

Methods in Quaternary Ecology #3. Plant Macrofossils

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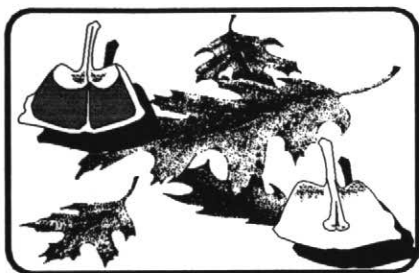
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Résumé de l'article

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Methods in Quaternary Ecology #3. Plant Macrofossils

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Summary

Plant macrofossils consist of reproductive and vegetative plant parts visible to the unaided 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 phyto-geographic 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 millennia.

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



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.

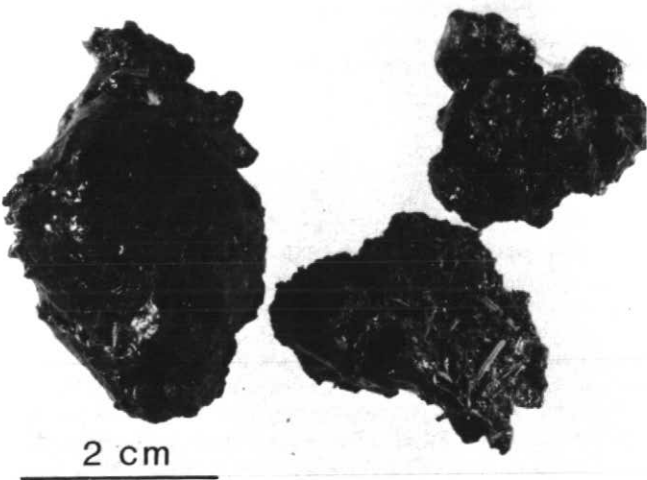


Figure 2 (above) Fossil middens of *Neotoma cinerea* from Interior British Columbia. Such middens serve as urination perches making them hard, dark and shiny, thereby preserving a varied assortment of plant macrofossils. These specimens are about 1110 years old. They contain *Pseudotsuga menziesii* needles,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

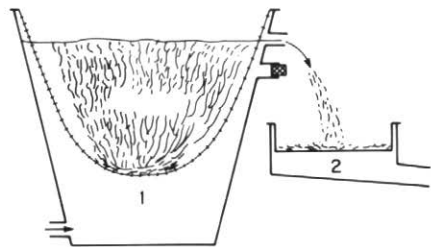
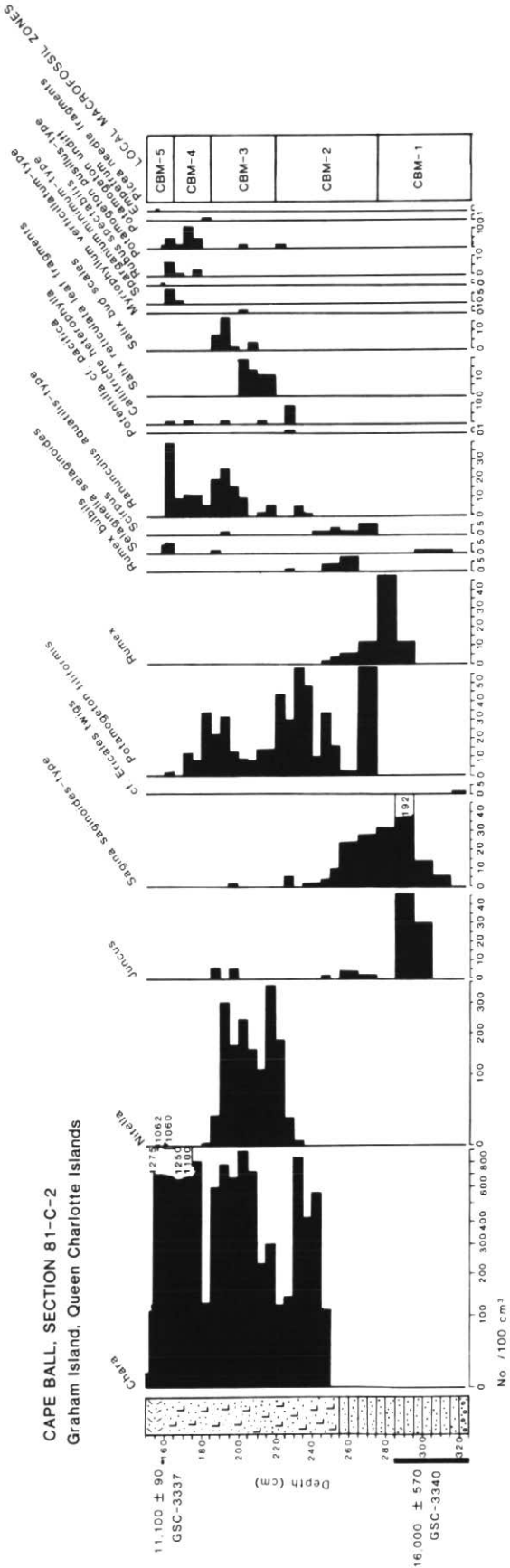


