STUDIES ON NORTH AMERICAN QUATERNARY BRYOPHYTE SUBFOSSILS
I. A NEW MOSS ASSEMBLAGE FROM THE TWO CREEKS FOREST BED OF WISCONSIN[1]

NORTON G. MILLER[2]

SUMMARY

Plant fossils in an exposure of Two Creeks Forest Bed peat about 11,850 years old, near Green Bay, Wisconsin, include 32 species of mosses representative of a variety of forest and nonforest habitats. The assemblage, which contains few aquatics and many calciphiles, establishes that a diverse flora of temperate, boreal, and arctic mosses occurred in northwestern Wisconsin just prior to and during active glaciation. Most of the mosses identified presently grow in Wisconsin or elsewhere in the upper Great Lakes area, but two, *Aulacomnium turgidum* and *Hypnum bambergeri*, now rarely occur farther south than arctic and subarctic regions. Present-day occurrences of some of these species in the Great Lakes region may, in part, date from the period when forest bed sediments accumulated. The represented vegetation, an open, more or less dry *Picea glauca* woodland with rich fens and dry sites, perhaps on dune sand, is inferred from pollen spectra, mosses, cones, seeds and twigs obtained from the peat.

The Two Creeks Forest Bed is a buried organic deposit first described in detail from exposures along the shore of Lake Michigan near the base of the Door Peninsula in northeastern Wisconsin. The forest bed contains a record of vegetation and soil that developed during an ice-free period between two glacial advances late in Wisconsinan time. Both glaciations overrode northeastern Wisconsin leaving behind tills which under- and overlie the forest bed. These deposits, the buried forest bed, and associated sediments contain a record of environmental conditions that may extend back 14,000 radiocarbon yrs B.P. The forest bed is generally considered to represent part of the interval between 11,000 and 12,500 yrs B.P. (Black, 1970).

Paleobotanical and paleoenvironmental studies of the buried forest were first carried out by Wilson (1932, 1936) who provided a comprehensive analysis of the deposits and their contained fossils. Foremost among plant materials recovered were mosses, 19 of which were identified in forest bed peats and clays from two sites (Cheney, 1930, 1931; Wilson, 1936). The orientation and manner of growth of certain mosses in the

[1] The first in a series aimed at providing a better understanding of the development of distribution patterns of North American bryophytes during Pleistocene and Holocene times. The usual American usage of Holocene, i.e., postglacial time, which extends from about 10,000 yrs Before Present (B.P.) to now, is being followed, even though some feel that the "postglacial" is best treated as a subdivision of the Pleistocene. Because the geologic setting and general paleobotany of deposits containing fossil Bryophyta help to determine what environmental conditions prevailed when burial occurred, these topics are treated to some extent also. To document the sometimes fragmentary remains of bryophytes encountered in Quaternary sediments, illustrations or citations of published drawings of fossil material are generally provided. The term subfossil indicates that specimens, though found in a fossil context, are not petrified or coalified, but consist of essentially unaltered tissues that almost always lack cellular contents.

[2] Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138

deposits, distribution of species within the sediments, and the preponderance of aquatic and subaquatic mosses facilitated reconstruction of the plant communities represented and geological events associated with deposition of the upper till. Culberson (1955) also studied mosses in the forest bed and reported species not previously found. In addition, mosses are mentioned by Schweger (1969) as occurring in a deposit of Two Creeks peat about 50 km northwest of exposures along the Lake Michigan shore. The vegetation of northeastern Wisconsin during Two Creeks time, based on pollen analysis, has been treated by West (1961) and Schweger (1969).

LOCATION AND GEOLOGIC SETTING

The forest bed exposure under consideration occurs in Scott, Wisconsin, mostly in the southwest quarter of Sect. 23, T. 24 N. / R. 21 E., on the Norbert F. Peters farm, about 6.5 km northeast of the city of Green Bay. According to unpublished data assembled by the late F. T. Thwaites when he visited the pit on 30 June and 1 July 1958, the sediments were exposed on a north-south trending wall of a borrow pit, then about 75 m long and 10 m deep (Fig. 1 & 2). The topmost deposit was a pale red glacial till, the base of which was fairly level and not over 2.5 m below the top of the exposure. Sediments below the till, however, were mixed and were not organized into horizontal strata to any great extent. At certain places dark red, obscurely stratified clay occurred immediately beneath the till, but at others sand was present. Thwaites' manuscript notes record that peat, associated logs, and other woody materials (Fig. 2) occurred intermixed with the clay at an isolated position along the wall. However, in 1957, Pfleger (Rubin & Alexander, 1960, p. 153) noted an organic rich silt and sand layer about 2 m thick with tree trunks and forest litter below the till. Since active digging was going on at this time, these observations indicate the organic bed and associated sediments were variable laterally. Red clay also underlies the peat, but sediments beneath this clay were covered or remained unexcavated, and therefore are not described in information available to me.

Stratigraphic relationships at the Peters' borrow pit are less clear than at comparable exposures along the western shore of Lake Michigan, but Thwaites (ms. notes) interpreted deposits in the two areas similarly. He considered sediments at the pit to have been laid down in a lake impounded in front of the ice that produced the upper till. In his opinion, the peat-log mass was rafted in because of the absence of roots in the position of growth. R. F. Black, who studied the site several times in the 1960's, interprets (in litt.) the organic matter as having been incorporated into lake sand when the rising lake level drowned the forest in front of the advancing ice. He notes that none of the trees were in growth

FIG. 1. Sediments exposed on west-facing north-south wall of borrow pit near Green Bay, Wisconsin, summer 1958. Organic deposit about midway up the wall. (Photograph courtesy of H. H. Iltis.)

FIG. 2. Close-up of most of the organic deposit showing logs and other woody material; deformed peat layer visible at left. Summer 1958. (Photographs courtesy of H. H. Iltis.)

position and that the organic bed was folded and disturbed greatly by the overriding ice. Although these workers indicate possible redeposition of organic materials, some of the blocks of sediment I studied have an unmixed vertical succession of species that is consistent with a shift from more or less dry and open forest communities to those that are wetter. At least part of the forest bed, therefore, appears to have been preserved as it had accumulated.

The following age determinations have been published for wood associated with peat in the borrow pit: 11,940 ± 390 yrs B.P. (Y–147X, Preston *et al.*, 1955, p. 958) and 11,140 ± 300 yrs B.P. (W–590, Rubin & Alexander, 1960, p. 153). These determinations agree favorably with the generally accepted age of the Two Creeks Forest Bed, 11,850 ± 100 yrs B.P. (Broecker & Farrand, 1963), which has been taken by some to mark the end of Twocreekan time (Black & Rubin, 1968).

To summarize, the Two Creeks forest developed on lacustrine sediments deposited out of a lake that stood higher than the present level of Lake Michigan. The lake beds accumulated on till whose precise age is not known but is often correlated with an advance of the late Woodfordian Cary ice or a somewhat more recent readvance. This lower till was not recorded at the Peters' borrow pit but can be seen along the shore of Lake Michigan and elsewhere in the immediate area. Forest became established on the lake sediments following a lowering of the lake level, and soil development and peat accumulation occurred. Glacier ice readvanced into the region about 11,850 yrs B.P. causing the lake level to rise and destroy the forest. Lacustrine sediments accumulated on top of the soil for some time following this date. Ice later spread over northeastern Wisconsin and then receded, leaving behind a deposit of reddish drift generally considered to correlate with the Valders till, described from somewhat farther south in Wisconsin. Recent data published by Evenson (1973) indicate that till above the forest bed is younger than the Valders, although this interpretation has been contested by Black (1974; see also Evenson *et al.*, 1974). Evenson (1973) has proposed the name Two Rivers till for that present above the Two Creeks forest bed.

