

Late-Quaternary history of the alpine flora of the New Hampshire White Mountains
Histoire de la flore alpine des White Mountains du New Hampshire au Quaternaire supérieur
Geschichte der alpinen Flora im Spät-Quaternär in den White Mountains von New Hampshire

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Résumé de l'article

On observe, dans les White Mountains, une flore distincte de 73 espèces de plantes vasculaires et de nombreux bryophytes dans la toundra alpine d'environ 20 km² de superficie des White Mountains. La répartition de ces plantes au Quaternaire supérieur a été reconstituée à partir des études polliniques et macrofossiles dans la région des Lakes of the Clouds (1 542 m) dans la zone alpine du mont Washington. On a par la suite comparé les résultats avec le pollen et les macrofossiles des dépôts du tardiglaciaire des basses terres de l'ouest de la Nouvelle-Angle-terre. Les paléo-flores des basses terres comprenaient 43 espèces de plantes vasculaires, dont 13 espèces font également partie de la flore alpine contemporaine des White Mountains. La majorité des espèces de la paléoflore a des affinités avec les espèces du Labrador, du Québec nordique et du Groenland, comme c'est le cas des mousses dans les dépôts des basses terres. Les premiers macrofossiles déposés dans les Lakes of the Clouds ont été des mousses arctiques-alpines de sol acide. Même si les mousses de terrains ouverts et les plantes vasculaires ont continué à se manifester tout au long de l'Holocène, ce qui témoigne de la persistance de la toundra alpine, les fossiles de *Hylocomiastrum umbratum* montrent que la forêt (peut-être sous forme de krummholz) a couvert un plus grand espace près du bassin de 7 500 à 3 500 BP. Aucune plante calciphile n'a été trouvée dans les sédiments des Lakes of the Clouds inférieurs. Les contraintes climatiques sur la flore alpine pendant l'oscillation du Dryas récent et peut-être aussi au cours d'autres périodes du tardiglaciaire ont peut-être contribué à la perte de certaines espèces de plantes dans la zone alpine des White Mountains.

LATE-QUATERNARY HISTORY OF THE ALPINE FLORA OF THE NEW HAMPSHIRE WHITE MOUNTAINS

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ABSTRACT A distinctive flora of 73 species of vascular plants and numerous bryophytes occurs in the ca. 20 km² of alpine tundra in the White Mountains, New Hampshire. The late-Quaternary distribution of these plants, many of which are disjuncts, was investigated by studies of pollen and plant macrofossils from lower Lakes of the Clouds (1542 m) in the alpine zone of Mount Washington. Results were compared with pollen and macrofossils from lowland late-glacial deposits in western New England. Lowland paleofloras contained fossils of 43 species of vascular plants, 13 of which occur in the contemporary alpine flora of the White Mountains. A majority of species in the paleoflora has geographic affinities to Labrador, northern Québec, and Greenland, a pattern also apparent for mosses in the lowland deposits. The first macrofossils in lower Lakes of the Clouds were arctic-alpine mosses of acid soils. Although open-ground mosses and vascular plants continued to occur throughout the Holocene, indicating that alpine tundra persisted, fossils of a low-elevation moss *Hylocomiastrum umbratum* are evidence that forest (perhaps as krummholz) covered a greater area near the basin from 7500 to 3500 yBP. No calcicolous plants were recovered from sediments at lower Lakes of the Clouds. Climatic constraints on the alpine flora during the Younger Dryas oscillation and perhaps during other cold-climate events and intervening periods of higher temperature may have led to the loss of plant species in the White Mountain alpine zone. Late-glacial floras of lowland western New England were much richer than floras of areas above treeline during late-glacial time and at the present.

RÉSUMÉ *Histoire de la flore alpine des White Mountains du New Hampshire au Quaternaire supérieur.* On observe, dans les White Mountains, une flore distincte de 73 espèces de plantes vasculaires et de nombreux bryophytes dans la toundra alpine d'environ 20 km² de superficie des White Mountains. La répartition de ces plantes au Quaternaire supérieur a été reconstituée à partir des études polliniques et macrofossiles dans la région des Lakes of the Clouds (1542 m) dans la zone alpine du mont Washington. On a par la suite comparé les résultats avec le pollen et les macrofossiles des dépôts du tardiglaciaire des basses terres de l'ouest de la Nouvelle-Angleterre. Les paléo-flores des basses terres comprenaient 43 espèces de plantes vasculaires, dont 13 espèces font également partie de la flore alpine contemporaine des White Mountains. La majorité des espèces de la paléoflore a des affinités avec les espèces de Labrador, du Québec nordique et du Groenland, comme c'est le cas des mousses dans les dépôts des basses terres. Les premiers macrofossiles déposés dans les Lakes of the Clouds ont été des mousses arctiques-alpines de sol acide. Même si les mousses de terrains ouverts et les plantes vasculaires ont continué à se manifester tout au long de l'Holocène, ce qui témoigne de la persistance de la toundra alpine, les fossiles de *Hylocomiastrum umbratum* montrent que la forêt (peut-être sous forme de krummholz) a couvert un plus grand espace près du bassin de 7500 à 3500 BP. Aucune plante calciphile n'a été trouvée dans les sédiments des Lakes of the Clouds inférieurs. Les contraintes climatiques sur la flore alpine pendant l'oscillation du Dryas récent et peut-être aussi au cours d'autres périodes du tardiglaciaire ont peut-être contribué à la perte de certaines espèces de plantes dans la zone alpine des White Mountains.

ZUSAMMENFASSUNG *Geschichte der alpinen Flora im Spät-Quaternär in den White Mountains von New Hampshire.* In den etwa 20 km² alpiner Tundra in den White Mountains, New Hampshire, gibt es eine charakteristische Flora von 73 Arten von vaskulären Pflanzen und zahlreichen Bryophyten. Die Spät-Quaternär-Verteilung dieser Pflanzen, von denen viele segmentiert sind, wurde mittels Studium der Pollen und Pflanzen-Makrofossilien von den unteren Lakes of the Clouds (1542 m) in der alpinen Zone von Mount Washington untersucht. Die Ergebnisse hat man mit Pollen und Makrofossilien von spätglazialen Ablagerungen in den westlichen Niederungen Neu-Englands verglichen. Die Paläofloren der Niederungen enthielten Fossilien von 43 Arten vaskulärer Pflanzen, von denen 13 in der gegenwärtigen alpinen Flora der White Mountains vorkommen. Die Mehrheit der Arten in der Paläoflora besitzt geographische Affinitäten zu Labrador, dem nördlichen Québec und Grönland, was auch für die Moose in den Ablagerungen der Niederungen zutrifft. Die ersten Makrofossilien in den unteren Lakes of the Clouds waren arktisch-alpine Moose von sauren Böden. Obwohl Moose offener Gebiete und vaskuläre Pflanzen durch das ganze Holozän hindurch weiter vorkommen und so zeigen, dass alpine Tundra weiterbestand, belegen Fossilien von einer leichten Mooserhebung *Hylocomiastrum umbratum*, dass Wald (vielleicht in Form von Krummholz) ein größeres Gebiet in der Nähe des Beckens von 7500 bis 3500 Jahren v.u.Z. bedeckte. In den Sedimenten bei den unteren Lakes of the Clouds wurden keine kalkliebenden Pflanzen gefunden. Klimatische Zwänge, die auf die alpine Flora während der Schwankungen des jüngeren Dryas und vielleicht während anderer Kaltklima-Ereignisse und dazwischenauf tretenden Perioden wärmerer Temperaturen gewirkt haben, mögen zum Verlust von Pflanzen-Arten in der alpinen Zone der White Mountains geführt haben. Die spätglaziale Flora der Niederungen von West-Neu-England war viel reicher als die Flora oberhalb der Baumgrenze während der spätglazialen und gegenwärtigen Zeit.

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INTRODUCTION

The high-elevation, treeless vegetation of the Presidential Range in the New Hampshire White Mountains has attracted much attention since the late 1700s. Early studies of the alpine flora emphasized previously unreported species and noted the taxonomic affinities of plants in an area that is isolated from other alpine regions in eastern North America and from the Arctic. Pease (1964) provided a comprehensive review of the relationships of the White Mountain flora to floras in other parts of the circumboreal/circumpolar zone, and also of early speculation on the geographic affinities of alpine plants in the White Mountains.

Seventy-four species of vascular plants are listed by Pease (1964) as being "essentially alpine" in the White Mountains. His list needs few changes to bring it in line with contemporary taxonomic concepts. Two species, *Calamagrostis nubila* Louis-Marie and *Euphrasia williamsii* Robinson, are now placed by systematists in the synonymy of *C. canadensis* var. *langsдорffii* (Link) Inman and *E. oakesii* Wettst., respectively. A recently described fir-moss, *Huperzia appalachiana* Beitel & Mickel, joins Pease's list, making a total alpine flora of 73 vascular plant species. There is one endemic vascular plant species in the White Mountains, *Potentilla robbinsiana* Oakes ex Rydb., which occurs in the alpine zone of both the Presidential and Franconia ranges (Cogbill, 1993).

Löve and Löve (1965, 1966) present a less conservative taxonomic assessment of the Mount Washington flora and the cytological and taxonomic basis for recognizing a somewhat larger number of species. However, Pease (1964) provides a good point of departure for considering the late-Quaternary distributional history of the alpine flora of Mount Washington, because the species concepts he employed are morphological, allowing them in most instances to be related to plant remains found in Pleistocene and Holocene sediments.

The flora of the alpine zone of the White Mountains consists of calcifuge species, many of which are also present in northwestern Europe (the amphi-Atlantic distribution pattern). Some are found across the circumpolar latitudes, with gaps of variable size and location. Many species in Pease's list (1964) also occur in other alpine areas of northeastern North America. For example, 41 of the 73 are recorded from the High Peaks Region of the eastern Adirondack Mountains, New York (Ketchledge and Fitzgerald, 1993); 58 occur on the summit or slopes of Mount Katahdin, Piscataquis County, Maine (Campbell *et al.*, 1995; Dibble *et al.*, 1990); and 67 occur in mountains on the Gaspé Peninsula, Québec (Scoggan, 1950). At least 47 of the species are present in the flora of West Greenland (Fredskild, 1996). In these four alpine or arctic areas, which are either south or north of the Presidential Range, a variable number of additional arctic or alpine species are present. These are plants of cliffs and ledges below the alpine zone, or in the case of West Greenland, where the flora consists of 397 vascular plant species (Fredskild, 1996), in distinct habitats in the ubiquitous, discontinuous tundra vegetation and barrens of this region.

The Presidential Range, and specifically Mount Washington, is also a southern outlier for arctic and alpine bryophytes, although that flora less well documented (Grout, 1940). The mosses *Arctoa fulvella* (Dicks.) B.S.G., *Aulacomnium turgidum* (Wahlenb.) Schwaegr., *Grimmia donniana* Sm., *Kiaeria blyttii* (Schimp.) Broth., and *K. starkei* (Web. & Mohr) Hag. (Grout, 1940; Crum and Anderson, 1981), and the hepatics, *Anthelia juratzkana* (Limpr.) Trev., *Gymnomitrium concinnatum* (Lightf.) Corda, and *G. coralloides* Nees (Schuster, 1974), are noteworthy arctic-alpine bryophytes of the alpine zone of Mount Washington.

The alpine flora of the White Mountains is often assumed to be a remnant of an arctic and northern flora that followed the disintegrating Laurentide Ice Sheet. This generalization has been widely accepted as an explanation for the occurrence of isolated populations of arctic and boreal plants on other mountains and in exposed (treeless) sites in eastern North America. The concept can be traced to Edward Forbes' influential essay (1846) on the geographic origins of the British flora and fauna in relation to Pleistocene glaciation and as an outcome of postglacial migrations. The model Forbes presented was quickly adopted in North America (for example, Gray, 1862), and all more recent work in Europe and North America has supported this simplified generalization.

