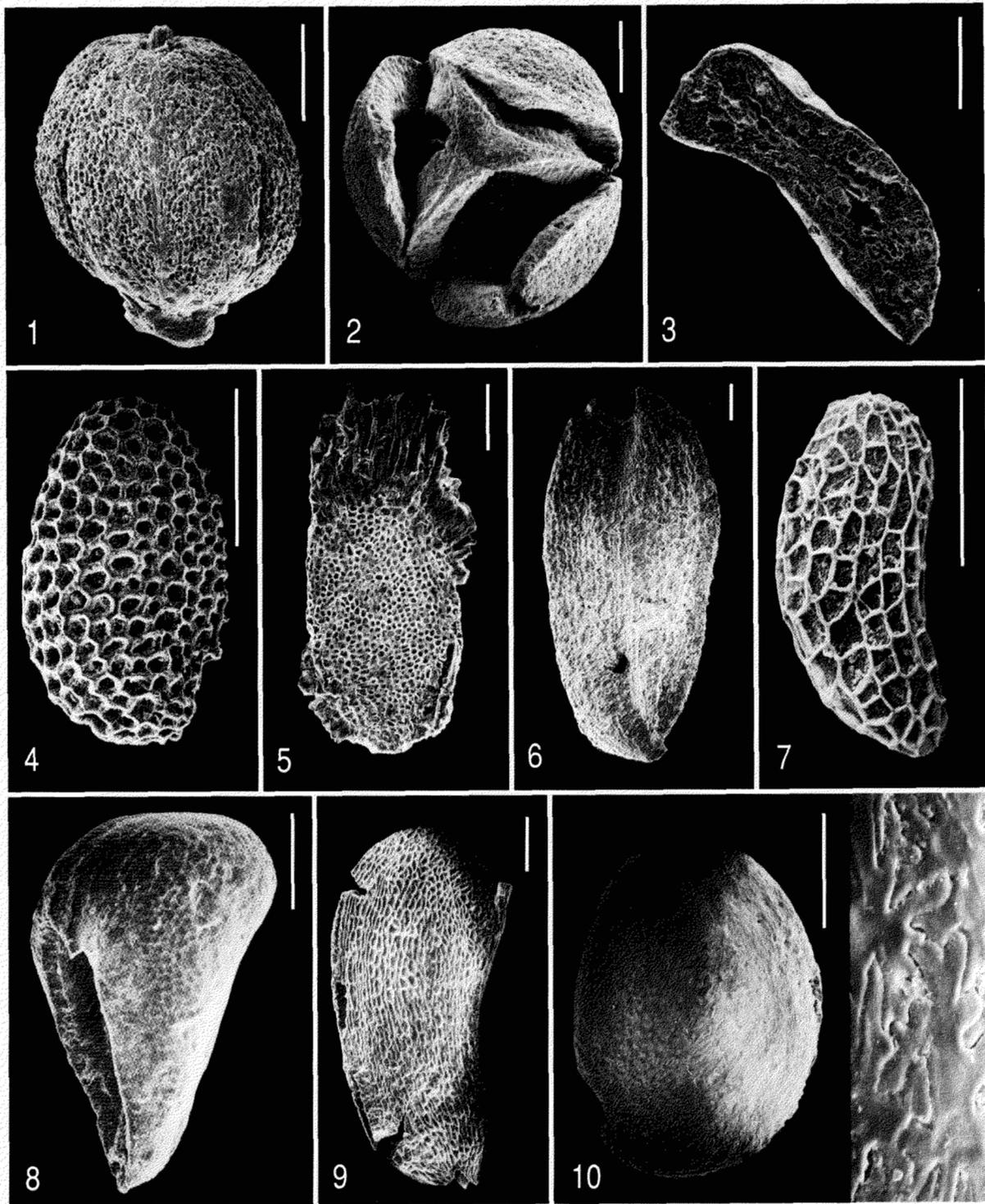


FIG. 4. Scanning Electron Micrographs of selected fossils. Scale bar = 300 μ m, unless otherwise noted. 1) cf. *Paliurus* sp. (Rhamnaceae): fruit. GSC-95883. High-level alluvium (Beaver Peat site, Figs. 10, 11), Ellesmere Island, N.W.T. Sample: FG-88-53b (SEM 41.330). Slightly oblique view of fruit with germination valves closed. 2) cf. *Paliurus* sp. (Rhamnaceae): fruit. GSC-95882. Cone Bluff, Porcupine River, Alaska. Sample: MRA 7-25-80-2 (SEM 41.080). Open germination valves as normally seen. 3) *Pinus* subsect *contortae* (?) sp. (Pinaceae): cross-section of leaf. GSC-99138 Prince Patrick Island, Beaufort Formation. Sample: FG-87-18a (SEM 41.570). Flattened needle shows widely spaced vascular bundles and few large resin canals as in species of subsection *contortae*. 4) *Diervilla* sp. (Caprifoliaceae): seed. GSC-99139 Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample: MRA 7-23-85-5 (SEM 40.938). 5) *Weigela* sp. (Caprifoliaceae): seed. GSC-99140. Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample: MRA 7-23-85-2 (SEM 40.975). 6) *Liriodendron* sp. (Magnoliaceae): seed. GSC-99141 Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample MRA 7-7-88-3 (SEM 41.244). Micropylar end is at bottom of photograph. 7) *Boschniakia rossica* (Cham. & Schlecht.) Fedtsch.: seed. GSC-99142. High-level alluvium, Ellesmere Island, N.W.T. Sample FG-88-10c (SEM 41.522). 8) *Decodon* sp. (Lythraceae): seed. GSC-99143 Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample: MRA 7-24-85-5 (SEM 40.741). Germination valve is missing. 9) cf. *Sagisma* Nikitin (Alismataceae): fruit. GSC-99144. Mary Sachs gravel, Duck Hawk Bluffs, Banks Island, N.W.T. Sample MRA 7-7-88-3 (SEM 41.246). This specimen contained a single recurved seed of the *Sagittaria* type. 10) *Nymphoides* sp. (Gentianaceae): seed. GSC-99145. High-level alluvium (Beaver Peat site, Figs. 10, 11), Ellesmere Island, N.W.T. Sample FG-88-8b (SEM 41.499). Notch indicates micropylar area. Magnified portion (SEM 41.481) shows surface with cells having highly undulate to stellate walls.

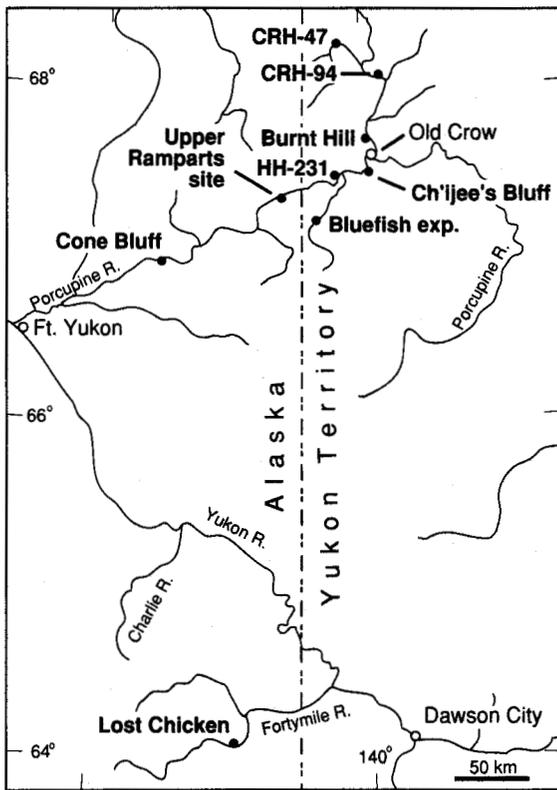


FIG. 5. Interior Alaska and Yukon localities.

autochthonous peat horizons occur near the base of the silt unit. The lower peat is associated with standing spruce stumps. The upper peat buries the stump horizon and is interbedded with Lost Chicken tephra, zircons from which have a fission-track age of about 2.1 Ma (Naeser *et al.*, 1982). Pollen spectra from both peats contain significant percentages of pine (Matthews, 1970b).

The mosses from the two peat units have been studied by Janssens (1980). The lower peat is an *in situ* deposit consisting exclusively of *Sphagnum lenense*. The other peat contains a mixture of *Sphagnum* and *Drepanocladus* fragments, representing a peatland pool.

Most of the vascular plant fossils reported here come from the upper peat. In this unit leaf fragments of *Larix* are abundant and show that the site was located within a larch woodland. Rare charred pine and spruce needles likely represent surrounding upland forests. The pine fossils refer to one of the species having medial resin canals (subsection *Cembrae*; Critchfield, 1986); therefore, they represent an Old World species or an extinct relative (see Discussion). *Sambucus* (Caprifoliaceae) and *Aracites globosa* also occur in the upper peat horizon. Both are characteristic of many of the other northern assemblages discussed here.

Like Lava Camp, Lost Chicken is a site that should be revisited and recollected. The section was badly slumped in 1974 but in recent years has been freshened and at times has displayed excellent exposures of the peats and associated tephra. Lost Chicken can be reached by road. There is no other "logistically easy" site in interior Alaska that would yield a greater scientific dividend if it were revisited.

Cone Bluff: Porcupine River, Alaska

Cone Bluff is a low cut-bank near the downstream end of Henderson Slough on the Porcupine River (Fig. 5). The

sediments at the exposure consist mostly of coarse to medium sands interbedded with lenses of coarse detrital organic debris.

Conifer cones (under study by R. Stockey, University of Alberta, Department of Botany) are abundant, possibly because the organic detritus is well sorted and biased for larger fossils. Several different types of conifer needles are present (Table 2), including *Larix*, *Abies* and five-needle pine, *Pinus* (*Strobus*). The latter are too poorly preserved to allow easy determination of the position of the resin canals. Among the other macrofossils are *Epipremnum crassum*, *Aracites globosa*, *Comptonia*, *Myrica*, *Paliurus* and *Sambucus*, all typical of many of the other late Neogene assemblages discussed here.

Upper Ramparts Site: Porcupine Canyon, East Central Alaska

Near the Alaska/Yukon border, the Porcupine River flows through a canyon created during the late Pleistocene by a major diversion of glacial meltwaters (Thorson and Dixon, 1983). At some places the walls of the canyon expose peats and tree stumps buried by flood basalts of probable mid-Miocene age (Brosge and Reiser, 1969; Plumley and Vance, 1988). The Upper Ramparts site (Fig. 5), located approximately 20 km below the Yukon-Alaska border in the upper ramparts of the Porcupine canyon, displays two basalt flows and an interbedded peat. The lower flow has buried a few trees, one of which has been tentatively identified as *Abies*. Except for *Abies*, all plant macrofossils listed in Table 2 come from the peat sandwiched between the two basalt flows.

Although it was baked when buried by the overlying lava, the peat has yielded a few identifiable plant macrofossils, including *Menyanthes*, *Epipremnum crassum*, *Aracites globosa*, *Hypericum* (Hypericaceae) and *Aldrovanda* (Droseraceae) (Fig. 3:9). The last-named plant occurs in European and Asian floras ranging from Tertiary to Quaternary age (Friis, 1985) and may also be present in the Miocene Severno-Pekul'neveemskaja flora from Chukotka (Fig. 1; Nikitin, 1979a). *Aldrovanda vesiculosa* L., the only extant species of the genus, is a submerged aquatic plant widespread in the Palearctic region (Lawrence, 1951). The *Aldrovanda* fossils reported here more than likely represent the first North American record of this taxon. They are another example of Palearctic elements in the Neogene floras of the North American Arctic.

The Upper Ramparts site was the object of detailed stratigraphic and paleobotanical research by a joint U.S. Geological Survey/Geological Survey of Canada team in the summer of 1990. Obviously the list presented in Table 2 will soon need revision. When that occurs, new radiometric dates on the basalts that overlie the organic horizons should also be available.

Ch'ijee's Bluff: Bluefish Basin, Northern Yukon

Ch'ijee's Bluff (= Twelvemile Bluff or HH-228 of other reports) is a 4 km long exposure on the Porcupine River downstream from the village of Old Crow (Fig. 5). The stratigraphy of the section is discussed briefly by Matthews *et al.* (1987; 1990a). Most of the sequence is of Quaternary age; probably only the basal two units are Tertiary.