Figure 3 (above) The earliest sieve apparatus for extraction of plant macrofossils designed by Andersson (1892). A hose is attached to the inflow spout at the base, the water is circulated in the bowl and net (1), the fine debris floats off and is caught on a screen (2) (after Backman, 1965). Some laboratories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



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 diamictic 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 μ m 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 HNO₃ and H₂O₂ 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 $\times$). 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 (GreatRex, 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 hydrosere 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 subsequently 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

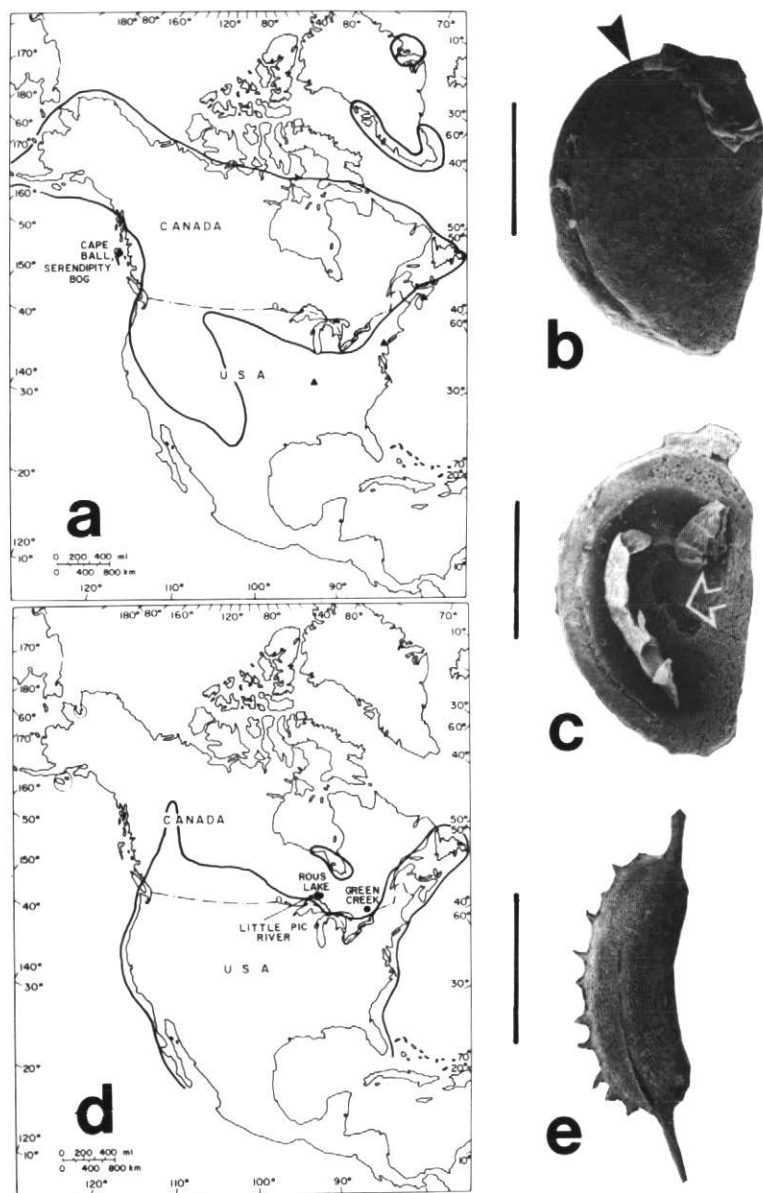


Figure 5 (a) Modern distribution of *Potamogeton filiformis* in North America. (After Mason, 1957; Porsild and Cody, 1980; Packer, 1983; Brayshaw, 1985). The dots (new records) and triangles (from Watts, 1979; Mott *et al.*, 1982; Jackson and Miller, 1983) indicate Late Quaternary fossil localities. 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 boundaries. Both of these plants achieve their best growth in shallow water bodies with high pH and conductivities. The amount of free carbon dioxide in the water available for photosynthesis 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 carbon sources for photosynthesis. Other factors 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 macrophytes can be used as paleoclimatic indicators (Warner, 1984a) although they seem to have much potential in paleolimnological reconstructions (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). Subsequently, European biostratigraphic schemes have been replaced largely by pollen chronologies with plant macrofossils playing a subordinate role. The use of plant macrofossils 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, unpublished). *Najas guadalupensis* has been recovered from the interglacial deposits at Toronto and from purported interglacial deposits in the James Bay Lowlands (Licht-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 misleading 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 reported previously from North America. In light of such ancient phylogeographic connections during Tertiary time, some plant macrofossils may prove useful as biostratigraphic 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 obtained, 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 northward expansion up to 5 km north of its present 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 macrofossil analyses especially on lake and peatland 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 alluvial sequences may be too coarse for the preservation of pollen and only plant macrofossils may be preserved in paleosols, calcareous 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. Phytogeographic extinctions are not known in Canada, and those reported by Penhallow are referable to modern taxa (Warner, 1986). Possible Quaternary extinctions occurred 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 records need verification (see references in Warner, 1986).

