Methods in Quaternary Ecology 11. Bryophytes

Jan A. Janssens
Department of Ecology, Evolution, and Behavior
University of Minnesota
318 Church Street S.E.
Minneapolis, Minnesota 55455 USA

Summary

Mosses are common fossils in Quaternary sediments. The fragments can be readily identified to species, and no fossils found in Quaternary sediments represent extinct species. Because of the detailed ecological information available from living populations, the Quaternary record of fossil mosses is superbly suited for paleoenvironmental reconstruction of peatland development and of other moss-rich habitats, and particular information is here presented concerning bryophyte fossils in Canadian deposits. New numerical techniques are being developed to establish quantitative bryophyte paleoecology in its own right among Quaternary disciplines.

Introduction

Bryophytes are an artificial group of primitive embryophytes, comprising the mosses, liverworts, and hornworts (Schofield, 1985; Crandall-Stotler, 1984; Mishler and Churchill, 1984, 1985). They are mostly terrestrial, autotrophic (green) plants with two morphologically distinct generations during their life cycle: (1) an autotrophic gametophyte or sexual generation and (2) a partially parasitic sporophyte or asexual generation, **attached to the gametophore** (Figure 1). Bryophyte diversity, approximately 14,500 species worldwide, is higher than in any other group of terrestrial plants except angiosperms (Scagel *et al.*, 1982). In addition, the expansion of bryophyte, and particularly *Sphagnum*, dominated landscapes (peatlands) during the Quaternary Period and the preservation of *Sphagnum* remains in peat have resulted in the speculation that there is more carbon stored in *Sphagnum*, alive and dead, than in any other plant (Clymo and Hayward, 1982).

The fossil record of bryophytes begins in the Paleozoic (Schofield, 1985; Krassilov and Schuster, 1984; Oostendorp, 1987). During the later Tertiary (Neogene) and Quaternary Periods the record, owing to the presence of numerous fossils referable to extant species, conveys abundant paleoenvironmental information (Miller, 1984). Phylogenetic considerations are based, however, exclusively on the study of extant groups, with only secondary attention given to the fossil record because of poor preservation of relevant systematic characters. However, many pre-Tertiary fossils actually can be interpreted in light of cladistic study based on extant mosses and liverworts (Mishler and Churchill, 1984).

Quaternary moss remains are easily recovered from Quaternary deposits and most can readily be identified to species. Fossil liverworts and hornworts, however, are exceedingly rare (Steere, 1942; Miller, 1984). Their haphazard occurrence, mainly in Holocene or interstadial/glacial peats and organic-rich deposits, is evident from the catalogs published for North America by Miller (1980a) and Janssens (1984). The poor Quaternary record of the liverworts and hornworts is in sharp contrast to detailed descriptions of Paleozoic, Mesozoic, and Tertiary species (Harris, 1939; Hueber, 1961; Grolle, 1985; Oostendorp, 1987; Schuster and Janssens, 1989).

Moss fragments are commonly extracted from peats (Janssens, 1988), lake sediments (Birks, 1976), and detrital (allochthonous) deposits (Miller, 1973). Leafy stems are most commonly recovered, but *Sphagnum* remains are usually detached stem and branch leaves (Janssens, 1983a, 1988). Rarely sporophytes (Figure 2) or calyptrae are found (Conolly and Dickson, 1969; Brassard and Blake, 1978; Janssens and Baker, 1984; Miller, 1987). Except for those of *Sphagnum* and hornworts, spores are only occasionally differentiated into genera or species by palynologists (Dickson, 1973, 1986). Considerable potential exists, however, for the use of sculpture patterns in identifying bryophyte

Figure 1 *A short turf of* Bartramia pomiformis *with exserted, mature sporophytes. The gametophores are clustered in a clonal population. (Photo provided by Dr. R.M. O'Clair, Juneau, Alaska.)*

spores (Horton, 1982; Boros and Jarai-Komlodi, 1975).

In this paper, I discuss the development of Quaternary paleobryology by focussing on the more important sites in Canada and North America. Some field and laboratory procedures are outlined, with notes on taphonomy and paleoenvironmental reconstruction. Peatland development, paleobryogeography, evolution and putative extinct species, and future directions for research are discussed. Recent catalogs of fossil species and reviews with exhaustive bibliographies on Quaternary fossil bryophytes are found in Dickson (1973), H.A. Miller (1982), N.G. Miller (1976, 1980a,b,c, 1984), Odgaard (1981), Birks (1982), Janssens (1984), and Dickson (1986). Quantification of data has been attempted (Janssens, 1983a; Wasylikowa, 1986), and future developments will include refinements of those techniques (Birks, 1985; Janssens, 1988).

Historical Development in Canada

Quaternary fossil bryophytes have been studied in North America for over a hundred years (H.A. Miller, 1982; N.G. Miller, 1976, 1980a, 1984; Birks, 1982). Only one published study from the United States predates those from Canada (Pratt, 1876). The first Canadian records were published by Hinde in 1877 (Miller, 1976). Fossil moss remains were extracted by G.J. Hinde and W.A. Johnson from exposures along the Scarborough Bluffs near Toronto and were identified by John Macoun and T.P. James. Several other studies published during the latter part of the nineteenth century reported moss fossils from the Toronto and Ottawa areas and from along the Missinaibi River (Miller, 1980a). Few records were published between 1900 and 1958, and detailed information started to accumulate only after the latter date. Published reports of North American bryophyte fossils were compiled by Miller (1980a) and Janssens (1984). A new catalog is in preparation by N.G. Miller and J.A. Janssens. Most of the 50 Canadian sites at which fossil bryophytes have been studied or are under study (51 papers) are located in the Arctic Islands (17 sites), Ontario (9), Yukon (6), Quebec (7), British Columbia (4), Alberta (2), Northwest Territories (2), Saskatchewan, Manitoba, and Labrador. Most of these sites (23) are Holocene. Many others represent Wisconsinan interstadial deposits or are interglacial, usually with poor direct-dating control (20). Another ten are late-glacial deposits. The Worth Point deposit described originally by Kuc (1974a) is probably of Early Quaternary age (Matthews, 1989). The Beaufort Formation localities on the Arctic Islands, once thought to be of Quaternary age, are not discussed here in detail because they are now known to be Neogene (Matthews, 1987, 1989; Matthews *et al.*, in press). These floras are clearly boreal, and all of the fossil mosses belong to extant species. The remains are preserved without diagenesis (Kuc, 1973, 1974b; Kuc and Hills, 1971).

The most significant lists of species for single locations with well-documented stratigraphy, radiometric dates, or both were published by de Vries and Bird (1965), Mathewes (1973), LaSalle *et al.* (1979), Hughes *et al.* (1981), and Stewart and England (1983). All are discussed below.

Southern Saskatchewan: A late-glacial moss assemblage of 16 species and 1 variety was identified by C.D. Bird from a kettle-hole deposit near Moose Jaw, Saskatchewan (de Vries and Bird, 1965). The mixed nature of the fossil assemblage is indicated by the presence of abundant well-preserved fragments of *Drepanocladus aduncus,* a semi-terrestrial wetland moss, and of upland species such as *Thuidium abietinum, Bryoerythrophyllum recurvirostrum,* and *Tortula mucronifolia*.

British Columbia: W.B. Schofield identified 22 moss species, from a late-glacial and early-Holocene lake-sediment sequence in Marion Lake, southwestern British Columbia (Mathewes, 1973). All of the species presently occur in the area and represent either terrestrial or epiphytic habitats. The presence of epiphytes, as *Antitrichia curtipendula* and *Isothecium stoloniferum,* is exceptional. Furthermore, eight of the species represented are endemic to western North America.

Figure 2 *Sporangium of* Barbula fallax *from a full-glacial assemblage, southeastern Iowa. (Modified from Janssens and Baker, 1984).*

Southern Quebec: LaSalle *et al.* (1979) described an interstadial Mid-Wisconsinan arctic-subarctic deposit from Vallée-Jonction, Quebec, from which W.C. Steere identified 12 terrestrial and wetland species. Mosses that do not belong to the present regional flora include the arctic species *Aulacomnium turgidum* and *Didymodon asperifolius.* All are characteristic of aquatic, semi-terrestrial, or stream-side habitats.

Ellesmere Island: An early-Holocene detrital assemblage of fossil bryophytes was recovered from emergent marine delta deposits at Clements Markham Inlet, northern Ellesmere Island, by Stewart (1981). I identified 25 taxa indicating rich-fen, dry-tundra, and fluvial habitats. All of these mosses occur in the region, and the fossil flora represent approximately one-fourth of the total extant bryoflora of Ellesmere Island (Brassard, 1976).

Northern Yukon: An interstadial deposit from the Hungry Creek section in the Bonnet Plume Basin, northern Yukon Territory, contained a large fossil bryophyte flora (Hughes *et al.*, 1981). The allochthonous assemblage is situated on bedding planes of superimposed sand and silt layers, which were overridden by the late Wisconsinan Hungry Creek glacial advance. Preservation of the abundant fossils is excellent, which suggests minimal reworking. I identified 39 species plus seven additional taxa to section and genus. The family Amblystegiaceae, indicating a highly minerotrophic peatland, was best represented. Other species represent communities ranging from lake-edge to rock-outcrop and dry upland habitat. Some arctic-alpine species are also present. *Hylocomium splendens,* represented by its luxuriant, sympodially branched wefts growth-form, suggests the presence of spruce forests growing nearby during deposition of the alluvial unit; the site is presently subarctic–subalpine.

Summary: Table 1 lists the 20 moss species that have 10 or more Quaternary records for Canada. It is compiled from published sources (Miller, 1980a; Janssens, 1983b, 1984) and from unpublished reports (Miller and Janssens, in preparation). Twelve of the 20 species belong to the family Amblystegiaceae (brown mosses). Nine of the 20 are rich-fen indicators and two *(Drepanocladus lycopodioides* var. *brevifolius* and *Aulacomnium turgidum)* are mainly subarctic or arctic.

