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SUBFOSSIL BRYOPHYTES IN EASTERN BERINGIA: THEIR PALEOENVIRONMENTAL AND PHYTOGEOGRAPHICAL SIGNIFICANCE

by

JAN A.P. JANSSENS

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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ABSTRACT

Eight hundred and eighty two new subfossil records of bryophytes are reported. The specimens were extracted from unconsolidated Pleistocene and Holocene sediments by screening. Five hundred and twenty-two of the records are from a complex sequence of Late Pleistocene age in the Old Crow Basin in the northern Yukon Territory, Canada, while other samples analysed are from Alaska, Alberta, Greenland, Iowa, Northwest Territories, Nova Scotia, Ontario and Quebec. Attention is drawn to microscopic morphological characters that differentiate the 145 different taxa. Habitat descriptions, recent North American distribution ranges and the known subfossil record in North America are compiled for each taxon.

The few liverwort records contrast sharply with the numerous mosses reported. On the other hand, the Amblystegiaceae (457 records) are strongly over-represented by comparison with the present day flora. Most extant *Drepanocladus* species have been found in samples of Late Pleistocene age (250 records). A key to identify fragmentary *Drepanocladus* material has been constructed and each species is defined by a diagnosis. A newly described species, *D. crassicostatus*, is characterized by an excurrent costa, denticulate margins and poorly developed alar cells. It is an extremely common subfossil in arctic and subarctic lacustrine and transported sediments, and is closely related to the European *D. trichophyllus*. *Drepanocladus crassicostatus* is known from only a few, scattered, present-day populations in North America, but its apparent scarcity may reflect lack of collections. It is found in highly minerotrophic waters, in contrast with the oligotrophic habitats characteristic of *D. trichophyllus*.

The preserved bryophytic remains in the Old Crow Basin sequence make it possible to aid in the reconstruction of the Late Pleistocene and postglacial vegetation history of eastern Beringia. Geomorphological evidence indicates that the basin was flooded at least twice and that these floods correlated with the major advances of Keewatin ice. During the long intervening period fluviatile sediments were deposited and in this inorganic matrix of sands, silts and clays were abundant organic remains. Most bryophytes are members of transported assemblages. However, some mixed and autochthonous samples were also recovered.

During the Gold Hill and early Old Crow Intervals (80,000 to 40,000 years ago) forests developed. This is indicated by the increase in bryophytes growing in mesic habitats. *Leptodontium flexifolium*, a possible remnant of a late Tertiary mesophytic flora, was still present during these intervals in the Old Crow Basin. This oceanic and montane species presumably became extinct north of the Southern Appalachians during the Late Wisconsinan. The formation of an extensive erosion surface, 65,000 years ago, suggests the optimal phase of the interstadial. The landscape was a mosaic of rich fen habitats, well developed *Picea* forest communities and drier upland calcareous tundra (with numerous moss taxa). *Sphagnum* was much less abundant than it was during the more mesophytic postglacial period. The later part of the Old Crow Interval (40,000 to 25,000 years ago) saw the onset of a very dry and probably cold period. Some southern Yukon moss assemblages indicate steppe-tundra vegetation. Bryophytes in the Old Crow Basin are derived exclusively from rich fen communities. *Sphagnum* is completely lacking. Also, there is no evidence of trees and shrubs. However, during the same period extensive rich bryophyte assemblages southeast of the basin in the Richardson Mountains indicate the survival of extremely diversified *Picea* forest until immediately before the appearance of Keewatin ice.

During the following Duvany Yar Interval that coincided with the last flooding of the basin in the northern Yukon, sterile clays were deposited and there is no bryophyte record in the Old Crow localities. The interval came to an abrupt end 13,000 years ago. The basin drained and extensive peat accumulations started by 9000 years ago. More mesophytic communities are suggested by the bryophyte assemblages, and *Sphagnum* became abundant for the first time.

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I. INTRODUCTION

A. Phytogeography and Fossil Data

The post-Darwinian period gave the discipline of plant geography new life. What began as the mere description of the spatial relationships of plants became one of the much needed lines of evidence on evolution itself. Basic data of the plant phytogeographer include plant ranges, geological features and fossil records. However, there are two different approaches to the study of these data. The floristic plant geographer tries to correlate evolutionary divergence, migration, and distribution patterns of a taxon with past events of the earth's history. Causal links between these data can be speculated upon. On the other hand, the ecological plant geographer attempts to reconstruct the history of communities and vegetation types, and speculates on their origins.

It is clear that phytogeography is very much a speculative science [illegible] distinction between floristic and ecological plant geography is reflected in the basic approaches used by phytogeographers. Two extremes in the continuum between floristic and ecological plant geography can be observed: one is represented by the person who uses the present ranges of taxa as primary data and speculates on the origins and previous distribution. He refines these hypotheses by correlation with geological and climatological events, ecophysiology, fossil data, morphological adaptations and ecology. The other extreme is represented by the person who has fossil assemblages available and considers them as his primary data base. More or less detailed phytogeographical hypotheses are then built by reconstructing the distribution of vegetation units through time.

What follows is a chronological discussion of the developments of some diverse concepts in North American phytogeography. It will soon be very clear that the classification of phytogeographers into an ecological and a floristic group is extremely arbitrary. One of the earliest and most eminent botanists in North America who turned his attention to phytogeography was Asa Gray. He studied, for the first time, the floristic affinities between eastern (primarily, but also western) North America and eastern Asia (especially Japan) (Gray 1846). The floristic entities common to both areas had already attracted the attention of Halen, a student of Linnaeus (*cf.* Fernald 1931). Gray (1859) reported the botanical results of the United States North Pacific Exploring Expedition and listed nearly 600 species of temperate Japanese plants. He gave their known occurrences in northern Asia, Europe, western and eastern North America. Twenty-one species had disjunct distributions between Japan and eastern North America. Other students (for example Sharp (1939) on bryophytes) added to the details of the floristic affinities, and Li (1971) reviewed the list of vascular plants in light of modern taxonomic concepts.

The most striking relationship was revealed by the identical species of vascular plants that are common on both continents and by the vicarious species pairs, or sets of congeneric species. Gray (1859) wrote that:

> "There has been a peculiar intermingling of the eastern American and eastern Asian floras, which demands explanation."

It is pertinent to note here that in this pre-Darwinian time leading biologists of the day were proponents of special creation and it is thus remarkable that Gray (1859), in an attempt to explain the relationships between the American and Japanese flora, wrote the following:

> "All the facts known to us in the Tertiary and post-Tertiary, even to the limiting line of the drift, conspire to show that the difference between the two continents Asia and America as to temperature was very nearly the same then as now, and that the isothermal lines of the northern hemisphere curved in the directions they do now. A climate such as these facts would demonstrate for the fluvial epoch would again commingle the temperate floras of the two continents at Bering's Strait, and earlier – probably through more land than now – by the way of the Aleutian and Kurile Islands. I cannot imagine a state of circumstances under which the Siberian elephant could migrate, and temperate plants could not ... Under the light which these geological considerations throw upon the question, I cannot resist the conclusion, that the extant vegetable kingdom has a long and eventful history, and that the explanation of apparent anomalies in the geographical distribution of species may be found in the various and prolonged climatic or otherwise physical vicissitudes to which they have been subject in earlier times;– that the occurrence of certain species, formerly supposed to be peculiar to North America, in a remote or antipodal region affords of itself no presumption that they were originated there ..."

Gray's later work (1860, 1873 & 1878) added considerable detail to his revolutionary concepts.

Around the same time, in the latter half of the eighteenth century, many biologists, following Schouw (1823), believed that species originated where they are found and that many plant taxa are polytopic in origin. Bigelow and Agassiz, opposed the idea that plants could undergo any significant migration. Both argued (during a meeting of the American Acadamy, related in Cain 1944) that circumpolar, homogeneous biota, created by polytopic origin and local expansion, gave rise to disjunct ranges by subsequent dying-out of types in the intervening areas. Gray (1873) could not agree with them and stated that the flora, as well as the fauna, migrated to new areas under the compulsion of climatic changes, with disjunctions resulting from these migrations. Gray feared that the concept of polytopic origin would remove the entire question of plant migration out of inductive science. He brought forth two lines of evidence that suggested why plant migration was possible: 1) the enormous multiplying powers, and facilities and means of dissemination of all living organisms, and 2) the ever increasing paleontological evidence of the previous occurrence, in areas that are different from moderns ones, of extant species.

Perhaps as a result of Gray's concepts and influence among early botanists, an historical perspective and the idea of extensive migrations have dominated floristic plant geography. Asa Gray attributed disjunct ranges to subsequent disruption of earlier intercontinental continuity. and he also believed in migration of flora and fauna that resulted in biota far from their center of origin. Hooker (1878) accepted the idea of plant migrations and he was the first to suggest that the relative impoverishment of the European flora, by comparison with the North American, was the result of different topography. The east-west trend of mountains and bodies of water in Europe and western Asia accounted for in the extinction of many forms during the forced, southward migrations of biota in the Pleistocene, while in eastern Asia and eastern North America there was an possibility for southward retreat during the ice advance because natural barriers were lacking.

In the beginning of the twentieth century numerous contributions by Fernald expanded the data-base of floristic geography and substantiated the migration concept. Fernald frequently concerned himself with the problem of disjunct ranges, especially in eastern North America and eastern Asia. It is apparent from the following (Fernald 1931) that he considered disjunct taxa occurring in these areas to be survivors of ancient Tertiary vegetation:

> "Viewed from the standpoint of availability for occupation by flowering plants, the oldest large section of the region is the southern half of the Appalachian Upland, extending from central New York to northern Georgia and northern Alabama, and west of the Mississippi represented by the Ozark Plateau. Never, since it was first occupied by Angiosperms, has the Appalachian Upland of the United States (and Canada) been invaded by seas; and, except for its northern extension, it lies wholly south of the limits of the Pleistocene glaciation. ... In the ancient Appalachian Upland ... the outstanding phytogeographic feature is, of course, the great mesophytic forest of Mesozoic or early Cenozoic genera. ... Not only ... are these Appalachian genera of today the genera of thousand ages; their species are also ancient and usually sharply differentiated... When the hundreds of species of Appalachian angiospermous genera are compared with their old world representatives the general conclusion is apparent: that in nearly all groups the species of the Western Hemisphere are completely segregated from those of the Eastern; that we have stable or essentially stable specific entities."

The idea that plants could survive north of the extent of glaciation was first proposed to explain the occurrences of certain relictual elements in the western Norwegian flora and also the close relationships of that flora with that of Greenland and Iceland (Blytt, Sernander, Wille, Hansen & Nordhagen: see Dahl 1945 for a review). However, Fernald (1925, 1931) was largely responsible for attracting attention to the potential significance of "nunataks" in North American phytogeography.

Among Fernald's major contributions were his studies of plant distributions in the area around the Gulf of St. Lawrence and his development of the nunatak theory. He studied a considerable number of plants, many of which were either considered endemic, or identical with (or very closely related to), plants found elsewhere only in the western mountains or more rarely in parts of continental Asia. Moreover, he showed that these plants have, in eastern North America, a very local and restricted distribution, found only in areas that may have been unglaciated during the Pleistocene. Later on, he supposed that several of the plants survived in northern localities during the Pleistocene and migrated to where they are now found, but were not derived by eastward migration from the western mountains.

Fernald's nunatak theory was challenged by Wynne-Edwards (1937), who correlated the localization of many arctic-alpine species in the Gulf of St. Lawrence region with the availability of certain soil conditions (calcareous rocks), and pointed out that more acid rocks, even if they were nunataks, do not have local relicts. He (1937) adhered to the "orthodox" views which preceeded the nunatak theory of Fernald as is evident from the following statement:

> "... it is propounded that the arctic-alpine flora of eastern North America has formed a single unit since pre-Wisconsin times; that in those times it occupied suitable habitats in latitudes similar to or higher than now; that with the advance of the Wisconsin glaciation it was driven southward and outward; and finally with the retreat of the ice a recolonization of suitable habitats took place."

In summary, the controversy between Fernald's and Wynne-Edwards' concepts centers around 1) the potential for plants to survive harsh climates of nunataks 2) and the ability to recolonize deglaciated terrain rapidly in edaphically favorable spots (also see for example, Crum 1972). An answer to the nunatak dilemma can only come after many more intensive paleobotanical, autecological and geological studies, and from detailed climatic reconstruction (such as the CLIMAP project (Gates 1976)).

During the first half of this century plant ecologists introduced some new and diverse conceptual ideas that influenced ecological, as well as floristic, plant geography. Clements (1918) stated that attention must first be turned to the biome, or the plants and animals of a particular area or habitat. This emphasis, together with his climax concepts, are essential to understanding much of what happened to ecological phytogeography and paleoecology prior to 1955. He (1918) stated that:

> "... the plant community is a complex organism, with structure and functions and with a characteristic development, ... In paleo-ecology the concept of the biome, or biotic community, seems to have peculiar value, as it directs especial attention to the causal relations and reactions of the three elements-habitat, plant, and animal."

In his pioneer publication, Clements (1916) outlined the basic paleoecological principles. He stressed uniformitarianism (" ... processes of succession [were] essentially the same during geological time as today ... ", "Climatic areas must have supported climax vegetation in geological times as they do now, ... ", and "Two climatic climaxes cannot occupy the same territory simultaneously, ... ". These principles led to an holistic concept of an association and to the mono-climax hypothesis. The climatic climax in its largest expression, the biome, such as the eastern North American hardwood forest, is a recognizable and definable unit. He wrote (1916):

> "It seems impossible that genera which we now know as boreal, temperate and tropical should have existed in the most complex and uniform mixture through a vast region characterized by a warm climate, and then have completely differentiated by later climatic changes ... into three great forest climaxes."

The occurrence of *Stipa* in the Oligocene of the Florissant of Colorado, indicated not merely the existence of prairie but also a grassland climate and a grazing fauna.

Clements did, however, accept that a biome could become separated by migration into different parts and that these could evolve separately and differentiate. He discussed this differentiation in considerable detail with respect to the modern Mohave and Colorado deserts, which evolved from the Madro-Tertiary Element. Recently, Axelrod (1958, 1976) has added to the paleobotanical history of the Madro-Tertiary flora and indicated a Mexican origin of the vegetation. Some plants in the desert area were considered to be indicators of past conditions on the area that in the late Tertiary supported the Sierra Madrean Element (rich conifer-hardwood forest). New discoveries of macrofossils of subalpine taxa in the late Tertiary floras indicated that these specimens were not transported down from the subalpine forest (as Clements would have indicated), but represent species that were actually living in the rich conifer-hardwood forest.

Clements (1916) pointed out that each major climatic shift produced a corresponding clisere defined by a series of climax formations or zones which follow each other in a particular region in consequence of a distinct climatic change, and leave behind relicts of each climax type in formerly occupied regions. The numerous members of the boreal forest found disjunct south of the glacial limits were considered as relicts of Pleistocene climaxes.

Gleason (1926) was opposed to Clements' earlier concepts of mono-climax and vegetation association. He wrote (1926):

> "Plant associations exist; we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with their environment, we can frequently discover their past history and make inferences about their future. ... [But the] duration of an association is in general limited. Sooner or later each plant community gives way to a different type of vegetation, constituting

> the phenomenon known as succession. ... We find variation of environment within the association, similar associations occupying different environments, and different associations in the same environment. It is small wonder that there is conflict and confusion in the definition and classification of plant communities. Surely our belief in the integrity of the association and the sanctity of the association-concept must be severely shaken. Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that the association is not an organism, scarcely even a vegetation unit, but merely a *coincidence*? ... Under the individualistic concept, the fundamental idea is neither extent, unit character, permanence, nor definiteness of structure. It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either with or without mutual influence, of the result of causes in continuous operation. ... Climax vegetation represents a stage at which effective changes have ceased, although their resumption at any future time may again initiate a new series of successions. ... Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration."

It is significant to note that Gleason came to the above conclusions by studying the geographical distribution, migration, phylogeny and comparative morphology of *Vernonia*, for which he had no fossil data.

Chaney (1924), in his study of the Bridge Creek Flora in Oregon, compared the fossil redwood flora with the present day Californian association. He concluded that the *Sequoia* forest of the Tertiary was somewhat more diversified and less homogeneous than that of today. He referred fossil taxa, previously erroneously identified and considered to be tropical, to temperate genera. A similar incongruous assemblage was found in the Goshen Fossil Flora of Oregon (Chaney & Sanborn 1933). The flora consisted of a mixture of tropical rain-forest and temperate rain-forest species, in a coastal situation. However, extensive transport of the temperate element did not seem likely and in this case Chaney and Sanborn suggested, in contrast to Chaney's conclusions on the Bridge Creek Flora, that

> "The relationship of the Goshen Flora both to the tropical rain-forest of Panama and to the tropical rain-forests of Costa Rica and Venezuela is consistent with its composition, including as it does an almost equal number of species whose modern equivalents occupy the lowland and middle slope forests. It may be concluded that the Goshen flora represents a forest of a type intermediate between the modern tropical rain-forest and the temperate rain-forest. *It is possible that there is no such forest now in existence* [italics mine], because of climatic changes since the early Tertiary which have restricted the more temperate genera to the upper elevations, leaving only the tropical types in the original habitat near sea-level."

This conclusion generated considerable controversy (Cain 1944), and Clements expressed his opinion (*in litt.* to Cain) as follows:

> "The conclusion as to the dual nature of the Goshen forest transgresses my understanding of the natural (ecological) law and it is equally contrary to the concept of climax and the origin by adaptation. I cannot entertain it until a climax of this character is found."

In summary, Chaney offered two unique and diverse explanations for incongruous fossil assemblages and in this way his paleobotanical work is the earliest in North America to illustrate the controversy between Clementian and Gleasonian concepts. In 1940, the forest migrations, by that time well documented by numerous fossil assemblages across the continents led Chaney to

> "... refute the hypothesis of continental drift. Forests under compulsion of climatic change, rather than the continents on which they live, appear to have been the wanderers during the history of life upon the earth."

Mason clearly supported Gleason's concept. In amplifying a list of principles of plant geography by Good (1931), he became opposed to Clements' interpretation of vegetation patterns (Mason 1936). Clements had said (Cain 1944):

> "It is not the extremes of the environmental factors which are of importance, but the means.",

while Mason's (1936) first principle read:

> "Plant distribution is primarily controlled by the distribution of climatic factors and in any given region the extremes of these factors may be more significant than the means."

Mason clearly aligned himself in Gleason's camp with the following:

> "Migration is brought about by the transport of individual plants during their motile dispersal phases and the subsequent establishment of these migrules. ... The evolution of floras is dependent upon plant migration, the evolution of species, and the selective influences of climatic change acting upon the varying tolerances of the component species."

In addition Mason wrote (1947) that:

> "Plant migration must be construed as a movement of an interbreeding population and not as a movement of individuals, or as a movement of floras. ... Environmental diversity must be met and overcome through the development of races of the species population whose tolerance spans are sufficiently diverse to enable the population to cross by inhabiting such areas."

Also, he carried Gleason's concept of the coincidental nature of the plant community one step further (Mason 1947):

> "The plant community then, possesses only coincidental unity based upon like simultaneous environmental tolerances for the over-all environmental

> factors ... The pattern of area, therefore, reflects only the condition of the environment to which the species populations inhabiting it are adapted. The pattern of area has no historical significance whatsoever that applies to the immediate flora as such. Historical fact pertaining to the flora must, of necessity, be established independently of the present pattern of area occupied by the flora. ... Thus the pattern of area, whether it be referred to as a 'natural area' a 'progressive equiformal area' (Hultèn 1937) or any other concept of area that endows it with historical significance in relation to its species population, must first be thought of in terms of environmental conditions prevailing today to explain the flora that may exist upon it."

The implications of these concepts are evident (Mason 1947):

> "Floristic history, because of the lack of reality and precise associations through time and because of the lack of functional unity of the plant community, becomes the history of an aggregation of independently operating dynamic systems, each of which is meeting its problems in its own way. ... From the nature of these dynamics it would be impossible to conclude that such a flora as the redwood forest has migrated as a whole from the north where it may have originated, because the redwood forest in its various elements originated at different times and at many points over the area it traversed and some of its elements developed in association with other floras from whence they migrated into association with the redwood flora. ... It is difficult under these conditions, and in terms of such dynamics as herein outlined, to envisage such floristics as an Arcto-Tertiary flora (Chaney 1936) in contrast to a Madro-Tertiary flora (Axelrod, *Mss.*) as accounting for floristic sources and centers of origin during Tertiary times. Such concepts of floristic organization and development demand unity and stability of communities in time and space beyond what is possible in the light of the nature of floristic dynamics such as are bound up with the genetics of the population, the physiology of the individual and the diversity and fluctuation of the environment."

These ideas have been discussed again and again during the following decades (Wolfe 1978, and most recently Janssens *et al.* 1979 and Wolfe & Tanai 1980).

Mason (1947) pointed out that:

> "If we assume now that the poles have been stationary as most astronomers insist that they have, and if we assume that the continents and ocean basins have been perpetuated in the present places through geological time as many geologists insist that they have, we must conclude that no tropical, warm temperate or even temperate forest flora, could possibly live and develop in high arctic latitudes. ... Thus far we can only conclude that if forest flora of the past actually lived and developed under such conditions in the high latitudes of the north, they could only have done so under permission of very different physiological relations than prevail in plants associated in similar floras today. To an informed biologist such a conclusion seems preposterous."

Now, even after the successful development of the theory of continental drift, this same intriguing problem of how temperate taxa could have survived in a high latitude photoperiod regime is still with us (Wolfe 1978). Following Mason's observation (1947):

> "Unfortunately the fossil record as revealed to us is so discontinuous and incomplete and fraught with misidentifications, as to be very unreliable as

> a means of developing even the framework of the story ... The fossil record of this story is badly in need of taxonomic reevaluation by experts in the various groups of plants represented."

It is clear that the presently greatly improved fossil record has done nothing at all to solve the dilemma and has probably even enhanced it. Wolfe (1978) even suggests that the tilt of the Earth's axis was less during the early Tertiary periods.

In summary, the major dilemmas of present day paleoecology were outlined in the work of the first paleoecologists in North America. They worked primarily with Tertiary assemblages, but as will be indicated in the following, these problems are also relevant to Quaternary vegetation history.

One of the major causal factors in the distribution of plants and communities at the present time is their Pleistocene history. The "glacial theory", stating that the long recognized drift deposits were of glacial or lacustrine origin, instead of being derived from a catastrophical flood, originated in Europe during the mid 1800's and was maintained and defended by Agassiz in North America (Pratt 1876). It replaced the 'universal flood' theory which lasted in one form or another until the 20th century.

Early forms of the glacial theory viewed the North American ice sheet growing southward from the North Pole and extending into mid-latitudes (Flint 1943). The effects this ice advance had on the North American biota became an obvious question in need of a solution. What follows here is a short summary of the Late Quaternary vegetational history of North America (Wright 1971, 1976, 1977, 1981 and others). Most of what is known relates to the Late Wisconsinan and postglacial history in northcentral and northeastern United States. By comparison, relatively little work has been done elsewhere in North America. Northwestern North America will be discussed in detail in Chapter V.

The effects of episodic Pleistocene cooling on the distribution of the Tertiary deciduous forest south of the glacial border in eastern North America has been the subject of considerable disagreement in the literature. Braun (1950, 1955), together with Cain (1943, 1944) and Iltis (1965) adhered to the viewpoint of Gray (1846), considering the rich deciduous hardwood forest a remnant of the Tertiary holarctic flora, and adopted the Clementsian view of plant communities. They postulated that the glacial periods had no major impact upon the southeastern flora and that this flora has remained largely stable and intact since the Tertiary.

After study of the vegetation of southern Ohio, Braun (1928) concluded that in eastern North America

> "... during [the Illinoian] glacial stage, all vegetation was forced southward. Arctic and coniferous belts intervened between the ice and the more southern deciduous forest. These were probably not wide, for the effects of glacial refrigeration do not seem to have extended far beyond the limits of the ice cap."

Braun (1937) also suggested that

> "Even if altitudinal limits of forest types had been lowered considerably during the Glacial Epoch, there would still have remained numerous breaks in continuity of the mountains, where valleys intervene ... It is not difficult to conceive of sufficient lowering of altitudinal limits as to permit spruce-fir summit forest more extensive than in the Great Smoky Mountains today. It is difficult to conceive of southward movement of a spruce-fir forest to Tennessee, *without displacing all extremely southern and Coastal Plain species*. If these were displaced, their presence now could be explained only by recent migrations, migrations into occupied territory. But the time has not been long enough to account for their return to the isolated stations in which they now occur."

Braun's work closed an era of speculative floristic plant geography. Most paleoecological work of the 1950's refuted her concepts and conclusions. However, the source for this turning point, Gleason (1926), were already established long before the mid-century.

A vegetation map of North America indicates that the major vegetational regions of the continent in general reflect the modern climatic pattern. Tundra extends from the North Slope of Alaska northeast across the Arctic Archipelago, southeast over the northern continental Northwest Territories and in a narrow fringe farther along the Hudson Bay coast, northern Ungava and Labrador. The boreal forest (*Picea glauca, P. mariana, Pinus banksiana, Abies balsamea, Betula papyrifera, Populus tremuloides*) forms a narrow belt from central Alaska in the west, widening towards the southeast and reaching Lake Superior. It covers most of northern Quebec and Labrador. Extensions of the boreal forest are found in the Black Hills. A transitional conifer-hardwood forest (*Pinus strobus, P. resinosa* and *Tsuga canadensis* as dominants) is found around the Great Lakes area and extends south into the Appalachian Mountains. The temperate hardwood forest (*Quercus, Carya, Fagus, Ulmus, Tilia, Acer, Betula, Castanea*) south of the Great Lakes area, is extremely rich even farther south in the lowlands of the southeastern United States and extends from Minnesota and New York to the Gulf Coast. Tall-grass prairie (west of the deciduous forest) gives way to short-grass prairie towards the

Rocky Mountains and *Artemisia* becomes more common The Rocky Mountain vegetation exhibits altitudinal zones with the major species change from one mountain range to the next Sagebrush (*Artemisia tridendata*), chaparral and desert shrubland are dominant towards the south and at lower elevations

Detailed knowledge of the vegetation history covers only the Late Wisconsinan and Holocene periods Early Wisconsinan encompasses the time from the end of the Sangamonian interglacial (? 100,000 BP) to the beginning of the Port Talbot interstadial (55,000 BP) The Late Wisconsinan ice advanced about 25,000 BP Few fossiliferous sediments of Early Wisconsinan age have been studied with one of the major reasons perhaps being the absence of absolute dating techniques

There are no interglacial fossil plant records known from the Southwest During the Wisconsinan, the climate was such that lacustrine clays were deposited in pluvial lakes During the so-called pluvial period, the areal extent of *Pinus* (but also *Picea*, *Abies* and *Pseudotsuga*) expanded and tree-line was lowered (1000 m) Modern vegetation returned rapidly in the period of 12,000 to 10,000 years ago The Holocene vegetational record in the western United States is sparse In the north, a dry middle Holocene period is indicated (Hypsithermal, Altithermal, Xerothermic) Dating of this dry interval has proven that it is not synchronous in all areas

All the pollen records of the Pacific Northwest have conifer pollen as the main arboreal component (*Pinus*, *Larix* and *Pseudotsuga*). Most studies are lateglacial and postglacial. During the postglacial, forest succession proceeded from a *Pinus* forest to *Tsuga* west of the Cascades, to *Tsuga* and *Picea* in the north along the Alaskan panhandle, to *Pseudotsuga* and *Quercus* inland in the drier valleys and even to grassland east of the Cascades.

Glaciations, including the Wisconsinan, are marked by a tundra-steppe mosaic in Alaska, the Yukon and the Mackenzie Delta area. Trees (*Picea* and *Larix*) were present in small areas during warmer interstadial phases. Postglacial history starts with the succession from herb tundra to shrub tundra, followed by *Picea-Betula* woodland and around 8000-5000 years ago by a *Picea-Alnus* forest.

Few studies have been done in eastern glaciated northern Canada. The pre-Wisconsinan and late Tertiary studies in the Arctic Archipelago indicate a succession of hardwood forest, coniferous forest, forest-tundra ecotone and tundra during several stages of the late Tertiary and Quaternary periods. Rapid and early deglaciation is known to have occurred on Ellesmere Island and eastern Greenland (Blake, *in litt.*). Postglacial vegetation communities were formed rapidly and remained relatively unchanged during the Holocene.

The classical phytogeographical conflicts between the concepts of Clements and Gleason centered upon the history of the vegetation of the southeastern United States during the Pleistocene (Gibson 1980). The early botanical exploration of the southern Appalachians led to an appreciation of the enormous species diversity of the flora. As related before, this intrigued such botanists, as Asa Gray and E. Lucy Braun, who adopted the view that the richness of the area could be equated with long term stability. On purely comparative chorological grounds the Appalachian Mountains were considered a refugium for the eastern deciduous forest (Braun 1950, 1955) with the glacial episodes postulated to have had no major impact on the flora. A full-glacial map of the vegetation in the Southeast would differ little from a map with the present day zonation. However, Deevey (1949), a palynologist, indicated severe cold conditions during glacial maxima. He postulated drastic displacement of the deciduous forest as far south as Mexico and Florida.

Proponents of these opposing views used data from the same sites to support their hypotheses. For example, Braun (1950) suggested that several relicts of the 'Arcto-Tertiary geoflora' are present in the Tunica Hills (southeastern Louisiana). The paleobotanical information, however, indicates the presence of *Picea glauca* and *Larix* in the Pleistocene deposits of the region (Delcourt & Delcourt 1977, 1979). Numerous other sites in the southeastern United States have supported this evidence of the presence of associations between boreal and temperate plants, and have led to reconstructions of full-glacial vegetation zonation east of the Rocky Mountains (Delcourt & Delcourt 1979, Delcourt *et al.* 1980 and Wright 1971, 1976, 1977, 1981) as is summarized below.

In the Great Lakes region, Berti (1975) interprets the fossil evidence from middle Wisconsinan sediments as indicating an open vegetation with a climate drier (and possibly warmer?) than today. However, his sequence is interrupted by Mid-Wisconsinan tills associated with macrofossils of tundra plants. The forest-tundra ecotone clearly must have been nearby, but fossil pollen samples have an abundance of *Pinus* (> 60 %) along with tundra herbs (Berti 1975). Since pine does not reach the tree-line at the present time no modern pollen surface sample has ever been found with this combination.

Sangamonian records are known from Illinois (Grüger 1972a, 1972b), Indiana (Kapp & Gooding 1964) and Ontario (Terasmae 1960) These interglacial records, as well as the postglacial, are characterized by *Quercus* and other hardwood types, and by abundant *Ulmus, Fraxinus, Carpinus* and *Taxodium*. *Liquidambar* is found in the Don Beds in Ontario, yet this tree is not found in the Toronto area at the present. The subsequent Wisconsinan herb zone lasted until 35,000 years ago. Prairie and *Quercus* savanna are implied during Early and Middle Wisconsinan times, while *Artemisia* indicated drier prairie environments. The unexpected result is a Middle Wisconsinan Midwest that is drier and not much colder than today. Later, forests expanded and *Picea* reached eastern Kansas by 25,000 BP (Grüger 1973) and southern Illinois by 21,000 BP. *Quercus* persisted in southern Illinois but prairie was gone by the beginning of the Late Wisconsinan.

In the Ozark Mountains of western Missouri, a *Pinus banksiana* parkland covered the landscape during the Mid-Wisconsinan (King 1973) and *Picea* migrated into the area 25 to 20,000 years ago. Today *Quercus* and *Pinus* dominate the Ozark Upland, but the present species of pine is a southern type (*Pinus echinata*) and no modern North American assemblages resemble the Mid-Wisconsinan Ozark pine parkland.

In summary, the vegetation of the United States east of the Rocky Mountains during the Middle Wisconsinan was mostly prairie and open woodland with *Quercus* in the east and *Pinus banksiana* in the west. The prairie gradually diminished throughout the Middle Wisconsinan and parkland invaded. At the beginning of the Late Wisconsinan, boreal forest elements became dominant with *Quercus* persisting in the south and *Pinus* becoming infrequent.

In the southeastern United States, the piedmont vegetation was a *Quercus-Carya-Taxodium* assemblage during Mid-Wisconsinan time (Watts 1973). This implies a climate as warm as today, while on the coastal plain a predominance of herbs indicate a dry climate. *Betula, Quercus* and *Alnus* gave way to invading boreal forest types during the Late Wisconsinan (Whitehead 1972, 1973) with dryness most strongly expressed in southcentral Florida during Mid-Wisconsinan time (Watts 1975).

Numerous study sites are known for Late Wisconsinan sediments. In the following summary most attention will be paid to those reconstructions that clearly underline the controversy between phytogeographical concepts, outlined in the first section, and the fossil data. In central Minnesota, a narrow tundra zone bordered the ice lobes during the Late Wisconsinan advances (Birks 1976). At the end of the Late Wisconsinan, shrub tundra and later *Picea* forest invaded. Periglacial climate is also indicated in the northern part of the Great Lakes area, in New England and in the Appalachians as far south as Maryland (Maxwell & Davis 1972). During maximal ice advance (Wright 1981) periglacial tundra did not exist from Ohio to South Dakota. Rather, ice was in immediate contact with a wide boreal forest belt, perhaps 1000 km broad, extending in the south from central Georgia around the southern end of the Appalachian Upland to Tennessee and then west to the Mississippi Valley and south to Louisiana. The belt had thus the same width as today but was displaced completely south (Delcourt & Delcourt 1979). However, the boreal biome had a different composition from that of the present. It lacked *Pinus banksiana* in the Mid-West, although this tree was present in abundance in the Middle Wisconsinan. Relatively high pollen frequencies of temperate hardwoods (*Fraxinus nigra, Ulmus, Carpinus, Carya* and *Quercus*) have also been recovered. Cyperaceae and *Artemisia* pollen are found in higher values than in surface samples from the modern boreal forest. In conclusion, no satisfactory modern analogues for the Late Wisconsinan *Picea* forest can be found, not even in Labrador, where *Pinus banksiana* is missing.

South of the boreal forest the record is poor. There is no evidence of the Great Lakes transition forest. The extremely diverse, temperate hardwood forest must have been very restricted. No trace of it is found in Late Wisconsinan sediments of the Florida peninsula. The climate was very dry and a xeric *Pinus-Quercus* woodland occurred there. It is possible that some of the hardwood forest elements survived on the loess bluffs of the Mississippi Valley and southward in Mexico (Delcourt & Delcourt 1977, 1979). It is very likely that many of them were mixed with boreal elements in suitable habitats.

There is considerable variation found in the postglacial records throughout the northeastern United States. It is evident that there is no synchroneity in the migration of forest species. The major trees migrated at different rates from their Late Wisconsinan refugial areas. Preliminary maps of these migrations have been produced (Davis 1976). *Pinus banksiana* spread very rapidly and reached Minnesota 10,000 years ago. *Pinus strobus* followed by 7200 BP. *Quercus* followed the pines and became the major pollen producer when *Pinus* became restricted to its present ranges. *Tsuga* reached the Great Lakes area 6000 years ago. *Fagus* and *Carya* came later. *Castanea* barely reached the eastern Great Lakes when it was destroyed in the 1920s. To the north, in the glaciated area, it is clear that migration followed deglaciation with a much smaller lag phase. *Picea, Larix* and *Abies* immigrated immediately after ice retreat. Fluctuations have been seen at the northern limits of their extended ranges throughout the Holocene epoch. To the south of the glaciated area interpretations are not as clear. Several indications point to successional sequences (such as lake filling) instead of climatic change. Sea level rise induced the formation of swamps in Georgia and Florida with the uplands in Florida becoming less xerophytic 6000 years ago. This contrasts with the drying trend of the Hypsithermal interval in the northern United States where *Quercus, Ulmus, Carpinus* and other temperate hardwoods replaced the boreal forest in the lateglacial. The warming trend continued there, including the increase in dryness. First *Quercus* woodland and then *Quercus* savanna and prairie replaced the temperate hardwood forest in Minnesota. In the present prairie areas, prairie succeeded the boreal forest immediately. Present tendencies are the return of hardwoods into the prairie and conifers into the hardwood forest in the northern United States.

Conclusions and Summary

Plants migrate as individual species (Gleason 1926), so that communities only migrate when most of their elements move. Associations rarely retain their composition. Past communties, even as recently as 5000 years ago in the southeaster United States, have no modern analogues.

Paleoecological methods are only workable tools when the tolerances of the taxa change slower than the climates of an area, and when the same processes were working during the past as at the present day (Uniformitarianism). Study of many facets of numerous fossil assemblages have proven that this is reasonably true.

Integration of phytogeographical concepts with fossil data is critical in the future. Interpretation from the fossil assemblages at the paleoenvironmental and climatological level are strongly influenced by the basic concepts. It can not be avoided that the concepts influence even the selection of the data available and thus the final conclusions. Only by carefully differentiating between facts and inference will it be possible to construct new concepts and rebuild older ones. At this time it is evident from work in the Quaternary of the United States and in northwestern North America that the Gleasonian concept of the coincidental nature of biota will dominate.

B. Statement of the Problem

Subfossil bryophytes have been neglected as an important tool for paleoecology in northwestern North America. Most previous work has concentrated on the deposits of Late Quaternary age in northcentral and northeastern United States (Miller 1976a, 1980a, c). Many less recent records are haphazardly scattered throughout this area and along the Quaternary time scale, many others are taxonomically outdated and still others have never been interpreted.

Before this work only three subfossil records were known from the Yukon Territory, and none for continental and arctic Alaska, while 410 mosses for the Yukon (Vitt 1974, 1976, Vitt & Horton 1978) and 415 for arctic Alaska (Steere 1978a). are known in the present bryofloras. In addition, there exists (Steere 1978a) "... the very distinct possibility that this number (415) will reach 475 or 500 eventually, ...". This number of species compares favorably with that of such large areas with great physiographic diversity as British Columbia (620), California (320) and Ontario (430).

After Hultén's work (1937) on the distribution of Beringian vascular plants, it can be thought that many bryophyte taxa could have survived in the area during the Pleistocene as well. Many subfossil bryophyte records from Pleistocene deposits in northern Beringia will prove this hypothesis (Chapter V).

In addition to phytogeographical information, subfossil bryophyte records can contribute to an understanding of the vegetation and landscape evolution. Numerous subfossil bryophyte records in close chronological and stratigraphical context are needed. The complex stratigraphical sequences in the Old Crow and adjacent Basins offered the opportunity to sample highly fossiliferous Pleistocene sediments and reconstruct local paleoenvironments in the northern Yukon. The reconstructions will be interpreted in relation to the paleoclimate, hydrology evolution and geomorphology of the basins. Several hypotheses will be tested.

C. The Significance of Subfossil Bryophytes

Well preserved subfossil bryophyte fragments can be identified at the species level. Small samples (< 1 g) can contain up to 30 different taxa and several thousand fragments. Such samples can be as easily extracted from large diameter cores as from bluff exposures along rivers and lakes. The uniform but still complex basic structure of bryophytes, makes it possible to use a reproducible and reliable measure of the preservation grade. The preservation of the specimens of a single species indicates the amount of transport or (in clearly autochthonous peats) the degree of humification of the peat. Differential preservation among species of the same assemblage points to a different pre-burial history on the several components of the sample.

Bryophytes are poor indicators of macroclimate or macro-environment (Miller 1980c). However, many taxa have clearly circumscribed habitat requirements and some detailed knowledge on the microclimate in which they live and their autecology os available (Chapter III). Subsequent detailed knowledge of local communities can then be used with good results in collaboration with pollen and macrofossil data to reconstruct Quaternary landscape evolution. Frgaments of Coleoptera have a similar size distribution as mosses. Although they are often less abundant in fossiliferous sediments, they can be used in similar ways in paleoenvironmental reconstruction (Matthews' papers). Such fossils can be identified to the species level, as well as the mosses. Also virtually all fragments from Pleistocene sediments represent extant species (Matthews 1979).

Bryophytes have clear, distinct distributional ranges and long-range dispersals have little significance in migrations (Crum 1972). Phytogeographical elements can be outlined after study of the present ranges and their speculated history can be substantiated and refined by the subfossil records (Chaper V).

II. MATERIALS and METHODS

A. Sources and Sites

Subfossil bryophytes (mostly in the form of single fragments) have been extracted from a variety of sediments. The samples were homogenous blocks of sediment, thought to be representative of a particular facies or horizon in the sequence. All of the sediment samples collected in the northern Yukon have been derived from riverbank exposures at numerous localities. A locality is a more or less continous exposure. It is divided into several stations, usually corresponding with homogenous portions of the bluff between two gullies or corresponding with a gully itself.

Sediments that are the richest in bryophytic contents may be fluviatile, deltaic or lacustrine, but contain detrital peat accumulations and highly organic silts. Often autochthonous peats (sediments consisting out of organic material) are mainly moss-peat, but these have a much lower species diversity than allochthonous accumulations. A bryophyte record is the presence of one species in one assemblage from a single sediment sample at one station. All bryophyte records from a single sample form an assemblage. Other sediments containing bryophytes are marine deltaic deposits, lacustrine silts, marl and detritus, and even organic silts flushed into hollow teeth. No tufa deposits containing bryophytes are known from the northern Yukon Territory. Bryophyte subfossil records from herbivore stomachs (mammoth) are only known from Siberia (Camus 1915, Farrand 1961, Solonevich, Tikomirov & Ukrainteva 1977). However, most likely this situation will be modified in North America in the near future; for example, Guthrie (University of Alaska) discovered a well preserved carcass of *Bison*, apparently with stomach contents in frozen Alaskan deposits (Schweger, personal communication). No clear association of any subfossil bryophytes with archeological material has been found in the northern Yukon Territory.

It is appropriate here to discuss peats as sediment types, because of their significant contribution to the subfossil record of bryophytes. It is essential that the main criteria for classifying peats are based upon detailed analysis of all aspects of the constituents of the organic deposits; unfortunately this system is not practical for field application. Troels-Smith (1955) and others have concentrated more on field application and developed a very sophisticated descriptive tool for the field.

The origin of the several components of the peat is the basis for the peat classification types. This classification, based on the peat components, can also be applied to the fossil assemblage types (see below, section D.) Sorting, abrasion and humicity are three features that have distinct states in different organic sediments Sorting could have been extensive, for example, the coarse allochthonous peat accumulations on top of the reworked lower lake clays in Yukon locality HH68-9 (see Chapter IV). An easy way to describe the degree of sorting utilizes the size variation of the components. Some more or less pure bryophytic peats evidently are so sorted that only fragments of around one cm length are preserved. Other samples contain only fragments from a certain size up (all smaller fragments are lost, for example the marine delta deposits in Clements Markham Inlet on Ellesmere Island, Bryological Report 401, see Janssens 1981). It is clear that such extreme sorting can act very selectively on the original material.

Abrasion is easily described when wood fragments are present in the peat sample. Rounded edges and the absence of bark on twigs indicate a high energy environment. This does not necessary imply that well preserved bryophytes will be absent in this material. They appear often to escape the rough treatment which left its obvious traces on the wood fragments.

Humicity (Troels-Smith 1955, p. 44 and p. 55), or the result of the process called humification (for example Von Post 1937, p. 211), indicates the degree of decomposition of peats. It is directly related to the ontogeny of the organic deposit, that is, the rate at which new organic remains become incorporated into the peat below the sulphide horizon, in the anaerobic zone of a mire system (Moore & Bellamy 1974, p. 99, and Clymo 1965). Other important factors are later disturbances, for example changes in water table (creating recurrence horizons) and the exposure of the peat deposits along riverbanks. There is a strong correlation between the external aspect of humicity (squeeze method applied in the field, see Troels-Smith 1955, p. 56-57) and the microscopic preservation aspect of the macrofossils. The reliability indices of the taxa in an assemblage (see below) are based mostly on several aspects of the preservation of the specimens. The range and mean of these indices give thus an indirect, but objective measure of the humicity of the peat source.

In extremely humicified peats no bryophytes are preserved at all. The only material that can be distinguished are very resistant structures, for example those composed of lignin, suberin and chitin. The second and third types of peats, mixed and autochthonous, can be discussed together, as the bulk of the materials or all of it is derived from organisms living *in situ*. Sorting and abrasion features are non-existent or negligible in these peats. Humicity is again variable and will dictate the success of the paleoenvironmental reconstruction.

The number of bryophytic fragments (per 100 g of the >1 mm fraction of the sample) varies from 200,000 in pure *Calliergon* peat (Bryological Report 352, see Janssens 1981) to 30 (Bryological Report 109) in fluviatile deposits. The only sediments encountered in this project which appear to be completely barren of bryophytes (and for that matter of all organic material, even pollen) are the glacio-lacustrine clays which were deposited during the existence of the latest glacial meltwater lake in the Old Crow and Bluefish Basins (see Chapter IV).

On the other hand, some Yukon strata are exceptionally rich in well preserved organic material. A very exciting source of subfossil bryophytes are all deposits and features associated with Disconformity A, Yukon Locality HH68-9. Bulk samples from material on this old surface as well as small peat block samples from features associated with this erosional contact contain very unusual assemblages. From Appendix 2 it is evident that this horizon has been extensively sampled. In fact, with respect to subfossil bryophytes, locality HH68-9 and its large exposure of Disconformity A provided the richest assemblages.

B. Extraction

Most samples consisted of unconsolidated sediments. Soaking in 10 % sodium-phosphate for three days ensured that all bryophytic material could be washed free from silt and sand. None of the autochthonous peat material from the northern Yukon Territory had clean cleavage planes from which faces could be prepared and bryophyte specimens picked by hand. All material has been screened on a 1 mm mesh size sieve and only this larger fraction has been analyzed (experience has proven that it is not worthwhile to work with smaller fractions than 1 mm).

Bryophyte stem fragments have been picked out from the screened sample under the stereoscope or with a binocular magnifier. They can be indefinitely preserved in a 70 % mixture of glycerol with water.

C. Identification

All specimens for identification were mounted on microscopic slides in Hoyer's solution (Anderson 1954). This semi-permanent medium ensured that dark specimens were sufficiently cleared and that small fragments can be soaked out or, in case of plastic coverslips, cut out for further study. Most material could be readily sectioned with a razorblade.

Preservation was extremely variable and it was essential to indicate this in order to give an idea of the reliability of identifications. Two factors, contributing to a particular preservation grade, can be distinguished. The first is the pre- and post-burial history of the specimen. This is illustrated when the preservation of elements of several communities of the same mixed assemblage (see below) is compared. Usually there is a strong contrast between the preservation of the fen component of the assemblage with that of the material of the nearby, topographically higher communities, flushed into the same deposition basin. The specimens of the upland component are usually very badly degraded and their abundancy is much lower.

The second factor is the species characteristic preservation aspect. Many species break down in a typical way. The leaves of *S. scorpioides* are usually strongly lacerated. *Calliergon giganteum* leaves split longitudinally from the apex. Leaves of *Rhacomitrium* species lose their apices and margins very rapidly, and many acrocarpous genera have a strong tendency to have only a few apices preserved. Mostly, they have a characteristic dark-gray color, while the hydrophilic Amblystegiaceae are golden-brown or rich dark-brown. *Polytrichum* and *Pogonatum* species turn opaque black in the fossilization process. Sometimes some of the original color is retained, for example the red leaf and costa bases in *Bryum pseudotriquetrum*.

Usually only the younger parts of the moss fragments are preserved. However, it is a rare occurrence when the growth apex of pleurocarpous stem or branch fragments is recovered (for example the apical falcate-second inrolled leaves of a *Scorpidium scorpioides* branch).

A reliability index was employed for each record of the fossil assemblages (see Janssens 1981) based mostly upon preservation characteristics. This is an expansion of the reliability measure given in Janssens (1977b), based on Dickson (1973). The index has been calculated for each taxon in a fossil assemblage and can range from 1 to 100. It takes into account 1) general sample characteristics (that is the total number of fragments and the % fragments identified to species level) and 2) specimen features (that is taxonomic level of identification, relative abundance of the taxa in the assemblage, and fragment and leaf preservation). The index permited to make comparisons between the reliability of the identification of a specific taxon among several samples. The range of the index for a particular assemblage gives an idea of the quality of the sample compared with others. More details on the calculation of the reliability index can be found in the introduction to Janssens 1981.

Abundancy was calculated by counting the number of fragments of each taxon and it can be expressed as a percentage of the total number of fragments in the assemblage. By analysing a great number of assemblages, I have developed the concept of five fairly natural abundancy classes. I have called them class 1, few, low, medium, and high, respectively meaning one single fragment, few up to 10 % of the total number of fragments, 10 to 50 %, 50 to 80 % and 80 to 100 %. Use of these classes helps in identifying the type of assemblage, as will be shown in the next section.

D. Classification of Assemblage Types

Subfossil bryophyte assemblages can be classified into three general types (Fagerstrom 1964), discussed below. Classification can often be attempted using only assemblage characteristics, such as species composition, abundancy and preservation. Sometimes sediment characteristics must also be used.

Autochthonous assemblages: the number of species is small (mean = four) but their preservation is usually excellent. Often clones or parts of populations in their natural growth form can be recovered by careful screening. The inorganic content of the samples is usually very low, consisting of wind blown silt and sand, and the sediment is classified as peat.

Mixed assemblages: a high number of species can be represented, but most sediment characteristics are the same as for autochthonous assemblages. The additional species are usually very infrequent and their ecology indicates topographically higher habitats which exist in close proximity to the depositional environment. Only very exceptionally have I found mixed assemblages in which the fen species constituted a minority group. Mixed assemblages are recognized by a distinct bimodal distribution of reliability indices (see Janssens 1981: Bryological Report 183 and 401).

Transported assemblages: most organic allochthonous or detrital sediments contain complex transported bryophyte assemblages. In well preserved and bryophyte rich material the number of species that can be obtained from only a few grams of sediment can be 30 or more (i.e. Bryological Report 435, see Janssens 1981). Preservation is extremely variable. The species composition often indicates the presence of two or three clearly distinct communities.

E. Taxonomic, Ecological and Chorological Studies

Essentially all taxa of the genus *Drepanocladus* were represented as subfossils. Most of the species of this genus have been frequently encountered in numerous samples. This motivated the taxonomic treatment of *Drepanocladus*, presented in Chapter III.

To study this genus, material from the following herbaria was obtained: ALA, ALTA, BR, C, COLO, H, DUKE, MICH, NY and S. In addition, numerous slides of my reference collection were used for quantitative studies. Most slides were prepared from collections of ALTA, BR, S and from personal herbaria.

Morphological descriptions have been based on material of extant populations, except in the case of *D. crassicostatus*. This species will be described as new and the preliminary description presented here is composed of information of numerous subfossil specimens and material of several extant populations.

The plate figures, illustrating the *Drepanocladus* taxa and some other taxa, were prepared with a drawing tube from representative subfossil specimens, cited in the legends. The habitat and distributional information for outside North America is a compilation of Crum (1973), Lawton (1971), Nyholm (1965), Steere (1978) and Vitt (1975). The recent distribution for North America has been constructed from collections of ALTA and CANM (solid dots on the maps) and from information in publications listed in the legends to the distribution maps (open circles). The fossil distribution is based on Miller (1980a), Kuc (1973e), Kuc & Hills (1971) and on my own analyses presented in Janssens 1981.

Appendix 1 lists the data base for water analyses, presented in habitat discussions. The water samples were collected in mires in Alberta, British Columbia and the Yukon Territory in the immediate vicinity of the bryophyte identified. Often, for upland taxa, water was squeezed out of the clones into the vials. The bryophyte collections will be deposited in ALTA and are at the present time in my personal herbarium. The Nalgene sample vials were frozen not later than 72 hours after collecting. A test indicated that there were no significant differences in pH and conductivity values between field measurements and laboratory measurements on the same unfrozen samples up to five days after collection. pH values became usually strongly erratic after five days and there was a fast lowering of conductivity values at that time. pH was measured in the laboratory with an electronic single probe pH meter at 20° C. Conductivity was measured by a electric meter at 20° C and the values were expressed in microScm^{-1}. They were not corrected for the contribution of H^{+} ions. Ca^{++} and Mg^{++} concentrations ([Ca^{++}] and [Mg^{++}]) in the water samples were determined with an atomic absorption spectrophotometer. Na^{+} and K^{+} concentrations ([Na^{+}] and [K^{+}]) were measured by a flame photometer. Cation concentrations are expressed in ppm.

The descriptions for all the taxa, other than *Drepanocladus*, have been based on a comparison of fossil specimens and material of extant populations. Most of the material for comparison has been provided by ALTA. Most of the habitat and chorology information was compiled from Crum (1973), Lawton (1971), Nyholm (1956-1969), Steere (1978) and Vitt (1975). Additional publications are listed in the text. Also, some water sample analysis values are reported for these taxa.

III. SUBFOSSIL BRYOPHYTE RECORDS

A. Introduction

Previously published records of the taxa discussed here can be found in Miller (1980a). The families that are not represented in the subfossil collections listed below and that have a fossil record in North America are the Cephaloziaceae, Ptilidiaceae and Ricciaceae in the liverworts, and the Andreaeaceae, Splachnaceae, Fontinalaceae, Cryphaeaceae, Leucodontaceae, Neckeraceae and Theliaceae in the Musci. The diagnostic features given in the species discussions are based upon my taxonomic concepts and experiences, and upon a comparison between living populations and fossil fragments. Habitat and Recent Distribution have been compiled from literature sources cited in Chapter II. The heading "Subfossil Distribution in North America" lists Miller's (1980a) state localities followed by my new reco[illegible] Within each subfossil distribution record the entry follows the sequence: locality, date or age, report (see Janssens 1981), relevant literature and an indication in case of low reliability identification (see Chapter II). An attempt is made, in case no radiometric date is available, to classify the records into one of the following general time classes: Pleistocene, pre-Wisconsinan, Early Wisconsinan, Wisconsinan and Holocene. This classification is in many cases very tentative and is discussed in detail in Chapter V.

B. Hepaticae

Liverworts are extremely poorly represented in the North American record. Only species of the families Lophoziaceae, Porellaceae, Cephaloziaceae, Ptilidiaceae and Ricciaceae are listed (Miller 1980a, Kuc 1973e, Janssens 1981). Thirteen records are known for the continent. Reasons for this poor representation and comparison with the fossil record in the British Isles are given in Chapter IV. Only two species of Lophoziaceae were present in my samples.

Lophoziaceae

A conservative classification for the family, outlined in Schuster (1966, p. 231) is adopted here. The genera *Anastrophyllum*, *Gymnocolea* and *Lophozia* have a fossil record (Miller 1980a, Jovet-Ast 1967 and Dickson 1973). Miller (1980a) recorded *Anastrophyllum minutum* (Schreb.) Schust. from interglacial deposits of Banks Island in addition to *Lophozia*, discussed below.

The family has succubously inserted, frequently lobed leaves. Underleaves are often strongly reduced. It is never possible to key out poorly preserved material and records are often listed as 'Lophoziaceae', *Lophozia* species or *Lophozia s.l.* (Miller 1980a).

Lophozia

Four species are recognized in the North American fossil record. *Lophozia hatcheri* (Evans) Steph. is known from Holocene deposits in Greenland (Miller 1980a). *Lophozia quadriloba* (Lindb.) Evans occurred in the same sample as the record of *Anastrophyllum minutum*, mentioned above. Also in the same deposits, some unidentified *Lophozia* species were recorded (Miller 1980a). In my collections two other species from this genus are represented and discussed below. Their diagnosis outlines the most characteristic features of these species, but is not unique. Because of the numerous taxa in the Lophoziaceae, the high variability of the characters and the poor preservation of the material, these identifications have only a low reliability. They are derived by comparing reference material of common taxa and by elimination.

Lophozia floerkei (Web. *et* Mohr) Schiffn.

Diagnostic features. – *Leaves* concave, 2 to 4 lobed, the lobes obtusely pointed; *margins* at the base with cilia, composed of short, rectangular or round cells; *underleaves* bifid to the base, with narrow lanceolate lobes and marginal cilia.

Habitat. – In heath vegetation, often frequent in the bottom layer of *Betula* woodland or of low alpine *Betula nana* shrub heath. It grows in coniferous forest and also in wetter habitats, sometimes in poor fens. It is not yet found on decidedly calcareous substrates, with its survival in forests depending on the ability to grow virtually erect and at a rapid rate on a substrate of *Picea* and *Abies* needles with a low pH.

Recent Distribution. – Circumboreal and disjunct in the Cordillera of Peru. Montane and subarctic species. North America: Alaska to Ellesmere Island in the north, disjunct to Colorado, New Mexico, Maine and Vermont in the south. Montane districts of western and central Europe, ubiquitous in Scandinavia.

Subfossil Distribution in North America. – (1) HH68–9, Old Crow Basin, Yukon Territory; Holocene peat, 0 to 10 cm below surface; Bryological Report 143.

Lophozia rutheana (Limpr.) Howe

Diagnostic features. – *Leaves* large, 2.5 to 3.0 mm wide, shallowly bilobed; *margins* at the base sometimes with 1 to 3 small and short cilia; *medial cells* very large, to 40 micrometers in diameter; *underleaves* large, 1.7 mm long and bi- to tri-fid.

Habitat. – Typical rich fen species. In calcareous *Thuja* bogs and swamps. Often associated with *Drepanocladus revolvens* and *Scorpidium scorpioides*. In the tundra it is usually fo[illegible]ound depressions. On wet lake margins.

Recent Distribution. – Circumpolar. Ranges in North America from Alaska to Greenland, Newfoundland and Labrador, southward in suitable sites in Alberta, British Columbia, Manitoba, the Great Lakes region in Michigan, New York, the Hudson Bay lowlands of northernmost Ontario and Quebec. Widespread in northern Europe, eastward into Asiatic U.S.S.R..

Subfossil Distribution in North America. – (1) HH68–9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148.

C. Musci

There are numerous reports of mosses in Quaternary sediments (Miller 1976b, 1980a, b, c). Most formerly published records are from glaciated areas in the northern and eastern United States. The following treatment by family lists all additional records from my samples and discusses the diagnostic features (based on living and subfossil specimens), habitat and present and past distribution of the taxa.

Sphagnaceae

Sphagnum

The record of subfossil *Sphagnum* taxa is meagre. Only 13 out of 54 species presently known for North America are represented in subfossil collections compared with the essentially complete representation of the species of *Drepanocladus*. The reasons for this poor representation are the poor preservation capabilities of *Sphagnum* and the arctic latitudes and continental position of most of my collections (no members of the genus have a High Arctic distribution). The British Quaternary record (Dickson 1973) illustrates this point clearly: most of its *Sphagnum* records are Flandrian or interglacial. Only sparse *Sphagnum* remains are known from Devensian sites. However, even in the North American recent Holocene peats, *Sphagnum* material is very susceptible to oxidation and hydrolysis and the fragments soon degrade and become unrecognizable. Worse, the resulting hydrolyzed material forms a glue that makes the preparation of the other bryophyte components in the assemblage extremely difficult. Stem material is rarely found, while branch leaves are abundantly present. This makes identification to the species level nearly impossible. An empty theca was found in the 2,000,000 year old Lost Chicken assemblage in Alaska.

In addition to the taxa listed below, the following species have a fossil record in North America: *S. balticum* (Russ.) Russ. *ex* C. Jens., *S. nemoreum* Scop., *S. compactum* DC. *ex* Lam. *et* DC., *S. palustre* L., *S. papillosum* Lindb., and *S. subsecundum* Nees *ex* Sturm (Miller 1980a).

Sphagnum centrale C. Jens. *ex* H. Arnell *et* C. Jens.

Diagnostic features. – *Branch leaves* cucullate, widely ovate; *chlorophyllose cells* in transverse section narrowly elliptic or sharply triangular, sometimes narrowly exposed on the abaxial or adaxial surface of the branch leaf. *Stem* epidermal cells with thickenings in spiral bands.

Habitat. – In woods, *Salix* thickets, often in the shaded, forested areas of fens. The species occurs in more minerotrophic conditions than *Sphagnum magellanicum*.

Recent Distribution. – Circumboreal. North America: widespread throughout Canada south of 60° latitude, and found south to New York and Indiana in the United States.

Subfossil Distribution in North America. – (1) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425.

Discussion. – This species belongs to the section *Sphagnum*, the species of which are characterized by cucullate, widely ovate leaves and spiral bands in the epidermal cells of branches and stems. These fibrils are not always easy to distinguish in poorly preserved material. *Sphagnum magellanicum* can be differentiated from *S. centrale* by the wider elliptic, never triangular, shape of the chlorophyllose cells in transverse section. In *S. centrale* these cells never reach the abaxial or adaxial surface of the leaves. Collapsed fossil leaves of these two taxa are difficult to interpret and many transverse sections have to be studied.

Sphagnum fuscum (Schimp.) Klinggr.

Diagnostic features. – *Stem leaves* lingulate, entire or notched, >1 mm long; *hyaline cells of the branch leaves* with large (2 to 6 micrometer) elliptic, weakly ringed pores on abaxial surface; *chlorophyllose cells* triangular in transverse section, exposed on the adaxial surface. *Stem* dark-brown, with 4-5 layered hyalodermis.

Habitat. – Forming hummocks in open and semishaded habitats, associated with coniferous trees. In bogs, fens and muskegs. pH 5.6 (n=1), conductivity 112 microScm^{-1} (n=1), Ca concentration 5 ppm (n=1), Mg concentration 0.7 ppm (n=1), Na concentration 13.5 ppm (n=1), K concentration 7.3 ppm (n=1).

Recent Distribution. – Circumpolar. North America: from Alaska to Newfoundland, Labrador and Greenland, most of Canada and the northern United States, farther south in the mountains. Europe, Asia, Japan.

Subfossil Distribution in North America. – (1) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Distinguished from other taxa of the section *Acutifolia* by its brown stem, *S. fuscum* is probably one of the most common taxa of this group in continental North America. I do not know if the stem of the green *Sphagnum* taxa changes color during fossilization. Therefore, the identification of dark-brown stemmed *Sphagnum* section *Acutifolia* material remains tentative.

Sphagnum girgensohnii Russ.

Diagnostic features. – *Stem leaves* lingulate, lacerate across the apex; *chlorophyllose cells of branch leaves* triangular in transverse section, exposed on the adaxial surface. *Stem* not dark-colored, with a three-layered hyalodermis.

Habitat. – In shaded, coniferous forests, but rarely directly in muskeg and fen habitats, beside lakes and rivers in *Salix* thickets.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Labrador, south through Canada to the northern United States from New England to Washington, farther south in the mountains to North Carolina in the east and California in the west. Europe, Asia, Japan, Java.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New records: (1) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat; Bryological Report 289.

Discussion. – *Sphagnum girgensohnii* belongs to section *Acutifolia* as does the more common *S. fuscum*. *Sphagnum fuscum* is differentiated from *S. girgensohnii* by its dark-brown or black stem and entire stem leaves. Living plants of *Sphagnum girgensohnii* never have any trace of red coloration, which differentiates them from *S. russowii*.

Sphagnum lenense H. Lindb. *ex* Pohle Plate 1

Diagnostic features. – *Plants* small, compactly branched; *stem leaves* < 1 mm, round-lingulate, deeply lacerated in the upper portion of the apex, often to the midpoint of the leaf. *Stem* black or dark brown.

Habitat. – On moist soil among bushes, on hummocks, banks, and mounds in poor fens. In various types of tundra, in *Sphagnum* tundra bogs, in tundra-like subalpine shrubzones and in forest tundra. Rarer in paludal coniferous forest.

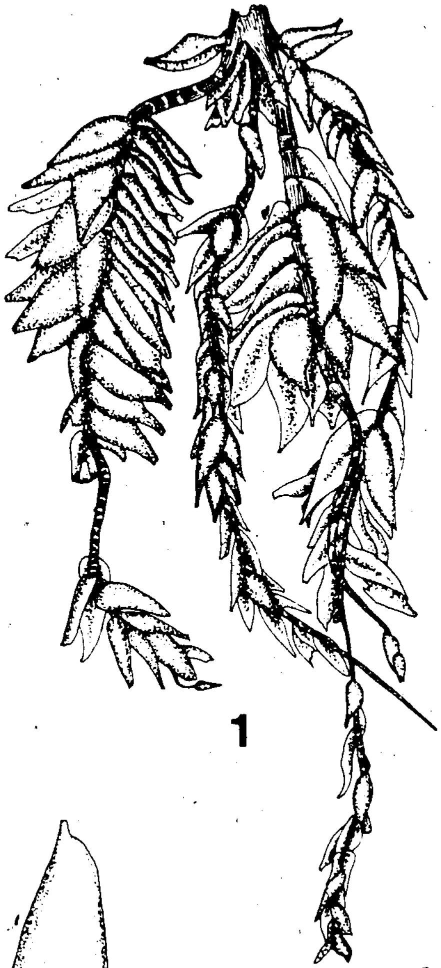
Recent Distribution (Plate 2). – Circumpolar. Subarctic species. North America: widely distributed between 60 and 70° latitude. Only found north of 70° in the Barrow area, Alaska and south of 60° in the Alaskan Peninsula and northeastern Quebec. Northern U.S.S.R.

Subfossil Distribution in North America. – (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) Lost Chicken area, Lost Chicken Mine, Alaska; 1,400,000 – 2,000,000 B.P.; Bryological Report 357, Matthews 1970.

Discussion. – *Sphagnum lenense* plants are easily recognized by their short compact branches and dark stems. *Sphagnum riparium* Angstr. also has deeply lacerate stem leaves, but they are much larger (>1 mm). The stem leaves of *S. lindbergii* are lacerate right across the apex and not with a deep cleft in the middle. They are up to 2 mm long or more. *Sphagnum fuscum*, another species with a dark colored stem, belongs to the section *Acutifolia* and has the chlorophyllous cells exposed on the adaxial side of the

Plate 1. *Sphagnum lenense* H. Lindb. *ex* Pohle (Bryological Report 357).

1. Fascicle, well preserved cluster of branches (x25).
2. Stem leaves (x50).
3. Stem transverse section with hyalodermis and cortex (x500).
4. Branch leaves (x50).
5. Medial hyaline cells and surrounding chlorophyllose cells of branch leaf, adaxial view (x500).
6. Medial hyaline cells and surrounding chlorophyllose cells of branch leaf, abaxial view (x500).
7. Transverse section through branch leaf, chlorophyllose cells exposed on the abaxial side (x500).



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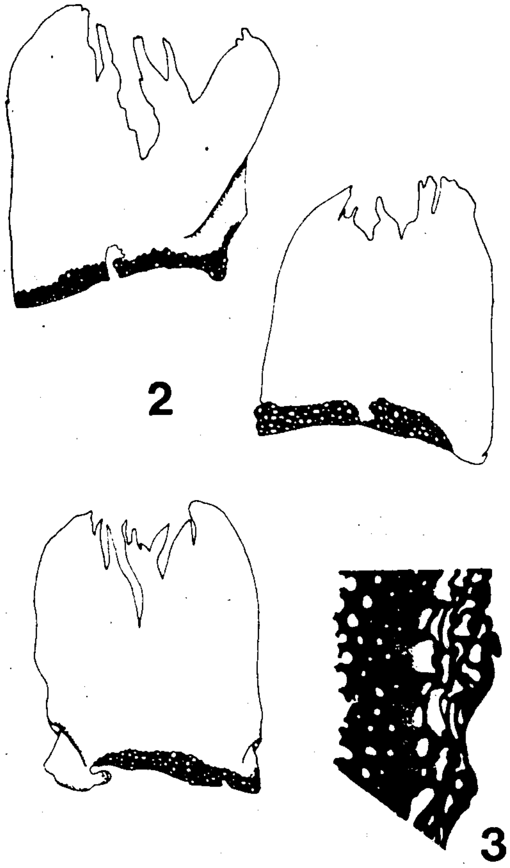

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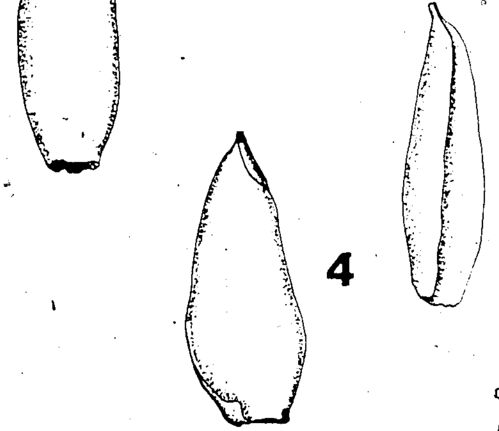

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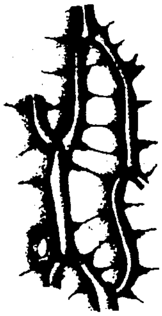

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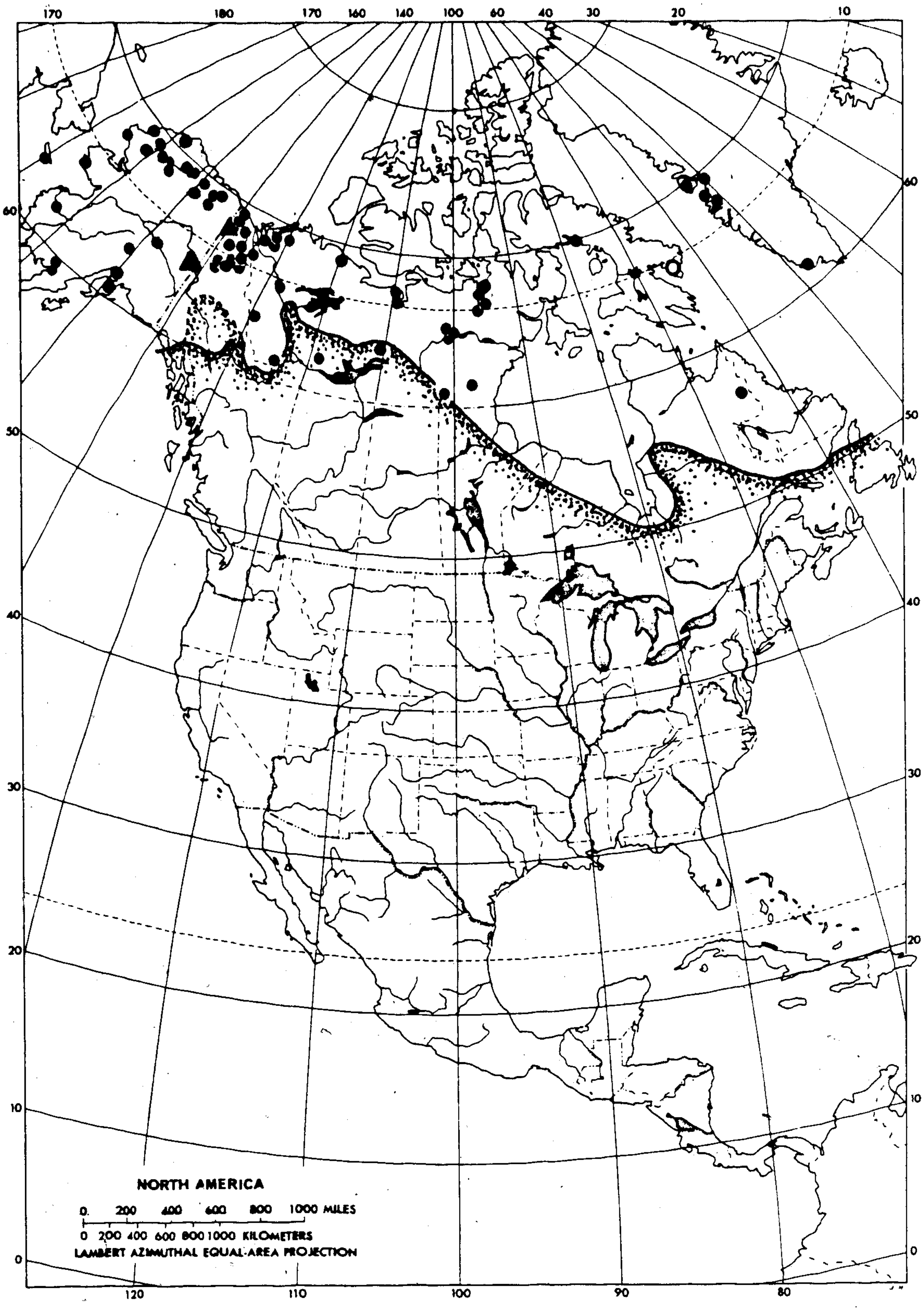
Plate 2. The present day and subfossil distribution of *Sphagnum lenense* H. Lindb. *ex* Pohle. Solid dots: present day distribution based on specimens in ALA, ALTA, C, CANM, COLO and NY. Open circle: uncertain locality. Triangle: Holocene river detritus (Yukon) and Plio-Pleistocene Lost Chicken locality (Alaska). Solid and broken shadowed line: maximal northward extend of *Pinus* in North America, based on maps in Hultén (1968), Hosie (1975) and Viereck & Little 1975.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NORTH AMERICA
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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

branch leaves. *Sphagnum lenense* belongs to the section *Cuspidata*, characterized by exposure on the abaxial side.

The two million year old record of the Lost Chicken locality in eastern Alaska is exceptional. Although it is the oldest record of *Sphagnum* for the continent, the material is perfectly preserved, actually better than any other *Sphagnum* material I have seen. The species is very abundantly represented in the autochthonous peat. For more discussion see Chapter IV and V.

Sphagnum magellanicum Brid.

Diagnostic features. – *Branch leaves* cucullate, widely ovate; *chlorophyllose cells of branch leaves* in transverse section widely elliptic, not exposed on the surface of the leaf. *Stem* epidermal cells with spiral bands.

Habitat. – In wide carpets or hummocks, exposed. In bogs, poor fens and woody peatland. It forms small hummocks or occurs on the side of larger hummocks. Relatively oligotrophic, pH 6.5 (n=1), conductivity 137 microScm^{-1} (n=1), Ca concentration 4.5 ppm (n=1), Mg concentration 0.5 ppm (n=1), Na concentration 10.8 ppm (n=1), K concentration 9.2 ppm (n=1).

Recent Distribution. – Circumpolar, bipolar. North America: Labrador to Alaska, south to the gulf of Mexico and California. Central America, South America to Tierra del Fuego, Falkland Islands. Europe, Azores, northern, eastern and central Asia, Japan. Australia.

Subfossil Distribution in North America. – Alberta, British Columbia and New York (Miller 1980a). New records: (1) HH75-24, Bluefish Basin, Yukon Territory; probably pre-Wisconsinan; Bryological Report 173. (2) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (3) Ballaine Lake, Fairbanks area, Alaska; 1770 ± 70 B.P. (USGS-31); Bryological Report 430, Hamilton *et al.* 1980.

Discussion. – The very characteristic ovate leaves and fibrils in the epidermal cells of the stem and branches make members of the section *Sphagnum* the easiest to recognize in the fossil material. *Sphagnum magellanicum* is by far the most common subfossil of this section in continental North America. See the discussion of *S. centrale* for the differentiation of *S. magellanicum*

Sphagnum squarrosum Crome

Diagnostic features. – *Fragments* robust; *stem leaves* finely, evenly fringed along margins and across apex; *branch leaves* squarrose, sometimes straight; *chlorophyllose cells* with outer walls finely papillose, narrowly elliptic or sharply rectangular in transverse section, not or narrowly exposed on the abaxial surface of the branch leaf.

Habitat. – In wet, shaded habitats and depressions. At fen margins, in minerotrophic seepages, beside lakes and streams. In *Picea* forests.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Labrador, troughout Canada and the northern and central United States, south in the mountains to North Carolina and Tennessee in the east and Arizona and California in the west. Europe, northern and central Asia, Japan.

Subfossil Distribution in North America. – Greenland, Iowa and Northwest Territories (Miller 1980a). New records: (1) Ballaine Lake, Fairbanks area, Alaska; 3110 ± 100 B.P. (USGS-30); Bryological Report 427, Hamilton *et al.* 1980. (2) Ballaine Lake, Fairbanks area, Alaska; 890 ± 175 B.P. (AU-17); Bryological Report 431, Hamilton *et al.* 1980.

Discussion. – *Sphagnum teres* is less robust than *Sphagnum squarrosum*. The leaves of the former commonly are not squarrose. Poorly preserved material can cause difficulties in identification to the species level. The section *Squarrosum* is differentiated from other *Sphagna* by finely papillose outer walls of the chlorophyllose cells and evenly fringed stem leaves.

Sphagnum teres (Schimp.) Angstr. *ex* C. Hartm.

Diagnostic features. – *Fragments* slender; *stem leaves* finely, evenly fringed along margins and across apex; *branch leaves* imbricate to spreading, straight; *chlorophyllose cells* with outer walls finely papillose, narrowly elliptic or sharply rectangular in transverse section, not or narrowly exposed on the abaxial surface of the branch leaf.

Habitat. – In floating mats, on hummocks (beside streams in alpine habitats), in sedge communities near open water. Beside lakes and in streams, in *Alnus*, *Salix* and *Betula* thickets, and in late snow-melt areas.

Recent Distribution. – Circumboreal and circumpolar. North America: from the Arctic south to Pennsylvania, Ohio, Michigan, Illinois, Iowa, North Dakota, Colorado, Montana, Idaho and California.

Subfossil Distribution in North America. – Greenland and Northwest Territories (Miller 1980a). New records: (1) Milford Gypsum Quarry, Milford, Nova Scotia; >50,000 B.P. (GSC-1642); Bryological Report 413.

Discussion. – See the discussion under *S. squarrosum* for the differentiation of that species from *S. teres*.

Sphagnum section *Acutifolia* Wils.

Diagnostic features. – Taxa belonging to this section are differentiated by the following combination of character states: one hanging branch per fascicle in most species, a well developed hyalodermis (3–4 layered) on the stem and chlorophyllose cells that are exposed on the adaxial surface of the branch leaves. Some of the most common taxa in continental North America belong to this section, including *S. girgensohnii*, *S. warnstorfii* (green stem) and *S. fuscum* (dark stem). Often, stem and stem leaves are nor preserved and identification to species level is then not possible.

Subfossil Distribution in North America. – Alberta (Miller 1980a). New records: (1) HH68–9, Old Crow Basin, Yukon Territory; Holocene peat, 20 to 30 cm below surface; Bryological Report 145. (2) HH68–9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148. (3) HH68–9 (station 1–2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (4) HH68–9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (5) HH68–9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (6) Cape Deceit Quaternary Exposure, Near Deering (station 5–6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 332, Matthews 1974a. (7) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (8) HH72–54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434.

Sphagnum section *Cuspidata* (Lindb.) Schlieph.

Diagnostic features. – Taxon belonging to the section *Cuspidata* are differentiated from other Sphagna by the following combination of character states: two hanging branches per fascicle, a poorly developed hyalodermis on the stem or none and chlorophyllose cells which are exposed on the abaxial surface of the branch leaves. *Sphagnum lenense*, discussed above, belongs to this group.

Subfossil Distribution in North America. – Alberta (Miller 1980[illegible] records: (1) HH68–9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (2) HH68–9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (3) Ballaine Lake, Fairbanks area, Alaska; 3110 ± 100 B.P. (USGS–30); Bryological Report 427, Hamilton *et al.* 1980.

Sphagnum unidentified species

Subfossil Distribution in North America. – (1) Snake River area, Yukon Territory; 11,700 ± 90 B.P. (GSC-2693) and 11,800 ± 170 B.P. (GSC-2745); Bryological Report 41. (2) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 1 (3) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (4) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (6) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (7) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (8) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (9) Lost Chicken area, Lost Chicken Mine, Alaska; 1,400,000 - 2,000,000 B.P.; Bryological Report 357, Matthews 1970. (10) Lost Chicken area, Lost Chicken Mine, Alaska; 1,400,000 - 2,000,000 B.P.; Bryological Report 359, Matthews 1970. (11) HH68-9 (station 3), Old Crow Basin; Yukon Territory; Early Wisconsinan?; Bryological Report 391.

Fissidentaceae

Fissidens

The genus *Fissidens* has a poor North American subfossil record. Only four species out of 39 reported for the Continent at the present time (Crum *et al.* 1973, Ireland *et al.* 1980) are represented as subfossils. Miller (1980a) listed *F. osmundoides* Hedw. from Iowa (Aftonian) and New York State (Lateglacial) and *F. taxifolius* Hedw. from Indiana (Sangamonian). My collections are listed below. They were annotated by R.A. Pursell, who wrote the following comments about them:

> "The plants ... (Bryological Report JJ 261) are *Fissidens bryoides* Hedw., *sensu lato*. No one, however, would disagree if you want to call them *F. viridulus* (Sw.) Wahlenb. ... The second set of slides (Bryological Report JJ 280), are the more interesting. I have compared the two fragments with *F. osmundoides*. The only other possibility is *F. taxifolius*. The costae in this species, however, are much more robust and generally excurrent. I feel certain that these fragments do represent *F. osmundoides*. [In these subfossils] ... there has been a shortening of the costae. If you have more material to demonstrate this, I see no reason why you could not propose a variety based on this character state."

It was not possible to extract more specimens of this taxon out of the tiny sample (originally a pollen sample).

Subfossil Distribution in North America. – (12) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 261, as *Fissidens bryoides* Hedw., *sensu lato*, confirmed by R.A. Pursell. (13) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *Fissidens cf. osmundoides* Hedw., confirmed by R.A. Pursell.

Ditrichaceae

Ceratodon

A few poorly preserved specimens can probably be assigned to *Ceratodon purpureus* (Hedw.) Brid. None of these specimens has the characteristic, irregular denticulation of the upper margin preserved.

Subfossil Distribution in North America. – Indiana, Minnesota, New York and Vermont (Miller 1980a). New records: (14) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265, as *cf. Ceratodon purpureus.* (15) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *cf. Ceratodon purpureus.* (16) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302, as *cf. Ceratodon purpureus.*

Distichium

No material with sporophytes was preserved in any of the samples. It was thus not possible to identify the small gametophytic fragments to species level. Luxurious forms of *Distichium capillaceum* (Hedw.) B.S.G. are the only *Distichium* specimens having a distinct gametophytic habit. They are large and have strongly squarrose-recurved leaves. The small forms of *D. capillaceum* on the other hand are indistinguishable from *D. hagenii* Ryan *ex* Philib. and *D. inclinatun* (Hedw.) B.S.G. However, *D. capillaceum* is the most common species of the three so all the fossil records are tentatively listed under this taxon. The distichous leaves of the species of this genus are differentiated from *Fissidens* leaves by the absence of apical and abaxial laminae and by their narrower, tubulose, subulate leaves with papillose medial cells.

Distichium capillaceum

Diagnostic features. – *Leaves* distichous, with a sheathing base and a long flexuose or squarrose-recurved subula; *medial cells* with a rough cuticle, showing low, elliptic papillae. These papillae are oriented longitudinally on the leaf.

Habitat. – Grows mostly on calcareous soil and in rock crevices, in mesic situations. In montane and tundra habitats. pH 7.7 (n=1), conductivity 856 microScm^{-1} (n=1), Ca concentration 125 ppm (n=1), Mg concentration 49 ppm (n=1), Na concentration 11 ppm (n=1), and K concentration 5 ppm (n=1).

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Greenland, south to New York to Iowa in the east and Colorado and Arizona in the west. Hawaii, Mexico to Patagonia. New Zealand, Australia, New Guinea.

Subfossil Distribution in North America. – Greenland, Indiana, Minnesota, New York, Northwest Territories, Ontario, Vermont and Wisconsin (Miller 1980a). New records: (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580a ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21, as *Distichium cf. capillaceum.* (2) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176, as *Distichium cf. capillaceum.* (3) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178, as *Distichium cf. capillaceum.* (4) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23, as *Distichium cf. capillaceum.* (5) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23, as *Distichium cf. capillaceum.* (6) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271, as *Distichium cf. capillaceum.* (7) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308, as *Distichium cf. capillaceum.* (8) HH68-9 (station 10), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological

Report 385, as *Distichium cf. capillaceum.* (9) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401, as *Distichium cf. capillaceum.* (10) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435, as *Distichium cf. capillaceum.*

Discussion. - Some of the small *Distichium* fragments could be *D. inclinatum*, a species characteristic of and probably relatively common along stream banks (D.G. Horton, personal communication).

Ditrichum

All material is poorly preserved. However, the diagnostic features *D. flexicaule* are usually clearly visible. All the subfossil specimens that were prepared could thus be identified to this species. Miller (1980a) listed one record of another taxon, *D. lineare* (Sw.) Lindb. from a deposit of unknown age near Aurora, North Carolina.

Ditrichum flexicaule (Schwaegr.) Hampe

Diagnostic features. - *Plants* tomentose; *leaves* erect-spreading with ovate-lanceolate base and long subula, shoulder usually not pronounced; *costa* wide, diffuse; *medial and upper cells* irregular, varying from rectangular to quadrate or subquadrate; *marginal cells* below and at the shoulder area longer and nar often linear at the margin itself.

Habitat. - On calcareous soil and in rock crevices. In meadows and on beach ridges in the High Arctic.

Recent Distribution. - Circumboreal. Bipolar. North America: from Alaska to Greenland and south to Vermont, Michigan, Iowa in the east and Colorado in the west. Guatemala and Colombia. Europe, Algeria, Caucasus, Madeira, northern Asia. New Zealand.

Subfossil Distribution in North America. - Michigan, Minnesota, New York, Northwest Territories and Wisconsin (Miller 1980a). New records: (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (2) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (3) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (4) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (5) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (6) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383. (7) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (8) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401. (9) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425.

Discussion. – The best preserved fragments are derived from luxurious forms. The leaves are long and the plants abundantly tomentose. The smaller forms can be recognized by the linear marginal cells at the shoulder area of the leaf. The medial and upper cells are very irregular in shape, contrasting with the more elongate and regular shape of small forms of Dicranaceae. The costa in all subfossil specimens is wide and not clearly delimited.

Dicranaceae

Dicranella

Subfossil *Dicranella* specimens are differentiated from those of *Dicranum* species by their poorly developed alar cells and small size. *Dicranella* can be differentiated from another genus in the Dicranaceae with a fossil record, *Oncophorus*, by the former having non-sheathing, gradually narrowed ovate-lanceolate to lanceolate leaves. Four speciesof *Dicranella* are represented in the North American record (Miller 1989a): *D. heteromalla* (Hedw.) Schimp. (Wisconsin), *D. palustris* (Dicks.) Crundw. *ex* Warb. (British Columbia), *D. schreberiana* (Hedw.) Schimp. (New York) and *D. varia* (Hedw.) Schimp. This last species is the most common in the fossil record and is also the only one in my collections from the Yukon Territory.

Dicranella varia (Hedw.) Schimp.

Diagnostic features. – *Leaves* lanceolate with a keeled subula; *costa* strong, clearly defined, with the narrow lamina forming a keeled subula above; *margins* narrowly recurved along most of their length, irregularly denticulate above; *medial cells* narrowly rectangular, thin-walled.

Habitat. – On damp, disturbed and calcareous soil, particularly on clay. On moist banks of ditches and along roads, also on solifluction soil.

Recent Distribution. – Circumboreal. North America: from Alaska to Nova Scotia, south to California and the Gulf of Mexico. Central America. Europe, Azores, Madeira, Canaries, northern Africa. Asia.

Subfossil Distribution in North America. – New York and Vermont (Miller 1980a). New record: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174.

Discussion. – Leaves of the other *Dicranella* species are characterized by having plane margins or a wider, diffuse costa.

Dicranella unidentified species

Subfossil Distribution in North America. – Wisconsin (Miller 1980a). New Record: (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23.

Dicranum

All the subfossil *Dicranum* specimens in my collections were annotated by W. Peterson. The following information is based on his thesis (Peterson 1979) and personal communication, in addition to the references listed in Chapter II.

Dicranum fragments are very distinctive fossils: more than any other acrocarpous moss, the color of their thick cell walls is modified to a dark-brown or black during fossilization. This feature is shared by *Aulacomnium* and some pottiaceous taxa in a lesser degree. The pleurocarpous mosses do not react in this way.

My collections are listed and discussed below. Additional taxa found in North America are: *D. elongatum* Schleich. *ex* Schwaegr. (Greenland), *D. fuscescens* Turn. (New York and British Columbia), *D. leioneuron* Kindb. (Northwest Territories) and *D. majus* Sm. (Alaska).

Dicranum acutifolium (Lindb. *et* Arn.) C. Jens. *in* Weim (Miller 1980a).

Diagnostic features. – *Leaves* straight to slightly curved, keeled; *apex* acute; *medial cells* irregular, varying from shortly rectangular to quadrate, not or weakly porose; *alar cells* in a bistratose group.

Habitat. – On slightly calcareous substrates, in forest areas surrounding mires and fens. In tundra, *Dryas* heath and montane-boreal forest.

Recent Distribution. – Circumboreal. North America (see Fig. 52 in Peterson 1979): from Alaska to Greenland, south in the east to New England and in the western mountains to New Mexico. Most common in the northwestern part of the continent. Europe, Asia.

Subfossil Distribution in North America. – (1) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 0 to 10 cm below surface; Bryological Report 143. (2) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – The closely related *D. fuscescens* Turn. and *D. elongatum* Schleich *ex* Schwaegr. are characterized by a more regular pattern of upper and medial cells. As well, *D. elongatum* has a unistratose alar cell region.

Dicranum angustum Lindb.

Diagnostic features. – *Leaves* narrowly lanceolate, not keeled; *apex* acute; *costa* without abaxial lamellae; *margins* entire; *medial cells* elongate, clearly porose.

Habitat. – Usually associated with *Sphagnum* species, in wet habitats. Widely distributed in the coniferous forests, with increasing frequency northwards. It is a fen moss and grows usually in loose tufts or as solitary stems among *Aulacomnium palustre*, *Calliergon sarmentosum*, *Calliergon stramineum*, *Dicranum majus*, *Drepanocladus revolvens*, *D. uncinatus*, *Sphagnum balticum*, *S. warnstorfii* and *Tomenthypnum nitens*.

Recent Distribution. – Circumboreal. North America (see Fig. 58 in Peterson 1979): from Alaska to Greenland, southward in the Canadian Rocky Mountains to Banff National Park. Europe: Scandinavia. Asia: Siberia.

Subfossil Distribution in North America. – (1) HH75-24, Bluefish Basin, Yukon Territory; probably pre-Wisconsinan; Bryological Report 173.

Discussion. – This species is morphologically very close to *Dicranum scoparium* Hedw.

The latter is differentiated by the presence of lamellae on the abaxial side of the costa.

Dicranum groenlandicum Brid.

Diagnostic features. – *Leaves* lanceolate, with a more or less widely ovate-lanceolate base, straight or curved; *apex* acute to narrowly obtuse, with a few teeth; *costa* without abaxial lamellae; *margins* entire; *medial and upper cells* elongate, very thick-walled, porose; *alar cells* not reaching the costa.

Habitat. – In mesic tundra, also in heath vegetation at higher elevations. Forming large hummocks similar to those of *D. elongatum*. It is found mainly on non-calcareous soil, rich in humus and often on old *Sphagnum* hummocks.

Recent Distribution. – Circumboreal. Arctic-alpine species. North America (see Fig. 45 in Peterson 1979): from Alaska to Ellesmere Island, Labrador and Newfoundland, south to southern Ontario, Alberta and British Columbia. Svalbard, Fennoscandia, Siberia and Japan.

Subfossil Distribution in North America. – (1) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (2) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (3) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (4) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat, Bryological Report 289. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (6) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (7) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – The very similar *D. angustum* has narrow lanceolate leaves. *Dicranum elongatum* has shorter upper cells, longer leaves and unistratose alar region. Other *Dicranum* taxa have shorter or thinner walled medial cells, or a costa with abaxial lamellae.

Dicranum scoparium Hedw.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New record: (1) HH68-9, Old Crow Basin, Yukon Territory, Holocene peat, 0 to 10 cm below surface; Bryological Report 143, as *Dicranum cf. scoparium*.

Discussion. – The very poorly preserved material has the appearance of a young *D. scoparium* plant. The costa is not completely developed. No abaxial lamellae can be observed.

Dicranum undulatum Brid.

Diagnostic features. – *Leaves* undulate, long lanceolate with an ovate-lanceolate base, strongly keeled; *apex* broad; *medial cells* very irregular and shortly rectangular, with sinuose, thick walls.