METHODS

Ten large, dry blocks of sediment (*ca.* 20 × 10 × 10 cm) were placed individually in beakers, covered with a solution of 0.5% trisodium phosphate and heated gently to loosen clays and silts and rewet the plant materials (Benninghoff, 1947). Inorganic materials were washed from the organic fraction through a small mesh sieve with distilled water after about 3 hr of treatment. Residues were soaked for several hours in distilled water to leach out all trisodium phosphate and were bottled in distilled water or 70% ethyl alcohol until studied microscopically.

To determine the variability of residues, subsamples removed from a well-mixed slurry of the wet fossil material were separated into their component species. The area occupied by individual taxa was determined by measuring a tightly packed layer of fragments, one plant deep, using a grid divided into square centimeters. This procedure was repeated twice for two residues to establish the reproducibility of the sampling method, and data from three additional sediment blocks were gathered. Data for individual samples were calculated in percentages.

A sample of the organic material cut from the center of a dry sediment block was analyzed for pollen following procedures outlined in Faegri and Iversen (1964). Pollen counts from inorganic sediments were not made because of possible contamination and uncertainty about the original orientation of sediment blocks in the exposure.

RESULTS

A compact moss layer, resting directly on an accumulation of forest litter or soil, occurred in each sediment block. The combined thickness of the organic material varied from sample to sample but the maximum noted was 5 cm. Intermixed clays and silts were absent except for a small amount of inorganic sediment found with plant fragments along the upper and lower limits of the organic layer. No plant fossils were found embedded in the silts and clays which under- and overlie the organic horizon.

Pollen analysis and vascular plant megafossils. Pollen counts obtained from samples of the thin (*ca.* 3 cm thick) moss layer in two sediment blocks are given in Table 1. The principal trees represented are spruce (*Picea* spp.) and tamarack (*Larix laricina*) which together account for about 80% of the percentage base. Pine pollen is nearly absent. About 15% of the sum consists of various nonarboreal (NAP) taxa, especially members of the Cyperaceae, which comprise about one-half of the NAP totals. These pollen assemblages agree with results obtained by West (1961) from samples of Two Creeks peat exposed along the shore of Lake Michigan, with the exception of somewhat higher spruce (80%) and lower Cyperaceae (usually < 5%) representation in most of his spectra. A pollen spectrum in Schweger (1969) from sediments at the borrow pit contains much less spruce (*ca.* 40%) and more Cyperaceae and Gramineae (*ca.* 45%) than either spectra reported here. Though differing quantitatively, the counts are similar in terms of pollen types represented, and the differences probably relate to the mixed nature of the "composite sample" Schweger processed (i.e., peat and organic silt mixed). My analyses were of single, relatively thin, strata.

The organic bed contains abundant cones, twigs and needles of spruce and tamarack (Fig. 3–9). Seeds of the two genera were also found, but no other seeds (or fruits) were noted. Although some spruce cones are

Table 1. POLLEN CONTENT OF MOSS LAYER AT THE PETERS' BORROW PIT, BROWN CO., WISCONSIN

AP[a]	Sample 1 n	Sample 1 %	Sample 2 n	Sample 2 %
Pinus	2	0.6	2	0.5
Picea	241	68.5	271	71.5
Larix	31	8.8	35	9.2
Betula	—	—	1	0.3
Carpinus-Ostrya	—	—	2	0.5
Quercus	4	1.1	1	0.3
Carya	1	0.3	1	0.3
Ulmus	1	0.3	1	0.3
Populus	9	2.6	10	2.6
AP totals	289	82.1	324	85.5
NAP[a]				
Alnus	—	—	1	0.3
Myrica	—	—	1	0.3
Salix	7	2.0	2	0.5
Cyperaceae	23	6.5	24	6.3
Gramineae	8	2.2	11	2.9
Ambrosia	7	2.0	7	1.8
Artemisia	7	2.0	5	1.3
Xanthium	1	0.3	—	—
High-spine Compositae	10	2.8	4	1.1
NAP totals	63	17.9	55	14.5
MISC[b]				
Polypodiaceae	3	0.8	7	1.7
Moss spores	—	—	1	0.2
Unidentifiable	24	6.4	17	4.2

[a] Percentage base = sum arboreal pollen (AP) + nonarboreal pollen (NAP)
[b] Percentage base = sum AP + NAP + MISC

FIGS. 3–9. Cones and twigs from Two Creeks peat at Peters' borrow pit.—3–5. Cones of *Picea glauca* (Moench) Voss.—6. Probable cone of *Picea mariana* (Mill.) B.S.P.—7–8. Cones of *Larix laricina* (DuRoi) K. Koch.—9. Twig of *Larix laricina*.

small for the species, most were identified as white spruce (*Picea glauca*) because the cones are at least two times longer than broad and their scales have entire margins. Because cones beneath living white spruce trees are somewhat variable in size and may be decayed to the point that the scale margins are no longer entire, identifications were made using only well-preserved specimens. About nine of every ten cones in the sediment blocks were of *P. glauca*, the remainder being assignable to *P. mariana*.

Bryophyte remains. Mosses in some sediment blocks were preserved mostly as unfragmented plants, indicating that water transport was minimal and that *in situ* burial probably occurred. Other sample residues contain mixtures of species from different habitats, and in these cases it seems likely that the assemblage was brought together by moving water. No liverworts were found.

In order to determine species composition at various levels in the organic bed, two sediment blocks showing clay—moss/forest litter—clay layering were cut in two vertically and the cut edges were soaked in water to facilitate examination. A compact, peaty forest litter, 3 to 4 cm thick was present in both blocks. Materials of *Drepanocladus uncinatus* and *Thuidium abietinum* (subordinate) occurred near the top of the litter, together with cones and needles of white spruce and tamarack. While both of these mosses occur in a variety of nonforest habitats, *D. uncinatus* is a typical species of moist to dry conifer stands, and *T. abietinum* is sometimes found in open white spruce forests on dry soil. Downward in the litter, the mosses drop out and the amount of degraded plant material increases. Above the forest litter and on top of the mosses was a dense mat of *Tomenthypnum nitens,* which generally occurs in wet, calcareous habitats that can be forested or open. Relatively few conifer needles and no cones were found with this moss, indicating a decline in the abundance of trees at the site. A shift from more or less dry to wetter conditions indicates a rise in the water table possibly relating to flooding associated with the advance of glacier ice or to periglacial activity.

