Methods in Quaternary Ecology #3. Plant Macrofossils

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Summary

Plant macrofossils consist of reproductive and vegetative plant parts visible to the un-aided eye. Lakes and peatlands are the most common repositories for the preservation of Quaternary plant macrofossils; however, natural tar seeps, calcareous nodules, spring deposits, packrat middens, and fossil dung are important sources of plant remains also. In Canada, the first plant macrofossils were collected in the mid-1800s, with a brief period of activity around 1900 before the beginning of modern Quaternary plant macrofossil analyses around 1960. Taphonomic studies indicate that plant macrofossils can be transported, sorted and redeposited long distances, which complicates paleoecological reconstructions. Plant macrofossils are valuable in geological studies of environmental history and climatic change; however, the use of plant macrofossils for biostratigraphic correlation must await further research. Four broad phytogeographic patterns are recognizable on the basis of Quaternary plant macrofossil records in Canada, and plant macrofossils can be used to trace the evolutionary origins of the modern flora.

Introduction

Almost everyone has observed plant macrofossils in the making, be it leaves floating on a lake in the autumn, once forested lands flooded by dams and reservoirs, drifted plant debris around river inlets and tidal marshes, or perhaps some have seen the woodrat in the twilight hours busily gathering food and material for its nest. All of these processes contribute to accumulations of plant parts that may be preserved for many years or even millenia.

Macroscopic plant remains were discovered in Quaternary deposits over 200 years ago (Mannion, 1986a). Subsequently, the identification of plants by their macroscopic remains has grown into an important and useful branch of Quaternary ecology. In contrast with many pollen and spores, macrofossils are more readily identified to the species.

A macrofossil is any plant part which is visible to the naked eye and which becomes incorporated into a sedimentary sequence or geological deposit. Identifiable plant macrofossils often include reproductive structures such as seeds, bracts, cones, sporangia, megaspores, and complete inflorescences or the vegetative parts of plants such as wood, twigs, leaves, and rhizomes. Macroscopic remains of bryophytes, algae, and fungi are common, but details of their role in Quaternary ecology are dealt with in other papers of this series.

This paper reviews potential sources for plant macrofossils, field sampling techniques, and laboratory processing procedures. The role of plant macrofossils as indicators of Quaternary environments and biostratigraphy, and their use in assessing the phytogeographic and evolutionary origins of the modern flora is discussed. Plant macrofossils have important implications for archeology and paleoethnobotany, but their use in these fields is not considered here. The geographic focus is Canada. Recent reviews give details on the use of plant macrofossils in Europe (Dickson, 1970; Birks, 1980; Wasylikowa, 1986; Grosse-Brauckmann, 1986; and Mannion, 1986a,b,c).

Historical Development

The first observations of macroscopic plant remains were made by workmen clearing and digging drainage ditches in peatlands for agricultural expansion in the early 1800s in northern Europe (Barber, 1981). In Canada, the first notice of plant macrofossils in peatlands was not until Ganong's (1891, 1897) investigations in New Brunswick.

The recording of plant macrofossils from Quaternary geological formations in Canada began with Dawson's paper in 1857. He reported fossil wood, leaves and marine algae in calcareous concretions from what today are known as Champlain Sea deposits near Ottawa (Figure 1).

Plant macrofossils did not achieve much impact in geology until the 1870s and 1880s, though Dawson (1857, 1866) in Canada, Lesquereaux (1859) in America, and Heer (1862) in Britain made new discoveries in the intervening period. Real interest in plant macrofossils from geological deposits began in 1870 in Sweden with Alfred G. Nathorst (1873), and subsequently Andersson (1888, *vide* Tralau, 1963) in Scandinavia, Weber (1891, *vide* Tralau, 1963) in Germany, and Reid (1892, *vide* Tralau, 1963) in Britain. Hollick (1892) and Knowlton (1896) in the United States and Dawson and Penhallow (1890) in Canada made the first contributions in North America. These early studies concentrated simply on compiling species lists with little regard given to the stratigraphic position of the fossils. Consequently, it is difficult to ascertain the age of these early plant records as many stratigraphic descriptions are incomplete or inaccurate, and most sites long since have changed or disappeared. Perhaps the most significant contributions made during this early period of investigation are the remarkably accurate paleoenvironmental reconstructions (Warner, 1986).

With the advent of pollen analysis around 1920, attention was diverted from plant macrofossils in North America. Nonetheless, in Europe, Knud Jessen maintained the tradition of plant macrofossil analysis, and successfully demonstrated the merits of combining the stratigraphic and chronological precision of pollen analysis with the taxonomic detail of plant macrofossils (Jessen and Milthers, 1928). One paper on plant macrofossils from an interstadial deposit

2 cm

Figure 1 *Purported* Populus balsamifera *leaves in concretions from Green Creek, Ottawa reported by Dawson in 1866 (Redpath Museum # 7407). These specimens were figures 2 and 3 in his 1866 paper.*

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Figure 2 *(above)* *Fossil middens of* Neotoma cinerea *from Interior British Columbia. Such middens serve as urination perches making them hard, dark and shiny, thereby preserving a varied assortment of plant macrofossils. These specimens are about 1110 years old. They contain* Pseudotsuga menziesii *needles,* Juniperus scopulorum *branches, and Rosaceae thorns (Specimens collected by R.J. Hebda).*

Figure 3 *(above)* *The earliest sieve apparatus for extraction of plant macrofossils designed by Andersson (1892). A hose is attached to the inflow spout at the base, the water is circulated in the bowl and net (1), the fine debris floats off and is caught on a screen (2) (after Backman, 1965). Some laboratories in Scandinavia continue to use this apparatus today.*

Figure 4 *(right)* *Representative plant macrofossil diagram from a late Quaternary site on eastern Graham Island, British Columbia (from Warner, 1984b). Five local macrofossil zones can be recognized. Generally, the sequence suggests wet sand habitats along a pond margin with* Juncus, Sagina saginoides-*type, and* Rumex, *followed by an increase in wetland and submerged vegetation such as* Chara, Nitella, Potamogeton filiformis, *and* Ranunculus aquatilis-*type, which ended with development of emergent aquatic and marsh communities with* Sparganium minimum-*type,* Scirpus, *and* Potamogeton pusillus-*type.*

CAPE BALL, SECTION 81-C-2
Graham Island, Queen Charlotte Islands

near Vancouver, British Columbia was published during this period (Draycott, 1948). This was the only paper until the first papers appeared from the present period of plant macrofossil investigations (Terasmae, 1959; Terasmae and Fyles, 1959; Schofield and Robinson, 1960; Ritchie and DeVries, 1964).

Sampling Procedures and Laboratory Methods
Abundant and well-preserved plant macrofossils occur in any natural environment where aerobic activity has been minimal, accumulation of enclosing materials was rapid, and deposition was in a low-energy environment. Lakes and peatlands provide the most common repositories for plant macrofossils. Plant macrofossils are most valuable when analysis can be performed in conjunction with other paleoecological indicators and on samples in stratigraphic sequence from cores, monoliths or open faces. Inter- and post-glacial deltaic, alluvial, colluvial and diamicton deposits provide other opportunities to collect stratigraphic plant macrofossil samples.

Less conventional, non-stratigraphic sources for plant macrofossils include calcareous nodules such as those in post-glacial Champlain Sea deposits near Ottawa or purported occurrences in the Sangamonian Don Formation at Toronto (Penhallow, 1904).