Habitat. – Mire species, frequently found in muskeg. Rarely on soil or wood. Forming compact mats on *Sphagnum* hummocks. Often associated with *Aulacomnium palustre*, *Meesia uliginosa*, *Tomenthypnum nitens*, *Catoscopium nigritum* and *Campylium stellatum*. pH 6.65 and 6.80 (n=2), conductivity [illegible] and 202 microScm^{-1} (n=2), Ca concentration 14.5 and 15.4 ppm (n=2), Mg concentration 4.3 and 15.4 ppm (n=2), Na concentration 12.0 and 12.1 ppm (n=2) and K concentration 5.3 and 13.6 ppm (n=2).

Recent Distribution. – Circumboreal, subarctic. North America (see Fig. 56 in Peterson 1979): from Alaska to Labrador and Newfoundland, south to North Carolina in the east and Wyoming and Washington in the west. Europe: Fennoscandia and the mountains. Siberia, Japan.

Subfossil Distribution in North America. – Iowa (Miller 1980a). New records: (1) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150 B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40, as *Dicranum undulatum*, approaching *Dicranum acutifolium*.

Discussion. – The fossil specimens are intermediate between *D. undulatum* and *D. acutifolium*. W. Peterson (*in litt.*) gave the following analysis of them:

> "The areolation is closer to ... [*D. acutifolium*] but the leaf shape, papillae on the costa and the marginal serrations suggest ...[*D. undulatum*]. There are no intact leaf tips except those on the reduced male leaves. ... These plants are not unexpected. In my thesis I speculated that the Beringia area was the probable place where *D. acutifolium* evolved from *D. undulatum*. Perhaps these specimens represent some phase in this evolutionary line."

Dicranum unidentified species

Subfossil Distribution in North America. – Greenland and Wisconsin (Miller 1980a). New records: (1) Your Creek area, Alaska; 5615 ± 110 B.P. (I–10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I–10,925); Bryological Report 201, Hamilton 1980a, p. 23. (3) HH68–9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (4) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC–2792); Bryological Report 269. (5) HH68–9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370.

Oncophorus

Only three poorly preserved fragments in my collections can be tentatively assigned to *Oncophorus*. They are similar to *Dicranella* fragments, but have a wider, more or less sheathing base.

Subfossil Distribution in North America. – (6) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I–10,525); Bryological Report 177, as *cf. Oncophorus* species. (7) HH68–9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308, as *cf. Oncophorus* species. (8) HH72–54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435, as *cf. Oncophorus* species.

Encalyptaceae

Subfossil Encalyptaceae leaves are differentiated from some similar pottiaceous leaves (e.g. *Tortula* and *Desmatodon*) by the thickened and colored, transverse walls of the basal cells instead of the equal thickness of transverse and longitudinal walls in the pottiaceae forms with differentiated basal cells.

All specimens were annotated by D.G. Horton. The information below is extracted [illegible]rton (1980) or by personal communication.

Bryobrittonia

Bryobrittonia longipes (Mitt.) Horton

Diagnostic features. – *Leaves* widely ovate-lanceolate; *apex* acute; *costa* ending in the apex; *margins* crenulate in the upper half; *medial cells* quadrate, mamillose; *basal cells* shortly rectangular along the costa, longer and narrower at the margin.

Habitat. – In moist shaded places on calcareous silt, often near streams or in flood areas, on alluvial banks and slumped sediments exposed along rivers.

Recent Distribution. – Circumpolar. Arctic-alpine species. North America: Alaska, Yukon Territory, Arctic Islands, Northwest Territories, British Columbia and Alberta. Siberia, Greenland.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23.

Discussion. – Other Encalyptaceae specimens are differentiated from *B. longipes* entire margins and papillose upper cells.

Encalypta

Only two specimens in my collections can be assigned to a taxon at the species level, namely *E. alpina* Smith. The other specimens are listed under *Encalypta* unidentified species, but some indication to their relationship is given. The only species listed in Miller (1980a) is *E. procera* Bruch (Vermont and Wisconsin).

Encalypta alpina Smith

Diagnostic features. – *Leaves* ovate-lanceolate to lanceolate; *apex* very narrowly acute and stoutly apiculate; *costa* well defined, shortly excurrent; *margins* plane, entire.

Habitat. – On seepage and solifluction slopes, gravel, drier meadows, and wet clay or calcareous silt of river banks, on disturbed peat banks and in crevices of cliffs. Often mixed with such other bryophytes as *Distichium capillaceum*, *Meesia uliginosa*, *Cyrtomnium hymenophylloides*, *C. hymenophyllum*, *M. thomsonii*, *Myurella julacea*, *Barbilophozia quadriloba*, *Orthothecium imbricatum*, and *Pohlia cruda*.

Recent Distribution. – Arctic-alpine species. North America: from Alaska to Greenland, south in the Rocky Mountains to Colorado. Iceland, Svalbard, Great Britain, Europe, Morocco, Himalayas, China, northern Asia, Japan.

Subfossil Distribution in North America. – (1) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328, as *Encalypta cf. alpina*. (2) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Encalypta unidentified species

Subfossil Distribution in North America. – (1) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980; a calyptra. (2) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980; as *Encalypta cf.*

rhaptocarpa. (3) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (4) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (5) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401, as *Encalypta cf. procera.*

Pottiaceae

This large family with many genera and numerous species has a poor subfossil record. Many taxa are small and the fragmentary material is difficult to identify. They characteristically occur in dry or pioneering types of habitats, not suited for good fossilization.

Barbula

Barbula belongs to the subfamily Trichostomoideae, differentiated from the Pottioideae by two stereid bands in the costa. Leaves of *Barbula* and *Didymodon* are characterized by recurved margins and short, subquadrate basal cells, that are shortly rectangular towards the costa. The two genera are closely related and several authors treat all species as *Barbula* (*e.g.* Nyholm 1954–1969). K. Saito (1975) and R.H. Zander (1978a) redefined the genera on gametophytic characters. Many taxa of *Barbula* were placed in *Didymodon* by these authors. My subfossil collections of *Barbula* were all annotated by R.H. Zander as *Didymodon acutus* (Brid.) K. Saito var. *acutus*. I list and discuss these fragments below under *Barbula acuta* in order to be conform to Janssens (1980b), the *Index Muscorum* (Van der Wijk *et al.* 1959) and the filing system in ALTA.

Barbula acuta (Brid.) Brid.

Diagnostic features. – *Leaves* small, 1.0 to 1.5 mm long, widely ovate-lanceolate, erect, weakly keeled; *apex* acute; *costa* stout, clearly defined below, disappearing in the apex of the leaf; *margins* recurved, unistratose, entire; *medial cells* rounded to subquadrate, thick-walled, sometimes slightly nodose, smooth; *basal cells* quadrate to shortly rectangular at the margins, towards the costa longer, thick-walled throughout.

Habitat. – Most frequent in dry situations, on calcareous rock outcrops and dry slopes.

Recent Distribution. – North America-Europe. North America: Alaska, Yukon (Slims River area) and Alberta, disjunct to Utah, Colorado, Texas, and Kansas. Mexico. Europe, northern Africa.

Subfossil Distribution in North America. – (1) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (2) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (3) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (4) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (5) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Species of *Barbula* and of *Didymodon* that are closely related to *B. acuta*, are differentiated by strongly keeled leaves and papillose cells (*Didymodon asperifolius* (Mitt.) Crum, Steere *et* Anderson and *Barbula vinealis* Brid.), bistratose margins and propagulae (*Didymodon rigidulus* Hedw.: for more details see discussion under the latter) or by an excurrent costa (*Barbula icmadophylla* Schimp. *ex* C. Müll. and *B. ditrichoides* Broth.).

Bryoerythrophyllum

Bryoerythrophyllum recurvirostrum (Hedw.) Chen

Diagnostic features. – *Leaves* narrowly lanceolate; *apex* acuminate-apiculate; *costa* ending in the apex; *margins* revolute except at the apex and the base, entire, except with a few irregular teeth at the apex; *medial cells* quadrate, with numerous hollow-cylindrical or C-shaped papillae; *extreme upper cells* smooth, rhomboid, sharply pointed; *basal cells* narrowly rectangular, thin-walled and gradually changing into the medial cells.

Habitat. – On calcareous soil and rock, in rock crevices, on logs and rotten wood, on beach ridges and in mesic meadows. In exposed situations it is found together with *Desmatodon latifolius*, *Encalypta rhaptocarpa* and *Stegonia latifolia*. In shaded and mesic places it is associated with *Isopterygium pulchellum*, *Myurella tenerrima* and *M. julacea*.

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Greenland, Newfoundland and Labrador, south throughout Canada into the United States, extending farther south at higher elevations, reaching North Carolina in the east and to Texas, New Mexico, Arizona and California in the west. Mexico, Guatemala, Iceland, Svalbard, Europe, Africa, China, Himalayas, northern U.S.S.R., Japan, Tasmania, New Zealand.

Subfossil Distribution in North America. – New York, Northwest Territories, Vermont and Wisconsin (Miller 1980a). New record: (1) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 261.

Discussion. – *Bryoerythrophyllum recurvirostrum* is a very characteristic species. The above listed combination of diagnostic features characterize no other taxon. Other taxa with narrowly lanceolate leaves, similar in aspect to those of *Bryoerythrophyllum*, are *Tortella*, *Trichostomum*, some *Barbula* and *Didymodon* species, *Gymnostomum* and *Eucladium*. All these genera, together with *Bryoerythrophyllum*, belong to the subfamily Trichostomoideae. *Tortella* is mostly distinguished by a sharp, V-shaped demarcation between basal and medial cells, with the basal cells extending higher along margins. For the difference between *Trichostomum* with *Tortella*, see the discussion under the latter. *Barbula* and *Didymodon* have shorter, subquadrate, thick-walled basal cells. *Gymnostomum* has margins recurved on only one side or plane, and thick-walled, short-rectangular basal cells. *Eucladium verticillatum* (Brid.) B.S.G. is denticulate at the leaf shoulder.

Desmatodon

Desmatodon and *Tortula* are the only two genera of the Pottioideae with a North American fossil record. The subfamily is characterized by a single stereid layer in a transverse section through the costa. *Desmatodon* is tentatively identifiable from *Tortula* by less abruptly differentiated basal cells. *Desmatodon ellesmerensis* Brassard has been placed in synonymy with *Pseudocrossidium revolutum* (a Trichostomoideae) by Zander, discussed below. The only North American subfossil representative of the genus *Desmatodon* is a single specimen of *Desmatodon leucostoma*, annotated by Zander.

Desmatodon leucostoma (R. Br.) Berggr.

Diagnostic features. – *Leaves* broadly ovate-lanceolate; *perichaetial leaves* similar to vegetative leaves; *apex* acute; *costa* stout, sharply defined, ending in the apex, in transverse section with well developed abaxial stereid band, no enlarged epidermal abaxial cells, large medial guide cells and a thin-walled adaxial epidermal cell group; *margins* partly bistratose, sharply revolute except at the base and apex; *medial cells* irregularly quadrate, thin-walled, densely papillose, papillae hollow or C-shaped; *basal cells* extending halfway up the lamina of the leaf, longly rectangular and thin-walled, slightly shorter towards the margins.

Habitat. – On gravelly beach ridges, rock crevices and disturbed banks. Particularly common around old lemming burrows, where it occurs with *Funaria microstoma*, *F. polaris* and *Desmatodon heimii* var. *arctica*. It is usually found with sporophytes. Steere (1978a) classified the species in the arctic circumpolar element, characteristic of calcareous silt and frost boils in exposed habitats.

Recent Distribution. – Circumboreal. Arctic and sub-arctic. North America: from Alaska to Greenland, south through the Rocky Mountains to Alberta and Colorado. Svalbard, mountains in Europe, northern and arctic asiatic U.S.S.R., central Asia.

Subfossil Distribution in North America. – (1) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267.

Discussion. – Leaves of some *Barbula* and *Pseudocrossidium* species approach those of *Desmatodon leucostoma* in general aspect. They are differentiated by shorter and more thick-walled basal cells and often by the development of two stereid bands of the costa; the lamina is narrower in relation to the width of the costa; the perichaetial leaves are differentiated from the cauline ~~and the~~ papillae are simple.

Didymodon

See the introduction to *Barbula* for the relationships to *Didymodon*. Only *Didymodon tophaceus* (Brid.) Lisa is listed from tufa deposits of unknown age in California and Oklahoma by Miller (1980a).

Didymodon rigidulus Hedw.

Diagnostic features. – *Leaves* widely ovate-lanceolate, slightly erect-recurved, weakly keeled; *apex* acute; *costa* stout, wide in relation to lamina width, disappearing into the multistratose lamina at the apex, in transverse section epidermal cells with large lumina, two well developed stereid bands and large guide cells; *margins* recurved, bistratose, entire; *medial cells* subquadrate to rounded, in distinct longitudinal rows, firm-walled, smooth or slightly rough, without clearly developed papillae; *basal cells* shortly rectangular, thin-walled, gradually differentiated from medial cells.

Habitat. – On calcareous rocks, walls and soil, on earth-covered boulders, in wet habitats, often on rocks in streams.

Recent Distribution. – Circumboreal. North America: from Alaska through British Columbia and Alberta to Oregon and at higher elevations to Arizona, New Mexico, Texas and Mexico, disjunct in New Brunswick, Michigan and Ontario, Ohio, Tennessee and Florida, also in Greenland and Newfoundland. South America, Iceland, mountains of Europe, North Africa, Caucasus, northern and arctic Asia, China, Japan.

Subfossil Distribution in North America. – (1) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434.

Discussion. – *Barbula acuta* is very close to *Didymodon rigidulus*. Both are small plants with short, wide and stiffly erect leaves. The costa is stout below and ill-defined above. *Barbula acuta* is differentiated by unistratose margins and upper lamina. Intergradations between these two taxa are likely (R.H. Zander, *in litt.*). No characteristic propagulae were preserved with the subfossil *D. rigidulus* specimen.

Gymnostomum

Gymnostomum is differentiated from the other genera of Trichostomoideae by entire margins that are plane or narrowly recurved on one side only. *Gymnostomum aeruginosum* Sm. is known as a subfossil from a lateglacial deposit in New York (Miller 1980a). A single specimen from Anaktuvuk Pass, Alaska, was annotated as *Hymenostylium recurvirostre* (Hedw.) Dix. by R.H. Zander. This record is discussed below under *Gymnostomum recurvirostrum* following Janssens (1980b) and Ireland *et al.* (1980). *Hymenostylium*, if recognized as a genus, is segregated from *Gymnostomum* by its systylious capsule (Crum 1973) and elongate medial leaf cells (R.H. Zander, *in litt.*).

Gymnostomum recurvirostrum Hedw.

Diagnostic features. – *Leaves* widely to narrowly ovate-lanceolate, weakly erect-recurved and keeled; *apex* sharply acuminate; *costa* stout to poorly defined, ending close to the apex; *margins* subentire (papillose-crenulate), narrowly recurved o at the medial portion, rarely plane; *medial cells* shortly rectangular to quadrate, firm-walled, clear or weakly papillose with a ,few, low hollow or C-shaped papillae; *basal cells* poorly differentiated from medial cells, more rectangular, walls, slightly nodose.

Habitat. – On wet calcareous cliffs, rocks and soil. Under some conditions forming tufa. In arctic areas intermixed with other fen mosses in wet tundra.

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Greenland, Newfoundland and Labrador, south to Texas and Arizona in the west, widespread in the east, south to Tennessee and Arkansas. Mexico, Central and South America, Europe, Africa, Asia, New Zealand, New Guinea.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23.

Discussion. – *Gymnostomum aeruginosum* is distinguished from *G. recurvirostrum* by plane leaf margins and less sharply acute apex.

Leptodontium

Leptodontium belongs to the subfamily Trichostomoideae, but does not develop the two stereid bands in the costa, as discussed below. In contrast with the other Trichostomoideae with a North American subfossil record, it is coarsely and irregularly denticulate along the upper part of the margins.

Leptodontium flexifolium (Dicks. *ex* With.) Hampe *in* Lindb. Plate 3

Diagnostic features. – *Leaves* lingulate, carinate above and scarcely sheathing below, *apex* broadly acute and often mucronate; *margins* recurved in lower 1/2–2/3 and denticulate in the upper 1/3; *costa* ending 3–8 cells below the apex; *laminal cells* papillose, with 4–7 low, cup– to c–shaped or flat, bi– to trifid papillae over each lumen; *inner basal cells* differentiated in the lower part of the sheathing base, short rectangular, papillose.

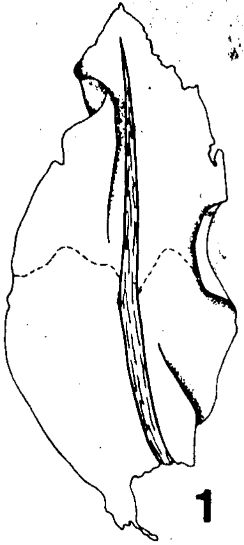
Habitat. – On soil, logs, trees and rock.

Recent Distribution. – Scattered pantropical and circumboreal. North America (Plate 4) : Southern Appalachians, Mexico. Central America, Andes, Europe, Africa, Himalayas, China, Formosa, Japan, southeastern Asia and Hawaii. Found at high latitudes in the tropics and subtropics, usually above 2000 m, in the Southern Appalachians restricted to the spruce–fir zone. Lesser altitude in Europe, to less than 300 m in Great Britain.

Subfossil Distribution in North America (Plate 4). – (1) HH68–9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (2) HH68–9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370.

Plate 3. *Leptodontium flexifolium* (Diks. *ex* With.) Hampe *in* Lindb. (Bryological Reports 174 and 370)

1. Upper perichaetial leaf (x50).
2. Lower leaves (x50).
3. Costa and lamina transverse sections (x500).
4. Leaf apex (x500).
5. Medial leaf cells (x500).
6. Basal leaf cells (x500).



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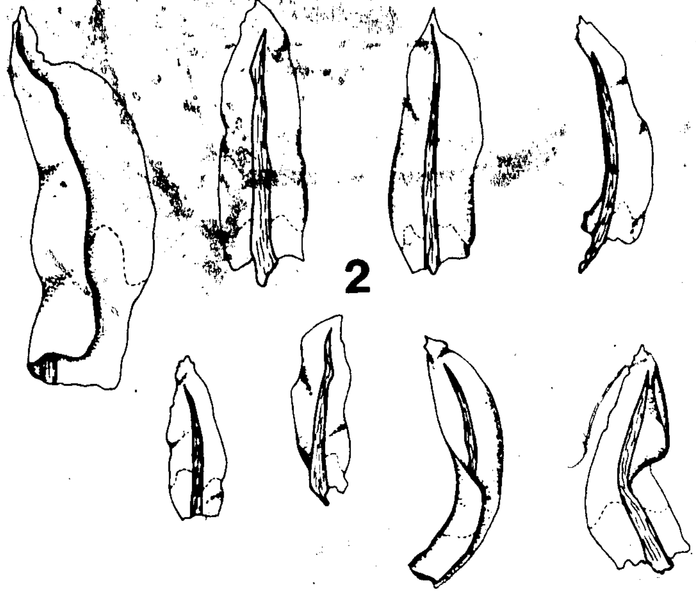

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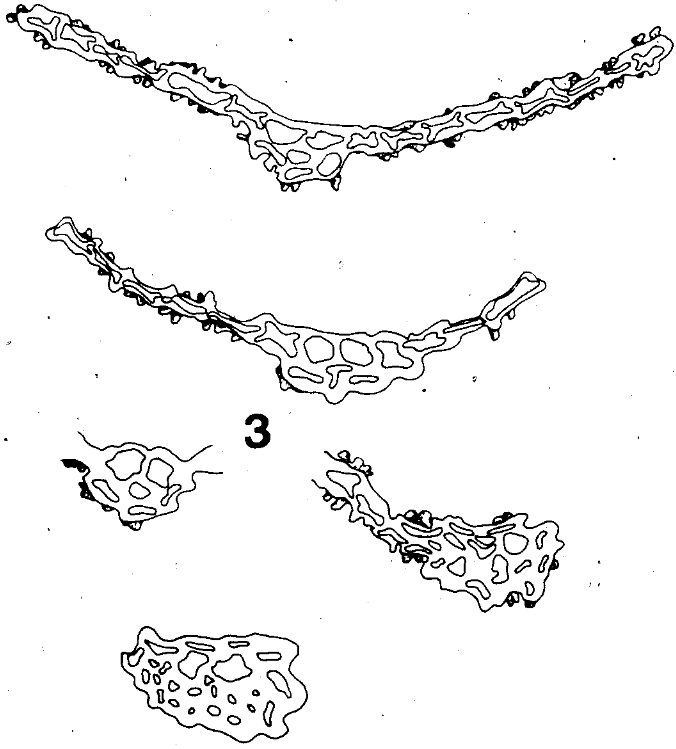

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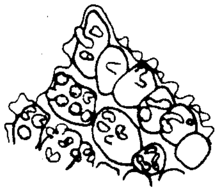

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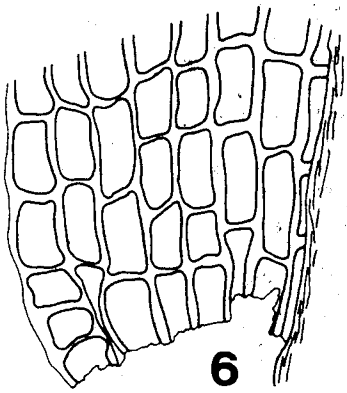

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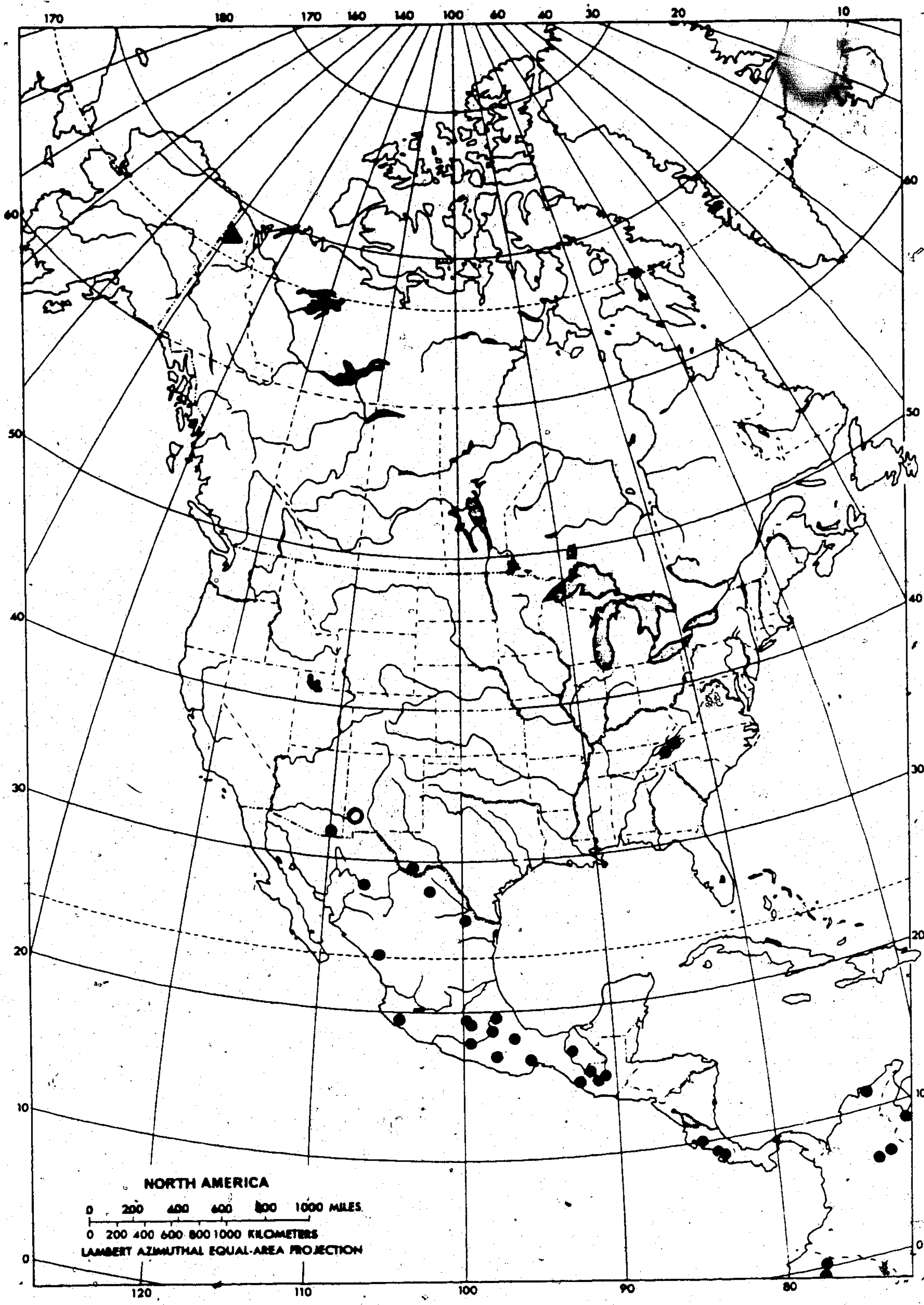
Plate 4. The present day North American distribution and subfossil records of *Leptodontium flexifolium* (Diks. *ex* With.) Hampe *in* Lindb. Solid dots: present day distribution based on Janssens & Zander (1980). Open circle: uncertain locality. Triangle: subfossil Wisconsinan record.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Discussion. – The three subfossil specimens show the following features: a few indistinct teeth are present near the apex on some leaves along their margins, laminal papillae are hollow (c-shaped); leaf base rather well differentiated and wide; leaves ovate; upper leaf margins plane and costa ending below apex.

Other species with leaves that are morphologically close in at least some features are (1) *Gymnostomum aeruginosum*, which has a narrower, more rounded apex; (2) *Barbula convoluta* Hedw., which has a stronger costa, and a more prominent keel and a generally a non-apiculate apex (or if apiculate, then the costa nearly reaches the apex), and (3) *Bryoerythrophyllum recurvirostrum*, which has leaf margins recurved to near the apex and a costa ending very nearly in the leaf apex.

K. Saito (Tokyo) agreed with this identification and pointed out that the cross section of the leaf of *Leptodontium* is distinctive. The typical leaf cross section of a species of *Leptodontium* shows an adaxial stereid band without a layer of epidermal cells over it. However, in such small specimens as the above subfossils, several combinations of rediced character-states are possible, including what may look like epidermal cells over the guide cells, but those are actually unthickened stereid cells. The only element of uncertainty in our identification is the poor development of denticulation along the upper part of the leaf margins. However, small, flagellated forms have often been observed with poor development of this feature.

Pseudocrossidium

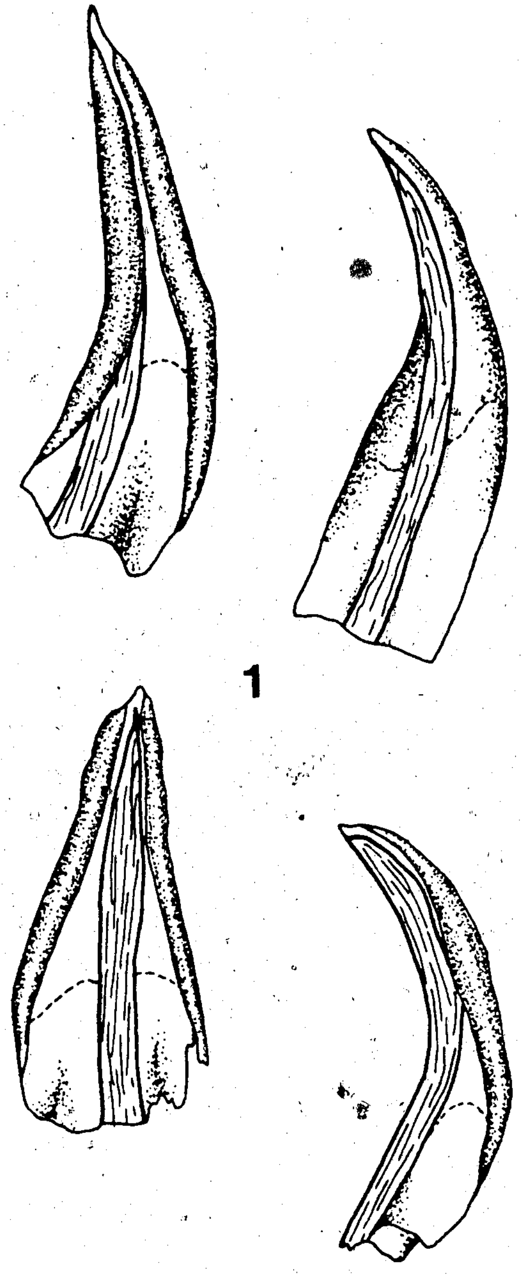
Pseudocrossidium (Trichostomoideae) in North America is segregated from *Barbula s.l.* by its broadly revolute upper leaf margins, composed of strongly chlorophyllose cells and by the poor development of the adaxial stereid band in the costa (as in *Leptodontium*).

Pseudocrossidium revolutum (Brid. *in* Schrad.) Zander Plate 5

Diagnostic features. – *Leaves* apiculate to short-mucronate, erect-spreading when moist, less than one mm long and 0.3 mm wide at the base; *margins* strongly revolute along entire length; *costa* strong; *medial and upper cells* rounded-quadrate and strongly

Plate 5. *Pseudocrossidium revolutum* (Brid. *in* Schrad.) Zander (Bryological Report 308)

1. Leaves. (x100).
2. Costa transverse section (x600).
3. Medial leaf cells (x3000).
4. Basal leaf cells (x1000).



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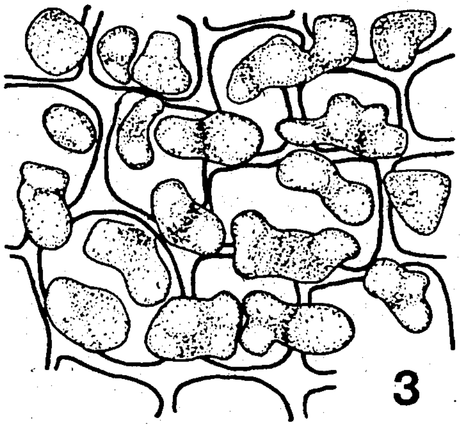

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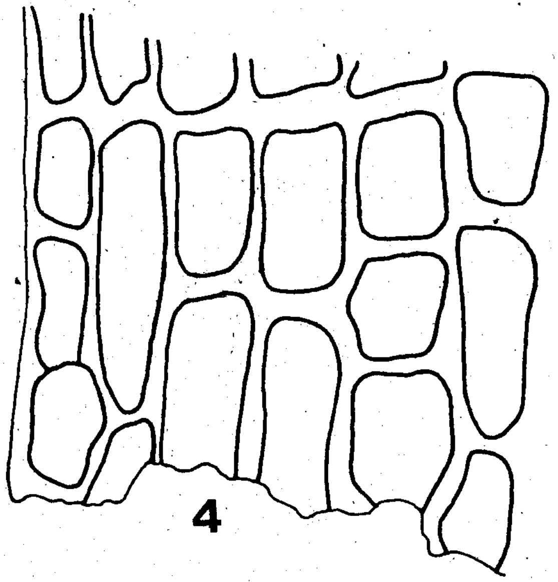


4

papillose with c-shaped papillae on both surfaces; *marginal cells* less papillose; *basal cells* shortly rectangular.

Habitat. – Soil, rock, north-facing cliffs, calcareous outcrops. On Ellesmere Island it has been reported to occur on fine, calcareous silt near lemming burrows (Brassard 1971a, b).

Recent Distribution. – North America – Europe. North America (Plate 6) : British Columbia, Ellesmere Island, Yukon Territory, Oregon, California. Ecuador(?), Europe, Canaries, Madeira, Algeria, Morocco, Tunis. Persia, Mesopotamia.

Subfossil Distribution in North America. – (1) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308.

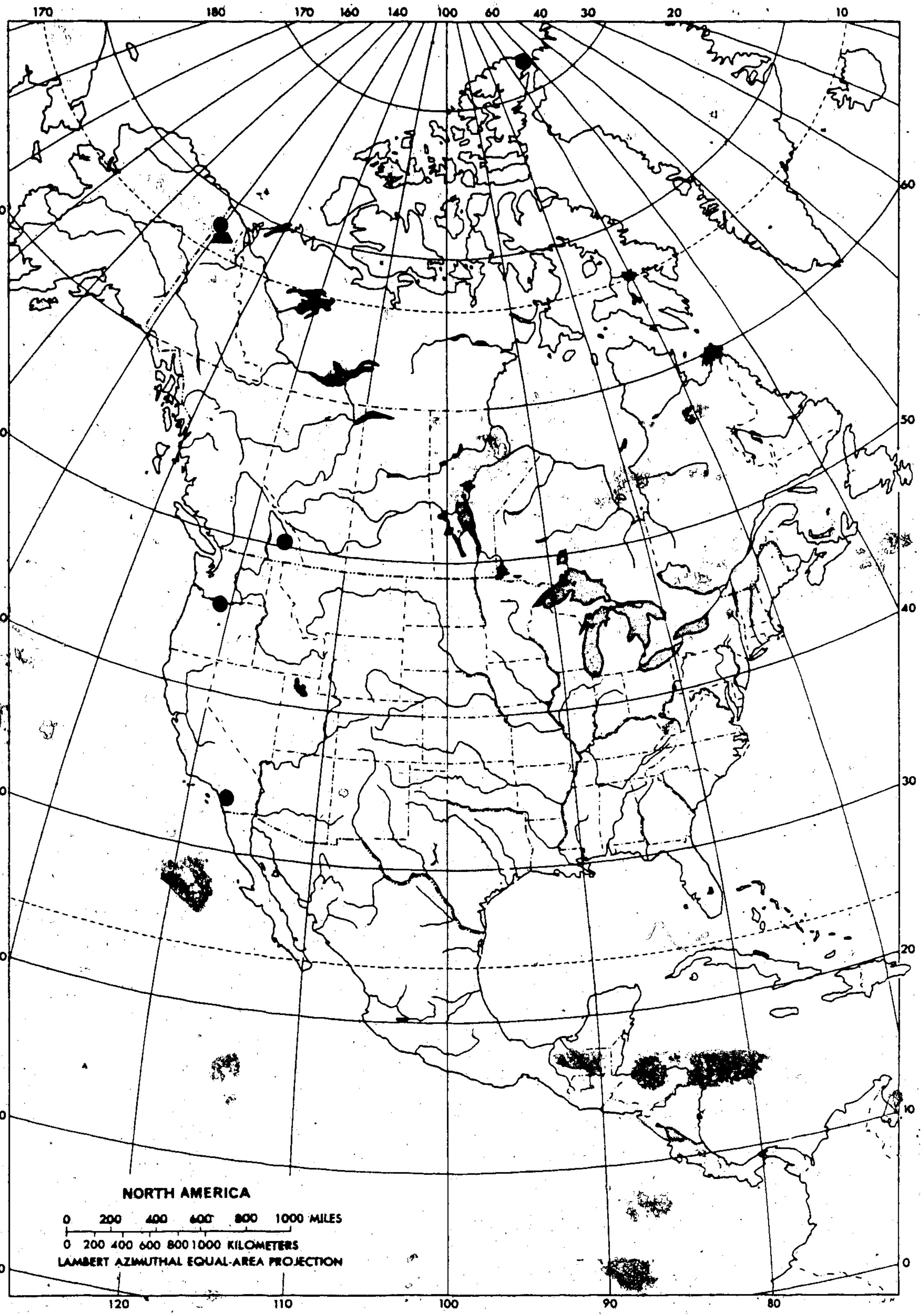
Discussion. – The subfossil specimen shows the above mentioned diagnostic character states clearly. In transverse section the leaf has strongly recurved margins with the cell walls smooth or low papillae on the abaxial surface, but with very coarse papillae on the upper adaxial surface. The costa possesses a crescent-shaped stereid band abaxially, but no adaxial band.

Tortella

Tortella exemplifies the characteristics that define the Trichostomoideae; narrowly lanceolate leaves and two stereid bands in the costa. The leaves are distinguished from other members of this subfamily by a sharp V-shaped demarcation between the smooth basal cells and the papillose upper cells, with the basal cells extending higher along the margins than along the costa.

It is the most commonly represented subfossil genus in the Pottiaceae. Miller (1980a) listed several records of *T. fragilis*, *T. inclinata* (Hedw. *f.*) Limpr. and *T. tortuosa*.

Plate 6. The present day North American distribution and subfossil records of *Pseudocrossidium revolutum* (Brid. *in* Schrad.) Zander. Solid dots: present day distribution based on Janssens & Zander 1980. Triangle: subfossil Wisconsinan record.


NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
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Tortella arctica (H. Arnell) Crundw. *et* Nyh.

Diagnostic features. – *Leaves* narrowly lanceolate, straight to slightly flexed, weakly keeled; *apex* narrowly acute, sometimes approaching a subula; *costa* black, stout and wide in relation to the width of the lamina, sharply defined, disappearing into the apex; *margins* plane, entire; *medial cells* rounded to subquadrate, thick-walled and densely papillose, papillae low; *basal cells* elongate to narrowly rectangular, with thicker longitudinal than transverse walls, porose, extending up to at least half the length of the lamina along the margins and often as a single row into the apical one third of the leaf, the demarcation between medial cells not as abrupt and not in a such sharply defined V-shape as in other *Tortella* species.

Habitat. – In extensive mats on wet soil, in swamps and meadows, in small drains from large snowpatches, associated with a community of vascular plants such as *Carex stans*, *Saxifraga cernua* and *Ranunculus sulphureus*. Other moss species are *Drepanocladus lycopodioides* var. *brevifolius*, *Bryum neodamense* and *Scorpidium turgescens* . It is found in large mats in the transition zone from the upland dry areas to hummocky sedge-moss meadows on Devon Island, together with *Schistidium holmeanum* and *Oncophorus wahlenbergii* and in the wetter sites with *Catoscopium nigritum*. These transition zones are often wet in the early season because of snowmelt seepage and become drier as the season progresses.

Recent Distribution. – Circumboreal. Arctic-alpine species. North America: Alaska, Yukon, Arctic Archipelago, northeastern Canada, Greenland, disjunct in Colorado. Siberia, northwestern Yunnan.

Subfossil Distribution in North America. – (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – *Trichostomum arcticum*, the most common species of Pottiaceae in my subfossil collections, is very similar in appearance to this species. However, *Trichostomum* is easily distinguished by its basal cells that do not extend up along the margins. Other *Tortella* species have a much more clearly defined V-shaped demarcation between basal and medial cells. The leaves of *T. tortuosa* which are undulate and strongly flexuose, are usually very poorly preserved. The costa is narrower and light-brown, not black. The medial cells have much higher papillae and are rounded instead of subquadrate. Some of the marginal basal cells form teeth at their upper ends. *Tortella fragilis* leaves have a fragile subula, but the basal cell character states are more reliable in distinguishing it from *T. arctica*. The other *Tortella* species are less narrowly lanceolate, often with an obtuse or apiculate apex.

Tortella fragilis (Drumm.) Limpr.

Diagnostic features. - *Leaves* narrowly lanceolate, stiff and straight or slightly erect-recurved; *apex* subulate; *costa* well defined, stout, extending beyond the apex in a long subula if preserved; *medial cells* subquadrate or rounded, thick-walled, densely papillose, papillae low; *basal cells* elongate to narrowly rectangular, thin-walled to moderately thick-walled, extending up, forming a clearly defined V-shaped demarcation.

Habitat. - On calcareous soil, rock or on alluvial silt, exposed or in crevices.

Recent Distribution. - Circumboreal. Bipolar. North America: from Alaska to Greenland and Newfoundland, south into the northern United States, in the east to New Jersey, the Great Lakes and Iowa, in the west to Nevada and Colorado. Iceland, Svalbard. Europe, northern Africa, Asia, Japan. Campbell Island.

Subfossil Distribution in North America. - Minnesota, Vermont and Wisconsin (Miller 1980a). New record: (1) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - For the differentiation from other *Tortella* species, see the discussion of

T. arctica.

Tortella tortuosa (Hedw.) Limpr.

Diagnostic features. – *Leaves* from a narrowly ovate-lanceolate base subulate, strongly flexuose and erect-recurved, undulate; *costa* narrow, clearly defined, not forming a subula in the apical part of the leaf; *margins* wavy, plane, entire except somtimes subentire in the basal part; *medial cells* rounded, thick-walled, densely papillose, papillae high; *basal cells* elongate, narrowly rectangular, very thin-walled, clearly demarcated from medial cells, extending along the margins to one third the total leaf length.

Habitat. – On calcareous rock and soil, commonly found on cliffs and boulders. In tundra often as solitary stems among *Distichium capillaceum*, *Isopterygium pulchellum*, *Mnium thomsonii* and *Myurella julacea*.

Recent Distribution. – Circumpolar. North America: Greenland to Alaska, south to Connecticut, Pennsylvania, the Great Lakes area, Iowa, Montana and Oregon, at higher elevations to Texas and Nevada. Iceland, Svalbard, Europe, northern Africa and central Asia. Japan.

Subfossil Distribution in North America. – Greenland, New York and Wisconsin (Miller 1980a). New records: (1) HH69-21, Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 103, as *Tortella cf. tortuosa*. (2) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (3) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980.

Discussion. – For differentiation from other taxa, see the discussion under *T. arctica*.

Tortula

Tortula belongs to the subfamily Pottioideae. The basal cells are often abruptly differentiated from the medial cells as in *Encalypta*, but do not have thickened transverse walls as in the latter. All the fossil material in my collections was annotated by R.H. Zander and B.D. Mishler.

In addition to records of *T. ruralis* (see below), Miller (1980a) listed a lateglacial record of *T. mucronifolia* Schwaegr. from Saskatchewan.

Tortula norvegica (Web.) Wahlenb. *ex* Lindb.

Diagnostic features. – *Leaves* ovate to ovate-lanceolate; *apex* obtuse to apiculate, mucronate or with a short, brown (in fossils), weakly denticulate hairpoint; *costa* stout, well defined, extending beyond the apex as mucro or short hairpoint; *margins* narrowly recurved along most of their length; *medial cells* subquadrate, densely papillose with 3 to 5 C-shaped papillae; *basal cells* forming ovoid patches in the lamina, hyaline and thin-walled and often degraded, narrower and brown along the costa and margins.

Habitat. – On calcareous rocks, boulders and loose soil, usually in late snow melt areas. In *Dryas* he[illegible]ciated with *Hypnum revolutum* and *Grimmia apocarpa* on rocks, with *Thuidium abietinum*, *Ditrichum flexicaule*, *Hylocomium splendens*, *Hypnum bambergeri* and *Plagiochila asplenoides* on soil.

Recent Distribution. – Circumboreal. Arctic-alpine species. North America: from Alaska to Greenland, Labrador and Newfoundland, southward in the western mountains through Alberta and British Columbia to California and Nevada, eastward in Canada to Manitoba, Quebec and Ontario. Iceland, mountains in Europe, northern U.S.S.R. and Himalayas.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23, as *Tortula cf. norvegica*. (2) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980.

Discussion. – *Tortula ruralis* leaves are very similar. They are distinguished by a hyaline awn (most often not preserved in fossil material), in contrast to the red awn in living plants of *T. norvegica*, by being more strongly spreading-recurved and having less clearly differentiated basal cells. *Tortula mucronifolia* has acute, ovate-lanceolate leaves with smooth or weakly papillose cells.

Tortula ruralis (Hedw.) Gaertn., Meyer *et* Scherb.

Diagnostic features. – *Leaves* squarrose-recurved, strongly keeled; *apex* obtuse; *costa* black, well-defined, extending beyond the apex as a hyaline hairpoint; *margins* strongly revolute along most of their length; *medial cells* subquadrate, densely papillose with C-shaped papillae; *basal cells* gradually differentiated from the medial cells, brown, shorter towards the margins and costa.

Habitat. – On soil and rock in dry, sunny, calcareous habitats. Often associated with *Hypnum revolutum*, *Grimmia apocarpa*, *Ditrichum flexicaule*, and *Encalypta rhaptocarpa*. Also found on trees, beach ridges and in drier meadows.

Recent Distribution. – Circumboreal. North America: Alaska to Greenland, south to the northern half of the United States in the east and to Mexico in the western mountains. Iceland, Svalbard, Europe, northern and central Asia, Japan. Africa.

Subfossil Distribution in North America. – New York, Northwest Territories, Vermont and Wisconsin (Miller 1980a). New records: (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (2) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (3) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308, as *Tortula cf. ruralis*. (4) HH68-9 (station 10), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 385, as *Tortula cf. ruralis*. (5) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – See the discussion of *T. norvegica* for differentiation with other *Tortula* species.

Tortula unidentified species

Subfossil distribution in North America. – (1) HH75–24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2[illegible]3–2); Bryological Report 271. (2) HH68–9 (station 7), Old Crow Basin, Yukon Ter[illegible] ± 60,000 B.P.; Bryological Report 308.

Trichostomum

Trichostomum is only represented by *Trichostomum arcticum* (=*T. cuspidatissimum* Card. *et* Ther.). *Trichostomum tenuirostre* (Hook. *et* Tayl.) Lindb., listed in Miller (1980a), is *Oxystegus tenuirostre* (Hook *et* Tayl.) Steere, differentiated from *T. articum* by more broadly acuminate leaves.

Trichostomum arcticum Kaal.

Diagnostic features. – *Leaves* narrowly lanceolate, keeled, flexuose and erect-recurved; *apex* narrowly acute; *costa* stout, well-defined, black, reaching into the apex, but not forming a subula; *margins* plane, or narrowly revolute on one side, papillose-crenulate; *medial cells* subquadrate, thick-walled, densely papillose with low, hollow papillae; *basal cells* linear, elongate to narrowly rectangular, wider towards the margins, gradually shorter and grading into the medial cells.

Habitat. – On calcareous soil in rather moist to wet tundra.

Recent Distribution. – Circumboreal. Arctic-alpine species. North America: Alaska to Greenland, south in the western mountains to northern British Columbia. Svalbard, arctic Scandinavia and northern and arctic U.S.S.R..

Subfossil Distribution in North America. – (1) Your Creek area, Alaska, 5615 ± 110 B.P.

(I-10,568), Bryological Report 183, Hamilton 1979a, Fig. 5. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (3) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271, as *Trichostomum cf. arcticum*. (4) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391.

Discussion. – *Trichostomum arcticum* is the most common fossil species of the Pottiaceae. It is similar to *Tortella arctica* but there is no distal extension of the basal cells along the margins. The leaves in *Tortella arctica* are stiffer and less flexuose, and the costa is wider in the upper half of the leaf, often forming a subula.

Grimmiaceae

The only genera with a subfossil record in the family are *Grimmia* and *Rhacomitrium*. *Grimmia* has only a Holocene record: *G. torquata* Hornsch. *ex* Grev. is known from Greenland and *G. alpicola* is discussed below. *Rhacomitrium*, a far smaller genus, is slightly better represented. All of the common taxa have a subfossil record (see below).

Grimmia

Grimmia alpicola Hedw.

Diagnostic features. – *Leaves* broadly ovate-lanceolate, slightly erect-recurved and keeled, lamina partly bistratose; *apex* narrowly obtuse or acute; *margins* entire, partly bistratose; *costa* stout, well-defined, reaching into the apex; *medial cells* rounded to irregularly angled, thick-walled, nodose, roughened by very small and low papillae; *basal cells* shortly rectangular, occasionally longer, densely chlorophyllose, evenly thick-walled or slightly nodose to smooth.

Habitat. – On calcareous or acidic rocks, near swift-running water, sometimes at the base of talus slopes and on moss tundra. Often in habitats that are occasionally or seasonally submerged. Submerged in fresh water pools on the Ellesmere Island Ice Shelf (Brassard 1971c).

Recent Distribution. – Circumpolar. North America: from Alaska to Ellesmere Island and Newfoundland, south to New Brunswick, Pennsylvania and Tennessee in the east and to British Columbia, Idaho, Montana, Wyoming, California and Texas in the western mountains. Mexico, Ecuador, Svalbard, western Europe, northern and arctic Asia, mountains of central Africa, Australia.

Subfossil Distribution in North America. – (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – *Grimmia* species can be differentiated from similar looking pottiaceous forms by the typical nodose or sinuose areolation of the medial and basal cells. *Grimmia alpicola* is defined by the combination of character states listed in the diagnosis.

Rhacomitrium

Rhacomitrium leaves are characterized by their narrowly rectangular, strongly sinuose or nodose basal and sometimes medial cells. The leaves are often narrower and longer than in *Grimmia* species and more strongly keeled and erect–recurved.

Rhacomitrium canescens (Hedw.) Brid.

Diagnostic features. – *Leaves* ovate–lanceolate, strongly keeled and erect–recurved; *apex* acute, with a short or long hairpoint that is strongly papillose but not denticulate; *costa* thin, black and well defined, reaching into the apex; *margins* revolute in the lower half of the leaf, often only along one side; *medial cells* shortly rectangular, strongly nodose, papillose; *basal cells* narrowly rectangular with thin transverse walls and very thick, strongly nodose longitudinal walls; *alar cells* in a narrowly triangular group along the margins, thick–walled, yellow and smooth.

Habitat. – A pioneer of sandy soil, gravel or wet rock, often in the flood zones along streams, shores and seepages. From lowlands to subalpine regions. On silt surfaces between *Salix* and *Populus* in the early stages of the succession on river deposits (Viereck 1970) together with *Polytrichum juniperinum* and *Ceratodon purpureus*. In association with *R. lanuginosum* in larger crevices of granitic rocks. Also on calcareous rocks.

Recent Distribution. – Circumboreal. More common in acidic and oceanic areas. North America: from Alaska to Greenland, south to New England and the Great Lakes region in the east and to Montana and California in the west. Svalbard, Europe, Asia, Japan.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New records: (1)

Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (2) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (3) Kitchener, Ontario; 6900 B.P.; Bryological Report 273.

Discussion. – Other North American *Rhacomitrium* taxa known as subfossils have smooth upper leaf cells.

Rhacomitrium lanuginosum (Hedw.) Brid.

Diagnostic features. – *Leaves* narrowly ovate-lanceolate to lanceolate, deeply keeled; *costa* thin, consisting of only two layers of cells in transverse section; *margins* narrowly or widely recurved, often on one side only, entire; *medial and basal cells* elongate to narrowly rectangular, with very thin transverse walls and thick nodose longitudinal walls, smooth;

Habitat. – On acidic rocks (rarely on calcareous) in fell fields and on talus, often forming conspicuous mats, in tundra.

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Greenland, Labrador and Newfoundland, south into New England in the east and in the western mountains in the west. Extensively scattered in the Southern Hemisphere and on tropical mountains.

Subfossil Distribution in North America. – Greenland and the Northwest Territories (Miller 1980a). New record: (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23.

Discussion. – Other *Rhacomitrium* species with smooth leaf cells have isodiametric or shortly rectangular medial and upper cells, short obtuse leaves or no hairpoint. The awns of the subfossil *R. lanuginosum* specimen were not preserved, but the upper margins showed clearly that it has been present before.

Rhacomitrium unidentified species

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 2[illegible] Hamilton 1980a, p. 23. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23, as *Rhacomitrium cf. heterostichum.* (3) Kitchener, Ontario; 6900 B.P.; Bryological Report 273, as *Rhacomitrium cf. sudeticum.*

Bryaceae

Bryum, *Leptobryum* and *Pohlia* have a North American subfossil record. In most cases, species of *Bryum* and *Pohlia* can be only identified with complete gametophytic and sporophytic material. Most identifications below are thus listed tentatively. For the distinction between the three genera, see the introduction to *Leptobryum*.

Bryum

The most common species encountered in subfossil assemblages is the variable *B. pseudotriquetrum*. The subfossil material complying with the diagnostic features listed below is recorded under this species as *B. cf. pseudotriquetrum*. Fragments clearly deviating from the diagnosis (usually by non-decurrent leaves with a plane border and thin-walled medial cells). are listed under *Bryum* unidentified species. Several other *Bryum* taxa are listed in Miller (1980a).

Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer *et* Scherb.

Diagnostic features. – *Leaves* ovate-lanceolate to ovate, distinctly decurrent; *apex* acute, cuspidate, acuminate or cucullate and obtuse (*f. neodamense*); *costa* stout, ending in the apex or shortly beyond, often red or reddish, even in the fossils; *margins* revolute along the whole length, often denticulate near the apex; *medial cells* rhomboid-hexagonal, thick to moderately thick-walled, sometimes porose, narrower to linear at the margins and very thick-walled, forming a border.

Habitat. – On moist calcareous soil and in rich fens. pH 7.2–7.7 (n=13), conductivity 251–856 microScm^{-1} (n=13), Ca concentration 24–124 ppm (n=8), Mg concentration 10–49 ppm (n=8), Na concentration 4.2–13.0 ppm (n=8) and K concentration 0.7–5.2 ppm (n=8).

Recent Distribution. – Circumboreal. North America: Alaska, Northwest Territories, Greenland, Labrador, south to Ontario. Svalbard, throughout Europe, arctic U.S.S.R., Altai Mountains.

Subfossil Distribution in North America. – Greenland, Idaho, Kansas, Michigan, Minnesota, New York, Northwest Territories, Saskatchewan, Vermont and Wisconsin (Miller 1980a). New records: (1) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159, as *Bryum cf. pseudotriquetrum.* (2) Sunwapta Pass; Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62, as *Bryum cf. pseudotriquetrum.* (3) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21, as *Bryum cf. pseudotriquetrum.* (4) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174, as *Bryum cf. pseudotriquetrum.* (5) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178, as *Bryum cf. pseudotriquetrum.* (6) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5, as *Bryum cf. pseudotriquetrum.* (7) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23, as *Bryum cf. pseudotriquetrum.* (8) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205, as *Bryum cf. pseudotriquetrum.* (9) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980, as *Bryum cf. pseudotriquetrum.* (10) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *Bryum cf. pseudotriquetrum.* (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302, as *Bryum cf. pseudotriquetrum.* (12) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308, as *Bryum cf. pseudotriquetrum.* (13) Kitchener, Ontario; below 8800 B.P.; Bryological Report 324, as *Bryum cf. pseudotriquetrum.* (14) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a, as *Bryum cf. pseudotriquetrum.* (15) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391, as *Bryum cf. pseudotriquetrum.* (16) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401, as *Bryum cf. pseudotriquetrum.* (17) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435, as *Bryum cf. pseudotriquetrum.*

Bryum unidentified species

Subfossil Distribution in North America. – Alaska, Alberta, British Columbia, Greenland, Minnesota, North Carolina, Northwest Territories, Ontario, Pennsylvania and Wisconsin (Miller 1980a). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (3) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 1000 B.P. (GSC-2756); Bryological Report 118. (4) Koyukuk River, 6 km downstream from Henshaw Creek, Alaska; 52,800 ± 1300 B.P. (QL-1283); Bryological Report 168. (5) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (6) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (7) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (8) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I-10,509); Bryological Report 181, Hamilton 1979b, p. 41. (9) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (10) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (11) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (12) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (13) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (14) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (15) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (16) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (17) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (18) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (19) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (20) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan;

Bryological Report 435.

Leptobryum

Leptobryum and *Pohlia* leaves are linear or narrowly lanceolate and not distinctly bordered. The genus *Bryum* is differentiated by broader leaves, usually with a well-developed border, and shorter leaf cells. *Leptobryum* has linear leaves with a broad costa, occupying half the width of the leaf at the base. There is only one North American species.

Leptobryum pyriforme (Hedw.) Wils.

Diagnostic features. – *Leaves* linear-lanceolate, straight or flexuose; *apex* acuminate; *costa* wide, diffuse, occupying half or more of the [illegible] and filling the upper half of the leaf; *margins* plane, entire; *medial cells* elongate, thin-walled, lax.

Habitat. – In slightly damp habitats, on bare disturbed soil, sandy peat banks, decaying wood, occasionally on rock in wetter places and on burnt patches together with *Funaria hygrometrica*, *Bryum* species, *Ceratodon purpureus*, *Dicranella* species and *Pohlia nutans*.

Recent Distribution. – Cosmopolitan. In North America: Greenland to Alaska, south to California, Arizona and New Mexico in the west, throughout eastern North America.

Subfossil Distribution in North America. – Saskatchewan (Miller 1980a). New records: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (2) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370.

Pohlia

For the distinction with *Bryum* and *Leptobryum*, see the introduction under the latter. All my *Pohlia* specimens were annotated by J. Shaw. The fragments which were too poorly preserved and did not conform to the diagnoses given below are classified under *Pohlia* unidentified species.

Pohlia nutans (Hedw.) Lindb.

Diagnostic features. – *Leaves* oblong-lanceolate to lanceolate; *costa* extending into the apex; *margins* plane, denticulate in the upper half; *medial cells* elongate, narrowly rectangular, thick-walled, slightly narrower towards the margins, but not forming a distinct border.

Habitat. – On moist soil, humus or rotting wood in mires, in heaths and forest or associated with *Sphagnum*, rarely in rock crevices. Usually an upland species.

Recent Distribution. – Widespread in temperate and polar areas. North America: from Alaska to Greenland and south throughout most of the United States. Europe, Asia, Japan, and temperate regions of the southern hemisphere.

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a). New records: (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21, as *Pohlia cf. nutans*. (2) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat; Bryological Report 289.

Discussion. – For differentiation from *P. wahlenbergii*, see the discussion under the latter. *Pohlia cruda* is very similar to *P. nutans*. It can be recognized from the latter by the shiny tufts, a characteristic that is of little value in determing subfossil material.

Pohlia wahlenbergii (Web *et* Mohr) Andr

Discussion. — About half of the *Pohlia* material can be tentatively assigned to *P. wahlenbergii*. The medial cells are lax and thinner walled than in *P. nutans*. Otherwise, leaf fragments of the two species are very similar.

Subfossil Distribution in North America. - Greenland and possibly Indiana (Miller 1980a). New records: (1) HH75-24, Bluefish Basin, Yukon Territory, probably pre-Wisconsinan; Bryological Report 173, as *Pohlia cf. wahlenbergii*. (2) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5, as *Pohlia cf. wahlenbergii*. (3) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23, as *Pohlia cf. wahlenbergii*. (4) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *Pohlia cf. wahlenbergii*.

Pohlia unidentified species

Subfossil Distribution in North America. - Alaska and Greenland (Miller 1980a). New records: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174, as *cf. Pohlia* species. (2) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (3) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (4) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (5) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401. (6) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (7) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Mniaceae

Most North American genera in the Mniaceae are represented in the fossil record *Leucolepis menziesii* (Hook.) Steere *ex* L. Koch is known from Holocene deposits in British Columbia (Miller 1980a). *Rhizomnium punctatum* (Hedw.) Kop. and *R. pseudopunctatum* (Bruch *et* Schimp.) Kop. are also listed by Miller (1980a). The genera *Mnium*, *Cyrtomnium*, *Plagiomnium*, *Pseudobryum* and *Cinclidium* are all present in my collections and discussed below.

The main characters differentiating these genera are leaf border development and structure, leaf shape and rhizoid structure (Koponen 1975b). *Leucolepis*, *Pseudobryum* and *Mnium stellare* Hedw. lack a differentiated border. *Leucolepis* has narrowly elliptic or triangular leaves. The two other taxa have wider, elliptical leaves and are differentiated by cell shape. *Mnium stellare* has isodiametric cells, while *Pseudobryum* has elongated cells with sharp ends.

Mnium and *Plagiomnium* have a differentiated border with teeth (not always present on single leaf specimens of *Plagiomnium*). The border is bi- to multistratose in *Mnium* and has teeth in pairs. *Plagiomnium* has a unistratose border and single teeth.

Cinclidium, *Rhizomnium* and *Cyrtomnium* have an entire, differentiated border. Identification of fragmentary leaf material of these genera can cause trouble. *Cyrtomnium* has cordate, acute to acuminate leaves with uniform areolation. In *Cinclidium* the apiculate leaves are at the widest near the middle and the cells are larger toward the costa. *Rhizomnium* commonly has a strongly developed, multistratose border and a reddish color.

Cinclidium

All my *Cinclidium* material was annotated by T. Koponen and G. S. Mogensen. Three of the four North American species are represented in my collections. Several poorly preserved specimens are listed under *Cinclidium* unidentified species and some of them approach *C. subrotundum* Lindb. The other three species are listed below. The treatment is based on Koponen (1975b) and Mogensen (1973) in addition to the works listed before in the introduction to this chapter.

Cinclidium arcticum (B S G) Schimp

Diagnostic features *Leaves* elliptic longer than wide narrowly and longly decurrent *apex* acute to shortly acuminate *margins* unistratose *medial cells* not in rows isodiametric to slightly elongate

Habitat In all types of arctic meadows but particularly the wetter areas and seepage zones originating from late snowmelt in rich fens

Recent Distribution Circumpolar Arctic alpine species North America from arctic Alaska (also in the Yukon) to Greenland south to Manitoba (Hudson Bay) Svalbard Fennoscandia northern U S S R World distribution map published in Steere (1978a)

Subfossil Distribution in North America Northwest Territories (Bathurst Island) (Miller 1980a) New records (1) HH75-1 Rock River Yukon Territory >43 000 B P (GSC-2585), Bryological Report 33 (2) Mackinson Inlet Ellesmere Island Northwest Territories, >52,000 B P (GSC-2677) Bryological Report 164, Blake & Matthews 1979 (3) Clements Markham Inlet, Ellesmere Island Northwest Territories 6400 ± 60 B P (SI-4314), Bryological Report 401

Discussion - *Cinclidium latifolium* and *C. subrotundum* are distinguished from *C. arcticum* by their widely elliptic leaves, often broader than long *Cinclidium stygium* has a more apiculate leaf and elongate medial cells in regular, diagonal rows

Cinclidium latifolium Lindb

Diagnostic features - *Leaves* broadly elliptic or circular, *apex* shortly apiculate; *margins* unistratose, broadly reflexed; *medial cells* shortly elongate, irregularly angled

Habitat - In open tundra at the edge of pools, in rich fens and seepage areas, in contact with calcareous ground water.

Recent Distribution Circumpolar Arctic species North America from arctic Alaska to Greenland south to the western coast of the Hudson Bay Svalbard Siberia World distribution map published in Steere (1978a)

Subfossil Distribution in North America (1) HH72 54 (station 3) Hungry Creek Yukon Territory Wisconsinan Bryological Report 435

Discussion *Cinclidium subrotundum* has the same leaf shape as *C. latifolium* but is easily distinguished by its multistratose plane or slightly recurved border obtuse apex and large elongate medial cells For the differentiation with the other two *Cinclidium* taxa see the discussion under *C. arcticum*

Cinclidium stygium Sw

Diagnostic features *leaves* elliptic longer than wide not or shortly decurrent *apex* longly acuminate or apiculate *margins* unistratose *medial cells* in diagonal rows slightly elongate

Habitat - In rich fens frequently associated with *Campylium stellatum* *Drepanocladus revolvens*, *Paludella squarrosa* and *Sphagnum warnstorfii* Near springs and among sedges in pools Also in moist rock-crevices More tolerant to different substrates than other species of *Cinclidium*

Recent Distribution - Circumboreal Not in high arctic areas North America Greenland to Alaska and south to Quebec, New York, and Michigan in the east and Saskatchewan, Alberta and British Columbia in the west, common in the Rocky Mountains Northern, western, eastern and central Europe, Altai, Kamchatka

Subfossil Distribution in North America - (1) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 175, as *Cinclidium cf. stygium* (2) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological

Report 176, as *Cinclidium cf. stygium*. (3) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (4) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (5) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - See the discussion under *C. arcticum* for the differentiation with other species of the genus.

Cinclidium unidentified species

Subfossil Distribution in North America. - (1) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980. (2) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980.

Cyrtomnium

Cyrtomnium specimens are poorly preserved. However, they can be recognized relatively easily by their uniform areolation (cells at the costa have the same average size as the ones towards the margins) and by leaves that have their maximal width below the midpoint. *Rhizomnium, Cinclidium* and non-denticulate *Plagiomnium* taxa have elliptic leaves with cells enlarged towards the costa.

Two species are represented in my collections. *Cyrtomnium hymenophyllum* has longly and narrowly decurrent leaves with a border composed of one or two rows of parallelogram-shaped cells. *Cyrtomnium hymenophylloides* leaves are not decurrent and have a border of two or three rows of elongate to linear cells. In my material the medial leaf cells of the latter are larger than in *C. hymenophyllum*.

Cyrtomnium hymenophylloides (Hüb.) Kop.

Diagnostic features. – *Leaves* cordate-ovate, not decurrent; *apex* bluntly acute; *margins* bordered by two or three rows of elongate to linear cells; *medial cells* varying from isodiametric to shortly elongate and irregularly angled, average diameter 38.75 micrometer.

Habitat. – On moist soil in crevices of calcareous rocks and in seeps. Associated with *Blephrostoma trichophyllum, Distichium capillaceum, Isopterygium pulchellum* and *Orthothecium intricatum.*

Recent Distribution. – Circumpolar. Arctio-alpine species. North America: from Alaska to Greenland, Newfoundland, Quebec and Nova Scotia, south to New England in the east and into Manitoba, Alberta and British Columbia in the west.

Subfossil Distribution in North America. – (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Cyrtomnium hymenophyllum (B.S.G.) Kop.

Diagnostic features. – *Leaves* cordate-ovate, narrowly and longly decurrent; *apex* obtuse; *margins* bordered by one or two rows of parallelogram-shaped cells; *medial cells* very irregular, varying from quadrate to variously angled isodiametric to rhomboid or hexagonal, average maximal diameter 23.50 micrometers.

Habitat. – On moist calcareous soil and in seepy habitats in tundra. Associated with *Campylium stellatum, Ditrichum flexicaule, Hypnum bambergeri, Orthothecium chryseum, Timmia norvegica* and *Tomenthypnum nitens.*

Recent Distribution. – Circumpolar. Arctic species. North America: from Alaska to Greenland, south to the Yukon and Northwest Territories. Mountains in Fennoscandia, Siberia.

Subfossil Distribution in North America. – (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I–11,010); Bryological Report 171, Hamilton 1980a, p. 21, as *Cyrtomnium cf. hymenophyllum*. (2) HH68–9 (station 1–2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 175, as *Cyrtomnium cf. hymenophyllum*.

Mnium

Two *Mnium* species are represented in the subfossil record of North America. *Mnium marginatum* and *M. thomsonii* are discussed below.

Most *Mnium* species have a multistratose border with double teeth. In some subfossil material this characteristic border is often poorly preserved and the teeth are not preserved at all. Therefore, some of the identifications below are listed tentatively.

Mnium marginatum (With.) Brid *ex* P. Beauv.

Diagnostic features. – *Leaves* narrowly elliptic; *apex* acute–acuminate to apiculate; *margins* bordered by a bistratose border below, unistratose above, with sharp, double teeth from halfway up to the apex in the upper leaves, lower leaves often entire; *medial cells* isodiametric to slightly elongate, moderately thick–walled with clear corner thickenings, larger towards the costa, average size 28.10 micrometers at the midpoint between costa and border.

Habitat. – On humus, rotten wood, damp soil or rock exposures in forests. Most commonly along creek banks.

Recent Distribution. – Cicumboreal. North America: from Alaska to (most likely not in the Yukon) to Newfoundla, south in all provinces of Canada except Saskatchewan, and Prince Edward Island, in the west to Colorado and California, otherwise only in the northernmost United States. Svalbard, Europe and northern Asia.

Subfossil Distribution in North America. - Wisconsin (Miller 1980a). New record: (1) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - *Mnium thomsonii*, the only other *Mnium* species in my subfossil collections, is very similar to *M. marginatum*. The former is distinguished by its uniform and small cell size that is only one half or one third of the cell size of *M. marginatum*. *Mnium marginatum* also has larger cells than *M. lycopodioides*.

Mnium thomsonii Schimp.

Diagnostic features. - *Leaves* narrowly elliptic; *apex* acute-acumniate; *margins* bordered by a bistratose border with blunt, double teeth or entire in the upper one third; *medial cells* uniform in size, average diameter 13.10 micrometers (in the subfossil material; in the reference collection the cell size is somewhat larger), isodiametric, varying from rounded to variously angled, moderately thick to thick-walled with clear corner thickenings.

Habitat. - On calcareous soil and rock in moist habitats.

Recent Distribution. - Circumboreal. North America: from Alaska to Greenland and Newfoundland, south in the Coast Range and the Rocky Mountains. In eastern North America to Gaspé and Lake Superior area. Europe and Siberia, Himalayas, China and Japan.

Subfossil Distribution in North America. - Vermont (Miller 1980a). New records: (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. - For the distinction with *M. marginatum*, see the discussion under the latter.

Mnium unidentified species

Subfossil Distribution in North America. – (1) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I–10,525); Bryological Report 178, as *Mnium* species *s.l.*. (2). HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302, as *Mnium* species *s.l.*. (3) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434, as *Mnium* species *s.l.*.

Plagiomnium

Only *P. ellipticum* is represented in my collections. The specimens were annotated by T. Koponen. Miller (1980a) listed *P. insigne* (British Columbia) and *P. medium* (Alaska) as Holocene subfossil specimens. He also recorded several specimens from Kansas, Minnesota and the Northwest Territories as *Mnium affine*. However, this taxon is now considered as either *P. ciliare* or *P. ellipticum*. Being the only species of the genus growing in mire habitats in the north, *P. ellipticum* is the most likely species in these records.

Plagiomnium species are distinguished from other taxa of the Mniaceae by their differentiated border with single marginal teeth. The fragments are often distinctly complanate.

Plagiomnium ellipticum (Brid.) Kop.

Diagnostic features. – *Leaves* not decurrent, elliptic; *apex* acute (sometimes shortly apiculate); *margins* bordered with an unistratose border with small teeth consisting of one cell, or entire in poorly developed material; *medial cells* lax, thin walled, the ones at the costa two to three times the size of the marginal laminal cells.

Habitat. – In a variety of such wet habitats as muskegs, fens, alluvial meadows, river and lake shores, seepages, preferring a peat substrate. Associated with *Cirriphyllum cirrosum*, *Meesia triquetra*, *Brachythecium turgidum*, *Aulacomnium palustre* and *Tomenthypnum nitens*. pH 7.3 and 7.4 (n=2), conductivity 32.2 and 698 microScm^{-1} (n=2), Ca concentration 32.8–82.3 ppm (n=3), Mg concentration 6.3–12.4 ppm (n=3), Na concentration 5.2 and 10.1 ppm (n=2) and K concentration 1.3–16.3 ppm (n=3).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Newfoundland, throughout Canada and south to the northern United States, farther south in the western mountains. Svalbard, Europe, northern Asia.

Subfossil Distribution in North America. – Kansas, Minnesota and Northwest Territories (Miller 1980a: as *Mnium affine* Bland *ex* Funck). New records: (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I–10,925); Bryological Report 201, Hamilton 1980a, p. 23. (2) HH68–9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 261, as *Plagiomnium cf. ellipticum*. (3) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC–2792); Bryological Report 269. (4) HH72–54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Leaves of most other *Plagiomnium* species differ from *P. ellipticum* leaves by being denticulate to the base or by being decurrent. Forms of *P. rostratum* without marginal teeth are essentially identical with similar forms of *P. ellipticum*. However, the two species are very different in habitat requirements. *Plagiomnium rostratum* grows on dry calcareous rocks.

Pseudobryum

One species of this genus, *P. cinclidioides*, is known in North America. Miller (1980a) listed one record of a Holocene deposit in Greenland. The other record is dicussed below. For the distinction between *Pseudobryum* and the other genera of the Mniaceae, see the introduction to the family.

Pseudobryum cinclidioides (Hüb.) Kop.

Diagnostic features. – *Leaves* elliptic and non-decurrent; *apex* obtuse; *margins* not or weakly bordered; *medial cells* in diagonal rows, hexagonal or rhomboidal.

Habitat. – In wet marshy and boggy tundra. Often in swampy depressions or dried-up pools in mixed woods and hardwood swamps. Associated with *Aulacomnium palustre, Calliergon richardsonii, C. sarmentosum, Mnium punctatum, M. rugicum, Philonotis fontana* var. *pumila* and *Sphagnum teres.*

Recent Distribution. – Circumboreal. North America: from Alaska to Newfoundland and Greenland, south through most of Canada and the northern United States, reaching Virginia at higher elevations. Europe, northern Asiatic U.S.S.R., central Asia and Japan.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New records: (1) Milford Gypsum Quarry, Milford, Nova Scotia; >50,000 B.P. (GSC-1642); Bryological Report 413.

Aulacomniaceae

Aulacomnium

All North American species of the genus have a fossil record except *Aulacomnium androgynum* (Dickson 1973, Jovet-Ast 1967). *Aulacomnium heterostichum* is represented in the Eocene by a closely related species, *A. heterostichoides* (Janssens *et al.* 1979). *Aulacomnium acuminatum*, *A. palustre* and *A. turgidum* all have a Quaternary subfossil record and are discussed below.

Aulacomnium subfossil specimens are typically black or dark-brown, as discussed under *Dicranum*. The genus is easily recognized by unipapillose cells with nodose walls.

Aulacomnium acuminatum (Lindb. *et* H. Arnell) Kindb.

Diagnostic features. – *Leaves* lanceolate, imbricate; *apex* sharply acute to narrowly to broadly acuminate; *margins* narrowly revolute along most of their length except at the extreme apex, entire; *medial cells* isodiametric to slightly elongate, strongly nodose, corner thickenings appearing (in LM) perforated transversely through the leaf, a single, simple, low papilla (not higher than wide) at the central part of the cell; *basal cells* less nodose and smooth, irregular, varying from shortly rectangular to rounded or sometimes subquadrate.

Habitat. – On moist or dry soil, usually in calcareous, open tundra. On hummocks in sedge-moss meadows, often associated with *Aulacomnium turgidum* and *Tomenthypnum nitens*. At the bases of rock outcrops, particularly in moist zones resulting from snowmelt. pH 5.20–7.85 (n=12), conductivity 32–486 microScm^{-1} (n=12), Ca concentration 4.5–52.5 ppm (n=10), Mg concentration 0.5–16.6 ppm (n=10), Na concentration 4.2–13.2 ppm (n=10) and K concentration 0.05–13.60 ppm (n=10).

Recent Distribution. – Circumpolar. Arctic species. North America (Vitt & Horton 1979):

from Alaska to Greenland, south to northern British Columbia in the west and disjunct to west-central Alberta and to southern Ontario in the east. Siberia.

Subfossil Distribution in North America. – New York (Miller 1980a) and Quebec (LaSalle *et al.* 1978). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33, as *Aulacomnium cf. acuminatum*. (2) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159; as *Aulacomnium cf. acuminatum*. (3) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I-10,509); Bryological Report 181, Hamilton 1979b, p. 41, as *Aulacomnium cf. acuminatum*. (4) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5, as *Aulacomnium cf. acuminatum*. (5) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat; Bryological Report 289, as *Aulacomnium cf. acuminatum*.

Discussion. – Living populations of *A. acuminatum* are easily distinguished from *A. palustre* populations by their bright, yellow-green color, straight, erect or imbricate leaves and the absence of propagulae. However, with fragmentary subfossil material, none of these features is helpful in identification. Therefore, I had to rely on less constant, more subtle microscopic character states to differentiate the two species. The leaves of *A. palustre* are often more ovate-lanceolate, they are flexuose and not stiff, erect-spreading and only imbricate in the variety *imbricatum* that is characterized and distinguished from *A. acuminatum* by its yearly increments, tomentose stems and shorter leaves. The apex of *A. palustre* is frequently denticulate or denticulate-papillose, and the margins are usually not revolute in the upper one third. The medial cells in *A. palustre* are less thickly walled and nodose, and do not form clear transverse perforations in the corner thickenings. Often the papillae are higher and narrower in *A. palustre* than in *A. acuminatum*. All these above listed characters are very variable in both species and not any of the specimens could be identified unambiguously to *A. acuminatum*.

Aulacomnium turgidum is easily distinguished from *A. palustre* and *A. acuminatum* by ovate, obtuse leaves. The areolation approaches much more the cell structure of *A. acuminatum* than that of *A. palustre*.

Aulacomnium palustre (Hedw.) Schwaegr. (including the variety *imbricatum* B.S.G.)

Diagnostic features. – *Fragments* often abundantly tomentose; *leaves* lanceolate to ovate-lanceolate, flexuose, erect-spreading to imbricate; *apex* sharply acute in the upper leaves, often bluntly acute to narrowly obtuse in the lower leaves; *margins* narrowly revolute for at least the lower 3/4 of their length, sometimes denticulate or denticulate-papillose in the upper one third; *medial cells* isodiametric, varying from quadrate to variously angled, not or slightly nodose, moderately thick-walled, corner thickenings when present not clearly transversely perforated through the leaf, a single, simple papilla at the central part of the cell, these papillae are often higher than wide; *basal cells* smooth, shortly rectangular.

Habitat. – On moist or wet soils, in bogs or fens, on wet rocks. On Devon Island often associated with *Polytrichum juniperinum* and *P. alpinum*. Only exceptionally really submerged.

Recent Distribution. – Circumboreal. Bipolar. Common in the boreal region, rare elsewhere. North America: Alaska to Greenland and south to Florida in the east and California in the west. Brasil, Bolivia, Patagonia. Svalbard. Northern, western, eastern and central Europe, Spain, Algeria, Asia. Australia, Tasmania, New Zealand.

Subfossil Distribution in North America. – Greenland, Iowa, Minnesota, New York, Northwest Territories, Vermont and Wisconsin (Miller 1980a). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (3) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 49. (4) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ±

60,000 B.P., Bryological Report 68. (5) HH69-21 (station 1), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 101. (6) HH69-21, Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 103. (7) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 0 to 10 cm below surface; Bryological Report 143. (8) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (9) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (10) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I-10,509); Bryological Report 181, Hamilton 1979b, p. 41. (11) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig 5. (12) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 261. (13) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (14) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (15) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (16) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980. (17) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *Aulacomnium cf. palustre.* (18) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; below >39,000 B.P. (I-4099); Bryological Report 335, Matthews 1974a. (19) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (20) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; >39,000 B.P. (I-4099); Bryological Report 342, Matthews 1974a. (21) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (22) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425.

Discussion. – *Aulacomnium palustre* is one of the commonest subfossils. It is easily identified by the diagnostic features listed above. See the discussion of *A. acuminatum* for the distinction of the two species when only fragmentary material is available.

Aulacomnium turgidum (Wahlenb.) Schwaegr.

Diagnostic features. – *Leaves* ovate to ovate- or oblong-lanceolate, imbricate to spreading, *apex* obtuse, *margins* narrowly revolute in the basal one third or plane, entire; *medial cells* isodiametric, weakly to strongly nodose, corner thickenings appearing (in LM) perforated transversely through the leaf, a single, simple and very low papilla on the central part of the cell; *basal cells* smooth, irregular, varying from shortly rectangular to rhomboid and quadrate.

Habitat. – In arctic-alpine regions on calcareous soil, often found intermixed with *A. acuminatum* on larger, drier hummocks in sedge meadows (Devon Island), or with *Drepanocladus uncinatus* and *Hylocomium splendens* in crevices and at bases of rock outcrops . The ecology is rather complex. It occurs mainly and often abundantly in *Dryas* heath, associated with *Dicranum muehlenbeckii*, *Hylocomium splendens*, *Ptilidium ciliare* and *Tomenthypnum nitens*, but is also found in many other habitats as irrigated or flooded rocks, calcareous as well as siliceous. It has been found in subalpine mixed mires. pH 5.2 and 6.3 (n=2), conductivity 18.6 and 40.7 microScm^{-1} (n=2), Ca concentration 3.8 and 7.9 ppm (n=2), Mg concentration 0.9 and 1.0 ppm (n=2) and K concentration 0.05 ppm (n=1).

Recent Distribution. – Circumboreal and circumpolar. Arctic-alpine species. North America (Miller 1980b): from Alaska to Greenland and Labrador in the north, south to northern British Columbia, the Jasper area in Alberta in the west and Lake Superior, northern New York and New Hampshire in the east. Northern and arctic zone of Europe, mountains of western and central Europe, of central Africa, northern and arctic zone of Asia, central Asia, Siberia, Korea, Kamchatka, Japan.

Subfossil Distribution in North America. – Greenland, New York, Northwest Territories and Wisconsin (Miller 1980a, b). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (3) HH68-9, Old

Crow Basin, Yukon Territory, Holocene peat, 200 to 150 cm below surface, Bryological Report 159 (4) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska, 10,580 ± 150 BP (I-11,010), Bryological Report 171, Hamilton 1980a, p. 21 (5) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 BP (I-10,925), Bryological Report 201, Hamilton 1980a, p. 23 (6) HH68-9 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 262 (7) HH68-9 (station 11), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 265 (8) St Eugene, Quebec, 11,050 ± 130 BP (QU-448), Bryological Report 279, Mott *et al.* 1980 (9) St Hilaire, Quebec, 10,100 ± 150 BP (GSC-2200), Bryological Report 280, Mott *et al.* 1980, as *Aulacomnium cf. turgidum* (10) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?, Bryological Report 299 (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory, Early Wisconsinan?; Bryological Report 302, as *Aulacomnium cf. turgidum* (12) HH68-9 (station 9), Old Crow Basin, Yukon Territory, Early Wisconsinan?; Bryological Report 370. (13) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – See the discussion of *A. acuminatum* for the distinction between *A. turgidum*, *A. palustre* and *A. acuminatum*.

Meesiaceae

This primarily circumboreal family has three genera. Two, *Meesia* and *Paludella* have a good subfossil record. Of the third genus, the monotypic *Amblyodon*, subfossil specimens have been only found in the British Flandrian deposits (Dickson 1973). *Amblyodon dealbatus* is distinguished from other Meesiaceae by having lax, thin walled medial cells, varying from rhomboidal to hexagonal-elongate and by its oblong-lanceolate leaves with a short acute apex. The areolation is strongly reminiscent of the cell structure of the Funariaceae but the narrower leaves easily distinguish *Amblyodon*.

Meesia and *Paludella* are differentiated by their three dimentional leaf shape and by their cell surface ornamentation. *Paludella squarrosa* has strongly squarrose-recurved, obovate leaves. The upper cells are isodiametric and unipapillose-bulging on both surfaces. *Meesia* species have erect, wide spreading or squarrose leaves and smooth, mostly rectangular upper cells.

Meesia

All three of the *Meesia* species listed in Ireland *e (1980) are represented in my subfossil collections. The characters differentiating these species are leaf shape, margin and costa structure.* *Meesia triquetra* has decurrent leaves that are sharply denticulate in the upper portion. The leaves have a poorly developed stereid band in the costa as is the case in *M. longiseta*, but the latter is distinguished from *M. triquetra* by its entire, partially recurved margins and less squarrose leaves. *Meesia uliginosa* has a well-developed abaxial and poorly developed adaxial stereid band in the costa and has narrower, ligulate leaves, a very wide costa, and narrowly recurved or revolute margins.

All subfossil material of *Meesia* is moderately blackened by fossilization with preservation is often perfect.

Meesia longiseta Hedw.

Diagnostic features. – *Leaves* ovate-lanceolate, erect-spreading to slightly recurved, not decurrent or very narrowly decurrent; *apex* sharply acute to very narrowly obtuse; *costa* homogeneous or the central cells smaller than the abaxial and adaxial layers; *margins* plane or narrowly recurved on one side only, entire or in a few leaves with weak denticulation at the apex; *medial and basal cells* rectangular, varying from 2:1 to 5:1, a few scattered cells with sharp ends, smooth, walls moderately thick, black.

Habitat. – In rich fens, on damp shores, on moist and calcareous soil in *Picea mariana* woodland.

Recent Distribution. – Circumboreal. North America: in the glaciated areas of eastern US and adjacent Canada: from Alaska to Greenland in the north, south to Idaho in the west and Illinois and Ohio in the east. Northern, eastern and central Europe, Siberia, Kamchatka.

Subfossil Distribution in North America. – Alberta (Miller 1980a). New records: (1) Koyukuk River, 6 km downstream from Henshaw Creek, Alaska; 52,800 ± 1300 B.P. (QL-1283); Bryological Report 168. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (3) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Meesia triquetra (Richt.) Angstr.

Diagnostic features. – *Leaves* ovate-lanceolate, strongly squarrose, broadly decurrent; *apex* acute; *costa* with stereid cells in the center; *margins* plane, sharply denticulate in the upper half and in luxurious forms along the entire length, with strongly recurved teeth along the lower margins; *medial cells* varying from large, shortly rectangular cells (3:1 to 2:1) in the middle part of the leaf to very small quadrate to irregularly angled cells in the upper part, or rectangular throughout; *basal cells* narrowly rectangular, in the decurrent leaf base more rounded.

Habitat. – In rich fens, sometimes on damp shores. Common in wet sedge-moss meadows and streamsides, with *Calliergon giganteum* and *Cinclidium arcticum*. pH 7.0-7.5 (n=16), conductivity 338-505 microScm^{-1} (n=16), Ca concentration 24.1- 77.5

ppm (n=8), Mg concentration 11-22 ppm (n=8), Na concentration 4.4-25.0 ppm (n=2) and K concentration 8.7-15.3 ppm (n=8).

Recent Distribution. - Circumboreal. North America: Alaska, Yukon and Northwest Territories in the north, south to California, Nevada, Michigan, and New York. Northern, eastern and central Europe, Spain, northern Asia, China.

Subfossil Distribution in North America. - Greenland, Minnesota, New York, Northwest Territories and Ontario (Miller 1980a). New records: (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (3) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 118. (4) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 163, Blake & Matthews 1979. (5) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 165, Blake & Matthews 1979. (6) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (7) Section Creek, 9 km upstream from Sagavanirktok River, Alaska; 12,690 ± 180 B.P. (I-10,567); Bryological Report 182, Hamilton 1979b, p. 29. (8) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (9) Shoran Lake, Banks Island, Northwest Territories; 10,200 ± 130 B.P. (GSC-2673); Bryological Report 283. (10) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302, as *Meesia cf. triquetra*. (12) Kitchener, Ontario; below 8800 B.P.; Bryological Report 322. (13) Kitchener, Ontario; below 8800 B.P.; Bryological Report 323. (14) Kitchener, Ontario; below 8800 B.P.; Bryological Report 324. (15) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (16) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434. (17) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Meesia uliginosa Hedw.

Diagnostic features. – *Leaves* ligulate to lanceolate–ligulate, not decurrent; *apex* obtuse; *costa* very wide, occupying more than half of the leaf base, with a clearly defined stereid band on the abaxial side and less well developed band on the adaxial side; *margins* narrowly recurved to strongly revolute along the entire length except at the apex, entire; *medial cells* uniformly rectangular throughout the leaf, slightly shorter towards the apex; *basal cells* narrowly rectangular.

Habitat. – On moist soil in rich fens, on wet rocks in streams and along lakes, and in moist rock crevices; a distinct calciphile.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Newfoundland, south through Canada and the northernmost United States, reaching Nevada and California in the western mountains. Iceland, Svalbard, European mountains, northern U.S.S.R., China.

Subfossil Distribution in North America. – Greenland, New York and Northwest Territories (Miller 1980a). New records: (1) HH68–9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (2) HH75–24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (3) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI–4314); Bryological Report 401.

Paludella

See the introduction to the family for distinguishing features of the genus *Paludella*. The genus is monotypic and *P. squarrosa* is a common, often beautifully preserved fossil. The specimens in my collections are less blackened than the *Meesia* fragments.

Paludella squarrosa (Hedw.) Brid.

Diagnostic features. – *Leaves* strongly squarrose-recurved, ovate to obovate, not or longly and narrowly decurrent; *apex* shortly acute; *margins* plane or slightly recurved, crenulate; *medial cells* rounded or quadrate, moderately thick-walled, strongly bulging-papillose on the adaxial side, bulging on the abaxial side; *basal cells* rectangular, thin-walled.

Habitat. – In intermediate fens, in ecotonal regions between forests and fens, around springs, rarely and poorly developed in drier habitats, on damp soil or rocks.

Recent Distribution. – Circumboreal. North America: Alaska to Greenland, south to New York, Michigan, Wyoming and Montana. Northern, western, eastern and central Europe, northern Asia.

Subfossil Distribution in North America. – Greenland and New York (Miller 1980a). New records: (1) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148. (2) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159. (3) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Catoscopiaceae

This monotypic family has a fossil record in North America (see below) and Poland (Holocene and Pleistocene, Jovet-Ast 1967). It is absent from the British record (Dickson 1973). *Catoscopium nigritum* specimens preserve very poorly and are often difficult to identify. The cell and margin structure described below, distinguishes the leaf fragments from similar fragments of *Ceratodon purpureus* specimens, often equally poorly preserved.

Catoscopium

Catoscopium nigritum (Hedw.) Brid.

Diagnostic features. – *Leaves* broadly-lanceolate, stiff and straight, tubulose above; *costa* wide, occupying up to half the leaf base, with an adaxial and abaxial stereid band; *margins* entire, plane, or slightly recurved in the shoulder area; *medial cells* irregular, varying from narrowly rectangular to rounded, quadrate or subquadrate, evenly thick-walled or the transverse walls thicker; *basal cells* wider, mostly rectangular, often variously angled, shorter towards the margins, thick-walled.

Habitat. – On damp calcareous soil and peat. On flushed slopes, banks of streams or lakes, in rich fens and on solifluction terraces. Typically growing in small bulging hummocks on the sides of larger hummocks. In late snow melt areas and wet transition zones of meadows.

Recent Distribution. – Circumboreal. North America (Miller 1980b): Alaska to Greenland, south to New Brunswick, New York, Michigan and Iowa in the east and British Columbia, Alberta and northern Montana in the west. Northern, western, eastern and central Europe, Pyrenees, Caucasus. Northern and central Asia.

Subfossil Distribution in North America. – Greenland, Michigan and Vermont (Miller 1980a, b). New records: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ±

60,000 B.P.; Bryological Report 174. (2) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (3) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (4) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (5) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – *Ceratodon purpureus* differs from *Catoscopium* by its strongly recurved margins and denticulate apex. The upper cells are isodiametric. *Meesia longiseta* is differentiated from *C. nigritum* with its more strongly erect-recurved leaves and more rectangular, thinner walled upper cells. The specimens are less obviously blackened by fossilization than *Meesia* fragments.

Bartramiaceae

The genera *Plagiopus*, *Bartramia*, *Conostomum*, *Philonotis* and *Breutelia* have a fossil record. *Breutelia* (Flandrian) and *Plagiopus* (Devensian) have only British records (Dickson 1973). While *Conostomum* was found in glacial deposits of Poland (Jovet-Ast 1967) and *Bartramia* was listed for Italy (Jovet-Ast 1967), Britain (Dickson 1973) and North America (British Columbia, Holocene: Miller 1980a).

Philonotis represents most of the records. In North America, one species with two of its varieties are recorded (Miller 1980a). Several other species are listed from Late Tertiary and Quaternary deposits in Belgium, Switzerland, Germany, Denmark and Poland (Janssens 1977a, Dickson 1973 and Jovet-Ast 1967).

Philonotis

The only species in the North American record is *P. fontana*. It is the most common species of the genus presently found on the continent and numerous modifications occur. Several of these have been given, perhaps unnecessarily, varietal status. See the discussion below for the distinction between this species and other taxa in the genus.

Philonotis leaves are superficially similar to those of *Pohlia* leaves in shape and areolation. However, *Pohlia* leaves are differentiated by their longer and narrower ovate-lanceolate shape with cells that are less thick-walled and smooth.

Philonotis fontana (Hedw.) Brid.

Diagnostic features. – *Leaves* ovate-lanceolate to lanceolate, erect or slightly secund; *apex* slenderly acuminate; *costa* reaching into the apex or beyond; *margins* plane above, revolute below, sharply denticulate, often from the base to the apex, sometimes only above, teeth sharp and sometimes recurved at the base; *medial cells* rectangular or oblong, linear towards the margins, papillose at the upper ends on the adaxial surface and at the lower end on the abaxial surface of the leaf, papillae larger or sometimes present only on the cells towards the margins.

Habitat. – In wet generally calcareous habitats and on wet rocks. In late snow melt areas, beside streams and springs, in seepages, in fens with moving water. pH 6.25–6.55 (n=3), conductivity 34.9–40.5 microScm^{-1} (n=3), Ca concentration 3.5 and 4.5 ppm (n=2), Mg concentration 0.065–0.085 ppm (n=3), Na concentration 3.6–4.6 ppm (n=3) and K concentration 1.0–1.3 ppm (n=3).