Methods

Field sampling procedures: Samples for bryophyte-fossil analyses are often bulk samples taken from freshly cleaned natural exposures. Moss remains are commonly concentrated along bedding planes or as dispersed detritus and peat lenses in inorganic sediments. Care should be taken not to dry field samples completely because

Table 1 Quaternary mosses with more than 10 Quaternary records in Canada (Miller, 1980a; Janssens, 1983b; Janssens, 1984; Miller and Janssens, in prep.)

Scorpidium scorpioides [1,2]	54
Tomenthypnum nitens[2]	47
Drepanocladus exannulatus[1]	43
Calliergon giganteum[1,2]	42
Drepanocladus lycopodioides var. *brevifolius*[1,3]	32
Calliergon richardsonii[1,2]	28
Drepanocladus crassicostatus[1]	25
Drepanocladus revolvens[1,2]	25
Meesia triquetra[2]	21
Bryum pseudotriquetrum[2]	20
Aulacomnium palustre	20
Calliergon trifarium[1,2]	19
Drepanocladus fluitans[1]	19
Campylium stellatum[1,2]	18
Drepanocladus aduncus[1]	17
Hylocomium splendens	16
Drepanocladus sendtneri[1]	14
Aulacomnium turgidum[3]	14
Ditrichum flexicaule	11
Distichium capillaceum	10

[1] *belongs to the family Amblystegiaceae (brown mosses)*
[2] *rich-fen indicator*
[3] *subarctic-arctic species*

this causes the moss remains to become brittle and susceptible to damage before and during laboratory processing. If humified *Sphagnum* peats are completely dried no amount of soaking can restore the original texture, and dispersal of the fossil fragments in water becomes extremely difficult. When bulk samples are pre-screened in the field to reduce the volume of the inorganic component, a preservative such as phenol should be added to the screened macrofossil remains to limit fungal growth. Alternatively, samples can be frozen.

Lake-sediment and peatland samples are obtained from cores or monoliths (Figure 3). Coring devices have been discussed most recently in Berglund (1986) for a wide variety of sediments and in Wright *et al.* (1984) and Janssens (1987) for Holocene peat deposits.

Laboratory methods and identification: Bulk samples and subsamples of peat or lake sediment are wet-screened in the laboratory before fossil bryophytes are extracted. KOH solution, which is quite destructive to moss remains, should not be used to disperse the sample. Instead, a mild wetting agent, such as Aerosol OT (Fisher), is preferred. Boiling is rarely necessary. Dilute HCl can help to break up a slightly consolidated calcareous matrix and does little damage to mosses. A 300-μm mesh screen is sufficient to retain significant moss remains. Screened material can be stored in glycerine before extracting

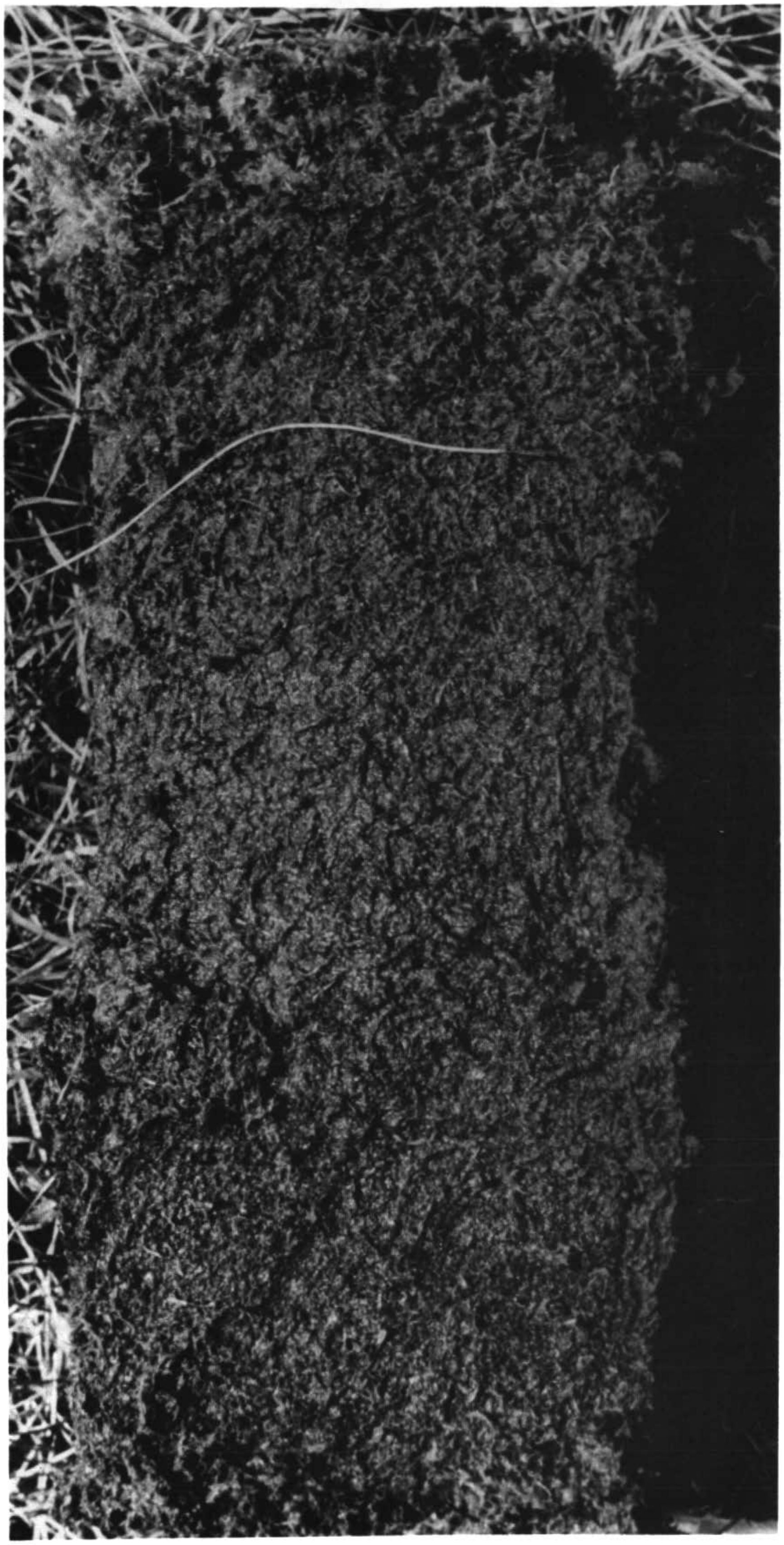

Figure 3 *Peat monolith extracted from a "muskeg" peatland on Douglas Island, Juneau area, southeastern Alaska. Living* Sphagnum lindbergii *constitutes the top 5 cm of the monolith. The next 25 cm constitutes the aerobic acrotelm layer with well-preserved* Sphagnum *peat (Ingram, 1983; Verry, 1984), overlying the catotelm of more decomposed, anaerobic peat. (Photo by the author).*

fossil fragments. Detailed techniques for volumetric measurement, identification, and quantification of *Sphagnum* species in Holocene peats are given by Janssens (1987, 1988). For leafy mosses other than *Sphagnum*, it is sufficient to detach the best-preserved leaves from the fossil fragment and mount both fragment and detached leaves under two separate coverslips on a microscope slide in Hoyer's solution (Schuster, 1966, p. 335). The specimens are then identified under a compound microscope with standard keys (Crum, 1984; Nyholm, 19541969; see also the list of manuals in Dickson, 1986), and with reference collections of slides and herbarium specimens. Dichotomous keys for the identification of fossil *Sphagnum* and *Drepanocladus* fragments are available in Janssens (1983b, 1987).

Presentation of results: Differential breakage of fragments does not allow counts of stem or leaf remains to be performed easily (Watts and Winter, 1966; Birks, 1970; Rybníček, 1973; Janssens, 1983a). Abundance estimates are commonly based on volumetric estimates or on a combination of these estimates and tallies of fragments (Rybníček and Rybníčková, 1968; Aaby and Jacobson, 1979; Dickson, 1981; Janssens and Barnosky, 1985). For instance, Rybníček and Rybníčková (1968) commonly screen 100 mL to estimate moss fragments and other plant macrofossils volumetrically. Countable fragments are tallied. Both volumetric estimates (in %) and counts re converted to a 7-point scale of relative abundance.

Sub-sampling of sediments with widely varying amounts of bryophyte material is more efficient when an exotic marker is added. Poppy seed, which has dispersal characteristics similar to bryophyte fragments, has proven useful (Janssens, 1983a). Only with the results of future studies on shoot densities, differential decomposition, and other taphonomically significant variables will actual counting of fragments be preferable to volumetric estimates or a combination of these estimates and fragment counts.

The most elaborate method of presenting results has been developed for Holocene autochthonous peats (Janssens, 1987, 1988). Standardized methods are essential for accurate quantitative inference (Birks, 1985). The first challenge in measuring the abundance of different species in a peat assemblage is the representation of *Sphagnum* species and other mosses on a common, comparative scale that reflects the volumetric contribution of each taxon to the total peat component. Janssens (1988, table 2) gives an example of such an assemblage and its quantification. The complexity of handling *Sphagnum* fragments is caused by the extensive fragmentation of their remains as compared with other mosses. No attempts have yet been made to compensate for selective decomposition (Clymo, 1965) and differential fragmentation (Rybníček and Rybníčková, 1968) among related species. Because of problems associated with quantification, qualitative aspects are still important, such as the presence or absence of certain "indicator" species (Rybníček, 1973). Techniques for quantitative inference are further discussed in the Paleoenvironmental Reconstruction section below and by Birks (1985).