Unit 1 is exposed intermittently during periods of exceptionally low water. Upstream it consists of blue-grey clayey

TABLE 2. Plant macrofossils from Porcupine River localities (Alaska/Yukon) and Lost Chicken, interior Alaska and Yukon

	Cone Bluff ¹	Upper Ramparts ²	Ch'ijee's Bluff ³		Lost Chicken ⁴	Bluefish ⁵	
			1	2		A	B
Actinorhizal nodules				+			+
BRYOPHYTES			+	+			
Sphagnales							
<i>Sphagnum lenense</i> Lindb. f. ex. Pohle					+		
<i>S. macrophyllum</i> var. <i>burinense</i> Maass					cf.		
<i>S. magellanicum</i> Brid.					+		
<i>S. sect. Cuspidata</i>					+		
Dicranales							
<i>Cratoneuron filicinum</i> (Hedw.)							+
<i>Ditrichum flexicaule</i> (Schwaegr.) Hampe							+
<i>D. groenlandicum</i> Brid.							+
Hypnobryales							
<i>Calliergon giganteum</i> (Schimp.) Kindb.							+
<i>C. richardsonii</i> (Mott.) Kindb. ex Warnst.							+
<i>Drepanocladus</i> spp.					+		
<i>D. sendtneri</i> (Schimp ex. H. Müll) Warnst.							+
<i>D. exannulatus</i> (B.S.G.) Warnst.							+
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.							+
VASCULAR PLANTS							
Selaginellaceae							
<i>Selaginella selaginoides</i> (L.) Link							+
Pinaceae							
<i>Abies</i> sp.	+	+		+	?		
<i>Larix</i> sp.	+			+	+	+	+
<i>L. minuta</i> Vassk. ⁶				cf.			
<i>Picea</i> sp.	+				+		
<i>Picea mariana</i> type							+
<i>Pinus</i> two-needle type							
<i>Pinus contorta</i> Dougl.				cf.			
<i>Pinus</i> five-needle type undiff.	+				+	+	
<i>P. subsect. Cembrae</i>				+	+	+	
<i>P. subsect. Eustrobi</i>					+		
<i>P. monticola</i> Dougl.				cf.			
Sparganiaceae							
<i>Sparganium hyperboreum</i> Laest.	+			+	+		+
Potamogetonaceae							
<i>Potamogeton</i> sp.				+	+		+
<i>P. Richardsonii</i> (Benn.) Rydb.							+
Alismaceae							
<i>Alisma</i> sp.					?		
Gramineae.							
<i>Glyceria</i> sp.	cf.						
Cyperaceae							
<i>Carex</i> spp.	+	+		+	+	+	+
<i>C. aquatilis</i> type							+
<i>C. rostrata</i> type							+
<i>Eleocharis</i> sp.							+
<i>Eriophorum</i> sp.							+
Araceae							
<i>Arctites globosa</i> (C.&E.Reid) Benn.	cf.	+			+		+
<i>Epipremnum crassum</i> C.&E.Reid	+	+					+
Salicaceae.							
<i>Salix</i> sp.					+		
Myricaceae							
<i>Comptonia</i> spp.	+						+
<i>Myrica</i> sp.	+			+	+		+
Betulaceae							
<i>Alnus</i> (<i>Alnobetula</i>) sp.	+			+			+
<i>Alnus incana</i> (L.) Moench					+		+
<i>Betula</i> arboreal type		+		+	+		+
<i>Betula</i> dwarf shrub type							+
Polygonaceae							
<i>Polygonum amphibium</i> L.							cf.
<i>Rumex</i> sp.							+
Nymphaeaceae							
<i>Brasenia Schreberi</i> Gmel.							+
<i>Nuphar</i> sp.							+
Ceratophyllaceae							
<i>Ceratophyllum demersum</i> L.							+
Ranunculaceae							
<i>Ranunculus hyperboreus</i> Rottb.					+		+

(continued)

TABLE 2. (continued)

	Cone Bluff ¹	Upper Ramparts ²	Ch'ijee's Bluff ³		Lost Chicken ⁴	Bluefish ⁵	
			1	2		A	B
<i>R. Macounii/pensylvanicus</i> type				+			
<i>R. lapponicus</i> L.							+
Cruciferae							
<i>Rorippa islandica</i> (Oeder) Borbas.				+			
Droseraceae							
<i>Aldrovanda</i> sp. ⁶		+					
Saxifragaceae							
<i>Chrysosplenium</i> sp.							+
Rosaceae							
<i>Dryas</i> sp.				+			+
<i>Potentilla</i> sp.	+		+		+		+
<i>P. palustris</i> L. Scop.				+	+		
<i>P. norvegica</i> L.							cf.
<i>Prunus</i> sp.							+
<i>P. Maximoviczii</i> Ruprecht							cf.
<i>Rubus idaeus</i> L.			+				
Empetraceae							
<i>Empetrum nigrum</i> L.				+			
Rhamnaceae							
<i>Paliurus</i> sp.	cf.						cf.
Hypericaceae							
<i>Hypericum</i> sp.		+					
Lythraceae							
<i>Decodon</i> sp.	+						
Haloragaceae							
<i>Myriophyllum spicatum/exalbescens</i> type							+
Hippuridaceae							
<i>Hippuris</i> sp.				+		+	+
Araliaceae							
<i>Aralia</i> sp.	+					+	
Umbelliferae							
<i>Cicuta</i> sp.					+		
Cornaceae							
<i>Cornus stolonifera</i> Michx.	+	+					
<i>C. canadensis</i> L.				cf.			
Ericaceae							
<i>Andromeda</i> sp.	+			+	+	+	+
<i>Chamaedaphne</i> sp.				+	+		+
<i>Ledum</i> sp.							+
<i>Vaccinium</i> sp.	+						
genus? two types	+						
Gentianaceae							
<i>Menyanthes trifoliata</i> L.	+	+		+	+	+	+
<i>Menyanthes</i> small form	+	+		+			+
Caprifoliaceae							
<i>Sambucus</i> sp.	+			+	+	+	+

¹ Cone Bluff — Samples MRA 7-25-80-2 and MRA 7-25-80-3; Porcupine River, Alaska (66°52.5'N; 143°34.79'W), lower end of Henderson Slough.

² Upper Ramparts — Sample MRA 7-20-80-3; Porcupine River, Alaska (67°19.83'N; 141°19.8'W), approximately 20 km below the Alaska/Yukon border on the south side of the river.

³ Ch'ijee's Bluff — Porcupine River, Yukon (67°28'N; 139°54'W), approximately 9.7 km southwest of the village of Old Crow. Formerly known as Twelvemile Bluff. "Ch'ijee's 1" is a pooled flora of fossils from several samples in unit 1. "Ch'ijee's 2" is from unit 2. All samples collected in 1985 by Matthews.

⁴ Lost Chicken Mine — Upper pit (64°4.5'N; 141°54.87'W), near Chicken (Fortymile District), Alaska. Samples collected in 1966 by Matthews.

⁵ Bluefish Section — HH 75-24 (67°23.1'N; 140°21.7'W), Bluefish River in Bluefish Basin, Yukon. A=Sample MRA 7-13-87-5; B=Sample MRA 7-13-87-1, both collected by Matthews in 1987.

⁶ Taxa shown in bold-face type either represent extinct genera (at least in North America) or the fossils referred to the taxon probably represent extinct species.

silt with a few large stumps in growth position and an abundance of woody detritus and conifer cones. At the downstream end of the section (the only other place where the lower unit is visible), rusty, partly cemented sand and sandy silt contain flattened wood, cones and other organic debris. Unit 1 is overlain unconformably (?), by unit 2, which consists of white, quartz-rich alluvial sand interbedded with coarse detrital organic horizons. Unit 2 is capped at all parts of the section by a thick sequence (unit 3) of silt and clayey silt, which appears to represent one or more lacustrine episodes. Paleomagnetic studies (Pearce *et al.*, 1982) suggest that the base of unit 3 is at least as old as the latter part of the Matuyama chron.

Ch'ijee's 1 (Table 2) is from silt in the lowest part of unit 1. The list for Ch'ijee's 2 includes fossils from three widely separated samples in unit 2: one from organic debris within the clean white sands at the downstream part of the section; another from sands at the upper contact of the unit at the upstream part of the exposure; and a third from semi-autochthonous fine organic silt filling a small depression in the sand of the upper part of unit 2.

Previous investigations showed that unit 1 contains cones of *Larix* (cf. *Larix minuta*), two- and five-needle pines and spruce (Matthews *et al.*, 1987). Pine needles are very rare, but at least one displays medially positioned resin canals typical of subsection *Cembrae* (e.g., Fig. 3:4).

Also from unit 1 are seeds of *Sambucus* and a few endocarps of *Myrica*. The latter clearly belong to the subgenus *Gale*, which contains the extant North American species *M. gale*. The lateral scales are missing on the fossils, so it is impossible to know if they had the long scales typical of fossil species *M. eogale* Nikitin.

Ch'ijee's 2 contained abundant needles of *Picea* and *Larix*, rare needle fragments of *Abies* and seeds of a number of other herbs and shrubs. *Aracites globosa* is present, but *Epipremnum* appears to be absent. It may have become extinct in the northern Yukon by the time the sample was deposited.

Bluefish Exposure: Bluefish Basin, Northern Yukon

The Bluefish exposure is located on the Bluefish River in the Bluefish Basin of the northern Yukon Territory (Fig. 5). It consists of a sequence of lignite and alluvium that is interrupted by a younger channel sequence (Fig. 6). The younger channel sequence is probably entirely of Quaternary age (McCourt, 1982). Early pollen analyses of the lignite at the base of the section suggested it might be of late Tertiary age (Schweger, unpubl. data), and this is confirmed by the results presented here.

Plant fossils listed in Table 2 come from both the lignitic zone (sample A) near the base of the exposure and one of the more prominent horizons of detrital peat (sample B) located in unit 6a about 6 m above the lignite (Fig. 6).

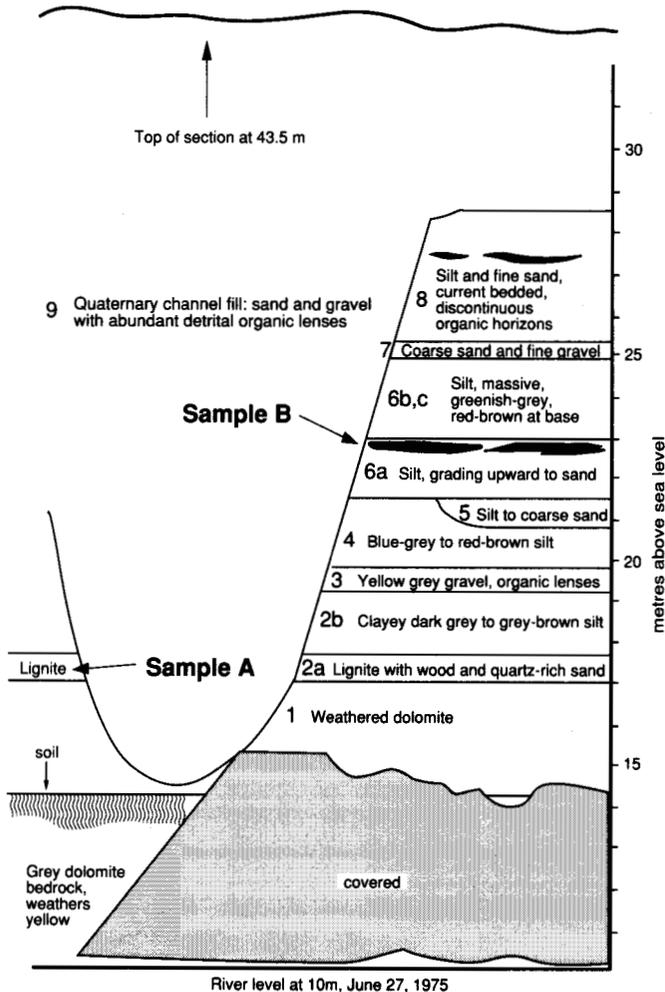


FIG. 6. Stratigraphy of the Bluefish section, northern Yukon.

The bryoflora (identified by J. Janssens), from a level near that of sample B, includes species of *Calliergon*, *Drepanocladus* and *Scorpidium scorpioides*. All three grow today in wetlands of the northern Yukon. The vascular macroflora from sample B is dominated by well-preserved *Carex* and other aquatic or wetland plants. Seeds of the extinct plant *Epipremnum crassum* (Fig. 3:2) are also extremely abundant and equally as well preserved as the other fossils. *Aracites globosa* is present, though rare. *Larix* needles are the dominant conifer fossil, but a few needles of the *Picea mariana* type, with two resin canals, are also present. Fossils of pine were not seen.

Poorly preserved *Pinus* needles do occur in the lignite collected for sample A. They are of the type seen in subsection *Cembrae* (see Discussion, Pines . . .) and probably represent an extinct species closely related to an extant Asian species. The lignite also contains *Epipremnum* and *Aracites*, as well as several other extinct taxa: *Comptonia*, *Paliurus* and *Prunus* cf. *Maximoviczii*. These differences imply that sample A is much older than sample B.

Gubik Formation: Fish Creek Site, Northern Alaska

The Gubik Formation, occurring along the Alaskan coastal plain, contains marine and nearshore deltaic sediments that have yielded molluscs entirely of Pacific affinities. This means that the entire formation postdates the opening of Bering Straits at approximately 3 Ma (Hopkins and Marincovich, 1984). Some Gubik sediments contain conifer wood and pollen, which suggests that the tree line was well north of its present limit during deposition of part of the unit.

The Fish Creek site (Fig. 7) is a key Gubik locality (Repenning *et al.*, 1987), partly because it contains many types of fossils, enabling cross checks on conclusions relating to age and paleoenvironments. The upper unit, thought by Repenning to be approximately 2.4 Ma in age, probably represents a marine regression. Pollen from these sediments indicate cooling conditions and developing shrub tundra. A small plant macrofossil flora from this unit is listed in Table 3. It shows that *Larix* was growing near the site, well north of its present limit, but in other respects the flora has a very modern aspect. For example, it does not contain extinct taxa, such as *Aracites globosa*. The flora also lacks extant genera, such as *Sambucus* and *Pinus* (*Strobus*), that do occur at the 2 Ma old Lost Chicken site.

Niguanak Site: Northern Alaska

Like Fish Creek, the Niguanak site (Fig. 7) contains many types of fossils, among them insects, pollen, wood, bryophytes and vascular plants. Unfortunately it has not yet

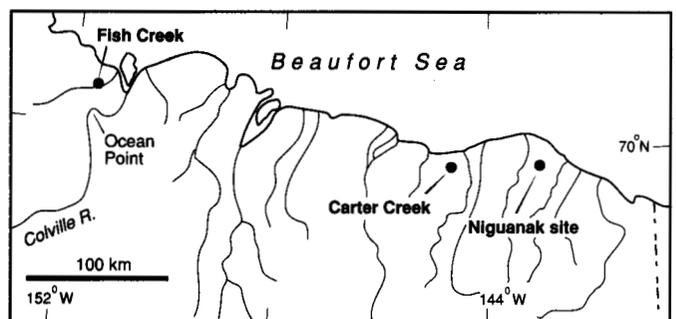


FIG. 7. Alaska coastal fossil localities.