Recent Distribution. – Circumboreal and in montane equatorial regions. North America: Greenland to Alaska, throughout the continent south to Mexico. Europe, Azores, Canaries, Madeira, eastern African Mountains, northern and central Asia, Japan.

Subfossil Distribution in North America. – Alaska, Greenland, Northwest Territories, Oklahoma and Vermont (Miller 1980a). New records: (1) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I–10,525); Bryological Report 178. (2) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC–2200); Bryological Report 280, Mott *et al.* 1980. (3) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI–4314); Bryological Report 401.

Discussion. – Other *Philonotis* species are distinguished by uni–papillose cells (only papillae at the upper or the lower end of the cells). Often, these taxa have narrower leaves. Several varieties of *P. fontana* are based on the variable length of the costa and on the shape of the leaf apex.

Timmiaceae

Timmia

Five of the six *Timmia* species have a fossil record. *Timmia comata, T. bavarica* and *T. megapolitana* have European and Russian records (Jovet-Ast 1967). *Timmia austriaca* and *T. norvegica* are known from European and North American deposits (Miller 1980a).

Timmia leaves resemble *Polytrichum* leaves in shape but do not have adaxial lamellae. The only species in my collections is represented by a single specimen of *T. austriaca*.

Timmia austriaca Hedw.

Diagnostic features. – *Leaves* lanceolate from an oblong base, the base forming a homogeneous brown sheath; *apex* narrowly obtuse; *costa* stout, ending just below the apex, smooth; *margins* irregularly and usually denticulate in the upper part, incurved above, plane below; *limb cells* quadrate, weakly mamillose on the adaxial side; *sheath cells* rectangular, narrowed to a linear shape towards the margins, smooth or papillose

Habitat. – On wet hummocky or gravelly slopes or soil, in crevices of rock outcrops, around bird perches. In wet tundra meadows and in seepages.

Recent Distribution. – Circumboreal (Brassard 1980). North America (Miller & Ireland 1978a): most abundant in the southwestern Cordillera. From Alaska to Greenland and Newfoundland, through the western mountains to New Mexico and disjunct to South Dakota, upper Michigan, Quebec, and New Brunswick in the east. Europe, northern Asia.

Subfossil Distribution in North America. – Vermont (Miller 1980a, Miller & Ireland 1978a). New records: (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – Other *Timmia* species are differentiated by a pale, yellow or hyaline sheathing base or by a sheath with some papillose cells.

Orthotrichaceae

This large family has a very poor fossil record. *Zygodon viridissimus* has two Flandrian records in the British Isles (Dickson 1973). The genus is represented in Pliocene deposits of Germany. *Ulota* has a few Flandrian records in Britain and a Holocene record in Czechoslovakia. *Orthotrichum* is represented by three species: *O. diaphanum* of Devensian age in Britain, *O. obtusifolium* of the Two Creeks Forest Bed in Wisconsin and *O. speciosum*, discussed below.

Orthothrichum speciosum

Diagnostic features. – *Leaves* narrowly ovate-lanceolate to lanceolate; *apex* narrowly acute; *margins* revolute along the entire length, except at the apex; *medial cells* irregularly rounded to elliptic, very thick-walled, commonly with two high, simple or forked papillae; *basal cells* elongate, strongly porose and very thick-walled.

Habitat. – Mostly on trees in temperate forests, rarely on rocks farther north in boreal and tundra areas. In the high arctic on gravelly slopes (Vitt 1973).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Newfoundland, south to the Great Lakes area in the east and to Oregon, Idaho and Montana in the western mountains. Europe, northern Africa and northern Asia.

Subfossil Distribution in North America. – (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401, as *Orthotrichum cf. speciosum*.

Discussion. – Sporophytes are necessary to identify this species with a high reliability.

Leskeaceae

Lescuraea, *Leskea* and *Pseudoleskeella* are the three genera in this family with a fossil record. *Lecuraea* has a few records of Late Devensian age in Britain and is known from deposits of the penultimate glaciation in Poland (Dickson 1973). Several species of *Leskea* and *Pseudoleskeella* are known from the Pliocene of the U.S.S.R. and the Netherlands, and from the Holocene of Czechoslovakia (Jovet-Ast 1967, Dickson 1973). Two North American records are known. Miller (1980a) reported *Leskea australis* Sharp. *in* Grout, of unknown age for North Carolina. One specimen of *Pseudoleskeella* is present in my collections.

The family is perhaps closely related to the Thuidiaceae. The principal difference between the two families is based on peristome characteristics.

Pseudoleskeella

This genus (*sensu stricto*) is characterized by a pleurocarpous habit, small and simple paraphyllia, small ovate-lanceolate leaves with an apiculate apex and with plane and entire margins. The areolation is the most characterstic feature of the vegetative plants. The medial cells are rounded, oval or shortly elongate, and smooth or papillose on the abaxial side of the leaf. The walls are sometimes strongly thickened.

Pseudoleskeella tectorum (Funck *ex* Bird.) Kindb. *ex* Broth.

Diagnostic features. – *Leaves* widely ovate-lanceolate; *apex* shortly acuminate; *costa* double, one branch often reaching to the middle of the lamina; *margins* plane, entire; *medial cells* rhomboid to shortly elongate (3:1 to 6:1), with clear corner thickenings, firm-walled, marginal cells shorter, parallelogram-sh *basal cells* varying from elliptic to rounded, quadrate and subquadrate.

Habitat. – On calcareous rock, usually in crevices and protected places, on trees, rarely on soil or siliceous rocks.

Recent Distribution. – Circumboreal (Lewinsky 1974: world distribution map but very incomplete for North America). North America: from Alaska to Greenland, Newfoundland and Labrador, south troughout Canada and northern United States, in the western mountains through Alberta and British Columbia to Arizona and New Mexico, east to Manitoba. Mexiço. Svalbard, mountains in Europe and arctic USSR.

Subfossil Distribution in North America. – (1) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267.

Discussion. – The similar *Leskea nervosa* (Brid.) Loeske is differentiated from *Pseudoleskeella tectorum* by a single costa ending in the apex. Other *Pseudoleskeella* species are distinguished by nearly isodiametric or papillose medial cells

Thuidiaceae

Several of the circumboreal genera in this family have a good fossil record *Heterocladium* is found in a Holocene deposit in British Columbia (Miller 1980a) and in several deposits of various Neogene ages in Germany, Poland and the USSR (Dickson 1973, Jovet-Ast 1967) *Anomodon* is reported from Iowa (Aftonian), Washington DC (Wisconsinan) and North Carolina (Wisconsinan) by Miller (1980a) and is reported from numerous Neogene and Pleistocene deposits in Europe (Jovet-Ast 1967) *Claopodium* has two extinct and one extant species represented in Pliocene deposits in Duab Caucasus (Abramova & Abramov 1959). Other records of the genus are known from France, Poland and the U.S.S.R (Jovet-Ast 1967) *Helodium* is frequently found in Pleistocene deposits of Belgium (Janssens 1977a), Switzerland, Poland and Germany (Jovet-Ast 1967) The North American records are discussed below *Thuidium* is represented by various species in European Neogene and Pleistocene deposits (Jovet-Ast 1967). Three species are known from the North American Pleistocene. Two are discussed below. The third, *T. delicatulum*, has an Aftonian and Wisconsinan record (Miller 1980a).

Thuidium and *Helodium* are pleurocarpous genera characterized by leaves with a very well developed costa, unipapillose cells and paraphyllia on the stem and branches. These paraphyllia are often very well preserved

Helodium

This genus is distinguished from *Thuidium* by filiform paraphyllia with cells longer than wide. These paraphyllia are not only found on the stem and branches, but also on the base of the costa and along the basal margins of the leaves (cilia). *Helodium blandowii* is the only species of the genus with a fossil record. It is a common Pleistocene fossil in Britain (Dickson 1973), where it is now extinct, and in Belgium (Janssens 1977a), where it is now extremely rare. It is also known from glacial deposits in Switzerland, Poland and Germany (Jovet-Ast 1967).

Helodium blandowii (Web. *et* Mohr) Warnst.

Diagnostic features. – *Branches* with filiform, branched paraphyllia with cells longer than wide; *leaves* broadly ovate; *apex* shortly acuminate; *margins* denticulate, with recurved teeth and cilia in the basal part; *medial cells* rhomboid or oblong, unipapillose, papillae usually at the upper end.

Habitat. – In wet calcareous fens (rarely in fens without tree or shrub layers) and marshes, usually with percolating water, along streams and ditches. Associated with *Mnium pseudopunctatum*, *Paludella squarrosa*, *Sphagnum teres*, *S. warnstorfii*, and *Tomenthypnum nitens*.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Newfoundland and Labrador, widespread throughout Canada, in the northern United States from New England to Washington, reaching Arizona and Nevada in the western mountains. Europe, northern Asia, Japan.

Subfossil Distribution in North America. – Greenland and Northwest Territories (Miller 1980a). New records: (1) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262.

Discussion. – Species of *Thuidium* are differentiated from *Helodium blandowii* by their laminal paraphyllia with quadrate cells and the absence of cilia at the leaf base.

Thuidium

See the *Helodium* introduction for the differentiation between the two genera.

Thuidium abietinum (Hedw.) B.S.G.

Diagnostic features. – *Fragments* unipinnately branched; *leaves* without marginal cilia; *paraphyllia* laminal or branched filiform, cells quadrate ,papillose with papillae at the upper end of the cells.

Habitat. – On sandy, gravelly or organic soil in well drained, usually calcareous habitats. Frequently on old dunes or dry hill sides, in open, coniferous stands, in *Dryas* heath, on ledges, at bases of cliffs or among talus rocks. Rather generally associated with *Rhytidium rugosum*, *Hypnum bambergeri* and *Tortula ruralis*. More compact and more regularly pinnately branched when growing in more exposed and drier habitats. Often found in areas much exposed to wind with *Tortula ruralis* and *Tomenthypnum nitens*.

Recent Distribution. – Circumboreal. Arctic and alpine–montane species. North America: Greenland to Alaska and south to Arizona, Colorado, Iowa, Indiana and Virginia at higher elevations. Europe, northern Asiatic U.S.S.R., central Asia, China and Japan.

Subfossil Distribution in North America. – New York, Northwest Territories, Saskatchewan, Vermont and Wisconsin (Miller 1980a). New records: (1) HH68–9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (2) HH68–9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62. (3) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I–11,010); Bryological Report 171, Hamilton 1980a, p. 21. (4) Your Creek area, Alaska; 5615 ± 110 B.P. (I–10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (5) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I–10,784); Bryological Report 200, Hamilton 1980a, p. 23. (6) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I–10,925); Bryological Report 201, Hamilton 1980a, p. 23. (7) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (8) Cape Deceit Quaternary Exposure, Near Deering (station 8); Alaska; 12,420 ± 1080 B.P. (I–4781); Bryological Report 351, Matthews 1974a.

Discussion. – The other *Thuidium* species are distinguished from *T. abietinum* by their bi- or multipinnate branching. See the discussion of *Helodium blandowii* for the distinction from *Thuidium*.

Thuidium recognitum (Hedw.) Lindb.

Diagnostic features. – *Fragments* bi-pinnately branched; *leaves* without marginal cilia; *paraphyllia* filiform or lanceolate with short cells, papillose with papillae at the upper end of the cells.

Habitat. – On moist calcareous soil, humus, rocks or logs. In wet or moist woods, open swamps or meadows.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Labrador and Newfoundland, throughout Canada and west from New England through the northern United States to Montana and Idaho, south to Georgia, Mississippi, Missouri, Kentucky, and Kansas. Europe, northern Africa, Japan, northern Asia.

Subfossil Distribution in North America. – Wisconsin (Miller 1980a). New records: (1) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383.

Discussion. – Other bipinnately branched *Thuidium* species are distinguished by paraphyllia with papillae not restricted to the cell ends.

Amblystegiaceae

Amblystegium

Amblystegium serpens (Hedw.) B.S.G.

Diagnostic features. – *Fragments* frequently but irregularly branched; *branch leaves* small, usually < 1 mm, erect-spreading to spreading, ovate-lanceolate with slenderly acuminate apex; *stem leaves* often twice as large; *costa* reaching half way up in the lamina; *margins* entire or weakly denticulate; *medial cells* rhomboid, 5:1 to 3:1, thin-walled, towards the apex longer and narrower, becoming gradually shorter, rectangular and quadrate at the base.

Habitat. – Usually on soil, on rotten wood and humus in moist to wet habitats.

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Greenland, Newfoundland and Labrador, throughout Canada and the United States, especially in th and central states. Central and South America, Europe, Asia, Japan, North Africa and New Zealand.

Subfossil Distribution in North America. – Alberta, Iowa, Louisiana, Saskatchewan and Wisconsin (Miller 1980a, including *A. juratzkanum* Schimp.). New records: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (2) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 -- 1,800,000 B.P.; Bryological Report 341, Matthews 1974a.

Discussion. – The small leaves and large, wide cells (so that the leaves are composed of only a strikingly small number of cells) are clear features to differentiate the two representatives of the genus *Amblystegium* represented in the fossil record from *Leptodictyum*. The two species are distinguished from *Hygroamblystegium* by the less well developed costa and the absence of a clear shoulder area on the leaf (Kanda 1975). The character states differentiating *A. serpens* and *A. varium* are discussed under the latter. *Amblystegium juratzkanum*, given species rank in Ireland *et al.* (1980), is probably only a modification of *A. serpens*. In its extreme form it is differentiated in somewhat larger and stiffer plants and more widely spreading leaves.

Amblystegium varium (Hedw.) Lindb.

Diagnostic features. – *Fragments* frequently but irregularly branched; *leaves* very variable in size, 0.5 to 2 mm long, spreading to erect-spreading, ovate-lanceolate with acuminate apex; *costa* reaching into the apex; *margins* entire, or sometimes denticulate in the upper half; *medial cells* rhomboid, 5:1 to 3:1, thin walled, not strikingly more elongate towards the apex, *basal cells* gradually shorter, rectangular and quadrate in the base.

Habitat. – Usually on soil, on humus, logs and rocks in moist to wet shaded habitats. In calcareous areas.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Labrador, throughout Canada and the northern United States, especially in the eastern part, Mexico. Haiti, South America, Europe, northern Africa, Asia, Japan.

Subfossil Distribution in North America. – (1) Chandalar River, 3 km east of Caro, Alaska; >30,000 B.P.; Bryological Report 184. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (3) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (4) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (5) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (6) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (7) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Plants of *A. varium* are frequently larger and stiffer than those of *A. serpens*. Other differentiating features are the costa reaching high in the apex and the more uniform areolation (apical cells not longer than medial) in *A. varium*. The margin is mostly slightly denticulate, as was suggested by Grout (1928–34). The large forms of *A. varium* are distinguished from *Leptodictyum trichopodium* by the shorter areolation and from *Hygroamblystegium tenax* by the less well developed costa and the more lanceolate leaf shape with a slender apex (compare also Nyholm 1965). Another species with leaves similar to *Amblystegium varium* is *Rhynchostegiella compacta* (C. Müll.) Loeske (Brachytheciaceae). However, the cells in the latter are much longer and narrower than in *Amblystegium*. *Rhynchostegiella* can be differentiated from *Leptodictyum trichopodium* (the cells are very similar) by the narrower ovate–lanceolate leaves, the costa that reaches much higher into the apex and the recurved tips of the marginal teeth (straight tips in *L. trichopodium* if it is not an entire form). Branched protonema–like cell strands are often present in the apical part of the *Rhynchostegiella* leaves or along the abaxial side of the costa.

Calliergon and *Calliergonella*

Some of the information compiled in the Habitat and Recent Distribution sections of the *Calliergon* and *Calliergonella* species treatments is derived from Karczmarz (1966, 1971) and Wynne (1945) in addition to the works cited in Materials and Methods. The maps of the present day distribution of *C. giganteum*, *C. richardsonii* and *C. trifarium* are based on ALTA and CANM specimens and on some additional information from papers listed in the captions to the figures.

C. obtusifolium Karcz., *C. orbicularicordatum* (Ren. *et* Card.) Broth. and *C. wickesiae* Grout are not represented in the fossil record. *C. cordifolium* (Hedw.) Kindb. (Miller 1980a) has been found as a subfossil only in the eastern part on the continent and is represented by a doubtful specimen (Geological Survey of Canada, Paleobotanical Collections, !) from Banks Island in the Canadian Arctic (Kuc 1974c). The extinct Quaternary species *C. aftonianum* Steere, *C. hansenae* Steere and *C. kayianum* Steere are discussed under *C. richardsonii*. *Calliergon subsarmentosum* Kindb. (Janssens 1980b) is discussed in relation with *C. giganteum*.

Calliergon giganteum (Schimp.) Kindb. Plate 7

Diagnostic features. – *Stem and branch leaves* ovate-cordate, branch leaves sometimes ovate-oblong; *costa* reaching in most mature leaves to the apex; *apex* cucullate; *alar cells* in a large convex group that reaches the costa except for one or two basal cells in between costa and the group, cells strongly differentiated, walls thin and hyaline, often not preserved.

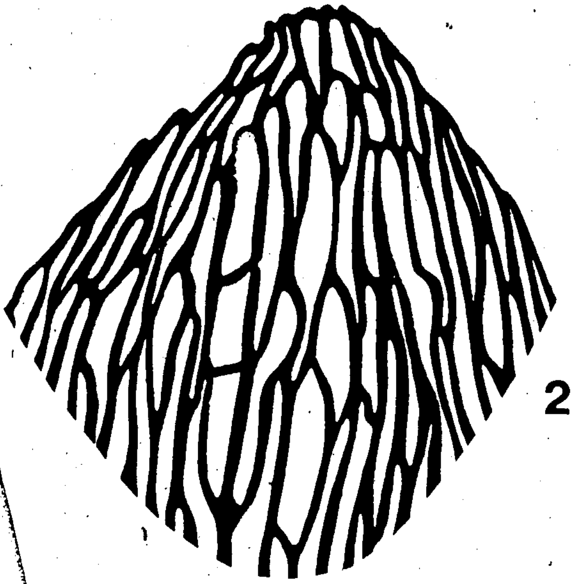
Habitat. – In rich fens, sedge-moss meadows, ditches, beside lakes and pools, sometimes completely submerged. pH 7.1 to 7.5 (n=3), conductivity 197 to 475 microScm^{-1} (n=3), Ca concentration 3 to 28 ppm (n=3), Mg concentration 3 to 22 ppm (n=3), Na concentration 10 to 22 ppm (n=3), K concentration 0.0 to 3.5 ppm (n=3).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Labrador and Newfoundland, south to Pennsylvania, Michigan and Minnesota in the east and to Washington, Idaho and Wyoming in the west. Europe, northern Asia.

Subfossil Distribution in North America . – Alaska, Greenland, Iowa, Minnesota, North Dakota, Northwest Territories and Pennsylvania (Miller 1980a). New records: (1) Silver Creek, Slims River drainage, Yukon Territory; 30,100 ± 600 B.P. (Y-1385); Bryological Report 2, Schweger & Janssens 1980. (2) Snake River area, Yukon Territory; 11,700 ± 90 B.P. (GSC-2693) and 11,800 ± 170 B.P. (GSC-2745); Bryological Report 41. (3) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (4) HH69-21 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 102. (5) HH69-21, Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 103. (6) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 109. (7) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148. (8) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (9) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 163, Blake & Matthews 1979. (10) Mackinson Inlet,

Plate 7. Calliergon giganteum (Schimp.) Kindb. (Bryological Reports 269 and 276)

1. Leaves (x50).
2. Leaf apex (x500).
3. Medial leaf cells (x500).
4. Alar leaf cells (x200).



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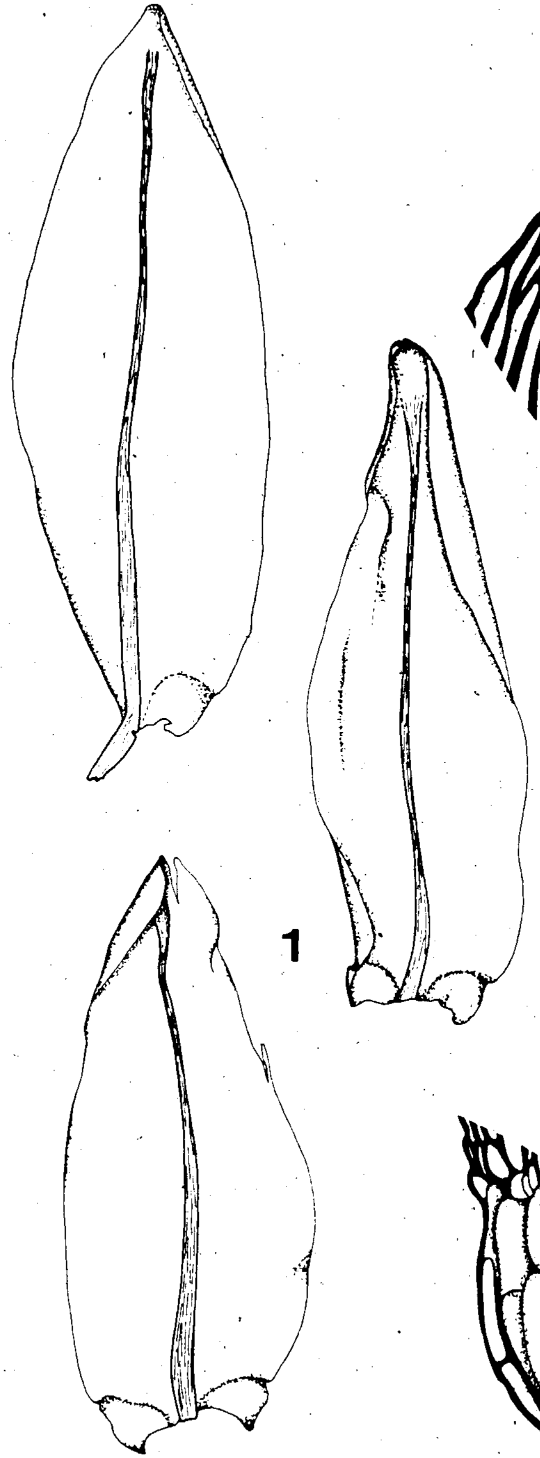

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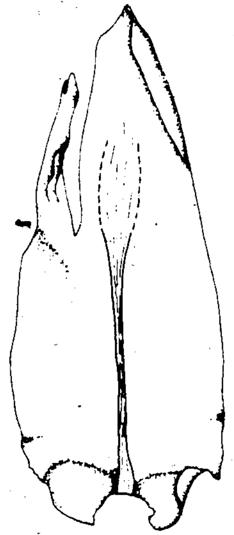

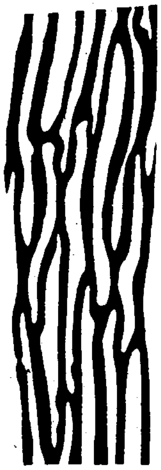

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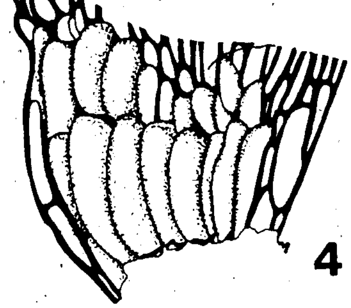

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Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 164, Blake & Matthews 1979. (11) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 165, Blake & Matthews 1979. (12) Chandalar River, 2.5 km downstream from Caro, Alaska; >42,000 B.P.; Bryological Report 166. (13) Koyukuk River, 6 km downstream from Henshaw Creek, Alaska; 52,800 ± 1300 B.P. (QL-1283); Bryological Report 168. (14) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (15) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (16) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (17) Section Creek, 9 km upstream from Sagavanirktok River, Alaska; 12,690 ± 180 B.P. (I-10,567); Bryological Report 182, Hamilton 1979b, p. 29. (18) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (19) Tulunga River, 8 km upstream of east fork, Alaska; 33,220 ± 1760 B.P. (I-11,012); Bryological Report 198, Hamilton 1980a, p. 19. (20) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (21) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (22) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (23) CRH 11 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 266. (24) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (25) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (26) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (27) Kitchener, Ontario; below 8800 B.P.; Bryological Report 276. (28) Shoran Lake, Banks Island, Northwest Territories; 10,200 ± 130 B.P. (GSC-2673); Bryological Report 283. (29) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 294. (30) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 295. (31) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (32) Kitchener, Ontario; below 8800 B.P.; Bryological Report 322. (33) HH75-24, Bluefish Basin, Yukon Territory;

Wisconsinan?; Bryological Report 325. (34) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (35) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (36) Cape Deceit Quaternary Exposure, Near Deering (station 1-2), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 346, Matthews 1974a, as *Calliergon cf. giganteum*. (37) Cape Deceit Quaternary Exposure, Near Deering (station 5-6), Alaska; 400,000 - 900,000 B.P.; Bryological Report 352, Matthews 1974a. (38) 228HH, Bluefish Basin, Yukon Territory; >37,000 B.P. (GSC-2783), ± 60,000 B.P.; Bryological Report 362. (39) HH68-9 (station 14), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 387. (40) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 389, as *Calliergon cf. giganteum*. (41) Milford Gypsum Quarry, Milford, Nova Scotia; >50,000 B.P. (GSC-1642); Bryological Report 413. (42) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434. (43) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435. (44) Lake 2 km southeast of Kap Inglefield, Inglefield Land, Greenland; Holocene?; Bryological Report 437.

Discussion. - All the subfossil specimens are characterized by distinct, bulging alar cell groups. In some poorly preserved leaves the cell groups can disintegrate and leave a distinct gap, even when the leaves are still on the stems. None of the material could be assigned to the closely related *C. cordifolium* (Hedw.) Kindb. When compressed by a coverslip, the subfossil material of *C. giganteum* frequently is characterized by a longitudinal split along the costa at the apex. In some material the costa is very broad and approaches the form *crassicostatum* (Karczmarz 1971, p. 85). Other material has narrowly ovate-lanceolate branch leaves. Two such fragments (Bryological Report 169 & 276, PLate 7), were classified under *C. subsarmentosum* Kindb. (Janssens 1980b). However, they are comparable to *C. giganteum* var. *hystricosum* Roth *et* Bock (Karczmarz 1971, p. 86). The narrowly ovate-lanceolate leaves of both specimens are characterized by crenulations in the upper half and by nematogon initials among the apical cells. The apex shape and denticulation are reminiscent of *Drepanocladus tundrae-D. pseudostramineus* leaves (see discussion under these taxa). The well differentiated alar cells form a strong, convex and bulging group, very unlike the alar cell structure in *C. sarmentosum*. These alar cell groups reach the costa in the branch leaves, in contrast with the stem leaves. In the latter taxon, a few undifferentiated basal cells (characterized by thick, porose walls) are inbetween the costa and the alar cells.

In my opinion the type specimen of *C. subsarmentosum* (S!) is also *C. giganteum* (*cf.* var. *hystricosum*). *Calliergon subsarmentosum* was described by Kindberg (1909a, b, Steere & Crum 1977) from material collected by J. Macoun "on wet earth, Shawnigan Lake, Vancouver Island, British Columbia, June 18th, 1908". Both the Kindberg papers (1909a, b) provided essentially the same short and insufficient description. The branch leaves are incorrectly characterized as very small. No reasons are given for its presumed close relationship with *C. sarmentosum*. Grout (1931, p. 98) studied material determined as *C. subsarmentosum*, but collected earlier than the type by Macoun on July 13, 1906 on Vancouver Island, British Columbia (Robinson 1959). Grout's slides, mentioned in Robinson's paper, could not presently be located at DUKE (Anderson, *in litt.*). Grout briefly described the morphological features, and these clearly underline the close relationship with *C. giganteum*. However, he considered the material as "merely a slight variation" of *C. sarmentosum* and cited *C. subsarmentosum* as a synonym of *C. sarmentosum*. This was followed by Wynne (1945, p. 144) after she studied Grout's slides.

Robinson (1959) studied subfossil *Calliergon* fragments collected by Fries (1962) from lateglacial deposits at Weber Lake, Minnesota (Miller 1980a). He also re-examined Grout's collections at DUKE and concluded that the fossils are very similar to the latter material. He provided a comparison between *C. sarmentosum* and *C. subsarmentosum* and concluded that both are distinct taxa. He did not attempt to relate *C. subsarmentosum* to any other taxon in the genus *Calliergon*. The bulk sample of the *Calliergon* peat was kept by Fries, but I have not yet been able to trace this.

Karczmarz (1971, p. 16, 80, 126, 128) studied the type material of *C. subsarmentosum* (S) and placed the species (Kindberg 1909a) in synonymy with *C. giganteum* (Karczmarz 1968, 1971, p. 80, Robinson *in litt.*). He made a reference to Kindberg (1909a). Presumably an error, he put the same taxon (referring there to Kindberg (1909b)) in synonymy with *C. sarmentosum* (Karczmarz 1971, p. 126 (see also

Steere & Crum 1977). There is no annotation label attached to the packet of the type specimen from S that I studied.

Calliergon megalophyllum Mik.

Diagnostic features. – *Stem and branch leaves* widely cordate-ovate, 4 to 6 mm long, plicate; *alar cells* strongly differentiated, inflated and with hyaline walls, the group not reaching the costa.

Habitat. – In minerotrophic lakes, pools in fens.

Recent Distribution. – Circumboreal. North America: Alaska and Northwest Territories. Europe, Asia.

Subfossil Distribution in North America. – (1) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308, as *Calliergon cf. megalophyllum*.

Discussion. – Steere (1978a) suggested that it might well be that this species does not occur in North America. Weber's specimen (ALTA) from Colorado being a much smaller plant without plicate leaves is not *C. megalophyllum*, but *C. richardsonii* (!). However, material from Alaska (e.g. Steere 15563 in ALTA), identified by Steere as *C. richardsonii*, approaches *C. megalophyllum* much more closely. The fossil plant from the Old Crow Basin is also much larger than all other *Calliergon* specimens in my fossil collections. No definite taxonomic conclusions can be brought forward without comparative studies of *C. megalophyllum*, *C. macounii* (Karczmarz 1966b) and *C. richardsonii* in the field and from North American herbarium specimens. *Calliergon megalophyllum* is very common in suitable habitats in eastern Fennoscandia (Tuomikoski 1940). Clearly it is not so common in North America as it is in Scandinavia. Most likely, if it was formerly as abundant in North American lakes as it presently is in Scandinavian, it would be a common fossil (see the discussion of *Drepanocladus crassicostatus*).

Calliergon richardsonii (Mitt.) Kindb. *ex* Warnst.

Diagnostic features. – *Stem and branch leaves* widely cordate-ovate, branch leaves sometimes narrowly ovate; *costa* reaching mostly half way up in the lamina; *alar cells* strongly differentiated, inflated and with hyaline cell walls almost reaching the costa.

Habitat. – On organic substrate, on gravel and rocks in arctic regions. In the mountains it grows in intermediate and rich fens, in valleys of rivers and streams.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Labrador and Newfoundland, south to the Great Lakes area in the east, in the western mountains south to Alberta and disjunct to Wyoming. Northern, eastern and central Europe, Svalbard, northern and central Asia.

Subfossil Distribution in North America. – Iowa, Minnesota, Northwest Territories and Vermont (Miller 1980a). New records: (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34, as *Calliergon cf. richardsonii*. (2) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (3) HH68-9 (station 8), O[illegible] Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48, as *Calliergon* [illegible] *richardsonii*. (4) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 [illegible]yological Report 54. (5) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62. (6) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 109, as *Calliergon cf. richardsonii*. (7) HH68-9 (station 9), Old Crow Basin, Yukon Territory: 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 120, as *Calliergon cf. richardsonii*. (8) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 140 to 150 cm below surface; Bryological Report 157. (9) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159, as *Calliergon cf. richardsonii*. (10) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (11) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p.

21, as *Calliergon cf. richardsonii*. (12) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (13) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (14) Chandalar River, 3 km east of Caro, Alaska; >30,000 B.P.; Bryological Report 184. (15) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (16) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (17) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (18) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269, as *Calliergon cf. richardsonii*. (19) Kitchener, Ontario; between 6900 B.P. and 7700 B.P.; Bryological Report 274. (20) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (21) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (22) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (23) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341; Matthews 1974a. (24) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (25) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (26) HH68 9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (27) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - The main feature differentiating *C. richardsonii* from *C. giganteum* is the poorly developed costa, usually branched in the upper part and only extended half way up the lamina. The branch leaves of *C. richardsonii* can be narrowly ovate-lanceolate. Such form of *C. richardsonii* in the subfossil record, with narrowly ovate-lanceolate branch leaves and a very short, weak costa, was described as the extinct *C. aftonianum* Steere (1942) from Aftonian deposits in Iowa. This is probably an aquatic form that is commonly found as a subfossil and much less frequently encountered in herbarium material (e.g. Vitt 24193 and Peterson 4883 in ALTA!). Kuc (1974a) commented on the taxonomic value of *C. aftonianum* while discussing the Late Cenozoic distribution of that taxon (see also Miller 1980a). He pointed out the close relationship with *C. richardsonii*.

Steere (*in litt.*) came to the same conclusion regarding this taxon. As with the other extinct Quaternary taxa (*C. hansenae* Steere, *C. kayianum* Steere, *Camptothecium woldenii* Grout, *Drepanocladus apiculatus* Steere, *Drepanocladus minnesotensis* Williams and *Neocalliergon integrifolium* Williams), Steere concluded that at least some of them may represent abnormal forms of extant species (see also Miller 1980b, p. 21–22 and Wynne 1945, p. 133). Except for *C. aftonianum*, I did not recognize in my fossil collections any of the above mentioned extinct taxa that were redescribed and discussed by Kuc (1974a, p. 7–8). In Janssens (1980b), *C. aftonianum* is still accepted as a distinct species. Further study of living populations of *C. richardsonii* will probably lead to the recognition of *C. aftonianum* as a distinct form, or even a subtaxon of *C. richardsonii*, still living in an aquatic environment.

Calliergon sarmentosum (Wahlenb.) Kindb.

Diagnostic features. – *Leaves* narrowly ovate; *apex* cucullate and in some leaves shortly apiculate; *alar cells* well but gradually differentiated from the basal cells, inflated, the cells towards the costa with brown thickened walls, the ones on the outside of the ovoid alar cell group with thin hyaline walls.

Habitat. – On irrigated rocks and on organic soil. In mires, mostly poor fens, and rocky tundra, beside lakes and streams, in mountains often submerged in streams and in late snow melt areas.

Recent Distribution. – Circumboreal. Bipolar. Arctic–alpine species. North America: from Alaska to Greenland, Newfoundland and Quebec, south to New Englandin the east, Montana and Colorado in the west. Bolivia, Peru and Patagonia, Svalbard, northern Europe, the Alps, Kenya, northern and central Asia. South Island of New Zealand, Antarctica.

Subfossil Distribution in North America. – Greenland, Kansas, Minnesota and Northwest Territories (Miller 1980a). New record: (1) St Eugene, Quebec; 11,050 ± 130 B.P. (QU–448); Bryological Report 279, Mott *et al.* 1980.

Discussion. - Other *Calliergon* species are distinguished from *C. sarmentosum* by more abruptly differentiated alar cells or by the different shape of the alar cell group.

Calliergon stramineum (Brid.) Kindb.

Diagnostic features. - *Leaves* oblong-ovate; *apex* obtuse; *alar cells* gradually differentiated, in a long narrow group reaching up along the margins; *apical cells* frequently partially differentiated in nematogon initials.

Habitat. - Often submerged in shallow pools, in fen and bogs, occasionally admixed with *Sphagnum*. pH 7.9 (n=1), conductivity 450 microScm^{-1} (n=1), Ca concentration 42 ppm (n=1), Mg concentration 18 ppm (n=1), Na concentration 25 ppm (n=1), K concentration 1.4 ppm (n=1).

Recent Distribution. - Circumboreal. Bipolar. North America: from Alaska to Greenland, Labrador and Newfoundland, throughout Canada and south to New England and Michigan in the east and Montana, Idaho, Wyoming and Colorado in the west. Europe, northern Asia, Japan and Australia.

Subfossil Distribution in North America. - Greenland, Minnesota, Northwest Territories, Iowa and Wisconsin (Miller 1980a). New record: (1) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - Other *Calliergon* species are differentiated from *C. stramineum* by better developed alar cells or by the different shape of the alar cell group.

Calliergon trifarium (Web. *et* Mohr) Kindb.

Diagnostic features. - *Fragments* unbranched; *leaves* concave, imbricate, ovate; *costa* frequently short, branched or double; *alar cells* gradually differentiated, the row at the insertion of the leaf inflated, with thick brown walls, the alar cells reaching the base of the costa.

Habitat. – In tufts or as solitary stems intermingled with rich fen bryophytes. Often associated with *Scorpidium* species, *Meesia triquetra* and *Drepanocladus* species in rich fens and calcareous spring seepages. Submerged types only exceptionally found in lakes. pH 7.2 to 7.7 (n=15), conductivity 229 to 602 microScm^{-1} (n=15), Ca concentration 19 to 54 ppm (n=10), Mg concentration 5.2 to 23.0 ppm (n=10), Na concentration 5.4 to 27.8 ppm (n=10), and K concentration 0.7 to 2.5 ppm (n=10).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Newfoundland and Labrador, south to Pennsylvania and the Great Lakes area in the east and to Oregon and Montana in the western mountains. Fennoscandia, western, eastern and central Europe, North Asia.

Subfossil Distribution in North America. – British Columbia, Greenland, Iowa, Michigan, Minnesota, Ohio, Ontario, Wisconsin and Yukon Territory (Miller 1980a). New records: (1) CRH 11, Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 3, as *Calliergon cf. trifarium*. (2) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (3) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (4) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (5) HH69-21 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 102. (6) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (7) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (8) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (9) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (10) Kitchener, Ontario; between 6900 B.P. and 7700 B.P.; Bryological Report 274. (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (12) Kitchener, Ontario; below 7700 B.P.; Bryological Report 320. (13) Kitchener, Ontario; below 8890 B.P.; Bryological Report 322. (14) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (15) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 389. (16) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 392. (17) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (18) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Calliergon unidentified species

Subfossil Distribution in North America. - Minnesota and Northwest Territories (Miller 1980a). New records: (1) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159. (2) Chandalar River, 3 km east of Caro, Alaska; >30,000 B.P.; Bryological Report 184, as *cf. Calliergon* species. (3) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (4) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (5) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (6) Kitchener, Ontario; below 8800 B.P.; Bryological Report 322. (7) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (8) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (9) Cape Deceit Quaternary Exposure, Near Deering (station 1-2), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 340; Matthews 1974a, as *cf. Calliergon* species. (10) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (11) Cape Deceit Quaternary Exposure, Near Deering (station 5-6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 345, Matthews 1974a, as *cf. Calliergon* species. (12) HH68-9 (station 12), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 386, as *cf. Calliergon* species. (13) HH68-9 (station 7), Old Crow Basin, Yukon Territory; Wisconsinan; Bryological Report 424. (14) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Calliergonella cuspidata (Hedw.) Loeske

Diagnostic features. – *Leaves* widely ovate-cordate, often with a sharp apiculus or shortly acute; *costa* absent or short and double; *alar cells* strongly differe[illegible]ed, inflated and thin-walled, in a convex group not reaching the middle of the leaf base. *Stem* with inflated epidermal cells, outer walls thin, forming a continuous hyalodermis.

Habitat. – In rich fens and sedge meadows, in ditches and eutrophic swamps. pH 7.0 to 7.5 (n=3), conductivity 66 to 410 microScm^{-1} (n=3), Ca concentration 8 to 76 ppm (n=3), Mg concentration 1.4 tp 9.7 ppm (n=3), Na concentration 8.1 to 27.1 (n=3), K concentration 0.0 to 0.4 (n=3).

Recent Distribution. – Circumboreal. Bipolar. North America: common in the east: Labrador and Newfoundland, south to Tennessee, in the west in a few scattered localities (British Columbia and California). South America: Argentina. Europe, northern Africa, Asia, Jamaica, Macaronesia, New Zealand.

Subfossil Distribution in North America. – Alberta (Miller 1980a). New records: (1) Wagner Property, Edmonton area, Alberta; Holocene peat, 60 to 70 cm below water surface; Bryological Report 206. (2) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 263, as *cf. Calliergonella cuspidata*.

Discussion. – The closely related *Calliergon* species can be distinguished by their single and well developed forked costa. In western North America (and in New Zealand) *C. cuspidata* is probably recently introduced (Schofield 1974). The species is distinctly weedy and is commonly found in mesic and acid habitats.

Campylium

Species of the genus *Campylium* are distinguished by their ovate-cordate leaf base with an abrupt constriction at the insertion and the long slender upper part of the lamina, forming an tubular apex. *Campylium* species often have long, narrow and thick-walled medial cells, a useful character state to differentiate between small *Campylium* specimens and *Amblystegium* fragments. The medial cells become gradually shorter in the basal part of the lamina. Subfossil fragments often have a characteristic yellow or golden color, in contrast with many other members of the Amblystegiaceae, which are reddish-brown or dark-brown.

Only two species and one variety are presently recognized in my collections. As a result of critical study of the material that I named *C. chrysophyllum* (Brid.) J. Lange, *C. polygamum* (B.S.G.) C. Jens. and *C. radicale* (P. Beauv.) Grout in Janssens (1980b) it is clear that these fragments are poorly preserved forms of the more common species discussed below. The three above mentioned taxa have published fossil records listed in Miller (1980a).

The present day distribution of *C. stellatum* and its variety *arcticum* is based on herbarium material studied (see the captions to the figures). The other information in compiled as explained in Chapter II.

Campylium hispidulum (Brid.) Mitt.

Diagnostic features. – *Leaves* wide-spreading to squarrose, around 1 mm long, flat at the base, concave at the middle of the lamina and tubulose at the apex; *costa* reaching half way up the lamina or shorter and branched; *margins* often finely denticulate all around or sharply denticulate at the base and entire towards the apex, or completely entire; *medial cells* thick or thin-walled, smooth; *alar cells* numerous or few, small, quadrate, in gradually differentiated groups.

Habitat. – On moist calcareous soil, bases of trees, decaying bark and stumps.

Recent Distribution. – Circumboreal. North America: from Alaska to Labrador, throughout

Canada south to British Columbia and Montana in the west, and in eastern, midwestern and central United States. Mexico. Central and South America, Europe, Asia and Japan.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23, as *Campylium cf. hispidulum*. (2) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (3) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370.

Discussion. – No attempt was made to distinguish the variety *sommerfeltii* (Myr.) Lindb. in the fossil material. This taxon is considered by Grout (1928–34) to have fewer differentiated alar cells. The variety *cordatum* Grout (1928–34), with numerous alar cells, is considered by Crundwell and Nyholm (1962b) as the endemic North American *C. hispidulum*. It is only found in the United States (Alabama, Tennessee, Missouri, Kansas, Minnesota, Illinois, Ohio, Pennsylvania, New Jersey) and for Canada in Ontario and New Brunswick. These authors also renamed material called *C. hispidulum* by many European and North American bryologists as *C. sommerfeltii* (Myr.) Bryhn. This taxon is truly widespread and its distribution is the one reported above. Material named *C. sommerfeltii* by European bryologists is renamed *C. calcareum* Crundw. *et* Nyholm, an endemic European taxon. These new combinations are very confusing and further work on this problem is needed.

Campylium stellatum (Hedw.) C. Jens. var. *stellatum*

Diagnostic features. – *Leaves* erect-spreading to squarrose, straight, 1 to 2 mm long, weakly concave in the basal part, tubulose or flat in the upper half; *costa* short, double or absent; *margins* entire; *medial cells* often porose; *alar cells* gradually or more abruptly differentiated from shorter basal cells, or inflated, thin-walled and hyaline, or inflated, thick-walled and brown, not reaching the costa.

Habitat. – On more or less calcareous soil, sometimes on rocks in moist or wet habitats.

In fens, along streamsides, in roadside ditches, in seepage areas around springs. The pH ranges from 6.9 to 7.9 (n=36), conductivity 66 to 1040 microScm^{-1} (n=36), Ca concentration 2.8 to 116.0 ppm (n=27), Mg concentration 1.4 to 51.6 ppm (n=29), Na concentration 6.3 to 28.2 ppm (n=28) and K concentration 0.0 to 7.2 ppm (n=28).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Labrador and Newfoundland, rare in the Arctic Archipelago, south to Pennsylvania and Ohio, disjunct to North Carolina in the east, through the western mountains to British Columbia, Alberta and Montana, disjunct to Wyoming, Colorado and New Mexico. Europe, Svalbard, Caucasus, northern and central Asia, Korea, Japan.

Subfossil Distribution in North America. – Alaska, Alberta, Indiana, Iowa, Michigan, Minnesota, New York, North Carolina, Northwest Territories, Vermont and Wisconsin (Miller 1980a). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) CRH 12, Old Crow Basin, Yukon Territory; 35,500 B.P. (GSC-2507); Bryological Report 40. (3) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148. (4) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (5) Koyukuk River, 6 km downstream from Henshaw Creek, Alaska; 52,800 ± 1300 B.P. (QL-1283); Bryological Report 168. (6) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (7) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (8) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (9) Wagner Property, Edmonton area, Alberta; Holocene peat, 60 to 70 cm below water surface; Bryological Report 206. (10) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (11) CRH 12 (station 2); Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (12) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (13) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; >39,000 B.P. (I-4099); Bryological Report

350, Matthews 1974a. (14) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383. (15) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (16) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (17) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - Subfossil material is characterized by the frequent absence of the alar cell groups, because of imperfect preservation. The distinctive variety *arcticum* is discussed below.

Campylium stellatum var. *arcticum* (Williams) Sav.-Ljub.

Diagnostic features. - *Leaves* erect-spreading to squarrose, straight, 1 to 2 mm long, strongly concave in the lower half and channeled in the upper half; *costa* stout, double or absent; *margins* entire; *medial cells* often porose; *alar cells* gradually differentiated, inflated, hyaline or orange, numerous, reaching to the base of the costa and often also along the margins half way up the basal part of the leaf.

Habitat. - In hummocky tundra, on streamsides and pond shores. Locally very abundant in the high arctic.

Recent Distribution. - Endemic to North America: Ellesmere Island, Devon Island, Melville Island, Banks Island and Baffin Island.

Subfossil Distribution in North America. - (1) Section Creek, 9 km upstream from Sagavanirktok River, Alaska; 12,690 ± 180 B.P. (I-10,567); Bryological Report 182, Hamilton 1979b, p. 29. (2) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (3) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (4) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302.

Discussion. – This distinctive variety is distinguished by strongly concave leaves. This feature causes them to disrupt or fold when mounted on a slide. The huge adaxially convex, bulging alar cell groups are very obvious when the leaves are observed attached on the stem.

Campylium unidentified species

Subfossil Distribution in North America. – Minnesota and Northwest Territories (Miller 1980a). New records: (1) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I–10,509); Bryological Report 181, Hamilton 1979b, p. 41. (2) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC–2200); Bryological Report 280, Mott *et al.* 1980.

Cratoneuron

Species of this genus are differentiated from other Amblystegiaceae by their cordate–lanceolate leaves with a stout costa.

Cratoneuron filicinum (Hedw.) Spruce

Diagnostic features. – *Leaves* straight to falcate–secund, cordate–lanceolate, abruptly narrowed at the insertion, upper part gradually and longly apiculate; *costa* stout, reaching into the apex or occasionally shorter and branched; *margins* sharply denticulate all around or only weakly at the base; *medial cells* around 5:1, walls thick but not porose; *alar cells* gradually but clearly differentiated from the basal cells, walls thick, brown. *Stem* with few lanceolate paraphyllia.

Habitat. – On rock and trees on moist soil. In fens along streams and in seepage areas. Often associated with other *Cratoneuron* species, as well as *Calliergon* and *Philonotis* species.

Recent Distribution. – Circumboreal. Bipolar. North America: from Alaska to Newfoundland, south to Alabama, Texas, New Mexico and California. Europe, Madeira, northern Africa, northern, western, central and eastern Asia. New Zealand.

Subfossil Distribution in North America. – Alberta and Minnesota (Miller 1980a). New records: (1) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 114. (2) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (3) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (4) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391.

Discussion. – Very few paraphyllia are present or preserved. However, the species is easily distinguished by its stiff, cordate-lanceolate leaves, stout costa reaching up high into the apex, short medial cells with thick walls and differentiated alar cells. Occasionally, the costa is short and branched. Branches with only this type of leaves are very confusing (see Bryological Report 174). They can be found on good *C. filicinum* specimens (e.g. Vitt 19273, ALTA!). It is unknown if there is any relation of this feature with habitat.

Drepanocladus (including *Calliergidium*)

Nineteen taxa of the genus *Drepanocladus* have been found in the North American Cenozoic record. Fifteen are present in my own collections. Of the remaining four two have been considered extinct. *Drepanocladus minnesotensis* Williams 1930 is apparently closely related to *D. aduncus* (Wynne 1944a) or *D. exannulatus* (Miller 1980a), while *D. apiculatus* Steere 1942 appears close to *D. revolvens* (Wynne 1944a). *Drepanocladus lycopodioides* (Brid.) Warnst. was identified by Coleman in deposits of the Scarborough Beds of Toronto and by Kuc from Holocene material of Banks and St. Patrick Islands (Miller 1980a). *Drepanocladus revolvens* var. *intermedius* (Lindb. *ex* C. Hartm.) Grout is not recognized as a separate taxon in my classification of *Drepanocladus* (see discussion under *D. revolvens*). I have not been able to locate these specimens and no opinion can be given on the value of these records.

Other extant North American *Drepanocladus* species that have not yet been found among the subfossil bryophytes from the Quaternary deposits are *D. procerus* (Ren. *et* H. Arnell *ex* Husn.) Warnst., *D. schulzei* (Limpr.) Loeske (= *D. fluitans* var. *uncatus* (Hedw.) Warnst., *D. berggrenii* (C. Jens.) Roth, *D. purpurascens* (Schimp.) Loeske, *D. capillaceus* (Mitt.) Broth. *D. jamesii-maccounii* (Kindb.) Grout., *D. latifolius* (Lindb. *et* H. Arnell) Warnst. and *D. pseudosarmentosus* (Card. *et* Ther.) Perss. The discussion under *D. crassicostatus* contains more information on the status of *D. trichophyllus* in North America. *Drepanocladus procerus*, formerly known only from Europe, was recorded for the first time in North America from the vicinity of the Attawapiskat River in the Hudson Bay Lowlands by Persson & Sjörs (1960). This species was locally very abundant in the intermediate fen types in the area. *Drepanocladus procerus* was also annotated from Alaskan material by Persson (Persson & Sjörs 1960) and listed for Newfoundland and British Columbia (Ireland *et al.* 1980). It is closely related to *D. exannulatus* and *D. purpurascens*, the latter not treated in Tuomikoski's paper (1949) but recognized by Persson (Persson & Gjaerevoll 1957). *Drepanocladus procerus* is differentiated by quadrate alar cells forming a distinct, fragile group that does not extend to the costa. The costa is strong, convex at the back and nearly decurrent on the stem. Leaves are strongly falcate-circinate with entire margins (except at the apex). *Drepanocladus purpurascens* is distinguished from *D. exannulatus* by auricles formed by a singly row of strongly elongated alar cells reaching the costa. Several of the fossil *D. exannulatus* specimens in my collection display this feature, but intergradations of this extreme structure with the typical *D. exannulatus* structure of two to three tiers of alar cells and the lack of any other differentiating character states does not warrant the separation of these taxa. *Drepanocladus schulzei* can morphologically be considered within the variability of *D. exannulatus*, but is autoicous (Nyholm 1965, Persson & Sjörs 1960). Sex determination is nearly always impossible in subfossil material.

A detailed analysis of the relationships among the genera *Calliergon*, *Calliergonella* and *Drepanocladus* is given in Tuomikoski & Koponen (1979). New characters used are the presence or absence of nematogons (initials of rhizoids in the leaf, usually cells at the apical part, differentiated in size and shape from the surrounding laminal cells) and the branching pattern (radial *versus* dorsiventral). *Calliergonella*, differentiated from the other Amblystegiaceae by non-decurrent leaves, a rudimentary costa, a hyalodermis, dorsiventral branching and the absence of nematogons, is questioned to belong to this family (Tuomikoski & Koponen 1979). All *Calliergidium* species described belong to other genera. *Calliergidium pseudostramineus*, the species discussed below as *D. pseudostramineus*, is described as *Warnstorfia tundrae* and closely related to *W. fluitans*. The genus *Warnstorfia* contains the species *W. fluitans*, *W. tundrae*, *W. exannulata*, *W. trichophylla* and *W. procera*. The taxa are charaterized by radial branching patterns, nematogons and micronemata, non-plicate perichaetial leaves, few paraphyses, poorly developed annulus, an exostome with scalariform, uneven sides, acuminate leaves, more or less denticulate and well differentiated alar cells. Closely related to *Warnstorfia* are the genera *Calliergon*, *Sarmenthypnum* and *Loeskhypnum*. *Calliergon* is differentiated from *Warnstorfia* by ovate, cucullate and decurrent leaves. Included are *C. giganteum*, *C. cordifolium* and *C. megalophyllum* (= *C. macounii* in North America). Other taxa will have to be reevaluated. *Sarmenthypnum* is intermediate between *Warnstorfia* and *Calliergon* and contains *S. sarmentosum*. It is characterized by the red color, a single functionless nematogon cell and non-decurrent alar cells. *Loeskhypnum* contains *L. badium* and *L. wickesiae*, differentiated from other taxa by the firm cell structure at the base of the leaf.

A second large group outline by Tuomikoski & Koponen (1979) is the genera *Sanionia*, *Scorpidium*, *Limprichtia* and *Drepanocladus*. These taxa have more or less two-sided branching, macronemata but no nemtogons, plicate perichaetial leaves, many paraphyses, a differentiated annulus and an even-sided exostome. *Scorpidium* includes not only *S. scorpioides* and *S. turgescens* (both only distantly related), but also *S. lycopodioides*, *S. trifarium*, *S. vernicosum*, *S. brevifolium* and *S. lapponicum*, taxa described here as *Calliergon* or *Drepanocladus* species. The genus *Limprichtia* contains *L. revolvens* and *L. intermedia*, two species which are doubtfully distinct (see the discussion under *D. revolvens* below). The genus *Drepanocladus sensu stricto* (Tuomikoski & Koponen 1979) has complanate, distichous branching, macronemata, entire margins and well developed alar cells. Three groups can be recognized: (1) the orthophyllous form, including *D. aduncus* and its extreme form, *D. simplicissimus*; (2) forms which are never orthophyllous and have a small group of alar cells, *D. sendtneri*, *D. tenuinervis* and *D. brachiatus* (Australia); (3) and forms with an excurrent costa, *D. capillifolius* and *D. longifolius* (South America). The genus *Sanionia* is unique and monotypic: *S. uncinatus*.

The *Drepanocladus* species constitute 23.4 % of the total of 1648 North American Late Cenozoic subfossil bryophyte records (Kuc & Hills 1971, Kuc 1973e, Miller 1980a and Janssens 1981). The following keys are based on study of herbarium material deposited in ALTA, BR, CANM, DUKE, MICH and S.

Introduction to the multiple access key to the species of *Drepanocladus*

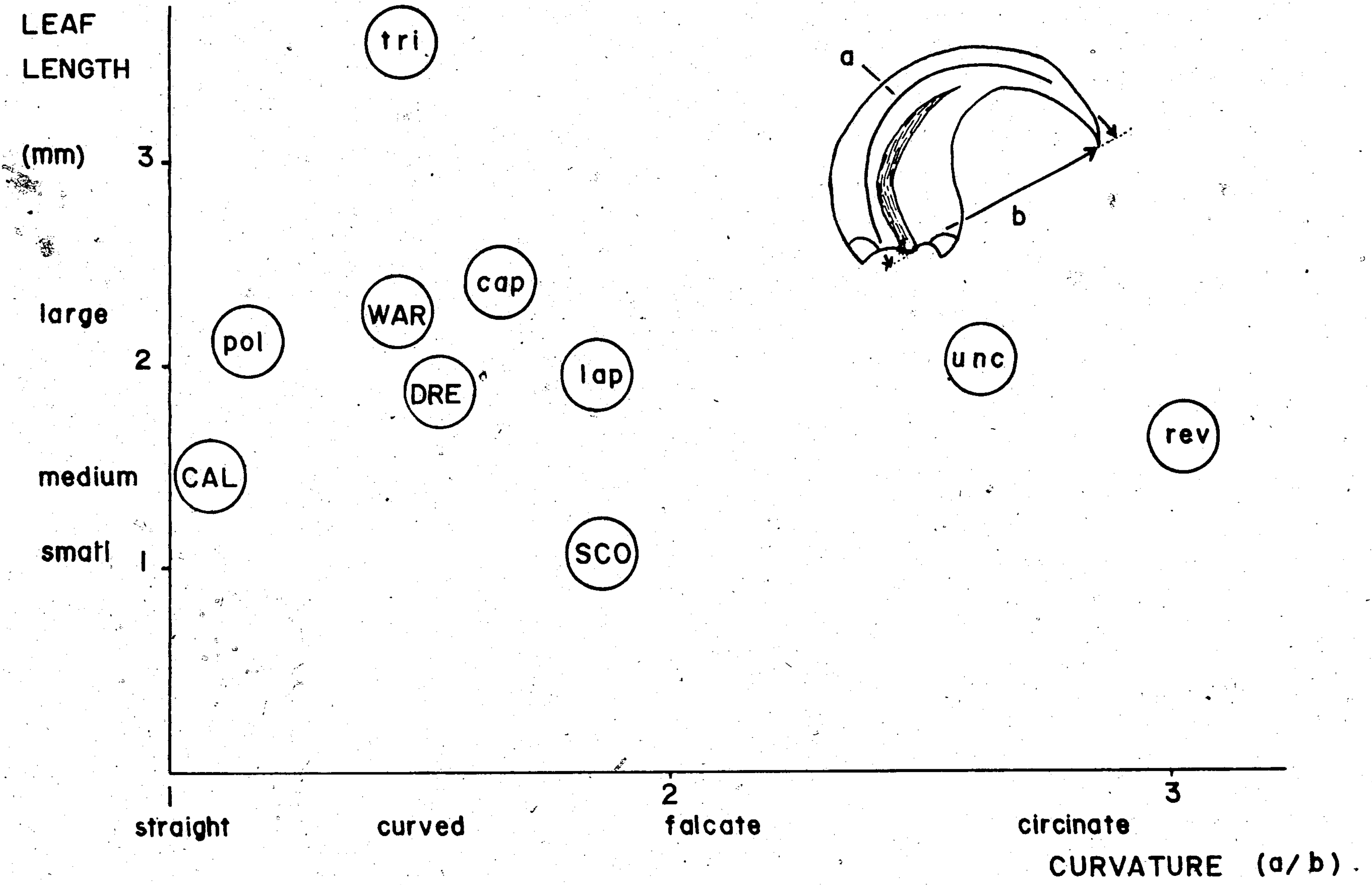
This multiple access key to all *Drepanocladus* taxa, known as fossils in North America, is structured in the same way as the key to species of *Sphagnum* in Alberta (Vitt & Andrus 1977). To construct the key with edge punch analysis cards, consult Vitt & Andrus (1977). For users basically familiar with the genus *Drepanocladus*, the following key offers the opportunity for identification of fragmentary material, a very common feature of subfossil specimens. However, for users without concepts of the taxa of these genera, it is necessary to discuss the relative value of the characters and their states, because not all of them have the same value in guiding the user to the correct identification.

Most important are the character states associated with the alar cells. Character states 33 and 34 (extent of the alar cell region) essentially differentiate the *Warnstorfia* and *Calliergidium* groups from the other taxa (Plates 14:3 and 11:5). Character states 35 to 37 (differentiation of alar cells) are explained by Plates 17:4 and 53:3 respectively. Another reliable character is the structure (entire or denticulate) of the leaf margin. However, it is of less value in subfossil material, because teeth often are not preserved or the aquatic forms (common as subfossils), are characterized by poorly developed denticulation.

In addition to the above characters, a number of character states are very helpful when present. These states, together with a reference to a figure and occasionally some notes on their interpretation, are as follows: (1) Circinately curved leaves (character state 4), Plate 41:1. This very characteristic feature will be always found in younger (or apical) leaves of *D. uncinatus* and in all leaves of *D. revolvens* fragments. (2) ovate leaves (character state 5), Plate 17:1. ([illegible]e leaves (character state 11), Plate 50:1. (4) apiculate (character state 15), Plate [illegible] narrowly obtuse (character state 16), Plate 38:1, and hooked leaf apices (character state 17), Plate 38:1. (5) branched or forked costa (character state 23), Plate 29:1. (6) costa reaching into the apex and beyond (character state 27), Plate 23:1. (7) pentagonal stem transverse section (character state 47), Plate 47:2. Some care must be taken with this character. Many subfossil bryophyte stems are strongly compressed or desiccated, creating the illusion of an angular transverse section. However, a well preserved *D. tundrae* pentagonal stem transverse section (Plate 47:2) clearly shows ridges of cells with narrow lumina. The cells from the inner part of the stem are thin walled, large and smooth, not flattened. It is important to keep in mind that the ridges are built up by stem cells, not by cells from decurrent leaf lamina, as in Plate 26:2. (8) absence of central strand (character state 49), Plate 32:2. Several good sections must be made because often in young and aquatic material the central strand is less than normally developed. (9) formation of a continuous hyalodermis (character state 50), Plate 41:3. Again care must be taken to examine well preserved material.

To check the identification some assistance can be obtained by considering the leaf length and leaf curvature index, displayed in Plate 8. This graph is based on measurements of 269 representative specimens (ALTA, CANM, S and BR). The number of specimens measured per taxon can be found in parentheses after the name of the taxon in the legend for Plate 8. Because of the notorious variability of the species of the genus *Drepanocladus*, absolute measures of the species portrayed in this graph are only marginally helpful. The most interesting differentiating features among taxa or groups of taxa are listed below. (1) *Drepanocladus pseudostramineus* (C. Müll.) Roth and *D. tundrae* are mostly orthophyllous and the plants are smaller than those of the *Warnstorfia* group (*Drepanocladus exannulatus* and *D. fluitans*), with which they are closely related. More information on this complex of species can be found in the species discussion sections.

Plate 8. Relation between leaf length and curvature of major *Drepanocladus* taxa. The leaf length is the mean of the number of specimens listed in parentheses after the taxa below. The curvature (a/b) is the mean of the same number of taxa, except for *D. revolvens* and *D. uncinatus*. For these two taxa it is the lower limit to the 95 % confidence interval around the mean. CAL: *D. pseudostramineus* (2) and *D. tundrae* (8); DREP: *D. aduncus* var. *aduncus* (47), *D. capillifolius* (4), *D. sendtneri* (6) and *D. aduncus* var. *polycarpus* (12); WAR: *D. exannulatus* (34) and *D. fluitans* (32); SCORP: *D. badius* (26), *D. vernicosus* (6) and *D. lycopodioides* var. *brevifolius* (26); pol: *D. aduncus* var. *polycarpus* (12); tri: *D. trichophyllus* (5); cap: *D. capillifolius* (4); lap: *D. lapponicus* (4); rev: *D. revolvens* (30); unc: *D. uncinatus* (28).


LEAF
LENGTH
(mm)
3
large
2
medium
small
1
1
straight
curved
2
falcate
circinate
3
CURVATURE (a/b)
tri
cap
WAR
pol
DRE
lap
CAL
SCO
unc
rev
a
b

(2) *Drepanocladus aduncus* var. *polycarpus* is mostly orthophyllous. However, the alar cell structure (see the species discussion) is a much better character for differentiation from the other species of the true *Drepanocladus* taxa (*Drepanocladus aduncus, D. capillifolius* and *D. sendtneri*). (3) A helpful feature in differentiating *D. trichophyllus* from *D. capillifolius*, or for that matter from all other *Drepanocladus* taxa, is the length of the leaves. There is essentially no overlap with *D. capillifolius*. However, this is less valid for the North American species *D. crassicostatus*, which is closely related to *D. trichophyllus*. (4) *Drepanocladus badius, D. lycopodioides* var. *brevifolius* and *D. vernicosus* are the smallest taxa. One of the most reliable character states to distinguish between two closely related species, *D. vernicosus* and *D. lapponicus*, is the leaf length. *Drepanocladus revolvens* and *D. uncinatus* are the only species displaying truly circinate leaves. This character state is much more constant in *D. revolvens* than for *D. uncinatus*.

Two graphs, Plate 9 and 10 illustrate the relationship of conductivity (see Chapter II for more details) and pH for several *Drepanocladus* taxa. These taxa were the most commonly collected with water samples. Species located at the low end of the minerotrophic gradient (*D. fluitans* and *D. vernicosus*) show a high variability in pH. In highly minerotrophic waters (conductivity above 300 microScm^{-1}) *D. aduncus* and *D. revolvens* are the most commonly collected species. The pH is always above 7.

Multiple access key to species of *Drepanocladus*

Character	Character State
	LEAF
Curvature of leaf	1. straight: 1, 2, 4, 5, 6, 7, 10, 13 2. curved: 1, 2, 4, 5, 6, 7, 10, 12, 13 3. falcate: 1, 3, 5, 6, 7, 8, 9, 11, 12, 14, 15 4. circinate: 11, 14, 15

Plate 9. Relationship between pH and conductivity for several *Drepanocladus* taxa. Triangle: *D. aduncus*. Dot: *D. fluitans*.

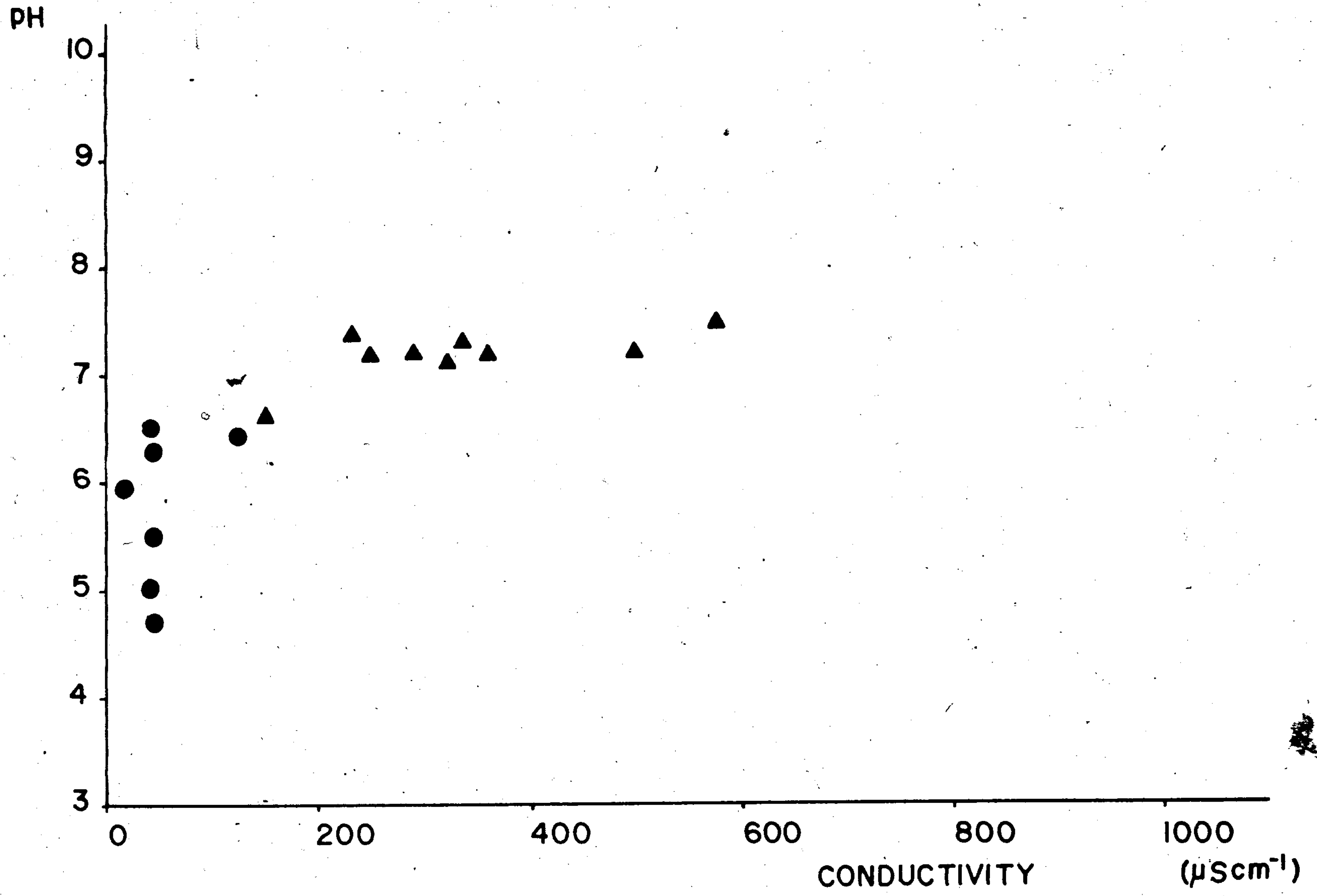
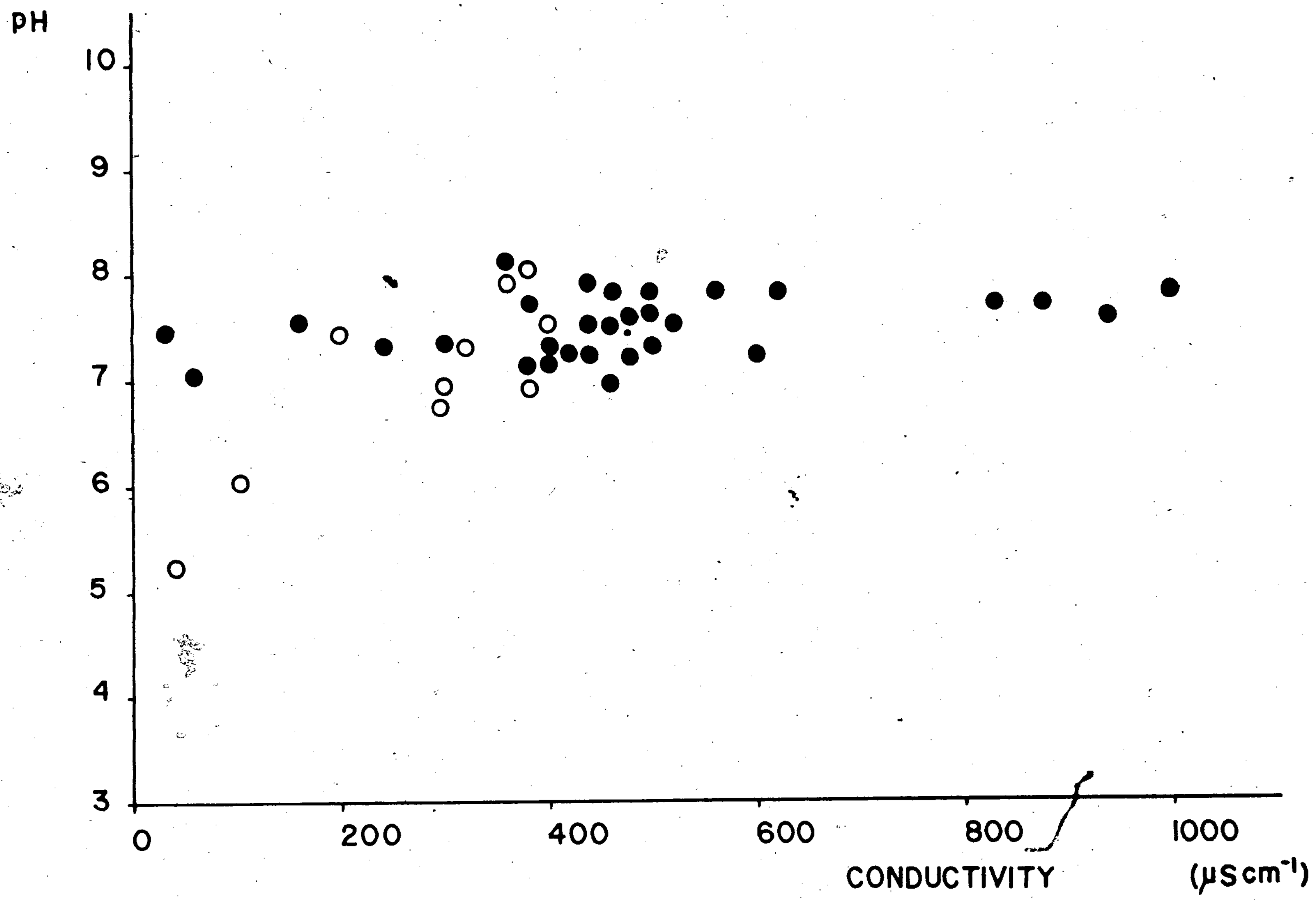

pH
10
9
8
7
6
5
4
3
0
200
400
600
800
1000
CONDUCTIVITY
(µScm⁻¹)

Plate 10. Relationship between pH and conductivity for several *Drepanocladus* taxa. Solid dot: *D.* [illegible]*olvens*. Open circle: *D. vernicosus*.


pH
10
9
8
7
6
5
4
3
0
200
400
600
800
1000
CONDUCTIVITY
(µS cm⁻¹)

Shape of leaf	5. ovate: 4 6. widely ovate-lanceolate: 2, 3, 6, 7, 8, 12 7. ovate-lanceolate: 1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15 8. lanceolate: 4, 12, 14
Leaf surface	9. concave: 3, 6, 7, 8, 9, 10, 11, 12, 15 10. plane: 1, 2, 4, 5, 6, 7, 10, 13 11. plicate: 14
Leaf decurrency	12. decurrent: 2, 4, 6, 10, 13 13. not decurrent: 1, 3, 4, 5, 6, 7, 8, 9, 11, 12, 14, 15
Leaf apex shape	14. acuminate: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15 15. apiculate: 4 16. narrowly obtuse: 1 17. hooked: 10, 13

MARGIN

Denticulation of leaf margin	18. denticulate: 5, 6, 7, 10, 13, 14 19. denticulate at the base only: 1, 4, 12 20. entire: 1, 2, 3, 4, 8, 9, 11, 12, 15

COSTA

Strength of costa	21. strong, clearly outlined, in section convex on both sides: 1, 2, 4, 5, 6, 10, 12, 13, 14, 15 22. weak, poorly outlined, in section plane convex: 1, 3, 7, 8, 9, 11, 14, 15
Branching of costa	23. branched or forked: 3, 7, 9

24. single: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15

Length of costa

25. ending around the middle of the lamina: 3, 7, 9, 11
26. ending in the upper half of the lamina: 1, 2, 6, 8, 10, 11, 12, 13, 14, 15
27. reaching into the apex and beyond: 4, 5

MEDIAL CELLS

Wall thickness

28. thin: 1, 2, 4, 6, 7, 14, 15
29. moderately thick: 1, 5, 6, 10, 13, 14, 15
30. thick: 3, 5, 6, 8, 9, 10, 11, 12, 13, 15

Cell wall pitting

31. porose: 3, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15
32. smooth walled: 1, 2, 4, 6, 7, 8, 10, 14, 15

ALAR CELLS

Extent of alar cell group

33. reaching costa: 2, 5, 6, 7, 10, 13
34. not reaching costa: 1, 3, 4, 6, 9, 11, 12, 14, 15

Differentiation

35. well differentiated: 1, 2, 4, 6, 10, 11, 12, 13
36. poorly differentiated: 3, 5, 7, 8, 9, 12, 14
37. not differentiated: 3, 8, 15

Color of cell walls

38. hyaline: 1, 2, 4, 6, 7, 10, 11, 13, 14
39. yellow: 6, 7, 8, 13, 14
40. yellow-brown to dark brown: 3, 5, 6, 8, 9, 12, 15

Wall thickness

41. thick: 3, 5, 6, 8, 9, 12, 14, 15

42. thin: 1, 2, 4, 6, 7, 8, 10, 11, 13, 14

Pitting of cell walls

43. porose: 3, 8, 9, 12, 15

44. smooth: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14

STEM

Transverse section shape

45. circular: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 14, 15

46. angular: 2, 3, 4, 10, 13

47. pentagonal with prominent ridges: 13

Central cells differentiated from inner cortical cells (thicker walls and smaller lumens)

48. yes: 1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14

49. no: 8, 15

Differentiated epidermal cells (inflated, outer walls thin)

50. forming hyalodermis: 11, 14

51. present, but not forming complete hyalodermis: 4, 6, 7, 10, 14

52. absent: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 15

SPECIES LIST

1. *D. aduncus* (Hedw.) Warnst.
2. *D. aduncus* var. *polycarpus* (Bland *ex* Voit) Roth
3. *D. badius* (C.J. Hartm.) Roth
4. *D. capillifolius* (Warnst.) Warnst.

5. *D. crassicostatus* Janens.
6. *D. exannulatus* (B.S.G.) Warnst.
7. *D. fluitans* (Hedw.) Warnst.
8. *D. lapponicus* (Norrl.) Smirn.
9. *D. lycopodioides* var. *brevifolius* (Lindb.) Mönk.
10. *D. pseudostramineus* (C. Müll.) Roth
11. *D. revolvens* (Sw.) Warnst.
12. *D. sendtneri* (Schimp.) Warnst.
13. *D. tundrae* (H. Arnell) Loeske
14. *D. uncinatus* (Hedw.) Warnst.
15. *D. vernicosus* (Lindb. *ex* Hartm.) Warnst.

Dichotomous key to species of *Drepanocladus*

Based on the characters and character states evaluated in the introduction to the multiple access key, the following dichotomous key is constructed. This key is more difficult to use with poorly preserved material than the mutiple access key, but will better guide the user who is unfamiliar with the value of the different characters in the genus *Drepanocladus*.

1. Alar cells differentiated and reaching the costa, stem transverse section circular to pentagonal with prominent ridges, central cells differentiated from inner cortical cells (thick walls and narrow lumina) . . . . 2.

1. Alar cells undifferentiated or there are several basal cells between differentiated alar cells and the costa, stem transverse section circular, central cells differentiated from inner cortical cells (thick walls and narrow lumina) or undifferentiated . . . . 7.

  2. Margins entire, costa strong, single, ending in the upper half of the leaf, walls of the medial cells thin, alar cells well differentiated, hyaline, with thin walls . . . . .

. . . . *D. aduncus var. polycarpus*

2. Margins denticulate throughout (study several leaves of the fossil fragments, denticulation preserves badly), costa strong or weak, branched or single, short to reaching into the apex and beyond, walls of medial cells thin or thick, alar cells distinctly to indistinctly differentiated, hyaline to dark-brown, with thin or thick walls . . . . 3.

3. Leaves orthophyllous, apex shortly acuminate, narrowly obtuse or hooked, alar cell group widely and longly decurrent, stem transverse section circular to pentagonal with prominent ridges . . . . 4.

3. Leaves falcate-secund to strongly curved, apex acuminate, never blunt, alar cell group not broadly decurrent, stem transverse section circular . . . . 5.

4. Stem transverse section distinctly angular, mostly pentagonal with prominent ridges, formed by cells with narrow lumina . . . . *D. tundrae*

4. Stem transverse section circular to slightly angular . . . . *D. pseudostramineus*

5. Leaves narrowly constricted and with weak costa reaching halfway up in the leaf, alar cells always poorly differentiated . . . . *D. fluitans*

5. Leaves with wide base at insertion and with strong costa, reaching higher than the middle of the leaf or reaching into the apex and beyond, alar cells well to poorly differentiated . . . . 6.

6. Costa reaching beyond the apex, alar cells poorly differentiated, epidermal cells of the stem with thick walls . . . . *D. crassicostatus*

6. Costa ending in the upper half of the leaf or reaching into the apex, alar cells well

differentiated, some of the epidermal cells of the stem inflated and with thin outer walls . . . . *D. exannulatus*

7. Leaves strongly plicate, young leaves strongly denticulate in upper part, epidermal cells of the stem commonly forming a continuous hyalodermis, central cells differentiated from inner cortical cells (thick walls and narrow lumina) . . . . *D. uncinatus*

7. Leaves smooth (not plicate), entire, epidermal cells of the stem sometimes forming a continuous hyalodermis, central cells differentiated from inner cortical cells (thick walls and narrow lumina) or undifferentiated . . . . 8.

8. Alar cells well differentiated (sometimes in a small tight group, not always present on the leaves: look at the stems!), margin mostly denticulate along the basal part or entire, costa single, stem transverse section with central cells always differentiated from the inner cortical cells . . . . 9.

8. Alar cells poorly differentiated or undifferentiated, margin always entire, costa often branched or forked, stem transverse section with central cells differentiated from inner cortical cells (thick walls and narrow lumina) or undifferentiated . . . . 12.

9. Epidermal cells of stem inflated and with thin outer walls, forming a continuous hyalodermis, leaves circinate to strongly falcate-secund, margin entire (except at the apex in some young leaves), alar cells clearly differentiated, two to five, in a small distinct group . . . . *D. revolvens*

9. Epidermal cells of stem with thick walls or some of them inflated and with thin outer walls, but never forming a continuous hyalodermis, leaves falcate or falcate-secund, margin denticulate at the base, alar cells well to poorly differentiated, never in a small tight group . . . . 10.

10. Costa reaching into the apex and beyond . . . . *D. capillifolius*

10. Costa ending in the upper half of the leaf . . . . 11.

11. Walls of alar cells dark-brown, thickened, costa strong, to 100 micrometer wide, medial cell walls thick, porose . . . . *D. sendtneri*

11. Walls of alar cells hyaline, thin, costa weaker, not as wide, medial cell walls thin to moderately thickened, smooth . . . . *D. aduncus*

12. Stem transverse section with central cells not differentiated from the inner cortical cells, costa single, ending in the upper half of the leaf . . . . 13.

12. Stem transverse section with central cells differentiated from the inner cortical cells (narrow lumina and thick walls), costa often branched, ending in the middle of the leaf . . . . 14.

13. Leaves 1.5 to 2.5 mm long, fragments frequently pinnately branched . . . . *D. vernicosus*

13. Leaves 2.5 to 4.0 mm long, fragments unbranched . . . . *D. lapponicus*

14. Leaves erect-spreading, apex acuminate, medial cell and apical cell walls thick and usually not porose . . . . *D. lycopodioides var. brevifolius.*

14. Leaves imbricate, apex frequently apiculate, medial and apical cell walls usually strongly thickened and porose . . . . *D. badius*

Drepanocladus aduncus (Hedw.) Warnst. var. *aduncus* Plate 11

Description (n=47). – *Leaves* falcate-secund to straight, ovate-lanceolate, not to weakly decurrent, (1.2)2.3–2.8(6.3) mm long, maximal width (0.4)0.7–0.8(1.3) mm, basal width (0.2)0.3–0.4(0.7) mm; *apex* slenderly acuminate; *margins* entire or weakly denticulate at the base only; *costa* weak to strong, ending in the upper part of the lamina; *upper leaf cells* elongate, sometimes oblong-hexagonal, walls thin to moderately thick, rarely porose, (17)51–64(120) micrometer long, (3.5)5.6–6.5(11.0) micrometer wide; *alar cells* in a small group not reaching the costa, clearly differentiated, inflated, shortly rectangular to rounded-quadrate, walls hyaline, thin. *Stem* with a circular transverse section, diameter (130)220–270(490) micrometer, central strand weakly developed, epidermal cells with thick outer walls.

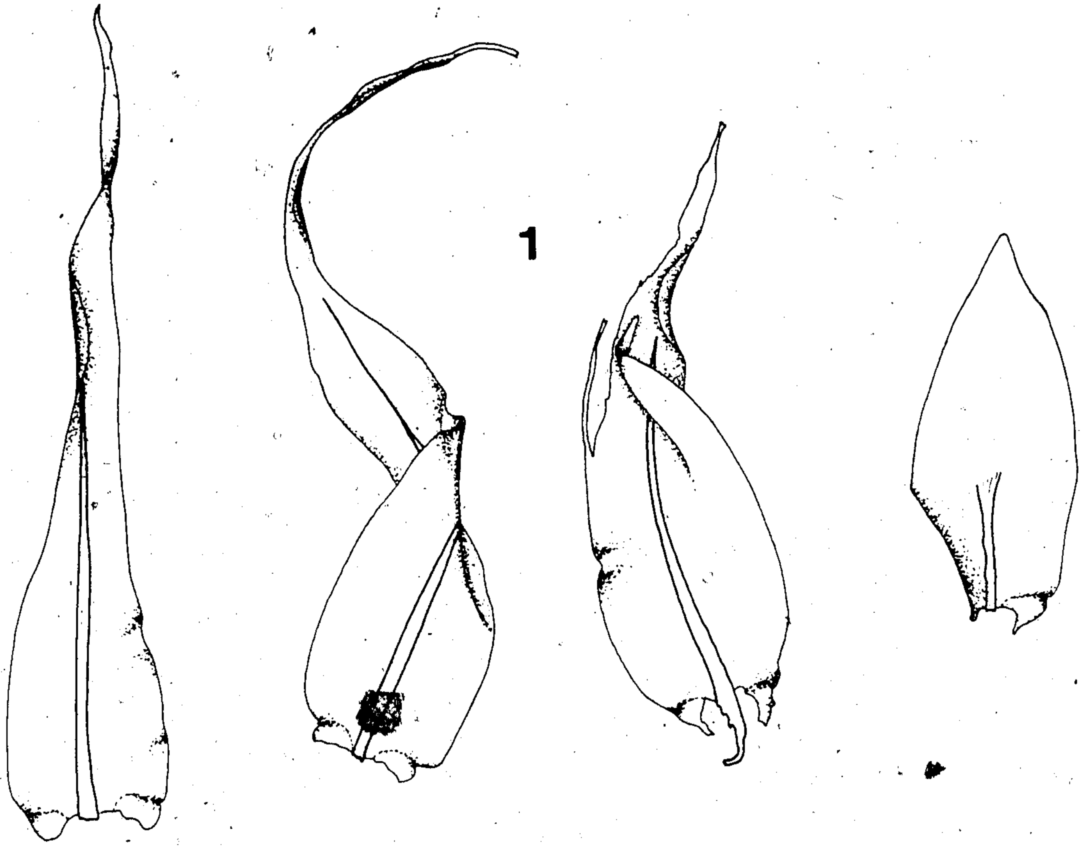
Habitat. – In fens, in seepages, beside lakes and pools in calcareous areas, sometimes in brackish water. On stumps and logs in wet *Betula* forests or in moderately rich fens. Together with *Calliergon giganteum*, *Calliergonella cuspidata*, *Campylium stellatum*, *Plagiomnium ellipticum* and *Tomenthypnum nitens*. The species grows relatively well in phanerogam vegetation. The highest concentration of salt measured in brackish habitats was 3.8 %. pH 6.6 to 7.5 (n=9), conductivity 150 to 575 microScm^{-1} (n=5), Ca concentration 23–61 ppm (n=5), Mg concentration 7.7–23.3 ppm (n=5), Na concentration 1.2–25.0 ppm (n=5) and K concentration 0.05–18.40 ppm (n=5).

Recent Distribution. – Circumboreal and arctic-alpine. North America (Plate 12) : from Alaska to Greenland, uncommon in the Canadian Arctic Archipelago, south to New England, Ohio, Indiana, Illinois, Mississippi, Missouri, Nebraska, Colorado, Arizona, California and Mexico. Elsewhere in Peru, Iceland, Europe, Algeria, northern and central Asia, Australia, New Zealand, Kerguelen.

Subfossil Distribution in North America (Plate 13) . – California, Indiana, Iowa, Minnesota, New York, North Carolina, Ontario, Saskatchewan, Vermont and Wisconsin (Miller 1980a). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585);

Plate 11. *Drepanocladus aduncus* (Hedw.) Warnst. var. *aduncus* (Bryological Reports 114, 115, 178, 267)

1. Leaves (x38).
2. Marginal cells halfway up the leaf (x240).
3. Medial leaf cells (x240).
4. Stem transverse section (x240).
5. Alar cells and undifferentiated basal cells (x240).



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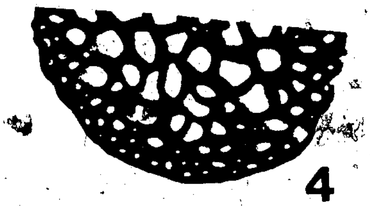

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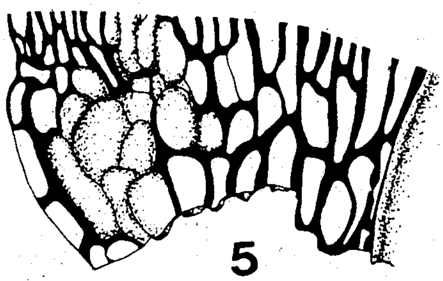

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Plate 12. The present day North American distribution of *Drepanocladus aduncus* (Hedw.) Warnst. var. *aduncus*, based on specimens in ALTA and CANM (solid dots), and Steere (1978a) and Tuomikoski *et al.* (1973) (open circles).