Taphonomy

Study of the ontogeny of death assemblages is important for paleoenvironmental reconstruction. Selective decomposition (Steere, 1942; Clymo, 1965; Janssens, in prep.) and transport (Glaser, 1981; Miller, 1984; Warner and Barnett, 1986) are two important processes that alter the composition of fossil assemblages. Both processes affect even autochthonous peats as indicated by poor recovery of ubiquitous bog liverworts (Duckett and Clymo, 1988) and the representation of hummock and hollow species in single fossil assemblages (Janssens and Engstrom, in prep.). In detrital deposits, reworking of older deposits often leads to mixed assemblages that are characterized by distinctly different preservation of the components, heterogeneous assemblages, and differential fragment lengths (Janssens, 1981; Miller, 1984).

Etiolation and aquatic modifications are often encountered in bryophytes from terrestrial habitats that became dislodged and grew under water before burial (Dickson, 1973). The presence of aquatic modifications is used in paleoenvironmental reconstruction (Janssens and Glaser, 1986). Some of the post-burial history of fragments can be gleaned from the index of reliability devised by Dickson (1973), and elaborated by Janssens (1983a, 1987), Janssens and Zander (1980), Odgaard (1982), and Schweger and Janssens (1980).

Paleoenvironmental Reconstruction

Distributional shifts were the first inferences made from fossil bryophyte records. With the development of better stratigraphical control and dating techniques, more significant qualitative paleoclimatic and paleoenvironmental inferences were made possible. Quantitative paleoenvironmental inference, suggested by models for paleoclimatology, has been developed only recently (Birks, 1985).

Commonly, Quaternary paleoenvironmental inference has been based on apparent climatic and environmental tolerances of individual species (Dickson, 1986) or on their value as syntaxonomic "indicators" for certain mire communities. H.H. Birks and Mathewes (1978) compared complementary macrofossil and pollen evidence in a paleoecological study of the late-glacial and early-Holocene development of Abernethy Forest, Scotland. The present distribution and edaphic preferences of *Calliergon trifarium* in Scotland were considered in the paleoenvironmental reconstruction of rich-fen communities based on bryophyte and vascular-plant macrofossils and pollen types of local origin. A similar approach was used by Webb and Moore (1982) in reconstructing stadial late-glacial paleoenvironments in southeastern Scotland. For example, bare-ground communities and late-snowmelt areas were suggested by the presence of *Salix herbacea* and *Polytrichastrum alpinum*. An exceptionally diverse Middle Weichselian moss assemblage from Jutland allowed Odgaard (1982) to postulate a treeless landscape dominated by herbs and dwarf shrubs. The climate was non-oceanic, and mean July temperatures were probably between 8° and 10°C. A different approach was taken by Rybníček (1973), who compared past and present mire communities in Czechoslovakia using a synecological approach. The presence of certain key species, rather than listing individual species, classified the fossil assemblages into predefined past community types. These predefined past community types are comparable to phytosociological units recognized in present-day mires. Paleoenvironmental reconstruction throughout a profile was based on a dated sere of community types that replaced each other through time.

Because of the absence of deep rooting systems, mosses are much more specific indicators of peatland habitat conditions than vascular plants (Janssens *et al.*, in press). Obviously only extant mosses that have been studied sufficiently in relation to environmental gradients can be used. Some of the most common and best-studied species, however, have such wide-ranging edaphic and climatic tolerances that they are of little indicator value in paleoenvironmental or paleoclimatic interpretations. *Hylocomium splendens* (Tamm, 1953) is an example. More detailed study of growth-forms and modifications of these common species can nevertheless indicate valuable paleoenvironmental aspects (Miller, 1984). The sympodial growth form of *Hylocomium splendens* remains of Sangamonan age from Hungry Creek in the Yukon Territory indicates the presence of a forest-floor community where presently no trees grow (Janssens, 1981; Hughes *et al.*, 1981). Aquatic modifications of *Scorpidium scorpioides* contribute to the understanding of the broader extent of marl pools in late-glacial-rich fens in contrast to the present limited occurrence of this habitat type (Janssens, 1981).

There is some evidence from phytocenological studies (Rybníček and Rybníčková, 1968) and from fossil records (Janssens *et al.*, 1986) that species represented in late-glacial assemblages may have had ecological requirements that differed from those in their extant populations. This problem is indicated by the presence of non-analogous assemblages (death assemblages without a modern analog: Birks and Birks, 1980), and sometimes can be explained by the possible existence of ecotypes (Gorham, 1956, in press; Green, 1968; Damman, 1977). The existence of different ecotypes in mosses (structurally identical populations only differentiated by edaphic or climatic requirements) has been suggested several times, *e.g.*, for *Sphagnum imbricatum* and *S. flavicomans* (Green, 1968; Tolonen and Tolonen, 1984; Flatberg, 1986). It is increasingly evident that there is a genetic basis for the habitat differentiation among populations of the same species growing in different regions (Longton, 1976, 1988; Dietert, 1980; Wyatt and Anderson, 1984; Sveinbjörnsson and Oechel, 1983; Shaw *et al.*, 1987; Shaw, 1987). However, the role of composition is most often still ignored. Presently, the most practical approach is to derive paleoecological inferences from the **total** known tolerance range of the species, including all putative ecotypes. Reference data sets should ideally encompass the entire distributional range of relevant species (Birks and Birks, 1980).

Another approach to paleoenvironmental reconstruction using macrofossils has been successfully employed by Wolfe (1978) with Tertiary leaf floras. It can be quite independent of taxonomic identification, but uses certain structural features, such as leaf outlines and margins, that differentiate along climatic gradients. Nothing has been attempted in this way with fossil bryophytes, but classification of bryophyte growth-forms (Gimingham and Birse, 1957; Gimingham and Smith, 1971) could possibly lead to a similar technique (Miller, 1980c; Janssens, 1981; Odgaard, 1981).

Old Crow Basin, detailed study: Janssens (1981) recognized six groups of fossil-moss assemblages for the Yukon refugium, some characterized by different growth-form spectra. These groups were formed by collating all fossil assemblages (65) from numerous sediment samples collected along exposures in the Old Crow Flats, northern Yukon Territory. The area was never glaciated and is the easternmost extremity of the large Beringian Pleistocene refugium (Hopkins *et al.*, 1982). The assemblage groups are illustrated by their growth-form spectra in Figure 4 along with a simplified composite section of the Old Crow River Quaternary exposures. The oldest assemblages are from Lower Lake clays and the thick alluvial deposit over-lying them. These sediments are all older than 149 ka, the age of Old Crow tephra (Westgate, 1988), and, at some sites, the lake clays are known to be of Plio/Pleistocene age (Schweger, 1989). The alluvial section grades into an overlying paleosol, abruptly truncated by a disconformity (Morlan, 1980) and strongly disturbed by periglacial activity. The paleosol and associated autochthonous peats postdate the Happy Interval and probably belong to the latter part of the Boutellier Interval, a period of intermediate climate and less extensive glaciation in Beringia (65,000-30,000 years age; Hopkins, 1982; Schweger and Janssens, 1980). This period was followed by the last cold and dry periglacial interval of the Pleistocene in unglaciated Beringia, the Duvanny Yar Interval (30,000-13,000 years ago). Locally, on the Old Crow Flats, the Duvanny Yar period is represented by the Upper Lake clays. The alluvial fossiliferous sediments below these sterile lake clays indicate the steep drying and cooling trend before the formation of the periglacial lakes. As shown in Figure 4, most Old Crow sections are capped by Holocene peat.

Six assemblage groups, illustrated by their growth-form spectra and species diversity in Figure 4, support the previously outlined Beringian paleoenvironmental reconstruction. All fossils were assigned a most common growth form (Janssens, 1981).

The habitat of a moss species is partially correlated with its strategy to obtain and retain the available water for growth (Birse, 1958; Gimingham and Smith, 1971; Longton, 1988). In Arctic or Antarctic regions, summers are short and favourable periods for growth are irregular. The growth form of a bryophyte will influence critically its survival since dense growth forms, such as small cushions, and turfs without branches are often effective in restricting water loss. The species with these growth forms are most commonly found in more exposed environments. Carpet-forming species (tall turfs with spreading branches such as *Sphagnum* spp.) and large cushions are found in swampy habitats provided with a permanent water supply. Tall turfs with erect branches and loose structure, and thus relatively little influence upon water conservation, often grow both in habitats with significant evaporation stress and on tall hummocks in more water-logged conditions. Often other mechanisms (for example cuticularization, and lamina and lamellae movement) also operate to restrict water loss. Most mat growers exhibit an extreme variability. Typically developed smooth and rough mats are never in contact with the water table, as is also the case with wefts (Tamm, 1953) that are mostly associated with forest-floor habitats. More robust forms approach carpets and are found in swampy habitats (for example, species of *Drepanocladus*).

In Figure 4, the seven different growth forms (tall turfs with erect branches, with spreading branches, with tomentum, short turfs, rough and smooth mats, and wefts) are grouped together in four classes (small turfs, tall turfs, mats, and wefts). The proportions of each class in the six assemblage groups are reflected in the height of the histogram bars. Proportions are calculated on the basis of the number of records for each fossil species in the assemblages. Species with two common growth forms are scored twice.

The Lower Lake Clay and Midsection assemblages consist mostly of detrital remains. Turfs are dominant over mats and wefts. A slightly higher proportion of mats is recorded in the more autochthonous set of assemblages associated with the paleosol below disconformity A (probably formed during the more moderate climate of the Boutellier Interval; Hopkins, 1982). This assemblage group has also the largest number of species (63) for the entire Old Crow Flats stratigraphy. In contrast, the sediments below the Upper Lake clays, which represent late Wisconsinan advance of the Laurentide ice sheet, have few species. Most of these assemblages consist of a few, transported, poorly preserved fossils. No weft-formers are evident and mats are dominant. High-energy fluvial habitats are suggested for the period before the formation of the upper glacial lakes. The growth-form spectrum of the Holocene peat cap is based on autochthonous peat samples, except for a few detrital samples immediately above the sterile glacio-lacustrine sediments.