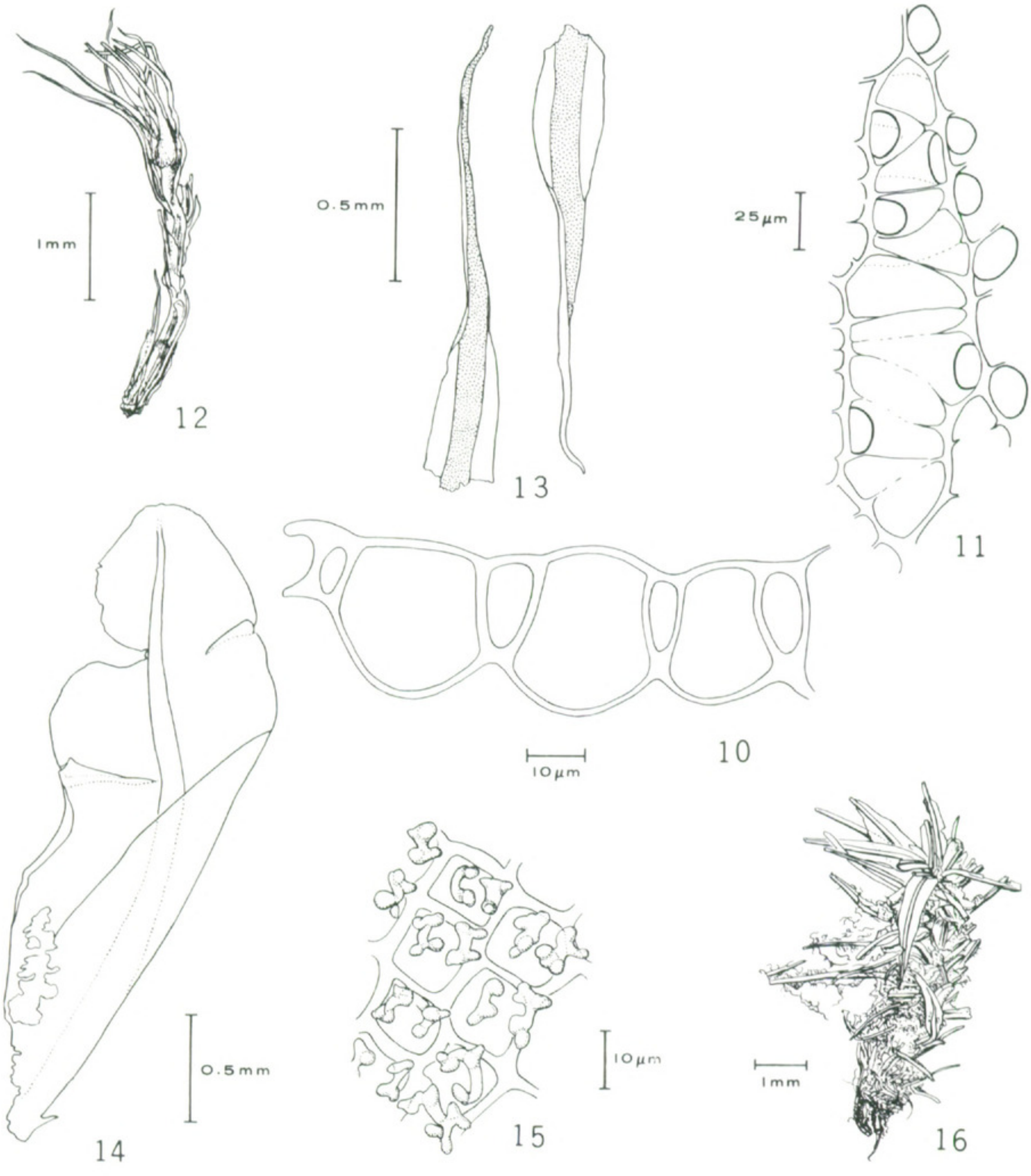
Variability in the composition of moss assemblages obtained from five sediment blocks is given in Table 2. Three of the samples yielded fifteen or more species while two had eight or nine. Some species occur in all samples but others are present in just one or a few. Four samples are dominated by *Tomenthypnum nitens* and from one to seven subdominant species occur with it. About half of the identified species are rare either in a given sample or in all examined materials. It is tempting to conclude that numerical relationships between species listed in the table also held in nature. However, the percentage values, which though similar to field determined estimates of percent cover, are not strictly comparable to measurements of abundance in nature for at least two reasons: sample residues are in part mixtures of species from distinct communities that may have existed at different times, and it is impossible to reconstruct the orientation of the mosses as they actually grew, therefore making measurements of area only an approximation of the original situation.

Mosses identified in the forest bed are given below, with an indication of their abundance in the residues. The following scale is used: rare—10 or fewer fragments; sparse—11 to 20; rather abundant—21 to 40; abundant—41 to 60; and very abundant— > 60. A fragment varied from isolated leaves to leafy branches to essentially complete plants. Notes are also given on the present distribution of identified taxa (particularly in the Great Lakes region), diagnostic characteristics and the occurrence of structures associated with the sexual reproductive cycle (e.g., archegonia, antheridia, sporophytes, etc.). Unless otherwise specified, a record documenting a recent collection of the species in Wisconsin has been found (see Cheney & Evans, 1944; Forman, 1967). Species indicated by an asterisk have not been previously reported from the forest bed. Crum's recent book (1973) on the mosses of northern Michigan contains helpful notes on the habitat preferences of many of the species found in the forest bed.

TABLE 2. AREAS (PERCENT COVER) OCCUPIED BY MOSS SUBFOSSILS IN SAMPLES ONE TO FIVE

Sample–Subsample Designation	1		2		3	4	5
Species	a*	b*	a*	b*			
Tomenthypnum nitens	67.9	67.2	54.7	52.8	70.3	83.8	13.9
Bryum pseudotriquetrum	7.7	7.3	10.1	12.2	0.8	0.3	3.3
Campylium polygamum	8.8	6.4	9.1	11.2	6.3	7.6	9.0
C. stellatum	1.6	1.8	8.1	6.1	6.3	trace	3.3
Brachythecium turgidum	—	0.2	5.1	4.1	—	—	34.4
Ditrichum flexicaule	1.1	1.8	4.1	4.1	9.3	—	16.4
Drepanocladus uncinatus	4.4	9.1	—	—	3.9	1.3	—
Thuidium abietinum	5.5	3.6	—	—	—	6.7	16.4
Hylocomium splendens	1.1	0.5	—	—	2.3	—	—
Scorpidium turgescens	—	—	—	—	0.8	—	—
Hypnum bambergeri	—	—	4.1	4.6	—	—	—
Distichium capillaceum	trace	trace	3.0	4.1	—	—	2.5
Drepanocladus aduncus var. *polycarpus*	—	—	1.5	1.0	—	trace	—
Eurhynchium pulchellum	0.7	0.9	—	—	—	—	—
Amblystegium serpens	0.5	0.4	trace	—	—	0.3	0.2
Tortella fragilis	—	0.5	trace	—	—	—	—
Drepanocladus sp.	—	—	—	—	—	—	0.4
Bryoerythrophyllum recurvirostrum	—	—	0.2	—	—	—	—
Dicranella heteromalla	0.2	0.2	—	—	—	—	—
Mnium marginatum	0.2	0.2	—	—	—	trace	—
Tortella sp.	0.2	—	trace	trace	—	—	trace
T. tortuosa	—	—	—	—	—	—	0.2
Myurella julacea	—	—	trace	trace	—	—	trace
Encalypta procera	—	—	trace	trace	—	—	trace
Aulacomnium palustre	—	—	—	—	—	—	trace
A. turgidum	—	—	—	—	—	—	trace
unknown	—	—	—	—	—	—	trace
TOTALS	99.9	100.1	100.0	100.2	100.0	100.0	100.0

*From samples analyzed for pollen



FIGS. 10–16. Subfossil mosses from Two Creeks peat at Peters' borrow pit.—10. *Sphagnum papillosum* Lindb., cross section of branch leaf.—11. same, hyaline cell and pores, outer face of branch leaf.—12. *Dicranella heteromalla* (Hedw.) Schimp., plant with apical antheridial cluster.—13. same, two leaves.—14. *Encalypta procera* Bruch., leaf.—15. same, cells and papillae from upper part of leaf.—16. *Tortella fragilis* (Drumm.) Limpr., plant with leaf tips mostly broken off.

**Sphagnum papillosum* Lindb.—Rare, one branch leaf only. Identified on the basis of trapezoidal chlorophyllose cells, which are broader on the inner than outer face, presence of a resorption furrow, and hyaline cells with relatively few pores. No papillae occur on the inner lateral walls of hyaline cells, making the material var. *laeve* Warnst. A fairly common, widespread species in the Great Lakes region. Fig. 10 & 11.

Ditrichum flexicaule (Schwaegr.) Hampe—Abundant, leafy plants matted together or solitary, in one case intermingled with *Bryum pseudotriquetrum*, *Campylium stellatum* and *Tortella fragilis*. Not known to occur in Wisconsin but present in the Straits of Mackinac region, Michigan. Fossil material from New York State is illustrated in Miller (1973).