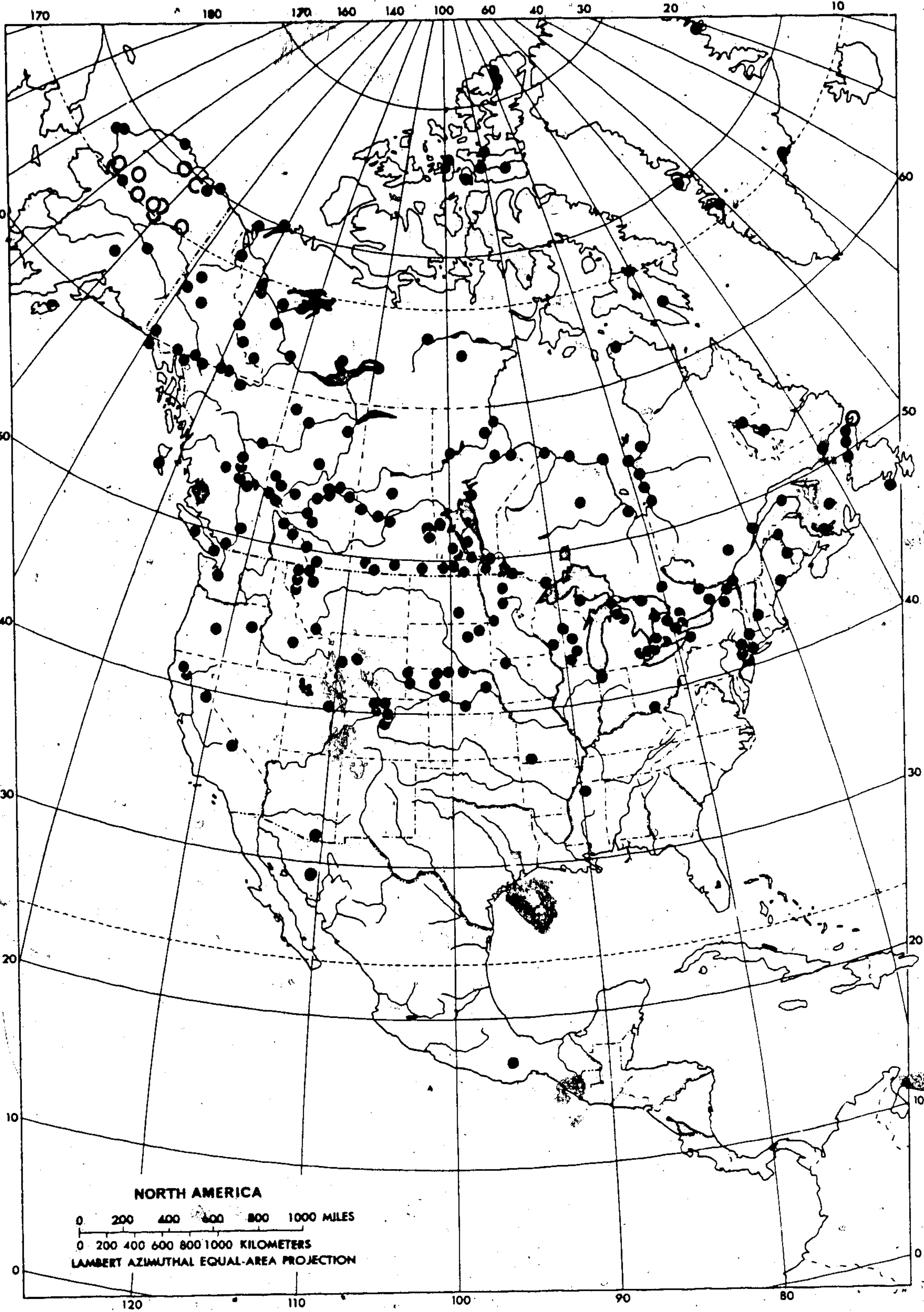
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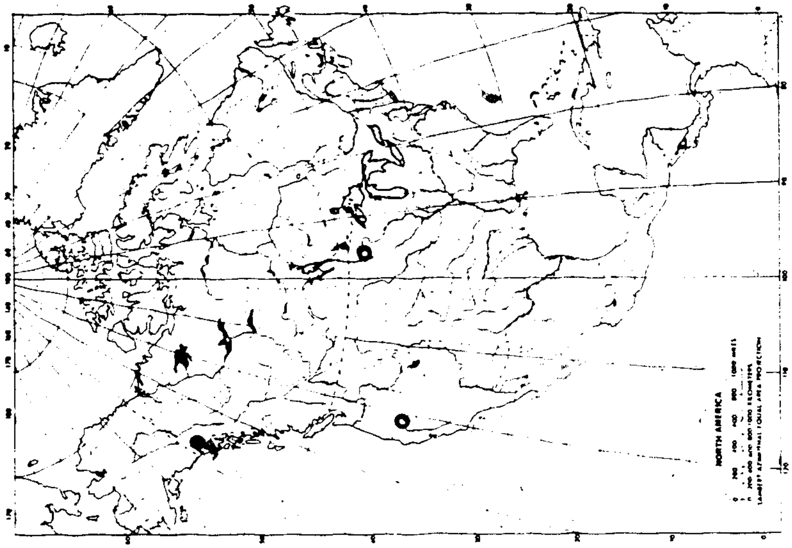
Plate 13. The subfossil North American records of *Drepanocladus aduncus* (Hedw.) Warnst. var. *aduncus*. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.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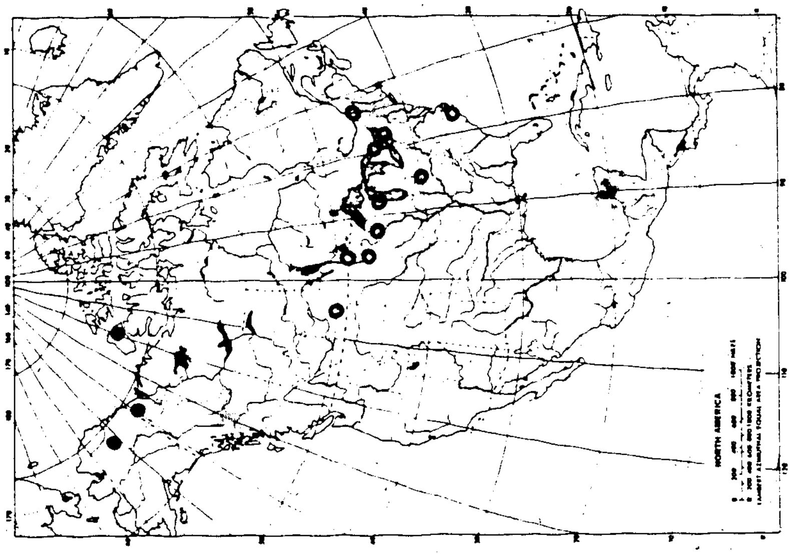
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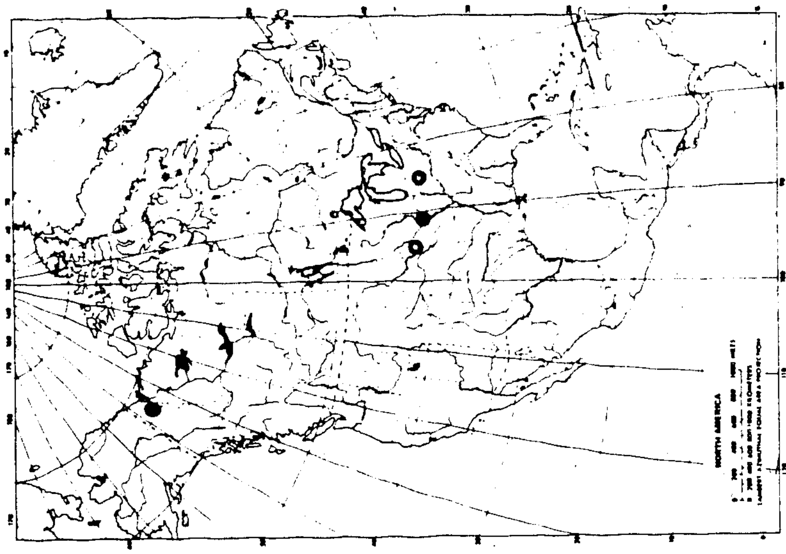
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Bryological Report 33. (2) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (3) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 109. (4) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 114. (5) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 115. (6) HH68-9, Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 134. (7) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (8) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (9) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (10) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (11) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 264, as *D. cf. aduncus*. (12) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (13) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (14) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (15) Shoran Lake, Banks Island, Northwest Territories; 10,200 ± 130 B.P. (GSC-2673); Bryological Report 283. (16) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 294.

Diagnostic Features and Discussion. - Specimens of *D. aduncus* are differentiated from other fossil *Drepanocladus* fragments by mostly distant, curved to falcate-secund leaves and yellow to yellow-brown color. The cell walls are thin and the cells are sometimes short, approaching the length of those of some *Amblystegium* species. The alar cells are more or less strongly inflated, but in the var. *aduncus* the alar cell group does not reach the base of the costa. No teeth are present along the margins, except rarely along the basal part. For the importance of the alar cells in distinguishing the varieties *aduncus* and *polycarpus*, see the discussion under the latter. *Drepanocladus aduncus* var. *kneiffii*, a form with distant, straight leaves and with short medial cells, is sometimes found, but these character states are not at all exclusively associated with each other. Short cells are often found in small strongly falcate-secund leaves. It is not possible to form a clear concept of this latter variety. Another common taxon in the *Drepanocladus* group, considered here as a separate species, *D. capillifolius*, is very distinct. Its differentiating features are listed in the discussion of that species.

One of the most important aspects of the ecology of *D. aduncus* is its ability to thrive well within a luxurious vascular plant vegetation. It is commonly found in ditches subject to fluctuating water level and creeping over dead litter. It is the *Drepanocladus* species which is the most commonly associated with disturbance (e.g. road ditches) and eutrophication (e.g., influx of nutrients from farmland or silt).

Drepanocladus aduncus var. *polycarpus* (Bland. *ex* Voit) Roth Plate 14

Description (n=12). – *Leaves* straight to slightly falcate-secund, widely ovate-lanceolate, decurrent, (1.4)2.4–3.9(5.5) mm long, maximal width (0.7)0.8–1.0(1.3) mm, basal width (0.2)0.3–0.5(0.7) mm; *apex* acuminate; *margins* entire; *costa* strong, ending in the upper half of the lamina; *upper leaf cells* elongate to shortly elongate, (26)57–86(106) micrometer long, (4.5)5.5–7.3(8.6) micrometer wide, walls thin; *alar cells* in a large group reaching the costa, well-differentiated, walls thin. *Stem* with circular or angular transverse section, diameter (230)240–290(380) micrometer, central strand well developed, epidermal cells small and with [illegible]s.

Habitat. – In rich fens, sometimes submerged. On stumps and logs in wet *Betula* forests.

Recent Distribution. – Circumboreal. North America (Plate 15) : rare in the southern Yukon and Northwest Territories, Greenland, common in southern parts of Canada and south to Wisconsin, Iowa, Wyoming, Nevada and California. Europe, Asia.

Subfossil Distribution in North America (Plate 16) . – Michigan, Saskatchewan, Wisconsin (Miller 1980a). New records: (1) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 47. (2) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 120. (3) Kluane Lake,

Plate 14. *Drepanocladus aduncus* var. *polycarpus* (Bland. *ex* Voit) Roth (Bryological Reports 47, 178 and 267)

1. Leaves (x35).
2. Stem transverse section (x224).
3. Alar leaf cells (x560).
4. Marginal leaf cells halfway up the leaf (x560).
5. Medial leaf cells (x560).

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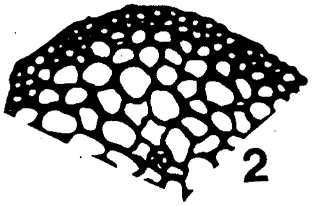

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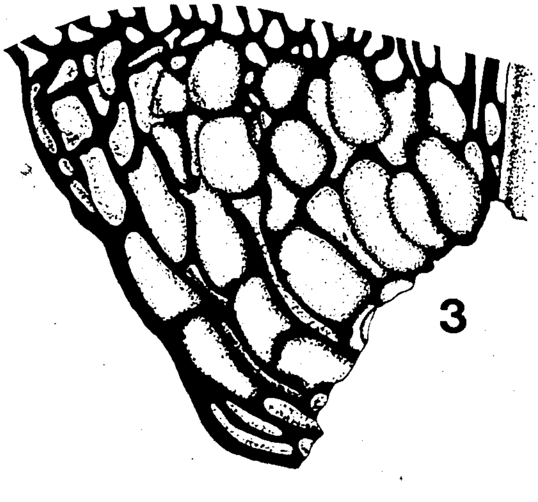

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Plate 15. The present day North American distribution of *Drepanocladus aduncus* var. *polycarpus* (Bland. *ex* Voit) Roth based on specimens in ALTA and CANM.

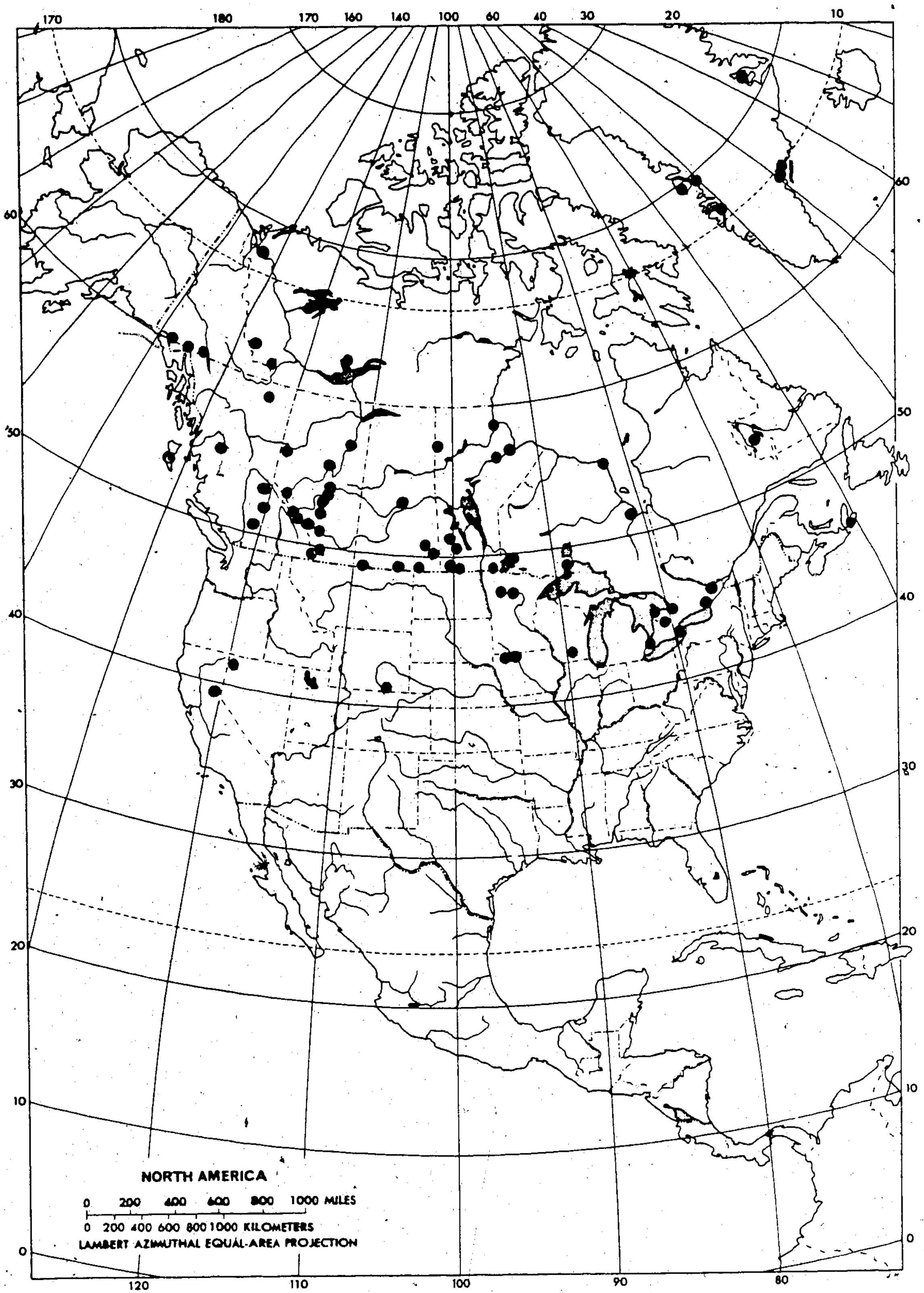
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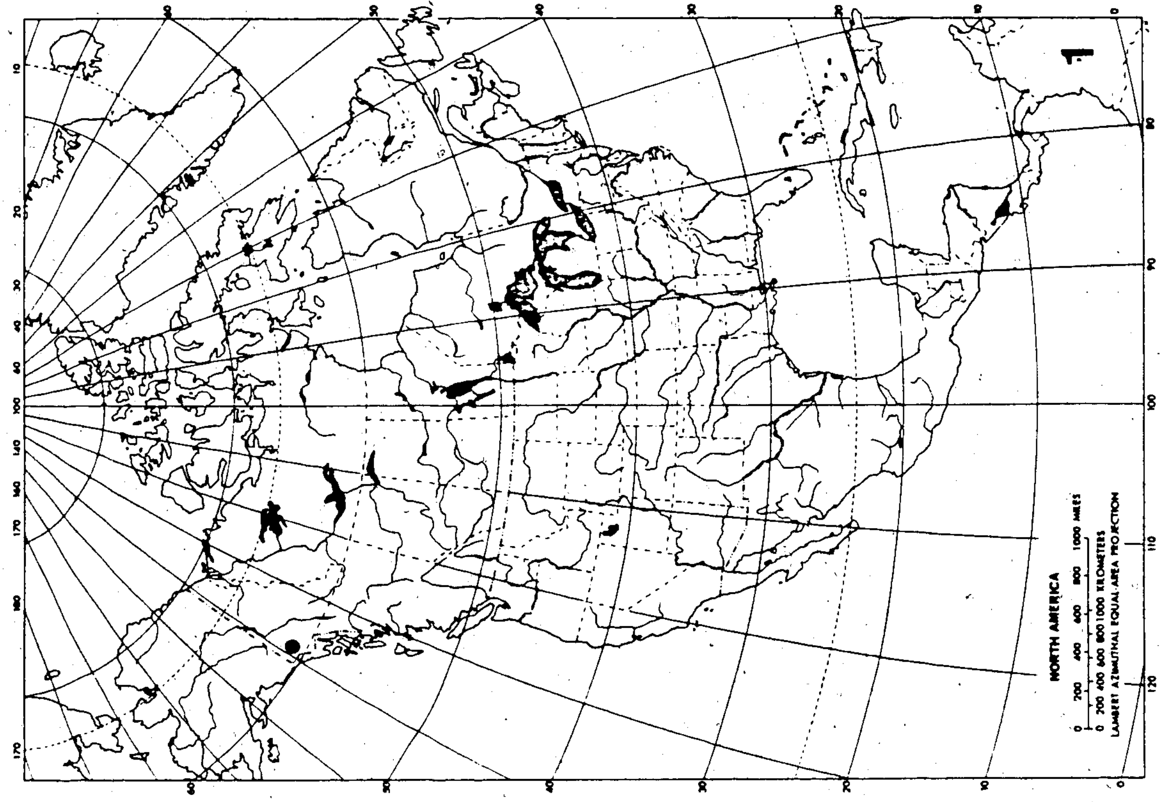
Plate 16. The subfossil North American records of *Drepanocladus aduncus* var. *polycarpus* (Bland. *ex* Voit) Roth. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.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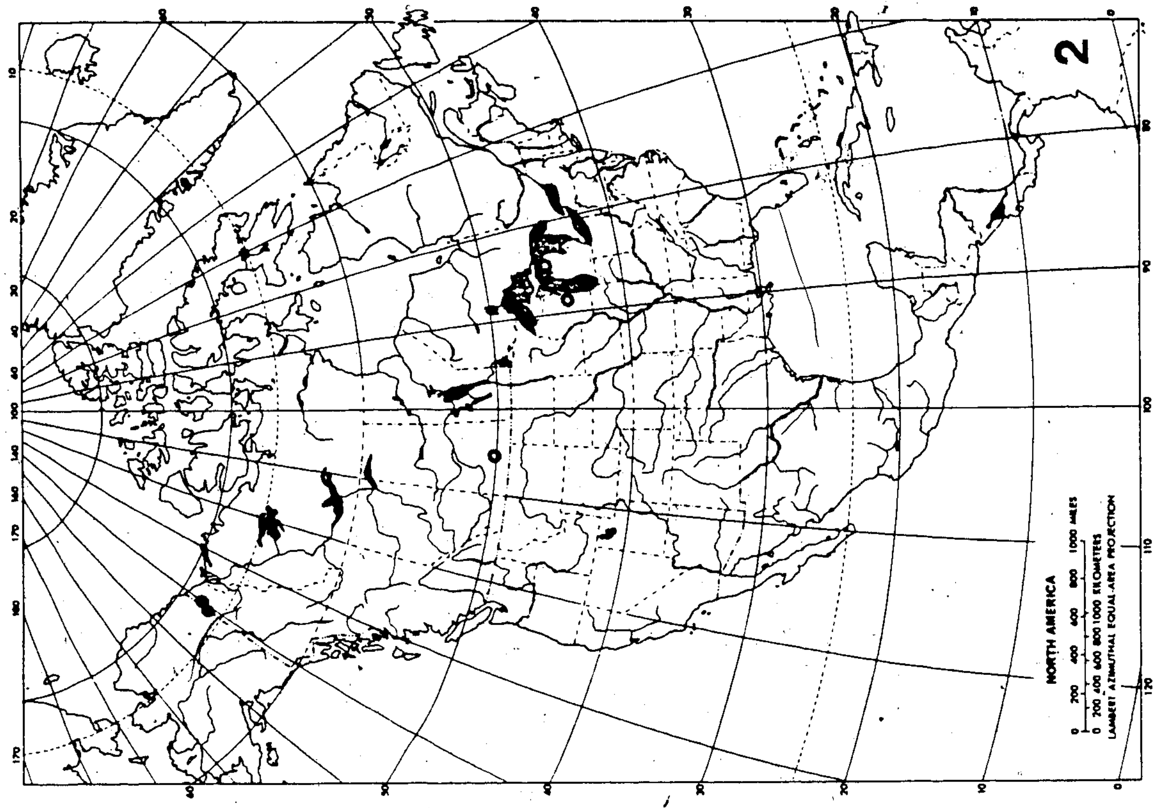
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south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (4) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (5) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Diagnostic Features and Discussion. - The alar cell structure is one of the most reliable characters to differentiate *Drepanocladus* species (see also Lodge 1959, 1960). When these features are applied as a primary character to the differentiation of *D. aduncus* var. *aduncus* and var. *polycarpus*, the most satisfactory concepts for these two taxa result. The strongly differentiated, decurrent alar cell groups that reach the costa in the variety *polycarpus* are associated with a short areolation of medial cells, large, widely ovate-lanceolate and mostly straight leaves and a strong costa. The margin is always entire. My concept does not completely correspond with that of Crum (1973), who described the leaves as slightly to strongly falcate-secund. My ideas are more closely related to those of Nyholm (1965) and Grout (1924-34), except that the leaves of the material that I studied tend to be more elongate and more slenderly acuminate than those illustrated by the latter authors.

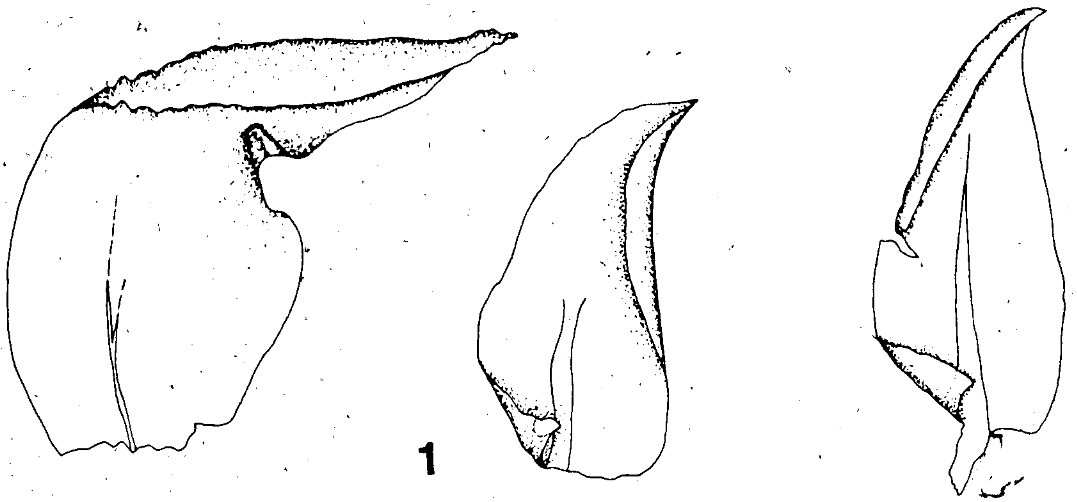
The small number of collections did not warrant any more detailed information on the ecology of the variety. Because it is commonly found among collections named *D. aduncus*, it is assumed that this taxon has a very similar habitat.

Drepanocladus badius (C.J. Hartman) Roth Plate 17

Description (n=26). - *Leaves* falcate-secund, ovate to broadly ovate, strongly concave, imbricate, (1.4)1.8-2.1(2.8) mm long, maximal width (0.5)0.7-0.8(1.1) mm, basal width (0.2)0.3-0.4(0.5) mm; *apex* shortly acuminate to frequently apiculate; *margins* entire; *costa* weak, very often branched or forked, reaching half way up; *upper leaf cells* elongate, (39)52-59(71) micrometer long, (5.5)7.0-7.7(8.7) micrometer wide, walls thick, porose; *alar cells* not or poorly differentiated, enlarged, shortly rectangular, walls brown and thick, porose. *Stem* with most frequently a slightly angular transverse section, diameter (160)225-255(290) micrometer, central strand present, epidermal cells with

Plate 17. *Drepanocladus badius* (C.J. Hartman) Roth (Bryological Reports 109 and 281)

1. Leaves (x42).
2. Medial leaf cells (x670).
3. Stem transverse section (x268).
4. Basal cells and poorly differentiated alar cells (x268).



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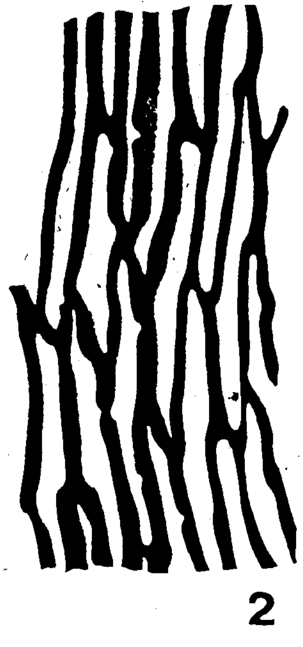

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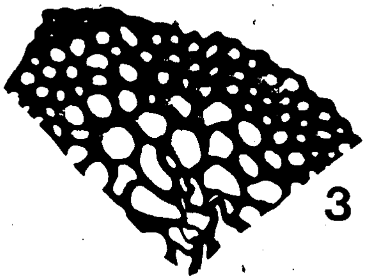

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thick outer walls.

Habitat. – A species of wet habitats, frequently found in more shallow parts of intermediate to rich fens, on irrigated rocks and beaches, sometimes exposed to salt water. Carpets which are completely free from other mosses are rarely seen. The species usually grows associated with *Aulacomnium palustre*, *Calliergon sarmentosum*, *C. wickesii*, *Campylium stellatum*, *D. exannulatus*, *D. revolvens*, *D. uncinatus*, *Paludella squarrosa*, *Scorpidium scorpioides*, *Sphagnum warnstorfii* and *Tomenthypnum nitens*. pH ranges from 4.4 to 7.3.

Recent Distribution. – Circumboreal. Subarctic-arctic species. North America (Plate 18) : common in Alaska and Yukon Territory, rare on the Arctic Archipelago, Greenland, northern Newfoundland, Labrador, northern Quebec and along the Hudson Bay coast, mountains in Alberta and British Columbia. Northern Europe, northern Asia, Svalbard and Japan.

Subfossil Distribution in North America (Plate 19) . – Northwest Territories (Miller 1980a). New records: (1) CRH 12, Old Crow Basin, Yukon Territory; 35,500 B.P. (GSC-2507); Bryological Report 40. (2) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 109. (3) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (4) Stewart Point, Banks Island, Northwest Territories; 9080 ± 160 B.P.; Bryological Report 281.

Diagnostic Features and Discussion. – *Drepanocladus badius* is closely related to *Calliergon wickesiae* Grout and *Scorpidium turgescens* (T. Jens.) Loeske. All three taxa are characterized by incrassate, porose cells, an ovate leaf shape, apiculate apex and poorly developed costa, which may be absent, single and short, double, prominent or inconspicuous, in individual leaves of the same fragment. *Drepanocladus badius* can be differentiated because of its falcate-secund leaves and long acuminate apex.

Plate 18. The present day North American distribution of *Drepanocladus badius* (C.J. Hartman) Roth based on specimens in ALTA and CANM (solid dots), and Steere (1978a), Tuomikoski *et al.* (1973) and Lewinsky (1971) (open circles).

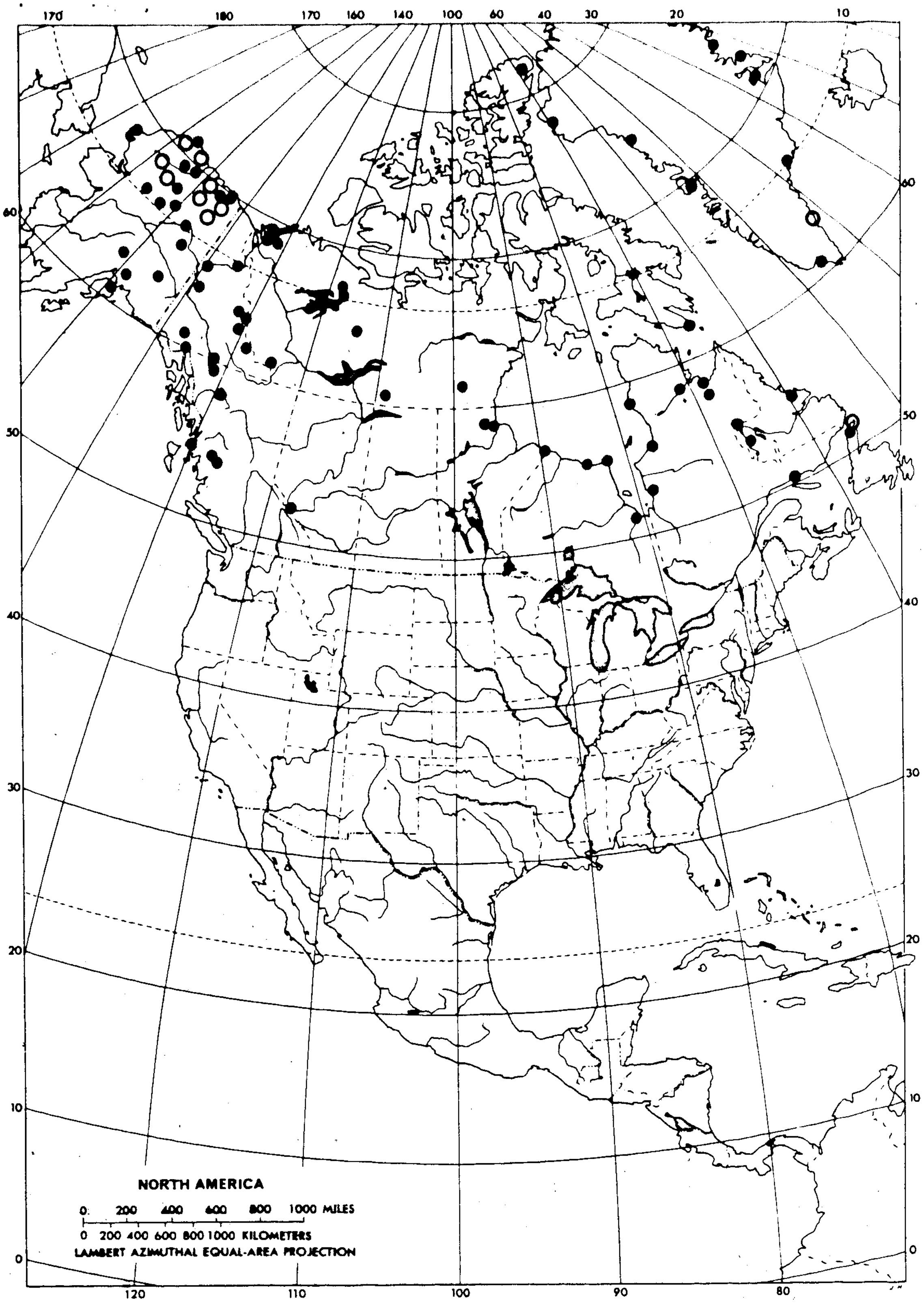
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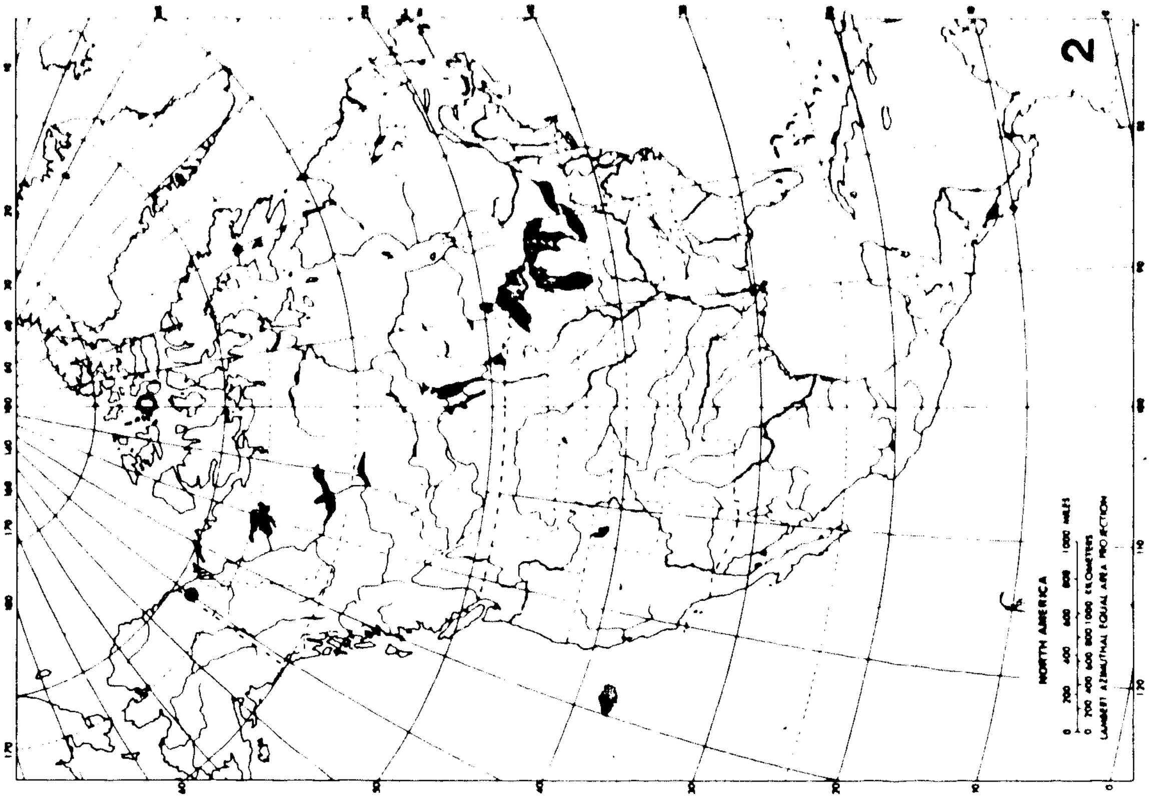
Plate 19. The subfossil North American records of *Drepanocladus badius* (C.J. Hartman) Roth. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.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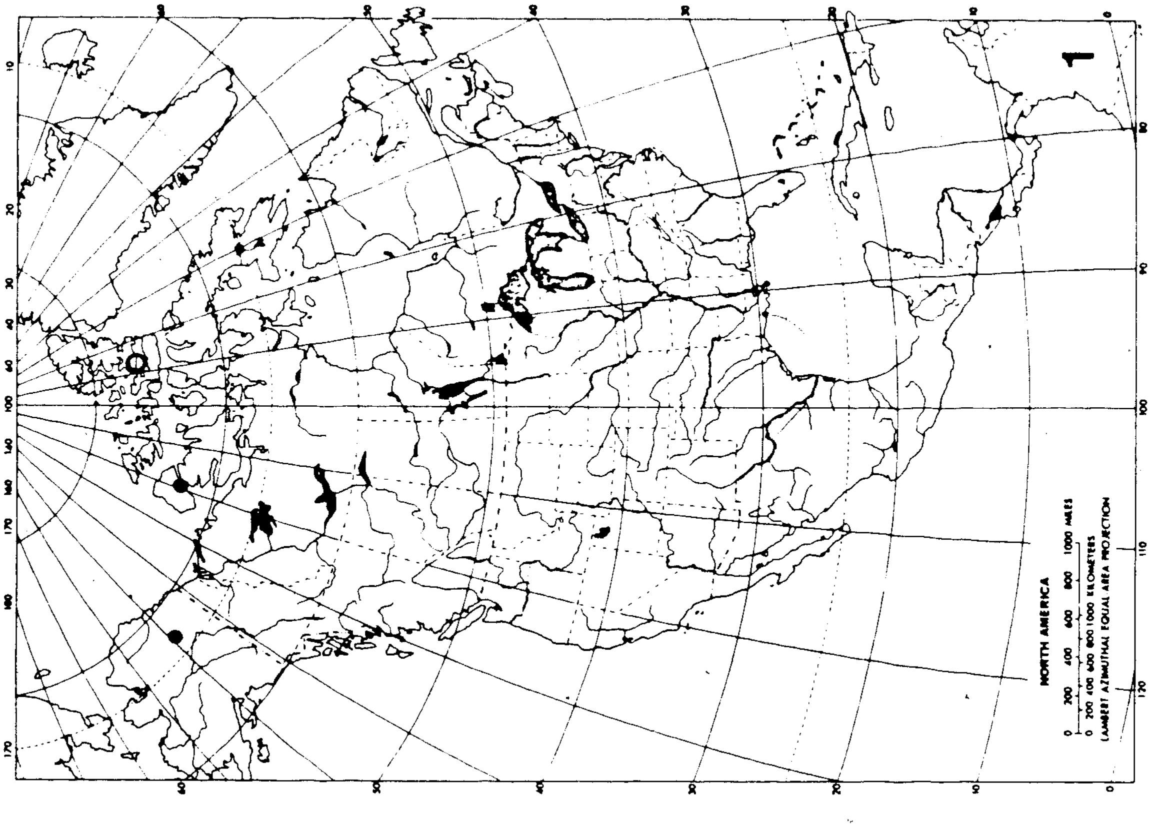
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Scorpidium turgescens and *Calliergon wickesiae* differ from *D. badius* with their straight leaves and short apiculate apices. The difference between the former taxa is more subtle and is primarly based on costa characteristics. Usually some leaves of *C. wickesiae* will clearly exhibit a single costa running to the upper half of the leaf. More study is needed to correlate the costa features with other character states so that these two taxa can be based on a sounder basis.

Drepanocladus capillifolius (Warnst.) Warnst. Plate 20

Description (n=4). – *Leaves* straight to slightly secund, lanceolate to ovate lanceolate, plane, more or less decurrent, 2.4–3.9 mm long, maximal width 0.3–0.9 mm, basal width 0.2–0.4 mm; *apex* slenderly acuminate; *margins* sometimes weakly denticulate at the base, entire; *costa* strong, longly reaching into the apex and beyond; *upper leaf cells* elongate, 50–70 micrometer long, 4.8–7.6 micrometer wide, walls thin; *alar cells* in a small group not reaching the costa, moderately well differentiated, inflated, shortly rectangular to rounded-quadrate, walls thin, hyaline. *Stem* with angular or circular transverse section, diameter 180–250 micrometer, central strand present, epidermal cells sometimes inflated, with thin outer walls, but never forming a continuous hyalodermis.

Habitat – Mostly immersed along the margins of more or less minerotrophic lakes, submerged to two meters in depth.

Recent Distribution – Circumboreal. Scattered within the northern hemisphere distribution of *Drepanocladus aduncus*. North America (Plate 21): Yukon Territory, Mackenzie District, Hudson Bay area and Great Lakes area, in the western mountains only in Colorado, Utah and California. Europe, Algeria, northern and central Asia.

Subfossil Distribution in North America (Plate 22). – Ontario (Miller 1980a). New records: (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) Snake River area, Yukon Territory; 11,700 ± 90 B.P.

Plate 20. *Drepanocladus capillifolius* (Warnst.) Warnst. (Bryological Reports 34: 41 and 269)

1. Leaves (x38)
2. Medial leaf cells (x240)
3. Alar leaf cells (x240)

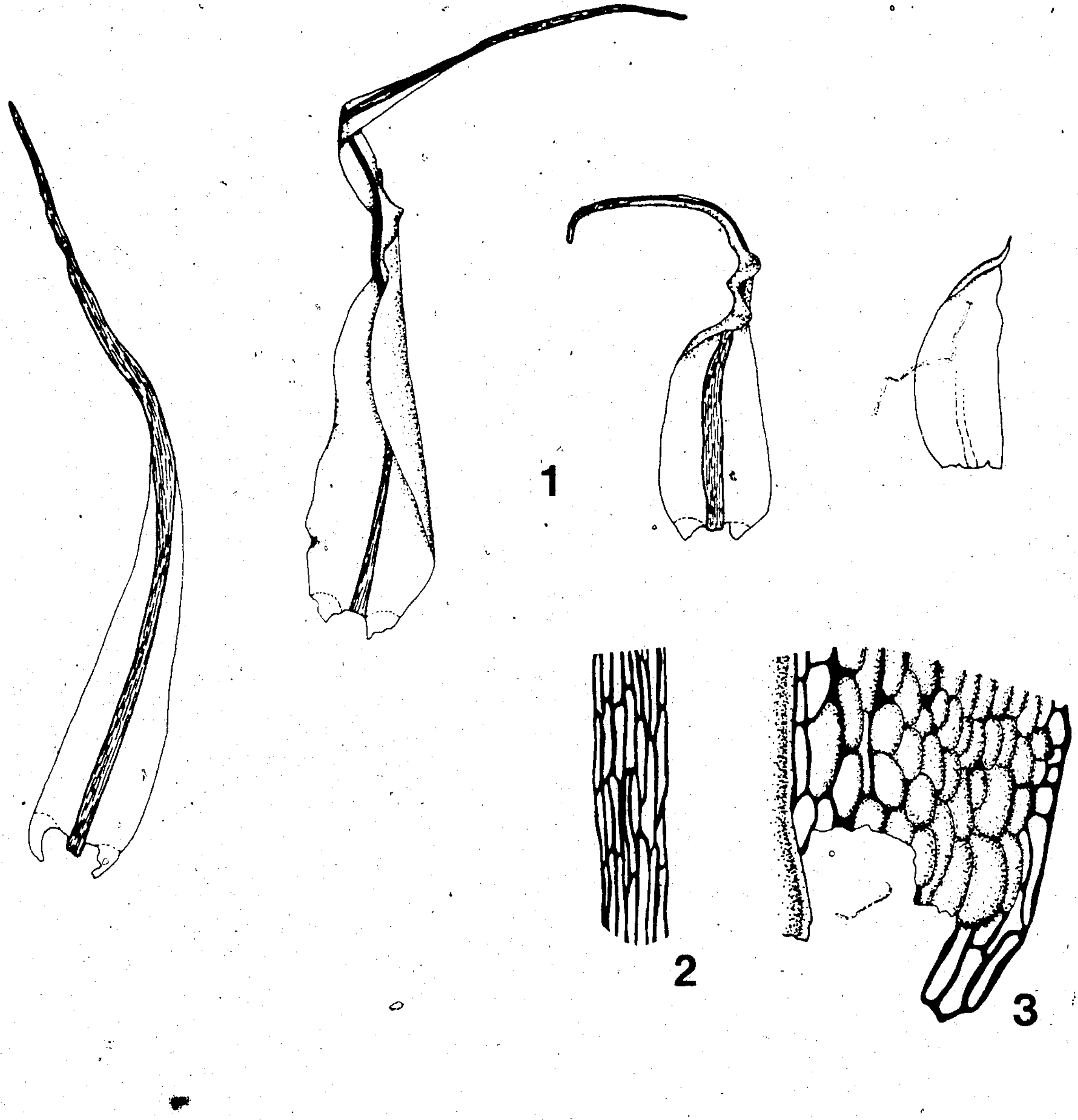
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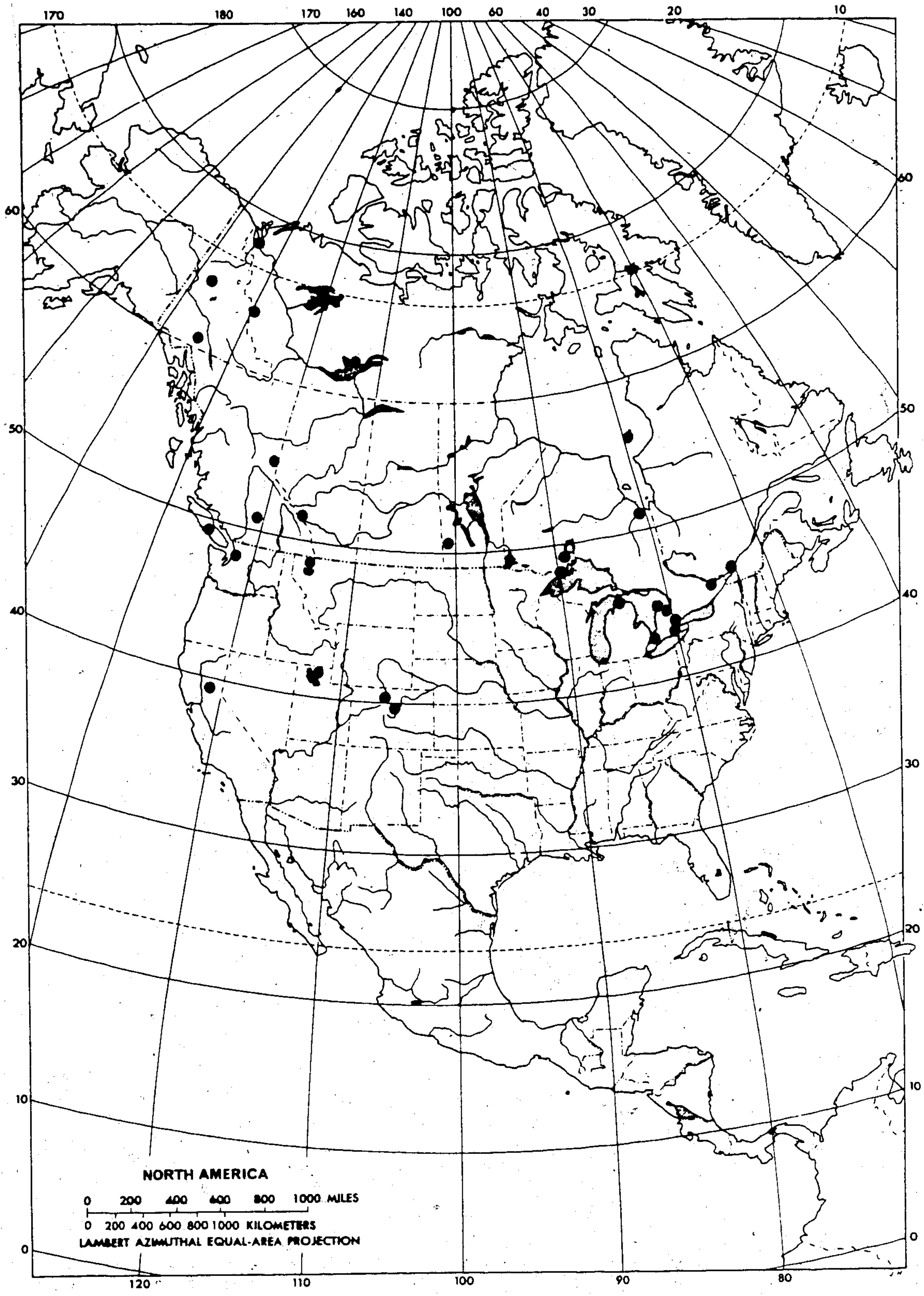
Plate 21. The present day North American distribution of *Drepanocladus capillifolius* (Warnst.) Warnst. based on specimens in ALTA, CANM, NY and C.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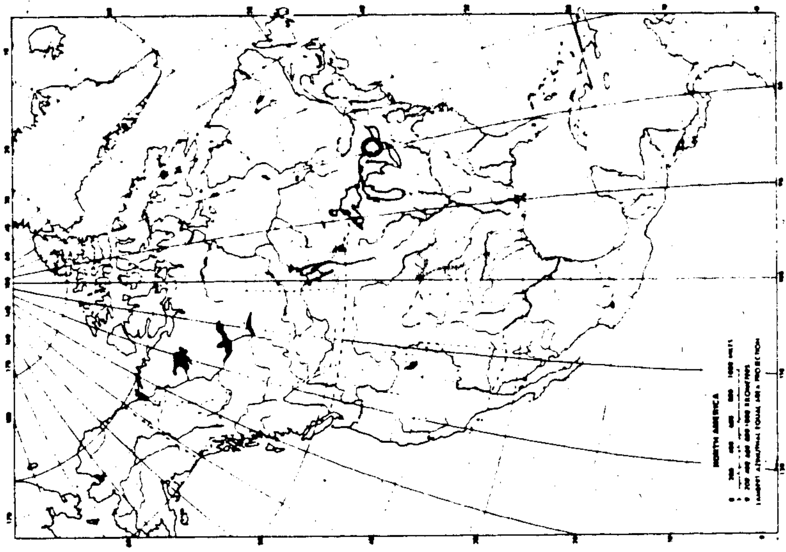
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 22. The subfossil North American records of *Drepanocladus capillifolius* (Warnst.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.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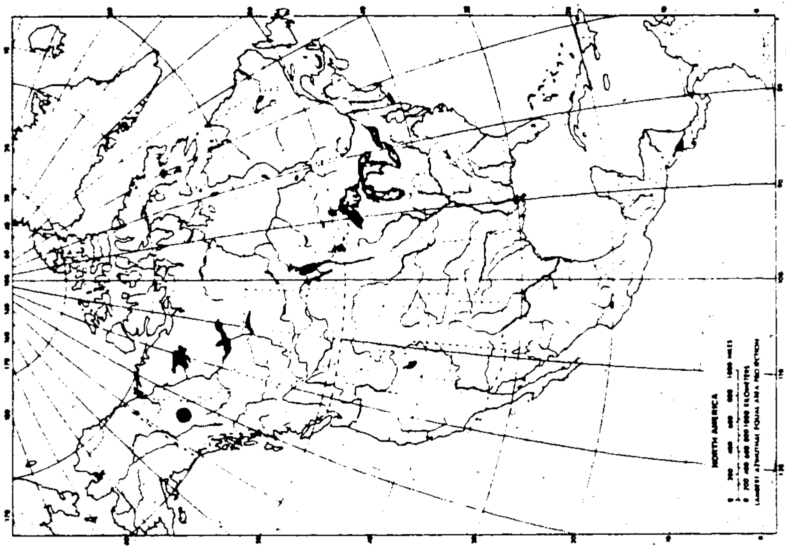
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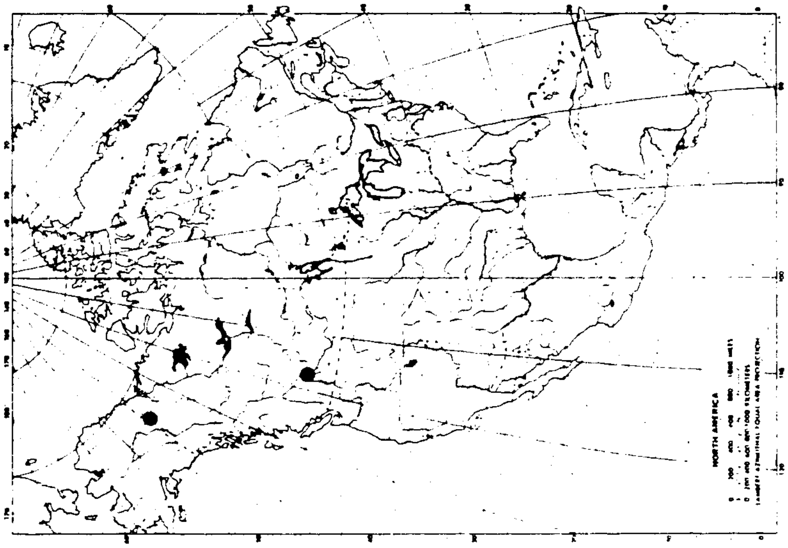
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(GSC-2693) and 11,800 ± 170 B.P. (GSC-2745); Bryological Report 41. (3) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (4) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (5) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (6) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (7) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (8) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370.

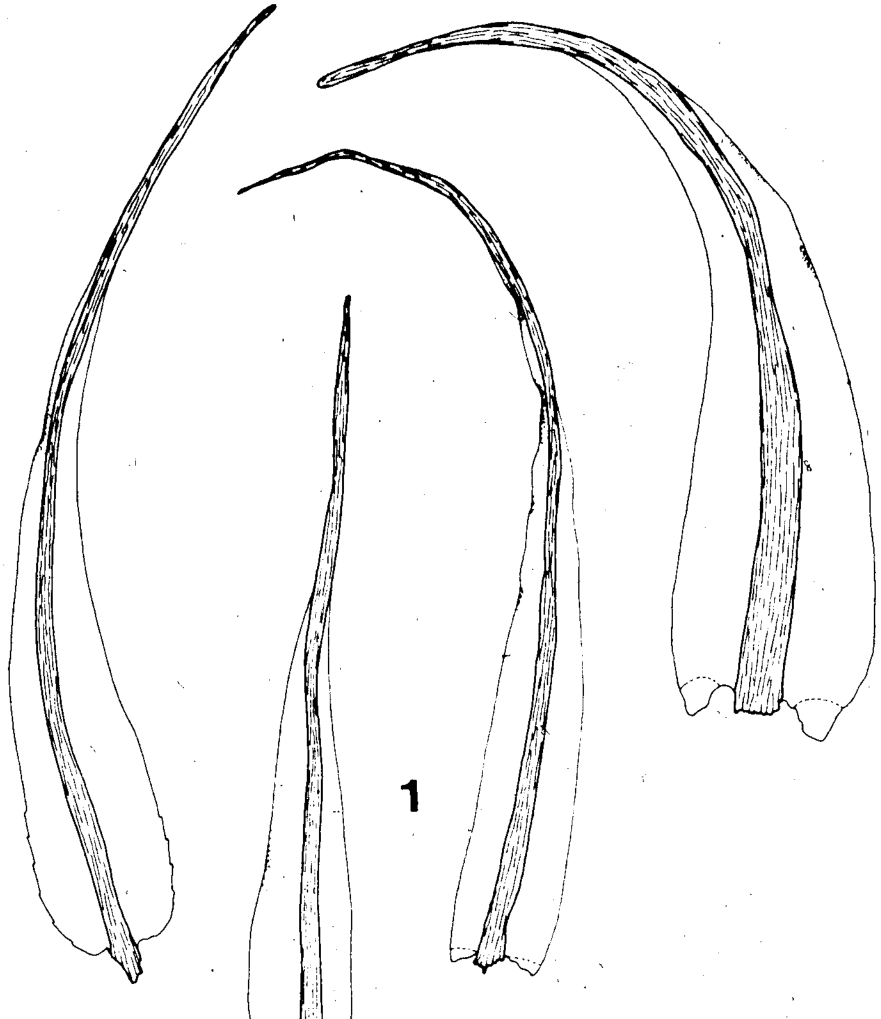
Diagnostic Features and Discussion. - The taxa *D. aduncus* var. *aduncus*, *D. capillifolius* and *D. aduncus* var. *polycarpus* are clearly defined; I can not agree with Crum (1973) who considers *D. capillifolius* a merely an aquatic form of both *D. aduncus* var. *aduncus* and var. *polycarpus*. Alar cell, as well as medial cell morpholgy of *D. capillifolius* is more closely related with that of the variety *aduncus* than with that of the variety *polycarpus*. The alar cell group does not reach the costa in *D. capillifolius*. Marginal teeth are frequently present along the basal part of the leaf, but never in the upper half. The leaves are very narrow and the costa is wide and extends beyond the lamina in the apex.

Drepanocladus crassicostatus Janssens (tentative name to be validated and described later) Plate 23

Description (n=41). - Note: this description is based on fossil specimens (27) and 14 extant populations (ALTA, CANM, NY, COLO and DUKE). *Leaves* straight to slightly curved, ovate-lanceolate to narrowly lanceolate, 3.8-5.9 mm long, maximal width 0.6-1.0 mm, basal width 0.3-0.7 mm; *apex* slenderly acuminate; *margins* denticulate; *costa* strong, longly reaching beyond the apex, biconvex in transverse section, with two stereid bands; *upper leaf cells* elongate, 44-88 micrometer long, 4.7-6.3 micrometer wide, walls thick to moderately thick, porose; *alar cells* in a diffuse group, usually reaching the costa, poorly differentiated, slightly inflated, rectangular, walls brown, moderately thickened. *Stem* with a circular transverse section, diameter 270-420 micrometer, central strand well developed, epidermal cells with thick outer walls.

Plate 23. *Drepanocladus crassicostatus* Janssens (Bryological Reports 54, 62, 159, 167, 308 and 434)

1. Leaves (x35).
2. Stem transverse section (x220).
3. Alar leaf cells (x220).
4. Costa transverse section (x220).
5. Marginal cells halfway the leaf (x560).
6. Medial leaf cells (x560).



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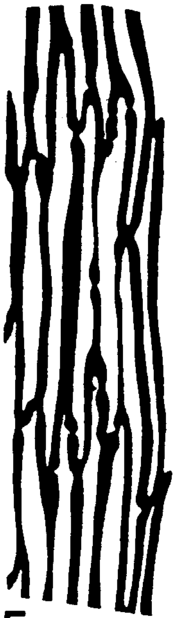

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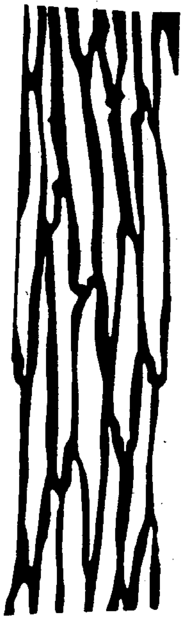

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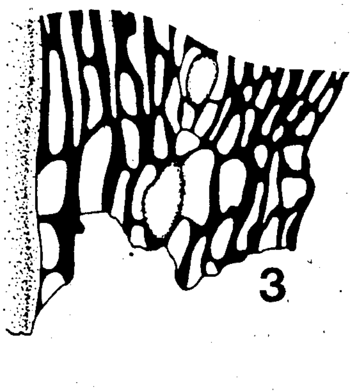

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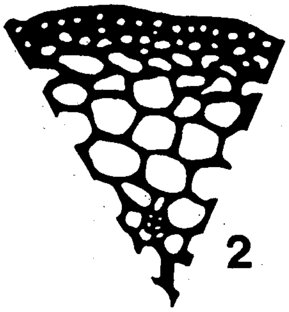

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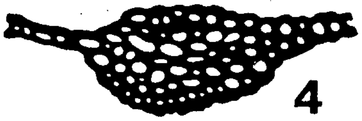

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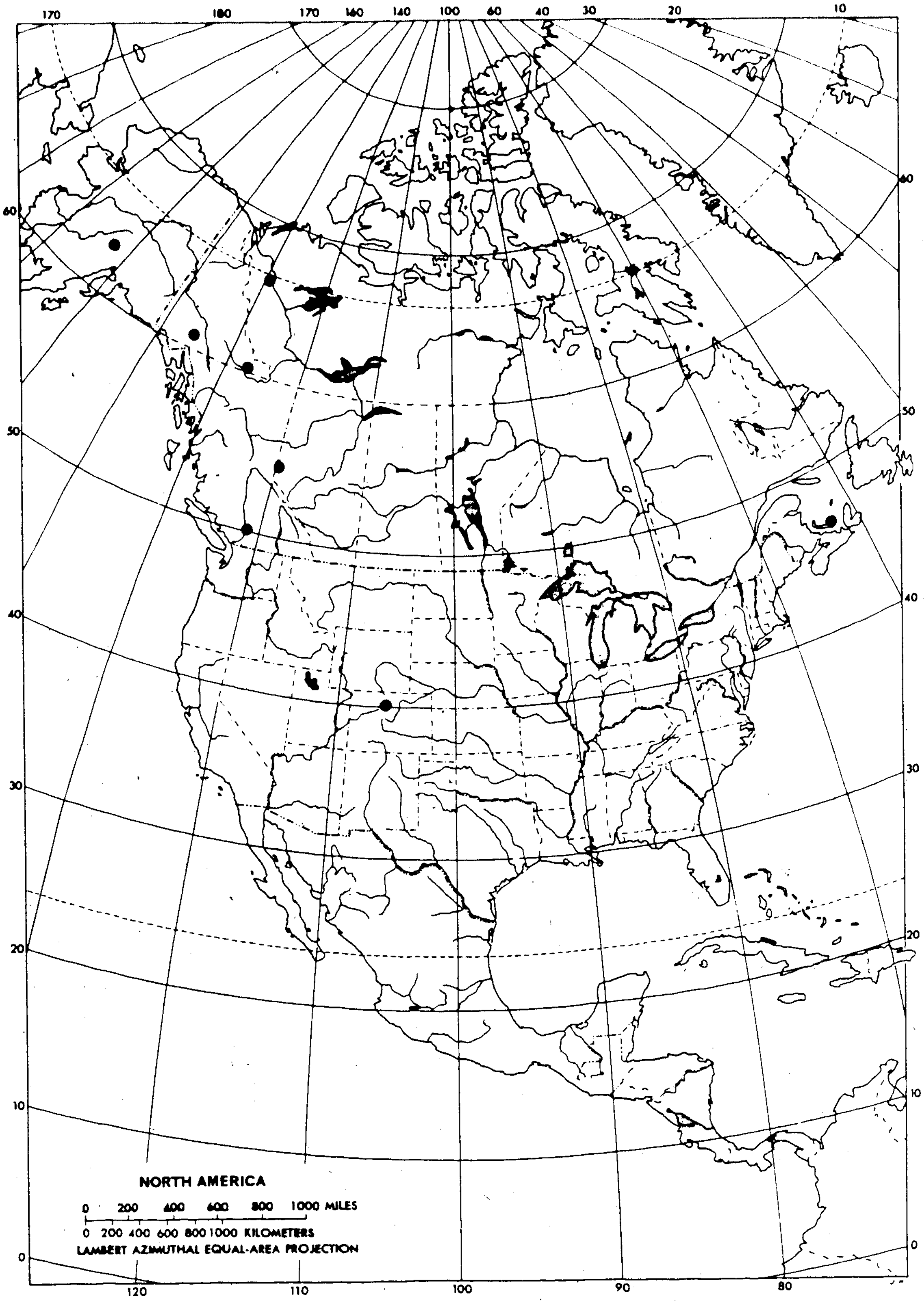
Habitat. - The two North American specimens of *D. crassicostatus* collected by myself with watersamples indicate high minerotrophic conditions: pH measurements of 7.7 and 7.9, conductivity 500 and 920 microScm^{-1}, Ca concentration 19 and 77 ppm, Mg concentration 37 and 42 ppm, Na concentration 22 and 42 ppm, K concentration 0 and 0.8 ppm.

Recent Distribution. - North America only (Plate 24) : Alaska, southern Yukon Territory and Mackenzie District, westcentral Alberta and southeastern British Columbia, disjunct to Colorado and Nova Scotia.

Subfossil Distribution in North America (Plate 25) . - (1) Chalmer's Bog, circa 15 km southwest of Turner Valley, Alberta; 18,500 ± 1090 B.P. (GSC-2670); Bryological Report 42, Jackson 1979. (2) Chalmer's Bog, circa 15 km southwest of Turner Valley, Alberta; 18,400 ± 380 B.P. (GSC-2668); Bryological Report 43, Jackson 1979. (3) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (4) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 54. (5) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62. (6) HH69-21, Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 103; as *Drepanocladus cf. crassicostatus*. (7) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 108. (8) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 116. (9) HH68-10, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159. (10) Chandalar River, 2.5 km downstream from Caro, Alaska; >42,000 B.P.; Bryological Report 166. (11) Koyukuk River, 9 km upstream from Henshaw Creek, Alaska; Pleistocene; Bryological Report 167. (12) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (13) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (14) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (15) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150 B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40. (16) HH68-9

Plate 24. The present day North American distribution of *Drepanocladus crassicostatus* Janssens based on specimens in ALTA, CANM, C, COLO and NY.

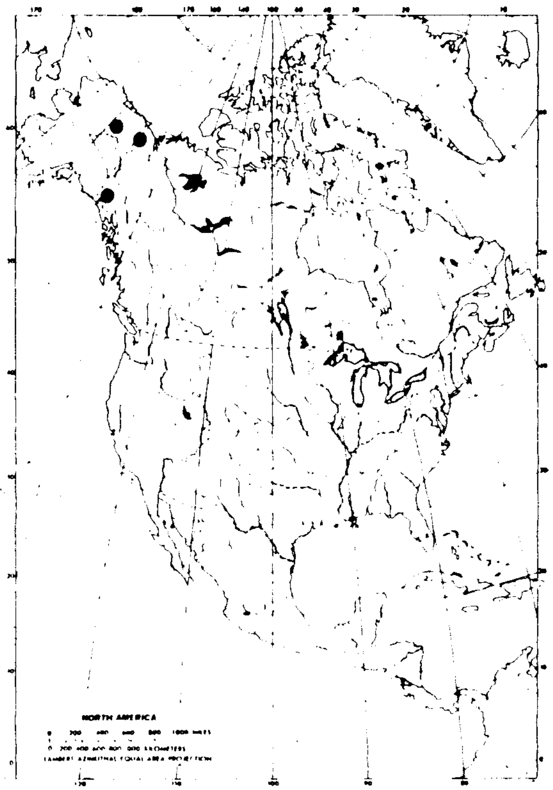


NORTH AMERICA

LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 25. The subfossil North American records of *Drepanocladus crassicostatus* Janssens. Based on Appendix 1.

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.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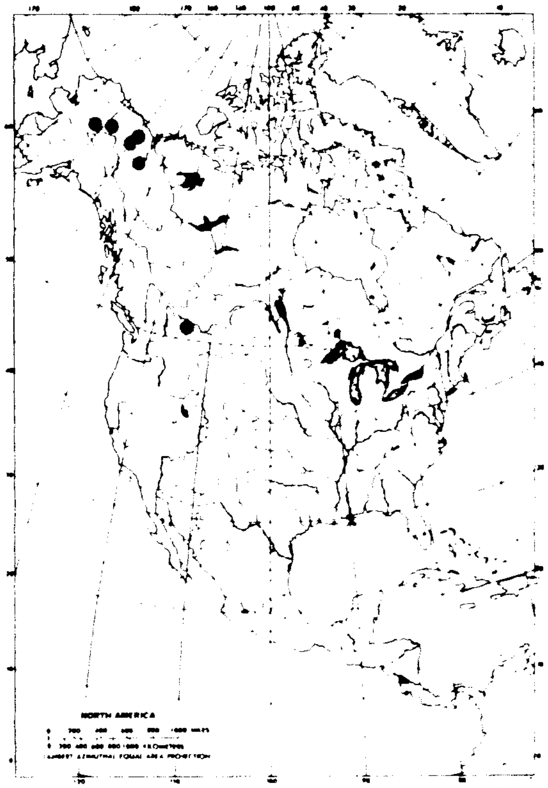
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LAMBERT AZIMUTHAL EQUAL AREA PROJECTION

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(station 2), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 262. (17) HH68-9 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 264. (18) HH68-9 (station 11), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 265. (19) CRH-12 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 267. (20) HH75-19, Old Crow Basin, Yukon Territory, pre-Wisconsinan?, Bryological Report 272. (21) HH68-9 (station 7), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 308. (22) HH75-24, Bluefish Basin, Yukon Territory, Wisconsinan?, Bryological Report 326, as *Drepanocladus* cf. *crassicostatus*. (23) 228HH, Bluefish Basin, Yukon Territory, >37,000 BP (GSC-2783), ± 60,000 BP, Bryological Report 362. (24) HH68-9 (station 14), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 387. (25) HH69-21 (station 3), Old Crow Basin, Yukon Territory, ± 60,000 BP, Bryological Report 388, as *Drepanocladus* cf. *crassicostatus*. (26) HH72-54 (station 3), Hungry Creek, Yukon Territory, Wisconsinan, Bryological Report 434. (27) HH72-54 (station 3), Hungry Creek, Yukon Territory, Wisconsinan, Bryological Report 435.

Diagnostic Features and Discussion. - Subfossil material of *D. crassicostatus* is very common. It comprises 15 % of all the identified *Drepanocladus* records. Moreover, this new species is often very abundant in the assemblages. Its structure suggests a similarity with *D. trichophyllus*, an aquatic species. However, many character states deviate from those of *D. trichophyllus*. The alar cell structure is drastically different. *Drepanocladus trichophyllus* exhibits very clearly differentiated alar cell groups, strongly decurrent and comparable with those of *D. tundrae*. In *D. crassicostatus* the differentiation is poor and the alar cell groups are essentially not decurrent. Other differences are the poor denticulation and the complete absence in *D. crassicostatus* of the macroscopic aspect of *D. trichophyllus*. In the latter the branches are clearly characterized by brush-like tips (Tuomikoski 1949). The leaves at the end of the branches are straight and tightly rolled together in a pencil-like configuration. The most distinct common feature that *D. crassicostatus and D. trichophyllus* share is the strongly developed costa, reaching far beyond the apex and biconvex in transverse section, displaying abaxial and adaxial stereid bands. A forthcoming paper will compare in detail the morphological and anatomical differentiation between *D. crassicostatus*, *D. trichophyllus* and *D. capillifolius*.

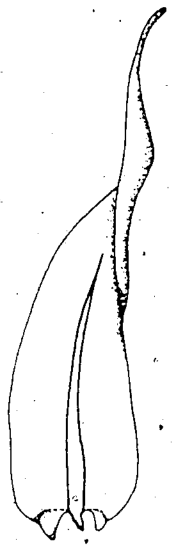
North American specimens, named *D. trichophyllus*, from ALTA, CANM, COLO, DUKE and NY were studied and compared with material from C and S. The North American specimens appeared to be other taxa of the *Warnstorfia* group. Some specimens are *D. crassicostatus* but none of the specimens were similar to the characteristic Fennoscandian *Drepanocladus trichophyllus*. At present I have seen no North American specimens with a costa reaching into the apex and beyond, well differentiated alar cells and the macroscopic aspect of *D. trichophyllus*. Persson's Alaskan specimens are not present in ALA (Persson & Shacklette 1959, Murray, *in litt.*). Persson & Gjaerevoll (1957) offered the suggestion that unstudied forms of the *Warnstorfia* group are present in alpine-arctic areas of North America. Most likely this applies to the material which I named *D. crassicostatus*. *Drepanocladus trichophyllus* is known as a subfossil from Late Weichselian sediments in western Norway (Ovstedal & Aarseth 1975). The authors mention that they observed the very typical alar cell structure and leaf shape of this species. The taxonomic status, ecology and distribution of *D. crassicostatus* in relation to *D. trichophyllus* will be discussed in the forthcoming paper. A comparison of the habitat of *D. trichophyllus* and of the extant populations of *D. crassicostatus* indicate differences. *Drepanocladus trichophyllus* occurs in moderately minerotrophic mires, floating or submerged, usually in non-calcareous water. In the Torneträsk area, Sweden, water analyses resulted in the following values: pH ranges from 5.0 to 6.5, conductivity 5–40 microScm^{-1}, Ca concentration 14 ppm, Mg concentration 6.6 ppm, Na concentration 14 ppm, K concentration 4.7 ppm, S concentration 44 ppm, P concentration 0.2 ppm and Fe concentration 14 ppm (Sonesson 1966). The two North American specimens of *D. crassicostatus*, collected by myself with water samples, indicate more minerotrophic conditions: see the habitat discussion above.

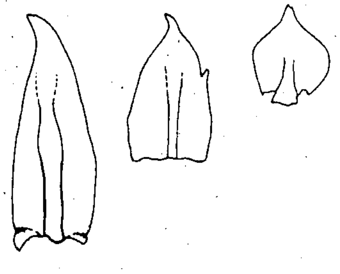
Drepanocladus exannulatus (B.S.G.) Warnst. Plate 26

Description (n=34). – *Leaves* strongly falcate-secund to straight, narrowly to widely ovate-lanceolate, more or less decurrent, (1.4)2.9–3.5(4.8) mm long, maximal width (0.4)0.6–0.7(1.1) mm, basal width (0.2)0.3–0.4(0.8) mm; *apex* slenderly acuminate; *margins*

Plate 26. *Drepanocladus exannulatus* (B.S.G.) Warnst. (Bryological Reports 48, 54, 173, 176, 260, 272, 302, 308 and 322)

1. Leaves (x31).
2. Stem transverse section (x200).
3. Marginal cells halfway up the leaf (x500).
4. Medial leaf cells (x500).
5. Alar leaf cells (x200).





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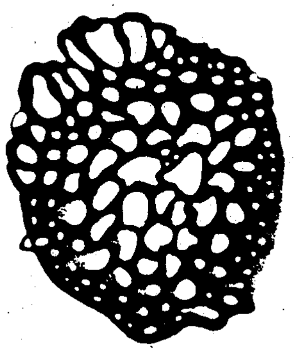

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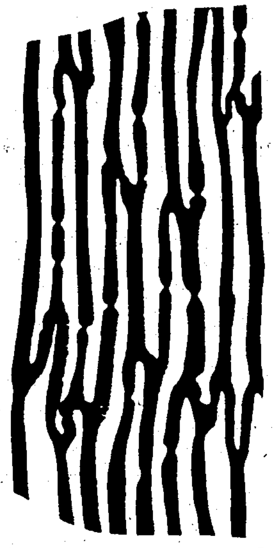

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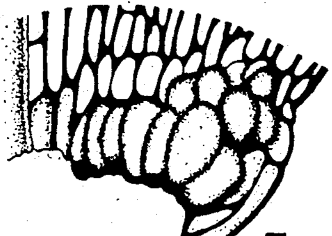

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denticulate; *costa* strong, ending in the upper half of the lamina or reaching into the apex in large aquatic forms; *upper leaf cells* elongate, (36)68–87(134) micrometer long, (3.8)5.6–6.8(9.2) micrometer wide, walls thick or thin, sometimes slightly porose; *alar cells* in a large group, in one to three regular tiers, often reaching the costa, clearly differentiated, inflated, shortly to longly rectangular or ovoid, walls yellow or brown, thin or slightly thickened. *Stem* mostly with a circular transverse section, diameter (160)250–310(460) micrometer, central strand always developed, often several of the epidermal cells inflated, with thin outer walls, but never forming a continuous hyalodermis.

Habitat. – In poor fens, ditches and non-calcareous springs, immersed in pools and lakes. Often associated with *Calliergon stramineum, C. cordifolium, C. richardsonii, Aulacomnium palustre, Hypnum lindbergii, Polytrichum commune* and *Sphagnum* species. pH (4.1)4.5–7.6(9.0), (n=10), conductivity 20–860 microScm^{-1} (n=4) Ca concentration 1.6–71 ppm (n=9), Mg concentration 0–51 ppm (n=9), Na concentration 0–29 ppm (n=9), K concentration 0–17 ppm (n=9). The species is absent in extremely rich fens. It is often a member of the bottom flora of lakes.

Recent Distribution. – Circumboreal. Common, except in Arctic areas. North America (Plate 27) : from Alaska to Greenland, Labrador and Newfoundland, south to new England and Wisconsin in the east, Colorado, Utah and Oregon in the west. Europe, northern, western, eastern and central Asia.

Subfossil Distribution in North America (Plate 28) . – British Columbia, Greenland, Iowa, Michigan, Minnesota, New York, Northwest Territories, Ontario, Vermont, Yukon Territory (Miller 1980a). New records: (1) Riverbar near HH75–9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) Riverbar of base camp at HH68–9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (3) HH68–9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (4) HH68–9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 54. (5) HH75–24, Bluefish Basin, Yukon Territory; probably pre-Wisconsinan; Bryological

Plate 27. The present day North American distribution of *Drepanocladus exannulatus* (B.S.G.) Warnst. based on specimens in ALTA and CANM (solid dots), and Lewinsky (1971), Steere (1978a) and Tuomikoski *et al.* (1973) (open circles).

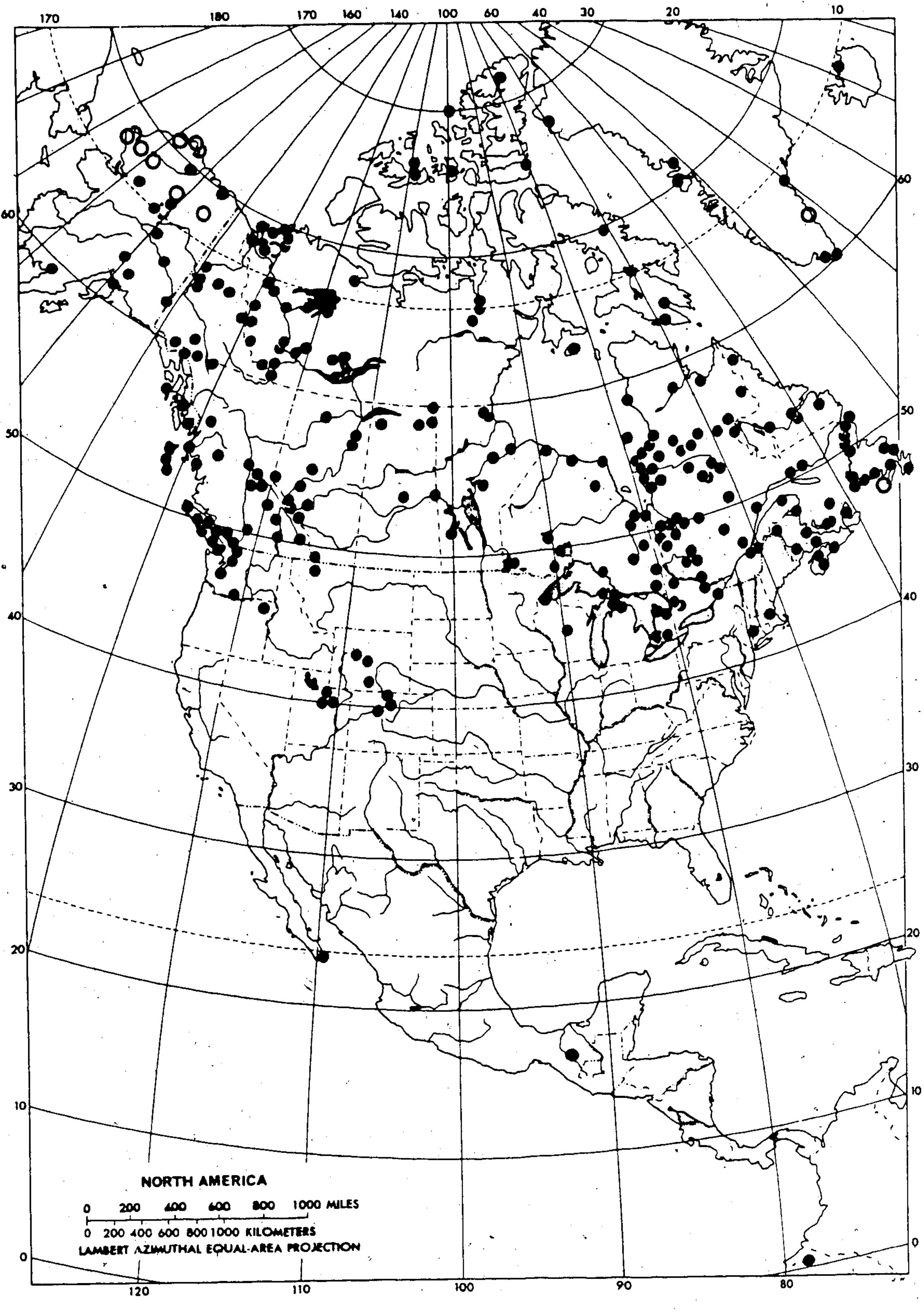
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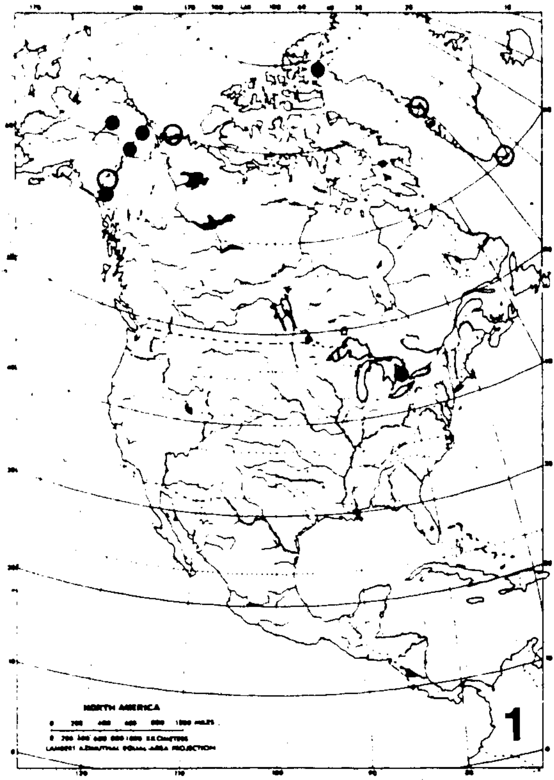
Plate 28. The subfossil North American records of *Drepanocladus exannulatus* (B.S.G.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a), Kuc & Hills (1971), Kuc (1973c).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.
4. Late Tertiary.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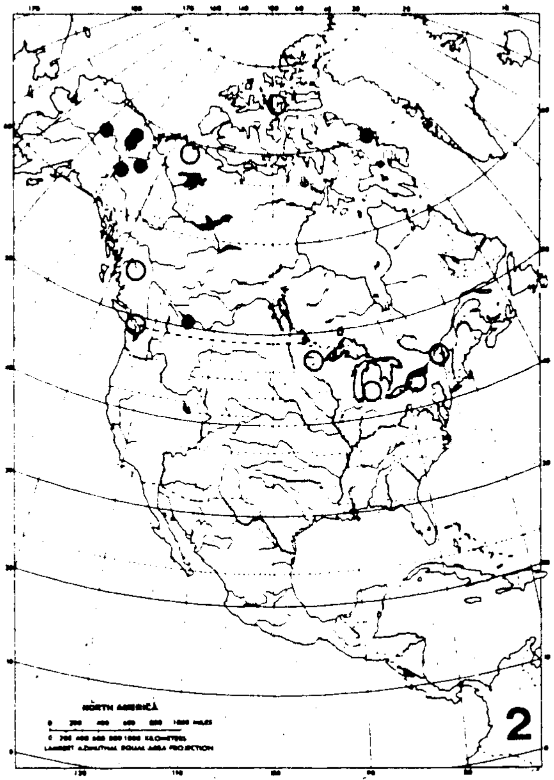
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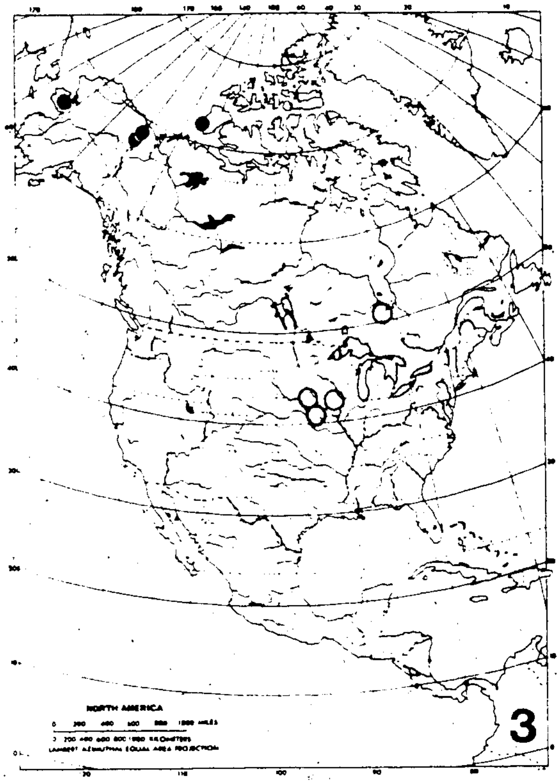
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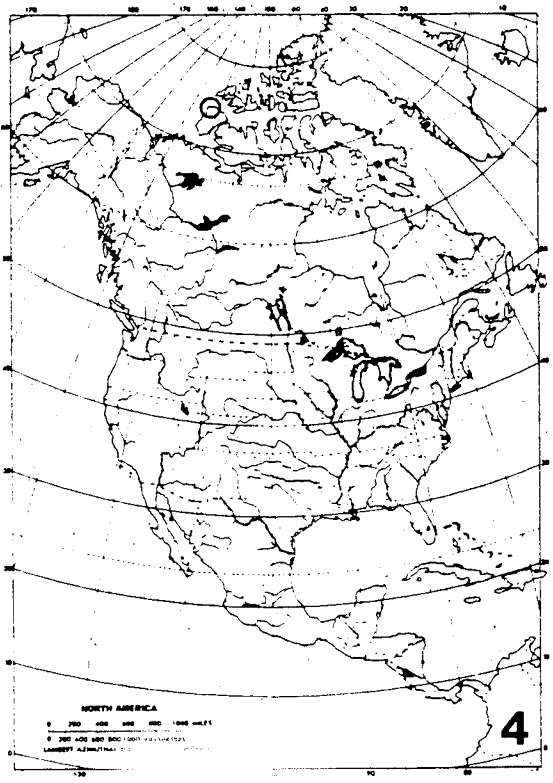
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Report 173. (6) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174. (7) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (8) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (9) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (10) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (11) Chandalar River, 3 km east of Caro, Alaska; >30,000 B.P.; Bryological Report 184. (12) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (13) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (14) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (15) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (16) Kitchener, Ontario; below 8800 B.P.; Bryological Report 275. (17) Chalmer's Bog, circa 15 km southwest of Turner Valley, Alberta; below 18,500 ± 1090 B.P. (GSC-2670); Bryological Report 285, Jackson 1979. (18) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (19) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (20) Kitchener, Ontario; below 8800 B.P.; Bryological Report 322. (21) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (22) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (23) Cape Deceit Quaternary Exposure, Near Deering (station 5), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 333, Matthews 1974a; as *Drepanocladus cf. exannulatus*. (24) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a; as *Drepanocladus cf. exannulatus*. (25) 228HH, Bluefish Basin, Yukon Territory; >37,000 B.P. (GSC-2783), ± 60,000 B.P.; Bryological Report 362. (26) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 384. (27) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (28) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 392. (29) Baird Inlet area, Ellesmere Island, Northwest Territories; sample at top of core, Holocene; Bryological Report 409. (30) Baird Inlet area, Ellesmere Island, Northwest Territories; sample at top of core, Holocene; Bryological Report 410. (31) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (32) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

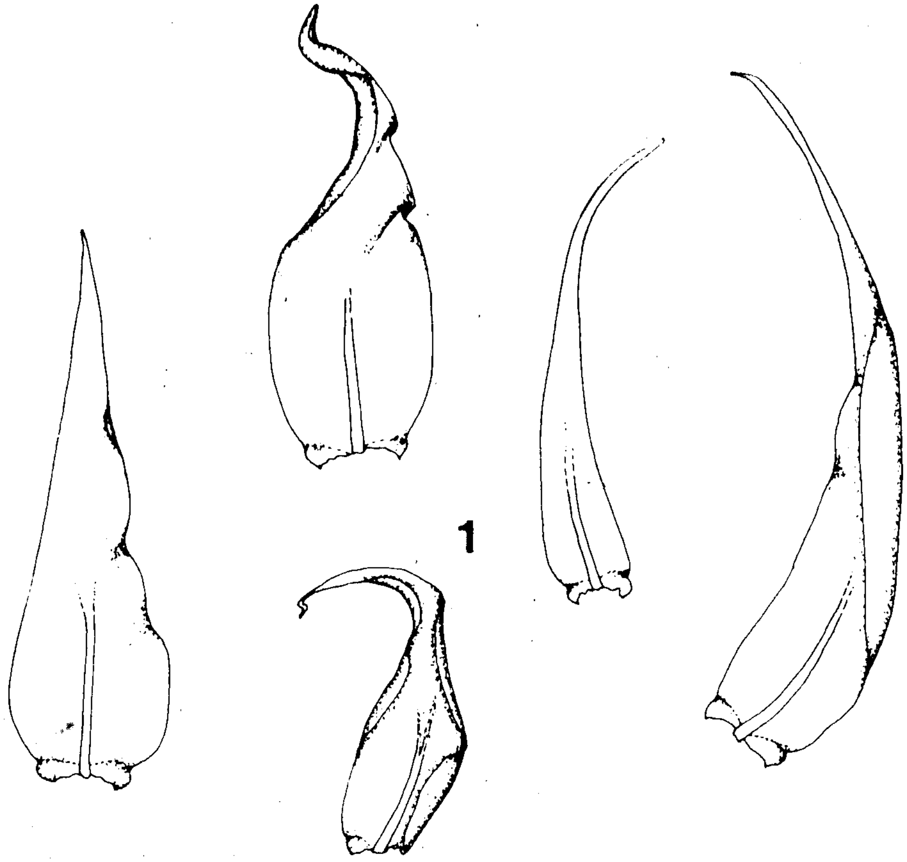
Diagnostic Features and Discussion. – *Drepanocladus exannulatus* can best be differentiated from the other species in the *Warnstorfia* group by the more or less enlarged epidermal cells of the stem. Often a group of epidermal cells, seen in a transverse section of the stem, are clearly enlarged by comparison with the cortical cells and have thin outer walls. In addition, the species is distinguished from *D. fluitans* by well-developed denticulation, a less conspicuous constriction at the base of the leaf and more clearly differentiated alar cells. From *D. tundrae* it differs in its generally circular transverse section of the stem, the less decurrent alar cell groups and the more falcate-secund leaves. From *D. crassicostatus* it is distinguished by a costa ending into or before the apex. None of the North American Quaternary subfossil material is similar to the common Fennoscandian species *D. procerus*. This species is characterized by strongly falcate-secund, concave leaves with a short, decurrent costa, that is slightly convex in transverse section and by the absence of epidermal cell differentiation on the stem.

Drepanocladus fluitans (Hedw.) Warnst. Plate 29

Description (n=32). – *Leaves* moderately falcate-secund to straight, ovate-lanceolate to broadly ovate-lanceolate, (1.3)2.7–3.7(6.2) mm long, maximal width (0.3)0.6–0.7(1.4) mm, basal width (0.2)0.3–0.4(0.5) mm; *apex* slenderly acuminate, often flexuose and twisted, sometimes forming rhizoids from nematogon cells; *margins* mostly denticulate; *costa* weak, ending half way up the lamina, frequently branched; *upper leaf cells* elongate, (48)84–103(142) micrometer long, (4.3)6.3–7.2(9.3) micrometer wide, walls thin; *alar cells* in a large diffuse group, usually reaching the costa, moderately differentiated, shortly rectangular to rounded-quadrate, not clearly arranged in tiers, walls yellow to hyaline, thin, not porose. *Stem* with a circular transverse section, diameter (1.60)220–260(360) micrometer, central strand present, epidermal cells small and with

Plate 29. *Drepanocladus fluitans* (Hedw.) Warnst. (Bryological Reports 39, 116, 157, 166 and 302)

1. Leaves (x40).
2. Marginal leaf cells halfway up the leaf (x640).
3. Medial leaf cells (x640).
4. Stem transverse section (x256).
5. Alar leaf cells (x256).



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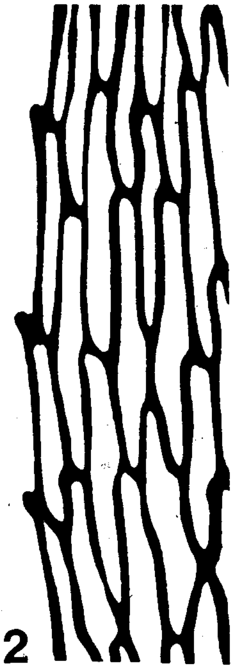

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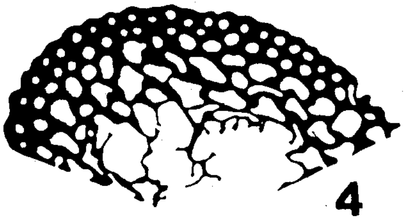

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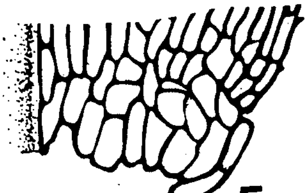

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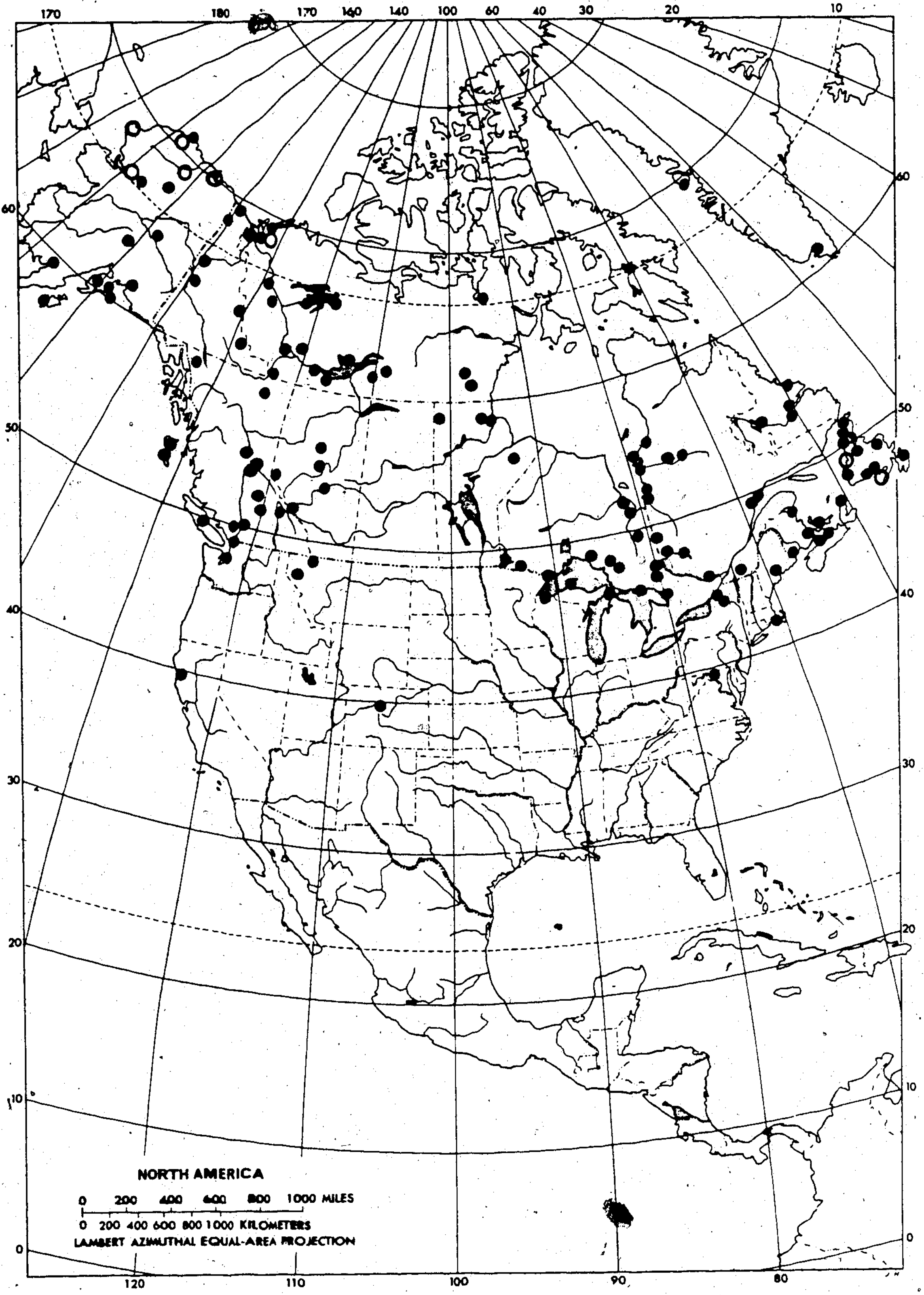
thick walls

Habitat - In poor fens and pools and lakes with oligotrophic water, in acid bogs and on wet acid rocks. Often with *Sphagnum* species and *Calliergon stramineum*. Many of its habitats indicate a highly dynamic environment (changes in water level and/or anthropogenic influence). pH 4.8-7.5 (n=7), conductivity 19-215 microScm^{-1} (n=7), Ca concentration 2.4-35.9 ppm (n=7), Mg concentration 0.0-8.9 ppm (n=7), Na concentration 4.0-25.4 ppm (n=7), K concentration 0-11 ppm (n=7). *Drepanocladus fluitans* is one of the most acidophilous species of the genus. It is the first species to appear in depressions in bogs, where the stagnant water is very acid and intensely brown from decomposed humus.