Packrats, or woodrats *(Neotoma)* build bulky dens in caves, cliffs and river canyons in British Columbia and throughout the United States. Their waste piles or middens usually contain a rich assortment of plant fragments which can be preserved for thousands of years in the arid scrublands and deserts (Figure 2). Fossil ground squirrel, mammoth and giant ground sloth dung contain plant remains *(i.e.*, Mead *et al.*, 1986). In the United States, calcareous spring deposits and tar seeps are important sources of plant macrofossils (Haynes, 1985). Among the most spectacular plant macrofossil records are purported 9000 year old seeds that germinated after being thawed and planted (Porsild *et al.*, 1967).

Storage and extraction of plant macrofossils in the laboratory varies with the nature of the sample. Wet field samples should be frozen or refrigerated, but they can be stored unrefrigerated for several months if sealed tightly to prevent dessication. Dry field samples should be kept dry until processing. Wet samples are preferred over dry ones as the wet macrofossils are less readily damaged during processing and analysis.

Extraction of fossils is relatively simple. Washing on a screen (usually 250 μm mesh) with a gentle jet of warm tap water sometimes after soaking overnight in water is usually all that is required for the majority of samples (Figure 3). A nest of sieves of different mesh sizes may be used when large volumes are processed. Chemicals should

be avoided if at all possible, and when stubborn samples are involved, treatment for a few minutes in a mild detergent, a weak base *(i.e.*, KOH) in the case of peats, or weak acids *(i.e.*, HCl) in the case of calcareous sediments, can be used. Treatment with HNO_3 and H_2O_2 as advocated by Wasylikowa (1986) is not recommended because these chemicals can degrade plant remains. Submergence in an ultrasonic bath for about one minute to break down samples with no apparent damage or alteration to the macrofossils is preferred over chemical treatments.

The retained residue is sorted in water under a binocular microscope (magnification 8 to 40×). All identifiable remains are stored in 95% ethanol and glycerine in stoppered vials or in glycerine in plastic boxes. One or two drops of phenol can be added to prevent fungal growth.

The identification of plant macrofossils is based on comparison with modern reference collections. There are a number of publications containing photographs and drawings of fossil specimens. Montgomery (1977) is a valuable aid for southern Canadian floras. Delcourt *et al.* (1979) give a comprehensive bibliography of seed atlases and other publications useful for plant macrofossil identification.

Plant macrofossil data are most conveniently presented on a graph, with relative frequencies or macrofossil concentrations on the abscissa and depth on the ordinate axis (Figure 4). For leaf or stem fragments, or other plant remains that are difficult to count accurately, their presence can be recorded by an abundance scale. In some cases, tables or species lists are adequate.

Taphonomy and Interpretation of Plant Macrofossil Data
Generally, it is assumed that plant macrofossils are deposited not far from the parent plant, thereby making them valuable paleoecological indicators. However, in the case of many environments, the initial place of rest is temporary, and the plant remains can be transported some distance before being fossilized at the study site.

Plant macrofossils are the end product of processes that lead to their incorporation and preservation in the sediment. Consequently, the plant fossil assemblage represents only a fraction of the total flora that lived at the time of deposition. Knowledge of the factors that influence the accumulation of potential plant macrofossils in sediments can be understood best by observing modern processes. Such factors include natural biotic dispersal mechanisms and seed productivity, dynamics of stream and river hydrology, origin of storm flotsam accumulations on beaches or winter ice, or woodrat foraging habits.

Most macrofossil assemblages in Canada have been deposited in or by water.

Numerous studies have demonstrated the capabilities of streams and rivers entering lakes to carry potential plant macrofossils great distances (Drake and Burrows, 1980; Hill, 1981; Holyoak, 1984; Spicer and Wolfe, 1987). Plant remains in montane lakes are particularly conducive to long-distance transport as streams may carry remains from high elevations to lowland lakes. Differentiation of distant *versus* local fossil components is nearly impossible, and perhaps the best way is simply to be aware of retransport possibilities, most often reflected by the sedimentology of the enclosing deposits. Small lakes and ponds lacking surface feeder streams most likely contain locally derived plant remains.

Potential plant macrofossils are affected by both water and biological sorting during transport and deposition (Spicer, 1980). Consequently, sorting can lead to the preservation of biased assemblages and misleading paleoecological inferences. Plant remains reflect the hydrodynamic characteristics of the site, in that low-energy environments where settling velocity is slow, contain small or more delicate plant parts and high energy environments tend to yield the more resistant seeds, cones and wood (Spicer, 1980, 1981; Collinson, 1983; Ferguson, 1985; Spicer and Wolfe, 1987). Consideration of transport and sorting processes aided in the interpretation of plant macrofossils in a late Quaternary deltaic sequence in southern Ontario as these processes probably contributed to a mixed assemblage of plant species which do not live together in the same vegetation zone today (Warner and Barnett, 1986). However, only sorting and little, if any, transport was apparent from macrofossils in another deltaic deposit in northern Ontario (Bajc *et al.*, 1986). Problems of interpretation are compounded with sub-till organic deposits where the physiography of the pre-glacial landscape is often unknown. Retransport of plant macrofossils may produce incongruent pollen and plant macrofossil assemblages, though in his early studies in the Yukon Territory, Matthews (1975) considered only the pollen to be retransported.

Wind can contribute to transport and sorting by regulating the size or type of leaves that may fall on a lake, by carrying seeds that are adapted to wind dispersal, or by blowing plant macrofossils over flat snow and ice covered landscapes (Spicer, 1981; Glaser, 1981; Ferguson, 1985).

Reworking of deposits may mix macrofossils that are older than their contemporary assemblages. A recent study of plant macrofossils in alluvial deposits in the Mississippi River Valley demonstrated the dating and interpretation problems of the older components in such assemblages when only younger components fortuitously were dated (Givens and Givens, 1987). Matthews

et al. (1986) discussed the possibilities of mixed Tertiary and Quaternary fossils in deposits in Arctic Canada. One site in southern Ontario revealed that a discordant radiocarbon date on wood was probably due to reworking and incorporation of the older wood into a much younger plant assemblage (Warner and Barnett, 1986). Karrow et al. (1977) described what are thought to be Middle Wisconsinan plant remains in a Late Pleistocene esker deposit, suggesting retransport in glacier meltwaters. It seems that multiple radiocarbon dates on various materials will become necessary to ascertain the representativeness of plant macrofossils where retransport is likely. In at least one instance, Warner et al. (1987) obtained several radiocarbon dates on a Holocene macrofossil assemblage preserved in alluvial sediments and found good consistency among the dates, which suggests that reworking is not always a problem. Other obvious examples of reworking is the presence of wood in till or peat balls in ice-contact deposits (Heusser, 1973; Berti, 1975).

Further studies are needed to understand the origin of plant macrofossils in other less conventional deposits. The genesis of calcareous concretions such as those at Green Creek remains a mystery (Gadd, 1980).

Some of the most useful taphonomic studies involve surface samples from lakes (Birks, 1973; Dunwiddie, 1987) and peatlands (Great-Rex, 1983). For example, among submerged aquatics, Najas flexilis seeds are over-represented because they produce prolific quantities annually, while perennial species such as Brasenia schreberi produce far fewer seeds in relation to its cover abundance (Birks, 1973). In contrast to lakes, where seeds can be transported around the basin, seeds in surface peats generally originate from plants within one metre of the sampling point, except for wind-dispersed propagules (GreatRex, 1983).