Distichium capillaceum (Hedw.) B.S.G.–Abundant, gametophytic materials only. Referred here with fair certainty, but the related *D. inclinatum* (Hedw.) B.S.G., which differs primarily on the basis of sporophyte characters, may also be present. Forman (1967) cites collections of *D. capillaceum* from rotting logs and soil at forested sites on the Door Peninsula. Fossil material illustrated in Miller (1973).

**Dicranella heteromalla* (Hedw.) Schimp.–Rather abundant. Not reported before from North American Quaternary deposits. Some specimens bear antheridia. Fig. 12 & 13.

Encalypta procera Bruch–Rather abundant, occurring mainly as isolated leaves or as stem fragments with few leaves, only one large leafy plant found. Preservation fair; upper leaf cells with forked papillae; lower hyaline, nonpapillose cells mostly decayed. All leaves lack any indication of an awn; filiform brood bodies are absent. No doubt still a member of the Wisconsin flora, since records of *Encalypta streptocarpa* Hedw. in Cheney and Evans (1944) probably refer to *E. procera.* Apparently not recognized previously as a fossil in North America. Fig. 14 & 15.

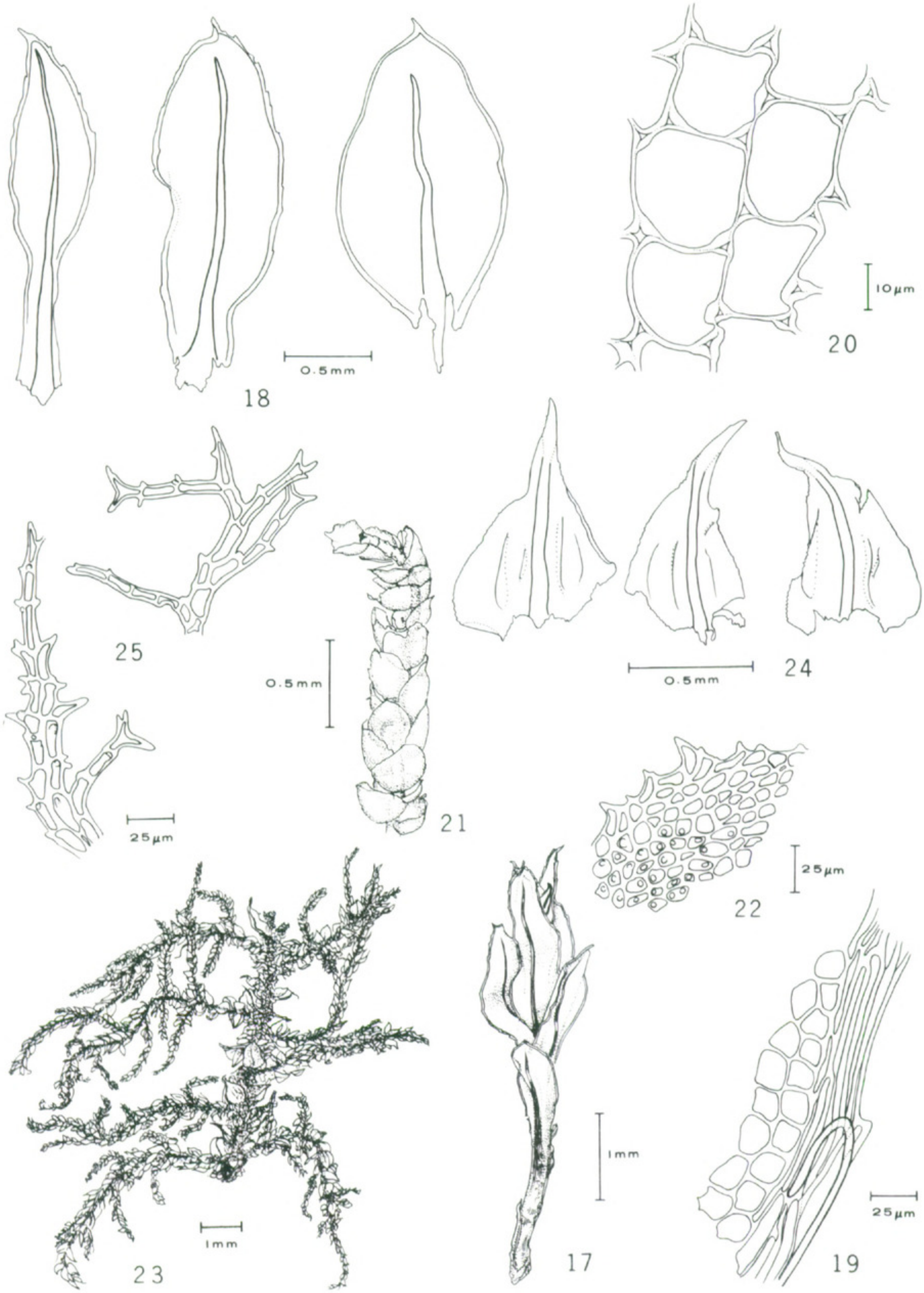
**Trichostomum tenuirostre* (Hook. & Tayl.) Lindb.–Rare, eight well-preserved leafy plants. The specimens agree well with most herbarium collections so-named, but North American materials of *Trichostomum* need revision. Leaves of the fossil specimens clearly show the typical region of basal hyaline cells that do not extend up the margin as in *Tortella.* Apparently unknown in the present flora of Wisconsin but occurring in the Upper Peninsula of Michigan. No records of its fossil occurrence in North America are known to me.

Tortella fragilis (Drumm.) Limpr.–Sparse, mostly leafy plants, a few with setae, and several isolated leaves. An infrequent moss of calcareous situations in the Great Lakes region. Fig. 16.

**T. inclinata* (R. Hedw.) Limpr.–Rare, three plants, somewhat poorly preserved but with certain leaves showing the characteristic concave, ± cucullate apex. A rare moss in the Great Lakes area where it has been collected most often on dune sand. Unknown from Wisconsin but reported from several counties bordering the Straits of Mackinac, Michigan. A previous fossil record exists from northwestern New York State in a deposit a few hundred years older than the Two Creeks Forest Bed (Miller, 1973, q.v. for illustrations of fossil material).

T. tortuosa (Hedw.) Limpr.–Rather abundant, leafy plants, preservation generally good. This species and *T. fragilis* are known from recent collections made in Door County, Wisconsin, at stations near the fossil bed. Illustrations given in Miller (1973).

**Bryoerythrophyllum recurvirostrum* (Hedw.) Chen–Sparse, somewhat degraded leafy plants. Fossil material illustrated in Miller (1973).



FIGS. 17–25. Subfossil mosses (cont.).–17. *Mnium marginatum* (With.) Brid. ex P. Beauv., plant.–18. same, three leaves from same plant.–19. same, leaf margin with a paired teeth.–20. same, upper leaf cells.–21. *Myurella julacea* (Schwaegr.) B.S.G., fragment of plant.–22. same, edge of leaf with teeth and papillose cells.–23. *Thuidium recognitum* (Hedw.) Lindb., nearly complete plant.–24. same, stem leaves from same plant.–25. same, paraphyllia.

**Tortula ruralis* (Hedw.) Gaertn., Meyer & Scherb.—Rare, two leaves. Identification probable but the characteristic roughened awn is poorly preserved. A common calciphile usually of open, ± dry situations throughout the Great Lakes area. Illustrations in Miller (1973).

Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.—Abundant, leafy plants and a few isolated leaves. Many plants were found matted together, and some individuals in such clumps carried a broken seta. Sporophyte bearing plants were searched for archegonia and/or antheridia, but out of approximately 25 specimens, only two could be shown to be synoicous and two dioicous (only archegonia seen). Plants of the two types were not intermixed in the same clump. One plant with a terminal antheridial cluster was also found. Dioicous collections of this species are sometimes referred to var. *pseudotriquetrum* and synoicous ones to var. *binum* (Schreb.) Lilj. Other species of *Bryum* may be present in the fossil materials, but in the absence of capsules and peristomes, identifications could not be made. Leaves of fossil *B. pseudotriquetrum* from New York State are illustrated in Miller (1973).