TABLE 3. Niguanak and Fish Creek (Alaska) plant macrofossils

	Niguanak ¹	Fish Creek ²		Niguanak ¹	Fish Creek ²
Actinorhizal nodules	+		Pinaceae		
BRYOPHYTES		+	<i>Abies</i> sp.	?	
Sphagnales			<i>Larix</i> sp.	+	+
<i>Sphagnum</i> sp.	+		<i>Picea</i> sp.	+	
<i>S. imbricatum</i> Hornsch. ex Russ.	+		<i>Pinus</i> subsect. <i>Eustrobi</i>³	+	
<i>S. magellanicum</i> Brid.	cf.		Potamogetonaceae		
<i>S. teres</i> (Schimp.) Aongstr ex C. Hartm.	cf.		<i>Potamogeton</i> spp.	+	+
<i>S. sect. <i>Acutifolia</i></i>	+		<i>P. Richardsonii</i> (Benn.) Rydb.	+	
<i>S. sect. <i>Cuspidata</i></i>	+		<i>P. pectinatus</i> L.		+
<i>S. sect. <i>Subsecunda</i></i>	+		<i>P. alpinus</i> Balbis.		+
Dicranales			<i>P. filiformis</i> Pers.		+
<i>Ceratodon purpureus</i> (Hedw.) Brid.	+		Cyperaceae		
<i>Dicranum</i> sp.	+		<i>Carex</i> spp.	+	+
<i>Distichium capillaceum</i> (Hedw.) B.S.G.	+		<i>Carex aquatilis</i>		+
<i>Ditrichum flexicaule</i> (Schwaegr.) Hampe	+		<i>Eriophorum</i> sp.	+	
<i>Oncophorus wahlenbergii</i> Brid.	+		Salicaceae		
Pottiales			<i>Populus</i> sp.	+	
<i>Didymodon</i> sp.	+		<i>Salix</i> sp.	+	+
<i>Tortella tortuosa</i> (Hedw.) Limpr.	cf.		Betulaceae		
<i>Tortula</i> sp.	+		<i>Alnus</i> sp.	+	
Grimmiales			<i>A. crispa</i> Ait.		+
<i>Racomitrium canescens</i> (Hedw.) Brid.	+		<i>Betula glandulosa</i> type	+	+
Bryales			<i>Betula arborea</i> type	+	+
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	+		Caryophyllaceae		
<i>Bryum</i> spp.	+		<i>Stellaria</i> sp.	?	
<i>Cinclidium arcticum</i> (B.S.G.) Schimp.	cf.		<i>Melandrium</i> sp.		+
<i>Pohlia</i> sp.	+		Genus?		+
<i>Philonotis fontana</i> (Hedw.) Brid.	+		Ranunculaceae		
<i>Meesia triquetra</i> (Richt.) Aongstr.	+		<i>Caltha</i> sp.	+	
Hypnobryales			<i>Ranunculus hyperboreus</i> Rottb.	+	
<i>Brachythecium turgidum</i> (C.J.Hartm.)			<i>R. lapponicus</i> L.	+	
Kindb.	+		<i>R. trichophyllus</i> type		+
<i>Calliergon giganteum</i> (Schimp.) Kindb.	+		Saxifragaceae		
<i>Campylium stellatum/arcticum</i> type	+		<i>Chrysosplenium</i> sp.	?	
<i>Climacium dendroides</i> (Hedw.)			Rosaceae		
Web.&Mohr	+		<i>Dryas</i> sp.	+	+
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	+		<i>Potentilla norvegica</i> L.	+	
<i>D. exannulatus</i> (B.S.G.) Warnst.	+		<i>Potentilla</i> sp.	+	+
<i>D. revolvens</i> (Sw.) Warnst.	+		<i>Rosa</i> sp.	?	
<i>D. uncinatus</i> (Hedw.) Warnst.	+		Violaceae		
<i>Eurhynchium pulchellum</i> (Hedw.) Jenn.	+		<i>Viola</i> sp.	+	
<i>Hygrohypnum polare</i> (Lindb.) Loeske	+		Haloragaceae		
<i>Hylocomium splendens</i> (Hedw.) B.S.G.	+		<i>Hippuris</i> sp.	+	+
<i>Hypnum pratense</i> Koch ex Spruce	cf.		Ericaceae		
<i>H. revolutum</i> (Mitt.) Lindb.	+		<i>Empetrum nigrum</i> L.	+	
<i>Rhytidadelphus triquetrus</i> (Hedw.) Warnst.	cf.		<i>Andromeda polifolia</i> L.	+	
<i>Rhytidium rugosum</i> (Hedw.) Kindb.	+		<i>Chamaedaphne</i> sp.	+	
<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	+		<i>Arctostaphylos alpina/rubra</i> type	+	
<i>Thuidium abietinum</i> (Hedw.) B.S.G.	+		<i>Vaccinium</i> sp.	?	
<i>Tomenthypnum nitens</i> (Hedw.) Loeske	+		Gentianaceae		
Polytrichales			<i>Menyanthes trifoliata</i> L.	+	+
<i>Pogonatum urnigerum</i> (Hedw.) P. Beauv.	+		<i>Menyanthes</i> small type		+
<i>Polytrichum juniperinum</i> Hedw.	cf.		Caprifoliaceae		
VASCULAR PLANTS			<i>Lonicera</i> sp.	+	
Equisetaceae					
<i>Equisetum</i> sp.	+				

¹Northern Alaska unnamed tributary to Niguanak River at 69°49.3'N; 143°05.2'W.

²Northern Alaska, Fish Creek, 24 km south of Arctic Coast at 70°16'N; 152°01'W.

³Taxa shown in bold-face type either represent extinct genera (at least in North America) or the fossils referred to the taxon probably represent extinct species.

yielded vertebrate fossils. A detailed discussion of the site is planned for a future paper. All that need be said here is that Niguanak is not clearly correlated with the Gubik Formation, though it may well be as young as the early part of the Gubik.

The Niguanak moss flora (Table 3) is one of the richest yet recorded from an arctic site. All of the species listed in the table grow in northern Alaska today. The same cannot be said of the vascular plants, for in addition to

Larix and *Picea*, neither of which reaches the Alaskan coast today, the flora also includes leaf fragments of a five-needle pine (subgenus *Strobus*). The needles have external resin canals like those in subsection *Eustrobi* (see Discussion, Pines . . .); hence they may represent one of the North American white pines or whitebark pine, *Pinus albicaulis*. Fossils similar to those of the shrubby Asian species *P. pumila* occur at some of the other sites discussed here, and *P. pumila* may have been the species that grew at

Niguanak, since its shrubby growth form and tree line adaptation conform with the open character of the vegetation indicated by other Niguanak plants (Table 3) and insects (Matthews, 1986).

Plateau Cap Gravels: Horton River Area, N.W.T.

Sediments known as the Plateau Cap Gravels occur beneath the Smoking Hills uplands along the West River, a tributary to the Horton River near the north coast of the Northwest Territories (Mathews *et al.*, 1989). Estimates of the age of these deposits range from late Pleistocene (Mathews *et al.*, 1989) to Tertiary (Vincent, 1990-this issue; Yoranth *et al.*, 1969).

The fossils listed in Table 4 clearly suggest a Tertiary age. Some of the taxa, such as *Actinidia*, have been seen only in the Mary Sachs gravel (see below). All of the identified wood samples from the site are referred to the *Pinus strobus* type (Jetté, 1988), which is not the type of wood seen in Quaternary sediments from the region.

It could be argued that the gravel is of Quaternary age (Mathews *et al.*, 1989) and that the fossils listed in Table 4 are rebedded from an older unit. If this were so, we should observe two distinct suites of fossils: those of undisputed Quaternary age, consisting of well-preserved macrofossils of typical northern taiga species; and a smaller group of anomalous poorly preserved "old" forms. Just such a "mixed" flora has been documented from Holocene deposits at Hutchinson Bay on the Tuktoyaktuk Peninsula (Fig. 1; Table 7; Matthews, 1988) and at an exposure on the Pasley River on Boothia Peninsula (Fig. 1; Dyke and Matthews, 1987). The Plateau Cap gravels assemblage consists entirely of "old" forms; hence it is almost certainly pre-Quaternary.

Mary Sachs Gravel: Southern Banks Island, N.W.T.

Fyles (1990-this issue) discusses the way in which the concept of the Beaufort Formation has become confused due to casual application of the name to sediments that are probably much older than the deposits on Prince Patrick Island, where the Beaufort Formation was first defined (Tozer, 1956). To overcome this confusion, Fyles suggests that certain deposits long considered part of the Beaufort Formation should be excluded from it. The Tertiary deposits at Duck Hawk Bluffs (Fig. 8) are in this category. For them, Fyles proposes the informal name Mary Sachs gravel.

Mary Sachs gravel (MSg) consists largely of sand and gravel with numerous horizons of wood and semi-compressed but friable organic debris. At one station along the exposure, a channel consisting of silty sediments is inset in the gravel (Matthews, 1989a). This silt unit yielded many of the smaller, delicate macrofossils (e.g., cf. *Sesuvium*, *Ludwigia*) listed in Table 4.

The flora from MSg is one of richest ones documented from the North American Arctic. Both in terms of its diversity and taxonomic content, the MSg flora resembles the Mamontova Gora flora from the Soviet Union (Fig. 1) (Volkova *et al.*, 1986). The Chukotkian Severno-Pekul'neiveemskaja suite (Fig. 1) also contains several plants that occur in the Mary Sachs gravel: *Glyptostrobus*, *Metasequoia*, *Dulichium*, *Aracites*, *Epipremnum*, *Morus*, Vitaceae, *Hypericum*, *Decodon*, *Microdiptera/Mneme* (as *Diclidocarya*), *Diervilla*, *Weigela* and *Sambucus* (Nikitin, 1979a; Baranova and Biske, 1979).

The MSg assemblage contains a number of taxa that have not been encountered in any of the other samples discussed here. *Liriodendron* (Magnoliaceae) (Fig. 4:6) is one example. The genus is presently represented in the Western Hemisphere by the tulip tree (*Liriodendron tulipifera* L.), which grows in the eastern United States and southernmost Canada. Another extant species of *Liriodendron* occurs in Asia and *Liriodendron* fossils are known from several Miocene floras in Siberia and eastern Europe (Friis, 1985; Lancucka-Srodoniowa, 1966).

Actinidia (Actinidiaceae) is another taxon that occurs in a number of European assemblages. Two different species

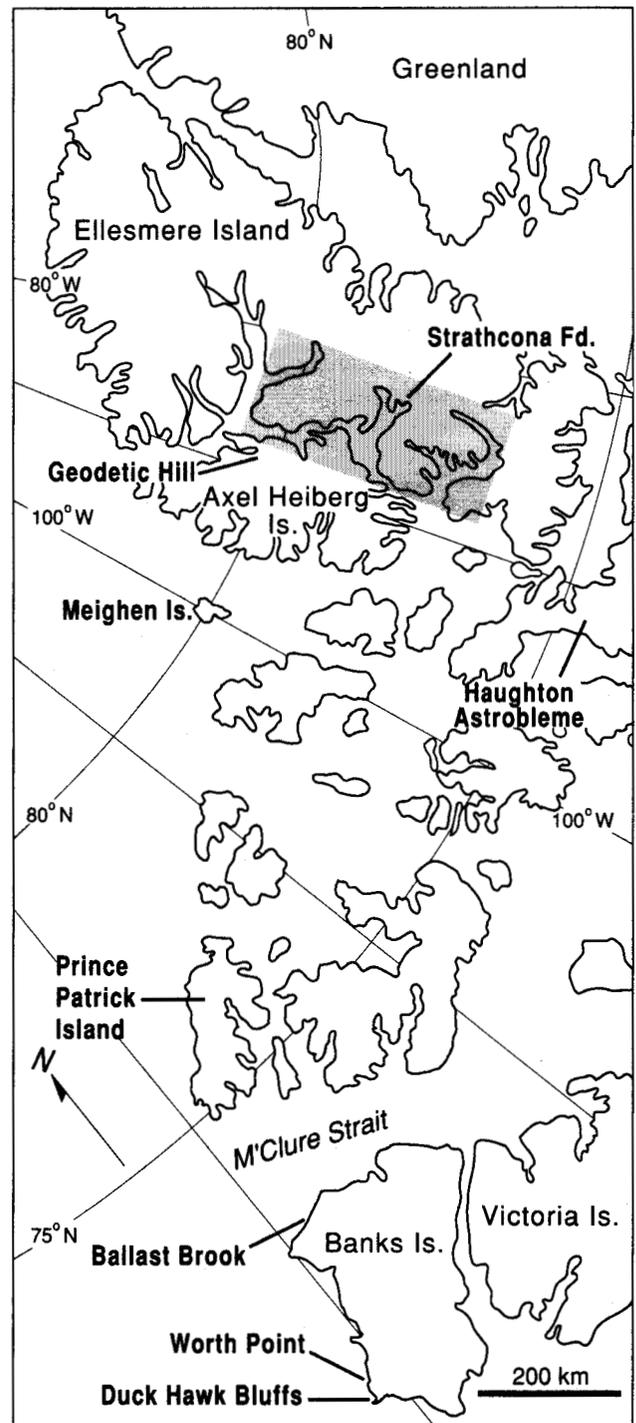


FIG. 8. Late Tertiary sites in the Canadian Arctic Archipelago. Stippled area is the region shown in Figure 10.

TABLE 4. Plant macrofossils from the West River (Horton River area) N.W.T., Mary Sachs gravel (S. Banks Island, N.W.T.) and the Ballast Brook beds (N. Banks Island, N.W.T.)