Biostratigraphy

The most valuable use of plant macrofossils in Quaternary geology is in the reconstruction of local environments and the history of past climates. Interglacial and interstadial plant macrofossils can be exceptionally difficult to interpret. It appears that the majority have been reworked or transported to some degree, and dating control may be poor. An in situ sub-till peat deposited in a shallow backwater channel on the Queen Charlotte Islands, British Columbia is an exception. Plant macrofossils reveal gradual hydroseral development from open water, through a shallow peatland and open fen phase with Hippuris vulgaris, Veronica scutellata and Menyanthes trifoliata, which eventually transformed into a Sphagnum peatland with Selaginella selaginoides (Warner et al., 1984a). This sequence of peat development closely resembles Holocene developmental processes in the same region (Warner, 1984b), suggesting that the timing and ordering of

peat development were similar during Middle Wisconsinan time in this region.

By virtue of their aquatic habitat, macrofossils of submerged aquatic macrophytes perhaps are the most common elements in lacustrine fossil plant assemblages. Extensive waterbodies in the past, such as pluvial and proglacial lakes, meltwater channels, and small ponds probably provided an efficient dispersal network and diverse habitats for colonization. The rapidity with which aquatic macrophytes colonize newly deglaciated areas is often thought to be due to efficient dispersal agents, most probably water. Potamogeton filiformis (Figure 5a) and Zannichellia palustris (Figure 5b) are two examples of aquatic macrophytes that

spread rapidly into previously glaciated regions, and subseqently have undergone range contractions within the last 10,000 years in Canada. Two possible hypotheses may explain the previous more widespread distributions. The first suggests that local extinctions and range contractions reflect climatic responses to colder temperatures, and the second proposes that natural ontogenetic processes changed living conditions in the aquatic environment which lead to the demise and local extinction of certain aquatic species.

In view of the cosmopolitan distribution of P. filiformis and Z. palustris in habitats ranging from intertidal estuaries to alpine water bodies, climate does not have any apparent
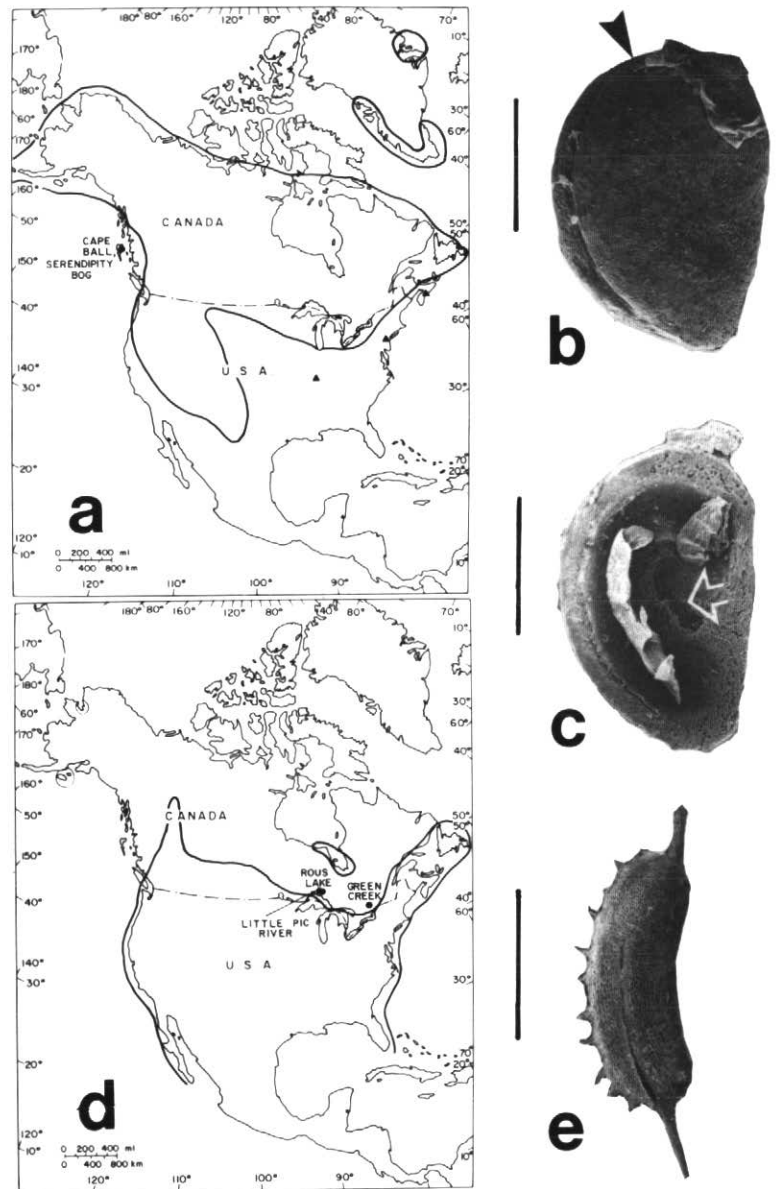
Figure 5 (a) Modern distribution of Potamogeton filiformis in North America. (After Mason, 1957; Porsild and Cody, 1980; Packer, 1983; Brayshaw, 1985). The dots (new records) and triangles (from Watts, 1979; Mott et al., 1982; Jackson and Miller, 1983) indicate Late Quaternary fossil localities. Fossil endocarps of P. filiformis, (b) arrow indicates saddle between beak and lid of endocarp, (c) arrow indicates characteristic cavity in endocarp loop. (d) Modern distribution of Zannichellia palustris in North America. (After Porsild and Cody, 1980; Riley and MacKay, 1980; Packer, 1983; Brayshaw, 1985). Dots indicate Late Quaternary range extensions. (e) Fossil seed of Z. palustris. Scale bars equal 1 mm.

direct influence on distributional bound-
aries. Both of these plants achieve their best
growth in shallow water bodies with high pH
and conductivities. The amount of free car-
bon dioxide in the water available for photo-
synthesis is limited. *P. filiformis* and *Z.
palustris* would be placed at a competitive
advantage over other aquatic macrophytes
not capable of using low amounts of free
carbon dioxide or bicarbonate as their car-
bon sources for photosynthesis. Other fac-
tors such as water depth, substrates,
turbidity, and dispersibility undoubtedly
played a significant role in regulating the
past distributions of certain submerged
aquatic macrophytes. Much more ecological
information is needed before aquatic macro-
phytes can be used as paleoclimatic indica-
tors (Warner, 1984a) although they seem to
have much potential in paleolimnological re-
constructions (Birks *et al.*, 1976).

The first biostratigraphic schemes were
developed on the basis of plant macrofossils
which gave rise to the Aspen, Pine, Oak, and
Alder zones in Scandinavia (Steenstrup,
1841, vide Mangerud *et al.*, 1974). Subse-
quently, European biostratigraphic schemes
have been replaced largely by pollen
chronologies with plant macrofossils playing
a subordinate role. The use of plant macro-
fossils for biostratigraphic correlations in
Canada is hampered simply by the paucity of

studied sites covering a wide geographic
and time range. The Sangamonian deposits
at Toronto, Ontario contain a number of
"southern" plant species whose modern
ranges have reached the southern fringes of
the Great Lakes region only since mid-
Holocene time and are not known from any
other older Quaternary deposit in North
America (Kerr-Lawson, 1985; Warner, un-
published). *Najas guadalupensis* has been
recovered from the interglacial deposits at
Toronto and from purported interglacial de-
posits in the James Bay Lowlands (Lichti-
Federovich, 1974). These are the only two
records for this taxon in Canada. Can we
assume temporal contemporaneity for the
two deposits? Probably this would be a mis-
leading conclusion in view of the reliability of
aquatic macrophytes as paleoecological
indicators.