Recent Distribution. - Bipolar, circumboreal and austral. North America (Plate 30) : Alaska, Yukon and Northwest Territories (but not in the Arctic Archipelago), Greenland, south to Newfoundland, New England, the Great Lakes area in the east, Colorado and California in the west. Ecuador, Europe, Azores, Canaries, southern and southeastern Africa, northern Asia, Korea, Japan, New Zealand, Tasmania, Kerguelen Islands.

Subfossil Distribution in North America (Plate 31) . - Alberta, Iowa, Minnesota, New York, Ohio, Ontario, Yukon Territory (Miller 1980a). New records: (1) Muskiki Lake, 30 km eastsoutheast of Mountain Park, Alberta; 8300 ± 435 B.P. (S-1523); Bryological Report 39. (2) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (3) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 114. (4) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 115; as *Drepanocladus cf. fluitans*. (5) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 116. (6) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 140 to 150 cm below surface; Bryological Report 157. (7) Chandalar River, 2.5 km downstream from Caro, Alaska; >42,000 B.P.; Bryological Report 166. (8) Anaktuvuk River; 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (9) Kluane Lake,

Plate 30. The present day North American distribution of *Drepanocladus fluitans* (Hedw.) Warnst. based on specimens in ALTA and CANM (solid dots), and Steere, Holmen & Scotter (1971), Steere (1978a) and Tuomikoski *et al.* (1973) (open circles).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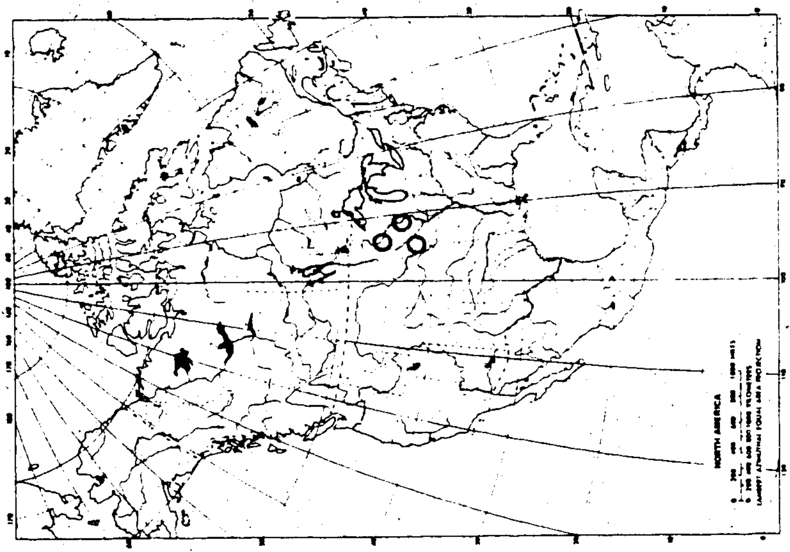
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 31. The subfossil North American records of *Drepanocladus fluitans* (Hedw.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.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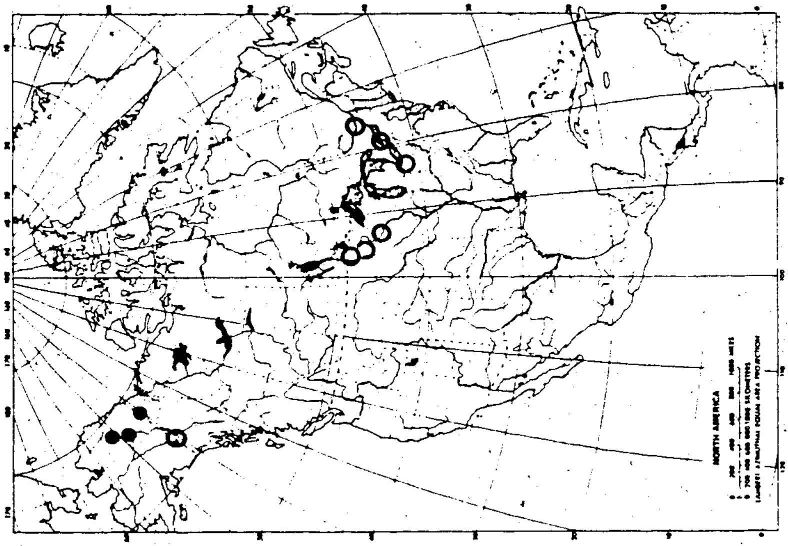
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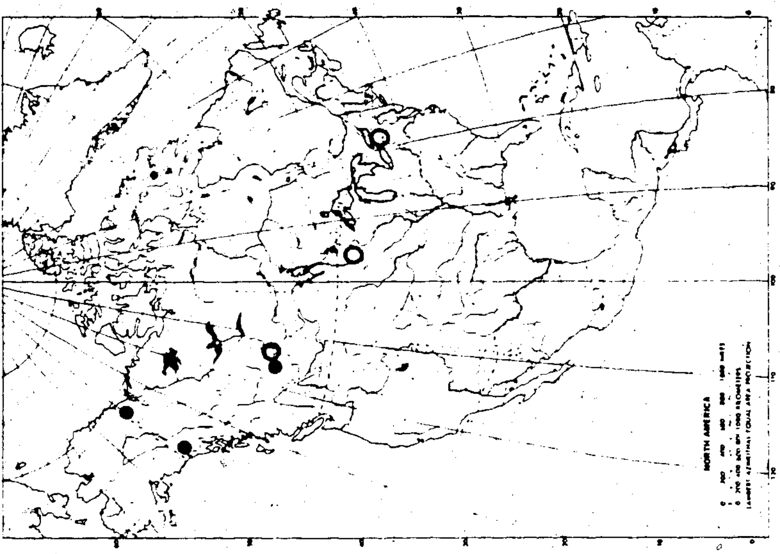
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south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (10) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 263. (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (12) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (13) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 384, as *cf. Drepanocladus fluitans*. (14) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (15) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

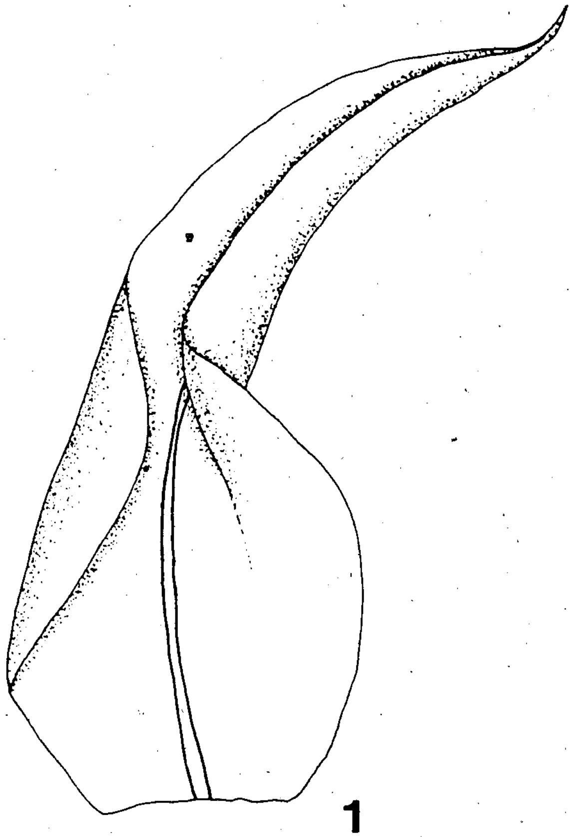
Diagnostic Features and Discussion. – Subfossil specimens are sometimes found which are too poorly preserved to place them in either *D. fluitans* or *D. exannulatus*. However, typically developed and well preserved fragments are very easily distinguished. *Drepanocladus fluitans* is a much smaller plant (except the strongly etiolated aquatic forms), having leaves with a strongly contracted base, a very weak costa, thinner-walled cells and less differentiated alar cells. The structure of the latter is again one of the most reliable characters to differentiate between these two *Drepanocladus* taxa. Some orthophyllous forms of *D. fluitans* can be mistaken for *Leptodictyum riparium* (Hedw.) Warnst. The two species can be distinguished by the wider medial cells, the very gradually differentiation [illegible] alar cells and the absence of nematogon initials in *L. riparium*. *Drepanocladus* [illegible]*tans* and *D. exannulatus* differ in the tolerance for lower concentrations of cations and the lower pH of *D. fluitans*. The southern hemisphere populations are possibly taxonomically related types or recent introductions (Schofield 1974). More critical studies are needed on these populations.

Drepanocladus lapponicus (Norrl.) Z. Smirn. Plate 32

Description (n=4). – *Leaves* falcate-secund, ovate-lanceolate to broadly ovate-lanceolate, weakly concave, sharply constricted at the basal width, 2.4–4.0 mm long, maximal width 1.0–1.4 mm, basal width 0.6–0.9 mm, *apex* shortly acuminate; *margins* entire; *upper leaf cells* elongate, 49–98 micrometer long, 4.1–4.8 micrometer wide, walls thin to thick,

Plate 32. *Drepanocladus cf. lapponnicus* (Norrl.) Smirn. (Bryological Reports 206)

1. Leaf (x54).
2. Stem transverse section (x344).
3. Basal leaf cells (x860).
4. Medial leaf cells (x860).



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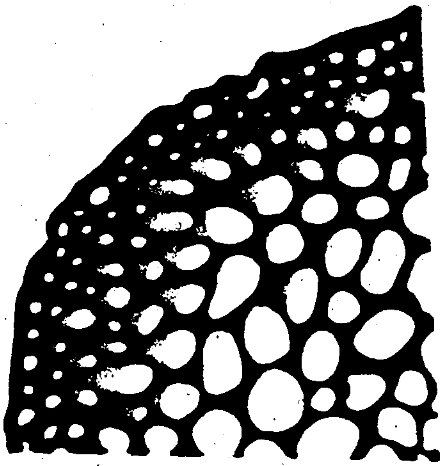

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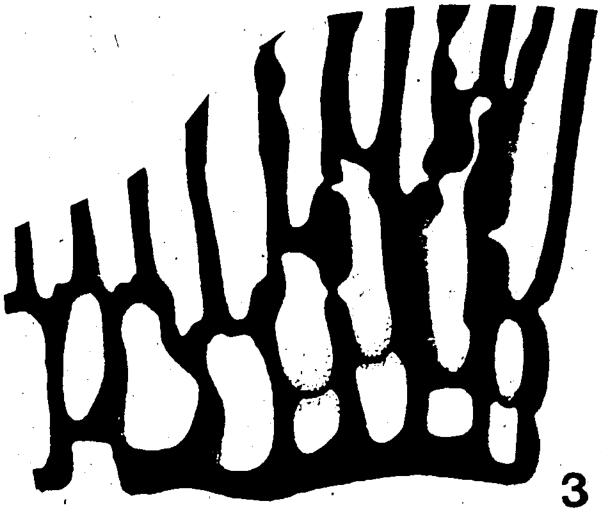

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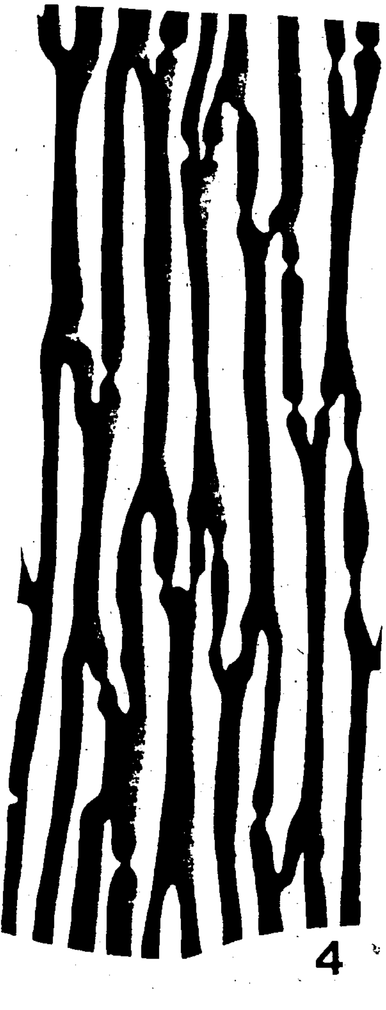

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sometimes porose; *alar cells*, rectangular, walls brown, thick and porose or slightly inflated and the walls thinner and yellow. *Stem* with circular transverse section, diameter 288–372 micrometer, no central strand, epidermal cells small and with thick outer walls.

Habitat. – In fens, beside lakes and streams. Associated with *Calliergon richardsonii*, *D. exannulatus*, *D. tundrae*, *D. revolvens*, *D. vernicosus* and *Scorpidium scorpioides*.

Recent Distribution. – Circumboreal, very rare. North America (Plate 33) : Yukon Territory, British Columbia and Alberta, Hudson Bay coast. Northeastern Europe, Asia.

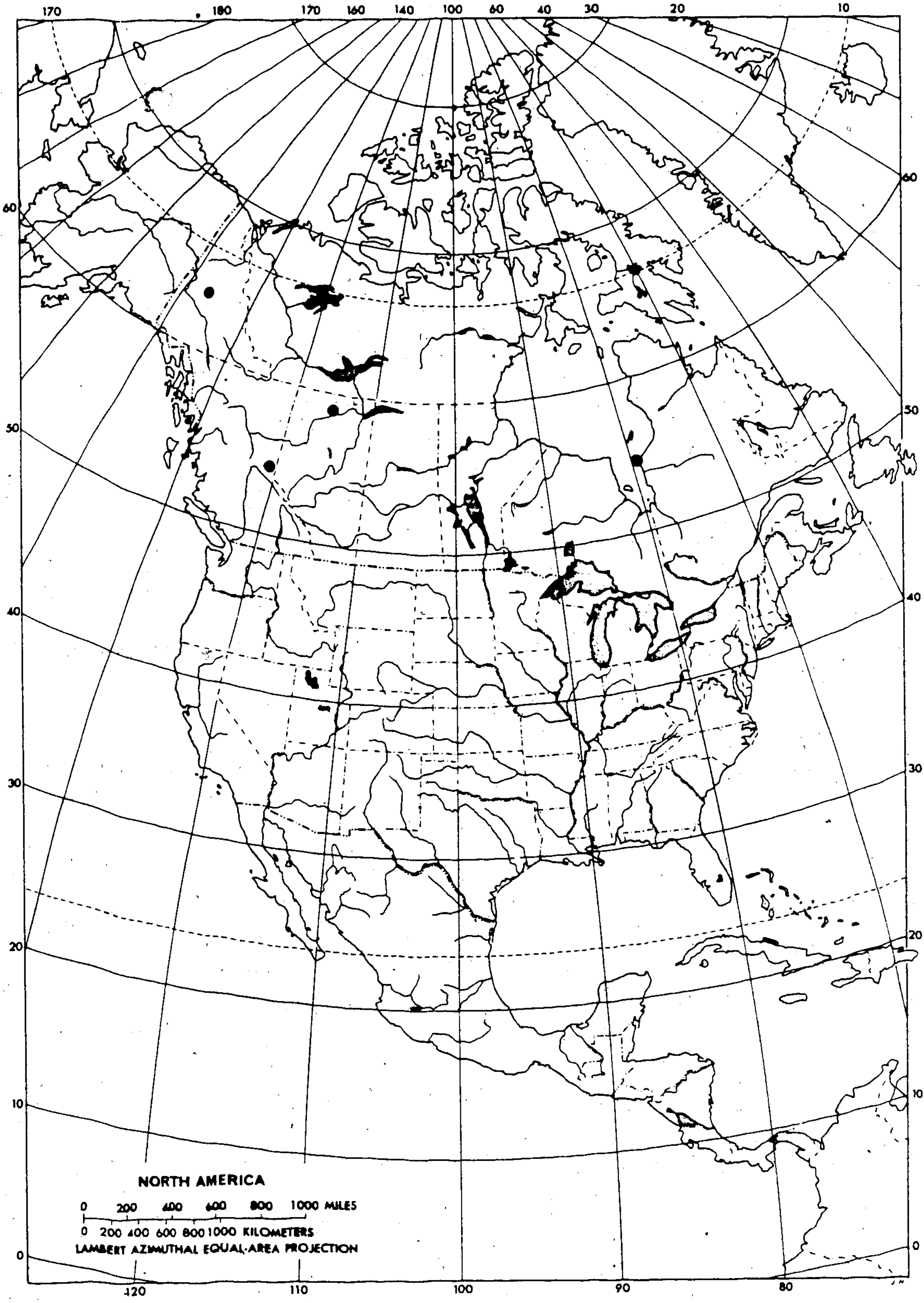
Subfossil Distribution in North America (Plate 34) . – (1) Wagner Property, Edmonton area, Alberta; Holocene peat, 60 to 70 cm below water surface; Bryological Report 206; as *Drepanocladus cf. lapponicus*. (2) HH75–24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC–2373–2); Bryological Report 271; as *Drepanocladus cf. lapponicus*.

Diagnostic Features and Discussion. – *Drepanocladus lapponicus* is a large turgid species, and not unlike *Scorpidium scorpioides* in aspect (Tuomikoski & Koponen 1979). The plant fragments of *D. lapponicus* are not branched, while even in the subfossil material of *D. vernicosus* pinnate branching is evident. The leaves are widely ovate–lanceolate and the alar cells are often more differentiated than in the closely related *D. vernicosus*.

Drepanocladus lycopodioides var. *brevifolius* (Lindb.) Monk. Plate 35

Description (n=26). – *Leaves* falcate–secund, ovate–lanceolate, (1.2)1.8–2.3(3.8) mm long, maximal width (0.5)0.8–0.9(1.2) mm, basal width (0.2)0.3–0.4(0.5) mm; *apex* acuminate; *margins* entire; *costa* weak, often branched in the upper part, reaching half way up the lamina; *upper leaf cells* elongate, (40)51–62(103) micrometer long, (5.5)7.2–8.2(11.0) micrometer wide, walls thick, porose, at least in the basal half; *alar cells* in a small or large diffuse group, poorly differentiated, irregular, walls brown, thick, sometimes

Plate 33. The present day North American distribution of *Drepanocladus cf. laponnicus* (Norrl.) Smirn. based on specimens in ALTA and CANM (solid dots), and Holmen and Scotter (1971) (opem circels).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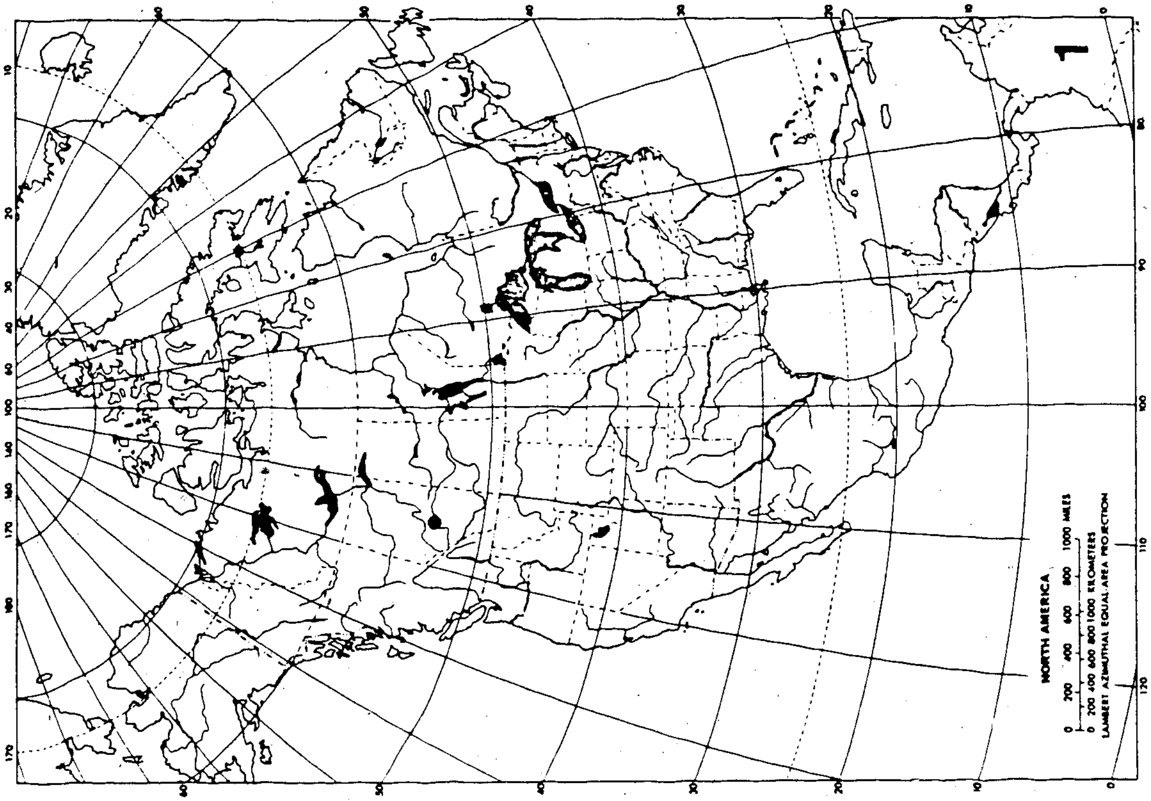
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 34. The subfossil North American records of *Drepanocladus cf. laponnicus* (Norrl.) Smirn. Based on Appendix 1.

1. Holocene.
2. Wisconsinan.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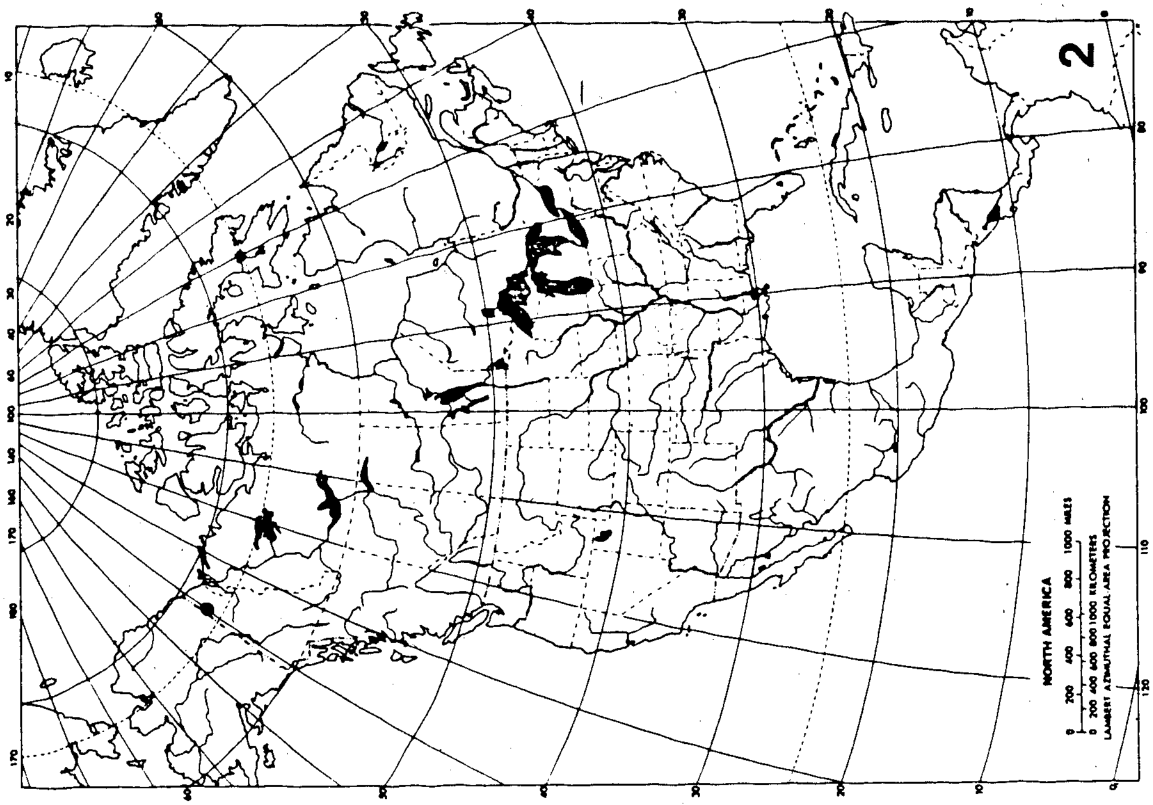
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Plate 35. *Drepanocladus lycopodioides* var. *brevifolius* (Lindb.) Mönk. (Bryological Reports 2, 115, 176, 198)

1. Leaves (x40).
2. Stem transverse section (x256).
3. Marginal cells halfway up the leaf (x640).
4. Alar and basal leaf cells (x256).
5. Medial leaf cells (x640).


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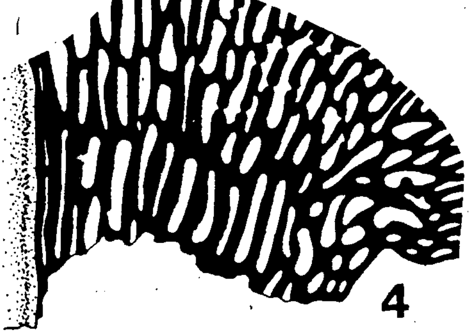
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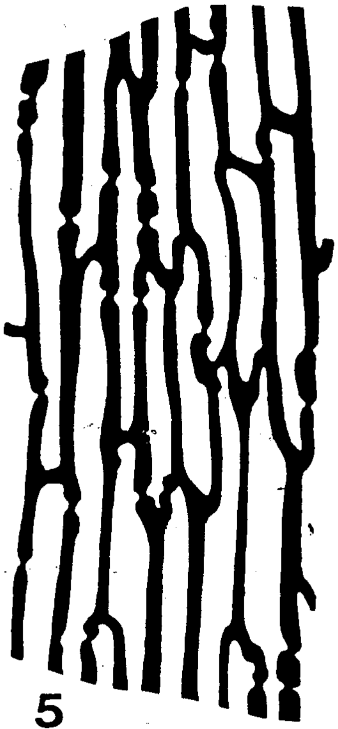
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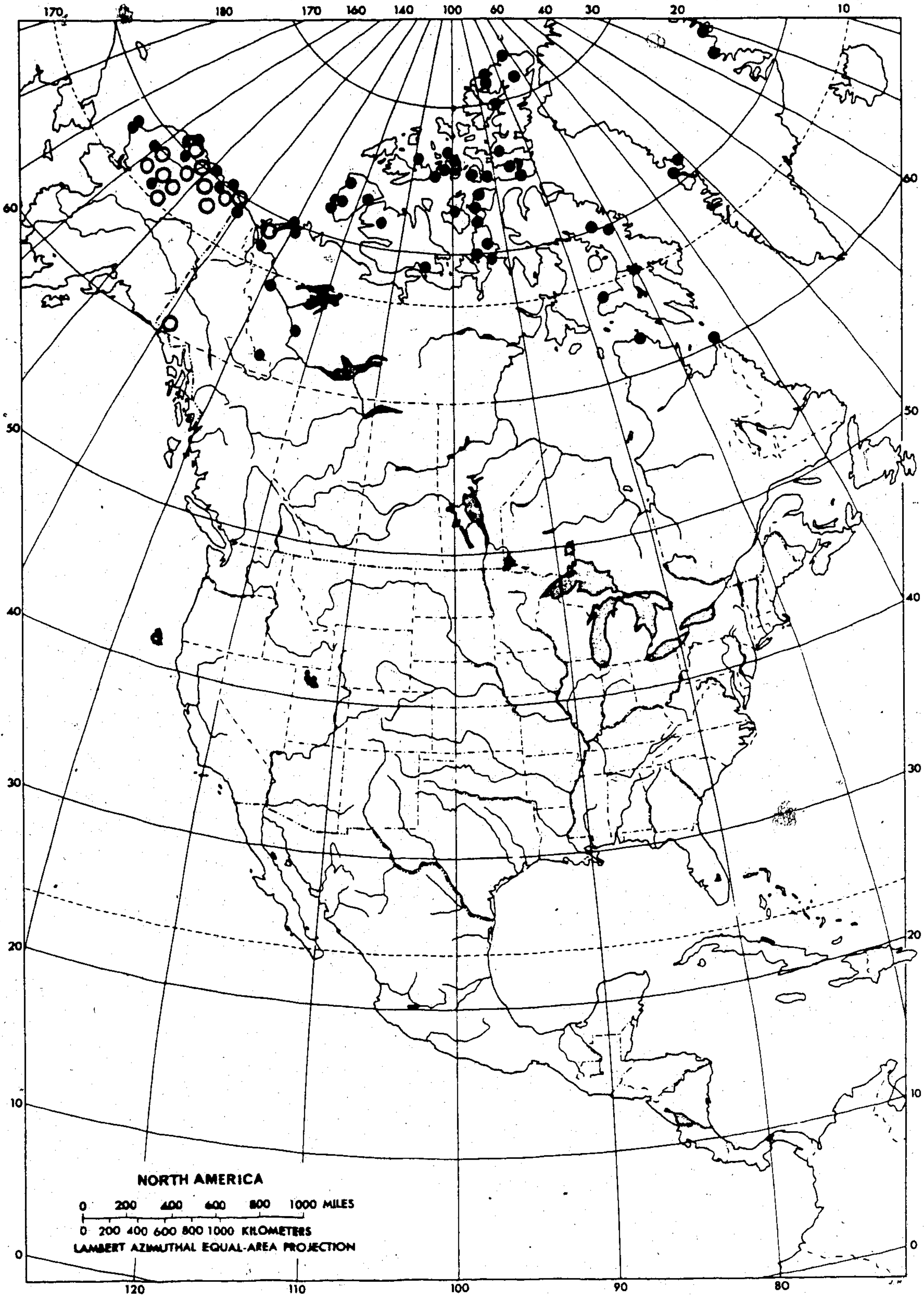
porose. *Stem* mostly with a circular transverse section, diameter (170)200-240(330) micrometer, central strand present, epidermal cells small and with a thick outer wall.

Habitat. - In rich fens and shallow pools and often in mesic habitats. In small streams with intermittent water discharge. It occurs on Devon Island together with *D. revolvens* and is among the most common of the meadow mosses in arctic areas. One pH measurement of 5.6, conductivity of 14 microScm^{-1}, Ca concentration of 7.2 ppm, Mg concentration of 1.9 ppm, Na concentration of 13.3 ppm and K concentration of 0.05 ppm.

Recent Distribution. - Circumpolar. Arctic-alpine species. North America (Plate 36) : not south of 60° N latitude. Alaska, Yukon Territory (St. Elias Mountains), Mackenzie Valley, very commonly in the Arctic Archipelago, northern Quebec and Labrador. Northern Asia.

Subfossil Distribution in North America (Plate 37) . - Greenland (Miller 1980a). New records: (1) Silver Creek, Slims River drainage, Yukon Territory; 30,100 ± 600 B.P. (Y-1385); Bryological Report 1, Schweger & Janssens 1980. (2) Silver Creek, Slims River drainage, Yukon Territory; 30,100 ± 600 B.P. (Y-1385); Bryological Report 2, Schweger & Janssens 1980. (3) CRH 11 (station 5), Old Crow Basin, Yukon Territory; >51,000 B.P. ([illegible]559-2), ± 60,000 B.P.; Bryological Report 32. (4) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (5) CRH 12, Old Crow Basin, Yukon Territory; 35,500 B.P. (GSC-2507); Bryological Report 40. (6) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (7) HH6[illegible]-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (8) HH69-21 (station 1), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 101. (9) HH69-21 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 102. (10) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 115. (11) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 116, as *Drepanocladus lycopodioides* var. *brevifolius*. (12) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 117, as *Drepanocladus lycopodioides* var. *brevifolius*. (13) HH68-9 (station 9), Old Crow Basin, Yukon Territory;

Plate 36. The present day North American distribution of *Drepanocladus lycopodioides* var. *brevifolius* (Lindb.) Mönk. based on specimens in ALTA and CANM (solid dots), and Douglas & Peterson (1980), Holmen & Scotter (1971) and Steere (1978a) (open circles).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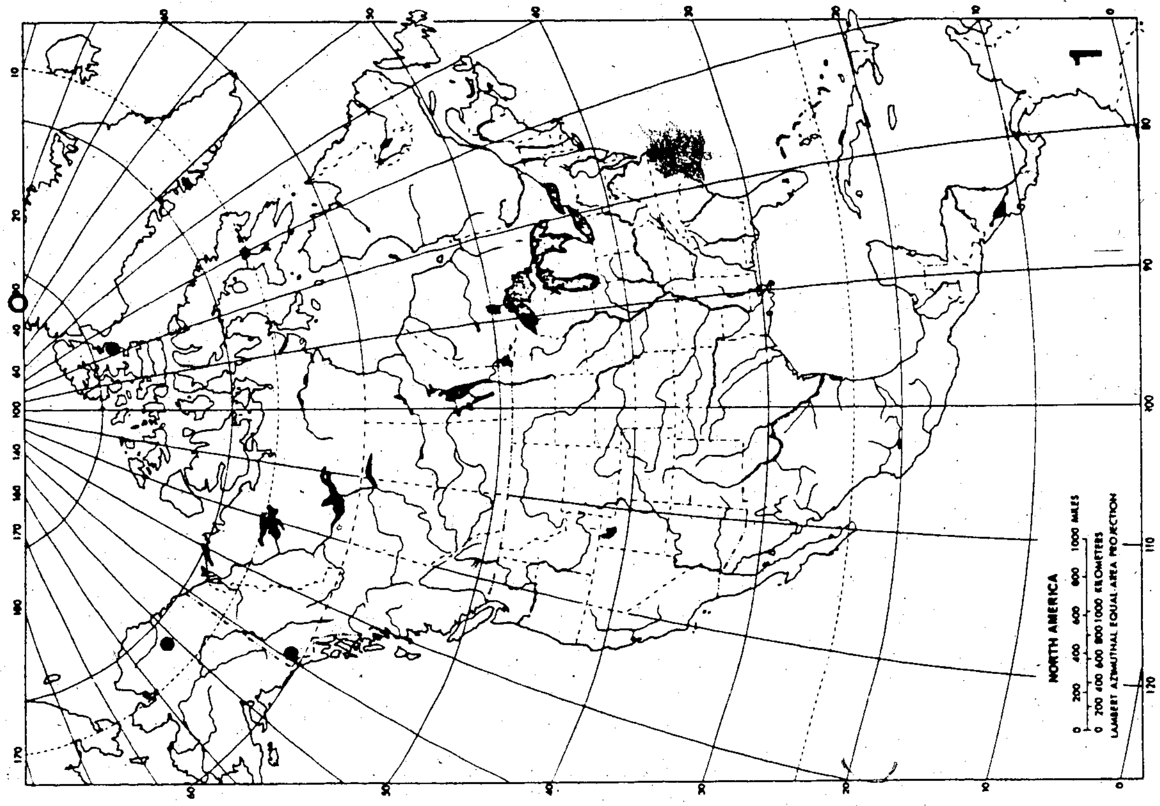
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 37. The subfossil North American records of *Drepanocladus lycopodioides* var. *brevifolius* (Lindb.) Mönk. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.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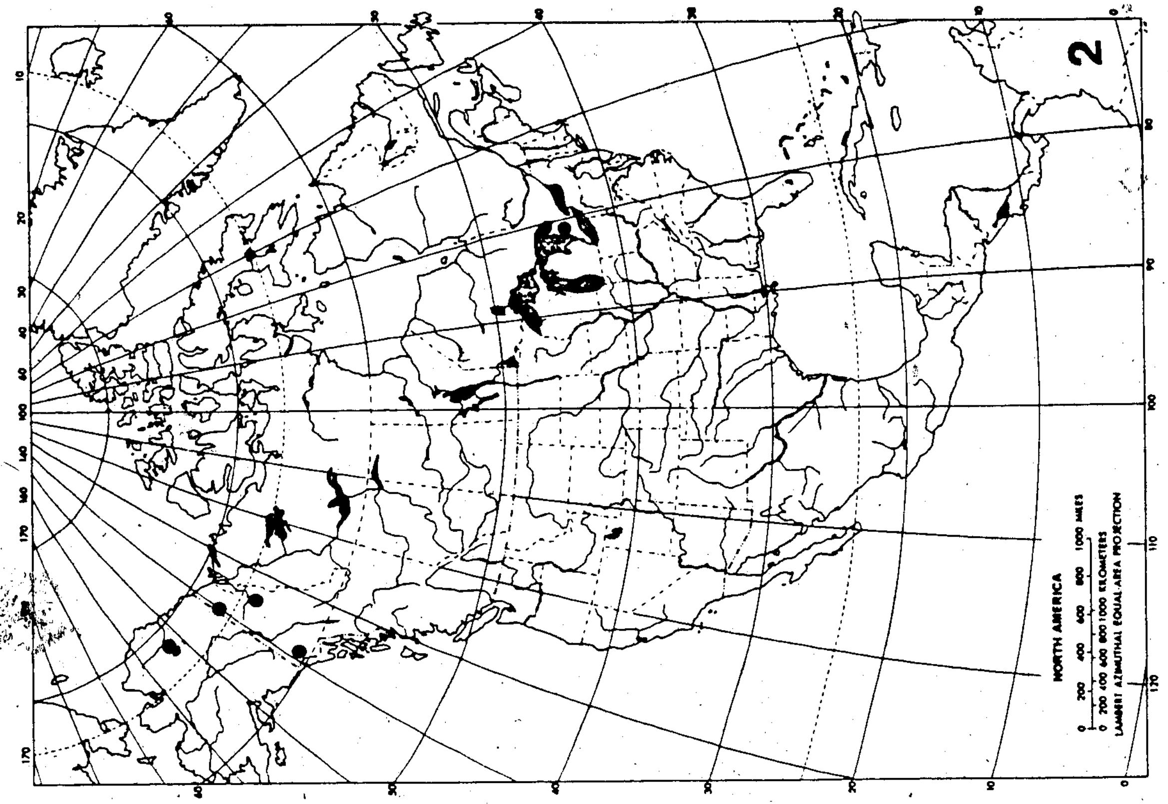
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38,800 ± 2000 B.P. (GSC-2756); Bryological Report 118, as *Drepanocladus lycopodioides* var. *brevifolius*. (14) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 120, as *Drepanocladus lycopodioides* var. *brevifolius*. (15) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (16) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (17) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178, as *Drepanocladus lycopodioides* var. *brevifolius*. (18) Tulunga River, 8 km upstream of east fork, Alaska; 33,220 ± 1760 B.P. (I-11,012); Bryological Report 198, Hamilton 1980a, p. 19. (19) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (20) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (21) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (22) CRH 11 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 266, as *Drepanocladus lycopodioides* var. *brevifolius*. (23) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (24) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (25) Wingham, Ontario; ± 12,100 B.P.; Bryological Report 277. (26) HH68-9 (station 10), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 319. (27) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326, as *Drepanocladus lycopodioides* var. *brevifolius*. (28) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (29) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (30) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 384. (31) HH68-9 (station 12), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 386. (32) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (33) Baird Inlet area, Ellesmere Island, Northwest Territories; 98 cm below bottom of lake, Holocene; Bryological Report 411, as *Drepanocladus lycopodioides* var. *brevifolius*. (34) Baird Inlet area, Ellesmere Island, Northwest Territories; 102 cm below bottom of lake, Holocene; Bryological Report 412. (35) HH68-9 (station 9), Old Crow

Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425, as *Drepanocladus lycopodioides* var. *brevifolius*; (36) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Diagnostic Features and Discussion. – The variety *brevifolius* is distinct from the common European, arctic species, *D. lycopodioides* var. *lycopodioides*. This latter taxon is a much larger plant, with widely ovate-lanceolate and less falcate leaves, with a better developed costa and alar cell group. In the variety *brevifolius* the alar cells are poorly differentiated and in a large diffuse group. Most commonly there are many small quadrate cells. Leaves are frequently strongly falcate-secund. *Drepanocladus lycopodioides* var. *lycopodioides* is similar in appearance to *D. lapponicus* and *Scorpidium scorpioides*, while the variety *brevifolius* more closely resembles *D. revolvens* var. *intermedius*. The distribution of *D. lycopodioides* var. *brevifolius* was previously considered oceanic (Kucyniak 1955). However, many specimens from localities in continental areas are now known. The Wisconsinan Ontario record is strongly disjunct.

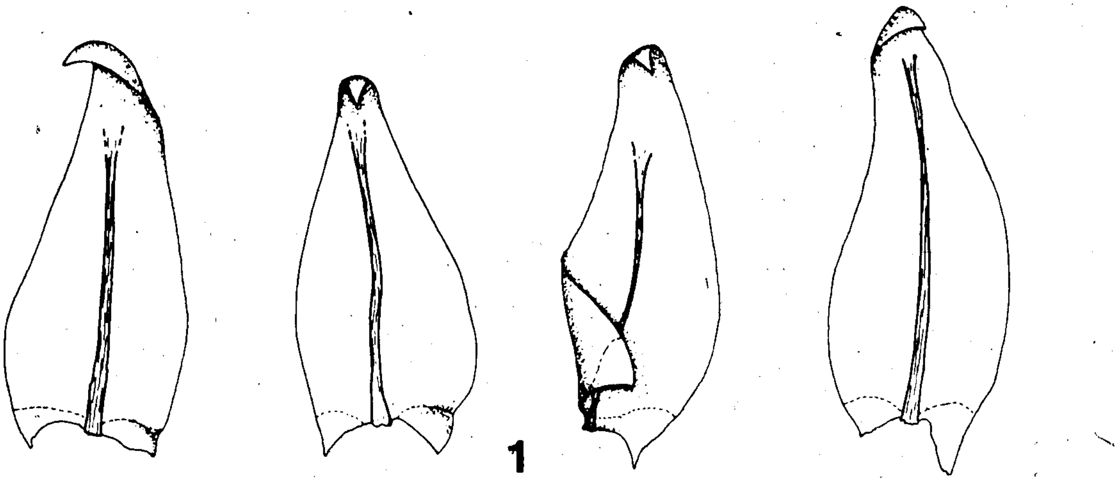
Drepanocladus pseudostramineus (C. Müll.) Roth Plate 38

Description (n=2). – *Leaves* straight to slightly curved, ovate-lanceolate, decurrent, 2.0–3.0 mm long, maximal width 0.8–1.0 mm, basal width 0.4–0.5 mm; *apex* shortly acuminate to narrowly obtuse, very commonly hooked; *margins* weakly denticulate; *costa* strong, ending high up in the upper half of the lamina; *upper leaf cells* elongate, 60–100 micrometer long, 6.0–7.5 micrometer wide, walls thick to moderately thick, sometimes porose; *alar cells* in a distinct group reaching the costa, clearly differentiated, strongly inflated, ovoidal, walls thin, hyaline. *Stem* with a circular to angular transverse section, central strand developed, epidermal cells sometimes slightly inflated and with thin outer walls, forming a weakly developed hyalodermis.

Habitat. – In poor fens and pools in wet tundra and near waterfalls. Probably an acidophilous species, but on the Reindeer Reserve (Holmen & Scotter 1971) found intermixed with *Scorpidium scorpioides*.

Plate 38. *Drepanocladus pseudostramineus* (C. Müll.) Roth (Bryological Reports 4:35)

1. Leaves (x42)
2. Medial leaf cells (x670)
3. Marginal leaf cells halfway up the leaf (x670)
4. Alar leaf cells (x268)



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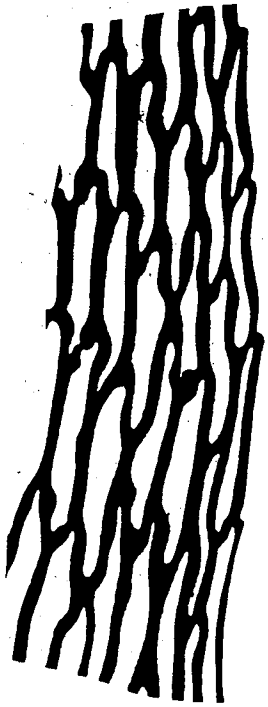

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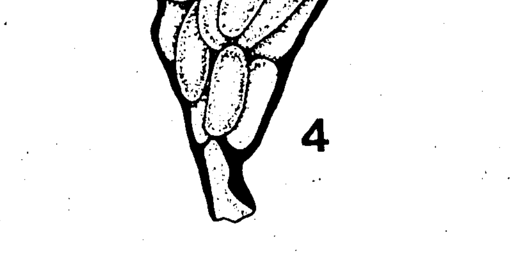

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Recent Distribution. – Rare. North America (Plate 39) : Alaska, Mackenzie delta, Alberta, southern British Columbia, Washington in the west, Hudson Bay coast, Labrador and Vermont in the east. Fennoscandia, the Alps.

Subfossil Distribution in North America (Plate 40) . – (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) CRH 79 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (3) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326; as *Drepanocladus cf. pseudostramineus*. (4) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434. (5) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Diagnostic Features and Discussion. – I agree fully with Tuomikoski & Koponen (1979) who indicate that *D. pseudostramineus* (*Calliergidium pseudostramineum* (C. Müll.) Grout) clearly to *Warnstorfia*, as does *D. tundrae*, and that both are closely related to *D. (Warnstorfia) fluitans*. Character states in common between the three above mentioned taxa are leaves that are often straight, the nematogon initials (differentiated apical cells), the weak denticulation, the weak costa and the ovate leaf base with a narrow constriction. The *D. tundrae–D. pseudostramineus* group differs from *D. fluitans* in better developed alar cell differentiation and often blunt apex. More information about *D. tundrae* and *D. pseudostramineus* is found in the *D. tundrae* discussion. For the distinction between leaves of *D. pseudostramineus* and those of *Eurhynchium pulchellum*, see the latter.

Drepanocladus revolvens (Sw.) Warnst. Plate 41

Description (n=30). – *Leaves* circinate to strongly falcate-secund, ovate-lanceolate to narrowly ovate-lanceolate, (1.4)2.1–2.6(4.5) mm long, maximal width (0.4)0.6–0.7(1.0) mm, basal *apex* slenderly acuminate, flexuose and spirally twisted; *margins* entire; *costa* faint, reaching the middle of the lamina or higher up; *upper leaf cells* elongate, (34)51–69(130) micrometer long, (3.8)5.0–5.7(7.8) micrometer wide, walls thick, porose;

Plate 39. The present day North American distribution of *Drepanocladus pseudostramineus* (C. Müll.) Roth based on specimens in ALTA and CANM (solid dots), and Holmen & Scotter 1971 (open circles).

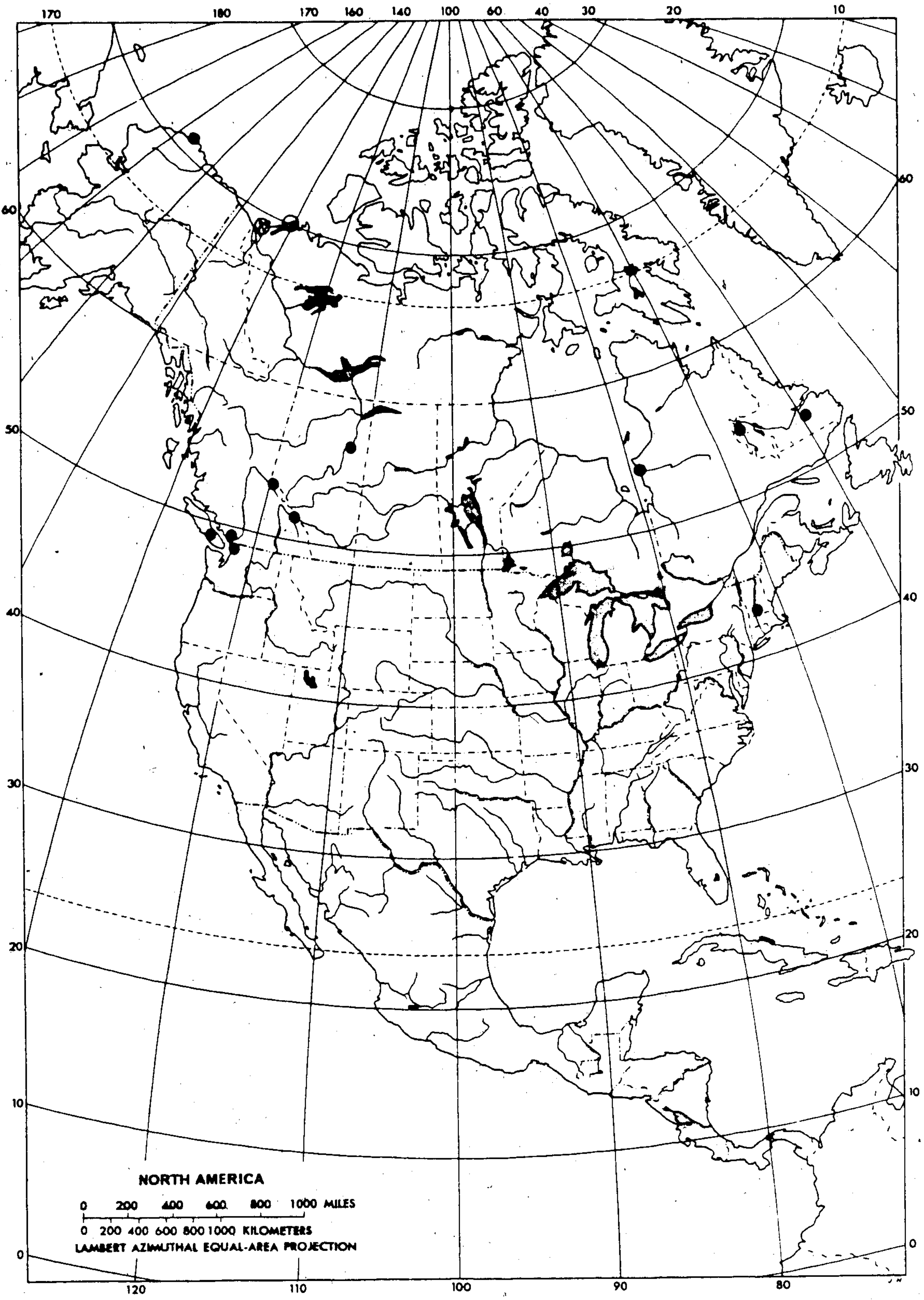
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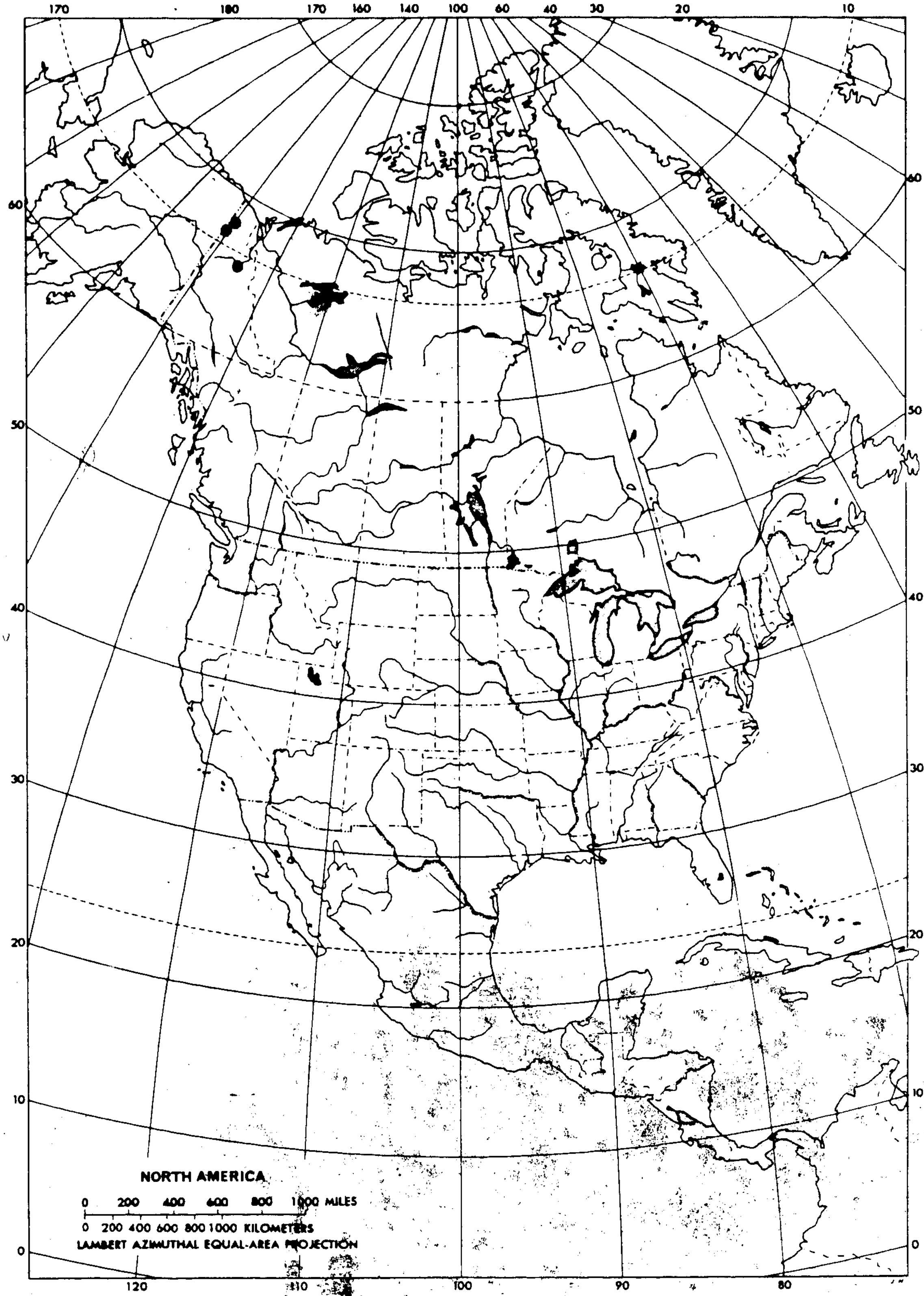
Plate 40. The Wisconsinan North American distribution of *Drepanocladus pseudostramineus* (C. Müll.) Roth based on Appendix 1.



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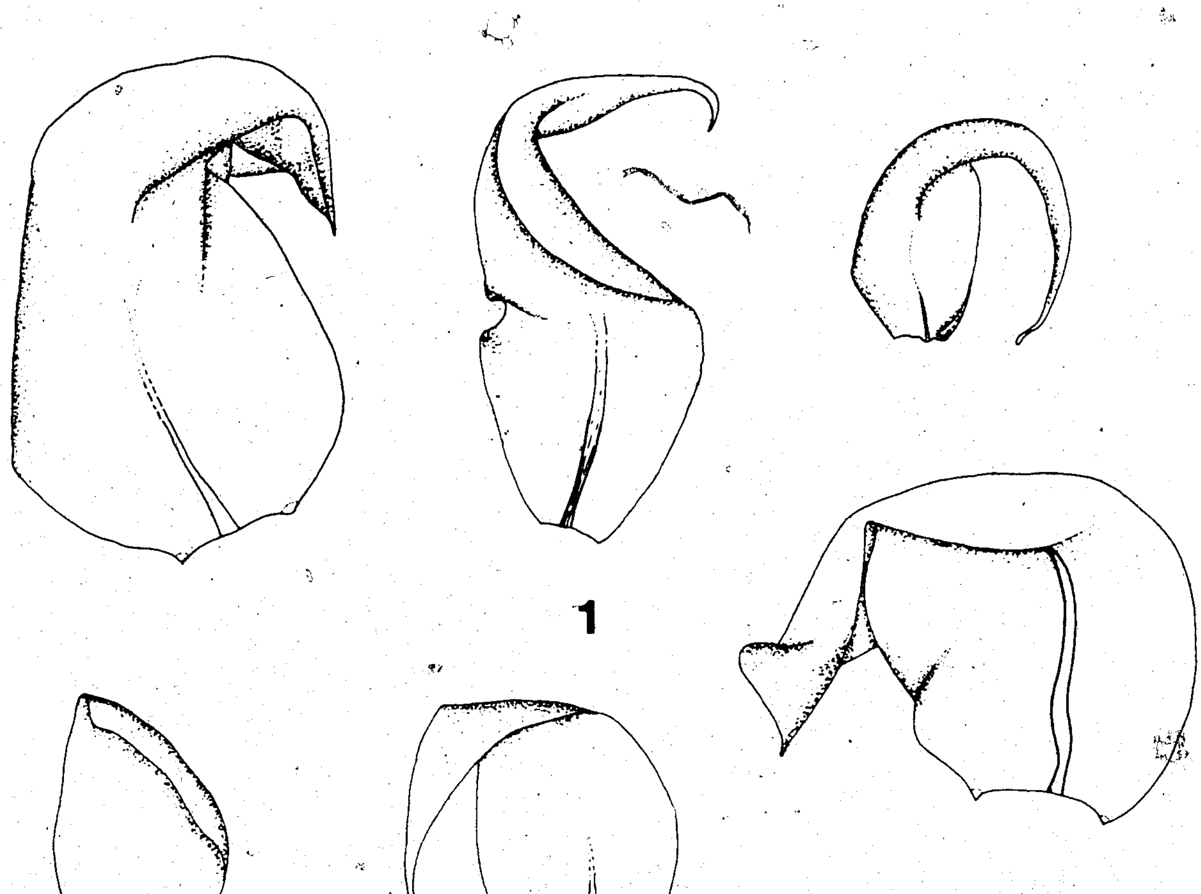
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 41. *Drepanocladus revolvens* (Sw.) Warnst (Bryological Reports 162, 164, 165, 200 and 434)

1. Leaves (x42)
2. Alar and basal cells (x268)
3. Stem transverse section (x268)
4. Medial leaf cells (x670)



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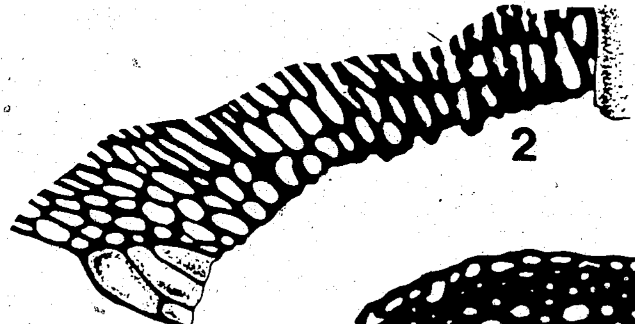

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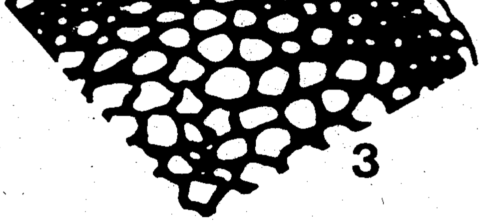

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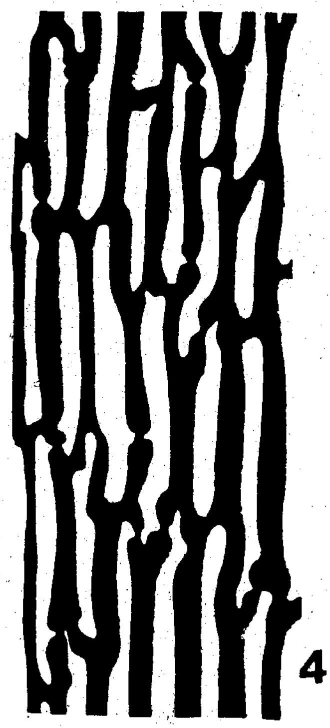

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alar cells in a very small group, two or five cells maximum, clearly differentiated, inflated, ovoidal, commonly lost during the preparation, walls thin, hyaline. *Stem* with circular transverse section, diameter (150)220–250(340) micrometer, central strand well developed, epidermal cells inflated, with thin outer walls, forming a very well developed hyalodermis.

Habitat – In fens, sedge-moss meadows, beside streams, in pools. On moist soil, along snow beds, ice furrows and in depressions on rock outcrops. It is one of the most conspicuous elements in rich fens. Often associated with *Campylium stellatum* and *Scorpidium scorpioides*. pH range (6.9)7.3–7.6(8.1), (n=52), conductivity (32)400–530(1070) microScm^{-1} (n=52), Ca concentration (3)33–60(160) ppm (n=43), Mg concentration (0)16–24(53) ppm (n=43), Na concentration (5)15–25(100) ppm (n=43), K concentration (0.0)0.7–3.6(18.8) ppm (n=43).

Recent Distribution. – Circumboreal. Common throughout its range, some southern hemisphere localities. North America (Plate 42) : Alaska, Yukon and Northwest Territories, common in the Arctic Archipelago, Greenland, Labrador, Newfoundland and continental Canada, south as outliers to the Great Lakes area, Iowa, Colorado and Montana. South America (Tierra del Fuego), scattered in western and central Europe, more common in northern Europe, Svalbard, northern Asia, Japan, Papua-New Guinea (Mount Wilhelm).

Subfossil Distribution in North America (Plate 43) . – Alberta, Greenland, Iowa, Michigan, Minnesota, New York, Northwest Territories, Ontario, Pennsylvania, Vermont, Wisconsin (Miller 1980a). New records: (1) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 50 to 60 cm below surface; Bryological Report 148. (2) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al*. 1978, p. 62. (3) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 163, Blake & Matthews 1979; as *Drepanocladus cf. revolvens*. (4) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 164, Blake & Matthews 1979. (5) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 165, Blake &

Plate 42. The present day North American distribution of *Drepanocladus revolvens* (Sw.) Warnst based on specimens in ALTA and CANM (solid dots), Holmen & Scotter 1971, Lewinsky 1973, Steere (1978a) and Tuomikoski *et al.* (1973) (open circles).

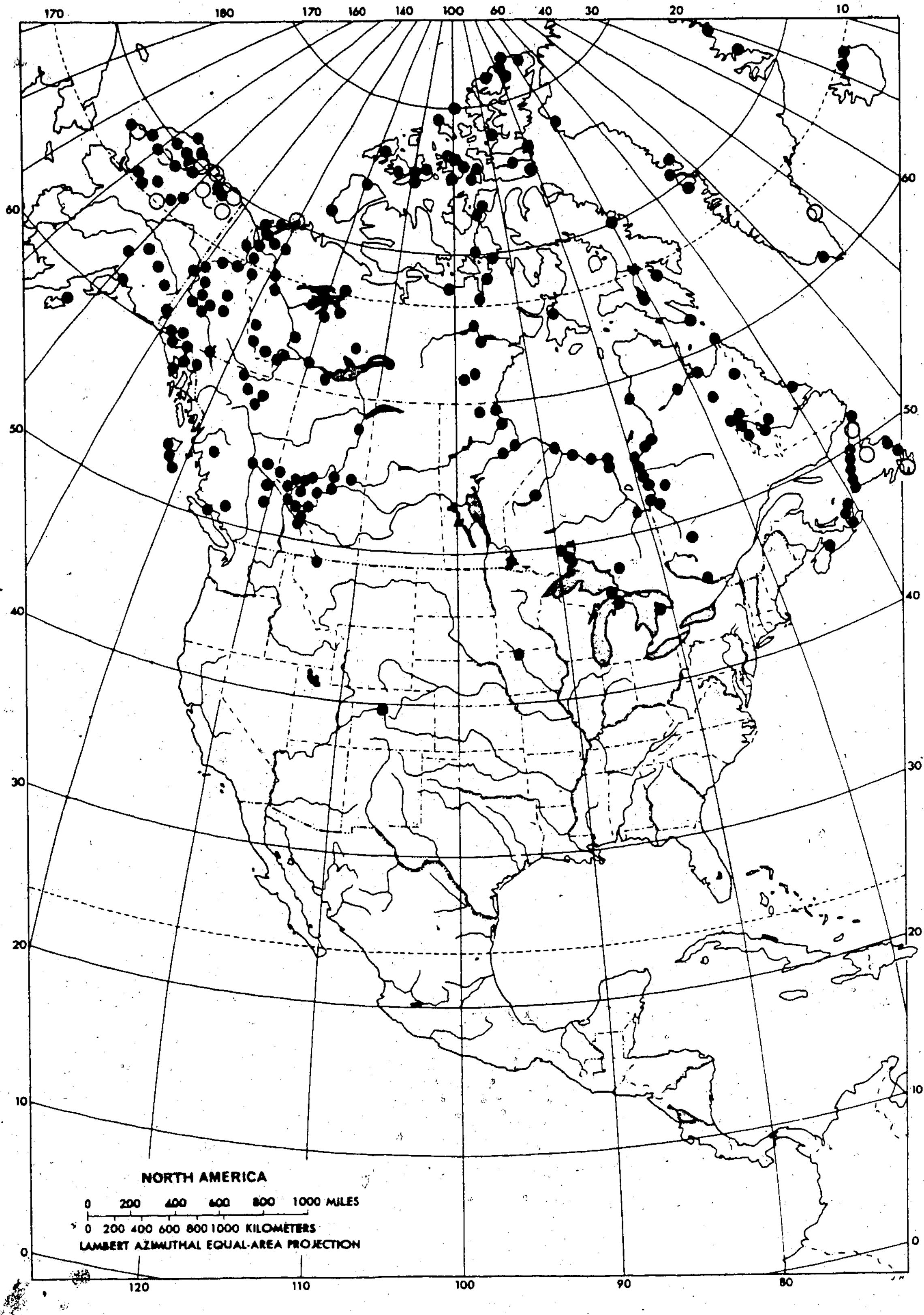
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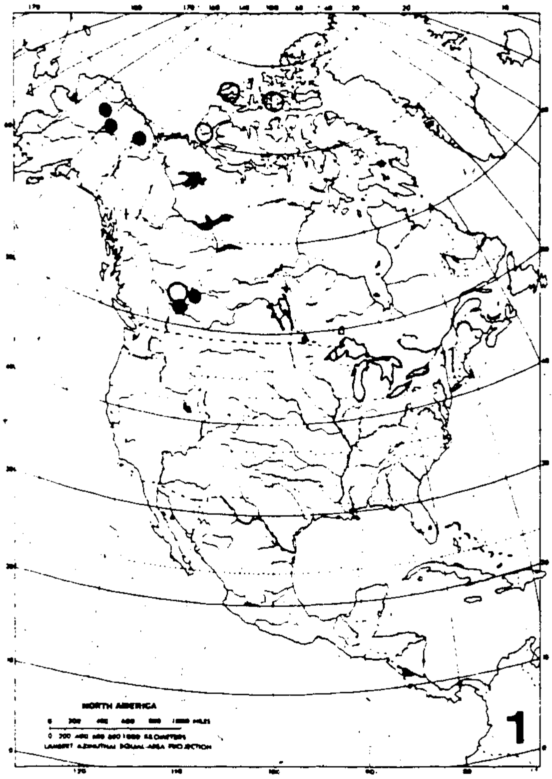
Plate 43: The subfossil North American records of *Drepanocladus revolvens* (Sw.) Warnst Solid dots: Appendix 1. Open circles: Miller (1980a), Kuc & Hills (1971) and Kuc (1973c).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.
4. Late Tertiary.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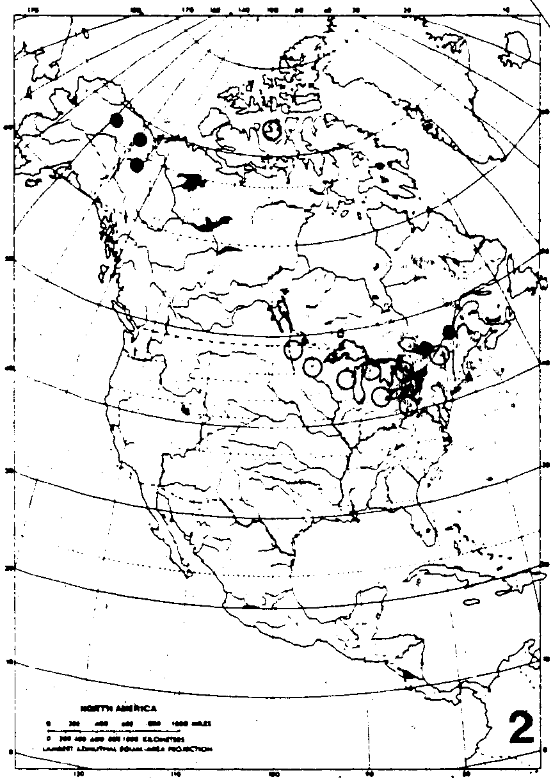
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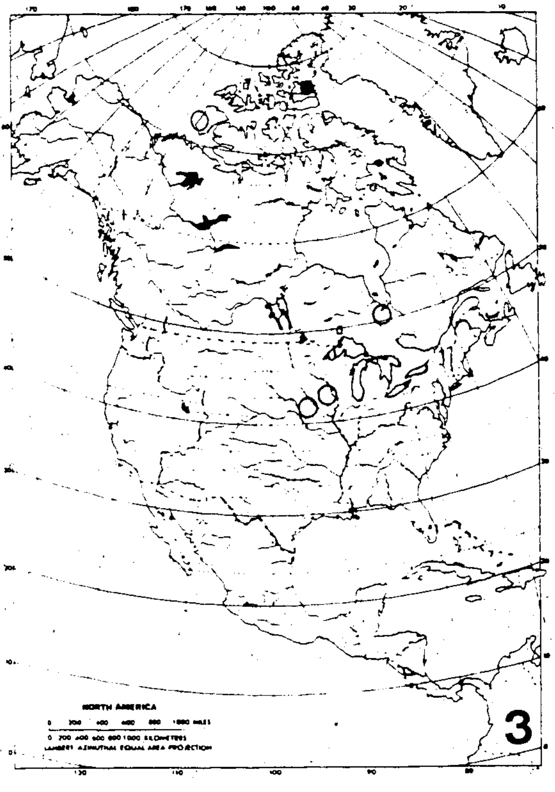
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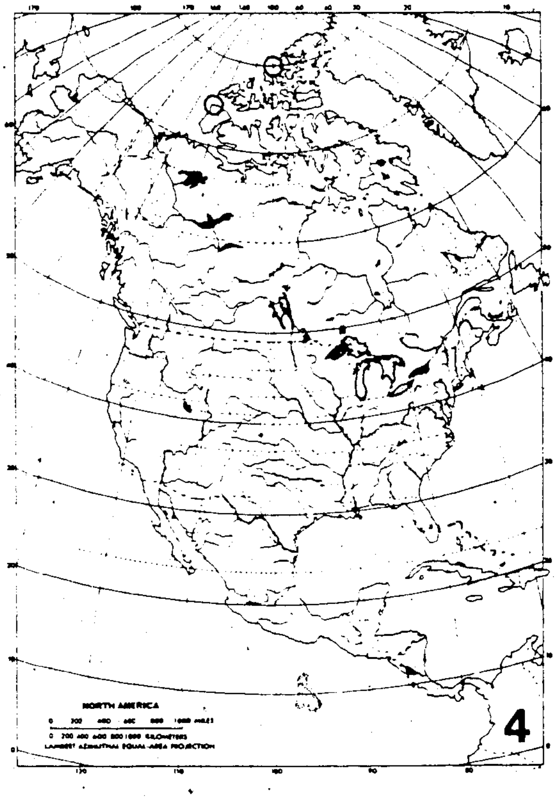
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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

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Matthews 1979. (6) Section Creek, 9 km upstream from Sagavanirktok River, Alaska; 12,690 ± 180 B.P. (I-10,567); Bryological Report 182, Hamilton 1979b. p. 29. (7) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (8) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (9) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (10) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267; as *Drepanocladus cf. revolvens*. (11) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980; as *Drepanocladus cf. revolvens*. (12) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980; as *Drepanocladus cf. revolvens*. (13) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434.

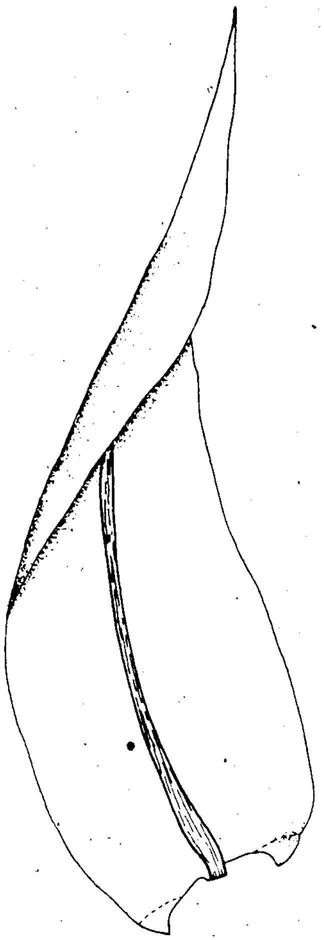
Diagnostic Features and Discussion. - Characteristic are the small, thight alar cell groups, composed of only a few cells, and the strongly circinate leaves. Also the lower leaves of a fragment are strongly falcate-secund which is not the case in the other *Drepanocladus* taxa with circinate leaves. *Drepanocladus revolvens* is quite isolated from all other *Drepanocladus* species (see also Tuomikoski *et al.* 1973, Tuomikoski & Koponen 1979: in *Limprichtia*). The only taxon closely related is *D. revolvens* var. *intermedius*. Most likely, both taxa are indistinguishable as subfossils, because the characteristic red color of the variety *revolvens* commonly will not preserve. Many bryologists consider the variety *intermedius* a less calciphilous taxon (see for example Bird *et al.* (1977)). It would be instructive to study the relationships between the two varieties more fully and to clarify their respective ecological requirements.

Drepanocladus sendtneri (H. Müll.) Warnst. Plate 44

Description (n=6). - *Leaves* strongly falcate-secund to slightly curved, ovate-lanceolate to widely ovate-lanceolate; 1.9-4.1 mm long, maximal width 0.6-1.0 mm, basal width 0.3-0.5 mm; *apex* slenderly acuminate; *margins* entire, sometimes a few teeth at the

Plate 44[illegible] *Drepanocladus sendtneri* (Schimp.) Warnst. (Bryological Reports 115, 176, 266 and 294)

1. Leaves (x42)
2. Medial leaf cells (x670)
3. Stem transverse section (x268)
4. Alar and basal leaf cells (x268)



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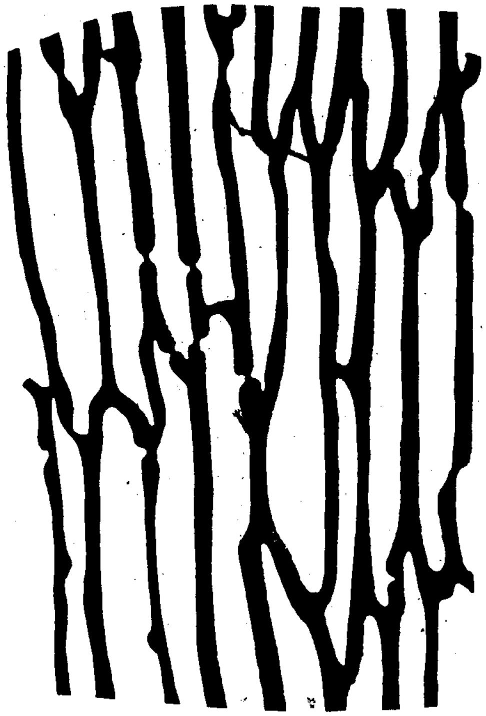

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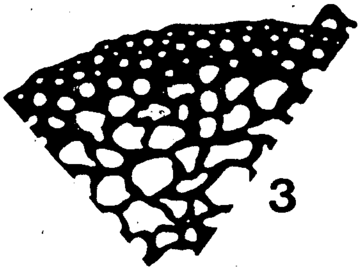

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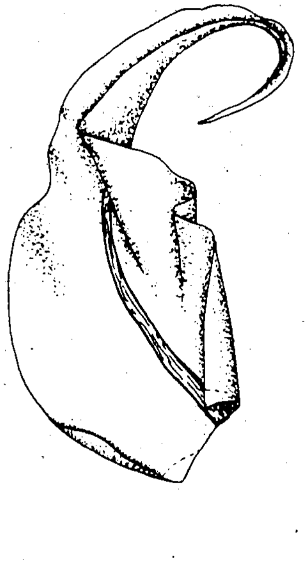

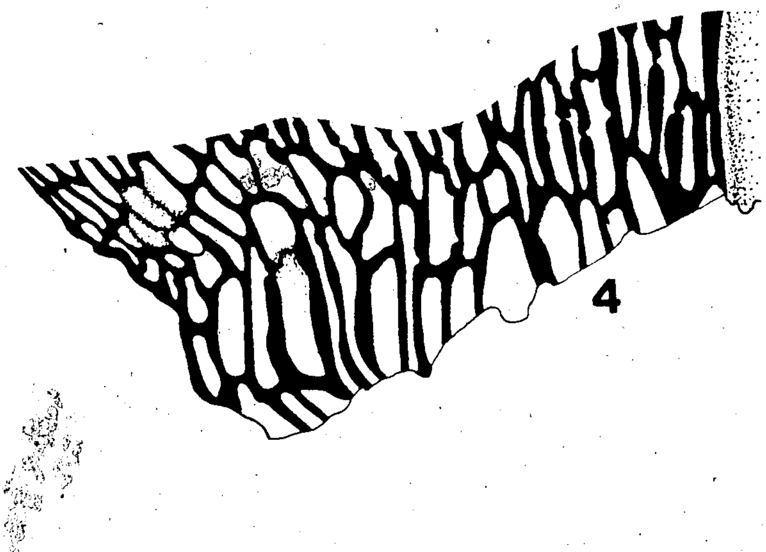

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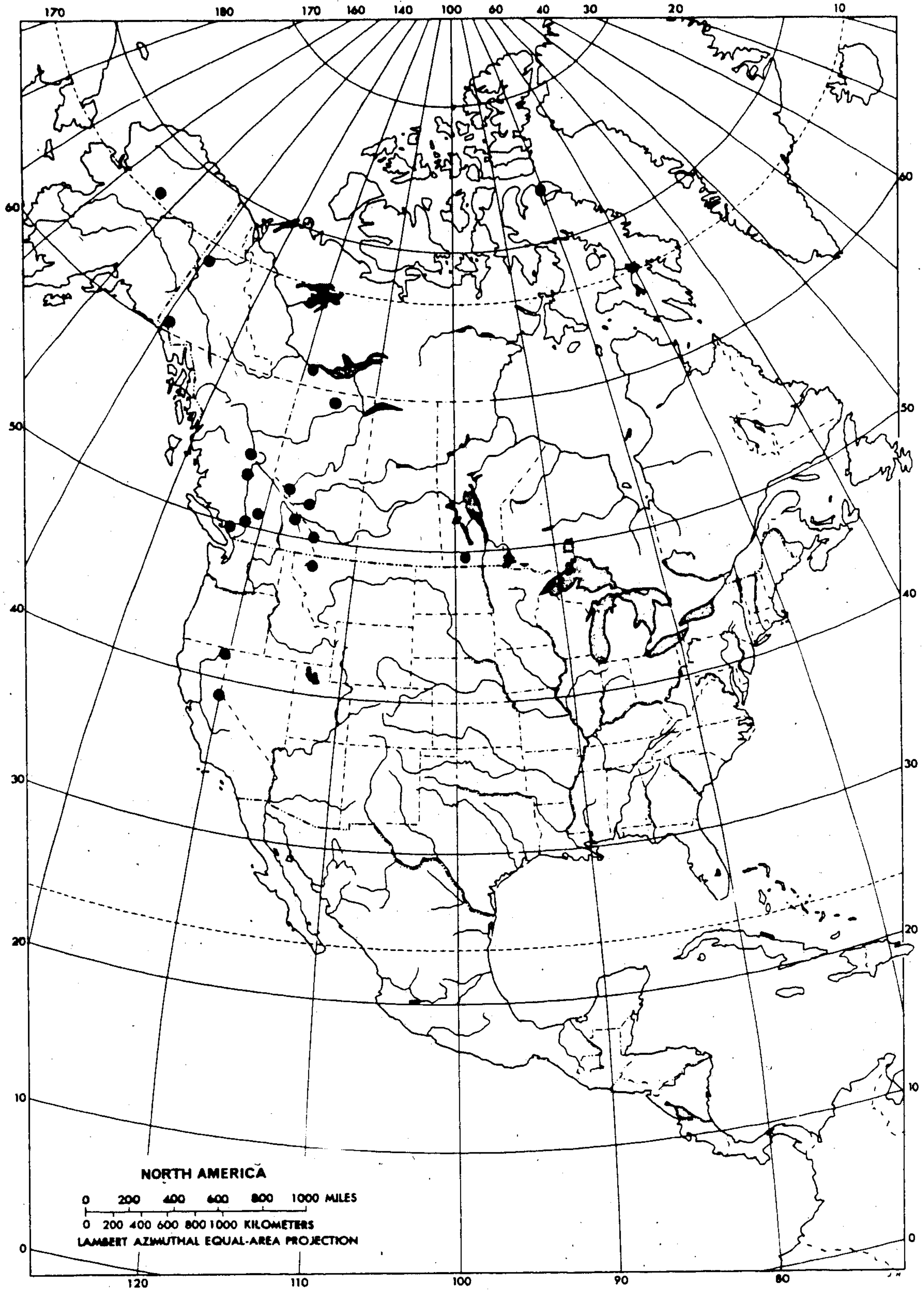
base; *costa* stout, 40–100 micrometer wide at the base, ending in the upper half of the lamina or reaching into the apex; *upper leaf cells* elongate, 42–64 micrometer long, 4.8–6.6 micrometer wide, walls thin, porose; *alar cells* in a diffuse group, not reaching the costa, rectangular, well to slightly differentiated, inflated, walls dark-brown, thick and porose. *Stem* with a circular transverse section, diameter 150–300 micrometer, central strand weak, always present, epidermal cells small and with thick outer walls.

Habitat. – In pools and shallow lakes in calcareous areas, in rich fens, even in brackish water.

Recent Distribution. – Circumboreal, rare. North America (Plate 45) : mostly western in distribution, Alaska, Yukon Territory and Mackenzie District, Baffin Island, British Columbia, Alberta and southern Manitoba, south to Montana and California. Europe, northern Asia.

Subfossil Distribution in North America (Plate 46) . – Alberta and Wisconsin (Miller 1980a). New records: (1) CRH 11 (station 5), Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 36. (2) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (3) HH69-21, Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 103. (4) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 115. (5) HH68-9 (station 9), Old Crow Basin, Yukon Territory; 38,800 ± 2000 B.P. (GSC-2756); Bryological Report 120. (6) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159. (7) Koyukuk River, 6 km downstream from Henshaw Creek, Alaska; 52,800 ± 1300 B.P. (QL-1283); Bryological Report 168; as *Drepanocladus cf. sendtneri*. (8) Anaktuvuk River, 0 (n=6).8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (9) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (10) CRH 11 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 266. (11) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 294. (12) HH68-9 (station 7), Old Crow Basin, Yukon

Plate 45. The present day North American distribution of *Drepanocladus sendtneri* (Schimp.) Warnst. based on specimens in ALTA and CANM (solid dots).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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

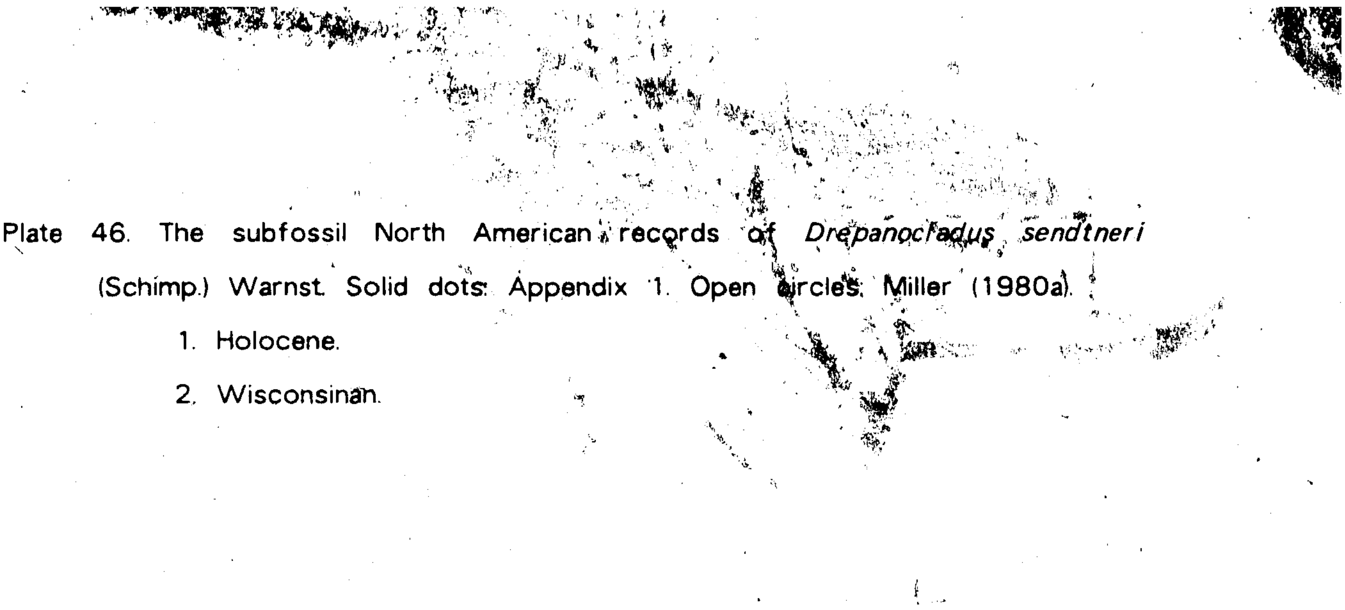
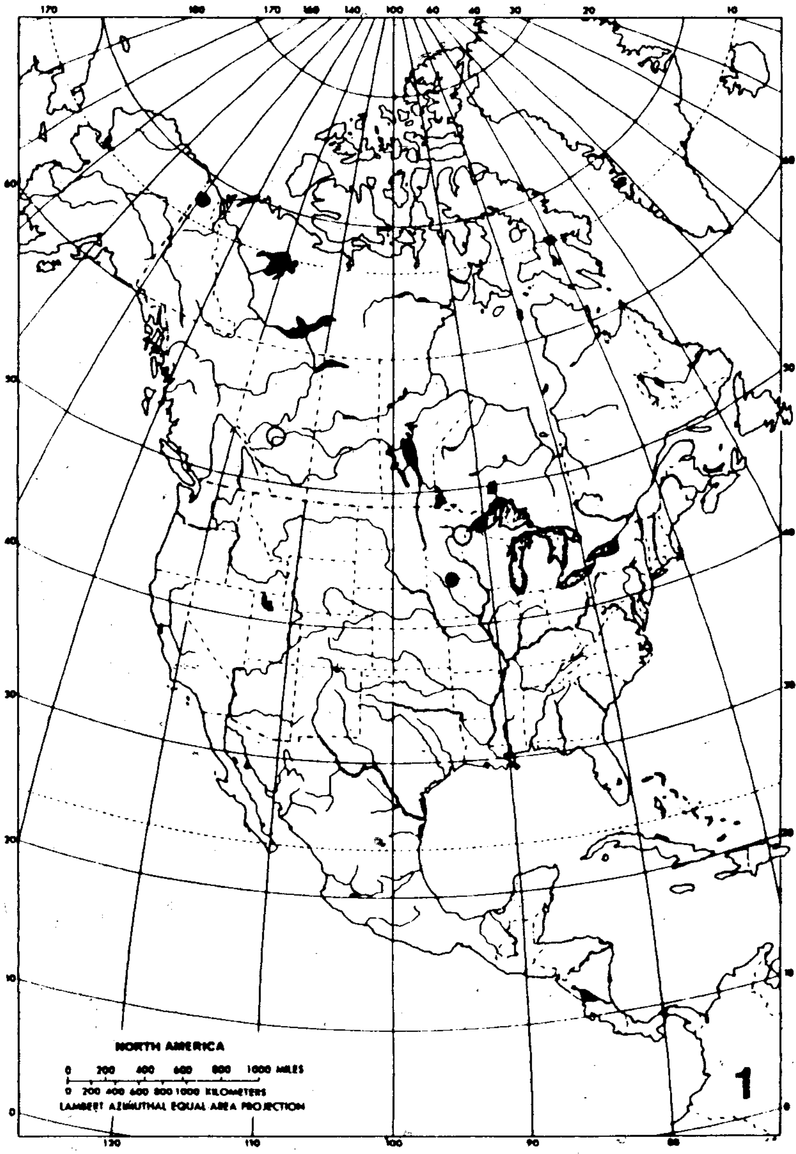


Plate 46. The subfossil North American records of *Drepanocladus sendtneri* (Schimp.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.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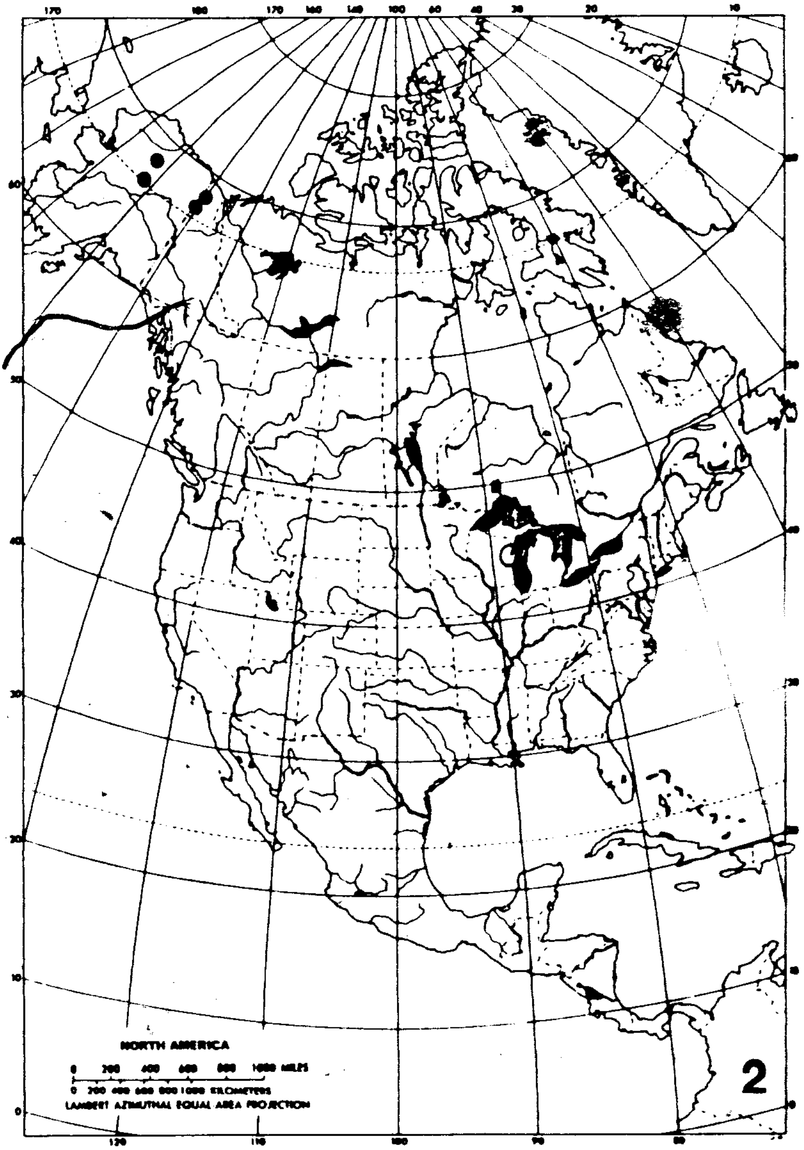
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LAMBERT AZIMUTHAL EQUAL AREA PROJECTION

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Territory; ± 60,000 B.P.; Bryological Report 308. (13) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (14) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (15) Bog near Hanlontown, Iowa; ± 1000 B.P.; Bryological Report 454, Welch 17346 (CANM).