	West R. ¹ Horton R. area	Duck Hawk Bluffs ² Mary Sachs gravels	Ballast Brook ³ Ballast Brook beds		West R. ¹ Horton R. area	Duck Hawk Bluffs ² Mary Sachs gravels	Ballast Brook ³ Ballast Brook beds
Amber	+			<i>Nymphaea</i> sp.			+
"old megaspore"	+			Aizoaceae			
Characeae				<i>Sesuvium</i> sp.		cf.	
<i>Chara/Nitella</i> type	+			Ranunculaceae			
VASCULAR PLANTS				<i>Ranunculus (Batrachium)</i> sp.		+	
Pinaceae				<i>R. hyperboreus</i> Rottb.		cf.	
<i>Abies</i> sp.	+			Magnoliaceae			
<i>Abies grandis</i> (Dougl.) Lindl.		cf.		<i>Liriodendron</i> sp.		+	
<i>Larix</i> sp.	+	+	+	Capparidaceae			
<i>Larix omoloica</i> Dorof. ⁴		cf. ⁵	cf. ⁵	<i>Cleome</i> sp.		+	
<i>Picea</i> sp.	+	+	+	<i>Polanisia</i> sp.		+	
<i>Picea banksii</i> Hills and Ogilvie		+ ⁵	+ ⁵	Crassulaceae			
<i>Pinus</i> five-needle type undiff.	+	+	+	<i>Sedum</i> sp.		+	
<i>P. itelmenorum</i> Vassk.		+ ⁵	+ ⁵	Saxifragaceae			
<i>Pinus</i> two-needle type undiff.				genus?		+	
<i>P. palaeodensiflora</i> Dorof.		+ ⁵	+ ⁵	Rosaceae			
<i>P. funebris</i> Kom.		cf. ⁵	cf. ⁵	<i>Potentilla</i> sp.		+	
<i>Tsuga</i> sp.	+	+		<i>Rubus</i> sp.	+	+	
Taxodiaceae				Euphorbiaceae			
<i>Glyptostrobus</i> sp.		+	+	<i>Phyllanthus (Phyllanthus)</i> sp.		+	
<i>Metasequoia</i> sp.	+	+	+	Rhamnaceae			
<i>M. disticha</i> (Heer) Miki		+ ⁵		<i>Paliurus</i> sp.	cf.	cf.	
<i>Taxodium</i> sp.		+		Vitaceae			
Cupressaceae				<i>Vitis</i> sp.	cf.		
<i>Thuja occidentalis</i> L.		cf.	cf.	Actinidiaceae			
Sparganiaceae				<i>Actinidia</i> sp.	+	+	
<i>Sparganium</i> sp.	+	+		Hypericaceae			
Potamogetonaceae				<i>Hypericum</i> sp.		+	
<i>Potamogeton</i> sp.	+	+		Violaceae			
<i>P. Richardsonii</i> (Benn.) Rydb.		cf.		<i>Viola</i> sp.	+		
Alismaceae				Lythraceae			
<i>Sagisma</i> sp.		cf.		<i>Decodon</i> sp.	+		+
Cyperaceae				<i>Microdiptera/Mneme</i> type		+	
<i>Carex</i> spp.	+	+		Onagraceae			
<i>Dulichium vespiforme</i> C.&E. Reid		cf.		<i>Ludwigia</i> sp.		+	
Araceae				Hippuridaceae			
<i>Aracites globosa</i> (C.&E. Reid) Benn.	+	+	+	<i>Hippuris</i> sp.	+		
<i>Epipremnum crassum</i> C.&E. Reid		+		Araliaceae			
Myricaceae				<i>Aralia</i> sp.	+	+	
<i>Comptonia</i> spp.		+	?	Ericaceae			
<i>Myrica</i> (Gale) sp.		+		<i>Andromeda polifolia</i> L.		+	cf.
<i>M. eogale</i> Nikit.		cf.		<i>Arctostaphylos alpina/rubra</i> type		+	
Juglandaceae				<i>Chamaedaphne</i> sp.		+	?
<i>Juglans eocineria</i> H,K&S		+ ⁵		<i>Vaccinium</i> sp.			+
Betulaceae				Gentianaceae			
<i>Alnus (Alnobetula)</i> sp.		+	+	<i>Menyanthes trifoliata</i> L.	+		+
<i>Alnus incana</i> (L.) Moench		cf.		<i>Menyanthes small form</i>		+	+
<i>Betula</i> sp.	+			<i>Nymphoides</i> sp.			+
<i>Betula</i> dwarf shrub type		+		Verbenaceae			
<i>Betula</i> arboreal type		+	+	<i>Verbena</i> sp.		+	
<i>Betula apoda</i> Nikit.		cf.		Labiatae			
<i>Tubela</i> sp.			cf.	<i>Lycopus</i> sp.	+		
Moraceae				<i>Teucrium</i> sp.		+	
<i>Morus</i> sp.		+		Solanaceae			
Polygonaceae				<i>Solanum/Physalis</i> type	+	+	
<i>Rumex</i> sp.	+	+		Caprifoliaceae			
Chenopodiaceae				<i>Diervilla</i> sp.		+	
<i>Chenopodium</i> sp.		+		<i>Sambucus</i> sp.	+	+	
Nymphaeaceae				<i>Weigela</i> sp.	?	+	
<i>Nuphar</i> sp.	+						

¹ Sample VH 88-067, 068, West River (69°12.4'N; 127°02.5'W); collected by J-S. Vincent, 1988.² Pooled list from several samples collected at stations C, G and H, Duck Hawk Bluffs, southwestern Banks Island (Vincent, 1990-this issue). Samples collected by Matthews, 1983 and 1988.³ Sample "Lower Beaufort Lignite," right bank of Ballast Brook (74°18.58'N; 123°W), approx. 5 km above junction of unnamed creek. Collected by Matthews in 1972.⁴ Taxa shown in bold-face type either represent extinct genera (at least in North America) or the fossils referred to the taxon probably represent extinct species.⁵ Taxa were identified on the basis of cones and other megafossils by Hills (1975).

are probably present in MSg. The smaller one (Fig. 3:1) is similar to fossils from the Horton River site mentioned above.

The genus *Phyllanthus* (Euphorbiaceae), like many of the other taxa identified in MSg, has a markedly southern distribution today. Only eight native species occur in North America (Webster, 1970) and none of them grows in Canada. *Phyllanthus* fossils have been recovered in Neogene deposits from Europe and Asia (Dorofeev, 1963; Lancucka-Srodoniowa, 1966), but this is the first report of the genus from the Neogene of the North American Arctic. The fossils (Fig. 3:7) have seven longitudinal ribs with fine transverse striae, similar to the extant *P. amarus* (subgenus *Phyllanthus*) and to the two fossil species *P. triquetra* (Nikitin) Dorof. and *P. compassica* Dorof. described from the U.S.S.R.

The fruit tentatively identified as *Sagisma* (Fig. 4:9) is similar to illustrations of *S. turgida* Nikitin from the U.S.S.R. (illustrated in Dorofeev, 1963). Like most Alismataceae fruits, it is laterally compressed and thin walled. There is no evidence of a marginal wing. The seed (not shown in the figure) is typical of *Alisma*, *Sagittaria* and other genera within the family.

Ballast Brook Beds: Northern Banks Island, N.W.T.

The Ballast Brook region (Fig. 8) on northwestern Banks Island has long been known as a source of Tertiary plant fossils (Heer, 1868). Hills (1969; Kuc and Hills, 1971) was the first to describe the stratigraphy at Ballast Brook. He divided the thick sequence of gravels, sand and peat into two units: a lower one approximately 40 m thick with compressed wood from large trees and a 4 m thick peat ("lignite," according to Hills, 1969), which can be traced for several kilometres; and an upper unit made up of sand and gravel with lenses of uncompressed wood and finer organic debris. Fyles (1990-this issue) removes the lower unit from the Beaufort Formation, proposing the alternate designation "Ballast Brook beds."

All of the fossils listed as "Ballast Brook beds" in Table 4 (except those identified earlier by Hills) come from a single sample of the peat collected by Matthews in 1973. The peat contains abundant remains of the conifer *Glyptostrobus* (Taxodiaceae). *Glyptostrobus pensilis* Koch is a monotypic relict growing today only in China (van Gelderen and van Hoey Smith, 1986). The genus was widely distributed during the Tertiary (Wolfe, 1977; Czeccott, 1959; Nikitin, 1979a; Il'jinskaja, 1968). Although *G. pensilis* grows in a paratropical climate today, its extinct relatives must have been capable of surviving more temperate conditions, because *Glyptostrobus* fossils occur in the late Miocene/Pliocene Clamgulchian deposits in the Cook Inlet region of Alaska (Fig. 1) (Wolfe, 1977). This paper shows that *Glyptostrobus* grew even farther north during the Neogene. Wolfe (1977) suggests that *Glyptostrobus* is more characteristic of high latitude Tertiary macrofloras than *Metasequoia*, which also occurs in the Ballast Brook beds.

Seeds of *Epipremnum crassum* (Araceae) are abundant and exceptionally well preserved in the peat. Field work in June 1990 revealed clusters of *Epipremnum* seeds at the base of the peat where *Glyptostrobus* leaf mats occur. This shows that *Epipremnum* and *Glyptostrobus* were probably members of the same plant community.

Several of the fossils from the peat are very similar to illustrations of nuts of the betulaceous form genus *Tubela* (Dorofeev, 1982). The fossils consist of an *Alnus*-like nut

enclosed in a wingless sack. Similar specimens have been seen at a few of the Prince Patrick and Ellesmere Island sites described below.

Beaufort Formation: Prince Patrick Island, N.W.T.

The name Beaufort Formation was first used by Tozer (1956) for unconsolidated, wood-bearing sand and gravel resting unconformably on Devonian and Cretaceous bedrock in the Mould Bay area of Prince Patrick Island (Fig. 9). Since 1956, similar deposits have been mapped on many of the western islands of the Queen Elizabeth Archipelago as well as on northern Banks Island. The strata on Prince Patrick Island form a clastic wedge thickening to the northwest. A typical site at the thin edge of the wedge, such as Beaufort Reference Section 1 (Fig. 9) (= Devaney Section 1 of Matthews *et al.*, 1990b), is characterized by recurring packets of cross-bedded, medium to coarse sand and pebbly sand. These are interspersed with subsidiary amounts of gravel, rippled and horizontal fine sand, silty or clayey "mud," wood beds and beds of fine plant detritus. Such sequences represent sandy, braided river deposits, with the coarse facies being channel and bar deposits and the finer, wood-bearing strata representing low-stage overbank deposits (Devaney and Fyles, 1988; Fyles, 1990-this issue).

The fossil moss flora from Prince Patrick Island (Table 5) is diverse (Matthews *et al.*, 1990b), and unlike the bryoflora at Meighen Island (from an essentially autochthonous peat; Kuc, 1973), it includes more taxa that grow in marshes, fens and floodplain sites than grow in mature woodland.

Among the vascular plant fossils listed in the table are needles and wood of several types of conifers. *Abies* is represented by rare needle fragments as well as wood (Mott, 1968). One addition to the flora published in Matthews *et*

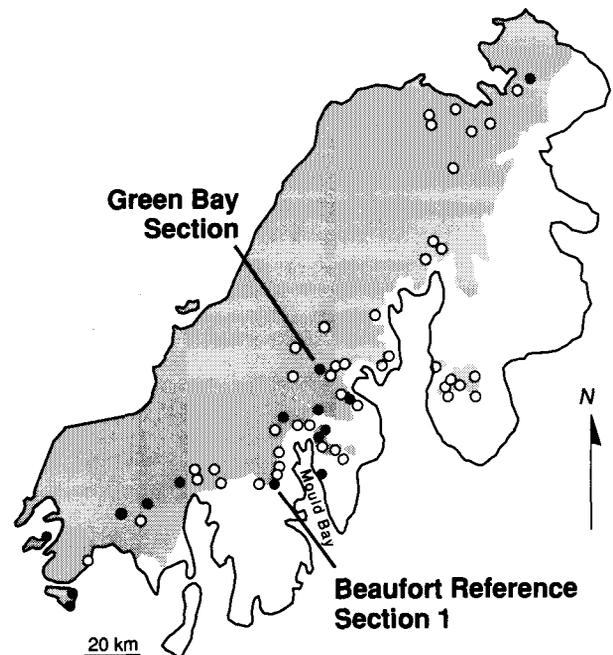


FIG. 9. Prince Patrick Island fossil localities. Black circles indicate localities that have yielded plant macrofossils and/or insect fossils. Stippled region indicates extent of the Beaufort Formation on the island. Note that most sample sites are located on the eastern part of the Beaufort terrain and thus sample only the thin edge of the thick Beaufort clastic wedge. Beaufort Reference Section 1 is located within the region where Tozer (1956) first defined the Beaufort Formation.

TABLE 5. Plant macrofossils from the Beaufort Formation *sensu stricto*

	Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³		Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³
Amber		+		<i>A. riparium</i> (Hedw.) B.S.G.		+	
Actinorhizal nodules		+	+	<i>Brachythecium</i> sp.		+	+
Characeae				<i>Calliergon giganteum</i> (Schimp.) Kindb.	+	+	+
<i>Chara/Nitella</i>		+		<i>C. orbicularicordatum</i> (Ren. & Card.) Broth.			+
BRYOPHYTES				<i>C. aftonianum</i> Steere			+
Sphagnales				<i>C. richardsonii</i> (Mitt.) Kindb. ex Warnst.			+
<i>Sphagnum</i> sp.	+			<i>Campylium stellatum/arcticum</i> type		+	
<i>S. fuscum</i> (Schimp.) Klinggr.	cf.			<i>C. polygamum</i> (B.S.G.) C. Jens.	+	+	+
<i>S. recurvum</i> B. Beauv.			cf.	<i>Climacium dendroides</i> (Hedw.) Web. & Mohr			+
<i>S. teres</i> (Schimp.) Aongstr. ex C.Hartm.	+	+		<i>Cratoneuron filicinum</i> (Hedw.) Spruce		+	
<i>S. sect. Acutifolia</i>	+	+		<i>Drepanocladus revolvens</i> (Sw.) Warnst.	+	+	+
<i>S. sect. Sphagnum</i>		+		<i>D. exannulatus</i> (B.S.G.) Warnst.	+	+	+
<i>S. sect. Subsecunda</i>		+		<i>D. fluitans</i> (Hedw.) Warnst.		+	
Dicranales				<i>D. pseudostramineus</i> (C.Müll.) Roth	?	+	
<i>Ceratodon purpureus</i> (Hedw.) Brid.		+		<i>D. aduncus</i> (Hedw.) Warnst.		+	
<i>Dicranum</i> sp.		+		<i>D. uncinatus</i> (Hedw.) Warnst.		+	+
<i>D. leioneuron</i> Kindb.			+	<i>D. lycopodioides</i> var. <i>brevifolius</i> (Lindb.) Mönk.		cf.	
<i>Distichium capillaceum</i> (Hedw.) B.S.G.		+		<i>D. lycopodioides</i> (Brid.) Warnst.			+
<i>Ditrichum flexicaule</i> (Schwaegr.) Hampe		+	+	<i>Hylocomium splendens</i> (Hedw.) B.S.G.		+	+
<i>Oncophorus wahlenbergii</i> Brid.		+	+	<i>Hypnum</i> sp.		+	+
Pottiales				<i>H. hamulosum</i> B.S.G.			+
<i>Bryobrittonia longipes</i> (Mitt.) Horton		+		<i>Myurella tenerrima</i> (Brid.) Lindb.			+
<i>Tortella fragillis</i> (Drumm.) Limpr.		+		<i>Orthothecium chryseum</i> (Schwaegr. ex Schultes) B.S.G.		+	+
Grimmiales				<i>Pleurozium Schreberi</i> (Brid.) Mitt.		+	+
<i>Racomitrium</i> sp.		+		<i>Scorpidium scorpioides</i> (Hedw.) Limpr.	+	+	
<i>R. heterostichum</i> var. <i>microcarpum</i> (Hedw.) Brid.			+	<i>Thuidium abietinum</i> (Hedw.) B.S.G.	+	+	+
<i>Schistidium apocarpum</i> (Hedw.) B&S in B.S.G.		cf.	+	<i>Tomenthypnum nitens</i> (Hedw.) Loeske	+	+	+
Bryales				Polytrichales			
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.		+	+	<i>Polytrichum alpinum</i> Hedw.		cf.	+
<i>A. acuminatum</i> (Lindb. & H. Arnell) Kindb.		+		<i>P. juniperinum</i> (Hedw.) P.Beauv.			+
<i>A. turgidum</i> (Wahlenb.) Schwaegr.		+		VASCULAR PLANTS			
<i>Bryum</i> spp.		+		Selaginellaceae			
<i>B. pseudotriquetrum</i> (Hedw.) Gaertn., Meyer & Scherb.			+	<i>Selaginella</i> sp.		+	
<i>Cinclidium arcticum</i> (B.S.G.) Schimp.		+	+	Pinaceae			
<i>C. latifolium</i> Lindb.		+	+	<i>Abies</i> sp.	?	+	
<i>Cyrtomnium hymenophyllum</i> (B.S.G.) Holmen			+	<i>Larix</i> sp.	+	+	+
<i>Meesia triquetra</i> (Richt.) Aongstr.	+	+		<i>Larix omolica</i> Dorof. ⁴	cf. ⁵		
<i>M. longiseta</i> Hedw.		+		<i>Picea</i> sp.	+	+	+
<i>M. uliginosa</i> Hedw.			+	<i>Picea banksii</i> Hills & Ogilvie	+		+
<i>Mnium marginatum</i> (With.) Brid. ex P. Beauv.		cf.	+	<i>Pinus</i> two-needle type	+		+
<i>Paludella squarrosa</i> (Hedw.) Brid.		+	+	<i>P. subsect. Contortae</i>		+	
<i>Philonotis fontana</i> (Hedw.) Brid.		+	+	<i>P. paleodensiflora</i> Dorof.	+		+
<i>Plagiomnium ellipticum</i> (Brid.) Kop.			+	<i>P. funebris</i> Kom.	cf. ⁵		+
<i>Pohlia</i> sp.		+	+	<i>Pinus</i> five-needle type undiff.	+		+
<i>P. nutans</i> (Hedw.) Lindb.		+	+	<i>P. itelmenorum</i> Vassk.	+		+
<i>P. cruda</i> (Hedw.) Lindb.			+	<i>P. subsect. Cembrae</i>		+	
<i>P. wahlenbergii</i> (Web. & Mohr) Andr.			+	<i>P. subsect. Eustrobi</i>		+	+
<i>Pseudobryum cinclidioides</i> (Hüb.) Kop.			+	<i>Tsuga</i> sp.		+	
<i>Timmia</i> sp.		+		Taxodiaceae			
<i>T. austriaca</i> Hedw.			+	<i>Metasequoia</i> sp.		+	+
<i>T. norvegica</i> Zett.			+	<i>Sciadopitys</i> sp.		+	+
Hypnobryales				Cupressaceae			
<i>Amblystegium</i> sp.		+		<i>Thuja occidentalis</i> L.		?	+
				Sparganiaceae			
				<i>Sparganium</i> sp.		+	