Macrofossil studies on the north slope of
Alaska have proven useful in distinguishing
Quaternary and Tertiary deposits (Matthews,
1987b, c). The Tertiary deposits contain a
number of Old World plant taxa such as
Epipremnum and *Aracispermum* not re-
ported previously from North America. In
light of such ancient phytogeographic con-
nections during Tertiary time, some plant
macrofossils may prove useful as bio-
stratigraphic indicators to differentiate
Pliocene and Pleistocene deposits.

The study by Gagnon and Payette (1981) is
one of the finest examples of the use of plant
macrofossils in reconstructing past climates
(Figure 6). Over 700 *Larix* wood specimens,
on which 67 radiocarbon dates were ob-
tained, were collected near treeline in the
area of Nouveau Québec. *Larix* reached the
area around 4500 years B.P. Subsequently
between 3500-2700 and between 2000-1600
years B.P., it underwent two periods of north-
ward expansion up to 5 km north of its pres-
ent northern limit. Reproduction by only seed
makes *Larix* a good paleoclimatic indicator in
contrast with other northern trees such as
Picea which can reproduce vegetatively in
spite of climatically severe growing seasons.

Numerous studies have demonstrated the
merits of combining pollen and plant macro-
fossil analyses especially on lake and peat-
land deposits (e.g., Karrow *et al.*, 1975;
Hughes *et al.*, 1981; Mott *et al.*, 1981; Warner
et al., 1984b; Schwert *et al.*, 1985; Baker *et
al.*, 1986). Under certain circumstances the
enclosing sediments such as deltaic or al-
luvial sequences may be too coarse for the
preservation of pollen and only plant macro-
fossils may be preserved in paleosols, cal-
careous concretions, mammal dung, or
packrat middens. Plant macrofossils should
be studied concurrently with pollen if at all
possible to avoid biased or incomplete
paleoenvironmental reconstructions.

Phytogeography

As a rough approximation, about 2.5% of
Canada's modern flora has been found in
the Quaternary fossil record. Phyto-
geographic extinctions are not known in
Canada, and those reported by Penhallow
are referrable to modern taxa (Warner,
1986). Possible Quaternary extinctions oc-
curred in the United States (Beals and
Melhorn, 1961; Blackwell, 1982).

Published plant macrofossil records exist
for no less than 100 sites in Canada. Based
on published records and on some of my
unpublished work, four broad Quaternary
phytogeographic patterns are recognizable.
I have not included the early reports of
Dawson and Penhallow because these rec-
ords need verification (see references in
Warner, 1986).

Selected representatives in each group are:
(a) Northern range extensions during the
penultimate, Sangamonian Inter-
glacial:
Taxa in this group are from sites in
Ontario:
Chamaecyparis thyoides
Elatine triandra var. *americana*
Najas guadalupensis sensu lato
(Figure 7a)
At present, these taxa are restricted to the
eastern and southeastern Unites States.
Some taxa extended as far north as the
James Bay Lowlands, which suggests a ma-
jor contracted range since the last inter-
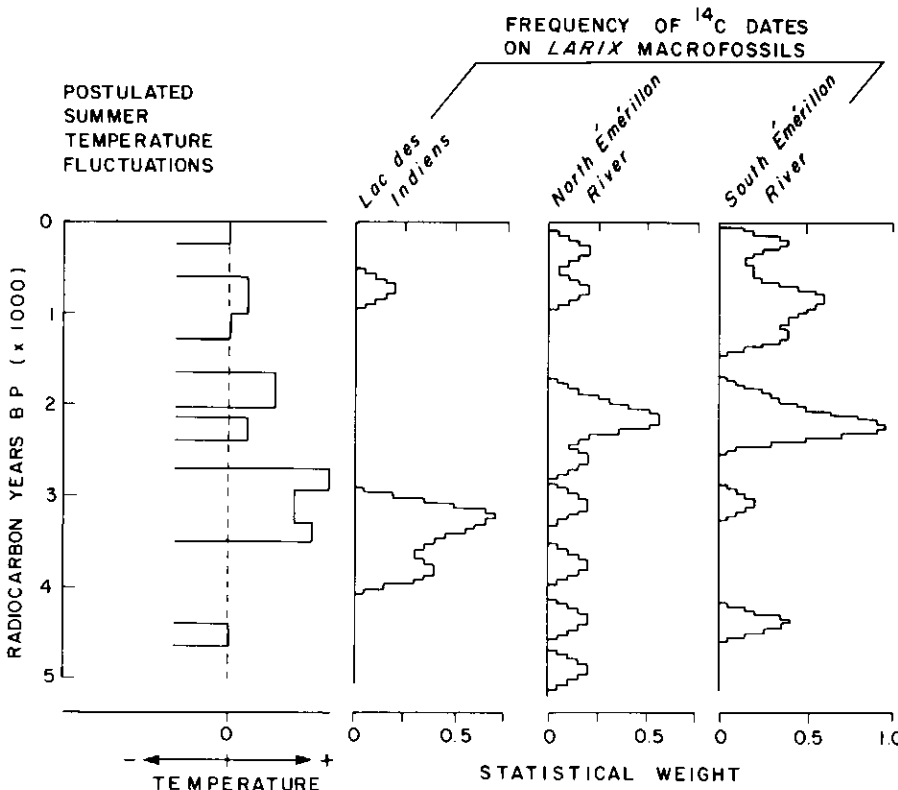glaciation. The presence of *Chamaecyparis*

FREQUENCY OF ¹⁴C DATES
ON *LARIX* MACROFOSSILS

POSTULATED
SUMMER
TEMPERATURE
FLUCTUATIONS

Figure 6   *The frequency of radiocarbon dates on* Larix *macrofossils north of its modern range indicate two
periods of northward treeline expansion in the past 5000 years in the area of Nouveau-Québec. (Adapted
from Gagnon and Payette, 1981).*

thyoides at Toronto during Sangamonian time (Kerr-Lawson, 1985) suggests an old inland origin for the Coastal Plain-Great Lakes disjunction that may have persisted south of the ice limit during later advances.

(b) Middle Wisconsinan disjunctions or range extensions:

Taxa showing this distribution include:
Southern Ontario
Dryas integrifolia (Figure 7b)
Betula glandulosa
Saxifraga oppositifolia (Figure 7c)
Alaska and Yukon Territory
Alisma gramineum
Scuttellaria galericulata
Najas flexilis
Alnus incana (A. rugosa)

The presence of *Saxifraga oppositifolia* and *Dryas integrifolia* in southern Ontario and in southern Quebec (Matthews *et al.*, 1987; Warner *et al.*, 1987) suggests that the Arctic-Alpine or Holarctic-Montane disjunctions were probably in place since Middle Wisconsinan time. These taxa likely grew in ice marginal zones moving north-south several times with glacier positions before

assuming modern distributions. Some components such as *Dryas integrifolia* maintained the Arctic-Alpine disjunction on into early Holocene time and presumably to the present along the north shore of Lake Superior (Bajc *et al.*, 1986).