Selected representatives in each group are:

- (a) Northern range extensions during the penultimate, Sangamonian Interglacial:
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 United States. Some taxa extended as far north as the James Bay Lowlands, which suggests a major contracted range since the last interglaciation. The presence of *Chamaecyparis*

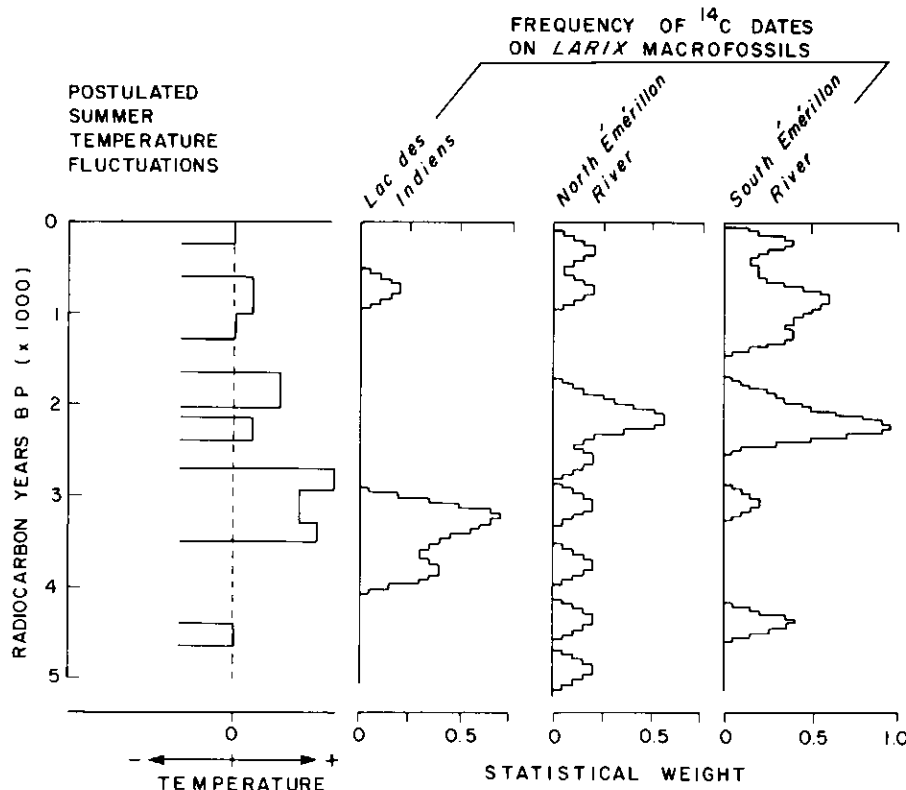


Figure 6 The frequency of radiocarbon dates on *Larix* macrofossils north of its modern range indicate two periods of northward treeline expansion in the past 5000 years in the area of Nouveau-Québec. (Adapted from Gagnon and Payette, 1981).