(continued)

TABLE 5. (continued)

	Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³		Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³
<i>S. hyperboreum</i> Laest.	cf.	cf.	cf.	Ranunculaceae			
Potamogetonaceae				<i>Caltha</i> type	?		?
<i>Potamogeton</i> spp.	+	+	+	<i>Ranunculus</i> sp.		+	+
<i>P. epihydrus</i> Raf.	cf.			<i>R. (Batrachium)</i> sp.			+
<i>P. filiformis</i> Pers.	cf.		cf.	<i>R. hyperboreus</i> Rottb.		cf.	
<i>P. spirillus</i> Tuck.	cf.			<i>R. lapponicus</i> L.	cf.	+	+
Scheuchzeriaceae				<i>R. Macounii/pensylvanicus</i> type	cf.	cf.	
<i>Triglochin maritimum</i> L.	cf.			<i>R. sceleratus</i> L.			cf.
Alismaceae				<i>Thalictrum</i> sp.		+	
<i>Alisma</i> sp.	?			Papaveraceae			
<i>Sagittaria</i> sp.		?		<i>Papaver</i> sp.		+	+
Gramineae				Capparidaceae			
<i>Glyceria</i> sp.	?	?	cf.	<i>Cleome</i> sp.	+	+	
genus?		+	+	<i>Polanisia</i> sp.	+		
Cyperaceae				Cruciferae			
<i>Carex</i> spp.		+	+	<i>Rorippa islandica</i> (Oeder) Borbas.		+	+
<i>C.</i> sect. <i>Acutae</i>		+	+	<i>Draba</i> sp.		+	
<i>C. aquatilis</i> Wahlenb.			cf.	genus?			+
<i>C.</i> sect. <i>Chordorrhizae</i>			+	Saxifragaceae			
<i>Dulichium vespiforme</i> C & E.				<i>Parnassia</i> sp.		+	
Reid	cf.			<i>Saxifraga</i> sp.		+	
<i>Eleocharis</i> sp.		+		<i>S. oppositifolia</i> L.		+	+
<i>E. palustris/uniglumis</i> type		+	+	Rosaceae			
<i>Rhynchospora capitellata</i> (Michx.)				<i>Crataegus</i> sp.			cf.
Vahl.		+		<i>Dryas</i> sp.		+	+
<i>Scirpus</i> sp.		+		<i>Fragaria</i>		+	
<i>S. validus</i> Vahl.		+		<i>Physocarpus</i> sp.	+	+	+
Araceae				<i>Potentilla</i> sp.	+	+	
<i>Aracites globosa</i> (C. & E. Reid)				<i>P. anserina</i> L.		+	
Benn.	+	+	+	<i>P. palustris</i> (L.) Scop.	cf.	cf.	cf.
<i>Epipremnum crassum</i> C. & E.				<i>P. norvegica</i> L.	cf.	cf.	cf.
Reid	+	+		<i>Prunus</i> sp.		+	
Juncaceae				<i>P. Maximoviczii</i> Ruprecht		cf.	
<i>Luzula/Juncus</i> type		+	+	<i>Rubus</i> sp.	+		
Salicaceae				<i>R. ideaus</i> L.	cf.	cf.	cf.
<i>Populus</i> sp.		+	+	Leguminosae			
<i>Salix</i> sp.	+	+	+	<i>Hedysarum</i> sp.			?
Myricaceae				Callitrichaceae			
<i>Comptonia</i> spp.	+	+	+	<i>Callitriche</i> sp.			?
<i>Myrica eogale</i> Nikit.	cf.	cf.	cf.	Empetraceae			
Juglandaceae				<i>Empetrum nigrum</i> L.		cf.	+
<i>Carya</i> sp.		+ ⁵		Rhamnaceae			
Betulaceae				<i>Paliurus</i> sp.		cf.	
<i>Alnus</i> sp.		+	+	Hypericaceae			
<i>A. (Alnobetula)</i> sp.			+	<i>Hypericum</i> sp.	+	+	
<i>A. crispa</i> Ait.		+		Violaceae			
<i>A. incana</i> (L.) Moench	+	+	cf.	<i>Viola</i> sp.	+	+	+
<i>A. tertiaria</i> Dorof.			cf.	Lythraceae			
<i>Betula apoda</i> Nikit.	+	cf.		<i>Decodon</i> sp.	+	+	
<i>Betula</i> arboreal type	+	+	+	<i>Microdiptera/Mneme</i> type	+	+	
<i>Betula</i> dwarf shrub type	+	+	+	Haloragaceae			
<i>Tubela</i> sp.		cf.		<i>Myriophyllum</i> sp.	+	+	
Polygonaceae				<i>M. spicatum/exalbescens</i> type	+	+	
<i>Oxyria digyna</i> (L.) Hill		+	+	Hippuridaceae			
<i>Polygonum</i> sp.	+	+		<i>Hippuris</i> sp.	+	+	+
<i>Rumex</i> sp.	+	+		Araliaceae			
<i>R. arcticus</i> Trautv.			cf.	<i>Aralia</i> sp.	+	+	
Chenopodiaceae				Umbelliferae			
<i>Chenopodium</i> sp.	+	+	+	genus?		+	
<i>C. gigantospermum</i> Aellen	cf.			Cornaceae			
Portulacaceae				<i>Cornus</i> sp.	+	+	+
<i>Claytonia</i> sp.	+	+		<i>C. stolonifera</i> Michx.	+	cf.	
Caryophyllaceae				Ericaceae			
<i>Melandrium</i> sp.		+		<i>Andromeda polifolia</i> L.	+	+	+
<i>Silene</i> sp.		+		<i>Cassiope tetragona</i> (L.) D. Don			cf. ⁵
genus?		+	+	<i>Chamaedaphne</i> sp.	+	+	+
Nymphaeaceae				<i>Ledum palustre</i> L.			cf.
<i>Nuphar</i> sp.	+	+	+	<i>Oxycoccus</i> sp.			+
<i>Nymphaea</i> sp.	+			<i>Vaccinium</i> sp.	+	+	+

(continued)

TABLE 5. (continued)

	Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³		Ballast Brook, ¹ Banks Island	Prince Patrick Island ²	Meighen Island ³
<i>Vaccinium</i>			+ ⁵	Labiatae			
<i>Vitis-Idaea</i> L. genus?				<i>Lycopus</i> sp.			+
Primulaceae				<i>Teucrium</i> sp.			+
<i>Primula</i> sp.		?		Caprifoliaceae			
Gentianaceae				<i>Sambucus</i> sp.	+		+
<i>Menyanthes trifoliata</i> L.	+	+	+	<i>Weigela</i> sp.			+
<i>Menyanthes small form</i> ⁴	+	+		Compositae			
Verbenaceae				genus? (at least two)			+
<i>Verbena</i> sp.	?	+					

¹ Pooled flora of several samples taken at various levels in "upper unit" at 74°20'N; 123°10'W (Geological Survey of Canada Loc. C-5552: Kuc and Hills, 1971).

² Pooled flora from several samples in Beaufort Formation on Prince Patrick Island. See Figure 9 for location of sites and Matthews *et al.* (1990b) for information on individual fossil floras.

³ Pooled flora from several samples from the terrestrial deposits on Meighen Island. Mosses identified by Kuc (1973). Vascular plants are from samples collected by Matthews in 1973 and 1975.

⁴ Taxa shown in bold-face type either represent extinct genera (at least in North America) or the fossils referred to the taxon probably represent extinct species.

⁵ Indicates species identified by L.V. Hills on the basis of cones and leaves. A single *Carya* nut was reported in Hills (1975); however, the exact location of the collection site is unknown and we are not even certain that the specimen still exists. The find requires confirmation.

al. (1990b) is *Tsuga*, but it is rare compared to spruce, larch and pine.

Leaves of both five-needle pine (subgenus *Strobus*) and two-needle pine (subgenus *Pinus*) have been found at some Prince Patrick sites. The latter type is rare and only one needle has been sectioned (Fig. 4:3). Like pines in the subsection *Contortae*, it possesses widely separated fibrovascular bundles and few resin canals. Because of its widely separated fibrovascular bundles, the fossil in Figure 4:3 cannot belong in the same group as either *Pinus paleodensiflora* or *P. funebris* (Harlow, 1931), two-needle pines to which Hills (1975) referred some of the female cones from the Beaufort Formation on Banks and Meighen islands.

Some of the triangular-shaped five-needle pine leaves possess three medially positioned resin canals (e.g., Fig. 3:4) like some of the species in the subsection *Cembrae* (see Discussion, Pines . . .). Samples from one site also contained needle fragments of the *Eustrobi* type with external resin canals. Thus at least three species of pine (two representing subgenus *Strobus* and one representing subgenus *Pinus*) are now known to occur in the Beaufort Formation on Prince Patrick Island.

Some of local floras from individual sites on Prince Patrick Island display floristic differences that may be indicative of age differences (Matthews *et al.*, 1990b). The most pronounced deviations occur in the flora from the fine detritus in the lower part of the Green Bay section (Fig. 9) (Matthews *et al.*, 1990b). Not only is that assemblage unusual for its more depauperate flora, but it also stands out because it contains delicate specimens not preserved in other samples. It could represent a younger Beaufort unit or alternatively a post-Beaufort assemblage containing rebedded Beaufort fossils. We favour the first explanation.

Other local floras on Prince Patrick Island contain taxa not seen at any other site on the island. But what cannot be seen from the list in Table 5 is that such fossils (e.g., *Metasequoia* and *Microdiptera/Mneme*) are usually rare and poorly preserved. They may in fact be rebedded from older units.

Beaufort Formation: Ballast Brook, Northern Banks Island, N.W.T.

Sand and gravel containing wood and detrital organic

horizons characterize the upper unit (Hills, 1969) or Beaufort Formation *sensu stricto* (Fyles, 1990-this issue) along the lower reaches of Ballast Brook on northern Banks Island (Fig. 8). In 1868 Heer described spruce cones (*Pinus MacClurii*) from the Ballast Brook region. A little over 100 years later similar cones were collected and described as *Picea banksii* (Hills and Ogilvie, 1970).

One of the exposures along Ballast Brook (Geological Survey of Canada locality C-5552) reveals an autochthonous peat bed that contains abundant, well-preserved mosses (Kuc and Hills, 1971). These and vascular plant fossils from strata below the peat at C-5552 are listed in Table 5. In the summer of 1990 additional macrofossil samples were collected at a site across the valley and upstream from C-5552, so the list in Table 5 will likely soon need revision. A surprising finding of the 1990 work is that the uncompressed wood in the Beaufort Formation at Ballast Brook (upper unit of Hills, 1969, and Matthews, 1987) represents trees that grew very slowly, much like trees in taiga areas today.

Beaufort Formation: Meighen Island, N.W.T.

Sand and gravel containing lenses of organic debris and the occasional autochthonous peat horizon interfinger with marine clay on the western part of Meighen Island. Fyles (1990-this issue) considers this entire package of sediments to represent the Beaufort Formation. The marine facies contain molluscs and foraminifera that provide the best available evidence of the age of the Beaufort Formation on Meighen Island (see Discussion, Age . . .).

The 42 types of mosses listed in Table 5 were identified by Kuc (1973). They all come from several samples collected along a single mossy, wood-bearing peat bed. The peat, representing partly forested peatland, contains the typical mosses of such a site, including *Ditrichum flexicaule*, *Dicranum leioneuron*, *Cyrtomnium hymenophyllum*, *Bryum pseudotriquetrum*, *Aulacomnium palustre*, *Drepanocladus uncinatus*, *Campylium polygamum*, *Calliargon giganteum*, *C. richardsonii* and *Tomenthypnum nitens*.