Present-day detritus collected on river bars during the summer consists of material that was probably deposited during spring floods of the same year. Notwithstanding the different genesis of the material, the growth-form spectra of the peat cap and river-bar detritus are very similar. The bulk of the detrital river-bar moss fragments is probably derived from the easily eroded Holocene peat cap rather than the more consolidated Pleistocene exposures. Tall turfs, mainly *Sphagnum* and common peatland species, are dominant.

Other studies: In contrast to the few studies mentioned above, most bryophyte fossils have been recovered from deposits of a single age or as allochthonous fragments in lake and alluvial deposits, representing only brief stratigraphic intervals. Some studies on lake and peatland profiles, however, have produced a continuous stratigraphic record at a single site, often encompassing several thousands of years (Birks, 1976; Miller, 1984; Anderson *et al.*, 1986; Miller and Futyma, 1987; Janssens *et al.*, in press).

Many individual bryophyte species have little value for edaphic or paleoclimatic inference (Miller, 1980b, and see previous discussion on ecotypes). However, stratigraphic boundaries based on changes of common peatland bryophyte communities can be established, dated, and correlated among nearby coring sites and can support wide-ranging paleoclimatic inferences (Janssens *et al.*, in press). The nearly synchronous start of the development of the extensive oligotrophic mire over the entire Red Lake Peatland watershed correlates well with a major climatic boundary between the prairie period and the mixed conifer-hardwood period established by pollen

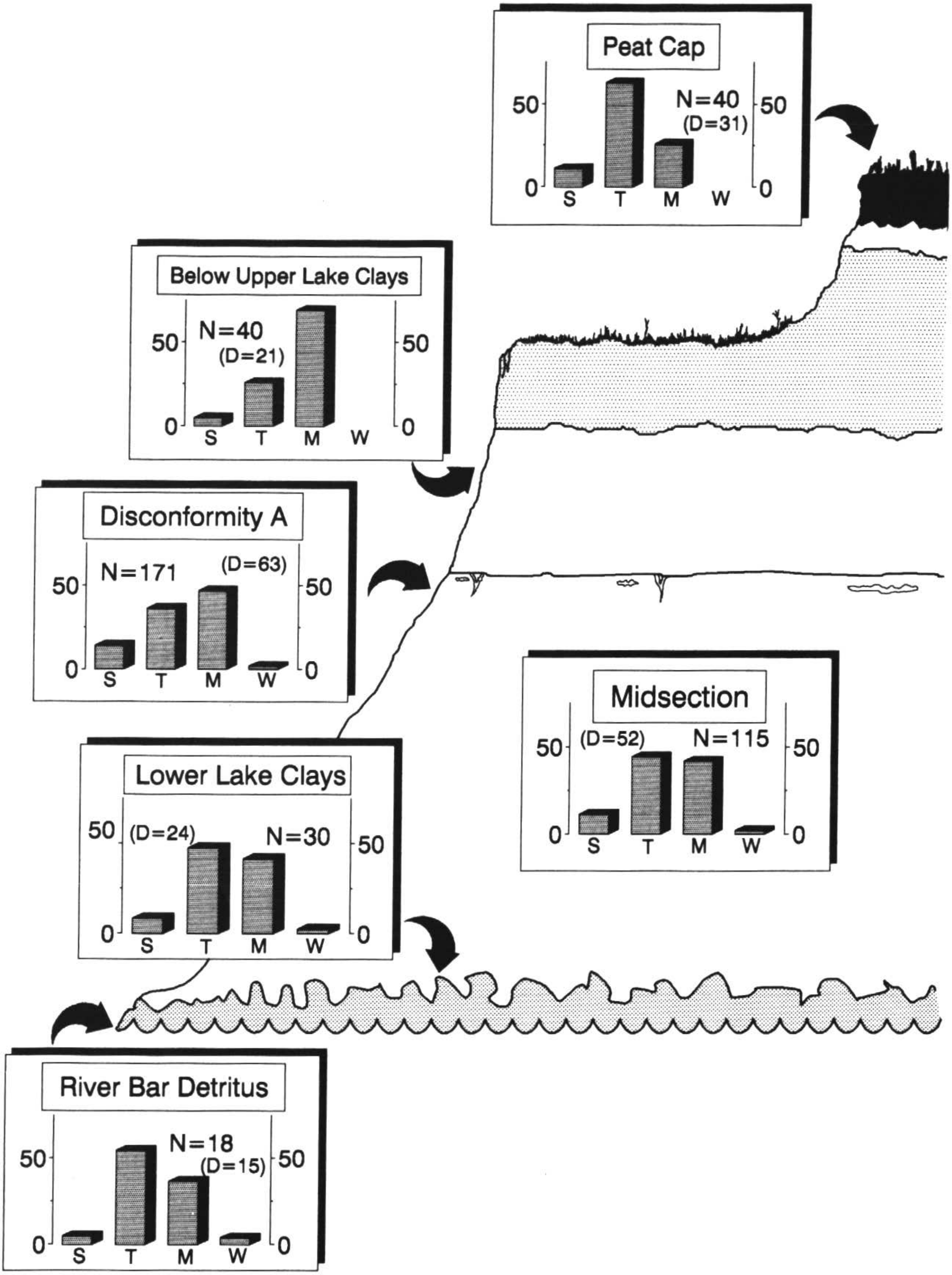

Figure 4 *Composite section along the Old Crow River in the Old Crow Flats basin and six groups of fossil-bryophyte assemblages, illustrated by their growth-form spectra. The Old Crow tephra (149 ka) is located just below Disconformity A. See text for discussion of chronostratigraphy and paleoenvironmental reconstruction.* ***N****, number of records;* ***D****, number of taxa;* ***S****, small turfs;* ***T****, tall turfs;* ***M****, mats; and* ***W****, wefts. (Compiled from Janssens, 1981; and Morlan and Matthews, 1978; see also Morison and Smith, 1987; and Schweger, 1989).*

analysis and radiocarbon dating at about 2750 years B.P. This paleoenvironmental reconstruction is supported by a number of core analyses similar to the one illustrated by Figure 5. pH optima and tolerances for each bryophyte species are estimated using WACALIB, a computer program for weighted-averaging regression and calibration (Janssens and Birks, in prep.). It was developed initially for reconstructing paleoenvironmental gradients of pH based on diatom assemblages from lakes affected by acid rain (Birks, 1987; Birks *et al.*, in press). The advantages of using numerical techniques (Birks and Birks, 1980) for the reconstruction of past peatland environments are (1) the possibility of using **all** taxa, irrespective of the amount of quantitative data accumulated, (2) the explicit nature and repeatable techniques of the method (the WACALIB reference data set for fossil mosses of North America will be available soon from the author), and (3) the discovery of unsuspected problems and the formulation of new ecological theory (Gorham and Janssens, in prep.).

No detailed bryophyte developmental sequence, correlated with climatic phases during the entire Holocene, exists for North American peatlands (the present continental peatlands are mostly about 5000 years old). In Europe, however, major climatic periods (the late-glacial Alleröd and Younger Dryas, and the Holocene Pre-Boreal and Boreal) show an excellent correlation with changes in peatland communities (Rybníček and Rybníčková, 1968), and the principal developmental phases, according to the Central European phyto-sociocenological system. After bog (oligotrophic mire) developed, no fundamental changes took place, but only changes in the proportion of more hydrophilic and more xerophilic species. During the "Little Ice Age" (15th-18th century) the extent of mires also increased substantially as attested by early records quoted in Gorham (1953).

Bryogeography, Evolution, and Putative Extinct Species

Bryogeographical conclusions have always been a major part of all studies of Quaternary fossil bryophytes. Even the most recent Holocene records have distinct phytogeographical importance (Janssens and Glaser, 1986). Most bryogeographic conclusions have been phrased in the context of glacial or rich-fen relicts (Miller, 1984, 1987; Rybníček and Rybníčková, 1968; Rybníček, 1973; Dickson, 1973) and some have also had phylogenetic relevance (Janssens *et al.*, 1986). Several late-glacial localities in North America have records of species that do not extend as far south at the present: *Cinclidium latifolium* (Janssens, 1984); *Aulacomnium turgidum* (Figure 6; Miller, 1984); *Aulacomnium acuminatum* (Miller, 1973; LaSalle *et al.*, 1979); *Hypnum bambergeri* (Miller, 1976). As well, not all Pleistocene or early Holocene refugia were south of the main continental glaciers (Miller, 1987): *Fontinalis flaccida* (Figure 7) was identified from lake sediments in southeastern Labrador (Janssens *et al.*, 1986), and *Leptodontium flexifolium*, a southern United States and Central American species, was present during the mild mid-Wisconsinan Boutellier Interval in Beringia (Janssens and Zander, 1980).