(c) Late Wisconsinan disjunctions or range extensions:
Coastal British Columbia
Selaginella densa (Figure 7d)
Hypericum scouleri (Figure 7e)
Potamogeton filiformis
Salix cf. *pedicellaris*
Sagina cf. *saginoides*
Dryas drummondii
Ontario and Southern Quebec
Elaeagnus commutata (Figure 7f)
Thalictrum venulosum
Taraxacum cf. *lacerum* (Figure 7g)
Shepherdia canadensis
Dryas integrifolia
Salix herbacea
Sibbaldia procumbens
Oxyria digyna
Carex bigelowii
Armeria maritima

Late Wisconsinan environments characteristically contained mixtures of plants which at present have temperate, boreal and subarctic distributions. During this period, Cordilleran plants such as *Dryas drummondii* and prairie-type plants such as *Shepherdia canadensis, Elaeagnus commutata,* and *Thalictrum* cf. *venulosum* were in eastern Canada (Miller and Thompson, 1979; Karrow and Warner, 1988). This suggests that the Eastern North American-Western North American disjunction was in place by this time. Similarly, plants of modern subarctic and arctic affinities such as *Dryas integrifolia, Oxyria digyna* and *Carex bigelowii* grew much farther south indicating that the Arctic-Alpine disjunction continued on into Late Wisconsinan time (*e.g.,* Birks, 1976; Watts, 1979; Mott *et al.*, 1981; Baker *et al.*, 1986).

Northern interior and central interior elements, such as *Salix* cf. *pedicellaris, Selaginella densa* and *Dryas drummondii* extended to the coastal regions of British Columbia. Northern (*Sagina* cf. *saginoides*) and southern (*Hypericum scouleri*) plants
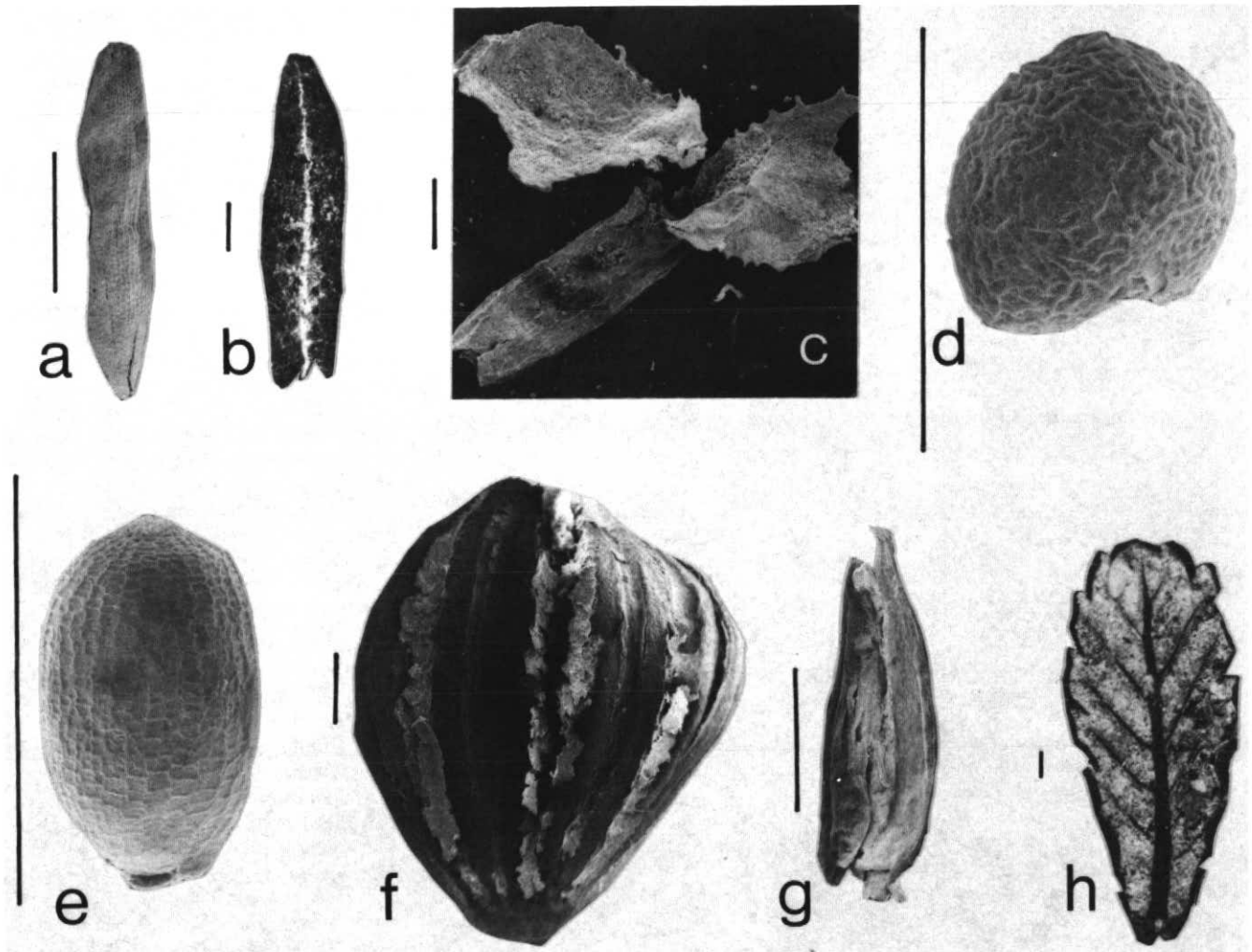

Figure 7 *Selected representative plant macrofossils.* (**a**) Najas guadalupensis sensu lato *seed,* (**b**) Dryas integrifolia *leaf (upper surface),* (**c**) Saxifraga oppositifolia *leaves,* (**d**) Selaginella densa *megaspore,* (**e**) Hypericum scouleri *seed,* (**f**) Elaeagnus commutata *seed,* (**g**) Taraxacum *cf.* lacerum *seed, and* (**h**) Dryas drummondii *leaf (under surface). Scale bar equals 1 mm except for (d) which is 0.5 mm.*

extended beyond their modern boundaries to the Queen Charlotte Islands on the west coast (Warner, 1984b).

(d) Holocene range extensions:
   Yukon
   Larix laricina
   Northern Quebec
   Larix laricina
   Ontario
   Dryas drummondii (Figure 7h)
   Pinus strobus
   cf. *Zizania palustris*
   Zannichellia palustris

Generally, the range extensions represent comparatively short distributional shifts on the order of 100 km or less. An exception is *Dryas drummondii* which represents persistence of the Western North American disjuncts in northern Ontario into and throughout Holocene time (Bajc *et al.*, 1986).

Evolutionary Changes and Paleoecology

The dramatic changes in ice extent, sea-level positions, presence of pro-glacial lakes, and climate during Quaternary time almost certainly pushed plants to their limits of environmental adaptation. Plant macrofossils have been measured for morphological changes as a means of assessing the evolution of different biotypes. In Europe, *Dulichium arundinaceum* and *Menyanthes trifoliata* have shown some degree of change (Birks, 1980); however, *Menyanthes* shows no morphological change during Quaternary time in Japan (Kokawa, 1960).