Vascular plant fossils listed in Table 5 come from several sites located both above and below the marine sediments. The list of taxa includes female cones of three species of pine (Hills, 1975): *Pinus itelmenorum* Vassk., a five-needle form;

P. paleodensiflora Dorof., a two-needle form; and *P. cf. funebris* Kom., another two-needle form similar to the extant *P. silvestris*.

The deposits also contain pine needles. None of the ones isolated to date are of the two-needle pine type. Most of the five-needle specimens have sparse to no serration on the needle margins and no stomata on the abaxial face and in cross sections reveal externally positioned resin canals. Fragments of large pine nuts, about the same size as those of *Pinus albicaulis* and *P. pumila*, are rare elements in some of the local floras. If the nuts and the needles come from the same species, they probably do not represent *P. albicaulis*, which has abaxial stomata. Thus it is likely that the nuts and needles represent the Asian species *P. pumila* or a related extinct species. *P. pumila* has closed cones that disintegrate after they fall to the ground (Critchfield, 1986), making it doubtful that its cones would preserve as fossils. Hence, the *P. itelmenorum* cones reported by Hills probably represent another five-needle pine species. In other words, the combination of cones, needles and nuts suggests that at least four species of pine grew on Meighen Island during Beaufort time. They were accompanied by both arboreal and shrub birch, poplar, alder, spruce, eastern cedar and larch.

Several of the Beaufort Formation sites on Meighen and Prince Patrick islands also contain fragments of the distinctive needles of another conifer — the Japanese umbrella pine *Sciadopitys* (Taxodiaceae). Similar needle fragments have been found in rebedded debris in interglacial sediments at Pasley River on Boothia peninsula (Fig. 1; Dyke and Matthews, 1987), although at the time of that report their identity was unknown. The Meighen Island and Prince Patrick fossils may also be rebedded from older deposits. However, *Sciadopitys* pollen occurs in the Late Pliocene part of marine cores near Greenland (e.g., de Vernal and Mudie, 1989); thus *Sciadopitys* may have grown somewhere in the Canadian Arctic Archipelago during the Pliocene.

Despite the investigation of a number of deposits and large collections of plant macrofossils, *Epipremnum crassum* has not been found on Meighen Island. We believe this means that it had become extinct in that area by the latter part of the early Pliocene. *Aracites globosa* is present in the flora. One fossil taxon that was not listed in the previous floral list from Meighen Island (Matthews, 1987) is *Crataegus*. The fossils were formerly provisionally referred to *Ilex*. If the specimens do represent *Crataegus*, they are markedly smaller than many of the extant North American species of that genus.

High-Level Alluvium: Ellesmere Island, N.W.T.

On Ellesmere Island 10-40 m of sand and gravel with rare organic horizons cap the eroded surface of the early Tertiary/late Cretaceous Eureka Sound Group. The alluvium was deposited prior to the down cutting responsible for the present valleys and fiords. J. G. Fyles, who first studied the deposits in the 1960s, has recently begun to reinvestigate the high-level alluvium ("high terrace sediments"; Fyles, 1962, 1989; Craig and Fyles, 1965) with the prime objective of locating sites that might yield plant and animal fossils of chronologic or paleoenvironmental significance.

Most of the samples are still under study, but the available evidence already shows that the high-level alluvium includes sediments as old as the Pliocene. We report here on selected

samples from several regions on Ellesmere Island (Fig. 10). The fossils listed under the heading "Beaver Pt." in Table 6 come from a site near the head of Strathcona Fiord where a lens of autochthonous peat and related detrital organic deposits are exposed over a distance of 1 km (Fig. 11). The peat contains beaver-cut wood and bones of what is probably an extinct beaver as well as an abundance of plant and insect fossils.

Scorpidium scorpioides dominates the bryophyte component of the Beaver Peat flora. Other species are less abundant, but most are typical of mineral-rich wetlands.

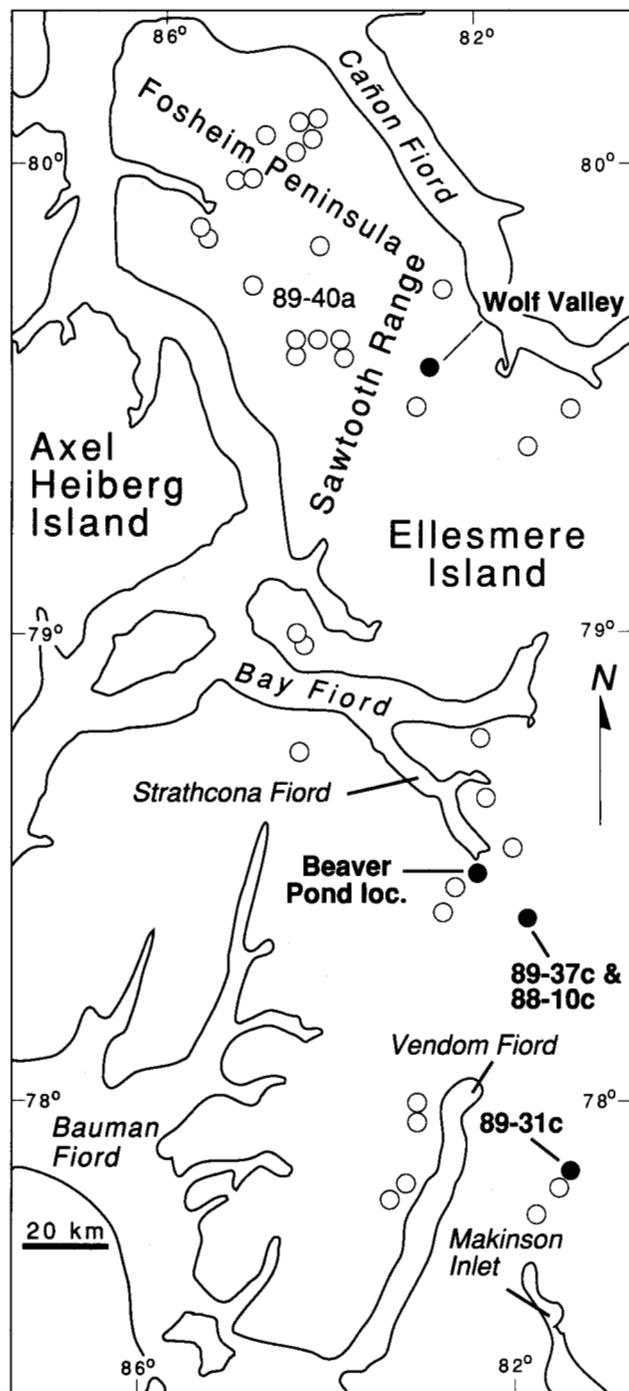


FIG. 10. Portion of Ellesmere Island (see Fig. 8) where the high-level alluvium has been studied. Circles indicate sites that have yielded wood or other plant materials. Black circles are sites referred to in this paper. Several of them are clustered around the site of the Beaver Pond Peat. See Figure 11 for details.

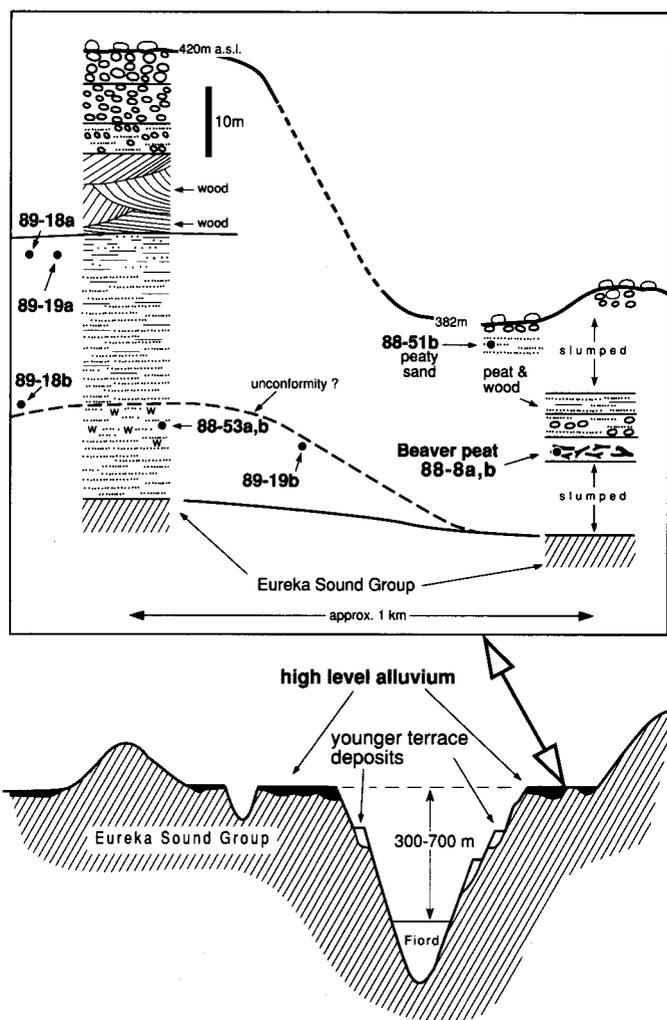


FIG. 11. Above: Stratigraphic setting of organic samples in the vicinity of the Beaver Peat locality, Strathcona Fiord, Ellesmere Island. Samples referred to in the text are shown in bold lettering. Based on a sketch by J.G. Fyles. Below: general stratigraphic setting of high-level alluvial deposits on Ellesmere Island.

Additional evidence of an older age for some of the high-level alluvial deposits comes from the floras labeled 37c/10c and 31c in Table 6. The most striking deviation from the Beaver Peat flora is abundance in the combined 37c/10c flora of *Epipremnum crassum*, *Cembrae* type pine needles and unknown seeds or fruits labeled "Cyperaceae type A" (Fig. 3:5). The latter were particularly abundant in sample 89-37c. They are very similar to illustrations of fossils identified as Cyperaceae genus? from the mid-Miocene FASTERHOLT flora in Denmark (Friis, 1985).

Sample 88-10c (10c in Table 6) represents an *in situ* wet forest bed. This is indicated by the following features: 1) the abundance of spruce needles, seeds and cones; 2) rarity of aquatic mosses; 3) presence of seeds of mesic forest understory plants such as *Rosa*, *Lonicera* and *Boschniakia rossica* (Fig. 4:7); 4) rarity of *Carex* and many of the other taxa usually found in wetland deposits; and 5) an arthropod fauna (Matthews, 1989b) containing species typical of conifer duff.

Many of the mosses from 88-10c (Table 6) are taxa that would form the mossy carpet of a damp, perhaps muskeg-like, spruce-larch forest. They include the "feather mosses," as well as species typical of damp mineral soil (*Aulacomnium*,

Thuidium, *Philonotis*) and slightly acidic-to-neutral tree ferns (*Dicranum leioneuron*, *D. bonjeanii*, *Tomenthypnum nitens*). The mosses of modern boreal forest floors form a fairly consistent group adapted to the rigors of this microenvironment, and sample 88-10c includes all the common members (e.g., *Dicranum* spp., *Ptilium crista-castrensis*, *Pleurozium schreberi*, *Hylocomium splendens*), as well as *Rhytidadelphus triquetrus*, which is a frequent associate of the group in Ontario (LaRoi and Stringer, 1976).

Of the twelve moss species in the assemblage, five (*D. leioneuron*, *D. bonjeanii*, *Ptilium crista-castrensis*, *Rhytidadelphus triquetrus*, *Pleurozium schreberi*) have northern limits in the central or northern boreal forest; another (*Hylocomium splendens*) is represented by a large, tripinnate form typical of that species' forest growth-form; and two (*Dicranum acutifolium* and *Aulacomnium acuminatum*) now have arctic-alpine distributions and are very rare in heavily forested regions. The remaining four species are widely distributed.

Fossils in the column labeled WV in Table 6 come from several samples of an extensive peat horizon exposed at Wolf Valley on the Fosheim Peninsula (Fig. 10). The list portrays a flora much less diverse than the others from Ellesmere Island. To some degree the flora is even more impoverished than indicated. For example, both *Picea* and *Larix* are listed, but these records represent rare needle fragments that may be rebedded from older units. Note in Table 6 the absence of *Thuja* and *Pinus* and presence of *Glyceria*, *Alnus crispa* and *Nuphar*. The first two are common associates in other samples from the high-level alluvium. The last three do not grow on Ellesmere Island today and their presence shows that, regardless of the impoverished flora, the climate was warmer than at present. It may even have been warmer than during any of the late Quaternary interglacials (Matthews *et al.*, 1986).

Geodetic Hill, Axel Heiberg Island, N.W.T.

Fossils listed in Table 6 under the column labeled "Axel H. Island" come from a thin peat bed in gravel capping the early Tertiary Buchanan Lake Formation at Geodetic Hill on Axel Heiberg Island (Fig. 8). The moss peat is better preserved than organic zones within the Buchanan Lake Formation and, unlike the latter, contains no amber. Thus it is clear that the peat bed and enclosing gravel are considerably younger than the Buchanan Lake Formation and its well-known forest beds (McMillan, 1986).

The mosses from the peat are taxa that grow in shallow peaty depressions and are widespread in present northern boreal and arctic regions. The assemblage is similar to a presumed post-Beaufort age autochthonous peat from Green Bay on Prince Patrick Island (Matthews *et al.*, 1990b) and to Holocene peats from Victoria Island.

The peat did not contain any fossils of conifers. It probably formed at a tundra site, but one only slightly beyond the limit of trees, because some of the mosses are usually found in boreal regions. Some of the vascular plants, such as *Ranunculus lapponicus*, now have their northern distributional limit in the low arctic tundra zone. Well-preserved seeds of *Aracites globosa* also occur in the Axel Heiberg peat.

Other Sites

In addition to the sites and floras discussed above, several others are important for purposes of the following discussion

or have been discussed in adequate detail elsewhere. These sites, with brief comment on their floras or their potential significance, are listed in Table 7.

DISCUSSION

Certain common themes or problems have emerged from the compilation of these floristic lists. One concerns the question of the Eurasian elements in the late Tertiary flora of arctic America, and a surprising new finding in this vein is that some of the Palaeartic taxa were conifers. A related theme concerns extinction and the reason why certain plants became extinct in North America but not Eurasia. Finally, any recounting of the sort attempted here would be incomplete without some speculations on the age of the floras. Only by doing this will we begin to learn how the North American arctic flora changed during the late Tertiary — knowledge critical for understanding how present biomes came into being and, more important, how they might change in the near future.