Some of the species that are quite rare in present mire communities were more widespread during late Pleistocene and early Holocene time (Miller, 1987). For example, *Calliergon trifarium* formed thick peat layers throughout Europe (Rybníček and Rybníčková, 1968) and in the west-central watershed profiles of the Red Lake Peatland (Janssens *et al.*, in press). It has a considerably restricted distribution today. *Meesia triquetra* is commonly associated with species of *Sphagnum* section *Subsecunda* in fossil assemblages (Rybníček, 1973), but, at present, the two are rarely found together (Dickson, 1973). Rybníček (1973) suggests that this undoubtedly results from drainage in mires. However, the extensive expansion of oligotrophic mire communities restricted available habitat for species such as *M. triquetra*. These oligotrophic mire communities are only known from the Atlantic in Europe

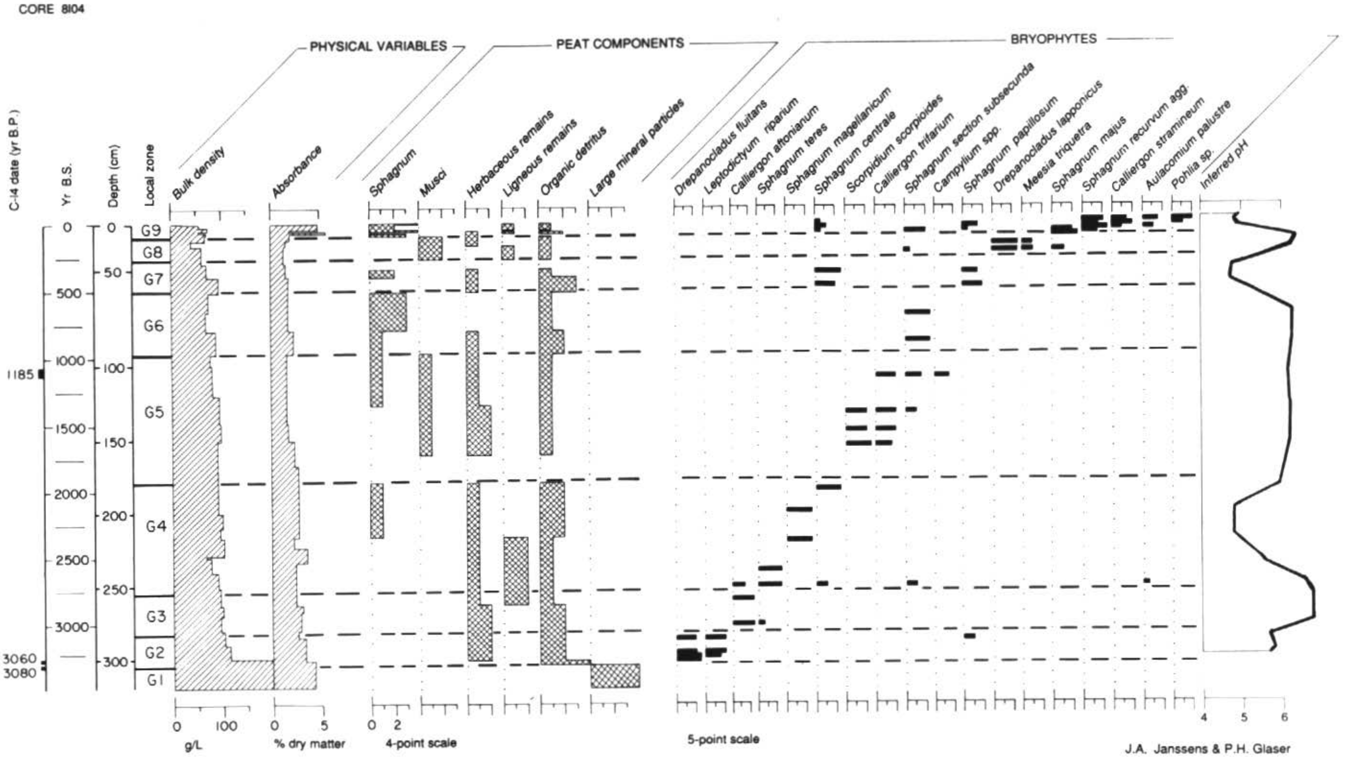

Figure 5 *Selected stratigraphic profiles versus calendar-year age for analyses from peat core 8104 of the Red Lake Peatland transect in northern Minnesota. The bryophyte profiles are discontinuous bar histograms at the level of each sample along a 5-point estimated volume scale (see Janssens (1987, 1988) for details). The inferred pH is estimated by weighted-averaging regression and calibration for each fossil-bryophyte assemblage using the FORTRAN program WACALIB. (From Janssens* et al., *in press.)*

(Rybníček, 1973) and from after the mid-Holocene warm period in continental North America (Zoltai *et al.*, 1988) and there is no preserved pre-Quaternary record of similar extensive deposits. This also suggests that speciation in *Sphagnum* could be very recent compared with the usual concept of bryophyte evolutionary rates. Compilation of the fossil record of *Sphagnum* (excluding doubtful spore records) does not give any clear hint of evolutionary development. The pre-Quaternary record is extremely meagre, and the Mesozoic records seem to be contaminants (Arnold, 1932; Reissinger, 1938). The order Protosphagnales, created by Neĭburg (1958) to accommodate the Permian fossil genera *Junjagia, Vorcutannularia,* and *Protosphagnum,* appears unrelated to the Sphagnales. Apart from the superficial resemblance in leaf-cell dimorphism these form species are structurally very different from *Sphagnum* (*e.g.*, well-developed costa and border present). In addition, the cell differentiation seen in photographs of these leaf areolations (Neĭburg, 1958, 1960) could sometimes be an artefact of fossilization: compression fossils often show the sideways collapse of large-lumened cells (as in present-day *Funaria* and *Splachnum* species) suggestive of an areolation pattern seen in *Sphagnum*. Moreover, pores or fibrils, other characteristic structures of *Sphagnum* branch-leaf cells, are not evident, but septae are (Oostendorp, 1987). The resolution of this artefact problem is not insignificant: the placement of *Sphagnum* in the moss clade is secondarily supported by the character complex of the Protosphagnales (Mishler and Churchill, 1984).

Few species of Quaternary age have been described as extinct (Miller, 1984), and none of these is still recognized as extinct. Even the late Tertiary Beaufort Formation (Kuc, 1973, 1974; Kuc and Hills, 1971; Matthews *et al.*, in press) contains no extinct species. It contains, however, *Calliergon aftonianum* (Kuc, 1974b), initially described as a Quaternary extinct moss from Aftonian deposits in Iowa (Steere, 1942). It is now recognized as a common Quaternary fossil (Kuc, 1974b; Janssens *et al.*, in press). It is indistinguishable from extant *Calliergon* populations found in the Lost River Peatland in northern Minnesota (Janssens and Glaser, 1986; Glaser *et al.*, in press). The fossil specimens are most likely a modification of the common *C. giganteum* or *C. richardsonii* (see also Miller, 1984, 1987). Similar conclusions have been drawn by Miller about the identity of *Drepanocladus minnesotensis* Williams (= *D. aduncus* var. *kneiffii*) and *Neocalliergon integrifolium* Williams (= *Scorpidium scorpioides*), based on study of type specimens (Figure 8; Miller, 1983). The morphological aspects of Tertiary and Quaternary fossil bryophytes are amazingly similar to those of the extant flora (Janssens *et al.*, 1979; Grolle, 1985) and contrast sharply with the well-known fossils of Mesozoic age (Harris, 1939;

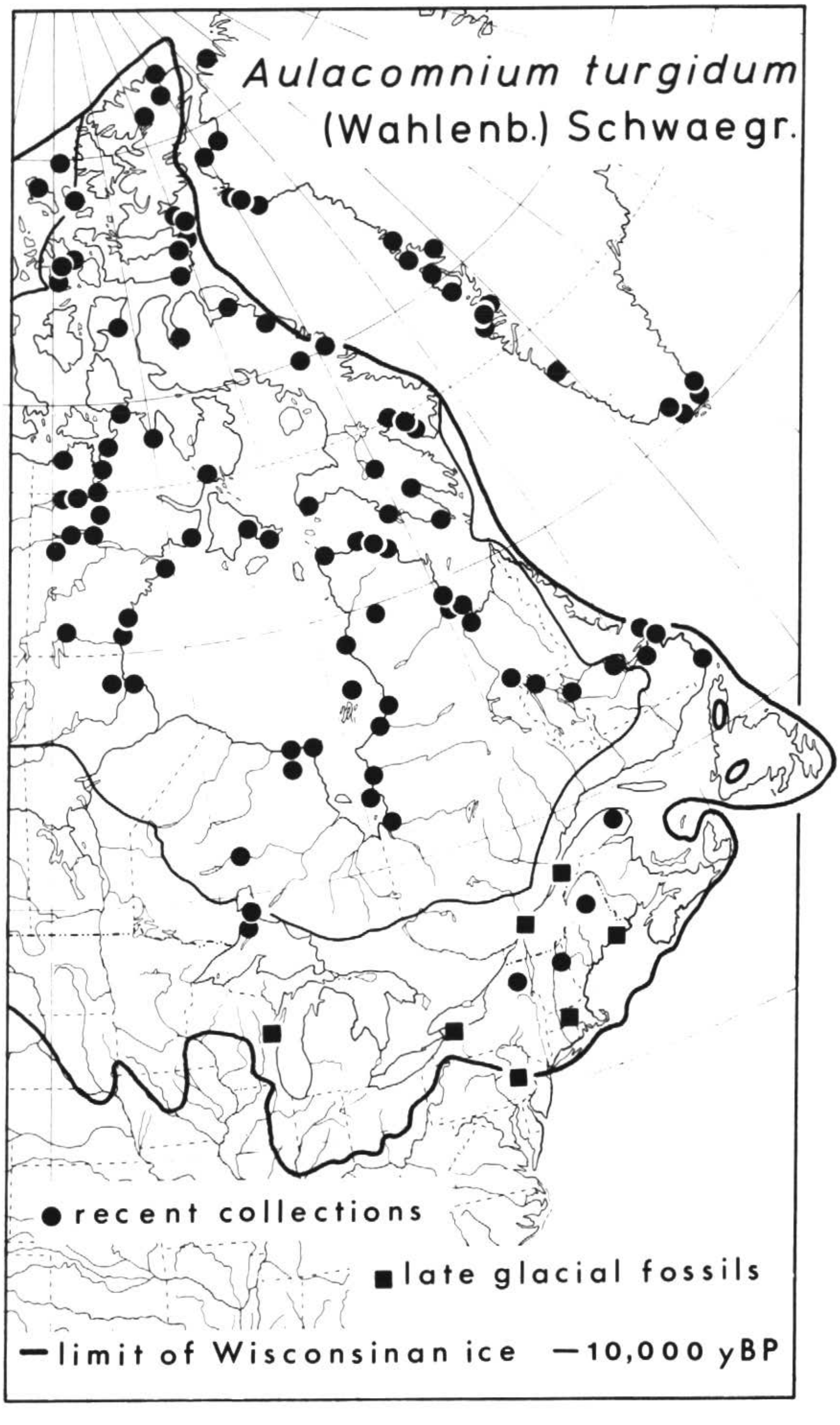

Figure 6 *Present and late-glacial distribution of* Aulacomnium turgidum *in eastern North America. (Modified from Miller, 1984).*