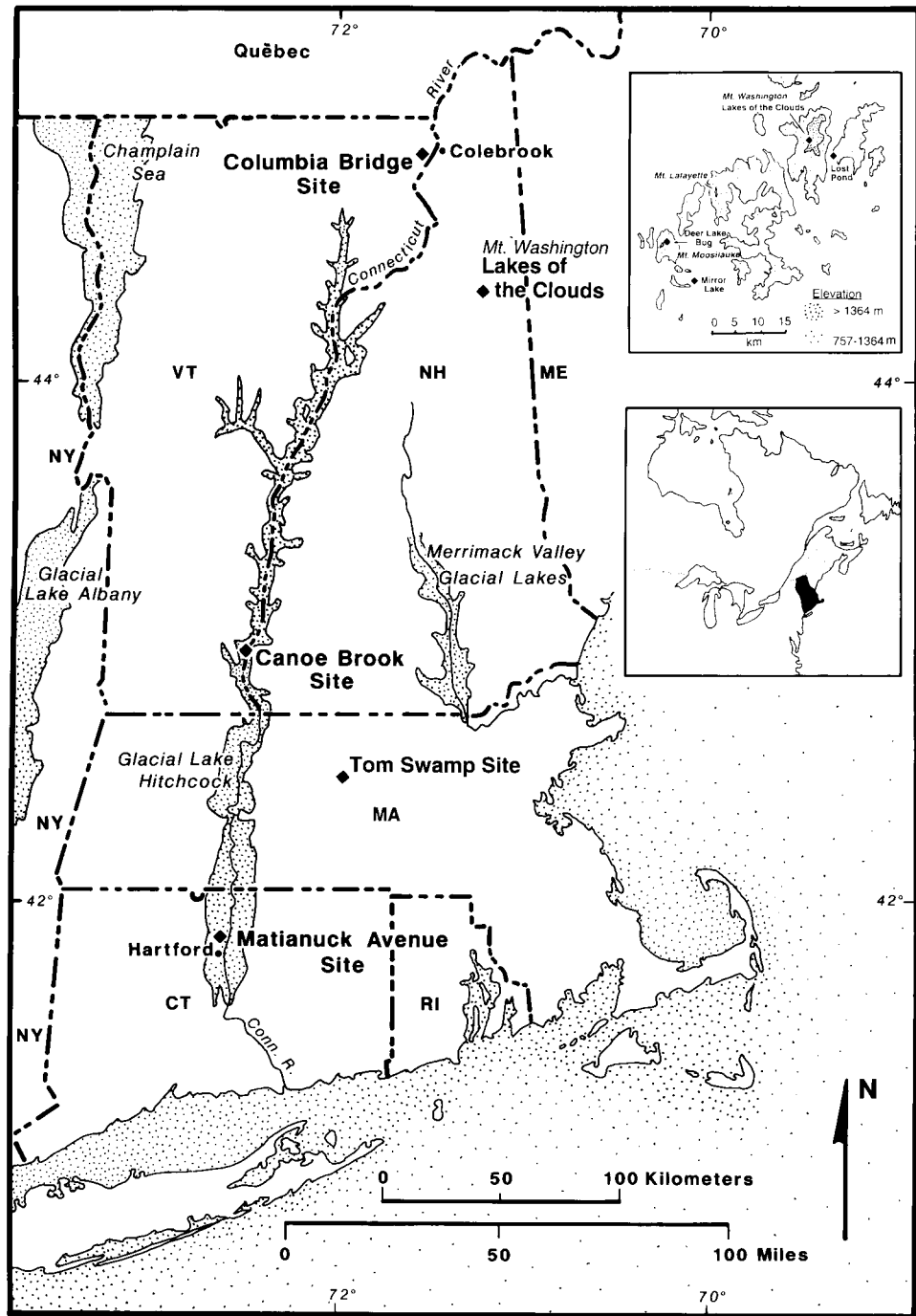
Paleobotanical studies of late-Quaternary sediments in New England provide a detailed record of the treeless vegetation that preceded the first forest communities to develop after the disappearance of glacial ice. Lowland deposits in the Connecticut River valley (Miller, 1992, 1995; Miller and Thompson, 1979), south and west of the White Mountains, contain macrofossils that document a diverse late-glacial flora and a variety of tundra plant communities. Pollen and plant macrofossils from lake sediments in the White Mountains (Davis *et al.*, 1980; Spear, 1989; Spear *et al.*, 1994) show evidence of late-Quaternary climate change, as well as fluctuations in plant populations. In this paper, we present new information about plant fossils in sediments in the lower Lakes of the Clouds (alpine zone of Mount Washington) and late-Pleistocene deposits in lowland New England beyond the White Mountains. These data provide new insights into the origin and persistence of the contemporary alpine flora of the White Mountains. In particular, we focus on evidence for late-Pleistocene and Holocene climate fluctuations and changing edaphic factors, which may have created bottlenecks that reduced the size of the flora. Finally, we relate these findings and our conclusions to Forbes' model, in which a steady unidirectional migration of plant species was proposed.

SETTING

The White Mountains, a part of the northern Appalachians, have alpine areas in the Presidential and Franconia ranges and the isolated Mount Moosilauke. The Presidential Range (Fig. 1) has the most extensive alpine zone, approximately 20 km² (Bliss, 1963), including Mount Washington (1917 m), the highest summit in northeastern United States. The White Mountains are largely Devonian metamorphic rock (Littleton Formation), with gneiss, schist, and quartzite forming the highest peaks (Billings *et al.*, 1946).

FIGURE 1. Map of New England showing location of study sites; insert (top), White Mountains, New Hampshire, with topography and location of sites discussed in text. (General map modified from Ridge and Larsen, 1990.)

Carte de la Nouvelle-Angleterre donnant la localisation des sites à l'étude. Médaille (haut) : les White Mountains du New Hampshire, topographie et emplacement des sites dont on parle dans le texte (modifié à partir d'une carte de Ridge et Larsen, 1990).



Both montane and continental glaciation shaped the White Mountains during the Pleistocene (Goldthwait, 1970, 1976). Montane glaciers preceded the Laurentide Ice Sheet, which completely overrode the summits during the Late Wisconsinan. After retreat of the Laurentide Ice Sheet (some time before 13,000 yBP), intense late-glacial frost produced periglacial features, including frost-shattered bedrock, stone nets, stone stripes, rock streams, and rock glaciers (Antevs, 1932; Goldthwait, 1940).

Steep climate gradients occur in the White Mountains. The mean annual temperature on the summit of Mount

Washington is -2.8°C , nearly 9.5°C below that in the valleys. The summit receives significantly more precipitation ($\sim 2\text{m}/\text{yr}$), is in heavy fog for some part of the day 310 days/yr, and experiences high winds (mean annual wind velocity 56.6 km/hr). Climate gradients are steeper above treeline than below (Bliss, 1966; Harries, 1966).

Five contemporary vegetation zones have been recognized in the White Mountains: (1) northern hardwoods (hemlock phase), $<450\text{ m}$; (2) northern hardwoods (spruce phase), $450\text{-}750\text{ m}$; (3) subalpine (spruce-balsam fir phase), $750\text{-}1220\text{ m}$; (4) subalpine (balsam fir phase), $1220\text{-}1500\text{ m}$;

and (5) alpine, >1500 m (Spear, 1989). Montane conifer forests of spruce and/or fir are found between 750 and 1450 m over large portions of the White Mountain National Forest. Treeline (the elevation above which trees are less than 2 m tall) generally occurs at 1500 m and corresponds to forest limit, the boundary above which trees cover less than 50% of the landscape (Spear, 1989). Treeline on the west slopes of the Presidentials is between 1465 and 1525 m, but it can reach as low as 1312 m on exposed northwest slopes. Treeline is higher on the more sheltered east slopes, usually between 1525 and 1588 m. The species limit, the elevation at which a species can no longer exist even as *krummholz*, is approximately 1700 m (Antevs, 1932).

A number of alpine plant communities occur above 1500 m, and they are distributed along environmental gradients of temperature, moisture, and wind exposure (Antevs, 1932; Bliss, 1963; Harries, 1966). Antevs (1932) suggested that wind exposure and snow cover were the main factors affecting the alpine vegetation. Bliss (1963) recognized nine communities: (1) exposed windswept sites with little or no winter snow, *Diapensia lapponica* L. prominent, (2) a widespread dwarf shrub heath-rush community associated with variable snow cover and on soil with good drainage, (3) dwarf shrub heath in areas of deeper snow, (4) snow banks (snow persisting until summer), (5) sedge-rush-dwarf shrub heath, (6) sedge-dwarf shrub heath, (7) sedge meadow, (8) streamside, and (9) bog. Differences between communities 5, 6, and 7 are gradational. Streamside and bog communities are associated with peat accumulation.

METHODS

Sediment deposited in Lakes of the Clouds (1542 m), small alpine ponds 1.7 km southwest of the summit of Mount Washington (Fig. 1), contains pollen and plant macrofossils from late-Quaternary alpine vegetation. The lower lake, the focus of our work, is the larger of the two. Its long and narrow watershed is about 15 ha and extends northeast up the flank of Mount Washington to an elevation of 1676 m (Buchanan, 1975). Maximum modern water depth has been 2.2 m.

FIELD

Spear cored lower Lakes of the Clouds in the summers of 1976 and 1977 from a plywood platform resting on two inflatable boats tied to shore. The raft was secured at a position near the center of the lake where sediments were the thickest. A 3.2-m-long column of sediment was taken with a 5-cm-diameter modified Livingstone piston sampler (Wright *et al.*, 1965) used in conjunction with 10.3-cm-diameter casing tube. Cores were extruded in the field, wrapped in plastic film and aluminum foil, and enclosed within two pieces of aluminum flashing for the hike off the mountain. Soft surface sediments were collected using a 2.5-cm plastic tube fitted with a piston.

Paleobotanical sites in the Connecticut River Valley southeast of the White Mountains (Fig. 1) are described in Miller (1993). The geology of the Matianuck Avenue site is

treated by Stone and Ashley (1992), and that of the Canoe Brook site by Ridge and Larsen (1990). Exposures of varved sediment from Glacial Lake Hitchcock were cleaned with shovels and mattocks, and large-volume samples were cut from the sections, wrapped in foil, and kept refrigerated until processed in the laboratory.

LABORATORY

Radiocarbon age determinations were obtained for bulk sediment samples from lower Lakes of the Clouds, as described in Spear (1989). Radiocarbon ages from the lowland sites along the Connecticut River Valley are either accelerator mass spectrometric (AMS) determinations of minute plant macrofossils of terrestrial origin or conventional radiocarbon age determinations of composite samples of small pieces of wood. The macrofossils were cleaned of adhering mineral matter, dried in an oven, and submitted for analysis. Radiocarbon ages (as *yBP*) are given as $\delta^{13}\text{C}$ corrected values, except those from lower Lakes of the Clouds for which $\delta^{13}\text{C}$ measurements are not available.

Standard laboratory techniques were used to characterize the sediments and prepare pollen and macrofossil samples, as described in Spear (1989) and Spear *et al.* (1994). Volumetric sediment samples were taken for pollen analysis. Pollen samples were treated chemically, using the procedures of Faegri and Iversen (1975). Highly inorganic samples were sieved (Cwynar *et al.*, 1979) to remove small residual organic and mineral particles (<10 μm) and to concentrate the pollen. Residues were mounted in silicone oil on microscope slides. A minimum of 300 terrestrial pollen grains were counted at a magnification of 400X for each level, with counts of 500 grains for many levels and for some about 1000.

Large-volume samples of varved sediment (4000 and 9600 mL) from the Lake Hitchcock sites were broken down in warm distilled water or 2% Na_2CO_3 . Small inorganic and organic particles in the resulting slurries were washed through a 250- μm -mesh sieve, and residues remaining in the sieve were examined at dissecting microscope magnifications to locate potentially identifiable fossils. Further details on sediment processing procedures are found in Miller (1993).

Plant fossils were stored in 70% ethyl alcohol. After cleaning with 00 or 000 artist's brushes and repeated dehydration/rehydration in alcohol/water, the fossils were placed on double-faced tape on stubs for scanning electron microscopy (SEM). Fossils received 10-15 \AA coating of gold-palladium (60:40) in a vacuum chamber (sputter-coater) before SEM examination. Magnifications recorded with each micrograph are presented as scale bars, which are accurate to within 10%. The scanning electron microscopy was done at the Museum of Comparative Zoology, Harvard University, and the SEM Laboratory of Northeastern University, in both instances employing an AMR Model 1000 microscope. A large library of SEM images of seed and fruits from herbarium voucher specimens in Miller's laboratory was used to help identify the fossils. This archive is based on a larger reference collection of seeds and other dispersible plant mate-

rials housed at the New York State Museum and broadly representing the vascular plant flora of all of northern North America.

For macrofossil analysis of sediment from lower Lakes of the Clouds, 50 mL samples were heated for approximately 2 h in a mild detergent solution and washed through a series of sieves (595- μm , 250- μm , 90- μm mesh). Moss fragments picked from the residues under 12X and 25X magnification were stored in glycerin. Fifty-five moss fragments were cleaned in distilled water, placed in Hoyer's solution, dissected, and, if necessary, sectioned for microscopic study. Thirty-eight (69%) could be identified. Although the remaining 17 fossils (31%) were either too fragmentary or too poorly preserved to allow full identification, 11 of these were named to genus and three others to family. Only one well-preserved but incomplete specimen could not be identified to species. The reference slide collection of dissected moss plants at the New York State Museum, which contains examples of most species in the northern North American bryoflora, facilitated identification.

Pollen percentages were calculated and plotted and macrofossil numbers were plotted using the stratigraph analysis program TILIA (developed by Eric Grimm, Illinois State Museum). We also used a subroutine within TILIA (CONISS—CONstrained Incremental Sums-of-Squares cluster analysis) to zone the pollen diagram. Pollen percentages and macrofossil numbers have been plotted against age rather than depth. The age of each sample was estimated from the age/depth relationship calculated by fitting a polynomial regression to several points. Spear (1981, 1989) described how the 1976 and 1977 cores were dated (five radiocarbon age determinations of bulk sediment samples) and fit together (pollen stratigraphic correlations). The bottom of the 1976 core (292 cm) is equivalent to 200 cm in the 1977 core. For the pollen percentage diagram in this paper (Fig. 2), the two cores were joined at this point, and pollen samples were overlapped for 20 cm. This diagram includes counts for an additional ten stratigraphic levels and lists more taxa than the summary diagram published by Spear (1989). The macrofossil diagram (Fig. 3) includes data from the 1976 and 1977 cores. We determined the ages of samples from each core, and plotted them as if they were in one stratigraphic section. This is a reasonable presentation of data from two different but adjacent cores, because macrofossil records are typically noisy and only crudely quantitative, and because we have only satisfactory radiocarbon age control. However, this procedure limits temporal resolution, and ages of vegetation boundaries can only be estimated to within 500 years.