**Mnium marginatum* (With.) Brid. ex P. Beauv.—Rather abundant, leafy plants and isolated leaves, preservation good but the double row of teeth along the leaf margin difficult to demonstrate. A few isolated leaves were broadly ovate (cf. Fig. 18). Upper leaf cells of fossil material are ± quadrate with thickened corners and vary in size from 20–28 μm. A widespread species in the Great Lakes region where it grows on soil and rock in open or more dense forests. Fig. 17–20.

**Aulacomnium palustre* (Hedw.) Schwaegr.—Rather abundant, leafy plants and isolated leaves, small marginal teeth sometimes apparent toward the leaf apex. A common moss in temperate and boreal America; occurring in a variety of usually moist to wet habitats including forests and open areas.

**A. turgidum* (Wahlenb.) Schwaegr.—Rare, one leaf-bearing stem tip and eight isolated leaves. Fossil materials identified as this species of *Aulacomnium* because the leaf apices are obtusely rounded and somewhat hooded. A predominantly arctic and subarctic moss in North America, and apparently not a member of the present flora of Wisconsin, the species occurs disjunctively near the north shore of Lake Superior. Fossil material of the species 12,100 yrs old is known from northwestern New York State (Miller, 1973, q.v. for illustrations); the species has been found in interglacial deposits on Banks Island, arctic Canada (Kuc, 1974).

**Orthotrichum obtusifolium* Brid.—Rare, two plants, preservation fair. Leaves of the fossils have bluntly rounded apices, unipapillose cells and plane margins. No brood bodies were seen. Identification probable but not positive because the fossil leaves in general have a shorter costa than that present in herbarium material. *Orthotrichum obtusifolium* occurs widely in north temperate and southern boreal North America, where it is a fairly common epiphyte, particularly on bark of species of *Populus* (Vitt, 1973), pollen of which occurs in the forest bed peat. The genus has apparently not been reported before from North American Quaternary deposits.

**Myurella julacea* (Schwaegr.) B.S.G.—Sparse, stem fragments with leaves, preservation fair to good. An uncommon species in the Great Lakes area where it grows on moist soil in forests, especially *Thuja* swamps, and sometimes on rock (e.g., crevices in cliffs) in ± open woods. No other North American Quaternary fossil occurrences are known. Fig. 21 & 22.

Thuidium abietinum (Hedw.) B.S.G.—Abundant, large plants and fragments, leaves sometimes decayed from stems and branches. Known from several Quaternary deposits elsewhere in North America.

**T. recognitum* (Hedw.) Lindb.—Abundant, complete plants and large fragments. Fossil material agrees in all characters with herbarium specimens. Not known with certainty from other North American Quaternary deposits. This moss and *T. abietinum* have been collected on the Door Peninsula and have a wide distribution in the Great Lakes area and elsewhere in North America. *Thuidium recognitum* occurs at open sites on soil and rock and less frequently in dry to moist, ± open forests. Fig. 23–25.

**Campylium polygamum* (B.S.G.) C. Jens.—Very abundant, leafy plants. Widely distributed in North America; in the Great Lakes region occurring on soil in bog forests, swamps, and wet open areas. Fig. 26 & 27.

C. stellatum (Hedw.) C. Jens.—Abundant, fossil materials sometimes recognizable at a glance by their rich, coppery brown color, but otherwise determinable by the leaves which have a short double costa (*vs.* costa strong and single in *C. polygamum*). Extending northward from the temperate zone in North America, *C. stellatum* often grows in ± open, calcareous habitats, especially rich fens, but also sometimes at forested sites. Fig. 28 & 29.

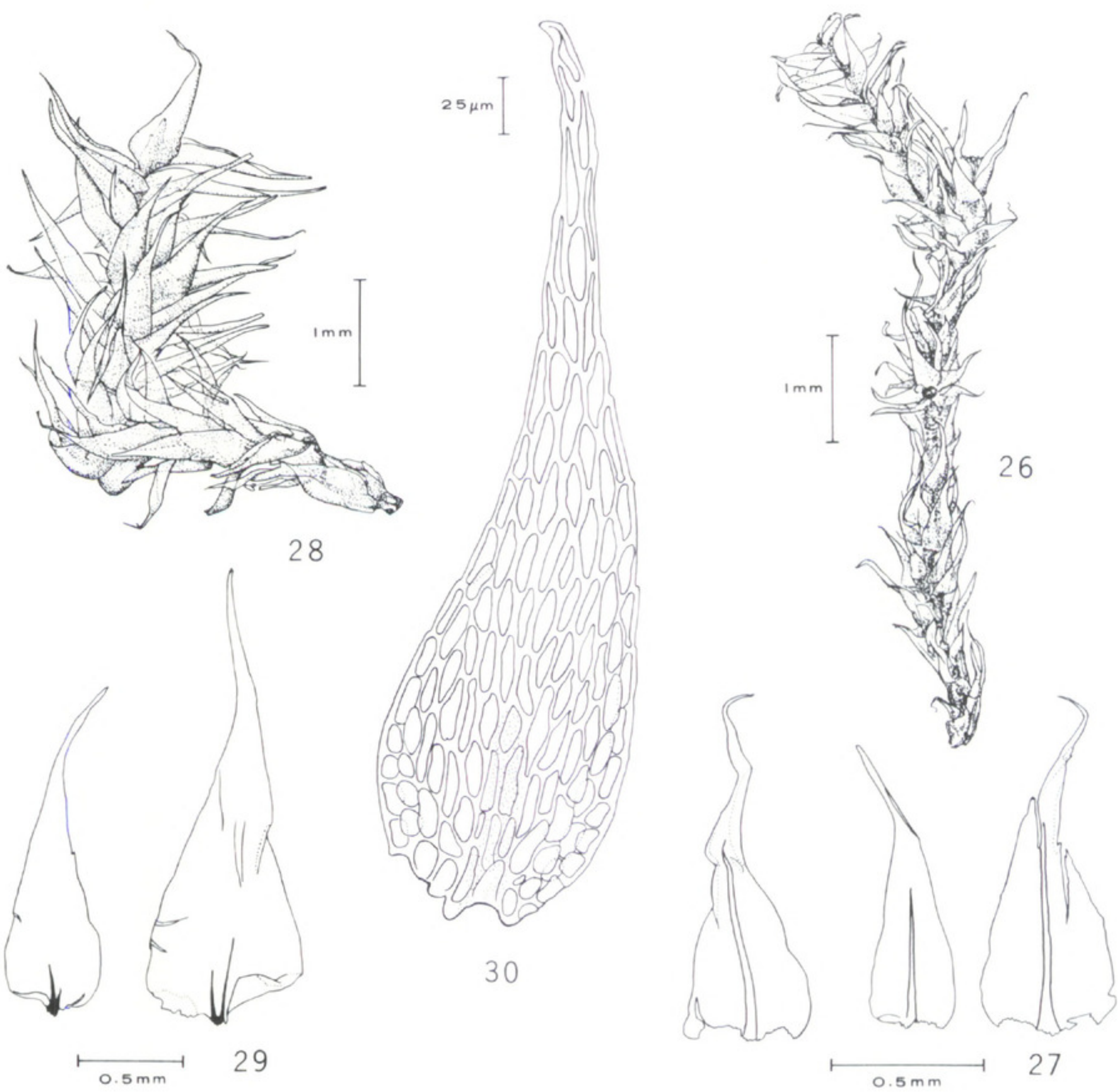
**Amblystegium serpens* (Hedw.) B.S.G.—Abundant, leafy stems mixed with other mosses or solitary. A common, widespread species of wet places, often on soil or rotting wood, in both forest and nonforest habitats. Not apparently recorded before as a subfossil in North America. Fig. 30.