Figure 7 *Fragment of* Fontinalis flaccida *recovered from early postglacial lake sediments from Lake Hope Simpson, southeastern Labrador.* **(1)** *gametophore fragment, 12 ×;* **(2)** *rhizoid, 220 ×;* **(3)** *leaf apex, 220 ×;* **(4)** *medial leaf cells, 330 ×;* **(5)** *alar leaf cells, 360 ×;* **(6)** *leaf, 70 ×. (From Janssens* et al., *1986).*

Krassilov and Schuster, 1984; Schuster and Janssens, 1989) that are uniquely different from anything now living.

Future Directions

The record of fossil bryophytes, pre-Quaternary as well as Pleistocene and Holocene, has, to date, played only a minor role in phylogenetic and taxonomic studies. The absence or non-preservation of many characters, presently used extensively in the taxonomic study of extant populations, will always limit the value of fossil bryophytes for tracing phylogenetic lines. Alternatively, additional autecological study will enhance the capability of using fossil bryophytes for paleoenvironmental inference. Development of the new empirical and statistical procedures will finally establish quantitative bryophyte paleoecology in its own right among other Quaternary disciplines.

Acknowledgements

I thank Barry Warner, the editor of this series, for his valuable help and persistent encouragement to complete this review. I also thank Norton Miller for critical remarks and permission to republish illustrations from his papers, and H.J.B. Birks, H.A. Crum, J.H. Dickson, E. Gorham, J.V. Matthews, Jr., B.D. Mishler, and H.E. Wright, Jr. for comments on the manuscript. Some of the research mentioned here was supported by Natural Sciences and Engineering Research Council (Canada) to D.H. Vitt, by contracts from the Minnesota Department of Natural Resources and the United States Department of Energy to H.E. Wright, Jr. and by grants from the United States National Science Foundation (DEB7922142) and the A.W. Mellon Foundation to E. Gorham.

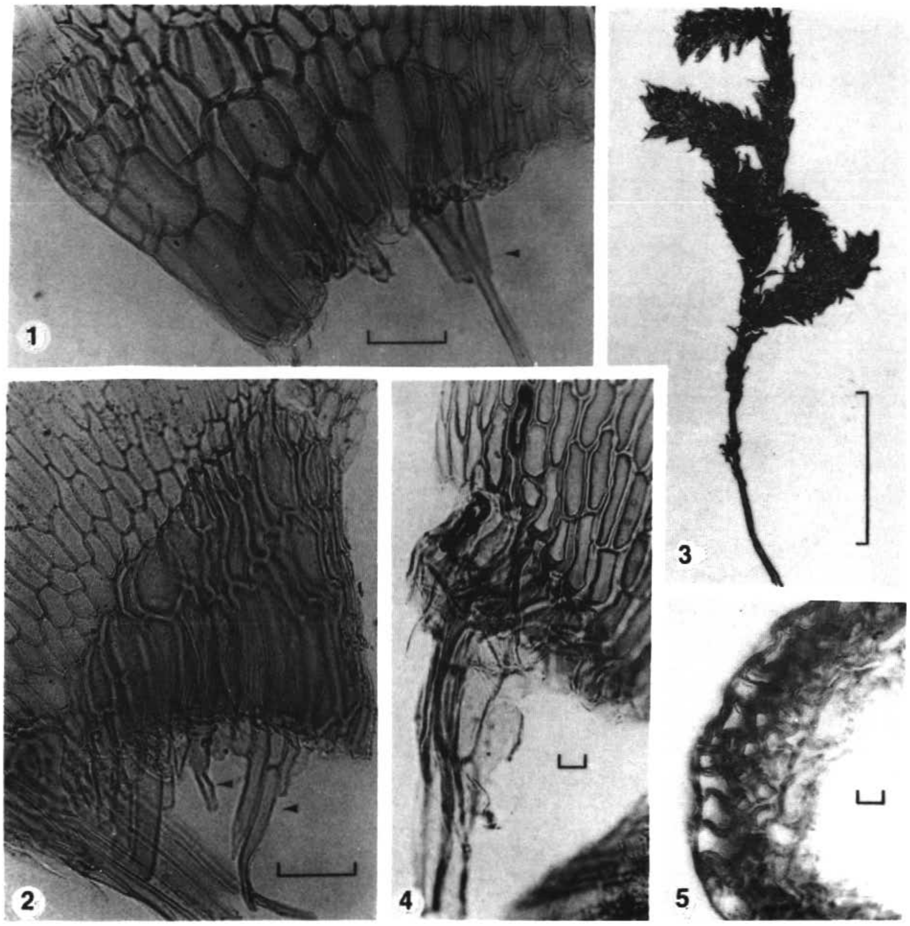

Figure 8 Drepanocladus minnesotensis (= D. aduncus *var.* kneiffii) *and* Neocalliergon integrifolium (= Scorpidium scorpioides). **(1-2)** D. minnesotensis: *alar cells of stem leaves with cortical cells of stem (at arrows) attached to leaf bases, scale = 50μm.* **(3-5)** Neocalliergon integrifolium. **(3)** *Plant, scale = 1 cm.* **(4)** *Alar region showing small group of enlarged cells at corner of leaf and enlarged cortical cells adhering to base of leaf, scale = 10μm.* **(5)** *Portion of transverse section of stem showing enlarged cortical cells, scale = 10μm. (From Miller, 1983).*

References

Aaby, B. and Jacobson, J., 1979, Changes in biotic conditions and metal deposition in the last millennium as reflected in ombrotrophic peat in Draved Mose, Denmark: Danmarks Geologiske Undersogelse, Årbog 1978, p. 5-43.

Anderson, R.S., Davis, R.B., Miller, N.G. and Stuckenrath, R., 1986, History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine: Canadian Journal of Botany, v. 64, p. 1977-1986.

Arnold, C.A., 1932, Microfossils from Greenland coal: Michigan Academy of Sciences, Arts and Letters, Papers, v. 15 (1931), p. 51-61.

Berglund, B.E., 1986, ed., Handbook of Holocene Palaeoecology and Palaeohydrology, J. Wiley & Sons, New York, 869 p.

Birks, H.H. and Mathewes, R.W., 1978, Studies in the vegetational history of Scotland. V: Late Devensian and early Flandrian pollen and macrofossil stratigraphy at Abernethy Forest, Inverness-shire: New Phytologist, v. 80, p. 455-484.

Birks, H.J.B., 1970, Inwashed pollen spectra at Loch Fada, Isle of Skye: New Phytologist, v. 69, p. 807-820.

Birks, H.J.B., 1976, Late-Wisconsinan vegetational history at Wolf Creek, central Minnesota: Ecological Monographs, v. 46, p. 395-428.

Birks, H.J.B., 1982, Quaternary bryophyte palaeoecology, *in* Smith, A.J.E., ed., Bryophyte Ecology: Chapman and Hall, London, p. 473-490.

Birks, H.J.B., 1985, Recent and possible future mathematical developments in quantitative paleoecology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 50, p. 107-147.

Birks, H.J.B., 1987, Methods for pH-calibration and reconstruction from paleolimnological data: procedures, problems, potential techniques, *in* Proceedings of Surface Water Acidification Programme (SWAP), Mid-Term Review Conference, Bergen 22-26 June 1987, p. 370-380.

Birks, H.J.B. and Birks, H.H., 1980, Quaternary Palaeoecology: Edward Arnold Publishers, London, 289 p.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. and ter Braak, C.J.F., in press, Diatoms and pH reconstruction: Royal Society of London, Philosophical Transactions, Series B, in press.

Birse, E.M., 1958, Ecological studies on growth-form in bryophytes. III. The relationship between growth-form of mosses and ground-water supply: Journal of Ecology, v. 46, p. 9-27.

Boros, A. and Jarai-Komlodi, M., 1975, An Atlas of Recent European Moss Spores: Akademiai Kiado, Budapest, 466 p.

Brassard, G.R., 1976, The mosses of northern Ellesmere Island, Arctic Canada III. New or additional records: The Bryologist, v. 79, p. 480-487.

Brassard, G.R. and Blake, W., Jr., 1978, An extensive subfossil deposit of the arctic moss *Aplodon wormskioldii*: Canadian Journal of Botany, v. 56, p. 1852-1859.

Clymo, R.S., 1965, Experiments on breakdown of *Sphagnum* in two bogs: Journal of Ecology, v. 53, p. 747-758.

Clymo, R.S. and Hayward, P.M., 1982, The ecology of *Sphagnum*, *in* Smith, A.J.E., ed., Bryophyte Ecology: Chapman and Hall, London, p. 229-289.

Conolly, A.P. and Dickson, J.H., 1969, A note on a Late-Weichselian *Splachnum* capsule from Scotland: New Phytologist, v. 68, p. 197-199.