RESULTS

PLANT MACROFOSSILS AND POLLEN FROM LOWLAND SITES

Late-glacial deposits from four lowland sites (Fig. 1), three southwest of Mount Washington (Matianuck Avenue, north-central Connecticut; Tom Swamp, central Massachusetts; Canoe Brook, southeastern Vermont) and one northwest of Mount Washington (Columbia Bridge, northeastern Vermont)

contain large, diverse, late-Pleistocene floras represented by pollen and vascular plant and bryophyte macrofossils. The age of a willow (*Salix*) twig from the southernmost of these, Matianuck Avenue, 265 km southwest of Mount Washington, was $13,540 \pm 90$ yBP, indicating that the assemblage dates roughly from the time the upper slopes of Mount Washington became ice free. The age of fossils in the three other deposits are younger (Table I) but contemporaneous with late-Pleistocene sediments deposited in lower Lakes of the Clouds. Additional details about the sites are presented in Table I.

Vascular plant macrofossils recovered at the four sites (Table II) were assigned to 65 taxonomic categories that convey different degrees of precision in identification. Forty-seven species (43 terrestrial; four aquatics [species of *Potamogeton* and *Brasenia schreberi* Gmel.]) were identified on the basis of technical characters, including seed-coat cell patterns revealed by scanning electron microscopy, leaf venation, or other anatomical details. However, it was not possible to identify all fossils to species, owing to incongruent differences between a fossil and herbarium reference specimens (a possible reflection of deficiencies or incompleteness of the reference collection) or the loss of diagnostic features in a fossil. When identifications are considered probable but not certain, the convention "cf." is used (Table II). Fifteen macrofossil types were identified to genus only, and three others were placed to family. Thirteen of the 47 fossils identified to species (28%) are of plants that occur in the contemporary flora of the alpine zone of Mount Washington and other mountains in the Presidential Range.

Fossils of 75 species of extant mosses were recovered and identified from sediments at the four sites (Miller, 1987a, b, 1993), including a few species also present in the contemporary alpine flora of Mount Washington.

Pollen assemblages from the four lowland sites, which are oldest in the south and progressively younger northward (Table I), showed significant regional trends. At the southernmost site, Matianuck Avenue, Connecticut, 70% of two replicate pollen spectra dated at $13,540 \pm 90$ yBP contained grass (40%), sedge (15%), and other herbs (14%), while spruce was poorly represented (5%). Northward, at Canoe Brook, Vermont, the total herb pollen percentage at $12,350 \pm 90$ yBP was 52% and consisted principally of sedge (30%), grass (6%), and other herb types (18%), with spruce pollen more frequent (13%). At the youngest site, Columbia Bridge, in far northwestern New England, total herb pollen percentages between $11,540 \pm 110$ yBP and $11,390 \pm 150$ yBP were the lowest (ave. 22%), and these were principally sedge (10-27% in four spectra). Spruce, however, was markedly higher (28%), and significantly greater amounts of oak, birch, and other deciduous trees were also registered at this site. The percentage of pine pollen at the three sites was remarkably consistent between 13,540 and 11,390 yBP: 20% at Matianuck, 21% at Canoe Brook, and 17% at Columbia Bridge.

Late-glacial Tom Swamp pollen spectra and associated macrofossils (Davis, 1958; Gaudreau, 1986; Miller, 1989) showed a prominent increase in spruce pollen just above sediment radiocarbon dated at $12,830 \pm 120$ yBP (Gaudreau,

Lower Lakes of the Clouds White Mountains, New Hampshire

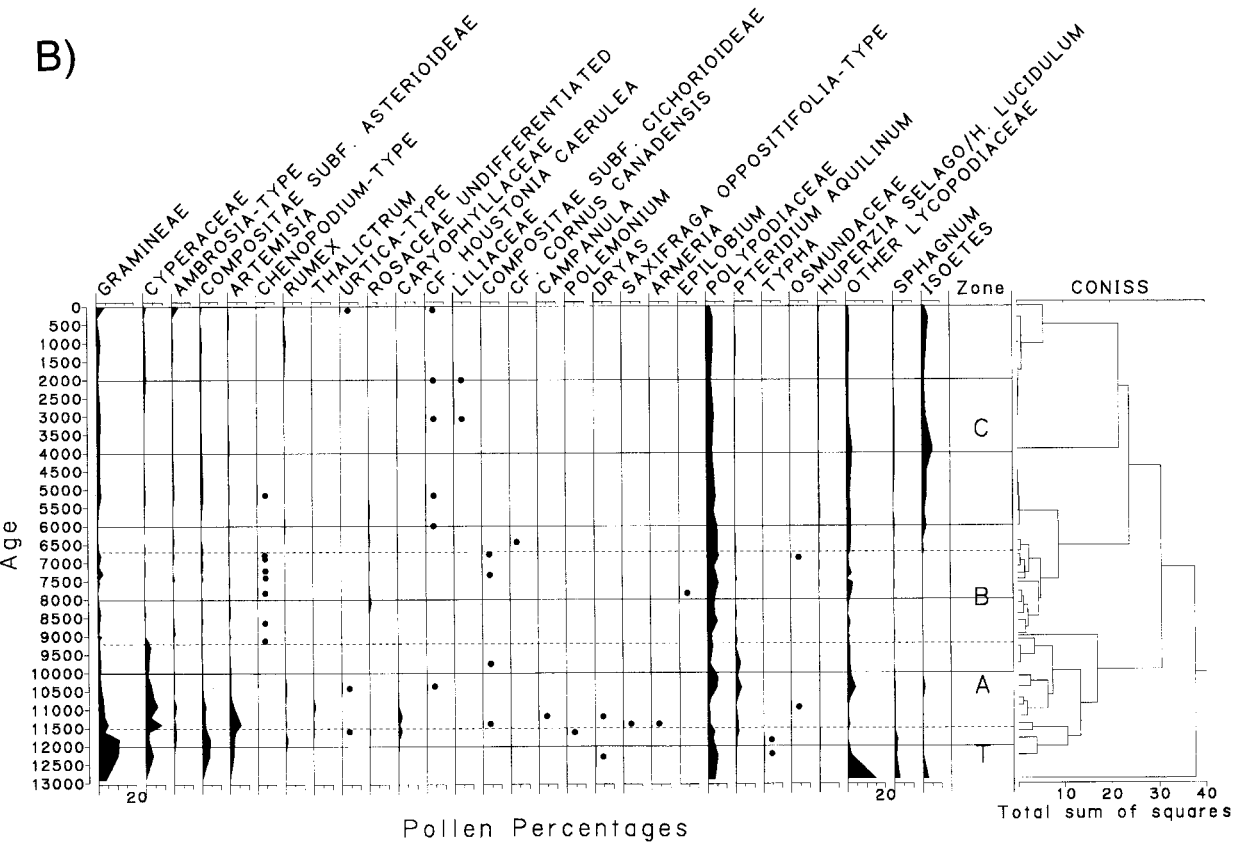
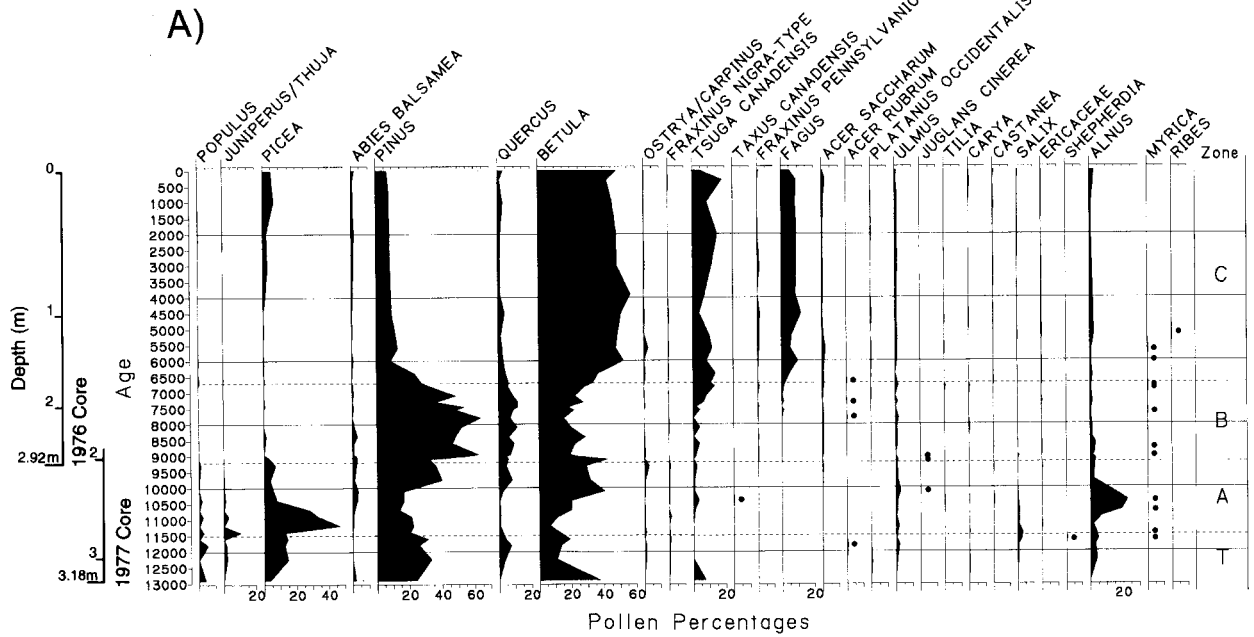


FIGURE 2. Pollen percentage diagram for lower Lakes of the Clouds: A) trees and shrubs, B) herbs. Dots indicate occurrences never exceeding 1%.

Diagramme de pourcentages polliniques de la région des Lakes of the Clouds inférieures ; A) les arbres et les arbustes ; B) les herbes. Les points signalent les pourcentages inférieurs à 1%.

Lower Lakes of the Clouds White Mountains, New Hampshire

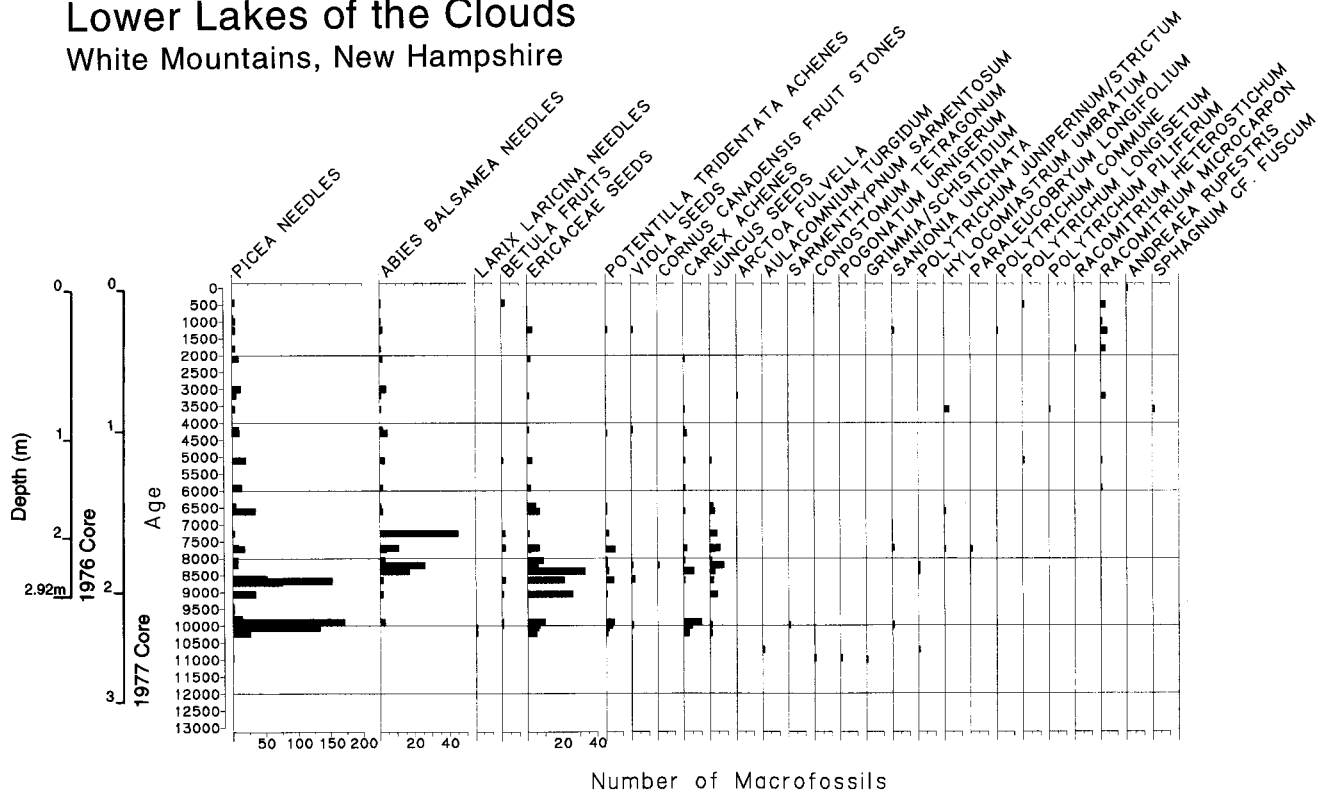


FIGURE 3. Plant macrofossil diagram for lower Lakes of the Clouds. *Diagramme des plantes macrofossiles des Lakes of the Clouds inférieurs.*