Fossil cones of *Picea* from coastal British Columbia were used to assess the degree of change within the last 10,000 years (Warner and Chmielewski, 1987). This study indicated that, in contrast with today, past spruce populations probably consisted of more introgressive populations of *P. sitchensis* and *P. glauca* that extended farther west before the two species assumed more or less independent distributions during Holocene time.

Some fascinating areas of research involving plant macrofossils which have received little or no attention in Quaternary botany lie in the areas of paleobiochemistry, past plant-animal interactions, mycology, and plant ultrastructure. One study on fossil *Picea* needles and wood from Michigan ranked the rates of degradation of various compounds through geological time which proved useful for studying processes of coalification (Meyers *et al.*, 1980).

Obvious examples of plant-animal interactions are beaver-gnawed *Picea*, *Pinus* and *Juniperus* branches (Aalto *et al.*, 1983), insect trails on logs (Figure 8), or evidence of herbivory including chewed or eaten seeds (Figure 9). Such studies may provide important clues to co-evolution, herbivory and mimicry, or the role of animals as dispersal agents and pollinators.

Bark, leaf and other plant tissues often possess fragmentary fungal remains, thereby providing an additional means of tracing the origin, interrelationships and evolution of major fungal groups throughout Quaternary time.

Heightened awareness by Quaternary botanists and their communication with experts in allied fields will lead to new and exciting aspects of Quaternary plant macrofossil analyses.

Figure 8 *Bark beetle trails on a Picea log dated 10,280 ± 100 years B.P. from southern Ontario (Karrow and Warner, 1988).*

References

Aalto, M., Donner, J., Hirvas, H. and Niemelä, H., 1983, Majavan jyrsimiä pesä- ja patopuita moreenin alla Vimpelissä: Geologi, v. 35, p. 137-139.

Andersson, G., 1892, Om metoden för växtpaleontologisk undersökning af torfmossar: Geologiska Förhandlingar, v. 14, p. 165-175, 506-508.

Backman, A.L., 1965, Växtpaleontologiska studier pa Aland: Acta Societas pro Fauna et Flora Fennica, v. 77, p. 1-45.

Bajc, A.F., Warner, B.G. and Morgan, A.V., 1986, Dating and paleontology of a postglacial fossil assemblage from the north shore of Lake Superior, Ontario, Program and Abstracts, 9th Biennial Meeting American Quaternary Association, Champaign, Illinois, p. 70.
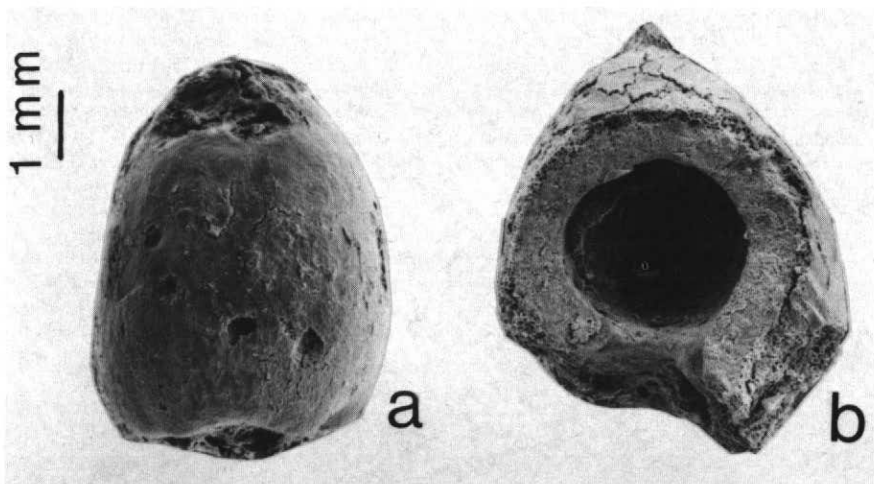

Figure 9 *Fossil Cladium mariscoides seeds of mid-Holocene age from a peatland deposit on Manitoulin Island, Ontario (Warner et al., 1984b). (a) Intact seed, and (b) partially eaten seed.*

Baker, R.G., Rhodes, R.S., Schwert, D.P., Ashworth, A.C., Frest, T.J., Hallberg, G.R. and Janssens, J.A., 1986, A full-glacial biota from southeastern Iowa, USA: Journal of Quaternary Science, v. 1, p. 91-107.

Barber, K.E., 1981, Peat stratigraphy and climatic change: A.A. Balkema, Rotterdam, 219 p.

Beals, H.O. and Melhorn, W.N., 1961, An extinct conifer, *Larix* (?) *pleistocenicum*, n. sp. from Yarmouth Interglacial deposits of Indiana: Journal of Paleontology, v. 35, p. 667-672.

Berti, A.A., 1975, Paleobotany of Wisconsinan interstadials, Eastern Great Lakes Region, North America: Quaternary Research, v. 5, p. 591-619.

Birks, H.H., 1973, Modern macrofossil assemblages in lake sediments in Minnesota, *in* Birks, H.J.B. and West, R.G., eds., Quaternary plant ecology: Blackwell Scientific Publishers, Oxford, p. 173-189.

Birks, H.H., 1980, Plant macrofossils in Quaternary lake sediments: Ergebnisse der Limnologie, v. 15, p. 1-60.

Birks, H.H., Whiteside, M.C., Stark, D.M. and Bright, R.C., 1976, Recent paleolimnology of three lakes in northwestern Minnesota: Quaternary Research, v. 6, p. 249-272.

Birks, H.J.B., 1976, Late Wisconsinan vegetation history at Wolf Creek, central Minnesota: Ecological Monographs, v. 46, p. 395-429.

Blackwell, W.H., 1982, Fossil "dogwood" from the Pleistocene of central Mississippi: Botanical Gazette, v. 143, p. 395-400.

Brayshaw, T.C., 1985, Pondweeds and bur-reeds and their relatives of British Columbia: British Columbia Provincial Museum, Occasional Paper 26, 166 p.

Collinson, M.E., 1983, Accumulations of fruits and seeds in three small sedimentary environments in southern England and their paleoecological implications: Annals of Botany, v. 52, p. 583-592.

Dawson, J.W., 1857, On the newer Pliocene and Post-Pleistocene deposits in the vicinity of Montreal, with notices of fossils recently discovered in them: Canadian Naturalist and Geologist, v. 2, p. 401-426.

Dawson, J.W., 1866, The evidence of fossil plants as to the climate of the Post-Pliocene period in Canada: The Canadian Naturalist, v. 3, p. 69-76.

Dawson, J.W. and Penhallow, D.P., 1890, On the Pleistocene flora of Canada: Geological Society of America Bulletin, v. 1, p. 311-334.

Delcourt, P.A., Davis, O.K. and Bright, R.C., 1979, Bibliography of taxonomic literature for the identification of fruits, seeds, and vegetative plant fragments: Oak Ridge National Laboratory, Environmental Sciences Division, Publication 1328, 84 p.

Dickson, C.A., 1970, The study of plant macrofossils in British Quaternary deposits, *in* Walker, D. and West, R.G., eds., Studies in the vegetational history of the British Isles: Cambridge University Press, Cambridge, p. 233-254.