Crandall-Stotler, B., 1984, Musci, hepatics and anthocerotes — an essay on analogues, *in* Schuster, R.M., ed., New Manual of Bryology, Volume 2: Hattori Botanical Laboratory, Nichinan, Japan, p. 1093-1129.

Crum, H.A., 1984, Sphagnopsida, Sphagnaceae, *in* North American Flora, Series II, Part 11: The New York Botanical Garden, 180 p.

Damman, A.W.H., 1977, Geographical changes in the vegetation pattern of raised bogs in the Bay of Fundy region of Maine and New Brunswick: Vegetatio, v. 35, p. 137-151.

de Vries, B. and Bird, C.D., 1965, Bryophyte subfossils of a late-glacial deposit from the Missouri Coteau, Saskatchewan: Canadian Journal of Botany, v. 43, p. 947-953.

Dickson, J.H., 1973, Bryophytes of the Pleistocene: Cambridge University Press, London, 256 p.

Dickson, J.H., 1981, Mosses from a Roman well at Abingdon: Journal of Bryology, v. 11, p. 559-560.

Dickson, J.H., 1986, Chapter 30: Bryophyte analysis, *in* Berglund, B.E., ed., Handbook of Holocene Paleoecology and Paleohydrology: J. Wiley & Sons, New York, p. 627-643.

Dietert, M.F., 1980, The effect of temperature and photoperiod on the development of geographically isolated populations of *Funaria hygrometrica* and *Weissia controversa*: American Journal of Botany, v. 67, p. 369-380.

Duckett, J.G. and Clymo, R.S., 1988, Regeneration of bog liverworts: New Phytologist, v. 110, p. 119-127.

During, H.J., 1979, Life strategies of bryophytes: a preliminary review: Lindbergia, v. 5, p. 2-18.

Flatberg, K.I., 1986, Taxonomy, morphovariation, distribution and ecology of the *Sphagnum imbricatum* complex with main reference to Norway: Gunneria, v. 54, p. 1-118.

Gimingham, C.H. and Birse, E.M., 1957, Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat: Journal of Ecology, v. 45, p. 533-545.

Gimingham, C.H. and Smith, R.I.L., 1971, Growth form and water relations on mosses in the maritime antarctic: Bulletin of the British Antarctic Survey, v. 25, p. 1-21.

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.

Glaser, P.H., Janssens, J.A. and Siegel, D.I., in press, Responses of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota: Journal of Ecology, in press.

Gorham, E., 1953, Some early ideas concerning the nature, origin, and development of peatlands: Journal of Ecology, v. 41, p. 257-274.

Gorham, E., 1956, On the chemical composition of some waters from the Moor House Nature Reserve: Journal of Ecology, v. 44, p. 377-384.

Gorham, E., in press, Biotic impoverishment of northern peatlands, *in* Woodwell, G.M., ed., The Earth in Transition, Patterns and Processes of Biotic Impoverishment: Cambridge University Press, in press.

Green, B.H., 1968, Factors influencing the spacial and temporal distribution of *Sphagnum imbricatum* Hornsch. *ex* Russ. in the British Isles: Journal of Ecology, v. 56, p. 47-58.

Grolle, R., 1985, Monograph of *Frullania* in Baltic amber: Prace Muzeum Ziemi, Warszawa, v. 37, p. 87-100.

Harris, T.M., 1939, *Naiadita*, a fossil bryophyte with reproductive organs: Annales Bryologici, v. 12, p. 57-70.

Hinde, G.J., 1877, The glacial and interglacial strata of Scarboro' Heights, and other localities near Toronto: Canadian Journal of Science, N.S., v. 15, p. 388-413.

Hopkins, D.M., 1982, Aspects of the paleogeography of Beringia during the late Pleistocene, *in* Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E. and Young, S.B., eds., Paleoecology of Beringia: Academic Press, New York, p. 3-28.

Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E. and Young, S.B., 1982, Paleoecology of Beringia: Academic Press, New York, 489 p.

Horton, D.G., 1982, The evolutionary significance of surficial spore characters in the Bryidae: Journal of the Hattori Botanical Laboratory, v. 53, p. 99-105.

Hueber, F.M., 1961, *Hepaticites devonicus*, a new fossil liverwort from the Devonian of New York: Annals of the Missouri Botanical Garden, v. 48, p. 125-132.

Hughes, O.L., Harrington, C.R., Janssens, J.A., Matthews, J.V., Jr., Morlan, R.E., Rutter, R.W. and Schweger, C.E., 1981, Upper Pleistocene stratigraphy, paleoecology, and archaeology of the northern Yukon Interior, eastern Beringia, 1: Bonnet Plume Basin: Arctic, v. 34, p. 329-365.

Ingram, H.A.P., 1983, Hydrology, *in* Gore, A.J.P., ed., Mires: Swamp, Bog, Fen, and Moor: Elsevier Publishing Company, Amsterdam, General Studies, Ecosystems of the World 4A, p. 67-158.

Janssens, J.A., 1981, Subfossil Bryophytes in Eastern Beringia: their paleoenvironmental and paleogeographical significance, Ph.D. dissertation, University of Alberta, 450 p.

Janssens, J.A., 1983a, A quantitative method for stratigraphical analysis of bryophytes in Holocene peat: Journal of Ecology, v. 71, p. 189-196.

Janssens, J.A., 1983b, Past and extant distribution of *Drepanocladus* in North America, with notes on the differentiation of fossil fragments: Journal of the Hattori Botanical Laboratory, v. 54, p. 251-298.

Janssens, J.A., 1984, Quaternary fossil bryophytes in North America: new records: Lindbergia, v. 9, p. 137-151.

Janssens, J.A., 1987, Ecology of peatland bryophytes and paleoenvironmental reconstruction of peatlands using fossil bryophytes, Manual for Bryological Methods Workshop, Mainz, FRG, 17-23 July 1987, Update August 1987, 68 p.

Janssens, J.A., 1988, Fossil bryophytes and paleoenvironmental reconstruction of peatlands, *in* Glime, J.M., ed., Methods in Bryology, Proceedings of the Bryological Methods Workshop, Mainz: Hattori Botanical Laboratory, Nichinan, Japan, p. 299-306.

Janssens, J.A. and Baker, R.G., 1984, A full-glacial bryophyte assemblage from southeastern Iowa: Journal of Bryology, v. 13, p. 201-207.

Janssens, J.A. and Barnosky, C.W., 1985, Late-Pleistocene and Early-Holocene bryophytes from Battle Ground Lake, Washington, USA: Review of Palaeobotany and Palynology, v. 46, p. 97-116.

Janssens, J.A., Engstrom, D.R. and Horton, D.G., 1986, *Climacium dendroides* and *Fontinalis flaccida*: fossils of the early postglacial of Labrador: Lindbergia, v. 12, p. 67-72.

Janssens, J.A. and Glaser, P.H., 1986, The bryophyte flora and major peat-forming mosses at Red Lake Peatland, Minnesota: Canadian Journal of Botany, v. 64, p. 427-442.

Janssens, J.A., Hansen, B.C.S., Glaser, P.H. and Barnosky, C.W., in press, Development of a raised bog complex in northern Minnesota, *in* Wright, H.E., Jr., Coffin, B. and Aasing, N., eds., Patterned Peatlands of northern Minnesota, in press.

Janssens, J.A., Horton, D.G. and Basinger, J.F., 1979, *Aulacomnium heterostichoides* sp. nov., an Eocene moss from central British Columbia: Canadian Journal of Botany, v. 57, p. 2150-2161.

Janssens, J.A. and Zander, R.H., 1980, *Leptodontium flexifolium* and *Pseudocrossidium revolutum* as 60,000 year old subfossils from the Yukon Territory: The Bryologist, v. 83, p. 486-496.

Krassilov, B.A. and Schuster, R.M., 1984, Paleozoic and Mesozoic fossils, *in* Schuster, R.M., ed., A New Manual of Bryology: Hattori Botanical Laboratory, Obi, Japan, p. 1172-1193.

Kuc, M., 1973, Fossil flora of the Beaufort Formation, Meighen Island, NWT-Canada: ERA, Canadian-Polish Research Institute, Biology and Earth Sciences, Series A, No. 1, Toronto, Canada, 44 p.

Kuc, M., 1974a, The interglacial flora of Worth Point, western Banks Island: Geological Survey of Canada, Paper 74-1B, p. 227-231.

Kuc, M., 1974b, *Calliergon aftonianum* Steere in Late Tertiary and Pleistocene deposits of Canada: Geological Survey of Canada, Paper 74-24, 8 p.

Kuc, M. and Hills, L.V., 1971, Fossil mosses, Beaufort Formation (Tertiary), Northwestern Banks Island, Western Canadian Arctic: Canadian Journal of Botany, v. 49, p. 1089-1094.

LaSalle, P., Martineau, G. and Chauvin, L., 1979, Lits de bryophytes du Wisconsin moyen, Vallée-Jonction, Québec: Canadian Journal of Earth Sciences, v. 16, p. 593-598.

Longton, R.E., 1976, Reproductive biology and evolutionary potential in bryophytes: Journal of the Hattori Botanical Laboratory, v. 41, p. 205-223.

Longton, R.E., 1988, The biology of polar bryophytes and lichens: Cambridge University Press, Cambridge, 391 p.

Luken, J.O., 1984, Net ecosystem production in a subarctic peatland, Ph.D. dissertation, Duke University.

Mathewes, R.W., 1973, A palynological study of postglacial vegetation changes in the University Research Forest, southwestern British Columbia: Canadian Journal of Botany, v. 51, p. 2085-2103.

Matthews, J.V., Jr., 1987, 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., Jr., 1989, New information on the flora and age of the Beaufort Formation, Arctic Archipelago, and related Tertiary deposits in Alaska: Geological Survey of Canada, Paper 89-1D, p. 105-111.