TABLE 7. Additional fossil localities (not discussed in text)

Site	Comments
Burnt Hill Bluff, Yukon (Fig. 5)	See Schweger (unpubl.) for information on pollen. Macroflora not yet studied. Contains Burnt Hill tephra (not yet dated) and well-developed forest soil (Tarnocai and Schweger, 1991).
HH-231, Yukon (Fig. 5)	Lake sediments of probable same age (minimum: Matuyama) as unit 3 at Ch'ijee's Bluff over sands containing large wood and organic detritus.
CRH-47, Yukon (Fig. 5)	Plant insect and vertebrate fossils associated with undated Surprise Creek tephra; paleomagnetic data suggest Brunhes age.
CRH-94, Yukon (Fig. 5)	Miscellaneous plant insect and vertebrate fossils associated with Little Timber tephra (minimum fission-track age — 1.2 Ma) (Matthews <i>et al.</i> , 1987).
Worth Point, Banks Island, N.W.T. (Fig. 8)	See Vincent (1990-this issue) for information on this site. Plant macrofossils include species now found near the tree line. The tree line was formed of <i>Larix laricina</i> . Extinct plants such as <i>Aracites globosa</i> are missing; hence flora appears to be younger than the Kap København 2 Ma flora.
Haughton Astrobleme, N.W.T. (Fig. 8)	Dated as early Miocene by K-Ar on shocked rock (Gomaa <i>et al.</i> , 1987). Macrofossil flora contains pine, spruce and larch (Whitlock and Dawson, 1990-this issue).
Pasley River, Boothia Peninsula, N.W.T. (Fig. 1)	Interglacial sediments containing rebedded late Tertiary fossils, including <i>Tsuga</i> , <i>Sciadopitys</i> , <i>Hypericum</i> , <i>Abies</i> (Dyke and Matthews, 1987). Suggests a late Tertiary site may exist in the area.
Kap København, Northern Greenland (Fig. 1)	Two Ma flora and insect fauna (Bennike and Böcher, 1990-this issue; Bennike, 1990). Indicates presence of forest tundra in northernmost Greenland. Flora contains <i>Thuja</i> , <i>Taxus</i> , <i>Picea</i> , an extinct <i>Larix</i> and <i>Aracites globosa</i> but no pine.
Hutchinson Bay, Tuktoyaktuk Peninsula, N.W.T. (Fig. 1)	Holocene deposit 2 m asl contains rebedded (?) fossils such as <i>Abies</i> , <i>Alisma</i> , <i>Myrica gale</i> , and <i>Sambucus</i> , indicating a nearby Tertiary source (Matthews, 1988).

Pines in Late Tertiary Arctic North America

Three different types of pine are represented by the fossil needles found in the samples discussed above. A few fossil needles from Prince Patrick Island represent a two-needle species related to or conspecific with one of the species in the subsection *Contortae* (Critchfield and Little, 1966). Hills (1975) referred cones from the Beaufort Formation to *Pinus paleodensiflora* and *Pinus funebris*. Neither is in subsection *Contortae* and their needles are anatomically quite different from those of the *Contortae* type (Harlow, 1931). Hence, three types of two-needle pine (the two mentioned above and one similar to *P. contorta*) may have grown in the Arctic during deposition of the Beaufort Formation.

Fossil needles represent at least two groups of five-needle pine (subgenus *Strobus*). One type of needle has external resin canals that are contiguous with cells of the dermal region; the other type has medial canals surrounded by mesophyll parenchyma and not touching the border of the fibrovascular region. Many of the latter have three canals located at each corner rather than the normal two located near the abaxial face.

Strobus species have been divided into two subsections by Englemann: subsection *Cembrae*, with all or some resin canals in the medial position (*P. cembra*, *P. sibirica*, *P. koraiensis*) or both medial and external, as in *P. armandii*; and subsection *Eustrobi*, with external resin canals (*P. pumila*, *P. albicaulis*, *P. flexilis* and *P. parviflora*) (Critchfield, 1986). More recent classifications group the species having seed-retaining cones and wingless seeds (e.g., *Pinus pumila* and *P. albicaulis*), but Critchfield (1986) argues that wingless seeds and seed-retaining cones probably evolved independently in several unrelated lineages. In his opinion, Englemann's system better reflects the evolutionary relationships among *Strobus* pines. In addition to medially positioned resin canals, all of the *Cembrae* species (*sensu* Englemann) have Eurasian distributions, wingless seeds and, except for *P. armandii*, seed-retaining cones. Of the *Cembrae* species, *P. cembra* and *P. sibirica* can be distinguished from all other pines because the walls of the mesophyll parenchyma are nearly devoid of folds.

Within subsection *Eustrobi*, *Pinus albicaulis* and *Pinus pumila* may be distinguished by seeds usually lacking spermoderm and needles with abundant stomata on the abaxial leaf surface but lacking marginal teeth — *P. albicaulis*; seeds with a partial spermoderm covering, no stomata on the abaxial leaf surface and possibly a few marginal teeth — *P. pumila*. Of the two species, *P. albicaulis* is North American, often occurring in alpine areas, and *P. pumila*, the Japanese stone pine, is an Asian shrub species that occurs at alpine sites in the southern part of its range and at the tree line near the Arctic Ocean (Critchfield and Little, 1966).

Eustrobi type needles are the only ones of the five-needle type to be found on Meighen Island and several of the high-level alluvium sites on Ellesmere Island. The fortuitous occurrence of both seeds and needles at one of the sites associated with the Beaver Peat on Ellesmere Island supplies strong circumstantial evidence that either *P. pumila* or an extinct, closely related species was growing there during the Pliocene. We believe that *P. pumila* was also one of the five-needle pines growing on Meighen Island, and its growth habit and autecology mean it is most likely the pine that grew in the open, tundra-like environment represented by the

Niguanak plants and insects. *Eustrobi* type pine needles from Prince Patrick Island may represent one or the other of the tall growing white pines rather than *P. pumila*.

One of the most surprising results of this synthesis is the discovery that one or more species of *Cembrae* type pines once grew in arctic North America. All of the needles referred to subsection *Cembrae* display convoluted walls on the mesophyll parenchyma, so they do not represent either *Pinus cembra* or *P. sibirica*. Many of the needles from the high-level alluvium and some from Prince Patrick Island have three resin canals like the specimen illustrated in Figure 3:4. This is similar to the condition reported for the Korean white pine, *P. koraiensis* (Harlow, 1931). The only difference is that some of the fossils have two rows of stomata on the abaxial (dorsal) surface, while *P. koraiensis* is reported to have none (Harlow, 1931). Because of this and until such time as a more detailed study is conducted, we refrain from referring the fossils to *P. koraiensis*.

Pine needles of the *Cembrae* type are not restricted to the Beaufort Formation. They also occur at Lava Camp, Lost Chicken, the lower part of the Bluefish Section and unit 1 at Ch'ijee's Bluff. The Lava Camp and Lost Chicken records are especially significant because taken together they show that *Cembrae* type pines grew in North America from late Miocene until about 2 Ma. Sometime after 2 Ma (probably during the Quaternary) the whole group disappeared from North America.

Examination of the internal anatomy of pine needles should become a routine procedure in future studies of Neogene plant macrofossils. The excellent preservation of the fossils at many northern sites means that such analyses can be performed using nothing more than a sharp razor. Needles from older sites, or samples in which the needles are crushed, will necessitate microtomed sections, special mounting procedures and probably staining in order to observe critical anatomical characters.

Extinct Plants

Two taxa that occur in many of the floras discussed here are *Epipremnum crassum* and *Aracites globosa*. Both are tentatively referred to the family Araceae, but future studies may change this assignment (Madison and Tiffney, 1976). In any case, they both undoubtedly represent extinct species. The fact that some of the deposits reported on here are autochthonous allows us to speculate on the possible autecology of these extinct taxa.

The records of *E. crassum* from Ellesmere Island are the most northern yet recorded. Even though *Epipremnum* is presently a subtropical plant (Madison and Tiffney, 1976), *E. crassum* must have been able to survive in an arctic light regime. Gregor and Bogner (1984) suggested that *Epipremnum crassum* was a wetland plant like its modern relatives. Our findings support that assumption. In addition, we show that *Epipremnum* nearly always occurs in assemblages containing fossils of trees, usually several types of conifers. It probably could not grow on tundra but did grow in regions dominated by mixed coniferous forests. On the other hand, *E. crassum* may not have been a true forest floor species because it is conspicuously absent from one assemblage, sample 88-10c, representing a spruce-dominated forest floor. It is tremendously abundant and exceptionally well preserved in an adjacent sample (89-37c), which on the

basis of the other macrofossils appears to represent semi-aquatic conditions.

The *Aracites* seeds seen in many of the samples discussed here are similar to those referred to the species *Aracites johnstruppi* in the Soviet and European literature (e.g., Buzek *et al.*, 1985) and to *Aracispermum* by Matthews (1987). They appear identical to illustrations and descriptions of specimens initially referred to *Hippuris* (as *Hippuris globosa*) by Reid and Reid (1915). Bennike (1990) discusses the nomenclatural confusion associated with this taxon and proposes the new combination *Aracites globosa* (C. Reid & E.M. Reid) Benn.

Several of the autochthonous peats discussed here contain *A. globosa* fossils. The Axel Heiberg assemblage shows that it grew slightly beyond the tree line and therefore could tolerate a low arctic tundra climate. Sample 89-18b (Fig. 11), which is dominated by *Aracites globosa*, represents vegetation barely within the tree line. In contrast, the *Aracites globosa* at Lost Chicken grew well within the limit of trees, probably in a poorly drained opening within a lowland larch forest surrounded by upland forests containing five-needle pines and spruce.

Like seeds of *Epipremnum*, *Aracites globosa* seeds are quite buoyant in water. This enhances the chances that the seeds will be carried into rivers and deposited in alluvium. If *Aracites* seeds were passively transported and distributed in the same way and to the same degree as are *Potamogeton* and *Nuphar* today, then absence of *Aracites* in a large collection of fossils from floodplain alluvium is probably a valid indication that the plant was either not growing or very rare in the entire drainage basin. For this reason we attach chronological significance (see Age and Correlation) to the absence of *Aracites* fossils in the Cape Deceit Formation and at the Fish Creek site.

Endocarps of *Comptonia* occur in many of the floras discussed here. Many of these specimens differ from the extant North American species *C. asplenifolia* by possessing well-defined longitudinal ribs. Nikitin (in Baranova *et al.*, 1976) lists several different ribbed species and varieties from the Mamontova Gora flora in the U.S.S.R. Numerous ribbed endocarps displaying great variation in rib development and size occur in single samples from the high-level alluvium on Ellesmere Island and the Cone Bluff locality in Alaska. Single specimens from such collections might be referred to different species, but when the whole series is seen, it is obvious that they represent a single extinct species with highly variable endocarp morphology. The fossils probably belong to one of the species already named from the U.S.S.R. (e.g., *C. baranovae* Nikit. or *C. longistyla* [Nikit.] Dorof.), but a positive statement will not be possible until type material is examined.

Two other types of *Comptonia* apparently occur in the floras discussed here. One, from the Mary Sachs gravel, is similar to illustrations of *C. debilis* V. Nikit. from the Mamontova Gora flora (Nikitin, in Baranova *et al.*, 1976). The other type, one specimen of which is illustrated in Matthews (1987), occurs in the Beaufort Formation at Ballast Brook and in one of the high-level alluvium samples from Ellesmere Island. It is superficially similar to *C. asplenifolia* but probably represents an extinct taxon.

Endocarps of *Comptonia* are as buoyant in water as seeds of *Aracites*. In addition they have thick walls, making them very tough and likely to survive transportation in rivers. This combination of characters explains why *Comptonia*

endocarps are so abundant in some samples or are practically the only fossils remaining when fossil preservation is poor. It also means that *Comptonia* endocarps are very likely to be rebedded from older deposits.

The tables show (bold-face type) many other taxa suspected to represent extinct genera and/or species. It will not be possible to make a final judgement for many of them until detailed study of type material is conducted.

Paleophytogeography

During the early Tertiary, North America was connected via a land bridge to Siberia and another across the enlarging North Atlantic to Europe. A major seaway in the U.S.S.R., the Turgai Straits, connected the arctic basin with the shrinking Tethys system. By Neogene time the connection across the North Atlantic was broken, or was at most a series of island stepping stones, and the Turgai Straits barrier had disappeared. A Beringian connection remained (Hopkins and Marincovich, 1984), meaning that the continents of the Northern Hemisphere were still much less isolated than at present. As well, the Arctic Archipelago was less insular than now. This combination of circumstances should have allowed easy exchange of flora and fauna between eastern Asia and the farthest reaches of the Canadian Arctic.

Many of the northern floras discussed here contain taxa that have previously been recorded from the Neogene of Asia. Some of the genera, such as *Weigela*, are presently extinct in North America; others now restricted to North America (e.g., *Dulichium*, *Diervilla*) once grew in Europe. The North Atlantic land bridge has been invoked to explain the former Holarctic distribution of such taxa (Tiffney, 1985), but now that fossils of many of them are being discovered virtually on the doorstep of Beringia, that area represents a more likely migration route.

The land bridge connecting east Asia and Alaska was in place when Lava Camp sediments were deposited. In order to explain the apparent North American character of the Lava Camp flora, Hopkins *et al.* (1971) proposed the existence on the land bridge of a tundra barrier that would have isolated forests of Asia and North America. We show here that forests existed almost to 80°N as late as the Pliocene, and Zyryanov (unpubl. data) concludes that a dark coniferous forest grew near the present-day New Siberian Islands during the late Miocene. It seems highly unlikely, in view of such findings, that tundra would have existed on the Bering land bridge in Late Miocene time. Besides, the need for such a barrier no longer exists because some of the new fossils found at Lava Camp (e.g., *Cembrae* type pine and *Paliurus*) show that its flora was not as distinct from that of contemporaneous east Asia as once thought.