TABLE I

Study-site characteristics, late-Pleistocene deposits of plant fossils, western New England

Name	Location	Elevation	Sediment Type	Sediment or Fossil Age	Bedrock
Matianuck Avenue, Windsor, Hartford Co., Connecticut	41°49'N, 72°40'W	30 m	fine sand above glacial lake varves	13,540 ± 90 yBP (Beta 59094, CAMS-4875)	arkose (sandstone), basalt (traprock) nearby
Tom Swamp, Petersham, Worcester Co., Massachusetts	42°31'N, 72°13'W	232 m	silty sand, coarse sand	12,830 ± 120 yBP (WIS-1210) 11,580 ± 110 yBP (WIS-1214) 10,080 ± 110 yBP (WIS-1212)	aluminous mica and quartzose schists, aluminous phyllite
Canoe Brook, Dummerston, Windham Co., Vermont	42°57'N, 72°33'W	100 m	fine sand and silt, (glacial lake varves)	12,350 ± 90 yBP (Beta 53663, CAMS-2667)	phyllite, mica schist, micaceous crystalline limestone, calcareous mica schist, quartzite, gray slate
Columbia Bridge, Essex Co., Vermont	44°51'N, 71°33'W	301 m	fine sand, silt, and clay, (glacial lake varves)	11,390 ± 115 yBP (WIS-919) 11,540 ± 110 yBP (WIS-961)	quartz-muscovite phyllite and schist, calcareous mica schist, quartzose and micaceous crystalline limestone
lower Lakes of the Clouds, Coös Co., New Hampshire	44°16'N, 71°19'W	1542 m	silt, fine and coarse sand	11,530 ± 420 yBP (I-10684) 10,300 ± 165 yBP (I-10683)	quartzite, mica schist

TABLE II

Late-Pleistocene plant macrofossils from lowland (non-montane) sites in western New England. The Matianuck Avenue and Canoe Brook assemblages are from varves of Glacial Lake Hitchcock, the Tom Swamp macrofossils came from silty or coarse sand layers at the bottom of a forested peatland, and the Columbia Bridge fossils were from varved sediments of a glacial lake located in the upper Connecticut River Valley. (* = present.)

	Fossil Type	Matianuck Avenue (1)	Tom Swamp (2)	Canoe Brook (1)	Columbia Bridge (3)
• <i>Arctostaphylos alpina</i>	fruit stone	*			
<i>A. uva-ursi</i>	fruit stone				*
<i>Arenaria humifusa</i>	seed			*	
<i>Armeria maritima</i>	calyx	*		*	
<i>Atriplex/Chenopodium</i>	seed	*			
• <i>Betula cf. glandulosa</i>	leaf				*
+ <i>Brasenia schreberi</i>	seed	*			
<i>Carex aquatilis</i>	achene with perigynium			*	*
<i>C. bipartita</i>	achene with perigynium				*
<i>C. spp.</i>	achenes	*	*	*	
<i>Cerastium cf. cerastioides</i>	seed			*	
<i>C. sp.</i>	seed	*			
<i>Draba sp.</i>	capsule		*	*	*
<i>Dryas drummondii</i>	leaf				*
<i>D. integrifolia</i>	leaf, achene, receptacle	*	*	*	*
<i>Elaeagnus commutata</i>	fruit				*
<i>Equisetum sp.</i>	stem			*	*
<i>Gentianopsis sp.</i>	seed				*
<i>Geum sp.</i>	calyx				*
• <i>Harrimanella hypnoides</i>	leaf, stems, capsule	*	*		
<i>Juncus spp.</i>	seed	*		*	
<i>Juniperus sp.</i>	leaf		*		
• <i>J. communis</i>	leaf, pollen and seed cones				*
<i>Ledum groenlandicum</i>	capsule, leaf				*
<i>Minuartia cf. dawsonensis</i>	seed				
• <i>M. groenlandica</i>	seed			*	
<i>M. rubella</i> and <i>cf. rubella</i>	seed	*		*	
• <i>Oxyria digyna</i>	fruit	*		*	*
<i>Parnassia sp.</i>	seed			*	
<i>P. cf. kotzebuei</i>	seed				*
<i>Picea sp.</i>	needle, cone				*
<i>Polygonum ramosissimum cf. var. prolificum</i>	achene				*
<i>Populus balsamifera</i>	capsule, leaf	*			*
+ <i>Potamogeton filiformis</i>	fruit stone				*
+ <i>P. perfoliatus</i>	fruit stone	*			
+ <i>P. pusillus</i>	fruit stone				*
<i>Potentilla spp.</i>	achene	*		*	*
<i>Ranunculus cymbalaria</i>	achene				*
+ <i>R. subg. Batrachium</i>	achene		*		
<i>R. spp.</i>	achenes	*		*	
• <i>Rhododendron lapponicum</i>	capsule				*
<i>Sagina cf. saginoides</i>	seed		*		
• <i>Salix cf. argyrocarpa</i>	leaf				*
• <i>S. herbacea</i>	leaf	*	*	*	*
<i>S. reticulata</i>	leaf	*		*	
• <i>S. uva-ursi</i> and <i>cf. uva-ursi</i>	leaf	*	*		*

TABLE II (continued)

Late-Pleistocene plant macrofossils from lowland (non-montane) sites in western New England. The Matianuck Avenue and Canoe Brook assemblages are from varves of Glacial Lake Hitchcock, the Tom Swamp macrofossils came from silty or coarse sand layers at the bottom of a forested peatland, and the Columbia Bridge fossils were from varved sediments of a glacial lake located in the upper Connecticut River Valley. (* = present.)

	Fossil Type	Matianuck Avenue (1)	Tom Swamp (2)	Canoe Brook (1)	Columbia Bridge (3)
<i>S. vestita</i>	leaf				*
<i>Saxifraga aizoides</i>	seed			*	*
<i>S. cf. flagellaris</i>	seed		*		
<i>S. oppositifolia</i>	seed, leaf, stem with leaves	*		*	
<i>S. paniculata</i>	seed			*	*
<i>Scirpus hudsonianus</i>	achene	*	*	*	
<i>Selaginella selaginoides</i>	megaspore				*
<i>Shepherdia canadensis</i>	seed				*
• <i>Sibbaldia procumbens</i>	achene	*		*	*
• <i>Silene acaulis</i>	seed	*	*	*	*
<i>S. involucrata</i>	seed	*		*	
<i>Stellaria crassifolia</i>	seed	*			
<i>Taraxacum</i> sp.	achene	*			
<i>Thalictrum alpinum</i>	achene	*			
• <i>Vaccinium uliginosum</i>	leaf, seed	*	*	*	*
<i>Woodsia ilvensis</i>	leaf				*
Undifferentiated Compositae	achenes	*	*	*	*
Undifferentiated Cruciferae	seeds	*		*	
Undifferentiated Gramineae	fruits	*			

Key: • = species occurring in the contemporary alpine flora of Mt. Washington (Pease, 1964); + = aquatics.

References: (1) Miller, 1992, 1995, and in preparation; (2) Miller, 1989; (3) Miller & Thompson, 1979.

1986). Immediately above that increase, spruce-needle abundance rises, and macrofossil remains of arctic-alpine plants are no longer present (Miller, 1989). Pollen spectra in sediments dated to older than 12,830 yBP contain high percentages of herb pollen (46%, ave. of six spectra), in which Cyperaceae (25%) and Gramineae (12%) were the most prominent (Gaudreau, 1986).

SEDIMENT LITHOLOGY— LOWER LAKES OF THE CLOUDS

No dramatic transitions are evident in the sediments from lower Lakes of the Clouds, which show gradational changes from fine detritus mud to gray silt and finally yellowish gray sand at the bottom (Table III).

POLLEN STRATIGRAPHY— LOWER LAKES OF THE CLOUDS

The composite pollen percentage diagram (Fig. 2) from lower Lakes of the Clouds provides a clearer record of the regional pollen stratigraphy than the summary diagrams published by Spear (1989). Although the regional stratigraphy is similar to that at low-elevation sites such as Mirror Lake at 200 m (Spear *et al.*, 1994), subtle differences provide evidence for the history of the alpine zone.

The order in which the pollen taxa for trees is presented in the diagram illustrates the development of the forest vegetation over the past 13,000 years. Pollen zones specified by

cluster analysis and shown on the diagram correspond to the time periods delineated by Spear *et al.* (1994).

Pollen from treeline and alpine taxa represent a small fraction of pollen assemblages at the lower Lakes of the Clouds. Pollen from plants restricted to high-elevation vegetation types is swamped by the more abundant and more heavily pollen-producing lowland species. Spear (1989) identified five pollen taxa characteristic of alpine surface-pollen assemblages, Caryophyllaceae, Cyperaceae, Ericaceae, *cf. Houstonia caerulea*, and *Huperzia selago* type, and four other late-glacial taxa (*Artemisia*, Gramineae, *Salix*, and Compositae subfam. Asterioideae) characteristic of open sunny and possibly cold environments. At lower Lakes of the Clouds, peak percentages of this category (~30%) occur in late-glacial sediments. The early Holocene is characterized by values averaging 2.2%, while percentages increase (to 3.9%) after 5000 yBP. On the basis of this information and evidence from macrofossils, Spear (1989) delineated the following time periods and vegetation changes at high-elevations on Mount Washington: deglaciation to 11,750 yBP—intense periglacial activity and sparse vegetation; 11,750-10,300 yBP—herb tundra and later shrub tundra; and at 10,300 yBP—shrubs tundra with krummholz trees.

The composite pollen percentage diagram from lower Lakes of the Clouds includes rarer pollen types, *Armeria*, *Campanula*, *Dryas*, *Polemonium*, *Rumex*, *Saxifraga oppositifolia*, and *Thalictrum*, much of which may have originated from arctic-alpine plants. Records of 22 likely arctic-alpine pollen types found at sites throughout western New England are

TABLE III
Lower Lakes of the Clouds Sediment Stratigraphy

Depth (cm)	Sediment Type	Color	Characteristics	Composition
0-160	loose fine detritus mud	Dark grayish brown 10 YR 2/1	Nig. 4 straf. 0, sicc. 1-2, elas. 2	Dg ⁺ Ld ² 3 Agl
160-200	fine detritus mud	Dark grayish brown 10 YR 3/1	Nig. 3 straf. 0, sicc. 2, elas. 2	Dg ⁺ Ld ² 3 As+Agl
200-225	compact fine detritus mud with transition to silt	Dark grayish brown 10 YR 4/1	Nig. 2-3 straf. 0, sicc. 2, elas. 2	Dg ⁺ Ld ² 2 Asl Agl
225-315	gray silt and fine sand	10 YR 4.5/1	Nig. 2-1 straf. 2, sicc. 2, elas. 1	Ld ² + Asl Agl Gs+
315-322	yellowish gray sand	10 YR 6/4	Nig. 0 straf. 0, sicc. 3, elas. 0	Agl Gal Gs2 Gg+

listed in Table IV. Although these types are not restricted to the alpine zone as a group, they are taken to indicate open, sunny, and cold conditions.

MACROFOSSIL STRATIGRAPHY— LOWER LAKES OF THE CLOUDS

No macrofossils of any strictly alpine vascular plants were recovered from sediments at the lower Lakes of the Clouds, although achenes of *Potentilla tridentata* Ait., an alpine-subalpine plant of exposed sites, first appeared in late-glacial sediments dated at 10,300 yBP (Fig. 3). Needles of *Picea* occur in highest abundance in the sediments of early Holocene age, but fall abruptly by 8500 yBP, when they were succeeded by abundant needles of balsam fir. Fir needles were common in samples from 8500 to 7000 yBP because of twigs in the sediment. In sediment younger than 7000 yBP no twigs were found; consequently, needle number decreased and remained low throughout the rest of the Holocene. Spruce needle representation increased somewhat beginning at ~6500 yBP and remained more or less constant until the late Holocene when the number declined. Seeds of Ericaceae were abundant in late-glacial sediments, as were achenes of sedges and seeds of rushes (*Juncus*).

Most moss fossils are represented by single occurrences, but five, *Racomitrium microcarpon* (Hedw.) Brid., *Hylocomiastrum umbratum* (Hedw.) Broth., *Polytrichum juniperinum* Hedw., *Sanionia uncinata* (Hedw.) Loeske, and *Polytrichum longisetum* Brid., occurred in two to seven samples (Fig. 3). Numerous fossils are of Holocene age, and a significant number of occurrences correspond to the late-glacial/Holocene transition. Four of the 19 species (Fig. 3) identified from late-Pleistocene and Holocene sediments are solely arctic-alpine: *Arctoa fulvella*, *Aulacomnium turgidum*, *Conostomum tetragonum* (Hedw.) Lindb., and *Sarmenthyphnum sarmentosum* (Wahlenb.) Tuom. & T. Kop. Fossils of the last three were found only in late-glacial sediments older than those that contained large numbers of spruce and later fir needles. A fossil of another moss, *Paraleucobryum longifolium* (Hedw.) Loeske was deposited in the early Holocene. This species grows on rock and sometimes also on tree bark, especially in the subalpine zone. Fossils of *Hylocomiastrum umbratum* occurred in Holocene samples from ca. 7800, 6700, and 3600 yBP.