Drepanocladus aduncus var. *polycarpus* (Bland. ex Voit) Roth—Rather abundant, leafy plants. An aquatic or semiaquatic moss, usually of open or wooded calcareous places, found throughout the Great Lakes region and northward. The variety is not known from other deposits of the forest bed, although vars. *aduncus* and *pseudofluitans* Sanio occurred in Wilson's samples (Cheney, 1930, 1931). Numerous reports of *D. aduncus* and some of its varieties are reported from Quaternary sediments elsewhere in glaciated portions of North America.

D. revolvens (Sw.) Warnst.—Rare, only two leafy fragments. Leaves of fossil material are nonstriolate and lack inflated alar cells. Recent collections of this and the following species have been made in Door County, Wisconsin (Cheney & Evans, 1944).

D. uncinatus (Hedw.) Warnst.—Very abundant, large fragments or intact plants, sometimes with one or several setae that lack capsules. Dense mats occurred in some sediment blocks. A common moss of open or dense boreal conifer forests; in the Great Lakes area occurring particularly in *Thuja* swamps. Fig. 31.

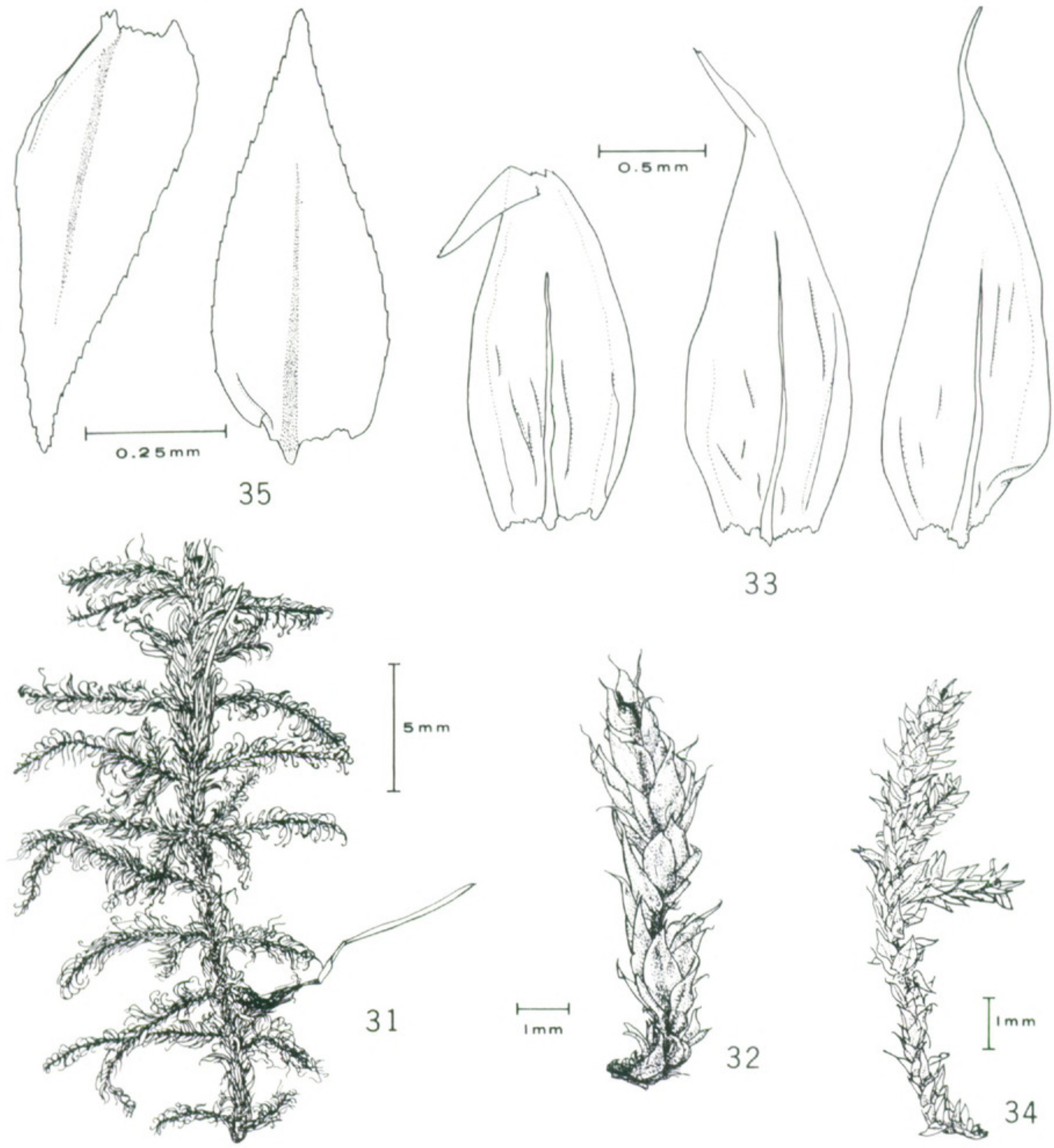
Scorpidium turgescens (T. Jens.) Loeske—Rare, two leafy plants. Unknown in the present flora of Wisconsin but found at several places in Michigan and adjacent areas, there reaching its present southern limit of distribution in central North America. Throughout its range, this moss occurs most frequently at wet, nonforest, calcareous sites, particularly rich fens. Illustrations of fossil material from New York State are in Miller (1973).



FIGS. 26–30. Subfossil mosses (cont.).—26. *Campylium polygamum* (B.S.G.) C. Jens., plant. —27. same, three leaves from same plant.—28. *C. stellatum* (Hedw.) C. Jens., plant.—29. same, two leaves from same plant.—30. *Amblystegium serpens* (Hedw.) B.S.G., leaf.

Tomenthypnum nitens (Hedw.) Loeske–Abundant, entire plants and fragments, one individual with two setae. Another calciphile, occurring in open or forested, wet habitats; found in North America from the Great Lakes region northward into the Arctic. Fossil material illustrated in Miller (1973).

**Brachythecium turgidum* (C. J. Hartm.) Kindb.–Abundant, leafy plants; large fragments (3–4 cm) have a few short branches. Stem and branch leaves are entire and in them the costa extends to just beyond the center of the leaf. Apparently unknown in the present Wisconsin flora, although the species has been collected in Michigan. Culberson (1955)



FIGS. 31–35. Subfossil mosses (cont.).–31. *Drepanocladus uncinatus* (Hedw.) Warnst., plant with two setae.–32. *Brachythecium turgidum* (C. J. Hartm.) Kindb., fragment of plant.–33. same, three leaves from same plant.–34. *Eurhynchium pulchellum* (Hedw.) Jenn., fragment of plant.–35. same, two leaves.

has reported *B. salebrosum* (Hoffm.) B.S.G. from samples of the forest bed. Fig. 32 & 33.

**Eurhynchium pulchellum* (Hedw.) Jenn.—Rather abundant, branched leafy plants and isolated branches. A species widespread in North America that usually grows on soil and rotting logs in forests; also extending northward to the tundra. A common moss of *Thuja* swamps and bog forests in the upper Great Lakes region. Fig. 34 & 35.

**Hypnum bambergeri* Schimp.—Abundant, fragments with and without short branches. A short double costa (occasionally single) and an elevated cluster of reddish-brown, thick-walled alar cells characterize leaves of the fossils, which match recent herbarium materials in all important characters. The present North American range of this moss is limited mostly to arctic and subarctic regions. The species is an apparent calciphile. Illustrations of fossil material from the Wisconsin locality are in Miller (1976).