The data presented here show that late Tertiary forests in the North American Arctic were floristically richer than modern boreal forests. This richness was due in part to the presence of many taxa now confined to Eurasia. Why do some plants (e.g., *Sambucus*, *Dulichium*) that once grew in arctic North America and Asia survive today in North America, while others (e.g., *Pinus pumila?*, *Cembrae* type pines, *Weigela*) are extinct there? The answer is surely related to the differing styles of Quaternary glaciation in North America and Eurasia. In the former area ice tended to block the southward retreat of plants living in the Arctic; in east Asia glaciation posed much less of a barrier. If this is the

answer, then we must also conclude that those plants that did not survive in North America were those that probably grew only in the Arctic. If they were wider ranging during the late Tertiary, they probably would have survived the disruptions of the Quaternary.

Compared to vascular plants, the arctic moss flora has changed relatively little since the late Tertiary. The fossil bryophyte flora reported here consists of over 80 species, and over 75% of these persist in arctic North America today. The remainder occur in boreal regions. No extinct mosses have been found at late Tertiary sites, and in only a few cases have atypical forms of common genera provoked comment (Kuc, 1973; Kuc and Hills, 1971; Ovenden, 1989). A long-term goal of one of the authors (Ovenden) is to develop a paleoenvironmental scenario that will reconcile the apparent stability of the arctic moss flora with the evident mutability of the vascular plant flora.

Age and Correlation

Figure 12 represents a preliminary attempt to correlate the floras discussed above. Floras that are independently dated by radiometric and/or paleontological criteria other than botanical are indicated by bold-face type. Note that very few of the floras are dated and that even fewer (those enclosed in boxes) occur in stratigraphic superposition.

The Cape Deceit Formation and Fish Creek beds are shown as nearly a million years younger than is reported in Repenning *et al.* (1987). Their floras are "modern," i.e., lack extant southern plants like *Sambucus* and extinct forms such as *Aracites globosa*, both of which are known to occur in other subarctic and arctic assemblages as young as 2 Ma. Admittedly, there is a danger in relying on such negative evidence, especially when sample size is small (as in the case of Fish Creek); however, the suggested age of the Cape Deceit Formation in Figure 12 is in line with Sher's (1986) estimate of its age, and recently Kaufman *et al.* (1990) have published Sr isotope results suggesting that the Fish Creek beds may be much younger than 2.4 Ma.

Repenning (1989) believes the Kutuiakh suite from the Krestovka River in northeastern U.S.S.R. (1.8-2.7 Ma) is correlative with some of the Fish Creek beds, but the Kutuiakh flora is markedly different. Among other plants, it contains both *Epipremnum crassum* and *Sambucus* (Nikitin, 1979a). Although there are several possible explanations for such a deviation, one of them is what we show in Figure 12: the Fish Creek beds as significantly younger than Kutuiakh.

Placement of the Niguanak flora in Figure 12 is very tentative. It may be a northern equivalent of the Lost Chicken flora or possibly younger than Lost Chicken. More study of floral and faunal remains is required in order to settle this question.

The flora from sample B at the Bluefish exposure is similar to the small macrofloras from the Begunovskia and Kutuiakh suites on the Krestovka River (Nikitin, 1979a). McCourt (1982), noting palynological similarities, suggested that unit 2 and/or unit 3 at Ch'ijee's Bluff might correlate with units 3-8 (and sample B) at the Bluefish section. But *Epipremnum* has not been found at Ch'ijee's Bluff, possibly an indication that the entire Ch'ijee's sequence is younger than unit 6 and sample B at Bluefish. On the other hand, *Pinus Cembrae* type needles and cones of a two-needle pine do occur in unit 1 at Ch'ijee's Bluff, so it is also possible that unit 1 is much

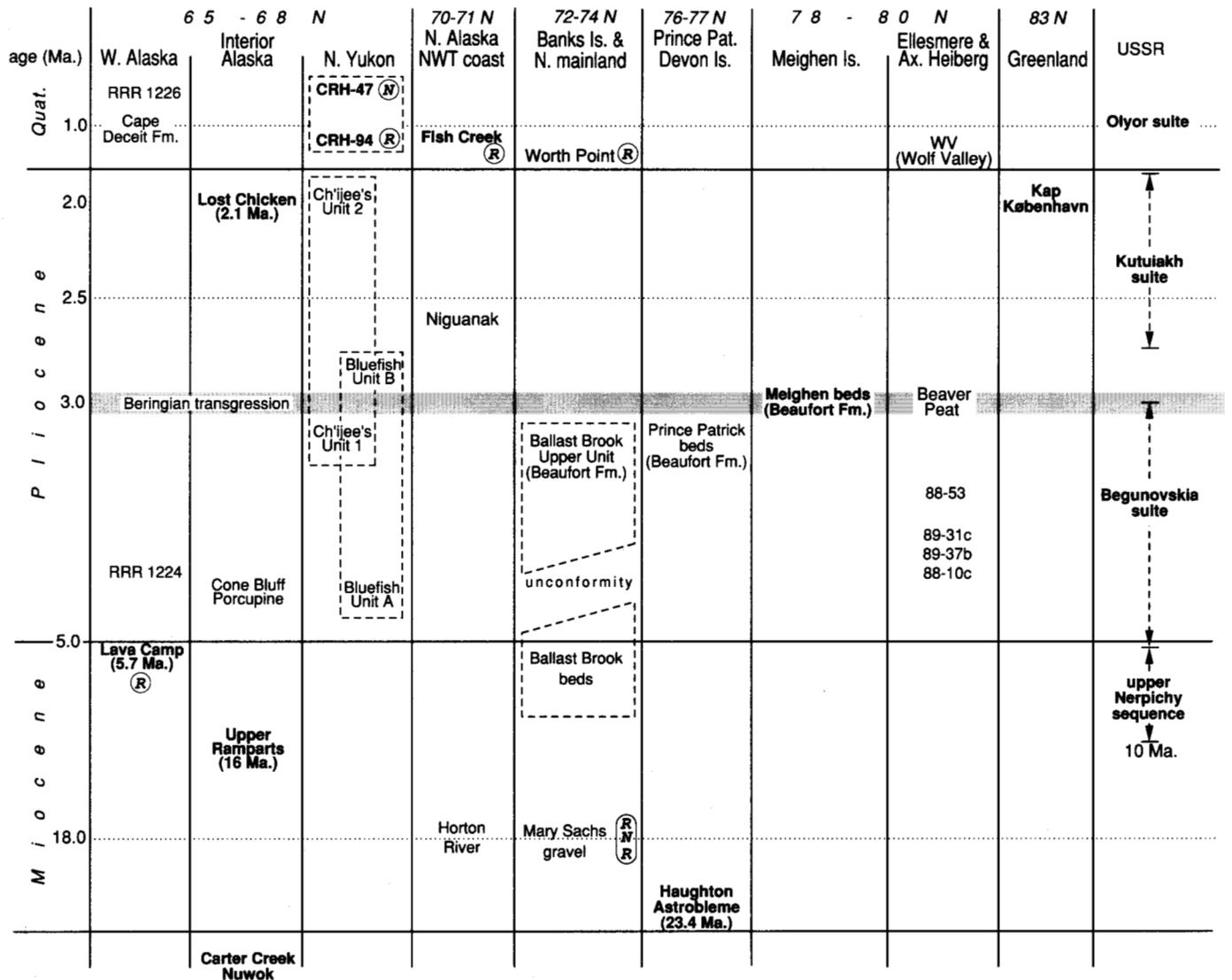


FIG. 12. Tentative correlation chart for samples mentioned here. Columns are arranged according to approximate latitude (except U.S.S.R. sites). Sites in bold-face text are those for which independent dates are available. Circled *R* and *N* indicate magnetic polarity, if known. Samples enclosed in dashed boxes are ones for which stratigraphic context (as shown) is known. Age of U.S.S.R. sites is from Baranova and Biske (1979) and Y. Zyryanov (letter to Matthews, 1990).

older than Bluefish sample B and that there is a great age difference between Ch'jee's units 1 and 2, with Bluefish unit 6a (and sample B) being of intermediate age (Fig. 12).

Hills (1975), relying chiefly on larger macrofossils such as cones and *Juglans* nuts, proposed a Seldovian age (late early and early Middle Miocene) for the sediments now called Mary Sachs gravel (Fyles, 1990-this issue). In support of this conclusion we note the known ranges of other taxa from Mary Sachs gravel. In east Asia *Metasequoia* last appears in the upper Miocene; *Sagisma* in the lower Miocene; *Actinidia* and perhaps *Taxodium* as late as mid-Miocene (Nikitin, 1979b). In contrast, the oldest Asian records of *Epipremnum crassum* and *Aracites* are apparently early Miocene. Taken together, the ranges of these taxa call for an early Miocene age. Independent dating is still required and may be realized when the minor magnetic polarity fluctuation within the sequence (Fig. 12; Barendregt and Vincent, 1990) is found in a dated marine sequence.

Several lines of evidence contribute to our estimate of the age of the Beaufort Formation on Meighen Island. 1) The Meighen Island marine unit contains fossils of *Arctica*, an Atlantic mollusc that probably became extinct in the Arctic Basin shortly after the Beringian transgression at about 3 Ma. 2) Foraminifera from Meighen Island suggest an age younger than the Miocene but older than approximately 2.4 Ma (McNeil, 1990-this issue). 3) Sr isotope analyses of *Arctica* shell fragments from Meighen Island place the age of the marine unit at between 2.5 and 5.1 Ma (Kaufman *et al.*, 1990; Matthews *et al.*, 1990b). And finally 4) Brigham-Grette *et al.* (1987) cite evidence suggesting that climate cooled markedly shortly after deposition of the marine unit and has remained cold ever since. This means that the Meighen Island marine beds most likely represent the last Pliocene interval of warm climate, which occurred about 3 Ma (Dowsett and Poore, 1990). Marine sediments in the Beaufort Formation on Meighen Island probably represent a eustatic high stand

of sea level, and the last such event in the world also occurred at approximately 3 Ma (Cronin, 1990).

Absence of interbedded marine sediments or other independent age criteria makes dating the Beaufort Formation deposits on Prince Patrick Island and on northern Banks Island difficult and speculative. Inevitably, one is forced into comparisons with the Meighen Island flora, and this involves assumptions and conclusions concerning the reason for the differences between the Meighen flora and those from Prince Patrick and Banks islands.

The Prince Patrick and/or Ballast Brook floras contain taxa such as *Cembrae* type pine, *Epipremnum*, *Microdiptera/Mneme*, *Cleome* and *Metasequoia*, which do not occur on Meighen Island. These distinctions could be viewed as evidence that Prince Patrick and Ballast Brook deposits are significantly older than Meighen Island. But it should be noted that none of these taxa dominates the Prince Patrick and Banks Island assemblages and some of them, such as *Epipremnum*, are quite likely to survive several cycles of rebedding. In other words, the floristic differences among the various Beaufort sites could be due to rebedded older fossils, leaving open the possibility that the floras are actually of approximately the same age.

Another explanation for the floristic distinctions of Beaufort Formation sites is that they reflect a latitudinal gradient (Hills, 1975), and Meighen Island, the most northern site, does have the most depauperate flora. However, such distinctions could also arise from differences in the continentality of the sites. Meighen Island was a maritime site around 3 Ma, while both northern Banks Island and especially the region from which most Prince Patrick Island samples come (Fig. 9) were probably tens to hundreds of kilometres inland, because the entire region of the western archipelago was at that time less fragmented than now.

Further complicating comparison of Beaufort Formation floras is that the plants listed from all three regions are pooled lists based on a number of local floras. The lists probably mask differences of chronologic significance. For example, if we were comparing the Meighen Island pooled flora with that from only the Green Bay site on Prince Patrick Island (Matthews *et al.*, 1990b), we would note their similarity and possibly conclude that they were about the same age. They may be, but it might be wrong to assume this was also true of the other Prince Patrick local floras.

The floral evidence does show that it is highly unlikely that the Beaufort Formation on Prince Patrick and northern Banks Island is younger than that on Meighen Island. It may be the same age or slightly older, as shown in Figure 12. Contrary to the suggestions in Hills (1975) and Fyles (1990—this issue), we do not believe the Beaufort Formation is as old as the Miocene. In other words, in terms of the Cook Inlet stages, the Beaufort Formation *sensu stricto* is entirely Clamgulchian in age (Wolfe, 1981).

Study of the stratigraphy and fossils from the high-level alluvium on Ellesmere Island is still in a nascent state. Nevertheless, the floras from various sites already suggest that the deposits span a great deal of time. Floras containing a number of extinct taxa, such as *Epipremnum*, *Decodon*, *Paliurus* and *Cembrae* type pines probably predate the Meighen Island Beaufort deposits (unless, of course, the absence of these taxa at Meighen Island is due to maritime influences). Sample 88-53, grouped with the Beaver Peat flora in Table 6, probably falls in this class; note (Fig. 11) that it

comes from below what is thought to be an unconformity in the sequence.

Floras compositionally similar to those associated with the Beaver Pond occur at a number of the high-level alluvium sites. Many of them appear to represent near tree line conditions. Floristically they are similar to floras from Meighen Island and are considerably richer than the 2 Ma Kap København flora. In Figure 12 we propose an age of about 3 Ma. Fortunately the Beaver Peat contains vertebrate fossils, which when studied should provide more definitive dating criteria.

The flora from Wolf Valley is an example of a third floral class from the high-level alluvium. It represents a warmer climate than at present but floristically is less diverse than floras of the Beaver Peat or Meighen Island type and even less diverse than the Kap København flora. Because of this, the Wolf Valley deposits are judged to be younger than 2 Ma (Matthews, 1990). Alternatively, the WV flora might represent a cool (i.e., floristically impoverished) period early in the Pliocene. If so, it would falsify a basic assumption used for dating late Tertiary floras, i.e., that the younger floras are the most impoverished.

When the time of extinction of plants like *Epipremnum crassum*, *Aracites globosa* and Cyperaceae Type A is established, their fossils should provide much better evidence for dating late Tertiary deposits than floristic comparisons. But dating by "last appearance" of a taxon also has problems, because extinction of a plant — particularly one that grew in the Arctic — is likely to be diachronous. *Epipremnum crassum* almost certainly became extinct on Ellesmere Island before the late Pliocene, when it disappeared from northern Europe (van der Hammen *et al.*, 1971), but how much earlier? How much earlier did *Aracites* disappear from Ellesmere Island than farther south, where it persisted until the early Quaternary (in Labrador, Klassen *et al.*, 1988; Finland, Aalto and Hirvas, 1987)?

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