DISCUSSION

PALEOFLORISTICS— VASCULAR PLANTS, LOWLAND SITES

Present geographic affinities of the 43 terrestrial species identified at the lowland sites are known from the following sources: Hultén and Fries (1986), Fernald (1950), Porsild (1957), Porsild and Cody (1980), Rousseau (1974), and Scoggan (1950). Some of the 43 species are represented in the contemporary montane floras of northeastern North America (Fig. 4): nine in the High Peaks Region of the Adirondacks (New York State), 15 on Mount Katahdin (Maine), 27 on the higher mountains of the Gaspé Peninsula and nearby areas (Québec), and 32 in an area encompassing northwestern Newfoundland, Labrador, and northern Québec. Thirteen occur in the alpine zone of Mount Washington, and one additional species at a nearby site in the White Mountains. The area containing the largest number of vascular plant species in common with identified macrofossil remains is northwestern Newfoundland, Labrador, and northern Québec, a region roughly 1400 km north of western New England.

Ten of the 43 species have contemporary ranges that include lowland areas and are not strictly arctic-alpine plants: *Carex aquatilis* Wahlenb., *Dryas drummondii* Richardson, *Elaeagnus commutata* Bernh. ex Rydb., *Ledum groenlandicum* Oeder, *Polygonum ramosissimum* Michx., *Populus balsamifera* L., *Ranunculus cymbalaria* Pursh, *Scirpus hudsonianus* (Michx.) Fern., *Shepherdia canadensis* (L.) Nutt., and *Woodsia ilvensis* (L.) R. Br. These plants presently occur in boreal and northern North America, in some cases southward to southern New York/northern Pennsylvania. None is in the contemporary alpine flora of the White Mountains. Fossils of nearly all of them came exclusively from the youngest lowland late-glacial deposit, Columbia Bridge, which dates to about 11,500 yBP. By then sufficient time had lapsed from the beginning of deglaciation to have allowed a mosaic of tundra, poplar woodland, and mixed woodland to co-exist regionally near late-glacial Columbia Bridge (Davis and Jacobson, 1985). This vegetation included species that now have southerly affinities, as well as others that eventually became extirpated in western New England but survive in areas to the north.

TABLE IV

Pollen types (genera or other taxonomic categories) containing arctic-alpine species. Pollen recovered from lake and pond sediments from sites in White Mountains and western New England

	Matianuck Avenue (1)	Tom Swamp (2)	Canoe Brook (3)	Columbia Bridge (4)	Mirror Lake (5)	Lost Pond (6)	Dear Lake Bog (7)	Lakes of the Clouds (8)
• <i>Armeria</i>	*	*						*
<i>Artemisia</i>		*		*	*	*	*	*
<i>Campanula</i>		*		*		*	*	*
Caryophyllaceae	*	*	*	*	*	*	*	*
Chenopodiaceae/ Amaranthaceae	*	*		*	*	*	*	*
Compositae subfam. Asteroideae	*	*		*	*	*	*	*
Compositae subfam. Cichorioideae	*	*	*					*
Cruciferae		*	*				*	*
<i>Dryas</i> undiff.		*	*					*
<i>D. drummondii</i>				*				
<i>Epilobium</i>		*	*		*	*		*
Ericaceae		*	*		*	*	*	*
cf. <i>Houstonia caerulea</i>							*	*
<i>Huperzia selago</i> type		*						*
• <i>Oxyria digyna</i>			*	*	*	*	*	*
<i>Polemonium</i>		*						*
Rosaceae undiff.		*	*	*	*	*	*	*
<i>Salix</i>		*		*	*	*	*	*
<i>Saxifraga</i> undiff.	*		*			*	*	*
cf. <i>S. oppositifolia</i>		*						*
<i>Thalictrum</i>	*	*	*		*	*	*	*

Key: • = arctic-alpine plants. References: (1) & (3) Miller, 1992, 1995, and in preparation; (2) Davis, 1958; (4) Miller & Thompson, 1979; (5) & (6) Spear *et al.*, 1994; (7) & (8) Spear, 1989.

One late-glacial plant, *Saxifraga* cf. *flagellaris* Willd., from Tom Swamp, is presently restricted to the High Arctic largely north of 70° latitude, and therefore is of considerable biogeographic interest. However, the identification of this species is tentative and on the basis of seed microstructure, the variability of which in northern species of *Saxifraga* is incompletely known.

Some of the vascular plants in western New England lowland late-Pleistocene deposits are also conspicuous members of the contemporary alpine flora of Mount Washington (Table II): *Arctostaphylos alpina* (L.) Spreng. (Fig. 18, 19), *Harrimanella hypnoides* (L.) Coville (Fig. 5, 6), *Minuartia groenlandica* (Retz) Ostenf. (Fig. 16, 17), and *Salix uva-ursi* Pursh (Fig. 7-10). In contrast, species not currently a part of the White Mountain flora, and for which no certain fossils have been found in late-Quaternary sediments from any of the lakes sampled in the White Mountains (Table II), are numerous and include the following: *Arenaria humifusa* Wahlenb. (Fig. 22, 23), *Silene involucreta* (Cham. & Schlecht.) Bocquet (*Melandrium affine* (Fries) Vahl) (Fig. 20), *Salix reticulata* L. (Fig. 11-13), *Saxifraga oppositifolia* L. (Fig. 26-31), *Thalictrum alpinum* L. (Fig. 14, 15), and others listed in Table II. The present ranges of species in this last group vary. Some include northern Labrador, adjacent parts of northern Québec, and nearby Greenland, with no stations south of the Gulf of St. Lawrence (e.g., *Silene involucreta*, *Salix reticulata*). Others are found in northern Québec and Labrador (with a few mostly along the Labrador coast) and also at a few disjunct stations

on the Gaspé Peninsula (e.g., *Arenaria humifusa*, *Saxifraga oppositifolia*, *Thalictrum alpinum*). One of the latter group, *S. oppositifolia*, occurs sporadically far to the south as a rare disjunct of open calcareous cliffs in northern Vermont (Fernald, 1950) and northern New York (Zika and Jenkins, 1992). The modern distribution of many of these species is more oceanic (maritime) than continental in northeastern North America. These data show that the Gulf of St. Lawrence is an important phytogeographical boundary. A large group of species once present on glaciated terrain to the south of this body of water is now restricted to areas north of the Gulf.

PALEOFLORESTICS— MOSSES, LOWLAND SITES

The biogeography of mosses represented in the lowland late-Pleistocene flora of western New England parallels that of the vascular plants. Fossils of 15 arctic-alpine species were identified from the lowland deposits. Six of these, *Cinclidium latifolium* Lindb., *Didymodon rigidulus* var. *icmadophilus* (Schimp. ex C. Müll.) Zander, *Encalypta alpina* Sm., *Tortella arctica* (Arnell) Crundw. & Nyh., *Trichostomum arcticum* Kaal., and *Pseudocrossidium revolutum* (Brid. in Schrad.) Zander, are exclusively subarctic or arctic species and are not treated in Crum and Anderson's comprehensive moss flora of eastern North America (1981), the geographic scope of which includes the southern edge of the boreal forest (i.e., from the Canadian Maritimes westward across Québec and Ontario to

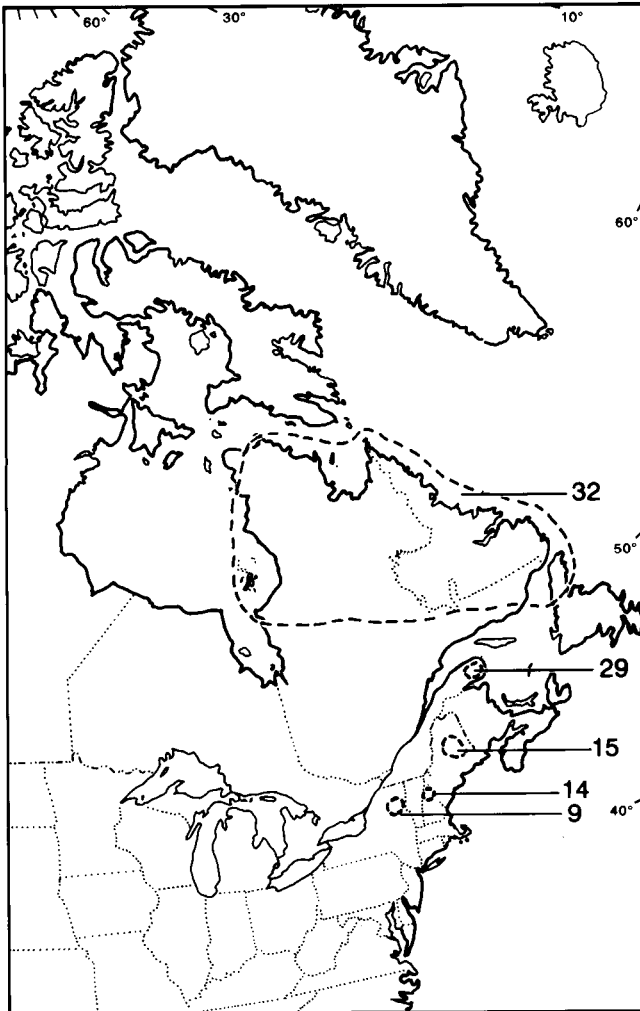


FIGURE 4. Map of eastern North America showing various areas with arctic and/or alpine plants and the number of species in the contemporary floras that are represented by macrofossils in late-glacial deposits in western New England.

Carte de l'est de l'Amérique du Nord présentant différentes régions comprenant des plantes arctiques ou alpines ainsi que le nombre d'espèces de la flore contemporaine représentées par des macrofossiles dans les dépôts tardiglaciaires.

Minnesota) south to the Gulf of Mexico. Fossils of other primarily subarctic and arctic species, which are now found only at a few disjunct stations along the southern limit of the boreal forest (Crum and Anderson, 1981) include: *Aulacomnium acuminatum* (Lindb. & Arnell) Kindb., *Bartramia ithyphylla* Brid., *Hypnum bambergeri* Schimp., *Timmia norvegica* Zett., *Tortula norvegica* (Web.) Wahlenb. ex Lindb., *Didymodon asperifolius* (Mitt.) Crum et al., *Hypnum revolutum* (Mitt.) Lindb., and *H. vaucheri* Lesq. The arctic-alpine moss *Cyrtomnium hymenophylloides* (Hüb.) T. Kop., which is represented by a late-glacial fossil from Canoe Brook, is now found at many disjunct stations in the northeastern United States and adjacent Canada that are isolated from areas of more continuous distribution in the Arctic (Miller and Mogensen, 1997). Its distribution is parallel to the current sporadic and isolated disjunct distribution of the vascular plant *Saxifraga oppositifolia*. Fossils of 75

species of mosses have been recovered from the four lowland deposits, and two of these, *Aulacomnium turgidum* (Wahlenb.) Schwaegr. and *Sarmenthyphnum sarmentosum* (Wahlenb.) Tuom. & T. Kop., are current members of the alpine flora of the White Mountains (Crum and Anderson, 1981).

PALEOVEGETATION—LOWLAND SITES

A reconstruction of late-Quaternary vegetation for northern New England (central Massachusetts northward) by Davis and Jacobson (1985) begins at 14,000 yBP when ice still covered large parts of Maine and northern Vermont and New Hampshire. The palynological and plant macrofossil records used in their synthesis show that tundra existed adjacent to the ice front at 14,000 yBP, with poplar woodland beginning to advance northward from the south and southeast.