Diagnostic Features and Discussion. – *Drepanocladus sendtneri* clearly belongs to the *Drepanocladus* group (*sensu* Loeske (1922), and Tuomikoski & Koponen (1979)). This is indicated by the entire leaf margins, the rounded-quadrate alar cells, which do not reache the costa as a group and the stem epidermis without a hyalodermis. Differentiating features for the species in this group are the frequently strongly developed costa and the thick-walled medial and alar cells. The leaf shape is extremely variable and ranges from long, slightly curved ovate-lanceolate leaves to short, widely ovate-lanceolate, strongly falcate-secund and concave leaves. The Fennoscandian *D. tenuinervis* Kop. (Koponen 1977) is closely related to *D. sendtneri*. *Drepanocladus tenuinervis* is a true aquatic, living in intermediate to highly minerotrophic lakes at a depth of two to six meter, and it is differentiated from *D. sendtneri* by a much weaker costa and thinner and less colored alar cell walls.

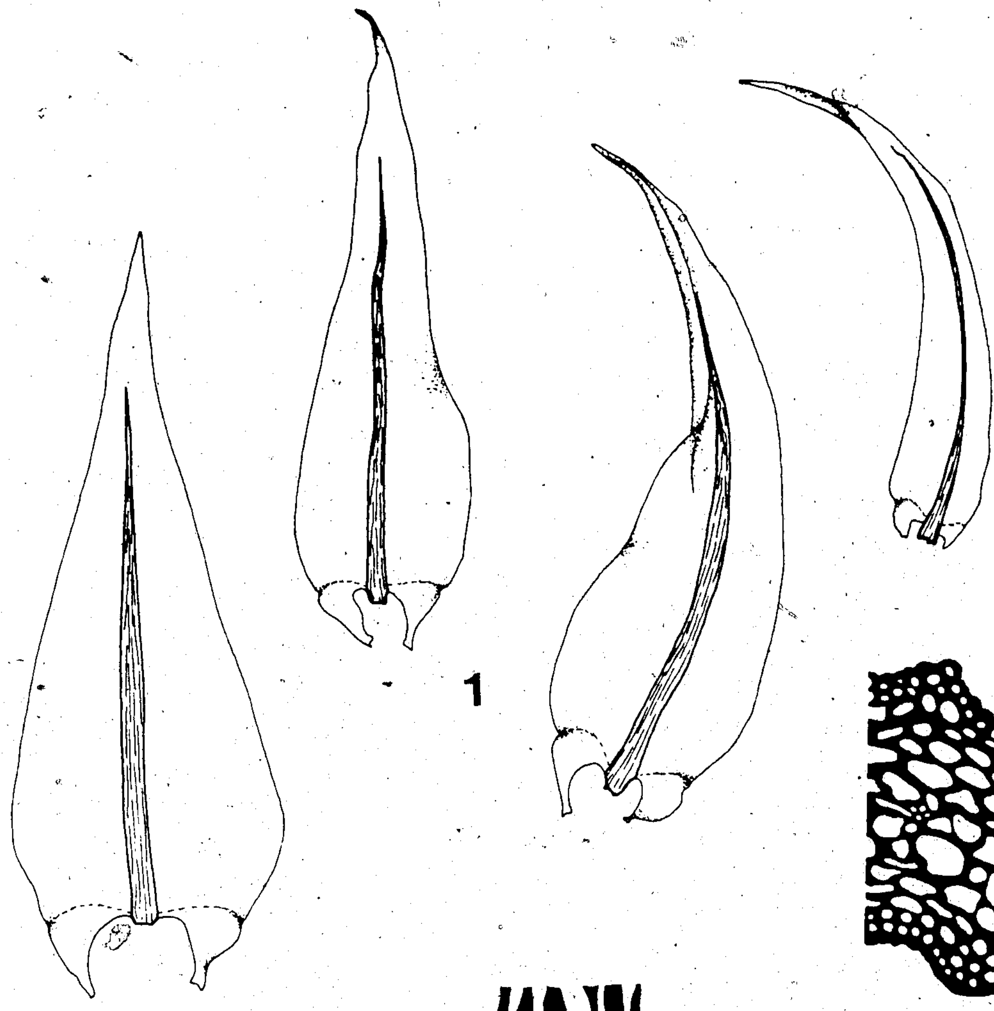
All the material determined as *D. sendtneri* in ALTA and CANM from localities east of Manitoba (except the Baffin Island specimen) appeared to be different taxa (see also Tuomikoski *et al.* (1 Apparently this species has a distribution in North America that is centered in the west.

Drepanocladus tundrae (Arn.) Loeske — Plate 47

Description (n=8). – *Leaves* straigth to sligthly curved, ovate-lanceolate, strongly decurrent, (1.8)2.1-3.0(3.1) mm long, maximal width (0.6)0.7-0.9(1.0) mm, basal width (0.3)0.4-0.6(0.7) mm; *apex* acuminate, sometimes hooked at the tip; *margins* denticulate to weakly denticulate; *costa* strong, ending in the upper half of the lamina; *upper leaf cells* elongate, (49)53-70(75) micrometer long, (5.6)-5.8-7.2(7.8) micrometer wide, walls moderately thick or thin, porose; *alar cells* in a broadly decurrent group, reaching the costa, clearly differentiated, inflated, ovoidal to rounded-quadrate, walls hyaline to

Plate 47. *Drepanocladus tundrae* (H. Arnell) Loeske (Bryological Reports 200, 295 and 302)

1. Leaves (x38)
2. Stem transverse section (x240)
3. Alar leaf cells (x240)
4. Marginal lead cells halfway up the leaf (x600)
5. Medial leaf cells (x600)



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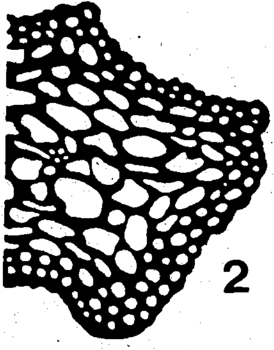

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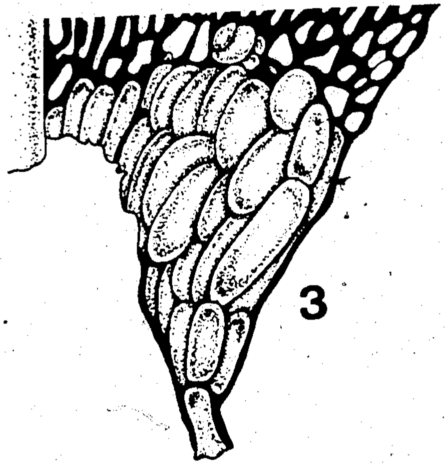

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yellow, thin to moderately thick. *Stem* with an angular transverse section, usually clearly pentagonal, diameter 250–450 micrometer, central strand well developed, epidermal cells small and with a thick outer wall.

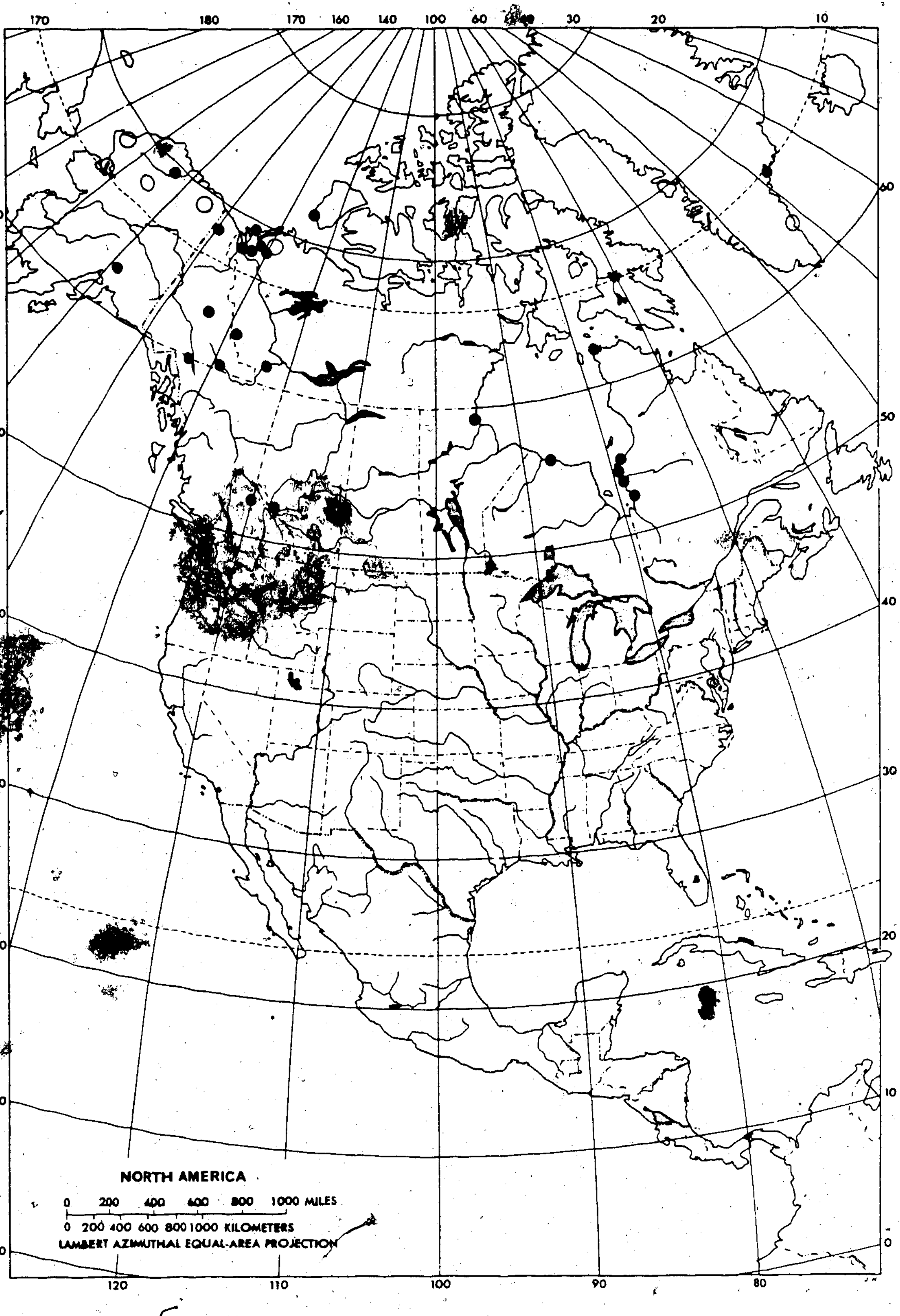
Habitat. – In rich fens, sometimes submerged in streams, lakes and pools of polygons and meadows. Mostly in exposed habitats, also in open *Picea* woodland.

Recent Distribution. – Circumboreal. North America (Plate 48) : Alaska, Yukon Territory and Mackenzie District, Banks Island, Greenland, Hudson Bay coast and mountains on the continental divide in Alberta and British Columbia. Svalbard, northern Europe and Siberia.

Subfossil Distribution in North America (Plate 49) . – Ontario (Miller 1980a). New records: (1) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (3) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 295. (4) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (5) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (6) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 392. (7) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434.

Diagnostic Features and Discussion. – *Drepanocladus tundrae* is clearly differentiated from the other taxa of the *Warnstorfia* group by a broadly decurrent mostly straight leaf often with a hooked apex. The stem transverse section is always angular and mostly distinctly pentagonal. This character state in subfossil material can be distinguished from a collapsed stem section by observing the intact, rounded cells, which form the ribs of the stem. *Drepanocladus tundrae* is closely related to *D. pseudostramineus*. The latter is distinguished by less decurrent alar cell groups, a more circular stem transverse section and often a blunt apex. However, forms are often encountered which are intermediate between these taxa. The taxonomic status of both species will be discussed in a

Plate 48. The present day North American distribution of *Drepanocladus tundrae* (H. Arnell) Loeske based on specimens in ALTA and CANM (solid dots), Holmen & Scotter 1971, Lewinsky 1973, and Steere (1978a) (open circles).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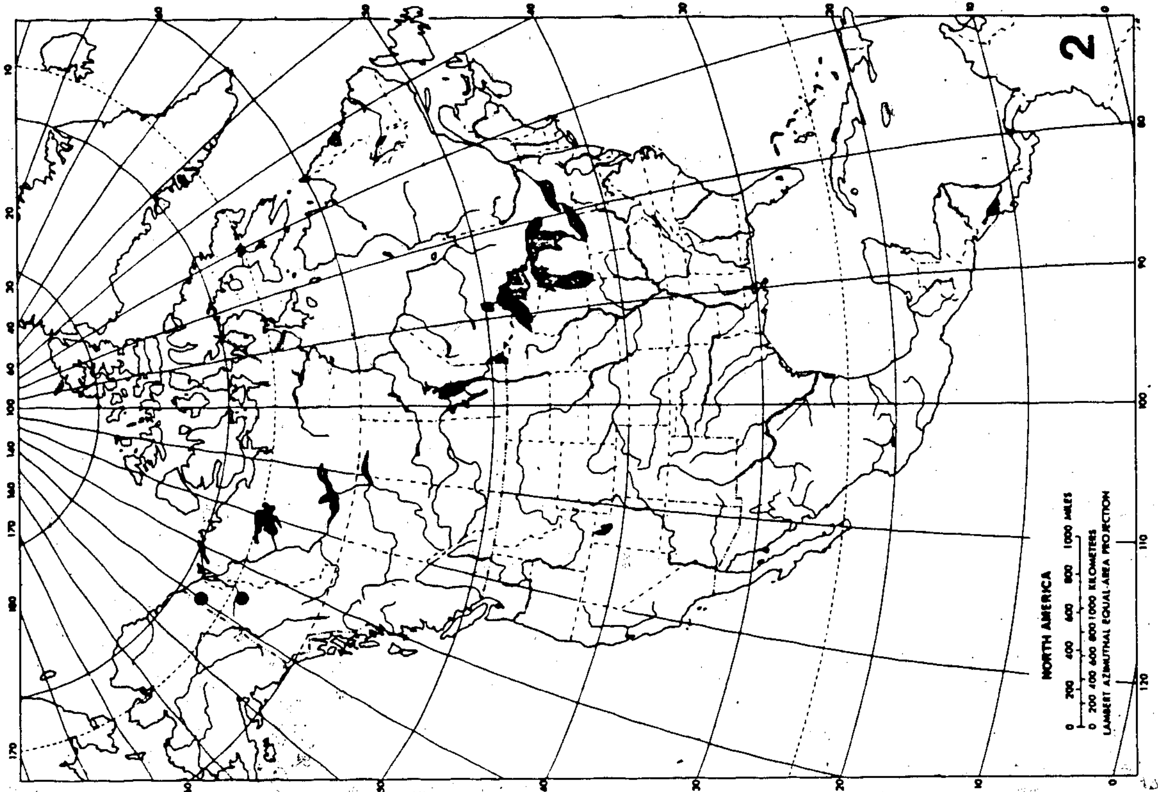
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Plate 49. The subfossil North American records of *Drepanocladus tundrae* (H. Arnell) Loeske. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.



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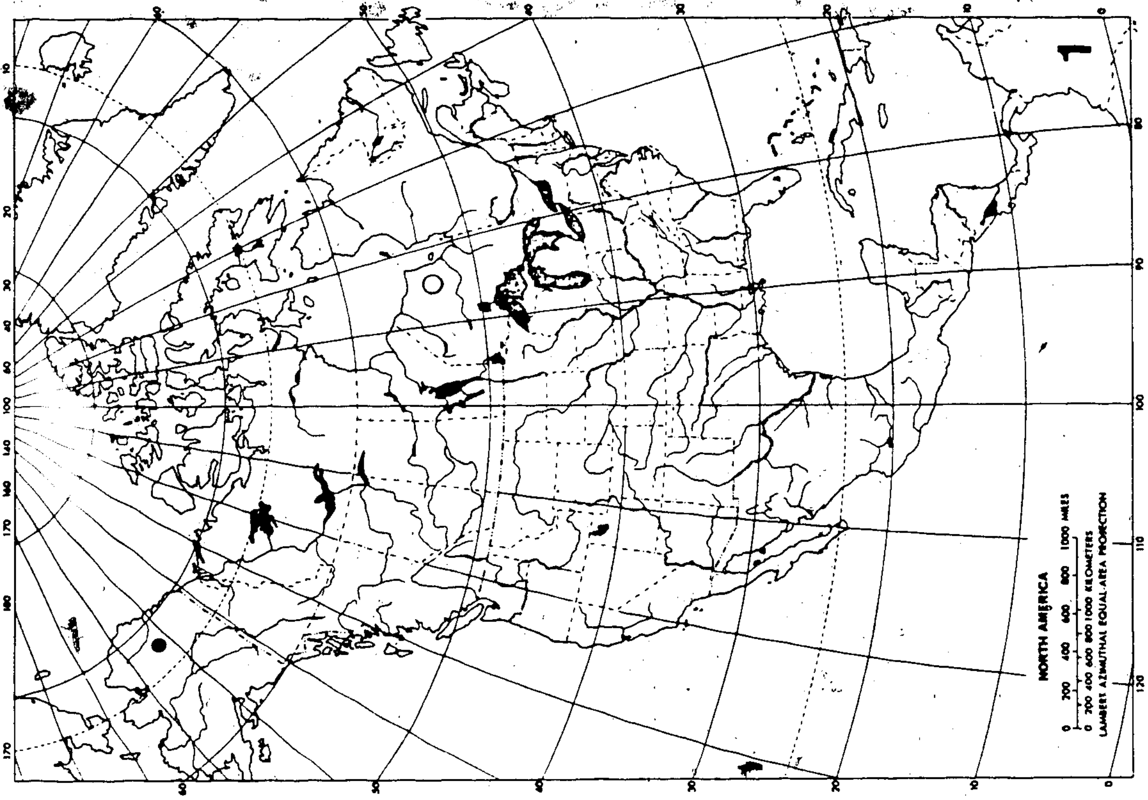

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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

forthcoming paper. At the moment, I believe that one of the two has to be reduced to varietal status. Tuomikoski & Koponen (1979) stated that both species form the connecting link between *Warnstorfia* and the true *Calliergon* species. The orthophyllous forms of both species with a hooked apex resemble closely some cucullate forms of *Calliergon* species with a narrow apex. Careful annotation of the *Warnstorfia* species in the major North American herbaria and additional collections will most likely indicate that *D. tundrae*–*D. pseudostramineus* are more commonly and evenly distributed over the Continent.

Drepanocladus uncinatus (Hedw.) Warnst. Plate 50

Description (n=28). – *Leaves* falcate-secund to circinate, ovate-lanceolate to lanceolate, plicate to smooth, not or weakly decurrent, (2.0)2.8–3.3(4.4) mm long, maximal width (0.4)0.6–0.7(1.0) mm, basal width (0.3)0.4–0.7(0.9) mm; *apex* slenderly acuminate, in young leaves flexuose and twisted; *margins* frequently sharply denticulate, mostly in the upper part; *costa* weak to strong, usually ending in the upper half of the lamina; *upper leaf cells* elongate, (33)52–66(124) micrometer long, (4.1)4.8–5.4(7.4) micrometer wide, walls thin to moderately thick, often porose; *alar cells* in a very small group, never reaching the costa, more or less clearly differentiated, some inflated, shortly rectangular or rounded-quadrate, walls hyaline or yellow, thin to moderately thick. *Stem* with a circular transverse section, diameter (153)254–317(480) micrometer, central strand well developed, epidermal cells inflated and with a thin outer wall, forming a hyalodermis.

Habitat. – On soil, gravel and over rock, on tree trunks, twigs and decaying wood. Common in *Dryas* heath, in the flood zone of streams, rivers and irrigated soil. Also seen in rich to poor fens and meadows. The species is not known to occur permanently submerged in lakes, but is common in periodically inundated areas. pH in aquatic environments ranges from 4.9 to 7.9 (n=6), conductivity from 15 to 385 microScm^{-1} (n=6), Ca concentration 2.4 to 13.2 ppm (n=6), Mg concentration 0.0 to 1.0 ppm (n=6), Na concentration 4.0 to 38.2 ppm (n=6) and K concentration 0 to 0.3 ppm (n=5).

Plate 50. *Drepanocladus uncinatus* (Hedw.) Warnst. (Bryological Reports 171, 201, 335, 342 and 401)

1. Leaves (x38)
2. Stem transverse section (x240)
3. Alar leaf cells (x240)
4. Medial leaf cells (x600)
5. Marginal leaf cells halfway up the leaf (x600)

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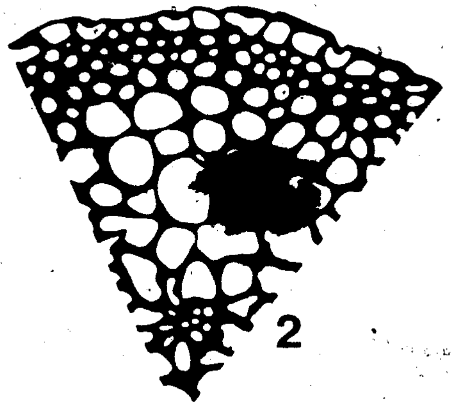

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Recent Distribution. – Circumboreal. Bipolar. Very common. North America (Plate 51) : from Alaska to Greenland, Labrador and Newfoundland, south to the Great Lakes area, northern New York and Vermont; Colorado, Utah, Idaho and California, disjunct to Mexico. South America, New Zealand, Kerguelen Islands and Antarctica.

Subfossil Distribution in North America (Plate 52) . – Greenland, Northwest Territories, Saskatchewan and Wisconsin (Miller 1980a). New records: (1) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 68. (2) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (3) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (4) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (5) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980; as *Drepanocladus cf. uncinatus.* (6) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; below >39,000 B.P. (I-4099); Bryological Report 335, Matthews 1974a. (7) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (8) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; >39,000 B.P. (I-4099); Bryological Report 342, Matthews 1974a. (9) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Diagnostic Features and Discussion. – *Drepanocladus uncinatus*, normally a mesophytic species, is sometimes found in wet habitats, often periodically inundated and thus frequently fossilized. Branch leaves formed during wet periods are characterized by an almost complete absence of plicae (*cf.* also Loeske 1910, p. 203). However, the stem leaves of *D. uncinatus* in these forms are still very distinct. They are strongly plicate, very long and strongly denticulate. In contrast with most branch leaves, they are straight. *Drepanocladus uncinatus* belongs to the species with a distribution restricted to former glaciated and periglacial areas.

Plate 51. The present day North American distribution of *Drepanocladus uncinatus* (Hedw.) Warnst. based on specimens in ALTA and CANM (solid dots), Holmen & Scotter 1971, Lewinsky 1973, Steere (1978a) and Tuomikoski *et al.* (1973) (open circles).

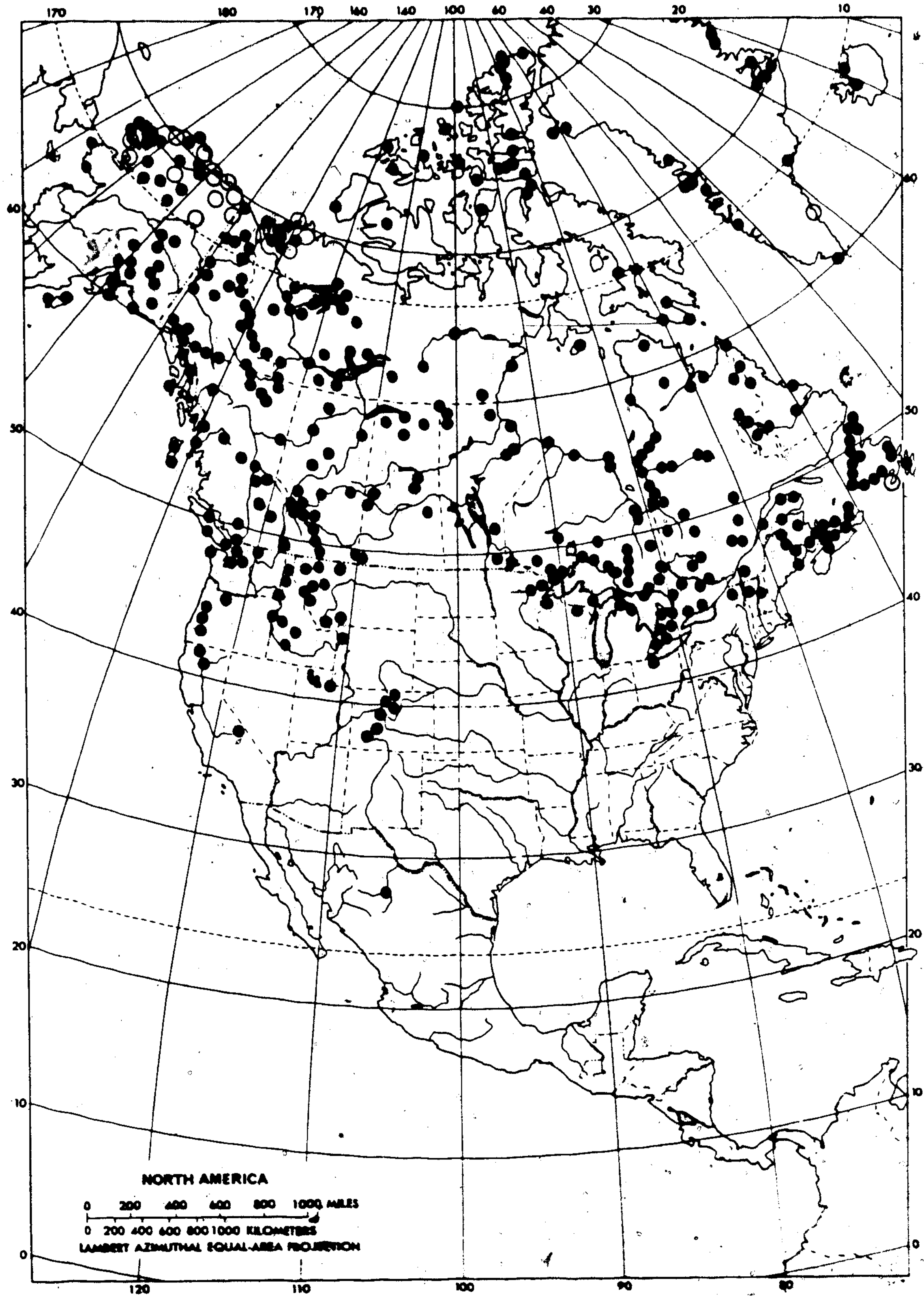
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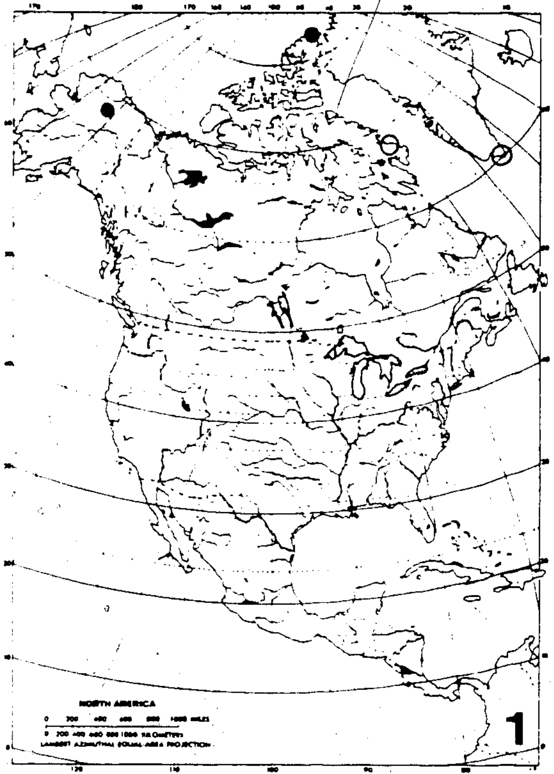
Plate 52. The subfossil North American records of *Drepanocladus uncinatus* (Hedw.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a) and Kuc (1973c).

1. Holocene.
2. Wisconsinan.
3. pre-Wisconsinan Pleistocene.
4. Late Tertiary.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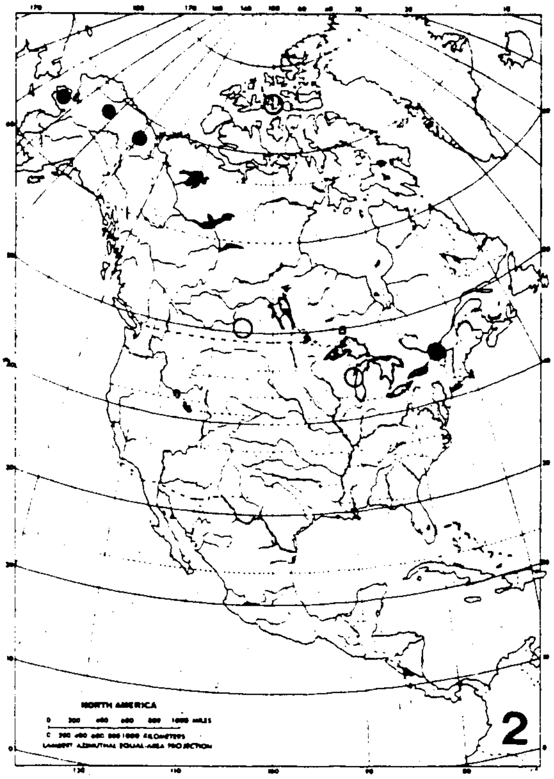
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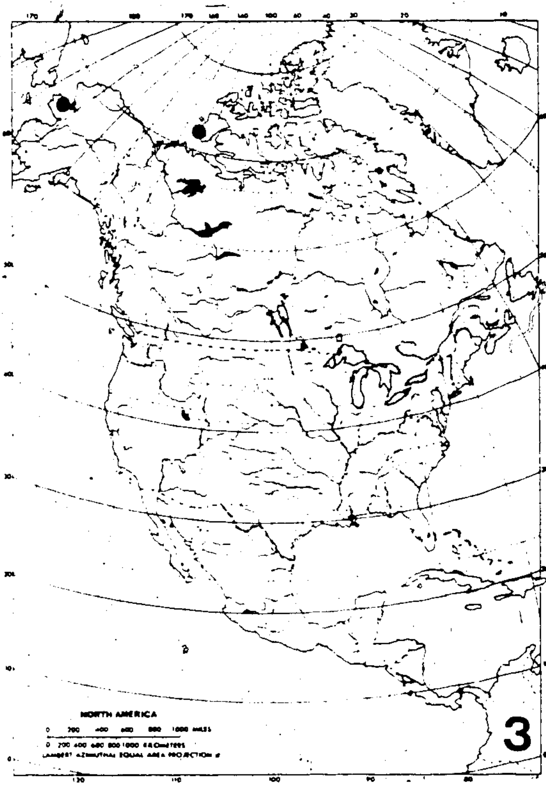
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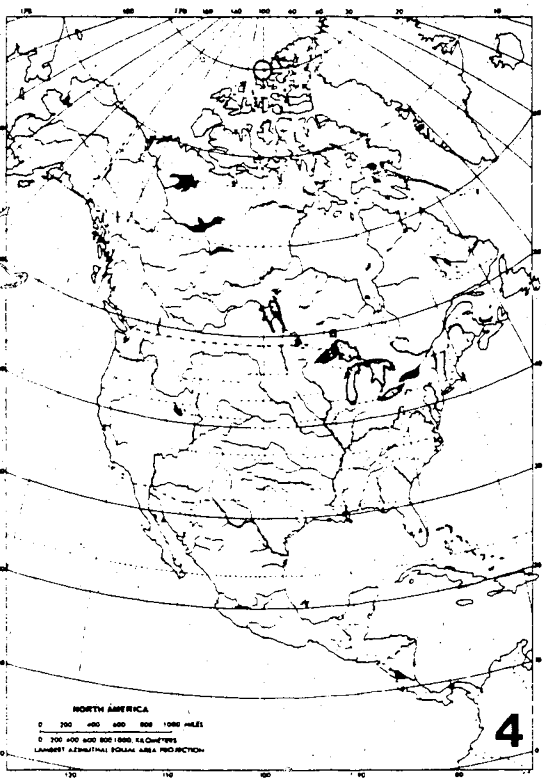
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Drepanocladus vernicosus (Lindb. *ex* C. Hartman) Warnst. Plate 53

Description (n=6). – *Leaves* falcate-secund to circinate, ovate-lanceolate, (1.6)1.7–2.5(2.7) mm long, maximal width 0.7–0.8 mm, basal width 0.5–0.7 mm; *apex* slenderly acuminate; *margins* entire; *costa* weak or strong, ending in the upper part of the lamina; *upper leaf cells* elongate, (31)41–73(75) micrometer long, (3.9)4.0–5.6(6.2) micrometer wide, walls thin or thick walled and porose; *alar cells* not differentiated from the other basal cells, rectangular, walls thick, porose and brown. *Stem* with circular transverse section, diameter (280)290–370(380) micrometer, no central strand, epidermal cells small and with thick outer walls.

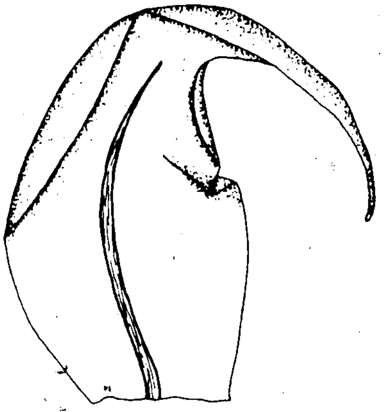
Habitat. – In moist or wet, often shaded habitats on calcareous substrata and in rich fens. Usually not submerged. pH ranges from 5.2 to 8.0 (n=13), conductivity 32–393 microScm^{-1} (n=13), Ca concentration 8–97 ppm (n=14), Mg concentration 1–23 ppm (n=14), Na concentration 3–66 ppm (n=14), K concentration 0–11 ppm (n=14).

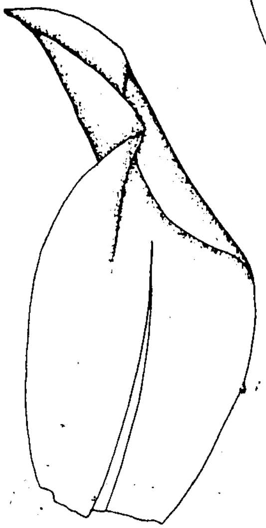
Recent Distribution. – Circumboreal. North America (Plate 54) : Alaska, Yukon Territory and Mackenzie District, Hudson Bay coast, Gaspe, Newfoundland and New Brunswick, south to the Great Lakes area, northern Minnesota, southern Manitoba, Saskatchewan, northern Montana and Washington.

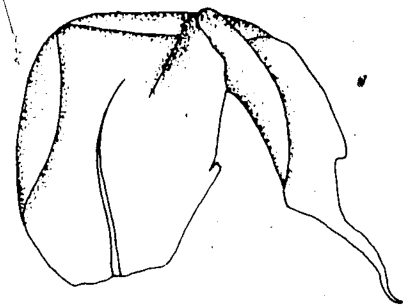
Subfossil Distribution in North America (Plate 55) . – Minnesota, New York, Vermont and Wisconsin (Miller 1980a). New records: (1) CRH 11, Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 3. (2) CRH 11 (station 5), Old Crow Basin, Yukon Territory; >51,000 B.P. (GSC-2559-2), ± 60,000 B.P.; Bryological Report 32. (3) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35; as *Drepanocladus cf. vernicosus.* (4) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (5) Wingham, Ontario; ± 12,100 B.P.; Bryological Report 278; as *Drepanocladus cf. vernicosus.* (6) Kitchener, Ontario; below 8800 B.P.; Bryological Report 321. (7) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325; as

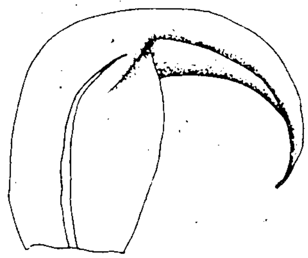
Plate 53. *Drepanocladus vernicosus* (Lindb. *ex* C. Hartm.) Warnst. (Bryological Reports 260, 321, 370 and 435)

1. Leaves (x43)
2. Stem transverse section (x276)
3. Basal leaf cells (x690)
4. Medial leaf cells (x690)









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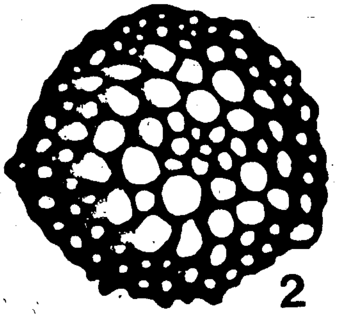

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Plate 54. The present day North American distribution of *Drepanocladus vernicosus* (Lindb. *ex* c. Hartm.) Warnst. based on specimens in ALTA and CANM (solid dots), and Holmen & Scotter 1971 (open circles).

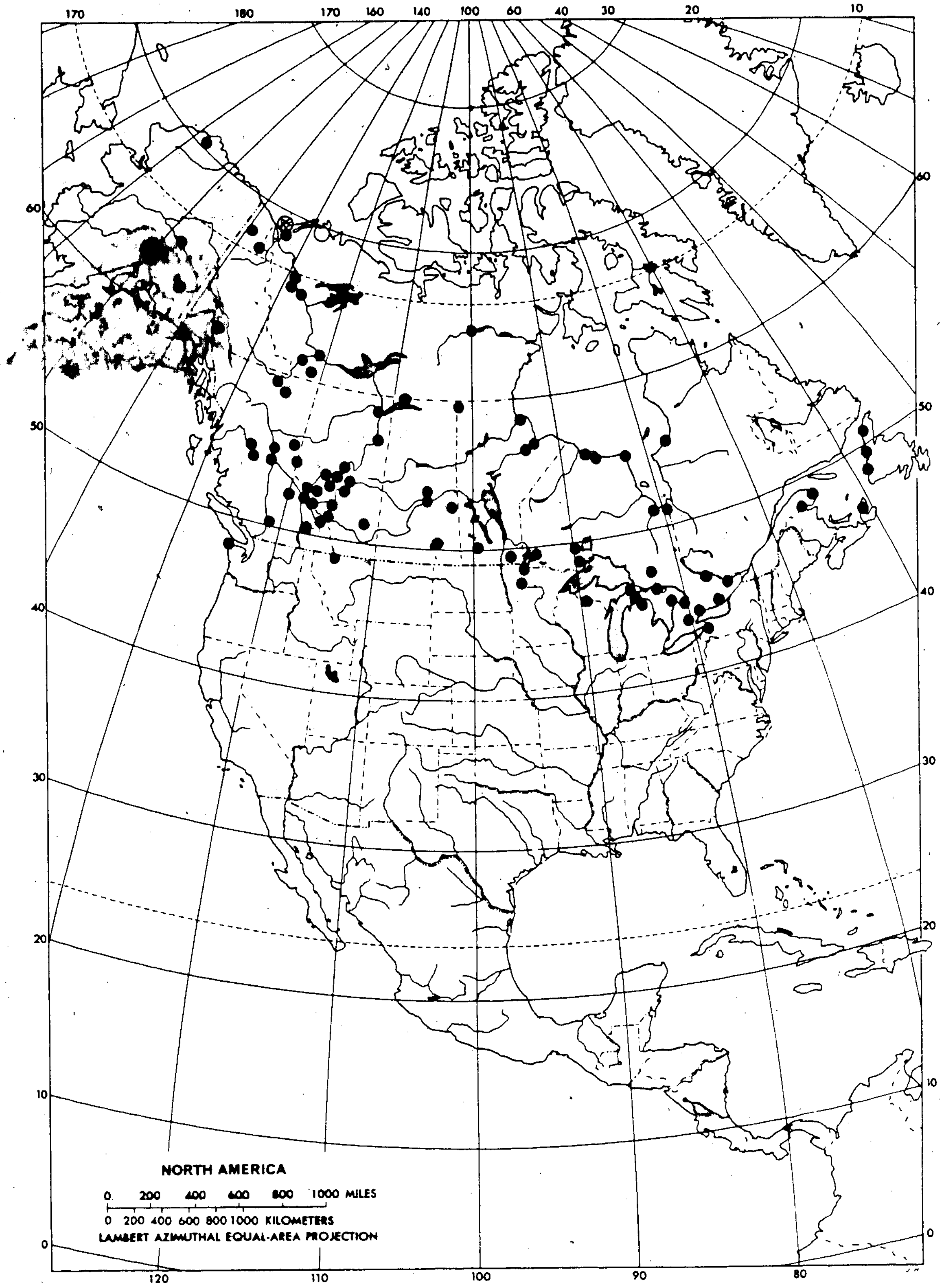
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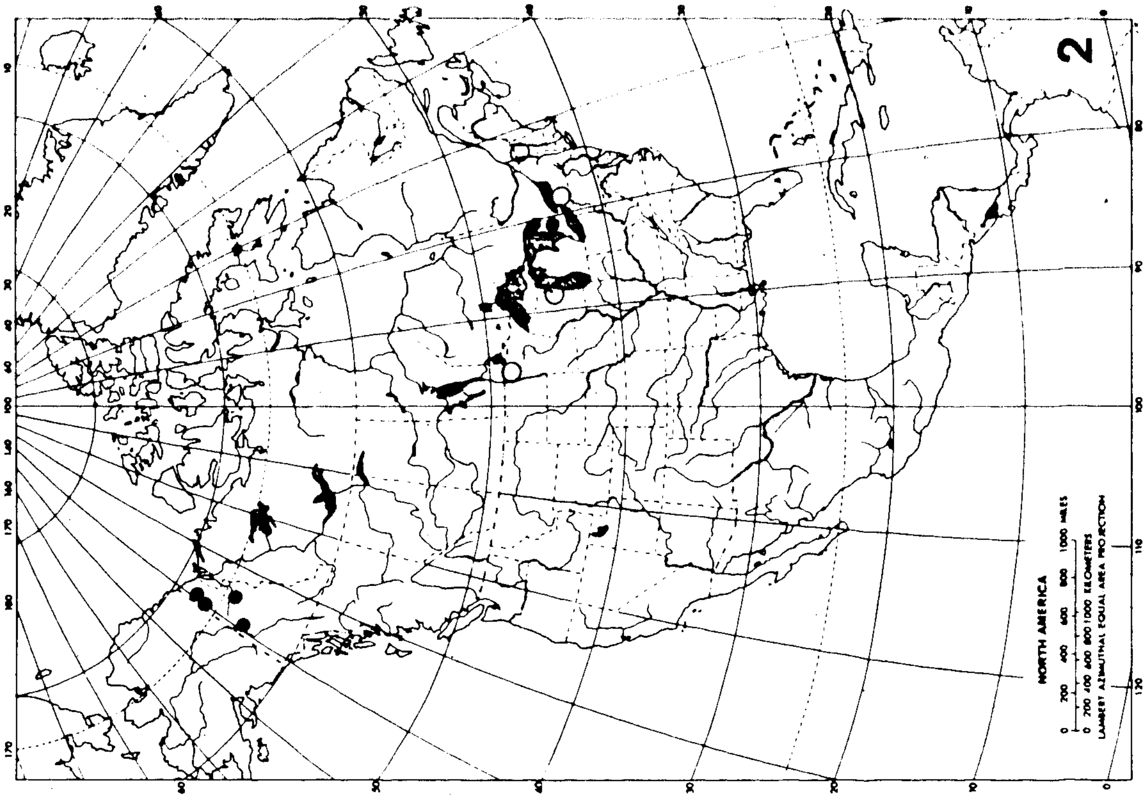
Plate 55. The subfossil North American records of *Drepanocladus vernicosus* (Lindb. *ex* c. Hartm.) Warnst. Solid dots: Appendix 1. Open circles: Miller (1980a).

1. Holocene.
2. Wisconsinan.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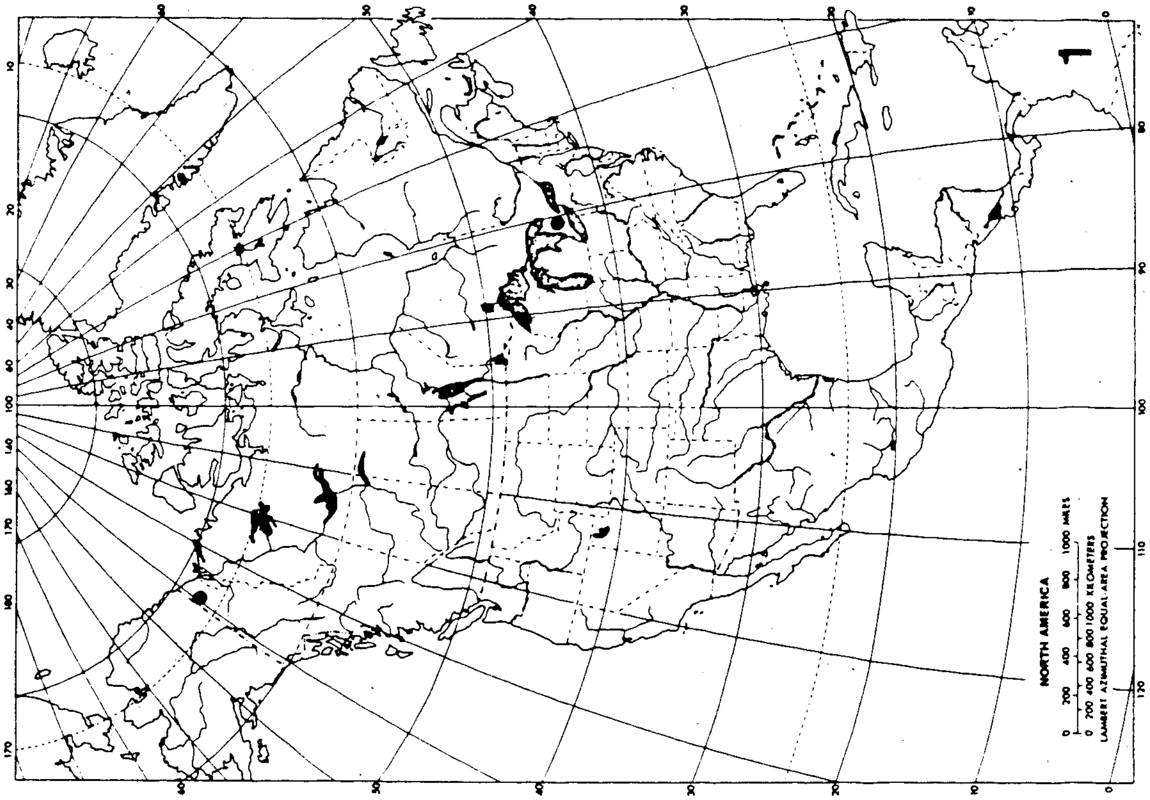
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Drepanocladus cf. vernicosus. (8) HH68-9 (station 9), Old Crow Basin, Yukon Territory. Early Wisconsinan?, Bryological Report 370. (9) HH72-54 (station 3), Hungry Creek, Yukon Territory, Wisconsinan; Bryological Report 435.

Diagnostic Features and Discussion. – The character states most reliable for recognizing *D. vernicosus* are the absence of a central strand in the transverse section of the stem and a complete lack of alar cell differentiation. Most of the plants are small. However, the subfossil fragments are frequently still pinnately branched.

D. vernicosus belongs to the species with a distribution restricted to former glaciated and periglacial areas. It is absent from the Arctic Archipelago (ALTA and CANM).

Drepanocladus unidentified species

Subfossil Distribution in North America. – Alaska, Illinois, Minnesota, Northwest Territories, Quebec and Wisconsin (Miller 1980a). New records: (1) CRH 11, Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 3. (2) CRH 11 (station 5), Old Crow Basin, Yukon Territory; >51,000 B.P. (GSC-2559-2), ± 60,000 B.P.; Bryological Report 32; as *cf. Drepanocladus* species. (3) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (4) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (5) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (6) CRH 11 (station 5), Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 36. (7) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (8) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (9) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (10) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62; as *cf. Drepanocladus* species. (11) HH69-21 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 102. (12) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 109. (13) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21.

(14) HH68-9 (station 1, 2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 176. (15) Your Creek area, Alaska, 5615 ± 110 B.P. (I-10,568), Bryological Report 183, Hamilton 1979a, Fig. 5. (16) HH68-9 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 262. (17) HH68-9 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 263. (18) HH68-9 (station 11), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 265. (19) CRH 11 (station 3), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 266. (20) CRH 12 (station 2), Old Crow Basin, Yukon Territory, ± 60,000 B.P., Bryological Report 267. (21) CRH 70 (station 2), Old Crow Basin, Yukon Territory, >37,000 B.P. (GSC-2792), Bryological Report 269. (22) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (23) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (24) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980. (25) HH68-9 (station 3), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 294. (26) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 295. (27) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (28) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?, Bryological Report 302. (29) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (30) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (31) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326. (32) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (33) 228HH, Bluefish Basin, Yukon Territory; >37,000 B.P. (GSC-2783), ± 60,000 B.P.; Bryological Report 362. (34) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (35) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 384. (36) HH68-9 (station 10), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 385. (37) HH68-9 (station 12), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 386. (38) HH68-9 (station 14), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 387. (39) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 389. (40)

HH68 9 (station 3) Old Crow Basin Yukon Territory. Early Wisconsinan? Bryological Report 391 (41) HH68 9 (station 3) Old Crow Basin Yukon Territory Early Wisconsinan? Bryological Report 392 (42) HH68 9 (station 7) Old Crow Basin Yukon Territory. Wisconsinan. Bryological Report 424 (43) HH68 9 (station 9) Old Crow Basin Yukon Territory Early Wisconsinan? Bryological Report 425 (44) Ballaine Lake, Fairbanks area Alaska, 3110 ± 100 BP (USGS 30). Bryological Report 427. Hamilton *et al.* 1980 as *cf. Drepanocladus* species (45) HH72 54 (station 3). Hungry Creek Yukon Territory Wisconsinan Bryological Report 434 (46) HH72 54 (station 3) Hungry Creek Yukon Territory Wisconsinan Bryological Report 435

Hygroamblystegium

Hygroamblystegium tenax (Hedw.) Jenn.

Diagnostic features. – *Leaves* around 1 mm long, ovate to ovate-lanceolate. *costa* reaching to the extreme apex, strong and often with a twist in the upper half. *apex* often bluntly acuminate; *margins* entire or subentire; *medial cells* short, 4:1 to 2:1, often shorter in the apex, becoming gradually shorter, rectangular and quadrate at the base.

Habitat. – In wet habitats, on stones and trees, also in running water.

Recent Distribution. – Circumboreal. North America from British Columbia to Newfoundland, but very rare in the west, essentially an eastern species south to Florida Arkansas, Arizona and Mexico. Europe, North Africa, Madeira and Caucasus.

Subfossil Distribution in North America. – Vermont (Miller 1980a). New records: (1) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178.

Discussion. – For the distinction between *Hygroamblystegium tenax* and *Amblystegium varium*, see the notes under the latter. Similar *Cratoneuron* leaves are distinguished by the cordate ovate shape with sharp teeth along the margins and by the elongate medial cells

Hygrohypnum

This genus is poorly represented in the fossil record (see also Dickson (1973)) The few specimens in my collections could not be assigned to any species with confidence

Subfossil Distribution in North America Indiana Northwest Territories Ontario Vermont and Washington D.C. (Miller 1980a including *Hygrohypnum eugyrium* (B.S.G.) Loeske *H. eumontanum* Crum Steere and Anders *H. luridum* (Hedw.) Jenn and *H. polare* (Lindb.) Loeske) New records (2) Clements Markham Inlet Ellesmere Island Northwest Territories 6400 ± 60 BP (SI 4314) Bryological Report 401 as *Hygrohypnum cf. luridum* (3) HH68 9 (station 8) Old Crow Basin Yukon Territory Early Wisconsinan? Bryological Report 62 as *cf. Hygrohypnum polare*

Discussion Like the other Amblystegiaceae the species of *Hygrohypnum* are frequently found in wet habitats However these taxa are particularly associated with running water This could explain their practical absence from the fossil record because such high energy environments are less suitable for fossilization

Scorpidium

Scorpidium scorpioides (Hedw.) Limpr

Diagnostic features – *Leaves* widely ovate to cordate-ovate, falcate-secund *apex* apiculate, *costa* short double, sometimes single and reaching to halfway up in the lamina or absent; *medial cells* with thick porose walls, *alar cells* gradually differentiated a few inflated and with thin hyaline walls

Habitat – In tufts or mats in moist or wet habitats on calcareous ground, often in fens mixed with *Drepanocladus revolvens*. On irrigated rocks, sometimes submerged in lakes or pools. Cited as an indicator of rich fens (Miller 1980c). The pH ranges from 6.9 to 7.8 (n=35), conductivity 66 to 1042 microScm^{-1} (n=35), Ca concentration 2.8–155.0 ppm (n=21), Mg concentration 1.5–51.6 ppm (n=21), Na concentration 2.6–27.8 ppm (n=20) and K concentration 0–15.3 ppm (n=20).

Recent Distribution. – Circumboreal. North America (Miller 1980c): from Alaska to Greenland, Labrador and Newfoundland, most common in the north, south to the Great Lakes area in the east and through the western mountains to Colorado and Utah in the west. Europe, northern Asia.

Subfossil Distribution in North America (Miller 1980c). – Alberta, British Columbia, Iowa, Manitoba, Minnesota, Northwest Territories, Wisconsin and Yukon Territory (Miller 1980a). New records: (1) Silver Creek, Slims River drainage, Yukon Territory; 30,100 ± 600 B.P. (Y-1385); Bryological Report 2, Schweger & Janssens 1980. (2) CRH 11, Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 3. (3) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (4) CRH 11, Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 37. (5) CRH 12, Old Crow Basin, Yukon Territory; 35,500 B.P. (GSC-2507); Bryological Report 40. (6) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 48. (7) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 61. (8) HH69-21 (station 1), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 101. (9) HH69-21 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 102. (10) Sunwapta Pass, Alberta; 6920 ± 100 B.P. (GSC-451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (11) Mackinson Inlet, Ellesmere Island, Northwest Territories; >52,000 B.P. (GSC-2677); Bryological Report 163, Blake & Matthews 1979. (12) Koyukuk River, 4 km downstream from Hawzerah Creek, Alaska; ± 60,000 B.P.; Bryological Report 169. (13) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (14) Anaktuvuk River, 2 km upstream from Itikmalaiyak Creek, Alaska; 1935 ± 80 B.P. (I-11,011); Bryological Report 172, Hamilton 1980, p. 24. (15) HH75-24, Bluefish Basin, Yukon Territory; probably pre-Wisconsinan; Bryological Report 173. (16) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (17) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150 B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40. (18) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (19) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (20) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (21) Wagner Property, Edmonton area, Alberta; Holocene peat, 60 to 70 cm below water surface; Bryological Report 206, as *Scorpidium cf. scorpioides*. (22) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (23) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (24) CRH 11 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 266. (25) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (26) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (27) HH75-19, Old Crow Basin, Yukon Territory; pre-Wisconsinan?; Bryological Report 272. (28) Kitchener, Ontario; 6900 B.P.; Bryological Report 273. (29) Kitchener, Ontario; between 6900 B.P. and 7700 B.P.; Bryological Report 274. (30) Kitchener, Ontario; below 8800 B.P.; Bryological Report 276. (31) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980. (32) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980, as *Scorpidium cf. scorpioides*. (33) Shoran Lake, Banks Island, Northwest Territories; just above 10,200 ± 130 B.P. (GSC-2673); Bryological Report 282. (34) Shoran Lake, Banks Island, Northwest Territories; 10,200 ± 130 B.P. (GSC-2673); Bryological Report 283. (35) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 294. (36) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (37) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (38) Kitchener, Ontario; below 7700 B.P.; Bryological Report 320. (39) Kitchener, Ontario; below 8800 B.P.; Bryological Report 321. (40) Kitchener, Ontario; below 8800 B.P.; Bryological Report 322. (41)

Kitchener, Ontario; below 8800 B.P.; Bryological Report 323. (42) Kitchener, Ontario; below 8800 B.P.; Bryological Report 324. (43) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 325. (44) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan?; Bryological Report 326, as *Scorpidium cf. scorpioides*. (45) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (46) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (47) HH69-21 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 388. (48) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391. (49) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 392. (50) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (51) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - *Scorpidium scorpioides* is a very characteristic fossil. It is also one of the most common Pleistocene bryophytes (see also Dickson 1973, p. 142). All fossil specimens have a rich dark-brown color. The preservation is often perfect (Janssens 1977b, Gistel-26 deposits and Bryological Report 172) and the fragments complete. Often intact apical parts of branches are found, composed of tightly inrolled leaves, that are characteristically falcate-secund. In the preparation of the slides, the apices of the broadly ovate leaves frequently split and appear lacerate. In less than perfectly preserved material, the short apiculus is eroded and usually only preserved on a few leaves.

The species is locally very abundant in rich fen pools and other highly minerotrophic, stagnant waters. It is considered a rich fen indicator (Miller 1973b). Calcium carbonates are frequently precipitated in these environments and the older parts of the plants are encrusted with lime. In autochthonous deposits marl is often intermixed with *S. scorpioides* peat. The habitat differentiation between *S. scorpioides* and *S. turgescens* is discussed by Miller (1980c). He based his conclusions on information taken from herbarium labels. *S. turgescens* is considered to be found more frequently on mineral substrata.

Scorpidium turgescens (T. Jens.) Loeske

Diagnostic features. – *Leaves* ovate to narrowly ovate, straight; *costa* short, double or absent; *apex* apiculate; *medial cells* with thick porose walls; *alar cells* gradually differentiated, always thick-walled and never strongly inflated.

Habitat. – On calcareous soil, in fens, on irrigated rocks. Rarely submerged in lakes. A distinct calciphile (but in the British Isles also reported from acidic substrates), mainly found in extreme rich fens. Associated with *Calliergon trifarium*, *Drepanocladus revolvens*, *D. tundrae*, *Meesia triquetra* and *Scorpidium scorpioides*. pH 7.3 to 7.7 (n=3), conductivity 181 to 493 microScm^{-1} (n=3), Ca concentration 19 to 78 ppm (n=3), Mg concentration 8.6 to 18.0 ppm (n=3), Na concentration 9 to 25 ppm (n=3), K concentration 0 to 1.5 ppm (n=3).

Recent Distribution. – Mainly circumboreal. North America (Miller 1980c): from Alaska to Greenland, Labrador and Newfoundland, south to New Jersey, Ohio, Indiana and Wisconsin in the east and to northern Idaho and Montana in the west; Queen Charlotte Islands. Ecuador, Bolivia. Northern and montane Europe, northern Asia.

Subfossil Distribution in North America. – Alaska, Greenland, Iowa, Michigan, Minnesota, New York, Northwest Territories, Vermont and Wisconsin (Miller 1980a, 1980c). New records: (1) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (2) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (3) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (4) HH68-9 (station 3); Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302.

Discussion. – The relationship of *Scorpidium turgescens* with *Calliergon wickesiae* and *Drepanocladus badius* is discussed under *D. badius*.

Scorpidium unidentified species

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a). New records: (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 174, as *cf. Scorpidium* species. (2) Kitchener, Ontario; 6900 B.P.; Bryological Report 273, as *cf. Scorpidium* species.

Brachytheciaceae

Brachythecium

As later explained in the discussion of *B. turgidum*, most of the subfossil material of *Brachythecium* is rather stenotypic and can be assigned to *B. turgidum*. Several other species of this large genus are represented in the literature by fossil records (Miller 1980a): *B. plumosum* (Hedw.) B.S.G., *B. rivulare* B.S.G. and *B. salebrosum* (Web. *et* Mohr) B.S.G. The only record I could check (G.S.C.!) was Kuc's specimen of *B. salebrosum* from Banks Island.

Brachythecium groenlandicum (C. Jens.) Schljak.

Subfossil Distribution in North America. – (1) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5, as *Brachythecium cf. groenlandicum*.

Discussion. – See below under *B. turgidum*.

Brachythecium turgidum (C.J. Hartm.) Kindb.

Diagnostic features. – *Fragments* unbranched; *leaves* spreading to erect, lanceolate to ovate-lanceolate, base concave, plicate; *costa* reaching into the upper half of the lamina, weakly developed; *margins* plane to frequently narrowly recurved or incurved, entire to weakly denticulate; *medial cells* elongate, linear, with sharp ends and thick, smooth walls; *alar cells* gradually and poorly differentiated, quadrate-rectangular, in an adaxially convex, bulging group, sometimes shortly and narrowly decurrent, cells in the decurrency usually rectangular, sometimes quadrate.

Habitat. – On moist or wet calcareous soil, in fens, on irrigated rocks, and on soil and rocks beside streams. pH 7.0 to 7.8 (n=7), conductivity 166 to 505 microScm^{-1} (n=7), Ca concentration 22 to 77 ppm (n=7), Mg concentration 12 to 16 ppm (n=7), Na concentration 12 to 25 ppm (n=7), K concentration 0.1 to 15.3 ppm (n=7).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland and Labrador, south in Quebec, Michigan and Montana. Northern and central Europe, Svalbard, northern Asia.

Subfossil Distribution in North America. – Wisconsin (Miller 1980a). New records: (1) Hulgothen Bluffs, Fish Creek, Alaska; 500,000 to 1,500,000 B.P.; Bryological Report 170. (2) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (3) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I-10,509); Bryological Report 181, Hamilton 1979b, p. 41. (4) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (5) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (6) HH75-24 (station 2), Bluefish Basin, Yukon Territory; above >53,000 B.P. (GSC-2373-2); Bryological Report 271. (7) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (8) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; below >39,000 B.P. (I-4099); Bryological Report 335, Matthews 1974a. (9) Cape Deceit Quaternary Exposure, Near Deering (station 8), Alaska; >39,000 B.P. (I-4099); Bryological Report 350, Matthews 1974a. (10) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383. (11) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – *Brachythecium turgidum* is distinguished from *Leptodictyum* species by having brachythecioid cells or medial cells with sharp points, (easiest to observe under a low power lens of the microscope), while the taxa in the Amblystegiaceae always have all their leaf cells with blunt ends. *Brachythecium* is an unwieldy genus. However, most of the subfossil material could be assigned, after careful study and elimination, to *B. turgidum*. This taxon is characterized by its essentially entire, often folded margins, narrowly lanceolate to ovate-lanceolate, plicate leaves and narrowly or not at all decurrent alar cell groups. The leaves are erect to erect-spreading and light-yellow in color. The fragments are always unbranched. *Brachythecium turgidum* is differentiated from *B. groenlandicum* in the leaf decurrencies: if they are present in *B. turgidum*, they remain attached to the stem when the leaves are scraped off, and they consist usually out of a few rectangular cells. In *B. groenlandicum*, the decurrency is usually broader, often remains attached to the scraped leaves and is composed of quadrate-rounded cells. This latter taxon also differs in habitat: in moist places on rocks (e.g. basalts) in mats, in late snow melt areas, or mixed with other bryophytes in heaths. It is thus essentially acidophilous. There is only one dubious fossil record of *B. groenlandicum*: see above.

Brachythecium unidentified species

Subfossil Distribution in North America. – (1) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a, as *cf. Brachythecium* species. (2) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383, as *cf. Brachythecium* species.

Cirriphyllum

Cirriphyllum cirrosum (Schwaegr. *ex* Schultes) Grout

Diagnostic features. – *Leaves* imbricate, concave, narrowly ovate; *apex* abruptly narrowed and long acuminate; *costa* short, usually reaching half way up the lamina; *margins* entire to weakly denticulate; *medial cells* elongate, narrow and thick-walled, shorter towards the base, walls smooth above, porose towards the base; *alar cells* gradually differentiated, quadrate.

Habitat. – On moist to wet calcareous soil in open tundra, on rocks, or in crevices and depressions. Common in the wetter parts of *Carex* meadows, and along streams and pond shores. In rock crevices farther south. Associated with *Meesia triquetra*, *Calliergon giganteum* and sometimes *Bryum cryophilum* in late snowbeds in the High

Arctic.

Recent Distribution. – Circumpolar. Arctic–alpine species. North America: from Alaska to Greenland, through the Rocky Mountains to Alberta and British Columbia, south to Washington and disjunct to Colorado, Manitoba. Iceland, Svalbard, mountains of Europe, Himalayas, arctic U.S.S.R., China, Japan, northern Africa.

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a). New record: (1) Your Creek area, Alaska; 5615 ± 110 B.P. (I–10,568); Bryological Report 183, Hamilton 1979a, Fig. 5.

Discussion. – *Cirriphyllum cirrosum* differs from *C. piliferum* (Hedw.) Grout by its narrower ovate leaves, denser areolation (narrower cells with thicker walls) and weaker costa. In contrast with *C. piliferum*, an European–eastern North American species, it is only found in arctic and alpine areas. There are no fossil records of *C. piliferum*.

Eurhynchium

Eurhynchium pulchellum

Diagnostic features. – *Leaves* widely spreading, ovate to ovate–lanceolate; *apex* bluntly acuminate or obtuse; *costa* short, usually reaching half way up the lamina and ending in an abaxial spine; *margins* sharply denticulate all around; *medial cells* elongate, linear, sinuose, thick–walled; *apical cells* abruptly shortened, often isodiametric; *alar cells* gradually differentiated, quadrate.

Habitat. – On soil, rock, rotting wood and tree–stumps or roots of trees in shaded habitats, chiefly in calcareous districts.

Recent Distribution. – Circumboreal North America: Alaska to Greenland in the north, south to California in the west and Virginia in the east. Mexico, Ecuador, Europe, Canaries, Algeria, Caucasus, northern, central, and eastern Asia, Japan.

Subfossil Distribution in North America. – Louisiana, Minnesota, Northwest Territories and Wisconsin (Miller 1980a). New records: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33. (2) HH68-9 (station 8), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 49. (3) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62. (4) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 64. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (6) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (7) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 370. (8) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425. (9) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – The only taxon approaching *E. pulchellum* in some aspects is *Drepanocladus pseudostramineus*. *Eurhynchium pulchellum* can be distinguished by its less developed alar cells, sharper denticulation, more numerous short isodiametrical cells in the blunt apex, suddenly shortened from the medial cells, and the shorter ovate leaf shape.

Tomenthypnum

Tomenthypnum nitens (Hedw.) Loeske

Diagnostic features. – *Fragments* pinnately or frequently densely branched on one side; *leaves* imbricate, narrowly ovate-lanceolate to lanceolate, strongly plicate, sharply and narrowly acuminate; *costa* single, strong or weak, reaching into the upper half of the lamina, often with abundant abaxial rhizoids formed in the lower leaves; *margins* entire; *medial cells* elongate, linear, very narrow, with blunt ends; *alar cells* gradually and poorly differentiated, quadrate and thick-walled.

Habitat. – In moist or wet habitats, often in rich fens mixed with other mosses. Associated with *Sphagnum warstorfii* and *Campylium stellatum*. On Devon Island it forms, along with *Aulacomnium turgidum*, *Campylium arcticum*, and *Orthothecium chryseum*, a conspicuous, but minor component of the higher hummocky sedge-moss meadows (Vitt 1975). It is also found in the mesic depressions of the rock outcrops, often with *Hylocomium splendens*, as well as in other mesic habitats. The pH ranges from 6.8 to 8.0 (n=25), conductivity 163 to 1068 microScm^{-1} (n=25), Ca concentration 13.2 to 115.0 ppm (n=19), Mg concentration 0.0 to 53.2 ppm (n=19), Na concentration 6.3 to 16.6 ppm (n=19) and K concentration 0.0 to 13.6 ppm (n=19).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Labrador and Newfoundland, south to New Jersey, Ohio, Michigan and Minnesota in the east and to northern Idaho and Montana in the western mountains, disjunct to southern Oregon, Wyoming, Utah and Colorado. Europe and northern Asia.

Subfossil Distribution in North America. – Alberta, Iowa, Minnesota, New York, Northwest Territories and Wisconsin (Miller 1980a). New records: (1) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (2) Riverbar of base camp at HH68-9, Old Crow Basin, Yukon Territory; recent detritus; Bryological Report 35. (3) CRH 11 (station 5), Old Crow Basin, Yukon Territory; ± 15,000 B.P.; Bryological Report 36. (4) Snake River area, Yukon Territory; 11,700 ± 90 B.P. (GSC-2693) and 11,800 ± 170 B.P. (GSC-2745); Bryological Report 41. (5) HH68-9 (station 8), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 62, as *cf. Tomenthypnum nitens*. (6) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 0 to 10 cm below surface; Bryological Report 143. (7) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 20 to 30 cm below surface; Bryological Report 145. (8) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 140 to 150 cm below surface; Bryological Report 157. (9) HH68-9, Old Crow Basin, Yukon Territory; Holocene peat, 200 to 150 cm below surface; Bryological Report 159. (10) Sunwapta Pass, Alberta, 6920 ± 100 B.P. (GSC 451); Bryological Report 162, Schweger *et al.* 1978, p. 62. (11) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska, 10,580 ± 150 B.P. (I-11,010), Bryological Report 171, Hamilton 1980a, p. 21. (12) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (13) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (14) Wind River, 50 km south of continental divide, Brooks Range, Alaska, 9380 ± 150 B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40. (15) Section Creek, 9 km upstream from Sagavanirktok River, Alaska; 12,690 ± 180 B.P. (I-10,567); Bryological Report 182, Hamilton 1979b, p. 29. (16) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (17) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (18) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (19) Wagner Property, Edmonton area, Alberta; Holocene peat, 50 to 60 cm below water surface; Bryological Report 205. (20) Wagner Property, Edmonton area, Alberta; Holocene peat, 60 to 70 cm below water surface; Bryological Report 206. (21) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (22) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 261. (23) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (24) CRH 11 (station 3), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 266. (25) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (26) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 269. (27) CRH 70 (station 2), Old Crow Basin, Yukon Territory; >37,000 B.P. (GSC-2792); Bryological Report 270. (28) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980. (29) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (30) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (31) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (32) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.;

Bryological Report 308 (33) Kitchener, Ontario, below 8800 BP, Bryological Report 322 (34) Kitchener, Ontario, below 8800 BP, Bryological Report 323 (35) Kitchener Ontario, below 8800 BP, Bryological Report 324 (36) HH75 24, Bluefish Basin, Yukon Territory; Wisconsinan, Bryological Report 328 (37) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska, 700,000 - 1,800,000 BP; Bryological Report 341, Matthews 1974a (38) HH68-9 (station 9), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 370 (39) HH79-1, Hungry Creek, Yukon Territory, 8700 ± 80 BP (GSC-2971); Bryological Report 383 (40) HH68-9 (station 3) Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 389 (41) HH68-9 (station 3), Old Crow Basin, Yukon Territory, Early Wisconsinan?, Bryological Report 392 (42) Clements Markham Inlet, Ellesmere Island, Northwest Territories, 6400 ± 60 BP (SI-4314); Bryological Report 401 (43) HH68-9 (station 9), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 425 (44) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 434 (45) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – The subfossil material of *Tomenthypnum nitens* is characterized by its rich-brown color, in contrast to the golden color of the living populations. Preservation of this very abundant and easily recognizable moss is often perfect (including branches and tomentum). The only North American taxa approaching its leaf structure are *Orthothecium, Homalothecium, Trachybryum megaptilum* (Sull.) Schof. and *Tomenthypnum falcifolium* Ren. *ex* Nich. *Orthothecium* is ecostate. However, it often takes some time in poorly preserved material of *Tomenthypnum nitens* to find the costa whiich is hidden by the folds. The use of pliant plastic coverslips has proven here to be of advantage: to apply partial pressure on a leaf to unfold it. *Homalothecium* and *Trachybryum megaptilum* are sharply denticulate. None of the fossil collections could be assigned to *Tomenthypnum falcifolium*. This species is characterized by falcate-secund leaves that are narrowed to the insertion (straight or slightly curved, lanceolate leaves in *T. nitens,* Vitt & Hamilton 1975). Leaves of *Drepanocladus uncinatus* can be differentiated from those of *T. falcifolium* by the denticulations along the upper part of the margin and the differentiated alar cells. The stem epidermis of *T. falcifolium* is formed by thick walled cells not forming a hylodermis as in *D. uncinatus*. Rhizoids practically always form on the abaxial side of the costa in *T. falcifolium*, but never occur in *D. uncinatus*.

The species of *Tomenthypnum* differ in habitat. *Tomenthypnum falcifolium* is found in poor fens, associated with *Sphagnum angustifolium* and *S. magellanicum*

Entodontaceae

All three North American genera of this family have a fossil record. *Entodon*, represented by one species, *E. concinnus*, is known as single, well preserved fragments in England (Dickson 1973) and Alaska (see below). In addition, there are Pleistocene and Pliocene occurrences in Poland and the U.S.S.R. (Jovet-Ast 1967). *Orthothecium* is only known in the North American Quaternary record. *Pleurozium*, a monotypic genus, is a very common fossil from postglacial times on in Britain (Dickson 1973) and is known from the Holocene of Belgium (Janssens 1977a) and from lateglacial and Holocene deposits in the Yukon and Alaska.

Members of this family are distinguished by imbricate, concave leaves that are often plicate, have a poorly developed or no costa and narrow, linear medial cells. There are no paraphyllia. *Entodon* and *Pleurozium* have obtuse or slightly apiculate leaves, *Orthothecium* has shortly acuminate to sharply acute leaves.

Entodon

Only *E. concinnus* has a fossil record.

Entodon concinnus (De Not.) Par.

Diagnostic features. – *Fragments* irregularly pinnately branched; *leaves* ovate to obovate, concave; *apex* obtuse; *costa* short and double or absent; *medial cells* elongate, with sharp ends, moderately thick-walled, slightly porose; *alar cells* numerous, in a long, narrowly triangular group extending up along the margins, rounded or quadrate.

Habitat. – On moist calcareous soil, often on rocks or fallen trees. On steep slopes and slopes covered with *Dryas*. Associated in mesic habitats with *Hylocomium splendens*, *Rhytidiadelphus triquetrus* and *Tomenthypnum nitens*. It is more common in drier habitats with such species as *Thuidium abietinum*, *Ditrichum flexicaule* and *Hypnum bambergeri*.

Recent Distribution. – Circumboreal. North America (Steere 1978a): from arctic Alaska to central Alberta, disjunct to Colorado and New Mexico in the west and disjunct to Newfoundland and to North Carolina in the east. Iceland. Europe, central and northern Asia. Japan.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a. p. 23.

Discussion. – *Pleurozium* is distinguished from *Entodon* by its shortly apiculate leaves, blunt ended medial cells and alar cell groups not extending along the margins. Leaves of both taxa are differentiated from *Calliergon* leaves by the absence of a single costa and less developed alar cells. *Scleropodium* (including *Pseudoscleropodium*) has a longer apiculus and a short, single costa.

Orthothecium

Orthothecium chryseum is the most commonly represented species in the North American fossil record. All localities are northern and my specimens fit the diagnosis of the variety *cochlearifolium* (Miller & Ireland 1978b).

Orthothecium chryseum var. *cochlearifolium* (Lindb.) Limpr.

Diagnostic features. – *Leaves* ovate-lanceolate, strongly plicate; *apex* shortly acuminate or sometimes narrowly obtuse, the tip sharply recurved; *costa* absent; *margins* entire, often narrowly recurved along the whole length; *medial cells* linear, thick-walled, porose; *alar cells* not differentiated.

Habitat. – In cushions in wet meadows, on hummocky slopes or at the margins of ponds and lakes. The species is often associated with rich fen taxa but occurs also in *Dryas* heath with *Ditrichum flexicaule*, and *Hypnum bambergeri*. On steep slopes it is found with *Cinclidium arcticum*, *Mnium blyttii*, *Cyrtomnium hymenophylloides*, *C. hymenophyllum* and *Timmia norvegica*.

Recent Distribution. – Circumpolar. Arctic species. North America: Alaska, Northwest Territories, Greenland. Svalbard, Northern Asia. The variety is recently recognized (Miller & Ireland 1978b) and probably has a wider range, like var. *chryseum.*

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a, as *Orthothecium chryseum*). New records: (1) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (2) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion. – Other *Orthothecium* species are distinguished by not or slightly plicate leaves or narrower, finely acuminate leaves. The variety *cochlearifolium* is differentiated from the variety *chryseum* by its shortly acuminate leaves with a strongly recurved tip.

Orhtothecium strictum Lor.

Diagnostic features. – *Leaves* ovate-lanceolate, straight, not plicate; *apex* sharply acute or acuminate; *costa* absent; *margins* narrowly revolute, weakly denticulate in the upper part; *medial cells* elongate, with sharp ends, moderately thick-walled, porose; *alar cells* not differentiated.

Habitat. – On moist calcareous soil or in rock crevices.

Recent Distribution. – Circumpolar. Arctic-alpine species. North America: from Alaska to Greenland and Newfoundland, south to Alberta and Colorado in the west. Svalbard, Fennoscandia and the Alps, arctic U.S.S.R., central Asia.

Subfossil Distribution in North America. – (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 391.

Pleurozium

Pleurozium schreberi (Brid.) Mitt.

Diagnostic features. – *Leaves* ovate or oblong, strongly concave; *apex* bluntly apiculate; *costa* short and double or absent; *margins* broadly incurved above, sometimes partially recurved, entire, weakly denticulate at the apex; *medial cells* shortly to longly elongate, with blunt ends, thick-walled and strongly porose; *alar cells* is a small oval group, gradually differentiated, thick-walled and brown.

Habitat. – On soil or forest litter, on rocks. It grows in mesic to dry, shaded habitats. It is most abundant in coniferous forests and very rare in tundra. When more nutrients are available it is usually replaced by *Hylocomium splendens*. Turgid forms are often seen in mires and poor fens on hummocks. pH 4.9–7.3 (n=3), conductivity 24–286 microScm^{-1} (n=3), Ca concentration 5.8–16.4 ppm (n=4), Mg concentration 0.7–4.8 ppm (n=4), Na concentration 10.3–41.0 ppm (n=4) and K concentration 0.3–13.5 ppm (n=4).

Recent Distribution. – Circumboreal. Bipolar species. North America: from Alaska to Greenland, south to New England in the east and Washington in the west, disjunct to higher elevations to North Carolina, Tennessee and Arkansas. Central and South America. Europe, Azores, Asia.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New records: (1) Snake River area, Yukon Territory; 11,700 ± 90 B.P. (GSC-2693) and 11,800 ± 170 B.P. (GSC-2745); Bryological Report 41. (2) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton, 1980a, p. 21.

Discussion. – See the discussion of *Entodon concinnus* for the distinction with other taxa.

Plagiotheciaceae

Only species of *Plagiothecium* were found as subfossils (Plagiotheciaceae: *sensu* Ireland *et al.* 1980). Miller (1980a) listed a late or postglacial record from Illinois of *P. cavifolium* (Brid.) Iwats. In Europe and the U.S.S.R., *Plagiothecium* species were found in Pliocene and Pleistocene deposits (Jovet-Ast 1967). Most British records are Flandrian (Dickson 1973). I collected one well preserved specimen that could be identified as *P. laetum*.

Plagiothecium

The genus is differentiated from *Stereophyllum* by having a double costa, whereas *Stereophyllum* has a well developed single costa, and from the genera in the Hypnaceae (*sensu* Ireland *et al.* (1980) e.g. *Isopterygium*, *Taxiphyllum*, *Hypnum* and *Ptilium*) by strongly decurrent, complanately inserted, often asymmetrical leaves.

Plagiothecium laetum B.S.G.

Diagnostic features. - *Leaves* distinctly complanately inserted, asymmetric, concave *apex* slenderly acuminate; *costa* very short with two unequal branches or absent; *margins* entire below, weakly denticulate at the apex, sometimes narrowly revolute; *medial cells* linear, slightly vermicular, moderately thick-walled, smooth, average width 5.0 micrometer; *alar cells* in a narrowly decurrent group, rectangular.

Habitat. - Usually on rotten logs, stumps, bases of trees, forest litter, and in rock crevices. In coniferous woods.

Recent Distribution. - Circumboreal. North America: from Alaska to Labrador, Newfoundland, south to North Carolina and Tennessee in the east and to California in the west, generally more common in the south), Europe, Asia, Japan.

Subfossil Distribution in North America. - (1) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat; Bryological Report 289.

Discussion. – Other *Plagiothecium* species are distinguished from *P. laetum* by smaller leaves, wider medial cells, and quadrate or rounded alar cells (Ireland 1969).

Hypnaceae

This large, heterogenous family has several genera represented as subfossils. *Hypnum* has the most records and is discussed below. *Hyocomium* is Eurasian and has Hoxnian and Flandrian records in Ireland, England and Brittany (Dickson 1973). *Ctenidium* is known from the Miocene of the Caucasus, the Pleistocene of Poland and from the Hoxnian, Late Devensian and Flandrian of the British Isles (Dickson 1973). *Taxiphyllum* and *Pylaisiella* are only known from North American localities (Miller 1980a). The genera *Isopterygium* and *Ptilium* are discussed below.

Hypnum

Six species are represented in my collections. An additional six species are listed by Miller (1980a). Many other records are reported by Jovet-Ast (1967), Dickson (1973) and Janssens (1977a). *Hypnum* specimens are often poorly preserved and many records have low reliability values.

The genus is differentiated by its falcate-secund leaves with a double or no costa, by differentiated alar cells and smooth medial cells. The fragments are mostly not pinnately branched.

Hypnum bambergeri Schimp.

Diagnostic features. – *Leaves* 1 to 2 mm long, falcate-secund to circinate, concave, ovate-lanceolate to lanceolate; *margins* plane or partially narrowly revolute, entire; *medial cells* thick-walled, often porose; *alar cells* quadrate to shortly rectangular, 3 to 5 along the margins, very thick-walled, dark-brown and porose. *Stem* with small, thick-walled epidermal cells.

Habitat. – On moist calcareous soil in arctic and alpine habitats. In *Dryas* heath, in fens associated with *Campylium stellatum, Dicranum muehlenbeckii, Distichium capillaceum, Ditrichum flexicaule, Mnium thomsonii, Orthothecium chryseum* and *Tomenthypnum nitens*. pH 6.8–7.8 (n=3), conductivity 46–166 microScm^{-1} (n=3), Ca concentration 8.2–22.4 ppm (n=3), Mg concentration 0.0–11.9 ppm (n=3), Na concentration 10.9–17.6 ppm (n=3) and K concentration 0.0–0.1 ppm (n=3).

Recent Distribution. – Circumpolar. Arctic-alpine species. North America (Miler 1976): from Alaska to Greenland, disjunct to northern Newfoundland and to the Gulf of St. Lawrence in the east, south through the western mountains to northern British Columbia and disjunct to central Alberta and the west coast of the Hudson Bay. Iceland, Svalbard, Scotland, northern Europe, Alps, northern and arctic U.S.S.R.

Subfossil Distribution in North America. – Wisconsin (Miller 1976b, 1980a). New records: (1) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (3) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (4) HH75-24, Bluefish Basin, Yukon Territory; Wisconsinan; Bryological Report 328. (5) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401. (6) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Other *Hypnum* species with small thick-walled epidermal stem cells on the stem are distinguished by their less thick-walled and non-porose alar cells.

Hypnum hamulosum B.S.G.

Diagnostic features. – *Leaves* small, less than 1 mm long, falcate-secund to circinate, plane or slightly concave, ovate-lanceolate; *margins* plane or narrowly revolute on one side, entire or weakly denticulate; *medial cells* thin-walled, smooth; *alar cells* few (3–5), quadrate or irregularly angled. *Stem* with strongly enlarged epidermal cells with a thin outer wall.

Habitat. – On calcareous soil, on rocks, in rock-crevi

Recent Distribution. – Circumboreal. North America: from Alaska to the Arctic Archipelago, south to the Hudson Bay coast in the east and throughout the western mountains to Utah in the west. Europe, northern Asia, central China, Japan.

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a). New record: (1) HH75-1, Rock River, Yukon Territory; >43,000 B.P. (GSC-2585); Bryological Report 33.

Discussion. – Other *Hypnum* species with a well developed hyalodermis on the stem are distinguished by their larger leaf size.

Hypnum lindbergii Mitt.

Diagnostic features. – *Leaves* falcate-secund, ± complanate, 1.5 to 2.0 mm long, plane or slightly concave, widely ovate-lanceolate; *margins* plane or partially narrowly revolute on one side, entire; *medial cells* thin-walled; *alar cells* strongly inflated, in a distinct auriculate group, brown and thicker walled towards the costa, hyaline and thinner walled towards the margins. *Stem* with enlarged epidermal cells with a thin outer wall.

Habitat. – On wet sandy or silty soil, rotten wood and humus. Often in habitats which are periodically inundated, such as swamps, the margin of lakes, ponds and under the *Salix* scrub in the floodzone of streams. In *Betula* forest, fens, moist meadows and seepages. Rather restricted to less calcareous substrates. Associated with *Aulacomnium palustre, Calliergon sarmentosum, C. stramineum, Circlidium dendroides, Drepanocladus uncinatus, Pogonatum alpinum* and *Polytrichum commune*.

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, Newfoundland and Labrador, across Canada from Nova Scotia to British Columbia and in the United States from New England to Washington, south to Florida and the Gulf of Mexico in the east and Colorado in the west. Iceland, Svalbard, Europe, northern and central Asia and Japan.

Subfossil Distribution in North America. – Minnesota (Miller 1980a). New records: (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200, Hamilton 1980a, p. 23. (2) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23.

Discussion. – *Hypnum pratense* is distinguished from *H. lindbergii* by its narrower lanceolate leaves and less abruptly differentiated alar cell groups. Other *Hypnum* species are distinguished from the two former taxa by their thick-walled epidermal stem cells or by their smaller, circinate leaves.

Hypnum pratense Koch *ex* Brid.

Diagnostic features. – *Leaves* falcate-secund to circinate, ± complanate, 1.0 to 1.5 mm long, strongly concave, narrowly ovate-lanceolate; *margins* plane or partially narrowly revolute, weakly denticulate at the apex; *medial cells* moderately thick-walled, smooth; *alar cells* quadrate, thin-walled, yellow or hyaline. *Stem* with epidermal cells with thin outer walls.

Habitat. – On humus-rich or organic soil. On lake shores in calcareous districts, often in rich fens, in wet alpine meadows and seepages. Associated mosses are *Brachythecium turgidum, Dicranum majus, Hylocomium splendens, Cyrtomnium hymenophyllum, Orthothecium chryseum* and *Tomenthypnum nitens.*

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland, throughout Canada and south to British Columbia and Colorado in the west and Florida in the east. Europe, northern Asia and Japan.

Subfossil Distribution in North America. – Vermont (Miller 1980a). New records: (1) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 64. (2) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150

B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40, as *Hypnum cf. pratense*. (3) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (4) REM 78-2, Old Crow Basin, Yukon Territory; surface sample of Holocene peat; Bryological Report 289. (5) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 302. (6) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 - 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (7) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. - See the discussion of *H. lindbergii* for distinction from other *Hypnum* taxa.

Hypnum revolutum (Mitt.) Lindb.

Diagnostic features. - *Leaves* 1.5 to 2.0 mm long, falcate-secund to curved, concave, ovate-lanceolate; *margins* strongly revolute at both sides; *medial cells* thin-walled, sometimes porose; *alar cells* numerous, quadrate and thick-walled. *Stem* with thick-walled epidermal cells.

Habitat. - On calcareous rock or gravel and around bird perches, often associated with *Tortula ruralis* and *Dryas*. Very widespread throughout the arctic in more xeric habitats than the other species of the genus.

Recent Distribution. - Circumboreal. Bipolar species. North America: from Alaska to Labrador, throughout Canada from Manitoba to British Columbia, in the western mountains south to Colorado, Utah, Texas, Arizona, New Mexico and California. Mexico, Svalbard, Europe, Asia and Antarctica (as fo. *pumilum* (Husn.) Ando).

Subfossil Distribution in North America. - Saskatchewan, Utah and Vermont (Miller 1980a). New record: (1) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Discussion - Other *Hypnum* species are distinguished by their plane or only partially recurved margins.

Hypnum vaucheri Lesq.

Diagnostic features. - *Leaves* 1.0 to 1.5 mm long, curved to falcate-secund, plane to weakly concave, ovate-lanceolate; *margins* plane or partially narrowly revolute on one side, denticulate above; *medial cells* short-oval in shape and moderately thick-walled, often porose; *alar cells* numerous, up to 25 cells along the margins, thick-walled. *Stem* with small, thick-walled epidermal cells.

Habitat. - On limestone or other calcareous rock, on thin calcareous soil and frequently in rock crevices in dry habitats and in exposed situations. It occurs in the lower part of the high alpine if suitable substrates are present. Species associated with the same habitat are *H. revolutum*, *Grimmia apocarpa* and *Tortula ruralis*.

Recent Distribution. - Circumboreal. North America: Alaska to Greenland, south to Newfoundland, Quebec and Ontario, widespread in the mountains of western Canada and the United States and south to Texas and Nebraska. Svalbard, mountains of Europe and temperate Asia.

Subfossil Distribution in North America. - Northwest Territories and Vermont (Miller 1980a). New records: (1) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (2) HH68-9 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 262. (3) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 308. (4) HH68-9 (station 14), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 387.

Discussion. - Other *Hypnum* species with thick-walled epidermal cells on the stem are distinguished by less numerous alar cells.

Hypnum unidentified species

Subfossil Distribution in North America. – (1) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?, Bryological Report 299. (2) HH68-9 (station 10), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 385.

Isopterygium

Subfossil records of this genus are known from the U.S.S.R., Czechslovakia and England (Dickson 1973). In addition, *I. tenerum* was found in a Wisconsinan deposit in North Carolina (Miller 1980a). The records of *I. pulchellum* are discussed below.

Fragments of *Isopterygium* are similar to *Plagiothecium* but are distinguished from the latter by their non-decurrent leaves.

Isopterygium pulchellum (Hedw.) Jaeg. *et* Sauerb.

Diagnostic features. – *Leaves* erect-spreading to secund, complanately inserted, symmetric, not decurrent, lanceolate; *costa* absent; *margins* subentire at the base or entire; *medial cells* elongate, smooth; *alar cells* few, 1–3 along the margins, quadrate, or none.

Habitat. – In shaded situations, in cliff crevices, on rocky banks, beach ridges and bases of trees and decaying wood and soil rich in humus. Often associated with *Blepharostoma trichophyllum, Distichium capillaceum, Mnium thomsonii, Myurella julacea* and *Pohlia cruda.*

Recent Distribution. – Circumboreal. Bipolar arctic-alpine species. North America: from Alaska to Greenland, across Canada and south to Pennsylvania and Wisconsin in the east and to California and Arizona in the west. Iceland, Svalbard, Europe, northern U.S.S.R., Japan, New Zealand.