**Hypnum pallescens* (Hedw.) P. Beauv.—Rare, one plant with branches and several unbranched leafy fragments; identified on the basis of serrulate leaves with a double costa and quadrate alar cells. At present found widely in north temperate and boreal North America (and extending southward in the mountains), this moss occurs in forests on the bases of trees and sometimes on humus or other substrata.

**Hylocomium splendens* (Hedw.) B.S.G.—Abundant, some nearly complete plants and fragments. A common moss of moist forest soil throughout boreal North America but also found northward into the tundra and southward in mountain forests. Recent collections from places on the Door Peninsula are cited by Cheney and Evans (1944).

DISCUSSION

The vegetation cover of northeastern Wisconsin during Two Creeks time has been interpreted as closed canopy spruce forest (West, 1961) or open boreal woodland (Schweger, 1969), two more or less floristically similar vegetation types occurring today at places in the North American boreal forest. Local variation in Twocreekan plant communities existed because fossil assemblages from different deposits vary in composition. Spruce, however, is uniformly the major arboreal component. Pollen or cones of white spruce predominate in some instances (West, 1961; this report); black spruce is more abundantly represented in others (Schweger, 1969; Wilson, 1936). In present-day boreal America white and black spruce usually occupy dry and wet soil sites respectively, and the same situation no doubt prevailed during Two Creeks time. Nonarboreal pollen (NAP) totals, indicative of the amount of open, nonforest vegetation, also vary. Spectra from some samples have as little as 5% NAP, others contain 20–25% or more. The existence of communities with herbs and shrubs is compatible with white and black spruce forests because similar mixtures of nonforest and forest vegetation now occur in parts of boreal America.

At the Peters' borrow pit megafossil material of white spruce is most abundant and lesser quantities of tamarack and black spruce occur. Forest communities on drier soil types must therefore have been prominent in the area during accumulation of forest bed sediments. Nonarboreal pollen is also sufficiently abundant to indicate the presence of plant communities containing or perhaps dominated by herbs, especially members of the Cyperaceae. The large assemblage of mosses found in the peat (Table 3) provides a way to define the communities more precisely, since all of the mosses represent extant species whose habitat preferences are known. The species are about evenly divided between those characteristic of forests and those occurring in nonforest habitats, several of which are indicated. Species listed more than once in the table are those that exhibit broad habitat tolerances.

The forest mosses support the view that dry to moist but not wet soil conditions prevailed. Species of dense to open forest stands are present. Some of them grow on litter or rotting logs in existing spruce forests (e.g., *Drepanocladus uncinatus, Eurhynchium pulchellum, Hylocomium splendens*); others occur on mineral or humus-rich soil (*Dicranella heteromalla, Bryoerythrophyllum recurvirostrum, Mnium marginatum*). It can be inferred that similar habitats existed in forests of Two Creeks time. Two epiphytic species, *Orthotrichum obtusifolium* and *Hypnum pallescens*, were found, although the latter occasionally grows on soil or rocks also. Some of the forest mosses are calciphiles. These perhaps grew on or close to calcareous substrata beneath the forest bed. Other species typical of acid substrata indicate that humus accumulation was fairly advanced. The variety of habitats indicates well established forest and not pioneer communities.

Of the nonforest mosses recovered from the peat, species of rich fen communities, which develop in association with shallow, calcium-rich water, are well represented. The distribution and character of rich fens are less fully known in North America than in Europe, although descriptions of some to the west of James Bay, Canada, are available (Sjörs, 1961, 1963; and Persson & Sjörs, 1960, for ecological data on mosses in this region). Species characteristic of wetter areas of rich fens are separated in the table from those often occurring in drier parts and emphasize the relative scarcity of aquatic mosses in the peat samples. The predominantly aquatic moss genera *Calliergon, Drepanocladus* and *Scorpidium* are better represented in forest bed exposures along the shore of Lake Michigan (Wilson, 1932, 1936) than at the borrow pit, perhaps indicating a greater abundance of poorly drained sites in the former area during Two Creeks time. A few mosses listed in the fen margin category (e.g., *Aulacomnium palustre, A. turgidum, Sphagnum papillosum*) prefer more acid substrata,

TABLE 3. SUBFOSSIL MOSSES, FROM TWO CREEKS FOREST BED EXPOSED AT PETERS' BORROW PIT, BROWN COUNTY, WISCONSIN, BY HABITAT TYPE

Forest: mostly humus or mineral soil	
Dicranella heteromalla	*Campylium polygamum*
Bryoerythrophyllum recurvirostrum	*Amblystegium serpens*
Bryum pseudotriquetrum	*Drepanocladus uncinatus*
Mnium marginatum	*Eurhynchium pulchellum*
Orthotrichum obtusifolium (tree bark)	*Hypnum pallescens* (tree bark)
Thuidium abietinum	*Tomenthypnum nitens*
T. recognitum	*Hylocomium splendens*
Nonforest: rich fen, aquatic or semiaquatic	
Campylium stellatum	*Scorpidium turgescens*
Drepanocladus aduncus var. *polycarpus*	*Tomenthypnum nitens*
D. revolvens	
Nonforest: fen margin, ± moist, mostly calcareous	
Sphagnum papillosum	*Aulacomnium turgidum*
Dicranella heteromalla	*Myurella julacea*
Distichium capillaceum	*Campylium polygamum*
Ditrichum flexicaule	*C. stellatum*
Tortella fragilis	*Amblystegium serpens*
Bryoerythrophyllum recurvirostrum	*Tomenthypnum nitens*
Bryum pseudotriquetrum	*Brachythecium turgidum*
Mnium marginatum	*Hypnum bambergeri*
Aulacomnium palustre	
Nonforest: moist rocks or mineral soil	
Distichium capillaceum	*Trichostomum tenuirostre*
Encalypta procera	*Mnium marginatum*
Tortella fragilis	*Aulacomnium turgidum*
Bryoerythrophyllum recurvirostrum	*Myurella julacea*
Nonforest: ± xeric, well-drained soil, e.g., sand	
Tortella tortuosa	*Thuidium abietinum*
T. inclinata	*T. recognitum*
Tortula ruralis	

and these perhaps grew on ± dry peat hummocks or other noncalcareous sites within fens. Mosses limited to rock or mineral soil in open or semi-forested situations were few (e.g., *Encalypta procera, Trichostomum tenuirostre*), although certain other species present in the peat sometimes grow in these habitats. The small group of mosses generally characteristic of xeric, open areas may have grown on well-drained dune or beach sand, which probably accumulated during fluctuations in the level of the lake then occupying the Lake Michigan basin.

Peat samples from the Peters' borrow pit have yielded a moss flora consisting of 32 extant species. The following seven additional mosses have been reported by previous workers from other exposures of the forest bed (Cheney, 1931, 1932; Culberson, 1955): *Brachythecium salebrosum* (Web. & Mohr) B.S.G., *Bryum tortifolium* Funck ex Brid., *Calliergon cordifolium* (Hedw.) Kindb., *C. stramineum* (Brid.) Kindb., *Drepanocladus sendtneri* (Schimp.) Warnst., *D. vernicosus* (Lindb. ex C. Hartm.) Warnst. and *Scorpidium scorpioides* (Hedw.) Limpr. No one ecological grouping of species dominates the flora, although aquatic or semiaquatic mosses may be more abundant at some localities. All species except seven are present members of the Wisconsin flora. Of these, however, five are known at stations in northern Michigan (Crum, 1973), and it is probable that they also occur in Wisconsin. Based on records cited in Cheney and Evans (1944) and Forman (1967), 16 of the 39 species (41%) are represented by recent collections from Brown, Door, Kewaunee and Manitowoc counties, which comprise the Door Peninsula.