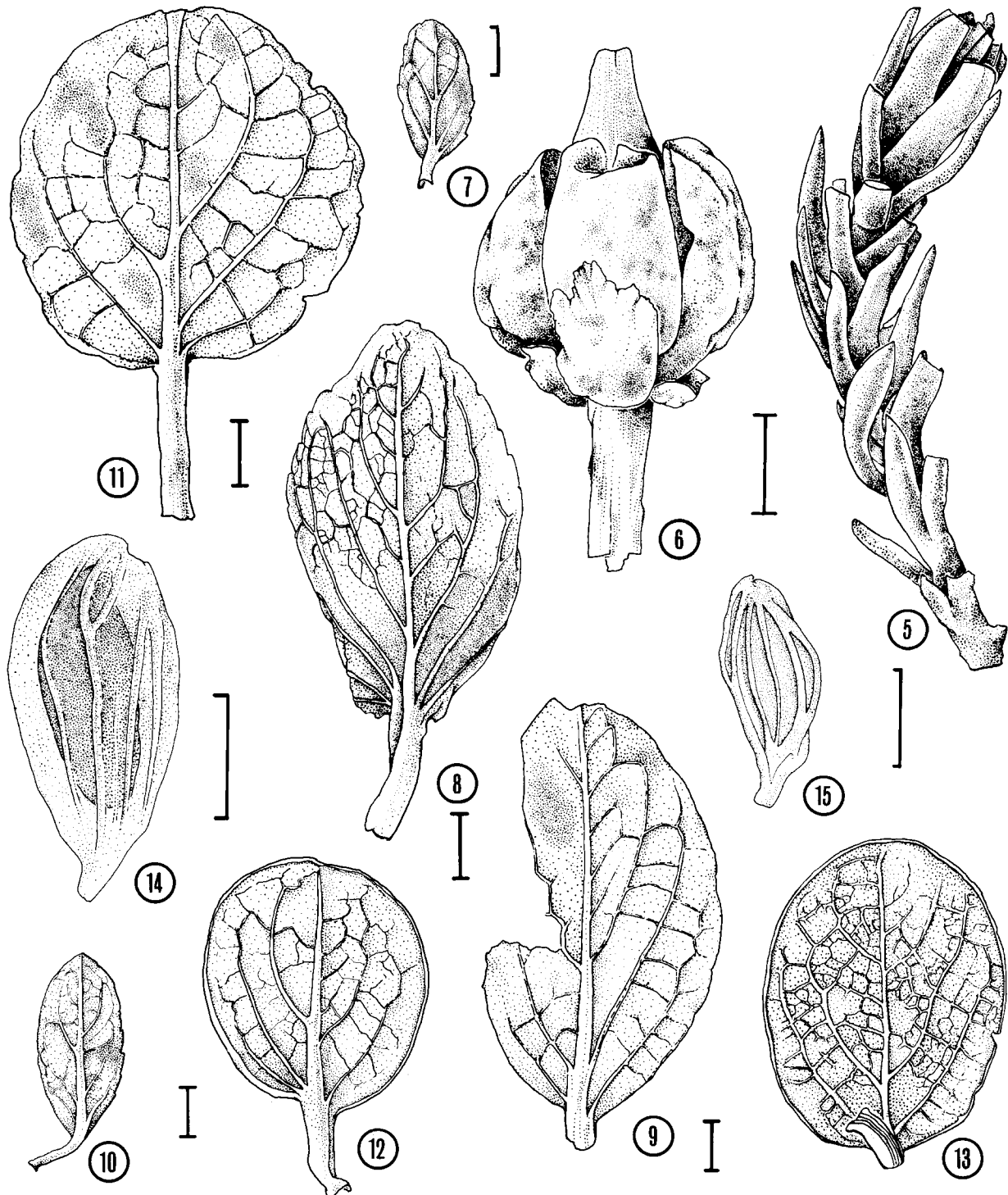
Data from the Matianuck Avenue site, central Connecticut, establish that a part of southern New England at 13,540 yBP had ericaceous shrub and sedge, grass, and herb tundra communities. Balsam poplar (*Populus balsamifera* L.) was the only tree represented in the macrofossil assemblage. Spruce pollen frequency was 5% of all tree, other woody plant, and herb pollen, indicating spruce trees in low density.

Tundra containing dwarf willows and many kinds of herbs and mosses existed near the Tom Swamp depositional basin, Massachusetts, at 12,830 yBP, and at Canoe Brook somewhat later (12,350 yBP). Spruce pollen was three times more frequent in the Canoe Brook sediment (14%), which suggests that spruce trees occurred in greater abundance than they had to the south a thousand years earlier. A mixture of tundra and forest communities existed in central New England at about 12,500 yBP. We suspect that the vegetation was not organized in a zonal pattern (north to south) but that complex patterns were present, reflecting differences in elevation, topography, bedrock, surficial geology, glacial lake position and extent, climate, and other factors that affect plant dispersal, occurrence, and community composition and structure.

Woodland, with spruce represented as macrofossils, occurred at Columbia Bridge at 11,500 yBP in association with shrubs and herbs that indicate open vegetation. It is likely, therefore, that in western New England the northward movement of a broad ecotone between tundra and spruce woodland occurred from 13,500 to 11,500 yBP.

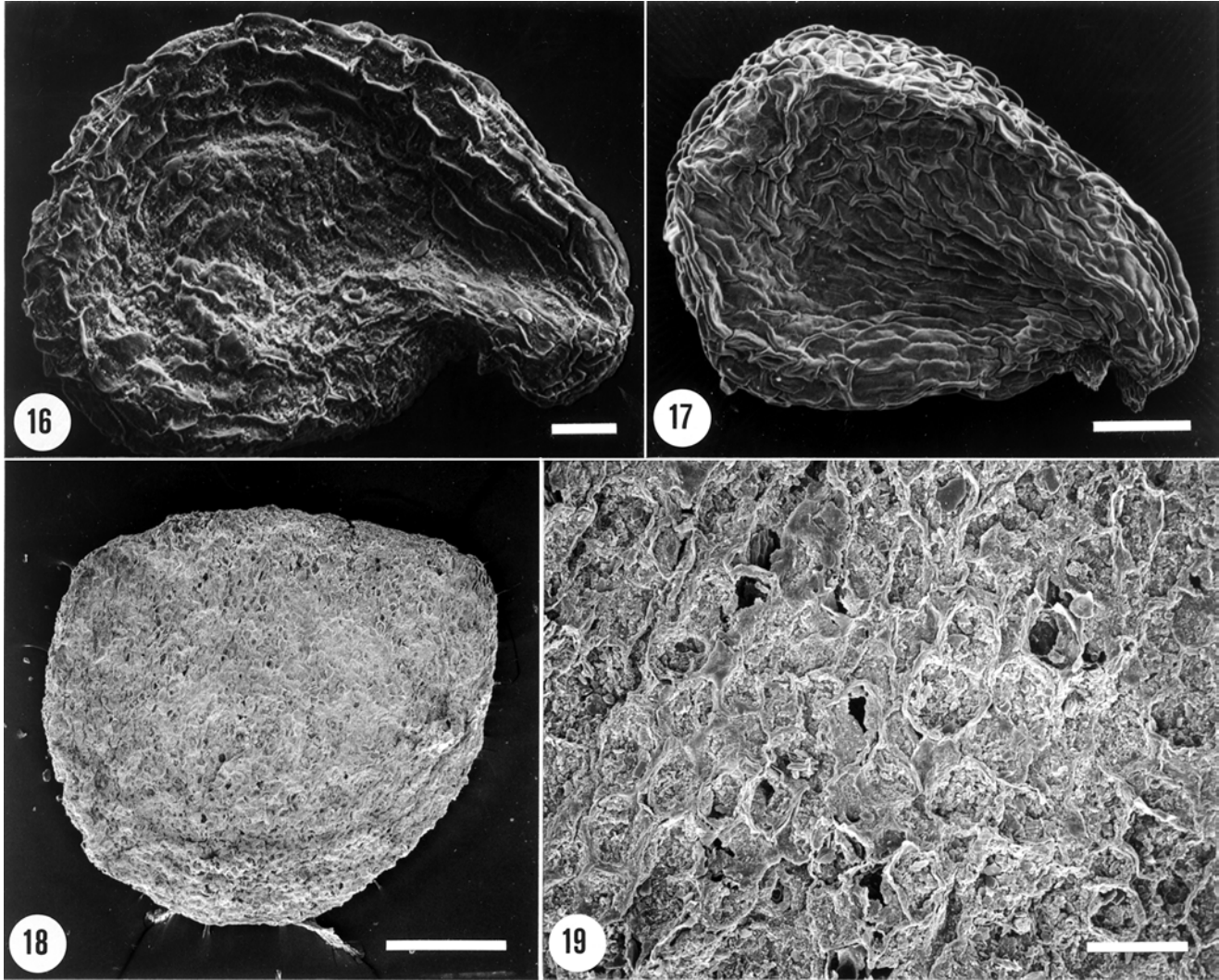
PALEOECOLOGICAL RECORD OF CHANGES IN THE WHITE MOUNTAINS ALPINE FLORA

Direct evidence of species loss or gain in the alpine flora during the late Quaternary is lacking. The best evidence for change would be the presence of macrofossils of arctic-alpine species that are not members of the modern flora. These presumably would have been extirpated during unfavorable conditions (e.g., a warm period). Unfortunately, the diversity of species in the vascular plant macrofossil record at lower Lakes of the Clouds is low and includes only species known in the contemporary flora. The diversity is not higher because lower Lakes of the Clouds is a low-energy depositional basin



FIGURES 5-15. Plant macrofossils from late-Pleistocene Matianuck Avenue site (Connecticut), representing species present (5-10) and absent (11-15) from the contemporary alpine flora of the White Mountains: 5, 6, *Harrimanella hypnoides*, 5, branch with leaves, 6, capsule; 7-10, *Salix uva-ursi*, four different leaves; 11-13, *S. reticulata*, three different leaves; 14, 15, *Thalictrum alpinum*, two achenes. (All scale bars 1 mm.)

Plantes macrofossiles du site de Matianuck Avenue (Connecticut) du Pléistocène supérieur représentant les espèces présentes (5-10) et absentes (11-15) de la flore alpine contemporaine des White Mountains: 5, 6, *Harrimanella hypnoides*, 5, rameau avec feuilles, 6, capsule; 7-10, *Salix uva-ursi*, quatre feuilles différentes; 11-13, *S. reticulata*, trois feuilles différentes; 14, 15, *Thalictrum alpinum*, deux akènes. (Echelle: 1 mm.)



FIGURES 16-19. . Fossil seed and fruit stone from late-Pleistocene Matianuck Avenue (Connecticut) and Canoe Brook (Vermont) sites, representing vascular plant species that still occur in the White Mountains, New Hampshire: 16, 17, *Minuartia groenlandica*, 16, fossil seed from Canoe Brook (scale bar = 100 μm), 17, seed from herbarium reference specimen for comparison (New Hampshire, Mt. Washington summit, Edmondson 5046 [NY]) (scale bar = 100 μm); 18, 19, *Arctostaphylos alpina*, 18, fruit stone from Matianuck Ave. site (scale bar = 0.5 mm), 19, cellular structure at surface of fossil (scale bar = 50 μm).

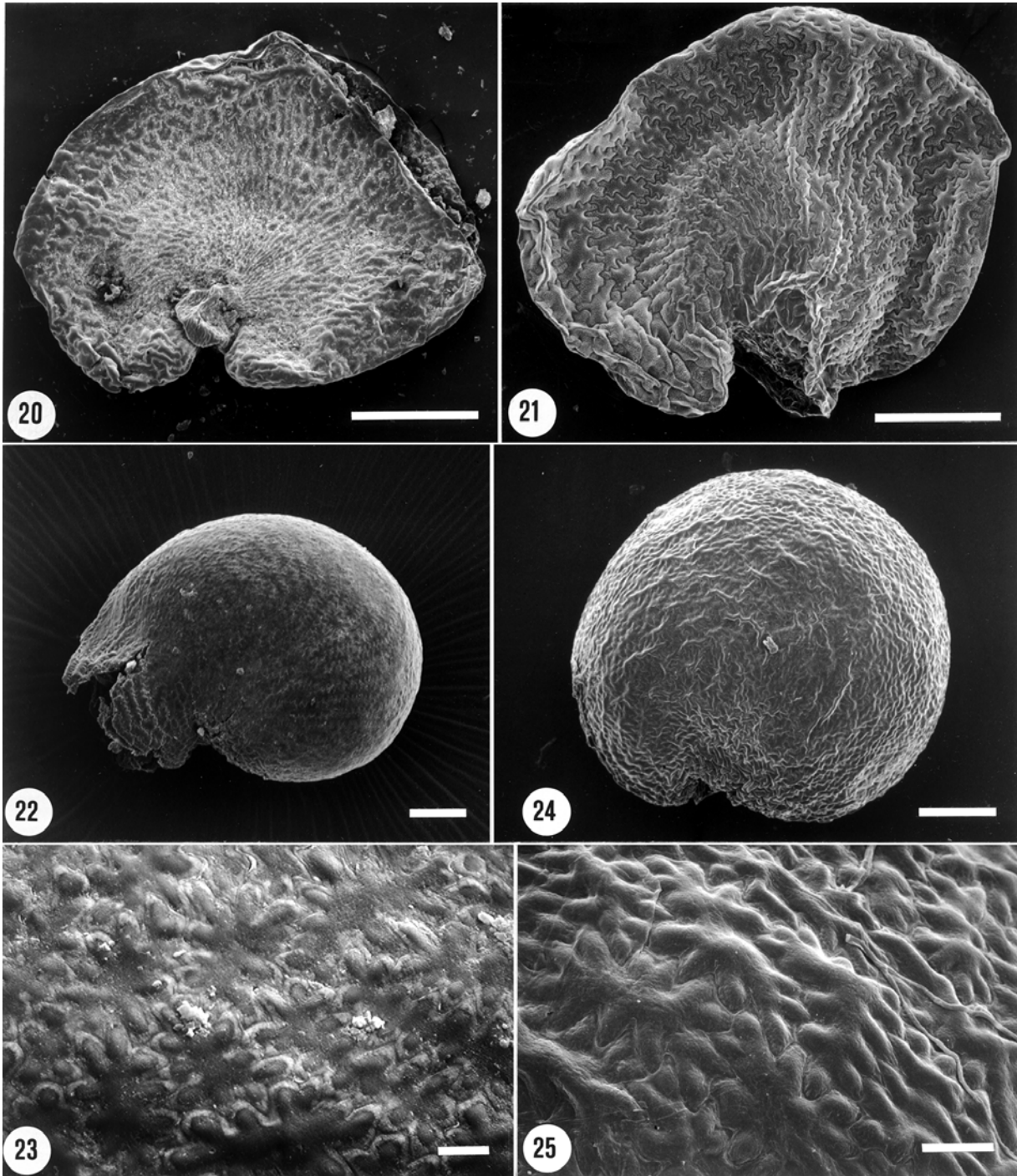
Graine fossile et noyau de fruit des sites de Matianuck Avenue (Connecticut) et de Canoe Brook (Vermont) du Pléistocène supérieur, représentant les espèces de plantes vasculaires qui existent encore dans les White Mountains du New Hampshire : 16, 17, *Minuartia groenlandica*, 16, graine fossile de Canoe Brook (échelle = 100 μm), 17, spécimen de l'herbier de référence pour fins de comparaison (New Hampshire, sommet du mont Washington, Edmondson 5046 [NY]) (échelle = 100 μm); 18, 19, *Arctostaphylos alpina*, 18, noyau de fruit du site de Matianuck Avenue (échelle = 0,5 mm), 19, structure cellulaire à la surface d'un fossile (échelle = 50 μm).

and receives little organic debris. Moreover, the volume of sediment used for macrofossil analysis (50 mL) was small and about two orders of magnitude less than that at the macrofossil rich, low-elevation Glacial Lake Hitchcock sites.