Matthews, J.V., Jr., Ovenden, L.E. and Fyles, J.G., in press, Plant and insect fossils from the late Tertiary Beaufort Formation on Prince Patrick Island, Northwest Territories, in press.

Miller, H.A., 1982, Bryophyte evolution and geography: Biological Journal of the Linnean Society, v. 18, p. 145-196.

Miller, N.G., 1973, Late glacial plants and plant communities in northwestern New York State: Journal of the Arnold Arboretum, v. 54, p. 123-159.

Miller, N.G., 1976, Quaternary fossil bryophytes in North America: a synopsis of the record and some phytogeographic implications: Journal of the Hattori Botanical Laboratory, v. 41, p. 73-85.

Miller, N.G., 1980a, Quaternary fossil bryophytes in North America: catalog and annotated bibliography: Journal of the Hattori Botanical Laboratory, v. 47, p. 1-43.

Miller, N.G., 1980b, Fossil mosses in North America and their significance, *in* Taylor, R.J. and Leviton, A.L., eds., The Mosses of North America: American Association for the Advancement of Science, San Francisco, p. 9-36.

Miller, N.G., 1980c, Mosses as paleoecological indicators of lateglacial terrestrial environments: some North American studies: Torrey Botanical Club, Bulletin, v. 107, p. 373-391.

Miller, N.G., 1983, The identity of the Pleistocene mosses of *Drepanocladus minnesotensis* and *Neocalliergon integrifolium* (Amblystegiaceae): Brittonia, v. 35, p. 87-92.

Miller, N.G., 1984, Tertiary and Quaternary fossils, *in* Schuster, R.M., ed., A New Manual of Bryology: Hattori Botanical Laboratory, Obi, Japan, p. 1194-1232.

Miller, N.G., 1987, Phytogeography and paleoecology of a late Pleistocene moss assemblage from northern Vermont: Memoirs of the New York Botanical Garden, v. 45, p. 242-258.

Miller, N.G. and Futyma, R.P., 1987, Paleohydrological implications of Holocene peatland development in northern Michigan: Quaternary Research, v. 27, p. 297-311.

Mishler, B.D. and Churchill, S.P., 1984, A cladistic approach to the phylogeny of the "bryophytes": Brittonia, v. 36, p. 406-424.

Mishler, B.D. and Churchill, S.P., 1985, Cladistics and the land plants: a response to Robinson: Brittonia, v. 37, p. 282-285.

Morison, S.R. and Smith, C.A.S., 1987, eds., Guidebook to Quaternary Research in Yukon: XXII INQUA Congress, Ottawa, Canada.

Morlan, R.E., 1980, Taphonomy and archeology in the Upper Pleistocene of the northern Yukon Territory: a glimpse on the peopling of the new world: Archeological Survey of Canada, Paper 94, 398 p.

Morlan, R.E. and Matthews, J.V., Jr, 1978, New dates for Early Man: Geos, Winter 1978, p. 2-5.

Neĭburg, M.F., 1958, Permian true mosses of Angaraland: Journal of the Paleontological Society, India, v. 3, p. 22-29.

Neĭburg, M.F., 1960, Listostebelnye mkhı iz Permskikh otlozhenii Angaridy: Akademiya Nauk SSSR, Trudy Geologicheskogo Instituta, Vypusk 19, Moskva, 104 p.

Nyholm, E., 1954-1969, Illustrated Moss Flora of Fennoscandia: C.W.K. Gleerup, Lund, 799 p.

Odgaard, B.V., 1981, The Quaternary Bryoflora of Denmark. I: Species list: Danmark geologiske Undersogelse, Årbog 1980, p. 45-74.

Odgaard, B.V., 1982, A Middle Weichselian moss assemblage from Hirtshals, Denmark, and some remarks on the environment 47,000 B.P.: Danmark geologiske Undersogelse, Årbog 1981, p. 5-45.

Oostendorp, C., 1987, The bryophytes of the Palaeozoic and Mesozoic: Bryophytorum Bibliotheca, Band 34: J. Cramer, Berlin-Stuttgart, 112 p.

Pratt, W.H., 1876, Report on a geological examination of the section of the bluffs recently exposed by the C.R.I. & P.R.R.: Davenport Academy Natural Sciences, Proceedings, v. 1, p. 96-99.

Reissinger, A., 1938, Die "Pollenanalyse" ausgedehnt auf alle Sedimentgesteine der geologischen Vergangenheit: Palaeontographica, v. 84B, p. 1-20.

Rybníćek, K., 1973, A comparison of the present and past mire communities of central Europe, *in* Birks, H.J.B. and West, R.G., eds., Quaternary Plant-Ecology: 14th Symposium of the British Ecological Society: Blackwell Scientific Publications, Oxford, p. 238-261.

Rybníćek, K. and Rybníčková, E., 1968, The history of flora and vegetation on the Blāoto Mire in southeastern Bohemia, Czechoslovakia: Folia Geobotanica Phytotaxonomica Praha, v. 3, p. 117-142.

Scagel, R.F., Bandoni, R.J., Maze, J.R., Rouse, G.E., Schofield, W.B. and Stein, J.R., 1982, Nonvascular Plants: an evolutionary survey: Wadsworth, Belmont, California, 570 p.

Schofield, W.B., 1985, Introduction to bryology: MacMillan Publishing Co., New York, 431 p.

Schuster, R.M., 1966, The Hepaticae and Anthocerotae of North America, east of the hundredth Meridian: Columbia University Press, New York, v. 1.

Schuster, R.M. and Janssens, J.A., 1989, On *Diettertia*, an isolated Mesozoic member of the Jungermanniales: Review of Palaeobotany and Palynology, v. 57, p. 277-287.

Schweger, C.E., 1989, The Old Crow and Bluefish Basins, northern Yukon: development of the Quaternary history, *in* Carter, L.D., Hamilton, T.D. and Galloway, J.P., eds., Late Cenozoic History of the Interior Basins of Alaska and the Yukon: United States Geological Survey, Circular 102B, p. 30-33.

Schweger, C.E. and Janssens, J.A., 1980, Paleoecology of the Boutellier Non-glacial Interval, St. Elias Mountains, Yukon Territory, Canada: Arctic and Alpine Research, v. 12, p. 309-317.

Shaw, J., 1987, Evolution of heavy metal tolerance in bryophytes II. An ecological and experimental investigation of the "copper moss", *Scopelophila cataractae* (Pottiaceae): American Journal of Botany, v. 74, p. 813-821.

Shaw, J., Antonovics, J. and Anderson, L.E., 1987, Inter- and intraspecific variation of mosses in tolerance to copper and zinc: Evolution, v. 41, p. 1312-1325.

Steere, W.C., 1942, Pleistocene mosses from the Aftonian Interglacial deposits of Iowa: Michigan Academy of Science, Arts and Letters, Papers, v. 27, p. 75-104.

Stewart, T.G, 1981, The Holocene paleoenvironment of Clements Markham Inlet, Northern Ellesmere Island, N.W.T., Canada, M.Sc. dissertation, University of Alberta, 135 p.

Stewart, T.G. and England, J., 1983, Holocene sea-ice variations and paleoenvironmental change, northernmost Ellesmere Island, N.W.T., Canada: Arctic and Alpine Research, v. 15, p. 1-17.

Sveinbjörnsson, B. and Oechel, W.C., 1983, The effect of temperature preconditioning on the temperature sensitivity of net CO_2 flux in geographically diverse populations of the moss *Polytrichum commune*: Ecology, v. 64, p. 1100-1108.

Tamm, C.O., 1953, Growth, yield and nutrition in carpets of the forest moss *(Hylocomium splendens)*: Meddelanden Fran Statens Skogsforskningsinstitut, Band 43 (1), 140 p.

Tolonen, K. and Tolonen, M., 1984, Late-glacial vegetational succession at four coastal sites in northeastern New England: Ecological and phytogeographical aspects: Annales Botanici Fennici, v. 21, p. 59-78.

Verry, E.S., 1984, Microtopography and water table fluctuation in a *Sphagnum* mire: Proceedings of the 7th International Peat Congress, Dublin, Ireland, 18-23 June 1985, Volume II.

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.

Wasylikowa, K., 1986, Analysis of fossil fruits and seed, *in* Berglund, B.E., ed., Handbook of Holocene Palaeoecology and Palaeohydrology: J. Wiley & Sons, New York, p. 571-590.

Watts, W.A. and Winter, T.C., 1966, Plant macrofossils from Kirchner Marsh, Minnesota — a paleoecological study: Geological Society of America, Bulletin, v. 77, p. 1339-1360.

Webb, J.A. and Moore, P.D., 1982, The late Devensian vegetational history of the Whitlaw Mosses, southeast Scotland: New Phytologist, v. 91, p. 341-398.

Westgate, J.A., 1988, Isothermal plateau fission track age of the late Pleistocene Old Crow tephra, Alaska: Geophysical Research Letters, v. 15, p. 376-379.

Wolfe, J.A., 1978, A paleobotanical interpretation of Tertiary climate in the Northern Hemisphere: American Scientist, v. 66, p. 694-703.

Wright, H.E., Jr., Mann, D.H. and Glaser, P.H., 1984, Piston corers for peat and lake sediment: Journal of Ecology, v. 65, p. 657-659.

Wyatt, R. and Anderson, L.E., 1984, Breeding systems in bryophytes, *in* Dyer A.F. and Duckett, J.G., eds, The Experimental Biology of Bryophytes: Experimental Botany, v. 19, p. 39-64.

Zoltai, S.C., Taylor, S., Jeglum, J.K., Mills, G.F. and Johnson, J.D., 1988, Wetlands of Boreal Canada, *in* Rubec, C.D.A., ed., Wetlands of Canada: Polyscience Publications, Montreal, Quebec, p. 97-154.

Accepted 10 November 1989.