Two mosses that occur in the borrow pit peat, *Aulacomnium turgidum* and *Hypnum bambergeri*, are far out of place based on their present ranges. While several disjunct stations for the former are known in the Thunder Bay District of Ontario, about 500 km north of Green Bay, the southern limit of its continuous distribution in North America roughly coincides with the northern edge of the boreal forest. The species also occurs southward in alpine regions both in the East and West. Found as far south as the Gaspé Peninsula, Quebec, in the East and near Banff, Alberta, in the West, *Hypnum bambergeri* also has a predominantly arctic and subarctic distribution in North America. Based on material in five herbaria (CANM, FH, MICH, NY, US), this moss presently is found no farther south in the midcontinent region than northern Manitoba, some 1200 km north of the fossil occurrence.

The presence of arctic and subarctic mosses in Wisconsin during Two Creeks time with others still found in the upper Great Lakes region and to the south is phytogeographically important. Such a mixed assemblage establishes that the Two Creeks flora was composed of species of different current geographical affinities. Existing disjunct stations for certain arctic species in the upper Great Lakes area may thus relate to Two Creeks time when such northern species occurred beyond their present ranges.

Other arctic and subarctic mosses present as fossils in deposits about 12,100 and 13,300 years old in northern Michigan and northwestern New York State are discussed in Miller (1973) and Miller and Benninghoff (1969).

While 95% of the Twocreekan moss flora of northeastern Wisconsin is still represented in this area or nearby, some of the calcicolous species currently are rare in the upper Great Lakes region and attain their greatest abundance northward. Certain of them and other species of similar distribution also occur to the east in the two deposits mentioned above. The species include *Catoscopium nigritum, Distichium capillaceum, Ditrichum flexicaule, Meesia uliginosa, Myurella julacea, Tortella fragilis, Scorpidium turgescens* and others. Their presence in the assemblages indicates that much of the Great Lakes region 13,300 to 11,850 years ago was edaphically (and climatically) suited to the occurrence of such calcicolous species. Since the mosses now occur in the same general region as they did during the waning phases of glacial activity in late Wisconsinan time, their present distribution in the Great Lakes area can be viewed as an example of persistence at suitable habitats. That the species may be recent immigrants is also possible but perhaps less likely because of evidence provided by the fossil record. Similar assemblages of subfossil mosses from postglacial deposits, i.e., those less than about 10,000 years old, will help establish the more or less continuous presence of the species. This topic is more fully discussed in Miller (1976).

The moss flora of northeastern Wisconsin during Two Creeks time was surprisingly diverse considering that it developed at a time of active glaciation. However, based on the richness of the flora as it is now known, study of material from other localities will continue to add species and improve the vegetation interpretation presented here and by other workers.

ACKNOWLEDGMENTS

Samples used in this study were collected by Hugh H. Iltis (University of Wisconsin, Madison) who wishes to acknowledge with appreciation support from that university's Research Committee of the Graduate School and Dean of Letters and Sciences. Iltis had earlier discovered the organic deposit in the company of Walter Büchmann. Samples of the organic bed were sent to me through the courtesy of W. C. Steere. I am grateful to Prof. R. F. Black of the University of Connecticut and Prof. Iltis for supplying descriptions of the borrow pit and of sediments exposed there. Howard Crum and L. E. Anderson examined some of the specimens on which the moss identifications are based, and I thank them for their comments. The habit drawings of mosses are the work of Marion Seiler whose care in their preparation is appreciated.

LITERATURE CITED

BENNINGHOFF, W. S. 1947. Use of trisodium phosphate with herbarium material and microfossils in peat. Science **106**: 325, 326.

BLACK, R. F. 1970. Glacial geology of Two Creeks Forest Bed, Valderan type locality, and Northern Kettle Moraine State Forest. Wisconsin Geol. Nat. Hist. Sur. Inf. Circ. 13. 40 pp.

————————. 1974. Late Pleistocene shorelines and stratigraphic relations in the Lake Michigan basin: Discussion. Geol. Soc. Amer. Bull. **85**: 659, 660.

———————— and M. Rubin. 1968. Radiocarbon dates of Wisconsin. Trans. Wisconsin Acad. Sci. Arts Letters **56**: 99–115.

Broecker, W. S. and W. R. Farrand. 1963. Radiocarbon age of the Two Creeks Forest Bed, Wisconsin. Geol. Soc. Amer. Bull. **74**: 795–802.

Cheney, L. S. 1930. Wisconsin fossil mosses. Bryologist **33**: 66–68.

————————. 1931. More fossil mosses from Wisconsin. Bryologist **34**: 93, 94.

———————— and R. Evans. 1944. The mosses of Wisconsin. Trans. Wisconsin Acad. Sci. Arts Letters **36**: 171–224.

Crum, H. 1973. Mosses of the Great Lakes forest. Contrib. Univ. Michigan Herb. 10. iii + 404 pp.

Culberson, W. L. 1955. The fossil mosses of the Two Creeks Forest Bed of Wisconsin. Amer. Midl. Nat. **54**: 452–459.

Evenson, E. B. 1973. Late Pleistocene shorelines and stratigraphic relations in the Lake Michigan basin. Geol. Soc. Amer. Bull. **84**: 2281–2297.

————————, W. R. Farrand and D. F. Eschman. 1974. Late Pleistocene shorelines and stratigraphic relations in the Lake Michigan basin: Reply. Geol. Soc. Amer. Bull. **85**: 661–664.

Faegri, K. and J. Iversen. 1964. Textbook of pollen analysis. 2nd Rev. Ed. 237 pp. Munksgaard. Copenhagen.

Forman, R. T. T. 1967. New and uncommon Wisconsin mosses. Bryologist **70**: 115–117.

Kuc, M. 1974. The interglacial flora of Worth Point, western Banks Island. Geol. Sur. Can. Paper **74–1B**: 227–231.

Miller, N. G. 1973. Lateglacial plants and plant communities in northwestern New York State. Jour. Arnold Arb. **54**: 123–159.

————————. 1976. Quaternary fossil bryophytes in North America: A synopsis of the record and some phytogeographic implications. Jour. Hattori Bot. Lab. *in press*.

———————— and W. S. Benninghoff. 1969. Plant fossils from a Cary–Port Huron Interstade deposit and their paleoecological interpretation. Geol. Soc. Amer. Special Paper **123**: 225–248 + *pl. 3*.

Persson, H. and H. Sjörs. 1960. Some bryophytes from the Hudson Bay Lowland of Ontario. Sv. Bot. Tidskr. **54**: 247–268.

Preston, R. S., E. Person and E. S. Deevey. 1955. Yale natural radiocarbon measurements II. Science **122**: 954–960.

Rubin, M. and C. Alexander. 1960. U.S. Geological Survey radiocarbon dates V. Amer. Jour. Sci. Radiocarbon Suppl. **2**: 129–185.

Schweger, C. E. 1969. Pollen analysis of Iola bog and paleoecology of the Two Creeks forest bed, Wisconsin. Ecology **50**: 859–868 + *1 pl.*

Sjörs, H. 1961. Forest and peatland at Hawley Lake, northern Ontario. Natl. Mus. Canada Bull. **171**: 1–31.

————————. 1963. Bogs and fens on Attawapiskat River, northern Ontario. Natl. Mus. Canada Bull. **186**: 45–133 + *pls.* 3–6.

Vitt, D. H. 1973. A revision of the genus *Orthotrichum* in North America, north of Mexico. Bryophytorum Bibliotheca 1. 208 pp. + *60 pls.*

West, R. G. 1961. Late- and postglacial vegetational history in Wisconsin, particularly changes associated with the Valders readvance. Amer. Jour. Sci. **259**: 766–783 + *2 pls.*

Wilson, L. R. 1932. The Two Creeks Forest Bed, Manitowoc County, Wisconsin. Trans. Wisconsin Acad. Sci. Arts Letters **27**: 31–46.

————————. 1936. Further fossil studies of the Two Creeks Forest Bed, Manitowoc County, Wisconsin. Bull. Torrey Bot. Club **63**: 317–325.