The vegetation history around Lakes of the Clouds shows fluctuations in the position of treeline and changes in the alpine plant communities over the past 13,000 years. Spear (1989) identified three major shifts in vegetation at this site: (1) 11,500 yBP—barren rock to sparse herb and later shrub tundra, (2) 10,300 yBP—herb and shrub tundra to a more continuous vegetation with krummholz and possibly some trees, and (3) 5000 to 6000 yBP—shrubby tundra with krummholz to

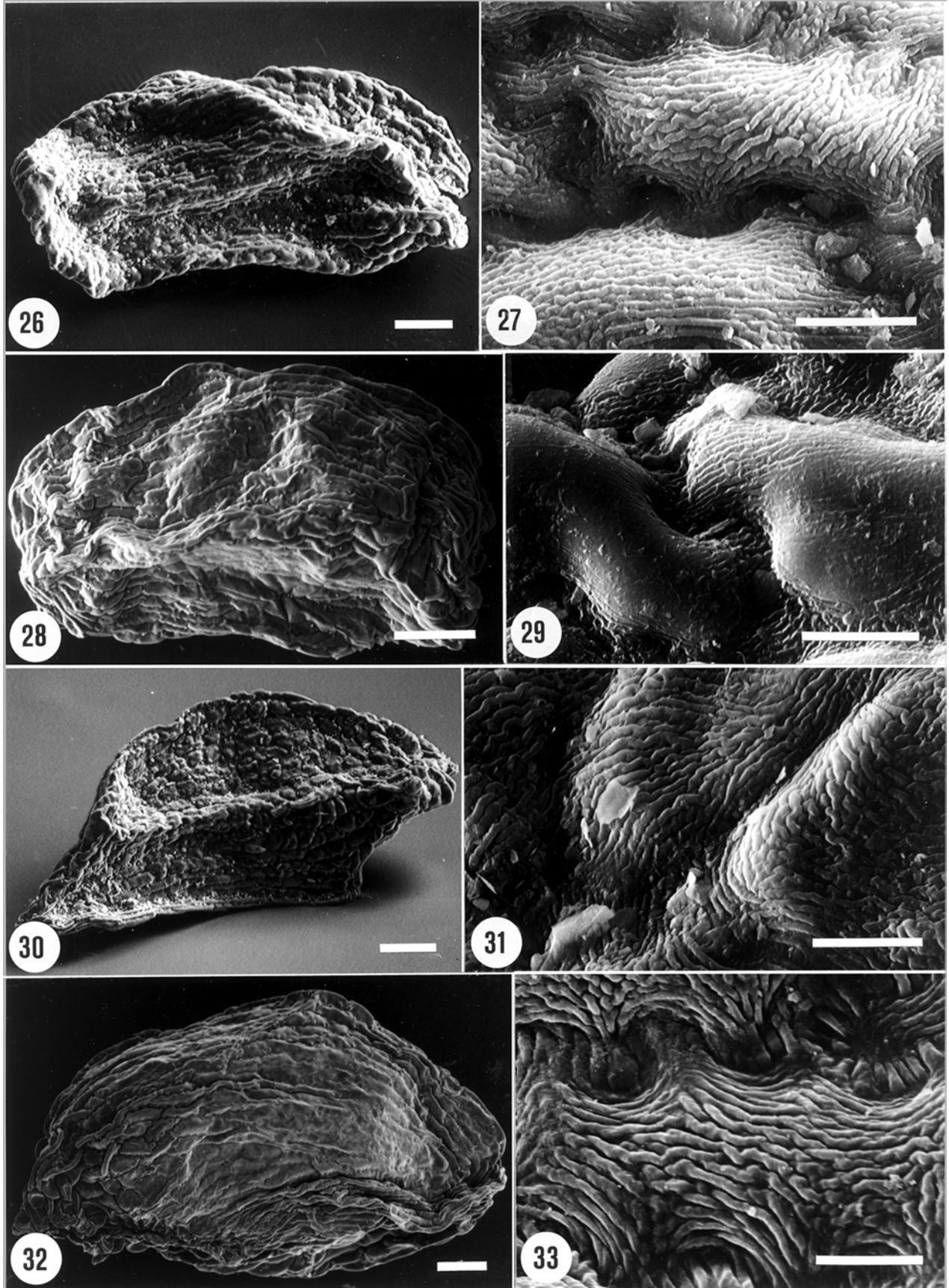
more open conditions. In addition, new evidence presented here indicates that trees may have been more abundant than previously thought and persisted at higher elevations longer, until at least 3500 yBP. These major vegetation shifts are likely to have involved changes in the species composition of the alpine flora.

The late-glacial plant macrofossil record from lower Lakes of the Clouds contrasts with that from lowland sites in a number of important respects. Late-glacial sediments older than 11,000 yBP at lower Lakes of the Clouds were barren of plant macrofossils. The oldest late-glacial sediments produced only moss fossils, principally of arctic-alpine species



FIGURES 20-25. . Fossil seeds from late-Pleistocene Matianuck Avenue (Connecticut) and Canoe Brook (Vermont) sites, representing vascular plant species that are not members of the contemporary New England flora: 20, 21, *Silene involucreta*, fossil, Matianuck Ave. (scale bar = 500 μ m); 21, seed from herbarium reference specimen (West Greenland, Disko Island, Nipisat, 21 Jul 1995, Miller 11,196 [NYS]) (scale bar = 250 μ m); 22, *Arenaria humifusa*, post-germination seed, Canoe Brook (scale bar = 100 μ m); 23, cells of seed coat, same seed (scale bar = 20 μ m); 24, *A. humifusa*, seed from reference specimen (West Greenland, Disko Island, Nipisat, 21 Jul 1995, Miller 11,203 [NYS]) (scale bar = 100 μ m); 25, cells of seed coat, same seed (scale bar = 20 μ m).

Graine fossile et noyau de fruit des sites de Matianuck Avenue (Connecticut) et de Canoe Brook (Vermont), représentant les espèces de plantes vasculaires qui ne font pas partie de la flore contemporaine de la Nouvelle-Angleterre. 20, 21, Fossile de *Silene involucreta*, Matianuck Avenue (échelle = 500 μ m) ; 21, spécimen de l'herbier de référence (ouest du Groenland, île Disko, Nipisat, 21 juillet 1995, Miller 11,196 [NYS]) (échelle = 250 μ m) ; 22, *Arenaria humifusa*, graine germée, Canoe Brook (échelle = 100 μ m) ; 23, cellules de tégument, même graine (échelle = 20 μ m) ; 24, *A. humifusa*, spécimen de l'herbier de référence (ouest du Groenland, île Disko, Nipisat, 21 juillet 1995, Miller 11,203 [NYS]) (échelle = 100 μ m) ; 25, cellules de tégument, même graine (échelle = 20 μ m).



that are present today in the alpine zone of Mount Washington and neighboring summits of the Presidential Range: *Aulacomnium turgidum*, *Conostomum tetragonum* (Hedw.) Lindb., and *Pogonatum urnigerum* (Hedw.) P. Beauv. Fossils of a fourth arctic-alpine moss, *Sarmenthyphnum sarmentosum*, were in sediments dating to the Pleistocene-Holocene transition (10,000 yBP). These are plants of acidic soil and rock in contrast to the lowland paleobryofloras of the same time period, which were dominated by calcicoles (Miller, 1993). Spruce needles are absent from sediments older than about 10,200 yBP at lower Lakes of the Clouds, indicating, as do the moss fossils, that the source area adjacent to the basin lacked trees and supported alpine tundra prior to 10,200 yBP. When spruce-needle deposition started, seeds of Ericaceae and achenes of *Potentilla tridentata* and sedges also began to appear in sediment, which likely marks the arrival of source plants in the watershed. *Potentilla tridentata*, a pioneer of open unstable mineral soil (Marchand and Roach, 1980) that grows over a broad elevational range, is a common plant in the alpine zone of Mount Washington.

Pollen of known and potential arctic-alpine species were recovered from late-glacial sediments at the lower Lakes of the Clouds (Spear, 1989), including *Armeria* sp., a plant that also has a late-glacial lowland fossil record in western New England. Other pollen types (genus determinations in most cases) recovered from lower Lakes of the Clouds that may have been produced by arctic-alpine species are listed in Table IV, and include Campanula, Compositae subfam. Cichorioideae, Cruciferae, Dryas, Epilobium, Polemonium, Saxifraga, and Thalictrum. Similar pollen assemblages are known also from several lowland late-glacial deposits in western New England (Table IV). Given the low pollen deposition rates in late-glacial sediments of lakes in the White Mountain region (Spear et al., 1994), indicating that some or even most of the pollen arrived by wind from a long distance, the pollen source area of these potential arctic-alpine plants cannot be established with certainty. However, some (e.g., *Armeria*, which has large, insect-transported pollen) probably originated from plants growing near Lakes of the Clouds or within their watersheds. Thus, the partial floristic similarity

FIGURES 26-33. *Saxifraga oppositifolia*, late-Pleistocene fossils and reference specimen: 26-31, fossil seeds from Canoe Brook (Vermont) site; 26, 28, 30, three seeds of different shape and preservation quality (scale bars = 100 μ m); 27, 29, 31, microstructure of seed coat cells, high magnification images of seeds in photographs immediately to the left (scale bars = 10 μ m); 32, seed from herbarium reference specimen (Québec, east coast Hudson Bay, Fishing Lake, 2 Aug 1939, Abbe et al. 3561 [GH]) (scale bar = 100 μ m); 33, seed coat microstructure of a part of the same seed (scale bar = 10 μ m).

Saxifraga oppositifolia, fossiles du Pléistocène supérieur et spécimen de référence : 26-31, graines fossiles du site de Canoe Brook (Vermont) ; 26, 28, 30, trois graines de différentes formes et plus ou moins bien préservées (échelle = 100 μ m) ; 27, 29, 31, microstructure du tégument, photographies à fort grossissement des graines situées immédiatement à leur gauche (échelle = 10 μ m) ; 32, spécimen de l'herbier de référence (Québec, côte orientale de la mer d'Hudson, Fishing Lake, 2 août 1939, Abbe et al. 3561 [GH]) (échelle = 100 μ m) ; 33, microstructure du tégument d'une partie de la même graine (échelle = 10 μ m).

between late-glacial vegetation of the Mount Washington alpine summit and lowland sites in western New England rests on moss fossils and pollen of vascular plants. However, this conclusion is tentative, because only small-volume samples of late-glacial sediment from lower Lakes of the Clouds were available for plant macrofossil analysis. More macrofossils are likely to be recovered from samples of larger volume, thereby potentially expanding the list of species.

The Holocene record of "forest" expansion into the alpine zone is supported by evidence from vascular plant macrofossils, rare pollen types, and mosses. The stratigraphic occurrence of *Hylocomiastrum umbratum* between 7500 and 3500 yBP follows the peak in numbers of needles of spruce and balsam fir. The autecology of *H. umbratum* is known primarily from specimens collected between 1879 and 1939 from 12 places in the region. Because *H. umbratum* grows on the forest floor, needles and seeds of overstory trees are present with the moss in herbarium specimens. This moss occurs over a wide elevational range but principally in montane spruce-balsam fir-birch and balsam fir forests, rarely up to perhaps 1500 m as recorded for Tuckerman Ravine on Mount Washington (Table V). Thus, its occurrence as fossils in lake sediment at lower Lakes of the Clouds above spruce-balsam fir forest provides evidence of forest communities (perhaps as krummholz) closer to lower Lakes of the Clouds, which is now 75 m above treeline.

Pollen from the insect-pollinated shrubs, gooseberry (*Ribes* sp.) and mountain maple (*Acer spicatum* Lam.), common in subalpine balsam fir and lower elevation forests, was also deposited between 7500 and 3500 yBP, indicating higher elevational occurrences for these plants. However, we do not envision the presence of closed forests much above Lakes of the Clouds on the summit cone of Mount Washington in the early Holocene, because achenes of *Potentilla tridentata*, a subalpine and alpine plant of unstable mineral soil, are found in sediments of this age, indicating areas without tree or shrub canopies near the lake. Spear (1989) reported finding *P. tridentata* on the bank of the Ammonoosuc River in an open area 90 m below treeline on the west slope of Mount Washington. Openings of this kind presumably existed in the subalpine forest or the higher elevation and more dense krummholz or stands of trees around Lakes of the Clouds in the middle Holocene.