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

Scutellaria 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

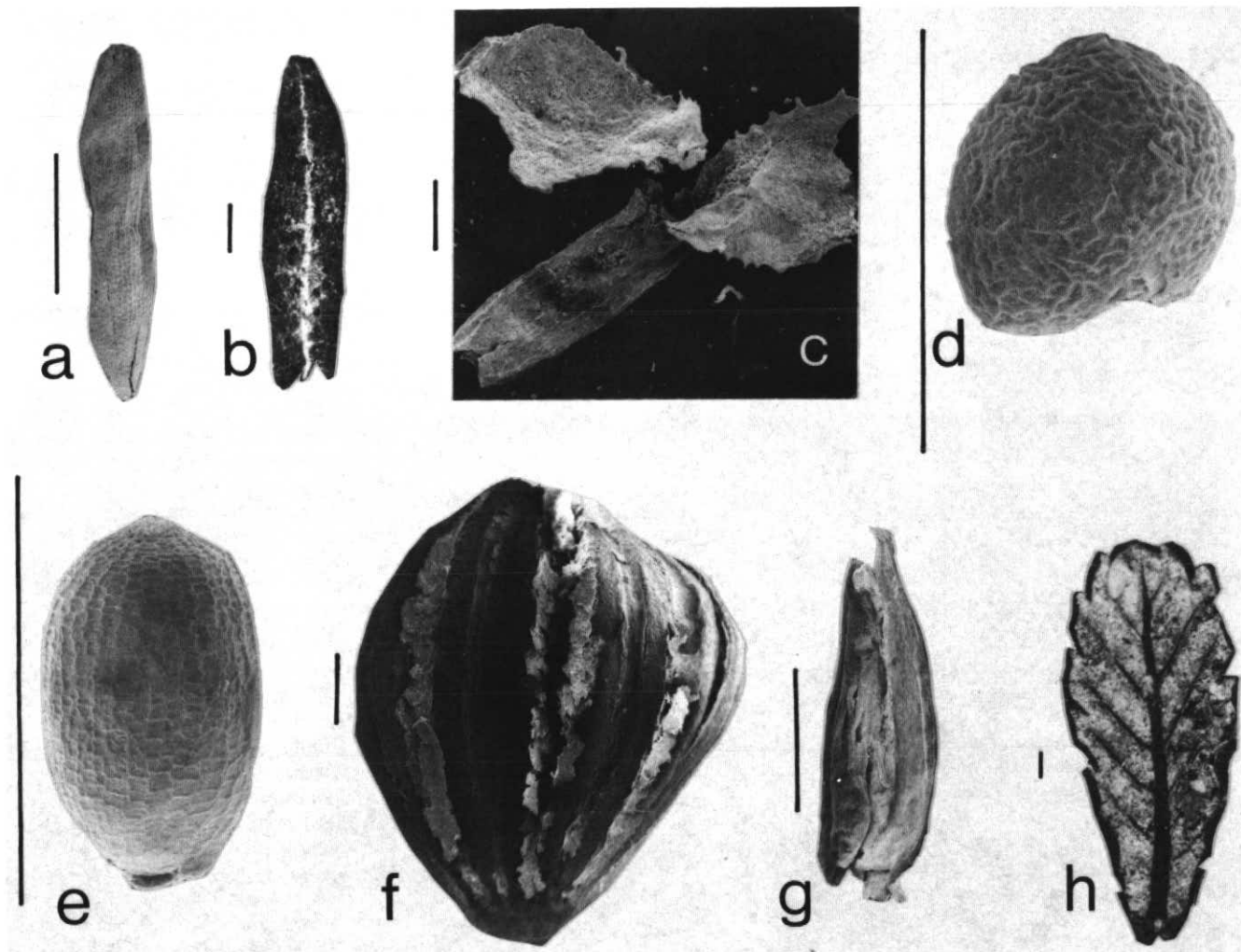


Figure 7 Selected representative plant macrofossils. (a) *Najas guadalupensis* sensu lato seed, (b) *Dryas integrifolia* leaf (upper surface), (c) *Saxifraga oppositifolia* leaves, (d) *Selaginella densa* megaspore, (e) *Hypericum scouleri* seed, (f) *Elaeagnus commutata* seed, (g) *Taraxacum cf. lacerum* 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 Paleoeecology

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.

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

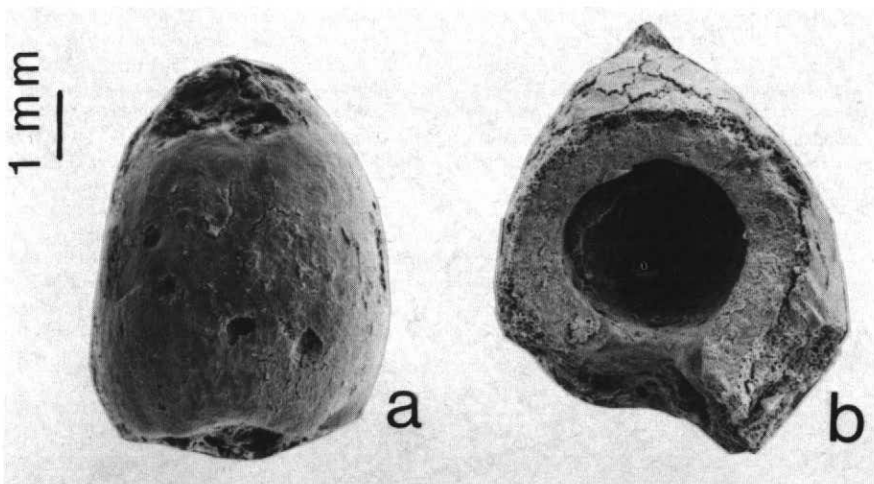


Figure 9 Fossil *Cladium mariscoides* seeds of mid-Holocene age from a peatland deposit on Manitoulin Island, Ontario (Warner *et al.*, 1984b). (a) Intact seed, and (b) partially eaten seed.

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