Subfossil Distribution in North America. – Greenland and Northwest Territories (Miller

1980a) New record (1) HH68 9 (station 2), Old Crow Basin, Yukon Territory + 60,000 B.P., Bryological Report 261

Discussion. – The above reported specimen and Kuc's fragments from Banks Island (Miller 1980a) were studied by Ireland and considered to be the more robust western form of *I. pulchellum* (see also his discussion, Ireland 1969, p. 57). The closely related *Taxiphyllum taxirameum* (Mitt.) Fleish., listed by Miller (1980a) on the basis of Wisconsinan and Holocene records from Washington, D.C. and Louisiana, is distinguished from *I. pulchellum* by shorter, acute, more widely ovate-lanceolate leaves with teeth at the apex.

Ptilium

Ptilium crista-castrensis has Miocene and Pliocene records in Europe and the U.S.S.R. (Dickson 1973). The single record for North America in listed below.

Ptilium crista-castrensis (Hedw.) De Not.

Diagnostic features. – *Fragments* regularly pinnately branched; *leaves* falcate-secund to circinate, plicate, not decurrent; *margins* plane, sharply denticulate in the upper half.

Habitat. – Common on rotten logs and coarse humus in boreal forest. Rare on moist soil in the tundra. pH 6.8 (n=1), conductivity 202 microScm^{-1} (n=1), Ca concentration 14.5 ppm (n=1), Mg concentration 4.3 ppm (n=1), Na concentration 12.0 ppm (n=1) and K concentration 13.6 ppm (n=1).

Recent Distribution. – Circumboreal. Typical broreal forest biome. North America: from Alaska to Greenland, Newfoundland and Labrador, throughout the boreal forest in Canada, and across the United States south to Tennessee and North Carolina in the east and Colorado at higher elevations in the west. Europe, Himalayas, Caucasus, central and northern Asia.

Subfossil Distribution in North America. – (1) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I–10,925); Bryological Report 201, Hamilton 1980a, p. 23.

Discussion. – *Hypnum* species are distinguished from *Ptilium* by their more irregular branching pattern, non-plicate leaves or less well developed denticulation.

Rhytidiaceae

Three of the four North American genera in this family have a fossil record. *Rhytidiadelphus* is known from Pliocene and Pleistocene deposits in western Europe, the U.S.S.R. and North America (Janssens 1977a, Dickson 1973, Miller 1980a, Jovet-Ast 1967). *Gollania* is reported from the Pliocene of Duab in the Caucasus (Abramova & Abramov 1959). *Rhytidium* is discussed below.

Members of this family are often grouped in the Hylocomiaceae. Both families are characterized by large plants, often pinnately branched, the stems frequently covered with paraphyllia, the medial cells elongate or linear, often papillose at the upper ends. The three genera mentioned above have no or very few paraphyllia. Members of these genera are not multi-pinnately branched.

Rhytidium

This monotypic genus has a good subfossil record. *Rhytidium rugosum* is known from Pliocene and Pleistocene deposits in the U.S.S.R., Poland, Sweden, Denmark and the British Isles. North America fossils are listed below. Identification of *R. rugosum* does not create any problems, not even with strongly fragmented material. The falcate-secund, rugose leaves have a single costa, vermicular, elongate medial cells, often with sharp papillae at the upper end of the cell on the abaxial side of the upper part of the leaf. The numerous alar cells are in a narrow, triangular group extending up along the margins.

Rhytidium rugosum (Hedw.) Kindb.

Diagnostic features. – *Fragments* unipinnately branched; *leaves* moderately falcate-secund, rugose, ovate-lanceolate; *apex* acuminate; *costa* single, reaching into the upper half of the leaf; *margins* narrowly revolute for most of their length; *medial cells* elongate, moderately thick-walled, several scattered cells in the upper part of the leaf papillose at their upper ends on the abaxial side of the leaf; *alar cells* numerous, isodiametric, varying from quadrate to rounded and subquadrate, extending up along the margins in a narrow triangular group.

Habitat. – On dry calcareous soil and rocks. On beachridges and rock outcrops. Often associated with *Orthotrichum speciosum* and *Dryas integrifolia* on Devon Island, not collected very often in the High Arctic . It is found frequently in the climax *Picea mariana/Sphagnum* forest at the end of a succession on river deposits (Viereck 1970).

Recent Distribution. – Circumboreal. North America: from Alaska to Greenland in the north, to Arizona, Colorado, Missouri, Tennessee and North Carolina in the south. Central America. Northern, western, eastern and central Europe, Spain, Morocco, Caucasus, northern, eastern and central Asia,

Subfossil Distribution in North America. – Northwest Territories (Miller 1980a). New records: (1) HH75–1, Rock River, Yukon Territory; >43,000 B.P. (GSC–2585); Bryological Report 33. (2) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I–11,010); Bryological Report 171, Hamilton 1980a, p. 21. (3) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150 B.P. (I–10,508), 9600 ± 85 B.P. (USGS–163); Bryological Report 180, Hamilton 1979b, p. 40. (4) Your Creek area, Alaska; 5615 ± 110 B.P. (I–10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (5) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I–10,925); Bryological Report 201, Hamilton 1980a, p. 23. (6) HH72–54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – The other North American genera of the Rhytidiaceae are differentiated from *Rhytidium* by their paraphyllia (*Rhytidiopsis*) or double costa (*Rhytidiadelphus* and *Gollania*). Asiatic genera are charaterized by straight leaves, shorter medial cells, double costa or bi-pinnately branching.

Hylocomiaceae

Of the several genera in this family, only *Hylocomium* has a fossil record. All four species of this genus are represented in the Pliocene and Pleistocene of the U.S.S.R. and Europe (Jovet-Ast 1967, Janssens 1977a, Dickson 1973). Only *Hylocomium splendens* has been found in North American deposits.

Preservation of this characteristic fossil is very variable. However, detached branches and leaves are easily identifiable.

Hylocomium

Hylocomium splendens (Hedw.) B.S.G.

Diagnostic features. – *Fragments* bi- to tri-pinnately branched, often with clearly defined yearly increments with the primary branching pattern sympodial and the secondary branching bi- to tri-pinnate; *stem leaves* ovate-lanceolate with a short or long apiculus, sharply denticulate, costa double, medial cells elongate to linear, vermicular; *branch leaves* ovate or elliptic, with a short blunt apiculus, crenulate at the apex, costa absent or short and double, medial cells linear, vermicular, thick-walled.

Habitat (Tamm 1953). – The species occurs from the lowlands up into the high alpine zone. It grows as weft[illegible]tter, rock and rotten trees in coniferous woods. In the arctic it is found at the bases of rock outcrops and boulders, in transition zones between meadows and beach ridges. It has a monopodial growth form (*cf.* "variety *alaskanum*") instead of the usual sympodial development when it is growing on sloping stones, on heaths and in deciduous forests. *Hylocomium splendens* avoids large open areas, and prefers the neighbourhood of trees. Only on steep slopes with trickling water it is rather independent of other vegetation. It is less tolerant of sunshine than *Pleurozium schreberi*. There is little or no contact with the substrate and its nutrient supply is found in rain, atmospheric dust and tree leachate. It is completely destroyed after fire. pH 6.3-7.3 (n=3), conductivity 19-444 microScm^{-1} (n=3), Ca concentration 7.9 and 32.0 ppm (n=2), Mg concentration 7.9 and 8.8 ppm (n=2), Na concentration 1.0 and 11.4 ppm (n=2) and K concentration 9.8 ppm (n=1).

Recent Distribution. – Common and often frequent in its circumboreal range. Bipolar. North America: from Alaska, Yukon, and Northwest Territories in the north to Georgia, Iowa, Colorado and California in the south. Europe, northern Africa, Asia, Japan. New Zealand.

Subfossil Distribution in North America. – Alaska, British Columbia, Greenland, Iowa, Minnesota, New York, Northwest Territories, Saskatchewan and Wisconsin (Miller 1980a). New records: (1) Stewart River, Yukon Territory; >50,000 B.P.; possible Sangamonian; Bryological Report 4. (2) Riverbar near HH75-9 along Porcupine River, Yukon Territory; recent detritus; Bryological Report 34. (3) HH68-9 (station 7), Old Crow Basin, Yukon Territory; ± 60,000 B.P., Bryological Report 64. (4) Anaktuvuk River, 0.8 km downstream from Irgkivik Creek, Alaska; 10,580 ± 150 B.P. (I-11,010); Bryological Report 171, Hamilton 1980a, p. 21. (5) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 177. (6) Kluane Lake, south shore, Yukon Territory; below 43 m of water; 2215 B.P. (I-10,525); Bryological Report 178. (7) Wind River, 50 km south of continental divide, Brooks Range, Alaska; 9380 ± 150 B.P. (I-10,508), 9600 ± 85 B.P. (USGS-163); Bryological Report 180, Hamilton 1979b, p. 40. (8) Wind River, 56 km south of continental divide, Brooks Range, Alaska; 9080 ± 150 B.P. (I-10,509); Bryological Report 181, Hamilton 1979b, p. 41. (9) Your Creek area, Alaska; 5615 ± 110 B.P. (I-10,568); Bryological Report 183, Hamilton 1979a, Fig. 5. (10) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6220 ± 140 B.P. (I-10,784); Bryological Report 200; Hamilton 1980a, p. 23. (11) Anaktuvuk Valley, thaw lake 2 km upvalley from Akmagolik Creek, Alaska; 6200 ± 120 B.P. (I-10,925); Bryological Report 201, Hamilton 1980a, p. 23. (12) North Fork Pass, Ogilvie Mountains, Yukon Territory; 11,250 ± 160 B.P. (GSC-470); Bryological Report 260. (13) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265. (14) St. Hilaire, Quebec; 10,100 ± 150 B.P. (GSC-2200); Bryological Report 280, Mott *et al.* 1980. (15) HH68-9 (station 3), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 299. (16) HH75-24, Bluefish Basin, Yukon Territory;

Wisconsinan?; Bryological Report 326, *cf. Hylocomium splendens*. (17) Cape Deceit Quaternary Exposure, Near Deering (station 6), Alaska; 700,000 – 1,800,000 B.P.; Bryological Report 341, Matthews 1974a. (18) HH79-1, Hungry Creek, Yukon Territory; 8700 ± 80 B.P. (GSC-2971); Bryological Report 383. (19) HH72-54 (station 3), Hungry Creek, Yukon Territory; Wisconsinan; Bryological Report 435.

Discussion. – Other genera of the Hylocomiaceae and species of the Rhytidiaceae are distinguished from *H. splendens* by their monopodial branching, or by sympodial branching not related to yearly increments (*Loeskobryum*), or by the absence of paraphyllia. Other species of *Hylocomium* have a single costa or strongly plicate leaves or do not produce clearly recognizable yearly increments.

Polytrichaceae

The genera *Polytrichum*, *Atrichum*, *Oligotrichum*, *Psilopilum* and *Pogonatum* have a fossil record (Jovet-Ast 1967, Dickson 1973, Janssens 1977a, Miller 1980a). *Psilopilum* is represented only in North America (Miller 1980a). *Atrichum* and *Oligotrichum* do not have a North American record.

Pogonatum

Pogonatum and *Polytrichum* are differentiated from the other genera of the Polytrichaceae by their distinctly sheathing leaves with a strongly widened costa and a narrow lamina in the limb. The fossil specimens are black or black-brown and opaque. *Pogonatum* can be distinguished from *Polytrichum* by a combination of vegetative character states. *Pogonatum* leaves have incurved margins that never overlap. The leaves are short and bluntly acute (never in *Polytrichum*) or sharply acute and longer, but then the marginal cells of the adaxial lamillae are papillose. *Polytrichum* species have smooth top cells on the lamellae.

The three *Pogonatum* species in the North American fossil record, two of them which are discussed below, are differentiated from the other taxa by their stiff, narrowly lanceolate leaves with numerous (>20), adaxial lamellae and denticulate margins. *Pogonatum alpinum*, *P. dentatum* and *P. urnigerum* can be distinguished from each other by the structure of the top cell of the lamellae, most easily observed in transverse section. Single good transverse sections are actually sufficient to identify the Polytrichaceae to species level. Both *P. urnigerum* and *P. dentatum* have coarsely papillose top cells. The latter also has very wide, slightly convex or flat topped marginal lamellae cells, while *P. alpinum* and *P. urnigerum* have narrow, elliptic, pear-shaped or rounded top cells. *Pogonatum alpinum* has finely papillose top cells (papillae <2.5 micrometer), while *P. urnigerum* has coarse papillae (>5 micrometer). However, this latter character state is not easy to distinguish in strongly blackened subfossil material.

Pogonatum alpinum (Hedw.) Röhl.

Diagnostic features. – *Leaves* from a long, widely ovate sheathing base narrowly lanceolate, concave and tubulose above; *margins* sharply denticulate at the apex; *marginal cells of lamellae* vertically elliptic, with thin or thick upper wall, papillose.

Habitat. – On moist or wet, acidic, neutral or somewhat calcareous soils, often over or among rocks; where there is churning of top soil due to frost action. In open tundra and heaths, in forests, sometimes in very wet places: in fens and in late snow-melt areas. pH 6.3 (n=1), conductivity 18.6 microScm^{-1} (n=1), Ca concentration 7.9 ppm (n=1), Mg concentration 1.0 ppm (n=1) and Na concentration 38.2 ppm (n=1).

Recent Distribution. – Circumboreal. Bipolar arctic-alpine species. North America: from Alaska to Greenland and Labrador, throughout Canada and northern United States southward at higher elevations to North Carolina in the east and California in the west. Southern Mexico, South America, Svalbard, Europe, northern and arctic U.S.S.R., central Asia, Japan. Africa, Tasmania, Australia, New Zealand. Antarctica.

Subfossil Distribution in North America. – Greenland and Northwest Territories (Miller 1980a). New records: (1) St. Eugene, Quebec; 11,050 ± 130 B.P. (QU-448); Bryological Report 279, Mott *et al.* 1980.

Pogonatum urnigerum (Hedw.) P. Beauv.

Diagnostic features. – *Leaves* from a short, widely ovate sheathing base narrowly lanceolate, tubulose; *margins* inflexed, coarsely denticulate along the limb; *marginal cells of the lamellae* rounded or ellipsoidal, with extremely thickened upper walls, papillose.

Habitat. – On open ground on leached sandy soil and in rock-crevices in dry and moist habitats. Beside streams, in sandpits.

Recent Distribution. – North America: from Alaska and British Columbia in the west to Nova Scotia and New England in the east. Europe, Azores, Canaries, Caucasus, northern, western and eastern Asia, Japan.

Subfossil Distribution in North America. – Greenland (Miller 1980a). New records: (1) HH68-9 (station 1-2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 176. (2) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314); Bryological Report 401.

Polytrichum

Species of *Polytrichum* are differentiated from *Pogonatum* taxa by the adaxially lamellae with smooth walled top cells of the adaxial lamellae. Only two taxa of this genus are represented in my collections. Miller (1980a) listed the following species with a North American fossil record: *Polytrichum commune* Hedw., *P. juniperinum* Hedw. and *P. strictum* Brid.

Polytrichum algidum Hag. & C. Jens.

Diagnostic features. – *Leaves* ovate-lanceolate from a short sheathing base, tubulose; *margins* plane or inflexed, entire; *marginal cells of the lamellae* twice as wide as the cells below, flat-topped or irregularly indented, thin-walled.

Habitat. – On calcareous or acidic soil, in wet places.

Recent Distribution. – Circumboreal. Arctic species. North America: from Alaska to Greenland, not south of 60° latitude. Svalbard, northern Europe and Asia.

Subfossil Distribution in North America. – (1) HH68-9 (station 11), Old Crow Basin, Yukon Territory; Early Wisconsinan?; Bryological Report 265.

Discussion. – Other *Polytrichum* taxa are differentiated from this arctic species by their denticulate, plane margins or by their strongly incurved margins, or by marginal cells of the lamellae which are not differentiated from the cells below. However, *P. ohioense* Ren *et* Card. and *P. commune* var. *yukonense* (Card. *et* Ther.) Frye are very similar, but can be distinguished by minor differences in the structure of the top cells of the lamellae. Both taxa have top cells with walls thicker than the walls of the cells below. In the latter mentioned variety, the top cells are distinctly notched and the wall thickenings form two bulging papillae.

Polytrichum juniperinum Hedw.

Diagnostic features. – *Leaves* lanceolate from a widely ovate sheathing base, tubulose; *margins* incurved and overlapping, entire; *marginal cells of the lamellae* narrowly vertically elliptic, as wide as the cells below, thin-walled.

Habitat. – On moist soil and humus, on *Sphagnum* hummocks, more rarely on dry soil and soil covered rocks. Late pioneer on burned peatlands, sometimes on decaying trees. Often associated with *Dicranum fuscescens*, *D. scoparium* and *Pleurozium schreberi*. pH 6.15 and 6.75 (n=2), conductivity 122 and 158 microScm^{-1} (n=2), Ca concentration 5.0 and 5.5 ppm (n=2), Mg concentration 0.6 ppm (n=2), Na concentration 11.4 and 12.4 ppm (n=2) and K concentration 7.5 and 11.6 ppm (n=2).

Recent Distribution. – Circumboreal. Nearly cosmopolitan. Bipolar species. North America: from Alaska to Greenland, Newfoundland and Labrador, south throughout Canada and northern United States, at higher elevations in North Carolina, Arkansas, California and Mexico. Europe, temperate Asia, in the southern hemisphere at higher elevations and latitudes.

Subfossil Distribution in North America. – Greenland, Massachusetts, New York, Northwest Territories and Vermont (Miller 1980a). New records: (1) CRH 12 (station 2), Old Crow Basin, Yukon Territory; ± 60,000 B.P.; Bryological Report 267. (2) Clements Markham Inlet, Ellesmere Island, Northwest Territories; 6400 ± 60 B.P. (SI-4314);

Bryological Report 401. (3) Milford Gypsum Quarry, Milford, Nova Scotia; >50,000 B.P. (GSC-1642); Bryological Report 413.

Discussion. – See the distinction under *P. algidum* for the differentiation with other *Polytrichum* taxa.

IV. SUBFOSSIL BRYOPHYTES and PALEOENVIRONMENTAL RECONSTRUCTION

A. Introduction

During the Pleistocene Northern Hemisphere glaciations the continental shelves, now covered by the Bering Sea and the Chukchi Sea, were exposed and connected the unglaciated regions in northeastern Siberia, Alaska and the Yukon. Beringia, a term first used by Hultén (1937) for this land bridge, and later expanded to include the vast landmass extending from the northern Yukon Territory to the Kolyma River in Siberia (150° E), has long been considered as a glacial refugium. Survivors of Pleistocene glaciations probably dispersed repeatedly from this area after deglaciation, and progressive equiformal distribution patterns can be constructed from study of the distribution of a large group of such surviving species. In addition, because of its Holarctic position, Beringia has played a strategic role in dispersal during the Cenozoic. The affect of the Bering Land Bridge on holarctic migrations is dependent on the vegetation cover it possessed throughout the Cenozoic this is discussed in Chapter V.

Most of my research in Beringia is centered in the Old Crow Basin, the largest of only four areas in the northern Yukon that are less than 400 m elevation. The other three are portions of the smaller Bluefish, Bell and Bonnet Plume Basins. The Old Crow Basin is a flat lowland covering 5500 km^2 in the northern Yukon. The basin is partly surrounded by the British Mountains to the north, the Richardson Mountains to the east and the Porcupine Plateau and the Old Crow Range to the south. The general elevation of the lowland is 300 to 400 m a.s.l. Topping thick deposits of fluvial and glaciolacustrine sediments of Pleistocene age is a mantle of Holocene peat and thaw lake sediments, the latter deposited in the numerous thermokarst lakes which occupy the basin. Permafrost is continuous and the active layer exceeds 30 cm in thickness. Active ice-wedge formation associated with low center polygons is taking place at the present time in the Holocene sediments of the basin.

Hughes (1969) and Morlan & Matthews (1978) have provided a summary of the geological history of the Old Crow Basin. It can briefly be summarized as follows. At two separate time periods large glacial meltwater lakes formed in the basin. In both lakes, thick layers of clay were deposited. The interval between the lacustrine clays beds is a sequence of sands and silts which were deposited by fluviatile processes. After drainage of the last glacial meltwater lake around 13,000 years ago, the Old Crow and Porcupine Rivers rapidly cut down through the Pleistocene sediments in the basin, resulting in their exposure in large cut-banks. Detailed studies of these exposures by members of the Yukon Refugium Project[1] in and outside the Old Crow Basin led to an appreciation of the complexity of the late Pleistocene history of the northern Yukon Territory. A short summary of the hydrological evolution of the northern Yukon during the Pleistocene follows. This sketch is based on John Matthew's ideas (1979), circulated to the members of the Yukon Refugium Project. The time-stratigraphical models applied to the Old Crow Basin will be discussed in more detail in Chapter V.

Three glacial meltwater lake basins have to be accounted for: the Old Crow, Bluefish and Bell basins (Plate 56). In addition three canyons are essential to the workings of the basin hydrology: the McDougall Pass, connecting the Bell Basin system with the Mackenzie River system, the Bell Canyon, between the Bell Basin and the Old Crow-Bluefish Basins system, and the Alaska-Yukon Border Pass (Porcupine River).

Before the deposition of the Lower Lake Clays, the Old Crow and the Bluefish Basins were subsiding, a continuation of local Tertiary tectonics. There was some external drainage of these basins and sedimentation was slow. The Bell Basin drained into the Mackenzie River through McDougall Pass.

During the first recorded glaciation in the eastern Richardson Mountains glacial meltwater filled all three basins. The Alaska-Yukon Border Pass served as an outlet and was eroded in stages, resulting in dropping water levels throughout the glacial epoch. The former Procupine River outlet at McDougall Pass was blocked by Keewatin Ice, and this resulted in a reversal of drainage as the Bell Basin discharged through Bell Canyon into the Yukon River system.

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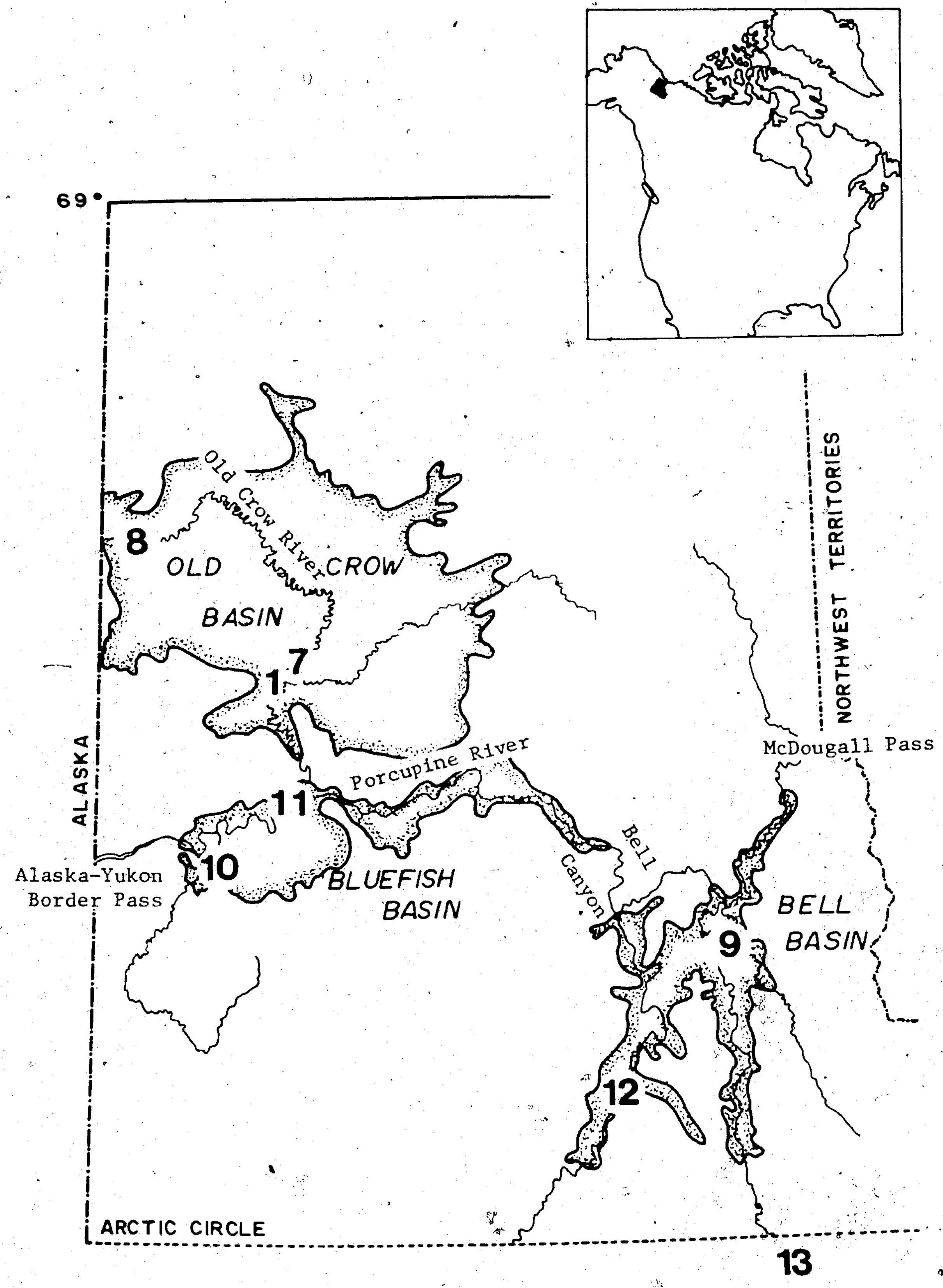
[1] The Yukon Refugium Project was launched in 1975 to study the late Pleistocene paleoenvironment of all unglaciated areas in the Yukon Territory (Morlan 1977f).

Plate 56. Glacial meltwater basins in the northern Yukon Territory. Map based on Hughes (1971) and Morlan (1978c). The maximum extent of the Late Wisconsinan glacial meltwater lakes is indicated by the stippling. The numbers are at the approximate location of the collecting localities (Table 2). Localities 1 to 6 are in the immediate vicinity of Locality 1. Locality 13 is off the map to the south.


69°
8
OLD CROW
BASIN
Old Crow River
7
1
ALASKA
NORTHWEST TERRITORIES
McDougall Pass
Porcupine River
11
10
Alaska-Yukon
Border Pass
BLUEFISH
BASIN
Bell
Canyon
BELL
BASIN
9
12
ARCTIC CIRCLE
13

With deglaciation, the meltwater supply ceased, the Old Crow and Bluefish Basins continued to drain into the Yukon River system, but the Bell Canyon may not have been eroded deeply enough to allow the Bell Basin to do the same. The Bell Basin water joined the Mackenzie River system through McDougall Pass. In the Old Crow and Bluefish Basins, residual lakes remained, reworking the top layers of the lower lacustrine clays. This explains the paleontological character of the upper part of these lacustrine clays. They are the oldest sediments in the northern Yukon that have been analysed for fossil bryophytes; however, their exact age has not yet been determined. During the subsequent warm period a flora and a fauna existed near Old Crow containing elements that are not found that far north at present.

Accumulation of fluvial sediments continued in the Old Crow and Bluefish Basins. A warm oscillation around 60,000 years ago halted the in-filling, thawed the ice wedges and created Disconformity A by erosion. This hiatus can be traced for over 40 km of the southern protion of the Old Crow Basin (Morlan 1978c). The oldest date on Disconformity A is more than 51,000 BP and a volcanic ash 30 cm below it has a maximum date of 80,000 years (Westgate, *et al.* 1978). No detailed dating of the fluviatile sequence below Disconformity A is possible at the present time. A pollen assemblage from the level of the exposure now known to coincide with Disconformity A has the following characteristics: 10 % *Picea*, 21 % *Betula*, 2 % *Pinus*, 6 % *Alnus*, 2 % *Salix* and around 25 % each for Gramineae and Cyperaceae (Lichti-Federovich 1973).

This evidence, plus the abundant plant and insect macrofossils recovered from along the Disconformity (Hughes *et al.*, manuscript in preparation), suggests that the regional climate was as warm or slightly warmer than at present during the erosional interval responsible for the formation of the contact (Matthews, *in litt.*). This period of climatic amelioration is also indicated by ice-wedge pseudomorphs and cryoturbation structures associated with the Disconformity. Many of these structures contain peats, bones, wood, shells of gastropods and pelecypods, and chitinous remains of insects, representing the ancient flora and fauna.

The Bell Basin was impounded a few times after the initial recorded flooding, with McDougall Pass and the Bell Canyon serving as outlets. No ponding occurred in the Old Crow and Bluefish Basins, because the Alaska–Yukon Border Pass was eroded deeply enough and the basins were filled up with sediment above the level of the pass.

During the Bonnet Plume glaciation, between 36,000 and 12,000 BP, McDougall Pass became obstructed with sediments, the Bell Canyon was cut to its present level and the water of the Peel was diverted once again to the Bell Basin and the Porcupine System. The Old Crow and Bluefish Basins were flooded by glacial meltwater flowing through the more effective Bell Canyon and they overflowed through the Alaska–Yukon Border Pass. According the Matthews' (*ibid.*) senario of events, the Bell Basin was not flooded continuously during this latter period. Around 13,000 years ago the Keewatin Ice Sheet retreated from the Richardson Mountains, creating the last rush of eastern glacial meltwater to effect the basins. In a short span of time the glacial meltwater cut down the Alaskan–Yukon Border Pass to its present level. Glacial meltwater supply was completely cut off when the Laurentide glaciers retreated to the east over the divide of the Richardson Mountains. The Old Crow and Bluefish basins were drained, exposing extensive plains with residual lakes . The development of permafrost in the clays resulted in formation of thermokarst or thaw lakes These thaw lakes began migrating over the basin floor and accummulated coarse detrital organics. Peat began to form in minerotrophic fens as the postglacial climate became wetter. The postglacial peat l[illegible] 1 to 2 m in thickness. At the present time the Old Crow Basin is covered with [illegible] of subarctic tundra vegetation and open *Picea glauca–Larix laricina* w[illegible] An account of the vascular plant flora of the region has been provided by Cwynar (1977) and Welsh & Rigby (1971).

Two sediment exposures, HH68–9 and HH68–10 (Plate 1), along the Old Crow River in the southcentral part of the Old Crow Basin, were studied in greatest detail. HH68–9 (Hughes 1969), is bluff along the right bank of the Old Crow River, 1500 m north and upstream from the confluence with Johnson Creek in the Old Crow Basin. Most of the 400 m long riverbank has a southerly exposure. Thawing of permafrost in the Upper Lake Clays during summer has created retrogressive thaw flow slides which form an extensive terrace high up in the section and obscure exposure of the most recent deposits in the Basin. The terrace and the underlying alluvial material is transected by several gullies, on the banks of which productive collecting stations occur. The Old Crow Basin sections, and more particularly the locality HH68-9, offer an excellent opportunity to study the Late Pleistocene (120,000 to 10,000 years ago) and postglacial history of eastern Beringia. The sequences discovered along the rivers in the Old Crow Basin are exposures of clay, sands and silts, deposited in a lacustrine or fluvial environment, and of *in situ* massive peats. Most sediments contain abundant remains of numerous such organisms as vascular plants (pollen, phytoliths, leaves and cones), bryophytes, diatoms, mammals (bones), pelecypods, gastropods, insects (mostly Coleoptera) and bryozoa (statoblasts). Evidence of Early Man is also found in the area and in one of the oldest context on the continent.

The sediment sequences indicate at least two periods of basin inundation, while the upper is dated to the last-glacial (30,000 to 12,000 BP), the lower is also tentatively correlated with advancing Keewatin Ice. The stratigraphic features, as well as the enclosed organisms, make it possible to reconstruct the precise history of this critical area in northwestern North America.

B. Results

The following sections of this chapter are restricted mostly to the discussion of the samples collected in the northern Yukon. Only these collections are numerous enough to span Late Pleistocene and Holocene history without major hiati. Other significant assemblages from outside the basins in the Yukon or from other parts of North America are discussed in Chapter V in relation to the Cenozoic history of Beringia. Plate 57 is a composite section through locality HH68-9 and neighbouring localities. It indicates the stratigraphic position of the analysed samples, collected by myself and members of the Yukon Refugium Project, listed by their Bryological Report Number. Table 1 lists additional samples from the same levels. Samples from other nearby Old Crow localities showing a similar stratigraphy, and from localities outside the Old Crow Basin are listed in Table 2. Janssens (1981) gives all detailed information and the analyses of each sample listed in Tables 1 and 2, while Appendix 2 summarizes the results of all analyses of samples from the northern Yukon Territory. Thirteen localities (Plate 56 and Table 2) are

Plate 57. Composite Old Crow Sequence showing the Bryological Report numbers for the samples collected and of analysed from HH68-9, HH68-10, HH69-21, CRH 11 and REM 78-2. Composition of the sequence: HH68-9, Stations 2, 3, 6, 7 and HH68-10, Holocene peat. Measurements by R.E. Gunn on HH68-9. Facies description[1] by R.E. Morlan based on HH68-9, Station 3 for −5.0 to +6.2 m, on HH68-9, Station 7 for above +6.2 m. Recent peat, description by J. A. Janssens based on HH68-10.

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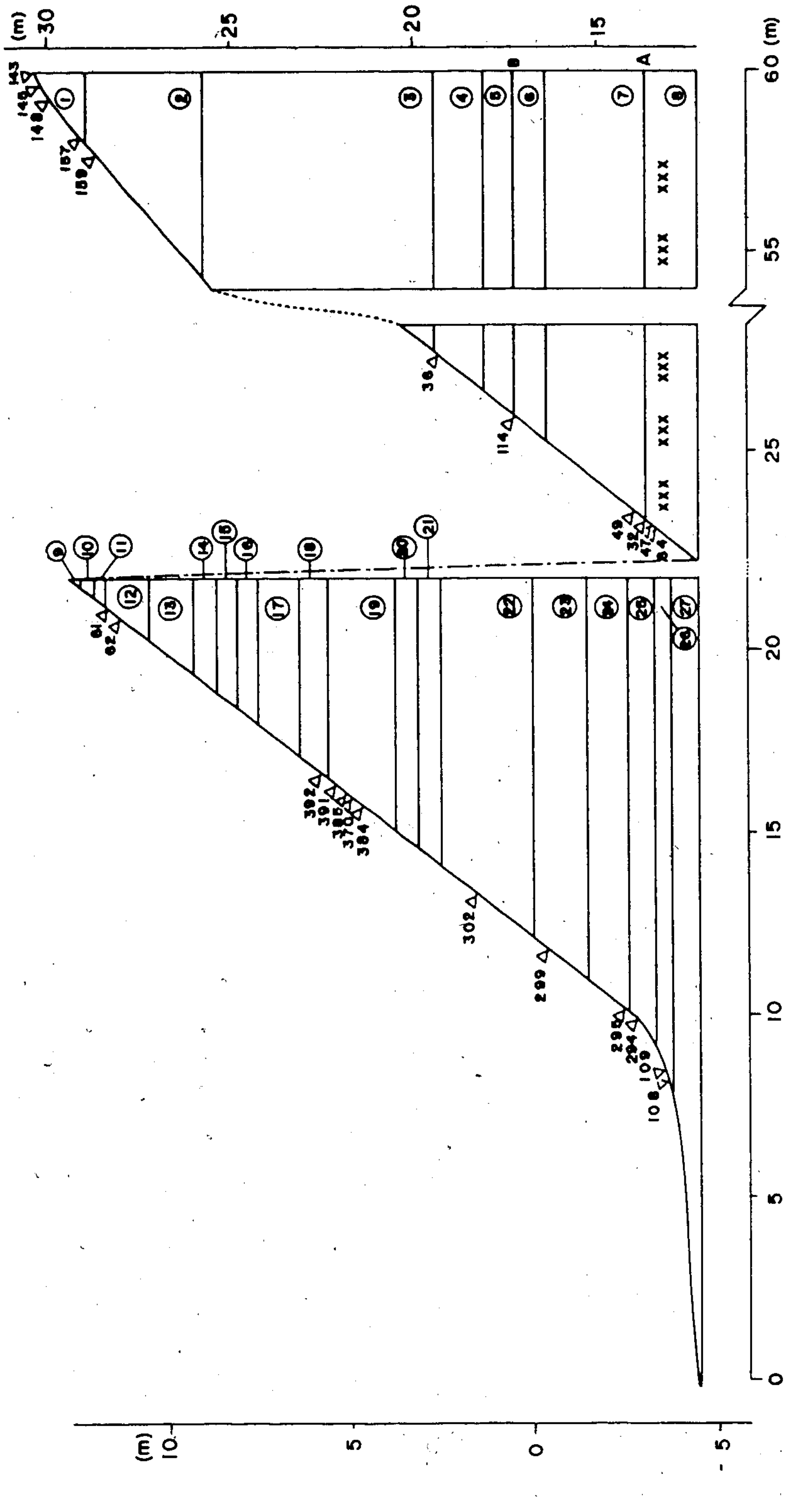
[1] Key to stratigraphic description:

1. Recent peat (HH68-10), not exposed in HH68-9.
2. Silts.
3. Gray clays with extensive development of retrogressive flowslides (only partially drawn on the fig.).
4. Variegated silts and clays.
5. Silts.
6. Cryoturbated and truncated silts.
7. Cryoturbated silts above and crossbedded silts and sands below.
8. Clay, with ash layer, and Disconformity A on top.
9. Crossbedded fine silts and sands.
10. Darkbrown silt.
11. Crossbedded fine sands.
12. Crossbedded clayey silt and silty sand.
13. Crossbedded clayey silts, very little sand in lenses.
14. Crossbedded silts and sands, detrital organics, gravel layer.
15. Crossbedded silts, oxidized, large wood.
16. Fine to coarse sand.
17. Organic silts, large wood.
18. Crossbedded sands, organics on bedding planes.
19. Crossbedded organic silts.
20. Sand and silt.
21. Bedded organic silts and sands.
22. Bedded silts and sands, discrete organic layers.
23. Bedded silts and sands with discrete organic layers, abundant pelecypods.
24. Faintly bedded silt, clay and sand with hematite nodules, scattered wood.
25. Gray-brown silts and sands.
26. Yellow-brown sands.
27. Dark gray silty clay, black with oxidized joints, scattered wood.



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108

Table 1. Additional Bryological Report Numbers for samples collected at the same level as samples indicated on Plate 57.

Sample #	Additional Bryological Report Numbers from the same level
32	48, 50, 54, 101, 134, 174–176, 262–264, 270, 362, 384, 386–388
36	37
47	68, 102, 261
49	308
114	115–118, 120
108	103, 265
143	289
370	425

Table 2. Localities studied in the northern Yukon Territory.

#	Locality name	Bryological Reports Numbers (Janssens 1981)
Old Crow Basin		
1a	HH68-9 (Upper Lake)	114-118, 120, 424.
1b	HH68-9 (Dis. A)	47-49, 54, 64, 134, 174-176, 261-264, 308, 384, 386, 387
1c	HH68-9 (Mid-Section)	61, 62, 294, 295, 299, 302, 319, 370, 385, 389, 391, 392, 425
1d	HH68-9 (Lower Lake)	108, 109, 265
1e	HH68-9 (river bars)	35
2	CRH 11	3, 32, 36, 37, 266
3	CRH 12	40, 267
4	CRH 70	269, 270
5	REM 78-2	289
6	HH68-10	143, 145, 148, 157, 159
7	HH69-21	101, 102, 103, 388
8	HH75-19	272
Bell Basin		
9	Rock River	33
Bluefish Basin		
10	HH75-24	173, 271, 325, 326, 328
Porcupine River		
11	228 HH	362
Upper Porcupine Section		
12	HH75-9	34
Bonnet Plume Basin		
13	Hungry Creek	383, 434, 435

represented in this latter appendix. Only one locality (HH68–9), has been subdivided here into its five major stratigraphical units. Each locality (or stratigraphical unit of HH68–9) represents from one to eighteen different samples (Table 2) as summarized vertically in the columns of Appendix 2. The rows of this appendix indicate the age distribution of a particular taxon. The age classification is based on three general periods: Pleistocene, Wisconsinan, and Holocene. The designation Pleistocene is used when it is not clear that the age is Wisconsinan or pre-Wisconsinan. [1]

A total of 522 records are presented here and summarized in Appendix 2. A record constitutes the presence of one taxon in a single sediment sample from a particular stratigraphical position at a single locality. Therefore, there can be several records of the same taxon in several samples from the same stratigraphical position, but exposed at different stations (for example Disconformity A at the several HH68–9 stations), from a single locality. The 522 records represent 111 taxa, 96 of which are identified to species or some infraspecific category. Mosses comprise 99.6 % of the records and 97.8 % of the species. The 10 commonest species are *Drepanocladus lycopodioides* var. *brevifolius* (27 records), *Scorpidium scorpioides* and *Tomenthypnum nitens* (each with 26 records), *Calliergon giganteum*, *C. richardsonii* and *D. crassicostatus* (each with 21 records), *D. exannulatus* (20 records), *Aulacomnium palustre* (13 records), and *D. sendtneri* and *C. trifarium* (each with 12 records). The Amblystegiaceae (8 of the above listed most common species are members of this family) represent 56.2 % of the records. The Brachytheciaceae (7.7 %), Aulacomniaceae (5.8 %) and Bryaceae (5.0 %) are the other most strongly represented families. A tabular summary of subfossil bryophytes results for the northern Yukon is given in Plate 56 to 58, Table 1 & 2, Janssens (1981) (*pro parte*) and Appendix 2. Some statistics are listed above.

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[1] This applies to most samples collected in the Mid-Section below Disconformity A. It has been assumed that the top of the lower lake clay was formed during Sangamonian time (Morlan & Matthews 1978). However, there exists severel alternative interpretations of the stratigraphy. It is possible that the top part of these clays are Early or Middle Wisconsinan in age and that the whole Mid-Section (18 m of sands and silts at HH68–9) was deposited during a short period before the formation of Disconformity A (around 60,000 years ago). The Mid-Section can then be considered as being formed by a rapid accumulation of fluviatile sediments in a point-bar system (Morlan, personal communication). On the other hand, the Lower Lake could be Early Pleistocene, even Late Pliocene, in age (Schweger, personal communication). More details on time–rock units can be found in Chapter V.

C. Subfossil and the Present Day Bryofloras of the northern Yukon Territory

Five moss species known from the fossil record of the Yukon have not been found there at present. *Leptodontium flexifolium* is disjunct from 4400 km south in the United States (Janssens & Zander 1980 and Plate 4). *Calliergonella cuspidata, Sphagnum centrale* and *Mnium marginatum* are found at the present time in neighbouring Alaska and British Columbia, but as yet not in the Yukon. However, both of the former species are identified at a low reliability level from HH68-9 samples. *Mnium marginatum* is found in the extraordinary Hungry Creek Bonnet Plume Basin assemblage (Bryological Report 435 (see Janssens 1981 for summaries of all Bryological Reports)). *Calliergon megalophyllum* is tentatively identified in a HH68-9 Old Crow Basin assemblage. The species presently is known from Alaska (ALTA!) and the Northwest Territories (Steere 1978a, Ireland *et al.* 1980).

While approximately 22 % of the bryophyte species in the present day flora of the Yukon are Hepaticae (Table 3), this same group is represented by only 2.2 % of the number of taxa in the subfossil record. In addition, the two subfossil hepatics recovered from postglacial dated samples (Bryological Reports 143 & 148) are probably only a few hundred years old. Very similar observations can be made on the contribution of the Hepaticae to the total North American subfossil record (summarized in Table 4) and to the British record (Dickson 1973). Only 7 of the 525 extant species of hepatics on the North American continent north of Mexico are known as subfossils. In the British Isles 18 liverwort subfossil taxa contrast with some 179 subfossil moss taxa. The present day flora of this region contains 285 liverworts and 675 mosses (Dickson 1973).

On the other hand, 47 % of the North American subfossil bryophyte records and 56 % of those from the northern Yukon are Amblystegiaceae. While the number of species of this family contributes only 4.4 % to the total number of species in the extant North American bryoflora (8.8 % for the Yukon), they are exceptionally well represented in the subfossil record: 16 % (North America) and 30 % (Yukon Territory). The higher frequency of Amblystegiaceae in the present Yukon bryoflora as compared with the North American flora is paralleled by their relative frequencies in the subfossil floras. In the record for the British Isles, 10 of the 30 most common species belong to the Amblystegiaceae and this accounts for 25 % of all the British records (Dickson 1973).

Table 3. Comparison between the present day and subfossil bryofloras of the Yukon Territory.

	Yukon present bryoflora[1]	Yukon subfossil bryoflora[2]
Bryophytes		
# of records		525
# of species	511	90
Musci		
# of records		523
# of species	401	88
Hepaticae		
# of records		2
# of species	110	2
Amblystegiaceae		
# of records		293
# of species	45	27

[1] Vitt & Horton 1979b and Ireland *et al.* 1980

[2] Appendix 2

Table 5. Representation of Hepaticae and Amblystegiaceae in the present day and Quaternary Subfossil bryofloras of the Yukon Territory, North America and the British Isles.

	Yukon	North America	Britain
Hepaticae			
subfossil flora	2.2 %[1]	2.8 %[2]	10.0 %[3]
present flora	22 %[4]	31 %[5]	42 %[3]
Amblystegiaceae			
subfossil flora	30 %[1]	16 %[2]	25 %[3]
present flora	8.8 %[4]	4.4 %[5]	4.6 %[6]

[1] Appendix 2

[2] Janssens 1981, Miller 1980a, Kuc 1973c and Kuc & Hills 1971

[3] Dickson 1973

[4] Vitt & Horton 1976b, Ireland *et al.* 1980

[5] Crum *et al.* 1973

[6] Warburg 1963

To conclude (Table 5) , the Hepaticae are under-represented in the fossil record by a factor 10 (4 in the British record), while the Amblystegiaceae are over-represented as fossils by a factor 3 to 4 (5.5 in the British record). The better representation of liverworts in the British subfossil flora is due to the great proportion of Flandrian records (Dickson 1973), while postglacial records in North America are scarce in comparison (Janssens 1981, Miller 1980a).

Groups of mosses not represented in the northern Yukon fossils are characteristic of particular habitats that are not conducive to fossilization. Thus, acidic saxicolous species, dry silt growers, ephemerals and corticolous species, for example Andreaeaceae, Orthotrichaceae, *Dicranella* species, *Dicranoweisia crispula*, *Coscinodon*, *Schistidium*, *Grimmia* and *Rhacomitrium* species are lacking. Also, curiously, some common bryophytes living in habitats with a high fossilization potential are noticeably absent, that is, many *Sphagnum* species, *Philonotis* species, *Myurella* and *Hygrohypnum* species. Some factors that might contribute to this absence are poor inherent preservation capabilities (*Sphagnum*) and high energy environments (*Hygrohypnum*). Future research in the northern Yukon should recover fossils of *Andreaeobryum macrosporum*, presently known to occur in the headwater region of the Peel and Porcupine Rivers on wet, calcareous rocks (Steere & Murray 1976); *Fissidens adianthoides*, common in fens; *Saelania glaucescens*, one of the drier calcareous soil growers; *Dicranum elongatum*, commonly found in bogs and tundra; *Bryobrittonia longipes*, on moist calcareous silt in floodplains and already in the Quaternary fossil record from Alaska (Bryological Report 201); *Barbula unguiculata* and *B. convoluta*, in the same habitat as *Bryobrittonia longipes*; *Gymnostomum recurvirostrum*, on calcareous rocks and in wet tundra (Bryological Report 201); *Rhacomitrium lanuginosum*, in large mats on acidic, and rarely on calcareous rocks (Alaska, Bryological Report 201); *Funaria hygrometrica*, which was probably abundant on disturbed soil in the basin floodplains during their Pleistocene development; *Pseudobryum cinclidioides*, common in mire systems and known from the Nova Scotian Quaternary fossil record (Bryological Report 413); *Climacium dendroides*, along streams and lakes; *Entodon concinnus*, on moist calcareous soil and already discovered in an assemblage from the Brooks Range (Bryological Report 201); *Ptilium crista-castrensis*, almost certainly

Table 4. Comparison of present day and subfossil bryoflora of North America

	North American present bryoflora[1]	North American subfossil record[2]
Bryophytes		
# of records		1663
# of species	1695	246
Musci		
# of records		1650
# of species	1170	239
Hepaticae		
# of records		13
# of species	525	7
Amblystegiaceae		
# of records		775
# of species	74	40

[1] Crum *et al.* 1973 and Stotler & Crandall-Stotler 1977

[2] Janssens 1981, Miller 1980a, Kuc & Hills 1971 and Kuc 1973c.

present during the warm interglacial and interstadials on the forested floodplains of the basins and now known as a subfossil from the same assemblage as the foregoing species; and *Polytrichum strictum*, a consistent component of acidic wet communities with *Sphagnum* species.

Neither sporophytes nor calyptrae have been extracted from any material collected in the Yukon Territory. However, they are not unknown for North America. I have extracted two fossil Hypnaceous capsules out of deposits from Ontario and an *Encalypta* calyptra from a Quebec sample. A *Sphagnum* sporophyte (probably *S. lenense*) was recovered from a two million year old deposit in eastern Alaska.

There are several possible explanations for the discrepancies between the subfossil records and the present-day bryofloras with respect to Hepatics, Amblystegiaceae and other taxa mentioned above. It is generally accepted that selective the under-representation of liverworts (Culberson 1955). Steere (1942) suggested different cell wall composition and structural differences as the reasons for the rarity of certain groups of bryophytes in the fossil record. Hydrophilic mosses are supposed to be more protected against decay by the presence of aromatic and antibiotic constituents in their cell walls (Steere 1942). An indication that cell walls of stem and leaves only mature at the end of the first year by the deposition of resistant products is given by the near absence of first year fragments and growth apices of pleurocarpous mosses among the subfossil fragments. Further study of cell wall composition and ultrastructure, and of the micro-organisms responsible for decay is badly needed to clarify the exact contribution of these factors to the skewed representation of certain groups of bryophytes in the fossil record. Clymo (1965) reviewed some of the conflicting literature on the presence of anaerobic organisms below the sulphide horizon in mires. He concluded that breakdown by micro-organisms was probably the for loss of matter from *Sphagnum*. His experiments illustrated selective destruction by showing that *S. papillosum* disappeared only half as fast than *S. cuspidatum* and *S. nemoreum* from the experimental set-ups.

However, it is evident that for some groups differential destruction is not the cause. Their absence can most easily be explained by considering that they grow in habitats without potential for fossilization, as for example corticolous species.

Summary

Most species with a fossil record in the Yukon are still in the present bryoflora of the Territory. However, *Leptodontium flexifolium* is a well documented example of a disjunct species [illegible] is absent in the Yukon at present (Plate 4), as well as the low reliability fos[illegible]ords of *Calliergonella cuspidata*, *Calliergon megalophyllum* and *Sphagnum centrale*. Hepaticae are strongly under-represented as fossils, while the Amblystegiaceae are over-represented. Some bryophytes are noticeably absent as fossils in the Yukon, but many of these are known from postglacial deposits in the Brooks Range and will probably be recorded fromn the Yukon in the future. Ultrastructural differences of cell-wall and the production of antibiotic substances and habitat preferences are responsible for the selective preservation.

D. Paleoecological Reconstruction: Approaches

Introduction

The majority of assemblages belong to the transported type (see Materials and Methods, and Table 6). Steere (1965) cautions that only the *in situ* deposited sediments (fossil peats and forest soils) are capable of giving reliable information about environmental conditions and climates. This viewpoint can be modified when the history of such largely transported and mixed assemblages as those from the glacial meltwater lake basins in the northern Yukon is considered in detail. All the samples have been collected along riverbanks composed of re-exposed fluviatile sediments and preserved in permafrost. No extreme topographical differences (and thus drastically different vegetation zones) are present between the localities and the headwaters of the small rivers cutting through the basins. In addition, it is clear, because of the extensive erosion and down-cutting of the river valleys during the late- and postglacial period, that the headwaters were in most cases much closer to the present day collecting localities. In conclusion, none of the species occuring in the northern Yukon assemblages could have been transported from exotic communities, but could have come from reworked flood

Table 6. Summary of the characteristics of the three types of assemblages, derived from the northern Yukon samples.

	Autochthonous	Mixed	Transported
Total			
number of assemblages	14	11	48
number of records	57	119	349
number of taxa	35	62	84
mean number of records per assemblage	4.1	10.8	7.3
mean number of records per taxon	1.63	1.92	4.15
Amblystegiaceae			
number of records	33	54	207
number of taxa	16	20	31

plain sediments. Therefore, despite the fact that most of the northern Yukon Yukon assemblages are mixed, the data obtained provide a sound basis for the reconstruction of Pleistocene and Holocene communities for this general area.

Disjuncts, Incongruous Samples and Modifications

There are four approaches in paleoenvironmental research to the analysis of data obtained from subfossil bryophytes. The first two methods will be briefly discussed below while the third and the fourth will be dealt with in the next part. All four methods will be illustrated in Chapter V.

The first approach makes use of the characteristic habitat features of a single taxon. The most significant conclusions are based upon those species no longer in the present-day flora of that area or that are found in unique associations. Two examples are discussed in detail in Chapter V.

A second approach to paleoenvironmental reconstruction, which is partially species independent (compare Chaney & Sanborn 1933 and Wolfe's papers), is based upon an analysis of structure modifications. Some modifications indicate submerged habitats for otherwise semi-terrestrial taxa or exposed habitats for otherwise shade-tolerant species. It is evident from the work of Lodge (1959, 1960) and Sonesson (1966), as well as from the discussions in Nyholm 1965 Mårtensson 1956, and Crum 1973, among others, that species in the genus *Drepanocladus* are extremely versatile in their morphological response to different environmental conditions. In a discussion of the taxonomy of several genera of Amblystegiaceae, Tuomikoski & Koponen (1979) clearly illustrated that the plasticity of *Drepanocladus* is also found in the large and unnatural genus *Calliergon.* (consult Chapter III for more details).

Except for the real and simulated deep-water experiments of Lodge (1959, 1960), no thorough study on correlations between morphological characteristics and habitat factors have been published. Lodge cultivated populations of *D. exannulatus* and *D. fluitans* under different conditions of submergence, salt concentrations and light intensities. Universal responses to aquatic habitat (associated with low light intensity at increased depth) are the production of narrower leaves, increase in cell length and internode length of the stem. Many of these responses are typical etiolation features. Lodge and later Sonesson (1966, for *D. trichophyllus*) came to the conclusion that the shape and structure of the differentiated alar cells are primarily genetically determined, while the shape of the leaves is strongly influenced by the environment. For further discussion see the *Drepanocladus* treatment in Chapter III.

Dickson (1973, p. 43) discussed the grossly modified leaves of a *Polytrichum commune* specimen that has been washed in a reservoir before burial and fossilization. The extreme length of the shoots of deep-water bryophytes is mentioned by several authors. Bodin & Nauwerck (1968) pointed out the slow growth of the deepest growing bryophyte plants and the depletion of their chlorophyll content. Some authors have described these aquatic forms as new species. For example, Savich-Ljubitskaja & Smirnova (1964, 1965) described two species, *Bryum korotkevicziae* and *Plagiothecium simonovii*, from perennial ice-covered lakes in Antarctica.

Better known deep-water taxa are *Drepanocladus trichophyllus*, *D. capillifolius* and *Calliergon megalophyllum* (Tuomikoski 1940, 1949, Tuomikoski & Koponen 1979). These taxa are commonly found in Fennoscandian lakes (Persson 1942, Malme 1978) and some appear to be true lake bryophytes. A treatment of deep-water bryophyte structure is in Persson (1944). Even though he studied only a small number of species, many typical modifications were shared by all of them. However, Persson mostly limited himself to pointing out how extremely different the aquatic forms are, without giving more than cursory detail of structure. *Bryum pseudotriquetrum* and *Cinclidium stygium* are distinguished from their normal terrestrial populations by robustness, lengthened shoots and squarrose-recurved leaves. The first species is, in addition, characterized by the absence of any branching, loss of differentiated border and complete sterility. A unique character state for the aquatic form of *Drepanocladus sendtneri* is the much thinner costa.

Scorpidium scorpioides is a species of Amblystegiaceae upon which no quantitative observations in relation to modifications have been made. However, it is an extremely common Pleistocene fossil (see also Janssens 1977a, 1977b). Observations of modifications in the field and study of the subfossil assemblages has led me to the conclusion that there are three distinct forms of this species. The luxurious form has short internodes, very large, concave leaves, and is often black or dark-brown. This first modification is found in autochthonous peat samples formed in extremely rich fens. In well preserved samples containing this modification, marl forms the matrix (Bryological Report 172 and Janssens 1977a, b, the Gistel sites). At present such marl deposits are formed in extremely rich fen pools, along the margins of which only the large, turgid forms of *S. scorpioides* live. The stems become encrusted with calcium carbonates, which give rise to the marl matrix. A second form of *Scorpidium scorpioides* has small leaves and is not turgid. This modification is found in what are obviously mixed or transported assemblages (for example Bryological Report 201). This form is commonly found intermixed with other bryophytes in more terrestrial habitats. A third very characteristic modification of this species is created by flood conditions. A sudden rise in the water level causes mats of the species to become floating. The new stems have long internodes and even larger, but less concave, leaves than the turgid forms. An example of this form in the fossil record is seen in Bryological Report 173. The mixed assemblage described in this report probably originated by a sudden rise in water level and by the influx of some components from nearby drier communities.

Drepanocladus species are the most abundantly recovered subfossils, so that more quantitative studies along the line of those performed by Lodge would greatly enhance the usefulness of the second approach in paleoenvironmental reconstruction. Most species of *Drepanocladus* are capable of growing in submerged situations. The most commonly found modifications in these aquatic plants or in the submerged parts of terrestrial plants are longer internode length, more orthophyllous, narrower leaves, and longer and narrower cells. The species of the subgenus *Warnstorfia* often have a reduction in the number and size of the marginal teeth. Some species have a longer relative costa length in the aquatic forms (for example Bryological Report 409).

I have found analysis of modifications to be very useful in interpretations of depositional habitats. For example, two samples (Bryological Reports 177 & 178) were collected from the bottom of Kluane Lake, 43 m below the present water level. They have been estimated to be approximately 2200 years old. The peat in the core had the aspect of an organic deposit, formed *in situ*. However, the bryophyte assemblage shows that the components were derived from different communities. In addition to the floristic information, it is clear that the communities which gave rise to the assemblages are terrestrial or semi-aquatic and not lacustrine, because of the complete absence of aquatic modifications in the *Drepanocladus* species. Most likely the peat was rafted into the lake during spring break-up. There is no other evidence to support the hypothesis that Kluane Lake had a water level 50 m lower 2000 years ago (Matthews, personal communication).

A similar situation is analysed in Bryological Reports 409 to 412 (Janssens 1981, Blake 1981). Abundant, well preserved material of *D. lycopodioides* var. *brevifolius* was recovered from 1 m below the bottom of an unnamed lake in the Baird Inlet region of Ellesmere Island, in an apparently autochthonous peat. The material is of Early Holocene age (8940 ± 170 BP, GSC-3009). This species has never been found as an aquatic moss, nor have I ever found any aquatic modifications in subfossil fragments. The collector of the samples proposed (Blake 1981) that the depression was formed during Holocene time after local deglaciation and that the water level gradual rose after the species had already invaded the pond. The initially porous moraine which forms the dam for the present day lake was blocked by the accumulation of fine mineral sediment and rising permafrost caused the area to be flooded. An alternative hypothesis is that *D. lycopodioides* var. *brevifolius* was living in a shallow pond on dead ice. The pond became gradually deeper when the ice wasted during the postglacial period. A clearly aquatic form of *D. exannulatus* was recovered from a few cm below the bottom of the lake in the same core, above the *D. lycopodioides* var. *brevifolius* peat. This confirms that a rise in water table occurred.

Analysis of modifications can also be used with bryophytes that are not characterstic of aquatic habitats. For example, *Hylocomium splendens* has two distinct growth forms, which are explained in more detail in Chapter III. One form, which is the monopodially branched, is found in arctic-alpine, exposed habitats. The other, luxurious, sympodially branched form is always associated with the boreal forest. Both forms are easy to differentiate in well preserved subfossil material. The material that has preserved branching in my collections all belongs to the sympodial form (Bryological Reports 4, 200, 201 & 383). The localities are Stewart River in the Yukon (63° N), Anaktuvuk Pass in Alaska (68° N) and Hungry Creek in the Yukon (65° N). The forest form of the bryophyte is associated in these samples with *Picea* needles and macrofossils of other boreal taxa, confirming the presence of trees in the environment. For the postglacial Anaktuvuk Pass sample this supports the evidence that tree-line was higher up and farther north during pre-Neoglaciation Holocene than at the present time (Hopkins 1972 and Chapter V).

Local and Regional Reconstruction

The third and fourth approaches to paleoenvironmental reconstruction are discussed in this section. Both are primarily based on the floristics of the assemblages. The third approach is the most commonly used method in paleoenvironmental research based on macrofossils (Miller 1980c). One attempts to reconstruct, on a local scale, the communities that gave rise to the fossil assemblage. The inferences drawn are based primarily on the ecology of the different species in the assemblage (see Chapter III). In addition, abundancy and reliability indices are used, as explained in the Chapter II. The conclusions that have been reached by analysis of each assemblage are contained in the Bryological Reports submitted to the Geological and Archeological Surveys of Canada, the United States Geological Survey and several other organizations and persons that provided the samples. These conclusions are not reproduced in the Summaries to the Bryological Reports in Janssens 1981. Several of these assemblages will be discussed in Chapter III. This third approach also resulted in the assignment of each sample to a type of assemblage (see Materials and Methods and Table 6).

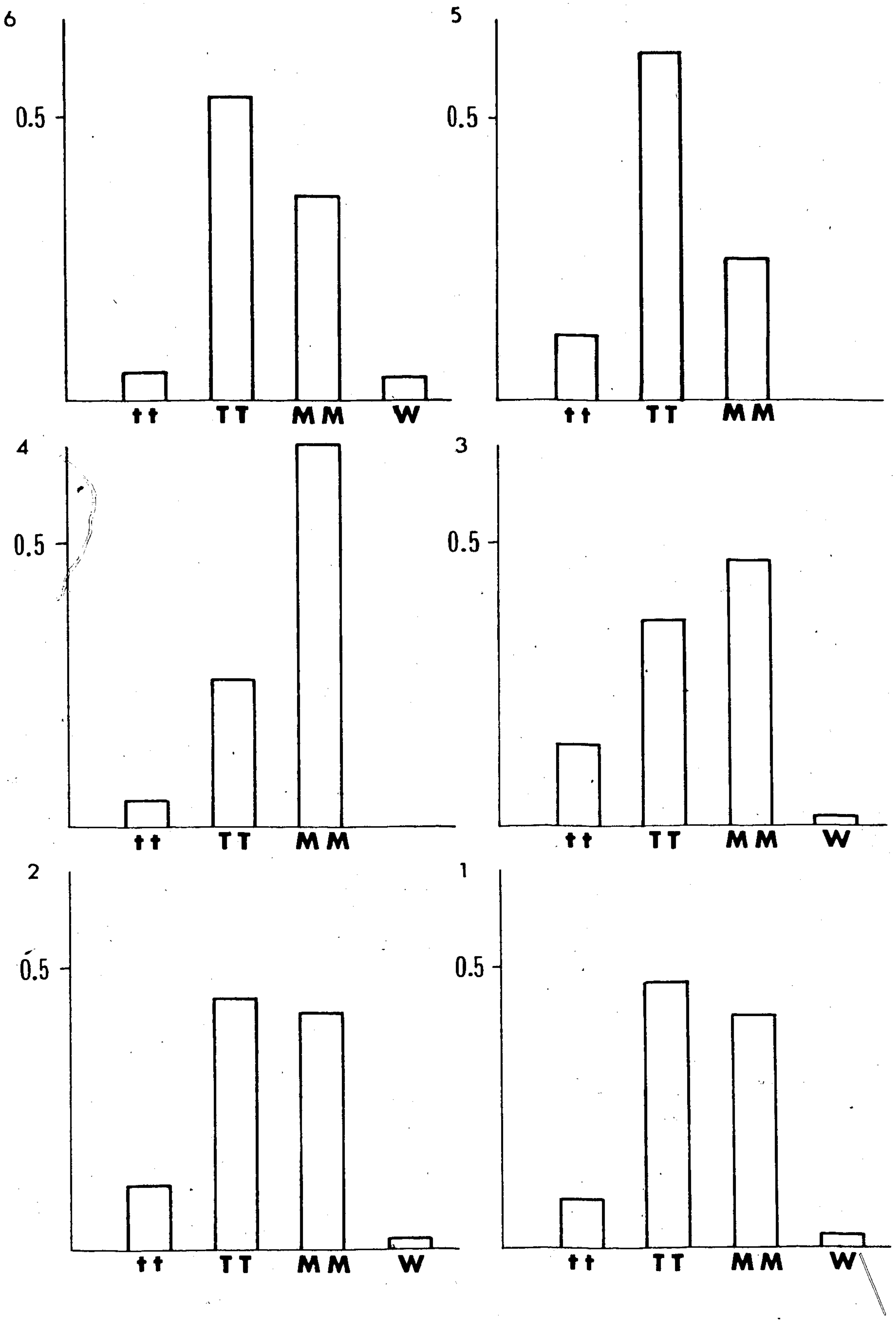
The fourth approach is to reconstruct the regional environments of the Old Crow Basin and adjacent areas. To my knowledge, this is the first time that macrofossil evidence alone is used on a regional scale for paleoenvironmental reconstruction. Six chronological/stratigraphical groups were formed from 65 assemblages out of 73 for the northern Yukon Territory. These are listed in Table 7. Some assemblages could not be used because there was no consensus about their age as there are several controversial time-stratigraphical models for the Old Crow Basin. These will be discussed later discussed in more detail. records and taxa for each group. What follows here is a synthesis of the ecological information each of the groups. The basis for this synthesis is the study of the bryophyte growth form distribution in the groups.

Table 7. Chronological assemblage groups of the northern Yukon Territory.

Assemblage Group	# of samples	# of records	# of taxa
6. Recent detritus	2	18	15
5. Postglacial peats	7	40	31
4. Late Old Crow Interval	11	40	21
3. Disconformity A	28	171	63
2. Mid-Section	13	115	52
1. Lower Lake	4	30	24

Appendix 2, summarizing all records of the northern Yukon, also indicates the predominant growth forms for all of the taxa recovered. This growth form classification is based upon that of Gimingham & Birse (1957) and Gimingham & Smith (1971), who suggested a descriptive system for the growth habit of terrestrial bryophytes, which they called growth form types. Their descriptions of bryophyte growth habits and my own observations of living populations in the field and dried herbarium specimens are the basis for the designation of the most common growth form or forms for each of the taxa listed in Appendix 2. The habit of a moss species is partially correlated with its strategy to obtain and retain the available water for growth (Birse 1958, Gimingham & Smith 1971). In northern or antarctic regions summer is short and favorable periods for growth are irregular. The growth form of the bryophyte will influence critically its survival. Such dense growth forms as small cushions, tall turfs with erect branches and small turfs are often effective in restricting water loss. The taxa with these growth forms are most commonly found in more exposed environments. Carpet forming species and large cushions are found in swampy areas that are provided with a permanent water supply. Tall turfs, having erect branches and loose structure, and thus relatively little influence upon water conservation, often grow in habitats with significant water evaporation stress and in more water-logged conditions (in the case of the rhizoidal form). Often other mechanisms (for example cuticularization, lamina and lamellae movement) are operating to restrict water-loss in these species. Most mat growers exhibit an extreme variability. Typically developed smooth and rough mats are never in contact with the water table (for example *Brachythecium* species). More robust forms approach carpets and are found in swampy habitats (for example *Drepanocladus* species). Plate 58 shows percentage histograms of the distribution of growth forms of the six groups. The eight different growth forms recorded for mosses in the northern Yukon (Appendix 2) are grouped together in three classes (small turfs, large turfs, mats and wefts). The proportion of each of these classes for the six groups is reflected in the height of the bars of the histograms in Plate 58. The percentages are calculated on the basis of the number of records. Records with two common growth forms are scored twice.

Plate 58. Percentage histograms of growth form distribution for the six assemblage groups of the northern Yukon Territory. tt = small turfs (t + to), TT = large turfs (Te + Trh + Td), MM = mats (Mr + Ms) and W = wefts (Gimingham & Birse 1958). For further explanation, see text.


6
0.5
tt
TT
MM
W
5
0.5
tt
TT
MM
4
0.5
tt
TT
MM
3
0.5
tt
TT
MM
W
2
0.5
tt
TT
MM
W
1
0.5
tt
TT
MM
W

Comparisons of differences and similarities among the growth form spectra (Plate 56) resulting in grouping the 6 assemblage groups into three stratigraphic zones (PLate 59). Zone I assembles groups one to three (the Lower Lake, Mid-Section and Disconformity A assemblages). Zone II is group 4 and Zone III are the postglacial autochthonous and detrital samples (groups 5 and 6). The differentiation of the zones is not only based on the growth form spectra, but also the relative amounts of rich fen, upland and aquatic indicators (see below), the type of assemblages and the preservation aspect of these assemblages (reflected in their mean reliability index). Table 8 lists the values for these parameters. In the remaining part of this section the three zones will be characterized. In Chapter V the vegetation history of the northern Yukon in relation to the history of Beringia will be discussed on the basis of these descriptions and the three other approaches.

Zone I, formed by the oldest assemblages, is the best documented. From it 316 records in 45 samples have been obtained and 85 different taxa are represented. Two thirds of the fossil assemblages oof this zone are transported. All the samples of the oldest group 1 of assemblages (group 1), the samples collected from the reworked Lower Lake Clays) consisted of transported detrital organics. The highest proportion of peats with an autochthonous aspect in Zone III were found in relation with Disconformity A. However, they were also transported as small blocks and deposited in features related to the hiatus.

Zone II has the lowest number of records and taxa. Most of the samples consist of a few transported, poorly preserved organics in a primarily mineral matrix of silts and sands. The mean reliability index of these samples was also lower than the index for the two other zones. Only group 4 constitutes this zone. It is clearly differentiated from Zone I below and Zone III above in the growth form spectra (Plate 58). by the dominance of mat growers and the absence of wefts. In Zone I the turfs (tt+TT) are dominant over the mats and wefts are always present. In Zone III the large turf growers (TT) are dominant and the mats contribute less than in Zone I.

Plate 59. Composite section through locality HH68-9, northern Yukon.

Assemblage Groups:

Zone III

6. Recent Detritus
5. Postglacial Peats

Zone II

4. Late Old Crow Interval

Zone I

3. Disconformity A
2. Mid-Section
1. Lower Lake

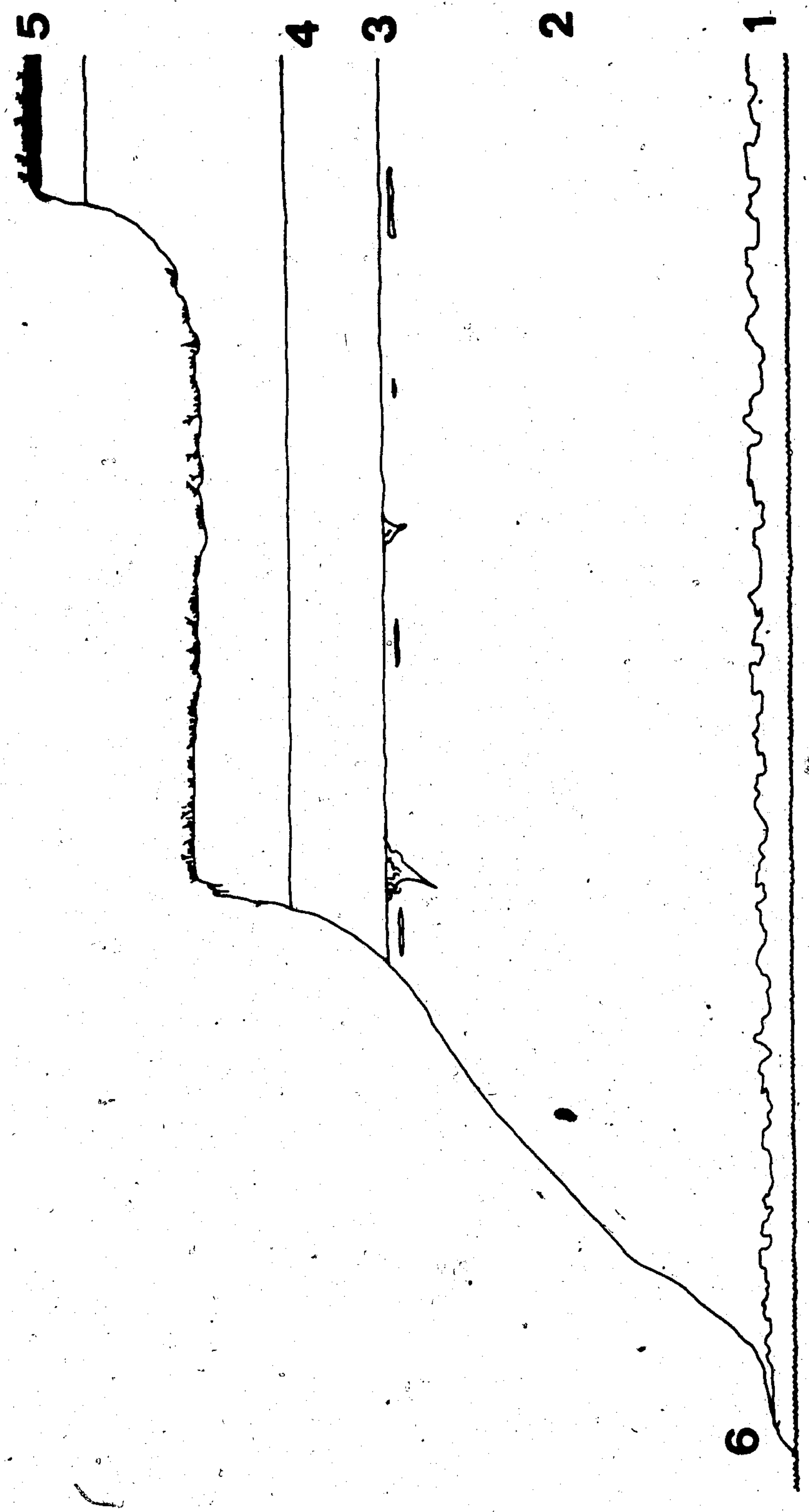

5
4
3
2
1
6

Table 8. Statistics for Zones I, II and III of the northern Yukon sequence.

	Zone I (Group 1 to 3)	Zone II (Group 4)	Zone III (Group 5 & 6)
Number of samples	45	11	9
Number of records	316	40	58
Number of taxa	85	21	41
Assemblage types			
% autochthonous	18 %	9 %	45 %
% mixed	15 %	9 %	22 %
% transported	67 %	82 %	33 %
Mean reliability index	45	42	52
Indicator Species			
% rich fen records	9 %	15 %	7 %
% aquatic records	5 %	5 %	2 %
% upland records	9 %	3 %	3 %

Zone III assembles two groups with completely different histories (groups 5 & 6). Group 5 consists of seven *in situ* peat samples, except for the oldest ones on top of the Upper Lake clays. These latter samples consist of reworked, coarse detrital organics deposited when the lakes were finally completely drained. Group 6 are present day detritus samples, collected on the river bars during the summer. The material was probably deposited during the spring floods of the same year. Notwithstanding this different origin of the deposits of Zone III, the growth form spectra are very similar (Plate 58). This leads to an important conclusion and the working hypothesis discussed in Chapter V. The preservation of Zone III samples was slightly better than for the other zones (see mean reliability index in Table 8). Forty-one different taxa are represented in this upper Zone III.

The identification of these three zones is not only the result of a comparison of the group growth spectra, but also based upon the relative abundance of indicator taxa (Table 8). These indicator taxa comprise upland, fen and aquatic species. Upland taxa are found exclusively in topographically high habitats and are most likely not found as living members of mire communities. Rich fen species are found exclusively in rich and extreme rich fens, characterized by a pH higher than 6.5 and a Ca^{++} concentration above 5 ppm (Sjörs 1950a, b, 1961a, b, 1963, Slack *et al.*, 1980, Miller 1980b). Two taxa are listed as aquatic mosses. The species classified as rich fen, upland or aquatic are indicated in Appendix 2. 15 % of the records of group 4 are from rich fen species. Together with the low representation of upland taxa, this supported the creation of Zone II for this assemblage group. Zone I is clearly differentiated from the two younger zones by the high incidence of upland taxa. Three times as many of its records are from upland species. Most of these are contributed by assemblage group 3 samples from the Disconformity, which is exceptionally rich in species. Zone III, the Holocene and present day assemblages, are the poorest in all three indicator species, having only half as many aquatics as the other, older zones.

Summary

All subfossil bryophyte fragments in the northern Yukon basins are derived from regional communities or *in situ* peats. Therefore, they can be considered reliable for paleoenvironmental reconstruction. Four approaches to paleoenvironmental reconstruction are utilized in the present study. One approach centers around species that are "incongruous" for the assemblages they occur in. A second approach deals with growth form and habitat modifications. Many well-defined modifications occur in the group of the Amblystegiaceae. These forms can be correlated with habitat features, primarily water level. Modifications also characterize some terrestrial bryophytes. In the case of *Hylocomium splendens*, use can be made of its differentiated forest and arctic-alpine forms. The third approach is to rely on the floristics of an assemblage to reconstruct local environments. Abundance and reliability measures are used to precisely define the conclusions. The fourth approach is a preliminary attempt at regional paleoenvironmental reconstruction. Assemblages are grouped in stratigraphic units. Growth form spectra and indicator taxa suggest similarities and dissimilarities among the groups. The groups outlined for the Old Crow Basin indicate the presence of three chronological zones. These periods suggest substantial landscape evolution in the Basin during Late Quaternary times.

V. SUBFOSSIL BRYOPHYTES and the CENOZOIC HISTORY of BERINGIA

A. Origin and early Tertiary Evolution

The Bering-Chukchi Land Bridge is a tectonic feature, correlated with plate tectonics, at least during most of its Tertiary and Quaternary history (Matthews 1979b, 1980b). During the Cretaceous the Pacific Kula Plate (now largely submerged), collided with the eastern Siberian, Beringian and northwestern North American platforms. This created early Tertiary fold belts along the collision line and made exchange of terrestrial biota between eastern Siberia and Alaska possible. This exchange was partly responsible for keeping the early, boreotropical Tertiary biota of Laurasia homogeneous. Prior to the Oligocene deterioration of climate, temperate broad-leaved deciduous forests were absent in the Northern Hemisphere. Most likely the early Tertiary forests were broad-leaved and evergreen, indicating the equability of the climate (Wolfe & Tanai 1980). Only in western Siberia were there significant water barriers to Holarctic dispersal during the early Tertiary. These were probably a connection of the southern Tethys Sea with the Arctic Ocean along the 65° meridian (Matthews 1980b). During the Eocene, the North American-Greenland plate drifted away from the Eurasian plate, breaking up Laurasia and connecting the Atlantic with the Arctic Ocean.

B. Miocene

By the Miocene, Beringian (Siberian), mid-continental North American and European biota had clearly differentiated from each other. This was a reflection of the disruption of Holarctic dispersal, which was caused more by world climatic deterioration than by sea barriers. During the Oligocene an abrupt cooling broke the connections of the broad-leaved evergreen forests over Beringia (Wolfe 1978) and the warmer middle Miocene did not restore any homogeneous biota with a Holarctic distribution. The existence of a circumpolar, homogeneous, Miocene Arcto-Tertiary Geoflora is now considered very controversial (Wolfe 1978, Wolfe & Tanai 1980). The Arcto-Tertiary Geoflora was defined by Chaney (1947) as an uniform, early Tertiary (at that time considered Eocene) temperate deciduous hardwood forest, very similar to the southern mixed mesophytic forest of the eastern United States. However, most of Beringia was too cool for mixed-mesophytic forest during the middle Miocene optimum and and it appears that the vegetation was not uniform. Since no physical barrier to Holarctic dispersal existed during this epoch (the Bering Strait was not yet formed and the Atlantic was in its early spreading stage), it seems that climate must have been the major factor contributing to the observed differentiation of the late Tertiary North American and Eurasian biota (Matthews 1980b). Wolfe & Tanai (1980) concluded that north of 65°, Beringia was covered by a rich northern coniferous forest, containing many more elements than the present taiga. It was dominated by Pinaceae (*Pinus, Picea, Tsuga, Abies* and *Larix/Pseudostuga*). The broad leaved genera were diverse and included *Betula* (dominant), *Fagus, Quercus, Carya, Pterocarya/Cyclocarya, Ulmus, Populus, Salix* and *Symphoricarpos*. Farther north the forest became totally coniferous. To the south there was an ecotone with the mixed northern hardwood forest or possibly a mixed mesophytic forest. The following genera occurred in these forests: *Metasequoia, Ulmus, Alnus, Fagus, Quercus, Carya, Pterocarya, Populus, Salix, Liquidambar, Platanus, Juglans, Betula, C*[illegible]*/Carpinus, Tilia, Acer, Ilex, Elaeagnus* and *Nyssa*. Still farther south the warmer elements, including *Lindera, Cercidiphyllum, Berchemia, Pterocarya* and *Cocculus*, were present in large numbers. The coastal area of southern Alaska was occupied by coniferous forest (Pinaceae dominated). Broad leaved members of this coastal forest were *Populus, Salix, Pterocarya, Alnus, Betula, Fagus, Ulmus* and *Acer*.

Traditionally (Chaney 1947, 1959), species in a fossil flora are assigned to an element (such as the Arcto-Tertiary element). These elements represent the region where the species originated. It is thus significant to consider to which elements the middle Miocene Alaskan assemblages belong because these elements comprise the flora that has been the basis for the Arcto-Tertiary flora, which in turn has been regarded as the type flora for the mixed mesophytic forest. Wolfe (1978) indicated that broad leaved deciduous forests appeared for a short period of time at middle and high latitudes of the Northern Hemisphere after the Oligocene deterioration. He listed two major sources for the components of these forests: (1) pre-adapted lineages present in the broad leaved evergreen forests prior to the climatic deterioration and (2) elements of the high elevation temperate coniferous forests that moved downslope. Three source areas are known for the components of the middle Miocene mixed northern hardwood deciduous and mixed mesophytic forests; thus, there are three elements, the East Asian, the West American and the Beringian (high latitude origin). For example, *Cercidiphyllum* and *Zelkova* are considered East Asian, *Ulmus, Carya*, and *Acer* West American and *Metasequoia, Fagus*, and *Salix* Beringian. Although some of these genera are no longer native to the area of the element they are assigned to, they are considered to belong to the element because they were present in the area before the Oligocene deterioration.

A fossil bryophyte species, discovered in Late Pleistocene sediments in the northern Yukon, could have some implications for the reconstruction of the Tertiary history of eastern Beringia (Janssens & Zander 1980, Bryological Reports 174 & 370). Even though there is no evidence of the presence of *Leptodontium flexifolium* in northwestern North America in late Tertiary times, Janssens & Zander concluded that this moss probably was a relict of the extensive Tertiary flora with subtropical affinities. *Leptodontium flexifolium* is found presently in oceanic-montane areas of Central and South America (Andes), in Europe, Africa (Cameroun, Zaire, Kenya), the Himalayas, China, Formosa, Japan, southeastern Asia and Hawaii. In the tropics and subtropics it occurs at high elevations, usually above 2000 m. In western Britain, *L. flexifolium* grows at places below 300 m elevation (Dickson 1973). North American stations are situated in Mexico, Arizona, New Mexico and North Carolina with the southern Appalachian populations restricted to the *Picea-Abies* zone above 1370 m elevation. Several other members of the Pottiaceae have similar disjunctive patterns of distribution. For example, the distribution of *Bryoerythrophyllum jamesonii* (Tayl.) Crum is basically Andean-Himalayan with only one New World station north of the Mexican-United States border (British Columbia: Queen Charlotte Islands, *Schofield 15257*, (UBC)) and it is present otherwise in Scotland, China, India, Tasmania and New Zealand (Zander 1979b). *Pterygoneurum lamellatum* (Lindb.) Jur. (Steere 1979) and *Molendoa sendtneriana* (B.S.G.) Limpr. (Zander 1976) show large arctic-temperate North American disjunctions while other species, for example *P. subsessile* (Brid.) Jur. and *Tortula bistratosa* Flow., have similar distributions, but with Cordilleran intermediate stations.

One explanation of the disjunctive pattern of *L. flexifolium* is that the distribution range was established in the north during early and middle Tertiary times. A

Mesozoic dispersal is very unlikely, considering that the only well known fossil bryophytes from that era are all extremely different from any of the now extant species. Only during the Paleocene, Eocene and early Oligocene periods, which were characterized by long periods of warm and equable climate (Leopold & MacGinitie 1972, Wolfe 1972, 1978, Janssens *et al.* 1979), were most species, or more likely their progenitors, capable of spreading over the North American continent. Later, drastic tectonic changes (for example orogenesis and vulcanism) and, most importantly, correlated climatological changes starting with the Oligocene deterioration and culminating in the glaciations of the Pleistocene, apparently broke up the formerly continuous distributions, selected pre-adapted species, segregated them in new vegetation units and restricted many populations to small refugial areas. The range of some species, including *L. flexifolium*, became very restricted and some taxa presumably became extinct in the more northern areas. *Leptodontium flexifolium* survived, apparently at least until the Wisconsinan, in the Old Crow Basin. It is quite possible that a living population of this species will be collected somewhere in northern North America in the future.

A more detailed reconstruction of the dispersal history of *L. flexifolium* can be proposed when its narrow autecological requirements are considered. The species is found in Hawaii, which indicates long-distance dispersal is possible and has happened at some time since the Miocene period. However, long-distance dispersal from Central America to the Yukon Territory during Wisconsinan time is considered very unlikely. Propagula of *L. flexifolium*, being larger and probably not as drought resistant as many diaspores of the species discussed by van Zanten (1978), are not likely to be transported northward by air currents from Central America. Dispersal by any of the many species of waterfowl migrating from the Gulf of Mexico area to the north is much more likely (Bellrose 1976). Several routes are in existence now (as well along the West Coast and over the continent) and it is apparent that similar migration patterns could have existed during Tertiary times, and the interglacial and interstadial periods of the Pleistocene. Recent studies of migration of waterfowl in northwestern North America (D.A. Boag, Department of Zoology, University of Alberta, personal communication) suggest that transportation by birds of wind-blown material floating on the water surface of lakes and ponds is much more frequent than was formerly thought. These studies have also shown that distances as great as 1500 km can be covered by waterfowl in 13 hours in exceptional situations (in this case during storm weather from Banks Island to northern Alberta). Birds follow the slow, northward transgression of the 1° C isotherm through the United States and southern Canada and the last northern leg of their spring migration flight is non–stop in contrast with the slow northward migration earlier.

Based on these recent findings and assuming no drastically different migration behaviour for birds during the Cenozoic, the following hypothesis for the distribution pattern of *L. flexifolium* in North America is proposed as the most likely: during Tertiary times before the strong aridification of western North America, mesophytic broad leaved deciduous and coniferous forests extended up to southern Alaska (Wolfe 1978). The equability of the climate and its strong oceanic aspect made it possible that the species could have had a more or less continuous distribution up to 60° latitude in habitats' similar to the ones found much farther south at the present time. The Old Crow Basin itself (at 68°) was inside the rich coniferous forest belt. However, the very unique character of the basins in the northern Yukon Territory (sheltered from the Arctic Ocean, with a strongly continental climate but abundant residual lakes and waterlogged organic substrates) made them a likely stop–over and breeding area for waterfowl (Bellrose 1976, p. 544). It is evident that we have no idea yet when the dispersal of the moss actually took place, but it is more likely to assume dispersal from hypothetical Tertiary now extinct southern Alaskan populations than from the extant Central America populations. It was also present in the northern Yukon before the formation of Disconformity A (Bryological Report 370).

C. Late Miocene and Pliocene

The rich coniferous forest in northern Beringia is of central significance with respect to the development of present subarctic and tundra biomes. The near absence of late Tertiary deposits in Canada is the cause of the tentative aspect of the reconstruction of the boreal life zone history in continental North America (Matthews 1979b, p. 54, fig. 2.6c). However, macrofossils from the Miocene–Pliocene Beaufort Formation of the northwestern Arctic Archipelago (from 73° to 83° N.) were studied by Hills (1975), Kuc &

Hills (1974), Kuc (1973e) and Matthews (1976b). The Beaufort Formation is a coastal plain deposit along the northwestern fringe of the Arctic Archipelago, extending from Banks Island in the south to Axel Heiberg Island in the north. The oldest deposits on Axel Heiberg Island (81° N.) indicate that hardwood forest elements were present during that epoch. Later, during the late Miocene, the mixed hardwood–coniferous forest ecotone extended as far north as Banks Island (73° N.). The oldest assemblages of subfossil bryophytes in North America are known from this island and these indicate a boreal forest vegetation (Kuc & Hills 1971).

The mosses in the Beaufort Formation deposit on Banks Island were recovered from a woody sapropel of fluvial origin. The moss fragments were deposited in a moderately minerotrophic pond (*Nuphar, Potamogeton, Sphagnum teres* and *Drepanocladus exannulatus*), surrounded by rich fens (*Meesia triquetra, Calliergon giganteum, Drepanocladus revolvens, Scorpidium scorpioides* and *Tomenthypnum nitens*). A few fragments of *Thuidium abietinum* indicated that nearby there were drier upland communities. Cones of *Picea banksii* (presumed progenitor of *Picea glauca*), *Pinus* and *Larix* were associated with the peat (Kuc & Hills 1971).

During the Miocene–Pliocene transition Meighen Island (80° N) was the site of an open woodland tundra with a circumpolar tundra zone in existence only at the end of the Pliocene (see below). Kuc (1973e) identified 44 mosses and one liverwort from a black peat layer exposed south of the Meighen Ice Cap. The bryophytes were associated with sharp angled (indicative of minor transport) fragments of wood (*Larix* and *Picea, Carex* and leaf fragments of *Salix* and *Dryas*). The age of the peat is now estimated to be late Miocene or Early Pliocene (J.V. Matthews, Jr., personal communication). Mosses with an extensive boreal distribution were found in the assemblage. They are still widespread in the Arctic Archipelago, but are generally more abundant in southern parts of the Arctic and subarctic areas. The typical forest form of *Hylocomium splendens* with sympodial branching was present, as well as the tundra form (mondpodial branching). Fragments of *Drepanocladus uncinatus* are well developed with strongly plicate leaves, as in the typical mesic form. Other taxa of this group are *Polytrichum juniperinum, Aulacomnium palustre, Drepanocladus revolvens, Bryum pseudotriquetrum, Meesia uliginosa* and *Thuidium abietinum.* The latter is found in xeric habitats and was part of the upland component in the mixed assemblage. Mainly boreal taxa, presently very rare in Arctic areas, were *Paludella squarrosa*, *Sphagnum recurvum* and *Pleurozium schreberi*. Not yet in the High Arctic at present, but recovered from the late Tertiary deposits, are *Climacium dendroides* (Horton & Vitt 1976), *Dicranum leioneuron* (restricted to the Canadian Maritime region, Peterson 1979) and *Pseudobryum cinclidioides*. Species that presently have a mainly arctic–alpine distribution are very abundant in the assemblage. Examples are *Calliergon richardsonii*, *Hypnum hamulosum*, *Cyrtomnium hymenophyllum*, *Cinclidium latifolium*, *Myurella tenerima*, *Philonotis fontana*, *Pogonatum alpinum*, *Timmia austriaca* and *T. norvegica*. This clearly mixed assemblage indicates a mosaic of subarctic forest and open fens, physiognomically very similar to the present day vegetation of the Old Crow region. The presence of arctic–alpine taxa in this assemblage and the absence of any indications of evolution or speciation supports the hypothesis that present tundra elements were already growing in late Tertiary alpine and open woodland habitats and were pre–adapted to open, exposed environments. All the subsamples of the peat indicate a very low abundance of *Sphagnum* material. This is in contrast with abundant *Sphagnum* remains in Holocene subarctic assemblages from the Old Crow region. If future studies of the Beaufort Formation or other high latitude late Tertiary samples confirm this near absence of *Sphagnum*, it may be possible that factors other than climate strongl[illegible]ited the present distribution of the genus in the High Arctic. Vitt & Pakarinen (1977[illegible]d out for the first time that *Sphagnum* is much more common in the Subarctic zone than in the High Arctic.