IMPACT OF SOIL DEVELOPMENT ON THE ALPINE FLORA

The large number of plant species identified from macrofossils permits an assessment of late-glacial soil conditions. Mosses associated with calcareous soil or bedrock predominate in the late-glacial record of New York-New England (Miller, 1987a, b, 1989), even when the fossils were recovered from areas of acidic bedrock and soil. This suggests that there was an initial period of base-rich, calcareous conditions associated with the leaching of transported or locally derived carbonate-containing minerals from the glacial drift. At Tom Swamp, Massachusetts (Miller, 1989), and Upper South Branch Pond, Maine (Anderson et al., 1986), the abrupt simultaneous appearance of spruce needles and dis-

TABLE V

Stated and estimated elevations for occurrences of *Hylocomiastrum umbratum* in the White Mountains, New Hampshire; data from voucher specimens in herbaria at Duke University (DUKE) and Harvard University (FH, FH-NEBC)

Location	Collector/Herbarium	Forest type ¹	Elevation (m) ¹
Mt. Washington, Tuckerman Trail	Grout, 10 Aug 1939 (DUKE)	<i>Abies</i>	1370-1525 (s)
Mt. Washington	E. Faxon, Jun 1889 (FH)	<i>Abies</i>	1220-1500 (e)
Mt. Washington	C. E. Faxon, 12 Jun 1879 (FH-NEBC)	<i>Abies, Betula, Picea</i>	750-1220 (e)
Mt. Washington, Crawford Bridle Path	E. & C. E. Faxon, 15 Jun 1883 (FH-NEBC)	<i>Abies, Picea</i>	750-1220 (e)
White Mts.	Wheeler, 1905 (DUKE)	<i>Abies, Picea</i>	750-1220 (e)
White Mts.	Pringle, 11 Jun 1879 (DUKE)	<i>Abies, Picea</i>	750-1220 (e)
Mt. Clinton	C. E. Faxon, 15 Jun 1883 (FH-NEBC)	<i>Picea</i>	450-750 (e)
Mt. Madison	Wheeler, Aug 1903 (FH-NEBC)	<i>Abies</i>	915 (s)
[Mt.] Randolph	A. F. A., 24 Jun 1927 (DUKE)	<i>Abies, Betula, Picea</i>	610 (s)
Mt. Willard	Cummings, 22 Jul 1880 (FH)	<i>Picea</i>	610-855 (e)
Mt. Willard	C. E. Faxon, 13 Jun 1884 (FH-NEBC)	<i>Abies, Picea</i>	610-855 (e)
Mt. Cannon	Kaiser, 13 Aug 1910 (DUKE, FH, FH-NEBC)	<i>Abies, Betula, Picea</i>	1070 (s)

¹ Forest type designations are on the basis of presence of needles and/or fruits of *Abies balsamea*, *Betula papyrifera*, and/or *Picea* (probably *P. rubens*) in the herbarium voucher specimen. For estimates (e), we used needle/fruit presence and the range over which the three tree species occur in the White Mountains, either singly or in combination, at the general collection locality. Stated elevations (s) were recorded by the collector.

appearance of calcicole mosses in the sediments indicate that edaphic conditions changed and litter accumulation and soil acidification began or intensified in response to larger spruce populations.

Macrofossil and pollen records at lower Lakes of the Clouds contain no evidence of an early calcicolous flora, perhaps for two reasons: the lowermost sediments (between 11,000 and 13,000 yBP) were devoid of plant macrofossils (or at least none was recovered from the sampled sediment), and/or the thin covering of glacial drift on the high alpine summit did not contain transported calcareous rocks and minerals (and no calcicoles grew nearby).

The oldest moss fossils recovered from lower Lakes of the Clouds are species of acidic substrata. The ecology of one of them, *Polytrichum juniperinum* Hedw. (*P. juniperinum/strictum*: Fig. 3) was studied on Mount Washington by Watson (1981) who reported that contemporary populations of it were most abundant in the alpine zone on organic soil of pH from 3.4 to 4.4.

A flora rich in calcicole mosses and vascular plants occurred in the lowland in Columbia Bridge area 80 km north-northwest of Mount Washington at 11,500 yBP, but fossils of none of the species was found in late-Pleistocene sediments of lower Lakes of the Clouds. Columbia Bridge and lower Lakes of the Clouds late-glacial sediments contained in common fossils of three mosses: *Pogonatum urnigerum*, *Polytrichum juniperinum*, and *P. piliferum* Hedw., which are all plants of acidic soil.

The late-Pleistocene flora of Mount Washington, and probably nearby Presidential Range summits, consisted of species of acidic sites, particularly moss species that are still members of the local contemporary flora. While the diversity of pollen types in late-glacial sediments suggests that the flora may have been richer floristically than indicated by the

recovered macrofossils, the Mount Washington late-glacial flora is depauperate when compared to the lowland floras of the same radiocarbon age. Edaphic factors (scarcity of calcareous bedrock and surficial deposits) and climatic ones (low mean annual temperatures, wind scouring) may have directly affected floristic diversity in contrast to sites in the lowland at which the climate was less severe and a greater variety of bedrock and other substrata occurred (Table I).

IMPACT OF CLIMATE CHANGE ON THE ALPINE FLORA

Evidence from sediments in the North Atlantic shows that climate oscillations since the end of the Wisconsinan glaciation, and especially in the Holocene, were much more regular and frequent than had been previously thought (Bond *et al.*, 1997). Changes in mean annual temperature were as great as 5-10°C over a period of several hundred years during late-glacial time. The Younger Dryas, a period of cold (glacial) climate beginning just prior to 10,000 yBP, has been recognized at sites in western Europe for nearly a century. Only recently has the Younger Dryas been convincingly documented from terrestrial sites near the Atlantic Coast of northern North America (Mott *et al.*, 1986; Peteet *et al.*, 1990; Mayle *et al.*, 1993). Using close-interval stratigraphic analyses of percent organic matter, pollen, plant macrofossils, and chironomids from lake sediments, and many AMS radiocarbon dates, Cwynar and his students (Mayle and Cwynar, 1995; Cwynar and Levesque, 1995; Levesque *et al.*, 1997) have been able to reconstruct past environments, including summer surface-water paleotemperatures (using a transfer function to convert chironomid assemblages to temperature estimates) in Atlantic Canada and Maine over a long period of late-glacial and early Holocene time. They identified three periods of climate deterioration: the Killarney Oscillation (11,200-10,900 yBP) with a 4-5°C decrease in

summer surface-water temperature, the Younger Dryas (10,800-10,000 yBP) when temperature dropped 5-12°C, and the Preboreal (Freisland) Oscillation (~9600 yBP) with temperature decreasing several degrees C (Levesque *et al.*, 1993, 1994; Cwynar and Levesque, 1995). Climatic fluctuations during the rest of the Holocene appear to have been much less dramatic.

The paleoecological record in the 1976 and 1977 sediment cores lacks the temporal resolution to reveal oscillations of a few hundreds of years. However, preliminary sediment weight-loss-on-ignition data from new cores collected during the summer of 1998 indicate that lower Lakes of the Clouds will be an excellent site for high resolution studies, including, we anticipate, changes in the abundance of plant fossils.

The first vascular plant macrofossils appear in the lower Lakes of the Clouds record near the end of the Younger Dryas and the beginning of the Holocene. Prior to that, the vegetation on the summit cone of Mount Washington seems to have been sparse. Goldthwait (1976) estimated that in the Presidential Range during the nunatak phase (mountain summits surrounded by glacial ice) and later in late-glacial time that the mean annual temperature was 7-8°C colder, and that intense periglacial activity occurred down to an elevation of 1585 m or perhaps even to 1370 m. Patterned ground, block nets, stripes and lobes are conspicuous in the alpine zone, although there is no evidence that they are currently active (Goldthwait, 1940, 1976). These features and many of the mid-elevation lake basins studied by Spear *et al.* (1994) formed during this time of unstable landscapes. The rock slide that dammed Carter Notch Ponds is perhaps another dramatic example of the intense frost action that occurred during this period. Recent more detailed investigations into sediment lithology and percent organic matter in lakes and ponds reported by Thompson *et al.* (1996) have detected the Younger Dryas fluctuation in the White Mountain region. Studies are now underway by L. Cwynar and R. Spear to document the ecological responses to these late-glacial climatic changes in the White Mountains.

The critical issue for this paper is whether alpine plants were trapped in a limited habitat as the climate changed, or whether they had ample time to disperse to favorable sites. Levesque *et al.* (1997), using fossil chironomid assemblages to infer summer surface-water temperature, described an exceptionally steep thermal gradient across the Canadian Maritime Provinces into Maine for parts of late-glacial time (during climatic transitions such as the beginning and end of the Younger Dryas). The inferred maximum temperature gradient across the late-glacial tundra-forest ecotone was 16°C per 100 km. Apart from a latitudinal gradient, a steep but varying altitudinal temperature gradient must also have existed in the White Mountains during parts of late-glacial time. To appreciate the scale and scope of arctic-alpine plant redistribution at this time, reconstructions of altitudinal climatic gradients and the rate at which climate changed are needed. Mayle and Cwynar (1995) estimated that the onset of the Younger Dryas occurred in a few decades. Within 50 years, the vegetation at some of their sites in New Brunswick

and Nova Scotia changed from spruce woodland to tundra in which grew arctic-alpine plants, for example, *Salix herbacea*, *Harrimanella hypnoides*, and *Dryas integrifolia* Vahl. Perhaps more important to the arctic-alpine flora is the termination of cold episodes, which would have led to decreases in the size of tundra habitats or eliminated them completely. The Younger Dryas ended in a few tens of years as abruptly as it started.

The paleoecological record at Lakes of the Clouds provides some tantalizing clues about changes in the alpine zone of Presidential Range during the Holocene. Treeline moved upslope during the early and middle Holocene (to about 3500 yBP). In fact, it may have reached as high as the current tree species limit (1700 m). Warmer conditions meant that less area was available for the alpine flora than earlier, and populations of some alpine plants may have been reduced or eliminated. From the pollen record of spruce increase, we infer that Neoglacial cooling began in the White Mountains about 2500 years ago. There is also some evidence that the peat deposits blanketing areas in the alpine zone date to about this time (Spear, 1989). The macrofossil record especially of *Potentilla tridentata* at Lakes of the Clouds indicates that open areas always existed around the Lakes, although the extent of the open plant communities varied during the Holocene.

CONCLUSIONS AND SUMMARY

1) This study provides a new stratigraphic record of moss fossils in sediments of lower Lakes of the Clouds. Four species, fossils of three of which occurred in late-glacial sediment, are arctic-alpine plants. Fossils of the forest moss, *Hylocomiastrum umbratum*, were deposited in the early to middle Holocene. Rare pollen types from late-glacial sediment (*Armeria*, *Campanula*, *Cruciferae*, *Dryas*, *Epilobium*, *Polemonium*, *Saxifraga*, *Thalictrum*) provide additional new evidence locally of the composition of the late-glacial flora.

2) Thirteen species of terrestrial vascular plants and two species of mosses occurring now in the alpine zone have been identified as fossils at lowland late-glacial sites in western New England. Of the 65 vascular plants identified at the lowland sites, 43 are plants of terrestrial habitats. Many have their geographic affinities with northwestern Newfoundland, Labrador, and northern Québec. The 75 species of mosses identified in late-glacial lowland deposits have the same geographic relationships as the vascular plants.

3) The alpine flora of the White Mountains is depauperate floristically when compared to the late-glacial lowland flora. The alpine zone does not contain the diversity of habitats found in the lowlands. The mosses are all species of acid soil and rock, and no evidence of an early calcicolous flora typical of lowland sites is present. Although no direct evidence of the extirpation of any arctic-alpine species exists, the vegetation record from lower Lakes of the Clouds establishes that climatic change could have led to species loss. Macrofossils of mosses indicate that forest expansion and/or treeline advance was more extensive and persisted longer than inferred by Spear (1989). On the basis of macrofossils of

spruce, balsam fir, and birch, Spear (1989) postulated early Holocene upward movement of treeline, ending some time before 6000 yBP. Macrofossil evidence from the Adirondack Mountains (Jackson, 1989; Whitehead and Jackson, 1990) and the White Mountains (Spear *et al.*, 1994) shows raised elevational limits for white pine (300 m), hemlock (300 m, Adirondacks; 200 m, White Mountains), and yellow birch (*Betula alleghaniensis* Britt.) (150 m, Adirondacks), which is interpreted as an increase in temperature of 1°C or more from about 9000 to at least 4000 yBP. Spear *et al.* (1994) attributed this to nonsynchronous changes at treeline and at low and mid-elevations. Our new evidence indicates that the vegetation response to the middle Holocene warm interval occurred at the same time along the mountain slopes. A period of higher mean annual temperature may have caused species loss and/or population decreases.

4) We suggest that future work in the region will greatly improve what is known about the Quaternary history of the alpine flora. Larger volume sediment samples from Lakes of the Clouds may produce an improved record of alpine floristic diversity. More detailed stratigraphic analyses of sediments (1 or 0.5 cm intervals) at sites at all elevations will refine temporal resolution and could detect short-term, late-glacial climate fluctuations and the loss of species.

5) The Forbes model provides an adequate description of the geographic origin of current floras on a broad continental scale. However, as detailed knowledge of late-glacial floras and tundra plant communities accumulates, a new model may be necessary.

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