Drake, H. and Burrows, C.J., 1980, The influx of potential plant macrofossils into Lady Lake, north Westland, New Zealand: New Zealand Journal of Botany, v. 18, p. 257-274.

Draycott, W.M., 1948, Pleistocene fossil beetle and vegetational remains in interglacial deposits; A summary report: Southern California Academy of Sciences, Bulletin, v. 47, p. 35-42.

Dunwiddie, P.W., 1987, Macrofossil and pollen representation of coniferous trees in modern sediments from Washington: Ecology, v. 68, p. 1-11.

Ferguson, D.K., 1985, The origin of leaf-assemblages - New light on an old problem: Review of Palaeobotany and Palynology, v.46, p. 117-188.

Gadd, N.R., 1980, Maximum age for a concretion at Green Creek, Ontario: Géographie physique et Quaternaire, v. 34, p. 229-238.

Gagnon, R. and Payette, S., 1981, Fluctuations Holocène de la limite des forêts de mélèzes, Rivière aux Feuilles, Nouveau-Québec: Une analyse macrofossile en milieu tourbeux: Géographie physique et Quaternaire, v. 35, p. 57-72.

Ganong, W.F., 1891, On raised peat-bogs in New Brunswick: Botanical Gazette, v. 16, p. 123-126.

Ganong, W.F., 1897, Upon raised peat-bogs in the Province of New Brunswick: Royal Society of Canada, Transactions, Series 2, v. 3, p. 131-163.

Givens, C.R. and Givens, F.M., 1987, Age and significance of fossil white spruce *(Picea glauca)*, Tunica Hills, Louisiana-Mississippi: Quaternary Research, v. 27, p. 283-296.

Glaser, P.H., 1981, Transport and deposition of leaves and seeds on tundra: A late-glacial analog: Arctic and Alpine Research, v. 13, p. 173-182.

GreatRex, P.A., 1983, Interpretation of macrofossil assemblages from surface sampling of macroscopic plant remains in mire communities: Journal of Ecology, v. 71, p. 773-791.

Grosse-Brauckmann, G., 1986, Analysis of vegetative plant macrofossils, *in* Berglund, B.E., ed., Handbook of Holocene palaeoecology and palaeohydrology: J. Wiley and Sons Ltd., Chichester, p. 591-618.

Haynes, C.V., 1985, Mastodon-bearing springs and Late Quaternary geochronology of the Lower Pomme de Terre Valley, Missouri: Geological Society of America, Special Paper 204, 35 p.

Heer, O.K., 1862, On the fossil flora of Bovey Tracey: Royal Society of London, Philosophical Transactions, v. 152, p. 1039-1086.

Heusser, C.J., 1973, Age and environment of allochthonous peat clasts from the Bogachiel River Valley, Washington: Geological Society of America, Bulletin, v. 84, p. 797-804.

Hill, R.S., 1981, Consequences of long-distance dispersal of plant macrofossils: New Zealand Journal of Botany, v. 19, p. 241-242.

Hollick, A., 1892, Palaeobotany of the Yellow Gravel at Bridgeton, N.J.: Bulletin of the Torrey Botanical Club, v. 19, p. 330-333.

Holyoak, D.T., 1984, Taphonomy of prospective plant macrofossils in a river catchment on Spitsbergen: New Phytologist, v. 98, p. 405-423.

Hughes, O.L., Harington, C.R., Janssens, J.A., Matthews, J.V., Morlan, R.E., Rutter, N.W. and Schweger, C.E., 1981, Upper Pleistocene stratigraphy, paleoecology, and archeology of the northern Yukon Interior, eastern Beringia, I. Bonnet Plume Basin: Arctic, v. 34, p. 329-365.

Jackson, S.T. and Miller, N.G., 1983, Paleoecology of a fossil plant assemblage from a Pre-Wisconsin till in southern Illinois: American Midland Naturalist, v. 109, p. 120-135.

Jessen, K. and Milthers, V., 1928, Stratigraphical and paleontological studies of interglacial fresh-water deposits in Jutland and Northwest Germany: Danmarks geologiske Undersogelse, Raekke 2, v. 26, p. 1-378.

Karrow, P.F., Anderson, T.W., Clarke, A.H., Delorme, L.D. and Sreenivasa, M.R., 1975, Stratigraphy, paleontology, and age of Lake Algonquin sediments in southwestern Ontario: Quaternary Research, v. 5, p. 49-87.

Karrow, P.F., Harrison, W. and Saunderson, H.C., 1977, Reworked Middle Wisconsinan (?) plant macrofossils from the Brampton Esker, southern Ontario: Canadian Journal of Earth Sciences, v. 14, p. 426-430.

Karrow, P.F. and Warner, B.G., 1988, Ice, lakes, and plants, 13,000 B.P. to 10,000 B.P.: The Erie-Ontario lobe in Ontario, *in* Laub, R.S., Steadman, D.W. and Miller, N.G., eds., Late Pleistocene and Early Holocene Paleoecology and Archeology of the Eastern Great Lakes Region: Buffalo Society of Natural Sciences, Bulletin, v. 33, (in press).

Kerr-Lawson, L.J., 1985, Gastropods and plant macrofossils from the Quaternary Don Formation (Sangamonian Interglacial), Toronto, Ontario, unpublished M.Sc. Thesis, University of Waterloo, 201 p.

Knowlton, F.H., 1896, Report on a collection of fossil plants from Morgantown, West Virginia: American Geologist, v. 18, p. 370-379.

Kokawa, S., 1960, Morphometric reconstruction of the compressed seed remains of *Menyanthes* in Japan: Journal of the Institute of Polytechnics, Osaka City University, v. D-11, p. 79-89.

Lesquereux, L., 1859, On some fossil plants of Recent Formations: American Journal of Science, Second Series, v. 27, p. 359-363.

Lichti-Federovich, S., 1974, *Najas guadalupensis* (Spreng.) Morong. in the Missinaibi Formation, northern Ontario: Geological Survey of Canada, Paper 74-1A, p. 201.

Mangerud, J., Andersen, S.T., Berglund, B.E. and Donner, J.J., 1974, Quaternary stratigraphy of Norden, a proposal for terminology and classification: Boreas, v. 3, p. 109-128.

Mannion, A.M., 1986a, Plant macrofossils and their significance in Quaternary paleoecology. Part I: Introduction: Progress in Physical Geography, v. 10, p. 194-214.

Mannion, A.M., 1986b, Plant macrofossils and their significance in Quaternary paleoecology. Part II: Applications: preglacial, interglacial and interstadial deposits: Progress in Physical Geography, v. 10, p. 364-384.

Mannion, A.M., 1986c, Plant macrofossils and their significance in Quaternary paleoecology. Part III: Applications: late glacial, postglacial and archaeological deposits: Progress in Physical Geography, v. 10, p. 517-546.

Mason, H.L., 1957, A flora of the marshes of California, University of California Press, Berkeley, 878 p.

Matthews, J.V., 1975, Incongruence of macrofossil and pollen evidence: A case from the Late Pleistocene of the northern Yukon coast: Geological Survey of Canada, Paper 75-1B, p. 139-146.

Matthews, J.V., 1987a, Late Quaternary plant and insect macrofossils from southern Quebec: International Union for Quaternary Research, 12th International Congress, Ottawa, Canada, Programme with Abstracts, p. 222.