During the late Miocene the northern Alaskan forests were coniferous (Wolfe & Hopkins 1967). Evidently, no continuous tundra biome existed around the pole at that time. Peneplanation of the land bridge occurred during the entire Tertiary. The Bering Strait, and the Bering and Chukchi Seas were formed until the end of the Pliocene (3.5 ma). At that time the Arctic Ocean froze over, tundra migrated south and Siberian tundra areas were united with those in North America in northern Beringia. Plant and beetle macrofossil studies (Hills 1975, Matthews 1976b, 1977) indicate continuity of tundra biota over Beringia for the first time. The circumpolar extent of tundra coincided or shortly pre–dated the formation of the Bering Seaway. In addition to the boreal elements, described above, steppe elements also were clearly present in North America during

Pliocene time (Webb 1977). Thus, the diversity of biomes in Beringia was greater at this time than at any other. In the north an ever increasing coastal and lowland tundra became firmly established and circumpolar. The Pliocene climatic changes and the inland continental aspect of Beringia made it possible for steppe elements to expand from central Siberia into inland Alaska and from the drying Southwest of North America to the north (see below). The former Miocene, rich coniferous forest became isolated on the two continents and this induced faunistic and floristic differentiation in the remaining southern Alaskan forest (Wolfe & Tanai 1980). *Pinus* still extended its range farther north than at present during the Pliocene–Pleistocene transition (Westgate *et al.*, in preparation). *Sphagnum lenense* and *S. magellanicum* were associated with these trees in east central Alaska (Bryological Reports 357 & 359). Pine does not reach the Lost Chicken area at the present time (Plate 2) and its range only overlaps with the range of *S. lenense* in the southern Northwest Territories. Another possible explanation for the presence of *S. lenense* in a *Pinus* woodland is a shift in habitat requirements of the moss. However, if one infers evidence based on morphological features, then that is not the case. Present day populations of *S. lenense* are indistinguishable from the subfossil material of the Lost Chicken site.

It appears that *S. lenense* survived glaciation as a Beringian element and perhaps also in some hypothetical refugium of limited temporal and spatial extent in eastern North America. It appears not to have expanded its range south or north after the last glaciation. *Pinus*, on the other hand, survived primarily in the vast refugium of the south and succeeded in reaching northward halfway to the Mackenzie system during the Holocene period.

During the Pliocene, Northern Hemisphere glaciations began (Guthrie & Matthews 1972, Matthews 1974a, 1979b, 1980b, Repenning 1980). Boreal elements were still present in western Alaska. The Cape Deceit Formation, exposed near Deering on the north coast of the Seward Peninsula, is at least 1.5 million years old. Besides the Lost Chicken samples, it is the oldest material I have worked on. Except for one (Bryological Report 341), all samples contained very poorly preserved bryophytes (Bryological Reports 332, 340, 345 & 346). The better preserved moss fragments of the Formation were accumulated among other detritus in a pond. Rich fen elements form the dominant component in the transported assemblage. *Hylocomium splendens*, *Eurhynchium pulchellum*, *Amblystegium serpens*, and *Larix* needles and cone scales suggest that treed communities were in the vicinity. As with the Coleoptera and mammal remains, the botanical evidence indicates the presence of subarctic tundra and an adjacent *Larix* tree-line. No phyletic evolution is evident in any of the plant macrofossil remains.

D. Summary of the Tertiary History

Beringia originated in the late Cretaceous. It was gradually peneplaned during the Tertiary. By Pliocene times the Bering Strait had fo[illegible] is thus evident that during the Tertiary there was ample opportunity for exchange of terrestrial biota between northeastern Asia and northwestern North America.

Climatic fluctuations, which began during the Late Eocene, induced differentiation in the holarctic boreotropical zone. Rich coniferous forest was present in Alaska during the middle Miocene optimum. South of the coniferous forest extended the mesophytic deciduous hardwood and coastal coniferous forests along the west coast of northwestern North America. The presence of *Leptodontium flexifolium*, a possible member of such a flora, in the northern Yukon during the Pleistocene (Plate 4), might have been the result of earlier dispersal of this species from the southern Alaskan forest.

Open woodland tundra on Meighen Island, north of eastern Beringia, is the first indication of the development of tundra during the Miocene-Pliocene transition. The formation of the Bering Strait coincided with the isolation of the eastern Siberian and western North American coniferous forest in Beringia and with the first circumpolar extent of this northern tundra. Steppe elements were introduced from Siberia and southwestern North America during the Pliocene. At the time of the onset of glaciations some boreal elements extended still farther west in eastern Beringia than at the present time.

E. Pleistocene

Introduction

By the onset of Pleistocene glaciations all true boreal elements had disappeared from the Arctic Archipelago and the interglacial sites studied contained indications of a tundra life zone. The present boreal and arctic biota can be traced back to floras and faunas of the Miocene. The primary effects of the Pleistocene glaciations were progressive impoverishment and recombination of those late Tertiary floras.

Paleoenvironmental studies in eastern Beringia, summarized and reviewed by Hopkins (1967, 1972), Morlan (1979), Matthews (1979b, 1980b), Ritchie & Cwynar (1979) and Schweger (1979), indicate that the region was not a refugium for the boreal and arctic vegetation *per se* (see for example Heusser 1967) of Canada and Alaska, but for many floristic elements of their biota. Present day boreal vegetation associations and their associated fauna were completely absent during the Late Wisconsinan. In addition, many of the tree taxa have not left any record and probably did not survive in the Beringian Refugium at all.

The most commonly reconstructed biome in Beringia, unique for Late Pleistocene time during glaciations, has been named tundra-steppe (Hopkins 1972), arctic-steppe (Matthews 1976c) or mammoth-steppe (Guthrie 1979). Pollen studies in Alaska and the Yukon Territory (Ager 1975, 1977, 1979, 1980, Colinvaux 1964, 1967a, b, c, 1973, Colbaugh 1968, Heusser 1963, 1967, Livingstone 1955, 1957, Matthews 1974a, b, Rampton 1971, Ritchie 1977, Ritchie & Cwynar 1979, Schweger 1976, 1979, Schweger & Janssens 1980) indicate that eastern Beringia was drier than the now existing alpine or lowland tundra in the area. Abundance of *Artemisia* pollen is the most commonly cited argument to support this steppe feature. Several grazing animals (*Bison, Saiga*, horse, mammoth) were the dominant faunal elements. However, Schweger & Habgood (1976), Matthews (1974b, 1976c), Ritchie (1977) and Ager (1979) indicated that neither grassland nor arctic-steppe was the predominant vegetation-type of Beringia, but that the landscape was a much more complex vegetation mosaic in which dry grassy habitats were widespread. This dryness was caused by the extreme continental aspect of the vast land bridge area and is also the main reason for the limited glaciation of Beringia.

Pre-Wisconsinan

The continentality of the glacial climatic episodes of the Pleistocene became manifest during the deposition of Unit 2 of the Cape Deceit Formation (Matthews 1974a). These sediments are of Early Pleistocene age. No well preserved bryophyte assemblages were recovered from these deposits (Bryological Reports 333 & 352). A slightly colder and clearly drier regional climate from the climate inferred from the above discussed Unit 1 was suggested by the near absence of bryophyte macrofossils, the accumulation of wind-blown silt, the abundance of *Artemisia, Carex* and Gramineae pollen, and by the low counts for *Betula* and *Alnus* pollen.

Interglacial warm floras are indicated by peat assemblages of the Deering Formation (Matthews 1974a) at Cape Deceit (Bryological Reports 335, 342 & 350) and by the Stewart River sample (Bryological Report 4) in the southcentral Yukon.

The climate was warmer than at present during the Kotzebuan (a pre-Illinoian interglacial) near Deering on the Seward Peninsula. The few, but perfectly preserved bryophyte fragments recovered are taxa associated with minerotrophic fens (*Aulacomnium palustre, Brachythecium turgidum* and *Campylium stellatum*) or found in shaded, forested habitats (*Drepanocladus uncinatus*, the well developed mesic form with strongly plicate stem leaves and well preserved branching). The rich fens and woody peat (both *Picea* species and arboreal *Betula*) and the presence of some Coleoptera tundra elements (Matthews 1974a) suggested a forest-tundra ecotonal region. The same taxa have not yet reached the area again during the present Holocene warming trend. Macrofossils of *Picea* have been found, although the low pollen accumulations of this species suggest a marginal climate for this tree.

No preserved bryophytes could be recovered from Sangamonian Interglacial sediments at Cape Deceit. However, one sample from the Stewart River locality, Yukon, can be assigned to this period. The sediment is a pure *Hylocomium splendens* peat, formed in a well developed *Picea* forest. It contains abundant spruce needles and twigs and the remains of several large-leaved dicots. The moss is clearly sympodially branched.

Wisconsinan

The best documented glacial period is the Wisconsinan. Abundant samples from the localities in the Old Crow Basin and adjacent areas were analysed for subfossil bryophytes (see Chapter IV). Three distinct zones were discovered throughout the exposed sequence. Comparison of the two groups of recent assemblages (group 5 and 6) in Zone III is the basis for the following working hypothesis. The similarity between growth form spectra of bryophyte assemblages of these postglacial *in situ* peats and recent river bar deposits (group 6 and 5) suggest that the alluvial detrital material strongly reflects the regional communities giving rise to *in situ* peat deposits. One assumption had to be made before this working hypothesis could be formulated: that the material contributing to the recent river bar deposits was mostly derived from postglacial peat exposures. Considerable experience with allochthonous samples has proven that this assumption is true. The postglacial peats are the only extensive organic deposits exposed to river action in the basins and their texture and buoyancy enable them to be carried longer distances as compacted organic blocks. On the other hand, the fluviatile allochthonous deposits, which constitute most of the other, older organic sediments, will break down more easily to numerous small fragments and the probability that bryophytes of this material will be reworked for the second time as recognizable fragments is much smaller. Based on this working hypothesis and by comparing the growth form distribution in Plate 58, I concluded that the bryophyte vegetation in the northern Yukon was very different during deposition of Zone II sediments. In addition, the communities that were present during the latter period can be clearly differentiated from those of the earlier period (Zone I). Also, there is a distinction between Zone I and Zone III growth form distribution, suggesting a different vegetation cover. Detailed discussion of the communities in relation to the vegetation history of Beringia follows later in this chapter.

First it has to be contemplated if the differentiation of these zones could be caused by selective preservation and that the differences in growth form distribution seen among the three zones are not just a manifestation of the over-representation of Amblystegiaceae. Several arguments can be used to reduce this concern to its relative importance. Table 9 indicates the preservation aspect of the assemblage groups by listing the mean of their composite reliability index. As pointed out before (Materials and

Table 9. Mean and ranges of the composite reliability index for the six assemblage groups of the northern Yukon samples. The proportion of autochthonous samples in each group is also given.

Zone	Group	Proportion of authochtonous samples	Range and mean of composite reliability indices
III	6	0 %	(42)-44-(46)
	5	57 %	(37)-60-(80)
II	4	8 %	(10)-42-(71)
I	3	21 %	(5)-47-(81)
	2	15 %	(20)-45-(75)
	1	0 %	(31)-44-(59)

Methods), the composite reliability index of an assemblage has made it possible to compare objectively the preservation among different assemblages. The slightly lower preservation for Zone II assemblages can not cause the drastic differences in growth form distribution. The only correlation seen in Table 9 is between assemblage type and preservation. Autochthonous samples are better preserved. No significant decrease correlated with age can be observed. After analysing many assemblages in North America, it has become clear that there exists no correlation between age and preservation of Quaternary samples. Actually, the best preserved subfossil bryophyte material is found in unconsolidated sediments of the Beaufort Formation, exposed on the northwestern coast of the Canadian Arctic Archipelago. The Formation is now considered to be of Miocene-Pliocene age. Pliocene-Pleistocene material from the Lost Chicken locality in Alaska (2,000,000 to 3,000,000 years old) is exceptionally well preserved also and it has been possible to identify specimens of *Sphagnum* at the species level (Westgate *et al.* in preparation, Bryological Report 357 and the discussion on *Sphagnum lenense* in Chapter III).

A group of bryophytes which appear to be under-represented in both Zone II and III are the upland species (see Table 8). This is partly caused by the classical effect, known in pollen analysis, and in vascular plant and insect macrofossil analysis, that more taxa are found when larger samples are investigated. However, a 10 % contribution of upland taxa in the small Lower Lake Clay assemblage group 6 is in line with the high value for these indicator taxa in the other Zone I assemblage groups. Therefore, I have concluded that selective preservation, based on the two considerations discussed above, can not be the cause of the differentiation among the three zones.

It is appropriate now to consider again the value of subfossil bryophytes for paleoenvironmental reconstruction. Reconstruction of local communities is important in a comprehensive review of the vegetation and landscape evolution (Miller 1980c). In addition, it influences, illustrates and adds evidence to taxonomic and phytogeographic concepts (Janssens & Zander 1980). Speciation rates and evolution in most groups of bryophytes is suggested to be slower than in vascular plants and some successful animal groups (Anderson 1963). Seven extinct fossil species were described from Quaternary deposits in North America (Steere 1942, Grout 1917, Williams 1930, Kuc 1974a). These taxa are members of the Amblystegiaceae and Brachytheciaceae. Most species in these families are known for their extreme phenotypic plasticity. Except for *Calliergon aftonianum*, all the extinct taxa have been considered by Kuc (1974a) to be forms of extant species of *Calliergon*, *Drepanocladus* and *Tomenthypnum*. In Chapter III, I have recognized *Calliergon aftonianum* as a distinct form of *C. richardsonii* (see Chapter III). The absence of any extinct forms of mosses contrasts sharply with the Pleistocene fossil record of mammals (Martin & Wright 1967), but is similar to the situation with insects (Matthews 1980b).

However, bryophytes are not good indicators of macroclimate (Miller 1980c). They can occur in isolated sites, far from their normal range of distribution (Billings & Anderson 1966, Steere 1965, Janssens & Zander 1980) because they occupy microenvironmental niches with rather uniform and stable microclimatic influences. Examples in the subfossil record are *Leptodontium flexifolium* (Janssens & Zander 1980) and *Sphagnum lenense* (Westgate *et al.* in preparation).

It is necessary that a complete reconstruction, on a regional scale, of past environments cannot be based on the bryophyte component alone (Matthews 1974a, Miller 1980c), but must incorporate as well information from pollen, insect and other macrofossil analyses. However, data from these sources are not yet available for the northern Yukon (Hughes *et al.*, manuscript in preparation). Thus, the following reconstruction of the vegetation history of the Old Crow Basin and adjacent areas is based primarily on the bryophyte data. Table 10 correlates the major Wisconsinan events in the Old Crow Basin, Silver Creek, Hungry Creek, Brooks Range and some less important areas from which subfossil bryophytes are known. It also gives a time frame and a tentative time-stratigraphical model (based on Hopkins 1981). This table can be referenced frequently during the following discussion.

Zone I is the best documented. The similarity of the assemblage groups throughout this Zone has lead me to support the hypothesis that the sequence from the top of the Lower Lake Clays to Disconformity A reflects one period of rapid accumulation of sediments (Morlan 1977b & 1978b). The presence of the same modification (see Chapter III) of the rare fossil *Leptodontium flexifolium* at Disconformity A and 9.5 m below it strenghtens this assumption. If the Lower Lake Clay

Table 10. Correlation chart of eastern Beringian Wisconsinan and Holocene localities

Dates (years BP)	Time-Rock Units	northern Yukon	Silver Creek	Hungry Creek (a) North Fork Pass (b) Snake River (c)	Brooks Range
0 8000-9000	Holocene	Zone III Assemblage Group 5 (Assemblage Group 6) mesic tree-line area *Sphagnum* growth increases during Holocene intermediate rich fens dry calcareous upland		(a) rich fens dry calcareous upland *Picea* by 8700 BP	forest communities minerotrophic fens calcareous upland tundra
9000 25,000	Late Wisconsinan (Upper Lake Clays and reworked top, Itkillik II)	sterile clays		(b, c) dry upland tundra intermediate fens	mesic tundra minerotrophic fens dry calcareous upland
25,000 40,000	Late Old Crow Interval (Middle Wisconsinan, Boutellier non-glacial interval in S. Yukon)	Zone II Assemblage Group 4 cold dry only bryophytes in rich fens *Carex*-moss meadow tundra in lowlands	tundra meadow and steppe	(a) *Picea* forest survives dry calcareous uplands fens	

Table 10. (Cont'd)

Dates (years BP)	Time-Rock Units	northern Yukon
40,000 65,000	Early Old Crow Interval (Middle Wisconsinan, Itkillik I/II	Zone I Assemblage Group 3 Disconformity A optimal rich fens, treed mires, lakes, numerous upland taxa, numerous forest indicators, arctic-alpine species
>65,000	Gold Hill Interval (Early Wisconsinan, Itkillik I)	Zone I Assemblage Group 2 Mid-Section warm rich fens and treed mires lacustrine habitats, few upland taxa, arctic-alpine species, forest indicators
		Zone I Assemblage Group 1 Lower Lake Clays cool rich and intermediate fens lacustrine habitats arctic-alpine species and upland taxa

in the southcentral Old Crow Basin localities is Illinoian, there has to be a major hiatus between it and the detrital organics on top of this clay. However, no other hiatus has been apparently observed throughout the sequence below Disconformity A (Matthews, personal communication). The major time-stratigraphical models applied to the Old Crow Basin will be discussed in the last section of this chapter.

The Lower Lake Clay assemblages form the oldest group of Zone I and of the total sequence. They consist of coarse detrital organics, incorporating charcoal, *Potamogeton* seeds, *Picea mariana* cones and large wood fragments with sharp edges but no bark (which indicates moderate transport). The rich and moderately minerotrophic fen bryophyte component is dominant in these assemblages (Appendix 2). It is best represented by numerous well preserved fragments of *Calliergon giganteum*, *Drepanocladus sendtneri*, *Scorpidium scorpioides* and *Tomenthypnum nitens*. Less abundant elements of [illegible] component are *Dicranum groenlandicum*, *Meesia uliginosa*, *Aulacomnium palustre*, *Calliergon richardsonii*, [illegible], *Drepanocladus aduncus*, *D. exannulatus* and *Hypnum pratense*. Well preserved fragments of *D. crassicostatus* suggest that some of the peat reworked in the assemblages was formed in pools or lakes. Upland taxa, or species growing in exposed habitats are represented by *Ceratodon purpureus*, *Tortella tortuosa*, *Aulacomnium turgidum* and *Polytrichum algidum*. Other mosses with a distribution clearly centered in the arctic regions and less common in the boreal zone were *D. badius* (Plate 18), *Drepanocladus lycopodioides* var. *brevifolius* (Plate 36) and *Campylium stellatum* var. *arcticum*.

The same species of the fen component, except *Meesia uliginosa*, are represented in the Mid-Section (Assemblage Group 2). However, several other taxa representing this latter component have been found: *Bryum pseudotriquetrum*, *Meesia triquetra*, *Catoscopium nigritum*, *Campylium stellatum* var. *stellatum*, *Cratoneuron filicinum*, *Drepanocladus capillifolius*, *D. fluitans*, *D. tundrae*, *D. vernicosus* and *Scorpidium scorpioides*. The aquatic species is still *D. crassicostatus*. *Polytrichum algidum* is absent from the upland component, but several other species were recovered: *Tortula ruralis*, *Trichostomum arcticum*, *Encalypta* species and *Thuidium abietinum*. In addition to *Campylium stellatum* var. *arcticum*, poorly preserved fragments of *Hygrohypnum polare* and *Trichostomum arcticum* indictate the presence of arctic species. A scarce component not present in the Lower Lake Clay assemblages is composed of species growing in mesic, often shaded and forested habitats: *Distichium capillaceum*, *Ditrichum flexicaule*, *Mnium* species, *Pohlia* species, *Campylium hispidulum*, *Eurhynchium pulchellum* and *Orthothecium strictum*. *Sphagnum* is represented by *S. magellanicum* and *S. centrale*. Both species are often found in treed mires with relatively minerotrophic conditions.

Assemblage Group 3, the uppermost samples of Zone I, are from the Disconformity. They consist of detrital organics which accumulated in erosion features (such as ice-wedge pseudomorphs). The minerotrophic fen species in these assemblages are *Bryum pseudotriquetrum*, *Plagiomnium ellipticum*, *Catoscopium nigritum*, *Helodium blandowii*, *Calliergon giganteum*, *Drepanocladus lycopodioides* var. *brevifolius*, *D. sendtneri*, *Scorpidium scorpioides*, *Tomenthypnum nitens* and *Hypnum pratense*. In addition to *D. crassicostatus*, the very rare aquatic *Calliergon megalophyllum* is also represented, indicating lake habitats. Numerous upland species were recovered (Plate 58), such as *Dicranella varia*, *Barbula acuta*, *Bryoerythrophyllum recurvirostrum*, *Pseudocrossidium revolutum*, *Tortula ruralis*, *Thuidium abietinum*, *Hypnum vaucheri* and *Polytrichum juniperinum*. Mesic and forested habitats are indicated by *Fissidens bryoides*, *Distichium capillaceum*, *Leptobryum pyriforme*, *Pseudoleskeella tectorum*, *Amblystegium varium*, *Campylium hispidulum*, *Drepanocladus uncinatus*, *Eurhynchium pulchellum*, *Isopterygium pulchellum* and *Hylocomium splendens* (forest form). Arctic-alpine taxa are represented by *Desmatodon leucostoma*, *Cyrtomnium hymenophyllum*, *Orthothecium chryseum* var. *cochlearifolium*, *Hypnum bambergeri* and *H. vaucheri*. The increase in the proportion of bryophytes indicating mesic and forested habitats is evidence that the climate was gradually becoming milder and became optimal for forest during the formation of Disconformity A. Geomorphological features as well as the abundant macrofossil remains of roots, twigs, wood and needles support the reconstruction.

An alternative hypothesis can be postulated for the change in vegetation and landscape evolution. Climatic factors play only a secondary role in affecting wetland biota. The hydrology and the influence of the minerotrophic ground water are of primary importance in the systems. Climate as such only influences the plant communities through the hydrological system. Bryophytes are unusual specific indicators of particular wetland communities (Miller 1980c and Rubnicek 1973).

During the time of deposition of Zone I, bryophyte taxa indicating mesic and more forested habitats increased. Forest cover became optimal during the formation of Disconformity A. The immediate cause of this shift from wetlands to mesic uplands could have been better drainage. This in turn was caused by the breakdown of a continuous permafrost during the milder climate.

The most abundant and commonest bryophytes in Zone I belong to the Circumboreal and Subarctic Phytogeographic Element (see Plate 42 in Chapter III). Eighty percent of the present Alaskan arctic flora (north of 66° N) belongs to this Element (Steere 1978a). The species in this Element are members of such communities as coniferous forests, mire systems, montane, alpine and lush arctic meadows. Most of the circumboreal ranges are located in formerly glaciated areas of the Northern Hemisphere. These circumboreal and subarctic species survived in Beringia and there is no doubt that they also survived in the vast continental refugia in the south in a wide boreal realm (Wright 1981). The populations, disjunct during maximal glaciation, were united again after extremely rapid recolonization (Crum 1972) of deglaciated terrain. This phytogeographic Element contains species with a wide ecological tolerance (or composed of several ecotypes?), as for example *Hylocomium splendens* and *Aulacomnium palustre*, as well as such specialists as *Scorpidium scorpioides*, a rich fen indicator. Some of the species were able to maintain an extensive distribution range outside the main glaciated areas, as for example *Fissidens bryoides* and *Drepanocladus aduncus* (Plate 12). Others, for example *D. revolvens*, have always been restricted to habitats created by glacial and periglacial activity, such as rich fens.

The presence of a temperate disjunct in the Mid Section and Disconformity A assemblages, *Leptodontium flexifolium*, is discussed above No other species belonging to the Temperate Disjunct Element (Steere 1978a), also called the 'Umiat Syndrome Element (Steere 1965, 1976), have been discovered yet in the northern Yukon or in Alaskan assemblages

Several of the species recorded in Chapter III belong to the Circumpolar Phytogeographical Element They are members of Zone I and other assemblages from northern areas (see Janssens 1981) Some of the species of this Element are strictly arctic, while others extend southward in the western mountains (Packer & Vitt 1974, Steere *et al*., Horton 1978, Steere & Scotter 1978a) The exact, or even approximate timing of the availability of a corridor throughout the foothill region of Alberta and northern British Columbia, connecting the southern refugia with the northern Yukon, is unknown (Rutter 1980) However, evidence is accumulating that many areas in the region were available for flora and fauna (and Early Man) for long periods during the latest glaciation and that limited, local ice surges were more common than long glaciation of the terrain. The well documented extension of the range of many arctic species (for example Horton 1978) through the western mountains has suggested that this area was available for biota during a longer period than the latest Late Wisconsinan deglaciation. Steere (1976) has argued convincingly that the species of the Circumpolar Element are not closely related to any taxa of more temperate climates. This suggests ancient relationships and long isolation of Tertiary species in the polar region. Often the closest relative is clearly subtropical or warm-temperate. The discussion on *Leptodontium flexifolium* is significant in this respect (Janssens & Zander 1980). The arctic species are a remnant of the pre-adapted taxa of a temperate-subtropical Tertiary flora. Several species recorded in Steere's tentative list of Circumpolar Arctic Bryophytes (Steere 1976) were present in Beringia and other northern areas during the Pleistocene (Table 11). They did not only survive the Pleistocene in the northern refugia, but also established some disjunct populations in southern refugia during the glaciations. *Aulacomnium acuminatum* was found in a Lateglacial deposit in New York State (Miller 1973b, 1980a, Vitt & Horton 1979). The species was also recovered from a Late Pleistocene deposit in Quebec (LaSalle *et al*. 1978). It is still found in southern Ontario (see Chapter III). Miller &

Table 11. Species of the Circumpolar Arctic Bryophyte Element (Steere 1976, 1980) present in northern Late Tertiary and Pleistocene assemblages (Janssens 1981, Miller 1980a, Kuc 1973c)

Taxon	Area	Age
Aulacomnium acuminatum	northern Yukon	Pleistocene
Cinclidium arcticum	Ellesmere Island	PLeistocene
	northern Yukon	Pleistocene
C. latifolium	northern Yukon	Wisconsin
Cyrtomnium hymenophyllum	arctic Alaska	Wisconsinan
	northern Yukon	Wisconsinan
Desmatodon leucostoma	northern Yukon	Wisconsinan
Drepanocladus badius	northern Yukon	Wisconsinan
D. lycopodioides	Meighen Island	Late Tertiary
D. lycopodioides var *brevifolius*	southern Yukon	Wisconsinan
	northern Yukon	pre-Wisconsinan and Wisconsinan
	arctic Alaska	Wisconsinan
Hygrohypnum polare	Bathurst Island	Pleistocene
	northern Yukon	Wisconsinan
Kiaeria glacialis	Banks Island	Pleistocene
Lophozia quadriloba	Banks Island	Pleistocene
Philonotis tomentella	Banks Island	Pleistocene
Tortella arctica	northern Yukon	Pleistocene
Trichostomum arcticum	northern Yukon	Wisconsinan

Benninghoff (1969) recorded *Bryum cryophilum* Mart from the Lateglacial of Michigan I discovered a specimen of *Drepanocladus lycopodioides* var *brevifolius* of Lateglacial age in a sample from Wingham Ontario (Plate 37) In addition some components of the Circumpolar Element have Holocene records in arctic areas (Janssens 1981 Miller 1980a) These include *Aulacomnium acuminatum* *Aplodon wormskjoldii* (Hornem) R Br *Bryobrittonia longipes* *Cinclidium arcticum* *Cyrtomnium hymenophylloides* *Drepanocladus badius* *D* *lycopodioides* var *brevifolius* *Kiaeria glacialis* (Berggr) Hag *Philonotis tomentella* *Schistidium holmenianum* Steere *et* Brassard (Bryological Report 402 in preparation *Tortella arctica* and *Trichostomum arcticum*

Two species associated with the Disconformity belong to the Steppe Bryophyte Element (Steere 1978a) *Desmatodon leucostoma* and *Pseudocrossidium revolutum* (*Desmatodon ellesmerensis* Brassard) are both found on calcareous silt in arctic regions They are disjunct from the southwestern deserts and steppes of temperate North America (Janssens & Zander 1980 and see Plate 6) Both species are still present in the northern Yukon They are considered as components that adapted themselves from the warm dry climate of steppes and subdeserts to cold and dry arctic climate A few small Alaskan assemblages in the Brooks Range confirm the warm interstadial period (Bryological Report 166) or indicated rich fen communities (Bryological Reports 168 169 & 184)

Zone II represents the assemblage below the Upper Lake (38 000-25 000 BP) As outlined above. the growth form distribution and species composition is very different from the Disconformity A, Mid-Section and Lower Lake assemblages It is also clearly differentiated from the postglacial samples Mat growers are dominant in the Zone II assemblages (Plate 58) and this is a reflection of the extremely high proportion of *Drepanocladus* records The most common taxon is *Drepanocladus lycopodioides* var *brevifolius* a species with a high arctic range at present (Plate 36) Also *D. badius* belongs to this group of species (Plate 18) All records in Zone II are from fen or lake species. except one upland taxon, *Barbula acuta* No *Sphagnum* material was recovered and most mire taxa indicate highly minerotrophic conditions (see also Schweger & Janssens 1980)

There is no evidence from bryophytes, nor from any other macrofossil remains (only *Carex* and *Potamogeton* achenes were recovered), of the survival of any tree species in the Old Crow Basin before the flooding by the Upper Lake. Dry upland habitats are indicated by wind-blown silt in the detrital peat samples and a macrofossil of *Artemisia* (capitula). Most of the fine detrital peat contained large reworked wood fragments. It is likely that the peat was formed in thaw-lakes, reworking older sediments. However, there is no evidence that the bryophyte component of the detrital peat consisted of reworked material of pre-Late Wisconsinan origin (see Table 8 and the discussion in Chapter IV).

After the warm period that created Disconformity A, the regional climate of the northern Yukon became probably dry and cold, or local drainage became increasingly impeded and permfrost more extensive. The only well preserved bryophyte component of the vegetation was the minerotrophic mire species. The macrofossil record and these bryophytes suggest a *Carex*-moss tundra in the lowlands and a steppe-like environment on the uplands.

This change from the period that formed the Disconformity was not sudden. Pollen records from alluvial sections including HH68-9, of the Old Crow Basin (Lichti-Federovich 1973) suggest a tripartite Mid-Wisconsinan interstadial vegetation. The lowest Mid-Section samples indicate a *Betula*-herb or Gramineae-herb assemblage with less *Picea* than Gramineae. These assemblages gave way to *Picea-Betula* dominated spectra, still below the later recognized Disconformity. During the formation of the latter hiatus assemblages were again dominated by Gramineae and herbs, and apparently this situation did not change before the flooding of the basin by the latest glacial meltwater lake. The Upper Lake Clays themselves are sterile. In conclusion, pollen data do not support the sharp distinction between Zone I and Zone II assemblages, based on the bryophytes. One of the reasons is the possibility of nearby sources of arboreal pollen, as will be discussed below. Another possible cause of discrepancy is that precise stratigraphical relationships between the early pollen work of Lichti-Federovich and present detailed knowledge of the Old Crow sequences are not yet outlined. I suggest that after the formation of the Disconformity a steep, but still gradual cooling of the climate took place and that most arboreal elements were eliminated from the Basin vegetation.

However, trees were still present in interior Alaska during this period of deforestation in the Old Crow Basin, 35,000 to 32,000 years ago (Matthews 1974b, Hopkins *et al.* 1981). Pollen diagrams suggest a *Carex*-moss tundra for the Fairbanks area, but the macrofossil record, including *Picea* indicated an open forest-tundra mosaic with scattered *Alnus* at 35,000 BP. Trees were apparently restricted to the lowlands. Later in the interval, more arboreal pollen is observed (*Alnus*, *Betula* and *Picea*) and macrofossils of *Betula papyrifera* are present. Tree-line moved to higher elevations. After 32,000 BP tree-line dropped again with the onset of colder climates. The Imuruk Lake pollen core (Colinvaux 1964, Colbaugh 1968) indicates shrub *Betula* tundra, followed by tundra vegetation. The warm interval in this site could be correlated with the Old Crow Disconformity A period.

In addition to those in Alaska, pollen work in the southern Yukon indicates a non-glacial interval around 35,000 BP (Rampton 1971, Schweger & Janssens 1980), as in the Fairbanks study area. When the alternative chronology of the Antifreeze Pond pollen record (Rampton 1971) is accepted, as outlined in Schweger & Janssens (1980), a shrub *Betula*-tundra landscape was present before 31,000 years. The Silver Creek samples of the Boutellier non-glacial interval (38,000 to 30,000 BP) suggest tundra meadow and steppe (Schweger & Janssens 1980, Bryological Reports 1 & 2).

It is possible to explain the differences between the interpretations of vegetation in the Fairbanks area and southern Yukon by consideration of the elevation differences. The lowland forest-tundra in the Fairbanks area (approximately 100 m a.s.l.) was replaced by *Betula* shrub tundra at Antifreeze Pond (approximately 700 m a.s.l.) and by tundra or tundra-steppe near Silver Creek (approximately 1300 m a.s.l.) Compared with the modern equivalents, this zonation shifted to lower elevations.

Two other localities in eastern Beringia indicate anomalously rich forested areas during this cooling period before the last major extent of the continental ice sheet 18,000 BP. One is south of Anchorage, where advancing valley glaciers blocked drainage patterns and formed a glacial meltwater lake. Paleoecological evidence indicate treed communities nearby (C.E. Schweger, personal communication). Another area is in the southeastern Yukon Territory. The Hungry Creek section provided some of the most controversial and intriguing problems for the glaciation history of eastern Beringia. Bryological Reports 434 and 435 are the result of analyses of two small samples of alluvial detrital material of this section. The last sample is the richest in number of species among all the samples I have ever processed. An additional characteristic is the complete absence of any dominant taxon or any differential preservation in the assemblage. All the material is perfectly preserved and all taxa reported are represented with a number of fragments of the same order of magnitude. The assemblage belongs clearly to the transported type, but the beautiful preservation rules out any reworking of older material, at least for the bryophytic component. Communities represented in the fossil assemblage are lakes, minerotrophic fens, well developed *Picea* forest (*Hylocomium splendens*) with rock outcrops (*Mnium marginatum*) and dry upland habitats. Even species that are characteristic for ecotonal areas between these communities were recovered. The local environments are completely and drastically different from the above described reconstruction for the Zone II assemblages, although they are of the same [illegible] These discrepancies between the Old Crow Basin and Hungry Creek environments are not easily explained. Hungry Creek is at a slightly higher elevation (450 m a.s.l.) and more of an upland site. However, the site was connected by the Peel River and the Bonnet Plume Basin with the Mackenzie River system [1] and is considered to be marginal to a large lake formed during the advance of the Keewatin Ice Sheet towards the Richardson Mountains. As in Anchorage, *Picea* forest probably survived until just before the advance of Keewatin ice in the Mackenzie Valley. An analog of this is seen in the history of the Two Creeks Forest Bed in Wisconsin (Schweger 1969). A small Alaskan assemblage from the Brooks Range indicates rich fen local environments and infers a cold climate, comparable to Zone II in the Old Crow Basin (Bryological Report 198).

No bryophytes, or any other macro– or microfossil are preserved or deposited in the Upper Lake Clays. However, outside the basins some lateglacial assemblages are known for the Yukon Territory. Mixed assemblages from North Fork Pass (11,250 BP, Bryological Report 260) in the westcentral Yukon and from the Snake River drainage (Bryological Report 41) in the eastern Yukon indicated a moderately rich minerotrophic fen and surrounding dry tundra upland habitats. A poorly preserved specimen of

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[1] The northern Mackenzie Valley could have been a Late Wisconsinan tree refugium, see Hopkins *et al.* (1981).

Hylocomium splendens did not contain information about forest vegetation. Both assemblages are too small to venture any regional environmental or climatological interpretation.

However, from the other side of eastern Beringia, on the Seward Peninsula of Alaska, more detailed information is available (Matthews 1974a). A steppe-tundra with *Poa*, locally abundant *Artemisia* and *Potentilla*, has been reconstructed. The climate was arid and colder than the earlier period. However, it was not too cold for the growth of dwarf *Betula*. Dry upland habitats are also indicated by a single record of *Thuidium abietinum* in a fibrous *Carex* peat sample (12,420 BP, Janssens 1981: Bryological Report 351). At present we have no clear evidence (except for *Populus balsamifera*) that trees survived in eastern Beringia after the Hungry Creek and Anchorage groves were destroyed (see also Hopkins *et al.* 1981).

Other lateglacial assemblages are from the Brooks Range. By 11,500-10,500 BP post deglaciation environments were available in the Sagavanirktok Valley (Janssens 1981: Bryological Report 182, Hamilton 1979b). A relatively productive mesic tundra meadow was present in the temporarily stabilized landscape. Bryological Report 171 (10,580 BP, Janssens 1981) indicated that by that time glacier ice had retreated from its last major readvance between 12,900 and 12,700 BP (Itkillik II age, Hamilton 1980a). The initial communities established were highly minerotrophic fens and drier calcareous upland tundra. Poorly preserved fragments of what was probably an arctic form of *Hylocomium splendens* and of *Pleurozium schreberi* were recovered in the assemblage.

Holocene

With the beginning of the Holocene, dramatic vegetation changes took place in eastern Beringia (Hopkins 1972, Murray 1978). Dwarf *Betula* shrub tundra became established and later *Picea* forest (with moose and caribou as major faunistic elements). This latter forest replaced the earlier biota completely by 5000 y BP. Trees migrated north through the eastern Rocky Mountains corridor, which was already well established by Late Wisconsinan time (Rutter 1980) and through the Mackenzie Valley system.[1]

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[1] Cold slightly minerotrophic lakes were present in the corridor area of Alberta (Janssens 1981: Bryological Report 42, 43 & 285), at 18,500 BP. *Drepanocladus exannulatus* (aquatic modification) and *D. crassicostatus* were covering the bottom or sides of these lakes. The radiocarbon dates on these moss peats is questioned by several people as being too old (B. Mott & L. Jackson, personal communication). However, it is indicated that bryophytes never use dissolved carbonates in aquatic systems, but that they rely on

The history of many trees in Beringia is still very controversial (Hopkins *et al.* 1981). However, there is quite good evidence that *Populus balsamifera* survived in Beringia during the Late Wisconsinan. Even today it is found far north and west of the major extent of other taxa in Alaska. There is some evidence the *P. tremuloides* and *Larix* could also have survived during this period. They were certainly not abundant and possibly reproduced only vegetatively. All other taxa, such as *Picea* species and arboreal *Betula*, were eliminated. The earlier concept of survival of tree species on the exposed southern continental shelf of Beringia (Heusser 1967, Hopkins 1972) is not accepted anymore (Hopkins *et al.* 1981). During the postglacial, the genus *Populus* reoccupied the region first (Ritchie 1977) and expanded very rapidly. This can be an indication of survival in the region. *Populus* was followed by *Picea*, arboreal *Betula* and *Larix*, and finally (5000 y BP) by *Alnus*. Present plant-site relationships in forested areas in Alaska are thus not older than 5000 years (Murray 1978). Extreme eastern Beringian areas (such as the Old Crow Basin) were forested earlier (see below and Hopkins *et al.* 1981).

A limited number of postglacial samples from eastern Beringia were analysed for subfossil bryophytes. The reason for this fairly incomplete record is the overall poor preservation of most postglacial peats or detrital organic sediments. The postglacial sequence that I tried to reconstruct completely was at locality HH68-10 (Table 2) in the Old Crow Basin. Only a few samples (Janssens 1981: Bryological Reports 143, 145, 148, 157 & 159) throughout the sequence contained sufficiently well preserved material to arrive at some conclusions. The basic problem with most samples was the extreme humidification of *Sphagnum* material in the autochthonous peats (see Chapter II).

The oldest dated Holocene peat sample (8700 BP) for the northern Yukon is from Hungry Creek (Janssens 1981: Bryological Report 383). It indicates the presence of *Picea* in the area (needles and luxuriously developed *Hylocomium splendens*). Other bryophytic components indicate rich fen communities and dry calcareous uplands. *Sphagnum* material was not found. The Old Crow sequence is not dated and it is not known when

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[1](cont'd)atmospheric CO_2 dissolved in the water (Hutchinson 1975, Ruttner 1947-48, 1948). This is the reason why high alkaline lakes, that have no dissolved CO_2, have no bryophyte flora. Because there exists no exchange of carbon between carbonate and dissolved CO_2 in the water, the carbon that bryophytes assimilate can never be "old carbon" (Broecker & Walton 1959). In addition, because the material dated was pure moss-peat, the dates cannot be too old because of fossil carbon assimilated by the mosses.

the first detrital peat accumulation began at this locality, probably 8000 to 9000 years ago (Hopkins 1981, manuscript in preparation). Rich fens, intermediate fens and ecotonal zones with forest groves are indicated. Aquatic lake bryophytes have been recovered also, as well as drier, calcareous upland species. *Sphagnum* is present from the start of the peat accumulation on, but probably increased throughout the Holocene, correlated by a rapid decrease in composite reliability index (most of the samples are so strongly humidified that it was not possible to construct an assemblage; they are not listed in Janssens 1981). The resolution of the Old Crow analyses for the Holocene is too coarse to allow for the reconstruction of the timing of the establishment of trees in the area. The surface samples contain several fragments of species such as *Dicranum* and liverwort species that usually are not sufficiently well preserved for specific identifications. In the future, additional collection and research in the area ought to concentrate on (1) surface sampling, (2) on correlation among Holocene peat stratigraphy contructed from several sources (exposed peat banks along rivers, wide diameter cores and detrital material of rivers and thaw lakes) and (3) on exact radiometric dating of the organic samples.

The oldest dated Holocene material for eastern Beringia are two Alaskan assemblages from the Brooks Range south of the continental divide (Janssens 1981: Bryological Reports 180 & 181). The detrital, fluvial, woody peat is older than 9000 years. The bryophytes are poorly preserved. This and other geomorphological features indicate extensive transport and probably reworking (Hamilton 1979b, Wind River exposures). If the bryophytes were derived from local communities, they indicate the presence of minerotrophic fens and calcareous upland habitats.

Two younger (6500–6000 BP), extremely well preserved assemblages are known from north of the continental divide in the Brooks Range (Janssens 1981: Bryological Reports 200 & 201). Another assemblage is known from south of the divide (Janssens 1981: Bryological Report 183). Trees are indicated in these assemblages by the presence of *Picea* macrofossils and well developed forest bryophytes, such as luxurious forms of *Hylocomium splendens* and *Drepanocladus uncinatus*. Other nearby communities were well developed rich fens, extensive dry calcareous and acidic (*Rhacomitrium*) tundra uplands, and alluvial habitats (with *Bryobrittonia longipes*). The two northern sites are out of the range of *Picea* at the present time (Viereck & Little 1975). By at least 6500 BP Anaktuvuk Pass was deglaciated and peat samples of younger Holocene age suggested a change to a more severe climate after 4750 BP (Hamilton 1980a). Neoglaciation in the Brooks Range began about 3500 BP. Trees never reached the pass during the later part of the Holocene after deglaciation.

In the Fairbanks area the Ballaine Lake samples also show Neoglaciation influence in central Alaska (Janssens 1981: Bryological Reports 427, 430 & 431, Hamilton 1980c). Some of the episodes recorded in these samples can be tentatively correlated with the climatic situation elsewhere in northern and central Alaska. *Picea* forest and poor minerotrophic fens were present 3000 years ago. The ice-wedge growth and the younger bryophyte samples indicate a colder climate (1800 and 900 BP) and probably even less minerotrophic conditions.

F. Summary of the Pleistocene History in Relation to Time-Stratigraphical Models

Relatively little is known of the pre-Wisconsinan period. Only a few interglacial assemblages have been studied and these are dated to the Kotzebuan (?) and Sangamonian Interglacials. However, there are indications that boreal biota reached farther west and north than at the present time.

The period of most interest is the interval between 120,000 and 10,000 years ago. It has been assigned the formal name Weichsel/Würm/Wisconsinan in the European and eastern North American literature. However, Hopkins (1981, manuscript in preparation) has argued that the application of a time-stratigraphical nomenclature developed in Europe or eastern North America is most inappropriate and partially misleading (see also Hopkins 1979). Therefore, I will apply his proposed alternative time-stratigraphical model for Beringia, while referring to the classical, eastern North American (Illinois) system and the Alaskan Brooks Range model (Hamilton & Porter 1975, Hamilton 1978c). Correlation with other time-stratigraphical (local and general) models in Siberia, Kamchatka, the Seward Peninsula, the Alaska Range, southern Yukon and Cordilleran systems can be found in Hopkins (1981, manuscript in preparation).

The Deering Interval followed the peak of the last interglacial from 120,000 to 80,000 years ago. The interval has been studied in the Cape Deceit section on the Seward Peninsula and the climate was only slightly more severe than now.

The Gold Hill Interval extended from 80,000 to 65,000 years ago (Early Wisconsinan, Itkillik I Glaciation). The Lower Lake Clay and Mid-Section assemblages in the Old Crow Basin probably belong to this interval. The top part of the Mid-Section is the Old Crow Tephra, 30 cm below Disconformity A in HH68-9. Unit 1 of the Deering Formation at Cape Deceit was also formed during this interval. The bryophytes in the above mentioned beds indicate that the climate became gradually milder and more extensively forested. It was optimal during the following Old Crow Interval.

The Old Crow Interval extended from 65,000 to 25,000 BP (Mid-Wisconsinan, Itkillik I/Itkillik II Interval). The type section for this interval is designated as those beds above Disconformity A (including all material inside the features of the Disconformity) and below the Upper Lake Clays at locality HH68-9. Part of the latter Old Crow Interval is the Boutellier nonglacial interval of the southern Yukon Territory. A general, steep drying and probable cooling trend is proposed for this later part of the Old Crow Interval, based on the arctic bryophyte communities (Zone II, Assemblage Group 4, and Silver Creek samples). Bombin (1980) suggested several climatic fluctuations within the Old Crow Interval beds.

The initial period of the Interval was clearly milder and more mesic than any other time between the last interglacial and the postglacial (Assemblage Group 3, Disconformity A samples). In contrast, the later part has no trees or shrubs and lacks *Sphagnum* completely. A dry and probably cold climate is suggested by the Old Crow data. However, pollen data suggest a still slightly milder climate and more diverse steppe-tundra than during the following Duvany Yar Interval. This latter interval extended from 25,000 to 13,000 BP (Late Wisconsinan, Itkillik II Glaciation). There are no fossiliferous sediments in the Old Crow Basin sequence and the Basin was flooded. The climate was extremely dry and probably cold.

The Duvany Yar Interval was interrupted by a sudden climatic change that began 14,000 or 13,000 years ago and coincided with the drainage of the Old Crow Basin. It ended with the initiation of Holocene peat accumulation 9000 to 8000 years ago. The period is named informally the "Birch period", because of the rapid rise of *Betula* pollen. No well studied sediments of this period are known from the northern Yukon Territory.

The peat accumulation in the Old Crow Basin started in the postglacial period as a detrital accumulation. Because of the poor preservation of the material collected, the reconstruction of the Holocene climatic fluctuations is too coarse to indicate any oscillations. The climate gradually became more mesic, and *Sphagnum* growth increased. Assemblages from the Brooks Range and other Alaskan localities indicate more extensive ranges for forested communities before Neoglaciation took place.

VI. SUMMARY and CONCLUSIONS

Important historical considerations on the vegetational history of North America include Lucy E. Braun's speculative floristic plant geography on the hardwood forests of the eastern United States. In her view no major displacement of the southern deciduous forests would have been necessary to accommodate boreal and arctic plants south of the maximal extent of the Laurentide Ice Sheet. Arctic and coniferous belts could have intervened between the ice and the stable, southern forests and a sufficient lowering of the altitudinal zonation would have permitted extensive spruce-fir summit forests, still leaving the southern associations intact. Her concept of vegetation units was Clementsian and the plant community was considered to be a complex organism making it impossible that taxa could have existed in other mixtures under analogous climates. The individualistic concept of plant associations, introduced by H.A. Gleason in 1926, considered a vegetation unit as a mere coincidence. Gleason stated that plants migrate as individual species, so that communities only migrate when most of the elements move and specific associations rarely retain their composition for any length of time. Gleason's ideas, along with Chaney and Sanborn (1933), and later many other paleoecologists, who tentatively advanced the idea that some past biota had a unique composition, were majors steps forward towards an integration of speculative plant geography and fossil data. It now offers the possibility to accomodate the rich and recently accumulated, new paleobotanical evidence into reasonable working hypotheses about the origin of present day biota.

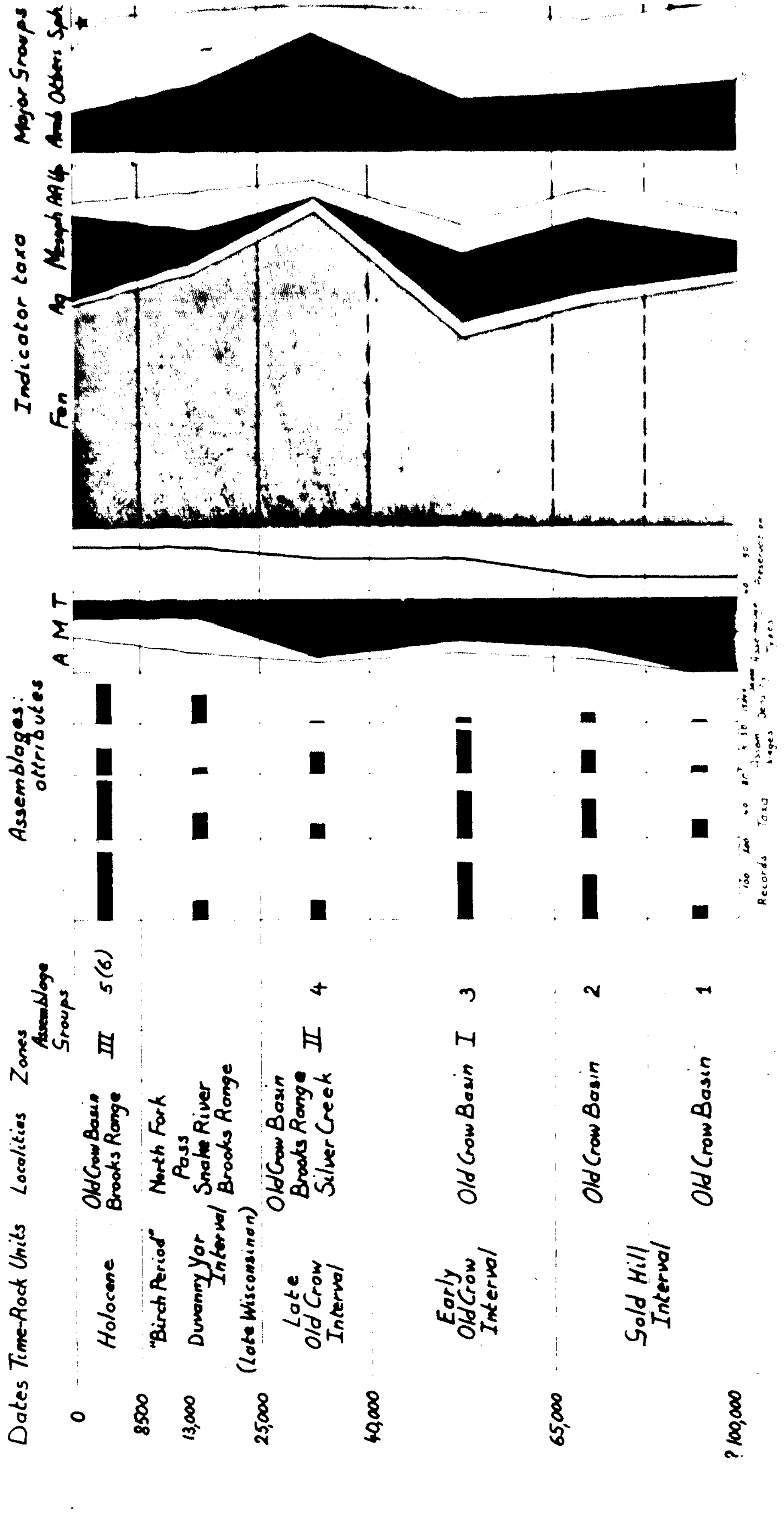
The work presented here is an attempt to utilize bryophytes, more particularly mosses, in the paleoenvironmental reconstruction and historical biogeography of eastern Beringia. This vast area, including Alaska and the Yukon, now has a rich moss flora. Beringia was never covered by extensive lowland glaciers and was a refugium for arctic and boreal elements during the Pleistocene. Well preserved bryophyte fragments are ubiquitous in the organic component of fluviatile, deltaic and lacustrine sediments and in postglacial peats. Continuous accumulations of such sediments are known in several localities in the Old Crow Basin in the northern Yukon Territory. The sequences, revealed by rapid Holocene downcutting of the rivers in the basin, were sampled with easy stratigraphical control. Often samples were screened in the field and the coarse organic component was picked for bryophytes in the laboratory. Additional samples, obtained through the Geological Survey of Canada and the United States Geological Survey and several other institutions and individuals, were processed. The data were used to supplement the Old Crow analyses. Abundancy and preservation was determined for each taxon recovered from a sample. The preservation grade was expressed by a reliability index that made it possible to compare samples. The fossil assemblages were classified into three types. 1) The transported type often with numerous taxa, 2) the autochthonous assemblages with a low species diversity and 3) an intermediate type, the mixed assemblages, with often numerous taxa, but distinguished from the transported type by the well preserved fen component, formed *in situ*. Identifications of 882 new records for North America were made and the specimens are deposited in ALTA. All 145 taxa have been provided with diagnoses and their morphology discussed. The descriptions are based on comparisons of living and fossil material, with emphasis on the distinctive microscopic features and certain aspects of the subfossil fragments. In addition to the descriptions, a compilation of habitat and distributional information is provided. New data on the physical environment of numerous species is provided (Appendix 1).

Five hundred and fifty-two records of subfossil bryophytes are reported from the northern Yukon assemblages. They represent 111 taxa, 96 of which are identified to species or some infraspecific category. Only two liverwort records are known, while the Amblystegiaceae are represented by more than half the number of records and eight of the commonest species belong to this family. Responsible for this selective preservation is the potential for fossilization correlated with habitat, the ultrastructural differences in cell walls and the production of antibiotic substances. Five species are not found at present in the bryoflora of the Yukon, but are in the fossil record: *Sphagnum centrale*, *Leptodontium flexifolium*, *Mnium marginatum*, *Calliergon megalophyllum* and *Calliergonella cuspidata*. All the bryophytes in the northern Yukon fossil assemblages are derived from transported material of regional communities or from *in situ* peats, so that all taxa could be used for paleoenvironmental reconstruction, to which there are four approaches. The first approach derives paleoecological and climatological information from a single species, the northern Yukon example being *Leptodontium flexifolium*. This species was found in two assemblages during the Gold Hill and Early Old Crow Intervals, dated 65,000 years or older It grows, at the present time, on organic substrates in lowlands of the temperate zone or in montane habitats in the subtropical belt At present it is found in North America north of Mexico only in the Southern Appalachian Mountains The presence of this species during the Old Crow Interval in the Old Crow Basin supports the reconstruction of the diversified flora of that period The second approach deals with growth form and habitat modifications. Many clearly outlined modifications can be described in the ubiquitous group of the Amblystegiaceae. These forms can be correlated with habitat features, mostly in relation to water level. In *Hylocomium splendens,* use can be made of its differentiated forest and arctic-alpine forms. The third approach leads to local environmental reconstruction, by relying on the floristics of an assemblage and the use of abundancy and reliability measures. The fourth approach is an attempt at regional paleoenvironmental reconstruction. Assemblages are grouped into stratigraphic units. Growth form spectra and indicator taxa suggest similarities and dissimilarities among the groups. The groups outlined for the Old Crow Basin indicate the presence of three chronological zones. These periods suggest substantial landscape evolution in the Basin during late Quaternary times.

Plate 60 is a illustration of the paleoenviromental reconstruction of eastern Beringian localities mentioned in this work and some attributes of their fossil bryophyte assemblages. The species diversity in the fossil assemblages is positively correlated with the number of samples processed and the number of records. However, there is no correlation with the relative proportions of indicator taxa or with major taxonomic groups. Density of bryophytic fragments in the organic component of the sediments is higher in autochthonous samples. Overall, preservation in autochthonous assemblages is also better. Landscape evolution and climate can be interpreted from the relative proportions of indicator taxa in the subfossil bryophyte assemblage groups. During the Gold Hill and Early Old Crow Intervals (65,000 to 40,000 BP), fossil bryophyte assemblages (Zone I, Assemblage Groups 1, 2 & 3) suggest that the climate gradually became milder and the Old Crow Basin more forested. The increase in mesophytic species and decrease of fen taxa and Amblystegiaceae indicate a warming trend and the availability of more shaded habitats. During the formation of Disconformity A in the Old Crow Basin (Assemblage Group 3, 65,000 BP) climate reached an optimum. This is

Plate 60. Reconstruction of the paleoenvironment of eastern Beringian localities during the Gold Hill, Old Crow, Duvany Yar, "Birch period" and Holocene intervals. The Zones and Assemblage Groups are for the Old Crow Basin localities.

Records, Taxa and Assemblages: absolute values, obtained by adding all assemblages listed in the localities column.
Density: average number of fragments in 100 g of the sediment fraction, > 1mm, in the samples.
Assemblage Types: A = autochthonous, M = mixed and T = transported (or allochthonous) assemblages.
Preservation: average of composite reliability indices of the assemblages.
Indicator taxa: Aq = aquatics, Mesoph = shade tolerant species, AA = arctic-alpine taxa and Up = species growing in dry calcareous upland tundra.
Major Taxonomic Groups: Amb = Amblystegiaceae and Sph = *Sphagnum*.
* = estimated increase of *Sphagnum* in Upper Holocene samples. The fossil assemblages with high *Sphagnum* content were not processed because of poor preservation.


Dates
0
8500
13,000
25,000
40,000
65,000
? 100,000
Time-Rock Units
Holocene
"Birch Period"
Duvanny Yar Interval
(Late Wisconsinan)
Late Old Crow Interval
Early Old Crow Interval
Gold Hill Interval
Localities
Old Crow Basin
Brooks Range
North Fork Pass
Snake River
Brooks Range
Old Crow Basin
Brooks Range
Silver Creek
Old Crow Basin
Old Crow Basin
Old Crow Basin
Zones
III
II
I
Assemblage Groups
5 (6)
4
3
2
1
Assemblages: attributes
Records
Taxa
Assem blages
Mean Density
A M T
Indicator taxa
Fen
Aq
Mesoph
AA
Major Groups
Amb
Others
Sph

confirmed by fossil assemblages in the Brooks Range, Alaska. During the Late Old Crow Interval (40,000 to 25,000 BP), the Old Crow Basin (Assemblage Group 4, Zone II), Brooks Range and Silver Creek fossil bryophyte assemblages indicate an abrupt cooling and drying of the climate. Bryophytes were only present in lowland, highly minerotrophic fens. Even though most assemblages are transported, there is only a very minor upland component in them, suggesting the absence of dry calcareous tundra and the presence of steppe. However, during this same period a diversified *Picea* forest still survived at the Hungry Creek locality. No bryophyte fossil assemblages were present in the Old Crow Basin sediments of the Duvany Yar Interval (25,000 to 13,000 BP) and the subsequent "Birch Period" (13,000 to 8500 BP). Bryophytes from the central Yukon and the Brooks Range indicate a less harsh climate during these Late Wisconsinan and Early Holocene periods than during the preceding Late Old Crow Interval in the northern Yukon. However, the complete sterility of the Upper Lake Clays in the Old Crow Basin suggests a continuation of the cold and dry climate. The proximity of the Keewatin Ice Sheet to the basin caused a harsher climate locally than farther west in Alaska and south in the central Yukon. During the Holocene, in northern and southern Yukon and in the Brooks Range of Alaska, climate gradually became more mesic, as indicated by the increased rate of peat accumulation and the increase in *Sphagnum*. Arctic-alpine taxa and rich fen indicators declined. Productive upland tundra became prominent. In the Brooks Range fossil bryophyte assemblages clearly support evidence of a pre-Neoglaciation (3500 BP) tree-line at a higher latitude and elevation than at the present time.

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APPENDIX 1: pH, CONDUCTIVITY and CATION CONCENTRATIONS of MIRE WATER SAMPLES

This appendix lists all the water sample analyses provided by M.H. Hickman (Department of Botany, University of Alberta) and D.H. Vitt. They are grouped per taxon in alphabetical order. The authority names for those taxa not mentioned in the chapter on the North American subfossil record are given. The samples identified with a number in the column Col. are collected by myself in Alberta, British Columbia and the Yukon Territory. The samples not identified with a number in the column Col. are provided by D.H. Vitt and are extracted from the data base for Vitt & Slack 1975, Slack *et al.* 1980 and Horton *et al.* 1979. Conductivity is not reduced for the contribution by H^+ cations. It is expressed in microScm^{-1}. The cation concentrations are expressed in ppm. See Methods and Materials for the procedures of collection and analysis.

Amphidium lapponicum (Hedw.) Schimp.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3862	8.15	915.25	5.00	14.4	61.6	39.3
3869	7.50	179.66	41.0	2.90	5.60	1.30
3871	7.80	188.14	5.75	2.90	5.80	1.50
3872	7.80	198.31	47.5	3.60	6.00	1.50

Aneura pinguis (L.) Dumort.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
	7.15	474.57	2.81	22.0	9.80	1.40
	7.20	432.20	27.9	23.0	9.50	1.10
	7.28	486.44				
	7.23	410.17	24.3	19.0	8.70	1.10
	7.35	488.14				
	7.25	505.08				
	7.35	491.52	33.1	18.0	11.0	1.40
	7.35	481.36			2.50	
	7.45	440.17	20.4	14.0	9.30	2.60
	7.27	423.73	24.3	11.0	4.70	.800
	7.27	406.78				
	7.20	369.49				
	6.98	445.76	24.1	15.0	4.40	1.00
	7.25	376.27				
	7.44	401.69				
	7.35	406.78	30.4	14.0	5.40	.700
	7.25	408.47				
	7.45	422.03				
	7.50	437.29	27.3	14.0	6.10	1.30

Aulacomnium palustre

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2834	5.20	32.203			4.28	.050
3226	7.00	66.102	8.43	1.46	8.12	.050
3228	7.00	66.102	8.43	1.46	8.12	.050
3828	6.60	142.37	10.8	2.95	10.3	9.2[illegible]
	7.28	486.44				
	6.95	391.52	30.9	14.0	13.0	8.70
	7.34	403.39	37.5	16.0	9.60	2.90
3841	7.85	286.44	52.5	9.95	9.50	1.10
3851	6.15	177.97	9.00	.855	13.2	9.10
3852	7.10	320.34	61.0	10.7	4.20	1.10
3858	6.50	137.29	4.50	.495	10.8	9.20
3859	6.80	201.69	14.5	4.25	12.0	13.6

Aulacomnium turgidum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
1608	5.20	40.678	3.84	.940	5.90	.050
2382	6.30	18.644	7.94	1.03	38.24	

Brachythecium frigidum (K. Müll.) Besch.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3870	7.75	21.525	4.30	4.65	6.20	1.60

Brachythecium turgidum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
1659	7.80	166.10	22.43	11.95	17.6	.120
3840	7.25	505.08	55.0	14.6	25.0	15.3
3845	7.75	359.32	71.5	15.0	13.0	1.10
3846	7.05	386.44	65.0	14.2	12.4	1.20
3847	7.10	389.83	66.0	14.0	12.8	1.60
3848	7.35	374.58	77.5	15.5	13.0	1.30
3849	7.15	384.75	66.5	15.5	13.4	1.30

Bryum pseudotriquetrum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3821	7.70	855.93	124.5	49.2	11.4	5.20
	7.30	474.58				
	7.23	410.17	24.3	19.0	8.70	1.10
	7.35	488.14				
	7.25	505.08				
	7.25	479.60				
	7.25	494.92	33.1	22.0	12.0	2.50
	7.44	401.69				
	7.35	406.78	30.4	14.0	5.40	.700
3839	7.35	338.98	50.0	11.0	11.1	.900
3848	7.35	374.58	77.5	15.5	13.0	1.30
3850	7.30	322.03	62.5	10.2	5.20	1.30
3857	7.20	250.85	39.0	9.65	4.20	1.70

Calliergon giganteum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2202	7.10	157.63	23.15	3.33	22.26	.050
	7.15	474.57	2.81	22.0	9.80	1.40
2713	7.50	196.61	27.49	7.50	12.68	3.34

Calliergon stramineum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2837	7.90	442.37	41.98	18.13	24.78	1.38

Calliergon trifarium

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2875	7.50	527.12	33.53	17.12	27.4	2.22
2877	7.20	601.69	54.29	18.27	27.82	2.50
2878	7.50	508.47	46.08	20.43	26.08	2.36
2868	7.60	477.97	26.29	18.56	24.84	1.66
2873	7.70	493.22	35.46	17.98	25.06	1.52
	7.32	405.08				
	7.20	432.20	27.9	23.0	9.50	1.10
	7.30	474.58				
	7.25	479.60				
	7.35	406.78	30.4	14.0	5.40	.700
	7.25	408.47				
	7.35	422.03				
	7.50	437.29	27.3	14.0	6.10	1.30
	7.30	228.81	18.7	5.20	5.40	1.40
3848	7.35	374.58	77.5	15.5	13.0	1.30

Calliergonella cuspidata

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2952	7.50	410.17	76.2	9.79	27.14	.400
3225	7.00	66.102	8.43	1.46	8.12	.050
3228	7.00	66.102	8.43	1.46	8.12	.050

Campylium stellatum

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
1659	7.80	166.10	22.43	11.95	17.6	.120
2218	7.00	384.75	27.74	7.78	14.84	.050
2443	7.60	181.36	19.29	8.64	9.08	.050
2868	7.60	477.97	26.29	18.56	24.84	1.66
2876	7.50	449.15	26.53	16.26	22.74	2.78
2866	7.50	467.80	27.25	18.13	24.44	1.66
2870	7.80	494.92	21.7	18.42	25.28	1.80
2871	7.90	491.53	23.15	18.27	28.2	1.94
2874	7.60	506.78	34.53	18.7	26.84	2.64
2877	7.20	601.69	54.29	18.27	27.82	2.50
2878	7.50	508.47	46.08	20.43	26.08	2.36
2702			20.49	23.3		
2952	7.50	410.17	76.2	9.79	27.14	.400
3225	7.00	66.102	8.43	1.46	8.12	.050
3226	7.00	66.102	8.43	1.46	8.12	.050
3809	7.75	906.78	134.	47.5	15.4	6.40
3811	7.80	622.03	91.0	28.1	10.2	5.60
3813	7.65	949.15	161.	51.6	15.8	5.90

3815	7.65	1042.4	150.	51.6	22.4	7.20
3816	7.70	930.51	135.	50.0	14.7	6.20
3817	7.70	876.27	151.	48.1	14.2	5.50
3819	7.70	832.20	117.5	45.0	12.1	5.70
	7.15	474.57	28.1	22.0	9.80	1.40
	6.90	457.62				
	7.32	405.08				
	7.28	486.44				
	7.23	410.17	24.3	19.0	8.70	1.10
	7.25	505.08				
	7.25	479.60				
	7.30	444.07				
	7.35	491.52	33.1	18.0	11.0	1.40
	7.35	481.36				
	7.25	494.92	33.1	22.0	12.0	2.50
	7.45	440.17	20.4	14.0	9.30	2.60
	7.15	379.66	34.0	10.0	6.30	2.70
	7.05	389.83				
	7.20	420.34	28.0	15.0	6.40	3.40

Climacium dendroides (Hedw.) Web. *et* Mohr

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3868	6.75	196.61	18.5	6.00	7.60	4.70

Cratoneuron commutatum (Hedw.) Roth.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
1703	7.00	286.44	46.08	17.12	10.06	2.64
2772	7.60	125.42	12.53	9.08	3.04	.050
3421	7.40	335.59	37.63	30.19	4.40	.050

Dicranella palustris (Dicks.) Crundw. *ex* Warb.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3226	7.00	66.102	8.43	1.46	8.12	.050
3863	6.55	37.797	3.50	.065	4.60	1.30

Dicranum polysetum Sw.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3859	6.80	201.69	14.5	4.25	12.0	13.6

Dicranum undulatum

Col.	pH	Cond.	[Ca^{++}]	[Mg^{++}]	[Na^{+}]	[K^{+}]
3826	6.65	169.49	15.4	4.50	12.1	5.30
3859	6.80	201.69	14.5	4.25	12.0	13.6

Distichium capillaceum

Col.	pH	Cond.	[Ca^{++}]	[Mg^{++}]	[Na^{+}]	[K^{+}]
3821	7.70	855.93	124.5	49.2	11.4	5.20

Drepanocladus aduncus

Col.	pH	Cond.	[Ca^{++}]	[Mg^{++}]	[Na^{+}]	[K^{+}]
2752	7.20	359.32	23.63	20.0	1.18	.050
2707			20.49	23.3		
3824	7.25	296.61	45.5	18.2	6.00	2.40
3829	6.60	147.46	24.6	7.70	5.80	2.40
3834	7.50	576.27	34.4	7.15	18.4	
3838	7.40	227.12	51.4	8.00	4.50	1.00
3839	7.35	338.98	50.0	11.0	11.1	.900
3840	7.25	505.08	55.0	14.6	25.0	15.3
3852	7.10	320.34	61.0	10.7	4.20	1.10
3857	7.20	250.85	39.0	9.65	4.20	1.70

Drepanocladus crassicostatus

Col.	pH	Cond.	[Ca^{++}]	[Mg^{++}]	[Na^{+}]	[K^{+}]
1793	7.90	500.00	18.8	42.4	21.68	.050
1805	7.70	923.73	76.97	37.23	41.64	.820

Drepanocladus exannulatus

Col.	pH	Cond.	[Ca^{++}]	[Mg^{++}]	[Na^{+}]	[K^{+}]
1808	9.00	311.86				
1810	8.40	440.68	37.39	29.26	29.2	1.38
1813	7.80	864.41	71.61	50.825	16.96	
				18.7		
3806	7.70	20.169	3.10	.450	0.	.200
	4.40	1.60	.200	2.90	.200	
	4.70	2.00	.300	2.90	.300	
	4.10	2.00	.300	3.40	.100	
	4.30	2.20	.300	3.00	.400	
	4.30	2.00	.300	3.30	.400	
	4.40	2.60	.300	3.00	.200	

Drepanocladus exannulatus var. *purpurascens* (Schimp.) Herz.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3863	6.55	37.797	3.50	.065	4.60	1.30
3865	6.25	40.508	4.50	.085	4.20	1.20

Drepanocladus fluitans

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2603	5.50	37.288	15.18	2.61	25.4	11.34
2620	6.40	111.86	14.7	4.33	9.06	.260
2662	4.80	38.983	5.53	1.17	13.12	.050
2664	4.90	38.983	7.70	1.46	11.16	.050
2713	7.50	196.61	27.49	7.50	12.68	3.34
2714	7.00	215.25	35.94	8.93	12.22	8.68
3673	5.90	19.153	2.40	.245	4.00	1.90

Drepanocladus lycopodioides var. *brevifolius*

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2329	5.60	13.559	7.22	1.89	13.34	.050

Drepanocladus revolvens

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
1803	7.80	559.32	28.46	38.95	16.02	.050
1815	8.10	369.49	44.87	13.67	40.84	.050
1855	7.70	372.88	106. 7 26.03	100.	18.78	
2064	7.40	32.203	5.29	.170	12.74	.050
2230	7.50	152.54	44.39	13.67	26.22	2.64
2457	7.30	233.90	37.39	12.52	49.68	.050
2665	5.40	37.288	9.87	2.47	5.09	2.64
2836	7.90	442.37	41.98	18.13	24.78	1.38
2837	7.90	442.37	41.98	18.13	24.78	1.38
2844	7.50	469.49	33.29	16.55	26.52	2.08
2727	7.10	405.08	44.15	19.42	12.24	2.50
2865	7.20	489.83	27.49	19.57	25.86	3.20
2866	7.50	467.80	27.25	18.13	24.44	1.66
2867	7.60	471.19	27.74	18.56	23.92	.960
2869	7.80	461.02	25.32	17.27	24.96	2.22
2870	7.80	494.92	21.7	18.42	25.28	1.80
2871	7.90	491.53	23.15	18.27	28.2	1.94
2873	7.70	493.22	35.46	17.98	25.06	1.52
2874	7.60	506.78	34.25	18.7	26.84	2.64
2733	7.30	291.53	28.94	14.97	9.70	.050
2868	7.60	477.97	26.29	18.56	24.84	1.66
2875	7.50	527.12	33.53	17.12	27.4	2.22
2876	7.50	449.15	26.53	16.26	22.74	2.78
2877	7.20	601.69	54.29	18.27	27.82	2.50
2878	7.50	508.47	46.08	20.43	26.08	2.36
3225	7.00	66.102	8.43	1.46	8.12	.050

3226	7.00	66.102	8.43	1.46	8.12	.050
3228	7.00	66.102	8.43	1.46	8.12	.050
3811	7.80	622.03	91.0	28.1	10.2	5.60
3813	7.65	949.15	161.	51.6	15.8	5.90
3814	7.75	1067.8	155.	53.2	16.6	5.70
3815	7.65	1042.4	150.	51.6	22.4	7.20
3816	7.70	930.51	135.	50.0	14.7	6.20
3817	7.70	876.27	151.	48.1	14.2	5.50
3819	7.70	832.20	117.5	45.0	12.1	5.70
	7.15	474.57	2.81	22.0	9.80	1.40
	6.90	457.62				
	7.32	405.08				
	7.20	432.20	27.9	23.0	9.50	1.10
	7.30	474.58				
	7.28	486.44				
	7.23	410.17	24.3	19.0	8.70	1.10
	7.25	505.08				
	7.25	479.60				
	7.30	444.07				
	7.35	491.52	33.1	18.0	11.0	1.40
	7.35	481.36				
	7.25	494.92	33.1	22.0	12.0	2.50
	7.45	440.17	20.4	14.0	9.30	2.60
	7.15	379.66	34.0	10.0	6.30	2.70
	7.05	389.83				
	7.20	420.34	28.0	15.0	6.40	3.40

Drepanocladus uncinatus

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
1484	6.40	61.017	9.39	.600	9.92	.050
1954	7.90	15.254	2.39	.500	4.04	.050
2218	7.00	384.75	13.25	.020	10.92	.050
2248	4.90	23.729	5.77	.740	15.7	.260
2382	6.30	18.644	7.94	1.03	38.24	0.05

Drepanocladus vernicosus

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
1682	6.90	301.69	23.15	10.94	10.86	5.74
2339	6.70	322.03	45.6	18.99	66.32	1.10
2636	6.00	94.915	8.43	2.18	4.96	11.2
2815	7.40	208.47	33.29	9.22	3.34	.050
2834	5.20	32.203			4.28	.050
2702			20.49	23.3		
2824			8.91	1.03	6.16	.050
3842	7.55	393.22	85.0	16.1	14.6	1.10
3843	8.05	383.05	96.5	16.3	12.4	1.10
3844	7.05	389.83	71.0	14.8	11.4	1.20
3845	7.75	359.32	71.5	15.0	13.0	1.10
3846	7.05	386.44	65.0	14.2	12.4	1.20
3847	7.10	389.83	66.0	14.0	12.8	1.60
3848	7.35	374.58	77.5	15.5	13.0	1.30
3850	7.30	322.03	62.5	10.2	5.20	1.30

Fissidens adiantoides Hedw.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2952	7.50	410.17	76.2	9.79	27.14	.400
3228	7.00	66.102	8.43	1.46	8.12	.050

Fissidens grandifrons Brid.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3869	7.50	179.66	41.0	2.90	5.60	1.30
3870	7.75	21.525	4.30	4.65	6.20	1.60
3872	7.80	198.31	47.5	3.60	6.00	1.50

Gymnocolea inflata (Huds.) Dumort.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2662	4.80	38.983	5.53	1.17	13.12	.050

Hygrohypnum luridum (Hedw.) Jenn.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3833	7.50	125.42	15.6	4.35	6.90	2.50
3860	7.95	89.831	6.00	2.80	3.70	1.20

Hylocomium splendens

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3831	6.90	254.24	32.0	8.80	11.4	9.80
	7.30	444.07				
2382	6.30	18.644	7.94	1.03	38.24	0.

Hypnum bambergeri

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
1675	7.80	45.763	8.18	2.00	13.36	.050
2166	6.80	162.71	13.25	.020	10.92	.050
1659	7.80	166.10	22.43	11.95	17.6	.120

Jungermannia pumila With.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3867	7.65	89.322	4.50	1.80	33.0	4.80

Leptodictyum riparium (Hedw.) Warnst.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3334	8.10	122.03	150.49 28.98	100.	4.04	

Meesia triquetra

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
	7.32	405.08				
	7.30	474.58				
	7.28	486.44				
	7.25	494.92	33.1	22.0	12.0	2.60
	7.27	423.73	24.3	11.0	4.70	.800
	7.27	406.78				
	7.20	369.49				
	7.00	445.76	24.1	15.0	4.40	1.00
	7.25	376.27				
	7.44	401.69				
	7.35	406.78	30.4	14.0	5.40	.700
	7.25	408.47				
	7.50	437.29	27.3	14.0	6.10	1.30
3839	7.35	338.98	50.0	11.0	11.1	.900
3840	7.25	505.08	55.0	14.6	25.0	15.3
3848	7.35	374.58	77.5	15.5	13.0	1.30

Philonotis fontana

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3863	6.55	37.797	3.50	.065	4.60	1.30
3864	6.25	34.915	.075	3.60	1.00	
3865	6.25	40.508	4.50	.085	4.20	1.20

Plagiomnium ellipticum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
1716			82.33	12.38	10.08	1.38
3835	7.40	698.31	32.8	6.35	16.3	
3850	7.30	322.03	62.5	10.2	5.20	1.30

Pleurozium schreberi

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2248	4.90	23.729	5.77	.740	15.7	.260
2099			10.84	2.18	10.32	.540
3827	7.30	286.44	16.4	4.85	41.0	13.5
3828	6.60	142.37	10.8	2.95	10.3	9.20

Pogonatum alpinum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2382	6.30	18.644	7.94	1.03	38.24	

Pogonatum dentatum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3863	6.55	37.797	3.50	.065	4.60	1.30

Pohlia sphagnicola (B.S.G.) Lindb. *et.* H. Arnell.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
	6.95	391.52	30.9	14.0	13.0	8.70

Polytrichum juniperinum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3853	6.75	157.63	5.00	.600	12.4	11.6
3854	6.[illegible]	122.03	5.50	.600	11.4	7.50

Polytrichum strictum Brid.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3825	6.50	289.83	19.0	4.60	20.4	15.3
3826	6.65	169.49	15.4	4.50	12.1	5.30
3828	6.60	142.37	10.8	2.95	10.3	9.20

Ptilidium ciliare (L.) Hampe

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2565			13.25	4.77	14.92	.400

Ptilium crista-castrensis

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
3859	6.80	201.69	14.5	4.25	12.0	13.6

Scapania paludosa (K. Müll.) K. Müll.

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2658			7.70	1.32		

Scorpidium scorpioides

Col.	pH	Cond.	$[Ca^{++}]$	$[Mg^{++}]$	$[Na^{+}]$	$[K^{+}]$
2877	7.20	601.69	54.29	18.27	27.82	2.50
3227	7.00	66.102	8.43	1.46	8.12	.050
3812	7.70	613.56	155.	27.5	10.0	3.50
3815	7.65	1042.4	150.	51.6	22.4	7.20
3822	7.80	932.20	150.	46.9	15.0	5.80
	7.15	474.57	2.81	22.0	9.80	1.40
	6.90	457.62				
	7.32	405.08				
	7.20	432.20	27.9	23.0	9.50	1.10
	7.30	474.58				
	7.28	486.44				
	7.23	410.17	24.3	19.0	8.70	1.10
	7.35	488.14				
	7.25	505.08				
	7.30	491.52	31.5	23.0	9.80	1.40
	7.25	479.60				
	7.35	491.52	33.1	18.0	11.0	1.40
	7.35	481.36				
	7.25	494.92	33.1	22.0	12.0	2.50
	7.27	423.73	24.3	11.0	4.70	.800
	7.27	406.78				
	7.20	369.49				
	6.98	445.76	24.1	15.0	4.40	1.00
	7.25	376.27				
	7.44	401.69				
	7.35	406.78	30.4	14.0	5.40	.700
	7.25	408.47				
	7.35	422.03				
	7.50	437.29	27.3	14.0	6.10	1.30
	7.40	220.34	28.3	7.30		
	7.20	225.42	24.0	7.40	4.90	1.70
	7.30	228.81	18.7	5.20	5.40	1.40
	7.65	222.03	21.5	5.30	2.60	.500
3839	7.35	338.98	50.0	11.0	11.1	.900
3840	7.25	505.08	55.0	14.6	25.0	15.3

Scorpidium turgescens

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2443	7.60	181.36	19.29	8.64	9.08	.050
2873	7.70	493.22	35.46	17.98	25.06	1.52
3848	7.35	374.58	77.5	15.5	13.0	1.30

Scouleria aquatica Hook.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3861	7.90	130.51	14.5	7.60	3.80	1.00
3867	7.65	89.322	4.50	1.80	33.0	4.80

Sphagnum angustifolium (C. Jens. *ex* Russ.) C. Jens *in* Tolf.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
	7.45	440.17	20.4	14.0	9.30	2.60
	6.95	391.52	30.9	14.0	13.0	8.70
3851	6.15	177.97	9.00	.855	13.2	9.10
3853	6.75	157.63	5.00	.600	12.4	11.6
3855	7.20	323.73	61.0	11.35	7.00	2.60

Sphagnum compactum DC. *ex* Lam. *et* DC.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2113			4.80	.890	3.04	.050

Sphagnum fuscum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3820	5.60	111.86	5.00	.685	13.5	7.30

Sphagnum imbricatum Hornsch. *ex* Russ.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3873	3.80	564.41	57.5	7.30	60.0	30.3

Sphagnum jensenii H. Lindb.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
	4.40		1.60	.200	2.90	.200
	4.70		2.00	.300	2.90	.300
	4.10		2.00	.300	3.40	.100
	4.30		2.20	.300	3.00	.400
	4.30		2.00	.300	3.30	.400
	4.40		2.60	.300	3.00	.200

Sphagnum lenense

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
1983			4.56	.200	10.82	6.86

Sphagnum magellanicum

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3858	6.50	137.29	4.50	.495	10.8	9.20

Sphagnum nemoreum Scop.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3832	5.90	157.63	7.40	.535	15.0	8.50

Sphagnum russowii Warnst.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
3825	6.50	289.83	19.0	4.60	20.4	15.3
3828	6.60	142.37	10.8	2.95	10.3	9.20
3854	6.15	122.03	5.50	.600	11.4	7.50
3856	6.90	132.20	6.00	1.10	8.40	8.70

Sphagnum subsecundum Nees *ex* Sturm

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2834	5.20	32.203			4.28	.050

Sphagnum warnstorfii Russ.

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
	7.45	440.17	20.4	14.0	9.30	2.60
	6.95	391.52	30.9	14.0	13.0	8.70
	7.15	435.59	32.2	13.0	12.0	5.10

Tomenthypnum nitens

Col.	pH	Cond.	[Ca⁺⁺]	[Mg⁺⁺]	[Na⁺]	[K⁺]
2166	6.80	162.71	13.25	.020	10.92	.050
3809	7.75	906.78	134.0	47.5	15.4	6.40
3810	8.00	833.90	91.0	47.5	11.8	4.60
3814	7.75	1067,8	155.0	53.2	16.6	5.70
3818	7.70	898.31	142.5	45.6	14.1	6.30
3821	7.70	855.93	124.5	49.2	11.4	5.20
3831	6.90	254.24	32.0	8.80	11.4	9.80
	7.28	486.44				

	7.25	505.08				
	7.25	479.60				
	7.30	44.07				
	7.45	440.17	20.4	14.0	9.30	2.60
	6.95	391.52	30.9	14.0	13.0	8.70
	7.15	435.59	32.2	13.0	12.0	5.10
	7.34	403.39	37.5	16.0	9.60	2.90
	7.15	379.66	34.0	10.0	6.30	2.70
	7.05	389.83				
	7.20	420.34	28.0	15.0	6.40	3.40
	7.00	427.12				
	7.20	422.03	24.7	15.0	6.90	3.40
	7.85	286.44	52.5	9.95	9.50	1.10
	7.05	389.83	71.0	14.8	11.4	1.20
[illegible]	7.30	322.03	62.5	10.2	5.20	1.30
3852	7.10	320.34	61.0	10.7	4.20	1.10
3859	6.80	201.69	14.5	4.25	12.0	13.6

APPENDIX 2: SUBFOSSIL BRYOPHYTES COLLECTED in the NORTHERN YUKON TERRITORY

Subfossil bryophytes were collected at 13 localities situated in the northern Yukon Territory. The thirteen localities are listed in Table 3. The IT & GF column indicates the Indicator Taxa and Growth Forms:

- Indicator Taxa: (see more details in text)
  - rf: rich fen species
  - up: upland species
  - aq: aquatic species
- Growth Forms:
  - Turfs: systems with parallel upright shoots
    - Te: tall, with erect branches
    - Trh: as Te, with dense tomentum
    - Td: tall turfs with divergent branches
    - t: as Te, but under 2 cm high
  - Mats: systems forming a generally dens extending horizontally over the substratum
    - Mr: rough mats, principal shoots horizontal, abundant short branches
    - Ms: smooth mats, branches in same plane as main shoots
  - Wefts: strangling shoots and branches often ascending and luxuriant
    - W: wefts

Three age classes are assigned (see text for more details)

- H: Holocene
- W: Wisconsinan
- [illegible] Pleistocene

Taxon	IT & GF	1a	1b	1c	1d	1e	2	3	4	5	6	7	8	9	10	11	12	13
Amblystegium serpens	Ms			P														
A. varium	Ms			P				W	W						W			W
Aulacomnium acuminatum	Te									H	H			P				
A. palustre	Trh		W	P	P	H		W	W		H	W,P		P				
A. turgidum	Te		W	P	P	H				H	H			P				
Barbula acuta	up, t							W					W		W			W
Brachythecium turgidum	Mr		W					W							W			H,W
Brachythecium species	Mr																	H
Bryoerythrophyllum recurvirostrum	up, t		W															
Bryum pseudotriquetrum	t		W	P							H							W
Bryum species	t	W	W	P				W	W				W	P	W		H	W
Calliergon giganteum	Td		W	P	P		W		W		H	W,P	W		W,P	W		W
C. megalophyllum	aq		W															
C. richardsonii	Td	W	W	P	P		W	W	W		H				P		H	W
C. stramineum	Ms																	W
C. trifarium	rf, Ms		W	P	P		W					W					H	W
Calliergon species	Td, Ms	W	W						W		H				W,P			W
Calliergonella cuspidata	Td, Ms		W															
Campylium hispidulum	Ms			P				W										
C. stellatum var. arcticum	Td			P	P													
C. stellatum var. stellatum	Td			P				W			H			P				H,W
Catoscopium nigritum	t		W	P				W										
Ceratodon purpureus	up, t			P	P													
Cinclidium arcticum	t													P				
C. latifolium	t																	W
C. stygium	t		W															W
Cratoneuron filicinum	Mr	W	W	P											P			
Cyrtomnium hymenophyllum	t		W															
Desmatodon leucostoma	up, t							W										
Dicranella varia	up, t		W															
Dicranum acutifolium	up, Te										H							W
D. angustum	Te														P			
D. groenlandicum	Te			P	P			W	W	H					P			W
D. scoparium	Te										H							
Dicranum species	Te			P	P				W									
Didymodon rigidulus	t																	W
Distichium capillaceum	t		W	P											W			W
Ditrichum flexicaule	t, Te			P											P			H,W

Appendix 2, northern Yukon Bryophytes

Taxon	IT & GF	1a	1b	1c	1d	1e	2	3	4	5	6	7	8	9	10	11	12	13
Drepanocladus aduncus var. *aduncus*	Mr	W	W	P	P			W	W					P				
D. aduncus var. *polycarpus*	Mr	W	W					W										W
D. badius	rf, Mr				P			W										
D. capillifolius	Ms		W	P					W								H	
D. crassicostatus	aq	W	W	P	P			W			H	W, P	W		P	W		W
D. exannulatus	Mr, Td		W	P	P	H							W		W, P	W	H	W
D. fluitans	Mr	W	W	P							H							W
D. lapponicus	Mr														W			
D. lycopodioides var. *brevifolius*	Mr	W	W	P	P		W	W	W			W			W, P			W
D. pseudostramineus	Td								W						P		H	W
D. revolvens	rf, Mr							W			H							W
D. sendtneri	Mr	W	W	P			W				H	P			P			
D. tundrae	Td			P			W											W
D. uncinatus	Mr		W															
D. vernicosus	Mr			P		H	W								P			W
Drepanocladus species	Mr, Td	W	W	P	P	H	W	W	W			W	W	P	P	W	H	W
Encalypta alpina	up, t														W			
Encalypta species	up, t			P														
Eurhynchium pulchellum	Ms		W	P										P				W
Fissidens bryoides	up, to		W															
Helodium blandowii	W		W															
Hygrohypnum polare	Mr			P														
Hylocomium splendens	W		W	P	P										P		H	H, W
Hypnum bambergeri	Ms		W												W			W
H. hamulosum	up, Ms													P				
H. pratense	Ms		W	P	P					H								W
H. vaucheri	up, Ms		W															
Hypnum species	Ms			P														
Isopterygium pulchellum	up, Ms		W															
Leptobryum pyriforme	up, t		W	P														
Leptodontium flexifolium	up, t		W	P														
Lophozia floerkei	t										H							
L. rutheana	rf, Ms, Te										H							
Meesia longiseta	t																	W
M. triquetra	rf, Te	W		P			W										H	W
M. uliginosa	t				P										W			
Mnium marginatum	t																	W
Mnium species	Te, t			P														W
Oncophorus species	t		W															W
Orthothecium chryseum var. *cochlearifolium*	Te		W															
O. strictum	Te, Ms			P														

Taxon	IT & GF	1a	1b	1c	1d	1e	2	3	4	5	6	7	8	9	10	11	12	13
Paludella squarrosa	Te										H							W
Plagiomnium ellipticum	Te		W						W									W
Plagiothecium laetum	Ms									H								
Pogonatum urnigerum	up, Te		W															
Pohlia nutans	t									H								
P. wahlenbergii	t														P			
Pohlia species	t		W	P											W			W
Polytrichum algidum	up, Te				P													
P. juniperinum	Te, t							W										
Pseudocrossidium revolutum	up, t		W															
Pseudoleskeella tectorum	up, Ms							W										
Rhytidium rugosum	W													P				W
Scorpidium scorpioides	rf, Ms		W	P	P	H	W	W				W	W		W,P			W
S. turgescens	Ms			P											W			
Scorpidium species	Ms		W															
Sphagnum centrale	Td			P														
S. fuscum	Td										H							W
S. girgensohnii	Td									H								
S. lenense	Td																H	
S. magellanicum	Td			P											P			
Sphagnum section Acutifolia	Td		W	P							H							W
Sphagnum section Cuspidata	Td			P	P													
Sphagnum species	Td		W	P							H				P			
Thuidium abietinum	up, W			P				W										
T. recognitum	up, W																	H
Tomenthypnum nitens	Td, W		W	P	P	H	W	W	W		H				W		H	H,W
Tortella arctica	Te, t													P				
T. fragilis	up, Te, t																	W
T. tortuosa	up, Te, t											P						
Tortula ruralis	up, t		W	P				W										
Tortula species	t, Te														W			
Trichostomum arcticum	Te, t			P											W			

Appendix 2, northern Yukon Bryophytes

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