Matthews, J.V., 1987b, Plant macrofossils from the Neogene Beaufort Formation on Banks and Meighen Islands, District of Franklin: Geological Survey of Canada Paper 87-1A, p. 73-87.

Matthews, J.V., 1987c, Potential importance of Arctic and Neogene floras for dating Pleistocene interglacials in northern North America: International Union for Quaternary Research, 12th International Congress, Ottawa, Canada, Programme with Abstracts, p. 222.

Matthews, J.V., Mott, R.J. and Vincent, J.S., 1986, Preglacial and interglacial environments of Banks Island: Pollen and macrofossils from Duck Hawk Bluffs and related sites: Géographie physique et Quaternaire, v. 40, p. 279-298.

Matthews, J.V., Smith, S.L. and Mott, R.J., 1987, Plant macrofossils, pollen, and insect fossils of arctic affinity from Wisconsinan sediments in Chaudiere Valley, southern Quebec: Geological Survey of Canada, Paper 87-1A, p. 165-175.

Mead, J.I., Agenbroad, L.D., Davis, O.K. and Martin, P.S., 1986, Dung of *Mammuthus* in the arid southwest, North America: Quaternary Research, v. 25, p. 121-127.

Meyers, P.A., Leenheer, M.J., Erstfeld, K.M. and Bourbonniere, R.A., 1980, Changes in spruce composition following burial in lake sediments for 10,000 yr: Nature, v. 287, p. 534-536.

Miller, N.G. and Thompson, G.G., 1979, Boreal and western North American plants in the Late Pleistocene of Vermont: Journal of the Arnold Arboretum, v. 60, p. 167-218.

Montgomery, F.H., 1977, Seeds and fruits of plants of eastern Canada and northeastern United States, University of Toronto Press, Toronto, 232 p.

Mott, R.J., Anderson, T.W. and Matthews, J.V., 1981, Late-Glacial paleoenvironments of sites bordering the Champlain Sea based on pollen and macrofossil evidence, in Mahaney, W.C., ed., Quaternary Paleoclimate: GeoAbstracts, Norwich, p. 129-171.

Mott, R.J., Anderson, T.W. and Matthews, J.V., 1982, Pollen and macrofossil study of an interglacial deposit in Nova Scotia: Géographie physique et Quaternaire, v. 36, p. 197-208.

Nathorst, A.G., 1873, Om Skånes nivå-förändringar: Geologiska Foreningens i Stockholm Förhandlingar, v. 1, p. 281-194.

Packer, J.G., 1983, Flora of Alberta, 2nd Edition: University of Toronto Press, Toronto, 687 p.

Penhallow, D.P., 1904, Notes on Tertiary plants from Canada and the United States: Royal Society of Canada, Transactions, Section IV, v. 10, p. 57-76.

Porsild, A.E. and Cody, W.J., 1980, Vascular plants of continental Northwest Territories, Canada, National Museums of Canada, Ottawa, 667 p.

Porsild, A.E., Harington, C.R. and Mulligan, G.A., 1967, Lupinus arcticus Wats. grown from seeds of Pleistocene age: Science, v. 158, p. 113-114.

Riley, J.L. and MacKay, S.L., 1980, The vegetation and phytogeography of coastal southwestern James Bay: Royal Ontario Museum, Life Science Contributions 124, 81 p.

Ritchie, J.C. and DeVries, B., 1964, Contributions to the Holocene paleoecology of west central Canada. A late glacial deposit from the Missouri Coteau: Canadian Journal of Botany, v. 42, p. 677-692.

Schofield, W.B. and Robinson, H., 1960, Late-glacial and post-glacial plant macrofossils from Gillis Lake, Richmond County, Nova Scotia: American Journal of Science, v. 258, p. 518-523.

Schwert, D.P., Anderson, T.W., Morgan, A., Morgan, A.V. and Karrow, P.F., 1985, Changes in Late Quaternary vegetation and insect communities in southwestern Ontario: Quaternary Research, v. 23, p. 205-226.

Spicer, R.A., 1980, The importance of depositional sorting to the biostratigraphy of plant megafossils, in Dilcher, D.L. and Taylor, T.N., eds., Biostratigraphy of fossil plants: Dowden, Hutchinson and Ross, Inc., Stroudsburg, p. 171-183.

Spicer, R.A., 1981, The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England: United States Geological Survey, Professional Paper 1143, p. 1-77.

Spicer, R.A. and Wolfe, J.A., 1987, Plant taphonomy of Late Holocene deposits in Trinity (Clair Engle) Lake, northern California: Paleobiology, v. 13, p. 227-245.

Terasmae, J., 1959, Palaeobotanical study of a buried peat from the Mackenzie River Delta area, Northwest Territories: Canadian Journal of Botany, v. 37, p. 715-717.

Terasmae, J. and Fyles, J.G., 1959, Palaeo-botanical study of late-glacial deposits from Vancouver Island, B.C.: Canadian Journal of Botany, v. 37, p. 815-817.

Tralau, H., 1963, The recent and fossil distribution of some boreal and arctic montane plants in Europe: Arkiv för Botanik, v. 5, p. 533-582.

Warner, B.G., 1984a, Commentary on plant indicator taxa in climatic reconstructions: Quaternary Research, v. 22, p. 266-268.

Warner, B.G., 1984b, Late Quaternary paleoecology of eastern Graham Island, Queen Charlotte Islands, British Columbia, Canada, Ph.D. Dissertation, Simon Fraser University, 190 p.

Warner, B.G., 1986, Early work in Quaternary botany in Canada: Geoscience Canada, v. 13, p. 39-44.

Warner, B.G. and Barnett, P.J., 1986, Transport, sorting and reworking of Late Wisconsinan plant macrofossils from Lake Erie, Canada: Boreas, v. 15, p. 323-329.

Warner, B.G. and Chmielewski, J.G., 1987, Biometric analysis of modern and late Pleistocene cones of Picea from western Canada: New Phytologist, v. 107, p. 449-457.

Warner, B.G., Clague, J.J. and Mathewes, R.W., 1984a, Geology and paleoecology of a Mid-Wisconsin peat from the Queen Charlotte Islands, British Columbia, Canada: Quaternary Research, v. 21, p. 337-350.

Warner, B.G., Hebda, R.J. and Hann, B.J., 1984b, Postglacial paleoecological history of cedar swamp, Manitoulin Island, Ontario, Canada: Palaeogeography, Palaeoclimatology, and Palaeoecology, v. 45, p. 301-345.

Warner, B.G., Karrow, P.F., Morgan, A.V. and Morgan, A., 1987, Plant and insect fossils from Nipissing sediments along the Goulais River, southeastern Lake Superior: Canadian Journal of Earth Sciences, v. 24, p. 1526-1536.

Warner, B.G., Morgan, A.V. and Karrow, P.F., 1988, A Wisconsinan interstadial Arctic flora and insect fauna from Clarksburg, southwestern Ontario, Canada: Palaeogeography, Palaeo-climatology and Palaeoecology. (in press).

Wasylikowa, K., 1986, Analysis of fossil fruits and seeds, in Berglund, B.E., ed., Handbook of Holocene palaeoecology and palaeohydrol-ogy: J. Wiley and Sons Ltd., Chichester, p. 571-590.

Watts, W.A., 1979, Late Quaternary vegetation of coastal Appalachia and the New Jersey Coastal Plain: Ecological Monographs, v. 49, p. 427-469.